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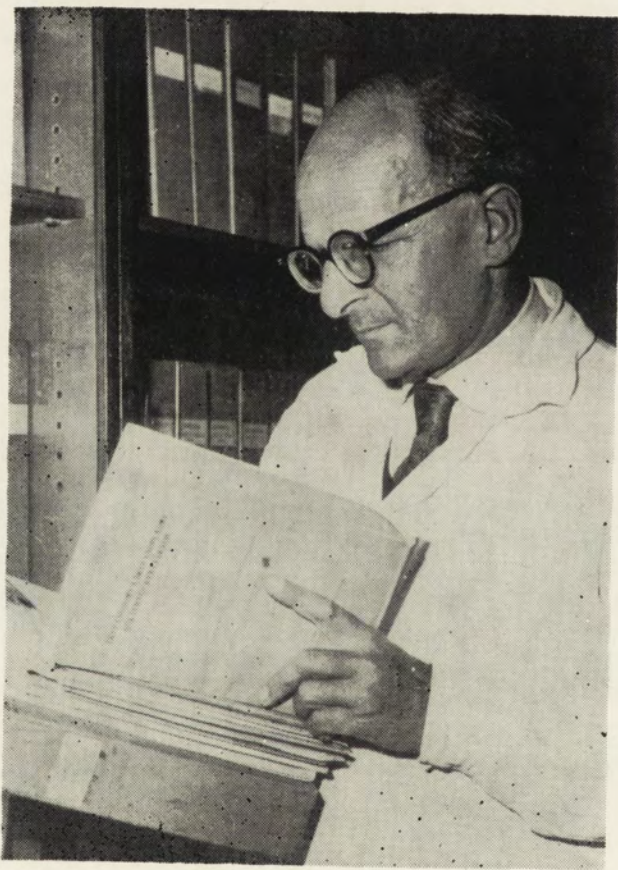
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OTTO JÍROVEC

(1907–1972)

On March 7th 1972, the eminent Czech protozoologist and parasitologist Professor Otto JÍROVEC succumbed to a serious circulatory disease after having undergone a series of painful major surgeries. His passing deeply grieved the scientific community and all of his innumerable friends; it ended a prolific life completely dedicated to a brilliant research work.

Born on January 1907 in Prague, Otto JÍROVEC started working in the zoological laboratory of the Czech protozoologist Václav Breindl at the Charles University as a volunteer while still attending high school. They became friends and Breindl's influence perhaps also contributed to his lifelong concentration on protozoology. After his regular enrolment at the university, he soon became a teaching assistant. He received his Ph. D. already in 1929 having submitted a thesis on trypanosomes experimentally devoid of kinetoplast. After graduation, he spent many months in some of the most prominent parasitological laboratories of that time — e.g., with E. Reichenow at Institut für Schiffs- und Tropenhygiene, with A. Lwoff at Institut Pasteur in Paris and with E. Brumpt at the Sorbonne. Following one year of teaching at the high school, he resumed his work at the Charles University. During the period of forced closure of Czechoslovak universities by the Germans in World War II he headed the parasitological laboratory of the State Institute of Health. After the war he became full professor and succeeded in building up a very active department of Parasitology and Protozoology. In 1953 he was elected member of the Czechoslovak Academy of Sciences. During the last decade of his life, he has been also the director of the Zoological Institute of the University.

Prof. JÍROVEC authored 233 scientific papers and about 250 articles published in popularizing and natural history magazines, in addition to eight books — the international public is familiar with his Protozoology (Czech edition 1953) and treatises on medical parasitology, which appeared in several editions in Czech and German.

He was an extremely versatile scientist; he was the spiritus agens in the development of Czechoslovak parasitology as a modern science, he was also active in hydrobiology, but primarily he has always been a protozoologist. From his own personal experience he was intimately acquainted with all protozoan groups. He was a pathfinder always anticipating the most important questions to be solved in a given problem or within a group of organisms and was competent enough to do so. Moreover, although engaged in basic research, he paid attention to practical use of achieved results and was at the beginning of today's successful cooperation between the basic research and the health service.

Of his numerous accomplishments, we have place enough here to list just a few — his work on kinetoplast lacking trypanosomes (1926–1928), on cytology of microsporidia (1932) and their taxonomy (1936), on taxonomy of haplosporidia (1932–1939), studies on experimental parasitism of free-living protozoa in invertebrates (1937), studies on protozoan parasitism of fish (1926–1942), on the use of protozoa as models for testing of drugs and antibiotics (1948), the discovery (1948) of STM-induced apochlorosis in *Euglena gracilis*. In post war years, he shifted more to medically important protozoa — discovery of *Pneumocystis carinii* as the agent of interstitial pneumonia, research of the role of *Trichomonas vaginalis* in humans and proposed prevention and treatment of trichomoniasis and studies on the epidemiology of human toxoplasmosis. He has proved the importance of parasitic diseases — especially of those caused by parasitic protozoa — in conditions of the temperate climate; this is one of his greatest merits.

On the organisatory level, he has accomplished as much as in his research. He fostered mutual scientific contacts among European protozoologists — he had especially cordial ties with French, Polish and Soviet colleagues — by promoting international meetings. The 1st International Congress of Protozoology, which was his initiative and was held under his chairmanship, started a continuing series of successful congresses. A series of honors reflects his outstanding achievements — the University of Clermont-Ferrand and Humboldt University of Berlin conferred upon him their honorary doctorates: he was awarded the Czechoslovak State Prize, he was President of the Czechoslovak Parasitological Society, honorary member of the Society of Protozoologists and served as Vice-President of the World Federation of Parasitologists; a complete list, however, would be very long.

Otto JÍROVEC was an excellent teacher. He attracted his students to work in his department not only by a lucid and pleasant presentation of his lectures, by the broad scope of his vast knowledge, but perhaps even more by his fascinating zeal for the research together with a kind, understanding personal approach to everybody. His department became a friendly, stimulating place where people felt at home, worked late in the evening, weekends included. Prof. JÍROVEC was an enormously dilligent and efficient worker and although constantly occupied by a number of very urgent tasks he knew how to find enough time for those asking his advice, judgement or help. He liked to socialize with people and everybody, including numerous foreign visitors, remembers with pleasure the evenings spent at his home.

His work will be carried on by his co-workers and students of whom he educated a great number; however, his loss will be painfully felt for a very long time. What gives him the best credit is that he will always be remembered not only as an imposing scientific authority but also as a man of highest integrity, a friend beloved and respected by all.

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Инфузории микробентоса островов Апшеронского и Бакинского архипелагов Каспийского моря

Ciliates from microbenthos of the islands of Apşeron-skij and Bakinskij archipelagos
of the Caspian Sea

Начиная с 1964 года нами проводились регулярные исследования инфузорий микробентоса песчаных грунтов Каспийского моря. Всего за период исследования было собрано и обработано свыше 800 проб, из которых 300 взяты на различных участках островов Апшеронского и Бакинского архипелагов, а также побережья Апшеронского полуострова.

Апшеронский и Бакинский архипелаги расположены в юго-западной части Каспийского моря. Они относятся к мелководному району Каспия и объединяют 13 крупных островов, а также большое количество камней, банок-рифов и других мелких островов, имеющих грязевулканическое происхождение. Прибрежные зоны большинства этих островов загрязнены нефтяными и буровыми отходами.

Грунты прибрежных зон островов в основном состоят из песка, глины, ракуши, ила с ракушей и камня. Наиболее распространенными грунтами являются песок и камень.

Острова Апшеронского архипелага расположены к востоку от Апшеронского полуострова и по климатическим условиям отличаются от островов Бакинского архипелага. К Апшеронскому архипелагу относятся три больших острова: Артем, Жилой и Нефтяные камни.

Острова Бакинского архипелага расположены южнее Апшеронского полуострова. Архипелаг включает 10 крупных островов (Ханлара, Песчаный, Вульф, Наргин, Дуванный, Булла, Глиняный, Лось, Свиной и Обливной).

Автор искренне благодарен доктору биол. наук И. Б. Райкову и канд. биол. наук А. В. Янковскому за ценные советы в работе.

Методика

Материалом настоящей работы послужили микробентические пробы, собранные за период 1966–1970 г. г. Работа была проведена в основном на 11-ти островах: Нефтяные камни, Жилой, Артем, Песчаный, Вульф, Дуванный, Булла, Глиняный, Лось, Свиной и Обливной.

Исследование инфузорий близ указанных островов проводилось до глубины 25 метров. Пробы отбирались стеклянной банкой (на мелководьях) или специальной драгой (в сублиторальной зоне). Собранные пробы, как правило, обрабатывались на месте в лаборатории экспедиционного судна. Определение инфузорий производилось как на живом, так и на импрегнированном серебром материале. Описания видов в основном даются на основании фиксированного материала, импрегнированного серебром по методике Шаттона и Львова (Chatton et Lwoff 1930), а также окрашенного по Унна или железным гематоксилином. Подробное описание указанных методов дано в наших предыдущих работах (Агамалиев 1966, 1967).

Для изучения вертикальной миграции и численности инфузорий в грунте пробы брали поршневой трубкой (диаметр 2 см) до глубины 18 см. Инфузории экстрагировались из этих проб по методу Улига (Uhlig 1964, 1965). Описание этого метода см. Агамалиев (1970).

Одновременно с пробами для фаунистического исследования отбирались образцы песка для гранулометрического анализа и определения в нем органических веществ. Определялись также соленость и температура воды.

Краткая характеристика островов Апшеронского и Бакинского архипелагов

Гидрологический режим островов Апшеронского и Бакинского архипелага несколько отличается от других районов Каспийского моря. Течения в районе островов носят ветровой характер. Господствующим ветром является северный. Последний более резко выражен на островах Апшеронского архипелага. На островах Бакинского архипелага преобладают северо-восточные ветры. Приливно-отливные явления выражены слабо.

В прибрежных зонах каждого острова имеются довольно разнообразные грунты. Песчаный грунт является наиболее широко распространенным. Температура воды прибрежной зоны островов летом равна 24–28°C, зимой и весной она понижается до 4°C. Соленость воды в период исследований колебалась в пределах 12.39–13.33‰.

(1) Остров Нефтяные камни расположен в районе, где дно моря покрыто тонким слоем наносов, состоящих из песка и ракуши. Песчаные грунты в основном распространены в мелководьях на глубине 25–30 м. В песках этого района сапробность составляет 0.48–0.53% органического вещества. Модальный размер песчинок равен 0.1–0.3 мм. Прибрежная зона этого острова наиболее сильно загрязнена нефтепродуктами, что влияет на видовое разнообразие псаммофильных инфузорий.

(2) Остров Жилой. Южный берег на всем протяжении песчаный, ровный, в то время как остальное побережье изрезано заливами. Грунты этих заливов в основном состоят из ракушечного песка и ракуши. На побережьях встречаются также и каменистые грунты. Песчаные грунты простираются до 10-метровой глубины. Сапробность составляет 0.37–0.59% органического вещества. Модальный размер песчинок варьирует в пределах от 0.1 до 0.7 мм.

Вокруг острова расположены действующие буровые и нефтедобывающие вышки. Все эти сооружения влияют на гидрохимический режим акватории острова Жилого.

(3) Остров Артем. На побережье имеется множество мелких бухт. Грунты этого района архипелага состоят в основном из песка, ракушечника, илистого песка и камня. Последний

чаще всего встречается в глубоководных частях акватории. Песчаные грунты широко распространены на мелководьях. С восточной и южной сторон острова до глубины одного метра грунт илисто-песчаный, местами илистый. Сапробность грунта составляет 0.41–0.57% органического вещества. Модальный размер песчинок варьирует от 1 до 2 мм.

Нефть и нефтепродукты загрязняют лишь прибрежные воды острова Артема. Однако грунты прибрежных зон острова чистые. Грунты, пропитанные нефтью, нами не обнаружены.

(4) Остров Вульф имеет побережье, изрезанное заливами. Грунты в основном состоят из песка с ракушей, илистого ракушечника и камня. Прибрежная зона острова загрязнена нефтяными отходами. За счет илистого грунта здесь сапробность повышена до 0.83% органического вещества.

(5) Остров Песчаный низменный, покрыт песком и ракушей. Прибрежные зоны этого острова отлогие и сложены песками. Остров соединен с Апшеронским полуостровом насыпной дамбой.

В связи с этим изменено течение вокруг острова. Остров Песчаный хорошо защищен от северных ветров Апшеронским полуостровом. Даже при сильных северных ветрах волнение моря здесь бывает незначительным. Грунты в основном состоят из мелкого однородного и гетерогенного песка с сапробностью 0.57–0.60% органического вещества. Модальный размер песчинок составляет 0.09–0.3 мм. Местами встречаются ракушечные и каменистые грунты. В отличие от других островов пески о. Песчаного (в отдельных бухтах) пропитаны нефтью и нефтепродуктами с сильным запахом сероводорода.

(6) Остров Дуваный имеет побережье с маленькими бухточками и пляжами. Грунты прибрежных зон этого острова состоят из песка, ракушечника, камня и серой вулканической глины. Пески этого района весьма разнородны ($M_0 = 0.2–1.0$ мм), с сапробностью 0.42–0.48% органического вещества. Каменистые грунты занимают глубоководную зону и северо-восточную часть побережья острова. Преобладание северо-восточных ветров способствует загрязнению северного побережья острова. Однако, в грунте запаха нефти и нефтепродуктов не наблюдается.

(7) Остров Булла — самый крупный остров Бакинского архипелага. Прибрежная зона острова изрезана заливами. Грунты состоят в основном из ила, песка и камней. Песчаные грунты широко распространены в юго-западной и северной частях острова. Модальный размер песчинок варьирует в пределах от 0.08 до 0.3 мм. Сапробность составляет 0.53% органического вещества. Господствующими ветрами здесь являются северо-восточные. В связи с этим северные прибрежные зоны острова загрязняются нефтью и нефтепродуктами. Загрязнение в основном наблюдается на поверхности воды. Грунт оказался чистым, не пропитанным нефтью.

(8) Остров Глиняный. Его северная прибрежная зона характеризуется наличием серой вулканической глины, местами перемешанной с песком и ракушей. Сапробность песка составляет 0.51% органического вещества, с модальным размером песчинок 0.1–0.5 мм. Нефтяное загрязнение здесь почти не наблюдается.

(9) Остров Лось. Прибрежная зона острова чистая, грунт в основном состоит из песка, илистого песка, ракушечника, глины и камня. Модальный размер песчинок составляет 0.1–0.6 мм, с сапробностью 0.49% органического вещества.

(10) Остров Свиной. Берега состоят из песчаного и ракушечного грунта. Местами встречаются каменистые грунты. Пески данного района Каспия состоят в основном из крупных гранул ($M_0 = 0.7–0.9$ мм). Местами встречаются мелкие гетерогенные пески, сапробность которых составляет 0.63–0.71% органического вещества. Как и на острове Дуваный, на о. Свиной преобладают северо-восточные ветры, что приводит к усиленному загрязнению нефтепродуктами северной прибрежной зоны.

(11) Остров Обливной. Грунты прибрежной зоны состоят в основном из камней. Местами встречаются пески разной зернистости ($M_0 = 0.7–1.3$ мм), с сапробностью 0.48–

0.63% органического вещества. Песчаные грунты занимают северо-восточную и юго-западную часть острова. Наряду с этим среди каменистых грунтов пятнами также встречаются песчаные грунты. В отдельных участках прибрежной зоны встречается серая вулканическая глина и илесто-ракушечные грунты. Нефтяного загрязнения в грунтах данного района не наблюдалось.

Таким образом, характеристика грунтов островов Апшеронского и Бакинского архипелага показала, что они по размеру песчинок отличаются друг от друга.

Гранулометрический анализ песка некоторых островов Бакинского архипелага (Дуванный, Булла, Свиной, Обливной) дан в наших предыдущих работах (Agamaliyev 1967). Поэтому в данной работе дается лишь гранулометрический анализ песка островов Артема, Жилого, Нефтяных камней, Песчаного, Вульфа, Глиняного и Лося. Для анализа песка было взято 5 наиболее типичных проб, кривые которых представлены на Рис. 1.

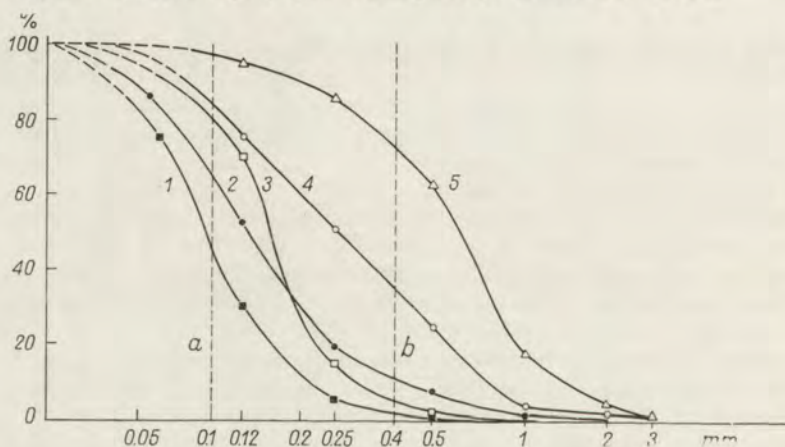


Рис. 1. Кумулятивные гранулометрические кривые пяти проб песка (1 — остров Глиняный; 2 — Нефтяные Камни; 3 — о. Песчаный; 4 — о. Артем; 5 — о. Жилой). По оси абсцисс — размер песчинок (логарифмическая шкала), по оси ординат — кумулятивный процент веса песка; *a* и *b* — границы развития типичной микропоральной фауны

Fig. 1. Collective granulometric curves of 5 samples of sand (islands: 1 — Glinjanyj, 2 — Neftjanye Kamni, 3 — Peščanyj, 4 — Artem, 5 — Žiloyj). Dimensions of sand grains (in logarithmic scale) plotted on abscissa, cumulative per cent of sand weight on ordinate, *a* and *b* — limits of development of typical microporal fauna

Кривые проб, взятых с островов Вульф и Лось, почти полностью совпадают с кривой № 1 (с о. Глиняного), поэтому на графике они не представлены.

Анализ кривых показывает, что на островах Апшеронского и Бакинского архипелагов встречаются разнообразные песчаные грунты с преобладанием мелкого песка.

Видовой состав инфузорий

В настоящее время из мезопсаммона Каспийского моря известно 230 видов инфузорий. Из них 208 видов найдено на западном побережье Среднего и Южного Каспия. Восточный берег Каспийского моря по видовому разнообразию инфузорий несколько уступает западному.

Что касается Апшеронского и Бакинского архипелагов Каспия, то этот район по своим гидрологическим и гидрохимическим режимам, а также по загрязненностью нефтью отличается от других районов моря. Однако, несмотря на нефтяное загрязнение прибрежных зон островов Апшеронского и Бакинского архипелагов и существенное общее объединение фауны инфузорий, резких качественных отличий состава фауны (ведущие формы остаются теми же, что и в других районах Каспия) здесь не наблюдается. Однако, при исследовании песчаных грунтов островов архипелага обнаружено несколько видов инфузорий, которые в других исследованных районах Каспия не встречались.

В Таблице 1 приводится список найденных видов инфузорий и отмечается нахождение каждого вида на отдельных островах архипелага. Всего было обнаружено 59 видов инфузорий, относящихся к 20 семействам. Шесть видов

Таблица 1

Table 1

Видовой состав псаммофильных инфузорий прибрежной зоны островов Апшеронского и Бакинского архипелагов Каспия

Occurrence of psammophilic ciliate species in littoral zone of Apşeronşkiş and Bakinskiş archipelagos of the Caspian Sea

Виды инфузорий Species of ciliate	Острова Islands											
	Артем	Жилой	Нефтяные камни	Песчаный	Вульф	Дуваный	Булла	Глиняный	Лось	Свиной	Обливной	
1	2	3	4	5	6	7	8	9	10	11	12	
Subclassis <i>Holotricha</i>												
Ordo <i>Gymnostomatida</i>												
Familia <i>Enchelyidea</i> Ehrbg.												
1. <i>Prorodon arenarius</i> Dragesco	+	+	—	+	—	+	+	—	—	+	+	
2. <i>P. discolor</i> var. <i>marinus</i> Kahl	—	+	—	+	—	+	—	—	—	+	+	
3. <i>Lacrymaria coronata</i> Cl. et L.	+	+	+	+	+	+	+	+	+	+	+	
4. <i>L. caudata</i> Kahl	—	+	—	—	—	+	—	—	—	—	+	
Familia <i>Trachelocercidae</i> Kent												
5. <i>Tracheloraphis prenanți</i> Dragesco	+	+	+	+	+	+	+	+	+	+	+	
6. <i>T. sarmaticus</i> Agam. et Koval.	—	+	—	+	—	—	—	—	—	—	—	
7. <i>T. teissieri</i> Dragesco	—	+	—	+	—	—	—	—	—	—	—	
8. <i>Trachelonema oligostriata</i> Raikov	+	+	+	+	+	+	+	+	+	+	+	
9. <i>T. binucleata</i> Agamaliev	+	+	—	—	—	+	—	—	—	—	—	
Familia <i>Amphileptidae</i> Bütschli												
10. <i>Litonotus lamella</i> Ehrbg.	+	+	+	+	+	+	+	+	+	+	+	
11. <i>L. cygnus</i> (O. F. M.)	—	+	—	+	—	+	+	—	—	—	—	
12. <i>Loxophyllum setigerum</i> Quenn.	+	—	—	—	—	+	—	—	—	+	—	
13. <i>L. multiplicatum</i> Kahl	—	+	—	+	—	+	+	—	—	—	—	
14. <i>L. uninucleatum</i> Kahl	—	+	—	+	—	+	—	—	—	+	—	

1	2	3	4	5	6	7	8	9	10	11	12
Familia <i>Trachelidae</i> Ehrbg.											
15. <i>Dileptus aculeatus</i> Dragesco	+	+	-	-	-	-	+	-	+	-	-
16. <i>Dileptus</i> sp.	-	-	-	+	-	+	-	-	-	-	-
Familia <i>Loxodidae</i> Bütschli											
17. <i>Remanella rugosa</i> Kahl	+	+	+	+	+	+	+	+	+	+	+
18. <i>R. granulosa</i> Kahl	+	+	-	+	-	+	-	-	-	-	-
Familia <i>Didiniidae</i> Poche											
19. <i>Mesodinium pupula</i> Kahl	+	+	+	+	+	+	+	+	+	-	+
20. <i>M. pulex</i> f. <i>rubrum</i> Lohman	-	+	-	+	-	+	-	-	-	-	-
Familia <i>Spathidiidae</i> Kahl											
21. <i>Spathidium fossicola</i> Kahl	-	+	-	+	-	+	-	-	-	-	-
22. <i>Paraspathidium fuscum</i> (Kahl)	+	+	+	+	+	+	+	+	+	+	+
Familia <i>Dysteriidae</i> Cl. et L.											
23. <i>Dysteria procera</i> Kahl	+	+	-	-	-	+	-	-	-	-	-
24. <i>Hartmannula entzi</i> Kahl	-	+	-	-	-	-	+	-	-	-	-
Familia <i>Chlamyodontidae</i> Stein											
25. <i>Chlamyodon triquetrus</i> (O. F. M.)	+	+	-	-	-	+	-	-	-	-	-
26. <i>Chilodonella subtilis</i> Kahl	+	-	+	+	-	-	+	-	-	-	-
Familia <i>Nassulidae</i> Fromentel											
27. <i>Chilodontopsis vorax</i> Stokes	-	+	-	-	-	+	-	-	-	+	-
Ordo <i>Hymenostomatida</i>											
Familia <i>Parameciidae</i> Kent											
28*. <i>Paramecium calkinsi</i> Wood.	-	-	-	+	-	-	-	-	-	-	-
29. <i>Paramecium</i> sp.	-	-	-	+	-	-	-	-	-	-	-
Familia <i>Frontoniidae</i> Kahl											
30. <i>Frontonia marina</i> Fab.-Dom.	+	+	+	+	-	+	+	+	+	+	+
31. <i>F. arenaria</i> Kahl	+	+	+	-	+	-	-	-	-	-	+
32. <i>Uronema marina</i> Dujardin	-	+	-	-	-	-	-	+	-	+	-
Familia <i>Pleuronematidae</i> Kent											
33. <i>Pleuronema marinum</i> Dujardin	+	+	-	+	-	+	+	-	-	-	-
34. <i>P. coronatum</i> Kent	+	+	+	+	+	+	+	+	+	+	+
35*. <i>Cyclidium bergeri</i> sp. nov.	-	+	+	-	-	-	-	-	-	-	-
36. <i>Cyclidium</i> sp.	-	+	-	-	-	-	-	+	-	-	-
37. <i>Histiobalantium majus</i> Kahl	+	+	-	+	-	+	-	-	+	+	+
Subclassis <i>Spirotricha</i>											
Ordo <i>Heterotrichida</i>											
Familia <i>Peritromidae</i> Stein											
38. <i>Peritromus faurei</i> Kahl	+	+	+	+	-	+	+	-	+	-	-
Familia <i>Spirostomatidae</i> Stein											
39. <i>Blepharisma clarissimum</i> Anigst	+	+	+	+	+	+	+	+	-	-	-

1	2	3	4	5	6	7	8	9	10	11	12
40. <i>Bl. salinarum</i> Florentin	—	+	—	—	—	—	—	—	—	—	—
41. <i>Parablepharisma pellitum</i> Kahl	—	+	—	+	—	—	—	—	—	—	—
42*. <i>Spirostomum teres</i> Clap. et Lachm.	—	—	—	+	—	—	—	—	—	—	—
Familia <i>Condylostomatidae</i> Kahl											
43. <i>Condylostoma arenarum</i> Spiegel	+	+	+	+	—	+	—	+	+	+	+
Ordo <i>Oligotrichida</i>											
Familia <i>Halteriidae</i> Cl. et L.											
44. <i>Strombidium sulcatum</i> Cl. et L.	+	+	—	+	—	—	—	+	—	+	—
45. <i>Strobilidium</i> sp.	—	+	—	+	—	—	—	—	—	—	—
Ordo <i>Hypotrichida</i>											
Familia <i>Oxytrichidae</i> Ehrbg.											
46*. <i>Holosticha manca</i> Kahl	—	+	—	+	+	—	+	—	—	—	—
47. <i>Amphisiella milnei</i> Kahl	—	+	—	—	—	—	—	—	—	—	—
48. <i>Urostrongylum caudatum</i> Kahl	+	—	+	—	—	+	—	+	+	—	—
49. <i>Keronopsis rubra</i> (Ehrbg.)	+	+	—	+	—	+	+	—	+	+	+
50*. <i>K. pernix</i> Wrzesn.	—	+	—	+	—	—	+	—	—	—	—
51. <i>Trachelostyla caudata</i> Kahl	+	+	+	+	+	+	+	+	+	+	+
Familia <i>Euplotidae</i> Ehrbg.											
52. <i>Euplotes raikovi</i> Agamaliev	+	+	—	+	—	+	+	+	+	—	—
53. <i>E. harpa</i> Stein	+	+	—	—	—	+	—	—	—	+	+
54. <i>Euplotes balteatus</i> Dujardin	—	+	—	—	—	+	—	—	—	—	—
55*. <i>Euplotes zenkewitchi</i> Burk.	—	+	—	—	—	—	—	—	—	—	—
56. <i>Diophrys scutum</i> Dujardin	+	+	+	+	+	+	+	+	+	+	+
57. <i>Uronychia transfuga</i> O. F. Müll.	+	+	—	—	—	+	+	—	—	+	+
Familia <i>Aspidiscidae</i> Stein											
58. <i>Aspidisca caspica</i> Agam.	+	+	—	+	—	+	+	+	—	—	—
59. <i>A. pulcherrima</i> Kahl.	—	+	—	+	—	+	—	—	—	—	—

(в таблице отмечены звездочками) являются новыми для Каспия. Один из них (*Cyclidium bergeri*) описывается впервые для науки. Эти виды были обнаружены в прибрежных зонах островов Песчаного и Жилого, где грунты загрязнены (пропитаны нефтью) и отличаются сильным запахом сероводорода.

Данные, приведенные в таблице, показывают, что отдельные острова по количеству обнаруженных видов отличаются друг от друга.

Остров Жилой по числу занимает первое место. Здесь было обнаружено 52 вида. Затем следуют о. Песчаный (40 видов), о. Дуваный (39), о. Артем (32), о. Булла (26), о. Свиной (22), о. Обливной (20), о. Глиняный (19), о. Нефтяные камни и о. Лось (по 18 видов). Остров Вульф оказался наиболее бедным (13 видов инфузорий).

Некоторые виды инфузорий являются массовыми формами района исследования. Для острова Артема, Свиного, Обливного такими формами были

Frontonia marina, *Diophrys scutum*, *Uronychia transfuga*. Для острова Дуванный, Жилой и Песчаный массовыми формами являлись *Remanella rugosa*, *Paraspathidium fuscum*, *Strombidium sulcatum*, *Condylostoma arenarium* и *Paramecium calkinsi*.

Сравнение обнаруженных видов инфузорий островов Апшеронского и Бакинского архипелагов с данными, полученными для морей Советского Союза, морей Западной Европы, Северной и экваториальной Атлантики показывает, что основные представители фауны островов являются микропоральными (66%). Наряду с этим в составе фауны есть также мезопоральные (20%) и эврипоральные (14%) экологические группы инфузорий.

Микропоральные виды в основном встречаются на островах Артем, Жилой, Песчаный, Дуванный и Булла, что связано с преобладанием там мелкого песка. Наряду с этим в крупнозернистых песках указанных островов в большом количестве встречаются также мезопоральные виды инфузорий. Последние преобладают на островах Свиной и Обливной, где наряду с крупнозернистыми песчаными грунтами встречается гравий и ракушечник с детритом.

Сезонная динамика

При сезонном изучении инфузорий островов Апшеронского и Бакинского архипелагов наблюдались три максимума в развитии фауны инфузорий, приходящиеся на весну, лето и осень (Рис. 2). Как видно из рисунка, инфузории своей наибольшей численности достигают в июне–июле. Зимой их численность минимальная.

В течение года температура воды варьировала от 4 до 28°C. При таком диапазоне температуры основная часть фауны состояла из эвритермных видов. К эвритермным видам, которые в районе исследования обнаружены в массовом количестве, можно отнести *Lacrymaria coronata*, *Tracheloraphis prenanti*, *Litonotus lamella*, *Remanella rugosa*, *Mesodinium pupula*, *Paraspathidium fuscum*, *Frontonia marina*, *Pleuronema coronatum*, *Peritromus faurei*, *Condylostoma arenarium*, *Keronopsis rubra*, *Trachelostyla caudata*, *Diophrys scutum*, *Uronychia transfuga*, *Aspidisca caspica* и др. Перечисленные виды и множество других видов инфузорий островов Апшеронского и Бакинского архипелагов имеют всесветное распространение.

Все эвритермные виды достигают максимума численности в летнее время года.

Зимой, при температуре 4–7°C в песках Апшеронского и Бакинского архипелагов наблюдается резкое снижение разнообразия видового состава фауны инфузорий и численности отдельных видов. Это, по-видимому, объясняется инцистированием многих форм инфузорий, а также миграцией их вглубь грунта.

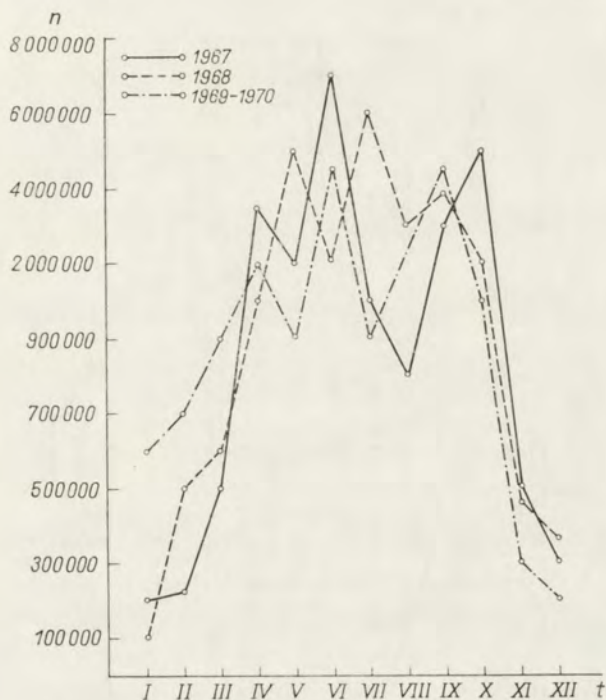


Рис. 2. Сезонная динамика численности инфузорий Апшеронского и Бакинского архипелагов Каспийского моря, n — количество экземпляров на m^2 ; t — месяцы
 Fig. 2. Seasonal frequency dynamic of ciliates of Apsheroniskij and Bakinskij archipelagos of the Caspian Sea; n — number of specimens per square meter, t — months

Сезонные колебания температуры играют важную роль в вертикальном распространении инфузорий. Последнее испытывает значительные изменения в разные сезоны года.

На Рис. 3 приводится вертикальное распределение псаммофильных инфузорий в мелких песках ($M_0 = 0.1-0.3$ мм) островов Апшеронского и Бакинского архипелагов в отдельные сезоны года. Как видно из рисунка, весной, летом и осенью основная масса инфузорий обнаруживается на верхних слоях песка (от 0 до 8 см глубины). При этом наибольшее видовое разнообразие инфузорий наблюдается в летнее время. К осени зона вертикального распределения инфузорий становится более вытянутой. Зимой картина вертикального распределения инфузорий резко меняется. В это время в верхних слоях песка (от 0 до 8 см глубины) инфузории почти не обнаруживались. Основное скопление инфузорий обнаружено в самых нижних слоях грунта (от 8 до 16 см).

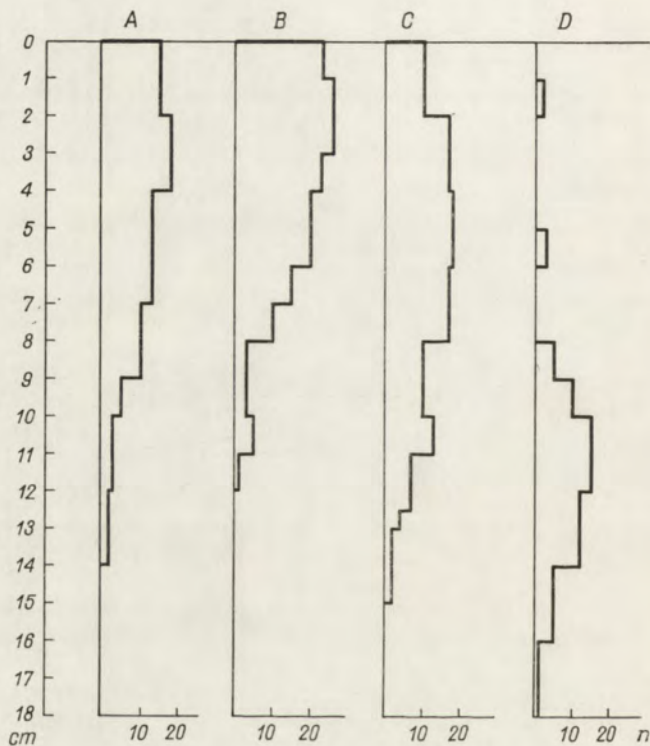


Рис. 3. Вертикальное распределение инфузорий в мелких песках ($M_0 = 0.1-0.3$ мм) островов Апшеронского и Бакинского архипелагов Каспия по отдельным сезонам года. А — весна, В — лето, С — осень, Д — зима, n — количество видов; на оси ординат глубина в см

Fig. 3. Vertical distribution of ciliates in fine sands ($M_0 = 0.1-0.3$ mm) of Apšeroniskij and Bakinskij archipelagos of the Caspian Sea in particular seasons. A — spring, B — summer, C — autumn, D — winter, n — number of species; depth in cm on ordinate

Описания видов

Paramecium calkinsi Woodruff, 1921 (Рис. 4, 5; Табл. I 1-3)

Солоноватоводная форма, впервые (в 1919 г.) была найдена Вудруффом в пресных водах Нью-Хейвена (штат Коннектикут, США).

Венрич (Wengich, 1928) в солоноватых лужах Вудс Холла (штат Массачусеттс, США) тоже обнаружил в большом количестве *P. calkinsi*. Позже Вихтерман (Wichterman 1950, 1951, 1953) переописал этот вид, основываясь на материале, собранном в соленых лужах (37.66‰) Уэст Барнстбейла (штат Массачусеттс, США).

Чешская исследовательница Даниелова (Danielová 1959) в природно загрязненных (мезосапробных) водоемах Чехословакии также обнаружила

в большом количестве *P. calkinsi*. Этот вид еще раньше был описан в литературе под названием *P. pyriforme* — из Марселя и *P. duboscqui bactocarium* — из Баньюльса (Gouret et Roeser 1886; Chatton et Brachon 1933).

Нам этот вид встретился в массовом количестве на Говсанском побережье Каспия и о. Песчаном.

Указанные районы были сильно загрязнены нефтью и нефте-продуктами. Песок имел сильный запах сероворода. Для изучения цилиатуры и ядерного аппарата было изготовлено большое количество препаратов. Описание этого вида дается на основании прижизненных наблюдений и серебрянных материалов.

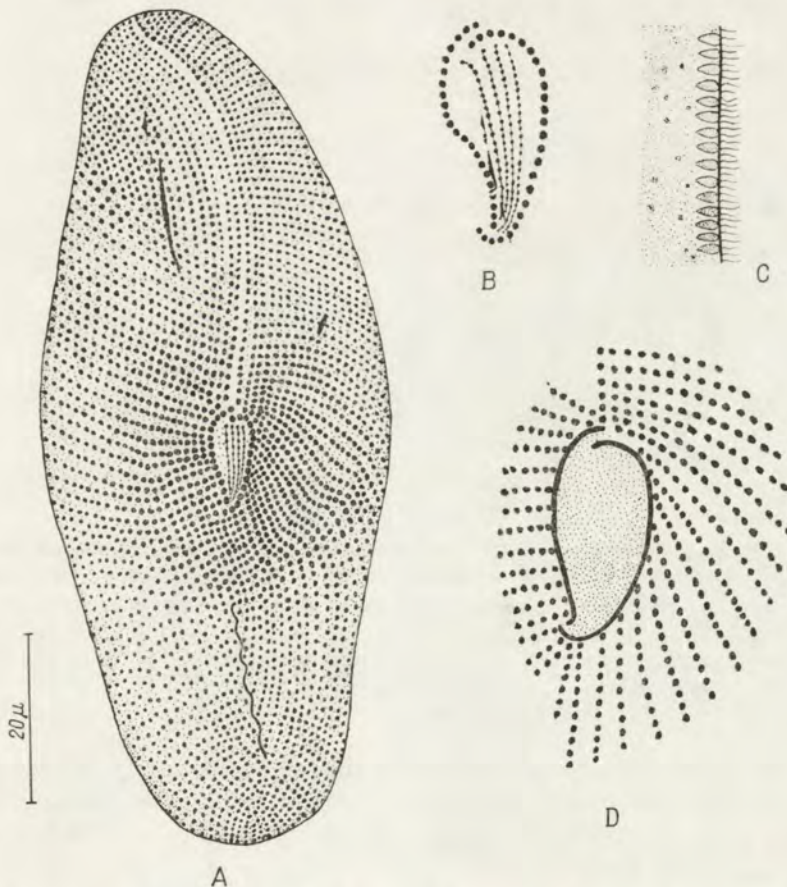


Рис. 4. *Paramecium calkinsi* Woodruff, 1921. А — общий вид с брюшной стороны, В — ротовой аппарат, вид квадрулуса, С — трихоцисты, D — система околоротовых рядов кинетосом (адесмокинет). Серебрение

Fig. 4. *Paramecium calkinsi* Woodruff, 1921. А — view of the ventral side, В — buccal apparatus with quadrulus, С — trichocysts, D — pattern of circumoral rows of kinetosomes (adescmokinets). Silver impregnation

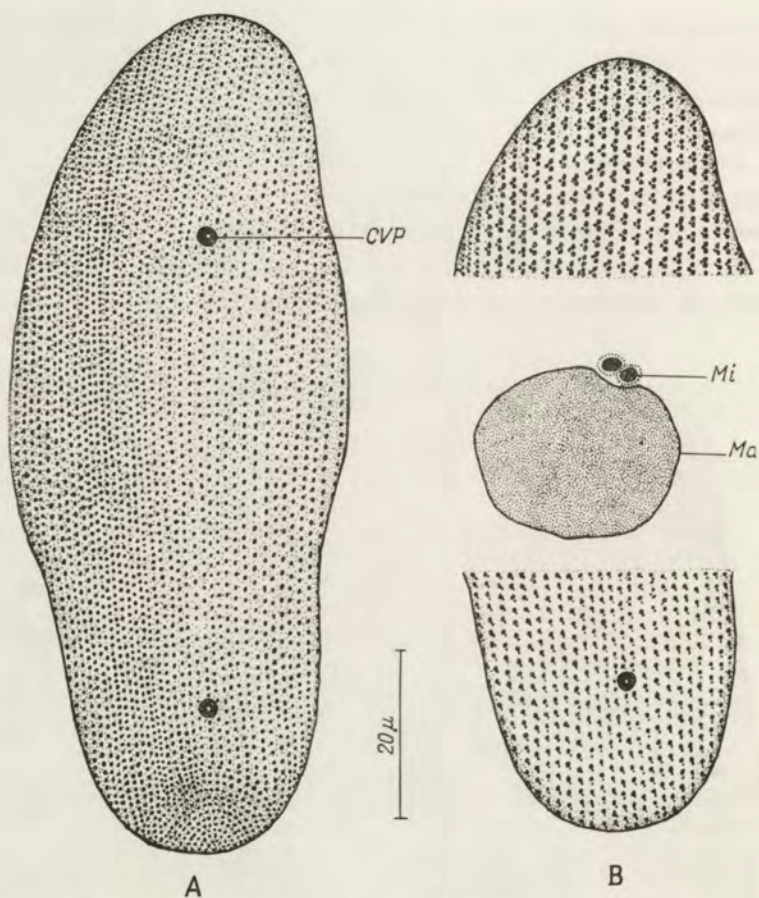


Рис. 5. *Paramecium calkinsi* Woodruff, 1921. А — общий вид со спинной стороны (серебрение), В — цилиатура переднего и заднего концов (серебрение) и ядра (гемалаун), Ма — макронуклеус, Ми — микронуклеус, CVP — поры сократительных вакуолей

Fig. 5. *Paramecium calkinsi* Woodruff, 1921. А — dorsal side of the body (silver impregnation), В — ciliature of the anterior and posterior body ends (silver impregnation) and nuclei (hemalaun), Ма — macronucleus, Ми — micronucleus, CVP — contractile vacuole pores

Тело вытянуто и закруглено на концах (Рис. 4 А, Табл. I 1). Живые инфузории в падающем свете коричневато-белые. Эктоплазма забита включениями. На живых инфузориях хорошо видны трихоцисты (Рис. 4 С). На фиксированных особях они не сохраняются.

Ресничный покров густой, на вентральной стороне тела он состоит из 45–50 меридианов. Кинетосомы этих рядов на заднем конце тела сильно сближены (Рис. 4 А). Рот расположен чуть ниже середины тела. На серебряных препаратах хорошо видна система вторичных околоротовых рядов кинето-

сом (адесмокинет), располагающихся перпендикулярно истинным кинетам (Рис. 4 А, D, Табл. I 2). Правый край перистоста несет 14–16 адесмокинетических рядов. Имеется две сократительные вакуоли. Их поры хорошо сохраняются на импрегнированных препаратах (Рис. 5 А, Табл. I 3). По спинной стороне проходит 43–45 меридиональных рядов. На заднем конце тела на кинетах кинетосомы образуют пары, на переднем они собраны по три.

Ядерный аппарат состоит из одного сферического макронуклеуса и двух тесно прилегающих к нему микронуклеусов (Рис. 5 В). По ядерному аппарату каспийская форма *P. calkinsi* стоит ближе всего к форме Вудруффа (Woodruff 1921).

Длина тела 110–140 м, а ширина — 40–50 м.

Биотоп: мелкий мезосапробный и полисапробный песок Каспийского моря (о. Песчаный).

Поскольку в литературе не имеется данных по серебрению *P. calkinsi*, мы не сможем дать детального сравнения каспийской формы этого вида с формами, описанными из других географических районов. Однако, нам удалось сравнить каспийскую форму с балтийской, на основании материалов А. В. Янковского. При этом выяснилось, что у каспийской расы *P. calkinsi* больше ресничных рядов (почти в два раза) во всех зонах тела и больше степень сгущения кинетосом в кинетах, чем у балтийской расы. Число адесмокинет справа у каспийской формы также больше (14–16), чем у балтийской расы (11).

Pleuronema coronatum Kent, 1881 (Табл. I, 4–6)

Pleuronema coronatum подробно описана в литературе и отмечена во всех изученных географических районах. Этот вид очень часто встречается в песках Каспийского моря. Подробное описание этой инфузории дается в наших предыдущих работах (Агамалиев 1968, 1970).

В настоящей работе даются лишь некоторые добавления к вышеуказанным описаниям. Описываемая форма в большом количестве была обнаружена на островах Апшеронского и Бакинского архипелагов.

Тело как у типичной формы (Табл. I, 4–6). Ресничный покров очень густой, равномерный, меридиональных рядов 60–70 (включая 3–4 предротовых меридиана). Буккальная полость спереди узкая, а сзади округлая. Ундулирующая мембрана занимает 3/5 длины тела. В глубине буккальной полости находится 14–16 длинных и 3–4 коротких радиальных ребер (Табл. I, 4, 5).

Ядерный аппарат характерен для *P. coronatum* и состоит из одного сферического макронуклеуса и 3–4 микронуклеусов.

Длина тела у фиксированных особей составляет 70–80 м, а ширина — 40 м.

Биотоп: мелкий и средний песок о. Жилого.

Главной отличительной чертой описываемой формы является большое число ресничных рядов, а также размер тела.

Cyclidium bergeri sp. nov. (Рис. 6, Табл. II, 7-9)

В настоящее время известно около десятка видов морских циклидиумов. Большинство из них описаны лишь на основании прижизненных наблюдений. Однако, в последние годы в литературе появились описания или переописания некоторых видов *Cyclidium*, сделанные по серебрянным препаратам.

В работах Берджера (Berger 1959), Берджера и Томпсона (Berger and Thompson 1960), Томпсона (Thompson 1958) дается подробное описание соматической и буккальной цилиатуры *C. glaucoma*. Польская исследовательница Чапик (Czapik 1963), на основании серебрянного материала изучала морфогенез цилиатуры *Cyclidium citrullus*. Дражеско (Dragesco 1963) в сап-робных песках близ Роскова обнаружил и описал новый вид *Cyclidium plouneouri*. Позже Боррор (Borror 1965) переописал *C. plouneouri* по серебрянным препаратам. В работах Боррора (Borror 1963) и Янковского (Jankowski 1964) дается также подробное описание *Cyclidium marinum*.

Во время работы на Каспийском море нами встречено много особей нового вида *Cyclidium bergeri* sp. nov. Этот вид в большом количестве обнаружен на о. Жилом, а также на восточном побережье Каспийского моря. Описание дается на основании прижизненных наблюдений и препаратов, импрегнированных серебром по методике Шаттона и Львова.

Форма тела овальная или яйцевидная, с закругленными концами (Рис. 6 А, В; Табл. II 7, 8). Буккальная полость занимает меньше половины тела. Она состоит из четырех элементов: ундулирующей мембраны и 3-х мембранелл (M_1 , M_2 и M_3). (Рис. 6 С; Табл. II 9). Длина буккальной полости составляет 20 μ . Позади буккальной полости начинается один короткий ряд ресничек, который не доходит до конца тела и оканчивается перед цитопигом. Реснички в этом ряду, по сравнению с другими рядами, расположены редко.

Ресничный покров состоит из 19-20 меридианов. Нам встретились 2 формы *C. bergeri*. У первой формы (Рис. 6 А) ресничные меридианы доходят до обоих концов тела. Меридиан, лежащий левее буккальной полости, на участке от нижнего конца второй мембранеллы (M_2) до нижнего конца ундулирующей мембраны состоит из тесно сближенных ресничек (Рис. 6 А; Табл. II 7). У второй формы (Рис. 6 В; Табл. II, 8) ресничные меридианы не доходят до заднего конца тела, где наблюдаются лишь беспорядочно разбросанные кинетосомы. Кроме того, у этой формы три ресничных меридиана (один лежащий справа от буккальной полости и два лежащих слева от нее) не доходят и до переднего конца тела, начинаясь на уровне начала ундулирующей мембраны. Цитопиг расположен ближе к заднему концу тела в посторальном меридиане.

Дорзальная сторона тела у некоторых особей несет 7-8, а у других до 10 рядов ресничек (Рис. 6 Е). На окрашенных препаратах хорошо видны вентральный и дорзальный аргиромы (Рис. 6 D).

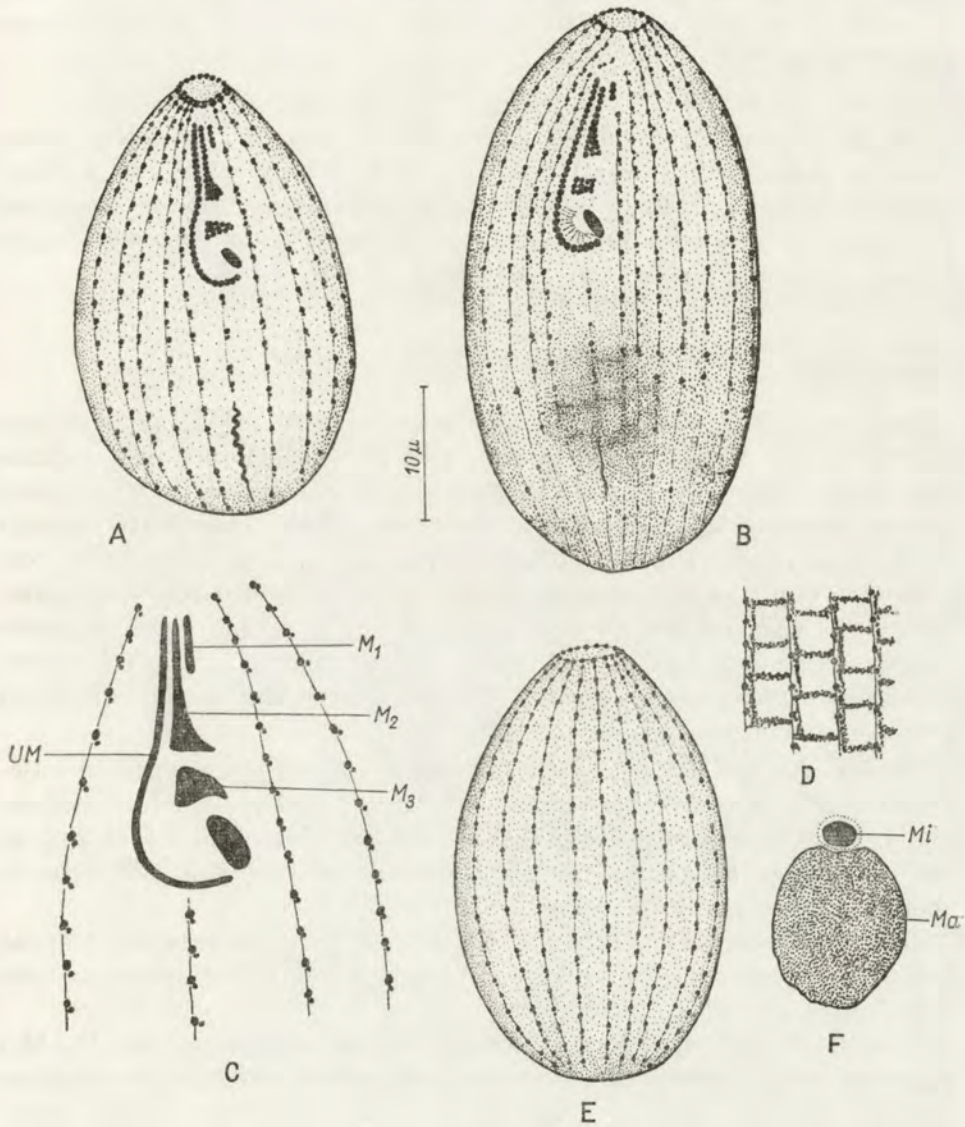


Рис. 6. *Cyclidium bergeri* sp. nov. А — первая форма, общий вид с брюшной стороны, В — вторая форма, общий вид с брюшной стороны, С — буккальный аппарат, D — строение спинного аргирома, E — общий вид со спинной стороны (A-D — серебрение) F — ядра (гемалаун), Ma — макронуклеус, Mi — микронуклеус, UM — ундулирующая мембрана, M₁, M₂, M₃ — мембранеллы

Fig. 6. *Cyclidium bergeri* sp. nov. A — first form, ventral side, B — second form, ventral side, C — buccal apparatus, D — structure of dorsal argyrome, E — dorsal side (A-D — silver impregnation), F — nuclei (hemalaun), Ma — macronucleus, Mi — micronucleus, UM — undulating membrane, M₁, M₂, M₃ — membranelles

Ядерный аппарат располагается в середине тела инфузории и состоит из одного округлого макронуклеуса и тесно прилегающего к нему микро-нуклеуса (Рис. 6 F).

Длина тела фиксированных особей 40–50 μ , ширина 25–30 μ .

Биотоп: мелкий и средний песок Каспийского моря. Настоящий вид отличается от описанных в литературе видов рода *Cyclidium* формой тела и характером цилиатуры: наличием одного посторального меридиана и сдвинутым назад цитопигом и ядерным аппаратом. Последний у всех описанных видов расположен ближе к переднему концу тела.

Histiobalantium majus Kahl, 1931 (Рис. 7)

Вид описан Калем (Kahl 1931) из пресной воды на основании лишь прижизненных наблюдений. Каль (Kahl 1931) впервые отметил, что представители рода *Histiobalantium* всегда имеют многочисленные сократительные вакуоли, макронуклеус, состоящий из нескольких частей. Дражеско (Dragesco 1968) переописывает *H. majus* по серебрянным препаратам из псаммона Роскова. Эта форма в Каспийском море встречается в большом количестве. Материал по данному виду был собран в средних и крупных песках островов Свиного и Обливного. На первый взгляд этот вид напоминает род *Pleuronema*. Однако на окрашенных препаратах их сразу можно различить по строению буккального аппарата.

Форма тела вытянуто-овальная, латерально сплюснутая (Рис. 7 А). Передняя половина тела очень темная, цитоплазма этой зоны богата включениями. Задняя часть тела прозрачная и обладает несколькими сократительными вакуолями, одна из которых очень объемистая. Под кутикулой имеются многочисленные трихоцисты (Рис. 7 В).

Буккальная полость широкая и занимает почти $2/3$ длины тела. Как и у рода *Pleuronema*, у этого вида существуют преоральные и посторальные швы (Рис. 7 А).

Буккальная цилиатура состоит из адоральных мембранелл (M_1 , M_2 , M_3) и ундулирующей мембраны. Последняя зигзагообразно идет по правому краю перистома, на самом конце делает петлю и, поднимаясь выше, образует поликинету, состоящую из 4–5 рядов тесно сближенных кинетосом. Вторая адоральная мембрана (M_2) самая широкая. Она состоит из 10 и более кинетосом и расположена параллельно первой (M_1). Третья мембранелла (M_3) более длинная и состоит из двух сближенных рядов кинетосом.

Ресничный покров густой, состоит из 90–110 меридиальных рядов. Передние и задние концы этих рядов упираются в преоральный и посторальный швы (Рис. 7 А).

Ядерный аппарат представлен макронуклеусом, который состоит из 2-х

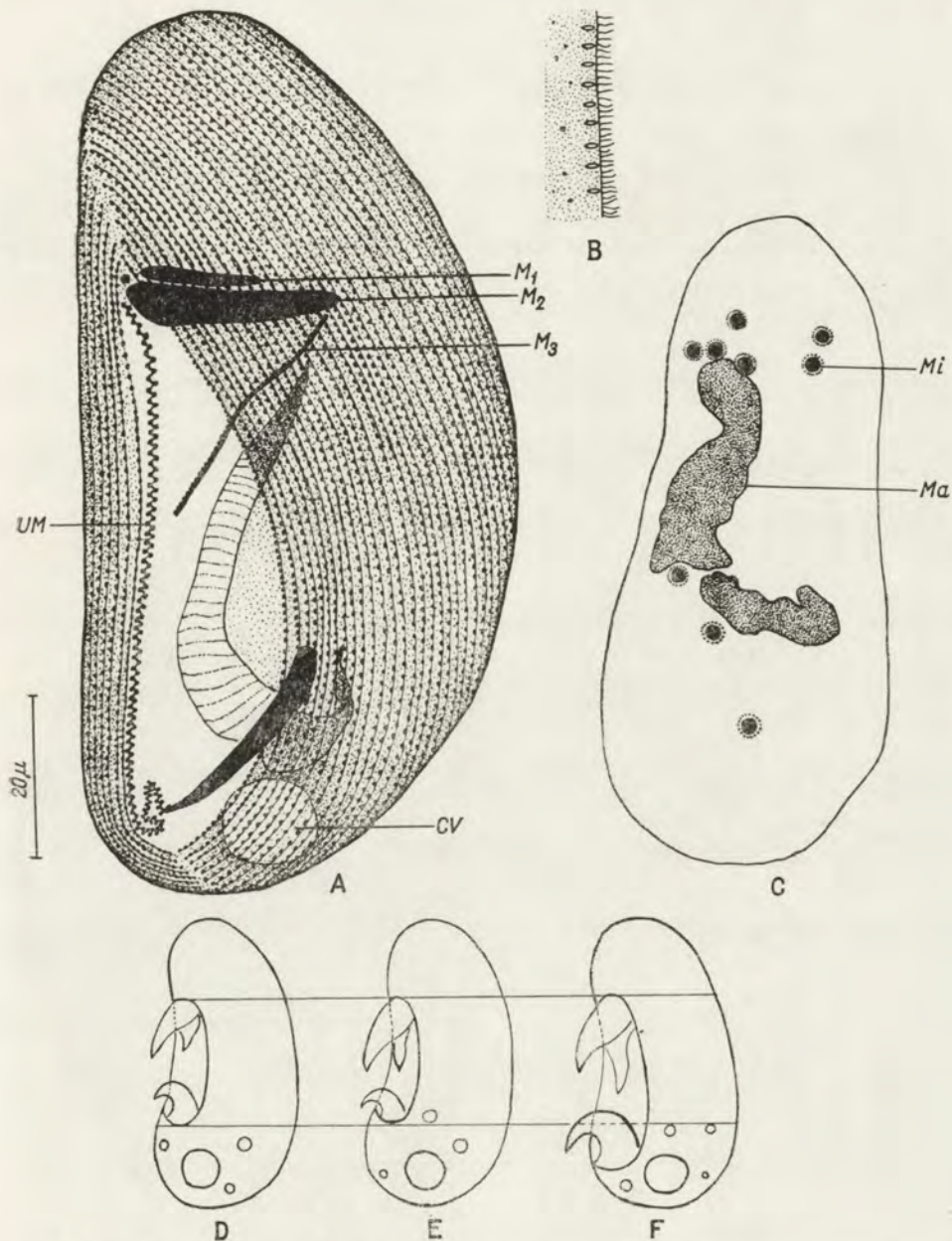


Рис. 7. *Histiobalantium majus* Kahl, 1931. А — общий вид с брюшной стороны (серебрение), В — трихоцисты, С — ядра (гемалаун), D-F — схемы: D — форма Каля (Kahl 1930-1935), E — форма Дражеско (Dragesco 1968), F — каспийская форма. Ма — макронуклеус, Ми — микронуклеус, CV — сократительная вакуоль, UM — ундулирующая мембрана, M₁, M₂, M₃ — мембранеллы

Fig. 7. *Histiobalantium majus* Kahl, 1931. A — ventral side (silver impregnation), B — trichocysts, C — nuclei (hemalaun) D-F — schemes: D — Kahl's form (Kahl 1930-1935), E — Dragesco's form (Dragesco 1968), F — caspian form. Ma — macronucleus, Mi — micronucleus, CV — contractile vacuole, UM — undulating membrane, M₁, M₂, M₃ — membranelles

частей. Вокруг макронуклеуса имеется от 7 до 9 микронуклеусов (Рис. 7 С).

Длина тела 150–300 μ , ширина — 70–120 μ .

Биотоп: средний и крупный мезосапробный песок Каспийского моря.

По большинству признаков каспийская форма *H. tajus* идентична форме Каля (Kahl 1931) и Дражеско (Dragesco 1968). Однако наша форма отличается от последних большим размером перистома и его смещением к заднему концу тела (см. Рис. 7 D–F).

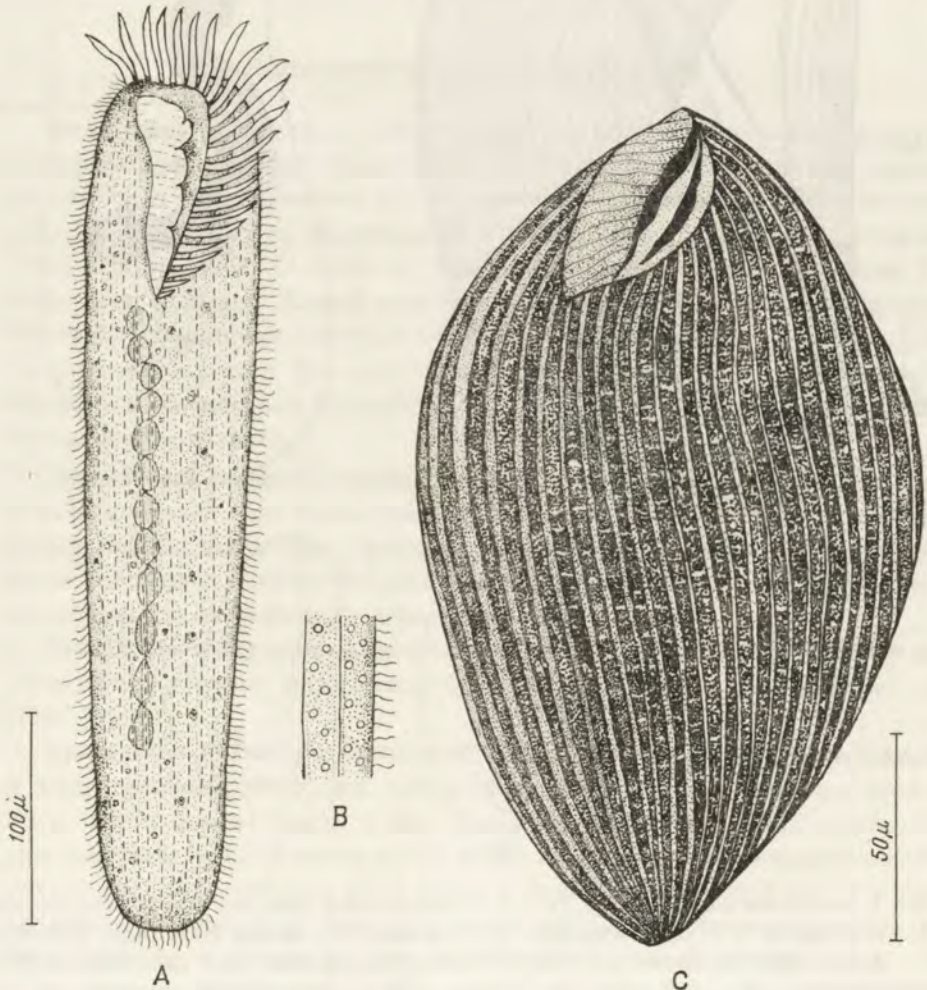


Рис. 8. *Condyllostoma arenarium* Spiegel, 1926. А — общий вид (прижизненно), В — трихоцисты, вид с поверхности тела, С — фиксированная особь (серебрение)

Fig. 8. *Condyllostoma arenarium* Spiegel, 1926. А — general view of living specimen, В — trichocysts, view of the body surface, С — fixed specimen (silver impregnation)

Condylostoma arenarium Spiegel, 1926 (Рис. 8)

Этот вид впервые был открыт Шпигелем (Spiegel 1926) и переописан Калем (Kahl 1930–1935), Форе-Фремье (Fauré-Fremiet 1950), Дражеско (Dragesco 1960), Боррором (Воггор 1963). Нам он встретился во всех районах побережья Каспийского моря. При изучении инфузорий островов Апшеронского и Бакинского архипелагов этот вид в массовом количестве обнаружен на о. Песчаном и Говсанском побережье Каспия, где имеется нефтяное загрязнение.

Форма тела цилиндрическая с несколько суженным задним концом (Рис. 8 А, С). Передний полюс тела занят неглубоким перистомом, снабженным ундулирующей мембраной и адоральной зоной мембранелл.

Ресничный покров состоит из 26–32 меридиальных рядов. Под кутикулой имеется беспорядочно расположенные протрихоцисты (Рис. 8 В). Макронуклеус четковидный, состоит из 8–15 узелков. Цитоплазма непрозрачная, забита разными включениями. Длина тела 350–600 μ .

Биотоп: мелкий полисапробный песок Каспийского моря.

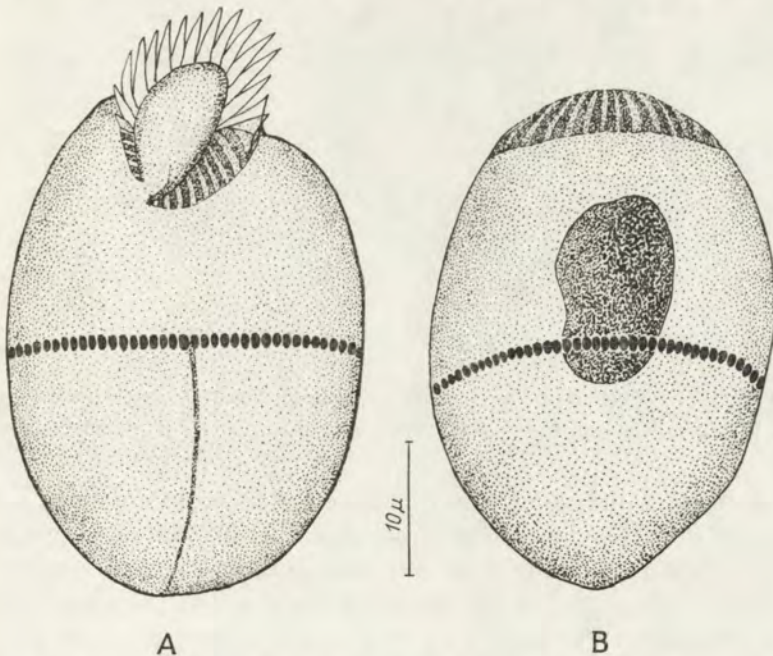
Strombidium sulcatum Clap. et Lachm., 1859 (Рис. 9)

Рис. 9. *Strombidium sulcatum* Clap. et Lachm., 1859. А — общий вид с брюшной стороны, В — общий вид со спинной стороны, серебрение

Fig. 9. *Strombidium sulcatum* Clap. et Lachm., 1859. А — ventral side, В — dorsal side, silver impregnation

Адоральная зона мембранелл состоит из 21–28 элементов (Рис. 9 А). Длина перистоста составляет 15–20 μ . Характерной чертой этого вида является наличие поперечного пояса, который огибает все тело инфузорий. При серебрении он выявляется очень хорошо и состоит из 60–80 фрагментов (Рис. 9 А, В). Инфузории очень подвижные и поэтому их часто можно найти в толще воды. В Каспийском море этот вид образует массовые популяции. При исследовании островов Апшеронского и Бакинского архипелагов Каспия он был обнаружен и в загрязненных нефтью песках о. Жилого.

Длина тела 40–50 μ , а ширина — 25–30 μ . Один макронуклеус. Микронуклеусы в наших препаратах не обнаружены (Рис. 9 В).

Биотоп: мелкий и средний песок Каспийского моря.

Strobilidium sp. (Рис. 10)

Эта форма в большом количестве обнаружена на западном побережье о. Артема и юго-западном побережье о. Жилого. Часто встречается и в песках восточного побережья Каспийского моря. Форма тела грушевидная, задний

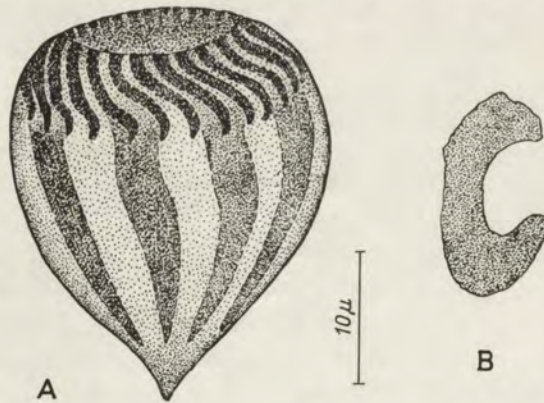


Рис. 10. *Strobilidium* sp. А — общий вид (серебрение), В — ядра (гемалаун)
Fig. 10. *Strobilidium* sp. А — general view (silver impregnation) В — nuclei (hemalaun)

конец заострен, а передний образует воронку и окружен адоральной зоной мембранелл (Рис. 10 А), число которых достигает 27. Живые инфузории в падающем свете коричневатые-белые. Эктоплазма забита разными включениями. Сократимость очень слабая. Вдоль тела хорошо видны ребрышки. Начинаясь в зоне мембранелл, они доходят почти до конца тела (Рис. 10 А).

Макронуклеус С-образный и располагается ближе к переднему концу тела (рис. 10 В).

Длина тела 30–40 μ , а ширина — 25 μ .

Биотоп: мелкий песок Каспийского моря.

Holosticha manca Kahl, 1932 (Рис. 11)

Первое описание этого вида приводится Калем (Kahl 1930–1935). Инфузории часто встречаются в песках островов Апшеронского и Бакинского архипелагов, а также на восточном побережье Каспийского моря. Описание дается на основании серебрянных материалов.

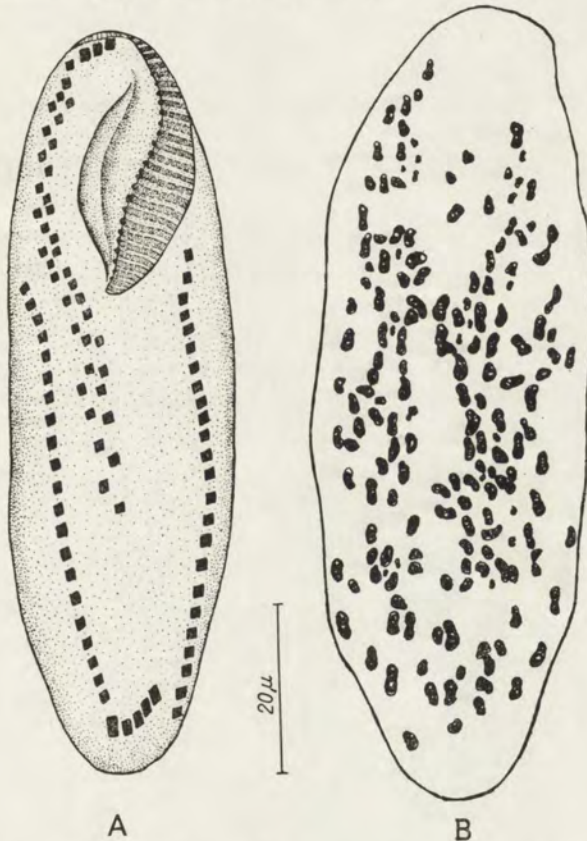


Рис. 11. *Holosticha manca* Kahl, 1932. А — общий вид с брюшной стороны (серебрение), В — ядра (гемалаун)

Fig. 11. *Holosticha manca* Kahl, 1932. А — ventral side (silver impregnation), В — nuclei (hemalaun)

Тело вытянуто в длину, сильно сплющено в дорзо-вентральном направлении (Рис. 11 А). Цитоплазма непрозрачная, забита включениями. Перистом небольшой (30 μ), занимает 1/3 длины тела. Адоральная зона состоит из 25–30 мембранелл. Брюшная сторона тела имеет два ряда маргинальных цирр и два ряда вентральных цирр. Последние, начинаясь у трех крупных фронтальных цирр, спускаются несколько ниже середины тела инфузории. Цирры в этих рядах расположены несколько беспорядочно (Рис. 11 А). Правые

и левые маргинальные ряды начинаются от нижней границы перистомальной полости и спускаются до конца тела. Каждый из них состоит из 22–28 цирр. 5 трансверсальных цирр расположены вблизи заднего конца тела. Ядра многочисленные, количество их варьирует от 150 до 220 (Рис. 11 В). Длина тела у фиксированных особей составляет 90–100 мк, а у живых — не более 120 мк.

Биотоп; мелкий мезосапробный песок Каспийского моря.

Amphisiella milnei Kahl, 1932 (Рис. 12)

Вид впервые описан Калем (Kahl 1932). Массами встречаются в песках восточного побережья Каспийского моря. Его можно встретить и в песках островов архипелага.

Тело вытянуто в длину и сплющено в дорзовентральном направлении (Рис. 12 А). Цитоплазма непрозрачная, забита включениями. Перистом не-

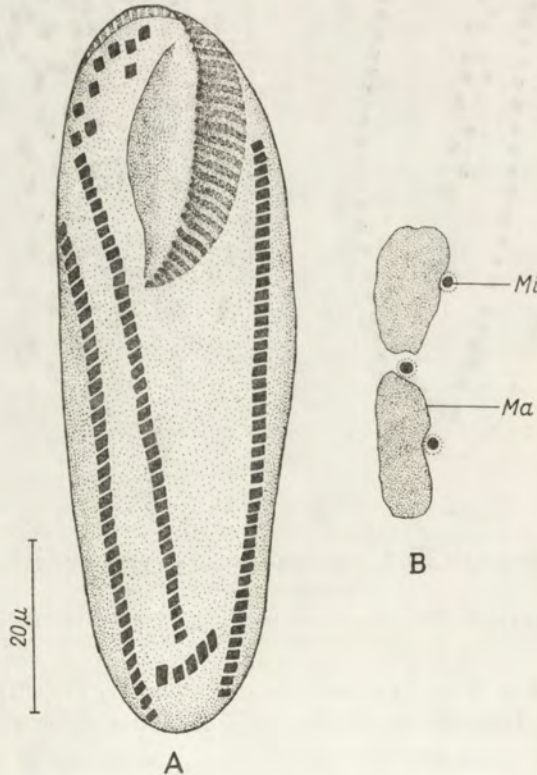


Рис. 12. *Amphisiella milnei* Kahl, 1932. А — общий вид с брюшной стороны (серебрение), В — ядра (гемалаун). Ма — макронуклеус, Ми — микронуклеус

Fig. 12. *Amphisiella milnei* Kahl, 1932. А — ventral side (silver impregnation), В — nuclei (hemalaun). Ма — macronucleus, Ми — micronucleus

большой, длина его составляет 35 μ . Адоральная зона состоит из 30–35 мембранелл. Брюшная сторона тела несет 6–9 фронтальных цирр, два ряда маргинальных и 1 ряд вентральных цирр (Рис. 12 А). Маргинальные цирры очень сближены друг с другом, каждый ряд состоит из 36–44 цирр. Трансверсальных цирр обычно пять, встречаются особи и с шестью трансверсальными циррами.

Ядерный аппарат состоит из 2-х овальных макронуклеусов и прилегающих к ним 2–3 микронуклеусов (Рис. 12 В). Длина тела 120 μ .

Биотоп: малкий песок Каспийского моря.

Euplotes zenkewitchi Burkovsky, 1970 (Рис. 13; Табл. II 10, 11)

Этот вид описан Бурковским (1970) из Кандалакшского залива Белого моря. Эта инфузория встретилась нам в песках о. Жилого. Сравнение каспийской формы этого вида с беломорской формой показано, что они по некоторым признакам заметно отличаются друг от друга. Поэтому мы даем описание каспийской формы на основании серебрянных материалов.

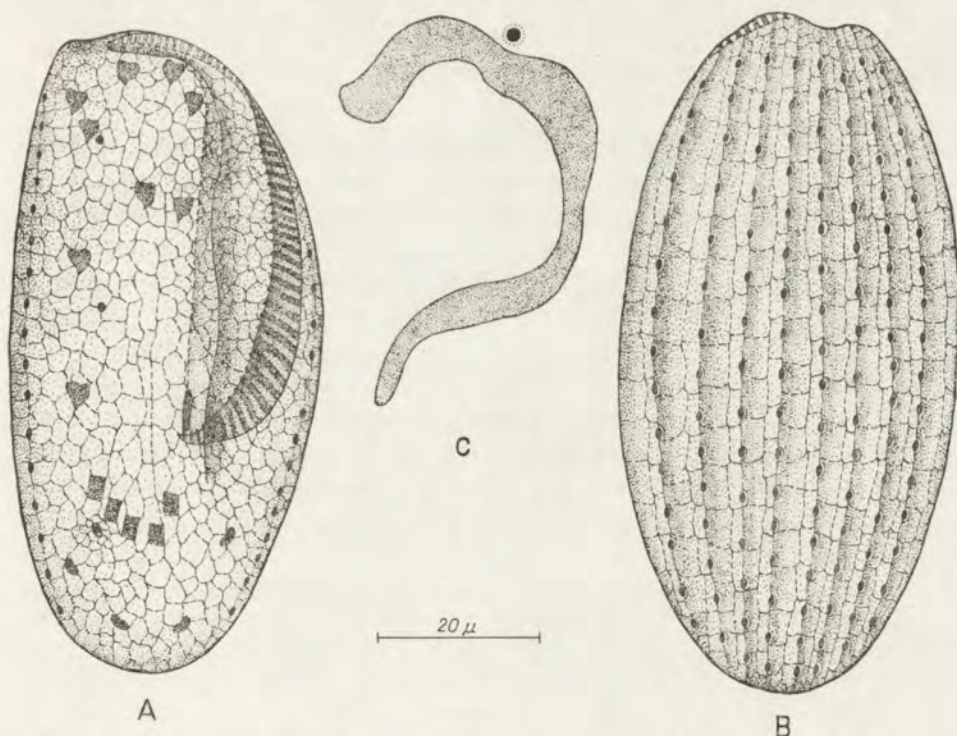


Рис. 13. *Euplotes zenkewitchi* Burkovsky, 1970. А — общий вид с брюшной стороны, В — общий вид со спинной стороны (А–В — серебрение); С — ядра (гемалаун)

Fig. 13. *Euplotes zenkewitchi* Burkovsky, 1970, А — ventral side, В — dorsal side (А–В — silver impregnation), С — nuclei (hemalaun)

Этот вид на первый взгляд напоминает *Euplotes muscicola* Kahl (1932), переописанный Тьюффро (Tuffrau 1960), но отличается от последнего иным строением дорзального межщетникового аргиромы.

Форма тела овальная (Рис. 13 А, В; Табл. II 10, 11). Цитоплазма непрозрачная, бесцветная. Перистом занимает больше половины тела, длина его составляет около 50–60 м. Адоральная зона состоит из 45–50 мембранелл. Брюшная сторона тела всегда имеет 9 фронто-вентральных, 5 трансверсальных и 3–4 каудальных цирры. На вентральной стороне тела имеются основания двух щетинок, расположенных на одной продольной линии (Рис. 13 А; Табл. II 10). У беломорской формы эти щетинки не обнаружены. Кроме того, у каспийской формы две задние фронто-вентральные цирры и правые передние расположены на одной продольной линии. Напротив, у беломорской формы две задние фронто-вентральные цирры расположены близ правого края тела. Имеется одна сократительная вакуоль. Обнаружено 8–10 латерально-дорзальных рядов щетинок (Рис. 13; Табл. II 11). В одном дорзальном ряду обнаруживается 16–18 щетинок. Аргиром межщетниковых рядов типа *E. patella*.

Ядерный аппарат, характерный для рода *Euplotes*, состоит из одного макронуклеуса и одного микронуклеуса (Рис. 13 С).

Биотоп: мелкий и средний песок Каспийского моря.

Длина тела 80–90 м.

Главной отличительной чертой каспийской расы *E. zenkewitchi* от беломорской является число каудальных цирр, число латерально-дорзальных рядов щетинок, число щетинок в одном дорзальном ряду и наличие 2-х щетинок на вентральной стороне тела. Вполне допустима вариабильность указанных признаков, поэтому мы не можем выделить эту форму в самостоятельный вид.

Diophrys scutum Dujardin, 1842

Этот вид, широко распространенный в песках Каспийского моря, встретился нам в большом количестве на островах Апшеронского и Бакинского архипелагов, а также на восточном побережье Каспия. В мелком песке восточного побережья (в районе Бекташе) среди обнаруженных особей встретилось много карликовых форм *D. scutum* размером 40–60 м. Адоральная зона у этих форм состояла из 25–35 мембранелл. В остальном карликовые формы имели типичное строение.

Резюме

В работе приводятся данные по фауне и экологии инфузорий микробентоса островов Апшеронского и Бакинского архипелагов Каспийского моря. Изучено около 300 проб песка, взятых с глубины от нуля до 25 метров на 11 остро-

вах (Нефтяные камни, Жилой, Артем, Песчаный, Вульф, Дуванный, Булла, Глиняный, Лось, Свиной, Обливной).

Грунты прибрежных зон островов в основном состоят из песка, глины, ракуши, ила с ракушей и камня. Характеристика грунтов показала, что острова архипелага по размеру песчинок несколько отличаются друг от друга. На всех островах преобладают мелкие пески с $M_0 = 0.1-0.3$ мм. Органические вещества в песках островов варьировали от 0.37 до 0.83%.

В песчаном грунте островов Апшеронского и Бакинского архипелагов всего было обнаружено 59 видов инфузорий, из которых шесть видов (*Paramecium calkinsi*, *Cyclidium bergeri*, *Spirostomum teres*, *Holosticha manca*, *Keronopsis pernix*, *Euplotes zenkewitchi*) являются новыми для Каспия. Один из них (*Cyclidium bergeri* sp. nov.) описывается впервые для науки. В статье дается описание вышеотмеченных, а также некоторых других видов (*Pleuronema coronatum*, *Histiobalantium majus*, *Condylostoma arenarium*, *Strombidium sulcatum*, *Amphisiella milnei*, *Diophrys scutum*), наиболее характерных для интерстициальной фауны Каспия. Приводятся также данные по сезонной динамике фауны инфузорий и их вертикальному распределению в разные сезоны года.

SUMMARY

In the present paper the data concerning the fauna and ecology of ciliates from microbenthos of the islands of Apšeroniskij and Bakinskij archipelagos of the Caspian Sea are given. About 300 samples of sand collected from 0 to 25 meters below the sea level in 11 islands (Table 1) were investigated.

The grounds of the littoral zone of islands were composed mainly of sand, clay, shells, loam with shells, and stones. Characteristic of the grounds have shown that the isles differ by dimensions of sand grains. Fine sand with $M_0 = 0.1-0.3$ mm dominates in all islands, the quantity of organic matter amounts from 0.37 to 0.83%.

In sandy grounds of the islands of Apšeroniskij and Bakinskij archipelagos 59 species of ciliates were found. Six species (*Paramecium calkinsi*, *Cyclidium bergeri*, *Spirostomum teres*, *Holosticha manca*, *Keronopsis pernix*, *Euplotes zenkewitchi*) were found for the first time in the Caspian Sea, one of them appeared to be a new species (*Cyclidium bergeri*). The descriptions of the above mentioned species, as well as some other species (*Pleuronema coronatum*, *Histiobalantium majus*, *Condylostoma arenarium*, *Strombidium sulcatum*, *Amphisiella milnei*, *Diophrys scutum*), the most characteristic of the interstitial fauna of the Caspian Sea, are included. The data concerning seasonal dynamic of the ciliate fauna as well as their vertical distribution in various seasons of the year are also given in the present paper.

Description of *Cyclidium bergeri* sp. nov.

Body oval or egg-shaped, rounded at both ends, 40–50 μ long, 25–30 μ wide (Fig. 6, Pl. II 7–9). Buccal cavity about 20 μ long, occupies less than half of the body. It is composed of 4 elements: an undulating membrane and 3 membranelles. Behind the buccal cavity a short row of loosely arranged cilia runs toward the posterior body pole. It ends before cytopyege.

Body ciliature is composed of 19 to 20 meridians. Two forms of *C. bergeri* are distinguished. In the first one the meridians reach both ends of the body. One kinety, lying to the left from the

buccal cavity, has densely arranged cilia in the segment from the level of the posterior end of second membranelle to the end of undulating membranelle. In the second form the meridians do not reach the posterior body pole; in this part only dispersed kinetosomes are present. Besides, in this form three kineties (one lying to the right and two to the left from the buccal cavity) do not reach the anterior body pole, beginning at the same level as undulating membrane. Cytopyge is situated near the posterior body end at postoral kinety.

On the dorsal side of the body there are usually 7–8 sometimes up to 10 kineties. Ventral and dorsal argyromes are clearly visible in stained preparations.

The nuclear apparatus is situated in the body; centre; it is composed of one rounded macronucleus and a micronucleus, tightly adhering to Ma.

Biotop — fine and medium sands of Žiloi isle of Apšeroniskij archipelago and eastern shore of the Caspian Sea.

The described species differs from all the representatives of the genus *Cyclidium* by the body shape and character of the ciliature. Occurrence of one postoral kinety and shifting of the cytopyge and nuclear apparatus toward the posterior body end in comparison with other species are the most important differences.

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ПОДПИСИ К ТАБЛИЦАМ I-II

1-3: *Paramecium calkinsi* Woodruff, 1921. 1 — общий вид с брюшной стороны, 2 — система околоротовых рядов кинетосом (адесмокинет), 3 — общий вид со спинной стороны
4-6: *Pleuronema coronatum* Kent, 1881. 4 — общий вид с брюшной стороны, 5 — вид радиальных ребер буккальной полости, 6 — общий вид со спинной стороны
7-9: *Cyclidium bergeri* sp. nov. 7 — первая форма, общий вид с брюшной стороны, 8 — вторая форма, вид с брюшной стороны, 9 — общий вид буккального аппарата
10-11: *Euplotes zenkewitchi* Burkovsky, 1970. 10 — общий вид с брюшной стороны, 11 — общий вид со спинной стороны

EXPLANATION OF PLATES I-II

1-3: *Paramecium calkinsi* Woodruff, 1921. 1 — general view of the ventral side, 2 — arrangement of circumoral rows of kinetosomes (adesmokineties), 3 — view of the dorsal side
4-6: *Pleuronema coronatum* Kent, 1881. 4 — general view of the ventral side, 5 — buccal cavity with radial ribs, 6 — view of the dorsal side
7-9: *Cyclidium bergeri* sp. nov. 7 — first form, general view of the ventral side, 8 — second form, general view of the ventral side, 9 — buccal apparatus
10-11: *Euplotes zenkewitchi* Burkovsky, 1970. 10 — general view of the ventral side, 11 — view of the dorsal side



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Arthur BORROR

Tidal marsh ciliates (*Protozoa*): morphology, ecology, systematicsSalzwassersumpfen Ciliaten (*Protozoa*): Anatomie, Ecologie, Systematik

Despite the known high productivity of tidal marshes and the potential these coastal wetlands have for supporting a rich and diverse microfauna, relatively few protozoologists have investigated the ditches, pools, and algal mats of coastal marshes. Compared with the ciliate fauna of other marine habitats such as the mesopsammon little is known of the extent or variety of the ciliate populations inhabiting coastal wetlands.

The earlier papers of Fauré-Fremiet 1912, Kahl 1928, and Kirby 1934 as well as more recent studies (Czapik 1962, Webb 1956) suggest that tidal marshes support populations of ciliates that may play significant ecological roles there. By means of their role in the decomposer food chain and as predators upon bacteria, ciliates may play a greater role than has been realized in flow of energy and in estuarine productivity in general.

During the past five years, investigations of the New Hampshire tidal marshes (Borrer 1965 a, b, 1966, 1968 a and 1969 b) have indicated that to interpret ecological data one must carefully assess identification procedures used in ecological studies. Many species of ciliates are morphologically similar; genera may be represented by more than one species simultaneously or may exhibit seasonal progression of species. Coupling of ecological methodology with careful systematics is not only necessary to bridge the gap between the ecologist and the taxonomically-oriented protozoologist but also to yield information relative to temporal changes in species composition of ciliate communities, and subtle microdistributional differences. This paper encompasses those species of ciliates that have been identified from collections in New Hampshire tidal marshes and serves as a reference for determination of interrelationships of these ciliates and physical and chemical factors associated with them. There are sufficient details on poorly known species to allow for an understanding of their external structure, internal structure, and taxonomic status.

This study was supported in part by grants (18050 FBW, 18080 FBW) from the Federal Water Pollution Control Administration.

Methods

Between July, 1964 and January, 1971, I collected ciliates either from a tidal marsh pool located near Route 1A at Odiorne's Point, Rye, New Hampshire, (L. 43°, 2'22" N.; L. 70°, 42'57" W.) or from a tidal marsh near Adams' Point, Durham, New Hampshire (L. 43°, 5'22" N.; L. 70°, 52'15" W.). The latter area became the focus of intensive study since 1968 with establishment of the Jackson Estuarine Laboratory of the University of New Hampshire on nearby Adams' Point. Samples were taken at various depths in tidal marsh ditches and pools as well as from surface mats of various algae (i.e., *Cladophora* and *Vaucheria*).

I either examined field collections immediately for living ciliates or filtered the collection through a series of filters employing nylon gauze of known mesh sizes. I maintained mass or clonal cultures of many species employing simple media such as rice grains, dried split peas, and hay infusion. I observed living individuals with dissecting microscopes and bright field photomicroscopes, corroborating cortical details by the NMF method (Borrer 1968 b, 1969 a) and the Chatton-Lwoff silver impregnation technique as modified by Corliss 1953, nuclear morphology by an iron hematoxylin method and Fielgen nuclear reaction. I used a camera lucida, a calibrated ocular micrometer, and a Nikon automatic photomicroscope employing high contrast copy film to record observations of morphology. Scales on all drawings indicate length of 10 µm.

Permanent preparations containing type material of new species have been deposited in the U. S. National Museum.

This is a contribution of the Jackson Estuarine Laboratory.

The following is a list of species of ciliates encountered in New Hampshire tidal marshes.

Gymnostomatida

Rhabdophorina

- Prorodon marinus*
- Stephanopogon apogon*
- Lacrymaria marina*
- Loxophyllum chaetonotum*
- Loxophyllum setigerum*
- Litonotus cygnus*
- Coleps tessellatus*
- Mesodinium pulex*
- Enchelyodon trepida*
- Spathidium* sp.
- Askenasia stellaris*
- Trachelonoma oligostriata*
- Metacystis striata*
- Placus salinus*

Cyrtophorina

- Trochilia sigmoides*
- Chlamydodon triquetrus*
- C. obliquus*
- C. lynchelliformis* n. sp.
- Trochilioides recta*
- Nassula labiata*
- Dysteria monostyla*
- D. marina*
- Cryptopharynx setigerus*

Trichostomatida

- Plagiopyla nasuta*
- Sonderia sinuata*
- Geleia simplex*
- G. orbis*
- Colpoda cucullus*
- Trimyema pleurispirale* n. sp.

Hymenostomatida

- Paratetrahymena wassi*
- Ophryoglena flava*
- Frontonia marina*
- F. microstoma*
- F. fusca*
- Paramecium calkinsi*

Scuticociliatida

- Uronema marinum*
- U. acutum*
- U. filificum*
- Uropedalium pyriforme*
- Paralembus hargisi* n. comb.
- P. marinus* n. comb.
- Pseudocohnilembus longisetus*
- Cohnilembus verminus*
- Cyclidium plouneouri*
- C. marinum*
- Paranophrys magna* n. sp.

<i>Pleuronema coronatum</i>	<i>Odontostomatida</i>
<i>P. smalli</i>	<i>Caenomorpha</i> sp.
<i>Peritrichida</i>	<i>Hypotrichida</i>
<i>Vorticella nebulifera</i>	<i>Trichotaxis pulchra</i> n. sp.
<i>V. striata</i>	<i>Holostricha diademata</i>
<i>Cothurnia simplex</i>	<i>Paraholosticha polychaeta</i>
<i>Zoothamnium</i> sp.	<i>Oxytricha halophila</i>
<i>Suctorida</i>	<i>Histiculus similis</i>
<i>Acineta</i> sp.	<i>Gastrostyla pulchra</i>
<i>Heterotrichida</i>	<i>Trachelostyla pediculiformis</i>
<i>Condylostoma arenarium</i>	<i>Euplotes mutabilis</i>
<i>Protocruzia depressa</i>	<i>E. trisulcatus</i>
<i>Peritromus faurei</i>	<i>E. crenosus</i>
<i>Gruberia lanceolata</i>	<i>E. bisulcatus</i>
<i>Parablepharisma bacteriophorum</i>	<i>E. harpa</i>
<i>P. chlamydephorum</i>	<i>E. charon</i>
<i>Oligotrichida</i>	<i>E. quinquecarinatus</i>
<i>Strombidium sulcatum</i>	<i>E. alatus</i>
<i>S. latum</i>	<i>E. minuta</i>
<i>S. kahli</i>	<i>E. crassus</i>
<i>S. viride</i>	<i>Diophrys oligothrix</i>
<i>S. styliferum</i>	<i>D. scutum</i>
<i>S. purpureum</i>	<i>Uronychia transfuga</i>
<i>Strobilidium caudatum</i>	<i>Aspidisca aculeata</i>
	<i>A. baltica</i>

Systematic section

Order *Gymnostomatida*

Suborder *Rhabdophorina*

Prorodon marinus Claparède et Lachmann, 1858

Length 81–117 μm , width 56–78 (–88) μm . Cell surface showing no obvious cortical sculpturing. Cytostome apical and anterior, circular, about 12.5 μm in diameter, lined with about 25 nematodesmata that extend about 25 μm into cell (Fig. 1, 2).

Ciliation. Ciliary rows number 41 to 60 not all bipolar, 3–4 μm apart at equator of cell separated by single rows of mucocysts. Anteriormost three cilia in each ciliary row doubled, used in feeding. Cilia near posterior pole elongated. Radial symmetry interrupted by three rows of relatively closely set cilia extending from cytostome 19–27 μm posterior along an area 4 to 5 μm wide.

Internal anatomy. Macronucleus elongate oval, usually equatorial, superficial, approximately 15 \times 12 μm , of uniform refractive index with scattered rela-

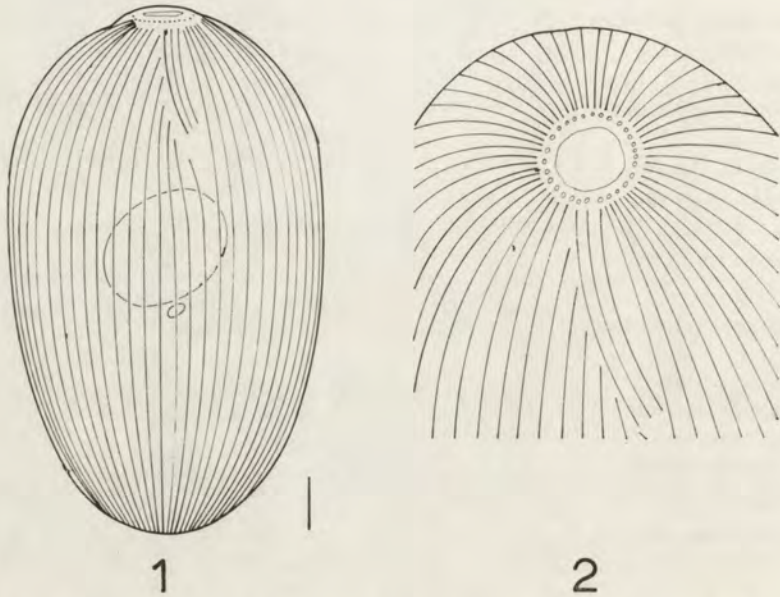


Fig. 1. *Prorodon marinus*, length 100 μm , lateral aspect, showing nuclear configuration and arrangement of ciliary rows. Scales on all drawings indicate length of 10 μm

Fig. 2. *P. marinus*, anterolateral aspect, showing arrangement of anterior ends of ciliary rows, and ends of nematodesmata around the cytostome

tively small spherical bodies of a lower refractive index (Fig. 1). Macronucleus single. Food vacuoles contain diatom shells (often 17 or more per cell, each approximately 30 μm in length) and remains (including the easily identifiable nucleus) of armored dinoflagellates.

Ecology. This species occurs fairly regularly and in large numbers at several places in tidal marshes both in spring and fall. During quantitative sampling during 1964 and 1965, this species reached greatest abundance in August; numbers diminished to zero in November and remained at zero until small numbers reappeared in March. They occur in high numbers during April and May.

Systematics. The most recent review of this genus (Kahl 1930) lists 29 species, most differentiated on the basis of size and shape. Since 1930, at least 22 additional species have been described.

Recent investigations of life history and morphogenesis in this genus (Czapik 1965, and de Puytorac and Savoie 1968) have suggested that body size, shape, and number of ciliary rows are sufficiently variable to be used only with caution in differentiation of species of this genus. If size depends upon the stage in the life cycle and nutritional state, then the number of nematodesmata may also be a dangerous criterion by which to differentiate species. The criteria of greatest value in differentiation of species in this genus seem to be nuclear structure, trichocyst arrangement, and extent and geometry of the triple rows of closely set cilia.

Of the 52 nominal species in this genus, 18 have an oval macronucleus with small evenly distributed nucleoli.

Of these, only two have trichocysts arranged as in the present population, *P. marinus* Claparède et Lachmann, 1858, and *Prorodon teres* var. *crassa* Kahl, 1927. The latter was considered a modification of *Prorodon teres* (Kahl, 1930). In 1960 Dragesco published a description of *Prorodon marinus* showing the macronucleus richly provided with nucleoli. He remarked on the numerous short interkinetal trichocysts implanted perpendicularly to the cell surface. Dragesco did not describe the arrangement of nematodesmata.

Placus salinus Dietz, 1964

Length 53–117 μm . Cell oval in longitudinal section and cross section; maximum width 41–80 μm . Anterior and posterior poles evenly rounded. Surface sculptured by approximately 30 spiral double-contoured ribs separated by grooves with strongly cross-ribbed surfaces (Fig. 5, Pl. I 53). Cytostome anterior, slit-like, 10 μm wide. Frontal plane containing cytostomal slit also contains longest cross diameter of cell and posterior suture. Shallow groove extending posteriorly from cytostome approximately 1/3 cell length, widening and deepening posteriorly. (In the following discussion the side of the cell bearing this groove is considered to the the animal's left). Cytoproct a long slit extending from posterior end of groove nearly 2/3 cell length. Water expulsion vesicle pore near posterior end of cytoproct.

Ciliation. Row of compound ciliature 27 μm long in postcytostomal groove (Fig. 4), consisting of 27 groups of cilia, each group diamond-shaped containing four stiff, erect cilia 6–7 μm long. Posterior end of postcytostomal groove with four–five single cilia, each apparently accompanied by barren basal body (Fig. 4).

Locomotory cilia in 29–31 rows, terminating anteriorly as in Fig. 4. In addition, cytoproct bordered by two ciliary rows. All rows spiral to animal's right through approximately 90° ending posteriorly at a suture. Water expulsion vesicle pore lies approximately midway on ventral side of posterior suture (Fig. 6). Somatic cilia closely set, emerging between microvilli that extend outward and to animal's left from edge of each ridge.

Internal anatomy. A series of two or three flattened alveoli and a row of trichocysts beneath cell membrane of each ridge (Fig. 5). Trichocysts also occur at each edge of compound cilia. Water expulsion vesicle large, posterior. Cytopharynx lined with approximately 40 double nematodesmata abutting surface in an oval approximately 10 \times 3 μm . Nematodesmata straight, progressing posteriorly near surface of cell approximately 150° away from (ventral to) postcytostomal groove, at least 50 μm long. An additional set of 25–30 fibers abuts bottom of posterior depression of postcytostomal groove, each approximately 14 μm long, extending inward and ventrally terminating in an oval approximately 7 or 8 μm wide. Food vacuoles containing remains of flagellates. Macronucleus enlongate, C-shaped,

of varying width. Anterior end of macronucleus ventral to cytopharynx, anterior to secondary nematodesmal fibrils. Macronucleus curves posterodorsally, terminating in posterior half of cell. Micronucleus not observed.

Ecology. Members of this genus occurred in the Adams' Point tidal marsh in October and November of 1968, and April and May of 1969–1971. The animal swims in a straight line with a clockwise twisting.

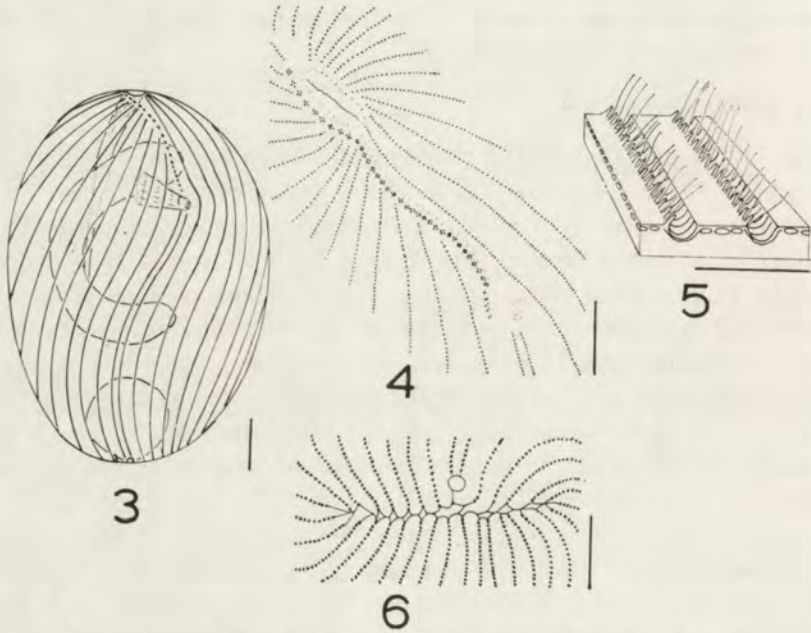


Fig. 3. *Placus salinus*, length 74 μm , left lateral aspect, showing ciliary rows, macronucleus, lateral and cytopharyngeal nematodesmata, and water expulsion vesicle and pore

Fig. 4. *P. salinus*, anterior aspect, showing slit-like cytostome surrounded by ends of nematodesmata, anterior ends of ciliary rows, and post cytostomal row of compound cilia. Stipple field at anterior end of double ciliary row represents superficial terminus of postcytostomal nematodesmata

Fig. 5. *P. salinus*, diagram of arrangement of cilia, microvillae, striated grooves, and alveoli, of a section of cortex

Fig. 6. *P. salinus*, posterior aspect, showing arrangement of posterior ends of ciliary rows that abut posterior suture, and position of water expulsion vesicle pore

Systematics. Since Kahl reviewed this genus in 1932, listing six species, two additional species have been described; *P. eforianus* Tucolesco, 1962 and *P. salinus* Dietz, 1964. During the 1920's and 1930's numerous investigators of the morphology of *Placus* (Mansfeld 1923; Kahl 1926, 1928, 1930; Sauerbrey 1928 and Noland 1937) have commented on the difficulty of observing these animals in life. The structures discussed above were observed in living individuals, nonetheless wet silvers and specimens prepared according to NMF and progressive-hematoxylin techniques were used for corroboration. Prior to Dietz's description

of *P. salinus*, all species known had spherical or condensed macronuclei. According to Dietz, the species ranged from 70–90 μm and has 32 ciliary rows. His drawing of the secondary fibrils closely approximates that of the present population and differs slightly from previous drawings of the structure in other species of the genus. The present population differs from those seen by Dietz in being more variable in size, and having slightly fewer ciliary rows.

The type of anterior termination of the ciliary rows and the presence of double cytopharyngeal nematodesmata lining the apical cytopharynx indicate a close relationship to the genus *Prorodon*, despite the degree of cortical specialization otherwise. Comparison of the feeding behavior of this species with some of the members of the genus *Prorodon* with specialized postcytostomal cilia (*Prorodon mimeticus* Kahl, 1932), as well as determination of the morphogenesis of the ciliature might shed further light on the systematic position of *Placus* in the *Holophryidae*. The fibers extending inward from the posterior end of the postcytostomal groove, like the railroad track organelle in *Chlamydon* remain, in the words of Kahl, "leicht sichtbar, aber schwierig zu verstehen".

Lacrymaria marina Kahl, 1932

These predatory ciliates occur relatively uncommonly in the tidal marsh.

Enchelyodon trepida (Kahl, 1932)

This species was described previously (Borror 1965 b).

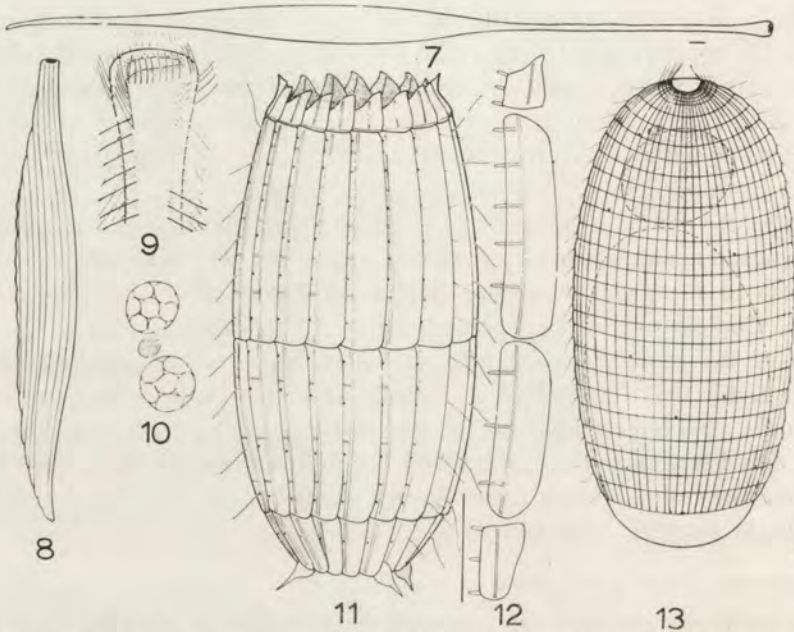
Stephanopogon apogon Borror, 1965

This species is of relatively uncommon occurrence in the tidal marsh. Closely related congeners occur in the interstices of particulate substrata (marine sands).

Trachelonema oligostriata Raikov, 1962

At full extension, length 390–620 μm (four specimens measured), width at widest point 19–23 μm . Neck 2–6 μm wide, comprising anterior third of animal. Posterior 1/5 of animal narrowed (Fig. 7). At full contraction, animal shortened by factor of three, at which time neck and tail each comprise only 1/5 of total length (Fig. 8). Cell oval in cross section, slightly more flattened on ciliated surface. Anterior end 10 μm wide, concave, bearing cytostome. Posterior tip bluntly pointed, angled to animal's left (Fig. 7). Narrow concavity 20–30 μm long from anterior end between left bristle row and left ciliary row (to be discussed below). Cell slightly dimpled where cilia arise.

Ciliation. Locomotory cilia ventral, in seven rows; left most two or three rows bipolar, others terminating against right side, accentuating scalloped margin (Fig. 8). Rows of sparse, stiff, nonmotile cilia at each edge of dorsal surface. Cytostome encompassed by whorl of closely set cilia. A row of approximately eight closely set cilia along dorsal side of narrow concavity, ventral to left bristle row (Fig. 9).



- Fig. 7. *Trachelonema oligostriata*, length about 400 μm . Anterior end to right
- Fig. 8. *T. oligostriata*, contracted specimen, ventral aspect, showing arrangement of ciliary rows
- Fig. 9. *T. oligostriata*, dorsal aspect of anterior end, showing anterior cytostome, longitudinal and circumcytostomal rows of cilia, and dorsal bristles
- Fig. 10. *T. oligostriata*, diagram of one of nuclear vesicles, with two macronuclei and one micronucleus
- Fig. 11. *Coleps tessellatus*, length 48 μm , lateral aspect, showing arrangement of cortical plates, spines, and positions of cilia (dots)
- Fig. 12. Four plates from one meridian of cortex of *C. tessellatus*, dissected to portray sculpturing and teeth
- Fig. 13. *Metacystis striata*, length 70 μm , lateral aspect. Concentric and meridional lines portray arrangement of cortical sculpturing. Posterior vacuole and nuclei also indicated

Internal anatomy. Diagonal strips of fine granules in unciliated dorsal cortex between ciliary rows, and around cytostome. Cytoplasm packed with oval disc-shaped inclusions. Nuclei in six to 12 vesicles, each with two macronuclei and one micronucleus (Fig. 10), scattered evenly along body axis.

Behavior and ecology. This species is thigmotactic, and difficult to study in the living condition inasmuch as the animal often lyses posterior to the head upon contact with the coverslip. Fixed specimens usually contract. This species was collected from the tidal marsh in October 1968 where it was numerous on the microfloral film of a fingerbowl culture. With it in culture were numerous *Uronema* spp., and the dinoflagellate *Oxyrrhis*.

Systematics. In 1960 Dragesco reviewed the family *Trachelocercidae*, erecting this genus for three species discovered among interstitial spaces of marine sand. Since then at least five more species have been described (Raikov 1962, 1963; Agamaliev 1966, and Kovaljeva 1966). None of these describe the bristle rows

or the circumcytostomal ciliature. Species in this genus currently are distinguished on the basis of length, number of ciliary rows, and nuclear structure. Of four species in this genus with as few as nine ciliary meridians, one, *T. oligostriata* as described by Raikov, agrees with the present population in length and arrangement of nuclei.

Coleps tessellatus Kahl, 1930

Length 46–49 μm ; width 21–27 μm (measurements of specimens fixed 30 sec in osmic acid fumes). Body ovate to cylindrical with truncate poles (Fig. 11), covered by approximately 18 longitudinal series of cortical plates, each series with four plates (Fig. 12). Each plate with a thickened longitudinal midline, a series of teeth on right edge, and a thin wing on left edge. Wings of each plate overlapping teeth of adjacent plate and anterior part of next plate posterior. Spine on anterior plates usually blunt, sometimes more acute. Plates of second tier with five teeth, those of other tiers with three teeth per plate. Fourth tier of plates with about three posterior teeth or spines. Anterior pole unarmored. Cytostome in cup-like depression. Posterior pole armored with six–seven irregular plates.

Ciliation. Cilia in approximately 18 rows, emerging between teeth of plates, approximately 10 μm long and 4 μm apart.

Internal anatomy. Macronucleus circular, central, approximately 13 μm in diameter, homogeneous, with adjacent spherical micronucleus. Cytopharynx 12 μm long, lined with poorly refractile nematodesmata. Anterior cytoplasm packed with irregular oval or circular bodies 1.5–2.3 μm in diameter. Food vacuoles contain flagellates. Water expulsion vesicle posterior.

Behavior and ecology. *Coleps* swims in a counterclockwise helix during forward and backward locomotion. When the ciliate locates food, forward progression stops while ciliary rotating of the cell continues, often with the posterior pole revolving. Then cell motion ceases. Feeding is accomplished while the anterior pole is held against the substratum. They may also travel with a slow progression along a substratum.

Coleps tessellatus was observed in May and September through December. During quantitative sampling during 1964 and 1965, *Coleps* occurred in June, August, September, and November, but was absent during the remainder of the winter and early spring.

Systematics. The genus *Coleps* was reviewed by Noland in 1925; the genus then included seven species. In 1930, Kahl listed 14 species. Since 1932, 11 additional species have been added to the genus.

Kahl's major contribution to the systematics of this genus was establishing a system of types of cortical plates based on morphology. This species possesses plate type three (Kahl system), in which there are teeth and a central ridge in each plate but no scalloped depressions or reticulated patterns. This feature is shared with at least seven other species.

Coleps tessellatus differs from all these in the exact conformations of the cortical plates. Individuals observed resemble closely those described by Kahl 1932 and Noland 1937.

Metacystis striata Stokes, 1893

Length 50–86 μm (usually over 62 μm), width 29–39 μm . Cell rounded posteriorly, truncate anteriorly, and nearly parallel sided; widest 2/3 of way posteriorly (Fig. 15). Anterior end concave, bearing cup-like, apical cytostome. Posterior pole hemispherical, limited by a thin membrane. Cortex finely cross-striated and longitudinally-striated by rectangular alveoli, each 1 μm wide and 3 μm long (Fig. 13). Each area so delineated bears a cilium and trichocyst. Approximately 15 water expulsion vesicle pores, randomly dispersed, positioned on alveoli as in Fig. 13.

Ciliation. Locomotory cilia in 63–66 parallel longitudinal rows, appearing in 22–24 whorls. Feeding cilia in six anterior whorls composed of the anterior six cilia of each ciliary row (Fig. 13).

Internal anatomy. Posterior 1/2–2/3 of cell usually filled by noncontractile, clear vesicle. Water expulsion vesicles small (5 μm diameter), numerous, independent of this vesicle. Macronucleus central, spherical, homogeneous. Conical cytopharynx lined by narrow truncate cone of 15 to 20 nematodesmata. Anterior cytoplasm often darkened by 30 to 50 refractile granules 1–2 μm long.

Behavior and ecology. The animal can swim rapidly in a counterclockwise helix along a narrow path. It can cruise over the substratum, sometimes gradually halting forward locomotion and spinning in a conical path with the apex in front of the organism. This species occurred in large numbers along the bottom of cultures containing rice grains, debris, and such ciliates as *Trachelonema oligostriata* and *Uronema filificum*. It was recovered from collections from Adams' Point taken in October and November of 1968.

Systematics. In 1930 Kahl reviewed the genus and included 11 species. Since then four other species have been described (Tucolesco 1962, and Dietz 1964). Species are separated on the basis of the number of circlets of cilia, size, and presence of a lorica. *M. daphnicola* Penard, 1922 has approximately the same number of circlets of cilia as the present population, but was described as being more elongate and narrow, and highly contractile. According to Stokes, *Meracystis striata* had but 20 circlets of cilia.

Mesodinium pulex Claparède et Lachmann, 1858

Length 23–31 μm , width 14–24 μm (usually less than 20 μm). Body circular in cross section. Shape as in Fig. 17.

Ciliation. Cilia equatorial, in two complex whorls. Anterior whorl with approximately 49 rows of simple cilia, each row 2–3 μm long. Posterior whorl with 40–43 double rows each 3 μm long (Fig. 18).

Internal anatomy. Cytopharynx lined with eight — 12 rods, each forked apically, $1.5\ \mu\text{m}$ wide and $6\ \mu\text{m}$ long, and capable of being retracted or extruded to at least half their length. Cytostome surrounded by a loose circlet of dense granules: similar granules (mitochondria?) scattered through anterior half of cell. Four whorls of granules underlying bases of ciliary groups (see Fig. 18). Cortex posterior of ciliary whorls relatively thin, easily ruptured during fixation.

Ecology. Members of this genus occur throughout the season in the tidal marsh. At Adams' Point, they have been found in collections in April, May, October, November, and December. In a series of monthly quantitative samples at Odiorne's Point, they occurred in each month except June, September, January, and March.

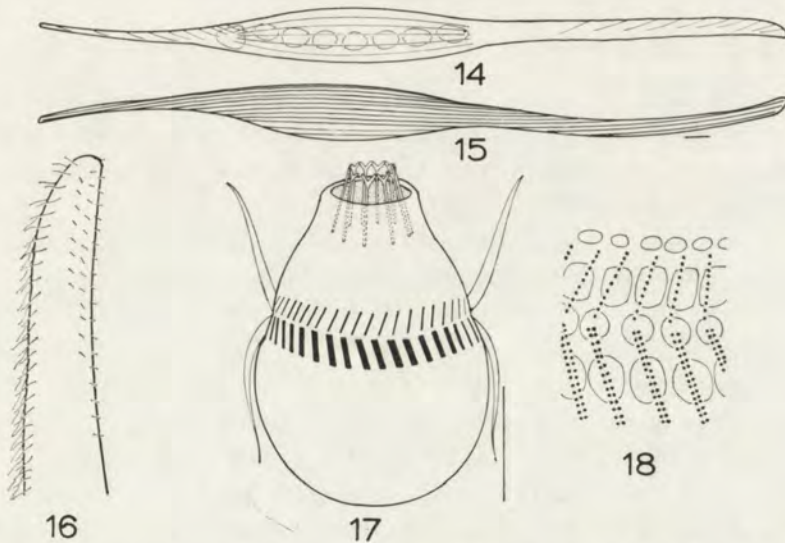


Fig. 14. *Litonotus cygnus*, length $325\ \mu\text{m}$, dorsal aspect, showing longitudinal ribs of midportion of animal, water expulsion vesicle, macronuclei, and trichocysts

Fig. 15. *L. cygnus*, ventral aspect, showing arrangement of ciliary rows

Fig. 16. *L. cygnus*, anterior end, dorsal aspect, showing row of cilia bordering cytostome dorsally, and dorsal bristle rows

Fig. 17. *Mesodinium pulex*, length $25\ \mu\text{m}$, lateral aspect, showing arrangement of ciliary organelles and oral nematodesmata

Fig. 18. *M. pulex*, diagram indicating positions of individual cilia in anterior and posterior ciliary girdles, and whorls of granules underlying cilia

Systematics. There are four species in this genus, with apparently no new species described in the last 35 years. Both Dragesco 1960 and Borror 1963 b noted the difference in orientation of the cilia of the two equatorial rows, and the functional differences in their cilia. Alligator Harbor, Florida populations of this species have oral stylets that are flat or slightly concave distally (Borror 1963 b) — distinctly different from the oral stylets of the New Hampshire tidal marsh popu-

lations. Whether or not this is a distinction worthy of erection of a new species cannot be assessed at this time. Arrangement of the cilia in this species differ but slightly from those of *M. pupula* and *M. rubrum* (Dragesco 1963 a, Taylor et al. 1971).

Askenasia stellaris Leegaard, 1920

This peculiar planktonic member of the family *Didiniidae*, that occurred in a diatom detritus substratum commonly at Alligator Harbor (Borrer 1963 b), also has been observed periodically in the New Hampshire tidal marshes.

Loxophyllum setigerum, another easily recognized gymnostome, occurs fairly regularly in the tidal marsh along with a considerable variety of closely related species, including *Loxophyllum chaetonotum* Borrer, 1965.

Litonotus cygnus (O.F.M., 1776)

Length 170 μm contracted, 325 μm fully extended, maximum body width 23 μm when extended. Minimum neck width 8 μm . Shape as in Fig. 15. Dorsal hump with about four longitudinal grooves (Fig. 14). Cytostome extending along convex edge of neck, about 1/3 body length.

Ciliation. Ventral surface with cilia in rows as shown in Fig. 15. One row of cilia borders cytostome dorsally. Right (aboral) body edge bearing a lateral bristle row. Two short bristle rows additionally at anterior end of "neck" (Fig. 16).

Internal anatomy. Macronucleus consists of four — seven oval bodies linearly arranged in central part of body (Fig. 14). Micronucleus not observed. Water expulsion vesicle posterior in main body section. Curved trichites present in cytopharynx and in caudal projection, particularly along oral margin.

Ecology, behaviour. This species apparently is of irregular occurrence in the tidal marsh, and was encountered in a sample containing members of the genera *Frontonia*, *Diophrys* and *Gastrostyla*. When it moves forward in straight lines along the substratum, it reacts to posterior stimulation by contracting into the "head", and reacts to anterior stimulation by contracting the body and reversing of the cilia. It can glide free of the substratum with little or no rotation of the body axis and with the neck extended.

Systematics. This genus now contains at least 27 species, characterized by contractility, elasticity, and flexibility. They differ from members of the genus *Loxophyllum* in being less rigid and possessing fewer trichocysts. Members of the closely related genus *Hemiophrys* exhibit metaboly, are more oval in cross section, and have rows of cilia terminating anteriorly against the ventral midline. Members of the genus *Amphileptus* supposedly are fully ciliated (Canella 1960). This species is recognizable by its extremely long contractile body form, large size, distribution of dorsal bristle rows, and pattern of ciliation. Members of the population observed have a longer caudal projection than those observed by Kahl 1931.

Spathidium sp.

Large individuals of this genus have been encountered irregularly in samples from the Adams' Point marsh, but in insufficient numbers to permit species identification. They are carnivores, feeding on other ciliates.

Suborder *Cyrtophorina**Cryptopharynx setigerus* Kahl, 1926

This is apparently of irregular occurrence in tidal marshes, where it occurs in low numbers. A few individuals in this species occurred in a sample collected in November, 1968. It is a bacteriovore.

Trochilia sigmoides Dujardin, 1841

This small cyrtophorine occurs in small numbers at irregular intervals in alga mats at the Odierne's Point tidal marsh station.

Trochilioides recta Kahl, 1928

Length 43–60 μm . Width 23–31 μm . Thickness about $2/3$ the width (16–20 μm). Cell truncate anteriorly, widest just posterior to anterior end, tapering gradually to evenly rounded but narrower posterior end. Dorsal surface evenly convex, the lateral surface converging ventrally, narrowing the ciliated portion of the ventral surface (Fig. 20). Buccal cavity anteroventral, with cytostome at its base. Edges

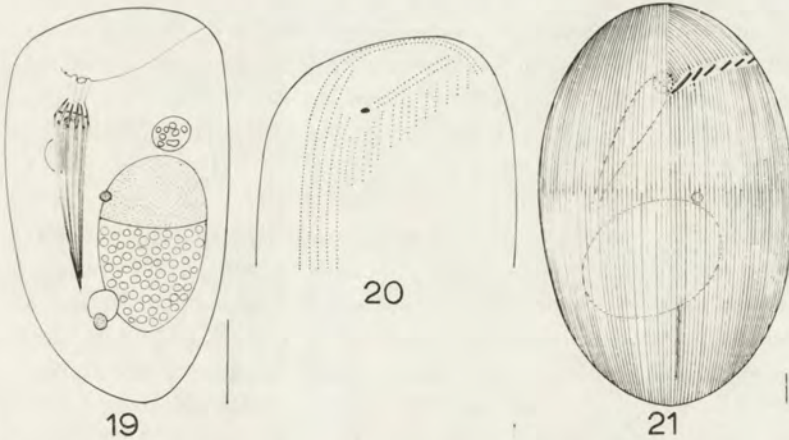


Fig. 19. *Trochilioides recta*, length 45 μm , ventral aspect of internal anatomy, showing macronucleus and single micronucleus, two water expulsion vesicles, position of stylus, food vacuole and cytopharyngeal apparatus

Fig. 20. *T. recta*, anterior end, ventral aspect, showing positions of cilia. Cytostome indicated by black dot

Fig. 21. *Nassula labiata*, length 132 μm , ventral aspect, showing ciliary meridians, cytostome, cytophyge, nuclei and arrangement of somatic membranelles

of cytostome raised as obvious cortical lips. A secretory papilla arises near posterior ends of ciliary rows.

Ciliation. Cilia in four groups of rows, labelled A, B, C, and D in this discussion (Fig. 20). Group A: 13–16 parallel short postbuccal rows. Group B: two rows extending from cytostome posteriorly beyond secretory papilla. Group C: three rows extending from secretory papilla anteriorly along right ventral surface; left row terminating near anterior end (other two rows curving along anterodorsal edge of buccal cavity, terminating a few micrometers posterior of anterior end on left lateral surface; at this termination, two additional short rows of cilia present). Group D: two close set rows of cilia, with a unified beat, extending to animal's left and anterolaterally from cytostome.

Internal anatomy. Macronucleus heteromerous, approximately 26 μm long, 17 μm wide consisting of anterior diffused section and posterior more granular portion (see Fauré-Fremiet 1957). Water expulsion vesicle small, near secretory papilla. Cytopharynx with two sets of fibrils. Narrow, poorly refractile fibrils extend posterior from cytostome at least 1/3 cell length. In addition, 10 oral trichites more obvious, approximately 23 μm in length, arranged as in Fig. 19.

Ecology. Members of this genus were discovered in collections from the Adams' Point tidal marsh in October, 1968 (rotting stems of *Spartina alterniflora*) and April, 1969 (a *Beggiatoa* mat).

Behavior. Members of this species can crawl slowly on the bottom of a culture dish or on filaments of *Beggiatoa*, and can swim slowly, often in groups. The water in their vicinity is more viscous than the surrounding medium, due to mucus they secrete. On glass they act as if they trail mucus; that is, swimming individuals can be slowed with a microneedle much as a spider can be caught by its trailing silk. It is likely that this capability would allow *T. recta* to contribute significantly to the physical aspects of the filamentous *Beggiatoa* substratum (see Picken 1937).

Discussion. In 1932 Kahl listed five species in this genus. Since then at least five additional species have been described (Fauré-Fremiet and Guilcher 1948; Tucolesco 1962; Fenchel 1965; and Jankowski 1967). *Ervillea striata* Buddenbrock, 1920 was placed in the genus *Trochiloides* (Kahl, 1932) but probably does not belong in the genus inasmuch as it differs significantly in buccal structure. Kahl distinguished other species on the basis of body shape. In size and shape the present population most nearly resembles *T. recta* Kahl, 1928. According to Kahl, however, the cytopharyngeal basket contains only six nematodesmata that reach the posterior end of the cell and then bend to the left. He described it as eating *Beggiatoa*. *Trochiloides oculata* Kahl, 1933 is larger (length = 100 μm), with the ciliary rows of group A longer. *Trochiloides filans* Fauré-Fremiet et Guilcher, 1948 is ectocommensal on planktonic copopods. *Trochiloides trivialis* Fenchel, 1965 has relatively long ciliary rows in group A, and a narrow unciliated vestibulum, and is ectocommensal on amphipods. *T. bathybius* Jankowski, 1967 has three rows of cilia in group D, each perpendicular to the long axis of the body, and five

rows of cilia in group C. *T. littoralis* Jankowski, 1967 has two rows of cilia in group D like *T. recta*, but differs in arrangement of ciliary rows in group A and C, body shape, and cytopharyngeal structure.

Nassula labiata Kahl, 1933

Length 117–154 μm , width 83–106 μm . Cell surface relatively smooth. Cell a flattened oval in cross section, the oral surface flatter than the aboral surface (Fig. 21). Cytostome approximately 1/4–1/5 way posteriorly, at floor of unciliated longitudinally oriented slit opening ventrally and to animal's left. Floor of slit marked by closely set cortical ribs that radiate from cytostome.

Ciliation. Somatic ciliature composed of 120–165 closely set meridians, as shown in Fig. 21. Some cilia arranged in 13 somatic membranelles arranged in a series beginning at midpoint of aboral surface and extending clockwise 180° to posterior corner of cytostome depression. Except for membranelle nearest cytostome, each is three cilia wide and approximately 10 cilia in length. Cilia of somatic membranelles in parallel rows, not hexagonally packed. Membranelle nearest cytostome approximately twice length of any of remaining ones, and consists of three series of cilia. In ventral aspect, about eight somatic ciliary rows course along right lip of cytostomal depression, ventral to pharyngeal basket.

Internal anatomy. Cortex armored with fusiform trichocysts. Pharyngeal basket contains 25–30 nematodesmata. Macronucleus large, oval, and central. Micronucleus not observed.

Ecology. This species is of irregular occurrence in New Hampshire tidal marshes; observed only in one collection.

Systematics. Since the most recent review of this genus (Kahl 1931), at least 13 additional species have been described. Members of the present population have the 3:2 length-width ratio of *Nassula ornata*. However, the arrangement and geometry of the cytostomal depression, easily observable in slides prepared according to the NMF method and the wet silver method fits Kahl's description of *Nassula labiata* closely. Most species in this genus are elongate and have a different cytostomal structure. Although rarely recorded, it appears that this can be considered a typical brackish water or tidal marsh ciliate, having been recorded before in this habitat (Kahl 1933; Tucolesco 1961; and Dietz 1964).

Chlamydodon obliquus Kahl, 1931

The morphology of this species has been described in detail previously (Borror 1963 b); the following information augments that description.

In the New Hampshire tidal marshes, members of this species often range from 210–240 μm , and are 130–165 μm wide; considerably larger and with approximately 25 nematodesmata instead of 16 compared to members of the Florida population.

Ecology. This widespread and commonly encountered ciliate is somewhat

thigmotactic, eating while virtually motionless against the substratum. It swims in a relatively straight path with a counterclockwise twist.

Chlamydodon triquetrus Müller, 1786

Although less common than the previous species, this relatively narrow member of the genus also is widespread in New Hampshire tidal marshes. Like the previous species, New Hampshire populations include larger individuals than those encountered in Florida (Borrer 1963 b); some individuals reach a length of 85 μm .

Chlamydodon lynchelliformis n. sp.

Length 42–54 μm , width 30–44 μm , thickness about 20–30 μm . Body oval in frontal section, terminally truncated. Oral surface flattened, dorsal surface humped. Anterior, posterior and lateral edges strongly grooved, containing peculiar railroad track organelle characteristic of this genus. Cytostome on cell surface, a small short transverse slit on midventral axis near anterior end (Fig. 22).

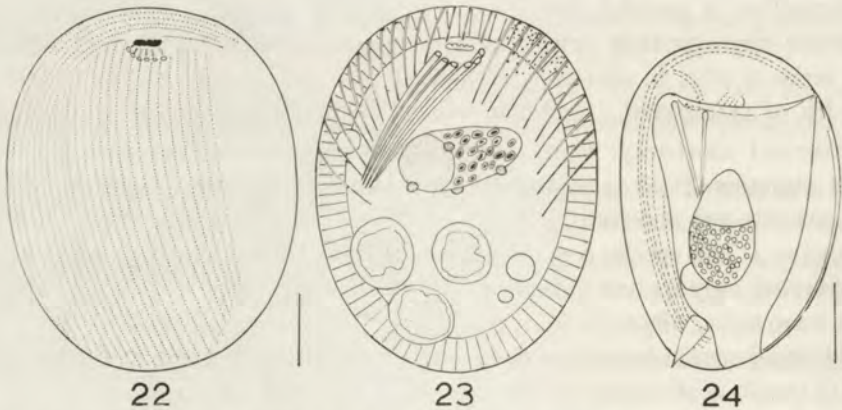


Fig. 22. *Chlamydodon lynchelliformis*, length 46 μm , ventral aspect, showing arrangement of cilia, and relationship between ends of nematodesmata (circles) and cytostome (black area)

Fig. 23. *C. lynchelliformis*, frontal section, ventral aspect, showing such internal structures as railroad-track organelle, trichocysts, water expulsion vesicles, nematodesmata, food vacuoles, and a macronucleus with four adjacent micronuclei

Fig. 24. *Dysteria marina*, length 39 μm , ventral aspect, showing arrangement of ciliary rows, nematodesmata, macronucleus and water expulsion vesicle

Ciliation. Cilia in approximately 25 parallel and curving rows, restricted to surface ventral to railroad track organelle, extending from right edge left across ventral surface, and covering approximately 4/5 of ventral surface (Fig. 22). Cilia in first three ciliary rows anterior to cytostome closely set and beat posteriorly, used in feeding.

Internal anatomy. Cytopharynx with 8 rods that extend dorsally, posteriorly, and to animal's right from cytostome. Railroad track organelle a complete circle. Macronucleus large, central, oval, heteromerous, accompanied by four micronuclei

(Fig. 23). Most of posterior cytoplasm with numerous food vacuoles containing green algae. Left anterior margin of cell with numerous yellow pigment granules. Two water expulsion vesicles one anteriorly near right margin, one near posterior left margin. Narrow, poorly refractile fibers extend from cortex towards central 1/3 of cell in a frontal plane in anterior half of cell, giving rigidity to anterior half of ventral surface. Unciliated surface underlain by numerous small (approximately 1 μm in length) vesicles.

Ecology. *Chlamyodon lynchelliformis* is sometimes abundant, but of irregular occurrence in surface mud of tidal marsh pools. Members of this species have been collected twice (once in October, 1968, and once in May, 1970). They apparently are of irregular occurrence in algal mats.

Systematics. Members of the populations of this species from New Hampshire tidal marshes are much smaller and have considerably fewer ciliary meridians than do most species in this genus with the exception of *C. minutus* Dragesco, 1965. His species is also small (average length: 50–60 μm) but differs from the present population in having 12 or 13 ciliary rows right from the cytostome that continue anterior to the cytostome. Members of the present population differ also from *Chlamyodon minutus* in the arrangement and position of other ciliary rows, disposition of the cytostome, number of micronuclei, number of contractile vacuoles, body shape, and disposition of the railroad track organelle. This constellation of factors seem to me to warrant erection of this new species.

Although clearly a member of the genus *Chlamyodon*, its simplicity of structure suggests the more primitive genus *Trithigmostoma*. Yet the body shape and alignment of ciliary meridians also suggest the more specialized members of the genus *Lynchella* (hence the specific name chosen) (see Deroux 1970). This further suggests that the genera *Chlamyodon* and *Lynchella* did not evolve separately from the genus *Trithigmostoma*, but rather that both may have had a common ancestor with characteristics resembling that of *Chlamyodon lynchelliformis*.

Dysteria monostyla (Ehrenberg, 1838)

Populations of this species encountered primarily during the late fall months in several New Hampshire tidal marshes conform in morphological details to those illustrated by Fauré-Fremiet 1965.

Dysteria marina Gourret and Roeser, 1886

Length 39–45 μm . Body shape and ciliation as shown in Fig. 24.

Ecology. This species coexisted with *D. monostyla*, at which times it could be distinguished by its shape and smaller size. It was discovered crawling on debris along with species of the genera *Uronema*, *Strombidium*, and *Frontonia* in collections enriched by addition of a split pea.

Systematics. The arrangement of somatic and vestibular cilia of this species (determined by the wet silver method) shows consistent differences from the close-

ly related *Dysteria ovalus* (Gourret et Roeser, 1886) as illustrated by Fauré-Fremiet 1965. *D. ovalus* apparently has four kineties, of which two continue to parallel the anterior edge of the organism. Members of the present population have five rows of cilia along the right edge of the body. In addition near the extreme left end of the two ciliary rows that border the anterior edge of the organism there is a short row of approximately eight cilia.

Order Trichostomatida

Plagiopyla nasuta Stein, 1860

Length 65–95 μm , width 38–57 μm . Body shape as indicated in Kahl's 1931 description (Fig. 25). Characteristic ribbed "Streifenband" extending from anterior right lip of vestibulum posteriorly along dorso-lateral surface about 2/3 body length.

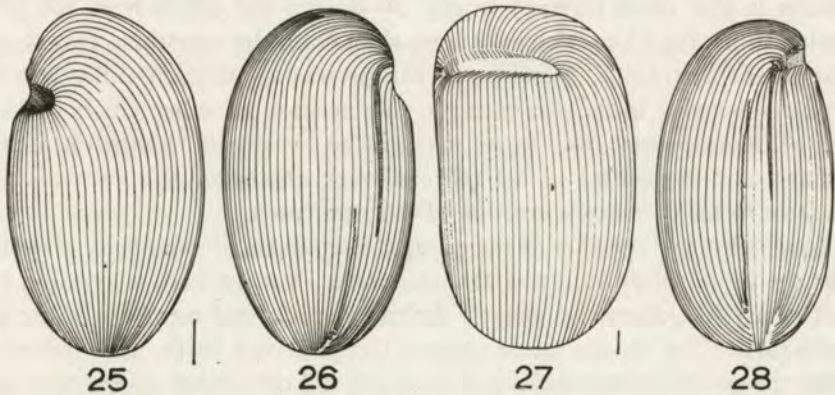


Fig. 25. *Plagiopyla nasuta*, length 75 μm , left lateral aspect, showing ciliary rows and opening of vestibulum

Fig. 26. *P. nasuta*, dorsal aspect, showing "Streifenband", cytoproct, and water expulsion vesicle pores

Fig. 27. *Sonderia sinuata*, length 145 μm , ventral aspect showing ciliary rows and opening of vestibulum

Fig. 28. *S. sinuata*, right lateral aspect, showing "Streifenband", cytoproct, and water expulsion vesicle pore

(Fig. 26). Cytoproct approximately 30 μm long, three ciliary meridians dorsal of "Streifenband", in posterior half of body. Two water expulsion vesicle pores just posterior to cytoproct at right end of suture at posterior end of ciliary rows.

Ciliation. Somatic ciliation as in Fig. 25 and 26. Cilia of vestibulum closely set in rows continuous with rows of somatic cilia. Entire vestibulum ciliated except for narrow unciliated suture zone along right wall (Fig. 29). Vestibular kineties immediately dorsal of this zone terminating against this zone and increase in length across dorsal wall of vestibulum. Kineties in left half of vestibulum and on ventral wall of vestibulum extend to posterior extremity of vestibulum. Macronucleus

large, oval, central. Water expulsion vesicle posterior. Food vacuoles contain remains of diatoms.

Ecology. Members of this species have been found at different seasons to be conspicuous members of the community of ciliates associated with *Beggiatoa* mats in the tidal marshes.

Systematics. Numerous authors have referred to the variability in size and shape within populations in this genus (Kahl 1931, and Jankowski 1964). Although the genus now contains about ten nominal species, little attention has been given to the validity of the characters distinguishing these species. In view of the apparent morphological variability within populations in this genus, and the broad area of overlap of characteristics of such nominal species as *P. marina*, *P. ovata*, and *P. nasuta*, it would seem appropriate to retain Stein's species name for members of this genus until significant species characters are determined. The present population agrees closely with those observed by Jankowski 1964 except for being slightly smaller.

Sonderia sinuata Kahl, 1931

Length 144–164 μm ; width 81–113 μm . Cell oval to circular in cross section; shape as shown in Figs. 27 and 28. "Streifenband" extending one half body length. Opening of vestibulum at right angles to long axis of body approximately 1/5 body length from anterior end. Vestibulum a dorsoventrally flattened funnel extending approximately one half body length. Cytoproct over one half body length extending horizontally between third and fourth kinety dorsal of "Streifenband". Water expulsion vesicle pore at posterior end of cytoproct.

Ciliation. Cilia in approximately 65–70 kineties. All kineties contributing to vestibular ciliature except three kineties that course between "Streifenband" and cytoproct. These latter rows terminating at right lip of vestibulum. Within each kinety cilia arranged in triplets, except in vestibulum and in zone immediately surrounding vestibular overture, where they are arranged in closely set series (Fig. 30). "Streifenband" cross-striated in specimens prepared according to the wet silver method. Somatic kineties terminating posteriorly along suture lines (Fig. 28). Surface with cylindrical symbiotic bacteria (?) among cilia.

Internal structure. Macronucleus large, oval, central; micronucleus not observed. Food vacuoles contain remains of diatoms. Adjacent to ventral cortex are approximately 50 skeletal rods approximately 25 μm long and 1 μm wide. These parallel long axis of body except they are more randomly oriented at the posterior end. No such rods appear to be associated with aboral surface.

Ecology. This species was encountered frequently during sampling of *Beggiatoa* mats in the fall, where it coexisted with members of the genus *Plagiopyla*.

Systematics. In addition to possessing the characteristics of the family *Plagiopylidae*, members of the genus *Sonderia* (originally erected by Kahl in 1931) are characterized by surface symbiotic bacteria, a "Streifenband", a prominent

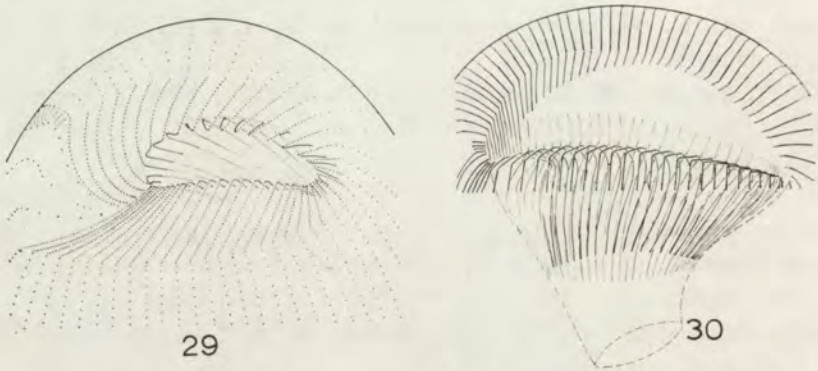


Fig. 29. *Plagiopyla nasuta*, anterior end, ventral aspect, showing arrangement of cilia on lips of and within vestibulum
 Fig. 30. *Sonderia sinuata*, anterior end, ventral aspect, showing arrangement of ciliary rows at lips of and within vestibulum

and characteristically arranged cytoproct and water expulsion vesicle (contrary to the observations by Kahl), and a uniquely arranged system of vestibular ciliation. Particularly characteristic, and allowing differentiation from *Plagiopyla*, is the presence of an unciliated expanse on the anterior vestibular lip (Fig. 30). Nevertheless, the kineties on the roof of the vestibulum are direct prolongations of dorsal somatic kineties; delicate lines in the nonciliated area can be seen in wet silver preparations to connect these ciliated regions.

The morphology of members of a population supposedly of this species recently has been described by Dragesco 1968 a on the basis of specimens prepared according to the silver-protein impregnation technique. A psammobiotic member of the genus (*S. labiata* Fauré-Fremiet et Tuffrau, 1955) resembles *S. sinuata* in arrangement of somatic kineties, cytoproct, and position of water expulsion vesicle but is considerably flatter and has a different arrangement of cilia on the vestibular overture.

Colpoda cucullus Müller, 1786

Although not heretofore convincingly recorded from marine habitats, members of this species were encountered during examination of collections from the tidal marsh during October and December 1968. The characteristic confirmation of the somatic ciliature, including the nine vestibular kineties (which are stomatogenic according to the results of Hashimoto 1966), and the two differentiated fields of vestibular ciliature could be seen in wet silver preparations.

Trimyema pleurispirale n. sp.

Length 20–44 μm , width 16–23 μm (usually less than 20 μm). Shape in frontal section as in Fig. 31. Cell circular in cross section. Except for elongate caudal cilium, all somatic cilia restricted to anterior half of cell, arranged in at least four spirals (a few individuals show a partial or even complete fifth spiral, and even

a few cilia of a sixth spiral). Cytopyge an elongate (approximately 8 μm) slit near posterior pole, lying in same latitude as cytostome and suture at ends of ciliary spirals. Water expulsion vesicle pore not observed.

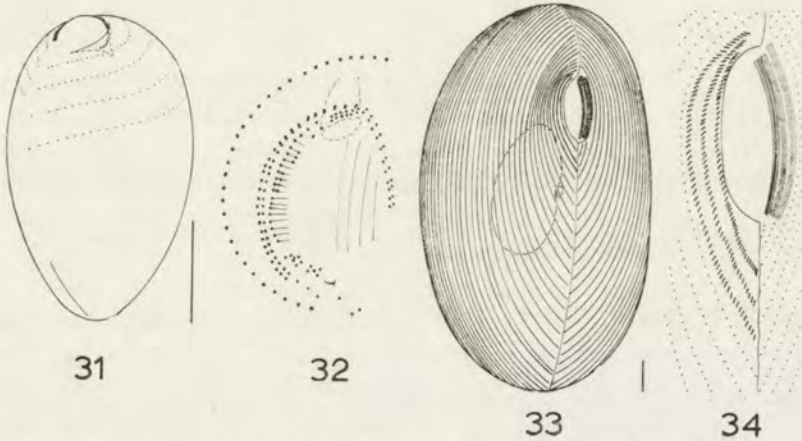


Fig. 31. *Trimyema pleurispirale*, length 25 μm , left ventrolateral aspect, showing position of vestibular cilia (dark anterior band) and somatic cilia (dots)

Fig. 32. *T. pleurispirale*, anterior aspect, depicting positions of cilia in anteriormost somatic whorl (single C shaped row) plus cilia of vestibular polykineties. Dash lines indicate region of cytostome. Light lines connected with some of vestibular cilia represent silver lines present in "wet-silver" preparations

Fig. 33. *Frontonia fusca*, length 118 μm , ventral aspect, showing ciliary rows, three vestibular kineties, and three peniculi. Also shown is arrangement of macronucleus and micronucleus

Fig. 34. *F. fusca*, vestibulum, ventral aspect, showing appearance of somatic and vestibular kineties and three peniculi

Vestibular structure. Vestibulum ciliated by cilia of an outer and an inner polykinety, each at least two cilia in width (Fig. 32). Outer polykinety originating near anterior-most terminus of first ciliary spiral, courses clockwise 180° while dipping posteriorly into vestibulum, terminating near cytostome. Throughout its length ciliary doublets (approximately 28 pairs of cilia) evenly spaced. Inner polykinety contains three regions. Anterior-most are two isolated tufts of approximately five cilia each. Next is a broad polykinety closely paralleling outer polykinety and extending from the two previously mentioned tufts down into vestibulum to cytostome. Posterior-most region of inner polykinety a J-shaped field of 16–20 pairs of cilia extending clockwise across floor of vestibulum deep beneath cell surface. Floor of vestibulum mediad of this polykinety bearing several faint argentophilic lines. Macronucleus spherical, central; micronucleus not observed.

Ecology. Members of this genus are bacterivores, and apparently occur only irregularly in New Hampshire tidal marshes.

Discussion. This genus was erected by Lackey 1925 for one species, *T. compressa*. Since then, at least 4 nominal species have been described, including *T. marimum* (Kahl, 1931), *T. claviforme* Kahl, 1933, *T. kahli* Tucolesco, 1962, and

T. alfredkahli Tucolesco, 1962. *Sciadostoma difficili* Kahl, 1926, and *S. minutum* are probably both junior synonyms of *T. compressa*. Ruinen 1938 placed *Palmarium salinum* Gajevskaja, 1925 in the genus *Trimyema*; however this is erroneous since Gajevskaja illustrated *Palmarium* as having an adoral zone of membranelles. Members of the genus previously have been examined by both the dry silver method (Klein 1930), and the wet silver method (Fauré-Fremiet 1962 and Jankowski 1964). These authors studied *T. compressa* and *T. marinum*, showing that the vestibular ciliature consists of two polykineties, but indicated that in these species there are three ciliary spirals. Inasmuch as size and shape varies considerably within populations of members of this genus and is quite probably affected by the salinity of the medium, it would seem to be too highly variable a character to be used for species determination.

All members of the population examined, however, differed from all previous descriptions of members of this genus in the number of ciliary spirals; the name of the new species was chosen to reflect this difference. The cilia of the inner vestibular polykinety were constant in arrangement among members of the population examined, and differed significantly from the arrangement of the inner polykinety in *T. marinum* (Fauré-Fremiet 1962).

Geleia simplex Fauré-Fremiet, 1951

Individuals apparently of this species are of irregular occurrence in small numbers in midsummer where they occur particularly in mats of pink sulphur bacteria, along with *Frontonia*, *Gruberia*, and other ciliates. Those individuals observed are relatively small (150–200 μm in length), are rounded posteriorly, have two macronuclei, and bear no anterior hook. The arrangement of buccal ciliature is similar to that described for *G. decolor* (Borror, 1963 b) and *G. swedmarki* (Dragesco, 1963). The ciliary field bordering the left edge of the buccal cavity is arranged in approximately 35 short cross rows of close set cilia. There are approximately 34 longitudinal somatic meridians. Food vacuoles contain diatoms. The only other species in this genus in this size range (*G. nigriceps* and *G. hyalina*) both are pointed posteriorly.

Gelei orbis Fauré-Fremiet, 1950

One individual originally observed in life, and subsequently preserved by the nigrosin mercuric-chloride formalin method (Borror 1968 b) has been observed from New Hampshire tidal marshes. This individual has the serpentine body form, nuclear configuration, and pointed posterior end previously shown to be characteristic of this species. This individual differed from those described previously (Fauré-Fremiet 1950, Fjeld 1955, Dragesco 1960) in having 70–75 ciliary meridians instead of 32–46 as previously recorded. The length of this individual (fixed and contracted) is 450 μm . The original length exceeded 1 mm. The nuclear complex contains two macronuclei and one micronucleus. The cell cortex is marked by a fine intermeridional granulation.

Order *Hymenostomatida**Paratetrahymena wassi* Thompson, 1963

This ciliate was identified from a collection made 6 July, 1964 at the Odiorne's Point pool station.

Ophryoglena flava Ehrenberg, 1833. When salinity is depressed locally by flows of fresh water or heavy precipitation, it may coexist in tidal marshes with members of other genera usually associated with fresh water, including *Paraholosticha* and *Colpoda*. *Ophryoglena* has not been recorded in any collections in which the salinity exceeds three parts/thousand.

Both *Frontonia marina* Fabre-Domergue, 1891 and *Frontonia microstoma* Kahl, 1932 occur in the New Hampshire tidal marshes. The latter species was found only once, whereas the first species is a widespread commonly encountered form.

Frontonia fusca (Quennerstedt, 1869)

Length 92–165 μm , width 51–110 μm . Buccal cavity 15–32 μm long, approximately 12 μm wide, situated 20–43 μm from anterior end. Body shape as in Fig. 33 and Pl. I 54. Water expulsion vesicle pores not observed.

Ciliation. Left wall of buccal cavity with three peniculi; right wall of vestibulum with three vestibular kineties (see Roque 1961). Field right of buccal cavity occupied by these three vestibular kineties approximately 5 μm wide at widest point (Fig. 34).

Internal structure. Macronucleus central, an elongate oval 22–43 μm , in length, 8–20 μm in width, with two small adjacent micronuclei. Food vacuoles contain desmids, diatoms, and filaments of blue-green algae. Near anterior end on right dorsolateral cortex is a pigment fleck 5–10 μm in diameter consisting of 25–30 spherical granules approximately 1 μm in diameter.

Ecology. Members of this species occur fairly regularly during the summer months in the tidal marsh, where they may be found in areas of high oxygen concentration, particularly in floating mats of filamentous green algae (e.g., *Cladophora*). This species is easily recognizable in fresh samples by the presence of the pigment fleck near the anterior end. The animal is relatively wider than other species in this genus identified from the salt marsh.

Systematics. The members of the local population resemble those studied by Kahl 1931 but generally are smaller, and have two micronuclei. An anterior pigment fleck also occurs in *Frontonia vernalis*, *Frontonia ocularis*, *Frontonia complanata*, and *Frontonia algivora* (Bullington, 1939).

Paramecium calkinsi Woodruff, 1921

Length 70–180 μm (usually about 100–110 μm); width 25–80 μm (usually about 50 μm). Conformation of the body, vestibulum, and buccal cavity similar to form

described by Woodruff 1921 and Kahl 1931. Cytopyge a post-buccal slit visible in wet silver preparations (Fig. 35). Water expulsion vesicle pores aboral (see Fig. 36).

Ciliation. Somatic cilia arranged in approximately 100 meridians as shown in Fig. 35. Buccal ciliature consisting of an endoral membrane approximately 10 μm long on right wall of buccal cavity near buccal overture, and a quadrulus and

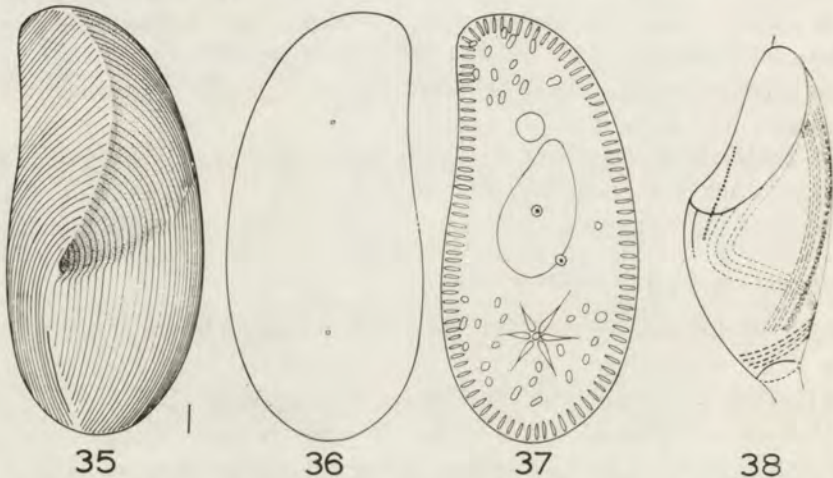


Fig. 35. *Paramecium calkinsi*, length 132 μm , ventral aspect, showing ciliary rows, cytopyge, buccal overture, and geometry of vestibulum

Fig. 36. *P. calkinsi*, dorsal aspect, showing positions of water expulsion vesicle pores

Fig. 37. *P. calkinsi*, frontal section, ventral aspect, showing water expulsion vesicles and radiating canals associated with posterior vesicle, macronucleus and two vesicular micronuclei, refractile reserve granules at anterior and posterior ends of cell, and trichocyst layer

Fig. 38. *P. calkinsi*, diagram of arrangement of buccal cilia, ventral aspect. Single row of large dots and circles represents bases of cilia of endoral membrane. Dotted and dash lines represent ciliary rows of the two peniculi and the quadrulus. Figures at top and bottom of illustration depict approximate geometry of buccal overture and cytostome respectively

two peniculi spiralling posteriorly along wall of buccal cavity (Fig. 38). Tuft of three-four caudal cilia present. Locomotory cilia 7 μm long.

Internal structure. Two water expulsion vesicles each with six radial canals. Posterior cilia approximately 14 μm long. In addition to contractile vacuoles, cytoplasm contains several smaller clear noncontractile vesicles. Just beneath trichocyst layer throughout cell particularly at ends of cell are 3–4 μm long refractile rods slightly wider at ends than at middle (approximately 50–60 of them). Discharged trichocysts about 20 μm long. Macronucleus large, central, shaped as a slightly inflated curved disc; two micronuclei, closely oppressed to macronucleus, vesicular. Each micronucleus approximately 4 μm in diameter, with central part approximately 1.5 μm in diameter (Fig. 37).

Ecology, Behavior. Members of this species occur regularly in tidal marsh pools, where they swim in a characteristic right hand helix.

Systematics. *Paramecium woodruffi* Wenrich, 1928, another estuarine species, differs from *P. calkinsi* in having three, four or more micronuclei scattered through the cell and not immediately adjacent to the macronucleus, and having a slightly yellowish color when cultured in sea water media (Wenrich 1928). So far *P. woodruffi* has not been discovered in the New Hampshire tidal marshes.

Order Scuticociliatida

Members of this order (Small 1967) are commonly encountered in this tidal marsh habitat. Members of the genus *Uronema* (*U. marinum*, *acutum* and *filificum*) are encountered regularly (Borror 1963 a, b, 1965 b). *Cohnilembus verminus* (Müller, 1773) occurs in relatively small numbers under natural situations, but often can be found to bloom in cultures. I have also identified *Pseudocohnilembus longisetus* Evans et Thompson, 1964 from collections from the Adams' Point and from the Odiorne's Point tidal marsh station.

Two species of *Cyclidium* (*C. plouneouri* Dragesco, 1963 and *C. marinum* Borror, 1963) occur regularly in the tidal marsh, and are distinguished by their buccal structures.

Uropedalium pyriforme Kahl, 1928

Length 19–22 μm ; width 14–20 μm (usually 15 \times 20 μm). Cell circular in cross-section, oval, widest anteriorly (Fig. 39). Some cells more pear-shaped than others. Buccal cavity 2/3 of way posteriorly, a deep pocket.

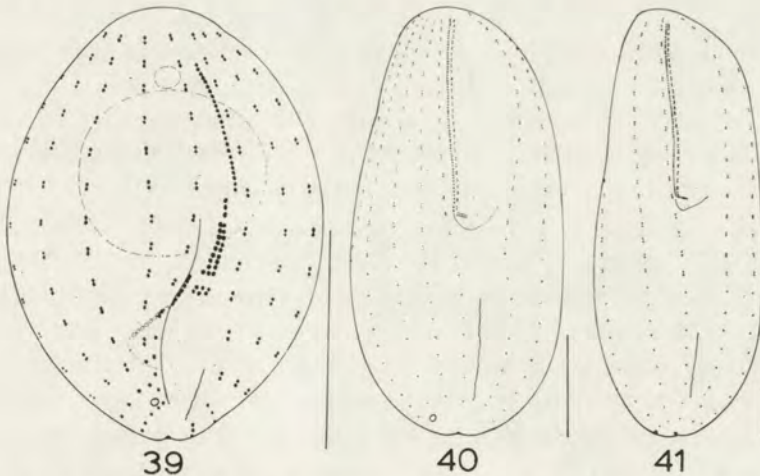


Fig. 39. *Uropedalium pyriforme*, length 20 μm , ventral aspect, showing positions of cilia, cytopharynx, and cytosome (dash-circle). Nuclei also indicated. Stippling indicates region of oral cavity. Circle indicates position of water expulsion vesicle pore

Fig. 40. *Paralembus hargisi*, length 41 μm , ventral aspect, showing arrangement of cilia (dots), region of buccal cavity (stipples) and cytopharynx and water expulsion vesicle pore

Fig. 41. *Paralembus marinus*, length 41 μm , ventral aspect, showing cortical features as in Fig. 40

Ciliation. Somatic cilia 6–7 μm long, in 14 meridians, 2–2.5 μm apart. Cilia 1–1.5 μm apart (much closer set than *Cyclidium*). Little apparent anterior posterior difference in interciliary distance. A strong pellicular ridge to right of each ciliary row. Anterior pole 3–4 μm wide. Cilia sometimes in pairs. Posterior pole 3 μm wide, with caudal cilium 12–15 μm long. Cytoproct an irregular zig-zag argentophilic structure between buccal cavity and posterior pole. Water expulsion vesicle pore at posterior end of second ciliary row right of buccal cavity. Cilia of buccal apparatus organized in four compound structures, the cilia of which are visible in specimens fixed 10 seconds in OsO_4 fumes and observed in temporary mount. Basal bodies of these cilia visible in specimens prepared according to wet sliver method. Undulating membrane sigmoid, along right lip of posterior end of buccal cavity, with 12–16 cilia. M_1 (alpha membranoid according to Small 1967) a single row of seven or eight cilia that beat along buccal cavity. M_2 (beta membranoid) triangular, M_3 (gamma membranoid) rectangular.

Macronucleus nearly spherical, in anterior half of body with adjacent micronucleus. Water expulsion vesicle terminal. Cytoplasm generally almost clear, except for food vacuoles containing rod-shaped bacteria, and six or seven crystals 1 μm in length.

Behavior. Somatic cilia beat to the animal's left, causing counterclockwise rotation of cell. The undulating membrane stands stiffly at an angle to the body surface and vibrates as a unit. In cultures in filtered sea water (six parts per thousand) and rice grains, the animals tend to swim near the bottom of the dish, and mass around the rice grains as if along a front of bacterial concentration. Locomotion of organisms varied with their distance from the rice grains. Those in a tight group near the grain (feeding?) swam in a wide tight counterclockwise helix going in one direction seven-eight turns, then abruptly going off in another direction, as if maintaining an optimum distance from the center of the attracting mass. In other parts of the culture where apparently no feeding was going on, cruising individuals not associated with high densities swam in a narrower, long helix.

Systematics. This species closely resembles *Homalogastra setosa* Kahl, 1926, a small ciliate discovered in samples of mosses. In addition to the habitat difference, members of these two genera are distinguished, according to Kahl, on the basis of behavior. *Uropedalium* is described as a very small salt water form "mit hastig schwankender (tanzender) Bewegung ohne Ruhepausen". The description above of the behavior of members of populations from New Hampshire tidal marshes is parallel to this, individuals feeding while in motion. By contrast, the genus *Homalogastra* was described by Kahl as comprising very small moss forms "mit stossweise gleitender Bewegung mit Ruhepausen". Kahl further describes members of the genus *Homalogastra* as feeding in motionless positions with groups of cilia spread laterally — a behavior pattern so far not observed in *Uropedalium*. Particularly characteristic of members of the genus *Uropedalium* is the geometry of the

helical path when swimming near a food source; a wide tight helix described by Kahl as "tanzender Bewegung".

Paralembus hargisi (Evans et Thompson, 1964) n. comb.

Length 37–55 μm (as short as 20 μm in tomites), width 17–23 μm . Buccal cavity 19–23 μm long. Body bluntly pointed anteriorly, rounded posteriorly, circular in cross-section.

Ciliation. Cilia arranged in 13–14 (usually 14) longitudinal or slightly sigmoid meridians, and an elongate caudal cilium. Cytopyge an elongate slit posterior of buccal cavity (Fig. 40). Water expulsion vesicle with 1–2 (usually 2) pores, at posterior ends of third and fourth ciliary meridians to right of buccal cavity. Unciliated pole slightly dorsal to anterior end 4–5 μm in diameter.

Buccal apparatus. Buccal cilia as in Fig. 40. See discussion under following species.

Internal structure. Macronucleus central with adjacent micronucleus. Water expulsion vesicle terminal.

Behavior. This species and the following reach high densities in finger bowl cultures to which a split pea is added. Practically none of the ciliates occur at the surface of the culture. Most swam near the bottom or fed on the substratum in large masses, often with the anterior end pushed against the starch grains.

Systematics. This species was originally described by Evans and Thompson as a member of the genus *Pseudocohnilembus* along with two other species, including *Pseudocohnilembus persalinus*, designated as the type species of their new genus. In 1966 Thompson described *Pseudocohnilembus marinus* from the Virginia coast (Thompson 1966). The morphogenesis of the type species of this genus has been described (Evans and Corliss 1964).

In 1931, Kahl erected the genus *Lemboides* for two new species from hydroids. He described the buccal apparatus as follows: "Das Wimperfeld des Peristoms ist auf die rechte Seite beschränkt worden; es ist eine membranoide Verschmelzung mehrerer Wimperreihen; es fehlt aber die Ausbildung der zweiten Membran, die *Lembus* hat; statt dessen ist hinten rechts eine kleine Seitentasche ausgebildet wie bei *Philaster*, aus der eine kleine Sondermembran schlägt." One species, *L. digitiformis*, measured 75–80 μm long. The second species, *L. rostrata*, was plump ovoid with an obvious anterior beak. It was later discovered (Kahl 1933) that the genus name *Lemboides* must fall as a junior synonym (it was preoccupied), and he erected the replacement name *Paralembus*.

When Evans and Thompson were reviewing characteristics of various hymenostome genera for possible assignment of their three new species, they concluded that none of the five or six genera conventionally included in the family *Cohnilembidae* at that time had buccal structures at all similar to those of their species. It would appear to me, however, that the combined inner and outer membranes that they described for members of this genus represent the "membranoid Versch-

melzung mehrerer Wimperreihen" cited by Kahl, and the short posteriorly directed group of buccal cilia at the posterior end of the inner and outer membranes (oriented at a 90° angle to these membranes in *P. marinus*, discussed below) corresponds to the "kleine Sondermembran" also described by Kahl.

It is not my intent to suggest that the name *Pseudocohnilembus* should fall as a junior synonym of *Paralembus*. This decision should be based on careful examination of the type species. However, the characteristics of specimens of *P. hargisi* and *P. marinus* studied both in life and in wet-silver preparations appear to differ from the two species of *Lemboides* described by Kahl in only minor features. For these reasons I am transferring these two species to the genus *Paralembus*.

Paralembus marinus (Thompson, 1966) n. comb.

Length 34–47 µm (no tomites observed), width 14–20 µm. Cell finger shaped, bluntly pointed anteriorly, rounded posteriorly, with obvious pellicular dimpling at bases of cilia (salinity of medium 30 parts per thousand). Morphology generally like the preceding species (Fig. 41). Somatic cilia in approximately 10 longitudinal slightly sigmoid meridians, approximately 30 cilia per meridian. Anterior unciliated pole approximately 1.5×3 µm in size. Cytopyge as in Fig. 41. One water expulsion vesicle pore, near posterior ends of first or second meridians to right of buccal cavity.

Buccal apparatus. Buccal cavity 16–18 µm long. Beginning approximately 3 µm from anterior pole (in the preceding species the outer and inner membranes of the buccal apparatus reach the anterior pole). Outer membrane approximately 2 or 3 µm longer than inner membrane. At posterior end of inner membrane is a membranelle-like group of basal bodies arranged at right angles to inner membrane (Fig. 41). These appear ciliated in living animals.

Behavior. See notes on previous species. The outer membrane of the buccal apparatus consists of equally spaced cilia in a single row that are stiff, erect, and vibratile. The inner group is a longitudinal series of ciliary doublets that do not form a unified membrane, but sweep within the buccal cavity.

Discussion. This description agrees with that given by Thompson in all major respects save the position of water expulsion vesicle pore. In specimens observed by Thompson, the single pore lies nearer the posterior end of meridian 4. This species like the preceding one is removed here from the genus *Pseudocohnilembus* and placed in the genus *Paralembus* Kahl, 1933 (a substitution name for the preoccupied *Lemboides* Kahl, 1931). The similarity of these two species to those described in the original publication on the genus *Lemboides* is sufficient in my opinion to warrant this transfer. See discussion under previous species.

Paranophrys magna n. sp.

Length 45–75 µm, width 17–25 µm, body circular in cross-section. Shape of frontal section shown in Fig. 42. Cytoproct postbuccal. Water expulsion vesicle pore at posterior ends of second meridian (Fig. 43).

Ciliation. Somatic cilia arising from pits in body surface, arranged in about 21 bipolar meridians. Anterior unciliated pole about 4.5 by 1.5 μm . Caudal cilium about 20 μm long. Buccal ciliature consisting of an undulating membrane and three linearly arranged fields of cilia (Fig. 42, Pl. I 56). Anterior most field a narrow triangle. Middle one rectangular with straight or slightly curved sides, about three-

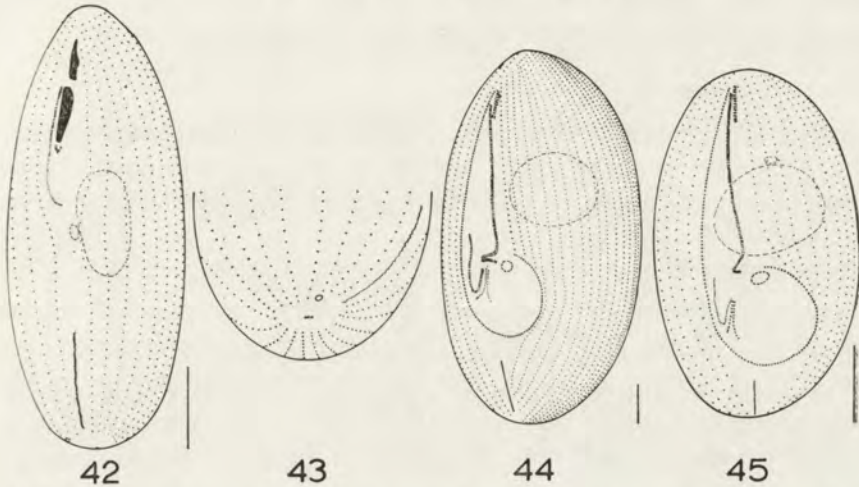


Fig. 42. *Paranophrys magna*, length 54 μm , ventral aspect, showing cortical features and arrangement of nuclei

Fig. 43. *P. magna*, right posteriolateral aspect, showing cortical features at posterior end

Fig. 44. *Pleuronema coronatum*, length 91 μm , ventral aspect, showing cytostome, cytophyge, and distribution of somatic and buccal cilia, as well as position of macronucleus

Fig. 45. *Pleuronema smalli*, length 44 μm , ventral aspect, showing cytostome, cytophyge, arrangement of somatic and buccal cilia, and nuclei

cilia wide, immediately to left of undulating membrane, and separated from first membranelle by strip about 1 cilium wide. Posterior-most membranelle a triangular field of 5-7 long cilia. Surface of buccal cavity to right of cytostome with argento-philic rib wall.

Internal anatomy. There is a single, central macronucleus near cytostome, with adjacent micronucleus (Fig. 42). Water expulsion vesicle small, posterior.

Behavior. Often reaching tremendous numbers in cultures seeded with a split pea, this ciliate has several types of locomotion. When it moves across open water, it swims in a counterclockwise helix straight ahead with no veering. Some individuals swim faster than others. When moving in contact with surface scum, they crawl slowly here and there with frequent changes of direction. The animal feeds by rubbing the buccal apparatus against the scum, often with the posterior end elevated.

Discussion. This species is encountered frequently in sampling both in the New Hampshire tidal marshes, and in the seawater system at the Jackson Estuarine

Laboratory. It is one of a series of morphologically similar *Philaster*-like hymenostome ciliates. The cortical morphology of this species is remarkably similar to that of *P. marina* Thompson et Berger, 1965. The arrangement of the buccal apparatus, the position of water expulsion vesicle pore and cytophyge, and the pattern of ciliation are all similar. The major differences are size and number of ciliary meridians; minor differences exist in arrangement of the buccal membranelles. I interpret these as species differences, and therefore erect a new species.

Pleuronema coronatum Kent, 1881

Length 80–100 μm , width 43–51 μm . Buccal cavity 41–56 μm long and approximately 13 μm wide at widest point. Approximately 40 ciliary meridians including three short prebuccal meridians (Fig. 44). Cytophyge a longitudinal slit posterior of buccal cavity. One macronucleus and two micronuclei present. Details of oral rib structure not studied.

Discussion. This species does not appear to be as regular in the salt marsh as the following species; at this writing it has only been discovered once. The morphological characteristics of members of this population match those of *Pleuronema coronatum* as listed by Dragesco 1968 b very closely, particularly those of the Roscoff population (see Dragesco 1960). It has a narrower buccal cavity and fewer pre-buccal meridians than populations of *P. coronatum* from Alligator Harbor, Florida (Borrer 1963 b). In view of the current lack of understanding of the validity of specific differences in members of this genus due to the lack of genetic experimentation, it seems most useful at present to retain species names for these obviously morphologically different groups until further comparative studies can be undertaken.

Pleuronema smalli Dragesco, 1968

Length 42–54 μm , width 24–37 μm . Buccal cavity length 34–38 μm , beginning 3–9 μm from anterior end. At widest point, buccal cavity approximately 12 μm wide. Approximately 28 ciliary meridians, including three-four preoral meridians. Buccal ciliature is shown in Fig. 45. Macronucleus spherical to oval and central, with two adjacent micronuclei. Details of oral ribs not studied.

Ecology. Members of this species have been found more regularly than the preceding species in New Hampshire tidal marshes, particularly associated with algae. Large numbers are sometimes associated with the interstitial water of surface mats of *Vaucheria*.

Discussion. The morphology of members of populations from New Hampshire marshes closely resembles that tabulated by Dragesco 1968 b. These two species of *Pleuronema* both possess a sigmoid bending of the precytostomal row of buccal ciliature, and obviously share many morphological characteristics.

Order *Peritrichida*

No concerted effort has been made during the course of these studies to identify all members of this order. Those that have been identified include *Vorticella nebulifera* Müller, 1773, *Vorticella striata* Dujardin, 1841, *Cothurnia simplex* Kahl, 1933, and an unidentified species of *Zoothamnium*. These occur regularly attached to strands of green algae but were often fragmented during concentration.

Order *Suctorida*

Unidentified species of the suctorian genus *Acineta* have been discovered irregularly in collections from coastal tidal marshes, where their exogenous budding and their feeding behavior (on *Holosticha*) has been observed.

Order *Heterotrichida*

Members of this order are often large and conspicuous and sometimes numerous in tidal marshes. Particularly characteristic are *Gruberia lanceolata* (Gruber, 1884) and *Peritromus faurei* (Kahl, 1932). Members of the genus *Gruberia* from New Hampshire tidal marshes seem morphologically identical to those studied at Alligator Harbor (Borror 1963 b). Use of the modified NMF method (Borror 1969 a) on *Peritromus faurei* corroborates descriptions of morphology previously published (Borror 1963 b). Another heterotrich occasionally encountered in collections from New Hampshire tidal marshes is *Protocruzia depressa* Ammermann, 1968. As studied with the modified NMF method (Borror 1969 a) the features of the external morphology agree closely with those described or illustrated by Ammermann 1968, so will not be discussed further here.

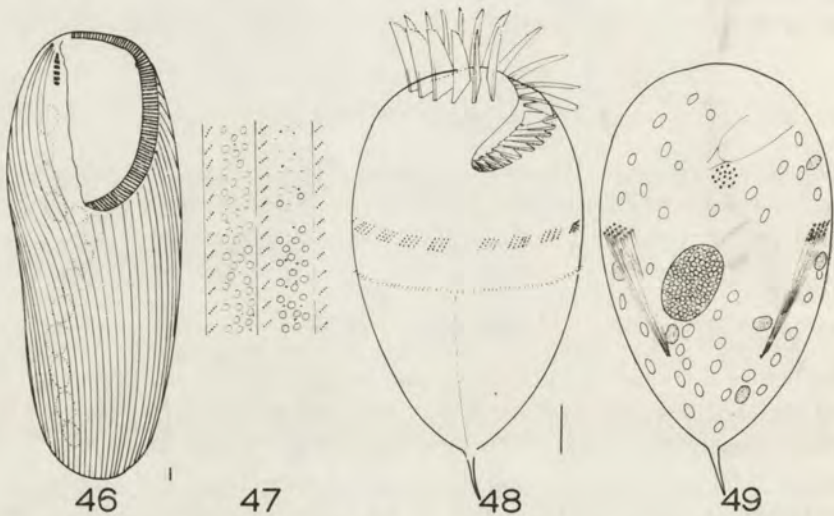
Parablepharisma bacteriophorum Villeneuve-Brachon, 1940 and *L. chlamydo-phorum* Kahl, 1932 are of regular occurrence in tidal marshes, where they are restricted to reducing zones low in oxygen content and high in sulfides.

Condylostoma arenarium Spiegel, 1926

Length 187–367 μm ; width approximately 100 μm . Buccal cavity 1/4–1/3 body length. Cell outline of larger individuals as in Fig. 46, shorter individuals relatively wider with relatively longer buccal cavity.

Ciliation. Somatic cilia about 10 μm long, arranged in approximately 40–64 longitudinal meridians. Within these meridians, cilia arranged in short oblique cross rows of two-four cilia each (Fig. 47). Anterior and left edges of buccal cavity bordered by zone of membranelles. Cilia at median edge of zone beat separately from rest of membranelles, forming a functionally distinct band. Membranelles deep in posterior portion of buccal cavity conform closely to arrangement de-

scribed for *C. magnum* (Tuffrau 1967). Right edge of buccal cavity bearing an undulating membrane two ciliary rows in width. Lateral to anterior end of undulating membrane, at anterior end of an otherwise unciliated field between buccal cilia-ture and ciliary rows of frontal field are four to six buccal cirri. This group of cilia 8–23 μm long, and approximately 2 μm wide. Length of group of buccal cirri posi-



- Fig. 46. *Condyllostoma arenarium*, length 360 μm , ventral aspect, showing ciliary rows, AZM, buccal cirri, and arrangement of macronuclei
 Fig. 47. *C. arenarium*, diagram of the arrangement of cilia, cortical contractile fibrils, and inter-meridional granulation of a short section of three adjacent ciliary rows
 Fig. 48. *Strombidium styliferum*, length 76 μm , lateral aspect, showing AZM and equatorial circles of simple cilia, points at which individual fibers of trichite girdle abut cell surface, and post-equatorial line (visable in "wet-silver" preparations)
 Fig. 49. *S. styliferum*, frontal section, ventral aspect, showing relative size and position of fibers of trichite girdle, eyespot near cytostome, macronucleus, and various cytoplasmic inclusions

tively correlated with body length within a population; individuals with shortest group of buccal cirri are small, whereas those whose buccal cirri measure over 20 μm in length are usually over 300 μm long.

Individuals in various stages of predivision morphogenesis were fixed and stained according to the NMF method (Borrer 1968 b). As observed by Villeneuve-Brachon 1940 the buccal cirri of the opisthe differentiate from a field of cilia derived from the same primordium as the undulating membrane.

Internal structure. All individuals observed, regardless of size, shape and length of buccal cavity had the pattern of intermeridional granulation shown in Fig. 47. Most individuals contained 13–16 macronuclear nodes.

Ecology. Members of this species were recorded regularly during summer and early fall from mats of *Cladophora* and *Vaucheria*, areas of high oxygen con-

centration. They usually occurred in small numbers with seldom more than one individual per sample.

Systematics. With the exception of a few caudate individuals whose morphology has been little studied, all members of this genus encountered so far in New Hampshire tidal marshes agree closely with Villeneuve-Brachon's description of *C. arenarium*. However, her description does not agree with the original description of the species by Spiegel 1926 nor with descriptions by other authors that have been assumed to be of this species (Kahl 1932, Bock 1952, Dragesco 1960, and Borrer 1963 b). Nomenclature of species in this genus (see discussion of this in Fjeld 1955) involves at least two homonyms, and probably numerous synonyms. Solution of these problems shall require not only perusal of old and obscure papers of the last century, but more insight than currently is available on factors affecting development of the buccal cirri. It has been known for many years that the number of macronuclear nodes as well as general body form fluctuates considerably in response to known environmental factors (Kiesselbach 1935).

Order *Odonotostomatida*

Members of this order typically inhabit zones of low oxygen tension. Occasionally, members of the genus *Caenomorpha* have been encountered during sampling of mud from the bottom of panne ponds in the upper part of the Adams' Point marsh.

Order *Oligotrichida*

The genus *Strombidium* is rich in species in the New Hampshire tidal marshes; at least six species have been found. Morphological and ecological relationships of four of these species (*S. sulcatum*, *latum*, *kahli*, and *viride*) have already been discussed (Borrer 1968 a). *Strombidium purpureum* Kahl, 1932 also occurs regularly in the tidal marsh, having been found throughout the ice-free season over several years. Members of this species are recognizable by the purple bacteria contained in the cytoplasm. In addition to these, the following species has been found.

Strombidium styliferum Levander, 1894

Length 70–76 μm , width 46–53 μm at greatest point. Extent of posterior elongation variable, from a blunt point to an elongate pointed tail (Fig. 48).

Ciliation. Equatorial belt of approximately 120 short cilia, interrupted posterior of cytostome. Zone of membranelles as in Fig. 48, 15 membranelles visible ventrally in buccal cavity, about six on frontal field visible ventrally. About eight membranelles visible from aboral side, arising from shallow, narrow anterior depressions.

Internal anatomy (Fig. 49). Trichocyst girdle touches surface a few micrometers anterior of ciliary girdle. Trichocysts arranged in a band that is broken

postorally. Within this band trichocysts arranged in approximately 14 bundles of approximately two dozen rods each, in small oblique rows of three or four trichocysts. Some individuals have far fewer trichocysts, having lost them in handling prior to observation. Each trichocyst approximately 25 μm long. Reserve granules particularly concentrated in anterior cone, about 3 μm long. A group of reddish granules near cytostome. Cytoplasm contains bluish-green and yellow-green bodies, perhaps remains of chloroplasts. Food vacuoles contain diatoms. Macronucleus elongate, central, spindle-shaped, equatorial but acentric toward buccal cavity, oriented longitudinally, about 20 μm long. No undulating membrane observed. A cortical reticulum is visible posterior to the ciliary girdle in specimens prepared according to the wet silver method.

Ecology, behavior. This species occurs regularly throughout the ice-free season in pools in the tidal marsh. The animal swims slowing in a straight line while spinning on the longitudinal axis, then turns and darts away in a different direction.

Systematics. This is a large and diverse genus with at least 50 nominal species described, of which at least six occur in New Hampshire tidal marshes. Four of these species show a dramatic diversity of morphology and feeding behavior (Borror 1968 a). The ecological interactions of this species complex is currently under study.

Anatomical features of members of this population agree closely with descriptions by Fauré-Fremiet 1924, and Kahl 1932. *S. styliferum* is apparently a typical tidal marsh species. It is characterized by its relatively large size and distinct conical appearance due to the anterior placement of the trichite girdle. Development of the posterior stylus is variable. Identification of this species on the basis of superficial examination of living material must take into account that it often occurs in association with the similarly-shaped *Strobilidium caudatum* Kahl, 1932. This latter species lacks the ciliary and trichite girdles, and has an entirely apical zone of membranelles and buccal cavity, as well as a horseshoe-shaped macronucleus.

Order *Hypotrichida*

This order is extremely richly represented in the New Hampshire tidal marshes. The various substrata available in the filamentous algal mat habitats provide many niches in which members of this order have been able to become dominant.

Genus *Paraholosticha*

One member of this essentially fresh water genus (*Paraholosticha polychaeta* Borror, 1966) has been described from the New Hampshire tidal marshes. This species apparently occurs in the marshes only during the times of the year when the salinity is lower than normal (three parts per thousand). Details are described elsewhere (Borror 1966).

Genus *Holosticha*

Holosticha diademata (Rees, 1884) is a ubiquitous denizen of cultures from many different stations in the New Hampshire tidal marshes, and was found in similar collections from the Gulf of Mexico. Apparently this species is one of the first bacteriovores of early successional stages. The peculiar anterior bend of the left marginal cirrus row, as well as the characteristic size, shape, and behavior, characterize this common ciliate.

Trichotaxis pulchra n. sp.

Length 174–248 μm ; width 37–74 μm , usually 50–60 μm . Thickness about 1/2 body width. Typical outline as in Pl. I 55; some abnormal individuals shorter, wider, variously with acute or indented posterior end. Buccal cavity about 1/3 body length. Ventral surface relatively smooth, except that buccal cirri arise from a shallow longitudinal groove to the immediate right of the buccal overture.

Ciliation. Zone of membranelles bordering anterior and left edge of buccal cavity, including approximately 50 membranelles, each approx. 10 μm long. Medial cilia of buccal membranelles beat separately from remainder of membranelles. Endoral cilia in 6–7 rows on roof of buccal cavity, beat posteriorly. Undulating membrane stiff, vibratile, inserted under right buccal overture. 6–7 buccal cirri each about 10 μm long, in groove to right of buccal cavity. One row of right marginal cirri each 8–10 μm long. Two rows (in all individuals observed) of left marginal cirri each approximately 10 μm long. Marginal cirrus rows overlapping at posterior end. Midventral cirri extending entire length of ventral surface, 9 μm long, except anterior most 3–5 that are approximately 12 μm long. Transverse cirri in L-shaped group of about 15 cirri. Dorsal cilia in at least 3 rows, cilia 3 μm long, 5 μm apart, erect, vibratile.

Internal structure. Many short oblique series of 2–6 cortical granules strikingly visible between dorsal ciliary rows. Each granule approximately 1 μm in length. Ventral cortex likewise granulated as follows: 2–4 oval granules lie between adjacent marginal cirri in all 3 rows, and are situated posterior and to the left of each midventral cirrus. Similar granules lie between bases of anterior most transverse cirri; the posterior most transverse cirri have practically no granules underlying them. Granules also lie between bases of buccal cirri. Longitudinal groups of closely packed granules, one or two granules wide border each row of marginal cirri. Ciliary rootlet fibrils at bases of cirri easily visible in life. Macronuclei difficult to discern in living specimens. In specimens prepared according to the Feulgen nucleal reaction, macronuclei appear as numerous scattered bodies. Cytoplasm generally relatively clear with pale brown inclusions and diatom shells. Food vacuoles with diatom shells and ingested ciliates. Water expulsion vesicle near left margin posterior to buccal cavity.

Behavior. When in contact with the substratum, the animal can crawl forward veering either right or left. The body is flexible dorsoventrally as well as laterally, allowing the animal to worm its way over and among clumps of detritus. Free-swimming occurs in a relatively ineffective counterclockwise helix, whereby the anterior end describes a wide arc while the posterior end drags along the axis of the helix.

Ecology. A population was encountered once, in a collection made in April, 1971.

Systematics. The genus *Trichotaxis* is characterized by possession of two rows of left marginal cirri and one row of right marginal cirri (Borrer 1972). Its members share with such genera as *Holosticha* and *Keronopsis* the possession of midventral cirri. Although some species are described as having two macronuclei, *T. stagnatilis* Stokes, 1891, the type species of this genus, possesses many macronuclei. A similar condition may also exist in *T. crassa* and *T. velox*. No other species in the genus *Trichotaxis* possess buccal cirri, or as many transverse cirri as in *T. pulchra*. Most have 4–6 transverse cirri; *R. stagnatilis* has 8 transverse cirri. Most members of the genus are found in fresh water except *T. crassa*, *T. euplotes*, and *T. velox*. *T. pulchra* is distinguishable by a constellation of morphological characteristics, including fragmented macronucleus, a row of buccal cirri, a relatively large number of transverse cirri, distinctive granulation of the cortex, and marine habitat. In addition, the individuals observed generally are larger than other species of *Trichotaxis*.

A similar linear series of buccal cirri as present in this population have been described also for *Holosticha multistylata* and *Pseudourostyla muscorum*, both described from the water film on mosses.

The specific name is based on the beauty of the cortical granulation in life and the striking preparations possible with the Nigrosin-mercuric chloride-formalin method. A representative slide containing paratypes has been deposited with the International Type Slide Collection, U. S. National Museum.

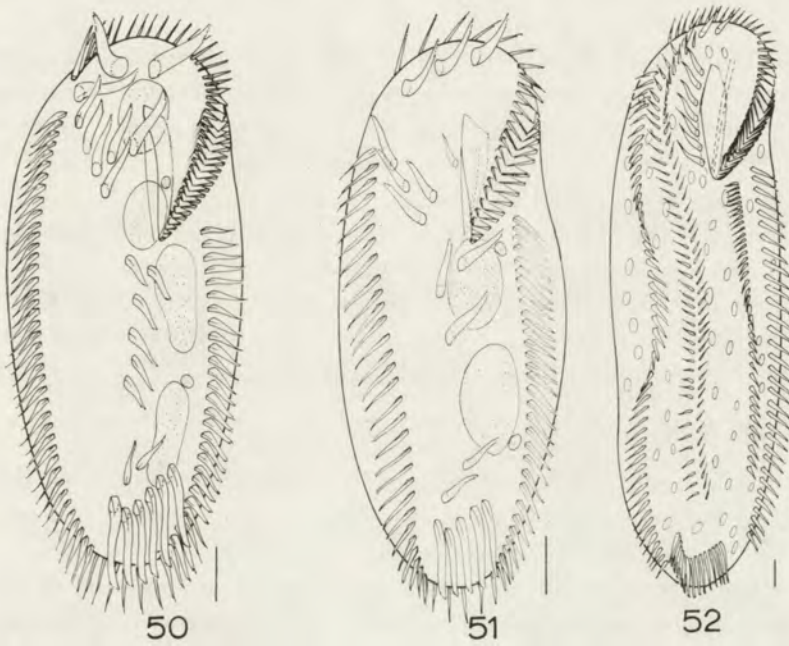
Genus *Gastrostyla*

Populations of *Gastrostyla pulchra* (Perjaslawzewa, 1885) morphologically identical with populations studied in Florida (Borrer 1963 a) occur in the New Hampshire tidal marshes.

Histiculus similis (Quennerstedt, 1867)

Length about 83–150 μm , width about 40–59 μm . Cell flattened ventrally, thickness about half the width. From lateral aspect, both anterior and posterior ends particularly thin. From ventral aspect, the anterior end is particularly blunt, with the widest part of the cell approximately 1/3 of way posteriorly. Buccal cavity 40–45 μm long (Fig. 50).

Ciliation. Cirri arranged as in Fig. 50. Marginal cirri approximately 15 μm long in single right and left rows that are confluent posteriorly, where the rows become virtually dorsal (Fig. 50). Transverse cirri overlapping posterior end slightly. Anterior-most three frontal cirri particularly strong. One buccal cirrus near base



- Fig. 50. *Histriculus similis*, length 90 μm , ventral aspect, showing AZM, undulating membrane and cirri, four macronuclei, and two micronuclei
 Fig. 51. *Oxytricha halophila*, length 90 μm , ventral aspect, showing ciliary organelles and nuclear configuration
 Fig. 52. *Trichotaxis pulchra*, length 187 μm , ventral aspect, showing ciliary organelles and finely distributed macronuclei

of undulating membrane. At least four rows of sparse, vibratile dorsal cilia. AZM (adoral zone of membranelles) includes approximately 40 units in which the mediad two-three cilia of each membranelle beat ventrally as a distinct ciliated field. Thus as in *Condylostoma arenarium* the AZM contains two functionally distinguishable ciliary organelles. On floor and right margin of buccal cavity are two longitudinal series of cilia. Undulating membrane mediad, vibratile, moving back and forth slightly as a unit. Between undulating membrane and AZM is a field composed of a single closely set row of cilia that beat posteriorly at an angle to surface.

Internal structure. Four vacuolate, refractile, distinct macronuclei and two micronuclei. Water expulsion vesicles numerous aborally, slightly to left of medial line, in a series. Relatively little cortical granulation. Food vacuoles contain green algae and diatoms.

Behavior. In contrast to *Oxytricha halophila*, with which members of this population were associated, these ciliates move in a manner more reminiscent of *Stylonychia* or *Euplotes*; that is, they move with relatively fast, frequent reversals posteriorly about one body length to offset a constant left hand veer when going anteriorly. The body does not bend from right to left; it is relatively stiff. The animal can correct this constant left hand forward veer without any reversal by a quick stop, then a slight turn and a restart. When encountering irregularities in the substratum the animal can bend dorsally or ventrally, turning up or curling down the frontal field and membranelles over the edge of a clump of detritus.

Systematics. Members of this genus resemble members of the genus *Oxytricha* except that the body is firm. There are seven species (Borrer 1972), with only two described since Kahl's 1932 review (Vörösváry 1950; Dragesco 1966). Members of the present population resemble those described by Quennerstedt in habitat and general form, and agree closely with populations described by Kahl 1932. *H. lemani* (Dragesco, 1966) is a similar species from fresh water with a different arrangement of cirri and a larger buccal cavity.

Oxytricha halophila (Kahl, 1932)

Length 62–99 μm , width 33–45 μm . Shape from ventral aspect as shown in Fig. 51. Cell thickness about half the width. Buccal cavity length 26–33 μm . Body flattened ventrally, oval in cross section.

Ciliation. Frontoventral cirri massive, in typical arrangement of members of this genus. Transverse cirri overlapping posterior end. Twenty-four right marginal cirri each 20 μm long, 8 μm apart in single row. Left marginal cirri similarly arranged. Dorsal cilia 4–5 μm long, 4 μm apart, in five or six dorsal rows. Rows of marginal cirri ventral, becoming lateral just prior to posterior end, and confluent posteriorly where they lie on dorsal surface (see Fig. 51). Terminal three or four marginal cirri bristle-like, approximately 16 μm long. When animal is maneuvering in a small place they can beat.

Buccal ciliature. Zone of membranelles includes approximately 25–30 membranelles, each with three closely set rows of cilia. Cilia on mediad edge of each membranelle beat independent of membranelle, form a narrow field of cilia. Right buccal overture anteriorly bordered by undulating membrane that courses posteriorly under right buccal lip along medial wall of buccal cavity. UM base appears double, the ciliary bases with 60° packing. Between base of the undulating membrane and AZM of roof of buccal cavity is a zone of endoral cilia that beat posteriorward. Bases of endoral cilia and bases of cilia of undulating membrane separated by a sharp ridge.

Internal anatomy. Cortical cytoplasm heavily granulated. On dorsal surface, spherical (approximately 0.5 μm diameter) single granules in linear oblique groups of two to five granules parallel dorsal ciliary rows. Rows of granulation similarly

on sides of ventral field. Between most massive frontal cirri each row of granules approximately 10 in number. Two macronuclei, each with a micronucleus. Water expulsion vesicle present. Posterior end of cell with irregular oblong granules approximately $4 \times 2 \mu\text{m}$. Food vacuoles contain chloroplasts and diatom shells.

Ecology, behavior. Members of this species became abundant on or near the surface scum of cultures derived from a collection made 18 December, 1968 from the Adams' Point tidal marsh. Individuals when free swimming do so in a narrow slow counterclockwise helix. Most individuals creep forward in a rapid irregular manner, showing a strong tendency to veer to the right. The cell is obviously not rigid; the animal can bend laterally. Members of this species thus were easily distinguished from *Histiculus*.

Systematics. The genus *Oxytricha* Ehrenberg, 1830 contains at least 29 species (Borror 1972) and is characterized by a contractile body and posteriorly confluent rows of marginal cirri. The caudal cirri if present are the modified posterior parts of the marginal rows. Since Kahl's review 1932, at least four species have been added to the genus (Kahl 1935, Chatton and Séguéla 1940, Gellért 1942, Tucolesco 1962). Members of this population agree with the original description by Kahl in nuclear configuration, arrangement of posterior cirri, and marine habitat. The other marine members of this genus (*O. ovalis*, *O. marina* and *O. discifera*) all differ in both shape and nuclear configuration from this species.

Genus *Trachelostyla*

Trachelostyla pediculiformis (Cohn, 1866) occurs regularly in small numbers in tidal marshes, particularly in association with areas of low oxygen concentration. Individuals of this species from New Hampshire appear morphologically identical with populations from the Florida coast studied previously (Borror 1963 b, Kool 1970).

Genus *Aspidisca*

Apparently only two species in this genus occur regularly in the New Hampshire tidal marshes. There are *A. aculeata* (Ehrenberg, 1838) and *A. baltica* Kahl, 1935, both described in detail previously (Borror 1965 b).

Genus *Diophrys*

This genus is represented by a confusing array of populations that differ from one another morphologically in the coastal New Hampshire area. In addition to the relatively well known *Diophrys scutum* (Dujardin 1841). I have also found *D. oligothrix* Borror, 1965.

Genus *Euplotes*

This genus has more members in the tidal marsh habitat than any other genus of ciliate. So far encountered in the tidal marsh are *E. charon* (Müller, 1773); *E. harpa* Stein, 1859; *E. minuta* Yokom, 1930; *E. alatus* Kahl, 1932; *E. mutabilis* Tuffrau, 1960; *E. trisulcatus* Kahl, 1932; *E. bisulcatus* Kahl, 1932; and *E. quinquecarinatus* Gelei, 1950. All these have been differentiated not only on the basis of living material and wet silvers, but also by specimens prepared according to the NMF method. In addition to these I have observed *E. crenosus* Tuffrau, 1960 on the basis only of material prepared according to the wet silver method. Some, such as *E. crassus* (Dujardin, 1841) and *E. vannus* (Müller, 1786) occur commonly on the open coast, but apparently do not occur with any regularity in tidal marshes.

Genus *Uronychia*

Members of this genus of the family *Euplotidae* occur regularly and in some abundance in the New Hampshire tidal marshes. All populations so far studied in detail appear ascribable to the species *Uronychia transfuga* (Müller, 1786) (see Borrer 1963 a).

Summary

Over 100 species of ciliates occur in New Hampshire saltmarshes. Anatomy, behavior, autecology, and systematic position of 29 species are discussed, including previously described species of the genera *Coleps*, *Colpoda*, *Condylostoma*, *Dysteria*, *Frontonia*, *Geleia*, *Histiculus*, *Litonotus*, *Mesodinium*, *Nassula*, *Oxytricha*, *Paralembus*, *Paramecium*, *Placus*, *Plagiopyla*, *Pleuronema*, *Prorodon*, *Sonderia*, *Strombidium*, *Trachelonema*, *Trochilioides*, and *Uropedalium*. Four new species are described in the genera *Chlamydon*, *Paranophrys*, *Trichotaxis*, and *Trimyema*. Two species are transferred from *Pseudocohnilembus* to *Paralembus*.

This serves as a reference for determination of interrelationships of these ciliates and associated environmental factors.

ZUSAMMENFASSUNG

Über 100 Arten von Ciliaten leben in New Hampshire Salzwasser Sumpfen. Anatomie, Betragen, Autecologie, und Systematik von 29 Arten sind vorgestellt. Diese einschliessen schon vorbeschriebenen Arten von dem Genera *Coleps*, *Colpoda*, *Condylostoma*, *Dysteria*, *Frontonia*, *Geleia*, *Histiculus*, *Litonotus*, *Mesodinium*, *Nassula*, *Oxytricha*, *Paralembus*, *Paramecium*, *Placus*, *Plagiopyla*, *Pleuronema*, *Prorodon*, *Sonderia*, *Strombidium*, *Trachelonema*, *Trochilioides*, and *Uropedalium*. Vier neue Arten sind im Genera *Chlamydon*, *Paranophrys*, *Trichotaxis* and *Trimyema* beschreiben. Zwei Arten sind von *Pseudocohnilembus* zu *Paralembus* übergetragen.

Dieses dient als Auskunft denn Bestimmung von Beziehungen zwischen Ciliaten und Umweltfaktoren.

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EXPLANATION OF PLATE I

- 53: *Placus salinus*, left lateral aspect, photomicrograph of specimen prepared according to Chatton-Lwoff silver impregnation technique, left lateral aspect
54: *Frontonia fusca*, ventral aspect; photomicrograph of specimen prepared according to NMF technique
55: *Trichotaxis pulchra*, ventral aspect; photomicrograph of specimen prepared according to NMF method. Note obvious row of buccal cirri adjacent to undulating membrane
56: *Paranophrys magna*, anterior end, ventral aspect; photomicrograph of specimen prepared according to Chatton-Lwoff silver impregnation technique; showing buccal apparatus



A. Borror

auctor phot.

Maria JERKA-DZIADOSZ

Cortical development in *Urostyla*. I. Comparative study
on morphogenesis in *U. cristata* and *U. grandis*Rozwój struktur powierzchniowych u *Urostyla*. I. Badania porównawcze
nad morfogenezą *U. cristata* i *U. grandis*

Patterns of cortical development of the hypotrichous ciliates have become the subject of numerous investigations in recent years (Wise 1965, Jerka-Dziadosz and Frankel 1969, Tuffrau 1969, 1970, Jerka-Dziadosz 1971). As a result of these investigations it has been stated, that in more evolved forms such as for instance *Euplotes* both oral and cirral primordia are formed without visible participation of a preexisting ciliature (Wise 1965, Diller 1966, Hufnagel and Torch 1967). In lower hypotrichs Tuffrau 1969, 1970 described topographical relation of the oral primordium for the opisthe to one of the ventral cirral rows (*Kahliella*) or one from the transverse cirri (*Stylonychia*, *Gastrostyla*). In *Urostyla weissei* Jerka-Dziadosz and Frankel 1969 described a direct incorporation of the kinetosomes from preexisting cirri into the oral primordium and cirral primordia as well. Comparative studies on the related species may add more information to the general problem of the role of preexisting ciliature in ciliate morphogenesis.

A study of the early stages of development of oral and cirral primordia in *Urostyla cristata* and *Urostyla grandis* has been carried out. The general pattern of morphogenesis of those two species was described in earlier papers (Jerka-Dziadosz 1963, 1964 a). Reexamination of early stages of the formation of primordia using the protargol technique seems to be necessary, since the earlier study on *U. weissei* (Jerka-Dziadosz and Frankel 1969) and results presented in this paper indicate clearly, that such complicated structures as the divisional primordia of ciliature in hypotrichous ciliates, stained with the iron hematoxylin after Parducz 1967, are very difficult to interpret clearly. The protargol technique gives much better results (see Tuffrau 1967, 1969).

The present communication provides a detailed description of the morphogenesis of ciliary organelles during binary fission in *U. cristata* Jerka-Dziadosz and *U. grandis* Ehrbg. The early stages of development, the sites of origin of primordia and the participation of preexisting ciliature in the process of ciliary pri-

mordia formation will be emphasized throughout. On the basis of this description an attempt will be made to compare the morphogenetic pattern in *U. grandis* and *U. cristata* to that in *U. weissei* and other hypotrichs. The problem of participation of preexisting ciliature will be discussed.

Materials and methods

The organisms used in this investigation were clones of *U. grandis* Ehrbg. collected in 1968 from the pond of Sadyba in Warsaw (Poland) and *U. cristata* Jerka-Dziadosz collected in August 1970 from the pond in Zaborów near Warsaw. The general culture methods for *U. grandis* were those described previously (Jerka-Dziadosz and Frankel 1969) for *U. weissei*. The culture medium was Pringsheim solution, while the food organism was *Tetrahymena pyriformis* GL-C washed from 2% proteose-peptone medium and transferred for 24 h into egg yolk solution.

The culture methods for *U. cristata* were as follows. The organisms were maintained in small Petri dishes, the culture medium was Pringsheim solution. Every other day half of the culture fluid was removed and *Aerobacter aerogenes* incubated for 24 h in 0.15% dried lettuce infusion was added. Once a week few drops of dried egg yolk solution was added.

In well-fed cultures of both species division occurred every 18–20 h at room temperature (18–21°C). Large cells presumably in late S phase and early dividers were picked up by micropipette and transferred directly into depression slides containing Bouin or Hollande fixative, for 5–10 min. They were then washed several times in tap water and then transferred onto a slide with Mayer's albumin. The cells were "enrobed" in a thin film of albumin, the excess of albumin was removed by micropipette. After coagulation of albumin in 96% alcohol, the protargol impregnation technique as described earlier (Jerka-Dziadosz and Frankel 1969) was employed. However, certain simplifications were introduced, mainly the concentration of potassium permanganate was 0.2%, instead of 5% used previously. Thanks to this the falling off of the albumin layer from the slide has been avoided.

Results

Cortical anatomy of non-dividing cells

Urostyla cristata

The general description of morphological features was given in an earlier paper (Jerka-Dziadosz 1964 a). The present description is based on specimens stained with protargol and will consider only the ciliary organelles. The first top drawing on the Fig. 1 represents the ciliary organelles on the ventral surface of *U. cristata*.

The peristome is bounded on the animal's left by an adoral zone of membranelles (AZM) made up 90–130 membranelles. Each membranelle consists of three long rows and one short row of basal bodies and cilia. The distal portion of the AZM curves to the right around the anterior end of the animal and ends close to the first marginal row of cirri. The basal plates of membranelles which lie on the anterior margin and on the right side of the cell are shorter than those closer to buccal cavity on the left side. On the right wall of the peristome are situated 2 undulating mem-

branes (UM). These are parallel to one another and separated by a space of several micrometers. The outer one ("preoral membrane") is longer and possesses longer cilia, while the inner one ("endoral membrane") is shorter, curves under the wall of peristome and bears shorter cilia.

Five systems of cirri are disposed on the ventral and marginal portions of the cell. The fronto-ventral cirri lying on the frontal and ventral area to the right and posterior to the peristome are arranged in two diagonal parallel rows. Those rows start at the anterior left side of the ciliate, then they curve parallel to the AZM and run posteriorly along the central meridian of the ventral surface till they reach an oblique short row of cirri. Close to the outer undulating membrane there is one isolated cirrus, which will be called "frontal cirrus No. 0". The ventral cirri are called those cirri of the two rows, which cover the central meridian posterior to the buccal cavity. The transverse cirri are situated close to the posterior end of the cell. These 12–16 cirri are disposed in a short diagonal row close to posterior terminations of the ventral cirral rows. These three groups of cirri: frontal, ventral and transverse will be subsequently designated as the FVT complex.

Two groups of rows of marginal cirri cover the spaces on the left and right side from the FVT complex. Each side is covered by seven longitudinal parallel rows of cirri. They will be numbered starting from the one closest to the FVT — on the left side to the left, and on the right side to the right.

The protargol preparation shows also the fiber system connected with the cirri and membranelles. Each cirrus possess three kinds of fibers: tangential, diagonal and transverse. The disposition of those fibers is similar to the ones described by other authors in several hypotrichous ciliates (Tuffrau 1965, Grim 1970).

The pattern of dorsal ciliary rows or kineties is drawn on the first left sketch in the lower line on the Fig. 1. The dorsal surface is covered by eight longitudinal rows of short single cilia. Those rows extend continuously from the anterior end of the animal to the posterior end.

The nuclear apparatus consists of about 50 pieces of macronucleus (Ma) and 6–8 micronuclei (Mi). They are clearly visible in protargol preparations.

Urostyla grandis

As in *U. cristata*, the general description of morphological features of *U. grandis* was given in an earlier paper (Jerka-Dziadosz 1963). This description based on protargol preparations contains only details of the arrangement of the ciliary organelles. (Fig. 3, first drawings in upper and lower rows). The arrangement of the oral ciliature of *U. grandis* differs insignificantly from the one of *U. cristata*. The left border of the peristome is bounded by the AZM, which consists of 60–70 membranelles. Each membranelle is made up of three rows of cilia. The basal plates of the membranelles which lie on the anterior end of the cell are shorter than the ones on the left margin of peristome. On the right margin of the buccal cavity are situated two undulating membranes (UM). The outer UM ("preoral membrane")

possess long cilia, closely packed, while the inner UM is shorter, curves under the outer one, and its cilia are shorter and dispersed at the distal end.

The somatic ciliature of the ventral side can be divided as follows: FVT complex, which covers the frontal area and the central meridian of the animal, and two groups of marginal cirri, which cover the left and right margins of the cell. About 24 frontal cirri, arranged in longitudinal rows, cover the frontal area. The first row which consists of about 9–13 cirri is situated parallel and very close to the outer UM. The next parallel rows consist successively of 5, 4 and 3 cirri. The ventral cirri consist of two parallel rows of cirri. They start next to the frontal cirri, to the right of them. These two rows of cirri pass along the central meridian of the ventral surface till they reach a short diagonal row of cirri. The transverse cirri are situated close to the posterior end of the cell, with 12–16 cirri which are arranged in a short oblique row. The anterior end of this row is directed to the anterior left margin of the cell.

Although the general pattern of arrangement of the cirri in the FVT complex is fairly constant, the number of cirri in each particular group of cirri varies considerably.

Marginal cirri consist of two groups of cirral rows, one on the left, the other on the right margin of the cell. The number of the row of cirri on each side varies considerably. Most frequently there are 5 rows on the left and 5 rows on the right side. Sometimes the animal may have 6 or 7 rows on one or both sides. On the left side the first marginal row (counted from the FVT complex to the left) runs from the AZM to the posterior end of the cell. The second or sometimes the third row is shorter and ends close to the equator of the ciliate. The next two or three rows extend continuously from the anterior to the posterior end. On the right side of the animal the first, short row (closest to the FVT) starts in the middle of the ventral surface and ends at the posterior tip. The remainder of the right marginal cirral rows run continuously from the anterior end to the posterior tip of the cell. Behind the transverse cirri both left and right marginal rows curve to the middle and join.

The cortical system also contains the fibers underlying the membranelles and cirri. This system is similar to that in *U. cristata*. Each cirrus possesses diagonal, transverse and longitudinal fibers.

The dorsal surface of *U. grandis* is covered by three longitudinal rows of short cilia. The cilia are widely spaced within a row. The rows run from the anterior to the posterior end of the animal.

The nuclear apparatus of *U. grandis*, described elsewhere (Tittler 1935, Raabe 1945, 1946) consists of about 80–100 pieces of macronucleus and 8–16 micronuclei.

Cortical development of *Urostyla cristata*

Morphogenesis during division in *U. cristata* is complex, involving the replacement of every element of the old oral and somatic ciliature. There are 4 major

sets of ciliary primordia: (1) the oral primordia (AZM and UM), (2) the ventral cirral primordia (FVT), (3) the marginal primordia and (4) the primordia of dorsal kineties. The first two groups of primordia will be described separately for the proter and opisthe. The marginal and dorsal primordia, owing to their similarity in proter and opisthe, will be described together.

A stage-by-stage summary of major cortical events are presented in Table 1 and schematically drawn in Figs. 1 and 2.

Table 1

Summary of cortical feature characterizing each stage of development of *Urostyla cristata*

Stage	1	2	3	4	5	6
AZM primordium for opisthe	first appears	expanded field	MB formation begins	MB formation proceeding	MB formation completed	final form attained
AZM primordium for proter	—	first appears within old inner UM	expanded sub-pellicular field joins old AZM	MB formation begins	MB formation proceeding	final form attained
UM primordia	fields begin to form	expanded fields	UMs and FC-1 begin to form	UMs and FC-1 begin to form	UMs nad FC-1 formation completed	—
FVT primordia	fields begin to form	elongate fields	anterior streaks begin to form	new frontal cirri begin to form	new transverse cirri differentiate	new cirral rows attain final form
Marginal primordia	—	—	fields begins to form	streaks from fields differentiate	new marginal cirri differentiate	cirral rows elongate
Dorsal primordia		new kineto's appear in kinety I	new kineto's appear in kineties 2-8	new kineties well developed	kineties elongate	final form attained
Ma	RB	RB	begining of coalescence	Ma fused	division of Ma	division of Ma

Oral and FVT primordia of the proter

Stomatogenesis of proter begins from disaggregation of the two old undulating membranes (Pl. II 7, 8, 9, 10). The process of dispersion begins at the anterior end of the UMs and proceeds posteriorly. The 2 UM-fields unite as they form. As a result, a kinetosomal field parallel to the AZM is formed. Inside the buccal cavity this field comes closer to the old AZM (Pl. III 11, 12, 13). Within the buccal cavity, as a continuation of the UM and AZM a sort of "pocket" filled up with kinetosomes is formed (stages 2-3). Some of those kinetosomes, which lie under the pellicle within the "pocket", become a primordium of the new AZM for the proter (see below).

Differentiation of the UM field starts at the late stage 3. The first step is the appearance of a fork at the anterior end of the UM-field. The kinetosomes of the right branch of this fork become more closely packed than in the remainder of the field. This branch develops during stage 4 into the 1st frontal cirrus (Pl. IV 15, V 21). The remainder of the field gradually differentiates in the 2 new undulating

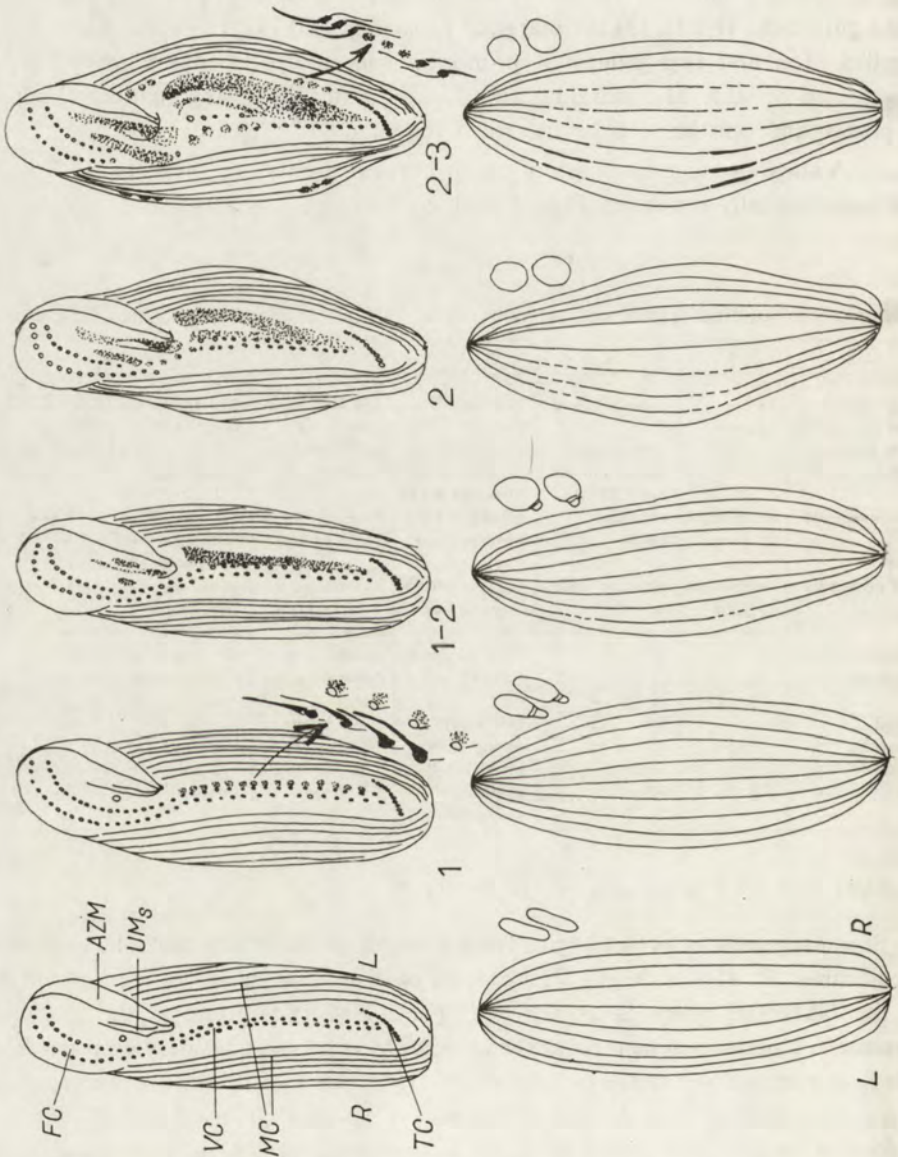


Fig. 1. Drawings of the ventral (upper row) and dorsal (lower row) surfaces of cells of *U. cristata* in stages 0-3 of preparation for division. The first drawings in the upper and lower row show the interdivisive specimen. The drawings are made from actual specimen, stained with protargol and identified by stage designation presented in Table 1. The numbers indicate the stages of development. Two pieces of Ma are drawn next to the right upper corner of the lower row drawing. The kinetosomal fields and new kinetosomes are indicated by areas of fine dots, while the streaks which will form the new cirri are shown as thin lines. At stage 5 and 6 the old cirri, which are destined to be resorbed, are omitted. Abbreviations: AZM - adoral zone of membranelles, UM - undulating membranes, FC - frontal cirri, VC - ventral cirri, MC - marginal cirri, TC - transverse cirri, R - right side of the cell, L - left side of the cell

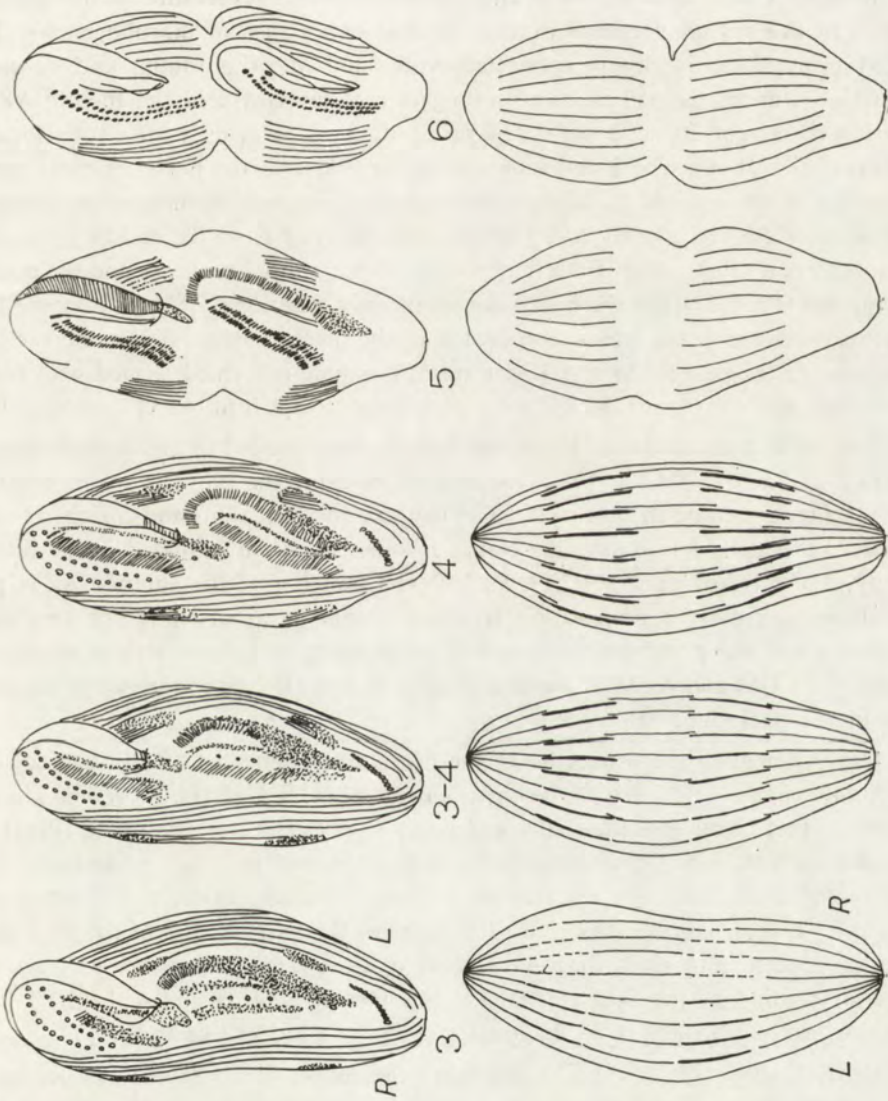


Fig. 2. Drawings of the ventral (upper row) and dorsal (lower row) surfaces of cells of *U. cristata* in stages 3-6 of preparation for division. The conventions employed are the same as those indicated for Fig. 1

membranes, which are parallel until stage 5 (Pl. V 22, 23), later the inner one curves inside, under the outer one.

The AZM primordium for the proter makes its appearance after disaggregation of the old UMs. On the right wall of the peristome, very close to the posterior part

of the inner UM a small group of kinetosomes appear. Proliferation of new kinetosomes in this region proceeds during the first two stages of morphogenesis. The AZM primordium is closely connected with the UM primordium, and develops posteriorly, under the pellicle as a prolongation of the UM-field and the old AZM. During the stages 2 and 3 the AZM primordium appears as a long subpellicular "pocket" (Pl. II 10). The kinetosomes which are close to the posterior-most membranelles of the original AZM become organized into new membranelles, whereas the old ones are successively resorbed "in situ". Starting from the middle of stage 4 almost all new kinetosomes from the "pocket" move up to the surface and the pocket disappears (Pl. V 22). On the both sides of the new anterior AZM one may see free kinetosomes, which are later incorporated to the membranelles. Below the surface, posterior to the new AZM and UM a new cytostome is formed, armed with fibers connected with the inner UM and with inner kinetosomes from AZM membranelles.

The AZM primordium in *U. cristata* has not been noticed in earlier observations (Jerka-Dziadosz 1964 a) probably because of using the Parducz's iron hematoxylin staining method in that study. The method does not stain non-ciliated kinetosomes, and small, delicate groups of kinetosomes, especially situated in the buccal cavity, are not distinguishable (Pl. VI 26). The presence of the anterior AZM primordium in protargol preparation is unmistakable, however, it is not very easy to distinguish the primordium since it is surrounded by heavily stained structures such as: the UM and AZM of proter and opisthe, and also the condensed or dividing Ma in the background (Pl. V 19).

Development of the primordia of the FVT complex begins with disaggregation of frontal cirrus No. 0, that is the cirrus closest to outer UM (Pl. II 8). The kinetosomes of that cirrus lose their cilia and begin to disperse in a small field (Pl. II 9), parallel to UM-field. Proliferation of new kinetosomes proceeds posteriorly. The old ventral cirri which are situated at the level of buccal cavity are incorporated to the FVT field. During stage 3 of development the basal bodies of the FVT-field become ordered into short diagonal streaks of cilia. This process begins from the anterior portion of the field (Pl. III 13, 14). During stage 3 and 4 the FVT-field is transformed into about 40 diagonal streaks in a ladder-like form.

Differentiation of new FVT cirri from the ladder-like primordium begins at stage 4 (Pl. IV 15, Pl. VI 21, 22, 23). The first streak of the "ladder" appears to be the right branch of the UM-field, which develops into the first frontal cirrus. Frontal cirrus No. 0 is formed from the inner part of the second streak. The remainder of the frontal and ventral streaks divide into two segments, and the 12-16 most posteriorly situated streaks divide into 3 segments. Each segment is then transformed in a cirrus. In this way two longitudinal row of cirri are formed at the frontal and ventral area, plus a third short row of cirri parallel to the posterior portion of the previous ones. This short row of cirri then curves to the left and moves posteriorly to reach the position of transverse cirri.

Oral and FVT primordia of the opisthe

The appearance of the AZM primordium for the opisthe is the first event of cortical morphogenesis associated with cell division in *U. cristata*. The old ventral cirri from the left row, which are situated posterior to the old AZM lose their sub-pelicular fibers. Around them, to their left, small fields of new kinetosomes are formed. Thus a longitudinal row of small kinetosomal fields associated topographically with the left row of ventral cirri appear (Pl. I 1-4). Next, extensive kinetosome proliferation occurs in the central meridian of the cell and a uniform, longitudinal field of basal bodies appears. The length of this field is about 1/3 that of the cell, with its anterior end situated a few micrometers posterior and to the left of the old AZM. Posterior end of this field terminate in close vicinity of the old transverse cirri. The posterior part of left and right ventral cirri are successively incorporated to the AZM field. During the 2nd stage of morphogenesis the anterior portion of the AZM-fields "detach" from the old ventral cirri and move to the left (Pl. I 3). Membranelles subsequently differentiate within the AZM-field. They initially appear in stage 3 in the right anterior corner of the field. Membranelle formation then spreads posteriorly and to the left (Pl. I 4) until the entire field has become organized into membranelles at stage 5. During differentiation of membranelles the new AZM curve to the right in the anterior region, to round up the anterior portion of the future opisthe.

The primordium of the undulating membranes (UMs) develops separately from that of the AZM. At stage 2, between the AZM primordium and right ventral row of cirri a thin longitudinal field of kinetosomes is formed (Pl. I 3, 4). The anterior, midventral portion of the left ventral row of cirri, which was previously "involved" in formation of the AZM-primordium, is now incorporated into the UM-field. The proliferation of basal bodies spreads posteriorly, and the primordium grows. The posterior portion of the UM and AZM primordium are continuous, and form a common field. They separate during later morphogenesis.

Differentiation of UM field into new UMs and first frontal cirrus proceeds in the same way as in proter. In the anterior portion a fork-like split is formed. The right branch of that fork is then transformed into the first frontal cirrus, the rest of the field divide longitudinally and forms two parallel membranes.

The primordium of the FVT for the opisthe begins to form during 2nd stage of morphogenesis. The old cirri from the right row of ventral cirri, which are situated near the equator of the cell, disaggregate and form few small groups of loose kinetosomes. Then the gaps between these groups are filled up with new basal bodies and a longitudinal field of basal bodies appear at stage three of division. The posterior portion of that field lies close to the posterior terminations of the UM and AZM fields (Pl. I 4, IV 6).

Differentiation of the FVT field into a ladder-like form of diagonal streaks of cilia, and later formation of new frontal, ventral and transverse cirri proceeds

in the same way as in the proter and thus will not be repeated here. It should be noted, however, that the development of the FVT complex in the proter always precedes of that in the opisthe. The opposite situation applies to the oral primordia, which are visible first in the opisthe and then in the proter. During the two last stages of development the differences between proter and opisthe disappear.

Marginal and dorsal primordia

Development of marginal and dorsal primordia proceeds in a very similar way in proter and opisthe. The kinetosomal fields which form the primordia of new marginal rows of cirri are built within one of the seven old marginal rows on each side at two levels, which correspond to the location of anterior and posterior peristomes. The marginal fields appear in stage 3, and are derived directly from the old marginal cirri. On the left side 3-4 old cirri from the first left marginal row in proter and opisthe lose their rootlets, and cilia (Pl. I 4). The kinetosomes disperse and form small fields. Proliferation of new basal bodies between the fields leads to longitudinal, uniform fields (Pl. IV 17). It should be stressed that old cirri from but only one row of old marginal rows take part in formation of a field which next differentiate into 7 rows of new left marginal rows of cirri. A similar situation appear on the right margin. Some cirri from the furthest-right row of old right marginal cirri form primordial fields of basal bodies, which develop into the primordium of the right marginal cirri (Pl. V 20).

Differentiation of new marginal cirri within left and right marginal fields proceeds in a very similar way (Pl. IV 18). Starting from the right anterior corner of the field, 7 longitudinal streaks of cilia are formed. Later, within each streak new cirri form by the aggregation of cilia. This process also begins from the right anterior portion of the field. It appear that within the same field the process of differentiation of new cirri occurs in the right anterior portion, whereas in the left posterior portion a process of proliferation of new kinetosomes simultaneously proceeds (a similar situation appear to happen within the AZM-field). The spaces between new marginal rows gradually enlarge, and the new marginal cirri become to occupy their final position, whereas the remainder of the old marginal rows are resorbed together with the anterior-most frontal cirri and the transverse cirri, which also do not participate in morphogenesis. The process of resorption of old ciliature takes place at the conclusion of the binary fission and is finished after separation of offsprings (Jerka-Dziadosz 1968).

The development of new dorsal ciliature in *Urostyla cristata* has not been described previously, owing to the difficulty of discerning the early stages of primordia development by Parducz's iron hematoxylin method. The dorsal primordia are formed in two zones within each of the 8 kineties, one is 1/3 and other 2/3 of the distance from the anterior to the posterior end of the cell (Pl. VI 24, 25). The process of formation of new kinetosome begins in the stage 2, occurring sequentially in kineties from 1 to 8. New unciliated kinetosomes arise anterior and posterior to

old ciliated ones, resulting in the formation of short files of kinetosomes. By the end of stage 3, the short files of kinetosomes formed within each kinety have merged, forming a continuous row of closely-spaced basal bodies, which is the new kinety. At about this time cilia grow out on the new basal bodies. Subsequently, in stage 4, the new kineties, now fully ciliated, detach from the old ones and begin to elongate with their cilia spreading apart. In the process of elongation the new kineties come to overlap the remaining parts of the old ones. The remaining portions of the old kineties are resorbed and replaced by the elongating new kineties.

In *U. cristata* no structures have been observed similar to the caudal cirri described in *U. weissei*, which in the latter organism are formed at the posterior terminations of dorsal kineties (Jerka-Dziadosz and Frankel 1969).

Nuclei

Nuclear events which occur during division have been generally described in earlier paper (Jerka-Dziadosz 1964). Since the protargol preparation stains cortical structures and the nuclear apparatus as well, it became possible to observe cortical and nuclear events simultaneously. At the time when stomatogenesis of the opisthe begins, a replication band (RB) can be clearly observed in all pieces of Ma. These bands are situated near to one of the ends of each piece of Ma. This indicates that the cell which enters the division process is at the late S phase of generation cycle. At the beginning of stage 3 of division, right after the RB has passed through Ma, each piece rounds up and the process of coalescence of macronuclear material of the cell begins. This fused Ma at stage 4 takes up a central position in the cell, at the end of stage 4 the first division of the Ma occurs, later on further segmentation of Ma into small pieces takes place. Micronuclear mitosis occurs at the time of first two divisions of the Ma in stage 5. The offspring of each Mi go to different cells.

Cortical development in *Urostyla grandis*

As in *U. cristata* every element of the oral and somatic ciliature of *U. grandis* is replaced during division. The preexisting ciliature participate extensively in the process of the primordia formation. There are 4 groups of primordia to be described: (1) oral primordia, (2) the FVT primordia, (3) the marginal primordia and (4) the primordia of dorsal kineties. As in the case of *U. cristata*, the first two classes of primordia will be described separately for proter and opisthe, whereas marginal and dorsal rudiments will be described jointly. A stage-by-stage summary of major cortical events are summarized in Table 2 and schematically drawn at Figs. 3 and 4.

Oral and FVT primordia of the proter

Stomatogenesis of the proter in *U. grandis* differs considerably from that one in *U. cristata*. The primordia of AZM and UM appear together as one compact group of basal bodies situated on the right side of the buccal cavity (Pl. VII 30-32),

Table 2

Summary of cortical features characterizing each stage of development in *Urostyla grandis*

Stage	1	2	3	4	5	6
AZM primordium for the opisthe	first appears	expanded field	membranelle formation begins	MB formation proceeding	MB formation completed	final form attained
AZM primordium for the proter	—	first appears within old inner UM	joins old AZM	membranelle formation begins	MB formation proceeding	final form attained
UM primordia	—	fields begin to form	expanded fields	UMs and FC-1 begin to form	UMs and FC-1 formation completed	—
FVT primordia	—	first three streaks appear	remaining streaks appear	new frontal cirri begin to form	transverse cirri differentiate	new cirral rows attain final form
Marginal primordia	—	—	streaks appear	streaks elongate	new marginal cirri differentiate	cirral rows elongate
Dorsal primordia	—	new kinetosomes in kinety 1 appear	new kinetosomes in kineties 2 and 3 appear	kineties elongate	kineties well developed	final form attained
Ma	RB	RB	begining of coalescence	Ma fused	division of Ma	division of Ma

close to the posterior end of the inner, "endoral", membrane. This group of kinetosomes join with basal bodies of the disaggregating old undulating membranes. The important feature which distinguishes the stomatogenesis of *U. cristata* and *U. grandis* is the participation in the latter species of old frontal cirri in the formation of the UM-AZM primordium complex. About 9-13 cirri from the row of frontal cirri closest to the UM become incorporated into the UM field. This process of incorporation starts from the posterior part of the row (Pl. VII 33). By stage 2 of division a longitudinal field of basal bodies which expands on posterior portions on the place of old UMs and the first row of frontal cirri appear. The expanded area becomes the primordium of AZM. The most posterior part of the old AZM begins to be resorbed at that time, and a "bare patch" is formed (Pl. VIII 35). This indicates that two quite different processes occur in close vicinity to each other: an extensive proliferation of kinetosomes in the UM-AZM primordium complex and a resorption of membranelles in the proximal part of old AZM. During stage 2 of development the kinetosomes from the posterior end of the UM-AZM field move to the right and join the rest of the old AZM (Pl. VIII 37). Kinetosomes of this part of the primordium begin to form new membranelles of the AZM. During stage 2 the process of formation of the AZM primordium take place in the buccal cavity, under the surface, later during stage 3 the buccal depression disappear and all oral structures become situated at the surface of the cell. Kinetosomes of the AZM primordium form "anarchic field"-like anlage around the posterior end of the AZM of the proter. During stage 4 the rest of the loose kinetosomes are organized into new membranelles, whereas the old membranelles are resorbed successively "in situ".

Differentiation of the UM-field starts at the end of stage 3. At the beginning a fork-like split appears in the anterior portion of the UM-field. The right branch of that fork later organizes into the first frontal cirrus, the rest of the UM field differentiates into two longitudinal parallel UMs. After separation of daughter cells the inner UM curves inside, underneath the outer one. The fibers connected with the kinetosomes of the inner membrane form the wall of the cytostome.

It is worth pointing out here that at early stages of development the posterior portion of UM and AZM primordium of the proter are situated in a depression under the pellicle, whereas very close to it, at the surface there are the AZM and UM primordia for the opisthe (Pl. VIII 34-37). On the Parducz's iron hematoxylin preparations this whole region of the cell seems to appear as a uniform longitudinal field of cilia, and has been described as such in the earlier paper published in 1963.

Formation of the FVT primordia of the proter takes place in the "bare path" at the frontal area, close to the UM-field. At stage 2 of division 3-4 longitudinal streaks of kinetosomes with short cilia appear (Pl. VIII 37). The process of appearance of basal body streaks proceeds from anterior to posterior. The streaks are oriented diagonally to the anterior-posterior axis of the animal, with their posterior terminations directed toward the AZM. Posterior streaks arise in very close vicinity of the UM-AZM primordium of the proter. As a result about 30 streaks in a ladder-like fashion are formed. The most posterior streak is situated parallel to the old marginal row, at the level at which new marginal cirri will first form. The old ventral cirri which had been present in the territory where the posterior portion of the "streak-ladder" is formed become incorporated into the primordia. They lose their cilia and fibers (Pl. IX 38-41).

The differentiation of new cirri from the ciliary streaks of the "ladder" has been described previously (Jerka-Dziadosz 1963). The first frontal cirrus is formed from the UM-field. The rest of the frontal cirri (about 23) are formed from the first five streaks of the "ladder". Within each streak a few cirri differentiate. From the first streak the one anterior-most cirrus move anteriorly, the rest shift toward the UM and form the row of cirri closest to UM (this row will be incorporated to the UM-field in the next division). Six cirri form in the second streak and in the next three streaks 5 to 3 cirri differentiate subsequently. All these become the frontal cirri. The rest of the "ladder" is transformed into the ventral and transverse cirri. In each streak 3-5 cirri are formed. The inner-most cirri (closest to UM) form a row of transverse cirri, whereas the remainder differentiate into two longitudinal rows of ventral cirri. During stage 5 and 6 the transverse cirri move posteriorly and to the left, until they reach their final position, after separation of the offspring (Pl. X 42-45).

Oral and FVT primordia of the opisthe

The AZM primordium of the opisthe of *U. grandis* originates and develops in a very similar fashion as the oral primordia for the opisthe in *U. weissei*. It appears

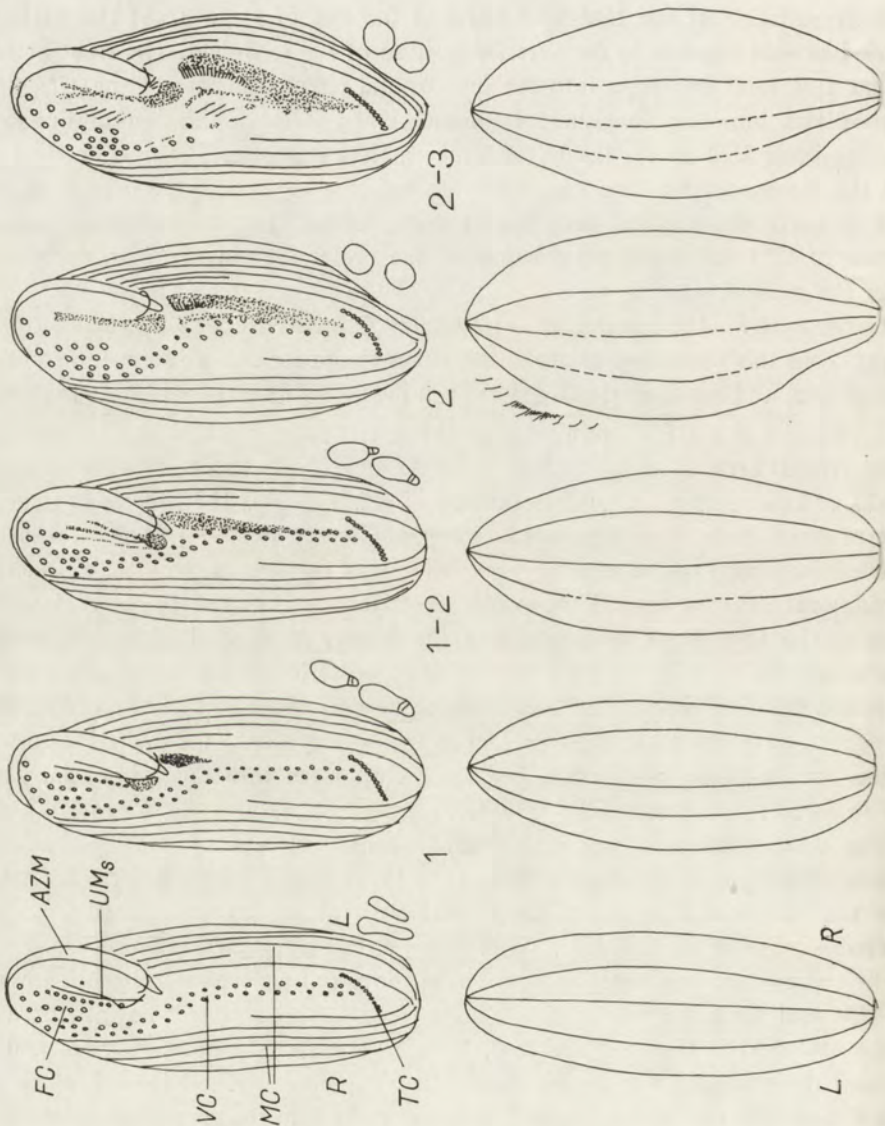


Fig. 3. Drawings of the ventral (upper row) and dorsal (lower row) surfaces of cells of *U. grandis* in stages 0-3 of preparation for division. The conventions employed are the same as those indicated for Fig. 1

as an elongated field of basal bodies situated in the space between the left row of ventral cirri and first left marginal cirral row (Pl. VII 28, 29). The anterior portion of the primordium is situated very close to the original buccal cavity, but direct contact with the old mouth has not been observed. During the first stage of development the number of kinetosomes within the AZM primordium increases

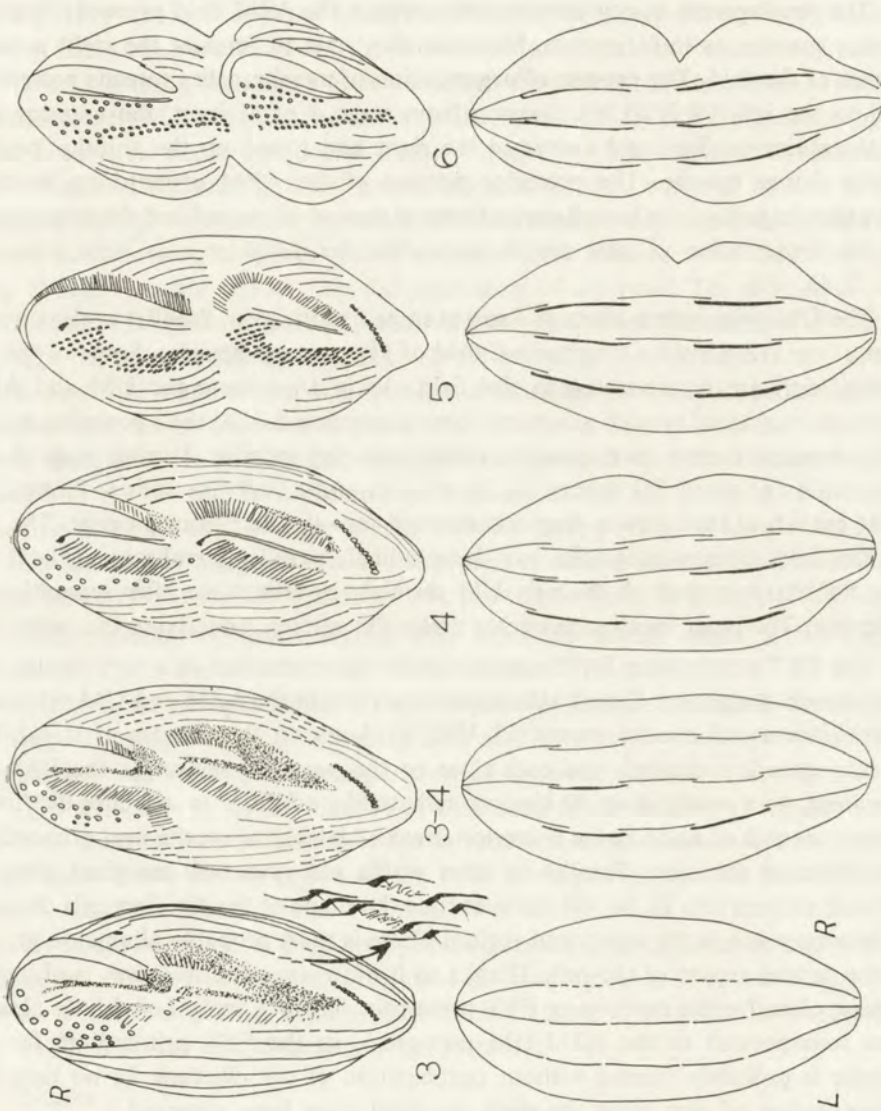


Fig. 4. Drawings of the ventral (upper row) and dorsal (lower row) surfaces of cells of *U. grandis* in stages 3-6 of preparation for division. The conventions employed are the same as those indicated for Fig. 1

considerably. Groups of new kinetosomes between old ventral cirral row can be observed. At the time the primordium grows, the old cirri from the left and later, right ventral cirral rows are incorporated to the primordium. The old cirri lose their cilia and subpellicular fibers and by stage 3 are no longer distinguishable within the field (Pl. VIII 36).

The development of new membranelles within the AZM field proceeds in a very similar manner as in *U. cristata*. Membranelles start to form at the right anterior corner of the field. The process of organization of membranelles spreads posteriorly and to the left (Pl. VIII 36). Starting from stage 4 of division, the anterior part of the membranelar band curves to the right and round up the anterior portion of the future opisthe. The posterior portion of the AZM primordium develops later than in proter, the buccal cavity forms at the end of stage 5 and the complement of the organization of new mouth ends after the daughter cells have separated (Pl. X 43, 45).

The UM primordium starts to form at stage 2 of division. Parallel to the anterior part of the AZM field a longitudinal field of kinetosomes appears. Some of the old ventral cirri are incorporated to this field. As in *U. cristata* the UM and AZM fields are very close to each other and form a common field at their posterior region. They separate during development starting from the anterior. During stage 4 differentiation of new UMs occurs. At the anterior end a fork-like split is formed, the right branch of that fork is then transformed into the first frontal cirrus. The rest of the field differentiates into two longitudinal, parallel membranes (Pl. X 45). The final arrangement of the new UM membranes take place after separation of offspring. The inner membrane curves under the surface, underlying the outer one.

The FVT primordium for the opisthe make its appearance in a very similar way as it does in the proter. Close to the anterior portion of the AZM and UM primordia a few kinetosomal streaks appear (Pl. VIII 36). Later on the process of streak formation spreads posteriorly and ends close to the posterior region of the UM primordium. As a result about 30 kinetosomal streaks originate in a ladder-like form. During stage 3 of division the posterior streaks "detach" from the oral primordium and move to the right. Parallel to them within old rows new marginal rows are induced to form (Pl. IX 38, 40). At that time the shape of the dividing cells changes. It become wider in the equatorial region. There is most probably allometric growth in the central region of the cell. Thanks to it old marginal cirral rows push apart, leaving place for the developing FVT primordia. The old ventral cirri have already been incorporated to the AZM-UM primordia, so the FVT primordium for the opisthe is probably formed without participation of old ciliature. In no time has incorporation of cirri from the right marginal rows been observed.

Differentiation of new frontal, ventral and transverse cirri from the ciliary streaks proceeds in the same way as in the proter. Anterior streaks develops into frontal cirri, posterior streaks develop into ventral cirri. The transverse cirri are formed from the distal terminations of about 12–14 posterior-most streaks.

Marginal and dorsal primordia

The marginal and dorsal primordia develop in a very similar way in proter and opisthe. The pattern of formation of marginal primordia in *U. grandis* differs signifi-

cantly from that in *U. cristata*. Marginal primordia of *U. grandis* appear as a kinetosomal streaks and some old cirri from each row participate in formation of marginal rudiments. During the stage 3 of development the cirri in the inner-most rows of old marginal cirri which are situated at the level of buccal cavity of the proter and opisthe lose their cilia and subpellicular fibers (Pl. IX 39). The constituent kinetosomes of a single cirrus change their mutual orientation, they come to assume a linear orientation and form short segments of kinetosomes. Such segments formed from a few neighbouring cirri join end-to end and form streaks. After their formation, the streaks elongate and overlap the preexisting ciliary rows. The process of streak formation takes place successively in all old marginal rows. The number of marginal streaks depends on the arrangement of old marginal cirri present in the dividing cells. Since the number and arrangement of marginal rows varies, some regulatory mechanisms can be observed in proter and opisthe as well. In adult cells the inner-most marginal row on the right margin is shorter than the rest. It starts from the middle of the cell and runs posteriorly. That means that the proter does not possess the first marginal row. During division two overlapping marginal streaks are formed within the second marginal row of the proter. A similar situation exists on the left side, where one of the old marginal rows (second or third) is shorter (Pl. X 42, 43).

Differentiation of new marginal cirri from the streaks starts at the stage 4, beginning from the anterior end of the streaks. The remainder of the marginal cirri, which do not participate in the process of streak formation, are resorbed during later stages of morphogenesis. Left and right rows which are closest to the dorsal side are resorbed after separation of daughter cells.

The primordia of dorsal kineties of *U. grandis* are formed in a very similar way as in *U. cristata*. New kinetosomes are formed within old kineties starting from the right-most kinety in two region of the cells, corresponding to the location of primordia on the ventral surface. The process of formation of new kinetosomes then occurs in the second and third kinety. New kineties grow in anterior and posterior directions, detach from the old dorsal rows and overlap them. The remaining portions of the old dorsal kineties are resorbed in later stages of division. In *U. grandis* as in *U. cristata*, no caudal cirri can be observed.

Nuclei

Nuclear phenomena which occur during division of *U. grandis* have been described by other authors (Tittler 1935, Raabe 1946, 1947). Protargol preparations utilized in this study make possible to correlate cortical events with nuclear ones. At the moment when morphogenesis starts, all of the pieces of macronucleus (about 60-90) possess replication bands (Pl. VI 27). After the replication bands pass through, each piece rounds up and the process of fusion of macronuclear segments begins. During G_2 of Ma, on the surface, the processes of formation, arrangement and primary differentiation of ciliary primordia take place. At stage 4, when the Ma

prepares itself to the first division, the process of differentiation of new cirri begins. Micronuclei divide simultaneously with the Ma. Offspring of each dividing Mi separate to different cells.

Discussion

The most important outcome of the present investigation is the clear demonstration that during division in *U. cristata* and *U. grandis* (1), both, anterior and posterior oral ciliatures are formed anew, and (2) those oral ciliatures are derived from apparently different sources. The results clearly show that old, somatic ciliature may participate in formation of oral and somatic ciliature, and also, that certain somatic cirri may differentiate from oral primordia.

The participation of preformed structures in morphogenesis of hypotrichous ciliates has been first presented in *U. weissei* by Jerka-Dziadosz and Frankel 1969. In this ciliate certain cirri undergo a process of disaggregation and reorganization to form linear arrays of ciliary units the "streak-segments", which later differentiate into new frontal, ventral and marginal cirri. In the present paper the pattern of cortical development of two other species of the genus *Urostyla* has been present. It become possible now to discuss three main questions of ciliate morphogenesis: (1) formation of primordia, (2) organization of primordial structures, and (3) the role of preexisting ciliature in morphogenesis.

Pattern of formation of primordia

There are two methods by which preformed cirri may participate in the formation of primordia. The primordia which are formed in the close vicinity of unchanged, old cirri, will be considered as the first method. To this category belong oral primordia of many studied species such as: *Kahliella*, *Opistotricha*, *Onychodromus*, *Gastrostyla*, *Stylonychia* (Tuffrau 1969, 1970, Groliere 1970). It is worth pointing out that in lower hypotrichs such as for instance *Urostyla*, *Kahliella* or *Hypotrichidium* the oral anlage appears close to the left postoral row of ventral cirri, whereas in higher *Hypotricha* such as *Opistotricha*, *Gastrostyla* and *Stylonychia* the oral anlage appears close to the left-most transverse cirrus (in both cases oral anlage is formed at the same meridian, on which the anterior mouth is situated). It should be noted however, that "stomatogenic" ventral cirri may later be incorporated to the primordium, whereas transverse "stomatogenic" cirri are never incorporated to the primordium (Tuffrau 1969, Frankel unpubl.). The primordia of the FVT primordium complex of hypotrichous ciliates in question originate also close neighbourhood of preexisting old frontal and ventral cirri, but (except in *Urostyla*) and perhaps *Kahliella* in the latter do not participate visibly in the process of primordia formation (Wallengren 1902, Hashimoto 1961, Tuffrau 1969).

The second manner of primordia formation thus far recorded only in the ciliates from genus *Urostyla* is the formation of cortical primordia with active participation of preexisting elements of the locomotory system. In *U. grandis* and *U. cristata* certain old cirri lose their subpellicular fibers and probably also cilia. Kinetosomes from basal plates lose their close packing and undergo, a transformation into an anarchic field or kinetosomal streak, with later proliferation of new kinetosomes taking place in both systems. The fate of the original kinetosomes from the dispersed basal plates is unknown. Theoretically two possibilities exist. (1) Kinetosomes may persist unchanged and during development gain new cilia and other accompanying structures depending on what complex structure they become part of (cirrus, membrane, membranelle). (2) Kinetosomes may be resorbed after dispersion and replaced by new ones, formed close to them. Since we do not possess any ultrastructural data and specific labelling method for kinetosomes, the resolving of those possibilities is so far impossible.

Organization of primordial structures

In the two species of *Urostyla* described in this paper, as well as in *U. weissei* described previously (Jerka-Dziadosz and Frankel 1969) two kinds of primordial structures can be distinguished. These are (1) kinetosomal fields, containing closely packed kinetosomes arranged in a seemingly random pattern, and (2) — kinetosomal streaks — containing close packed basal bodies arranged in a more or less longitudinal row. Kinetosomes in a streak are ciliated almost from the very beginning. Both kinds of primordial systems can be formed with — as well as — without the participation of preexisting cirri.

Oral primordia in almost all groups of *Ciliata* originate as a kinetosomal field (anarchic field) connected topographically with one or several kineties (see review of Tartar 1967). New somatic kinetosomes are formed within preformed kineties (Dippel 1968, Allen 1969, Sonneborn 1970) and can rather be considered as equivalent to a "streak".

In *U. cristata* all of primordial structures on the ventral surface originate as kinetosomal fields. Later, during development, membranelles differentiate within the AZM primordium, and two membranes differentiate within UM primordium. FVT and marginal fields form streaks and later differentiate into new cirri.

In *U. grandis* and also in *U. weissei* both kinds of primordial systems exist. Oral primordia appear as kinetosomal fields, whereas cirral primordia appear as streaks. It is worth mentioning here that in lateral fragments of *U. weissei* as well as *U. grandis* in which the left marginal cirri have been cut off, the primordium of these cirri is formed as a single kinetosomal field, whereas the FVT and right marginal primordia develop as in a normal proter (Jerka-Dziadosz, unpubl.). That means that the preformed structures somehow influence the organization of primordial structures (see also Jerka-Dziadosz 1972).

The role of preformed structures in stomatogenesis

In *U. grandis* and *U. cristata* a very interesting phenomenon occurs namely the process of formation of oral structures proceeds in a different way and with participation of different preexisting structures in different parts of the same cell at the same time.

The oral primordium for the proter of *U. cristata* originates inside the original peristome, close to inner UM, and develops under the surface. The basal bodies from both old UMs join to the primordium. During development from this primordium: new AZM membranelles, UM membranes and the first frontal cirrus differentiate. That means that the anterior mouth is formed with participation of basal bodies from preformed UMs but without participation of old cirri. On the contrary, oral primordia for the opisthe originate on the surface of the cell and with direct contact with postoral ventral cirri. The very interesting phenomenon of participation of the same cirri in the process of formation of two different primordia occurs here. The preformed cirri of the left postoral ventral row serve first as the "organization centres" for the anarchic field of the AZM primordium for the opisthe, and later, after the developed AZM primordium move away from them, they become incorporated into the UM-field. It seems that the proliferation of new kinetosomes occur twice around these cirri. A similar process takes place also in *Keronopsis monilata* during division (Janus and Jerka-Dziadosz, unpubl.). To summarize, in *U. cristata* the process of oral primordia formation is connected with the inner UM (endoral membrane) in the proter and with the left postoral cirral row in the opisthe.

In *U. grandis* participation of somatic cirri in the process of formation of both: anterior and posterior oral primordia has been described. However, in the process of formation of the anterior anlage the preexisting frontal cirri are involved, whereas in the opisthe the left ventral postoral cirral row is utilized. This situation is reminiscent of that described by Tartar (1967) for *Condylostoma* "... the formation of proter mouthparts is by a distinctly different course, involving different kinetics than those associated with the opisthal anlage" (Tartar 1967, p. 62).

The problem of recognition of the "stomatogenic kinety" in Hypotrichs remains to be discussed. Tuffrau 1969, 1970 suggested on the basis of observations on the formation of oral anlage for the opisthe in many hypotrichous ciliates, such as *Kahliella*, *Hypotrichidium*, *Gastrostyla*, *Stylonychia* and others, in which the primordium originates close to the postoral ventral row of cirri the left-most transverse cirrus, that these cirri be considered as the equivalent of stomatogenic kinetics of holotrichs and spirotrichs. He noted ... "En fait, quand les cinetosomes dont néoformes auprès du ou des cirres interessés cela ne vent pas dire que ces derniers sont par eux-mêmes stomatogenes, mais que leur presence traduit l'existence d'un certain territoires, des nouvelles structures buccales". It follows from many experimental studies (Uhlig 1960, Frankel 1960, Tartar 1961, Jerka-Dziadosz

1966, Nanney 1966, 1968) that the location of the site of primordium formation varies in relation to the preformed structures. The morphogenetically active territory is determined by its position within a new totality rather than by any fixed pre-existing ciliary elements. On the basis of an analyses of the location of the FVT primordia in several kinds of fragments of *U. weissei* it has been demonstrated, that the origin and location of the FVT primordia does not depend on the presence of the preformed cirri, which normally take part in divisional morphogenesis (Jerka-Dziadosz and Frankel 1969, Jerka-Dziadosz 1972). The question of the participation and role of the stomatogenic area of proter and opisthe in morphogenesis needs more work. The earlier observations on lateral fragments of *U. cristata* indicated that such fragments do regenerate although they possess only one kind of marginal cirri (Jerka-Dziadosz 1966). Similar fragments of *U. grandis* do not regenerate (Jerka-Dziadosz 1964 b). Three species of *Urostyla* which show such a great diversity in morphogenetic patterns seem to be a good system for an experimental analysis of the problem of transmission of cortical patterns and multidimensional information in development.

One more question remains to be discussed. In an earlier publication (Jerka-Dziadosz and Frankel 1969) it was pointed out that certain preformed structures never participate in morphogenesis (see also Frankel 1969). These are the old AZM membranelles the anterior most frontal cirri, transverse cirri and in *U. cristata* also, most of the marginal cirri (see Table 3). This lack of competence can be explained as follows: these are the most highly organized organelles and that their structure becomes fixed during ontogenesis in such a way, that they are no longer capable of gaining morphogenetic activity (Frankel 1969). Another possibility exists namely that the factor or factors which cause morphogenetic activity of definite regions of the ciliate cortex does not "reach" those fixed structures in normal development connected with cell division.

Comparative considerations

In previous study on development of *U. weissei*, the morphogenetic patterns within *Hypotrichida* has been compared. This section excludes *Euplotes* because the morphogenetic patterns in this genus are very different from those of other hypotrichs.

U. weissei represents morphogenetic pattern distinctly different from two other species (Table 4). The arrangement of dorsal kineties, their origin, the presence of caudal cirri and the lack of AZM primordium for the proter and the orientation of the cirral rows in relation to the streaks from which they form distinguish this species so clearly, that it seems that *U. weissei* should no longer remain in genus *Urostyla*. On the basis of observations on early stages of development of *Stylonychia mytilus*, made by Dr J. Frankel on protargol preparations of the latter species, can be noted that morphogenetic processes of *Stylonychia mytilus* and *U. weissei* are more similar than the processes within the genus *Urostyla*.

Table 3

Participation of preexisting ciliature in formation of primordial structures in hypotrichous ciliates (*Stichotrichina*)

Preexisting structures	<i>Urostyla cristata</i>	<i>Urostyla grandis</i>	<i>Urostyla weissei</i> *	<i>Stylonychia mytilus</i> **
Anterior AZM	—	—	—	—
Anterior frontal cirri	—	—	—	—
Transverse cirri	—	—	—	—
UMs	UM, AZM primordia and FC-1 of proter	UM, AZM primordia and FC-1 of proter	UM, AZM primordia and FC-1 of proter	UM, AZM primordia and FC-1 of proter
Frontal cirri close to UM	FVT primordium	UM primordium	FVT primordium	—
Ventral cirri	AZM, UM and FVT primordia of opisthe	AZM, UM and FVT primordia of opisthe	AZM, UM and FVT primordia of opisthe	—
Marginal cirri	one row on each side forms marginal primordial field	each row on both sides forms marginal streaks	marginal streaks	marginal streaks
Dorsal kineties	dorsal primordia	dorsal primordia	dorsal primordia for 3 rows on left side	dorsal primordia for 4 rows on left side

* Observations from Jerka-Dziadosz and Frankel 1969.

** Observations made by Dr. J. Frankel, based on protargol preparations of Strain 1 of *S. mytilus* from laboratory of Dr. Ammerman (Tübingen, GFR).

Comparing the morphogenetic processes of *U. grandis* and *U. cristata* the following similarities can be noted; (a) the beginning of morphogenesis in the late macronucleus phase S (similar as in *U. weissei* and *S. mytilus*), (b) anterior AZM and UM are replaced by new ones, (c) oral primordia for both proter and opisthe appear as a kinetosomal fields. However, there are differences in stomatogenesis between both species in question. In *U. grandis* cirri of the first frontal row are incorporated into the UM-AZM primordium for the proter, a phenomenon which was not described earlier. The cirri had differentiated in the previous generation from the FVT-complex primordium. A similar process also occur in two other species of *Urostyla* which can not be defined according to known descriptions (Janus and Jerka-Dziadosz, unpubl.).

In stomatogenesis of the opisthe of *U. grandis* and *U. cristata* there are small differences in the mode of appearance of the first kinetosomes of AZM primordium. One feature should be stressed: the morphological picture of oral primordia of the opisthe in stages 2 and 3 of *U. grandis* and *U. cristata* are extremely similar, except for the way they have originated.

Again, if one compares the well-formed primordia of FVT-complexes of *U. grandis* and *U. cristata* and neglects the mode they have appeared, one would observe quantitative differences only. In *U. grandis* 30 diagonal streaks of the FVT complex differentiate into: (1) transverse row, (2) fronto-ventral rows and a group of about 24 frontal cirri. In *U. cristata* 40 diagonal streaks of FVT complex differentiate into (1) transverse row, (2) fronto-ventral rows, plus 1 cirrus on the frontal area.

When one compares the mode by which the primordia in question have originated then the following differences would be noted: in *U. cristata* the FVT complex originate as a kinetosomal field, which in the proter begins to form from disaggregation of frontal cirrus No. 0, and in the opisthe from the right postoral ventral cirri; in *U. grandis* however, the FVT-complex originate as separate streaks of kinetosomes, which in the proter are formed in a region of the surface which lack parental cirri, whereas in the opisthe the right ventral cirri are partially incorporated to the FVT promordium.

The most distinct difference in morphogenesis of *U. grandis* and *U. cristata* is the way the marginal cirri are formed. As has been described in the result section, in *U. cristata* 7 rows of marginal cirri differentiate from a kinetosomal field, which has originated from several old cirri of only one row of the seven old marginal rows of cirri. The left marginal cirri appear within the first old left marginal row, the right within the seventh right marginal row. The remaining 12 rows of marginal cirri do not take part in normal divisional morphogenesis.

The marginal cirri in *U. grandis* appear in a distinctly different way. They originate as a kinetosomal streaks closely related, topographically with each of the old marginal rows of cirri. The first right marginal streak of the proter and opisthe appear exactly at the level of the posterior-most streak of the FVT complex and

Table 4
Comparison of developmental patterns in hypotrichous ciliates

New structures	<i>Urostyla cristata</i>	<i>Urostyla grandis</i>	<i>Urostyla weissei</i> <i>Stylonychia mytilus</i> *
Anterior AZM	primordia appear within inner UM membrane in the buccal cavity	primordia appear within inner UM membrane in the buccal cavity	persists unaltered
Anterior UMs	differentiate from field derived from disaggregation of old UMs	differentiate from field derived from disaggregation of old UMs and first row of frontal cirri	differentiate from field derived from disaggregation of old UM UMs
Posterior AZM and UMs	primordia incorporate ventral cirri	primordia incorporate ventral cirri	primordia incorporate one row of ventral cirri**
First frontal cirrus	develops from right anterior portion of UM field	develops from right anterior portion of UM field	develops from right anterior portion of UM field
FVT cirri other than FC-1	develop from about 40 diagonal streaks, differentiated in FVT field	develop from about 30 diagonal streaks	develop from 5-7 longitudinal streaks
Marginal cirri	develop from fields formed within one old marginal row on each side	develop from streaks formed in each old marginal row	develop from streaks formed in each old marginal row
Caudal cirri	No CC present	No CC present	develop from posterior ends of new dorsal kineties
Dorsal cilia rows	develop within old kineties and later replace them	develop within old kineties and later replace them	partly develop within old kineties and partly formed on right margin

* Observations made by Dr. J. Frankel, based on protargol preparations of strain 1 of *Stylonychia mytilus* from the laboratory of Dr. Ammerman (Tübingen, GFR).

** In *S. mytilus* AZM primordium for the opisthe appears close to the left-most transverse cirrus (Tuffrau 1969) and does not incorporate any ventral cirri.

parallel to it. The first left marginal streak originate at the same level as the first right one. The others marginal streaks appear in a medio-lateral sequence.

From the above considerations the general conclusion follows that maintaining of *U. grandis*, *U. cristata* and *U. weissei* in one genus is by all means artificial. In addition to the morphological differences there are differences in morphogenetic patterns which are not limited to the topography of primordia, but the differences appear also in the source of the initial material (preexisting structures) and in the pattern of its transposition into the primordial structure.

As it has been suggested by authors (Corliss 1967, 1968 Corliss and Roque, 1967, Small 1967, Borrer 1970 in addition to careful study on interclonal variability, morphogenetic patterns should be taken in consideration when natural systems of lower taxonomic units are considered.

It follows that the present taxonomic categories within the *Hypotrichida* are no good. The relationships of some ciliates formerly (Faure-Fremiet 1961) put in separate suborders may turn out to be much closer — namely *U. weissei*, *Stichotrichina* and *Stylonychia* (*Sporadotrichina*), while it seems that *U. weissei* and *U. grandis*–*U. cristata* should be in separate families, not only separate genera.

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Summary

The study of the early stages of development of oral and cirral primordia in *Urostyla cristata* Jerka-Dziadosz and *Urostyla grandis* Ehrbg. has been carried out, using the protargol technique. In both species anterior and posterior oral ciliatures are formed anew from different sources. The old somatic ciliature participates extensively in the formation of oral and cirral primordia.

In *U. cristata* all types of primordial structures on the ventral surface originate as kinetosomal fields. During development the FVT and marginal fields form kinetosomal streaks and later differentiate into new cirri. In *U. grandis* oral primordia appear as kinetosomal fields, whereas cirral primordia appear as streaks. In both species the anterior oral primordia are formed with participation of the inner undulating membrane of the preformed mouth.

On the basis of the description the problems of pattern of primordia formation, organization of primordial structures and the role of preexisting ciliature in morphogenesis are discussed.

STRESZCZENIE

Przeprowadzono badania porównawcze wczesnych stadiów rozwoju zawiązków oralnych, cirri i rzęsek grzbietowych u *U. grandis* Ehrbg. i *U. cristata* Jerka-Dziadosz, stosując barwienie protargolem. U obu gatunków orzęsienia oralne protera i opistora tworzą się od nowa. W obu komórkach potomnych wykorzystywane są inne elementy starego orzęsienia. Preformowane orzęsienie somatyczne w znacznym stopniu bierze udział w morfogenezie zarówno zawiązków oralnych jak i zawiązków cirri, natomiast z już wytworzonych zawiązków oralnych mogą różnicować się cirri.

U *U. cristata* wszystkie rodzaje zawiązków powstają w postaci pól kinetosomalnych, w trakcie rozwoju pola frontально-wentralno-transwersalne (FVT) różnicują się w paski rzęskowe, a następnie w cirri.

U *U. grandis* zawiązki oralne tworzą się w postaci pól kinetosomalnych, natomiast zawiązki cirri powstają jako paski kinetosomalne.

U obu gatunków przednie zawiązki oralne tworzone są z udziałem wewnętrznej membranelli undulans (UM).

Na podstawie opisów dyskutuje się zagadnienie sposobów tworzenia zawiązków, organizację struktur zawiązkowych oraz znaczenie preformowanego orzęsienia w morfogenezie.

Przeprowadzono porównanie wzorców morfogenetycznych u *Hypotricha*; stwierdzono, że dotychczasowe kategorie taksonomiczne są sztuczne i wymagają rewizji.

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Note added in the proof

Since the paper has been submitted for publication a paper of dr A. Borror appeared (Borror A. 1972: Revision of the order *Hypotrichida* (*Ciliophora*, *Protozoa*). *J. Protozool.*, 19, 1-23). The paper contains new systematic position of *Urostyla grandis* Ehrbg. *U. cristata* Jerka-Dziadosz and *U. weissei* Stein. According to this *U. grandis* remains in the family *Urostylidae* Butschli. *U. weissei* remains also in *Urostylidae* but has been put to new genus *Paraurostyla* Borror. *Urostyla cristata* has been put to the family *Holostichidae* Fauré-Fremiet in a newly formed genus *Pseudo-urostyla* Borror.

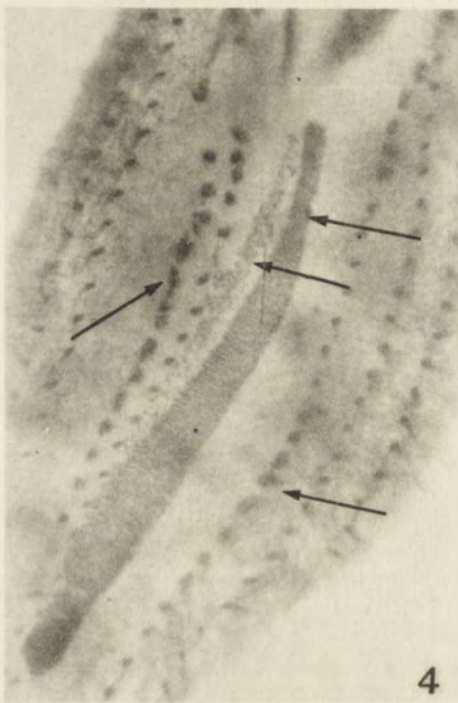
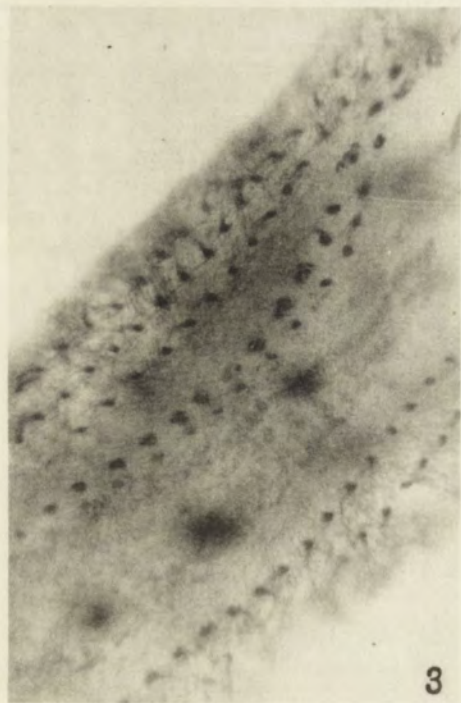
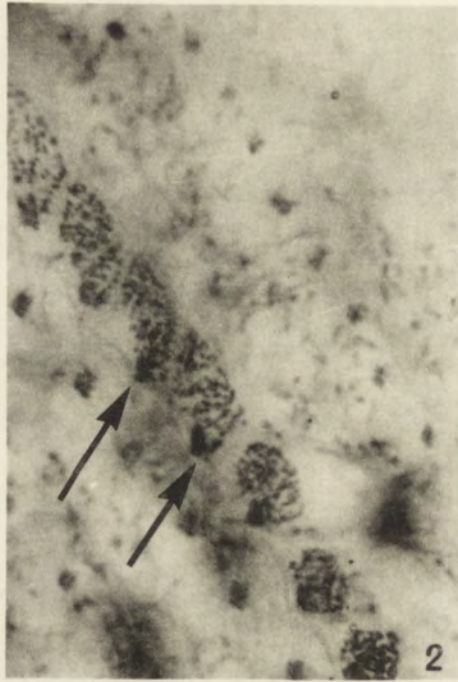
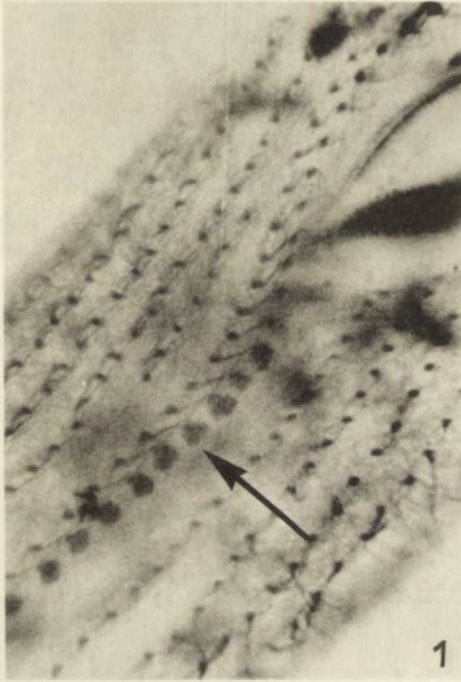
EXPLANATION OF PLATES I-X

Urostyla cristata Jerka-Dziasosz. Protargol impregnated specimens engaged in cortical morphogenesis associated with cell division. All photographs are printed in the same magnification and so that the anterior end is up and the animals left corresponds to the viewers right. The magnifications (in parentheses) indicate that of the microscopic objective.

- 1: The oral primordium (arrow) for the opisthe of a cell in stage 1 of development (40×)
- 2: High magnification of an oral primordium for the opisthe. The arrows indicate the old ventral cirri (100×)
- 3: The oral primordium for the opisthe in late stage 2 of development. Note the wide kinetosomal field to the left of old ventral cirral rows (40×)
- 4: The oral and cirral primordia for the opisthe in early stage 3 of development. The upper right arrow indicates the AZM primordium, the middle right arrow indicates the UM primordium, the lower right arrow indicates the old marginal cirri being disaggregated and engaged in the formation of marginal field. The left arrow indicates the FVT field for the opisthe being formed from old ventral cirri (40×)
- 5: An interdivisional specimen. The arrow indicates FC-0 (40×)
- 6: Anterior part of the cell in stage 2 of division. The upper arrow indicates the disaggregating FC-0. The lower arrow indicates the AZM primordium for the opisthe (40×)
- 7: The oral primordium for the proter in stage 2 of development. The arrow indicates the UM-field being formed close to the inner UM (100×)
- 8: The same specimen as on phot. 7 in different focus. The left arrow indicate the forming FVT field the right arrow indicates the UM field out of forms (100×)
- 9: The oral and FVT primordium for the proter in stage 2 of division. The inner UM is dispersed and forms a field going down inside the peristome. The outer UM is in the process of disaggregation. The arrow indicates the FVT field. Note that the old frontal cirri which are to be incorporated to the FVT field have lost their fiber rootlets (below the arrow) (100×)
- 10: The same specimen as phot. 9 focussed on the inner part of peristome. The right arrow indicate the edge of old AZM the left arrow indicates the "pocket" of kinetosomes in the extension of the UMs. In the cytoplasm around the mouth the rounded-up macronuclei can be seen (100×)
- 11: The oral primordium for the proter in stage 2 of development. The arrow indicates the UM-field (100×)
- 12: The oral primordium for the proter. UM-AZM kinetosomal pocket inside the cell (100×)
- 13: The same specimen as on phot. 12 focussed on the ventral surface. The upper arrow indicates the developed FVT field. The lower arrow indicates the site of the anterior UM-AZM primordium under the pellicle (40x)
- 14: The developing anterior FVT primordium at stage 3. Kinetosomal streaks are being formed (arrow). The UM field is seen in the center of the photography (100×).
- 15: The anterior UM and FVT primordium in stage 4 of development. FVT streaks are developed. The arrow indicates the fork-like branching in the anterior part of the UMs-field (100×)
- 16: Posterior oral and FVT primordia at stage 4 of development. Note the close vicinity of the FVT streaks and UMs (arrow) (100×)
- 17: The right marginal field of the opisthe at stage 3 of development. Note the second old marginal row unchanged (100×)
- 18: The developing right marginal field stage 3-4 of development. The upper arrow indicates the differentiating new cirri within the streaks in the right anterior corner of the field. The lower arrow indicates loose kinetosomes in the left posterior portion of the marginal field (100×)
- 19: The dividing specimen at stage 4 of division. The upper arrow indicates the right marginal cirri primordium, the lower one indicates the proximal end of the anterior oral primordium, next to it to the left the condensed Ma and Mi in prophase can be seen (40×)
- 20: Dividing cell at stage 3 of development. The arrow indicates the beginning of formation of the right marginal field (40×)
- 21: Differentiation of new frontal cirri within anterior FVT streaks. Note the frontal cirrus (arrow) formed within the UM-field (100×)
- 22: Proter at stage 5 of development. The proximal end of the AZM as now on the surface, surrounded by loose kinetosomes (40×)
- 23: Opisthe at stage 5 of development. Note the position of (arrow) FC-0 (40×)
- 24: Dorsal bristles of non-dividing cell surrounded by mucocysts (100×)
- 25: The primordia of dorsal kineties at stage 3 of development (100×)
- 26: The dividing cell of *U. cristata* at stage 3 of division stained with iron hematoxylin after Parducz. The kinetosomes of the UM-AZM primordium are not seen (100×)

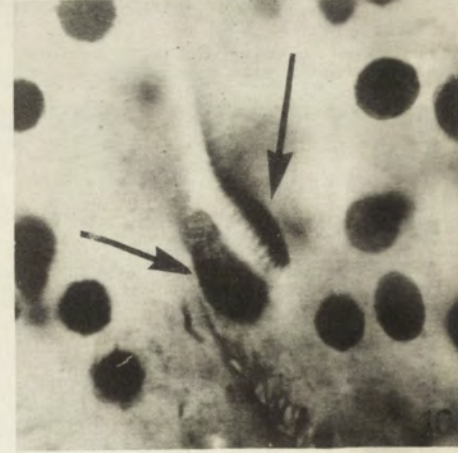
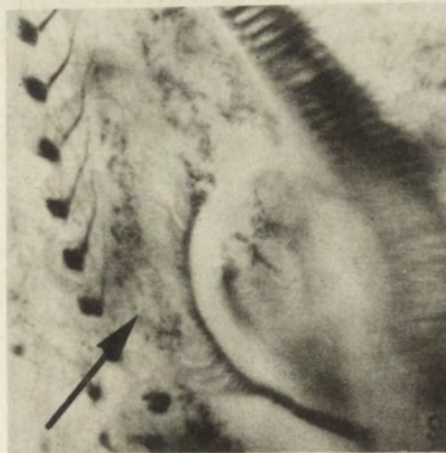
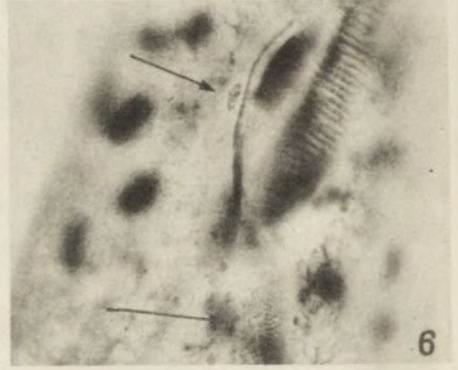
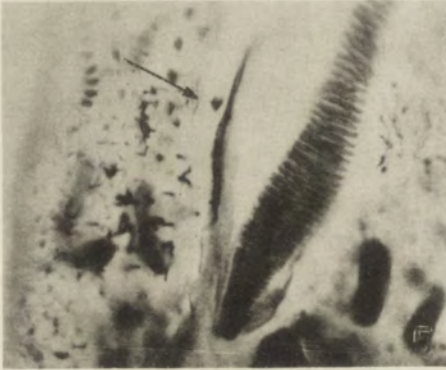
Urostyla grandis. Ehrbg. Protargol impregnated specimens engaged in cortical morphogenesis associated with cell division. The conventions employed are the same as those indicated for the preceding plates.

- 27: The macronuclei of the cell of *U. grandis* at stage 1 of division. The replication bands in the Ma can be seen
- 28: The AZM primordium for the opisthe of a cell in stage 1 of development (40×)
- 29: The AZM primordium for the opisthe of a cell in stage 1 of development (40×)
- 30-32: The anterior oral primordium of a cell at stage 2 of development at different focal levels. Note the distention of posterior end of the UM-field left arrow phot. 31, and the process of resorption of old AZM membranelles (right arrow, phot. 31) (100×)
- 33: The anterior oral primordium at stage 2 of development, the arrow indicates the disaggregating old frontal cirri which will be incorporated to the UM-field (40×)
- 34: Ventral surface of the dividing cell at stage 3 of development. The FVT streaks are forming. The arrow indicates the position of the anterior oral anlage behind it the posterior oral and FVT anlage is seen (40×)
- 35: The same cell as on phot. 34 focussed on the anterior AZM primordium. The left arrow indicates the UM-AZM primordium, the right arrow indicates the proximal portion of the old AZM being resorbed (40×)
- 36: The oral and FVT primordia for the opisthe at stage 3 of development. Note the close vicinity of the posterior part of FVT steaks and the UM-AZM primordia (40×)
- 37: The oral primordia for the proter at stage 3-4. The kinetosomal field join the old AZM membranelles. The rounded-up macronuclei in cytoplasm can be seen (40×)
- 38: The right marginal primordia of a cell at stage 3 of division. The arrows indicate the first marginal streaks for proter and opisthe. The FVT primordia are not in focus (40×)
- 39: An enlarged photograph of the right marginal streak of the proter. Note that the old marginal cirri which will form the streak (arrow) have no fibers (100×)
- 40: The developed FVT primordium for the opisthe at stage 4 (100×)
- 41: The differentiation of new cirri. The transverse cirri are derived from the posterior terminations of the posterior FVT streaks. Note the two UMs lying close to each other (100×)
- 42: Differentiation of new FVT and left marginal cirri in proter at stage 4-6 of division (40×)
- 43: Differentiation of FVT and left marginal cirri in opisthe at stage 5-6 division. Note the overlapping new rows of left marginal cirri (40×)
- 44: Differentiation of FVT and right marginal cirri in proter. Old frontal cirri not yet resorbed are seen in the anterior-right portion of the cell (40×)
- 45: Opisthe after separation. Note the two parallel UMs (40×).



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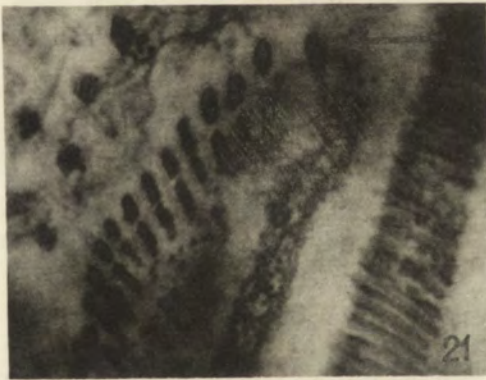
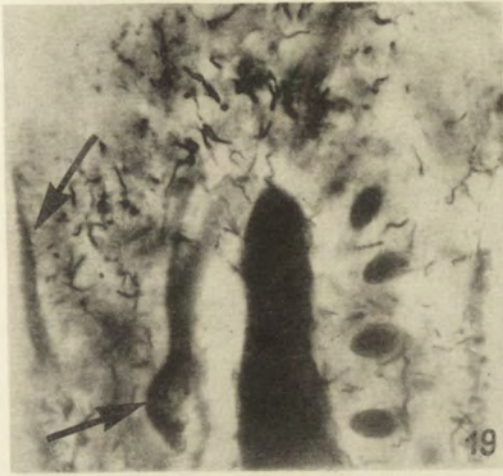
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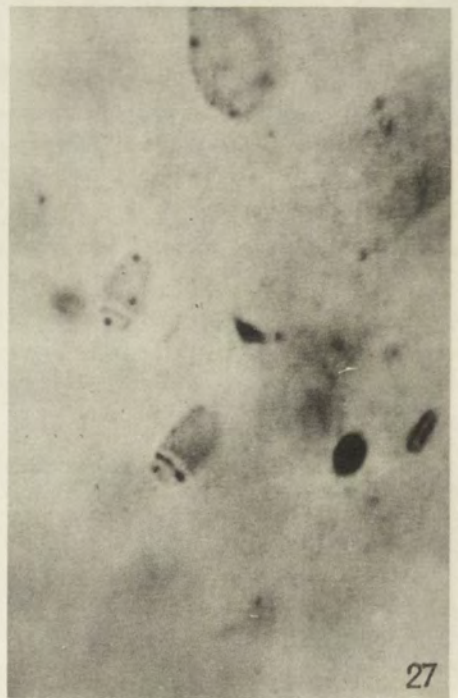
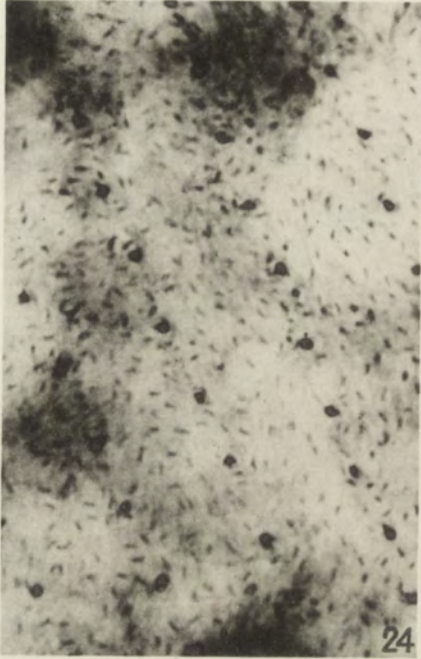
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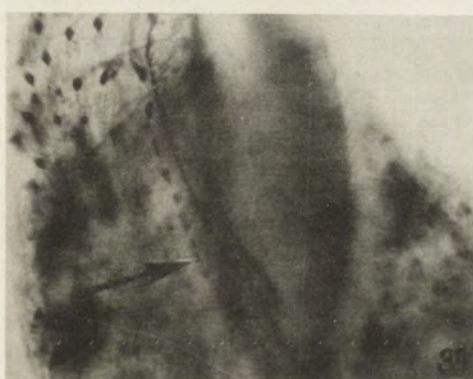
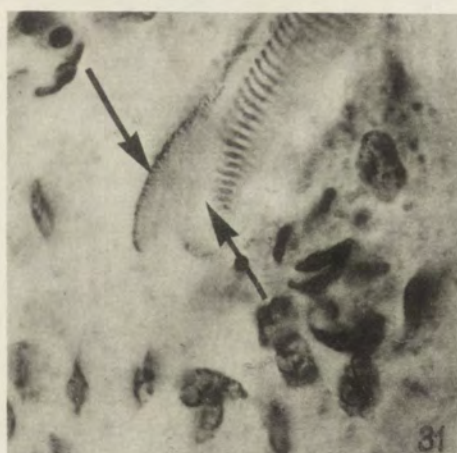
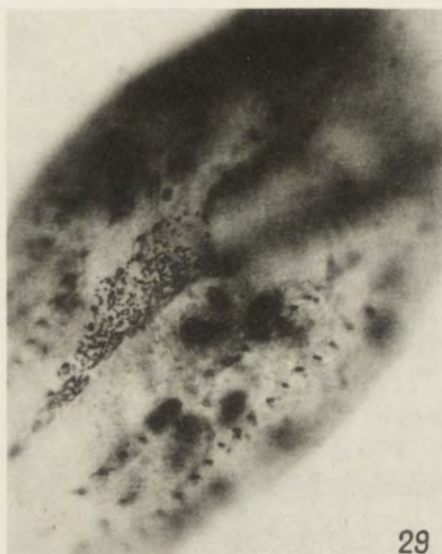
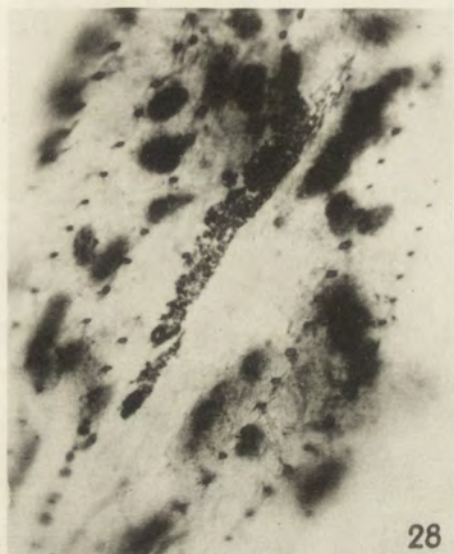
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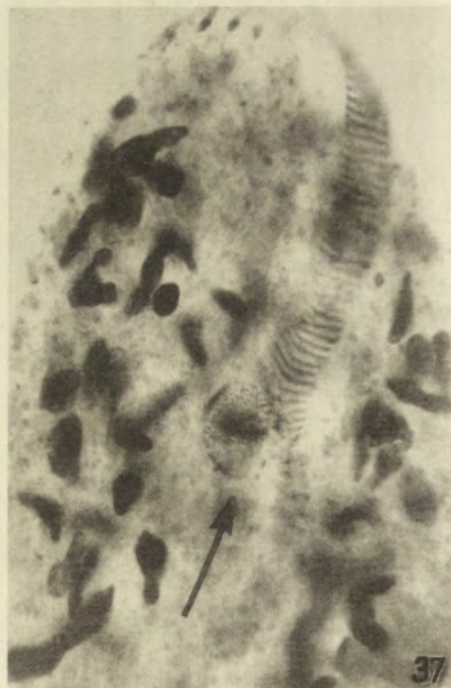
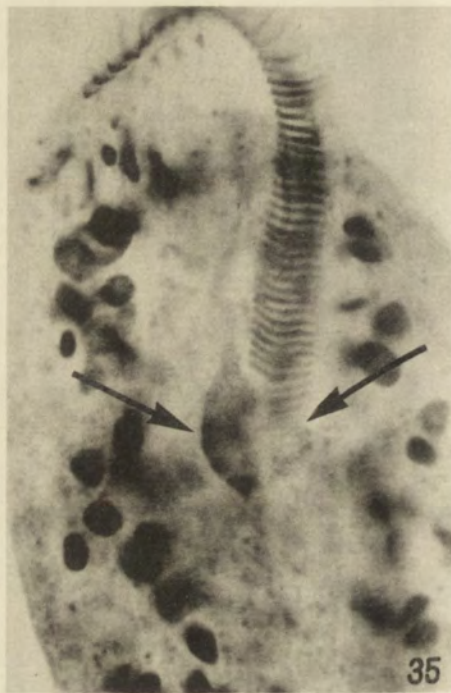
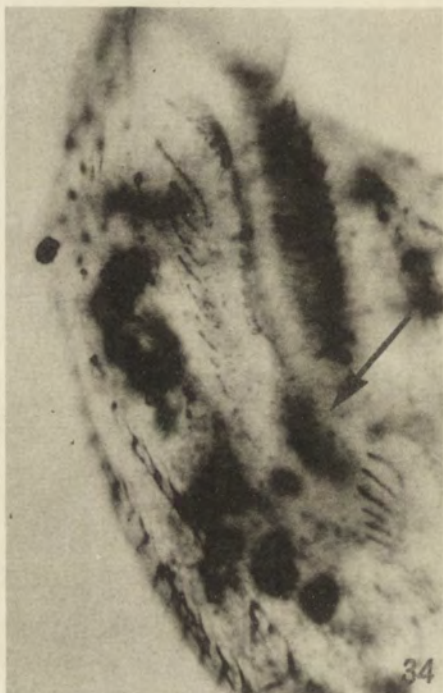
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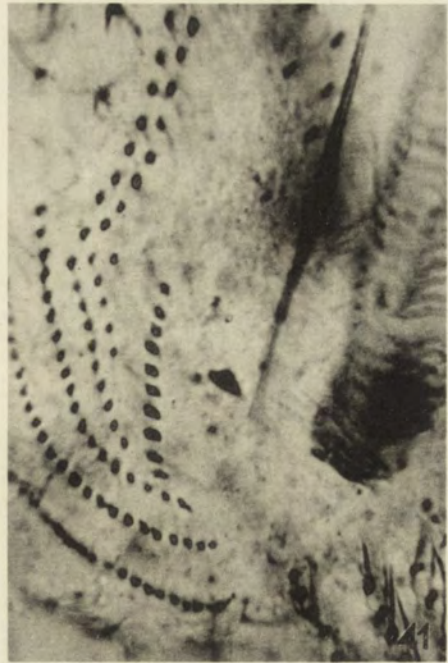
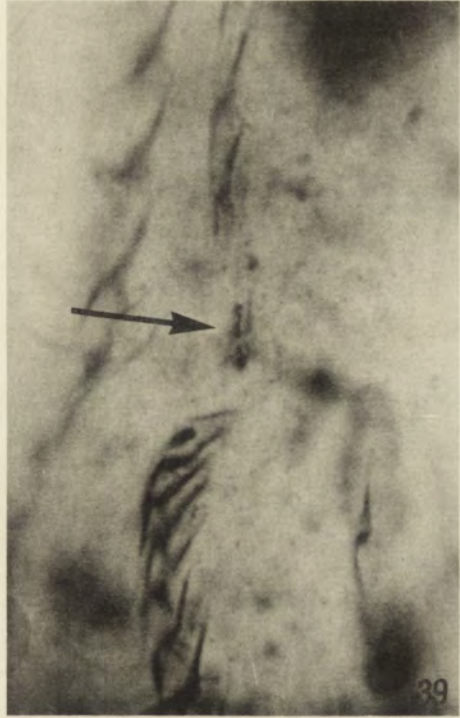
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A. R. KASTURI BAI and S. V. TARA

Studies on temperature induced division synchrony
in *Blepharisma intermedium*Studien über die Temperatur induzierte Synchrone Zell-teilung
in *Blepharisma intermedium*

Methods for inducing synchrony in protozoans are of importance as cell synchrony is finding increasing use with molecular biologists, cell biologists and developmental biologists who seek to understand cell division and cell specialization. Synchronous cells are also popular for cell physiologists and have been used for a variety of physiological experiments in which uniform testing material is required. In synchronous cultures the burst in cell division is the most apparent evidence of synchrony. Microorganisms like bacteria and protozoans form useful material for studies in synchrony and have been widely investigated. Among the different methods employed, temperature and light induced synchrony are of great importance. In the present investigation synchrony in division has been induced in *Blepharisma intermedium* Bhandary by temperature treatment. The cytochemistry of *Blepharisma* is described during the warm and cold treatment to find out whether the burst in cell division is reflected in a change in cell metabolism and cytochemistry of the ciliate.

Materials and methods

Pure culture of *Blepharisma intermedium* Bhandary grown in hay infusion fortified with horlicks was exposed to temperature shocks. Two methods were adopted — with the first method there were two temperature shifts — (1) from room temperature 26°C to cold 12°C for 95 h and 176 h and (2) from cold 12°C to warm 38°C for 17 h. With the second method, there were three temperature shifts (1) from room temperature 26°C to cold 12°C for 45 h and 72 h, (2) from cold 12°C to warm 38°C for 5 h and 24 h respectively, (3) from warm 38°C to room temperature 26°C for 14 h.

As the synchronous division was maximum in the first experiment, cytochemical investigations were made on ciliates acclimated to both cold and heat shocks for 95 h and 24 h respectively. Cytochemistry of the ciliates acclimated only to cold 12°C for 95 h and also of the ciliates grown at room temperature 26°C was studied without exposing them to heat shocks.

Both the acclimated ciliates and the normal ciliates were stained back to back to maintain identical experimental conditions. Carbohydrates and glycogen were tested by the PAS reaction (Pearse 1968), basic proteins by the mercury bromophenol blue (Ray and Hazra 1963) unsat-

urated lipids by Sudan black B (Baker 1946) sulfhydryl group by ferric ferricyanide method (Pearse 1968). The enzymes alkaline and acid phosphatases were tested by Gomori's technique (1957), succinic dehydrogenase by the method of Nachlas 1957 and urease by the method described by Sen 1930. Adequate controls were maintained for all the tests.

Observations

Ciliates grown at room temperature 26°C were pear shaped and bright pink in colour. At 12°C, there was change in the shape, but not in colour. They were more elongated and slender. At 38°C (after the cold shock) the ciliates were smaller and stouter than at room temperature. The ciliates regained their normal size and colour when they were allowed to recover at room temperature after the heat shock.

Division burst occurred 17 h after the onset of warm period in the first two experiments while in the third and fourth experiments, it occurred 14 h after the

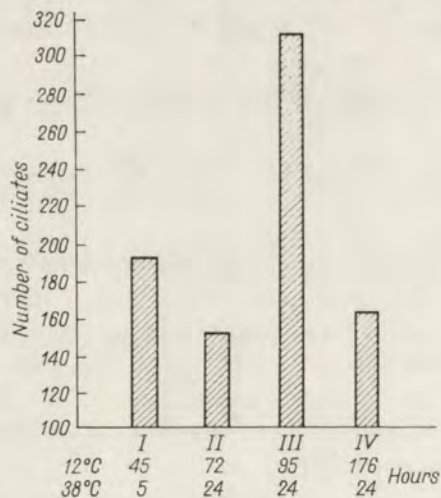


Fig. 1. The mitotic index of the four different experiments

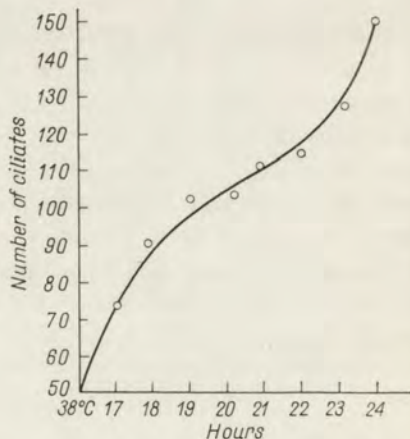


Fig. 2. The number of doublings that occur at intervals of one hour after the mitotic trigger is released starting from 17 h to 24 h during the warm period

cultures were kept to recover at room temperature. The mitotic index for the four experiments is given in Fig. 1. Maximum division synchrony was observed in the ciliates exposed to 12°C for 95 h and then transferred to 38°C. Figure 2 shows the number of doublings that had occurred at intervals of one hour after the mitotic trigger is released starting from 17 h to 24 h during the warm period.

Results of the cytochemical tests made on *Blepharisma* at 12°C and 38°C and room temperature are summarized in Table 1. There is positive reaction for all

Table 1
Cytochemistry of *Blepharisma intermedium* at different temperatures

	PAS	Mercury bromophenol blue	Ferric ferri-cyanide	Sudan black B	Succinic dehydrogenase	Alkaline phosphatase	Acid phosphatase	Urease
At 26°C								
Cytoplasm	±	+	±	±	+	+	±	±
Macronucleus	-	+++	-	-	-	±	+	-
Basal granules	++	++	-	-	±	±	-	+
Peristomial region	++	+++	±	±	±	-	+	+
Region surrounding the macronucleus	++	+	++	±	+	+	±	±
At 12°C								
Cytoplasm	+	++	+	+	++	++	±	±
Macronucleus	-	+++	+	-	-	+	-	-
Basal granules	++	++	±	+	+	+	+	+
Peristomial region	++	+++	+	+	+	+	+	+
Region surrounding the macronucleus	++	+	++	+	++	+	±	±
At 38°C								
Cytoplasm	++	++	+++	+	+++	±	+	±
Macronucleus	-	+++	±	-	-	+	-	+
Basal granules	+	++	±	+	++	+	±	+
Peristomial region	++	+++	++++	+	++	+	-	+
Region surrounding the macronucleus	+++	++	+++	+	++++	-	+	±

- Negative; ++ Strong; ± Weak; +++ Very strong; + Positive; ++++ Intense

the tests at the three temperatures but the intensity of the staining reactions differ indicating that there are considerable differences in the quantity of reacting substances present. Large amounts of proteins, carbohydrates, lipids and sulfhydryl groups are present and enzymatic activity is maximum at 38°C. Pl. I 1, 2, 3 show the localization of proteins, Pl. I 4, 5, 6 sulfhydryl groups at room temperature, 12°C and 38°C respectively. Pl. I 7 shows thiol accumulation during cytotomy. At 12°C these substances are more than the quantity present at room temperature, but less than the amount present at 38°C.

Discussion

Adaptations of organisms to the thermal state of the environment is related to change in their morphology and physiology (Kasturi Bai et al. 1969). The two manifestations of life-growth and reproduction are sensitive to temperature and are two separate phenomena. Processes of cell growth and processes leading to cell division may function simultaneously with their own characteristic rates indicating separate but interdependent processes (Scherbaum 1957). These two processes can be synchronized by exposing cells to alternate cold and heat shocks.

Methods for obtaining synchronous cultures have been summarized by James 1966. He distinguishes two different types of synchrony: (1) cycle oriented, and (2) division oriented. Division synchrony can result from cycle synchrony. The primary purpose of division oriented synchrony is the production of simultaneous cell divisions irrespective of the kind and duration of treatment that is necessary to bring about this result. In this investigation an attempt has been made to establish conditions of temperature acclimation that will produce the highest possible degree of synchronism in cell division. Emphasis is also laid on the evaluation of changes in the chemical constituents of the cells in connection with the temperature treatment and synchronized cell division. The two temperatures, 12°C and 38°C were chosen for definite reasons. It was found that a temperature of 12°C favoured cell growth and blocked fission. In an earlier investigation (Kasturi Bai et al. 1969) it was established that in the warm range fission was blocked in the ciliate at 38°C. Keeping these two temperatures constant, four different experiments were devised. In two experiments, exposure time to cold temperatures were altered (95 h and 176 h), maintaining the exposure time to warm temperature constant with only one temperature shift, cold to warm. In the other two experiments, the organisms were exposed to cold and heat shocks for different periods (45 h and 72 h at 12°C and 5 h and 24 h at 38°C) and then allowed to recover at room temperature. In these, there were two temperature shifts—from cold 12°C to warm 38°C and then to room temperature 26°C. The release mechanism responsible for division burst steps in at different times in the four experiments. In the first two experiments, the mitotic trigger or the release mechanism stepped in during the warm period 38°C. In the third and fourth experiments, this release mechanism stepped in at room temperature.

The synchronized *Tetrahymena* systems (Zeuthen 1964) demonstrate striking cases of dissociation between growth and division. Lower temperatures favour cytoplasmic growth rather than cell division (Padilla et al. 1966). During the synchronization with heat, there is continued though reduced rate of growth but no division. During the synchronous division, there is reduced rate of growth and increased rate of division. Results of our investigation on *Blepharisma* are similar to the *Tetrahymena* systems. At 12°C, *Blepharisma* is larger in size and large quantities of proteins, carbohydrates, lipids, thiol groups and enzymes are present, but there is no division.

Cytophysiological study of temperature adaptations of some free living ciliates show that the pattern of cell metabolism varies with changes in temperature (Polzansky et al. 1965). In *Paramecium caudatum* there are alterations of both cytoplasmic proteins, reserves of glycogen and neutral lipids decrease more markedly at 25–28°C than at 4–10°C. In *Tetrahymena* there is suppression of both RNA and protein accumulation at 34°C and 43°C. With the cytochemical techniques used, quantitative changes in proteins, carbohydrates, lipids, thiol groups, enzymes—alkaline and acid phosphatases, urease and succinic dehydrogenase could not be

determined in *Blepharisma* acclimated to 12°C and 38°C. However, it is known that the amount of colour developed by the reaction depends on the amount of reactive substances present (Pearse 1968). As the tests were carried out under identical conditions with adequate controls, the differences noticed in the intensity of the staining reactions could be due to differences in the quantities of reacting substances present in the cell. The staining reactions at 12°C are stronger than at room temperature, but at the same time they are weaker than at 38°C.

It is known that cellular processes like cytokinesis operate most effectively within a narrow temperature range, where as other processes, largely comprising cytoplasmic functions continue throughout the entire physiological temperature range of a cell (James 1966). In *Blepharisma intermedium* during the cold period though large quantities of the above mentioned substances are present, division does not occur and 12°C may not permit division.

Rapkin 1931 was the first to set forth the sulfhydryl theory of mitosis and the importance of thiol groups in cell division has been emphasized by Mazia 1959 and Nickerson 1959. Extensive evidence has accumulated to suggest that for division, proteins rich in SH groups are necessary and are synthesized at the end of the warm period in *Tetrahymena* (Zimmerman 1969). Plate I 7 shows concentration of proteins rich in SH groups round the macronucleus when cytotomy is taking place at 38°C. At 12°C such a concentration is not present. Added to this, the succinic dehydrogenase activity is maximum at 38°C showing that the rate of respiration is more than at 12°C and conditions are optimum for fission.

There is an universal pattern of biochemical events underlying cell division. Discussing the specificity of synchronizing agents, James 1966 made it clear that in most temperature induced systems, the DNA synthesis period is inhibited or delayed by the cold phase and is reinitiated by the warm phase, but the temperature changes cannot be interpreted as specific agents, in that one cannot expect their effects to be confined to one or a few such components. At the time the mitotic trigger is released in *Blepharisma* at 38°C, requisite quantities of carbohydrates, proteins, lipids, thiol groups, enzymes — phosphatases, succinic dehydrogenase and urease are present and hence fission rate is maximum.

Investigations are in progress to induce synchronous division in *Blepharisma intermedium* grown in axenic medium (Smith 1966) with temperature shocks and quantitative estimations of the different cell components will be made by biochemical methods.

Acknowledgement

Our grateful thanks are due to Prof. K. Pampapathi Rao, Head of the Department of Zoology, Central College, Bangalore University, B'lore, for his kind encouragement.

Summary

Synchronous division has been induced in the ciliate *Blepharisma intermedium* by exposing them to temperature shocks. Cytochemistry of the ciliates acclimated to the different temperatures has been studied for an evaluation of the changes in the chemical constituents of the cells in connection with temperature treatment and synchronized cell division.

ZUSAMMENFASSUNG

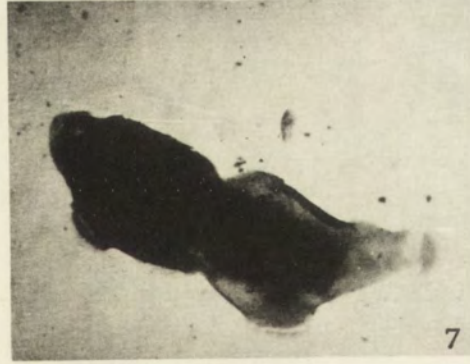
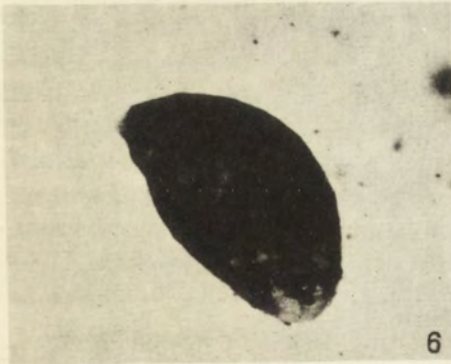
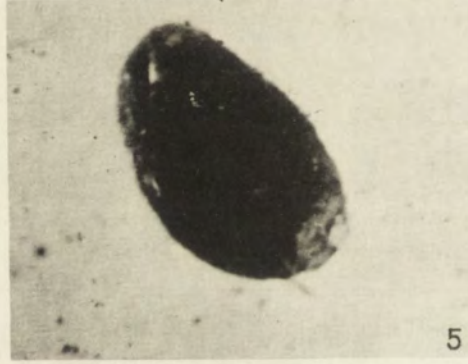
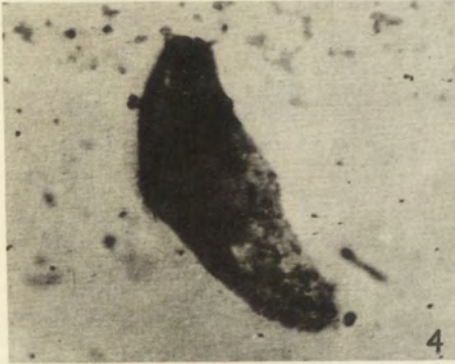
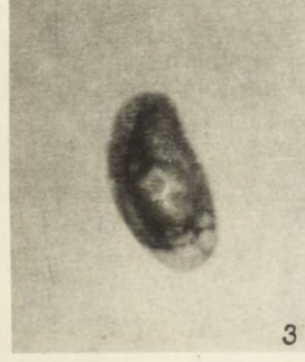
Synchrone Zellteilung wurde in *Blepharisma intermedium* aus der Klasse der Ziliaten herbeigeführt, indem man sie Temperaturstößen aussetzte. Die Zytochemie der an die warmen und kalten Temperaturen akklimatisierten Ziliaten wurde untersucht, um die Veränderungen in den chemischen Komponenten der Ziliaten in Zusammenhang mit den Temperaturstufen und der synchronen Zellteilung zu bestimmen.

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EXPLANATION OF PLATE I

- 1: The localization of proteins in *Blepharisma* grown at room temperature
- 2: The localization of proteins in *Blepharisma* acclimated to cold 12°C for 95 h
- 3: The localization of proteins in *Blepharisma* exposed to temperature shock — cold 12°C for 95 h and warm 38°C for 24 h
- 4: The localization of sulfhydryl groups in *Blepharisma* grown at room temperature
- 5: The localization of sulfhydryl groups in *Blepharisma* acclimated to cold 12°C for 95 h
- 6: The localization of sulfhydryl groups in *Blepharisma* exposed to temperature shock — cold 12°C for 95 h and warm 38°C for 24 h
- 7: The localization of SH groups at 38°C in *Blepharisma* during cytokinesis



A. R. Kasturi Bai and S. V. Tara

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Marek DOROSZEWSKI

The responses to bisections of dividing *Dileptus cygnus*Reakcje dzielącego się *Dileptus cygnus* na przecięcia

The problem of ciliate division presents structural and functional aspect as well.

The division morphogenesis had been described in a number of papers and a general picture of it becomes outlined although we are far from its exact understanding. In many morphogenetical studies the behaviour of ciliate in the course of division was mentioned as e.g., its loss of motility. However, the experimental study of formation of the new functional entity are very rare. The time of onset and character of activity of the new structures have not been studied neither was the moment of functional division of the ciliate. The morphogenetic studies have got ahead of those of the ciliate behaviour in division and may serve as a base of their research. The close relation of the two aspects of division problem — the structural and the functional — should be stressed. Movement surely plays an important role in the final separation of individuals. Golińska and Doroszewski 1964 ascertained the ciliary reversal in the posterior individual of *Dileptus anser* in the moment of conclusive separation. The studies of Seravin 1962 a, b on *Spirostomum* should be mentioned. He applied puncture with microneedle at different places of *Spirostomum* body prior to the moment of fission of two individuals. The essential result of his experiments was that *Spirostomum* responds as an entity till the moment of fission.

In the present study the bisection of the individual into two parts was performed and the movement of the arising fragments — as response to the operation — was observed. This proved to be either a forward or a backward movement. The experimental problem put forward in this research was to ascertain at which moment a new functional entity arises in the dividing individuals, i.e., when the new zones of reactivity to section appear in the dividing individuals. This might be looked upon as an certain indicator.

In the previous publications concerning the action of mechanical stimuli in *Dileptus*, the existence of two areas of response has been stated (Doroszewski 1963, 1965, 1970).

The "backward response area" is situated in the anterior body part and its stimulation evokes retreat. The "forward response area" is in the posterior body part and its stimulation evokes a forward movement. The manner of differentiation of those areas in division is the subject of the present research.

Material and methods

The studies were carried out on *Dileptus cygnus* Clap. et Lachm. Its motility is moderate: the protozoan is mostly lying at the bottom of container. This position provides conditions convenient for experimenting. Protozoa were cultivated in the Pringsheim's medium and fed with *Colpidia* and *Tetrahymenae*. For gaining dividing individuals, feeding was performed 24 h prior to experiment. The dividing individuals were fished out of the culture and placed on a concave slide in a drop of water rimmed by parafin oil. For section the knife made of steel needles were used. Observations were carried out under a binocular microscope. Every section was repeated approx. 100 times.

Results

Sections were carried out at various division stages, starting with one just beginning to appear. Sections performed at the initial stages of division gave similar results, therefore only the experiments on one of the final stages of division will be described.

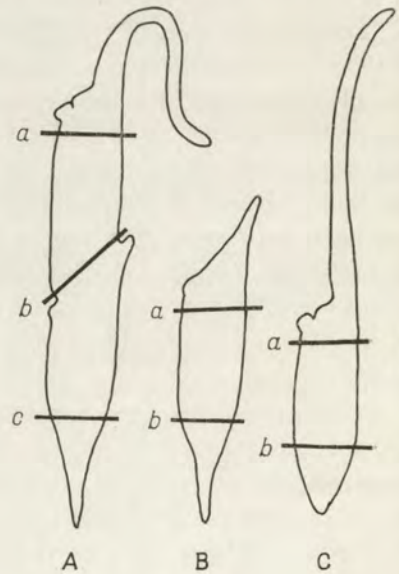


Fig. 1. Sections executed on the dividing *Dileptus cygnus*. A — Individual before division; *a* — section of proter on the level of cytostome, *b* — section along the division line, *c* — section of opisthor in the posterior part of body; B — Opisthor immediately after division, *a* — section behind the cytostome, *b* — section of the posterior body part; C — Proter immediately after division, *a* — section behind the cytostome, *b* — section of the posterior body part

The following sections were executed:

- (1) Section of proter closely behind the cytostome (Fig. 1, A *a*).
- (2) Section along the division furrow (Fig. 1, A *b*).
- (3) Section of opisthe in its posterior body part (Fig. 1, A *c*).

In every case the section *A a* involved the retreat of both arisen fragments, similarly as it occurs in the normal individual. The section *A b* was the most difficult to be performed because the resulting fragments were easily destroyed. This evoked also a withdrawal of both individuals, being, however not a rule: in some cases the anterior fragments started forwards whereas the posterior one withdrew. Uniform results were gained after the section *A c*. Both fragments started forwards, similarly as it occurs in a normal individual.

Sections were also carried out on new arisen individuals, immediately after division. They were as follows:

- (1) Section of proter just behind the cytostome (Fig. 1, *C a*).
- (2) Section of proter at the posterior body part (Fig. 1, *C b*).
- (3) Section of opisthor just behind the cytostome (Fig. 1, *B a*).
- (4) Section of opisthor in the posterior body part (Fig. 1, *B c*).

The section *C a* involved the backward movement which corresponds to the behaviour of normal individual. Sections *C b* caused also a backward movement in every case. This has been an unexpected result because in the normal individual this section brings about a forward movement.

The subsequent experiments brought evidence that just approx. 5 h after division, the distribution of reactivity in proter returns to the normal one, i.e., stimulation of the posterior sections involves a forward movement.

In the case of opisthor, the section *B a* involved permanently a backward movement. The section *B c* involved withdrawal. This scheme is similar to that one which is observed in the normal individual.

Discussion

The results gained with animals in the stage prior to the fission of individuals seem to speak in favour of the fact that at this stage the dividing individual responds like the normal individual, i.e., as one entity. The functional division has not yet occurred in it. This is proved by the fact that the response to stimulation of the anterior section is withdrawal, and to the posterior one — the forward movement. For a full ascertainment of this regularity, observations of the ciliary movement should be carried out in order to know whether the stimulation concerns the whole ciliate cell.

It is a characteristic fact that the section along the division line causes mostly a withdrawal in both new-arisen fragments. These sections are executed in the same region of cell where in the normal individual boundary of the "backward response area" and the transitory zone exists. The results of Seravin 1962 a, b gained on *Spirostomum* support also the view that the individual prior to division responds to external stimuli as an entity.

The study of reactions immediately after division proved to be interesting. In

opisthor, the pattern of reactivity is the same as in the normal individual. This phenomenon proceeds parallel to the morphogenetic processes since at the moment of division the whole zone of the buccal apparatus is already formed anew.

The reactions of proter are somewhat unexpected: it fails to behave like a normal individual after division, and possesses only the anterior area of the reactivity. The stimulation of posterior sections evoke in its withdrawal whereas in the normal individual they cause the forward movement. The return to the norm lasts about 5 h, which possibly may correspond to the time of morphogenetic processes. In proter those processes proceed at a slower rate, new structures fail to arise — as it occurs in the opisthor — only the regulation of the posterior body segment takes place.

Perhaps it is an example of relations between behaviour and morphogenesis: the morphogenetic stability is reflected in the stability of reaction in proter. In opisthe where the morphogenesis is very distinct — the differentiation of reaction appears soon. The formation of new parts is accompanied by new reactions. Possibly the developmental stages of proter and opisthor are not similar and proter is in some way delayed in his development. It behaves similarly as the anterior fragment of the normal individual. This may be supported by the experiments on reactions of fragments of *Dileptus* to the shake of water (Doroszewski 1968). It was shown in those studies that the anterior fragments reacts only by the withdrawal, whereas the posterior one manifests already differentiated reactions. In this case the return of reactivity to the norm in the anterior fragment lasts also approximately 5 h.

The achieved results suggest that in opisthor the new pattern of reactivity is formed before the fission of individuals while in proter it occurs much later.

Summary

The experiments had to ascertain at which stage of division the arising *Dileptus* individuals start to behave as a new functional entity. It was stated that prior to fission the dividing individual behaves normally. After the fission of individuals, opisthor shows already normal reactions whereas proter behaves like the anterior fragment of interdivision individual.

The author links those results with the phenomena of morphogenesis.

STRESZCZENIE

Doświadczenia miały za zadanie wykazanie w jakim momencie podziału powstające osobniki *Dileptus* zachowują się jako nowa całość funkcjonalna. Stwierdzono, że przed podziałem dzielący się osobnik zachowuje się normalnie. Po rozdzieleniu się osobników opistor wykazuje już normalne reakcje, natomiast proter zachowuje się jak fragment przedni osobnika międzypodziałowego. Autor wiąże te wyniki ze zjawiskami morfogenezy.

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NOTICE

The International Collection of Ciliate Type-Specimens, established in 1963 and recently transferred to the Smithsonian Institution, Washington, D. C., now contains 180 type-specimens representing 105 species. A paper has recently appeared (Corliss J. O. 1972. Current Status of the International Collection of Ciliate Type-Specimens and Guidelines for Future Contributors. *Trans. Amer. Micros. Soc.*, 91: 221–235) which gives an up-to-date report on the Collection. More importantly, perhaps, the paper predicts a rapid growth of the number of specimens in the near future and gives careful directions and guidelines for preparation, designation, and posting of types now residing in private research collections around the world. The advantages to the whole field of ciliate systematics of having a centrally located, well-known, international repository, where type material becomes "the property of science" and is available for comparative study in the future by all qualified specialists engaged in research work of a revisory nature, are many, as is widely recognized by protozoologists everywhere. The availability of techniques of silver impregnation makes possible the preparation of ciliate specimens which remain well-preserved indefinitely and which reveal infraciliary characteristics, of both free-living and parasitic forms, of basic taxonomic significance. Researchers are urged to deposit type-specimens, especially when new species are first being described. Reprints of the paper cited above, and answers to questions on the subject in general, may be obtained from Dr. John O. Corliss, Department of Zoology, University of Maryland, College Park, Maryland, 20742, U.S.A.

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ANNOUNCEMENT

On the occasion of the Second International Congress of Parasitology in Washington, D.C., in 1970 the World Federation of Parasitologists entrusted the organization of the Third International Congress of Parasitology (Third ICOPA) to Deutsche Gesellschaft für Parasitologie (DGP).

Third ICOPA will be held from August 25th to August 31st, 1974, in München, Kongress-Zentrum, Messengelände.