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Ordo *Thigmotricha (Ciliata—Holotricha)*

III

Familiae *Ancistrocomidae* et *Sphenophryidae*

I would like to consider two families in the third part of my monographic study: *Ancistrocomidae* and *Sphenophryidae* which Chatton et Lwoff 1949/50 couple (together with the family *Hypocomidae*) in tribus *Rhynchodea* opposed to tribus *Stomodea* including according to these authors: *Thigmophryidae, Conchophthiridae* and *Hemispeiridae*. As I mentioned before (part I pp. 26, 33) I do not consider as right to keep the family *Hypocomidae* Bütschli em. Chatton et Lwoff in the order of *Thigmotricha*. In my opinion its slight similarity to *Ancistrocomidae* consists merely on a convergency. However the families *Ancistrocomidae* and *Sphenophryidae* are closely related to one another so that *Sphenophryidae* may by considered as a highly specialized branch of *Ancistrocomidae*, whereas *Ancistrocomidae* refer directly to *Hemispeiridae*.

Familia *Ancistrocomidae* Chatton et Lwoff, 1938

syn.: *Hypocomidae* pro parte Chatton et Lwoff, 1922—1938 et auctores.

The history of the examinations of this family was rather paradoxical, it begun with the description of a species, presently not belonging to it at all. This species was *Hypocoma parasitica* described with the creation of a new genus *Hypocoma* by Gruber 1884 which enclosed it to *Hypotricha*. Plate 1888 noticed its sucking tentacle and recognized it as a transitional form between *Ciliata* and *Acineta*. Bütschli 1889 recognized *Hypocoma* as an organism close to *Chlamydodontidae* and create for it a family *Hypocomidae*. Collin 1907, 1912 recognizes *Hypocomidae* as neotenic *Acineta* having a ciliature composed of concentric elipses and he describes a new species *Hypocoma acinetarum*.

The studies on "*Hypocomidae*" from the gills of molluscs initiated Lichtenstein 1921, describing *Hypocoma patellarum* with non-concentric ciliature; Chatton et Lwoff 1922 describe a separate species *Hypocomella cardii* with the same ciliature. According to former assumptions, Chatton et Lwoff 1922 consider *Hypocomidae* as neotenic *Acineta* the more so that *Sphenophrya dosiniae* (fam. *Sphenophryidae*) described by them in 1921 was

a sedentary form and produced tomits resembling virtually to their *Hypocomella cardii.*

However the finding of such forms as *Hypocomides modiolariae* Ch. Lw., 1922 or *Hypocomides mytili* Ch. Lw., 1922 having "un rudiment de zône adorale" induced the French authors to exclude from *Acineta* both *Hypocomidae* as *Sphenophryidae* and to arrange them with *Ancistridae* Issel, 1903 and *Thigmophryidae* Ch. Lw., 1923, to a separate suborder *Thigmotricha* among *Holotricha Hymenostomata.* It is a paradox that the presence of a rudimental adoral apparatus in *Hypocomidae* serves to Chatton et Lwoff as an issue for the solution of this problem but afterwards they denied to it in their monography from 1949—1950!

The further analysis of similarities and differences in the scope of so conceived family of *Hypocomidae* led endly to the differentiation of two families within it (Chatton et Lwoff 1939 b), namely *Hypocomidae* s. str., embracing parasites of *Protozoa* and *Tunicata*, and *Ancistrocomidae* including parasites of *Mollusca.* The suborder *Rhynchodea* created in that way by Chatton et Lwoff could embrace 3 families: and the French authors held up to the end (1950) *Hypocomidae* among *Thigmotricha.*

The differentiating diagnoses of both families are presented as follows in the monograph of Chatton et Lwoff 1949 (p. 247):

1° *Hypocomidae* Bütschli s. s., emend. Ch. et Lw. *Rhynchodea* cilifères à l'état adulte. — La face dorsale seule est ciliée. La cinétie vestigiale est antéro-latérale droite. Le suçoir, plus long que large, est à point d'émergence dorsal. Sa longueur ne dépasse pas le quart de la longueur du cilié. Le macronucleus de l'ádulte est en fer à cheval. Une ou deux gastrioles centrales. Genres: *Hypocoma* Gruber, *Heterocoma* Ch. Lw. et *Parahypocoma* Ch. Lw.

2° *Ancistrocomidae* Ch. et Lw. *Rhynchodea* cilifères à l'état adulte. — Le système ciliaire est plus ou moins développé. En dehors du champs ciliaire dorsal, il y a souvant persistance d'un certain nombre de cinéties générales. La cinétie vestigiale, lorsqu'elle existe est postéro-ventrale droite. La suçoir, plus long que large, est à point d'émengence antérieur. Sa longueur est supérieure à moitié de la longueur du cilié. Il y a une seule exception: le genre *Hypocomidium.* Le macronucleus de l'adulte est sphérique ou allongé. Les gastrioles sont petites. Genres: *Goniocoma, Hypocomagalma, Holocoma, Ancistrocoma, Heterocinetopsis, Hypocomella, Hypocomidium, Hypocomina, Insignicoma, Crebricoma, Raabella, Ansisocomides, Hypocomatidium, Hypocomides, Isocomides, Enerthecoma, Syringopharynx, Cepedella.*

The decision of Chatton et Lwoff 1939 of separation of *Hypocomidae* from *Ancistrocomidae* is quite proper but in my opinion unconsequent. In my view the family *Hypocomidae* in its original and definite outline has nothing in common with *Thigmotricha* in general and slight similarities between *Hypocomidae* and *Ancistrocomidae* are only convergencies. I intend to touch once more this problem when the systematic and phylogenetic relationships of *Thigmotricha* with other groups of *Ciliata* will be discussed.

The family *Ancistrocomidae* purfified in this way seems to be a distinctly outlined and uniform group. All its representatives have several common features: an elongated body form, the adhesive-sucking tentacle, the lack of primary mouth and a strongly reduced ciliature in which the thigmotactic ciliature is longest preserved. However the family *Ancistromidae* is not

uniform in respect to its ciliature. Besides the forms in which the kineties cover the whole body and consist both the general and the thigmotactic ciliature, are these which preserved the rest of adoral kineties and of the thigmotactic ones, and finally these also which preserved merely the thigmotactic ciliature. Presumably their origin is not strictly monophyletic, it may be that the particular groups (subfamilies in my opinion) of *Ancistrocomidae* decent from different *Hemispeiridae* and arose in the way of a parallel evolution.

However the general description of the family may be reported as follows:

The body elongated to a different degree; from the ovoidal shape through the pear-shaped to banana-shaped. The anterior end of the body has a sucker which according to the idea of Chatton et Lwoff (quite adequate in my opinion) originated from the bouton adhesif in the anterior part of the body of some *Ancistrinae* and *Hemispeirinae*. This tentacle has undoubtedly an adhesive function which may be observed in the living material, and also a sucking function; a longer or shorter cytopharynx leads from it inside the plasma reaching in some species nearly the body end as i.e. in *Ancistrocoma pelseneeri* Ch. Lw. (Raabe 1936). This tentacle may be rather stiff, sometimes contractile, and in several forms retractable to the vesicular space. As it seems this tentacle is not able to suck larger, formed particles of food, and the digesting vacuoles are minute and they do not include these particles.

In many forms i.e. in *Ancistrocoma* occur in the body posterior end original creatures determined by Raabe 1936 as concretionary vacuoles and recognized by him as organellum corresponding to the statocyst. It is a vacuole filled with a transparent fluid in which is suspended a corpuscle or some corpuscles strongly refracting light or strongly staining e.g. by iron hematoxylin. Presumably these corpuscles constitute some remains of undigested food or metabolites of a ciliate deposited in vacuoles. The vibration of the corpuscles influenced by the movement of flowing water could indicate virtually its role as a signal for as animal concerning the presence or the lack of current; it could also allow for a safe detachment of the animal from the substract and the shift of place. Similarly Dogiel 1929 treats likely as statocysts in the ciliates of the family *Ophryoscolecidae*, living in the rumen and reticulum of *Ruminantia*.

The nuclear apparatus of *Ancistrocomidae* consists of a macronucleus which seems large comparing to the body size and is circular, oval or somewhat elongated, and of a sometimes relatively large micronucleus. Contractile vacuole lies in posterior part of the body, its activity is usually sligthly visible.

The locomotory apparatus of *Ancistrocomidae* is the more characteristic and allows to spin some phylogenetic conceptions. It consists of various number of kineties (from 30 going to the reduction up to 4!), running virtually from the base of the tentacle to the back of the body more or less meridionally however usually the meridional run is disturbed by the curvature of kineties towards the center of the thigmotactic area. The kineties are densely filled by kinetosomes, sometimes more rarely in their distal parts. The cilia are relatively long. As it is visible in the silver-preparations and especially on these effected by Klein's silver method, between the kineties, (especially between these which are more distant from one another) and on naked areas without ciliature there is a cover of more or less uniform argyrophilic net of fibrills. However there is a lack even of any trace of longer fibrills

corresponding to the anterior or the posterior sutures, or fibrills connecting several kineties as it occurs in *Hemispeiridae*. This development of the argyrophilic net on the area without ciliature is characteristic for many groups of *Ciliata*, as *Holotricha — Hypostomata, Hypotricha* and others. In the case of *Ancistrocomidae* the atrophy of principal fibrills which occurs in *Hemispeiridae* makes difficult the studies both on the topography of cortical organelles and on the phylogenetic relations.

It seems possible to distinguish three parties in the ciliature after Chatton et Lwoff 1950: the general ciliature, the differentiated thigmotactic ciliature and the relicts of adoral ciliature or adoral kineties of other *Thigmotricha*. If the adoral kineties are preserved they do not operate for driving the food but they co-operate with the remaining ciliature in the locomotoric and thigmotactic functions. According to my opinion the adoral kineties occurring in the representatives of the subfamily *Hypocomidinae*, preserved they original topography and may constitute an element in the body orientation of *Ancistrocomidae*.

I suggested (part I p. 33) a division of the family *Ancistrocomidae* in 3 subfamilies depending on the presence or lack of these particular parts of ciliature and their mutual relations. These subfamilies are: *Hypocomidinae* preserving besides the thigmotactic ciliature also the traces of the adoral kineties; *Ancistrocominae* which have besides the thigmotactic ciliature also the general one; and *Hypocomellinae* which have only the thigmotactic ciliature. The remembrance of the proposed division could do easy the description of the ciliature represented by *Ancistrocomidae* (Fig. 1).

The thigmotactic ciliature is this part of ciliature which is present in all *Ancistrocomidae*. Chatton et Lwoff 1950 differentiate three types of kineties system, namely (p. 396): "aire thigmotactique homogène — constitué par un seul champs de cinéties équidistances", "air thigmotactique divisée — constitué par deux champs de cinéties équidistances separées par une zone glabre au par une crête"... "aire thigmotactique hétérogène — constituté par deux système de cinéties inégalement écartés". Virtually this division as the authors stated, is not very important: "chez les Ancistrosomidés les choses sont singulièrement complexes". The thigmotactic field is such that its kineties run arcuately: the central ones are ranged nearly meridionally, the right of them are buckled to the right side, the left ones — leftwards; in this way they isolate and integrate the thigmotactic ciliature.

Chatton et Lwoff derive the thigmotactic zone in *Ancistrocomidae* from the same zone in *Hemispeirinae* therefore they find out in it a structure of a type closed in système sécant [1]. This assumption seems not indispensable. In my view *Ancistrocomidae* may be derived also from *Hemispeirinae* and *Ancistrinae* what may be indicated by other characters. The closure of the thigmotactic system according to the pattern of système sécant can in my opinion appear independently of the origin as a converging phenomenon occurring also in other *Ciliata*, as i.e. in *Hypostomata*, in *Conidophryidae* and others. This seems especially possible in the case when the arrangement of kineties is based on the plastic argyrophil net and there is a lack of connective polarized fibrills.

[1] However Chatton et Lwoff 1950 find out in *Hypocomidae* a continuation of models of *Ancistrinae* (= *Protophryinae*); this suggestion does not seem quite right in view of the individuality of *Hypocomidae*.

Fig. 1. Scheme of the system and evolution of *Ancistrocomidae* and *Sphenophryidae:* An — *Ancistrocominae*, A — *Ancistrocoma*, H — *Hypocomagalma;* Hd — *Hypocomidinae*, Ic — *Insignicoma*, Hs — *Hypocomides*, R — *Raabella*, Ac — *Anisocomides*, Ht — *Hypocomatidium*, C — *Crebricoma*, Is — *Isocomides;* Hl — *Hypocomellinae*, Hll — *Hypocomella*, H.q — *Hypocomella quatuor*, G — *Goniococoma*, Het — *Heterocinetopsis*, E — *Enerthecoma*, Hi — *Hypocomidium*, Hn — *Hypocomina*, Ca — *Colligocineta*; Sp — *Sphenophryidae*, *Gg* — *Gargarius*, P — *Pelecyophrya*, L — *Lwoffia*, S — *Sphenophrya*

The thigmotactic zone in *Ancistrocomidae* consists of kineties originating as a rule at the base of the tentacle and runing arcuately backwards in such a way that their ends again are often close to one another. In the case of the existing relicts of the general ciliature these kineties which are the nearest to the thigmotactic zone close it really système sécant. The length of the kineties of the thigmotactic ciliature is very different: they often outstretch slightly the middle of the body length; the shorter are the central kineties,

the longest are the kineties on the left side. The development of the thigmotactic ciliature within *Ancistrocomidae* tends in several directions: to the reduction of the number of kineties so strong i.e. in *Hypocomella quatuor* Raabe only 4 kineties are preserved! On the other hand it exists a tendency to a closer integration of the thigmotactic system by its closing that is by the approach of the ends of its marginal kineties to one another; this phenomenon occurs in many *Hypocomella*, distinctly in *Hypocomina* and in an extreme shape in *Colligocineta* (see part I p. 19).

The third development trend of the thigmotactic area with a reduction of the general ciliature may relay on the enlargement of the range of the thigmotactic zone. These relationships prevail in *Goniocoma macomae* (Ch. Lw.) and present some difficulties concerning the interpretation. The ciliature of *Goniocoma* covers the whole body and remembers these relations which occur in *Hypocomagalma dreissenae* Jarocki et Raabe; even the system of kineties is similar but specular opposite! Chatton et Lwoff 1950 accept in both cases the existence of the general ciliature and the thigmotactic zone and write (p. 397): "Chez *Goniocoma* la ciliature somatique se continue sans hiatus avec celle de l'aire thigmotactique à la gauche de celle-ci, tandis que chez *Hypocomagalma* cette continuité est à droite". Under this assumption the topographic interpretation is quite impossible. In this situation Raabe 1938, 1957 (see part I, p. 19) recognized that if *Hypocomagalma* has both the thigmotactic and general ciliature and their arrangement correspond to these observed in *Ancistrocoma*, therefore *Goniocoma* preserved only merely the thigmotactic ciliature, but this ciliature secondarily disseminated on the whole body surface and adopted the locomotoric role previously limited.

The general ciliature is preserved only in several forms which I arranged to the subfamily *Ancistrocominae*. The kineties of the general ciliature consist in *Holocoma* or *Ancistrocoma* a border line in both sides of the thigmotactic ciliature, in *Hypocomagalma* — rather only in the left side. They differ only slightly from the kineties of the thigmotactic ciliature by a more rare arrangement of kinetosomes, they are also larger, and the cilia seem bigger than the thigmotactic ones. In the general ciliature there is usually a distinct chiatus between the kineties corresponding clearly (according to Chatton et Lwoff) to the naked peristomial field of *Hemispeiridae*. Therefore the kineties on both sides of the chiatus may be numbered as kinety "1" — on the right side of chiatus and kinety "*n*" on its left side. I mentioned before concerning *Goniocoma*, in some cases the role of the general ciliature may be adopted secondarily by the thigmotactic ciliature.

The adoral kineties constitute a set of kineties of *Ancistrocomidae* concerning which there are the most inexact data reported by Chatton et Lwoff in their particular works and also for the reason of changing by them of some interpretations and conclusions. The French authors give in their earlier notes rather enigmatic data. They write in 1922: "La preuve en est que la bouche s'est oblitérée et que l'aire adorale elle-même a regressé au point qu'elle n'est plus représenté chez *H. modiolariae* n. sp. que par un segment d'helice d'un tiers de tour et chez *H. mytili* n. sp. par un segment beaucoup plus court encore, continué seulement par une dizaine de grands cils". In 1926 they report writing on *Ancistrocoma*: "Cette ciliature se compose: 1° de la frange pèristomienne droite à cils très longs dans sa région postérieure ou elle est enfoncée dans un sillon qui fait encoche dans le profil de la face

ventrale". The French authors based on the existence of this frange pèristomienne their whole system of *Thigmotricha* and on the relation of *Ancistrocomidae* to *Hemispeiridae* (or earlier *Hypocomidae* to *Ancistridae*). That's Chatton et Lwoff 1949, 1950 give up this interpretation (see part I, p. 26) and they preserve only the term "cinétie vestigiale" which conveys nothing, for marking the discussed segments of kineties if they do not deny their existence in *Ancistrocoma* in general.

The reason for withdrawing of Chatton et Lwoff 1949, 1950 from the previously accepted positions concerning the homology of vestigial kineties of *Ancistrocomidae* with adoral kineties of *Hemispeiridae* was as they report (p. 398): "L'étude de la stomatogenèse des *Hemispeiridae* nous a conduits à une conception claire de la ciliature prostomienne. L'examen des *Ancistrocomidae* imprégnés à l'argent ne nous a révélé dans la structure de la cinétie vestigiale, aucun caractère qui permette de la considérer comme l'équivalent de la ciliature prostomienne des *Hemispeiridae*". This is undoubtedly a fair point of view. But perhaps the French authors anticipated a too accurate recurrence i.e. in the morphogenesis of *Ancistrocomidae* of the processus occurring in the stomatogenesis of *Hemispeiridae*, together with the transition of the adoral kineties over the stage of ambihymenium? The biogenetic law would not be forcibly in the case of retrograded or virtually changed organs. The principle of deviation after Sjewiercow may operate in this case, or even the rule of archalaxis by which the recurrence of the ancestors' stages is totally abolish.

As I mentioned before, I do not only agree to the desertion of Chatton et Lwoff but inversely I extend their view on the remains of the adoral kineties in *Ancistrocomidae* (see part I, p. 26), namely in these which I arranged to the subfamily *Hypocomidae*. In my opinion the two often occurring, isolated and longer kineties, lying on the right from the thigmotactic field, may be just recognized as a parallel and the remainder of the adoral kineties of *Hemispeiridae*. These two isolated kineties occur in *Insignicoma, Anisocomides, Hypocomatidium, Hypocomides, Raabella* and *Crebricoma*. In *Insignicoma, Anisocomides* and *Hypocomides* one of them continues as a short segment of cilia. It may be assumed that it is this kinety which may be compared to the stomatogenic kinety. Although this segment is disrupt from its maternal kinety, as it may be assumed, its arrangement corresponds to the loop of the stomatogenic kinety. It seems that in spite of the unadequate description this segment was merely preserved in *Isocomides* as the last remainder of the adoral kineties.

Topographically the problem of homology of the differentiated kineties in *Ancistrocomidae-Hypocomidinae* with adoral kineties of *Hemispeirinae* seems less complicated when *Hypocomidinae* are not compared to *Ancistrumina* or *Ancistrum* but to *Proboveria*. In this species the adoral kineties are continuing with their spiral so far leftwards that the kineties of the general and thigmotactic ciliature break off before them.

In this situation what is about the problem of the body orientation in the representatives of the family *Ancistrocomidae*? *Ancistrocomidae* are a group strongly modificated and in connection with their transition to a really parasitic way of life *Ancistrocomidae* lost many structures which could serve to the body orientation of the more plesiomorphic *Hemispeiridae*. The flat sides of the body were there the lateral ones, the margin on which was the peri-

stomal field and the adoral kineties (in their original arrangement) was the ventral margin, the opposite was the dorsal one. The division on the left and the right side of the body was stressed by the arrangement of the anterior and posterior sutures. In *Ancistrinae* the thigmotactic field occupied the anterior part of the left side of the body shifting to the dorsal side in *Hemispeirinae*. In *Ancistrocomidae* the situation is more complicated.

Chatton et Lwoff 1950 present as follows their orientation system (p. 395—396): "Tous les *Ansistrocomidae* connus ont, sans exception, une aire thigmotactique individualisée qui marque leur face d'adhérence à l'hôte. Nous pouvons qualifier celle-ci de «dorsale» puisque l'aire thigmotactique occupe chez les *Hemispeirinae* la face dorsale, la face ventrale ayant été définie, conformément aux conventions les plus générales, par le point d'origine de la cinétie stomatogène, ici la cinétie prostomienne, 1. La ciliature prostomienne a disparu chez les *Ancistrocomidae*. Mais chez *Holocoma primigenius*, l'une des formes les plus primitives du groupe, il existe, entre deux cinéties opposées à l'aire thigmotactique, une zone glabre que nous considérons comme l'emplacement de la ciliature prostomienne disparue, c'est-à-dire comme représentant le secteur méridien ventral, bordé par les cinéties 2 et *n*. L'aire thigmotactique sera donc considerée comme dorsale. En l'absence de bouche cette orientation est arbitraire. Mais appeler la face thigmotactique ventrale parce que c'est par elle que se réalise l'adhérence au support serait plus arbitraire encore. Et la définition d'un méridien dorsal est nécessaire pour définir la droite et la gauche du cilié."

Chatton et Lwoff 1949, 1950 forejudged arbitrally that *Ancistrocomidae* are derived entirely from *Hemispeirinae* and that for this reason the thigmotactic zone lies dorsally in both groups. I think that *Ancistrocomidae* or at least their majority could equally be derived from *Ancistrinae*, having the thigmotactic zone situated distinctly on the left side of the body. I also suggest that in *Hemispeirinae* the thigmotactic zone, however has virtually a dorsal position, is derived mainly from the kineties on the left side of the body (see part II. p. 122). These kineties concide towards the posterior suture shifted to the anterior part and they transform into a symmetric system. For this reason the thigmotactic zone of *Ancistrocomidae* may be equally recognized as lying on the left body side as it is in all other families of *Thigmotricha*. Under this orientation the separated kineties of *Hypocomidinae* as well as the naked zone in *Ancistrocominae* could take a ventral position which is also consistent with the claims of Chatton et Lwoff (Fig. 2).

Independently of these considerations needed for practical reasons, a different point of view may be accepted. Whatever is the phylogenetic orientation of the thigmotactic zone in *Ancistrocomidae*, actually it is situated on the somewhat concave body side by which the organism clings to the base and to which is directed the sucker as a secondary apparatus of food taking. It is the ventral side therefore in the biological and physiological approach. If one would like to find some relations to the adoral kineties which would mark the ventral side, it is already there where we accept (according to my opinion) the existence of their remains in *Hypocomidae*, their final vestigial part is just located on the meridians of the thigmotactic zone. Therefore I would take the thigmotactic side of *Ancistrocomidae* as their ventral side. It seems extremely paradoxical in my view to consider this side as a dorsal one along the suggestions of Chatton et Lwoff.

The reproduction of *Ancistrocomidae* is effected by an equal division; the level of the division passes somewhat obliquely in a way that it cuts the arrangement of the thigmotactic kineties more or less in the middle. These kineties lie rather in the anterior part of the body of the dividing individual. The divisional processes were observed by Jarocki 1935 in *Hypocomella chattoni*, by Raabe 1938 in *Ancistrocoma pelseneeri* and in *Hypocomatidium sphaerii* (not. publ.), by Chatton et Lwoff 1950 in *Anisocomides zyrphaeae* and *Goniocoma macomae*. The differentiated kineties identified by myself as the remainders of the adoral kineties divide themselves in an ordinary way without any transformation (Raabe in *Hypocomatidium sphaerii* — not publ.). The origin and formation of the short isolated segments of kineties (cinéties vestigiales) is not elucidated.

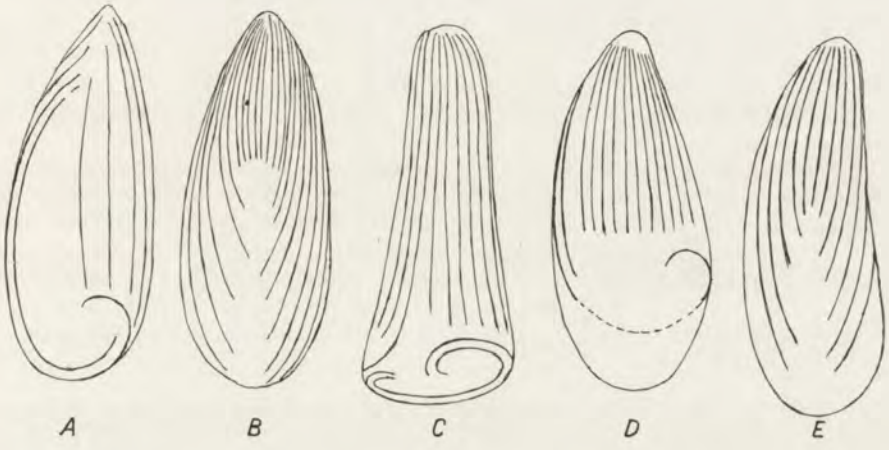

Fig. 2. Comparison of *Ancistrocomidae* with *Hemispeirinae* and *Ancistrinae:* A — adoral kineties and the oral field in *Ancistrospira*, B — the thigmotactic field in *Ancistrospira*, C — situation of the adoral spiral in *Boveria*, D — thigmotactic field and adoral kineties in *Insignicoma*, E — thigmotactic field in *Ancistrocoma*

The origin of the sucker with the gullett deserve a special attention as a new, substitutional apparatus of food taking in *Ancistrocomidae*. This sucker (suçoir of Chatton et Lwoff) affiliate from the bouton adhesif of *Hemispeiridae*. This homology concerns however the position and the external part of the suçoir but does not concern its inner part. Chatton et Lwoff 1950 find out that two forms arise during the division in the plasma of the dividing individual (i.e. *Hypocomella*) les ébouches des suçoirs", one of them would replace the degenerating sucking tentacle of the proter, the second one would transform into the sucker of the opisthe. A similar situation occurs also in *Sphenophryidae* (p. 443).

I was not able to find in this material the substitution of suçoir of the proter, but I have many times observed the lying up the sucker of the opisthe. I consider therefore the whole processus as a reliable one.

I consider however as unmotivated the thesis of Chatton et Lwoff 1949 that the anlage of the sucker arose in connection with kineties or kine-

tosomes with which it would be related over the first periods of time "par un filament sidérophile d'épaisseur voisine de celle du cinétodesme" (Ch. Lw., 1949 p. 244, 246, fig. XIX). The authors report (p. 246): "Si cette hypothèse est exacte, il y aurait chez les *Rhynchodea* une ou deux cinéties formatrices du suçoir, comme il y a chez les Hymonostomes une cinétie formatrice de la ciliature buccale". "La spherule qui se transforme en suçoir serait un cinétosome hypertrophié dérivant par division de l'un des cinétosomes de la cinétie formatrice". "Notre hypothèse de l'origine cinétosomienne de la sphérule s'appuie: 1° sur la constatation effective d'une liaison entre la sphérule et la cinétie; 2° sur l'analogie entre la formation du suçoir et celle trichocyste".

I suppose that here is the principal error: really these "cinéties formatives" or even the formative fibrills occur in *Hymenostomata* as well as in *Thigmotricha* (i.e. in *Conchophthirus* — R a a b e 1965) but they occur as anlage of the adoral ciliary compositions of the type UM or AZM. However the suçoir is not an adoral ciliary formation, but an oral composition like i.e. the oral basket of *Prostomata*. These oral compositions have a quite different origin. Moreover — their formation and transformation are not directly related to the transformation of ciliary systems and are subjected to a quite different mechanism.

The conjugation of *Ancistrocomidae* is effected by the connection of partners by the posterior ends of the body, therefore by the ends in which or next to which was situated certainly the primary buccal aperture of the initial forms. The conjugation was examined by R a a b e 1936, 1938 in *Ancistrocoma pelseneeri, Raabella helensis, Hypocomidium fabius* and *Goniocoma macomae* (also the simultaneous conjugation of three individuals!) by C h a t t o n et L w o f f 1950 in *Isocomides mytili* and by F e n c h e l 1965 in *Hypocomides astarte*.

Ancistrocomidae are real parasites especially of the respiratory surface of *Mollusca*, both *Chitones, Bivalvia* as well as *Gastropoda*, marine and fresh water species. As far the only exceptions are: *Heterocineta phoronopsidis* Kozloff, 1945, parazitizing on the tentacles of *Phoronidea* and *Ignotocoma sabellarum* Kozloff, 1961 parasitizing on the adoral cirri of *Polychaeta*. Moreover J a r o c k i 1935 mentions that some of the species of the genus *Hypocomella* (=*Heterocineta*) described by him parasitizing in the mantle cavity of *Gastropoda* may transfer the oligochaete *Chaetogaster limnaei* living in these cavities.

The parasites cling by their sucking tentacle to the gills or other respiratory surfaces of the host, but they are able to tear out and penetrate to these respiratory surfaces, or are floating freely usually performing spiral rotations. The ciliature of the thigmotactic surface serves as a locomotoric apparatus in the cases of freely floating. It would be supposed that the concrementic vacuole, which is at the back of the body, signalises to the ciliates the possibility of tearing and floating freely. This vacuole is especially developed in more elongated forms.

As it seems, *Ancistrocomidae* are rather strictly specific to their hosts, attached to their species or genera. If even the given species of parasites in many hosts distant systematically or ecologically, it is possible to distinguish different forms of parasite varying among them mainly by the number of kineties. This occurs i.e. in the case of *Ancistrocoma pelseneeri*, occurring in

Macoma, Mya, Pholas: this species proves a distinct variability in the number and arrangement of kineties even within the compass of the population from one host's individual. The problem which deserves a study is the separateness of the particular species' of the genus *Hypocomella*, described especially by Jarocki 1934, 1935 from the freshwater *Gastropoda*. It could not be excluded that these numerous species are merely forms of one species adapted to numerous hosts. Particularly the genus *Hypocomella* (=*Heterocineta*) is highly polyspecific and deserves a more detailed revision.

In view a conspicuous homogenity of the general plan of structure and in spite of differences that occur between the particular subfamilies differentiated here, the definition of the family *Ancistrocomidae* may be settled in a clear and univocal way. Chatton et Lwoff 1949 give a diagnosis prepared for the separation of *Ancistrocomidae* and *Hypocomidae*, but Chatton et Lwoff 1950 give instead the diagnosis a detailed description of the family. The diagnosis of Corliss 1961 seems unadequate: "Anterior suctorial tentacle. Body ovoid to pyriform in shape, with general somatic and thigmotactic ciliature, often restricted to anterior portion."

On the basis of these diagnoses and of the discussed characters, the definition of the family *Ancistrocomidae* may be presented as follows:

Familia *Ancistrocomidae* Chatton et Lwoff, 1939

syn.: *Hypocomidae* partim auctorum; *Cepedellidae* in Corliss, 1961.

Thigmotricha of a reduced buccal apparatus, secondarily replaced functionally by the sucking snout lying on the front body pole; it is homologous to the pointed body top of several *Hemispeiridae*. The adoral kineties undergo partial or complete reduction. A similar reduction concerns the general ciliature too. There remains, as a rule, more or less developed thigmotactic ciliature, first of all in the anterior part of the body. The body is pear- or banana-shaped, of small or middle dimensions (10—65 μ). The nuclear apparatus common; 1 Ma and 1 Mi. Division equal; conjugation of equal individuals with the hind body parts. Parasites of the mantle cavity of *Mollusca* (exceptionally in *Annelida* and *Phoronidea*).

Typus familiae: genus *Ancistrocoma* Chatton et Lwoff, 1926.

As it was stated in the part I and in view of the discussion in the present part of the description of *Thigmotricha*, the family *Ancistrocomidae* in my opinion may be divided into 3 subfamilies, namely:

subfamilia *Ancistrocominae* Chatton et Lwoff, 1939, Raabe, 1967
subfamilia *Hypocomidinae* Raabe, 1967
subfamilia *Hypocomellinae* Raabe, 1967.

Subfamilia *Ancistrocominae* Chatton et Lwoff, 1939, Raabe, 1967

According to previous statements, *Ancistrocomidae* ranged to this subfamily preserved the general ciliature besides the thigmotactic ciliature. Consequently the diagnosis of the subfamily may run as follows:

Subfamilia *Ancistrocominae* Chatton et Lwoff, 1939, Raabe, 1967

Thigmotricha — Ancistrocomidae of an elongated and relatively large body (30—60 μ). The ciliature occupies the great part of the body in longitudinal and in circumferential aspect and consists, as it seems, of partially preserved general ciliature embracing the thigmotactic ciliature as in parentheses ("système sécant"). Lack of differentiated adoral kineties. The nuclear apparatus common. Vacuoles of concrements can occur in the hind part of the body. Parasites of the mantle cavity of marine and fresh-water *Bivalvia*.

Typus subfamiliae: genus *Ancistrocoma* Chatton et Lwoff, 1926.

As things stand by now to the subfamily *Ancistrocominae* may be ranged the typical genus *Ancistrocoma* Chatton et Lwoff, 1926 then its very approximate genus *Holocoma* Chatton et Lwoff, 1950, unadequately described genus *Syringopharynx* Collin, 1914 and a clearly separate genus *Hypocomagalma* Jarocki et Raabe, 1932. The ciliature covers nearly the whole body surface of these ciliates; only an oblong girdle remains free from cilia. This row runs from the sucking tentacle towards the back of the body, and is homologous, after Chatton et Lwoff, with the naked row of peristomal field of more primitive *Hemispeiridae*. Also free from cilia is the naked field at the back of the body, beyond the range of shorter kineties of the thigmotactic ciliature.

The central part of the ciliature is filled by thigmotactic kineties; they are shorter than the kineties of the general ciliature, arranged more densely than the former ones, but they have distinctly somewhat smaller kinetosomes. Therefore the thigmotactic kineties form an individualized arrangement, passing in both sides, the right and the left one, into the arrangement of kineties of the general ciliature, which are longer as a rule, in any rate reaching further to the back of the body.

As we did concerning the *Hemispeiridae*, the body of the representatives of *Ancistrocomidae* is oriented in that way that as the anterior part of the body is considered this end, on which is the adhesive tentacle (suçoir), and we consider as the posterior end this one on which was located the declined primary buccal aperture. The thigmotactic side of the ciliate is considered as a ventral one. The body sides are considered from the "point of view of the protozoan" and not of the person looking at it (the left and right part and not the left-hand and right-hand part). In the calculations of kineties this one may be considered as kinety 1 which is on the right side of the naked field (according to Chatton et Lwoff it would correspond to

kinety 2, this kinety which confines the naked field from the left side is the kinety *n*, therefore we will consider the kineties clock-wise looking from apex of the body.

Genus *Ancistrocoma* Chatton et Lwoff, 1926

syn.: *Holocoma* Chatton et Lwoff, 1950: *Parachaenia* Kofoid et Bush, 1936.

This genus was created by Chatton et Lwoff 1926 for two species described at the same time: *A. pelseneeri* and *A. pholadis*. The authors tried to formulate precisely the diagnosis of this outstanding species: "Hypocomidés ayant conservé la ciliature générale des Ancistridés y compris la ciliature péristomienne de sorte que malgré l'absence de bouche l'orientation est encore possible. Cette ciliature se compose: 1° de la frange péristomienne droite à cils très longs dans sa région postérieure oú elle est enfoncée dans un sillon qui fait encroche dans le profil de la face ventrale. A sa droite un système des stries parallèles à cette frange, qui, comme elle sont légérement hélicoidales dextres. A la droite de ce système, un deuxième systéme de stries hélicoidales sénestres en sécance aves le premier dans la région postérieure du corps. Dans la région entérieure il y a, entre ces deux systèmes écartés un troisième système qui correspond à l'aire thigmotactique formée de l'*Ancistrospira intermedia* [2] au delà du système des stries sénestres un champ non cilié s'étendant jusq'à la frange péristomienne et qui représente un champ peristomien trés large. Pôle antérieur du corps atténué et pourvu d'un suçoir qui, á l'état de rétraction pas visible comme un petit bouton. Ciliature thigmotactique non différenciée".

The existence of the "frange péristomienne" individualized by Chatton et Lwoff was then demented by them in 1950; they reported: "Les impregnations argentiques ont permis de voir que cette frange peristomienne est en réalité une cinétie qui n'est pas differente des autres cinéties générales". Frange peristomienne searched by Raabe 1938 and reported by him as lying in the anterior body part, proves accordingly to the view of Kozloff 1945 — as an artefact. It must be recognized that *Ancistrocoma*, similarly to *Holocoma*, has no traces of adoral ciliature.

After the issue of the description of Chatton et Lwoff 1926, Kofoid and Bush 1936 described from *Mya arenaria* a new genus and species *Parachaenia myae* with an undefinited systematic position (in a view of a complete ignorance of any "*Hypocomidae*"). This species corresponds undoubtedly to the genus *Ancistrocoma*, what recognizes Kirby 1941 and finds Kozloff 1946 on his material, then Chatton et Lwoff 1950 and finally Fenchel 1965. Some doubts arise concerning the eventual arrangement of *Syringopharynx pterotrochae* Collia, 1914 to this genus; Chatton et Lwoff 1950 could not decide these problems.

Chatton et Lwoff 1950 created a new genus *Holocoma* for the species *H. primigenius* described at the same time. Virtually it would differ from the species of the genus *Ancistrocoma* merely by a somewhat larger number of kineties (19—23 instead of 12—15) and consequently by a narrower naked zone between the last and the first kinety. In principle the differences between *Holocoma primigenius* Chatton et Lwoff, 1950 and the species of the genus

[2] Enigmatic name never used before or after — certainly in concerns *A. veneris*? — Z.R.

Ancistrocoma are almost of the quantitative nature and not of qualitative one. I consider therefore as adequate to include *H. primigenius* into the genus *Ancistrocoma.*

The high variability in the number and disposition of kineties among individual species consists a real difficulty for the systematics within the genus *Ancistrocoma.* This variability may be affected besides the individual variability within the population, also by the ubiquity of individual species of parasites and the wide geographical and ecologic spreading of their main hosts (both *Macoma balthica* and *Mya arenaria*). The intricacy of these questions may be presented in the schedule of data coming from different authors (Table 1). Besides the differences in the number of kineties there are striking differences in their disposition. Generally as it is visible, a part of kineties of the general ciliature, lying on the left (according to our orientation) from the thigmotactic field is highly more numerous as the right part last kineties); what give arrangements: 2, 6, 5 or 3, 5, 6. It concerns both forms described as *Ancistrocoma pelseneeri* and *A. myae* and *Holocoma primigenius.* Only according to Chatton et Lwoff 1950 the relations for *A. pelseneeri* are quite inverse along the scheme 7, 5, 1 or 5, 7, 2. It seems correct to suppose that Chatton et Lwoff having to do with the individuals impregnated at both sides, focussed them badly and inversely interpreted the pictures however all others did it properly. I have no doubts as to my data, having to do with a one sided impregnated material according to the dry method, and paying a particular attention to the interpretation of pictures. I will discuss once more this problem presenting *Ancistrocoma pelseneeri.*

The definition of the genus *Ancistrocoma* Chatton et Lwoff, 1926 after the including in it the species *Parachaenia* Kofoid et Bush, 1936 and *Holocoma* Chatton et Lwoff, 1950 may be stated as follows:

Ancistrocoma Chatton et Lwoff, 1926

syn.: *Parachaenia* Kofoid et Bush, 1936; *Holocoma* Chatton et Lwoff, 1950; *Syringopharynx* Collin, 1914 (?).

Ancistrocomidae — Ancistrocominae of a strongly elongated (50 μ), banana-shaped body, slightly depressed in the thigmotactic area. The ciliature covers almost the whole surface of the body, with the exception of longitudinal stripe on the dorsal side and a small sector in the hind part of the body behind the thigmotactic area. The kineties are arranged generally in three complexes: the middle complex of several thigmotactic kineties reaching 1/2 of the body length and both lateral complexes, the left and the right, consisting of more and more long kineties, arc-like bent and directted with their ends to each other, making then a parenthetical system. The arrangement of kineties is or is not symmetrical to the median line of the ciliature. Ma elongated: in the hind part of the body there occur vacuoles of concrements. Parasites of the mantle cavity of marine *Bivalvia.*

Typus generis: *Ancistrocoma pelseneeri* Chatton et Lwoff, 1926.

Table 1

Comparison of the data concerning of *Ancistrocoma* sp. sp.

Name used	Author	No. of kineties	Scheme of ciliature			Host	Locality
H. primigenius	Ch. Lw. 1950	19—23	6	6—10	7	*Macoma balthica*	France
H. primigenius	Fenchel 1965	15—17	2—3	6	8	*Macoma balthica*	Baltic Sea
A. pelseneeri	Ch. Lw. 1926	13	2—3	8—9	1	*Macoma balthica*	Boulonge
A. pelseneeri	Ch. Lw. 1950	12—13	7	5	1	*Macoma balthica*	Pas de Calais
A. p. v. *pholadis*	Ch. Lw. 1950	14(13)	4—5	7	1	*Pholas candida*	Pas de Calais
A. pelseneeri	Raabe 1938	13—14	3	5	5—6	*Macoma balthica*	Baltic Sea
A. pelseneeri	Kozloff 1945	14	3	5	6	*Macoma, Mya*	San Francisco Bay
A. pelseneeri	Raabe, actual	13—15	2—3	5—6	4—6	*Macoma balthica*	Baltic Sea
P. myae	Kofoid, Bush 1936	15—16		—		*Mya arenaria*	San Francisco Bay
A. myae	Ch. Lw. 1950		3	6	3	*Mya arenaria*	Woods Hole
A. myae	Fenchel 1965	12	3	5	4	*Mya arenaria*	Kristineberg
A. dissimilis	Kozloff 1946	11(14)	3	4	4—5	*Pholadidea penita*	California
A. thorsoni	Fenchel 1965	18	2—3	8	7	*Abra nitida*	Gullimarfjord
S. pterotrocheae	Ch. Lw. 1950	14	6	2	6	*Pterotrochea coronata*	Méditerrané

Ancistrocoma primigenius (Chatton et Lwoff, 1950)

syn.: *Holocoma primigenius* Chatton et Lwoff, 1950; Fenchel 1965.

The body strongly elongated, slightly buckled. Length 41—50 μ (Ch. Lw.), 47—60 μ (F.), width 14—16 μ (Ch. Lw.), 8—12 μ (F.). Ma elongated ca 25×4 μ, lies in the medium part of the body; Mi spherical, 3 μ, lies next to Ma. Cilia 3.5—4.5 μ on the thigmotactic surface, others — 9—10 μ. The ciliature consists of 19—23 kineties according to Chatton et Lwoff. Fenchel reports the number of probably 15—17 kineties, however he stipulates for that he was not able to state it exactly. According to Chatton et Lwoff the kineties arrangement is as follows: the central part conceived in système sécant has 6—10 kineties, the right part (the left according to Chatton et Lwoff) — 7 kineties, the left one (the right according to Chatton et Lwoff) — 7 kineties. Fenchel reports the central system — 6 kineties, the left one — 8 kineties, the right — 2—3 long kineties (Fig. 3a, A, B, C).

The form reported by Fenchel is distinctly very near to the forms of *A. pelseneeri* which I found in *Macoma baltica* of the South Baltic Sea. It is still more surprising because the author finds that he did not met *Ancistrocoma pelseneeri* in the forms studied by him. The identification of the forms find by Fenchel as *H. primigenius* I accept however fide Fenchel.

Host: *Macoma balthica* (L.) — France (Ch. Lw.), Askö — Balthic Sea, but not Øresund, Kattegat (Fenchel).

Ancistrocoma pelseneeri Chatton et Lwoff, 1926

syn.: *Ancistrocoma pholadidis* Chatton et Lwoff, 1926; *Parachaenia myae* Kofoid et Bush, 1936; *Ancistrocoma myae* (Kofoid et Bush) — auctorum.

According to the original description of Chatton et Lwoff 1926 of the forms found in *Macoma balthica* (L.) — Pas de Calais: Body strongly elongated, somewhat buckled. Length 40—60 μ, width 6—10 μ. Ciliature: "Frange péristomienne droite parcourant la face ventrale en longue hélice sénestre... A ca droite un système hélicoidal dextre de 8 à 9 stries parallèles à la première... Au dela un système de trois stries hélicoidales sénestres... Dans les deux tiers anterieurs un système de deux stries... enfermé entre le système dextre et le système sénestre".

Chatton et Lwoff 1926 report for *A. pholadis* from *Pholas candida:* "Frange péristomienne droite une seconde strie de même course; sur la face droite un système de 2 franges légèrement sénestres". Chatton et Lwoff 1950 couple *A. pholadis* with *A. pelseneri*, but they treat it once as a separate species: (p. 411), once as varietas (p. 413). Moreover they write on the p. 412 that they met *A. pelseneeri* in *Macoma balthica* associated to *A. pholadis* (?!!). The description of 1950 does not contain any new data except that the ciliature of *A. pelseneeri* consists of 12—13 kineties. It results from the drawings of Chatton et Lwoff 1950 that the ciliary system from the right to left (after my own orientation) contains in *A. pelseneeri*: 7 sinistrorsal kineties (7th—13th), thigmotactic kineties (2th—6th) and one dextrorotatory kinety and in *A. pelseneeri* var. *pholadis* respectively: 4, 7, and 2 kineties. Chatton et Lwoff marked after all, that both the number and the system of kineties are highly variable. In any case it is typical for this

system that the kineties on the right from the thigmotactic arrangement are higher in number than on the left (Fig. 3a D, E, F, G).

Kofoid et Bush 1936 described from *Mya arenaria* of San Francisco Bay a new genus and species *Parachaenia myae,* assigned by Kozloff 1946 to the genus *Ancistrocoma.* Kozloff recognized on the basis of the observations of Raabe 1936 the identity of *A. myae* with *A. pelseneeri.* Chatton et Lwoff 1950 report their own data on *A. myae* originating from *Mya arenaria* from Woods Hole; their drawings agree in general drawings of Kozloff 1946 and Raabe 1936, but do not correspond to their own data concerning *A. pelseneeri.* Chatton et Lwoff 1950 consider then *A. pelseneeri* and *A. myae* as separate species (Fig. 3a H, I).

It is really striking that according to Raabe 1938, Kozloff 1945, Fenchel 1965, the *Ancistrocoma* examined by them had the central part of the system of kineties closed in système sécant, which consists of a complex with a reduced number of kineties (2—3) on the right, and on the left a more numerous complex of these kineties (5—6), (Fig. 3a K, L, M, N, O). This arrangement is confirmed by numerous preparations did by the dry silver method (Fig. 3a P, R, S).

A substantial difference is revealed between the data of Chatton et Lwoff and the data of all other authors depending on a specularly opposite presentation of the system of kineties. This is illustrated on the Table I.

In view of this concurrence of many authors, and of individual data only of Chatton et Lwoff, endly in view of a conspicuous adequacy of the forms from *Mya, Macoma* and *Pholas* I consider as admissible to find out an error of Chatton et Lwoff depending distinctly on the position of focus and on taking into consideration the more distant side from the observer as the near one. Then undoubtedly operates the habit. Recently my opinion was confirmed in the work of Khan 1969 and his personal communication recognizing that the ciliary system of *A. pelseneeri* is really inverse than consider Chatton et Lwoff.

After this identification, the data concerning *A. pelseneeri* may be reported as follows:

The body strongly elongated, somewhat buckled. Length 40—83 μ, width 10—20 μ, thickness 10—16 μ. Ma elongated, 11—16×4—7 μ lies in the middle of the body; Mi ovoidal or elongated, 1.2—2.1×3.2 μ, lies besides Ma. C.V. in the middle of the body; in the posterior part concrement vacuole or vacuoles. The long pharyngeal canal. Cilia 8—10 μ.

The ciliary system consists of 12—16 kineties. Its thigmotactic central part consists of relatively short kineties reaching $^2/_3$ of the body length; they run nearly meridionally and more or less parallely, 5—6 in number. On the right from them run 2 or 3 gradually longer, more rarely arranged kineties bent leftwards. On the left from the central complex run 4—6 kineties, also gradually longer, bent to the right and reaching nearly the body end (comp. Table I). The both lateral complexes of the general ciliature closed the thigmotactic kineties in a parenthetical system.

Hosts: Chatton et Lwoff 1950 repport *Macoma balthica* (L.), *Pholas candida* L. — Pas de Calais and *Mya arenaria* L. — Woods Hole, Mass. Kofoid et Bush report, that *A. myae* is only specific for *Mya arenaria* L. — San Francisco Bay. Kozloff 1946 found it mainly in *Mya arenaria* L., but also in *Cryptomya californica* (Conrad), *Macoma inconspicua* Brod. Sov.

Fig. 3a. *Ancistrocoma:* A, B — *A. primigenius* (after Chatton et Lwoff); C — *A. primigenius* (a. Fenchel); D, E, F — *A. pelseneeri* (a. Ch. Lw.); G — *A. pelseneeri* var. *pholadis* (a. Ch. Lw.); H, I — *A. myae* (a. Ch. Lw.); K, L — *A. myae* (a. Fenchel); M — *A. pelseneeri* (a. Raabe); N, O — *A. pelseneeri* (a. Kozloff), P, R, S — *A. pelseneeri* (Raabe, oryg. $AgNO_3$) ×1000

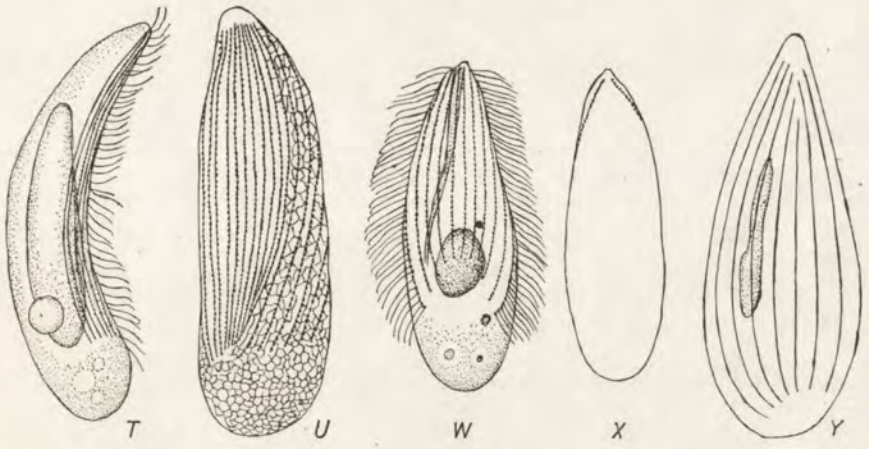

Fig. 3 b. *Ancistrocoma:* T, U — *A. thorsoni* (a. Fenchel); W, X — *A. dissimilis* (a. Kozloff); Y — *Syrinopharynx pterotrochae* (a. Ch. Lw. ×1000

(= *M. balthica*?), *M. nasuta* (Conrad), *M. irus* (Hanley) — San Francisco Bay and in *Macoma secta* (Conrad) — Tomales Bay, Calif.

Besides Chatton et Lwoff report this species in European seas: Raabe 1936, 1938 in *Macoma balthica* L. in south Baltic Sea, however he did not found it in intensively examined *Mya arenaria* L. Fenchel 1965 found it in *Mya arenaria* L — Helsingør and Kristineberg, Kattegat, but did not observed it in *Macoma balthica* L., where he met *A. primigenius*!

Ancistrocoma dissimilis Kozloff, 1946

The body elongated. Length 33—51 μ, width 10—14.5 μ, thickness 8—12 μ. Ma elongated, 6.8—13.7×5.4—7.2 μ, lies in the middle of the body, Mi ovoid, 2.2×2.4—3.2 μ. C.V. in the middle part of the body. The ciliature consists of 11, (rarely up to 14) kineties. The central thigmotactic complex embraces 5 kineties, more or less equal and reaching 3/5 of the body length; on the left usually 3—4, on the right 4—5 kineties, gradually becoming elongated and buckled, the marginal ones reach 3/4 to 4/5 of the body length (Fig. 3b W, X).

Host: *Pholadidea penita* (Conrad) — Moss Beach, California.

Ancistrocoma thorsoni Fenchel, 1965

The body elongated, slightly buckled. Length 46—61 μ, width 15—17 μ, Ma elongated, ca 30 μ, occupies a considerable part (3/5) of the body length. Mi spherical, 2—3 μ. C.V. in the middle of the body. The ciliary system consists of 18 kineties arranged in two sets: the proper thigmotactic complex consisting of 11 kineties with the distance of 1 μ between them, and on the left from it (on the right according to Fenchel) there is a complex of 7 kineties distant from one another by 7 μ. All the kineties end at a distance of about 1/5 of the body length from the posterior end (Fig. 3b T, U).

Host: *Abra nitida* (Müll) especially in the dense population — Gullmarfjord, W. Sweden.

Syringopharynx pterotrocheae Collin, 1914

The body elongated, the dimensions are: 55×25 μ. Ma cylindric. "Il y aurait 14 cinéties; 6 sur la face dorsale, 6 sur la face ventrale légèrement et incurvée, 2 sur les marges droite et gauche". Chatton et Lwoff 1950 in spite of the observations of this ciliate, did not propose any thing new or deciding to its description and conclude: "nous avons l'impression que les genres d'*Ancistrocomidae* que avons admis sont bien distincts du genre *Syringopharynx* qu'il conviendra bien entendu de réetudier" (p. 446—447). This ciliate must be recognized as genus et species inquirendae (Fig. 3b Y).

Host: *Pterotrochea coronata* — Villefranche-sur-Mer, Méditerrané.

Genus *Hypocomagalma* Jarocki et Raabe, 1932

This genus was created by Jarocki et Raabe 1932 for the species *H. dreissenae* described at the same time from the gills of *Dreissena polymorpha* from the Warszawa regions. The individual character of this species consists on the ciliature which covers the whole body in an inverse system than in the genus *Goniocoma* Chatton et Lwoff. This specific system finds confirmation in the described by Kozloff 1946 second species of the genus, namely *H. pholadidis* from *Pholadidea penita* (California).

The distribution of kineties of the representatives of the genus *Hypocomagalma* may be characterized as follows: the thigmotactic arrangement occupies a somewhat concave part of the body. Taking from the right, run several (2—3) kineties more and more short, then followed short kineties, nearly of the same length, next the kineties gradually elongate to the left, reaching the body end: the kineties of the general ciliature. These kineties are not confined to the thigmotactic surface, but they cover also the convex side of the body and their origin does not lye at the base of the sucker, but gradually further backwards, in this way they are at the border of a naked, narrow row, running along the last, right kinety (Fig. 4).

Kozloff 1946 remarks that the first two kineties on the right are distinctly longer than the next ones and are more distant from them and he suggests that: "perhaps these two rows are homologous with the one or two rows constituing the right ciliary complex of *Crebricoma carinata* (Raabe), *Insignicoma venusta* Kozloff, and species of *Hypocomides*." In that way they would correspond to the adoral kineties in my approach. In my opinion these first two (or three) kineties virtually somewhat isolated of the thigmotactic system, may be recognized as the last kineties of the general ciliature, therefore kineties $n, n-1$ and possibly $n-2$. In this case the naked field confined on the one hand by kineties $n, n-1$ and s.o., and on the other by the origin of the last, left kineties, this naked field may be recognized as adequate to the naked, paristomal field of *Hemispeiridae*. This situation remainds to some extend of the conditions in *Hemispeiridae* that the adoral kineties and further kineties (2, 3) often do not start at the apex, but are retracted and originate at the edge of the naked, peristomal field.

The diagnosis of the genus *Hypocomagalma* may be stated as follows:

Hypocomagalma Jarocki et Raabe, 1933

Ancistrocomidae — Ancistrocominae of a fairly elongated, pear-shaped body with somewhat concave thigmotactic area. The ciliature covers almost the whole body surface, with the exception of a little field behind the thigmotactic area. The ciliature consists of several, arc-like bant, thigmotactic kineties and somatic kineties lying on the left side, at first parallel to the former. The kineties of the general ciliature commence first at the body top, and afterwards more and more backwards, just at the right border of the thigmotactic field. Parasites of the mantle cavity of fresh-water and marine *Bivalvia*.

Typus generis: *Hypocomagalma draissenae* Jarocki et Raabe, 1933.

The genus *Hypocomagalma* embraces presently two species:

Hypocomagalma dreissenae Jarocki et Raabe, 1932

The body pearshaped, elongated (n.b. the drawings Jarocki et Raabe performed on the basis of dried preparations reveal a too wide body). Length 32—50 μ, width 14—19 μ, thickness 10—15 μ. Ma ovoid or fusiformed 9—24× ×6—7 μ, lies in the middle of the body, Mi 3—4 μ near Ma, C.V. in the middle of the body. The ciliature covers the whole body and consists of the thigmotactic zone having 7 kineties which reach more or less the half of the body length, bordered by two somewhat longer kineties on the right side, and on the left framed by a dense general ciliature (15 kineties). The first of these kineties (6) originate at the base of the sucker and go farther and range farther backwards; the next (9) begin gradually further to the back from this base so that the last one of them starts in the middle of the body length. *H. dreissenae* moves lively and ably even more ably than other *Ancistrocomidae*. The division was observed (Fig. 4 A, B).

Host: *Dreissena polymorpha* (Pall.), presumably on the whole area of its occurrence. I observed *H. dreissenae* in the region of Warszawa, in the Mazury lakes, and in the saltish waters (zalew Wiślany). I recognized it also out of Poland in the Balaton Lake (Hungary), in freshwaters of Bulgaria and Yugoslavia including the lake Ohrid. Fenchel 1965 examined it in *Dreissena* in the lakes near Kopenhagen.

Hypocomagalma pholadidis Kozloff, 1946

The body pear-shaped, elongated, without a distinct flattening of the thigmotactic surface. Length 63—89 μ, width 18—25 μ, thickness 16—21 μ. The cilia 9—10 μ long, Ma elongated, 12.5—20×5—8.9 μ lies obliquely in the anterior part of the body, Mi spherical 2.4—3.3 μ lies before Ma. The ciliature ranged similarly as in *H. dreissenae*, consists of two longer kineties lying on

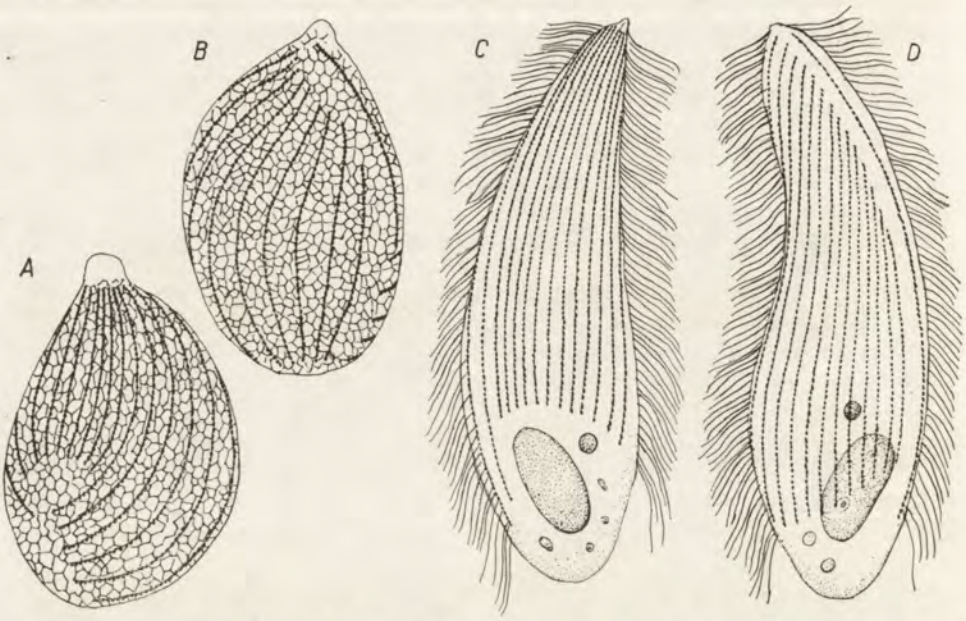

Fig. 4. *Hypocomagalma:* A, B — *H. dreissenae* (after Jarocki et Raabe); C, D — *H. pholadidis* (a. Kozloff) ×1000

the right of the thigmotactic surface and of 22—23 kineties constituing the thigmotactic surface and gradually passing into the general ciliature. These kineties at first are growing longer and originate at the base of the sucker, then reaching nearly the back of the body, they begin gradually farther from the apex (Fig. 4 C, D).

Host: *Pholadidea penita* (Conrad) — Moss Beach, California.

Subfamilia *Hypocomidinae* Raabe, 1967

As it was previously stated these genera were ranged to this subfamily whose representatives preserved besides the thigmotactic ciliature, some traces of adoral kineties of their ancestors in spite of the disappearance of the initial oral aperture. The diagnosis of the subfamily may be as follows:

Subfamilia *Hypocomidinae* Raabe, 1967

Thigmotricha — Ancistrocomidae of an in different grade elongated body, of medium size (20—70 μ). The ciliature consists of a functionally and probably genetically thigmotactic ciliature, limited to the somewhat concave body side, and of elements of the adoral kineties preserved in different grade: two kineties running arc-like from the apical pole, and, sometimes, the rudiment of the loop of one of them. Lack of general ciliature. Parasites of the mantle cavity of marine and fresh-water *Bivalvia*.

Typus subfamiliae: genus *Hypocomides* Chatton et Lwoff, 1922.

Under this assumption, many genera may be arranged to *Hypocomidinae* with differently shaped thigmotactic zone which still preserved on the right of this zone and in some distance the arcuately buckled, individual, long kineties, and sometimes a short segment of cilia (cinétie vestigiale), lying on their prolongation. This interpretation of the enterity of the differentiated kineties seems quite regular, if the space between them and the thigmotactic ciliature will be recognized as homologous of the naked peristomial field of *Hemispeiridae* and we will accept that the entire or nearly entire general ciliature disappeared. The preserved thigmotactic ciliature corresponds in this approach to the left body side of *Hemispeiridae*, what is especially striking when *Insignicoma* is compared to *Proboveria* (Fig. 2). For this reason, among the others I am able to derive *Hypocomidinae* rather from *Ancistrinae* than from *Hemispeirinae* (as would like Chatton et Lwoff 1950).

The degree of preservation of these kineties which we recognized (at least as a work hypothesis) as remains of two adoral kineties may be very different; in *Insignicoma* and *Hypocomides* there are big, individualized kineties reaching up to 3/4 of the body length, strongly buckled, and there is a short, vestigial kinety on their prolongation corresponding to the adoral spiral. It is similarly in *Anisocomides*. In *Isocomides* there exists a "lost" vestigial segment; it may be accepted that the both arcuated kineties disappeared completely. In the remaining genera (*Crebricoma*, *Raabella*, *Hypocomatidium*) only these archely buckled kineties remain, but there is a lack of their vestigial ending segment. Some interpretation difficulties affords the occurrence of only one kinety in *Raabella kelliae* Kozloff, 1946 and even of three those kineties in *Hypocomatidium jarockii* Ch. Lw., 1950.

The thigmotactic zone of *Hypocomidinae* could be different in its structure, it may be uniform, bipartite, or even composed of three series of kineties. Its kineties run almost meridionally or are buckled in such a way that arises a système sécant, (secondarily in my view). There are 7—32 kineties of the thigmotactic system.

Genus *Insignicoma* Kozloff, 1946

This genus created Kozloff 1946 for the species *I. venusta* described at the same time, in order to emphasize the highly individual kind of its ciliature. This form illustrates fairly the reduction process of the adoral ciliature and of the general ciliature of the type *Hemispeiridae — Ancistrinae*. There are here large, distinct kineties isolated from the ones and buckled arcuately. I find in them traces of the adoral kineties, and in their elongation a segment of a kinety rolled up over 180° — a vestigial kinety; it may be find out in it a roll of the adoral spiral. The thigmotactic zone is very spacious and is divided into two parts, every one of them has a dozen or so of kineties. The left part which is relatively farther of the adoral kineties, could be even recognized as a residual of the general ciliature; by now it is included to the thigmotactic zone and is completely assimilated within it (Fig. 5 A, B).

On the basis of a clear description of Kozloff and considering our own approach, the definition of the genus *Insignicoma* may be reported as follows:

Insignicoma Kozloff, 1946

Ancistrocomidae — Hypocomidinae of a pear-shaped, elongated body with flattened thigmotactic area. The apex of the body is narrowed and provided with a retractory sucking snout. The thigmotactic ciliature consists of 2 complexes: the right complex of several kineties reaching 1/2 of the body length, and the left complex of kineties running approximately meridionally. On the right side of the thigmotactic ciliature there are 2 long, arc-like bent kineties (adoral kineties) reaching far backwards; there exists also an arc-like transversal vestigial kinety, bent towards the front and cutting the hind parts of the thigmotactic kineties. Parasites of the mantle cavity of marine *Bivalvia.*

Typus generis: *Insignicoma venusta* Kozloff, 1946.

Presently to the genus *Insignicoma* belongs only one species:

Insignicoma venusta Kozloff, 1946

The body pear-shaped, elongated. Length 42—52 μ, width 18—21 μ, thickness 15—18 μ. Ma ovoidal or elongated measures 12—17×4.4—9 μ and lies in the posterior part of the body; Mi spherical, 2.4—4 μ lies anterior to Ma. C.V. in the middle of the body. The thigmotactic zone dominates in the ciliature; it is divided on two parts: the right one with gradually longer kineties, from the right to the left, but originating more and more from the sucker, 14—15 in number, and the left side with similarly arranged 16—17 kineties. On the right from them at some distance run two (adoral) kineties arcuately bent and parallel; on their elongation, on the left, runs an arch of the vestigial kinety directed by its curvature towards the space between two thigmotactic complexes. The cilia are 8—9 μ long, 12—14 μ on the vestigial arch (Fig. 5 A, B).

Host: *Botula californiensis* (Philippi) — Moss Beach, California.

Genus *Hypocomides* Chatton et Lwoff, 1922

This genus has been created by Chatton et Lwoff 1922 in order to differentiate two species described simultaneously namely *H. modiolariae* and *H. mytili.* These species have been characterized in following terms: "l'air adorale a régressé au point qu'elle n'est plus représentée chaz *H. modiolariae* n. sp. que par un segment d'hélice d'un tiers de tour, et chez *H. mytili* n. sp. par un segment beaucoup plus court encore, continué seulement par une dizaine de grands cils". "La ciliature générale a presque complètement disparu, tandis que l'aire thigmotactique seule s'est consérvée. Deux lignes ciliaires chez *H. modiolariae*, deux côtes sans cils chez *H. mytili*, les unes et les autres à gauche de l'aire thigmotactique, sont tout ce qui reste de la ciliature générale" (Fig. 5 C, D, Fig. 6 A, B).

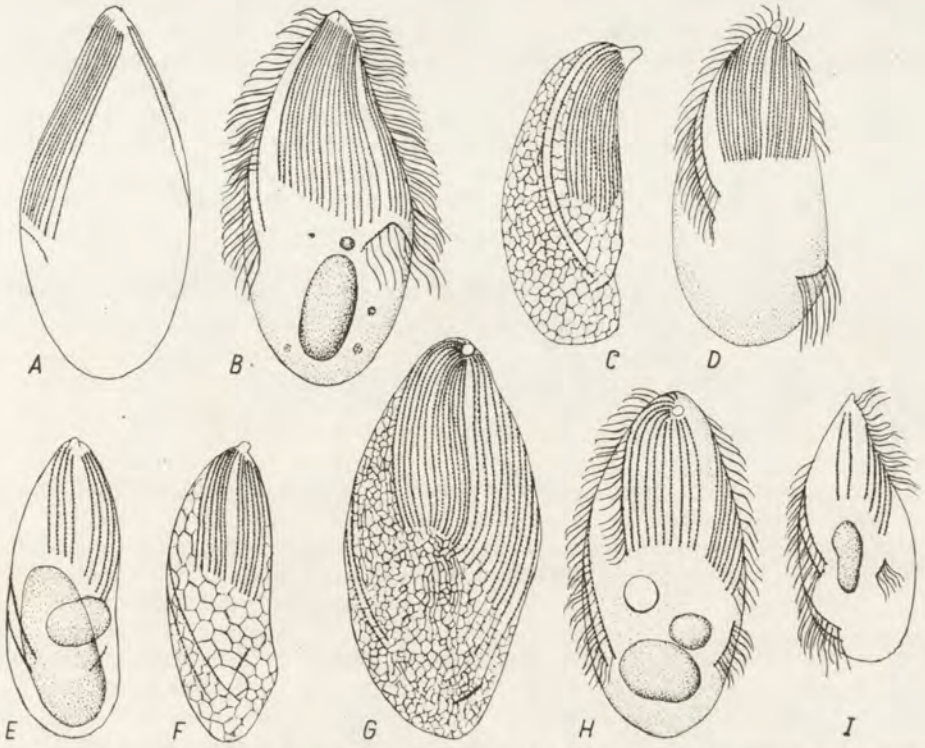

Fig. 5. A, B — *Insignicoma venusta* (after Kozloff); C, D — *Hypocomides modiolariae* (a. Ch. Lw.); E — *H. astarte* (a. Fenchel); F — *H. hiatellae* (a. Fenchel), G — *H. elsinora* (= *modiolariae* 1964 — a. *Fenchel*); H — *H. musculus* (a. Fenchel); I — *Anisocomides zyrphaeae* (a. Ch. Lw.) ×1000

Then Chatton et Lwoff 1926 described the third species from this genus: *H. zyrpaeae* Ch. Lw., 1926. The genus *Hypocomides* Chatton et Lwoff, 1924 set at this time "à la base de la famille, en contact immédiat avec les Ancistridés, dont ils ne diffèrent que l'absence de bouche fonctionelle, les *Hypocomides*: *H. modiolariae* et *H. mytili* qui sont une aire ciliare asymétrique comportant deux systèmes de stries, des vestiges de la ciliature générale et un segment résiduel de frange adorale, long et hèlicoidal chez le premier, trés court chez le second, correspondant à la partie moyenne et antérieure de la frange adorale des Ancistridés."

In view of rather enigmatic descriptions of Chatton et Lwoff which did not give an adequate idea concerning the structure of the ciliary arrangement of their species and genera, Raabe 1938 reported as *Hypocomides mytili* Ch. Lw. a ciliate originating also from *Mytilus edulis* from Hel; the last one did not correspond (as it has been shown) to the individuals of French authors. Kozloff 1946 following Raabe reported a repeated description of *"H. mytili"* from the coasts of America and descriptions of *H. botulae*, *H. parva* and *H. kelliae*. The situation was only elucidated when appeared the monograph of Chatton et Lwoff 1949—1950, reporting the first time the drawings of the studied forms and including a revision of the former

diagnosis. The authors leave within the genus *Hypocomides* Ch. Lw. 1922 only one species: *H. modiolariae*; two remaining species are differentiated by them in two new genera *Isocomides* and *Anisocomides*, and the species reported by Raabe 1938 and by Kozloff 1946 they placed in the new genus *Raabella*.

This decision of Chatton et Lwoff 1950 may be considered as proper both concerning the species ranged by mistake to the genus *Hypocomides* by Raabe and Kozloff, and their own species revealing among them principal differences. Fenchel 1965 filled up the genus *Hypocomides*, describing four farther species namely: *H. elsinora*, *H. musculus*, *H. astarte* and *H. hiatellae*.

On the base of this material the diagnosis of the genus *Hypocomides* may be stated as follows:

Hypocomides Chatton et Lwoff, 1922

Ancistrocomidae — Hypocomidinae of a pear-shaped, elongated body, with flattened thigmotactic area. The thigmotactic ciliature consists of a uniform complex of the meridionally arranged kineties, parallel to each other, reaching 1/2 of the body length. Two arc-like bent kineties, parallel to each other and reaching far to the end of the body (adoral kineties) run rightwards. On the prolongation of these kineties, behind the thigmotactic complex, lies transversally an arc-like bent vestigial kinety provided with strong cilia. Parasites of the mantle cavity of marine *Bivalvia*.

Typus generis: *Hypocomides modiolariae* Chatton et Lwoff, 1922.

Presently 5 species may be ranged to the genus *Hypocomides*:

Hypocomides modiolariae Chatton et Lwoff, 1922

The body elongated. Length 27—50 μ, width 15—27 μ. Ma elongated, Mi spherical. C.V. in the middle of the body. The thigmotactic zone includes nearly 20 kineties (on the drawing 21), running more or less meridionally, densely arranged and reaching 1/2 of the body length. On the right side two long, buckled kineties (belonging according to Chatton et Lwoff to the general ciliature); on their elongation, on the other side of the thigmotactic field, in the middle of the distance between the field and the body end — the arched segment of the vestigial kinety (Fig. 5 C, D).

Host: *Modiolaria* (= *Musculus*) *marmorata* Forbes — Roscoff.

Hypocomides elsinora Fenchel, 1965

The body pear-shaped, elongated. The length 50—62 μ, witdth approx. 24 μ thickness — 12 μ. Ma elongated, 10—20 μ, lies centrally; Mi, 3 μ, near Ma. C.V. in the middle of the body. The thigmotactic zone includes 13 kineties in the

right and 10 more and more longer kineties in its left part. On the right of it two long archely buckled kineties (adoral), on the left, in the posterior body part, a very short vestigial kinety (Fig. 5 G).

Host: *Musculus niger* (Grey) — Øresund, Kattegat (together with *Ancistrumina caudata*).

Hypocomides musculus Fenchel, 1965

The body elongated, truncated in the posterior part. Length 39—50 μ, width 22—30 μ, thickness approx. 18 μ. Ma elongated, 13×15 μ, lies in the posterior body end; Mi spherical, measures 5—7 μ. The thigmotactic zone counts 10+8 kineties. The adoral kineties slightly buckled, the vestigial longer than in *H. elsinora* (Fig. 5 H).

Host: *Musculus discolor* (L.) — Gullmarfjord.

These three species: *M. modiolariae*, *H. elsinora* and *H. musculus* are according to Fenchel 1965 "closely related ciliates living in closely related lamellibranchs. They form a special group within the genus being characterized by a high number (about 20) of thigmotactic rows".

Hypocomides hiatellae Fenchel, 1965

The body elongated. Length 30—43 μ, width 15—18 μ. Ma spherical, measures 9 μ, Mi 2—3 μ, lay out of the middle of the body. The thigmotactic field contains 5+6 equal-long kineties. The adoral kineties are long, a short and situated close to them vestigial kinety (Fig. 5 F).

Host: *Hiatella arctica* (L.) and *H. striata* (Fleur.) — Gullmarfjord, Kattegat; infestation 0—50%, slight — several specimens.

Hypocomides astarte Fenchel, 1965

The body elongated. Length 36—44 μ, width 17—20 μ, thickness 9—12 μ. Ma elongated, approx. 24×14 μ lies in the back of the body; Mi very large, 11×8 μ close to Ma. The thigmotactic field contains 4+5 kineties; kineties of the left part of arrangement grow gradually longer. Long adoral kineties, short vestigial kinety in the posterior body end (Fig. 5 E).

Host: *Astarte montagui* (Dilvyn) — Gullmarfjord, Kattegat; infestation 15—50%, usually few, in one case in mass.

Genus *Anisocomides* Chatton et Lwoff, 1950

This genus created Chatton et Lwoff 1950 for the differentiated species *H. zyrpaeae* Ch. Lw., 1926, separated from the genus *Hypocomides* Ch. Lw., 1922. This species really, as it was visible from its original description (even without drawings), differentiates rather distinctly from the typical species of the genus: *H. modiolariae* Ch. Lw., 1922 mainly because of its thigmotactic zone which is differentiated on several kineties complexes. Besides it occur here two arched adoral kineties and a short obliquely arranged segment of the vestigial kinety.

In comparison to the description of Chatton et Lwoff 1950 some changes of interpretation ought to be introduced indispensable in our diagram resulting from the drawings of the authors. Chatton et Lwoff 1950

both in their description and on the drawings XXVIII, 10 (here Fig. 5 Y) treat equally the kineties identified by them as 9—10 and 11—12. By now it results from their drawings 8 and 9 on Table X that the kineties 11 and 12 are distinctly differentiated, while the kineties 9 and 10 belong to the thigmotactic complex. The situation speaks for the recognition of these differentiated kineties as adoral kineties, and for the treatment of their rests as thigmotactic arrangement. The vestigial kinety, here very short and situated nearly meridionally, Chatton et Lwoff 1950 treat as a continuation of the declined kinety 1, lying on the left of the thigmotactic arrangement. There were no results of their endeavors in order to examine its origin during the division. In my opinion the vestigial kinety may be rather related to the kineties recognized by myself as adoral ones, similarly as I do it concerning the other genera of the subfamily *Hypocomidinae.*

Next to introducing of these alterations in the interpretation, the diagnosis of the genus *Anisocomides* may be stated as follows:

Anisocomides Chatton et Lwoff, 1950

Ancistrocomidae — Hypocomidinae of pear-shaped, elongated body with flattened thigmotactic area. The thigmotactic ciliature consists of 3 complexes: the madian complex of a few (2) meridionally directed kineties reaching 1/2 of the body length, the left complex of several arc-like bent, more and more longer kineties, and the right complex of a few (2) arc-like bent kineties. On the right side of the right complex there are 2 arc-like bent kineties reaching far backwards (the adoral kineties); there exists also a short vestigial kinety lying transversally behind the left complex. Parasites of the mantle cavity of marine *Bivalvia.*

Typus generis: *Anisocomides zyrpaeae* (Chatton et Lwoff, 1926), Chatton et Lwoff, 1950.

The genus *Anisocomides* contains one species:

Anisocomides zyrpaeae (Chatton et Lwoff, 1926)

The body of mean elongation, flattened on the side of thigmotactic surface. Length 19—38 μ, width 10—15 μ, thickness 7—10 μ. Ma ovoid after the division, 5—6 μ, cylindric before the division, up to 14 μ. Mi big, measures 3 μ. The thigmotactic field divided into three complexes: taking from the right 2 longer kineties run through it, then after some interval 2 short ones, meridionally arranged, further 5 progressively longer kineties. The adoral kineties run parallely to the two first thigmotactic kineties from the right and they reach the body end. On the left side of the posterior body part, behind the kineties of the thigmotactic ciliature, a short vestigial kinety run parallely to them (Fig. 5 Y).

Host: *Pholas* (*Zyrpaea*) *crispata* L. — Wimereux.

Genus *Isocomides* Chatton et Lwoff, 1950

Chatton et Lwoff 1950 created this genus for the species *H. mytili* differentiated from the genus *Hypocomides* Ch. Lw., 1922. This species differs virtually from the typus of the genus that is *H. modiolariae* Ch. Lw., 1922. In the first description Chatton et Lwoff indicated already the difference when they reported: "Deux lignes ciliaires chez *H. modiolariae*, deux côtes sans cils chez *H. mytili*... sont tout ce qui reste de la ciliature générale".

As it results from the descriptions and drawings of Chatton et Lwoff 1922, 1950 *Isocomides mytili* (Ch. Lw., 1922) preserved a uniform thigmotactic ciliature, consisting of 14—18 kineties reaching hardly a half of the body length and a short row of cilia — cinétie vestigiale. The thigmotactic field is bordered by something like ribs, reaching far backwards. There are no kineties which would be considered as remains of the adoral kineties (Fig. 6 A, B).

Finally in 1950 appears a more detailed description and some drawings of Chatton et Lwoff and it seems evident that the organisms reported by Raabe 1938 and Kozloff 1946 from the gills of the same host as *Hypocomides mytili* Ch. Lw., consist a different species, recognized rightly as a representative of a separate genus *Raabella* Ch. Lw., 1950.

The diagnosis of the genus *Isocomides* may be presented as follows:

Isocomides Chatton et Lwoff, 1950

Ancistrocomidae — Hypocomidinae of a pear-shaped, elongated body, with flattened thigmotactic area. The thigmotactic ciliature consists of a uniform complex of the meridionally arranged kineties, parallel to each other, reaching 1/2 of the body length. Backwards of it, there is a transversal, short vestigial kinety. The thigmotactic field is limited on both sides by two non ciliated lines, situated longitudinally and parallely to each other, and reaching far backwards. Parasites of the mantle cavity of marine *Bivalvia*.

Typus generis: *Isocomides mytili* (Chatton et Lwoff, 1922), Chatton et Lwoff, 1950.

The genus *Isocomides* includes one species:

Isocomides mytili (Chatton et Lwoff, 1922)

The body strongly elongated. Length 57—64 μ, width 20—22 μ. Ma elongated, lies in the posterior body part. C.V. in the middle of the body. The thigmotactic field uniform, but divided in the middle by a comb running meridionally: 8—10 kineties on the right of it, on the left 6—7 kineties reaching from the sucker to the half of the body length, ending equally, along the "equator". Behind them lies crosswise a short vestigial kinety. On the right of the thigmotactic system run "deux côtes non cilifères". On the drawings one line

is visible which run backwards; a similar form could exist also on the left of the thigmotactic ciliature. This species is slightly known and described (Fig. 6 A, B).

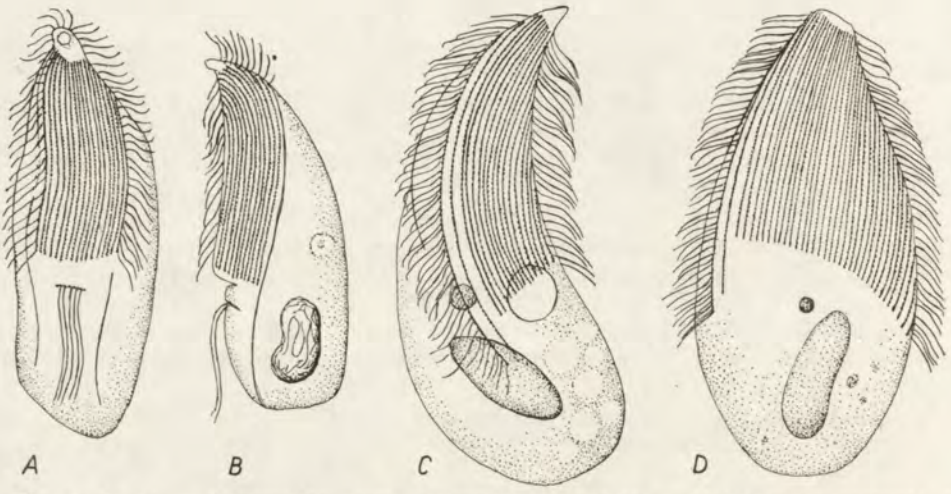

Fig. 6. A, B — *Isocomides mytili* (after Ch. Lw.); C — *Crebricoma carinata* (a. Raabe); D — *C. carinata* (a. Kozloff) ×1000

Host: *Mytilus edulis* L. — Roscoff, Sète, Ch. Lw., Gullmarfjord and Askö, Fenchel 1965.

Genus *Crebricoma* Kozloff, 1946

This genus created Kozloff 1946 in order to set an adequate place for the species found by himself at the coasts of San Francisco Bay, and formerly described from the Baltic Sea as *Hypocomina carinata* Raabe, 1934. This decision was just, because *H. carinata* does not correspond to the features of the genus *Hypocomina* Chatton et Lwoff, 1924, reported as this time rather vaguely. Also there was no clear description of the species typical of the genus, namely *H. patellarum* (Lichtenstein, 1921). The effect of this unprecized description was that also Kozloff 1946 ranged to the genus *Hypocomina* his new species *H. tegularum* corresponding rather to the genus *Enerthecoma* Jarocki, 1934. However the creation of the genus *Crebricoma* resolved the question of the species *H. carinata*, redescribed as the same time by Kozloff. Chatton et Lwoff recognized in their monograph of 1950 (not without reservations) the genus *Crebricoma* in the approach of Kozloff 1946, but its forms described as *C. carinata* (Raabe, 1934) they separated in an individual species *C. kozloffi*.

Slight difference which virtually occur between the descriptions of Raabe 1934 and of Kozloff 1946 result certainly from a variability of the species widely spread with its host, but also to some extent are due to the unadequateness of the descriptions of both authors. The great number of kineties in *C. carinata* is difficult to fix without the silver method, and the

distance among the particular parts of kineties or the differentiation of some of them may be poorly marked. For this reason the move of Chatton et Lwoff 1950 seems unjustified for me and I consider the both discussed forms as one species (Fig. 6 C, D).

The diagnosis of the species *Crebricoma* may be stated as follows:

Crebricoma Kozloff, 1946

Ancistrocomidae — Hypocomidinae of a long (60 μ), pear-shaped body, strongly narrowed anteriorly, with flattened and even concave thigmotactic area. The ciliature is a uniform, large complex of ca 30 kineties, covering densely the thigmotactic area and reaching on the convex part of the body. On the right side there are two longer, arc-like bent kineties, parallel to each other and to neighbouring thigmotactic kineties (adoral kineties). Parasites of the mantle cavity of marine *Bivalvia*.

Typus generis: *Crebricoma carinata* (Raabe, 1934), Kozloff, 1946.

Therefore this genus includes presently only one species:

Crebricoma carinata (Raabe, 1934)

syn.: *Hypocomina carinata* Raabe, 1934; *Crebricoma kozloffi* Ch. Lw. 1950.

The body elongated, distinctly narrowed in the posterior part, slightly buckled. Length 55—72 μ (Kozloff: 58—71 μ) width approx. 30 μ (K.: 27—39 μ), thickness K.: 22—31 μ. Ma 19—27×10 μ (K.: 13—24.3×5.6—11.7 μ) lies in the back of the body; circular Mi, 3 μ (K.: 2.7—3.6 μ) lies in front of Ma. C.V. at the half of the body length. There is a distinctly large and strong thigmotactic zone, which occupies the concavity of the body, numbering over twenty (Raabe) to over thirty (up to 34 — Kozloff) kineties, densely arranged next to one and reaching far over half of the body length. Two kineties longer and running at larger distances are distinct on the right of the thigmotactic arrangement more (Kozloff) or less (Raabe) distinctly — they may be recognized as adoral kineties. The marginal left kineties of the thigmotactic arrangement are also somewhat rarified (Fig. 6 C, D).

Host: *Mytilus edulis* L. — Baltic Sea (Gdańska Bay), Askö — Sweden, San Francisco Bay. Infestations do not occur very often and as a rule are not numerous.

Genus *Raabella* Chatton et Lwoff, 1950

This genus was created by Chatton et Lwoff for the species described by Raabe 1938 from the Baltic Sea as a *Hypocomides mytili* Ch. Lw., 1922 renamed on *Raabella helensis* Ch. Lw., 1950. The unquestionable mistake of Raabe 1938 resulted from a quite misleading description without

any drawings of *Hypocomides mytili* Ch. Lw., 1922, verified only in 1950. Consequently of this verification, Chatton et Lwoff 1950 included to the genus *Raabella* also the species' described by Kozloff 1946 as belonging to the genus *Hypocomides*, and distinctly approximated to *R. helensis*, namely: *H. botulae*, *H. parva* and *H. kelliae* (Fig. 7).

Among these species, three: *R. helensis* Ch. Lw., 1950, *R. botulae* Kozloff, 1946 and *R. parva* (Kozloff, 1946) correspond properly to the character of one genus. They have a thigmotactic ciliature divided in two zones: the medium one of short, straight kineties, and left zone — of arched kineties, which grow longer. Finally there are two long, strongly arched kineties, considered by me as adoral kineties. Only *R. kelliae* (Kozloff, 1946) differs from them having only one right, arched kinety. This feature is in my opinion very important, because it is concerning the adoral kineties which are decisive in my considerations. I could explain this character by a further reduction of the adoral kineties, namely by a complete atrophy of one of them.

If this character would be confirmed the species *R. kelliae* (Kozloff, 1946) could be qualified for the creation of a new genus for it.

The diagnosis of the genus *Raabella* may be stated as follows:

Raabella Chatton et Lwoff, 1950

Ancistrocomidae — Hypocomidinae of a pear-shaped, feebly elongated body (30 μ), with moderately flattened thigmotactic area. The thigmotactic ciliature consists of 2 complexes: the right complex of a few straight kineties reaching 1/2 of the body length, and the left complex of a few arc-like bent kineties reaching more backwards. On the right side there are 2 arc-like bent, long kineties, reaching far backwards (adoral kineties). Parasites of the mantle cavity of marine *Bivalvia*.

Typus generis: *Raabella helensis* Chatton et Lwoff, 1950.

The genus *Raabella* embraces by now three good species and one distinctly deviating from the type of the genus:

Raabella helensis Chatton et Lwoff, 1950

syn.: *Hypocomides mytili* Ch. Lw., 1922 — Raabe 1938, 1949, Kozloff 1946.

The body ovoidal, narrowed in front. Raabe 1938 distinguishes two forms, occurring together in the populations, but differing between them by dimensions and number of kineties; these are f. *major* and f. *minor*. Length: f. *major* 26—36 μ, f. *minor* 17—26 μ, according to Kozloff 34—48 μ, to Fenchel 20—30 μ; width f. *major* 19—21 μ, f. *minor* 15—17 μ, according to Kozloff 13—18 μ, according to Fenchel — 15 μ. Ma spherical, 8 μ, lies in the back of the body; Mi — 3 μ, before Ma at the half of the body length. C.V. slightly visible, in the back of the body (according to Kozloff — centrally).

The thigmotactic zone is formed into two complexes, the centrally lying complex of 6—8 kineties (Kozloff — 8, Fenchel — 5), running meridionally, arranged closely to one another and reaching only 1/3 of the body length, where they end equally, or nearly equally and the left set of kineties 5—6 in number (Kozloff — 8, Fenchel — 7—8) progressively longer to the left body part so that the last reach 1/2 of the body length. On the right, on a larger distance of the thigmotactic system, run two long, archely buckled and parallely running kineties, reaching nearly the body end (adoral kineties). Cilia 8.5—9 μ long (Fig. 7 A, B, C, D, E).

Among the two forms differentiated by Raabe 1938, f. *major* has the thigmotactic complex consisting of 8+6 kineties, f. *minor* — of 7+5 kineties. The forms described by Kozloff 1946 amounts to 7+9 (on the drawings 8+8, 7+8), and the both sets embrance kineties growing from the right to the left. In my own specimens from the Baltic Sea, kineties of the central com-

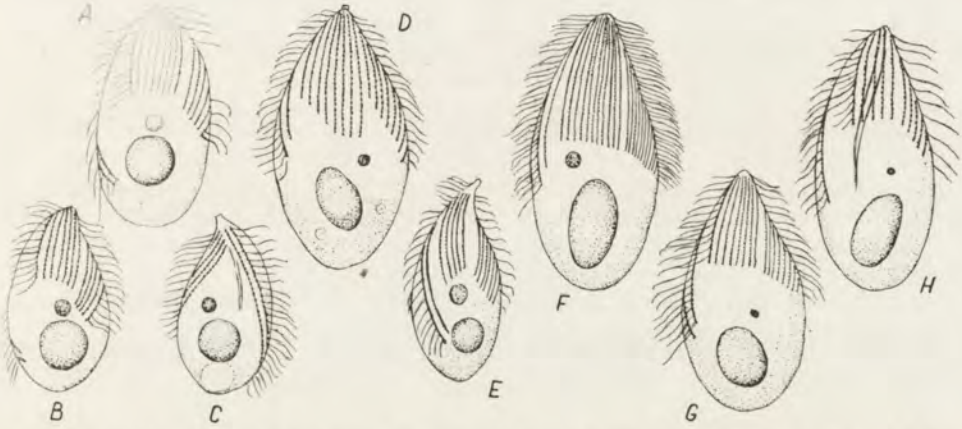

Fig. 7. *Raabella:* A — *R. helensis* f. *maior* (after Raabe); B, C — *R. helensis* f. *minor* (a. Raabe); D — *R. helensis* (a. Kozloff); E — *R. helensis* (a. Fenchel); F — *R. botulae* (a. Kozloff); G — *R. parva* (a. Kozloff); H — *R. kelliae* (a. Kozloff) ×1000

plex are cut parallely, but i.e. in *R. helensis* from *Mytilus minimus* from Adriatic, they really can grow longer from the left to the right. Fenchel 1965 in his description of *R. helensis* reports (p. 119): "The form described by Kozloff differs in several ways from the form of Raabe, and may be a different species, while the form described here does not differ in any way from that described by Raabe".[3] I suggest that all these forms belong to one species, and represent merely its geographic and ecologic variability — Fig. 7.

[3] Chatton et Lwoff 1950 report on the figure XXVI the drawing of *R. kelliae* (Kozloff) as *R. helensis* according to Kozloff. At the end of the description of *R. helensis* they mention the "*Enerthecoma properans* de Hel" which was newer described from sea. There are many examples of carelessness in the work of Chatton et Lwoff.

Hosts: *Mytilus edulis* L. — Baltic Sea, Skagerrak, Kattegat; San Francisco Bay; *Mytilus galloprovincialis* — Adriatic Sea (Split), Black Sea (Varna) — R a a b e, unpublished data; *Mytilus minimus* — Adriatic Sea (Split) — R a a b e, unpublished data.

Raabella botulae (Kozloff, 1946), Ch. Lw., 1950

The body meanly elongated. Length 31—39 μ, width 14—17 μ, thickness 12—14 μ. Ma, 9—13×4.7—7 μ, lies in the posterior of the body; Mi 2.4—3.2 μ, spherical, lies near Ma at the half of the body length. The central thigmotactic complex embraces 11 kineties, reaching 1/2 of the body length, ending equally and meridionally; the left complex embraces also 11 kineties, progressively longer, counting from the left to the right. Two long kineties on the right of the thigmotactic ciliature reach 3/4 to the body back. Cilia are 8—9 μ long (Fig. 7 F).

Host: *Botula californiensis* (Philippi) — but not *Botula falcata* (Could.) — Moss Beach, California — a slight infestation.

Raabella parva (Kozloff, 1946) Ch. Lw., 1950

The body meanly elongated. Length 21—29 μ, width 10—13 μ, thickness 8—11 μ. Ma ovoid, 4.2—8.2×4.2—5.3 μ lies on the back of the body; Mi 1.9—2.3 μ half of the body length. The central thigmotactic complex embraces 8 kineties, ending equally at the distance of 2/5 of the body length, the left complex embraces 8 progressively longer kineties. Two long kineties on the right reach 3/5 of the body length. Cilia 6—7 μ long (Fig. 7 G).

Host: *Botula californiensis* (Philippi), — but not *Botula falcata* (Gould.), separately or together with *R. botulae* — Moss Beach, California.

Raabella (?) *kelliae* (Kozloff, 1946) Ch. Lw., 1950

The body elongated. Length 31—37 μ, width 13—15 μ, thickness 11—13 μ. Ma ovoid, 7.8—14×3.9—7 μ lies at the posterior body end; Mi, 1.9×1.5 μ to 2.3×1.9 μ lies at the half of the body length. The central thigmotactic complex embraces 5 kineties, reaching 1/3 of the body length, ending equally; the left complex has also 5 kineties which grow longer. On the right of the thigmotactic arrangement occurs one kinety only; it fills the same position as fill two kineties in other species! (Fig. 7 H).

Host: *Kellia laperousi* Deshayes — Moss Beach California.

Genus *Hypocomatidium* Jarocki et Raabe, 1932

This genus has been created by J a r o c k i et R a a b e 1932, in order to differentiate the simultaneously described species *H. sphaerii* which differs among the freshwater *"Hypocomidae"* by its ciliary arrangement. Three complexes may be differentiated in this arrangement: the left one constituted of several kineties running in dextrorotatory arches, the middle one — of two sinistrorsal kineties finally the right one — also of two sinistrorsal kineties, but conspicuosly longer than the former ones. R a a b e 1938 treated this third complex as the remains of adoral kineties (similarly to these kineties

in *"Hypocomides mytili"* = *Raabella helensis*), and the two remaining complexes as a thigmotactic ciliature (Fig. 8).

Chatton et Lwoff 1950 not agreeing with this thesis, interpreted differently the ciliary arrangement: they take the left complex as a thigmotactic ciliature, and the two remaining so the two pairs of kineties — as "cinéties somatiques générales". At the same time Chatton et Lwoff described the new species ranged by them to the genus *Hypocomatidium*, as *H. jarockii*. This species represents in general the same type of structure of the ciliary system as *H. sphaerii*, but it last complex on the left embraces three (not two) kineties!!! If this difference would be verified in further examinations, then *H. jarockii* would be enclosed into a separate genus as having a different and quitely individual kineties arrangement seized by me as adoral kineties!. The phenomenon of triple kineties which I consider as adoral ones could be elucidated only in this way that it was the question of the first kinety of the former general ciliature which has been often among the *Hemispeiridae* differentiates from the other ones, subsequent kineties and follows the adoral kineties (comp. part I, pp. 15, 23).

Taking into consideration the both species assigned to the genus *Hypocomatidium*, the diagnosis of the genus may be stated as follows:

Hypocomatidium Jarocki et Raabe, 1933

Ancistrocomidae — Hypocomidinae of a pear-shaped body with flattened and even concave thigmotactic area. The thigmotactic ciliature consists of 2 complexes: the right complex of a few (2) arc-like bent kineties, and the left complex of several short, a little bent kineties. On the right side of the right complex there are 2 longer, arc-like bent kineties, reaching far backwards (the adoral kineties). Sometimes there are three such kineties! Parasites of the mantle cavity of fresh-water and marine *Bivalvia*.

Typus generis: *Hypocomatidium sphaerii* Jarocki et Raabe, 1933.

The genus *Hypocomatidium* embraces two discussed species:

Hypocomatidium sphaerii Jarocki and Raabe, 1932

The body elongated, enlarged at the back, slightly buckled. Length 30—45 μ, width 14—18 μ, thickness 9—12 μ. Ma elongated, 15—36×3—7 μ, lies at the half of the body length of its convex margin; Mi 3—4.5 μ is arranged in different ways. C.V. in the middle of the body. The ciliature consists of three complexes of kineties: two of them may be recognized as belonging to the thigmotactic ciliature; these are: the left complex of five kineties buckled slightly to the right, and the medium complex of two kineties running meridionally with a slight twist to the left. All these kineties reach nearly a half of the body length. On the right at a considerable distance (4.5—9 μ)

run two separated kineties in an arch strongly buckled to the left reaching 2/3 of the body length (Fig. 8 A, B).

Hosts: *Sphaerium corneum* L., *S. rivicola* Lam. — Jarocki et Raabe, the region of Warszawa; *Sphaerium lacustre* Müll., *S. corneum* L., *Pisidium casertanum* (Poli), *P. obtusale* (Lam.) — Dobrzańska 1958, small water bodies in N. Poland; presumably also other species of *Sphaerium* and *Pisidium* of Europe.

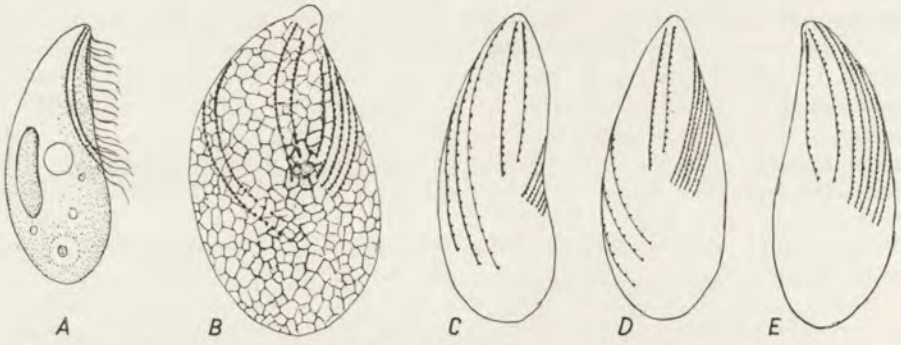

Fig. 8. *Hypocomatidium*: A, B — *H. sphaerii* (after Jarocki et Raabe); C, D, E — *H. jarockii* (a. Ch. Lw.) ×1000

Hypocomatidium (?) *jarockii* Chatton et Lwoff, 1950

The body elongated. Length 40—52 μ, width 14—18 μ. The lack of data concerning the nuclear apparatus. The ciliature is composed of three complexes: the left one 5—6 kineties, slightly dextrorotatory and densely arranged, the medium complex — two kineties running meridionally and largely dispersed, and the third complex of three kineties long and sinistrorsal, distinctly distant from the former ones. The length of kineties of these complexes is presented on the drawings of Chatton et Lwoff in different ways.

Chatton et Lwoff 1950 recognize only as a thigmotactic ciliature the left (right according to them) complex of 5—6 kineties, and they consider the two remaining as "cinéties somatiques générales". According to the orientation and interpretation accepted here, the two first complexes were recognized here as belonging to the thigmotactic ciliature, and the last one (three kineties) as in this case extended residue of adoral kineties (Fig. 8 C, D, E).

Host: *Nucula nucleus* L. — Banyuls-sur-Mer.

Subfamilia *Hypocomellinae* Raabe, 1967

According to the performed division of the family *Ancistrocomidae* these genera were ranged to this subfamily which representatives preserved only the thigmotactic zone of the ciliature, but they lost completely the general ciliature and the traces of the adoral kineties. The diagnosis of the subfamily may be therefore stated as follows:

Subfamilia *Hypocomellinae* Raabe, 1968

Thigmotricha — *Ancistrocomidae* of a rather feebly elongated body, of medium or small dimensions (15—50 μ). The ciliature consists, as can be assumed, of the thigmotactic ciliature only, limited to the front part of the flattened body side and consisting of kineties running longitudinally from the body top or making a parenthetical system. Even the cases of covering with the ciliature almost the whole surface of the body, may be explained as a secondary growth of the thigmotactic ciliature. Nuclear apparatus common. Parasites of the mantle cavity of marine and fresh-water *Bivalvia*.

Typus subfamiliae: genus *Hypocomella* Chatton et Lwoff, 1924.

8 or 9 genera may be ranged to the subfamily *Hypocomellinae*, and the main part of them distinguish oneself by a very convergent body structure, and especially of the thigmotactic zone. This zone is composed of a different number of kineties (from 12 to 4 kineties), usually running from the base of the sucker, more or less meridionally to the back of the body. This zone covers generally 1/2 to 2/3 of the body length. Its kineties deviate however from the meridional situation and very often are not of equal length: the medium ones usually the shorter, run more or less meridionally, the kineties of the right part of the field usually, numbering from its middle, are growing longer and buckle to the left. The left ones are conspicuosly progressively longer and deviate to the right. Thus the thigmotactic zone forms a rather integrated system, bordered by marginal kineties. It lies as the concave surface of the body which according to the previous considerations could be determined as the left side of the body in terms of phylogenesis, however biologically it becomes its ventral part.

The tendency of buckling leads to as arrangement which may form nearly a closed and concave oval, as in *Hypocomina patellarum* (Licht. 1921), and endly a completely closed arrangement, as in *Colligocineta furax* Kozloff, 1965, where the marginal kineties of the left and right body side link together by the distal ends.

Goniocoma macomae (Ch. Lw., 1922) is a completely individual exception from the subfamily *Hypocomellinae*, which body is nearly quitely covered with a ciliature. As I attempted to elucidate (p. 390), it is not the preserved general ciliature, but it is the thigmotactic ciliature spread secondarily over the whole body.

The genus *Hypocomella* (syn. *Heterocineta*, syn. *Hypocomatophora*) affords the more of systematic difficulties in the scope of the subfamily *Hypocomellinae*, from which are described several species, and it should be taken into consideration that some further may appear. The relation of this genus to the genus *Heterocinetopsis* is also not quite clear, as well as to the connected with it genus *Hypocomatophora*. The other genera differentiate rather properly.

Genus *Hypocomella* Chatton et Lwoff, 1924

syn.: *Hypocomatophora* Jarocki et Raabe, 1932; *Heterocineta* Mawrodiadi, 1927 (nomen nudum); *Heterocinetopsis* Jarocki, 1935 — partim.

This genus has been created by Chatton et Lwoff, 1924 for the species *H. cardii* Ch. Lw. 1922 differentiated from the genus *Hypocoma*. The authors are writing: "Le genre *Hypocomella*, que nous proposons pour *H. cardii* dont l'aire ciliare, tout en étant asymétrique, ne comprend qu'un seul système ciliaire et qui est dépourvu de frange adorale. Cette *Hypocomella*... est plus régressé des Hypocomidés que nous connaissons".

In the following years appeared the description of *H. macomae* Ch. Lw., 1926, which Chatton et Lwoff 1950 in a definite monography transferred to a separate genus *Goniocoma* Ch. Lw., 1950. Up to this monography the French authors did not publish any drawings nor outline of any of these species.

In view of this situation, Jarocki et Raabe 1932 created a new separate genus *Hypocomatophora* for the ciliate *H. unionidarum* described from the gills of *Unionidae*. The Polish authors mentioned at that time, that undoubtedly this species was included by Mawrodiadi 1913 as a development form ("primären Keim") to the fantastic development cycle of *Conchophthirus anodontae*!

Jarocki 1934 found in the later slightly known works of Mawrodiadi 1923, 1925, 1927, 1928 some allusions to these species, for which Mawrodiadi applied the name "*Heterocineta anodontae*". Jarocki admits that Mawrodiadi reports some mentions concerning this species "without clearly defining its exact nature and true position in the system of *Ciliata*". Moreover, some mentions of Mawrodiadi 1927 comparing "*Heterocineta*" to *Hysterocineta* could be evident, that Mawrodiadi found also *Ancistrumina* and included it to the development cycle of "*Heterocineta*". Quite unmotivated is the position of Jarocki 1934, recognizing *Hypocomatophora* as a younger synonym of "*Heterocineta*"; virtually the name "*Heterocineta*" should be recognized as nomen nudum, as did it Chatton et Lwoff 1950.

Jarocki 1934, 1935 describes 7 species from the freshwater *Gastropoda*, including them to the genus *Heterocineta;* the exact descriptions of the author give no proper idea of the shape of these species, as Jarocki gives only several photographs of some of them. After Jarocki also Kozloff 1946 described two species ranging them to the genus *Heterocineta*, namely *H. fluminicolae* and *H. goniobasidis* which are fit for the genus *Hypocomella* or *Heterocinetopsis* Jarocki 1935. *Heterocineta phoronopsidis* described by Kozloff 1945 deviates from other genera by some features of structure and by the specificity of the hosts group so far that a separate genus *Kozlefiella* g.n. may be created for it.

Chatton et Lwoff 1950 report finally the first drawing of *Hypocomella cardi* (Ch. Lw., 1922); this individual seems to be swelled or flattened. The authors perform a synonymization of the genera *Hypocomatophora Jar.* et Raabe and *Heterocineta* Mawrodiadi nom. nudum with the genus *Hypocomella*. Some reservations could arise if i.e. *H. cardii* (Ch. Lw., 1950 Fig. XVII) with the strongly buckled kineties and a wide thigmotactic field, would be compared to one of the species of Jarocki 1935 i.e. to *H. chattoni* or

H. raabei (Raabe 1938 Tab. VI, Fig. 5), which has an elongated, narrow thigmotactic field and slightly buckled kineties. However virtually between these shapes exist many transitional forms, and besides it different pictures may arise even in one species depending on fixation methods (the body swelling) or depending on drying (body flattening).

Chatton et Lwoff 1950 too peremptory and in many cases unproperly ranged several forms described as *Heterocineta* sp. sp. to the genus *Heterocinetopsis* Jarocki, 1935 in spite of the fact that the French authors preserved the genus *Heterocinetopsis* only provisionally. In this way the species *H. siedleckii* Jarocki, 1935, *H. krzysiki* Jarocki, 1934 and *H. lwoffi* Jarocki, 1934 included to this genus correspond in many ways to the genus *Hypocomella*. The species *H. unionidarum* (Jarocki et Raabe, 1932) arranged to *Heterocinetopsis* virtually proves a similarity of its highly asymmetric thigmotactic zone to the zone of *Heterocinetopsis*, but in other respects (i.e. the body shape) corresponds to the genus *Hypocomella*. Chatton et Lwoff 1950 ranged also to the genus *Heterocinetopsis* two species of Kozloff 1946: *H. goniobasidis* and *H. fluminicolae;* the first of them corresponds to the genus *Hypocomella*, and the second one may be ranged virtually in the genus *Heterocinetopsis*.

All the species of the genus *Hypocomella* Chatton et Lwoff 1924 have a pear-shaped body (not banana-shaped) strongly narrowed to the anterior end and bent towards the thigmotactic side. The thigmotactic ciliature constitutes one, asymmetric complex consisting of 4—12 kineties. The medium kineties are the shorter ones and they run meridionally, the somewhat longer kineties lye on the right side of the field, considerably longer are these lying at the left side of the field. The marginal kineties may be strongly bent to one another and they close to some extent the thigmotactic field (it is so i.e. in *H. cardii, H. katherinae, H. krzysiki, H. maziarskii*), or they run to three body back, leaving the thigmotactic field open to the posterior part (other species of the genus *Hypocomella*) — Fig. 9.

The definition of the genus *Hypocomella* may be set as follows:

Hypocomella Chatton et Lwoff, 1924

syn.: *Hypocomatophora* Jarocki et Raabe, 1932; *Heterocineta* Mawrodiadi, 1927 (nomen nudum); *Heterocinetopsis* Jarocki, 1935 partim.

Ancistrocomidae — *Hypocomellinae* of a pear-shaped, moderately elongated body, with flattened or concave thigmotactic area. The ciliature consists of one complex of uneven kineties, short and straight in the centre, more and more longer and arc-like bent towards the both sides of the thigmotactic area, especially on the left side. Number of kineties, 4 to 13. Parasites of the mantle cavity of marine and fresh-water *Bivalvia* and *Gastropoda*.

Typus generis: *Hypocomella cardii* Chatton et Lwoff, 1924.

Genus *Hypocomella* is the most abundant in species' genus among the *Ancistrocomidae* and embraces by now 14 species. I try to range them here according to the reduction of the number of kineties.

Hypocomella cardii (Chatton et Lwoff, 1922), Ch. Lw., 1924

syn.: *Hypocoma cardii* Chatton et Lwoff, 1922.

The body ovoidal, stocky. Length 20—30 μ, width 13—15 μ. Ma spherical, Mi elongated. The ciliature consists of 12—13 kineties starting on the base of sucker and running archely to the back. Taking from the right side (the left according to Chatton et Lwoff) run 8 kineties of near equal length reaching the half of the body length; the further kineties (4) are growing longer so that the last one reaches nearly 3/4 of the body length. The ciliates are strongly clinging by their sucker to the epithelium of the host (Fig. 9 A).

Host: *Cardium edule* L. — Roscoff, Boulogne-sur-Mer.

Fig. 9. *Hypocomella:* A — *H. cardii* (after Ch. Lw.); B, C — *H. unionidarum* (a. Jarocki et Raabe); D — *H. goniobasidis* (a. Kozloff); E, F — *H. katherinae* (a. Kozloff); G, H — *H. krzysiki* (a. Raabe); I, K — *H. makedonica* (a. Raabe), L — *H. janickii* (a. Kozloff); M — *H. lwoffi* (a. phot. of Jarocki); N — *H. chattoni* (a. phot. of Jarocki); O — *H. turi* (Raabe, oryg.); P, R — *H. raabei* (a. Raabe); S — *H. raabei* (a. Fenchel); T, U — *H. quatuor* (a. Raabe) ×1000

Hypocomella katherinae Kozloff, 1961

The body with an ovoidal outline, flattened and concave at one side, on which is the thigmotactic surface. Length 25—38 μ, width 10—12 μ (the body is considerably longer on the drawings!). Ma elongated (ratio 1 : 3), lies obliquely, slightly posterior to the middle of the body; Mi ovoid lies anterior to Ma. There is a long pharyngeal canal. C.V. posterior. Cilia 6 μ. The ciliature consists of 11 or 12 kineties. The anterior termini are arranged around the base of the sucker. The 7 or 8 right kineties are of the same length, the 4 left ones are progressively longer and considerably buckled to the right, they close the thigmotactic system in its posterior part at the left side (Fig. 9 E, F).

Host: the chiton *Katherina tunicata* (Wood), on ctenidia — Cape Arago region, Oregon, N. Am.

Hypocomella unionidarum (Jarocki et Raabe 1932)

syn.: *Hypocomatophora unionidarum* Jarocki et Raabe, 1932; *Heterocineta anodontae* Mawrodiadi — Jarocki 1934, 1935; *Heterocinetopsis unionidarum* : Chatton et Lwoff 1950.

The body elongated, strongly narrowed in the anterior part. Length 30—37 μ, width 16 μ. Ma 15—27×5—7 μ lies in the middle of the body length, Mi 3×4 μ lies near Ma. C.V. in the middle of the body. The ciliature consists of 11 (or 10) kineties, beginning at the base of the sucker. Taking from the right the first one reaches by an arch $^1/_2$ of the body length, the next 6 are progressively shorter, but the next 4 are progressively longer so that the last one reaches $^3/_4$ of the body length. The division and conjugation by posterior body parts are observed (Fig. 9 B, C).

Hosts: *Anodonta cygnea* L. and *Unio pictorium* L. in the Warszawa region (Jar. et Raabe); I met *Hypocomella unionidarum* in *Unionidae* in many regions of Poland, and in *Unio crassus* Retz. in the lake Ohrid, Yugoslavia (Raabe, 1966).

Hypocomella goniobasidis (Kozloff, 1946)

syn.: *Heterocineta goniobasidis* Kozloff, 1946; *Heterocinetopsis goniobasidis* : Chatton et Lwoff 1950.

The body elongated. Length 36—48 μ, width 15—20 μ, thickness 11—14 μ. Ma 10—13.5×4—5.5 μ lies in the middle of the body length, Mi 1.2—1.7 μ lies anterior to Ma. C.V. central. Cilia 9 μ long. The ciliature consists of 10 kineties. Taking from the right side, 6 kineties are running of nearly equal length reaching the half of the body length; next 4 kineties start progressively further of the sucker base and reach further and further to the posterior in this way that the last left kinety reaches $^2/_3$ or even $^3/_4$ of the body length (Fig. 9 D).

Host: *Goniobasis plicifera silicula* (Gould.) on the gills and the mantle cavity — Portland, Oregon, N. Am.

Hypocomella krzysiki (Jarocki, 1934)

syn.: *Heterocineta krzysiki* Jarocki, 1934; *Heterocinetopsis krzysiki* : Chatton et Lwoff 1950.

The body subovoid. Length 26—38 μ, width 14—15 μ, thickness 10—12 μ. Ma 7—15×4—7 μ, ovoid lies in the middle of the body length; Mi spherical, 2.2—3 μ, lies anterior to Ma.

The ciliature consists of 9 kineties. Taking from the right side: the first is longer than the next ones, the further 3 are progressively shorter, then the 5 are growing so that the last ones are "deflected to the right run arcuately to the median axis of the ventral surface, bounding the other rows posteriorly" (Jarocki 1934 p. 186). This closure of the thigmotactic arrangement of *H. krzysiki* constitutes its conspicuous distinctive character (Fig. 9 G, H).

Jarocki 1934, 1935 mentions that *H. krzysiki* proves a tendency to migrate on the body of *Chaetogaster limnaei*, parasitizing in *Bithynia*.

In the description of *H. krzysiki* reported by Chatton et Lwoff 1950 is included a whole passage concerning evidently *H. maziarskii*, quoted after Jarocki. In this way arises a chimera that could not be reciphered (p. 421). By the way Chatton et Lwoff consider both these species as belonging to the genus *Heterocinetopsis* Jarocki, 1935 without any reasons for it.

Host: *Bithynia tentaculata* (L.) — the region of Warszawa (Jarocki). I met this species in *Bithynia tentaculata* (L.) in the Mazury lakes (N. Poland), in salted-watered Zalew Wiślany and in Balaton Lake (Hungary).

Hypocomella siedleckii (Jarocki, 1935)

syn.: *Heterocineta siedleckii* Jarocki, 1935; *Heterocinetopsis siedleckii* : Chatton et Lwoff 1950.

Body subovoid. Length 27—35 μ, width 15 μ, thickness 10—12 μ. Ma of various shape, 12—18×4.5—7 μ lies in the middle of the body length. Mi spherical 3—3.4 μ, lies anterior to Ma. C.V. in the middle of the body. The ciliature consists of 9 kineties. From the right: one kinety somewhat longer and more bent, the two next progressively shorter, the two next the shortest ones, reaching nearly the half of the body length, the last 3 kineties are gradually longer, reach scarcely $^3/_4$ of the body length. All kineties start at the base of the sucking tentacle. No drawings or photographs.

Host: *Acroloxus lacustris* (L.) on the skin and pseudobranchium, Wilanów near Warszawa.

Hypocomella makedonica (Raabe, 1965)

syn.: *Hypocomatophora makedonica* Raabe, 1965.

The body elongated. Length 20—25 μ, width ca 8 μ. Ma ovoid, 10×4 μ lies in the middle of the body length; Mi, 3 μ close to Ma. C.V. (?) at the posterior body part. The ciliary system consists of 9 kineties. The first (right) kinety is bent right as a slight arch. It reaches beyond the half of the body length. The next 5 kineties are nearly parallel to it, but become gradually

shorter, so that the last one (the sixth) reaches scarcely as far as half of the body length. The system is closed by 3 kineties, bent leftwards, much longer than the other so that the last of them reach beyond $^3/_4$ of the body length. All the kineties initiate at the base of the tentacle, rarely the fifth or the sixth one is slightly shifted (Fig. 9 I, K).

Host: *Pseudamnicola sturanyi* Wst. (*Prosobranchia, Hydrobiidae*) — from the shallow litoral overgrown with *Chara,* on the depth of 5 m — Ohrid Lake.

Hypocomella janickii (Jarocki, 1934)

syn.: *Heterocineta janickii* Jarocki, 1934.

The body slightly elongated. Length 23—32 μ, width 12—17 μ, thickness 10—13 μ. Ma various-shaped, 6—12×3—6 μ lies rather in the posterior part of the body; Mi, 2—3 μ, lies anterior to Ma. C.V. in the middle, at the concave side of the body. Cilia 5—7 μ. The ciliature consists of 8 kineties. Taking from the right side — 4 short kineties, then 4 progressively longer so that the last ones reach $^2/_3$ of the body length; at the end of these kineties the kinetosomes are more rarely arranged. According to the data of J a r o c k i 1935, *Hypocomella janickii* moves numerously on the body of *Chaetogaster limnaei,* parasitizing in *Physa* (Fig. 9 L).

Host: *Physa fontinalis* (L.) often infestation (up to 100%) but not numerous, the region of Warszawa (J a r o c k i); *Physa cooperi* Tryen. — Mt. Eden, California (K o z l o f f 1946).

Hypocomella maziarskii (Jarocki, 1935)

syn.: *Heterocineta maziarskii* Jarocki, 1935.

Body longitudinally ovoid. Length 26—38 μ, width 13—16 μ, thickness 10—11 μ. Ma diversiform, 6—16×3—4.5 μ lies in the middle of the body length; Mi spherical 3 μ, lies anterior to Ma. C.V. central. The ciliature consists of 8 kineties. Taking from the right: the first one limits the thigmotactic field from the right side and reaches by its end so far, as the last, left kineties; the next 4 kineties are gradually shorter, next 3 — progressively longer and conspicuously bent close the arrangement from the left side. The last left kineties initiate further and further from the sucker. No drawings.

Host: *Coretus corneus* (L.), especially young, the region of Warszawa.

Hypocomella lwoffi (Jarocki, 1934)

syn.: *Heterocineta lwoffi* Jarocki, 1934; *Heterocinetopsis lwoffi* : Chatton et Lwoff 1950.

The body ovoid, slightly elongated. Length 20—32 μ, width 12—15 μ, thickness 9—10 μ. Ma diversiform, 6—17×3—6 μ, lies in the middle of the body length; Mi 3 μ, lies anterior to Ma. C.V. in the middle of the body. Cilia 8 μ. The ciliature consists of 8 (sometimes 7) kineties. Taking from the right: 5 kineties of the same length reach the half of the body length, next three

kineties are progressively longer reaching $^2/_3$ or ven $^3/_4$ of the body length. The right kineties initiate at the base of the sucker, the next further from it. The division and conjugation has been observed; it is effected not only by posterior ends but also in other positions (Fig. 9 M).

Host: *Viviparus fasciatus* O. F. M., mantle and tentacles — Wilanów (Warszawa region).

Hypocomella chattoni (Jarocki, 1934)

syn.: *Heterocineta chattoni* Jarocki, 1934.

The body elongated, sigmoidal. Length 27—38 μ, width 15—18 μ, thickness 10—12 μ. Ma, 12—17×3—5 μ, in the middle of the body length; Mi, 3 μ next to it. C.V. in the body medium. The ciliature consists of 7 kineties. Taking from the right, 4 kineties more or less of the same length reaching scarcely the half of the body length, next 3 kineties are gradually longer and the last of them reaches scarcely $^2/_3$ of the body length (Fig. 9 N).

Host: *Radix ovata* (Drep.), *R. auricularia* (L.), *Stagnicola palustris* (Müller), on mantle and tentaculae, slight infestation — Warszawa region.

Hypocomella turi (Jarocki, 1935)

syn.: *Heterocineta turi* Jarocki, 1935.

Body subovoid. Length 22—32 μ, width 15—16 μ, thickness 10—12 μ. Ma 6—16×3—6 μ, in the middle of the body length; Mi, 3—4 μ anterior to Ma. C.V. — centrally. The ciliature consists of 7 kineties. From the right: 4 kineties short and 3 next somewhat longer, reaching the half of the body length; the last left kineties initiate at the back from the base of the sucker (Fig. 9 O).

Host: *Tropidiscus planorbis* (L.), *Spiralina vortex* (L.) — Warszawa region (Jarocki). I have met *H. turi* in *S. vortex* from the Jeziorka river near Warszawa.

Hypocomella raabei Chatton et Lwoff, 1950

syn.: *Hypocomella cardii* Ch. Lw. : Raabe 1938.

The body elongated. Length 21—24 μ, width 8—11 μ. Ma spherical 6.5 μ, lies in the posterior part of the body; Mi, 1.5 μ, in the middle of the body length. C.V. slightly outlined. Concretion vacuoles were observed.

The ciliature consists of 6 kineties. From the right of the arrangement: 3 kineties slightly dextrorotatory gradually shorter, then 3 somewhat sinistrorotatory, progressively longer. The thigmotactic field narrow, elongated (Fig. 9 P, R, S).

Host: *Cardium edule* L. (recte *Cardium lamarcki*) south Baltic Sea, rarely and poor in number.

Chatton et Lwoff 1950 describe a new form of this species namely: *Hypocomella raabei* f. *roscoffiensis*, with a following character: the body

elongated, length 23—27 μ, width 13—14 μ. Ma somewhat elongated, subspherical, 9—11×5.5 μ. The ciliature consists of 7 kineties.

Host: *Cardium exiguum* Gm. et Pemp. — Roscoff.

Hypocomella quatuor Raabe, 1968

The body pear-shaped, elongated. Length 15—18 μ, width 6 μ. Ma 10 μ, lies in the middle of the body length; Mi, 3 μ, close to Ma. The ciliature consists scarcely of 4 kineties; the left ones are bent slightly to the left, the right to the right side. The thigmotactic field is rather narrow (Fig. 9 T, U).

Host: *Theodoxus fluviatilis* L., so far observed only in some Mazury lakes, N. Poland. In spite of examinations effected on *Ciliata* from *Theodoxus* in Poland, in Hungary, Bulgaria and Yugoslavia (the Ohrid lake included) I have any where met in this host a representative of the family *Ancistrocomidae*.

Genus *Heterocinetopsis* Jarocki, 1935

This genus created J a r o c k i 1935 for the species *H. reichenowi*, described at the same time from *Viviparus fasciatus*, which distinguishes itself rather clearly from those ranged by him to the genus *Heterocineta* Mawrodiadi. The differences consist both in a considerable elongation and in a cylindrical body form and in the structure of the thigmotactic ciliature conspicuously asymmetrical. Its right part includes more or less equal kineties reaching the half of the body length, the left one gradually longer bent kineties, reaching scarcely the body end. In comparison to the genus *Hypocomella* (= *Heterocineta*) the difference depends on the intensity of the features appropriate to its representatives however it is in that specific case sufficiently evident (Fig. 10 A).

The problem seems not so evident when it is the question of arrangement to the genus *Heterocinetopsis* of other species belonging to the genus *Heterocineta* and outstanding by a higher dissymetry of the thigmotactic system. C h a t t o n et L w o f f 1950 ranged here quite arbitrary many species, namely: *H. unionidarum, H. siedleckii, H. krzysiki, H. lwoffi, H. goniobasidis* and *H. fluminicolae*. In my view it is no quite valid because these species probably except for *H. fluminicolae* Kozloff, 1946, do not differ more evidently from these, which C h a t t o n et L w o f f 1950 left in the genus *Hypocomella* (= *Heterocineta*).

In spite of the secondary revision applied by myself and the enclosure to the genus *Heterocinetopsis* besides the species typical of the genus, also *H. fluminicolae* (K o z l o f f, 1946) and *H. ohridanus* Raabe, 1965, the borderline between this genus and the genus *Hypocomella* (= *Heterocineta*) is not so clear. Among the species ranged to the genus *Hypocomella, H. unionidarum* (Jarocki et Raabe, 1932) is close to the genus *Heterocinetopsis* and has conspicuously long kineties on the left part of the thigmotactic system. Probably the finding of other species would efface more this difference.

The diagnosis of the genus may be now presented as follows:

Heterocinetopsis Jarocki, 1935

Ancistrocomidae — Hypocomellinae of a banana-shaped, strongly elongated body (ca 50 μ). The ciliature is distinctly assymetrical: starting from the median kineties — there are arranged on the right side a few more and more long kineties, not surpassing 1/2 of the body length; on the left side the kineties are distinctly longer and bent so, that the last kineties reach almost the end of the body. Parasites of the mantle cavity of fresh-water *Gastropoda — Prosobranchia.*

Typus generis: *Heterocinetopsis reichenowi* Jarocki, 1935.

Only three species may be included to the genus *Heterocinetopsis:*

Heterocinetopsis reichenowi Jarocki, 1935

The body strongly elongated, cylindrical. Length 27—65 μ, width 12—15 μ. Ma ovoidal or elongated, 12—24×7—9 μ, lies in the centre of the body, Mi spherical, very small 1.5—1.7 μ, lies anterior to Ma. C.V. in the centre of the body. In the posterior body part numerous food vacuoles. Cilia 5—6 μ. The asymmetrical ciliary system consists of 12 kineties, the proximal ends of which commence just at the base of the tentacle at the same level, almost in contact with each other. Kineties 1—8 do not surpass 1/2 the length of the body; these kineties do not differ greatly in length, the 4th or 5th being the shortest. Kineties 9—12 become progressively longer, the 11th and 12th reach often almost to the end of the body (Fig. 10 A).

Host: *Viviparus fasciatus* Müller, frequent on branchia, vicinity of Warszawa.

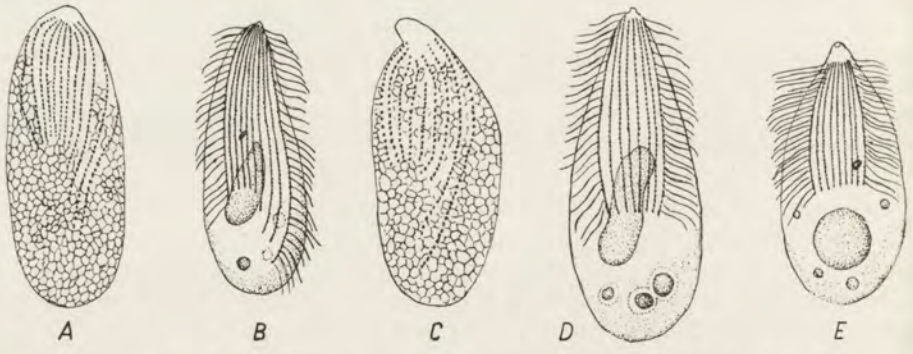

Fig. 10. A — *Heterocinetopsis reichenowi* (after phot. of Jarocki); B — *H. fluminicolae* (a. Kozloff); C — *H. ohridanus* (a. Raabe); D — *Enerthecoma properans* (a. Kozloff); E — *E. tegularum* (a. Kozloff) ×1000

Heterocinetopsis fluminicolae (Kozloff, 1946)

syn.: *Heterocineta fluminicolae* Kozloff, 1946.

The body strongly elongated. Length 30—36 μ, width 13—17 μ, thickness 10—12 μ. Ma 7.4—10×3.9—4.4 μ lies in the middle of the body length; Mi, 1.5×1.2 μ lies anterior to Ma. C.V. central. Cilia 6—7 μ. The ciliature consists of 10 kineties "the first 6 rows from the right side are approximately of the same length being about $^2/_3$ the length of the body. The last 4 rows become increasingly longer and incurved in such a way that they terminate one behind the other not far to the left of the midline. The longer row extends to the posterior end of the body" (Fig. 10 B).

Host: *Fluminicola virens* (Lea), on the gills and mantle, Portland, Oregon, N. Am.

Heterocinetopsis ohridanus Raabe, 1965

The body elongated, banana-shaped. Length 30—45 μ, width ca 15 μ. Ma ovoid, 10×6 μ lies in the middle body part; Mi 3 μ, close to Ma. C.V. slightly marked, in posterior body part. Concretions vacuoles appear often near Ma. The ciliary system consists of 9 kineties. The first kinety (starting from the rigth side of the area) reaches beyond $^1/_2$ of the body; the next 4 kineties are gradually somowhat shorter; they initiate gradually farther from the base of the tentacle. On the left side, the system is closed by 4 gradually longer kineties, bent left and less closely disposed. Especially two last kineties are distinctly longer so that the last one (the 9th) reaches nearly the body end (Fig. 10 C).

Host: *Ginaia munda* Sturany (*Prosobranchia, Hydrobiidae*) in Ohrid Lake, at the depth of about 15 m.

Genus *Kozloffiella* genus novum

I create this genus for differentiating of a specific species described by Kozloff 1945 as *Heterocineta phoronopsidis* and corresponding in many respects to the characters of the genus *Hypocomella*. Kozloff 1945 reports that his *H. phoronopsidis* "differs fundamentally from other species of *Heterocineta* in having a grove-like depression originating on the left side of the body near the anterior end and extending posteriorly along the dorsal surface close to the left margin". Kozloff points out that these forms did not occur in the representatives of the genus *Heterocineta* (=*Hypocomella*) familiar directly to him, nor in numerous species of Jarocki 1934. Virtually in view of a considerable monotony of morphology which is common among the species arranged here to the genus *Hypocomella*, this character would seem essential the more so that it is also connected with a far systematic position of the host (Fig. 11).

The role, importance and origin of this groove-like depression are unknown, anyhow it is not the place of the run any kinety and it does not reveal kinetosomes. This is clearly visible on living specimens. It may be admitted that this form plays a role in the life of *K. phoronopsidis* (Kozloff, 1945) on tentacules of *Phoronopsis*, therefore in the conditions different from these which are revealed in the mantle cavity and on the gills of *Mollusca*.

The genus *Kozloffiella* g.n. is created by me rather provisionally supposing

that perhaps the farther examinations on parasites of other groups of animals except for *Mollusca* would afford material which would confirm their individuality.

In this situation the diagnosis of the genus *Kozloffiella* g.n. may be presented as follows:

Kozloffiella genus novum

pro: *Heterocineta phoronopsidis* Kozloff, 1945.

Ancistrocomidae — Hypocomellinae of a pear-shaped, medium elongated body, with flattened thigmotactic field. The ciliature, similarly to *Hypocomella*, consists of one complex of uneven kineties, most court in the middle, more and more long towards both sides of the ciliated area, and especially towards the left side. On the dorsal, convex body side a distinct groove-like depression runs from the anterior pole backwards. Parasites of the antennae of *Phoronidea*.

Typus generis: *Kozloffiella phoronopsidis* (Kozloff, 1945).

The genus *Kozloffiella* g.n. embraces by now only one species:

Kozloffiella phoronopsidis (Kozloff, 1945)

syn.: *Heterocineta phoronopsidis* Kozloff, 1945.

Body pyriform. Length 26—37 μ, width 11—16 μ; thickness 6.5—11 μ. Ma oval or rod-shaped, 5.25—7.5×3—4.5 μ, in the middle of the body; Mi, 1.5—2.25 μ, in front of Ma. C. V. in the middle. The kineties, 8 in number, originate near the base of the tentacle. The first 5 kineties from the right are about 3/5 the length of the body, while the remaining 3 kineties become progressively longer and are influxed in such a way that they end one behind the other near the midline. A groove-like depression without any trace of ciliature, extend from the anterior end of the body posteriorly along the convex surface close to the left margin (Fig. 11).

Host: *Phoronopsis viridis* Hilton (*Phoronidea*), on the tentacles, Tomales Bay, California.

Genus *Enerthecoma* Jarocki, 1935

This genus was created by Jarocki 1935 for the individualization of *E. properans* Jarocki, 1935 from *Viviparus fasciatus* among other species of *Ancistrocomidae* which he found in the mantle cavity and on the body surface of the freshwater snails in the region of Warszawa.

This species differs from others ranged by Jarocki to the genus *Heterocineta* (=*Hypocomella*), by a strongly elongated body and by a symmetric thigmotactic arrangement consisting of kineties of the same length.

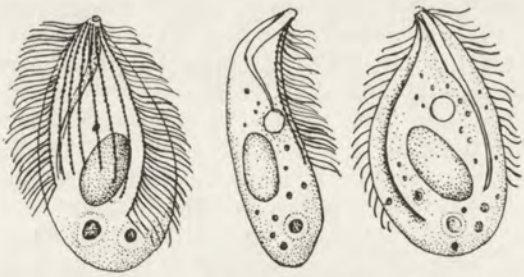

Fig. 11. *Kozloffiella phoronopsidis* (after Kozloff) ×1000

Enerthecoma properans Jarocki, 1935 was later found by Kozloff 1946 in *Viviparus malleatus* in North America; Kozloff confirms all characters which Jarocki has indicated before (Fig. 10 D). Chatton et Lwoff 1950 individualize unnecessarily the form of Kozloff as a quite new species *E. kozloffi*.

Only "*Hypocomina*" *tegularum* Kozloff, 1946 may be arranged from among many species of the subfamily *Hypocomellinae* to the genus *Enerthecoma*, having a more or less symmetric thigmotactic arrangement which deviates from the distinctly asymmetric arrangement in the representatives of the genus *Hypocomella* and other genera of the subfamily (except for *Hypocomina*).

The diagnosis of the genus *Enerthecoma* may be stated as follows:

Enerthecoma Jarocki, 1935

Ancistrocomidae — Hypocomellinae of a banana-shaped, strongly elongated body (ca 50 μ), with a flattened thigmotactic area. The ciliature consists of several kineties of equal length, reaching 1/2 the body length. A longitudinal elevation runs along the thigmotactic field in the middle line. Parasites of the mantle cavity of *Gastropoda — Prosobranchia*.

Typus generis: *Enerthecoma properans* Jarocki, 1935.

To the genus *Enerthecoma* may be arranged two species:

Enerthecoma properans Jarocki, 1935

syn.: *Enerthecoma kozloffi* Chatton et Lwoff, 1950.

Body symmetrical, lanceolate. The internal tubular canal leads from the tentacle to the antithigmotactic surface of the ciliate. Length 33—60 μ, breadth 15—22 μ, thickness 10—13 μ. Ma rod-like or ovoid, 8—88×5—7 μ, in the middle

of the body; Mi spherical, 3 μ, in front of Ma. The ciliary system consists of 8 (exceptionally of 7) practically parallel kineties forming a narrow thigmotactic area occupying about 2/3 of the body length. The middle of the area forms an inconsiderable longitudinal eminence, dividing the ciliary system into two laterial complexes. The right complex consists of 5, the left one of 3 kineties. As a rule, the kineties are of equal length. The kineties commence on the base of the tentacle at the same level. The kinetosomes are placed closely, in contact with each other (Fig. 10 D).

Host: *Viviparus fasciatus* Müller, on ctenidial filaments in great abundance — Vistula in the vicinity of Warszawa (Jarocki); *Viviparus malleatus* (Reeve) — an introduced snail in America — San Francisco, Riverside, California (Kozloff).

Enerthecoma (?) *tegularum* (Kozloff, 1946)

syn.: *Hypocomina tegularum* Kozloff, 1946, Chatton et Lwoff 1950.

Body pyriform. Length 26—36 μ, width 12—17 μ, thickness 9—11 μ. Ma spherical, 5.5—7 μ, in the posterior half of the body; Mi, 1.6—2.2 μ, anterior to the middle of the body. C. V. central. Cilia 6—7 μ. The kineties, 9 in number, are disposed in a shallow depression occupying the anterior half of the "ventral" surface. The first 5 kineties from the right side are slightly longer than the other 4 kineties (Fig. 10 E).

Host: *Tegula brunnea* (Philippi) on the ctenidium, Carmel Bay, California.

Genus *Ignotocoma* Kozloff, 1961

This genus was created by Kozloff 1961 for the species *I. sabellarum* from peristomial cirri of polychaete annelid of the family *Sabellidae*. These ciliates by the outline of their body and its inner structure closely resemble to the typical representatives of the genus *Hypocomella*. Kozloff separated this species in a new genus mainly on the base of a somewhat different system of kineties on the thigmotactic surface. This arrangement namely consists of two parts specifically combined with one another (see the diagnosis of the genus and the description of the species, Fig. 12 A, B).

It is assumed that the decision of Kozloff 1961 was undertaken under the influence of a complete individuality of the host's group of this species, similarly as in the case of the genus *Kozloffiella* g. n. it weighed in my decision of creating a separate genus. Kozloff noticed the similarity of his species with other genera of *Ancistrocomidae* from *Mollusca*, however he assumes that "there is a possibility that as additional sabellids and other polychaetes are examined, there will be brought to light an assamblage of ancistrocomids which will show some evolutionary tendencies totally independent of those known in the ciliates of this family found on molluscs".

The provisional diagnosis of the genus may be stated as follows:

Ignotocoma Kozloff, 1961

Ancistrocomidae — Hypocomellinae of a pear-shaped, medium elongated body, with the thigmotactic area with a ridge-like eminence extending along the area about the midline. The ciliature consists of several (7) kineties on the right, and several (8) on the left side of the area. The kineties are in each part arranged progressively more posteriorly toward the left side. Parasites of the peristomial cirri of *Polychaeta*.

Typus generis: *Ignotocoma sabellarum* Kozloff, 1961.

The genus *Ignotocoma* embraces presently only one species:

Ignotocoma sabellarum Kozloff, 1961

The body pear-shaped. Length 23—33 μ, width 12—16 μ, thickness 8.5—10 μ. Ma elongated lies obliquely beyond the half of the body length; Mi spherical or elipsoidal, lies anterior to Ma. A distinct pharyngeal canal bent right. C. V. in the middle of the body. Cilia 10—11 μ. The ciliature consists of 15 kineties and is divided on two complexes, in the main separated by a ridge-like eminence which extend along the thigmotactic surface about the midline of the body. The right complex consists of 7 kineties starting the right to the left gradually farther from the base of the tentacle, ending progressively farther backwards; the left complex forms 8 kineties also starting gradually farther from the base of the tentacle and they reach farther backwards. The initial parts of the kineties form a step; however their distal ends break off along a uniform line, running obliquely in the posterior body part (Fig. 12 A, B).

Host: *Schizobranchia insignis* Bush and *Endistilia vancouveri* (Kinberg), *Sabellidae*, on peristomial cirri — Coss Bay at Charleston, Oregon, N. Amer.

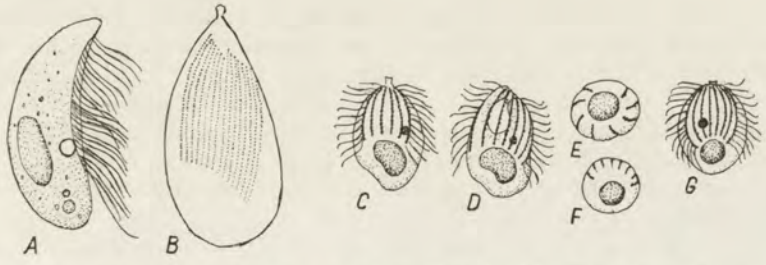

Fig. 12. A, B — *Ignotocoma sabellarum* (after Kozloff); C, D, E — *Hypocomidium fabius* (a. Raabe); F, G — *Hypocomidium granum* (a. Raabe) ×1000

Genus *Hypocomidium* Raabe, 1938

This genus created R a a b e 1938 for two species, which by their minute dimensions and by a simple ciliary system differentiate among *Ancistrocomidae*, namely for: *H. fabius* Raabe, 1938 from *Cardium edule* L. (on the first place) and *H. granum* Raabe, 1938 from *Mya arenaria* L. These are minute bulged organisms without a distinct thigmotactic concavity with several kineties running from the base of the tentacle so that they embrace 1/3 to 3/4 of the body circumference. The sucker consists also of an outstanding character inserted in an ampoule lying behind it (Fig. 12 C — G).

The simplification of the structure, the undifferentiation of kineties, the fact that they embrace a larger surface than the thigmotactic field itself, may results from the reduction of the body dimensions and may constitute in principle only a convergent phenomenon which could not forejudge the mutual kinship. There are no available data to analyze the phylogenetic aspect of this form.

The diagnosis of the genus *Hypocomidium* may be provisionally stated as follows:

Hypocomidium Raabe, 1938

Ancistrocomidae — Hypocomellinae of a small (ca 15 μ), grain-like body, rounded on both poles, without more distinct flattening or depression. The ciliature consists of several meridionally directed kineties, and embrace 1/3 to 3/4 of the body circumference. The snout is invaginated. Parasites of the mantle cavity of marine *Bivalvia*.

Typus generis: *Hypocomidium fabius* Raabe, 1938.

I range (provisionally) to the genus *Hypocomidium* two species:

Hypocomidium fabius Raabe, 1938

The body ellipsoidal, somewhat flattened on the one side on the posterior part, on the other side somewhat concaved. Length 12—17 μ, width circa 9 μ. The sucker 3 μ, introverted to the reservoir, is placed somewhat obliquely. Ma spherical or reniform 5 μ, lies in the posterior body part; Mi spherical, 1.7 μ usually anterior to Ma. The ciliature reduced to 8 kineties, running from the base of the tentacle mainly on the flattened body surface in such a way that the ciliature embraces 3/4 of the body circumference. The distance between the kineties ca. 1.5 μ, cilia ca. 5 μ long. A cross division; the conjugation by posterior ends, the individuals are arranged under the angle of 120° (Fig. 12 C, D, E).

Host: *Cardium edule* L. (recte *C. lamarcki*), 20% infestation, often in mass — south Baltic Sea with bays and gulfs; *Cardium edule* L., sometimes in mass — Vernenske lake, Varna, Bulgaria (R a a b e 1966 — not published).

Hypocomidium granum Raabe, 1938

The body elipsoidal, somewhat flattened on one side. Length 10—13 μ, width ca. 7 μ. The sucker introversed and set somewhat obliquely. Ma spherical, 3 μ, lies in the posterior part of the body; Mi, 1 μ lies anterior to Ma. The ciliature reduced to 8 kineties, running from the base of the sucker and occupying mainly the flattened body part. The kineties embrace only 1/3 of the body circumference and form a nearly closed, symmetric system which embraces the thigmotactic ciliature with dimensions ca. 9×7 μ. The cross division (Fig. 12 F, G).

Host: *Mya arenaria* L., rarely and small in number, usually at the absence of *Sphenophrya dosiniae* Ch. Lw. — south Baltic Sea.

Genus *Hypocomina* Chatton et Lwoff, 1924

This genus was created by Chatton et Lwoff 1924 recognizing a conspicuous individuality of the species *Hypocoma patellarum* Lichtenstein, 1921 in relation to other species of the genus *Hypocoma* Gruber, 1884. Chatton et Lwoff are writing on this matter: "Le genre *Hypocomina*, que nous créons pour *H. patellarum*, présente aussi les mêmes caractères de l'aire ciliaire (que *Hypocoma*), mais cette aire est très enfoncée au-dessous du niveau du tégument; pas de vestige de frange adorale". The farther examined differences induced the French authors to separate the family *Ancistrocomidae* (together with *Hypocomina*) from the family *Hypocomidae* s. str.

The unadequate description of Lichtenstein 1921 and the unclear remarks of Chatton et Lwoff did not allow for an adequate orientation concerning the characters of the genus *Hypocomina*. It results in an unjust arrangement to this species of both *H. carinata* Raabe, 1934 (recte *Crebricoma carinata*) and *H. tegularum* Kozloff, 1946) (recte *Enerthecoma tegularum*). This problem was elucidated only but the more detailed descriptions and drawings of Chatton et Lwoff 1950, concerning *Hypocomina patellarum* (except Fig. XXI which in spite of the subscription could not refer to this species!). The distinctions of the genus *Hypocomina* resulting from them confirmed my observations from Split and Rovinj (Yugoslavia) carried on *H. patellarum* and confirmed also the acquired there silver preparations (Fig. 13 A, B).

Hypocomina patellarum (Lichtenstein, 1921) differentiates distinctly itself from the other representatives of the family *Ancistrocomidae*. The body outline is not pear-shaped or banana-shaped as in others but is likely to a single bean of coffee. The placement of the sucker not on the apex but in the anterior flattened body part, the depression of the whole thigmotactic arrangement and its closing by a ridge-like eminence of integument — all this is striking yet at the first during observation in vivo. It is essential that the arrangement of the thigmotactic kineties, owing to their curvature, is apparently closed, but not in the same way and grade as in the genus *Colligocineta* Kozloff, 1965.

However these characters cannot be considered as strange to *Ancistrocomidae*: the thigmotactic arrangement has a tendency to be closed up also in some *Hypocomella*, but the concavity and the reduction of the thigmotactic surface is connected with a strong swelling of the body. In the case of this

swelling in other species and groups, the body surface covered only by an elastic argyrophilic net is considerably accentuated, however the parts covered by kineties do not spread, which give to the cortical layer a considerable stiffness.

The diagnosis of the genus *Hypocomina* may be stated as follows:

Hypocomina Chatton et Lwoff, 1924

Ancistrocomidae — Hypocomellinae of an oval body, convex on the dorsal, concave on the ventral thigmotactic side. The snout is shifted a little vantrally and not apically located as in other genera. The thigmotactic ciliature is somewhat deepened and embraced by an elevated border; there are several arc-like kineties, running together (but not joining) in the front and hind parts and forming a seemingly closed system. Parasites of the branchies of marine *Gastropoda — Prosobranchia* (*Patella*).

Typus generis: *Hypocomina patellarum* (Lichtenstein, 1921) Chatton et Lwoff, 1950.

Only one species is arranged to the genus *Hypocomina*:

Hypocomina patellarum (Lichtenstein, 1921)

syn.: *Hypocoma patellarum* Lichtenstein, 1921.

The body ovoidal in its outline, strongly flattened and concaved on the one side. Length 29—30 μ, width 15—15 μ, thickness 10—11 μ. Ma ovoid ca 8 μ (Z. R.), lies in the posterior part of the body; Mi very slight, lies close to Ma. C.V. slightly perceptible.

A well outlined thigmotactic surface is reduced to the oval in the anterior flattened body side which measures 10—15×15—20 μ (Z. R.) and surrounded by a cortical height. Its ciliature consists of 8—10 kineties, running backwards from the base of the sucker, the central kineties run straight on, the marginal ones are progressively bent like arches; these kineties converge slightly with each other in the posterior part of the field and consist a symmetric arrangement (Fig. 13 A, B).

Host: *Patella cerulea* L., on gills, moderate infestation in general in the company of *Urceolaria patellae* — Sète (Lichtenstein, Chatton et Lwoff), Split, Rovinj — Adriatic — (Raabe).

Genus *Colligocineta* Kozloff, 1965

Kozloff 1965 created this genus for the species *C. furax* described at the same time, originating from the peristomial cirri of *Sabellidae*. The decision of Kozloff was very right, for this ciliate represents a character which is not present in any representative of the family *Ancistrocomidae*,

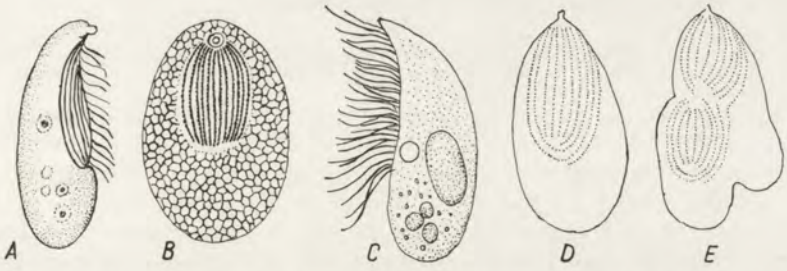

Fig. 13. A, B — *Hypocomina patellarum* (after Ch. Lw.); C, D, E — *Colligocineta furax* (a. Kozloff) ×1000

namely a real closure of the thigmotactic ciliature. The thigmotactic zone of *Colligocineta* resembles to the relations in some *Hypocomella* and especially in *Hypocomina*: it is a well outlined oval, occupying here near 1/3 of the body length; its kineties start as the base of the tentacle and run in form of an arch to the posterior, the right ones sinistrorsal, the left ones — dextrorotatory. The kineties of the middle are bipolar, the marginal left ones are connected by their distal ends with the marginal right. This is of course a secondary phenomenon. The divisional stages are forcible; in opisthe the broken fragments of all kineties are firstly bipolar and then are connected in right couples (Kozloff, 1965 — Fig. 13 C, D, E).

The interesting findings of Kozloff confirmed by his own statement (Kozloff, 1961) in the description of *Ignotocoma* that in *Polychaeta* may be expected the occurrence of many interesting forms of the family *Ancistrocomidae* or *Thigmotricha* in general.

The diagnosis of the genus *Colligocineta* may be reported as follows:

Colligocineta Kozloff, 1965

Ancistrocomidae — Hypocomellinae of an ovoid body, concave in the ventral thigmotactic area. The ciliary system occupies the anterior two-thirds of the ventral surface. At more anterior levels, ten kineties are invariably found. But in the posterior portion of the ciliary field, the kinety on the extreme right appears to be continuous with the kinety which is adjacent to the one of the extreme left. The kineties just medial to these two rows likewise appear to be continuous. However, in dividing ciliates, in the proter all of the ten rows are for a time completely separated. Parasites of the peristomial cirri of *Polychaeta*.

Typus generis: *Colligocineta furax* Kozloff, 1965.

One species belongs to the genus *Colligocineta*:

Colligocineta furax Kozloff, 1965

The body ovoidal in its outline, strongly flattened on one side. Length 27—38 μ, width 16—19 μ, thickness 11—13 μ. Ma elongated (ratio 2—3:1), lies obliquely in the middle of the body length; Mi spherical, lies anterior to Ma. C.V. near the middle of the body. The plasma in the posterior part of the body vacuolized and granulated. The sucker is transformed in a long cytopharynx. Cilia 11—12 μ. The ciliature consists of 10 kineties originating at the base of the tentacle and running backwards arcuately. The middle kineties (3th to 7th from the right side) break off more or less in the middle of the body length, however the marginal ones join together by their ends with the opposite ones. In fact, the kinety 1th meets the 8th, kinety 2th the 9th, kinety 10th is free (Fig. 13 C, D, E).

Host: *Laonome kroyeri* Malmgren, *Sabellidae*, on peristomial cirri — regions of San Jean Archipelago, Washington, on depth of 15 meters.

Genus *Goniocoma* Chatton et Lwoff, 1950

This genus was created by Chatton et Lwoff 1950 for the differentiation of the species *H. macomae* Ch. Lw. 1926 from the genus *Hypocomella* Ch. Lw. 1924. This species was separated for the reason that it does not correspond by the character of the ciliature which covers nearly the whole body of this ciliate, to the genus *Hypocomella* nor to any other genus of the family *Ancistrocomidae*. *Goniocoma macomae* may be juxtaposed concerning its ciliary cover only to *Hypocomagalma* Jarocki et Raabe, 1932 whatever the kineties arrangement is in both cases almost specularly inverse (comp. p. 404).

In the first description of 1921, *H. macomae* is in fact slightly different from the typical species of the genus: *H. cardii* (Ch. Lw., 1922), the French authors did not notice that its ciliature embraces the whole body. They reported: "Ciliature: champs de stries occupant la moitié anterieure de la face ventrale, formé de deux systèmes l'un droit de stries légerément dextres, l'autre gauche, de stries légèrement sénèstres un peu plus longues et un peu plus écartées que les premières." Raabe 1938 proved, that the right arrangement extends far beyond the thigmotactic field and enter on the convex side of the body however he also did not appreciate the number of kineties. Chatton et Lwoff 1950 document in their description and on the drawings that the thigmotactic arrangement closes in virtually the whole body, and their kineties reach the last kineties of the left system and they originate not from the body apex but along the last kinety from the left side under a certain angle. These suggestions are confirmed by my own later examinations.

The complete ciliature of *Goniocoma* consisting virtually of one complex, interpretes as I reported before (part I, p. 19, this part, p. 390) a thigmotactic ciliature spread on the whole body. The proper concave thigmotactic surface occupies the arrangement of kineties similar to that occurring in *Hypocomella*: the middle kineties are shortest and oriented meridionally, and the further ones from the middle are gradually longer and arcuately bent. There are

several of these kineties (6—7) on the left from the medium kinety, and the last of them reaches 3/5 of the body length. There are more of them on the right (20—25) — the first of them start at the apex near the sucker, the next ones originate gradually backwards along the last left kinety (Fig. 14).

The diagnosis of the genus *Goniocoma* may be stated as follows:

Goniocoma Chatton et Lwoff, 1950

Ancistrocomidae — Hypocomellinae of a pear-shaped, moderately elongated body, with a flattened or concave thigmotactic field. The ciliature, especially strongly developed, occupies almost the whole surface of the body, with the exception of a field in the hind part of the ventral (thigmotactic) body side. The whole ciliature can be regarded as a secondarily overgrown thigmotactic ciliature, and not as a primitive general ciliature. The depressed thigmotactic surface occupies a system of kineties similar to that of *Hypocomella*, but the kineties of the right side are more and more long and, passing on the dorsal side, begin more and more posteriorly on the left rand of the thigmotactic field. Parasites of the mantle cavity of marine *Bivalvia*.

Typus generis: *Goniocoma macomae* (Chatton et Lwoff, 1926) Chatton et Lwoff, 1950.

Only one species may be arranged to the genus *Goniocoma*:

Goniocoma macomae (Chatton et Lwoff, 1924)

syn.: *Hypocomella macomae* Chatton et Lwoff, 1924; Raabe 1934.

The body pear-shaped, strongly elongated in the anterior part and rounded in the posterior part. Length (according to the data of Chatton et Lwoff, Raabe and Fenchel): 24—39 μ, width 13—18 μ, Ma elongated, 11—17× ×5—7 μ lies in the posterior or somewhat beyond the body middle; Mi big, spherical, 3—4 μ lies close to Ma. C. V. central. Cilia 7—9 μ.

The ciliature consists of many kineties: 23—29, consisting a homogenous complex. The typical thigmotactic set, occupying the concavity in the anterior body part, has the structure of système sécant: from the short central kinety lie (or 7) kineties which turn off more and more to the left and growing longer in the way that the last one reaches ca 3/5 of the body length. There are on the right 17—24 kineties rolled up to the left and subsequently reaching the posterior part of the body toll its end. The first of them starts at the base of the sucker, the subsequent ones gradually from it, along the last kinety of the left arrangement. The last of these kineties are virtually short segments in the posterior part of the body connected with the body by a dense net of argyronems (Fig. 14 A, B, C, D).

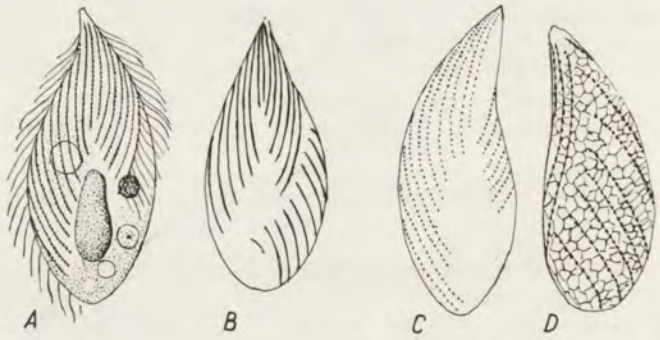

Fig. 14. *Goniocoma macomae:* A — after Raabe, B—a. Ch. Lw., C, D — a. Fenchel. ×1000

The division substransversal, the conjugation observed; Raabe 1938 reports cases of triple conjugation, with a complete synchronization of nuclear processes.

Host: *Macoma balthica* (L.) — Boulogne (Ch. Lw.), south Baltic Sea (Raabe); Fenchel observed *Goniocoma macomae* in *Abra alba* (Wood), but did not find it in *Abra nitida* (Muell.) nor in *Macoma balthica* (L.) — Gullmarfjord.

Familia *Sphenophryidae* Chatton et Lwoff, 1921

The family was created by Chatton et Lwoff 1921 for a single species and genus *Sphenophrya dosiniae* Ch. Lw., 1921 from the gills of *Dosinia exoleta*; the authors signalled similar organisms from other shellfish. This family was then approached as an individual indeed but belonging to *Suctoria* (*Acineta*). This position would be pointed out by an unciliated trophont and ciliated tomit arising from the trophont in the way of budding. Only in their later works Chatton et Lwoff excepted from *Suctoria* the family *Sphenophryidae* and created for it, together with *Ancistridae* and *Hypocomidae*, the order or suborder of *Thigmotricha*. At the same time they approach *Sphenophryidae* as a group the most adapted in this order to the parasitic way of life and the most specialized too.

The definition of *Sphenophryidae* as sedentary unciliated organisms in the trophic stage, but in tomit's stage with a ciliature and remembering the *Hypocomidae* (=*Ancistrocomidae*) allowed to include here of farther species and genera. Besides the new species of the genus *Sphenophrya* there are successively described: *Pelecyophrya tapetis* Ch. Lw., 1922, *Gargarius gargarius* Ch. Lw., 1934 (=*Rhynchophrya cristallina* Raabe, 1935) and *Lwoffia cilifera* Kozloff, 1955. This species, anyhow ciliated in the trophic stage, is so distinctly approximated to other representatives of the family that there are no doubts as to the possibility of its rank among the *Sphenophryidae*.

The *Sphenophryidae* are a group which in a completely clear and forcible way refer by the ontogenesis to its exit group that is surely to *Ancistrocomidae*. The tomits of all known forms are organisms with a pear-shaped body, narrowed in the anterior part (in the locomotoric and phylogenetic sense), and has a tentacle. One of the sides of the body on which are located the

thigmotactic ciliature, is somewhat concave — we called it in *Ancistrocomidae* the ventral side. The kineties run from the tentacle to the back of the body and form two complexes: the left one, consisting of 5—9 densely arranged kineties and the right one which consists usually of 2+2 (sometimes 2+3, 2+4 or 3) more rarified kineties. These complexes are buckled arcuately so that the ends opposite to the tentacle, that is the distal ends, are in contact. The silver impregnation proves that the whole body is covered by a rather dense argyrophil net like the body of *Ancistrocomidae* and of trofonts of *Sphenophryidae*.

This likeness and the undoubted homology of the tomits of *Sphenophryidae* to the representatives of the family *Ancistrocomidae* with a strongly reduced ciliature emphasized repeatedly Chatton et Lwoff, Raabe and other authors. Especially amazing is the likeness of the arrangement of kineties of the tomits of *Sphenophrya sphaerii* Miasn. to the *Hypocomatidium sphaerii* Jar. et Raabe (Raabe 1948). Dobrzańska 1960 pointed out the mutual likeness of tomits of many species and genera and she admitted that this similarity could indicates rather close monophyletism of this group.

For this reason the variability of the trophic sedentary forms of *Sphenophryidae* is very amazing as well as the transformation ways of the tomits into the trophont even among very approximate to each other representatives of one genus of *Sphenophrya*. Raabe 1948 payed attention to this problem comp. p. 452).

The idea of the variety of shape would be conceived comparing *Gargarius* with *Lwoffia, Pelecyophrya* or *Sphenophrya*. The differences concern not only the shape, but also the general architectonics of the body and consequently they assign its orientation. *Gargarius preserves* in general the shape and orientation of a tomit, or of initial forms with a structure of *Ancistrocomidae*: the body elongated in the midline frontback, the sucking tentacle well developed and conspicuously acting, two complexes of kineties arranged more or less parallely on both sides of the body. *Pelecyophrya* and *Lwoffia* prove larger modifications: they cling to the gills of the host not by a narrow tentacle, but by an elongated, gutte-shaped surface. In the species of the genus *Sphenophrya*, arises wide and usually long sole, consisting a wide surface by which the animal clings to the bottom, extended as a long boat.

The tentacle, the gutter-shaped pad or sole of *Sphenophryidae*, Chatton et Lwoff originate from the suçoir of *Ancistrocomidae*, and this one consequently from bouton adhesif of *Hemispeiridae*. This idea seems adequate, at least in the topographic sense. The arising of the apparatus of the suçoir or of other forms originating from it as food-taking apparatus needs farther elucidation. Chatton et Lwoff 1949/1950 consider that likely as in *Ancistrocomidae* (comp. p. 393) so in *Sphenophryidae*, in the early stages of division or budding, in the body of the proliferous animal appear two anlages of the adhesif-sucking formations in the shape of "cylindres sidérophiles". One of them would later replace the adhesif apparatus of the sedentary individual (proter), the second one moves to the area of the budding individual (opisthe) and becomes its adhesif apparatus. Chatton et Lwoff 1949/1950 prove the presence of such "ébouches des suçoirs" in *Pelecyophrya, Gargarius* and *Sphenophrya*. Mjassnikowa 1930 finds the occurrence of "rätselhafte Gebilde" in *Sphenophrya myae* and *S. sphaerii*, Raabe 1938, 1949 proves them in *S. sphaerii* and *S. dosiniae*. Kozloff 1955 observes them in *Lwof-*

fia, Dobrzańska 1958 in *S. dreissenae*. I would be accepted that really the adhesif apparatus in *Sphenophryidae* appears in the way of neoformation at least in the opisthe for the reason that the replacement of the old apparatus by a new one in the proter was not infallibly proved, however it seems very probable.

Chatton et Lwoff 1950 explain the homology and the divergent development of the adhesive-sucking formations in their "*Rhynchodea*" and they report as follows: "Le suçoir des *Ancistrocomidae* et des *Hypocomidae* est une formation relativement longue et étroite, le suçoir des *Sphenophryidae* est au contraire une formation courte, évasée et étirée. Chez *Pelecyophrya*, c'est un entonnoir aussi larger que long, aplati latéralement, a orifice formant une gouttière elliptique allongée. Chez *Sphenophrya*, c'est un entonnoir extrêmement court, formant une goutière étroite qui parcourt le cilie sur toute sa longueur. Chez *Gargarius*, le suçoir s'étend sur la face ventrale applatie" (Chatton et Lwoff 1950 p. 460). Chatton et Lwoff illustrate this description by the included drawing (Fig. 15), whose interpretation is not clear. Nobody knows e.g. what means the black beak marked on the adhesive surfaces (?).

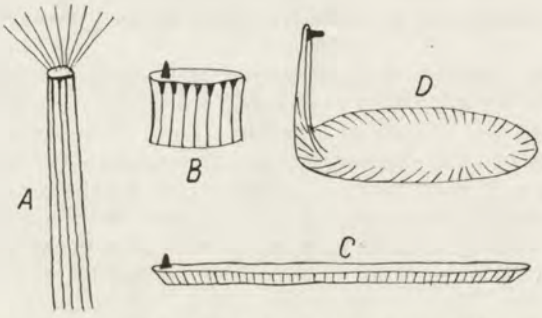

Fig. 15. Shape and transformations of the sucking tentacle (suçoir) in *Ancistrocomidae* and *Sphenophryidae:* A — *Hypocomella*, B — *Pelecyophrya*, C — *Sphenophrya*, D — *Gargarius*. From Chatton et Lwoff 1950, fig. XXXVII

The deep modification of the shape of the body of *Sphenophryidae* as compared to *Ancistrocomidae*, brings farther difficulties concerning the proper orientation of the body. Chatton et Lwoff come out from the shape of tomit which represents the structure of *Ancistrocomidae* and this body side, on which are kineties they consider as the dorsal side. However I consider it as the right in the phylogenetic sense (comp. p. 392). But both orientations have no meaning in view of farther transformations which undergoes a tomit when developing into a trophont. The difficulties concerning the interpretation are clearly visible in the considerations of Chatton et Lwoff 1950 (pp. 461—462):

"Chez *Pelecyophrya*, l'orifice du suçoir, du pourtour duquel partent les extrémités antérieures des cinéties, est manifestement antérieur. Mais il reste à définir, selon la tradition, une face dorsale et une face ventrale. Nous avons exposé les arguments qui nous ont amenés à conclure que la face ciliée des Ancistrocomidés évolués et celle des Hypocomidés devait être considérée

comme dorsale. Nous renons à répéter qu'en l'absence de bouche, la définition de la face dorsale, qui s'impose par des considérations de morphologie comparative, reste arbitraire. Elle l'est d'autant plus que le système de cinéties dorsales, primitivement unique ou homogène, se dissocie parfois en un système droit à cinéties serrées et un systéme gauche à cinéties espacées, lesquels se trouvent séparés nettement et plus ou moins écartés du fait du développment d'une crête dorso-méridienne".

"Les deux systèmes composant ce qui reste de la ciliature dorsale réduite peuvent donc se trouver déjétés latéralement. C'est ce qui se produit chez *Pelecyophrya*. Mais au moment du bourgeonnement, les secteurs postérieurs des deux systèmes ciliaires se rapprochent. L'on assiste alors à la formation d'un champ de cinéties subparallèles. Le suçoir néoformé de l'opisthe ou bourgeon apparaît entre les deux systèmes. Si, conformément à notre conclusion, ce systéme ciliaire est dorsal, on voit immédiatement que le système à 2 paires de cinéties écartées est gauche, le système à 5 cinéties serrées, droit. Par la suite, le suçoir émigrera au pôle antérieur et la *Pelecyophrya*, du fait d'un développement asymétrique sera comprimée latéralement et déjetée ventralement".

"Pour ce qui concerne la *Sphenophrya* — les choses sont plus compliquées. La zone d'affrontement ou hile correspond au pôle postérieur; elle est postérieure parce qu'elle correspond aux extrémités postérieures des cinéties et parce que c'est là que se formera l'opisthe. Mais le pôle postérieur ne correspond nullement à l'extrémité postérieure du cilié. Le pôle postérieur n'est pas la partie postérieure de l'animal, mais la zone qui porte les attributs morphologiques et physiologiques qui se trouvent en général coincider avec l'extrémité postérieure".

"Ceci dit, c'est entre les deux systèmes de cinéties du bourgeon que viendra affleurer le suçoir de l'opisthe. Si, conformément à notre conclusion, la ciliature est dorsale, le système à 3 cinéties espacées sera gauche, le système à 5 cinéties sera droit le cuçoir qui s'étend entre les systèmes droit et gauche sera dorsal".

Raabe 1949 discussing the differences, which occur in the metamorphosis of two species of the genus *Sphenophrya* (*S. dosiniae* and *S. sphaerii*) and referring to the interpretation applied by Chatton et Lwoff 1950 and Mjassnikowa 1930, concludes his considerations in following words (Raabe 1949, p. 127): "Il me semble que le problème de l'orientation du corps qui a une si grande importance pour fixer la phylogènese de nombreuses formes, perd de l'importance dans ce cas. Nous avons à faire aux formes très specialisées qui sont, pour ainsi dire des résultats finals actuels d'une certaine chaine évolutive. Des formes pereilles peuves aboutir aux transformations très poussées et complètement divergentes. Tâcher de fixer l'orientation propre du corps peut mener aux conclusions sans importance et tout à fait scolastique."

I thing that likely to the case of *Ancistrocomidae* (p. 392) it is possible to abstract from the phylogenetic considerations and recognize the practical orientation of the body, based on the actual topography of the organella. This orientation is not easy too for the reason that the tentacle of the tomit develops during the metamorphosis in different ways and the arising gutter or adhesive sole occupies an individual position relatively to the system of kineties not only in different genera but even in different species of the same

genus of the family *Sphenophryidae*. Dobrzańska 1950 expressed it correctly in her considerations and on her drawing 5.

According to this interpretation, the tentacle (suçoir), develops in *Ancistrocomidae* along the body midline and occupies an apical position; the same position it occupies in tomits of *Sphenophryidae*. But during the metamorphosis it develops in *Lwoffia* and forms a gutter oriented between the two rows of kineties; in *Pelecyophrya* it is oriented toward the opposite side, carrying the anterior ends of kineties; in *Gargarius* it elongates perpendicularly to the body midline and forms a protrusive beak; in *Sphenophrya* the tentacle gives a gutter entering between two rows of kineties, this gutter develops then into a sole perpendicular to the tomit's body midline.

Therefore it may be stated after the application of the orientation reported for *Ancistrocomidae*, then also for the tomits of *Sphenophryidae* that: the surface with thigmotactic kineties is the ventral surface and consequently the adhesive gutter in *Lwoffia* is shifted to the anterior part of the ventral side, but in *Pelecyophrya* inversely that is on the anterior part of the dorsal side, in *Sphenophrya* it develops towards the ventral side in its anterior part, deforming it completely and changing the midline of the trophont's body in relation to the tomit.

In this situation, the definition of the family *Sphenophryidae* to be formulated taking into consideration not only the shape of the trophont's body but the likeness of tomits and the process of metamorphosis. Corliss 1961 gives a following definition: "Short suctorial tentacle. Mature form without cilia, but budded larval form possesses several rows of somatic ciliature". This definition seems to be not adequate and unsufficient. I would like to propose therefore a following diagnosis:

Familia *Sphenophryidae* Chatton et Lwoff, 1921

Thigmotricha sedentary in the trophic stage, of various body shape. The ciliature is in general reduced; there are always preserved the kineties (with kinetosomes, but without cilia) arranged in groups and corresponding to the thigmotactic ciliature of *Ancistrocomidae* (of *Hypocomatidium* type). The tomites, of an *Ancistrocomidae* body shape, acquired the cilia on the sectors of kineties transferred from the ancestral individual. The settlement of tomites is bounded customarily with the loss of cilia and with the changes of body form in various directions. The food uptake occurs by the sucking snout or by the adhesive sole. Reproduction by budding; conjugation of trophic, sedentary individuals. The nuclear apparatus common. Parasites of the gills of marine and fresh-water *Bivalvia*.

Typus familiae: genus *Sphenophrya* Chatton et Lwoff, 1921.

Genus *Gargarius* Chatton et Lwoff, 1934

syn.: *Rhynchophrya* Raabe, 1935.

This genus was created by Chatton et Lwoff 1934 for the species *G. gargarius* described et the same time from the gills of *Mytilus edulis*. The authors pointed out in their description the likeness of *Gargarius* to *Pelecyophrya* and they report: "C'ést en fait, une *Pelecyophrya* quis'est ornée la face dorsale de deux peignes parallèles mais asymétriques, le droit plus dévelopé que le gauche, courant tous deux de l'avant vers l'arrière".

In view of the inadequacy of description and the lack of drawings in this work, Raabe 1935 described the second time this ciliate under the name of *Rhynchophrya cristallina*, reporting an detailed description and illustrations. The identity of *Gargarius* and *Rhynchophrya* was elucidated only in the definite work of Chatton et Lwoff 1950.

Gargarius occupies among the known genera of the family *Sphenophryidae* a position in many ways very approximate to *Ancistrocomidae*: the body elongated towards the line between the tentacle and the body back, the settlement on the gills with aid of a heavy tentacle, the arrangement of kineties in two longitudinal systems, the reproduction very near to the cross equal division. An individual character of *G. gargarius* is an additional adhesive apparatus (?) composed of cross slats.

The diagnosis of the genus may be stated as follows:

Gargarius Chatton et Lwoff, 1934

syn.: *Rhynchophrya* Raabe, 1935.

Sphenophryidae of an elongated, banana-shaped body, clinging on the substrate with an apical, somewhat obliquely directed sucking snout. On the dorsal side there is a specific system of transverse listels. On both sides of the body there are two perpendicular systems of cilialess kineties, of a few (4—5) kineties each. Reproduction by postero-terminal budding, resembling an equal fission. Parasites of the gills of marine *Bivalvia*.

Typus generis: *Gargarius gargarius* Chatton et Lwoff, 1934.

The genus *Gargarius* embraces by now only one species:

Gargarius gargarius Chatton et Lwoff, 1934

syn.: *Rhynchophrya cristallina* Raabe, 1935.

The body banana-shaped or cucumber-shaped. Length 40—60 μ, width ca. 15 μ. The tentacle is elongated in the shape of a bird's beak; it is sideway oriented under the angle of 45—90°. In the inverse side of the body somewhat on its right side (if one recognize the beak as oriented to the ventral side) lie several cross, protrusing slats — their meaning is unknown. Chatton et

Lwoff 1950 consider that these are "deux peignes parallèles des papilles" (p. 482). From the beak to the back of the body run obliquely two long fibrills; presumably they consist a reduction of the cytopharynx. Ma elongated, big ca 25×6 μ, lies in the middle or somewhat in the back of the body; Mi spherical, also extremely big, ca 5 μ, lies in different position close to Ma (Fig. 16).

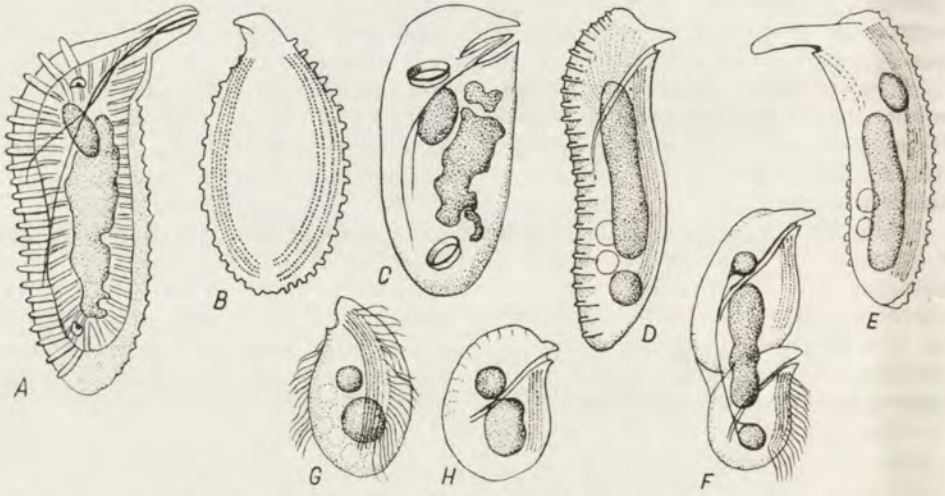

Fig. 16. *Gargarius gargarius:* A, B, C — after Chatton et Lwoff, D, E, F, G, H — a. Raabe. ×1000

The system of kineties without cilia is divided into two complexes running along the body in its both sides. On its right side run usually 4 parallel kineties, on the left 4—6 kineties arranged close to one another. The kineties run nearly over the whole body length.

The reproduction through gammation is approximate to the equal division; the transmitted to the opisthe parts of kineties get a ciliature. The tentacle forms early during the division. The conjugation is not observed.

Host: *Mytilus edulis* L. — Roscoff, Sète (Ch. Lw.), Baltic Sea, (Raabe).

Genus *Pelecyophrya* Chatton et Lwoff, 1922

Chatton et Lwoff 1922 created this genus for the species *P. tapetis* from *Tapes aureus*, described at the same time; they assign directly this genus to the family *Sphenophryidae* on the basis of the likeness of its structure and development to *Sphenophrya*. It is a similarity scarcely very general, because both the structure and development are very different in these two genera.

The body of *Pelecyophrya* is flattened laterally with a pear-shaped outline. One margin is uniformly convex, the second is somewhat concave and meshed, here lies the adhesive-sucking gutter. Along the convex margin run on one side several densely arranged kineties, corresponding to the left complex, on the other side two pairs of kineties corresponding to the right complex. It the anterior, sharpened part of the body, the kineties pass however on its opposite

side and reach the margins of the shifted here adhesive gutter. It must be recognized that the anlage of suçoir developing in a gutter shifts to the dorsal margin and carries the ends of kineties which are in contact with it. The divisional stages prove that really the system of kineties belongs to the ventral side of the body opposite to the gutter; these stages are: the interruption of kineties of the dividing individual occurs on the ventral side.

The reproduction occurs by gammation which resembles rather the cross-division, because the dimensions of proter and opisthe are nearly equal. The ends of kineties which fall to opisthe get the cilia. According to Chatton et Lwoff 1950, two anlages of tentacles arise during the division, one of which replace the reducing gutter of proter, the second one falls to the opisthe.

The diagnosis of the genus *Pelecyophrya* may be stated as follows:

Pelecyophrya Chatton et Lwoff, 1922

Sphenophryidae of a laterally flattened body of a shape of a somewhat obliquely oriented cap, adjacent to the substrate with a ridge-like attachement surface, shifted to the dorsal body ridge. On both sides, along the convex ventral border of the body, there are two systems of kineties without cilia — on the left side several kineties (5), on the right one — 2+2 kineties. The budding is apical from the engravure in the surface of the parent ciliate. Conjugation with the body sides. Parasites of the gills of marine *Bivalvia*.

Typus generis: *Pelecyophrya tapetis* Chatton et Lwoff, 1922.

Only one species belongs to the genus *Pelecyophrya*:

Pelecyophrya tapetis Chatton et Lwoff, 1922

The body with a pear-shaped outline, flattened laterally. Length?, width? At the posterior body apex there is an eliptic gutter, corresponding to the tentacle, shifted to the dorsal side of the body. Ma spherical, lies in the posterior part of the body; Mi tiny, ovoid, lies close to Ma. Kineties arranged in two rows, they initiate from the margin of the gutter and they pass to the

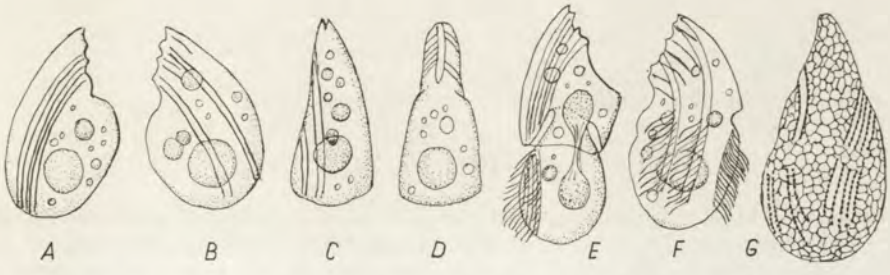

Fig. 17. *Pelecyophrya tapetis* (after Ch. Lw.), E, F, G — division. ×1000

ventral side of the body. The right complex two pairs of kineties form (2+2), the left — 5 kineties. The kineties reach nearly the posterior body margin (Fig. 17).

Host: *Tapes aureus* Gmel. (but not *T. decussatus* L. and not *T. pullastra* M.) — Roscoff.

Genus *Lwoffia* Kozloff, 1955

This genus was created by Kozloff 1955 for a sedentary species which belongs undoubtedly to *Sphenophryidae*, but preserving the ciliature in the trophic stage. The genus *Lwoffia* presents an individual type of structure: the body is rather strongly flattened laterally with an ovoidal outline. The dorsal margin is uniformly convex, the ventral one in its anterior part shows a cut occupied by the adhesive-sucking gutter. Both rows of kineties lie conspicuously at the sides of the body, on its flat surfaces. As in the majority of *Sphenophryidae* the left row consists of several densely arranged kineties, the right one forms two complexes of 2—3 kineties. The reproduction is effected by division; two nearly equal individuals arise, both of them have cilia. During the division the two primordia of the new suckers: one of them replace the adhesive gutter of the proter, the second one becomes the gutter of the opisthe.

The definition of the genus *Lwoffia* may be accepted after Kozloff:

Lwoffia Kozloff, 1955

Sphenophryidae with cilia persisting throughout the whole life. The body is laterally compressed, with an extensive ridge-like attachement surface which occupies the anterior end and the anterior part of the ventral surface of the body. The ciliature of the left side is composed of one group of rows; the ciliature of the right side is arranged in two groups of rows. The sucker is funnel-shaped in outline as viewed from the side, and is directed anterodorsally; it is considered to be a protoplasmatic channel. Parasites of the mantle cavity of marine *Bivalvia*.

Typus generis: *Lwoffia cilifera* Kozloff, 1955.

The genus *Lwoffia* embraces only one species:

Lwoffia cilifera Kozloff, 1955

Body laterally compressed, with the extensive attachment surface. Length 16—19 μ, width 14—25 μ. Ma — ? The ciliary system of the left side of the body is composed of 5 kineties. On the right side of the body, the kineties in the group nearer the attachment surface are 3 in number, and the kineties

in the group farther from the surface are commonly 2 or 3 in number, rarely one of 4 (Fig. 18).

Host: *Brachiodontes* (=*Mytilus*) *recurvus* (Rafin.), on the branchial filaments — Fort Myers, Florida, N. America.

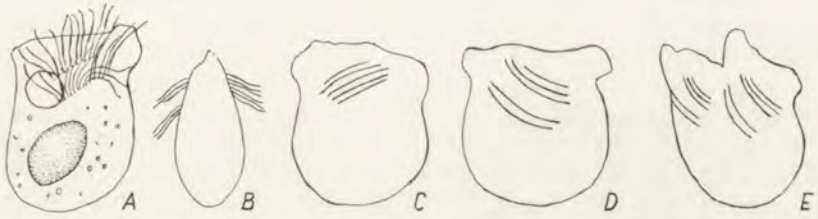

Fig. 18. *Lwoffia cilifera* (after Kozloff), E — division. ×1000

Genus *Sphenophrya* Chatton et Lwoff, 1921

This genus was created by Chatton et Lwoff 1921 for the species *S. dosiniae* described at the same time, as a genus typical of the new family *Sphenophryidae*. *S. dosiniae* was described from the branchia of *Dosinia exoleta*, however at the same time the authors signalize these ciliates also from other shell-fishes, mainly from *Cardium edule*.

The first description of Chatton et Lwoff 1921 give a sufficient idea of the species, genus and range of the created family *Sphenophryidae* (assigned initially to *Acineta*) and caused consequently an appearance of farther studies and descriptions. *S. myae* Mjassnikowa, 1930 from *Mya arenaria* reveals an identity with *S. dosiniae* Ch. Lw. (Raabe 1938); the further separate species is *S. sphaerii* Mjassnikowa, 1930 from *Sphaerium* (Raabe 1949). The form of *S. dosiniae* Ch. Lw. differentiated by Raabe 1938 from the branchia of *Cardium edule*, Chatton et Lwoff 1950 recognized as an individual species *S. cardii*. Then appeared the descriptions of *S. minor* Poljansky, 1951, *S. dreissenae* Dobrzańska, 1960 and finally *S. naumiana* Raabe, 1965.

All described species of the genus *Sphenophrya* Ch. Lw. are consisting with the reported by Chatton et Lwoff 1921 outline of the definition of the genus and reveal a high morphological similarity. Very similar, nearly identical are the tomit's stages lively resembling to *Ancistrocomidae*, and especially *Hypocomatidum*: their ciliary system consist 2+2 (or 2+3) kineties on the right side and several (5—7) kineties on the left side of the thigmotactic field (Raabe 1949, Dobrzańska 1960). Also similar in the general topography are the trophic stages: according to Chatton et Lwoff they have a shape of a naked snail or of a more or less elongated boat, clinging by its deck to branchia of the host. The system of kineties without cilia lies on one side of the body, with that both systems, the left and the right, converge at the body apex, corresponding to the posterior margin of the tomit's body, and they diverge towards the two ends of the body at its base. In spite of this convergency of the structure of tomits on the one hand and of trophonts on the other, the morphogenetic processes following the gammation, and mainly the transition of the tomit into the trophont, run in different ways not parallel in individual species (Raabe 1949, Dobrzańska 1960).

The budding occurs at the apical side of the trophont more or less in the middle of the body length. Yet before the marking of a lobe from which would arise the bud, the adapical ends of both systems of kineties break somewhat to the back and on their kinetosomes appear the cilia. Gradually these segments of kineties are pushed on the body of the forming bud. The argyrophil net covering the body of the ciliate (the dynamic net: Raabe 1949 — Fig. 22 H, J, K) participate actively or passively in these processes. At the same time, after the equal division of Mi occurs an unequal division of Ma and a new nuclei set moves to the body of the bud. As it was observed for some species, in the body of the budding trophic individual arise previously peculiar formations named by Chatton et Lwoff "baguettes tubulaires", by Mjassnikowa as "rätselhafte Gebilde" which have a form of elongated plates. One of them wanders on the body of a tomit and settles subpellicularly between the both complexes of kineties falling to it. It seems that it arises from it a sole of the future trophic individual. Slightly in a different way occurs the budding in a conspicuously short species in its trophic stage, that is in *S. dreissenae* Dobrzańska. Here the tomit is of nearly an equal size with the remaining individual (proter); after the separation from this individual it is like unfinished, he has not a typical pear-shaped outline of the body with a narrow sucker and moreover the cilia are not ever present.

The transformation of the tomit into a trophont run as it seems in different ways (Fig. 19). According to Chatton et Lwoff 1932 the tomit of *S. dosiniae* settles on ground not only by its sucker, but also with the space

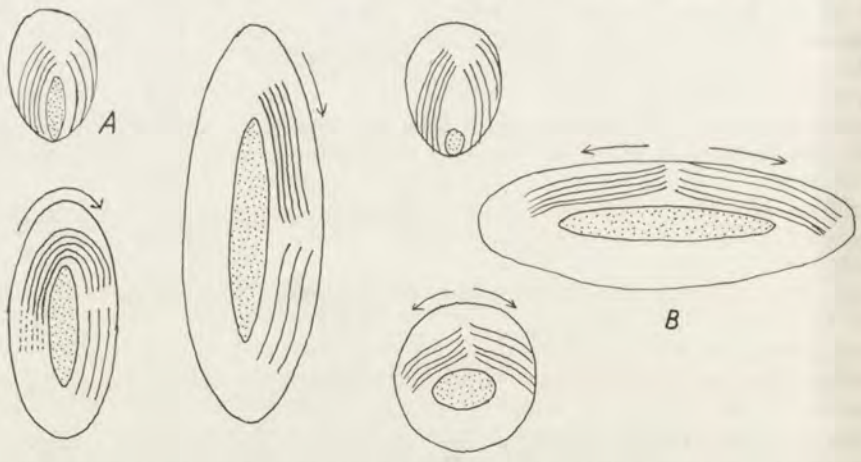

Fig. 19. Transformation of the tomit into the trofont in *Sphenophrya:* A — *S. dosiniae*, B — *S. sphaerii.* After Raabe 1949

between the rows of kineties occupied by the baguette tabulaire, which develops forming a sole. In the first periods of time after the settlement of the tomit it has on the one side of the elongated sole a complex of three rarely arranged kineties, on the other side the complex of 5 kineties more densely arranged. These rows are in contact with one another by its ends which are oriented to the posterior, enlarged, opposite to the sucker part of the body of the tomit. Consequently with the further evolution of the body, the complex of 3 kineties remain on its place, and the complex of 5 kineties wander

to its side in this way, that endly in an grown up trophont, both complexes lie on one side of its body being in contact in its central part. My own observations (R a a b e 1949) confirm this way of process (Fig. 20).

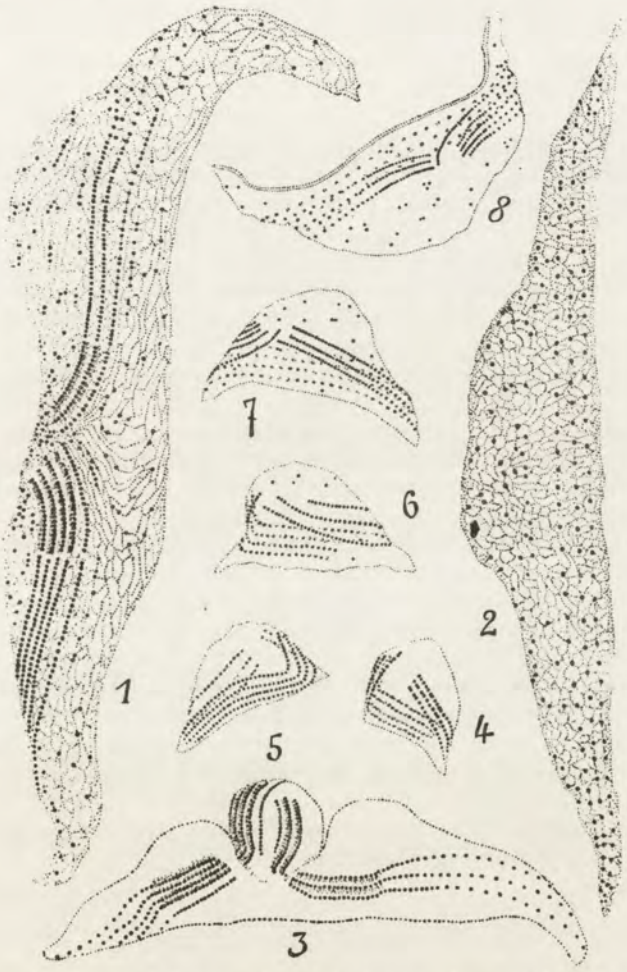

Fig. 20. The development of *Sphenophrya dosiniae* — from C h a t t o n et L w o f f 1931

M j a s s n i k o w a 1930 denies this run of transformation, presumably she based her view on the experience from the observation of these processes in *S. sphaerii*, where virtually they run differently.

The bud of *S. sphaerii* has not as it seems, the baguette tubulaire, or has a very short one and conjunct with the sucker. Its sucker is wide and somewhat extended to the back, towards the surface between the both complexes of kineties (in this case the right row contains 2+2 or 2+3 kineties, the left one contains 6 kineties). The tomit settles on the ground with its sucker, which develops transversally to the run of kineties. As a result of it the contact

between the both complexes of kineties is preserved in the part consisting the posterior body part of the tomit, but the opposite ends of kineties directed to the sucker of the tomit, and by now to the foot of trophont, diverge in both sides of the elongated body. As a result both complexes remain from the beginning on the same side of the trophont's body. So stands the matter both in the opinion of Mjassnikova 1930a, and of Raabe 1949. The difference consist only in the topographic interpretation: Mjassnikova considers that the sucker that is "Das Zäpfchen entspricht einem der Enden eines erwachsenen Individuums, welchen, lässt sich jedoch nicht feststellen", whereas Raabe considers that it transforms in a complete sole (Fig. 23).

The like manner as in *S. sphaerii* run the metamorphosis in *S. dreissenae* Dobrz., but here occurs a torsion of the body evoking a slight spiralization of the system of kineties in the trophont in their apical parts (Dobrzańska 1958, 1961).

Most species of the genus *Sphenophrya* have in their trophic stage a strongly elongated body. *S. dreissenae* Dobrz. provides in this respect an exception, and by its body shape approaches slightly to *Pelecyophrya* or *Lwoffia*. *S. dreissenae* may be considered as a form which is plesiomorphic as to its body construction. On the other hand the fact that its tomits not always have a ciliature or at most a highly reduced one, may be explained as a mark of a stronger advancement towards the complete reduction of ciliature, therefore as an apomorphic character. It must be recognized that the evolution has a mosaic character and that the particular developing features may get over this evolution a different degree of promotion and a different level.

For practical reasons abstracting from the evolutionary aspects of the topography of *Sphenophryidae*, the sole of *Sphenophrya* may be considered as the ventral side in that it constitutes an element squeezed in between both complexes of kineties (ventral, according to our practical interpretation — part III, p. 446). The margin opposite to the sole would be then the dorsal side. The kineties systems would be arranged laterally: the left which contains a higher number of densely arranged kineties, and the right, which contains less of them and rarely arranged. The same may be said about the left and right end of the elongated body.

In view of a considerable similarity of forms, the diagnosis of the genus *Sphenophrya* may be easy presented as follows:

Sphenophrya Chatton et Lwoff, 1921

Sphenophryidae of a shape of more or less elongated boot, adjacent to the substrate with the base ("deck"). On the side there is a system of kineties without cilia, divided into two complexes of parallel kineties; these complexes are near each other in the apical part of the body, and are going asunder towards the basis in two directions taking a parallel orientation to the base. The budding is apical, the division of Ma unequal. The conjugation occurs with the opposite body ends or with the bases. Parasites of the gills of marine and fresh-water *Bivalvia*.

Typus generis: *Sphenophrya dosiniae* Chatton et Lwoff, 1921.

We range by now among the genus *Sphenophrya* 6 species:

Sphenophrya dosiniae Chatton et Lwoff, 1921

syn.: *Sphenophrya myae* Mjassnikova, 1930.

The body strongly elongated, sharply ended on both tops. The sole is narrow, not protruding out of the body margins. The length 120 μ, width 10—20 μ, Ma elongated, often of irregular shape, measures ca 40×4 μ and lies in the central part of the body; Mi, 2—3 μ, lies close to Ma. C.V. next to Ma, its activity is slightly visible. The system of non ciliated kineties constitutes two complexes: the first complex consists of 5 kineties distant from one another ca 1 μ, and the last (by the sole) by 1.5 μ (on several drawings of Chatton et Lwoff 1950 there are 6 kineties in this complex); these kineties point from the center of the convex body side towards its sole and deviate to the left along the margin of the sole. The second complex contains 3 kineties distant from one another by 2—2.5 μ, they run from the peak point with the formers on the convex side of the ciliate's body towards its sole and to the left (Fig. 21 A—J, Fig. 22 A).

The reproduction by budding from the concave side of the body. The tomit measures 20×10 μ. The tomit transforms in trophont by the development of sucker into a sole. The system of 3 kineties remains at its place, the system

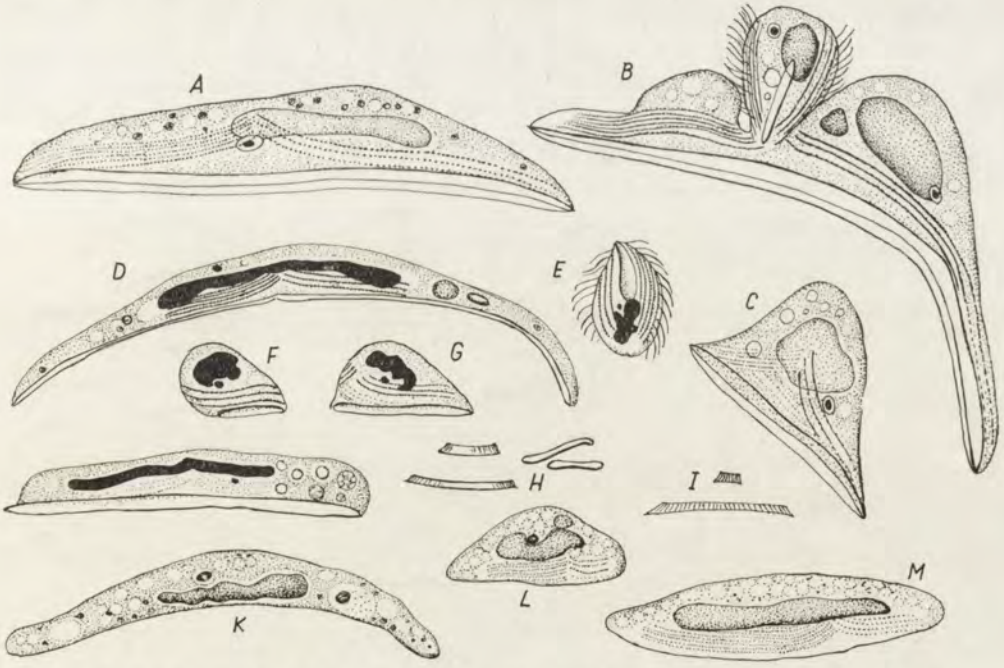

Fig. 21. *Sphenophrya:* A, B, C — *S. dosiniae* (after Chatton et Lwoff); D, E, F, G — *S. dosiniae* (a. Raabe); H — baguette tubulaire (a. Raabe); J — baguette tubulaire (a. Ch. Lw.); K — *S. cardii* (a. Ch. Lw.); L, M — *S. minor* (a. Poljansky). ×1000

of 5 kineties moves through the sharpened end of the body on the same side (Fig. 20). The conjugation occurs by the coupling of the sedentary individuals by the opposite ends of the body; the triple conjugation was observed (R a a b e).

Host: *Dosinia exoleta* L., *Venus ovata* Penn., *Corbula gibba* Olivi — Roscoff (Ch. Lw.); *Mactra solidissima* L., *Mya arenaria* L. — Woods Hole, Mass., N. America (Ch. Lw.); *Mya truncata* — White Sea (M j a s s n i k o v a); *Mya arenaria* L. — Baltic Sea (R a a b e). Sometimes mass occurrence.

Sphenophrya cardii Chatton et Lwoff, 1950

syn.: *Sphenophrya dosiniae* Ch. Lw., form from *Cardium*, — Raabe 1938.

R a a b e 1938 finds the occurrence of *Sphenophrya* in *Cardium edule* L. (recte *C. lamarcki* Reeve) from South Baltic Sea. He recognized this *Sphenophrya* as *S. dosiniae* Ch. Lw., 1921 on the basis of the identity of the kineties system. R a a b e differentiated also the populations originating from *Cardium* of Gdańsk Bay with a larger and thicker body, and the populations from the more freshwatered part of the Puck Bay with a smaller and more narrow body. C h a t t o n et L w o f f 1950, did not mention the studies of R a a b e 1938 and describe the new species *S. cardii* from *Cardium edule* L. of Roscoff on the basis of a different body outline in spite of the identity of the system of kineties with this of *S. dosiniae*. The same form finds F e n c h e l 1965 in *C. lamarcki* from Kattegat, recognizing it as *S. cardii*. I found a very like form in *C. edule* from the lake Varnenske close to the Black Sea. For the reason that all populations from *Cardium* reveal a morphological coincidence and differ from the typical *S. dosiniae*, I incline to the opinion of C h a t t o n et L w o f f 1950 and F e n c h e l 1965 and I preserve for them a separate species with following characteristic features:

Fig. 22. The variations of shape and size of marine *Sphenophrya:* A — *S. dosiniae* from *Mya arenaria* from the S. Baltic Sea, B — *S. cardii* from *Cardium lamarcki* form the deeper places of the Gulf of Puck (S. Baltic Sea), C — *S. cardii* from *Cardium lamarcki* from the more shallow places of the Gulf of Puck (S. Baltic Sea); from R a a b e 1938

Body elongated bluntly rounded on both ends. The sole wide, often protrudes besides the margin of the body. Length up to 120 μ, width 5—20 μ. Ma elongated, irregular, measures up to 40 μ of length and lies in the middle of the body; Mi next to Ma. The system of kineties (as in *S. dosiniae*): 5 kineties point to the right, 3 more distant from each other to the left. Tomits ca 20×8—10 μ; transformation as in *S. dosiniae* (Fig. 21 K, Fig. 22 B, C).

Hosts: *Cardium edule* L. — Roscoff (Ch. Lw.); *C. edule* and *C. lamarcki* Reeve — Øresund, but not Kristineberg and not Askö, Baltic — (F e n c h e l); *C. lamarcki* Reeve — Gdańsk Bay and Puck Bay, S. Baltic (R a a b e); *C. edule* L. — Varnenske Lake, Varna, Black Sea (R a a b e, not publ.).

Sphenophrya sphaerii Mjassnikova, 1930

Body elongated, rather stocky and bluntly ended. Length up to 135 μ, width 10—25 μ. Ma very long, sometimes as long as the body but folded in this case, sometimes short and thick; Mi minute, lies near Ma. The system of kineties (without cilia) consists of two complexes, they converge on the convex side of the body in its middle. One of them consists of 5—7 kineties (according to M j a s s n i k o v a 4—8) arranged close to each other they run from the apical point towards the sole and turn right; the second consists of 2+2 or 2+3 kineties (according to M j a s s n i k o v a 4—6 kineties) and point to the sole turning left. The budding occurs from the convex side of the body. The tomit measures ca. 25 μ. The tomit settles by its sucker on the ground and this sucker gradually develops into a sole so that both complexes of kineties which touch in the posterior end of the tomit diverge by their free ends in two sides towards the two body ends (Fig. 23). The conjugation is done by the opposite ends of the sedentary individuals; the threefold conjugation was observed (R a a b e).

Host: *Sphaerium corneum* L. — mouth of Newa-river (M j a s s n i k o v a); the lake Żarnowieckie, N. Poland (R a a b e); region of Strassbourg (Ch. Lw.).

Sphenophrya minor Poljansky, 1951

Body meanly elongated. Length 30—85 μ, width 13—20 μ. Ma elongated, long over a half of the body length; Mi dorsal from Ma, near C.V. The system of kineties: the right complex consists of 7—9 kineties arranged near each other, the left complex 3—4 more rarely arranged kineties. The author considers that *S. minor* can take as a food the cells of the host epithelium what would be proved by the presence of their nuclei in its cytoplasm (Fig. 21 L, H).

Host: *Cardium* sp — Vladivostok, Far East USSR (P o l j a n s k y).

Sphenophrya dreissenae Dobrzańska, 1958

Body of the shape of helmet, 30×30 μ, slightly flattened laterally, with one or two distinctly protruding processes on the body margins. The processes are not always equally distinct which seems to be associated with the position of the ciliate on the margin of the host's gill. Ma irregular, usually ovoid, ca 10×8 μ, lies in the middle of the body; Ma, 3—4 μ in diameter, lies on the side of Ma.

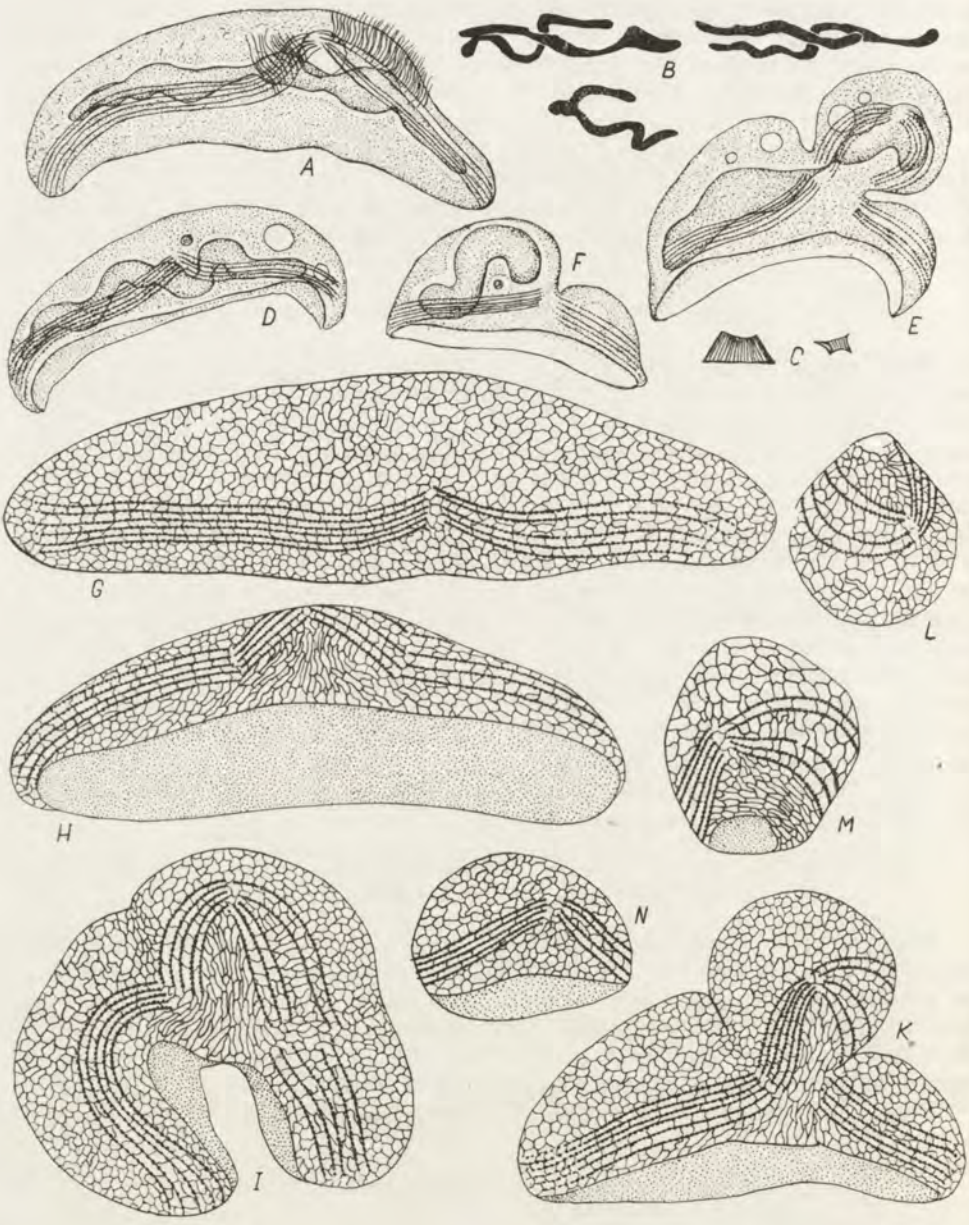

Fig. 23. *Sphenophrya sphaerii:* A — the general view and B — the forms of Ma (after Mjassnikova); C — the "rätselhafte Gebilde" (a. Mjassnikova); D, E, F — the trophont, the budding and the trophont after budding (a. Raabe); G, H — the trophonts, I, K — the budding, L — the tomit, M, N — the transformation rzono rodzaj *Kozlofiella* g. n. dla *Heterocineta phoronopsidis* Kozloff.

The system of kineties (with no cilia) is limited to one body side and is constituted by two complexes with converge on the apical body convexity. From this place one complex consisting of 4—5 kineties runs towards the base, turns right and sometimes passes in the other body side. Another complex composed of two pairs of kineties (2+2) diverges from the former one and deviates left. The apical parts of both complexes are somewhat spiral twisted (Fig. 24 A—D).

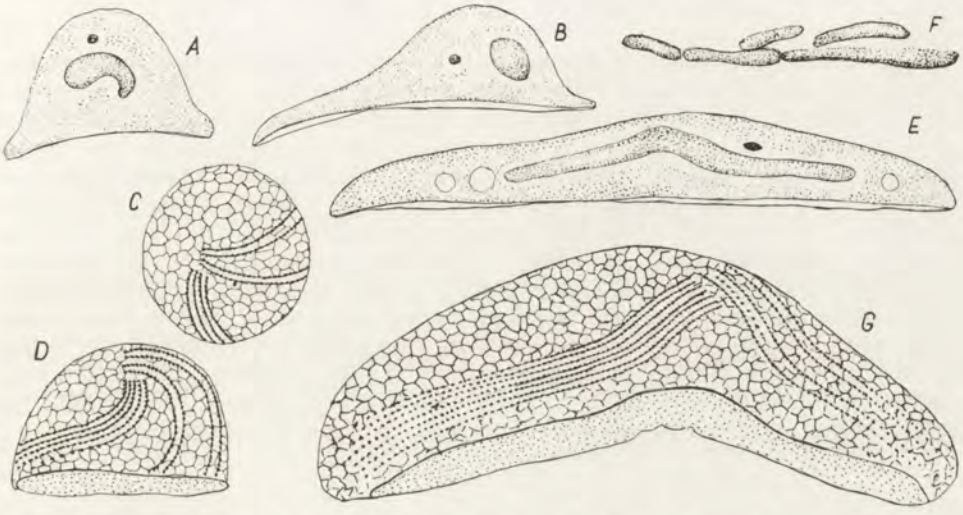

Fig. 24. *Sphenophrya:* A, B — *S. dreissenae* I. H. prep., C, D — *S. dreissenae* after $AgNO_3$ prep.; E, F, G — *S. naumiana*, general view, the shape of the Ma and the ciliate after $AgNO_3$ preparation (all after R a a b e); ×1000

The reproduction by budding, or rather by a division in two nearly equal individuals. It seems that the new individual separating from the sedentary one not always get cilia and does not flow off, but slips from the sister individual. Conjugation by the ends or soles.

Host: *Dreissena polymorpha* Pall. — environments of Warszawa and Mazury Lakes. N. Poland (D o b r z a ń s k a, R a a b e); Ohrid Lake, Yugoslavia (R a a b e). In the Ohrid Lake *Dreissena* could be met at different depth from 1/2 m to 50 m. In the case of mass occurrence (1% of mussels), other ciliates were found in very small numbers or were absent of all.

Sphenophrya naumiana Raabe, 1965

Body elongated, one of its ends is beak-shaped. Length 60—80 μ, width 12—18 μ. The sole is broad, 8 μ. Ma elongated, 50×10 μ, lies in the middle of the body; Mi, 3—4 μ, lies near Ma. The system of non ciliated kineties constitutes two complexes. The right complex consists of 6—7, sometimes even 9 kineties, runs turning from the peak point towards the sole (sometimes by a sharp bent), pointing concurrently to the sole and reaching as far as the body. The left complex consists of two pairs of kineties (2+2, or sometimes 2+3 and even 2+4) and runs diverging towards another body end (Fig. 24 E, F, G). Budding occurs at night; the bud measures ca. 17×10 μ.

Host: *Dreissena polymorpha* Pall. — Ohrid Lake, Yugoslavia. *S. naumiana* Raabe, 1965 was found rather irregularly in the Ohrid Lake both at the depth of 0.5 m and of 10 or 40 m. Mass occurrence in 1% of mussels. A simultaneous occurrence of *S. dreissenae* Dobrz. and *S. naumiana* Raabe in the same host individual was never stated.

Summary

The third part of the monograph on *Thigmotricha* comprises the elaboration of the families *Ancistrocomidae* and *Sphenophryidae*. These families are connected with the common, but in a different grade realized, tendency to the reduction of the ciliature, the atrophy of the primary mouth and to the passage to the nutrition with the secondary oral apparatus i.e. the sucker or the adhesive surface originating from the sucker. The characteristics of the families is given as well as the evolutionary paths and the division of the family *Ancistrocomodae* in three subfamilies: *Ancistrocominae, Hypocomidinae* and *Hypocomellinae*. The paper comprises the descriptions and definitions of the genera and the diagnoses of the species. Within the subfamily *Ancistrocominae* — *Holocoma* is included in the genus *Ancistrocoma*, while in the subfamily *Hypocomellinae* the genus *Hypocomatophora* and *Heterocineta* are included in the genus *Hypocomella*; the new genera *Kozloffiella* for the species *Heterocineta phoronopsidis* Kozloff was established.

STRESZCZENIE

Trzecia część monografii *Thigmotricha* zawiera opracowanie rodzin *Ancistrocomidae* i *Sphenophryidae*, które łączy wspólna, lecz w różnym stopniu realizowana, tendencja do redukcji urzęsienia oraz do zaniku pierwotnej gęby i przejściu do pobierania pokarmu przez wtórny aparat oralny — ryjek lub wytworzoną z niego powierzchnię czepną. Podano charakterystykę obu rodzin, omówiono kierunki ewolucyjne w ich obrębie i podział pierwszej z nich na podrodziny: *Ancistrocominae, Hypocomidinae* i *Hypocomellinae*. Podano opisy i diagnozy rodzajów i opisy gatunków. W obrębie podrodziny *Ancistrocominae* dokonano włączenia rodzaju *Holocoma* do rodzaju *Ancistrocoma*, w obrębie podrodziny *Hypocomellinae* włączono rodzaje *Hypocomatophora* i *Heterocineta* do rodzaju *Hypocomella* oraz stworzono rodzaj *Kozlofiella* g. n. dla *Heterocineta phoronopsidis* Kozloff.

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Urceolaria kozloffi sp. n., a symbiont of Brachiopods

Urceolaria kozloffi sp. n., un symbiont des brachiopodes

There have been no reports of symbiotic ciliates from brachiopods, but symbiosis has rarely been recorded in these hosts (Hyman 1959). In 1962 Dr. Eugene Kozloff suggested that I try to identify the mobiline peritrich that he had seen in brachiopods dredged from Puget Sound waters near the Friday Harbor Laboratories. Two species of brachiopods, *Terebratalia transversa* and *Hemithyris psittacea* are commonly found in dredge hauls near San Juan Island, Washington, and every individual of both species is infected with the ciliates.

The ciliates are identified as mobiline peritrichs by their left-winding adoral ciliature encircling a conspicuous peristome and an elaborate denticulate adhesive disc. In the living host they are attached by their discs to the tentacles of the lophophore, where they probably feed at the expense of the host's food supply.

The denticles on the adhesive disks are smooth, obliquely tangential to one another, and bear no radial processes. These characteristics identify the peritrich as a species of *Urceolaria*. The individuals from the two species are alike in respect to denticle number, disc diameter, and body shape. But a substantial proportion of individuals from both species of brachiopods have H-shaped instead of C-shaped macronuclei. Since macronuclear dimorphism has been reported for other species of *Urceolaria* (Caullery et Mesnil 1915, Colwin 1944, Lom 1958), the difference in macronuclear shape has not been deemed sufficient to separate these symbionts into two species. Therefore these urceolarians are described as a new species and named *Urceolaria kozloffi* in honor of Dr. Eugene Kozloff.

Materials and methods

Terebratalia transversa and *Hemithyris psittacea* were collected in dredge hauls in Puget Sound and maintained in running sea water in the laboratory. The numbers of symbionts decreased with time, but even after a month all the brachiopods were still infected.

To collect the ciliates, the valves of a brachiopod were forced apart, and the extirpated lophophore was repeatedly wiped back and forth over coverslips. The ciliates trapped in the mucus from the lophophores were transferred to the coverslip. To observe the living animal these coverslips were inverted on slides and sealed with vaspar. Other coverslips were dropped onto the

surface of various fixatives for subsequent staining. Fixatives used were Schaudinn's, Champy's, DaFano's, Hollande's and Bouin's. Permanent preparations were made using Heidenhain's iron haematoxylin, Ehrlich's haematoxylin, and the Feulgen stain for DNA. Organisms were impregnated with silver using Protargol or the Chatton-Lwoff method. The protocols for all staining procedures are those in Kirby's manual (Kirby 1950).

Living urceolarians were studied by phase and by brightfield illumination.

Observations

The living animal

In freshly made preparations the form of this species alters after two or three minutes. The organism contracts, assuming the rounded body outline usually seen in stained preparations. Before contraction the oral-aboral axis is about 20% longer than the width of the body. Measurements of three living specimens average 120 μ×100 μ. The peristome and collarette are slightly broader than the aboral end (Fig. 1). The broad peristome is slightly convex and is circled by the oral ciliary membranes which describe a 430° angle around it. When the organism contracts, the collarette covers the bases of the membranes, immobilizing them. Both membranes continue into the infundibulum and beat even when the peristomial cilia are stilled.

A large vacuole, which was not observed to contract, is found near the infundibulum between the arms of the macronucleus. Similar vacuoles in the same position have been reported from other urceolarians (Fig. 1).

About 2/3 of the body length from the oral pole is a stratum of refractile yellowish granules which cannot be recognized in stained material.

The aboral ciliary girdles are in constant movement even when the aboral end of the organism is appressed to detritus on the slide. The long (20 μ) powerful cilia appear to be coalesced, with undulations along their length that slap at the substrate. MacLennan 1939 suggests that it is the action of these beating cilia that holds the disc against the host epithelium and presses the margin of the disc down among the host cells. Bordering the outer ciliary girdle, very long cilia extend orad about 1/3 of the body's length. These marginal cilia are the "cirri" described in the early literature (Kahl 1935). They stay near the body, not beating outward, and cannot be recognized in stained material. (For a summary of forms with "cirri", see Raabe 1963).

The details of the adhesive disc are best studied in fixed material, although most structures are visible in life. The border membrane of this species is conspicuous, forming the transparent stiff walls of an inner cup between the girdles and the center of the adhesive disc (Plate I 5). The border membrane can sometimes be seen in living ciliates as they are attaching. Sandon 1965 believes that the beating of the diagonal rows of cilia of the aboral girdle pushes the margin of the disc and therefore the border membrane down and inward toward the main axis of the body, causing the border membrane to bite into the epithelium. In attached forms the denticles observed through the body are parallel to the oral-aboral axis. Their function would seem to be strengthening, (i.e. making rigid), the vault of the convex adhesive disc.

The macronuclear dimorphism was not recognized until the opportunity to study living ciliates was past. In the organisms studied, the micronucleus

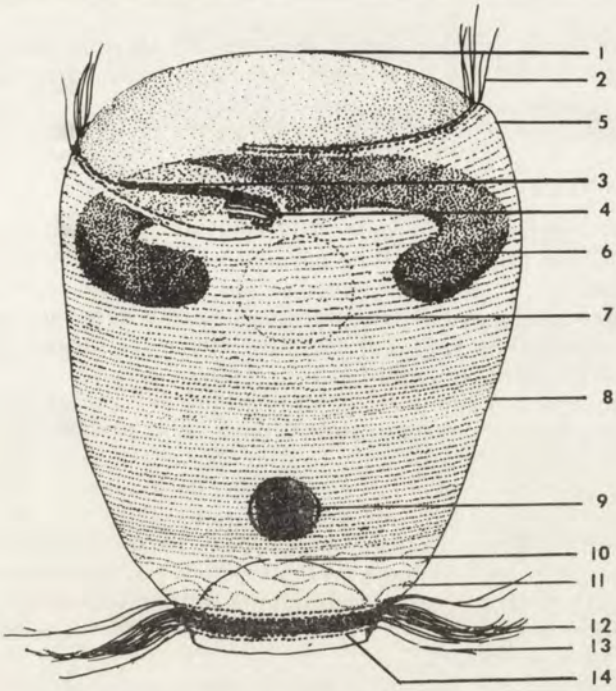

Fig. 1. Composite sketch of *Urceolaria kozloffi sp. n.* drawn from several specimens, each stained by a different method. (1) peristome (2) oral ciliature (3) polykinety (4) peniculus (5) collarette (6) macronucleus (7) vesicle (8) stria (9) micronucleus (10) center of adhesive disc (11) marginal cilia ("cirri", longer and upright in the living organism) (12) outer ciliary girdle (13) inner ciliary girdle (14) border membrane

appeared as a clear vesicle just anterior to the adhesive disc, and the macronucleus could be seen curving horizontally, directly beneath the collarette. However organisms with a V-shaped macronucleus would very likely counterfeit the shape and position of the micronucleus and macronucleus of the other form since the orally directed macronuclear connectives are usually thin and inconspicuous (Fig. 2).

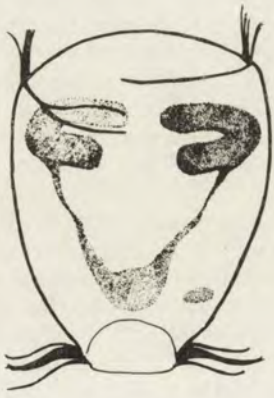

Fig. 2. Sketch of *Urceolaria kozloffi* sp. n. illustrating the position of the micronucleus and the H-shaped macronucleus

Under high magnification and favorable illumination the body surface shows fine horizontal striae like those encircling many vorticellids and other species of *Urceolaria*.

There is no trace of a velum in living or fixed organisms.

Stained preparations

The infraciliature and argyrome. The Chatton-Lwoff silver impregnation method reveals the regular pattern of pellicular striae encircling the body. Only the peristome and the adhesive disc are free of striae. The only asymmetry in the pattern of equidistant lines occurs in a zone just anterior to the aboral ciliary girdles (Fig. 1, Pl. I 2). Here the striae are thrown up in elaborate waves and anastomosing convolutions.

The Chatton-Lwoff method demonstrates that the infraciliature of the oral membranes conforms to the conventional pattern in peritrichs, a haplokinety, its kinetosomes staining as a single row of granules, and a polykinety, two granules wide. The two membranes closely parallel one another as they encircle the peristome, the haplokinety being distal to the polykinety. They separate at the buccal overture; the haplokinety running down the distal wall of the short infudibulum and the polykinety, now 4 kinetosomes wide, following the proximal wall of the infundibulum. Both membranes extend to the cytostome, where the polykinety is paralleled by a peniculus consisting of six short rows of kinetosomes.

The aboral ciliary girdles are formed of three parts; an outer haplokinety which probably gives rise to the "cirri" or marginal cilia, the outer ciliary girdle, a complex polykinety made up of closely set diagonal rods containing six or seven kinetosomes per rod, and a haplokinety, the inner ciliary girdle, adjacent to the border membrane. The center of the adhesive disc contains numerous scattered kinetosomes, and in some individuals the attached cilia could be seen. (Cilia have been described within the denticulate ring in *Urceolaria synaptae* (Colwin 1944) and *Urceolaria paradoxa*, and electron micrographs of *Trichodina urinicola* show barren kinetosomes in the center of the disc (Favard et al. 1963).

The denticles are best examined in living organisms or in ciliates stained by Heidenhain's iron haematoxylin. Their number ranges from 10 to 16, but usually falls between 12 and 14 (Fig. 4). Each denticle is smooth and slender, in width varying from a little more to a little less than a micron and about four micra long. They are diagonally articulated on one another, forming a circle or corona whose external diameter is about 17 μ.

The striated membrane is distal to the corona. The number of striations or pins per denticle is a taxonomic characteristic for *Urceolaridae*. In *U. kozloffi* the number is 7. The pins of the striated membrane are continuous with the finer and more numerous striae of the border membrane (Fig. 3).

Many organisms fixed in side view show the border membrane, resembling the sides of a conspicuous inner cup, but the border membrane is difficult to recognize when the attached organism has been fixed in situ on the coverslip and the aboral surface is thereby uppermost. The border membrane is transparent and takes up none of the stains used in this study. In some protargol preparations stain collects in granules at the rim.

On every slide from either host some individuals had a C-shaped macronucleus parallel to the peristome and in the region of the collarette. This is the

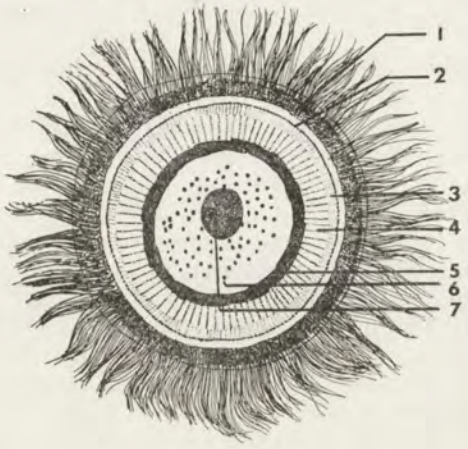

Fig. 3. Aboral view of *Urceolaria kozloffi* sp. n. (1) outer ciliary girdle (2) inner ciliary girdle (3) border membrane (4) pins (5) denticles (6) kinetosomes (7) micronucleus

typical shape and position of the macronucleus in vorticellids, and trichodinids, but *Urceolaria mitra* is the only other well-known member of this genus to have a macronucleus of this shape (H a i d e r 1963, R a a b e 1963).

The ends of the macronucleus are about 19 μ apart. The outline of the macronucleus is smooth and sausage-shaped and the interior contains Feulgen-negative vacuoles with a diameter of 2—3 μ. The micronucleus is a dark-staining ovoid body immediately above the adhesive disc (Fig. 3).

But always in company with these organisms are others of the same dimensions, whose macronuclei have the characteristic modified H-shape found in the majority of species of *Urceolaria* (H a i d e r 1963, N o b l e 1940). In these macronuclei the crosspiece of the H is bent aborad in a V extending to the adhesive disc where the apex of the V is inflated into a globular mass, occupying the position of the micronucleus in its companion (Fig. 2). The globular mass and the arms of the V are irregular in outline, and stain less intensely and homogeneously than the arms of the H. The micronucleus in these forms is oblate and located to one side of an arm of the V (Pl. I 4).

Conjugation takes place between two unlike partners (Pl. I 3). The microconjugant is noticeably smaller than the macroconjugant, although it appears complete in other respects. The microconjugant attaches to the side of the macroconjugant above the ciliary girdles. The macrogamete can only be recognized after attachment and subsequent nuclear events. Mass conjugation occurs, and many slides contain numbers of exconjugants. In these slides only organisms with H-shaped nuclei accompany the exconjugants.

Only two or three dividing organisms were recognized. In these organisms the macronucleus had condensed into a solid ball in the center of the body.

Protargol sometimes impregnates heavily certain fibrillar structures usually described as myonemes. Thick fibrils in groups of 2 and 3 insert on the inner edge of the denticles at a round granule. They rise orad, sometimes bifurcating before inserting on the peristome. Numerous smaller fibrils originate below the adoral ciliature. Frequently they branch before they reach the pellicle of the collarette. In some organisms a speckled band circles the organism in the collarette, each dot representing the terminus of a fiber (Pl. I 5).

Discussion

The most important point to be considered in a discussion of these ciliates is that they may not be a single species of *Urceolaria* with a dimorphic macronucleus but two separate species. However, macronuclear dimorphism has been described before in this genus and in *Trichodina*. Colwin 1944 has tentatively described from the gut of *Thione* two different strains of *U. synaptae* differing in size, macronuclear shape, and location in the gut. *U. patellae*, a form similar to *U. kozloffi* and with an H-shaped nucleus, is reported by Caullery et Mesnil 1915 to lose the arms of the H when heavily infected with zooxanthellae. Lom 1958 has described from salamanders three strains of *Trichodina urinicola*, two of which coexist in a single species of salamander and have slightly different macronuclei.

Further the constant presence of two species of the same genus in two genera of hosts is unusual.

In each form the number of denticles vary within the same narrow range, the form with the horseshoe shaped macronucleus averages 13.2 and the form with the H-shaped macronucleus 15 denticles. The diameter of the corona averages 15.8 μ in the former and 16.7 μ in the latter. These averages fall well

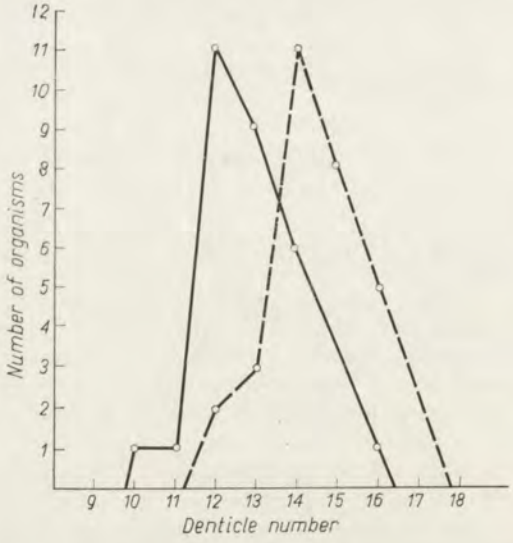

Fig. 4. Comparison of the number of denticles per organism of *Urceolaria kozloffi* sp.n. in individuals with H-shaped macronuclei (dashed line) and individuals with C-shaped macronuclei (solid line). Sample — 28

within the range variation within other described species (Noble 1940, Hirschfield 1949). If denticle number is a constant characteristic of a species, then these forms must be conspecific.

It is puzzling why only H forms are seen on slides with numerous exconjugants. Is it possible that the H-shaped nucleus represents a developmental stage, and the exconjugants are organizing H-shaped nuclei? The arms of the H resemble the horseshoe in size and staining reaction. The middlepiece may

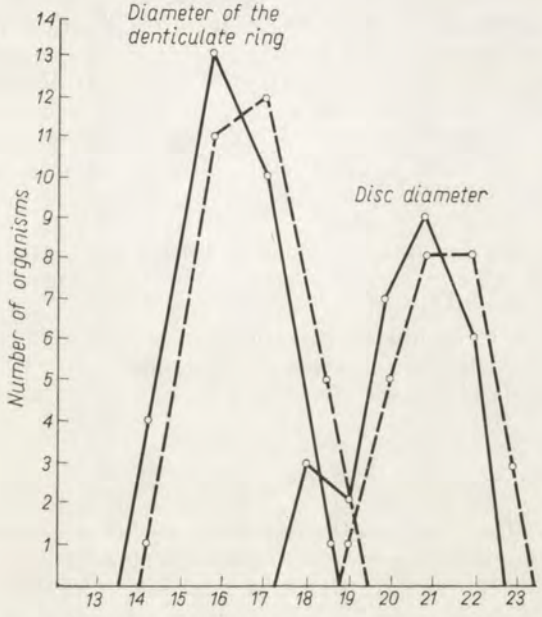

Fig. 5. Comparisons of the diameter of the denticulate ring and the diameter of the disc of *Urceolaria kozloffi* sp. n. in individuals with H-shaped macronuclei (dashed line) and individuals with C-shaped macronuclei (solid line). Sample — 28

stain so faintly that at first glance an organism will appear to have a horseshoe-shaped macronucleus. But faint-staining, vacuolate nucleoplasm, and irregular outlines are characteristic of the crosspiece of the H-shaped macronucleus.

The presence of marginal cilia place *Urceolaria kozloffi* in the subgenus *Leiotrocha* according to Lom's classification of the suborder. Raabe suggests the recognition of *Leiotrocha* Fabre-Domergue, 1888 as a valid generic name. *Urceolaria kozloffi* has the H-shaped macronucleus and cortical striations that would make it a species of *Leiotrocha* it were not for the individuals with the horseshoe-shaped macronucleus. If *U. kozloffi* were two species, the forms with horseshoe-shaped macronuclei would not be *Urceolaria* according to Raabe's classification, because of their cortical striations. Raabe believes that *Urceolaria* and *Leiotrocha* are very closely related, and *Urceolaria kozloffi* may represent an intermediate stage. I prefer to consider *Leiotrocha* a subgenus and designate the ciliate described in this report as *Urceolaria* (*Leiotrocha*) *kozloffi*.

Diagnosis of *Urceolaria* (*Leiotrocha*) *kozloffi* sp. n.

Body cylindrical but tapering slightly at the aboral end, contracting to subspherical when fixed. Macronucleus may be C-shaped, in anterior third of body, with a conspicuous micronucleus just above center of adhesive disc. Alternatively, macronucleus may be H-shaped with the arms in the anterior third of the body and middle piece bent aborad into a V above center of

adhesive disc, micronucleus then being posterior and distal to an arm of the H. Average body height and width 48×45 μ after fixation (Hollande's). Oral ciliature is a haplokinety and a polykinety two kinetosomes wide. Marginal cilia ("cirri") present; infraciliature of aboral ciliary girdle short diagonal rows of 7—8 kinetosomes. A haplokinety circles the adhesive disc at the outer base of the prominent border membrane. Disc diameter averages 16 μ; 10—16 smooth denticles — 7 pins per denticle; scattered cilia in the center of the adhesive disc; large fixed vacuole near infundibulum between arms of macronucleus; band of yellowish granules in lower third of body; macro- and microconjugants; pellicular striae encircle body except for peristome and adhesive disc.

Type host: *Terebratalia transversa.*

Additional host: *Hemithyris psittacea.*

Habitat: Attached to the tentacles of the lophophore of brachiopods.

Type locality: Puget Sound, Washington.

Summary

An inquiline ciliate from the lophophores of the brachiopods, *Terebratalia transversa* and *Hemithyris psittacea*, is described as a new species of *Urceolaria*: *U. kozloffi.* Individuals fixed in Hollande's fixative average 48 μ in height and 45 μ in width. The denticulate rings is 14 to 18 μ in diameter. The number of denticles ranges from 10 to 16 with about 7 radial pins per denticle. A prominent border membrane forms a cup, pendant from the adhesive disc. The base of the cup is strengthened by the denticulate ring which encircles a tuft of cilia in the center of the adhesive disc.

The macronucleus may be C-shaped and in the oral third of the body, perpendicular to the oral-aboral axis, or individuals may have an H-shaped macronucleus whose middle piece is bent aborad into a V just above the adhesive disc. In the former case the micronucleus is directly above the center of the adhesive disc; in the latter case the micronucleus is found in the aboral third of the body just below and to one side of an arm of the H.

RÉSUMÉ

Un inquilin cilié des lophophores des brachiopodes, *Terebratalia transversa* et *Hemithyris psittacea*, est décrit comme une nouvelle espèce *d'Urceolaria: U. kozloffi.* Les individus après fixation au liquide de Hollande mesurent environ 48 μ de longueur, sur 45 μ de largeur. Le diamétre de l'anneau segmenté measure de 14 à 18μ. Le nombre des pièces de l'anneau segmenté varie de 10 à 16 et il y a environ sept fibres coronales accompagnant chaque segment. La couronne, péripherique est très developpée et forme les parois marginales de la cupule adhésive. L'anneau segmenté encercle une touffe de cils.

Le macronucleus peut avoir la forme d'un C et être situé dans le tiers oral du corps, perpendiculaire a l'axe oral-aboral ou bien peut avoir la forme d'un H et dont la partie mediane est pliée en forme de V dans la direction aborale juste au dessus du centre de la cupule adhesive. Dans ce dernier cas le micronucleus est situé dans le tiers aboral du corps just en dessous et à coté de l'une des branches du H.

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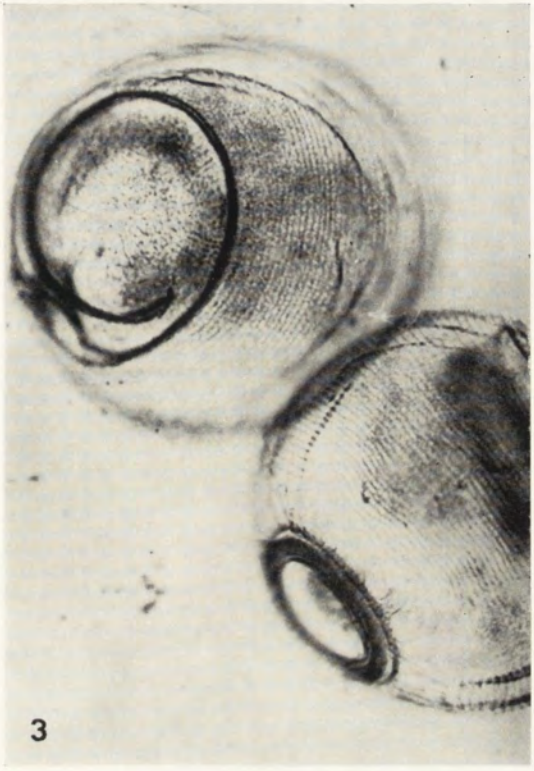
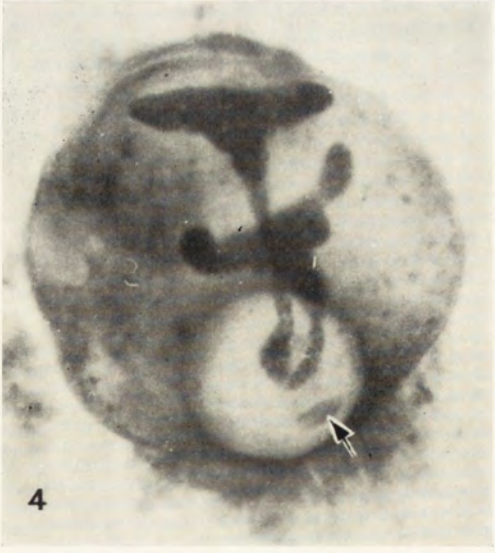
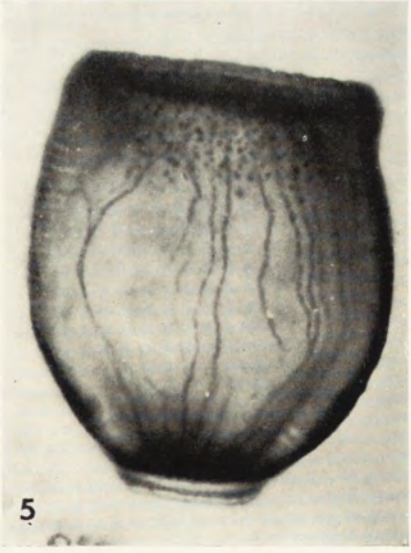
EXPLANATION OF PLATE I

Urceolaria kozloffi sp. n.

1: Oral surface of a Feulgen-stained preparation of *U. kozloffi* showing a C-shaped macronucleus
2: Chatton-Lwoff silver impregnation of the infraciliature and the argyrome. The pellicular striae above the aboral cilia are interrupted and convoluted. The kinetosomes in the center of the aboral disc are slightly out of focus
3: Protargol impregnation illustrating the size differences between conjugant partners
4: Latero-posterior view of an individual with an H-shaped nucleus. The arrov indicates the micronucleus. Feulgen stain
5: Protargol impregnation of myonemes in *U. kozloffi*. The granules at the oral end represent the termini of myonemes







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Инфузории мезопсаммона Кандалакшского залива (Белое море). I

The ciliates of the mesopsammon of the Kandalaksha Gulf (White sea). I

Фауна псаммофильных инфузорий Кандалакшского залива подробно изучалась И. Б. Райковым 1962. В настоящей работе приводится описание некоторых новых и наиболее массовых, ранее неизвестных для Белого моря видов. Описание даётся на основании прижизненных наблюдений и изучения фиксированного материала, импрегнированного серебром (Chatton et Lwoff 1930) или окрашенного гемалауном. Материал собран в районе биологической станции Московского университета в июне-сентябре 1967 года. Пользуюсь случаем выразить глубокую благодарность моим руководителям — сотруднику кафедры О. И. Чибисовой и профессору Л. А. Зенкевичу за постоянную помощь в работе.

Lagynophrya halophila Kahl, 1930 (Рис. 1)

Тело овальное или цилиндрическое, асимметричное, несократимое. Вентральная сторона прямая или вогнутая, дорсальная — выпуклая. Размеры 40—44×20—22 μ. „Хоботок" широкий, конический, сравнительно крупный и хорошо выраженный. На фиксированных препаратах он часто ввёрнут внутрь. 18—20 соматических кинет. Кинетосомы крупные, сгруппированы по 2—3. Расстояние между группами кинетосом в пределах одной кинеты и между соседними кинетами одинаково (2—3μ). Параллельно ресничным рядам тянутся ряды трихоцист.

Эндоплазма содержит разнообразные включения, особенно их много в передней трети тела, задняя треть свободна от каких-либо включений. Ротовые трихиты хорошо развиты. Макронуклеус эллипсоидный или овальный (5—6μ) с очень маленьким сферическим микронуклеусом. Сократительная вакуоль простая, терминальная.

Один из самых распространённых в Кандалакшском заливе видов. Встречается в песках разнообразной зернистости и сапробности, а также в слое детрита и в придонном слое воды.

Беломорская форма близка форме, описанной Калем, но характеризуется несколько меньшими размерами, более широкой формой тела, большим числом соматических кинет и их своеобразным строением.

Lacrymaria ovata sp. nov. (Рис. 2)

Тело эллипсоидное или овальное, слегка уплощенное в дорсо-вентральном направлении, несократимое. Размеры 60—64 × 30—32μ. „Шейка" отсутствует; „хо-

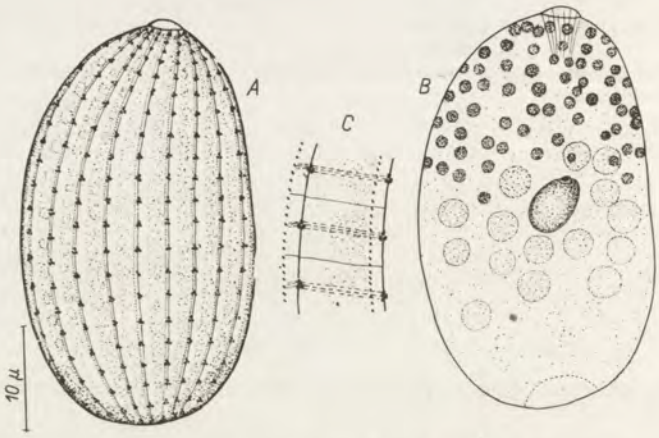

Рис. 1. *Lagynophrya halophila* Kahl, 1930. A — общий вид (тотальный препарат, себрение), правая сторона, B — оптический разрез; ядерный аппарат (гемалаун), C — фрагмент аргирома

Fig. 1. *Lagynophrya halophila* Kahl, 1930. A — general view (whole preparation, silver impregnation), right side, B — frontal section, nuclear apparatus (haemalaun), C — fragment of argyrome

боток" двучленный, крупный. Основание „хоботка" — 6μ, вершина 4μ. 16—20 слегка спиральных соматических кинет. Кинетосомы очень крупные. Расстояние между кинетосомами около 1μ. Максимальное расстояние между соматическими кинетами 5—6μ. Параллельно ресничным рядам тянутся ряды трихоцист. Реснички „хоботка", вдвое длиннее соматических, тесно прилегают друг к другу и образуют ярко выраженную спираль. Кинетосомы очень мелкие.

Эктоплазма плотная, но не блестящая, не панцировидная. Эндоплазма содержит большое количество разнообразных включений, тёмная, непрозрачная, часто вакуолизированная и пигментированная. Ротовые трихиты не выражены. Макронуклеус эллипсоидный (10μ), лежит в середине тела. Микронуклеус не обнаружен. Сократительная вакуоль простая, терминальная.

Очень радкий вид. Несколько экземпляров были найдены летом 1964 и 1967 годов в районе биологической станции Московского университета. Сублитораль (5—10 метров), мелкий и среднезернистый песок высокой сапробности.

Настоящий вид отличается от всех других видов этого рода своеобразной формой тела. Ближайшие виды *L. sphaericum* Lepsi, 1960 и *L. cohni* Kahl, 1935.

Cyclotrichium sphaericum Fauré-Fremiet, 1924 (Рис. 3)

Тело шарообразное, несократимое. Размеры 100—120×100—110μ. Всё тело, за исключением переднего полярного поля, несущего ротообразное углубление для приёма пищи, покрыто густыми ресничками. Меридиональных рядов 160—200. Ниже полярного поля 4—5 венчиков ресничек, отделённых друг от друга узкими концентрическими полями, лишёнными ресничек. Вместе они занимают от $^1/_4$ до $^1/_3$ длины тела. Реснички венчиков вдвое длиннее остальных.

Эндоплазма содержит разнообразные включения, сильно вакуолизированная, непрозрачная, тёмная. По полярному полю разбросаны длинные серповидные трихоцисты. Ротовое отверстие отсутствует. Макронуклеус лентовидный, при-

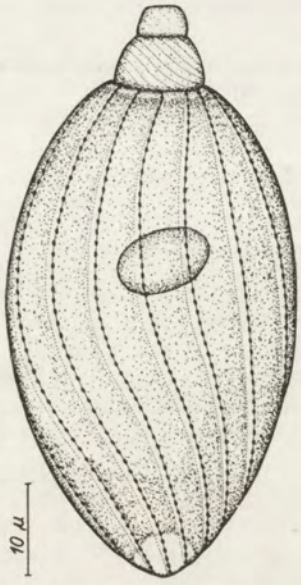

Рис. 2. *Lacrymaria ovata* sp. nov. Общий вид (тотальный препарат, серебрение)

Fig. 2. *Lacrymaria ovata* sp. nov. General view (whole preparation, silver impregnation)

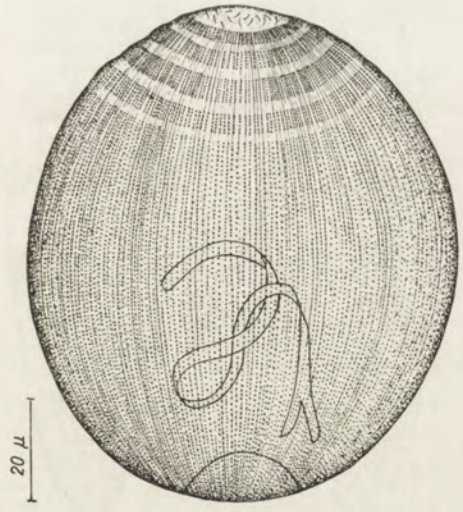

Рис. 3. *Cyclotrichium sphaericum* Fauré-Fremiet, 1924. Общий вид (тотальный препарат, серебрение)

Fig. 3. *Cyclotrichium sphaericum* Fauré-Fremiet, 1924. General view (whole preparation, silver impregnation)

чудливо свёрнутый, часто раздвоенный на одном из концов. Микронуклеус не обнаружен.

Один из самых массовых видов Кандалакшского залива. В некоторые месяцы (июль-август) достигает огромной численности, придавая воде буроватую окраску. Планктонная форма, но очень часто встречается в поверхностных слоях песка.

Беломорская форма характеризуется бóльшим числом венчиков и несколько меньшими размерами тела.

Loxophyllum levigatum Sauerbrey, 1928 (Рис. 4)

Тело ланцетовидное, лентообразное, сильно сплющеное с боков, слабо сократимое. Вентральная сторона спереди вогнутая, сзади выпуклая; дорсальная сторона выпуклая. Передний конец вытянут, заострен и загнут на дорсальную сторону образуя "клюв". Задний конец закруглен, часто перегибается на левую сторону. Размеры 250—300×35—60μ. Правая сторона равномерно покрыта мелкими ресничками (18—20 кинет). Кинетосомы и фибриллярные структуры правой стороны чёткие. Левая сторона с сильно редуцированным ресничным покровом. Из 8 кинет левой стороны только одна непрерывная. У остальных кинет кинетосомы выявляются преимущественно на концах; кинетосомы мелкие. Вдоль щелевидного ротового отверстия, занимающего до $^1/_4$ длины вентрального ребра, тянутся 2—3 предротовые кинеты, включающие тесно прилегающие друг к другу мелкие кинетосомы.

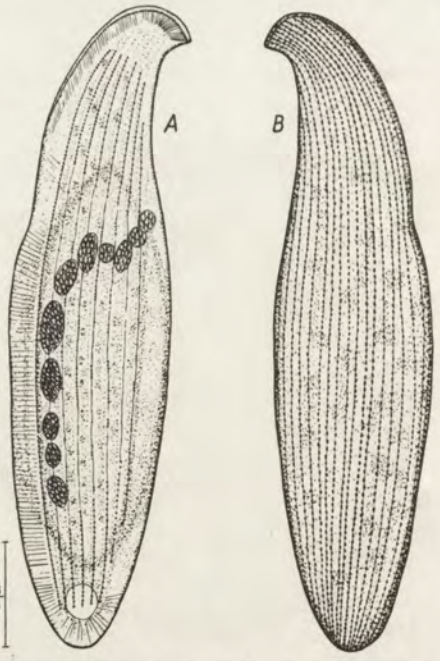

Рис. 4. *Loxophyllum levigatum* Sauerbrey, 1928. A — общий вид, левая сторона (тотальный препарат, серебрение); ядерный аппарат (гемалаун), B — правая сторона

Fig. 4. *Loxophyllum levigatum* Sauerbrey, 1928. A — general view, left side (whole preparation, silver impregnation), nuclear apparatus (haemalaun), B — right side

Вентральная краевая полоска прозрачная, несёт длинные тонкие, параллельно лежащие трихоцисты. Дорсальная сторона лишена трихоцист Эндоплазма прозрачная, мелкозернистая. Ядерный аппарат представлен 9—12 сложными образованиями (8—18μ), вытянутыми в цепочку. Сократительная вакуоль терминальная.

Один из самых массовых видов Кандалакшского залива. Мезопоральный вид, встречается в песках средней и крупной зернистости.

Беломорская форма характеризуется присутствием 8 сильно редуцированных кинет на левой стороне.

Loxophyllum asetosum sp. nov. (Рис. 5)

Тело продолговатое, асимметричное, сильно уплощенное, но не листовидное, сужено и закруглено на концах, несократимое. Левая сторона выпуклая, правая плоская или слегка выпуклая. Передний конец загнут на дорсальную сторону, задний — на вентральную. Размеры 80—160×25—40μ. Щелевидное ротовое отверстие занимаое от $^1/_4$ до $^1/_3$ длины брюшного ребра. Вдоль него тянутся 3—5 предротовых кинеты, включающие крупные тесно прилегающие кинетосомы. Подобное строение имеют также некоторые соматические кинеты в том месте, где они приближаются ко рту. Околоротовые реснички равны или несколько превосходят по длине реснички покрывающие всё тело. Ресничный покров неравномерный. Правая сторона несёт от 40 до 80 характерно расположенных кинет. Кинетосомы крупные, но значительно мельче предротовых, аргентофильные фибриллы вы-

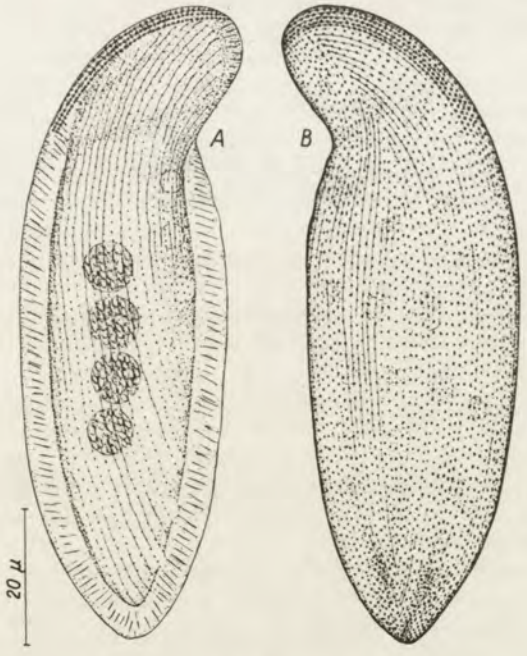

Рис. 5. *Loxophyllum asetosum* sp. nov. A. — общий вид, левая сторона (тотальный препарат, серебрение); ядерный аппарат (гемалаун), B — правая сторона

Fig. 5. *Loxophyllum asetosum* sp. nov. A — general view, left side (whole preparation, silver impregnation), nuclear apparatus (haemalaun), B — right side

ражены хорошо. Левая сторона тела бугристая, всегда несёт вдвое меньше кинет, чем правая. Кинеты на левой стороне включают очень мелкие кинетосомы, аргентофильные фибриллы выражены слабее, чем на правой стороне.

Вентральная и дорсальная краевые полоски обычно непрозрачные. Длинные трихоцисты, как правило, тянутся равномерно вдоль всего края тела инфузории. Эндоплазма непрозрачная, мутная. Ядерный аппарат состоит из 2—6 округлых образований сложного строения (6—8μ). Однако, чаще встречаются формы с 2 или 4 такими образованиями. 6—12 сократительных вакуолей лежат на дорсальной стороне тела.

Распространённый в Кандалакшском заливе. Встречается в песках средней и крупной зернистости. Литораль и сублитораль.

Настоящий вид близок к *L. setigerum* Quennerstedt, 1876 (переописан Petran 1963), но существенно отличается от него отсутствием краевых шипов и ротовых папилл, наличием сплошной кольцевой полоски трихоцист и слабо редуцированных соматических кинет на левой стороне, иной формой тела, своеобразным расположением ресничных рядов на правой стороне и более вариабильным числом сложных ядерных образований и сократительных вакуолей.

Frontonia tchibisovae sp. nov. (Рис. 6)

Тело продолговатое, асимметричное, сплющенное в дорсо-вентральном направлении, несократимое. Максимальная ширина приходится на переднюю треть тела. На обоих концах тело закруглено. Вентральная сторона плоская или слегка вогнута, дорсальная выпуклая. Правая сторона плоская, левая выпуклая. Размеры 80—180×30—60μ. Преобладают формы 100—120×30—35μ. Ресничный покров густой, равномерный, 110—130 меридиональных соматических кинет. Ротовое отверстие в первой трети тела, на брюшной стороне, в глубине довольно сложно устроенного вестибулюма (15—23μ). Буккальная цилиатура представлена одной фронтальной кинетой, включающей 6—7 крупных кинетосом, 4 вестибулярными кинетами и одной пароральной кинетой (ундулирующая мембрана). Кроме того, иногда на уровне нижнего края вестибулюма, между 3 и 4 вестибулярными рядами вклинивается ещё одна кинета, являющаяся, возможно, результатом редукции одной из вестибулярных кинет. Кинетосомы вестибулярных рядов значительно мельче и расположены тесней, чем кинетосомы, входящие в соматические кинеты. Слева от ротового отверстия расположены три пенникулуса. Длина первого пеникулуса составляет 15—18μ, он, как и следующий, состоит из 4 рядов тесно сближенных мелких кинетосом. Третий пеникулус состоит из 3 рядов кинетосом. Ниже и слева от вестибулюма — 7 посторальных кинет.

Трихоцисты многочисленные, веретенообразные. Эндоплазма непрозрачная, мутная, часто содержит различные включения. Ядерный аппарат представлен одним овальным или сферическим макронуклеусом (20—25μ) и 2—4 крупными (3—4μ) эллипсоидными микронуклеусами. Сократительная вакуоль открывается одной порой на дорсальной стороне.

Массовый, широко распространённый в Кандалакшском заливе вид. Встречается в песках разнообразной зернистости и сапробности, а также в слое детрита на поверхности грунта и в придонной воде.

Настоящий вид отличается от ближайшего вида *F. marina* Fabre-Dem., 1891, (Kahl 1930—1935, Bullington 1939, Borror 1963) по крайней мере семью признаками: присутствием 2—4 (вместо 2—3) микронуклеусов, фронтальной кинеты (которая для *F. marina* не описана), меньшим числом вестибулярных рядов, значительно меньшими размерами вестибулюма и первого пеникулуса, состояще-

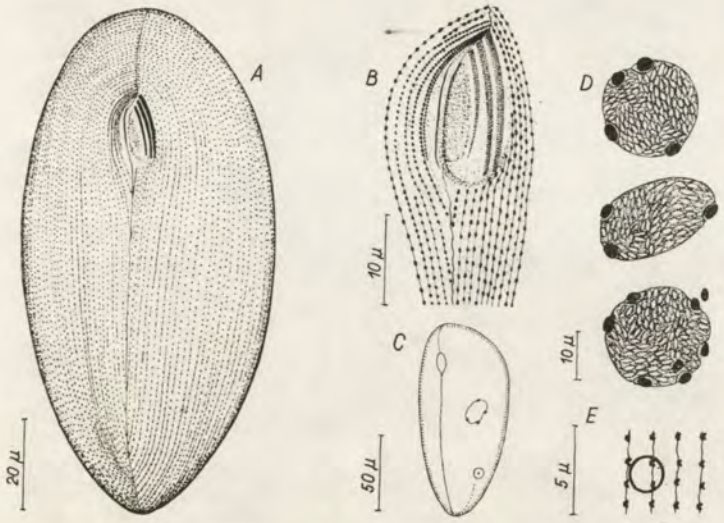

Рис. 6. *Frontonia tchibisovae* sp. nov. A. — общий вид (тотальный препарат, серебрение), B — цилиатура буккальной полости, C — типичная форма тела и относительное расположение органелл, D — типы ядерного аппарата (гемалаун), нижний рисунок — начало деления, E — фрагмент тела с порой сократительной вакуоли

Fig. 6. *Frontonia tchibisovae* sp. nov. A — general view (whole preparation, silver impregnation), B — ciliature of buccal cavity, C — typical shape of body, disposition of organella, D — types of nuclear apparatus (haemalaun), figure below — beginning of division, E — fragment of body with contractile vacuole pore

го из 4 (а не из 6) рядов ресничек, расположением поры сократительной вакуоли и 7 посторальными рядами ресничек. Все вышеперечисленные признаки признаются существенными в диагностике видов этого рода (Gil et Perez-Silva 1962, 1964 a, b, c).

Frontonia maris-albi sp. nov. (Рис. 7)

Тело продолговатое, асимметричное, сплющенное в дорсо-вентральном направлении, несократимое. Максимальная ширина приходится на последнюю треть. На обоих концах тело закруглено. Вентральная сторона вогнутая, дорсальная выпуклая. Правая сторона плоская или вогнутая, левая выпуклая. Размеры 80—140×30—50μ. Преобладают формы 100—120×30—40μ. Ресничный покров густой, равномерный, 120—140 меридиональных соматических кинет. Ротовое отверстие в первой трети, на брюшной стороне тела, в глубине довольно сложно устроенного вестибулюма (15—22μ). Буккальная цилиатура представлена тремя вестибулярными кинетами, одной предротовой кинетой. Фронтальная кинета отсутствует. Кинетосомы вестибулярных рядов значительно мельче и расположены тесней, чем кинетосомы, входащие в соматические кинеты. Слева от ротового отверстия расположены три пеникулуса. Длина первого пеникулуса составляет 15μ, он, как и следующий, состоит из 4 рядов тесно расположенных мелких кинетосом. Третий пеникулус состоит из 3 рядов кинетосом. Ниже и слева от вестибулюма — 5 посторальных кинет.

Трихоцисты многочисленные, веретенообразные. Эндоплазма непрозрачная,

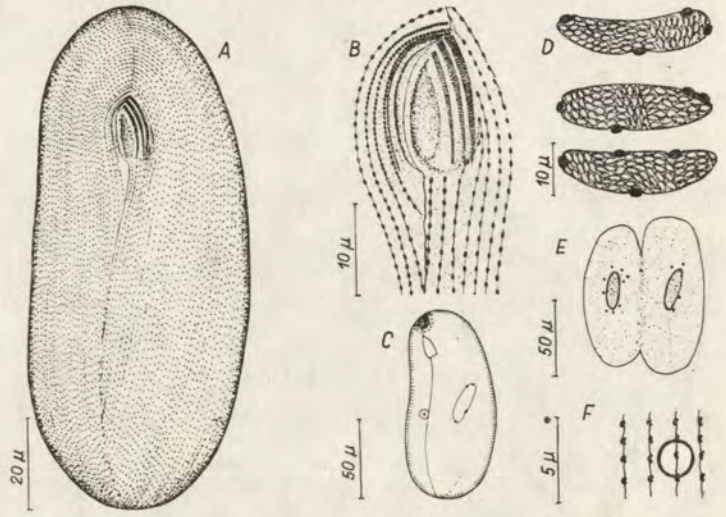

Рис. 7. *Frontonia maris-albi* sp. nov. A. — общий вид (тотальный препарат, серебрение), B — цилиатура буккальной полости, C — типичная форма тела и относительное расположение органелл, D — типы ядерного аппарата (гемалаун), E — конъюгация (гемалаун), F — фрагмент тела с порой сократительной вакуоли

Fig. 7. *Frontonia maris-albi* sp. nov. A — general view (whole preparation, silver impregnation), B — ciliature of buccal cavity, C — typical shape of body, disposition of organella, D — types of nuclear apparatus (haemalaun), E — conjugation (haemalaun), F — fragment of body with contractile vacuole pore

мутная, пигментированная. На переднем конце тела, справа имеется крупное темно синее или чёрное пигментное пятно, состоящее из 50—100 гранул (1,5—2μ). Ядерный аппарат представлен одним продолговатым реже эллипсоидным макронуклеусом (20—25μ) и 4 эллипсоидными микронуклеусами (2—3μ). Сократительная вакуоль открывается одной порой на вентральной стороне, в середине тела, вблизи посторальной аргентофильной линии.

Массовый, широко распространённый в Кандалакшском заливе вид. Встречается в песках разнообразной зернистости и сапробности, а также в слое детрита на поверхности грунта и реже в придонном слое воды.

Ближайшие виды: *F. fusca* Quennerstedt, 1869 (K a h l 1930—1935) и *F. arenaria* Kahl, 1935. Настоящий вид отличается от *F. fusca* четырьмя микронуклеусами и центральной сократительной вакуолью с одной порой. Из-за отсутствия в литературе описания буккальной цилиатуры *F. fusca* дальнейшее сопоставление этих видов невозможно. Новый вид отличается от *F. arenaria* также своим ядерным аппаратом, размерами вестибулюма и первого пеникулуса, формой тела, присутствием чёрного пигментного пятна и рядом других признаков. От своеобразной каспийской формы этого вида (A g a m a l i e v 1967) настоящий вид кроме того существенно отличается составом буккальной и соматической цилиатуры.

Pleuronema coronatum Kent, 1881 (Рис. 8)

Тело эллипсоидное, сильно сплющенное в дорсо-вентральном направлении, суженно и закруглено на концах, несократимое. Размеры 68—72×38—40μ. Ресничный покров густой, равномерный. Меридиональных рядов 36—40 (включая 6 па-

рабуккальных кинет). Ротовое отверстие открывается в последней трети тела, в глубине расширенной части длинного узкого перистома. Справа от перистома лежит крупная ундулирующая мембрана. Вблизи ротового отверстия расположены 4 мощные но короткие мембраны. Вглубь буккальной полости уходят многочисленные ряды тонких ресничек. Слева от перистома находится довольно длинная мембрана, она изгибается в виде крючка. Рядом лежит маленькая крючкообразная мембрана. Слева вверху видны ещё 3 мембраны, две из которых сложены из крупных кинетосом. Первая парабуккальная кинета характеризуется тесно сближенными кинетосомами, последняя (шестая) не отличается от соматических кинет, но значительно короче.

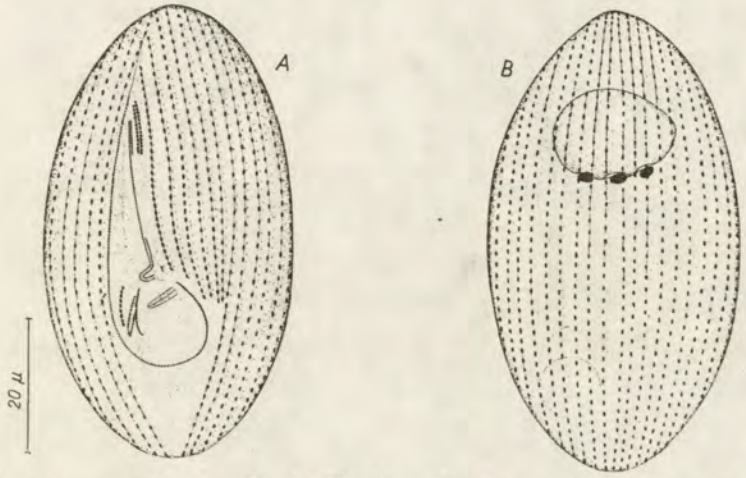

Рис. 8. *Pleuronema coronatum* Kent, 1881. A — общий вид, вентральная сторона (тотальный препарат, серебрение), B — дорсальная сторона; ядерный аппарат (гемалаун)

Fig. 8. *Pleuronema coronatum* Kent, 1881. A — general view, ventral side (whole preparation, silver impregnation), B — dorsal side; nuclear apparatus (haemalaun)

Трихоцисты многочисленные, веретенообразные. Эндоплазма прозрачная или слегка мутная, содержит разнообразные включения. Ядерный аппарат представлен крупным овальным макронуклеусом (16—20μ) и 3 эллипоидными микронуклеусами (2—3μ). Сократительная вакуоль в последней четверти (8—10μ).

Один из самых массовых видов Болого моря. Встречается в песках разнообразной зернистости и сапробности, в детрите и реже в придонной воде.

Оригинальное описание не удовлетворяет современным требованиям. Именно поэтому вид неоднократно переописывался (D r a g e s c o 1960, 1963a, 1965, B o r r o r 1963). Последне описание наиболее обстоятельное. Беломорская форма характеризуется большим постоянством размеров тела и числа парабуккальных кинет, а также некоторыми деталями строения буккальной цилиатуры.

Pleuronema marinum Dujardin, 1841 (Рис. 9)

Тело продолговатое, сильно сплющенно в дорсо-вентральном направлении, сужено и закруглено на концах, несократимое. Максимальная ширина приходится на последнюю четверть тела. Размеры 90—130×30—45μ. Ресничный покров густой, равномерный, меридиональных рядов 32—36 (включая 2 парабуккальных

кинеты). Справа от перистома лежит крупная ундулирующая мембрана. Вблизи ротового отверстия 4 мощные, но короткие мембраны. Вглубь буккальной полости уходят многочисленные ряды тонких ресничек. Слева от перистома находится довольно длинная прямая мембрана. К ней тесно прилегают ещё 4 мембраны. Первая парабуккальная кинета короче второй. Парабуккальные кинеты включают тесно лежащие кинетосомы.

Трихоцисты многочисленные, веретенообразные. Эндоплазма прозрачная или слегка мутная, седержит разнообразные включения. Ядерный аппарат представлен овальным макронуклеусом (15μ) и двумя сферическими микронуклеусами (2μ). Сократительная вакуоль субтерминальная.

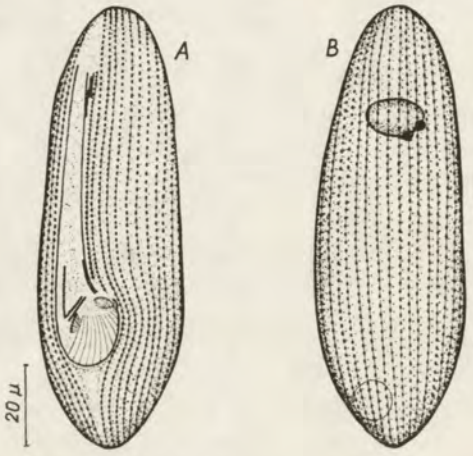

Рис. 9. *Pleuronema marinum* Dujardin, 1841. A. — общий вид, вентральная сторона (тотальный препарат, серебрение), B — дорсальная сторона; ядерный аппарат (гемалаун)

Fig. 9. *Pleuronema marinum* Dujardin, 1841. A — general view, ventral side (whole preparation, silver impregnation), B — dorsal side; nuclear apparatus (haemalaun)

Встречается значительно реже, чем предыдущий вид. Преимущественно мелкий песок разнообразной сапробности, детрит.

Оригинальное описание не удовлетворяет современным требованиям. Наиболее подробное переописание этого вида даёт B o r r o r 1963. Беломорская форма существенно отличается от последней и характеризуется двумя микронуклеусами, более вытянутой формой тела, втрое меньшими размерами макронуклеуса, двумя парабуккальными кинетами, несколько меньшим числом соматических кинет. Кроме того обнаруживаются некоторые различия в деталях строения буккальной цилиатуры.

Euplotes balteatus Dujardin, 1841 (Рис. 10)

Тело широкое, овальное, сильно сплющенное в дорсо-вентральном направлении, несократимое. Спереди, справа имеется выступ. Правая и левая стороны одинаково выпуклые. Размеры 70—90×50—60μ. Перистом большой, адоральная зона мембранелл (АЗМ) занимает $^3/_4$ длины тела и состоит из 50—55 мембранелл. Предротовая мембранелла хорошо выражена, расположена в глубине перистома, под перистомальной губой. На вентральной стороне прикрепляются 10 фронто-

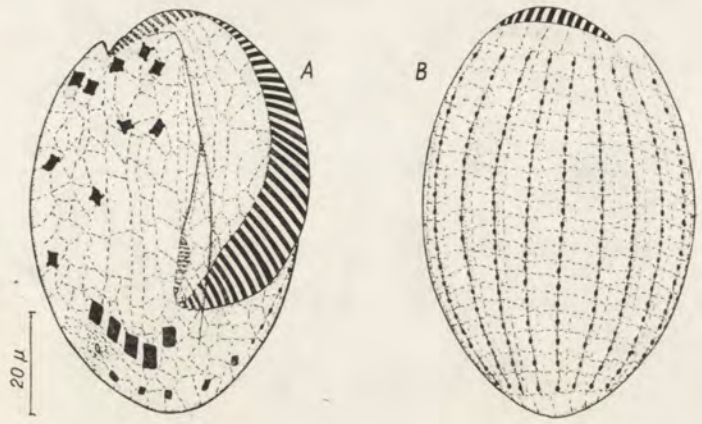

Рис. 10. *Euplotes balteatus* Dujardin, 1841. A — общий вид, вентральная сторона (тотальный препарат, серебрение), B — дорсальная сторона

Fig. 10. *Euplotes balteatus* Dujardin, 1841. A — general view, ventral side (whole preparation, silver impregnation), B — dorsal side

-вентральных, 5 трансверсальных и 4—5 каудальных цирры. Морфология вентрального и дорсального аргиромов дана на рисунке 10. На дорсальной стороне берут начало 9—10 латерально-дорсальных кинет. Каждый ряд включает около 20 щетинок.

Цитоплазма прозрачная, бесцветная. Макронуклеус в виде буквы "С", с одним сферическим микронуклеусом. Сократительная вакуоль субтерминальная.

Широко распространённый в Кандалакшском заливе вид. Встречается преимущественно в песках средней и крупной зернистости, на литорали.

Этот полиморфный вид неоднократно переописывался Beers 1954, Borror 1963, Dragesco 1963, Tuffrau 1964. Беломорская форма существенно отличается от всех других ранее описанных форм этого вида вдвое-втрое большим числом щетинок в латерально-дорсальных рядах, своеобразной морфологией вентрального и отчасти дорсального аргиромов, значительно большим числом мембранелл, входящих в АЗМ, и более округлой формой тела.

Euplotes zenkewitchi sp. nov. (Рис. 11)

Тело продолговатое, яйцевидное, спереди сужено и кончается выступом, сзади расширено и округлено; сильно сплющено в дорсо-вентральном направлении, несократимое. Размеры 70—90×45—55μ. Перистом большой, АЗМ занимает до $^2/_3$ длины тела и состоит из 50—60 мембранелл. Предротовая мембранелла хорошо выражена, расположена в глубине перистома, под перистомальной губой. На вентральной стороне прикрепляются 9 фронто-вентральных, 5 трансверсальных и 3 каудальных цирры. Морфология вентрального и дорсального аргиромов дана на рисунке 11. На дорсальной стороне берут начало 10 латерально-дорсальных кинет. Каждый ряд включает 14—15 щетинок.

Цитоплазма прозрачная, бесцветная. Макронуклеус со сферическим микронуклеусом. Сократительная вакуоль субтерминальная.

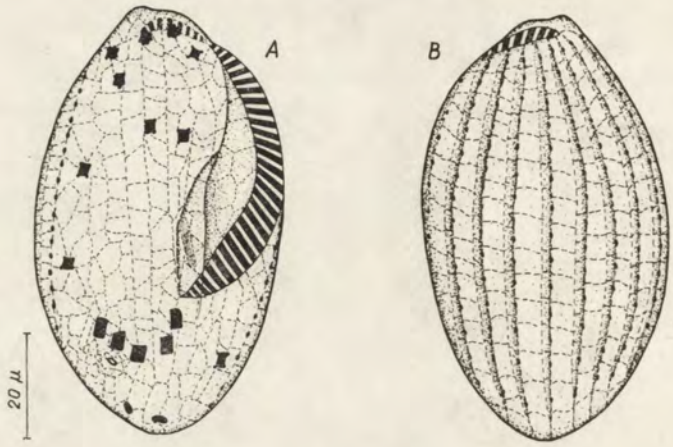

Рис. 11. *Euplotes zenkewitchi* sp. nov. A. — общий вид, вентральная сторона (тотальный препарат, серебрение), B — дорсальная сторона

Fig. 11. *Euplotes zenkewitchi* sp. nov. A — general view, ventral side (whole preparation, silver impregnation), B — dorsal side

Встречается на литорали в песках разнообразной зернистости и в наскальных заплесках.

Настоящий вид хорошо отличается от всех ранее описанных видов совокупностью признаков, главными из которых являются число и расположение фронто-вентральных и каудальных цирр, морфология вентрального и дорсального аргиромов, число дорсальных кинет, форма и размеры тела. Ближайшие виды *E. plumipes* Stokes, 1884, *E. muscicola* Kahl, 1932, *E. elegans* Kahl, 1932.

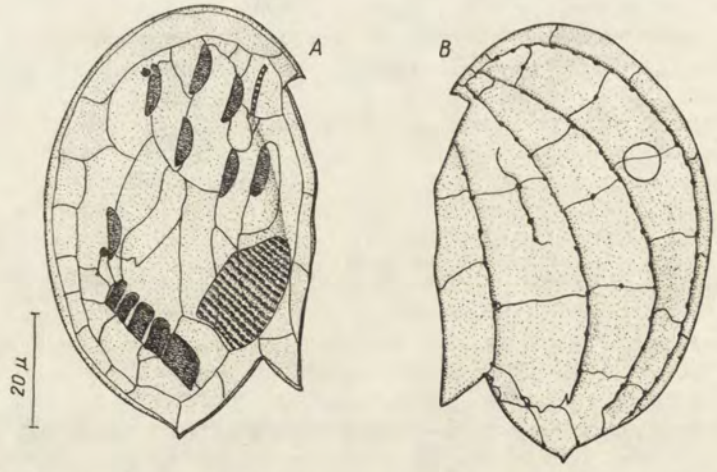

Рис. 12. *Aspidisca psammobiotica* sp. nov. A. — общий вид, вентральная сторона (тотальный препарат, серебрение), B — дорсальная сторона

Fig. 12. *Aspidisca psammobiotica* sp. nov. A — general view, ventral side (whole preparation, silver impregnation), B — dorsal side

Aspidisca psammobiotica sp. nov. (Рис. 12)

Тело овальное, асимметричное, сильно сплющенное в дорсо-вентральном направлении, несократимое. Правая сторона ровная, выпуклая; левая неровная, волнистая, снабжена двумя крупными острыми зубцами. Нижний вентральный зубец направлен наружу. На заднем конце, строго посередине имеется только один острый зубец. Вентральная сторона плоская, дорсальная выпуклая и несёт четыре киля. Размеры 65—85×40—50μ. АЗМ представлена двумя далеко отстоящими участками. Задний отрезок состоит из 16—18 мембранелл, передний — из 8—9 мембранелл. На вентральной стороне прикрепляются 7 фронто-вентральных цирр, 5 трансверсальных цирр. Вентральная цирра имеет цирру спутник. Вентральный и дорсальный аргиромы имеют характерное расположение. На дорсальной стороне — 4 полные и часто одна редуцированная кинета.

Цитоплазма прозрачная, бесцветная, мелкозернистая. Подковообразный макронуклеус с 2 сферическими микронуклеусами. Положение сократительной вакуоли изменчиво.

Обнаружен в массовом количестве в районе биостанции Московского университета. Песок разнообразной зернистости, литораль.

Этот вид входит в группу близкородственных видов *A. pulcherrima* Kahl, 1932 — *A. lyncaster* Stein, 1859. Эти виды отличаются между собой, главным образом, формой тела, особенно его заднего конца, количеством поперечных цирр, формой и строением АЗМ, аргиромом и рельефом дорсальной стороны. Настоящий вид занимает промежуточное положение между *A. lyncaster* Stein, 1959, *A. sedigita* Quennerstedt, 1867, *A. caspica* Agamaliev, 1967. Новый вид отличается от *A. lyncaster* (Petran 1963, Tuffrau 1964) другим строением АЗМ и присутствием 2 Ми и 4 кинет на дорсальной стороне, от *A. sedigita* 5 трансверсальными циррами и несколько иной формой тела, от *A. caspica* иной формой тела и отсутствием многочисленных зубцов на заднем конце тела, кроме того некоторыми деталями строения дорсального аргирома и присутствием 2 Ми.

Резюме

В работе приводится описание некоторых новых и наиболее массовых, ранее неизвестных, для Белого моря инфузорий: *Lagynophrya halophila* Kahl, 1930, *Lacrymaria ovata* sp. nov., *Cyclotrichium sphaericum* Fauré-Fremiet, 1924, *Loxophyllum levigatum* Sauerbrey, 1928, *Loxophyllum asetosum* sp. nov., *Frontonia tchibisovae* sp. nov., *Frontonia maris-albi* sp. nov., *Pleuronema coronatum* Kent, 1881, *Pleuronema marinum* Dujardin, 1841, *Euplotes balteatus* Dujardin, 1841, *Euplotes zenkewitschi* sp. nov., *Aspidisca psammobiotica* sp. nov. Описание даётся на основании прижизненных наблюдений и изучения фиксированного материала, импрегнированного серебром.

SUMMARY

Description of twelve infusorian species, dicovered in the sandy bottom of the White sea, is founded on study of living ciliates and of fixed material impregnated with silver by the Chatton and Lwoff (1930) method. Six species are new.

Lagynophrya halophila Kahl, 1930 (Fig. 1). Body oval, ventral side concave, dorsal side convex, 40—44×20—22 μ. 18—20 somatic kineties. Endoplasm with many

regular granules packing anterior two-thirds of body. Macronucleus (Ma) oval, with one micronucleus (Mi). Contractile vacuole (CV) posterior.

Lacrymaria ovata sp. nov. (Fig. 2). Body oval, "neck" absent, 60—64×30—32 μ. 16—20 slightly spiralled somatic kineties. Ma ellipsoid, 10 μ long. CV posterior. This species distinguish oneself by constant oval form of body.

Cyclotrichium sphaericum Fauré-Fremiet, 1924 (Fig. 3). Body spherical, 100—120×100—110 μ. Polar field small. 160—200 somatic kineties, 4—5 circular stripes of cilia. Ma band-like, CV posterior.

Loxophyllum levigatum Sauerbrey, 1928 (Fig. 4). Body lancet-like, band-like, 250—300×35—60 μ. Cytostome along convex ventral side, 60—70 μ long. 18—20 longitudinal kineties right, 8 reduced kineties left. Trichocysts (Trc) along ventral and dorsal sides. Nuclear apparatus consists of 9—12 oval parts. CV posterior.

Loxophyllum asetosum sp. nov. (Fig. 5). Body lancet-like, semicircular in cross-section, ends rounded, 80—160×25—40 μ. Cytostom 30—40 μ long. 36—72 strong somatic kineties right, 18—36 slightly spiral feeble kineties left. 3—5 particularly powerful paroral kineties. Trc along ventral and dorsal sides. Nuclear apparatus consists of 2—6 ovale parts. 6—12 CV along dorsal side.

Frontonia tchibisovae sp. nov. (Fig. 6). Body foot-shaped, 80—180×30—60 μ. 110—130 somatic kineties. Buccal cavity 15—25 μ long. Buccal ciliature includes frontal kinety, 4 vestibular kineties, paroral kinety (undulating membrane) and 3 peniculi. First and second peniculi composed of 4 rows of cilia, third peniculus of 3 rows. 7 postoral kineties. Ma oval, 20—25 μ long, with 2—4 Mi. CV dorsal, 30—35 μ from posterior end, with only one pore.

Frontonia maris-albi sp. nov. (Fig. 7). Body beans-shaped, 80—140×30—50 μ. 120—140 somatic kineties. Buccal cavity 15—22 μ long. Buccal ciliature includes 3 vestibular kineties, paroral kinety and 3 penniculi. First and second penniculi composed of 4 rows of cilia, third peniculus of 3 rows. 5 postoral kineties. Ma elongate, 20—25 μ long, with 4 Mi. CV ventral, central, with only pore.

Pleuronema coronatum Kent, 1881 (Fig. 8). Body oval, 68—72×38—40 μ. 36—40 somatic kineties including 6 short parbuccal kineties. Buccal ciliature consists of 9 membranes, undulating membrane and many small buccal rows of cilia. Ma oval, 16—20 μ long, with 3 Mi. CV subterminal.

Pleuronema marinum Dujardin, 1841 (Fig. 9). Body ellipsoid, 90—130×30—45 μ. 32—36 somatic kineties including 2 short parbuccal kineties. Buccal ciliature consists of 9 membranes, undulating membrane and many small buccal rows of cilia. Ma ovale, 15 μ long, with 2 Mi. CV subterminal.

Euplotes balteatus Dujardin, 1841 (Fig. 10). Body oval, 70—90×50—60 μ. Adorale zone of membranelles (AZM) with 50—55 membranelles. 7 frontal, 3 ventral, 5 anal, 4—5 caudal cirri. Bristles in 9—10 rows. Every row consists about 20 bristles. Ma C-shaped with only one Mi. CV subterminal.

Euplotes zenkewitchi sp. nov. (Fig. 11). Body oval, 70—90×45—55 μ. AZM with 50—55 membranelles. 7 frontal, 2 ventral, 5 anal, 3 caudal cirri. Bristles in 10 rows. Every row consists about 15 bristles. Ma with only one Mi. CV subterminal.

Aspidisca psammobiotica sp. nov. (Fig. 12). Body oval, 65—85×40—50 μ. Left margin with two sharp teeth, posterior margin with only one sharp tooth. AZM consisting of two parts, 8—9 membranelles in groove near anterior left margin, 16—18 membranelles in posterior buccal cavity. Dorsal side with 4 kineties. 7 frontal, ventral, 5 anal cirri. Ma C-shaped with 2 spherical Mi. CV with big pore.

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Some protozoan endosymbionts in Ohio-frogs

Quelques protozoaires des grenouilles en Ohio

The taxonomic history of the *Plagiotomidae*

Leidy 1849 established the genus *Nyctotherus* for *N. velox* from the millipede *Julus marginatus*, and the next year described *N. ovalis* from the cockroach *Blatta orientalis*, both at Philadelphia. Leidy defined the genus as "Body ovate, finely vibrillated, dilated posteriorly, compressed anteriorly; investing tunic granular and marked with longitudinal lines; anterio-inferiorly and middle line of the body furnished with a semicircle of large vibrillae, anterior to which is a large, granular areola; posteriorly, with a short fissure passing inwards."

Previously Ehrenberg 1838 had described a nyctotheran, *Nyctotheroides cordiformis*, but had placed it in the genus *Bursaria*. Stein 1867 counted four species in the genus *Nyctotherus*: *N. cordiformis, N. velox, N. ovalis* and *N. gyroeryanus* Stein.

Grassé 1928 suggested the subgenera *Nyctotherus* and *Nyctotheroides* for *Nyctotherus* spp. with and without a karyophore, a sling containing the nuclei. Corliss 1961 elevated these taxa to the generic level. The karyophore was first clearly described by Entz 1913 in *Nyctotherus piscicola* Daday, 1905, though he credited Schuberg 1887 with the elucidation of ciliate nuclear suspensors (diaphragms, discs, fibrils, etc.). Zulueta 1916 described the karyophore and its partitioning effect in *N. ovalis*.

Dujardin 1838 had described *Plagiotoma lumbrici* from earthworms, and Bütschli 1887 added *Nyctotherus* to this genus to form the *Plagiotomidae*. For recent references to *P. lumbrici* see Dworakowska 1967.

Amaro and Sena 1967 and 1968 have discussed the systematics of the two main genera, establishing three subgenera for *Nyctotherus* and five for *Nyctotheroides*, based upon the length curvature and/or form of the peristome. I believe their decisions lack immediate utility and prefer to use type of peristome as a specific criterion only.

Pseudonyctotherus is generically different from *Nyctotherus* and *Nyctotheroides* as it has scattered transparent vacuoles, no contractile vacuole or secondary vacuole, nor does it have an invagination of the pellicle or a tubule as cytopyge. It contains an excretory funnel like *Balantidium* (=*Paranyctotherus*) *kirbyi*. Sandon 1941 had added *Paranyctotherus kirbyi* to the *Plagiotomidae*, emending Rodriquez 1941. However, de Puytorac and Grain 1965, while establishing *Balantidium xenopi* from *Xenopus fraseri*, conclude that Sandon's organism from *Xenopus laevis* is actually a *Balan-*

tidium. Still the assignment of these two organisms to trichostome or spirotrich status may not be entirely settled. Is the structure of the cytopyge in *Balantidium kirbyi* and *Pseudonyctotherus corlissi* homologous?

B. kirbyi and *B. xenopi* are different from *P. corlissi* as their undulating membranes (UM) extend to the anterior of the adoral zone of membranelles (AZM), the buccal overture is forward and the peristome is oblique rather than S-shaped. The main features of *B. kirbyi* are shown in Fig. 1 and Pl. I 1.

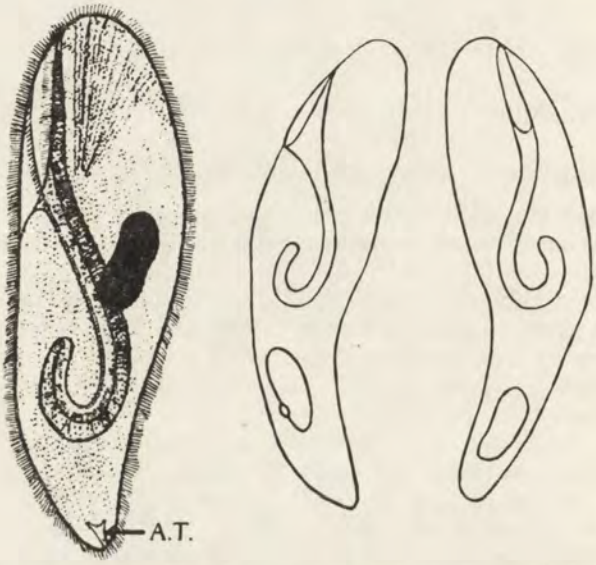

Fig. 1. *Paranyctotherus kirbyi*. The figure on the left (A. T. anal tube) is copied from Sandon 1941, and the two on the right from Rodrigez 1939

In cell shape, position of the buccal overture and peristome, and nuclear apparatus, nyctotherans are distinct from the type of the family, *Plagiotoma*. *P. lumbrici*, the single representative of the genus, is a flattened, elongate ovoid, whose AZM runs down the venter to and into the peristome two-thirds of the distance from the apex; its nuclear system is usually double, and the macronucleus a fragmented chain.

Some clarification of morphological terms seems advisable. The grand rule for all organisms is that the mouth is on the ventral side, thus the plagiotomid peristome and AZM open to the ventral side. This means that when the peristome is on the viewer's left, the uppermost side which is viewed is the left side. The buccal overture is the exterior extension of the peristome, and it is included in the shallow depression which makes up the ventral surface. In *Nyctotherus* this slight concavity, beginning as a groove adjacent to the AZM, extends one half to perhaps two-thirds the length of the cell, but in some *Nyctotheroides* spp., this ventral surface extends throughout the entire cell length. The peristome is a tubule entering the cell, and its entrance is the buccal overture. The cytostome is at the base of the peristome, and the family demonstrates no cytopharynx, i.e., structure below the cytostome. The term cytopharynx has been repeatedly misapplied to the peristome.

In order to provide succinct diagnoses of three closely related genera, and *Plagiotoma*, Leidy's definition of *Nyctotherus* is amended as follows.

> Endosymbiotic; cell ovate; uniformly ciliated; karyophore present; compressed anteriorly; quasiglobose posteriorly; ventral concavity bearing an S-shaped adoral zone of membranelles, beginning just short of the apex, continuing dorsal and inferiad into the peristome as its main component; buccal overture within the anterior half of the cell; peristome contains an undulating membrane; macronucleus anterior to the peristome; contractile vacuole(s) present; posterior invaginated cytopyge.

The other genera are now defined differentially.

> *Nyctotheroides* is like *Nyctotherus*, except that there is no karyophore, and it need not be compressed anteriorly. *Pseudonyctotherus* is like *Nyctotheroides*, except that a flattened funnel-shaped excretory apparatus is present terminating in a grooved tubule, and no contractile vacuole is evident.
>
> *Plagiotoma* is like *Nyctotheroides*, except that the cell is elongate, the buccal overture is within the posterior third of the cell, and the nuclear complement is usually double with the macronucleus chain-like.

In regard to *Balantidium* (=*Paranyctotherus*), its outstanding feature is its heavy peristomal membrane running anteriad, opposite the AZM; it also has an excretory funnel at least superficially similar to that of *Pseudonyctotherus* n. gen. Further, while a contractile vacuole is always present in *Nyctotherus* and *Nyctotheroides*, it is absent in *Balantidium kirbyi* and *Pseudonyctotherus corlissi*. Both Sandon and Rodriquez reported the former species as possessing a number of small vacuoles, often three, herewith corroborated. In *P. corlissi*, many specimens have four small scattered vacuoles, and some even five or six. Though *P. corlissi* has not evinced a contractile vacuole, there is a specialized pellicular area just above the excretory funnel on the ventral side. It commonly stains differently from the remaining pellicle, and is evident in Pl. I 2, 3.

In the main, ciliate systematics is dependent on the morphology of the cytostome and its ancillary structures. In the present context, a series of spirotrichs can be arranged in which the mouth is placed increasingly forward: *Clevelandella* and *Paraclevelandia* (peristome entering the cell at the vertex, see Kidder 1937), the *Plagiotoma*, followed by *Nyctotherus, Nyctotheroides* and *Pseudonyctotherus*.

In closing this discussion of the *Plagiotomidae* let me say, parenthetically, that I am not sure that *Balantidium kirbyi* and *B. xenopi* are so distantly related to *Pseudonyctotherus corlissi* as trichostome versus heterotrich. If they are so phylogenetically separated, then it follows that similarity in cytopyge is purely coincidental, i.e., convergent. A comparative electron microscope study of the respective cytopyges seems required in order to find out whether these structures are morphologically homologous; they may not be. Were they, then at that point of clarification, objections of various sorts might be forthcoming against the acceptance of convergence. Still if these cytopyges are homologous or closely analogous, then a notable example of environmentally-directed evolution would be evinced, since the organisms of the problem occupy the same ecological niche.

Endosymbionts known from *Hyla versicolor*, *Bufo woodhousei fowleri* and *B. terrestris americanus*

Division and conjugation of *Nyctotheroides cordiformis*, an apparently universal endosymbiont of frogs and toads, have been described by Wichterman 1937. He studied tadpoles, metamorphosing and adult *Hyla versicolor* from a pond near Woods Hole, Massachusetts. That *H. versicolor* from Ohio, as in the present case, has different endosymbionts than *H. versicolor* in Massachusetts is poor explanation. Differences in local ecologies seem far more effective in influencing infections than regional differences. In this investigation, Hocking County treefrogs had *Pseudonyctotherus corlissi* n. gen., n. sp. and *Opalina waltoni* n. sp., whereas some 15 kilometers south, Vinton County hosts had *N. sandoni* n. sp. and *O. wenrichi* n. sp. Wichterman's populations came from one environment, whereas mine, caught as breeding adults migrating to ponds in May, came from several sources. Reasons for infection remain conjectural as the total ecology is unknown (knowledge of other frog populations).

Also, a *Balantidium* sp. (ca. 157×92 μ, Pl. III 10) was rarely encountered in Vinton County *H. versicolor*, and *Bufo terrestris americanus*.

There are about 70 members of the flat multinucleate genus *Opalina*, established by Ehrenberg, in 1832, and most have been described by Metcalf 1923, 1940. From a metamorphosing *H. versicolor* at Leland, Michigan, Metcalf in 1923 described *O. hylaxena* (419×135 μ), similar to *O. obtrigonoidea* which, in turn, is like *O. triangularis* Ghosh, 1918, as pointed out by Walton 1946. The species is a member of the worldwide *obtrigona* complex, and its description inadequate, for it could also be *O. virguloidea*. Metcalf 1923 reported *Opalina* sp. from *H. versicolor chrysoscelis* Cope at New Braunfels, Texas, two forms of *O. hylaxena* from *H. versicolor* at Woods Hole, Massachusetts and a form from Tate, Georgia.

Protozoan endosymbionts reported from *Bufo woodhousei fowleri* are: *Opalina obtrigonoidea*, *O. obtrigonoidea* forma *plicata*, *O. triangulata*, *O. virguloidea*, *Nyctotherus cordiformis*, *Balantidium* sp. and *Hexamitus intestinalis*.

Protozoan endosymbionts reported from *Bufo terrestris americanus* are: *Haptophrya michiganensis*, *Karotomorpha swezyi*, *Leptotheca ohlmacheri*, *Nyctotheroides cordiformis*, *Trichomitus* (= *Tritrichomonas*) *augusta*, and *Opalina obtrigonoidea americana* and *O. obtrigonoidea americana*, forma *rugosa*.

Materials and methods

Specimens were examined living, or fixed in 6% glutaraldehyde buffered to pH 7.5, then stained with methyl green-pyronine, methylene blue, chromosome red (see Gurr 1965) and the Falg technique (see Gurr 1965). The Falg technique consists of staining with acid fuchsin in 4% acetic acid, rinsing then counterstaining with aqueous light green for polychroming effect. All photos were taken using Nomarski interference optics (Nomarski 1954 and Barer 1957). Specimens studied and photographed alive were narcotized. A coverslip was applied over specimens in 0.6% saline. Then the coverslip

was ringed with 3% chloral hydrate. A concentration gradient was set up so that while animals at the periphery were killed, those in the center were unaffected. This technique allows sufficient latitude for short-term study, relatively undisturbed by the motion of the organisms.

Results

Pseudonyctotherus corlissi n. gen., n. sp. [1]

Typical trophozoites of *P. corlissi* from *Hyla versicolor* in Hocking County, Ohio measure 196×117 μ. The length: breadth ratio approaches 1.6, and the shape is typically nyctotheran. However, the organism seems flattened throughout its length, rather than being distinctly quasiglobose posteriorly. The angle formed by the AZM at its turn into the cell, perhaps 100—130°, is 43% of the length of the cell from the apex. Thus the ventral exterior length of the AZM is similar to that of *Nyctotherus* and *Nyctotheroides* spp. The UM reaches out of the peristome to this angle. The AZM inside the peristome shows a dorsal ridge, common to the *Plagiotomidae*. The distal end of the peristome is a blind orifice (the cytostome), though occasionally a slight curved extention of the AZM (continuation band) is evident. Food organisms travel rapidly down the peristome and far into the posterior cytoplasm before stopping — something like a ball into a catcher's mit, the cytoplasm and of course the pellicle behind it acting as a cushion.

The macronucleus, roughly 66×29 μ, is a laterally flattened quasireniform structure, broader and thicker dorsally. It is very close to the right pellicle, and is very finely grained, almost homogenous, though of normal nucleolar content. The micronucleus, ca. 5×4 μ, is often located below the angle of the peristome near or also against the macronucleus at the reniform notch, and free in the anterior cytoplasm.

The cytopyge is a large ciliated tubule which expands within the cell to resemble a funnel flattened dorsoventrally. Sandon's statement on this organelle in *Balantidium* kirbyi is à propos, "It is broadly triangular in shape, sometimes with short prolongations, like uterine horns, at the anterior corners." The excretory apparatus in *Pseudonyctotherus corlissi* is proportionally at least three times longer than in Sandon's organism. The exit of this organelle is likely to be tufted as in Pl. I 2, but this character is variable. No contractile vacuole has been observed. In most specimens three to six small transparent vacuoles are noted, but they are not contractile. These are usually posterior, though such vacuoles have been noted anteriorly. One of these vacuoles is obvious and central in Pl. I 3. This Figure also shows a special pellicular area adjacent to the "funnel." One could speculate that it covers a potential contractile vacuole which might arise if the organism's osmotic requirements so demand, but actually the function of this pellicular area is unknown.

Ciliation is uniform and heavy. When in position as in Pl. I 2, peristome to the viewer's left, a fibrous ridge can be located parallel to the anterior AZM, just dorsal to the center of the right side. This ridge, also prominent in *Balantidium kirbyi*, is a suture line receiving opposing slanted kineties

[1] In honor of J. O. Corliss.

running anteriad on the right side. The anterior suture near the apex on the left side is left and perpendicular to the AZM which is beneath it, and typically nyctotheran.

The cyst, 27—40×30—42 μ, contains an ovoid macronucleus filling perhaps two-thirds of the cell, which is accompanied by the micronucleus.

Dimensions of *Pseudonyctotherus corlissi* are given in Table 1. Note that the AZM angle to cellular apex distance is available only in nyctotherans provided with a sharp angle. If the AZM is curved at the buccal overture, then the measurement cannot be obtained.

Table 1

Dimensions of *Pseudonyctotherus corlissi* in microns. N = 50

	Range	Arithmetic mean	Standard deviation	Standard error	Coefficient of variation (in %)
Length	175—216	196.0	10.3	2.0	5
Width	94—141	116.6	11.3	2.3	10
Ma length	55—75	66.3	4.7	0.9	7
Ma width	24—33	29.1	2.3	0.5	8
AZM angle to cellular apex	69—100	83.9	7.4	1.4	9

Nyctotheroides sandoni n. sp. [2]

Reminiscent of a rowing skiff pointed at both ends, *H. sandoni* from *Hyla versicolor* in Hocking Country is easily identified by its S-shaped macronucleus, in the living or stained state. In life the macronucleus is hyaline and stands out from the darker cytoplasmic background. Its general characteristics are shown in Pl. I 4, 5. *N. sandoni* averages 138×78 μ, and the sharp angle of the AZM is about 52% of the cell's length from the apex. That is to say the buccal overture is placed a bit lower than in many nyctotherans. The length: breath ratio is 1.8. This organism has a broad ventral concavity, particularly evident when the cell revolves in swimming, but its extent is muffled in most appearances as organisms are almost always encountered on their sides in life and on slides. A central cross-section would have the shape of a Gothic arch.

The organism usually glides on either side, preferring right side down. As a substrate-lover it swims rarely, as a rule only when the medium is purposefully agitated.

The angle formed by the AZM as it turns dorsally into the cell is very sharp, sometimes less than 90°. The distal end of the peristome is a blind orifice, the cytostome. The metachronic wave of the AZM begins at the cytostome as a pulse, and after traveling up the length of the AZM continues over the apex, and down the dorsal ciliature.

The distinctive macronucleus, ca. 48×20 μ, is finely grained, containing an average nucleolar complement. The micronucleus, ca. 4 μ in diameter, is

[2] In honor of H. Sandon.

usually located between the AZM angle and the lower ventral bend of the macronucleus as in Pl. I 4, 5.

The cytopyge is a grooved ventral tubule which cuts into the cell. It is more advanced than a simple invagination of the pellicle and common to the majority of nyctotherans. A pored contractile vacuole is present just posterior to the concavity of the ventral surface, anterior to the cytopyge. Other features are common to the genus, and it is stressed that there is no anterior flattening.

The dimensions of *N. sandoni* are given in Table 2.

Table 2

Dimensions of *Nyctotheroides sandoni* in microns. N = 25

	Range	Arithmetic mean	Standard deviation	Standard error	Coefficient of variation (in %)
Length	106—179	137.8	19.3	3.9	14
Width	50—106	78.2	17.8	3.6	23
Ma length	35—66	48.0	7.0	1.4	14
Ma width	13—23	20.2	3.0	0.6	15
AZM angle to cellular apex	53—106	71.9	14.7	2.9	20

Nyctotheroides amaroi n. sp. [3]

Reminiscent of a square-sterned rowing skiff, *N. amaroi* from *Bufo woodhousei fowleri* and *B. terrestris americanus* in Vinton County, is easily identified by its quasireniform macronucleus (ca. 62×21 μ), whose posterior boundary is straight-edged. The reader may decide, after viewing Pl. II 7 of this nucleus, that the configuration of the structure involved is somewhat defiant of descriptive language. In life the macronucleus seems granular, and has a cream-brown hue. The general characteristics of *N. amaroi* are shown in Pl. II 6 and 8. This spirotrich averages 175×94 μ, and the sharp angle of the AZM is about 46% of the cell's length from the apex. The length: breadth ratio is 1.9. Like *N. sandoni*, this organism has a broad ventral surface, and its midpoint cross-section would have the appearance of a Gothic arch. Also, *N. amaroi* is not compressed anteriorly.

The micronucleus has not been located, probably due to close adherence to the macronucleus.

The cytopyge and pored contractile vacuole are typical to the genus, and depicted in Pl. II 9. Note that the vertex of *N. sandoni* is more acute than that of the present species.

The dimensions of *N. amaroi* are given in Table 3.

Opalina waltoni n. sp. [4]

Typically polymorphic, following the general tendency that the number of nuclei and kineties increases as area increases, *O. waltoni* from Hocking County *Hyla versicolor* averages 139×80 μ. Infrequently a non-descript flat

[3] In honor of A. Amaro.

[4] In honor of the late A. C. Walton.

Table 3
Dimensions of *Nyctotheroides amaroi* in microns. N = 50

	Range	Arithmetic mean	Standard deviation	Standard error	Coefficient of variation (in %)
Length	112—224	175.4	29.2	4.1	17
Width	64—129	93.7	16.3	2.3	17
Ma length	35—78	61.6	11.2	1.6	18
Ma width	13—29	21.0	2.9	0.4	14
AZM angle to cellular apex	50—109	80.4	12.0	1.7	15

ellipsoid as in Pl. III 13 it is usually met with as a roughly bell-shaped form as in Pl. III 11. Pl. III 11—13, IV 14 adequately cover its range of polymorphism. The notable feature of the species is a notch on the viewer's left in Pl. III 11. This notch, or a semblance of it, is always evident in adults. In Pl. IV 14, a weak notch is present on the viewer's right near the center of the cell. The forms seen may have some order in the life cycle. For example forms with pointed caudas as in Pl. IV 14 may be terminal adults. However there are no obvious size differences in classes of forms, and it seems quite possible that these forms are not age-structure dominated.

The narrow suture line or falx is just posterior and parallel to the arc of the frontal edge. Often kineties angle into the falx, but they also meet at 180°, indicating an effect of polymorphism and possibly individual changes in torsion. Notch to the viewer's left, kineties are sigmoid along the uppermost surface, running parallel to the notch as in Pl. III 13, yet they are straighter in the return along the underside. Wessenberg's 1961 Figure 63 of *O. virguloidea* is representative of some *O. waltoni* trophozoites in regard to the configuration of kineties.

The protrophozoite (protrophont), rarely noted on slides, is spindle-shaped at the three-four nuclei stage. The cyst is ovoid, 15—19×19—21 μ.

The length and width of *O. waltoni* is given in Table 4.

Table 4
Dimension of *Opalina waltoni* in microns. N = 50

	Range	Arithmetic mean	Standard deviation	Standard error	Coefficient of variation (in %)
Length	59—181	139.3	25.4	3.6	18
Width	40—116	79.5	17.1	2.4	22

Opalina wenrichi n. sp. [5]

Most specimens of *O. wenrichi* from Vinton County *Hyla versicolor* are flat ovoids, having a straight posteriolateral edge, and a pointed cauda. Two forms are evinced as shown in Pl. IV 15, 16. Despite their clear differences in appearance, the parabolicities of the anterior thirds of both forms are iden-

[5] In honor of the late David H. Wenrich.

tical. *O. wenrichi* averages 111×66 μ. Its notable feature, aside from the posteriolateral straight edge, is a short pointed cauda. As *O. wenrichi* is highly asymmetric to its longitudinal axis, the straight edge can be said to belong to the larger area. When this line is on the viewer's right as in Pl. IV 15, the suture line or falx is uppermost and close to the anterior border.

Cysts are round to ovoid, about 20 μ in diameter. In temporary saline preparations, while most show only non-descript endoplasm, older cysts contain rapidly-whirling flagellated cells. The protrophozoite which emerges is comma-shaped. One of these cells at the four nuclei stage is shown in Pl. IV 17.

The length and width of *O. wenrichi* is given in Table 5.

Table 5

Dimension of *Opalina wenrichi* in microns. N = 50

	Range	Arithmetic mean	Standard deviation	Standard error	Coefficient of variation (in %)
Length	76—196	110.8	22.3	3.1	20
Width	36—92	66.0	14.0	2.0	21

Opalina virguloidea Metcalf, 1923.

O. virguloidea is a common Salientian endosymbiont of the *obtrigona* complex in North America. Populations of it were encountered in Vinton County *Bufo woodhousei fowleri*, captured in July at the close of the breeding season. Two forms were evident — a smaller oval and a larger triangular form. The ovals were found five times as often as the larger triangles, i.e., 83% of the population was in the juvenile phase. Pl. V 18, showing a cauda starting in a juvenile form, and other information here, confirms Wessenberg's 1961 account of the *O. virguloidea* life cycle. Working with *O. ranarum* near Dublin, El Mofty and Smyth 1964 showed that adult forms are found exclusively in the winter months, but that cysts and small forms are much in evidence in and after the hosts' breeding season in spring. Then adults in the population may drop to a low percentage. Similar information on the cyclic nature of opalinid activities had been presented by Sukhanova 1962. Seasonal characteristics in opalinids have been known since Zeller 1877.

Three *O. virguloidea* populations were assayed for size; a random sample of 65, 50 ovals only and 50 triangles only. Results in Table 6.

The random sample is normally distributed with kurtosis values of 3.64 for length and 2.10 for width, assuredly normal also. The slope (b) of juvenile forms is much greater than that of adults, but other statistical differences except for size averages are considered insignificant. The respective slope values are: random sample b = 0.30, ovals b = 0.79 and triangles b = 0.31.

The data above gives some idea of the range of dimensional factors found in one population, and how dimensions of populations may shift dependent on the percentage of large forms encountered. The only samples of expected similarity to the random sample above would be ones assayed in the same host at the same time of year at an approximately similar geographic location. The implication is that the dimensions of opalinid populations are affected by the host's photoperiodicity.

Table 6

Dimensions of *Opalina virguloidea* in microns

	N	Range	Arithmetic mean	Standard deviation	Standard error	Coefficient of variation (in %)
Random sample						
Length	65	66—263	137.5	48.2	6.0	35
Width	65	35—123	82.8	21.5	2.7	26
Selected ovals						
Length	50	78—162	119.0	20.9	3.0	18
Width	50	48—123	80.7	20.2	2.9	25
Selected triangles						
Length	50	68—268	205.5	55.9	7.9	27
Width	50	26—123	93.4	21.1	3.0	23

Opalina americana n. comb.

As noted, Metcalf 1923 has recorded *O. obtrigonoidea* and *O. obtrigonoidea plicata* from *Bufo woodhousei fowleri*, and *O. obtrigonoidea americana* and *O. obtrigonoidea americana rugosa* from *B. terrestris americanus*. I consider that all of these *obtrigona*-type opalinids are insufficiently described, and believe that the recorded descriptions could also apply to various races of *O. virguloidea*. Furthermore, the establishment of forms or subspecies of *Opalinidae* implies both that the species involved is well known, and that intraspecific variations are understood. Both of these assumptions are false.

I now suppress *O. obtrigonoidea plicata* as it is insufficiently described, and combine both *O. obtrigonoidea americana* and *O. obtrigonoidea americana rugosa* as *O. americana* n. comb.

Also note that Fowler's toad and the American toad interbreed in southern Ohio to produce hybrids.

Vinton County *B. terrestris americanus* were found infected with large numbers of a large, rugose opalinid, *O. americana*, and very few (4%) *Nyctotheroides amaroi*, as well as the infrequent (> 1%) *Balantidium* sp. depicted in Pl. III 10. Unlike *O. virguloidea* the juvenile form (Pl. V 21) of *O. americana* approximates the adult form Pl. V 20, though the juvenile is less elongate. The dimensions of *O. americana* are given in Table 7.

Table 7

Dimensions of *Opalina americana* in mirons. N = 100

	Range	Arithmetic mean	Standard deviation	Standard error	Coefficient of variation (in %)
Length	114—542	391.3	110.5	11.1	28
Width	36—143	101.5	19.1	1.9	19

On Opalinid identification

Shape differences between *Opalina waltoni* and *O. wenrichi*, and differentiation from other members of the genus are sufficient to validate them. Of course, both biological complexity and the group's taxonomic history lend towards confusion. Most statements on the *Opalinidae* could be suffixed with, "At least, I think that's right." The number of sureties on the group is low, in accord with the low number of discriminatory parameters, and high biological plasticity. In comparison to ciliates, expressly from the taxonomic viewpoint, the absence of a mouth leaves precisely that much less to study.

The size of nuclei, the configuration of kineties, cellular dimensions, life history, and particularly gross adult appearance, all play some part in identification. The species of host is also of aid, but assessment of host specificity is at present impossible. Natural interfaunation of opalinids amongst frog species is probable, demonstrated experimentally by Metcalf 1909 and corroborated by Cairns (personal communication) who in 1953 studied transfaunation of enteric protozoa from *Amphibia* and *Reptilia*. His published account dealt with trichomonads for the most part. The discriminatory criteria used here are mainly shape and size, which in turn approximates appearance. An overencompassing word such as 'appearance' is more useful than more precise criteria such as the number of kineties or nuclei as these vary with age. The taxonomist attempts to develop skill in pattern recognition through repeated sight of specimens and illustrations. The verbal areas of opalinid descriptions to date have very little import. Further, it is futile to recommend criteria which are difficult to ascertain in practice.

Two obvious situations which operate in counterpoint cause confusion in species differentiation. Stages of the life cycle and polymorphism may result in one species being identified as two or more, and the mixed infection of two or more opalinids in one host may eventuate in a garbling of entities. In the present investigation, it seems fortunate that single species infections were encountered one at a time.

O. virguloidea, identified primarily by recognition of juvenile stages as ovals, and *O. americana*, recognized by its plications and/or rugosities, as well as size, are easily designated taxonomically. However, both *O. waltoni* and *O. wenrichi* are compromised by the presentation of facsimiles in Metcalf's 1940 Figure 112 of *O. larvarum*. His Figure 112 a suits *O. wenrichi*, and Figure 112 a, a form of *O. waltoni*. Irony is introduced by the coincidence that Metcalf's Figure was drawn from one of Dr. Wenrich's slides. *O. larvarum* has been reported from *Rana clamitans*, *R. catesbeiana*, *R. cyanophlyctis* (India), *R. palustris*, *R. pipiens* and *R. sylvatica*. The possibility of either the present species falling into synonymy with *O. larvarum* Metcalf, 1923 seems slight. Metcalf may have been dealing with a mixed infection, but it is impossible to judge. In any event, *O. larvarum* dimensions are different, namely 46—68×72—75 μ. On the simplest basis: as neither *O. waltoni* nor *O. wenrichi* from *Hyla versicolor* can be matched to recorded descriptions, they are new.

Summary

Nyctotherus, *Nyctotheroides* and *Plagiotoma* of the *Plagiotomidae* are discussed, and *Pseudonyctotherus* n. gen. added. *Pseudonyctotherus* is like *Nyctotheroides*, except that a flattened funnel-shaped excretory apparatus is

present, and there are scattered transparent vacuoles but no contractile vacuole. *Pseudonyctotherus* shares these two features with *Balantidium xenopi* and *B. kirbyi*. The occurrence of similar cytopygeal structures in the heterotrich *Pseudonyctotherus* and the trichostome *Balantidium* may be coincidental, i.e., convergent. *P. corlissi* n. gen., n. sp. is ca. 196×117 μ, and has a quasireniform macronucleus ca. 66×29 μ. Its host is *Hyla versicolor* in southern Ohio. This treefrog also harbored *Nyctotheroides sandoni* n. sp. (ca. 138×78 μ), *Opalina waltoni* n. sp. (ca. 139×80 μ) and *O. wenrichi* n. sp. (ca. 111×66 μ). *Nyctotheroides amaroi* n. sp. (ca. 175×94 μ) from *Bufo woodhousei fowleri* and *B. terrestris americanus* is described. *O. americana* n. comb. from *Bufo terrestris americanus* is detailed, and representative of both *O. obtrigonoidea americana* Metcalf, 1923 and *O. o. americana rugosa* Metcalf, 1923. Additionally, *O. o. plicata* is suppressed. *O. virguloidea* from *B. woodhousei fowleri* is examined and Wessenberg's (1961) life cycle corroborated.

RÉSUMÉ

Nyctotherus, Nycteroides et *Plagiotoma* des *Plagiotomidae* ont été discutés et on a ajouté *Pseudonyctotherus* n. gen. *Pseudonyctotherus* est comme *Nyctotheroides* avec l'exception de l'appareil excrétiore qui est aplati et en forme d'entonnoir et aussi par la présence des vacuoles transparentes dispersées dans la cytoplasme mais pas de vacuole contractile. *Pseudonyctotherus* a ces deux traits en commun avec *Balantidium xenopi* et *B. kirbyi*. La présence des structures cytopygéales semblabes chez le Hétérotriche *Pseudonyctotherus* et le Trichostome *Balantidium* peut être accidentale c'est à dire convergente. *P. corlissi* n. gen., n. sp. mesure ca 196 μ×117 μ et possède un macronucleus quasireniforme ca 66×29 μ. Son hôte est *Hyla versicolor* dans le sud du Ohio. Cette grenouille est aussi le hôte pour *Nyctotheroides sandoni* n. sp. (ca 138×78 μ), *Opalina waltoni* n. sp. (ca 139×80 μ) et *O. wenrichi* n. sp. (ca 111×66 μ). On a décrit *Nyctotherus amaroi* n. sp. (ca 175×94 μ) du *Bufo woodhousei fowlei* et *B. terrestris americanus*. On a décrit en detail. *O. americana* n. comb. du *Bufo terrestris americanus* qui représente aussi *O. obtrigonoidea americana* Metcalf, 1923 et *O. o. americana rugosa* Metcalf, 1923. On a supprimé *O. o. plicata* en plus. On a examiné *O. virguloidea* du *B. woodhousei fowlei* et on a corroboré le cycle de Wessenberg (1961).

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EXPLANATION OF PLATES I—V

1: *Paranyctotherus kirbyi* from laboratory *Xenopus laevis*, showing the peristome and excretory apparatus. Living. ×500

2: *Pseudonyctotherus corlissi* n. gen. n. sp., showing the general form, AZM, macronucleus, peristome, vacuoles, excretory apparatus and adjacent specialized pellicle. Falg technique. ×500

3: Posterior area of *P. corlissi* showing peristome detail, food vacuoles, a central transparent vacuole, the specialized pelliele and adjacent cytopyge. Falg technique. ×925

4: *Nyctotheroides sandoni* n. sp., showing the S-shaped macronucleus, AZM, peristome, extensive ventral surface (viewer's left), and contractile vacuole. The micronucleus appears halfway between the AZM and the lower ventral edge of the macronucleus. Gurr's chromosome red. ×575

5: *N. sandoni* against the outside edge of a coverslip. The macronucleus, AZM and cytopyge are noterworthy. Living. ×575

6: *Nyctotheroides amaroi* n. sp., showing the macronucleus, AZM and peristome. Unna's polychrome methylene blue. ×500

7: Detail of the *N. amaroi* macronucleus. A small vacuole is evident above center. The portion of the peristome at the left affords the viewer orientation. Methyl green-pyronine. ×1500

8: *N. amaroi*, showing the extent of the ventral surface, the macronucleus, a vacuole over it and the contractile vacuole. Living. ×475

9: The vertex of *N. amoroi*, showing the cytopyge, the contractile vacuole ventral to it (above) and numerous food vacuoles. Living ×1350

10: A rarely noted *Balantidium* sp. from *Hyla versicolor*. Gurr's chromosome red. ×575

11: A typical trophozoite of *Opalina waltoni* n. sp. Falg technique. ×500

12: A common form of *O. waltoni*. Falg technique. ×500

13: Another common form of *O. waltoni*. Falg technique. ×500

14: A rarely encountered form of *O. waltoni*. Falg technique. ×500

15: *Opalina wenrichi* n. sp., one of two common forms. Living. ×700

16: *O. wenrichi*, the other common form, having a more acute cauda. Living. ×575

17: Juvenile form of *O. wenrichi*. Two nuclei are anterior, one central and another posterior. Living. ×1050

18: *Opalina virguloidea*. A juvenile form showing the beginning of a cauda. Living. ×550

19: *O. virguloidea* adult form, though less elongate than terminal adults. Living. ×500

20: *Opalina americana* n. comb., typical adults. Gurr's chromosome red. ×175

21: Juvenile form of O. *americana*, less elongate though resembling the adult form. ×500

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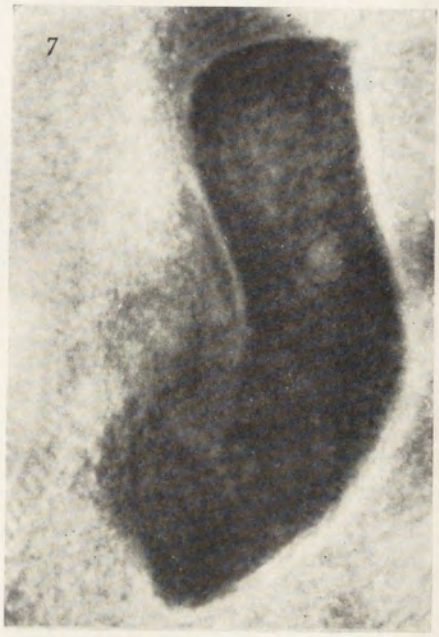

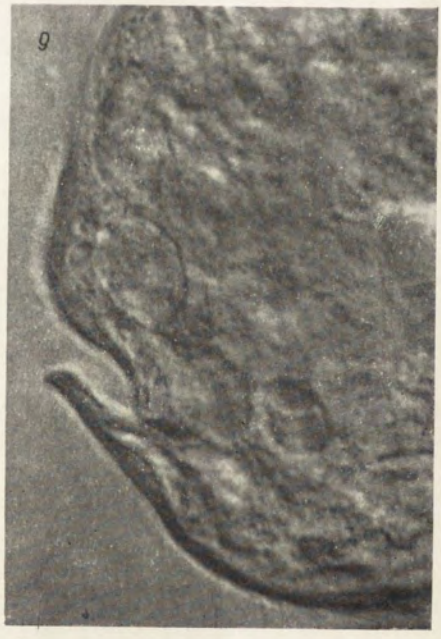

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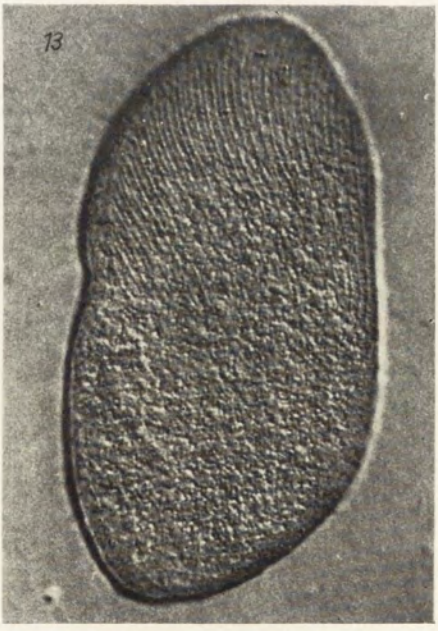

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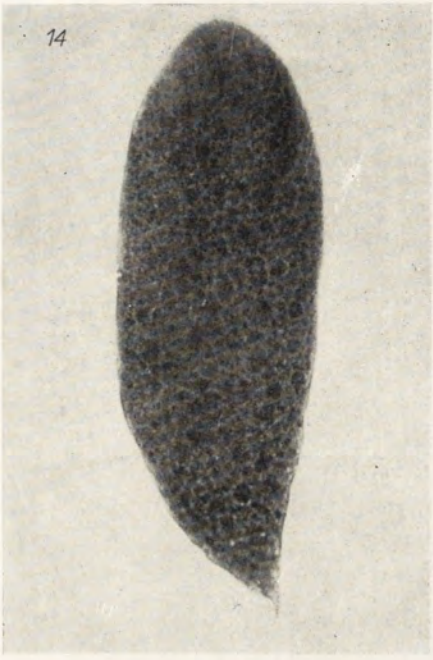

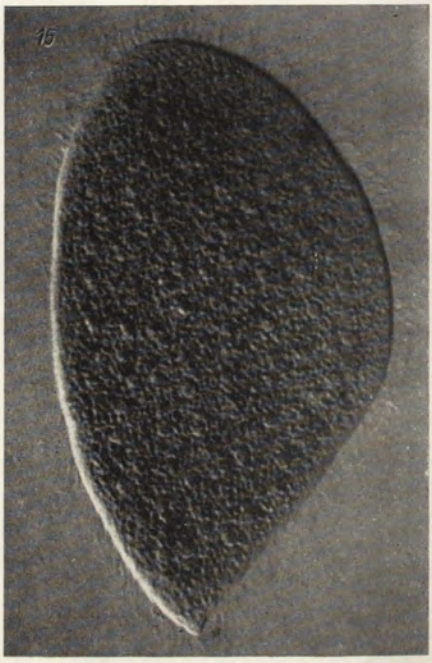

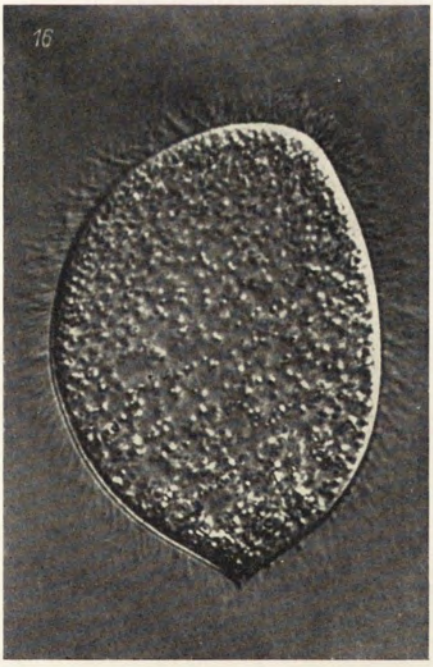

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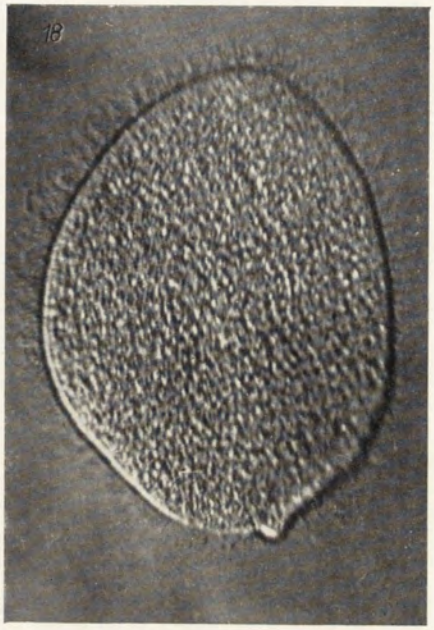

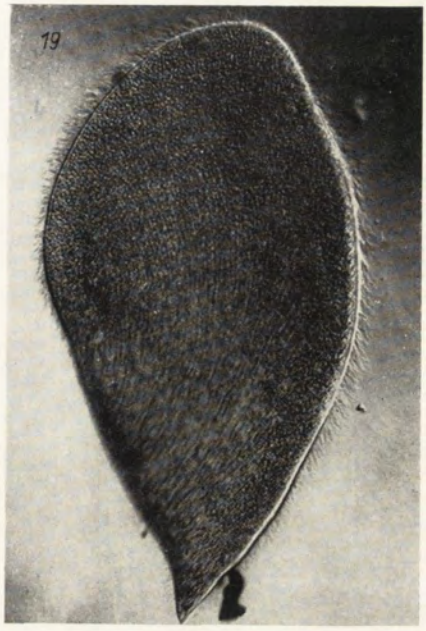

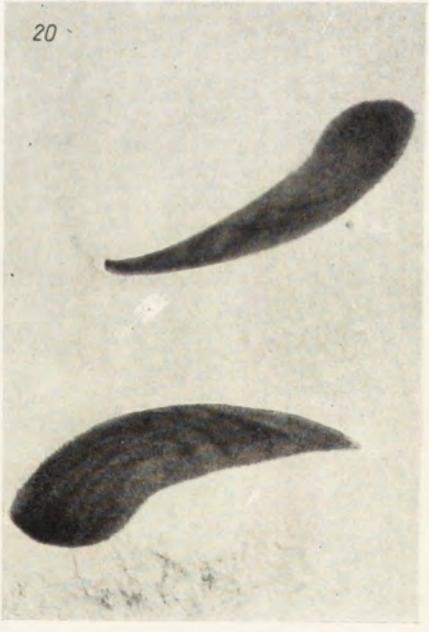

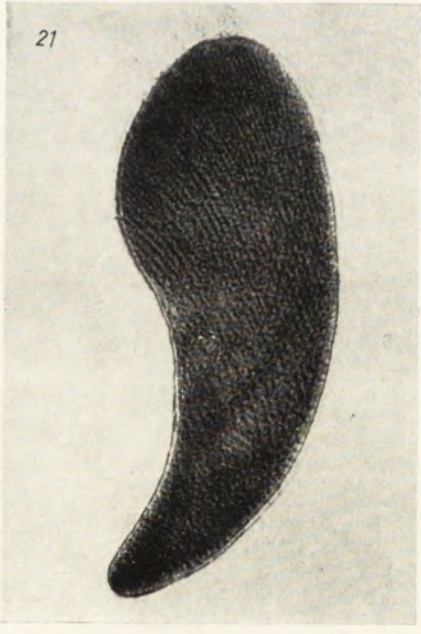

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Studies on the distribution of trichocysts in the normal life cycle and during regeneration of *Urostyla cristata* Jerka-Dziadosz, 1964 *(Hypotircha)*

Badania nad rozmieszczeniem trichocyst w normalnym cyklu życiowym i podczas regeneracji *Urostyla cristata* Jerka-Dziadosz, 1964 (*Hypotricha*)

One of the structures belonging to the cortex of *Protozoa* are trichocysts. They are organelles of a characteristic structure, with a property of exploding and extruding filaments. In some protozoa trichocysts exert toxic action (*Dileptus*) and serve for killing the pray for food.

It follows from the studies of Ehret and De Haller 1963 that trichocysts arise in endoplasm. Yusa 1963, 1965 studied the regeneration of trichocysts in *Paramecium* and in *Frontonia* impaired by electric shocks. He stated that trichocysts arise from membranous vesicles in endoplasm. Endoplasmic origin of trichocysts has also been stated in *Dileptus* by Dragesco et al. 1965.

Doroszewski and Golińska 1967 studied the distribution of trichocysts in the cell of *Dileptus* during regeneration and found that a store of trichocysts is present in endoplasm and that they are incorporated into the regenerating proboscis of this ciliate. The formation of trichocysts may possibly occur at various stages of the life cycle and is associated with the degree of feeding (Dragesco et al. 1965).

In *Hypotricha* trichocysts have not been described as yet and *Urostyla cristata* is the first ciliate of this group in which the occurrence of these structures has been ascertained.

Material and methods

Protozoa were cultivated in Petri dishes and fed with a standard lettuce medium with addition of *Aerobacter aerogenes*. The cultures were fed at one day intervals, having been rinsed in the Pringsheim's solution prior to feeding.

For revealing trichocysts, the silver impregnation method was applied using protargol according to Dragesco 1962. Material was fixed in saturated solution of mercuric chloride with 2% aqueous solution of OsO_4 (1:1) or in mercuric chloride only. Protargol and hydrochinon were used at temp. 40°. This method gives very variable results which are not always satisfactory

despite the uniform procedure. In the case of good results such structures become impregnated as: trichocysts, kinetosomes (especially the new-arising or young ones), sometimes fibers and the nuclear apparatus. The results of staining are not uniform even on the same slide.

Iron hematoxylin was also applied after a rapid fixation with saturated sublimate and 2% OsO_4 according to Párducz 1952. This method revealed successfully the ectoplasmic trichocysts extruded partially or completely.

To obtain a considerable number of fragments of ciliates bisected simultaneously, a special knife was used with 24 edges oriented horizontally (Jerka-Dziadosz 1968). This knife was adjusted to the head of a laboratory mixer with the maximal number of rotations about 1900/min. Ciliates densified by decanting were placed in a beaker of a 50 ml capacity. Then the knife was immersed into the culture and the ciliates were subjected to a mass operation for about 30 sec at approx. 300—400 rotations per minute. As result, each of the ciliates in the culture was bisected approximately twice. Immediately after operation ciliates were decanted, rinsed in the Pringsheim's solution, placed in a Petri dish and sampled at 30 min intervals till the conclusion of the regeneration proces i.e. for about 6 hours. The disposition of trichocysts was examined in fragments being at various phases of regeneration.

Results

Distribution of trichocysts in morphostatic individuals

The distribution of trichocysts in *Urostyla cristata* resembles to that of protrichocysts i.e. of mucocysts in *Urostyla grandis*. In the morphostatic individuals of *U. cristata*, trichocysts occur — as a rule — in ectoplasm only, being arrayed vertically to the surface. In some individuals, a few of them may be found in endoplasm (Pl. I 1—5). They are approximately of the same size and of similar structure as ectoplasmic trichocysts. On the ventral side (Pl. I 5) trichocysts are situated between the rows of cirri, rather densely, in a random irregular manner. The middle meridian of the body, on which the rows of ventral and transversal cirri lies, has a comparatively lower number of trichocysts.

On the dorsal side — similarly as on the ventral one — trichocysts are located between the rows of dorsal cilia (Pl. I 3). On the left side of the back, an empty band remains deprived of trichocysts. It corresponds to the position of the contractile vacuole canal which is formed periodically under the pellicle.

Only the distal parts of trichocysts sticking in the pellicle are stained with hematoxylin. They look like grains and resemble to mucocysts in *U. grandis* and *U. weissei*. After a poor fixation when OsO_4 or sublimate fail to penerate regularly into the whole cell, a part of trichocysts, mostly those of the frontal area, are stained with hematoxylin in their extruded state (Pl. II 6, 7). In such conditions, the filament protruding from the pellicle is seen, being slightly bent and terminating in a small swelling in the form of a ball. This ball resembles in its shape and size to a grain inserted into the pellicle at the place of a non-exploded trichocysts (Pl. II 7).

After application of protargol whole trichocysts are stained. They are rods, approx, 7—8 μ long, sticking vertically to the surface (Pl. II 9). Their distal ends are at the same level as kinetosomes. From the distal side trichocyst

looks like a grain — similarly as after staining with hematoxylin. In some cases, the exploded trichocysts are also stained with protargol. Then they have a feature of rather long (25—30 μ), folded filaments without distinct ends of their distal parts (Pl. II 8).

For proving the possibility of exploding of trichocysts in vivo, experiment was carried out using acetic acid in low concentration as the factor evoking the explosion. It stimulates the explosion of trichocysts in *Paramecium*. Exploding of trichocysts in *U. cristata* under the influence of acetic acid permitted to ascertain that: 1. Structures stained with different results after hematoxylin and protargol are all of the same nature and the differences in results are possibly involved by a specific fixation and staining. 2. Trichocysts of *U. cristata* respond to acetic acid similarly as those of *Paramecium*.

In living individuals of *U. cristata* trichocysts are invisible.

Distribution of trichocysts in dividers

After staining with protargol it is rather easy to distinguish the individuals of *U. cristata* which begin their division, the dividers, young post-divisional ciliates and those at various stages of physiological reorganization. A good indication of the life cycle stages is the nuclear apparatus being stained deep-brown after the protargol method.

As mentioned above, in the morphostatic individuals trichocysts fail to occur in endoplasm or are very scarce in it. A striking fact is their very high number in the endoplasm of dividing individuals with formed primordia (Pl. III 10, 13). It was ascertained after the examination of ciliates at different stages or division, that trichocysts begin to appear in a low number in those individuals in which the appearance of reorganization band is observed in the middle of each macronucleus. At this stage new kinetosomes are not yet visible at the surface. The number of trichocysts augments considerably in the individuals with a condensed macronucleus and remains at the same level till the division furrow is much advanced. This corresponds to the phase of the kinetosome formation, their arraying into rows and formation of the new cirri (Jerka-Dziadosz 1964). In the young individuals just after division, the endoplasmic trichocysts occur as well (Pl. III 12) but their number diminshes gradually. In proportion as the young post-divisional individuals grow up, in the course of formation of their definitive shape and of resorption of the paternal ciliature, trichocysts disappear in endoplasm and are observable only in the superficial layer of the cell. They are not detectable in endoplasm 40 min after fission.

The distribution of ectoplasmic trichocysts in dividers undergoes changes corresponding to the shift of primordia and of young cirri in the progeny individuals. At the places where new kinetosomes are being organized i.e. in the morphogenetic areas, the estoplasmic trichocysts disappear. It is not certain whether they are resorbed in situ prior to appearing of kinetosomes, or are "washed" out into the endoplasm. The translocation of the ectoplasmic trichocysts is very clearly seen in the region of the division furrow and in the anterior part of the opisthe (Pl. III 10). The middle meridians of trichocysts bend left and embrace the frontal area of the future opisthe. Unfortunately it is impossible to ascertain on the fixed and stained material whether this process indicates an active shifting of the whole parts of cortex and their growth, similarly at it may be observed in vivo in the case of growth and

shifting of AZM and of the frontal cirri (Jerka-Dziadosz 1967). It may be either a process of incorporation of endoplasmic trichocysts into the cortex of progeny individuals in the course of their formation.

Physiological reorganization

In the reorganizing individuals the distribution of ectoplasmic trichocysts undergoes modifications which are in harmony with the arising and developing primordia of the new cirri set (Jerka-Dziadosz 1965). On the ventral side (Pl. IV 17) in the places where new cirri are organized, trichocysts are absent (similarly as in the dividers). I could not be ascertained whether they are resorbed or shifted to the adjacent regions, or washed out into endoplasm. Some disturbances in the pattern and in accumulation of trichocysts near the morphogenetic areas may indicate the shifting of trichocysts. On the dorsal side, rows of kinetal cilia form the boundary of the meridional bands of trichocysts. The area between the 2nd and 3rd row of dorsal cilia is deprived of trichocysts. This is the meridian corresponding to the canalicle of the contractile vacuole (Pl. IV 15). The appearance of trichocysts in endoplasm corresponds to the morphogenetic processes which occur on the cell surface (Pl. IV 14, 16). The endoplasmic trichocysts occur in an insignificant number in the individuals at the first stage of reorganization, their number increases subsequently and begins to diminsh when the resorption of the old ciliature sets on.

Traumatic regeneration

As mentioned in the methods section, fragments were investigated since the moment of operation till the conclusion of the regeneration process. The morphogenetic phenomena belonging to the regeneration process i.e. formation of new ciliature, have been described in the previous publication (Jerka-Dziadosz 1965).

As to the ectoplasmic trichocysts, the fragment contains their part which derives from the operated morphostatic individual. On the dorsal side, an empty space is retained between the 2nd and 3rd row of cilia. It corresponds to the position of the contractile vacuole canalicle. On the ventral side, the pattern of trichocysts corresponds to the retained ciliature.

In the course of 15 min following the operation, the protargol method reveals that the traumatic surfaces differ distinctly from the remaining edge of the body. In the ectoplasm adjacent to the wound trichocysts are absent at this stage. In proportion as the wound is healing and the surrounding pellicle shrinks, the nearest trichocysts shift to the traumatic surface. About 30 min after bisection, the disposition of trichocysts on the body edges resembles to that in unimpaired individuals.

In the course of the first 2—2.5 hours — i.e. in the period of healing of the wound and of regulation of the fragment shape, trichocysts are not found in endoplasm. Simultaneously with appearing of the primordium of the new-regenerated ciliature on the surface, trichocysts appear in endoplasm, similarly as it has occurred in division and in physiological regeneration. Trichocysts persist in endoplasm till the moment of conclusion of the old ciliature resorption (Pl. V 18—21).

Summarizing the above facts, it may be stated that the ectoplasmic trichocysts occur in *Urostyla cristata* in morphostatic individuals, in dividers, in

reorganizers and in regenerating fragments. In the endoplasm of this ciliate trichocysts are present only in the periods of morphogenetic activity i.e. when the new ciliature is formed in division or in regeneration. Endoplasmic trichocysts appear in the moment of formation of kinetosomes and disappear at the period of resorption of the old ciliature.

As stated in the previous publication (Jerka-Dziadosz 1967) the regeneration of the fragments of dividers lasts twice as long as that of morphostatic individuals. In the fragments of dividers, prior to formation of the new regenerated ciliature, cirri, formed as result of division, had grown up and the patternal ciliature has been resorbed. The time from the conclusion of resorption of the pre-division ciliature till the formation of the new regenerated one amounts 2 hours. The fragments of dividers produce the regeneration ciliature within 5—6 hours after operation whereas the fragments of the morphostatic individuals (with the impaired AZM) form kinetosomes approximately 2—2.5 hours after operation.

The distribution of endoplasmic trichocysts in the divider fragments was studied for proving the association of trichocysts presence in endoplasm with the appearance of morphogenetic area on the surface.

Dividers with the fully formed primordia (the 4th and 5th stage) were selected from the culture and placed on slides. Proter and opisthe were bisected transversally in the middle of the body. Simultaneously a divider was bisected along the division furrow. In this way, four fragments were gained from one individual. Then, the material was fixed and stained at 30 min intervals since the moment of operation till the formation of the primordia of regeneration ciliature which takes place about 6 hours after operation. The fragments 2 hours prior to the onset of formation of the new ciliature (3—5 hours after operation) were examined most carefully.

It was stated that all the fragments contain trichocysts in endoplasm during all the regeneration period i.e. since the operation till the conclusion of resorption of ciliature after formation of the new regenerated ciliature. This period lasts for about 7 hours.

Trichocysts occur as well in the endoplasm of the divider fragments in the course of two hours preceding the formation of the regeneration primordia i.e. at this stage when in the fragments of morphostatic individuals trichocysts are not detectable in endoplasm. In a group of 41 divider fragments fixed 3—5 hours after operation, the absence of trichocysts in endoplasm was ascertained in 6 fragments (Pl. V 22). In the control non-operated individuals, fixed simultaneously with the experimental ones, the absence of endoplasmic trichocysts was stated since the stage of 1 hours after separation. It was found moreover that the anucleated fragments (gained from dividers at the stage of condensed Ma) contained much more trichocysts in endoplasm than the fragments with the nuclear apparatus (Pl. V 24).

Discussion

The first problem suggested by the above findings concerns the question whether the structures described in *Urostyla cristata* as trichocysts correspond to trichocysts of such ciliates as *Dileptus*, *Frontonia* or *Paramecium*.

The characteristic size (7 μ) and distribution of trichocysts in endoplasm as well as their capability of extruding structural filaments indicate their

similitude to trichocysts determined by Dragesco et al. 1965 as toxic trichocysts. However only the study of ultrastructure of trichocysts in *U. cristata* would permit a full affirmation of this hypothesis for this ciliate.

The function of trichocysts in *U. cristata* remains not elucidated either. The mass explosion of trichocysts has been observed in vivo only after the action of acetic acid. Any toxic properties after explosion have not been ascertained. After hematoxylin or protargol staining, individuals with single exploded trichocysts were found. It is however difficult to state whether the explosion was evoked by fixation or occurred prior to it and the ciliate became fixed in this state.

The occurrence of trichocysts in endoplasm of *U. cristata* may be accounted for by two possibilities. This may be the result of "washing" them out from the cortex into endoplasm at the stage when "empty" places on the surface are necessary for the morphogenetic areas on which kinetosomes of the new ciliature are organized. Another hypothesis is to consider them as an intermediate stage between the young trichocysts, not discernable in the optic microscope or non-stainable at the stage of the vesicle — on one — and the ectoplasm trichocysts, already incorporated into their final place — on the other side. The latter theory is in agreement with the studies of Ehret and De Haller 1963, Yusa 1965 and Dragesco et al. 1965 postulating the endoplasmic origin of trichocysts. The fact of disappearing of trichocysts from endoplasm at the final stage of morphogenesis and "filling" the ectoplasm with trichocysts in the places which were formerly deprived of them (the morphogenetic areas) speak in favour rather of the second possibility.

As known, in *Hypotricha* the whole ciliature is reorganized during division and regeneration. Divisional morphogenesis initiates by formation of the reorganization band in macronucleus (Raabe 1947, Gall 1959, Prescott and Kimball 1961) and by appearing of dispersed kinetosomes in the morphogenetic areas (Jerka-Dziadosz 1964, 1965, Jerka-Dziadosz and Frankel 1969 a, b, Wise 1965). Possibly the trichocyst formation in *U. cristata* begins also at the same time. It remains not elucidated whether the formation concerns "complementation" of the trichocyst set for the progeny individual (which receives only half of this set from the patternal individual) or is a full exchange of trichocysts.

A fact of interest is the occurrence of trichocysts in the endoplasm of fragments of dividers. In endoplasm of those fragments, trichocysts may be found in the whole course of regeneration process, from the moment of operation till the conclusion of resorption of the pre-regeneration ciliature. This fact may be explained by two postulations: 1. operation "prolongs" the predivisional formation of trichocysts till the onset of regeneration structure i.e. formation of regeneration trichocysts in the fragments of dividers would begin about 2 hours prior to the formation of new kinetosomes. Consequently, the delay of regeneration of the divider fragments would concern the formation of kinetosomes (Jerka-Dziadosz 1967) and not that of trichocysts. 2. Operation involves disturbances in the process of incorporation of trichocysts from endoplasm into ectoplasm. As effect of this, the trichocysts formed prior to division and those formed prior to regeneration occur side by side. In favour of the second possibility speaks the fact that some fragments of dividers occur in which trichocysts are absent in endoplasm (in 6 fragments out of 41 fixed 3—5 hours after operation).

The above observations, however not complete and requiring further, submicroscopical study, permit to ascertain that in *Hypotricha*, simultaneously with the morphogenetic processes as formation and arraying of kinetosomes, formation of the other structures belonging to the cortex — trichocysts — occurs.

Summary

The distribution of trichocysts in *Urostyla cristata* has been investigated in the morphostatic individuals, in dividers and in regenerating fragments. Trichocysts are of the form of rods about 7 μ long. They stick in pellicle vertically to the surface. They have a capability of extruding long folded filaments. During division and regeneration, presence of trichocysts was stated also in endoplasm. The endoplasmic trichocysts appear in the initial moment of formation of kinetosomes on the surface, and disappear after the conclusion of resorption of the old ciliature. They possibly pass to the superficial layers of the cell.

STRESZCZENIE

Zbadano rozmieszczenie trichocyst u *Urostyla cristata* u osobników morfostatycznych, podziałowców i fragmentów regenerujących. Trichocysty mają postać patyczków długości około 7 μ i tkwią w pellikuli prostopadle do powierzchni. Mają zdolność wyrzucania długiej pofałdowanej nici. Podczas podziału i regeneracji stwierdzono obecność trichocyst także w endoplazmie. Trichocysty endoplazmatyczne pojawiają się w chwili rozpoczęcia budowy kinetosomów na powierzchni, a zanikają po zakończeniu resorpcji starego orzęsienia, przechodząc prawdopodobnie do powierzchniowych warstw komórki.

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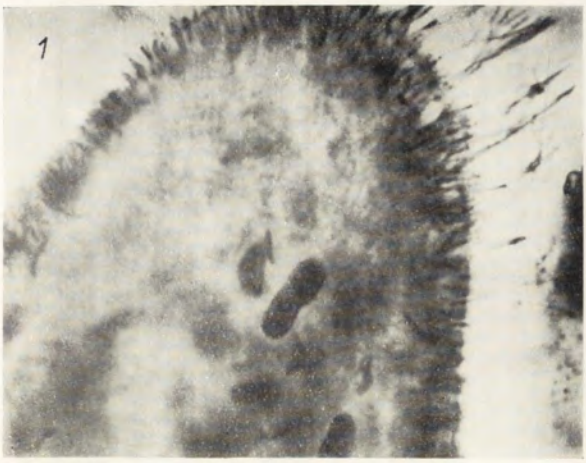
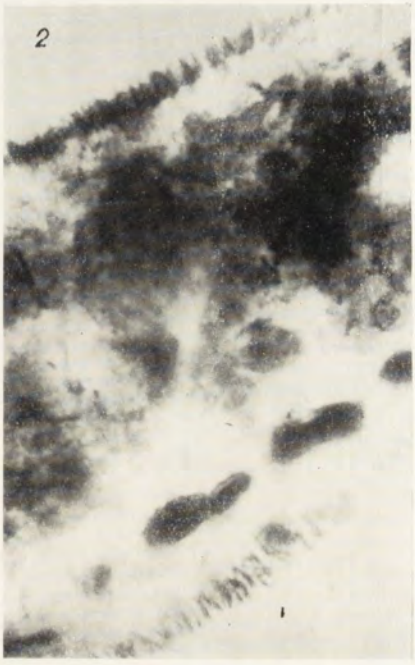
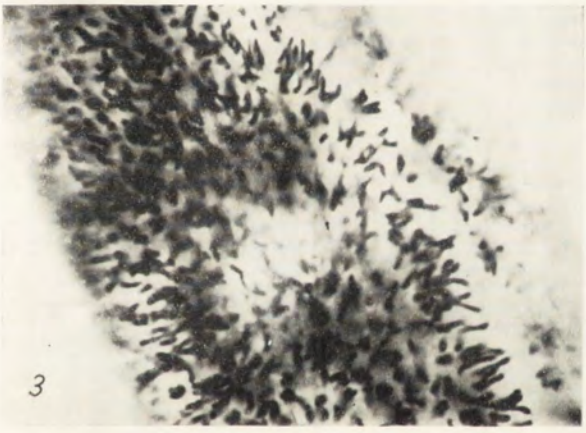
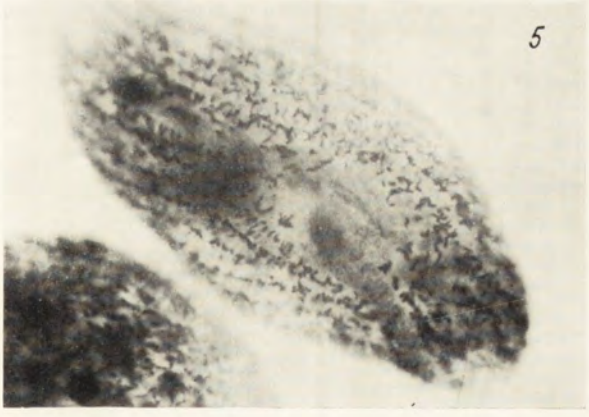
EXPLANATION OF PLATES I—V

Distribution of trichocysts in *Urostyla cristata*
1: Anterior part of a morphostatic individual. Anteriorly — exploded trichocysts. Optic section at the endoplasm level
2: Middle part of a morphostatic individual. Trichocysts on the body margins. Optic section at the level of endoplasm
3: Distribution of trichocysts on the dorsal side
4: Anterior part of a morphostatic individual
5: Distribution of trichocysts on the ventral side
6: Exploded trichocysts on the frontal area
7: Frontal area. Unexploded trichocysts between cirri
8: Optic section across the body margin. Exploded trichocysts
9: Same as 8. Unexploded trichocysts
10: Dividing individual. Trichocysts and nuclear apparatus inside
11: Same as 10. Ventral side. Bending of trichocysts in the anterior part of opisthe is seen
12: Young individual 30 min after fission. Trichocysts in endoplasm are present
13: Divider with a great number of trichocysts in endoplasm
14: Early stage of physiological reorganization. Trichocysts in endoplasm
15: Distribution of trichocysts on the dorsal side of reorganizer. On the right — canalicle of contractile vacuole
16: Late stage of reorganization. Trichocysts in endoplasm
17: Distribution of morphogenetic areas and of trichocysts on the ventral side of reorganizer
18: Endoplasm of regenerating fragment. Trichocysts and nuclear apparatus
19: Ventral side of a fragment of morphostatic individual 4 hrs after operation. Morphogenetic area in the middle
20: Endoplasm of regenerating fragment, 4 hrs after operation
21: Fragment of morphostatic individual 2 hrs after operation
22: Same as 21, 1 hr after operation. No trichocysts in endoplasm
23: Fragment of divider 2.5 hrs after operation. A few trichocysts in the middle
24: Same as 23.5 hrs after operation. Mi preserved. Ma absent. Very numerous trichocysts in endoplasm
25: Distribution of trichocysts on the dorsal side of fragment 1—5, 8—23 — protargol staining after Dragesco, 6, 7 — iron hematoxylin staining after Párducz









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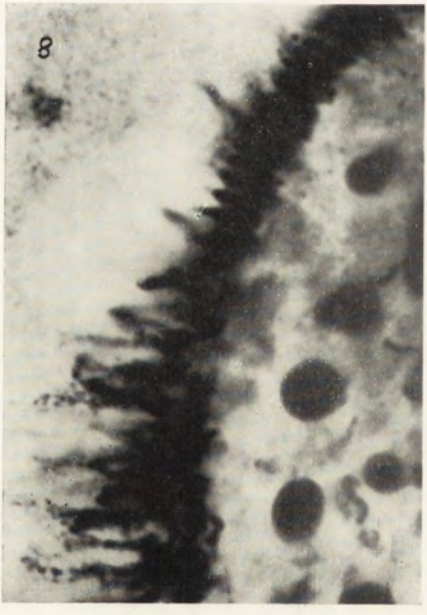

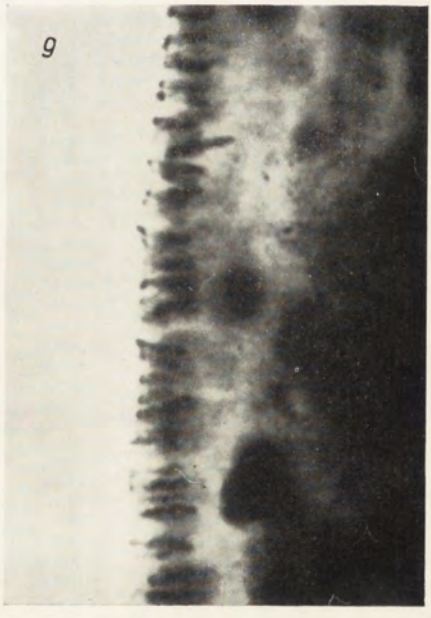

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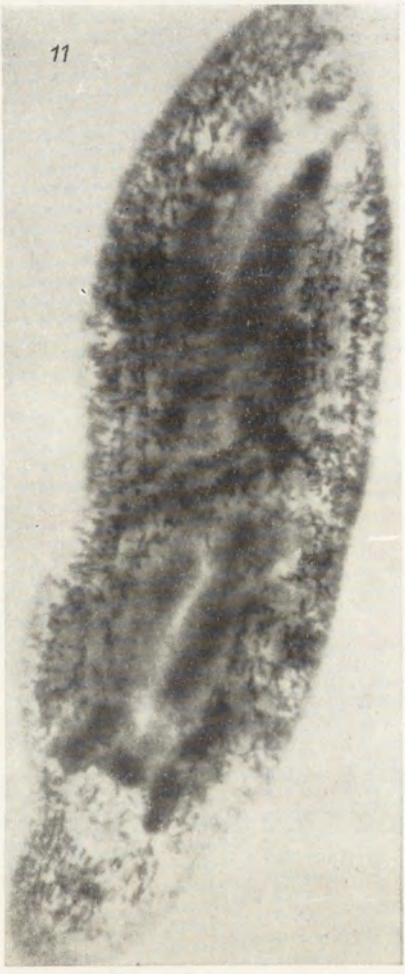

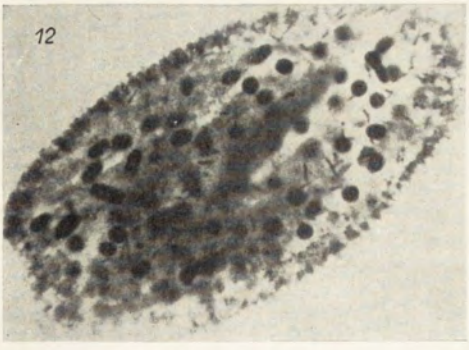

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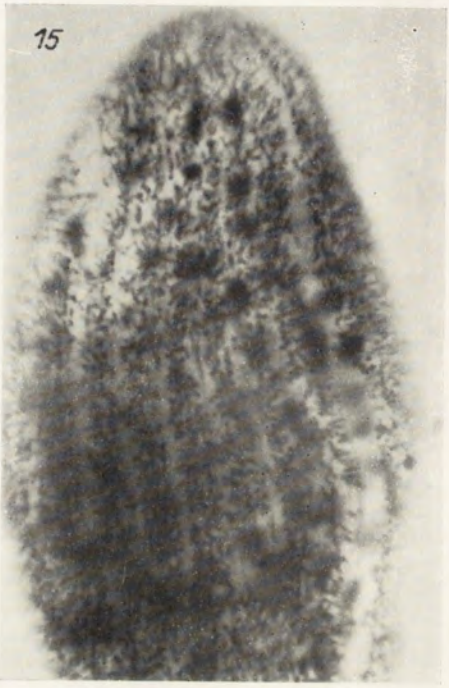

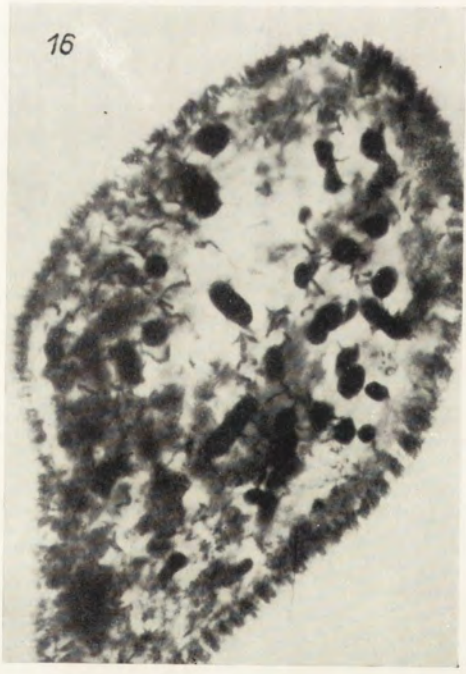

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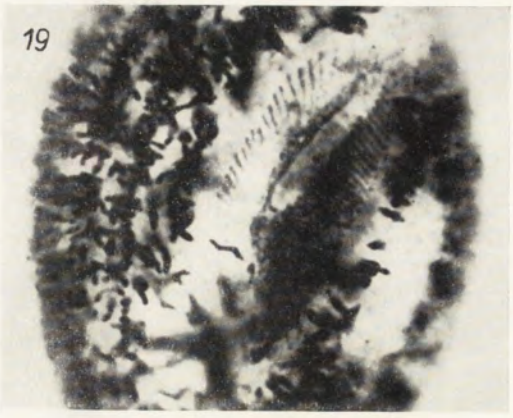

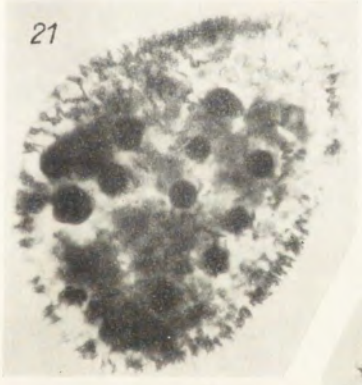

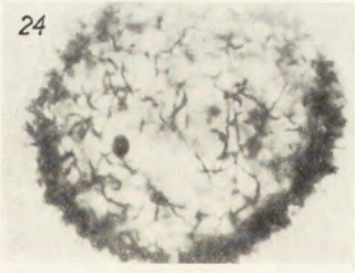

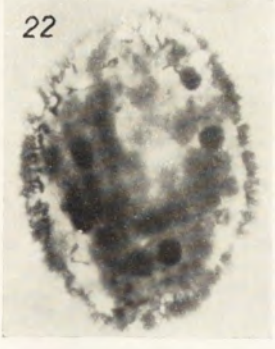

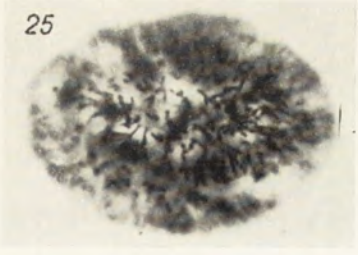

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Some relationships between the Red Flour Beetle, *Tribolium castaneum* (Herbst) *(Coleoptera, Tenebrionidae)* and *Lymphotropha tribolii* Ashford *(Neogregarinida, Schizocystidae)*

Observations sur les relations entre la néogrégarine *Lymphotropha tribolii* Ashford et le coléoptère ténébrionide, *Tribolium castaneum* (Herbst)

Lymphotropha tribolii Ashford, 1965 is a neogregarine pathogen of *Tribolium castaneum* (Herbst). In the original description, a few details were given of the pathogenicity, based on preliminary investigations. This paper presents the results of a wider range of studies designed to cover broadly the relationships between the parasite and its host.

The only broad study of a neogregarine which has come to my notice is that of McLaughlin 1965 who worked on *Mattesia grandis* McLaughlin, a parasite of Boll weevils, *Anthonomus grandis* Boheman. *M. grandis* affects adult beetles as well as larvae, and McLaughlin's work related mainly to adult infections, so is not directly comparable with the present study.

Apart from this work, most studies on the relations between neogregarines and their hosts have been incidental observations appended to taxonomic descriptions, but Jafri 1961, 1964 has shown that *Tribolium casteneum* adults infected with *Farinocystis tribolii* Weiser are hyper-sensitive to radiation, and Weiser has stated (1963) that the same parasite caused an enormous increase in the susceptibility of the beetles to D.D.T. Finlayson 1950 briefly investigated the mortality of *Laemophloeus* spp. infected with *Mattesia dispora* Naville.

L. tribolii infects the host larvae when spores are ingested accidentally, by cannibalism, or by necrophagy. The parasites develop in the haemocoele. In the life cycle there is limited asexual reproduction by schizogony, and infective spores are produced after about 15 days.

The infectivity, pathogenicity and maintenance of virulence of spores have been studied, as have the histopathology and the effects of disease on larval growth and activity. As *L. tribolii* does not infect adult beetles, it was possible to determine the effects of larval disease on the size, sex ratio, longevity and oviposition rate of surviving adults.

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The experiments were designed only to demonstrate gross effects of the disease. The results can therefore be regarded as significant either positively or negatively only as regards such effects.

General methods

Flour beetles were cultured from stocks held at Imperial College, where the original infections of *L. tribolii* were also found. All the species of *Tribolium* used were cultured in finely ground whole meal wheat flour, in sterilized containers. Eggs were obtained by sieving out the flour and rolling them repeatedly down paper to remove the remaining debris. Unwanted infections only occurred when this procedure was not carried out properly, or when more than one generation was allowed to develop in the same batch of flour.

Under the culture conditions used, at 28°C, eggs took 3—4 days to hatch, the larvae pupated after about 22 days, and the adults emerged after about a further 9 days. Thus, the whole life cycle was completed in about 35 days.

Young larvae were very difficult to handle without injury, so all ages were taken from the date of egg laying.

Dead larvae were separated by a combination of sieving and manual selection. New infections were established by adding powdered dead larvae to cultures in the required quantity.

The "spore powder" was estimated by first clearing larval tissue in KOH, then grinding it further to break up clusters of spores, and counting in a haemocytometer. It was invariably found to contain in the order of 10^8 spores per g. Standard doses could then be prepared by mixing the powder with flour in the required proportions. Early tests showed that the use of more than 10^6 spores per g of flour made little difference to the level of infection, or its course, so further experiments were carried out, except where stated otherwise, using this concentration (1% powder in flour w:w).

Maximum production of infective material was obtained either by giving light doses to young larvae, or by giving heavy doses to older ones. In this way, all the larvae died, and were large at the time of death, thereby containing many infective spores.

Histological studies were made as described by Ashford 1965 and histochemical studies used standard techniques as described by Pearse 1960.

Host range in species of *Tribolium*

50 eggs of the 5 available species of *Tribolium* were placed in 2.5 by 5 cm tubes containing 3 g of flour with about 10^7 spores of *L. tribolii* per g. Control tubes contained 50 eggs of each species, in sterile flour.

The pure flour medium is not very satisfactory for the development of *T. destructor* Uyttenboogart or *T. anaphae* Hinton, and only 8 and 16 of these species respectively survived to maturity in the control cultures. Of the other species, 22 *T. madens* (Charpentier), 27 *T. castaneum*, and 36 *T. confusum* (Duval) adults emerged. In the infected cultures, no adults developed in any save that of *T. confusum*, where 22 survived. Examination of these adults showed no signs of their having been infected.

The dead larvae were removed from the remaining cultures, and examination showed that all were infected with *L. tribolii*, and had died from the disease.

The low survival rate in control cultures and the cultures of *T. confusum* was probably due to cannibalism in the crowded conditions, and to the infertility of some of the eggs. The use of high population densities, which encourage cannibalism, would have allowed any low rate of infection to become apparent.

Thus, all readily available species of *Tribolium* are susceptible, except *T. confusum*, which is completely refractive. During the course of this study, further cultures of *T. confusum* were repeatedly exposed to infection, and they were never found to be susceptible.

The susceptibility of *T. castaneum* at different ages

Eggs of *T. castaneum* were collected at 10 day intervals, and allowed to begin development. When the third lot were beginning to hatch, batches of 20 larvae were taken from each age group, and exposed to concentrations of 10^7, 5×10^5 and 10^4 spores per gram. 20 further larvae of each age were reared in sterile flour.

The 20 larvae of each age to be exposed to each infective dose and 20 controls were reared in 2.5 by 5 cm tubes with 2 g of the requisite medium. The surviving adults were counted as they emerged.

Table 1 shows the figures obtained, which clearly indicate a decrease in susceptibility with age. The oldest larvae pupated within a few days of exposure, and were perhaps not infected for this reason. The 14 day larvae were exposed for long enough for the disease to develop fully, so their resistance must be due to the failure of a high proportion of the parasites to survive.

Repeated attempts were made to infect larvae aged 15 days or more, and while this was occasionally possible up to 16 days, it was very rarely so.

Table 1

Numbers (20) of *T. castaneum* reaching the adult state after exposure at different ages to different doses of *L. tribolii*

Age at infection	Dose (spores per g)			
	control	10^4	5×10^5	10^7
4 days	20	10	7	0
14 days	20	20	22	0
24 days	20	20	20	20

Adults also could not be infected even by freeding them on pure spore powder, which they consumed readily. Those adults which had emerged after infection as larvae commonly contained mature gametocysts of the parasite, but no adult was seen to have an actively developing infection.

When resistant larvae or adults were examined microscopically, after

exposure to massive doses, sporozoites were commonly seen in the mid-gut, but no further stages of the parasites. Resistance is, therefore, probably due to the failure of sporozoites to penetrate the gut wall, or to their failure to grow in the haemolymph.

Dosage and mortality

A series of fluor media was prepared containing fresh *L. tribolii* spores as follows: 10^7, 10^6, 10^5, 10^4, 10^3, 10^2 spores per g, by the serial dilution of a 10^7 spores per g medium.

Five eggs of *T. castaneum* were placed in each of five 2.5 by 5 cm tubes for each concentration of spores, and 1 g of the appropriate fluor was added. 25 individuals were thus allowed to develop, exposed to each infective level. In 2 repetitions of the experiment, the 10^7 spores per g dose was omitted, and 10 eggs were placed in each tube.

The surviving adults were counted as they emerged, survivors being defined as those which showed no external sign of infection on emergence.

Control mortality was measured similarly in larvae reared in sterile flour. A high control mortality was recorded as usual, being probably due to a combination of cannibalism and infertility. Abbott's formula was applied to account for this mortality.

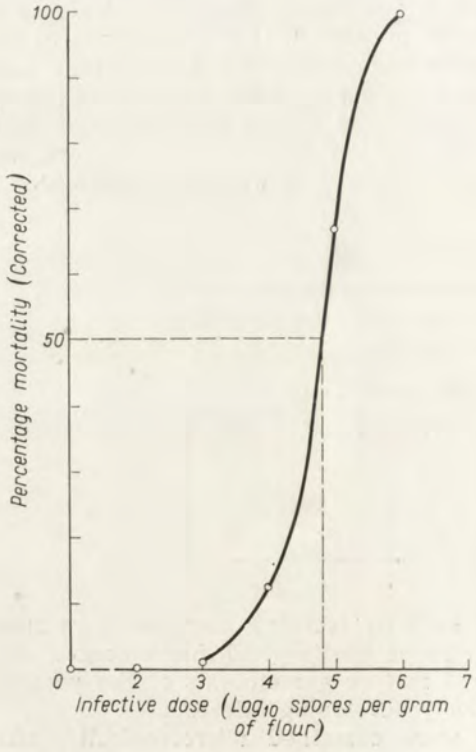

Fig. 1. Dosage mortality curve for *L. tribolii* in *T. castaneum* showing estimated L.C. 50 at about $10^{4.5}$ spores per g of flour

Fig. 1 shows the results obtained, and demonstrates that there is a correspondence between the dose to which larvae are exposed and their mortality. There is no "all or none" response to the disease, as might be expected if the parasites multiplied enormously within the host. Exposure to flour containing 1 000 spores per gm caused very little mortality attributable to the disease, but 10^6 spores per g caused almost 100% mortality.

A finer series of spore concentrations would probably not be useful without enormous replication. The concentration at which 50% mortality would be expected to occur (L.C. 50) may be be estimated as about $10^{4.8}$, and in spite of the variation inherent in this type of experiment, this value may probably be taken as repeatable within an order of magnitude.

Maintenance of virulence of *L. tribolii* spores

A fresh medium of spores in fluor was prepared, containing about 2×10^5 spores per g, which was expected to kill almost 100% of larvae reared in it. After an initial assay to prove this, the flour was divided into 3 parts, each to be stored at a different temperature. The conditions were chosen as representing those under which infective material might be kept in practice; 15°C, room temp. (20°C approx.) and 30°C.

The virulence of the spores in these media was assayed after 3 months and 9 months by determining the numbers of *T. castaneum* adults surviving from larvae reared in the medium. This assay method showed in general how long infective material might be kept without serious loss of potency.

1 g of flour was placed in each ten 2.5 by 5 cm tubes, and 12 newly laid eggs of *T. castaneum* were added. Adults were counted as they emerged, after incubation at 28°C. Control mortality was measured in larvae reared simultaneously, in sterile flour, and was taken into account using Abbott's formula.

The figures obtained are shown in Table 2. In the preliminary assay, 95.2% mortality (4.8% survival) occurred in the fresh medium. After storage for

Table 2

Percent survival to adult state of *T. castaneum* reared in *L. tribolii* infective fluor stored at different temperatures

Culture	Storage time						
	fresh spores		storage temp. °C	3 months		9 months	
	obs.	corr.		obs.	corr.	obs.	corr.
Uninfected	669	100		59	100	52	100
Infected	3.3	4.8	15	1.6	2.8	—	—
			R.T.	4.3	7.0	8.3	16
			30	2.5	4.2	21.8	41

Obs.: Observed percent survival.
Corr.: Results corrected by Abbot's formula for control mortality.
R.T.: Room temperature (= 20±5°C approx).
Note: The flour stored at 15°C for 9 months became mouldy and was not assayed.

3 months, there was no noticeable change in this figure at any temperature. After 9 months, a marked decrease in mortality occurred; flour stored at room temperature had retained the most potency, giving 85% mortality, but after storage at 30°C, only 59% of the larvae failed to develop.

Unavoidably, different batches of larvae were used in the successive tests, which may account for differences in control mortality. It can, however, be stated that although *L. tribolii* spores may be stored for considerable periods, they lose much of their potency if stored for 9 months at 30°C.

Extension of this experiment to a wider range of temperatures, and consideration of the effect of humidity are desirable in order to draw accurate quantitative conclusions.

External symptoms

Larvae which become infected with *L. tribolii* show no external symptoms until shortly before they die, or until encapsulated parasites (see below) become visible through the integument.

About 10 days after infection, some of those larvae which have received a massive dose show some darkening of the posterior abdominal segments. The rest of the body is slightly less opaque than in healthy larvae of the same age, owing to the degeneration of the fat body. At death, after 12 or more days, the larvae are straight, shrunken, and internally blackened. Desiccated corpses are dorso-ventrally flattened, and dark brown in colour. Accumulations of dead larvae smell strongly of yeast. In cultures with old infections, such larvae are commonly found to have been partially eaten. The only stage at which heavily infected larvae can be separated from healthy ones, or those which have died from other causes, is when they are moribund, or just dead, and immobile, shrunken, and blackened.

Larvae which have received a sub-lethal dose of spores develop normally, but more slowly than healthy ones. Pupation may be delayed for as much as a month. In these larvae, when the fat body becomes opaque and white just before pupation, the capsules surrounding the parasites become clearly visible externally as brown spots just below the integument. This symptom does not appear until at least 12 days after infection.

Many larvae were found to be intermediate between those described above, and some showed no externally visible signs of a light infection.

Larvae which survive an infection may pupate. Some of the pupae are speckled with capsules, while others show no external signs. Pupae which die do not blacken, they shrivel dorso-ventrally on drying out, and retain their live colour, which depends on the state reached by the developing adult inside. Apart from the capsules visible in some specimens, infected pupae while still alive are indistinguishable from healthy ones.

A large proportion of adults which die as the result of disease in the larvae, do so during or shortly after emergence. Such specimens are often grossly deformed in the development of their wings and elytra, and capsules are usually visible through the translucent cuticle of moribund teneral adults. Those which die prematurely, after emerging as apparently perfect insects show no differences from adults which die from other causes.

Histopathology

Encapsulation of the parasites by the host.

A conspicuous feature of *L. tribolii* infection is the host reaction, encapsulation, which it provokes. Encapsulated parasites were found in larvae, pupae and adults which had been exposed as young larvae to light or moderate infections. The capsules were clearly visible on external examination of larvae, pupae, or teneral adults, appearing as brown spheres, often in groups, mostly just below the cuticle. Those pupae which died, or would have been expected to give rise to deformed adults contained particularly large numbers of capsules, and a series of such pupae was examined histologically.

The capsules (Fig. 2) consist of two layers, though there is no clear demarcation between them. The outer layer is composed of haemocytes which have

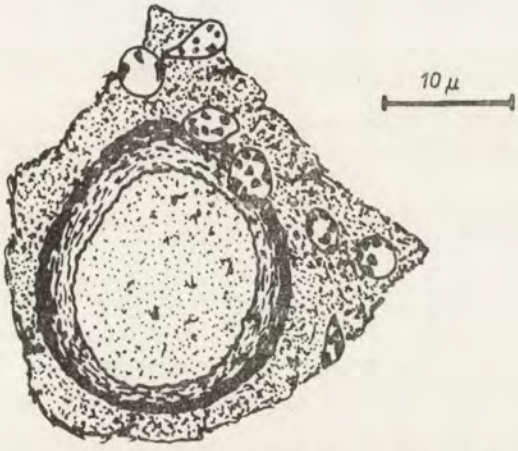

Fig. 2. Encapsulated gametocyst of *L. tribolii* from pupa of *T. castaneum*. Note degeneration of gametocyst contents. From a Giemsa stained section

aggregated round the parasite, forming a thick coat. The inner haemocytes in this layer are flattened and appear spindle shaped in sections. As haemocytes are very rare as free cells in healthy larvae, it was not possible to compare those in the capsule with normal ones.

The inner layer of the capsule, which is about 5 μ thick has a more homogeneous, fibrous texture, and is light brown in colour. This layer, which sometimes only partly surrounds the parasite bears a close superficial resemblance to insect cuticle. Individual cells and nuclei are not distinguishable, and it is difficult to be sure if this layer is composed of dead haemocytes, or is secreted by the surrounding layer of living cells.

The inner layer of the capsule stains heavily with Heidenhain's haematoxylin, and bright blue-green with Giemsa's stain. The haemocytes of the outer layer have cytoplasm which also stains heavily with Heidenhain's haematoxylin, and both their cytoplasm and nuclei stain red with Giemsa. The cell boundaries and nuclei are therefore difficult to distinguish. The outer haemocytes contain many small granules of PAS positive material, and this stain

colours the inner layer lightly and diffusely. The entire capsule stains heavily with mercury bromophenol blue, and while the outer layer is destroyed by boiling with KOH, the inner layer is not. After treatment with KOH, the inner layer does not stain with iodine. These tests indicate that the inner layer of the capsule is composed of a protein-polysaccharide complex of high inertia, which does not contain chitin. Also, proteins and polysaccharides are present in large quantities in the haemocytes of the outer layer.

A remarkable feature of encapsulation is that it only occurs around developing gametocysts of the parasites, which degenerate, their nuclei becoming indistinguishable, until the capsule finally contains only amorphous matter. Trophozoites, and gametocysts containing mature spores are not affected. The maximum development of encapsulation is illustrated in Pl. I 1, where many gametocysts have been destroyed, but many are mature, and not affected.

Capsules may be found from 12 days after infection, and may form in any part of the host's haemocoele. They are mostly close to the remnants of the fat body, where they often coalesce to form groups of 5 or more.

Encapsulation of the parasites was observed in all species of *Tribolium* which became infected, and was particularly prominent in *T. anaphae*.

Effects on the host's organs

Besides the phenomenon of encapsulation described above, the only histopathological effects of the disease which were noticed occurred in the fat body. The fat body of healthy *T. castaneum* larvae almost fills the haemocoele from any early age. In young larvae it comprises a group of cells with well defined margins, containing a few small granules. As the larva grows, the cells swell with increased volumes of reserve vacuoles, and individual cells become indistinguishable. The most conspicuous of the vacuoles stain heavily with Heidenhain's haematoxylin, obscuring the nuclei of the cells. They also stain with mercury bromophenol blue, and faintly with PAS, and may thus be interpreted as containing a mucopolysaccharide of high protein content. These are probably the equivalent of the "albuminoid spheres" (Wigglesworth 1950), commonly found in large numbers in insect fat body. In young larvae aged up to 6 days, the albuminoid spheres are small or absent, but they develop rapidly so that by 12 days the fat body is largely composed of them. They are variable in size, from 2 μ to 9 μ in diameter, mostly about 6 μ in old larvae.

Globules of lipid substance develop from an early age, and also increase in size and number as the larva grows. The lipid globules may best be observed as clear areas of the fat body in fixed preparations. In squashes in Sudan black in 70% ethanol they stain heavily, but cannot be measured, as they agglomerate on release from the cells.

The remaining vacuoles in the healthy fat body are of 2 kinds; one is proteinaceous, staining heavily with mercury bromophenol blue, and the other contains polysaccharide, staining heavily with PAS. These granules are present in the early fat body, and though they increase in number, they do not exceed 3 μ in diameter.

The nuclei of the fat body are rather uniform and constant in structure throughout the larval development. They are spherical, 5 μ to 6 μ in diameter, and contain from 2 to 6 darkly staining granules.

The nuclei are not affected noticeably by infection; the effect of *L. tribolii*

on the fat body may be interpreted mainly as slowing down its normal development, arresting it, and causing degeneration in heavy infections (Pl. I 2, 3).

The albuminoid spheres are most affected. These fail to develop in infected larvae, or do so only to a limited extent, and area almost entirely wanting in moribund specimens. The lipid globules are affected more slowly, persisting in small numbers in quite heavily infected larvae. At death, however, there is very little lipid material in the fat body.

While the fat body of healthy larvae occupies almost the entire haemocoele, the lack of development of storage vacuoles in infected larvae causes it to remain of constant size as the larva grows, and thus to occupy only a small proportion of the body cavity. The space thus made available is packed with parasites.

All the effects on the fat body described above seem to be reversible; in larvae in which a large proportion of the parasites have been encapsulated the albuminoid spheres and lipid globules may develop, and in surviving pupae the fat body has a normal appearance.

Effect on rate of larval growth

Infected larvae were conspicuously smaller than healthy ones of the same age. In order to investigate this retardation in growth, larvae from 2 heavily infected and 2 healthy cultures were weighed periodically throughout their development.

Larvae were cleaned of adhering flour particles by allowing them to crawl on paper and blowing off unwanted matter. In order to avoid inaccuracies due to water loss or starvation, they were weighed within one hour of removal from the culture. The youngest larvae were too small to weigh individually, so all larvae were weighed in groups of 20, and the average weight calculated and recorded. Dry weights were measured similarly after the same larvae had been desiccated overnight in an oven at 110°C.

Particularly in the middle of their development, larvae showed great variation in size, but the groups of 20 were thought to give a fair average. The live weight figures are presented graphically in Fig. 3 and show that infected and uninfected larvae cultured simultaneously show a distinct relationship with each other which is not so clear when larvae from different groups are compared. Slight differences in the consistency of the flour, and small variations in the temperature of the incubator are thought to be responsible for this. Only cultures reared simultaneously in identical conditions can be critically compared.

The results show that the disease had no measurable effect on the rate of growth until at least 6 days after exposure to infection. After 8 days, however, when the uninfected larvae were growing rapidly, the rate of increase in weight of infected larvae decreased. Infected larvae continued to grow at a greatly reduced rate until they died. Examination of the dry weights show no difference in pattern from live weights.

Effect of disease on larval activity

Activity in insects may be measured by a variety of methods, the results of each being open to different interpretations. In order to compare the activity of larvae of different ages and states of infection, it was necessary to

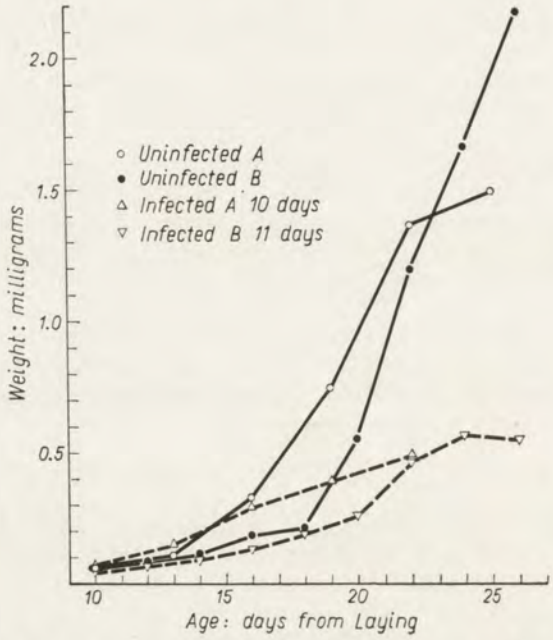

Fig. 3. Weights of *T. castaneum* larvae of different ages and states of infection

use a method which would be repeatable for larvae of all sizes. It was decided to count the number out of a batch of 10 larvae which moved in a 10 sec period. This number was usually more than 0, and almost always less than 10, and was thus suitable for repeated comparative readings.

Larvae were infected 10 days from egg laying, and at each age and state of infection, four batches of 10 infected and four batches of 10 healthy larvae were placed on filter papers and enclosed in nickel plated brass rings 2.5 cm in diameter. The rings were covered with a plastic petri-dish in order to eliminate air movements. The observations were carried out at a temperature of 20°C.

20 readings were taken from each of the 8 batches of larvae (4 infected and 4 control), in consecutive groups of 5, each group separated by an interval of 1 hour.

Table 3 shows the total score for each group of larvae observed, i.e. the sum of the numbers out of 10 larvae moving in 20, 10 sec intervals, spread in groups of 5 over 4 hours. The percentage activity is expressed as the average percentage moving in any group in any 10 sec period.

The results show that there is considerable variation in the activity of groups of larvae from identical cultures, under identical conditions. In all cases the average percentage activity is between 27% and 36%. While the individual estimates of activity varied between 15.5% and 52.5%, no pattern or trend is discernable in these results either in the figures for any one culture, or between the cultures.

It may be concluded that the disease has little if any effect on the activity of larvae, at least until very shortly before death.

Table 3

The activity of infected and unifected *T. castaneum* larvae of different ages

Culture	Group	Days from egg laying							
		10	12	14	16	18	20	22	24
Control	1	81	47	64	105	54	44	80	38
	2	74	54	58	62	53	51	62	53
	3	72	45	71	45	76	60	43	62
	4	63	71	71	69	44	65	63	101
	Total	290	217	264	281	227	220	248	254
	Mean %	36	27	33	35	28	27.5	31	32
Infected day 10	1	—	48	68	31	62	43	87	35
	2	—	54	49	44	74	59	89	55
	3	—	78	69	76	43	71	49	69
	4	—	46	63	63	52	68	51	80
	Total	—	226	249	213	231	241	276	239
	Mean %	—	28	41	27	29	30	36	30

Maximum indyvidual score = 200. Maximum total = 800.
Mean % = Total 1/8 to nearest whole number.

An interesting observation of the effect of the disease on the behaviour of some larvae may be recorded here. It was noticed that small numbers of infected larvae would crawl up on the filter paper in the culture jars. These larvae were invariably heavily infected and close to death. Uninfected larvae only left the culture medium in cases of severe overcrowding.

Effects of disease on surviving adults

L. tribolii is exceptional among neogregarines in that it only infects young larvae of its host, and that a proportion of infected larvae survive to become apparently normal adults. These adults contain no active stages of the parasite, but do contain encapsulated and mature gametocysts. In the following sets of data, the size, sex ratio, oviposition rate and longevity of surviving adults are discussed. The figures on size are supplementary data obtained from the dosage/mortality experiments. The oviposition rate and longevity were measured in adults surviving from cultures in which over 80% of the larvae had died, and in which all had been infected. Survivors are defined as those adults which were alive and perfectly normal in external appearance on emergence from the pupa.

The size of survivors

Estimates of the sizes of survivors were made by measuring the length of their elytra from the base of the scutellum to the tip. Measurements were made with a binocular microscope (20 times magnification), with an eyepiece scale with units equal to 1/14 mm.

Table 4
The elytra length of *T. castaneum* adults surviving exposure to different doses of *L. tribolii*

Dose spores per g survived	No measured	Elytra length (eyepiece units)	
		mean	range
0	32	34.9	32.0—37.5
10^2	38	34.9	31.5—38.0
10^3	33	34.5	31.0—37.0
10^4	32	34.4	31.5—37.0
10^5	12	34.0	25.0—36.5
10^6	no survivors	—	—

An apparent trend is shown by the figures, which are given in Table 4. The average elytra length of healthy adults (34.9) units) was slightly greater than that of those which had survived a heavy dose (34.0 units). The available number of adults surviving heavy doses was necessarily small, and the difference between the extreme means is well within the range about either one, so that no real significance can be attached to the results.

It seems, therefore, that while disease in the larval state may affect the size of surviving adults, the difference is very small.

The sex ratio of survivors

The sex ratio of adults from healthy cultures showed great variation for unknown reasons, being usually slightly biased in favour of females. Many sets of pupae from infected cultures were sexed, and as there was no apparent gross difference in the sex ratio caused by the disease, no comprehensive figures were recorded.

Longevity of survivors

From a culture in which all the larvae had been infected, pupae were removed and sexed. On hatching, adults (as below) were placed in 2.5 by 5 cm tubes with about 3 g of flour. Deformed adults, all of which died within 3 days of hatching were not used.

The tubes containing adults were examined every 5 days, and dead beetles were recovered. The flour was changed every 15 days. The survival rate up to 50 days was measured in 186 surviving adults and 197 adults from healthy cultures.

The results of this experiment, converted to percentages, are shown in Fig. 4. As there was no difference between the sexes, the figures have been pooled. Adults from healthy cultures had a high survival rate for the first 50 days. Those from infected cultures, however, had a distinctly lower survival rate for the first 25—30 days, during which time about 25% of the beetles died. After 30 days, the mortality rate of infected beetles was equal to that of healthy ones. About 100 individuals from each group were kept for a further 50 days, during which no mortality occurred.

Surviving adults may thus be separated into two distinct categories: those which are effected, and have a reduced life span (about 25%), and those which are apparently unaffected as regards their longevity (about 75%).

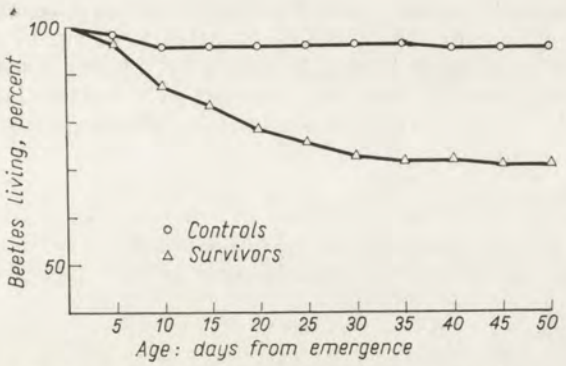

Fig. 4. Longevity of *T. castaneum* adults from healthy cultures and those from cultures in which 98% of larvae had died from *L. tribolii* infection

Oviposition rate of survivors

Pupae from a culture in which about 90% of the larvae had died were extracted and sexed. Adults were collected on the day of emergence, paired, and incubated in 2.5 by 5 cm tubes containing about 3 g of flour. One pair was kept in each tube. Every 3 days, the adults were removed and the flour sieved to separate eggs. The eggs were counted, and the adults and flour replaced. The flour was changed every 10 days.

A series of beetles from uninfected cultures were treated similarly, and the numbers of eggs laid by the two groups were compared. Surviving pairs in which the male died were discarded.

Table 5 shows that healthy females laid no eggs in the first 3 days of adult life, then laid at an increasing rate of up-to 18 eggs per day (usually about 10) for the whole length of the observed period.

Table 5

Eggs laid by *T. castaneum* females

A. Control. Adults from healthy cultures

Pair No.	Days from emergence														
	3	6	9	12	15	18	21	24	27	30	33	36	39	42	Total
1	0	6	19	26	27	33	38	30	29	30	28	49	46	38	399
2	0	2	13	28	34	41	46	42	43	40	34	53	53	43	477
3	0	0	13	21	27	37	27	31	27	24	26	46	48	45	372
4	0	0	5	11	17	26	26	25	21	23	24	41	39	34	292
5	0	7	18	18	21	34	37	33	36	29	27	42	48	46	396
6	0	8	21	29	31	32	28	27	27	25	24	43	47	44	386
7	0	12	36	45	44	45	42	36	46	51	42	51	52	49	551
8	0	1	6	9	23	31	26	21	25	26	24	40	39	28	229
9	0	9	16	14	19	38	42	38	33	31	27	36	40	39	382
10	0	9	12	21	30	41	35	29	30	31	28	48	40	40	394
11	0	4	26	25	29	44	36	27	29	32	29	47	49	45	422
Total	0	58	185	247	302	402	383	339	346	342	313	496	501	456	4370

As in the longevity experiment, the survivors may be clearly separated into two groups (Table 6). The females of pairs 6, 8, 10, 11 and 13 all died within 21 days of emergence having laid at most 14, and usually 0 eggs. The 9 remaining females lived for the whole period investigated, laying an average of 388 eggs each. This number compares very closely with the average of 397 eggs laid by healthy females.

Table 6

Eggs laid by *T. castaneum* females

B. Survivors

Pair No.	Days from emergence														
	3	6	9	12	15	18	21	24	27	30	33	36	39	42	Total
1	0	13	27	36	38	41	37	32	38	40	29	28	36	33	428
2	0	11	27	36	40	47	47	41	41	38	36	35	35	30	464
3	0	9	28	44	48	49	26	29	38	44	32	31	42	31	451
4	0	0	5	19	29	36	34	26	28	34	31	32	36	28	338
5	0	4	15	31	35	30	21	20	28	29	23	21	19	25	311
6	0	0	0	0	0	X		female	died						0
7	0	9	22	35	41	48	40	30	32	32	33	36	41	29	428
8	0	0	X	female	died										0
9	0	13	29	44	45	37	32	21	31	32	34	37	40	32	427
10	0	0	X	female	died										0
11	0	5	3	1	1	4	X	female	died						14
12	0	14	20	19	20	27	22	22	28	44	38	34	39	37	364
13	0	X	female	died											0
14	0	5	11	15	15	13	26	27	33	37	33	30	26	23	294
Total	0	83	187	280	312	332	285	248	297	330	289	284	314	268	3519

The graph, Fig. 5, shows the oviposition rates of healthy and surviving females. The two lines for survivors are based on egg counts averaged separately for the number of females originally surviving, and the number surviving at the time of the count. There is no meaningful difference between the oviposition of living survivors and healthy beetles, but when the total population surviving at emergence is considered, a considerable decrease is observed owing to the proportion which died early without laying.

Discussion

L. tribolii has been shown to infect 4 species of *Tribolium*, but not *T. confusum*. *Tribolium* species are closely related ecologically as well as taxonomically, and the range of hosts is not surprising. The anomalous refractivity of *T. confusum* is unexplained, but compares with that of *Cryptolestes turcicus* Grouve, which Finlayson 1950 failed to infect with *Mattesia dispora*, a parasite of other members of the genus.

Other neogregarines have been shown to infect larvae more readily than adults. For example, Weiser 1953 found adults of *T. castaneum* difficult to infect with *Farinocystis tribolii*, which killed many larvae. Old larvae and

Fig. 5. Oviposition rate of *T. castaneum* females from normal and infected cultures

adults have larger numbers of haemocytes than young larvae; possibly the sporozoites are destroyed by phagocytosis on entering the haemocoele. The presence of sporozoites in the guts of old larvae, and the absence of developing trophozoites in the haemocoele show that the resistive mechanism acts between these stages.

The importance of encapsulation must be slight in the case of heavy infections. Capsules were rarely found in these cases, and as they only formed round developing gametocysts, could not prevent any increase in number or volume of the parasites. In light infections the capsules isolate the parasites, killing them, and some benefit be had in this way. Encapsulation has not previously been reported in neogregarine infections. Salt 1963 a reviewed the subject in the case of metazoan parasites and concluded that the phenomenon occurred in the case of any foreign body, in the absence of factors (produced by parasites) to prevent it. During encystation of the gametocytes, a surface change does take place, which may be responsible for the breakdown of the parasite's defence mechanism. Salt 1963 b further suggests that parasites in unnatural hosts are commonly encapsulated. The possiblity thus arises that *Tribolium* spp. are not normal hosts to *L. tribolii*. The occurrence of unencapsulated mature gametocysts and encapsulated young ones in the same host is difficult to explain. Possibly the encapsulated parasites are early ones, which mobilized the host's entire supply of haemocytes, allowing later parasites to develop unhindered.

The parasite lives in the blood, and appears only to affect the fat body, causing its failure to develop, and eventually its degeneration. The lack of development of the fat body is not compensated for by the growth of the parasites, as the rate of growth of infected larvae (plus parasites) is far less than that of healthy larvae.

Brief studies (not presented here) on the rate of oxygen uptake and susceptibility to D.D.T. both showed no gross effect, and the lack of effect of disease on larval activity help to confirm that only the blood and food reserve organs are affected by the disease. The reversibility of the effects on the fat body support this view.

The disease thus prevents the normal development of larvae by chronic tissue starvation. Death which is sudden, and not preceded by marked symptoms may be the result of the inadequacy of food reserves at a critical moment such as ecdysis or metamorphosis. On the other hand, the blackening of larvae at the time of death possibly indicates physical internal damage, causing the alteration of blood proteins.

The studies on survivors indicate that the majority of these are unaffected as regards their longevity or oviposition rate, but some control of population numbers in addition to direct larval mortality accrues from the weakening and sterilization of about 25% of the survivors.

The limited intraspecific infectivity of this parasite, and the long time taken to kill the host probably preclude its direct use as a biological control agent. Flour contaminated with a lethal concentration of spores would be unacceptable in most communities. The spread of the disease into new areas, affected by *Tribolium*, would be facilitated by the long life of the spores, and might add one factor in the regulation of numbers, possibly yielding valuable returns.

Acknowledgements

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Summary

L. tribolii has been shown to infect 4 species of *Tribolium*, but not *T. confusum*. Young larvae only of *T. castaneum* could be infected, though older larvae, pupae and adults commonly died as the result of larval infection. A concentration in the order of 10^5 spores per g of culture medium caused 50% mortality. Spores maintained much of their virulence after storage at 20°C for 9 months. External symptoms were very slight, but internally, massive degeneration of the fat body occurred. Survival was probably aided in part by the encapsulation of parasites by the host's haemocytes. The larval growth rate was greatly reduced, but there was no effect on activity. Surviving adults were possibly slightly smaller than healthy ones; about 75% of these beetles had normal longevity and fecundity, but the remainder were almost sterile and died within 30 days of emergence.

RÉSUMÉ

Il a été prouvé que *L. tribolii* est capable d'infecter 4 espèces de *Tribolium* mais non pas *T. confusum*. Seules les jeunes larves de *T. casteneum* pourraient être infectées, bien que la mort des vielles larves, des pupes et des adultes resulte souvent de cette contamination. Une concentration de l'orde de 10^5 spores au gramme

de culture détermine une mortalité de 50%. Les spores ont conservé beaucoup de leur virulence après une conservation à 20°C durant 9 mois. Les symptômes externes étaint difficilement perceptibles mais par contre le taux de dégénération du corps adipeux était important. La survie était probablement facilitée en partie par un enkystement hémocytaire. Le taux de croissance des larves est sensiblement réduit, mais il ne se produit cependant aucun effet sur leur activité. Les adultes survivants paraissaient sensiblement plus petits que les adultes non contaminés. La longevité et la fecondité d'environ 75% de ces insectes survivants ne sont pas modifiées mais les autres sont presque tout à fait stériles et meurent dans le courant de 30 jours après leur éclosion.

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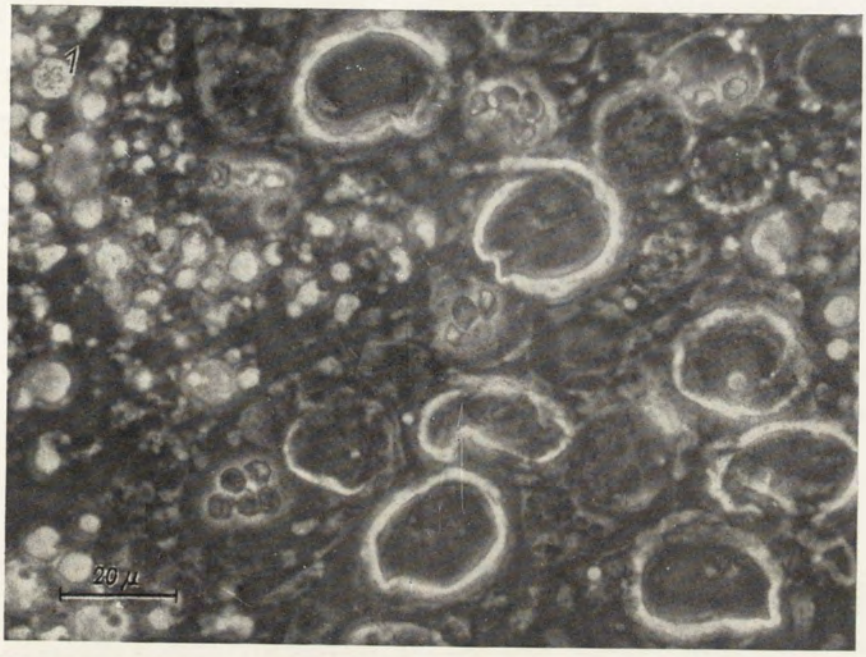
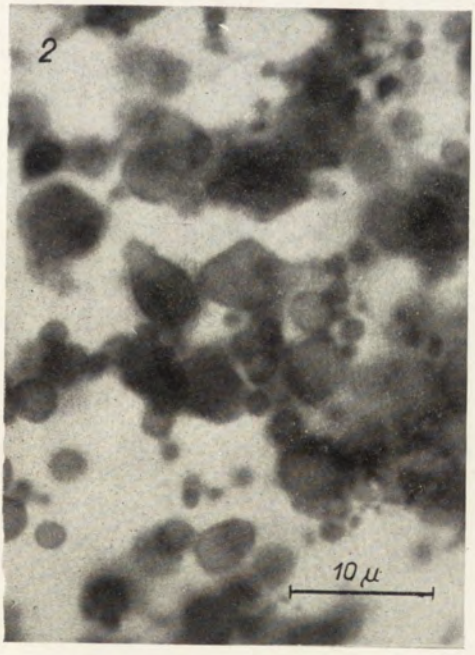
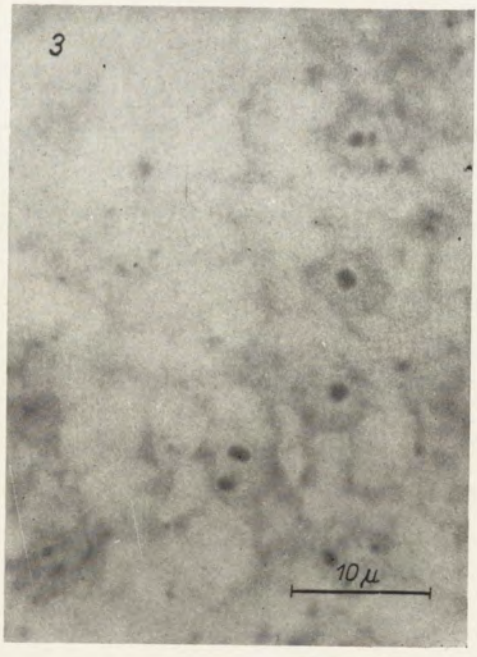
EXPLANATION OF PLATE I

1: *L. tribolii* in *T. castenum* moribund pupa. Showing encapsulated young gametocysts but gametocysts with mature spores unaffected. Unstained, negative phase contrast
2: *T. castaneum* section of healthy larval fat body. Heidenhain's haematoxylin shows albuminoid spheres. Clear spaces are lipid vacoules
3: *T. castaneum* section of infected larval fat body. Heidenhain's haematoxylin







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Primäre und induzierte Bewegungsstadien bei Osmiumsäurefixierung vorwärtsschwimmender Parameciен[1,2]

Primary and induced stages of movement after osmium-instantaneous-fixation of forward swimming *Paramecium*

Die Fixierungstechnik mit Osmiumsäure liefert für die Zwecke der Bewegungsanalyse cilienbesetzter Oberflächen gut erhaltene und färbetechnisch kontrastierbare Metachroniezustände (Gelei 1926, Párducz 1952, Grębecki 1964). Die bisherigen Erfolge der sog. Párducz-Methode auf dem Gebiet der Bewegungsphysiologie verschiedener Ciliaten beruhen in erster Linie auf einer qualitativen Bewertung des Fixierungsergebnisses (Literatur vgl. Párducz 1967). In den Hintergrund trat der früher stärker beachtete Umstand, daß die "Schnellfixierung" keineswegs alle Tiere momentan abtötet, sondern in größerem Umfang "physiologische Artefaktenbildungen" hervorgerufen werden (Párducz 1954). Diese Tatsache könnte aber der Angelpunkt einer Kontroverse über den Renormalisierungsprozeß bei der Fluchtreaktion von *Paramecium* sein (Párducz 1956, Grębecki 1956, Grębecki und Mikołajczyk 1968, Machemer 1969). Bei der Beurteilung eines Fixierungsergebnisses ist die Kenntnis der induzierten Bewegungsstadien in zweifacher Hinsicht von Wert: 1. Eine induzierte Schlagumkehr kann ein primäres Übergangsstadium beim Wechsel der Bewegungsrichtung vortäuschen; 2. quantitative Kriterien bei der Auswertung fixierter Stadien haben eine besser gesicherte Grundlage. In der vorliegenden Untersuchung wurden primäre und fixationsbedingte Stadien eines definierten Bewegungszustandes unterschieden und quantitativ ausgewertet.

Material und Methode

Paramecium multimicronucleatum aus Strohaufgußkulturen wurde in 1 mM $CaCl_2$-Lösung im Abstand von etwa 15 Stunden 2× geotaktisch gereinigt und konzentriert, dann zentrifugiert und erneut in 1 mM $CaCl_2$ verdünnt. Die Tiere schwammen in dieser Lösung fast ausnahmslos vorwärts.

Um den Häufigkeitsanteil der Fluchtreaktionen an den Bewegungen zu erfassen, wurde eine Probe makrographiert (Dryl 1961). In den photographisch

[1] Mit Unterstützung der Deutschen Forschungsgemeinschaft.
[2] Bernhard Rensch zum 70. Geburtstag.

aufgezeichneten Bewegungsspuren von 1800 Tieren fanden sich bei 1 sec Belichtung 45, bei 0.5 sec Belichtung 21 Fluchtreaktionen bzw. Umkehrungen.

Eine 0.5 ml *Paramecium*-Probe wurde in einer Blockschale mit der doppelten Menge Fixierlösung gemischt und nach Grębecki 1964 weiterbehandelt[3]. Beim Fixieren wurde beachtet, daß das OsO_4-$HgCl_2$-Gemisch zügig, aber nicht zu heftig, aus einer Spritze mit 2 mm Öffnung ausließen konnte. Die haematoxylingefärbten Präparate wurden äußerst vorsichtig in Alkohol entwässert, über Nacht in das Einbettungsmittel "Euparal grün" inkubiert und anschließend auf Objektträgern eingedeckt. Ohne Auswahl wurde ein Teil der Präparate quantitativ ausgewertet, d.h. jedes Stadium identifiziert und einer bestimmten Bewegungskategorie zugeordnet.

Verteilung der fixierten Bewegungsstadien

Bei der Einteilung der identifizierten Präparate sollten in erster Linie die primären Bewegungsstadien, d.h. normale Wellenmuster des Vorwärtsschwimmens, erfaßt werden. Ferner galt es, alle anderen Stadien in leicht unterscheidbare Untergruppen zu gliedern. Das Ergebnis zeigt die Tabelle 1.

Von insgesamt 467 untersuchten Präparaten trugen 21.6% normale, metachrone Wellenmuster. Bei einer weiteren, 17.9% umfassenden Gruppe war der Erhaltungsgrad des normalen Musters schlechter, jedoch nach den 3 Erkennungskriterien: Wellenverlauf, Form der regressiven Cilien und Cilienprofilbild (Machemer 1969) noch als Bewegungsstadium des Vorwärtsschwimmens zu identifizieren. Damit zeigten 39.5% der gefundenen Bewegungsstadien das vom primären Bewegungszustand her zu erwartende metachrone Muster. Bei 49.5% wurden verschieden weit fortgeschrittene Stadien der Schlagumkehr festgestellt. Diese Gruppe gliederte sich in etwa gleich große Anteile mit jeweils fortschreitender Schlagumkehr vom Vorderende bis zum Hinterende. Der Erhaltungsgrad restlicher metachroner Wellen blieb aus praktischen Gründen bei diesen Stadien unberücksichtigt. Eine vollständige Schlagumkehr war mit 7.3% relativ selten. Einige Präparate zeigten bei sonst allgemeiner Schlagumkehr Wellenmuster im Ventralbereich: bei 3.2% wurden Wellen des Vorwärtsschwimmens, bei 1.7% Wellen des Rückwärtsschwimmens festgestellt. Diese Muster erhielten getrennte Wertung, da nicht zu entscheiden war, ob ein Anfangsstadium der Schlagumkehr vorlag.

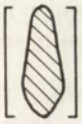
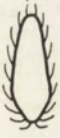
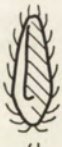
Schlüsse

Aus der makrographischen Lichtspuranalyse geht hervor, daß etwa 1% aller Tiere zu einem beliebigen Zeitpunkt Umkehrreaktionen ausführte, sofern man für diese Reaktionen eine Dauer von 0.5 sec veranschlagt. Demnach konnten primäre Stadien der Bewegungsumkehr das Fixationsergebnis kaum beeinflußt, keinesfalls aber hervorgebracht haben. Der große Anteil der fixierten Schlagumkehrstadien muß demnach auf induzierte, den Fixationsvorgang begleitende Umstände zurückgehen. Diese können nach Párducz 1951 1. auf der chemischen Reizwirkung und 2. auf rapiden Strömungserschei-

[3] Frau Hedy Hahn danke ich für sorgfältige technische Mitarbeit.

Tabelle 1

Häufigkeitsanteile verschiedener Bewegungsstadien nach der Fixierung vorwärtsschwimmender Paramecien

Stadium		Gefunden Anzahl	%	% identifizierte Stadien
	normale metachrone Wellen des Vorwärtsschwimmens	101	21.6	23.0
	Wellen des Vorwärtsschwimmens unvollständig erhalten, aber noch identifizierbar	84	17.9	19.1
	Zone der Schlagumkehr vom Vorderende bis zur Tiermitte	56	11.9	12.8
	Zone der Schlagumkehr unterhalb Tiermitte	66	14.1	15.0
	nur Caudalpol mit normalen Cilien	75	16.2	17.1
	vollständige Schlagumkehr, keine metachronen Wellen	34	7.3	7.7
	Wellen des Vorwärtsschwimmens ventral, sonst Schlagumkehr	15	3.2	3.4
	Wellen des Rückwärtsschwimmens ventral, sonst Schlagumkehr	8	1.7	1.8
Nicht zu identifizieren		28	6.0	

nungen beim Einfließen des Fixationsmittels beruhen. Eine Trennung beider Wirkungsmechanismen erscheint angesichts der variationsreichen Ausprägung der Schlagumkehr in den Präparaten nicht möglich.

Die Zahlenverhältnisse über die erhaltenen primären und induzierten Bewegungsstadien nach der Párducz-Fixation erlauben die allgemeine Feststellung, daß bei jeder Analyse schnellfixierter Ciliaten mit einem erheblichen Anteil von induzierten Bewegungsstadien gerechnet werden muß. Eine auf noch größerem Zahlenmaterial fußende und statistisch gesicherte Aussage würde im Einzelfall des Experiments wenig bedeuten, da zumindest die Begleitumstände der Fixierung — bisher — nicht normiert werden können. Als untere Grenze einer geeigneten, d.h. noch ausreichend "schnellen" Fixierung hat zu gelten, daß bei *Paramecium* die Trichocysten nicht oder in nur sehr geringem Umfang ausgestoßen wurden. Der Vorgang der Schlagumkehr läuft jedoch so schnell ab, daß offenbar eine vollkommene Momentanfixierung nicht zu erreichen ist.

Nach den vorliegenden Ergebnissen muß der Informationswert einer Párducz-Fixierung für die Beurteilung komplizierter Bewegungsabläufe in qualitativer wie in quantitativer Hinsicht etwas eingeschränkt werden. Dennoch erlauben die relativen Häufigkeiten erhaltener Metachroniestadien Rückschlüsse auf relative Häufigkeiten primärer Bewegungszustände (Machemer 1969). Umgekehrt müssen experimentelle Befunde, die sich ausschließlich auf metachroniefreie, fixierte Übergangsstadien gründen (Grębecki und Mikołajczyk 1968), als nicht ausreichend gesichert betrachtet werden.

Zusammenfassung

Die Osmiumsäure-Schnellfixierung von zu 99% vorwärtsschwimmenden Paramecien ergab, daß etwa 50% der Präparate fixationsinduzierte Schlagumkehrstadien zeigten. Bei etwa 40% der Präparate konnte das dem Vorwärtsschwimmen zugeordnete metachrone Wellenmuster identifiziert werden.

SUMMARY

Paramecia swimming forward at a rate of 99% were instantaneously fixed by osmic acid. Among the resulting preparations of individuals, 50% showed different stages of increasing ciliary reversal. The metachronal waves of forward swimming paramecia were identified in 40% of the preparations.

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