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Ordo *Thigmotricha* (*Ciliata — Holotricha*)

I

In the recent years the ciliated ordo *Thigmotricha* has atracted an increasing attention and interest for many reasons. Being a well established assembly of several families which are characterized by various adaptative changes, it may become a convenient material for the study of evolutionary trends in ciliates. Specific and deep-reaching transformations in the division and post-division reorganization processes enable to make interesting morphological and morphogenetical observations which contribute to elucidate the phylogenetic problems as well. At last — the strong morphological and physiological adaptations to the parasitic life allow to follow some interesting interdependence in the host--parasite ralations.

Realizing the advantages of the group under discussion and keeping in mind that the recent years added to its knowledge much interesting material, I approach my aim which was conceived years ago. I wish to summarize as far as possible our knowledge of *Thigmotricha* which have been the subject of my investigations for over 35 years. I wish to fulfill my purpose gradually, being compelled to carry on simultaneously all my other work and also for some editorial reasons. The introduction comprising a short outline of history of the investigations and a morpho-comparative characteristic of the order, will be followed by consecutive studies of separate families. The work will be concluded by remarks on the development and biology of *Thigmotricha* as well as by considerations on phylogeny, parasitism, ecology and chorology. Comparative juxtapositions are to orientate in the entire work and to facilitate the subsequent study of *Thigmotricha*.

I hope that this form of publication will only slightly delay my working out the whole problem and will give opportunity to my colleagues — as well as to the opponents — to express their views before the whole work is concluded.

The studies on ciliates, included presently to *Thigmotricha*, began over hundred years ago when Stein 1860 separated the genus *Ptychostomum*, Diesing 1866 — the genus *Hysterocineta*, and Quennerstedt 1867 described *Opalina mytili*, which was distinguished subsequently by Maupas 1883 as a new genus *Ancistrum*. Somewhat earlier, in 1838, Ehrenberg described a ciliate under the name *Leucophrys anodontae* which was placed by Stein 1861 in the new genus *Conchophthirus*.

Description of those species and genera cannot be recognized as the initia-

tion of the study on *Thigmotricha* as a systematic group. Nevertheless as an initial moment may be recognized the publication of a study in which the apparently remote forms were placed near one another for the first time, and their real relationship was ascertained on the ground of a morphological comparative analysis. Such publication is the dissertation of Issel 1903, in which the author associated such forms of the family *Ancistridae* as *Ancistrum* sp. sp., *Plagiospira* and *Boveria* indicating that they constitute links, or at least represent consecutive degrees, of the adaptive evolutionary process.

The subsequent publications containing some synthetic elements and a conscious investigation purpose are the works of Chatton et Lwoff, initiated by their publication in 1922 in which they established the order *Thigmotricha*, fusing in it *Ancistridae, Hypocomidae* (sensu lato) and *Sphenophryidae* considering that those families form a distinct and well grounded evolutionary trend. Chatton et Lwoff 1923 included a new family *Thigmophryidae* into *Thigmotricha* as an exit group to this order. Kahl 1934 included here *Conchophthiridae*, Raabe 1934, 1936 tries to show their link with other families. Raabe 1939, 1949 following the suggestions of Rossolimo 1925, includes here *Hysterocinetidae* (= *Ladidae*) as well.

No doubt, the crucial moment in the investigations on *Thigmotricha* was the publication of the monographic study of Chatton et Lwoff 1949—1950. This work announced for 25 years, was to elucidate many obscure points and ambiguities which appeared in the former publications of those authors. Unfortunately, this study analyzed in detailes only the families *Hemispeiridae, Ancistrocomidae, Hypocomidae* and *Sphenophryidae* leaving aside other families, and its general approach to problems is rather fragmentary and obviously not conclusive.

Subsequent studies — after the II world war — on the representatives of the order *Thigmotricha* were carried out by many authors. More general studies which formed continuous series and encroached upon the system and phylogenesis problems originate mostly of Cheissin 1931, Kozloff, Raabe and recently also of Fenchel. Fenchel 1965 attempted to give an outline of the phylogenetic tree of *Thigmotricha*.

In the considerations on *Thigmotricha* — similarly as on all the parasitic groups — arises inevitably the problem of their origin, their connection with the free-living groups which might be recognized as their exit groups.

Chatton et Lwoff in their first works devoted to *Thigmotricha* tried to find a form which might be accepted as an initial one, an exit form for this whole group. They had the well outlined evolutionary sequence in the families *Ancistridae* → *Ancistrocomidae* (formerly *Hypocomidae* s. l) → *Sphenophryidae*. It begins starts with the forms of a comparatively well developed general ciliature and goes through its reduction — only the thigmotactic ciliature being preserved — to the sedentary forms with an extremely reduced ciliature. Simultaneously occurred the reduction of the adoral ciliature and formation of the new mouth and at last — the adhesive surface. At the exit form of this evolutionary sequence Chatton et Lwoff 1926 recognized *Thigmophrya*, a form with a rich complete general ciliature, a thigmotactic ciliature non differentiated morphologically and — as they assumed — with no adoral kineties. *Thigmophrya* seemed to be the exit form — in the opinion of the authors — because it was supposed to resemble to the free living *Paramecium!*

This concept of Chatton et Lwoff 1926 was accepted with no reservation and discussion as a working opinion by Raabe 1936, 1949 and by Corliss 1961 as well as by the other authors.

Presently the anylysis of the extensive *Thigmotricha* material does not permit to keep it valid for many reasons. The suggestions of Chatton et Lwoff as to the link of *Thigmotricha* and *Paramecium* might be omitted since in the meantime *Paramecium* proved to be a ciliate highly specialized, with an adoral ciliature which is shaped specifically and in a different manner. Therefore *Paramecium* cannot be considered even as a model of a free-living exit form of *Thigmotricha*. However there are some more essential arguments:

1. The evolutionary paths which may be followed or imagined among *Thigmotricha* seem to indicate rather a tendency to shortening, rolling, or to reduction of the adoral kineties which were initially long. (It is seen well in *Hemispeiridae — Ancistrinae —* Raabe 1959). Consequently in the exit form should be anticipated the presence of long adoral rows running meridionally and not too well differentiated from the kineties of the general ciliature.

2. As it seems, the primitive forms of *Ancistrinae* — as before all *Ancistrumina or Ancistrum* — cleary approach the free-living forms of the features of *Cyclidium* or *Pleuronema* or at any rate of *Pleuronematidae*.

3. *Thigmophrya* however, as indicated by the studies of Fenchel 1964, has adoral rows highly reduced, more than it occurs in *Conchophthirus*.

It seems therefore justified — which is stressed by many authors and recently by Fenchel 1965 — that the ancestors of *Thigmotricha* should be looked for among the forms reminding of the presently living *Pleuronematidae*. Consequently the more primitive *Ancistrinae* i.e. *Ancistrum* or *Ancistrumina* should be accepted as the most plesiomorphic forms among *Thigmotricha*.

The way of development of those forms either towards *Boveria,* or to *Hemispeira,* or towards *Ancistrocomidae* and at last to *Sphenophryidae* seems to be clear and well motivated e.g. by Chatton et Lwoff 1949, 1950. Some difficulty may be found in tracing the origin of the forms abundantly ciliated as some *Ancistrinae, Conchophthiridae, Hysterocinetidae* and namely *Thigmophryidae* — from the forms of the *Ancistrumina* or *Ancistrum* type.

I assume — which will be discussed later more in detail — that the evolutionary paths of those families passed through the polymerization of the kineties of the general ciliature i.e. by its densification. All those families preserved well the general character of *Thigmotricha*: the lateral flattening of the body, the presence of the thigmotactic area in the left anterior body part, location of mouth on the ventral margin with a tendency of twisting the adoral kineties and shifting the buccal aperture backwards.

A similar evolutionary path might account for the origin of the group represented by the genus *Protanoplophrya* which has been recently joined to *Thigmotricha* (Corliss 1961) and perhaps, leads to *Astomata*. The paths to *Astomata* may possibly lead trough *Hysterocinetidae* or — perhaps — trough *Conchophthiridae* as well. These problems which have been discussed by many authors' will be considered again in this study.

The position of *Hypocomidae* s. str. (after exclusion of *Ancistrocomidae*) seems not to be clear. In spite of the effords of Chatton et Lwoff 1950, the structure of *Hypocomidae* seems to approach them rather to *Chlamydodontidae* or perhaps to *Apostomea* than to *Thigmotricha*. This problem needs further investigation.

According to the present state of our knowledge summarized in part in the taxonomic aspect by Corliss 1961, to the order *Thigmotricha* the following families are included:

Fam. *Hemispeiridae* König, 1894

Fam. *Thigmocomidae* Kazubski, 1958 pro *Thigmocoma acuminata* Kazubski, 1958

Fam. *Ancistrocomidae* Chatton et Lwoff, 1939

Fam. *Sphenophryidae* Chatton et Lwoff, 1921

Fam. *Hypocomidae* Bütschli, 1889, emend. Chatton et Lwoff, 1939 (?)

Fam. *Conchophthiridae* Kahl, 1931, 1934

Fam. *Thigmophryidae* Chatton et Lwoff, 1923

Fam. *Peniculistomatidae* Fenchel, 1965 — pro *Peniculistoma mytili* (De Morgan) Jankowski, 1964

Fam. *Hysterocinetidae* Diesing, 1866

Those families embrace presently over 50 genera, and 150 species.

For orientation in the similitudes and differences of those families, their most characteristic representatives are presented in Fig. 1.

General feature and orientation of the body

The great differentiation and many-sided specialization of the general architecture of the *Thigmotricha* body (Fig. 1) may evoke doubt whether is would be possible to trace a general type of their structure and a general manner of their body orientation. The opinions of the authors are especially controversive as to the orientation of the body even of their typical and only slightly modified representatives. The body side determined by some authors as the ventral one, is considered as one of the lateral by the others. There are even differences in the considerations concerning the kinetic or morphological anterior or posterior body end (the earlier and recent publications of Chatton et Lwoff).

I wish to remind the way of orientation applied by me for years (Raabe 1936, 1949, 1959) in my studies on *Hemispeiridae, Conchophthiridae, Hysterocinetidae* and others.

Considerations on this subject should begin by the analysis of the structure of forms which must be recognized as most plesiomorphic among ciliates, namely the *Gymnostomata — Prostomata* with a nearly axial symmetry and a cytostome located on the anterior body pole (apex), which constitutes also the point of confluence of undifferentiated meridional kineties. The situation becomes disturbed when the cytostome starts its backward and sideway migration, which occurs commonly. Then the apical complex of kineties may shift together with the cytostome which results in the asymmetry of their pattern and in a situation represented e.g. by *Gymnostomata — Hypostomata* and by some *Trichostomata*.

In *Hymenostomata* (as well as in *Thigmotricha*) occurs a shifting of the cytostome not together with the ends of kineties but between the kineties, along a line which constitutes the prolongation of the anterior suture of the kineties which is transformed into a linear (falx) from a point structure (apex) Just secondarily some kineties, the nearest to the cytostome, may be involved into its service. As a rule those are the adoral kineties situated on the right of cytostome (Fig. 2). In this situation the body side or its margin or more exactly the "body meridian" along which shifts the cytostome, should be accepted as the ventral one. The opposite margin is consequently the dorsal one and the division of the body into two lateral parts

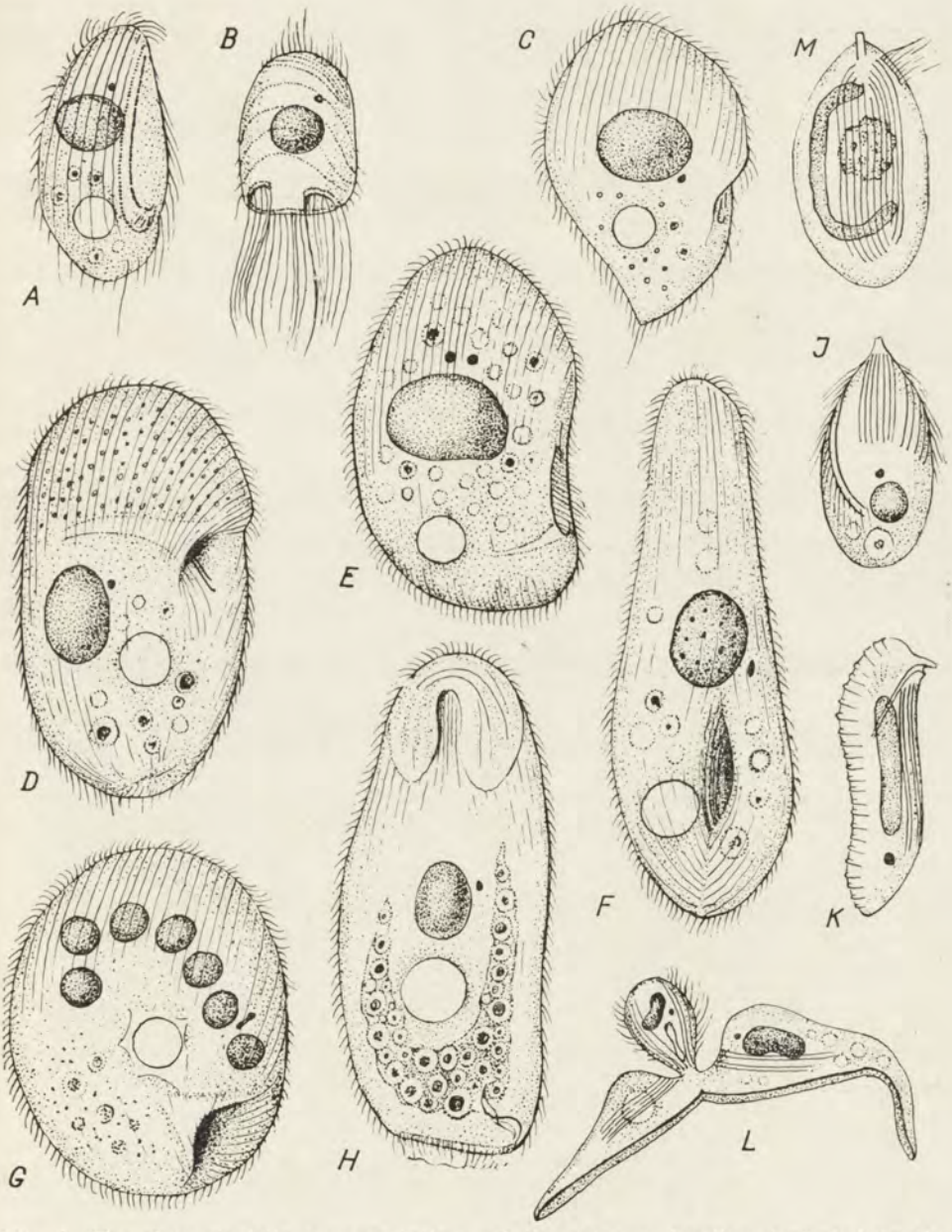

Fig. 1. The characteristic representatives of the various families included to the order *Thigmotricha*: A — *Ancistrumina* (*Hemispeiridae*, *Ancistrinae*), B — *Hemispeira* (*Hemispeiridae*, *Hemispeirinae*), C — *Thigmocoma* (*Thigmocomidae*), D — *Conchophthirus* (*Conchophthiridae*), E — *Peniculistoma* (*Peniculistomatidae*), F — *Thigmophrya* (*Thigmophryidae*), G — *Myxophyllum* (*Thigmophryidae*), H — *Hysterocineta* (*Hysterocinetidae*), J — *Raabella* (*Ancistrocomidae*), K — *Gargarius* (*Sphenophryidae*), L — *Sphenophrya* (*Sphenophryidae*), M — *Hypocoma* (*Hypocomidae*). After various authors

is indicated by: the anterior suture, the "meridian" with the cytostome and the posterior suture. This division corresponds to the division of the system of kineties into the left and right parts.

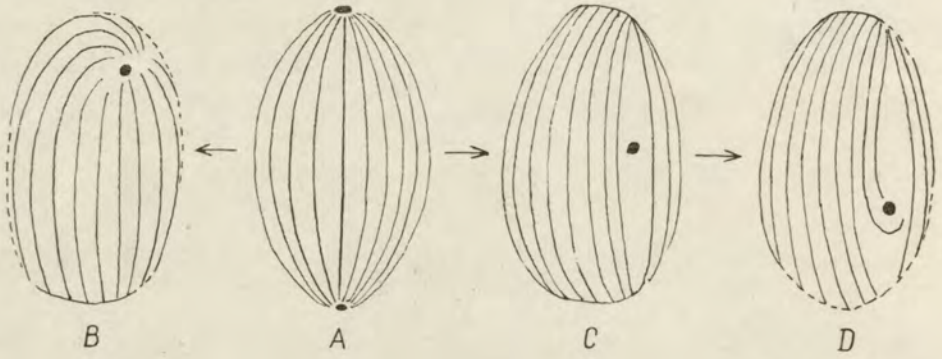

Fig. 2. Scheme of the shifting of the cytostome and of the kineties in *Ciliata*: A — *Gymnostomata* — *Prostomata*, B — *Gymnostomata* — *Hypostomata*, shifting of cytostome and apex, C — others *Holotricha*, shifting of cytostome along the oral meridian, D — separation of the adoral kineties. Oryg.

As to *Thigmotricha*, the structure of more plesiomorphic forms should be considered and interpreted. Those are the more simple *Ancistrinae* and the other *Hemispeiridae* with a similar structural pattern as well as *Conchophthiridae* or *Thigmocomidae*.

The body of those organisms (Fig. 3) is moderately elongated, of an ovoid outline, usually flattened, which allows to discern two relatively flat body sides and two rather more narrow margins. Along one of those margins or

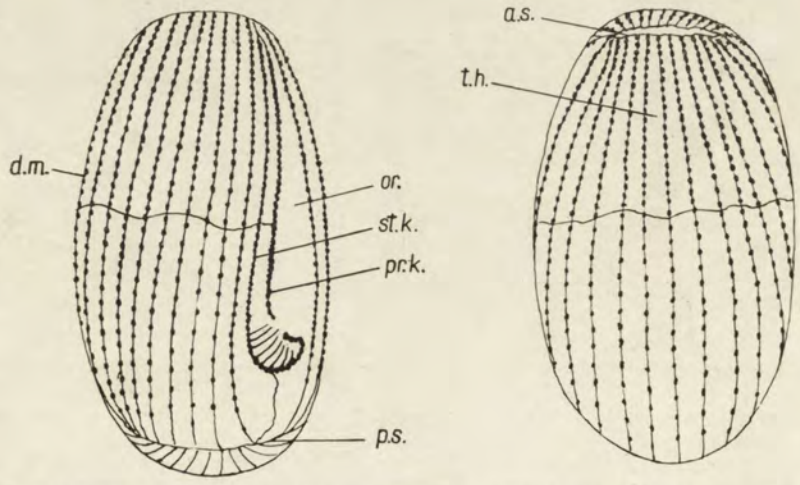

Fig. 3. Theoretical exit form of *Thigmotricha* — architectonic and orientation of the body, right and left body sides; *th* — thigmotactic area, *st. k* — stomatogenic kinety, *pr. k* — prostomal kinety, *d. m* —dorsal margin, *a. s* — anterior suture, *p. s* — posterior suture, *or* — nacked oral field. Oryg.

near it, run two, initially long, adoral kineties which form a loop around the cytostome in their posterior part. So this margin may be looked upon as the ventral one, whereas the opposite — as the dorsal, and the flattened body sides — as the left and right. One of the body ends namely this one on which the adoral kineties begin, and by which the ciliate moves foreward — is the anterior end. The posterior body end is the opposite one, the adoral kineties tend to reach it on their way to cytostome. The thigmotactic area lies in the anterior part of the left body side, the buccal apparatus tends to shift to the right side.

The disposition of kineties support very well and distinctly this orientation. In classical cases, kineties run nearly along the whole body: from its anterior pole or margin — as far as to the posterior one. In the anterior part, they are joined by the anterior suture which consists of one or two fibres which run parallel to the anterior body margin (sometimes with a certain shift to its left side). This suture is reached from both sides by the anterior ends of the kineties of the right and left body sides and in some more primitive cases also the adoral kineties. In the posterior end of the body, the kineties are joint by the posterior suture which has a form of fibril or a fibrillar netwark and is running parallel to the posterior body margin, sometimes shifted to the right side of the body. The posterior, abapical ends of the kineties of both body sides reach the posterior suture. The adoral kineties are here an exception: they twist round the peristome at a distance before the posterior body end.

Consequently the ventral area (which is naked except the zone of adoral kineties), the anterior and posterior sutures, as well as the dorsal body margin separate the right and left part of the ciliary system which correspond in the initial model to the right and left side of the body. Nevertheless the boundary of the left and right part of the ciliary system may undergo some shifting which is sometimes rather considerable. As a result, the left and right body side may correspond not exactly to the left and right parts of the kineties system.

The development of *Thigmotricha* followed several trends modifying the topographical picture of the structure scheme and body orientation which were discussed above as an exit situation.

Besides the plesiomorphic *Hemisperidae*, well correspond to the representatives of the families with an abundant ciliature as *Conchophthiridae*, or *Thigmophryidae*, *Hysterocinetidae* and even *Protanoplophrya* but even here various modifications may occur (Fig. 1).

Conchophthiridae have the body distinctly flattened: the left and right side of the ciliary system correspond to the left and right body side. In the representatives of the genus *Conchophthirus* occurs a distinct modification increasing the symmetry of the body. It concerns a strong shortening of the adoral kineties and their penetration into the peristomal funnel. The nearest to the cytostome kineties of the right body side i.e. kineties 2,3,4, etc. encroach into the peristomal funnel as well. This was namely the reason why many authors accepted the right side of the *Conchophthirus* body as the ventral one (basing on the presence of the mouth on it), and the left side as the dorsal one, neglecting the initial orientation established as well by the body shape as by the kineties system. Similar situation is in *Thigmophrya* (although its body is rather tapering) as in the other *Thigmophryidae* (*Conchophyllum*, *Myxophyllum*).

Hysterocinetidae show more accentuated asymmetry by a high and specific

development of the thigmotactic apparatus. However the pattern of the adoral kineties and of the anterior suture being the anterior margin of the sucker, permits to apply to it the same orientation (R a a b e 1939, 1949) and to recognize the side with the sucker as the left body side. In spite of considerable modifications in structure, the same may be applied to *Protanoplophrya*: its mouth lies on the ventral margin and separates two parts of the ciliary system and two body sides which are even more symmetric than in the other groups. In *Hysterocinetidae* occurred a process of shifting of the adoral kineties to a position parallel to the posterior body margin. In this way a situation arose in which the adoral kineties are in a vertical position to the kineties of the general ciliature (Fig. 1).

Similar situation as in *Ancistrinae* exists in *Thigmocomidae* in spite of their high modification in the ciliary apparatus as well as in *Peniculistomatidae* although their phylogenetic relations seem to be different than in *Thigmocomidae*.

The scheme presented above becomes distinctly complicated in the family *Hemispeiridae*, particularly in more specialized representatives of the subfamily *Ancistrinae* (*Proboveria* and *Boveria*) and *Hemisperinae* (*Plagiospira*, *Cheissinia*, *Hemispeira*). In those two evolutionary rows, the processes of retrogradation and spiralization of adoral kineties make a considerable progress till

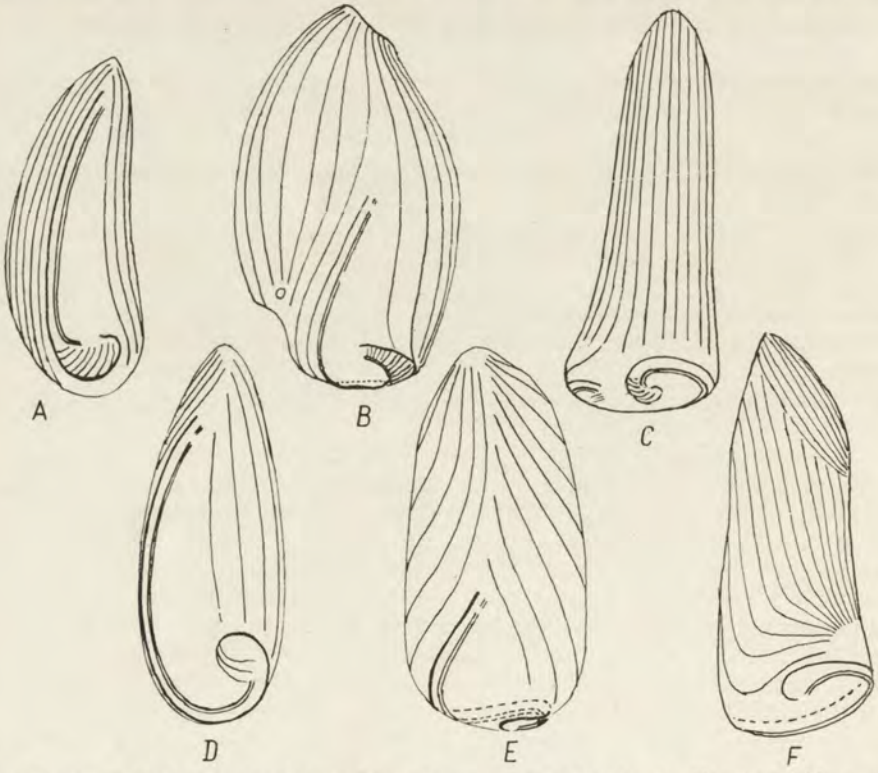

Fig. 4. Retrogradation and spiralization of the adoral kineties in *Hemispeiridae*: A — *Ancistrumina*, B — *Proboveria*, C — *Boveria*, D — *Ancistrospira*, E — *Plagiospira*, F — *Cheissinia*

the kineties are located around the posterior broadened body pole (Fig. 4). The trace of retrogradation of kineties i.e. the space between the kineties 2 and *n* still indicates the ventral margin of the body although in *Hemisperidae* the thigmotactic area occupies rather dorsal than ventral position. In extreme cases (*Hemispeira*), this area shifts completely to the body apex which produces its quite different architectonic and is even connected with its different orientation in relation to the substrate: the ciliate stands as if "upside down". A cone-shaped form arises of a nearly axial symmetry!

Already in the primitive *Ancistrinae* on the anterior body end appears a rather sharp, slightly bent protrusion called by Chatton et Lwoff "bouton adhesif". Those authors affiliate the adhesive-sucking apparatus of *Ancistrocomidae* their "suçoir" with this "bouton" which seems quite correct. At any rate in the representatives of this family appears a new apparatus for taking food from the host's body instead of the former cytostome which is pushed towards the posterior body region and becomes atrophied. In this way the anterior body pole becomes secondarily the oral pole, the position of the mouth ceases to help in orientation of the body, it fails to define its ventral side. Only the thigmotactic part of ciliature, preserved in all the forms, may indicate the left body side (or perhaps the dorsal one, as reported by Chatton et Lwoff 1950), although physiologically it is the ventral side, since it adheres to the substrate. The recognition of the thigmotactic surface of *Ancistroocomidae* as the left body side would support the view trat some two differentiated kineties which occur in some *Ancistrocomidae* e.g. *Hypocomides*, would be the remnant of the adoral kineties consequently lying — at least in their initial course — on the ventral body margin (Fig.5A).

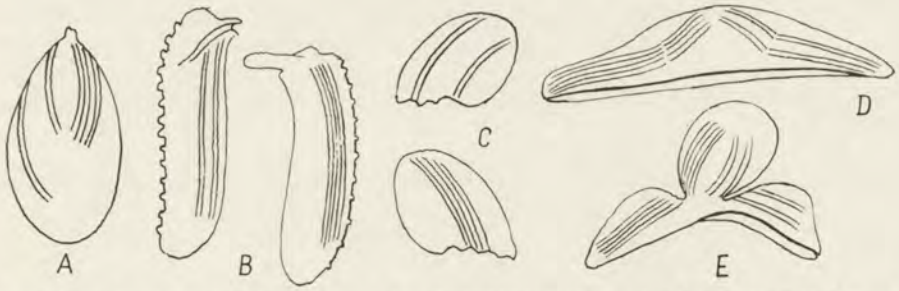

Fig. 5. The topographical relations in *Ancistrocomidae* and *Sphenophryidae*: A — *Hypocomatidium*, B — *Gargarius*, C — *Pelecyophrya*, D — *Sphenophrya*, E — budding *Sphenophrya*

However in the subsequent phylogenetic development which leads from *Ancistrocomidae* to *Sphenophryidae*, another reversion of the topographical interrelations occurs which still complicates the orientation of the body (Fig. 5). Only *Gargarius* has a structure resembling to *Ancistrocomidae* with its banana-shaped body. Its suçoir however is oriented obliquely or even vertically to the body axis, towards the thigmotactic area which makes this side functionally the ventral one. But the folds on te opposite side seem to perform an adhesive role too.

The architectonic of the evolutionary path represented by *Pelecyophrya*, *Lwoffia* and at last *Sphenophrya* presents a different problem. The tomits of all

those forms remind vividly *Ancistrocomidae* and before all *Hypocomatidium sphaerii* Jarocki et Raabe (Raabe 1949, Dobrzańska 1961), even by the pattern of their thigmotactic kineties, which are divided into two groups: on one side 2+2 (or 3), on the other 5—6 kineties. They show the same pattern in *Pelecyophrya* and *Lwoffia* on both sides of their flattened body. In the representatives of the genus *Sphenophrya* they are however all on one side. Both assemblies of the kineties unite in the convex body apex and diverge at its base (foot or sole) to both sides. A new apparatus for taking food from the substrate arises in the form of sole — especially in *Sphenophrya*. The secondary sucking apparatus suçoir — disappears. Chatton et Lwoff believe that the adhesive area arises of this suçoir by means of some dislocations, and this serves them for determination of the body sides of the elongated trophic form of *Sphenophrya dosiniae* Chatton et Lwoff. The processes of transition of the tomit into the trophont occur in a different way in separate representatives of the family *Sphenophryidae* and even in different species of the genus *Sphenophrya* (Raabe 1949), so that even the body architectonic may be interpreted in different way. Surely the problem is complicated and needs further study and a special discussion which will be done in the chapter dealing with the family *Sphenophryidae*.

It should be remarked that the body orientation of the sedentary forms in general is not a simple and easy problem. As example may serve the difficulties in the correct orientation of the body of *Peritricha* and in establishing homology with the other ciliates, and among *Holotricha* — the orientation of trophonts body of *Chonotricha* as related to *Gymnostomata* — *Hypostomata* (Dobrzańska-Kaczanowska 1963), or orientation of the trophont of *Conidophryidae* (Chatton et Lwoff 1936).

To the problems of general morphology and architectonic of the body belongs at last the question of spiralization of organisms or of some elements of their structure as well as of direction of this spiralization. This problem is of a special importance on account of the meaning of the spiralization direction of the cortical elements for the systematics of ciliates and for some phylogenetic conclusions bound with this problem.

Spiralization of the kineties in ciliates concerns in some cases their whole system i.e. it is the spiralization of all the kineties of the general ciliature. This is the case in *Heterotricha* as in numerous *Apostomea* (Chatton et Lwoff 1935). More frequently spiralization concerns only the adoral zone, without effect on the general ciliature. This phenomenon occurs among numerous *Holotricha*, is more or less characteristic for all the *Spirotricha* (except *Entodiniomorpha* which should be perhaps not included here) and — although in another relation — for all the *Peritricha*.

In *Thigmotricha* the spiralization concerns essentially only the adoral kineties which are generally — as a rule — twisted to the left in their terminal cytostomal ends. The parts of the adoral kineties which encroach into the peristome — as it takes place in *Hysterocinetidae* — are inside of it twisted and run on around ist walls. In *Hemispeiridae* (*Ancistrinae* and *Hemispeirinae*) an inclination to retrogradation and spiralization of adoral kineties exists till they occupy their place at the posterior body pole. In *Boveria* the spiral embraces more than 360°, in *Hemispeira* — scarcely over 180°. Among *Ancistrinae* a certain influence of the spiralization of the adoral kineties upon the neighbouring kineties of the general ciliature is marked. It concerns the kinety 2 before all, whereas the others keep their meridional position. In *Hemispeira*,

all the kineties of the general ciliature (much reduced in number) take a nearly parallel arrangment around the cone-shaped body. This is connected with the displacement of the adoral spiral to the posterior body pole and of the thigmotactic area to the anterior one.

In all the cases in *Thigmotricha,* the spiralization of the adoral kineties is always sinistral (anti-clockwise). In those cases when the adoral spiral is localized around the posterior body pole (as e.g. in *Boveria*), it is clear that it is involutive and adapical i.e. rolled up towards the middle of the pole area. As its beginning we accept the place which corresponds to the former union of the adoral kineties with the anterior suture, whereas its end — the place of location of the cytostome.

This situation deserves being stressed considering some concepts which trace the *Peritricha* from forms near to *Boveria.* (Fauré-Frémiet 1950, Corliss 1956). Raabe 1964 rejects this possibility because of a complete dissimilitude of *Peritricha* and of inadequacy of deriving an extensive and mostly free-living group of a narrowly specialized parasitic ancestor. As to the rotation of the spiral, Raabe stresses that it is in *Peritricha* sinistral, but is evolutive and abapical i.e. it untwists from the body pole. This problem will be discussed again with the phylogenetic problems of *Thigmotricha.*

General ciliature

I am inclined to accept the term of Chatton et Lwoff "ciliature générale" for the locomotoric ciliature covering initially the major part of the ciliate body, replacing by it the former term: "somatic ciliature", since the whole ciliature belongs to the somatic system in general and in *Thigmotricha* as well. As the "general ciliature" I consider the whole initial ciliatures, from which differentiate the secondary ones: the adoral ciliature which serves for driving food to cytostome, and eventually, the thigmotactic ciliature performing rather the function of adhesion but never postponding the locomotoric functions especially when it remains the only ciliature.

Among *Thigmotricha* occur groups (families) with a very dense general ciliature (*Conchophthiridae, Thigmophryidae, Hysterocinetidae, Protanoplohprya*), groups with a ciliature of a moderate density (the majority of *Hemispeiridae, Thigmocomidae*) and groups of a scarce general ciliature, in extreme cases with its entire reduction (part of *Hemispeiridae, Ancistrocomidae* and at last *Sphenophryidae*). Which one of those types of general ciliature should be recognized as the exit form for *Thigmotricha?* Should *Thigmophrya* be accepted as the exit form — as it was suggested by Chatton et Lwoff — just because of their abundant general ciliature, and their thigmotactic ciliature being not distinctly differentiated and which proved to be not correct lack of adoral kineties? Where should be placed the families of a abundant ciliature in the course of the phylogenetic tree of *Thigmotricha,* if as exit forms have been accepted forms like *Ancistrumina,* i.e. forms with a rather scarce ciliature similarly as *Pleuronematidae?*

The essential difficulty in considerations of those problems is involved by the general habit — as it seems not quite justified — to look in the evolution of ciliates and especially of their parasitic forms including *Thigmotricha,* for manifestation of reduction of kineties and kinetosomes (Chatton et Lwoff 1949, p. 238). The possibility of evolution by the increase of the number of

kineties is usually not accepted. It is postulated without discussion that the primitive forms had a very abundant ciliature and — which is rather correct — their ciliature was uniform and undifferentiated.

The evolution by polymerization of organs and multiplication of their number is however not only rare but even more common. Its importance was put forward by Dogiel 1929, and was pointed out by Raabe 1964, connecting it with the system of undulipodia, with the nuclear apparatus and with other systems. The phenomenon of polymerization of kineties occurs in *Protozoa* not so rarely and is manifested as well in their ontogenesis as in phylogenesis. No doubt it is distinct in the development of the trophont in *Opalina* where kineties multiply their number (from the side of falx or beyond it). In ciliates it occurs clearly in *Ichthyophthirius multifiliis* Foqué in the process of transition of tomits (with 43 kineties) into the trophic form (with 2040 kineties — Muggard 1947). It could be postulated that the process of ontogenesis in these cases — and at least in the case of *Ichthyophthirius* — is the recapitulation of the former parallel phylogenetic process.

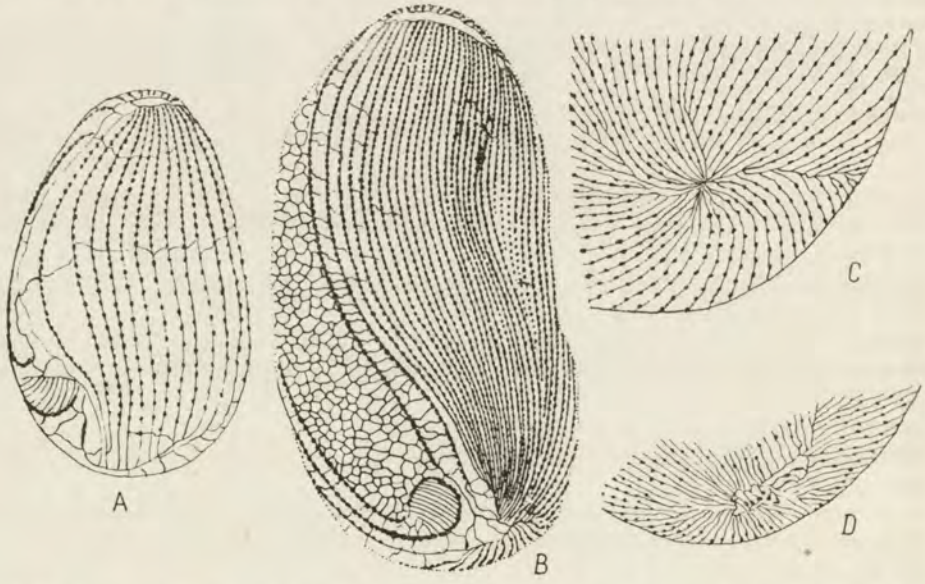

Fig. 6. Polymerization of kineties of the general ciliature in *Thigmotricha*: A — *Ancistrumina limnica* (Raabe), B — *Ancistrum mytili* (Quen.), C — the posterior suture in *Conchophthirus anodontae* (Stein) and D — in *C. unionis* Raabe, From Raabe

In *Thigmotricha,* the first manifestation of such a polymerization process would occur in *Hemispeiridae — Ancistrinae.* Here besides the forms accepted by me as the exit ones with a comparatively small number of kineties as e.g. *Ancistrumina,* appear some with a much higher number of kineties as *Ancistrum mytili* (Quen.) or *Protophrya* (Fig. 6 A, B). I consider these forms as representing the secondary increase of the number of kineties (polymerization) when compared to the exit forms nearer *Cyclidium* as *Ancistrumina.* A certain supplementary argument in favor of the primitivity of *Ancistrumina* may be the fact that the species of the genus *Ancistrum* (sensu meo), *Protophrya* or *Protophryopsis* are highly specific with regard to their hosts whereas the species of the genus *Ancistrumina,* as *A. limnica* (Raabe), *A. cyclidioides* (Issel) or *A. ovata*

(Cheissin), have a very broad range of hosts. So e.g. *A. limnica* occurs in many *Gastropoda* and *Unionidae* and not only on their gills or in mantle cavity but in the intestine as well. It might — in may opinion — speak in favor of the primitivity of *Ancistrumina*.

It seems worth acceptation that the polymerization process of kineties occurred in *Thigmotricha* as well, causing in effect a more dense ciliary coating of their body than it was in the exit forms. Such a dense coating of the body (besides the already mentioned *Hemispeiridae—Ancistrinae*) occurs also in *Conchophthiridae, Thigmophryidae* and *Hysterocinetidae* as well as in *Protanoplophrya*. They all are specialized groups embracing species of a rather high specifity concerning their hosts.

It is a striking but comprehensible fact that the polymerization of kineties is accompanied by the increase of the body dimensions. The species included by me into the genus *Ancistrum* (R a a b e 1959), have a much higher number of kineties as well as much considerable dimensions when compared with those which were included by me to the genus *Ancistrumina*. In a certain degree an inclination seems to be observed to retain the proportion of the number of kineties and the body width i.e. to retain similar distances between the kineties (R a a b e 1959). However in the organisms distinctly bigger i.e. *Thigmophryidae, Conchophthiridae* or *Hysterocinetidae*, the disposition of kineties becomes distinctly more dense and the distances between them diminish. This process is accompanied by densification of kinetosomes in kineties and appearance of general ciliature composed of short cilia. A general regularity deserves to be stressed: in places where kineties approach too much one to another as a result of the body shape, or they crowd together, the distribution of kinetosomes becomes more rarified, the number of kineties is reduced and confluent systems arise as it takes place in *Conchophthirus* in the place where kineties reach the posterior suture (Fig. 6 C).

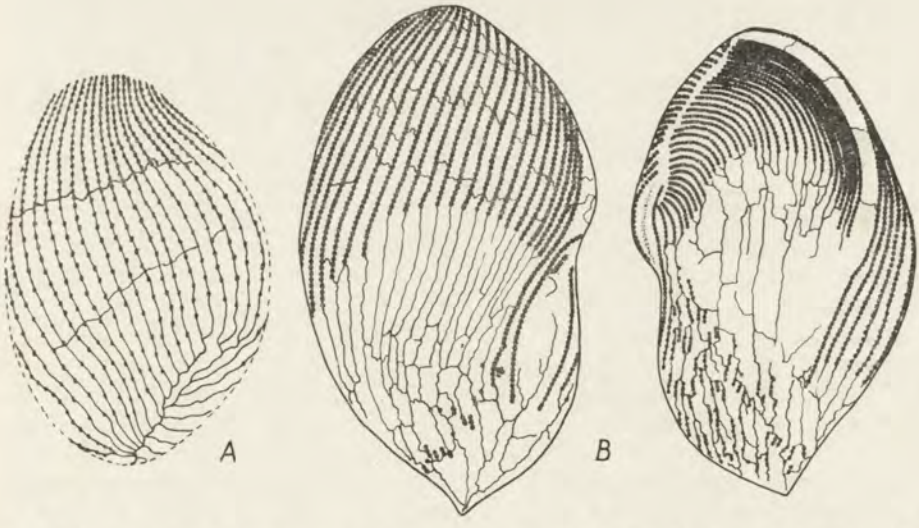

Fig. 7. Disposition of kinetosomes in kineties and their rarefaction in the posterior part of the body: A — *Ancistrumina*, B — *Thigmocoma*. From R a a b e and K a z u b s k i

Begining with the exit forms — as their model may serve *Ancistrumina* — two tendencies of the development of the general ciliature may be observed in *Thigmotricha*. One of them is the multiplication of the kineties leading to forms with a dense ciliature, the second one is the reduction of kineties leading over some *Hemispeiridae* to *Ancistrocomidae* and *Sphenophryidae*.

Fig. 8. The joining fibrils in *Thigmotricha*: A — *Ancistrumina limnica* (Raabe), B — *Ancistrum mytili* (Quen.), C — *Hypocomatidium sphaerii* Jar. Raabe, D — acetabule in *Hysterocineta cheissini* Raabe. From Raabe

Independently of the changes in the general ciliature (and some other changes in the ciliture), its system in *Hemisperidae, Thigmocomidae, Conchophthiridae, Hysterocinetidae* and mostly in *Thigmophryidae*, as well as in *Protanoplophrya* retains its common patern of structure (see the preceding chapter). The kineties of the general ciliature run from the anterior suture which corresponds to the anterior body margin, backwards to the posterior suture, which corresponds approximately to the posterior body margin. The anterior suture consists of one or two fibrils, the posterior one — rather of a fibrillar network. On the ventral margin of the kinety of the general ciliature, spaces arise in which the adoral kineties are located.

In the pattern of the kineties of the general ciliature, more or less distinct tendencies appear to a more loose disposition of their kinetosomes towards the posterior body end (Fig. 7). This tendency is distinct in *Hemispeiridae, Conchophthiridae, Hysterocinetidae* and being most striking in *Thigmocomidae*. Deviation of this regularity concerns only the first and last kineties of the general ciliature i.e. the kineties next to the adoral ones and the nacked peristomal area. This tendency is only slightly marked in *Thigmophryidae* and *Protanoplophrya*.

Besides the anterior and posterior suture, kineties are connected by some additional transverse fibrils — commissures. In *Ancistrumina* it is most frequently one fibril embracing the body in the equatorial plane, and sometimes are short additionary fibrils which join a few of neighbouring kineties. In *Ancistrum mytili* (Quen.), there are numerous short fibrils joining groups of kineties. A similar situation exists in *Conchophthiridae, Hysterocinetidae* and in *Protanoplophrya*. In the last ciliate the kineties are usually in fragments. On the territory of the naked peristomal area those fibrils bind the adoral kineties with the general ciliature. In some case e.g. in *Ancistrum* they form a dense network (Fig. 8).

It is interesting that those transverse fibrils or the fibrillar network appear in division in the place of disruption of kineties between the prother and opisthe, and persist till the full separation of fragments of kineties. The network of such fibrils joins the fragments of kineties in the place of injury (Raabe 1934). In the process of reduction of the general ciliature, the areas arise which are free of it. They become covered by a more or less dense and regular network of fibrils. When the ciliature atrophies on a larger area, a regular network of small meshes appears as it takes place in *Ancistrocomidae* and *Sphenophryidae* or on the acetabule of *Hysterocinetidae* (Fig. 8).

The elements belonging to the general ciliature but differentiated from it both topographically and functionally — are the parts of ciliature engaged secondarily into the function of the food-taking apparatus. Nearly in all the *Hemispeiridae* some kineties behave in a somewhat different way than the whole of the general ciliature. These are kineties nearest the stomatogenic kinety to the right, (the kinety 2 according Chatton et Lwoff) and often also the last kineties adjoining the adoral area on the left side i.e. the kineties n and $n-1$. Kinetosomes of those kineties of their posterior parts too are more dense than on the other kineties of the general ciliature and their cilia are sometimes more strong and collaborate with the cilia of the adoral kineties. This concerns mostly the kinety 2 which accompanies the spiralization of adoral kineties even in *Proboveria* and *Boveria* which belong to *Ancistrinae* whereas in *Hemispeirinae* it is not differentiated of the remaining kineties of the general ciliature. The extreme case of engaging the kineties of the general ciliature nearest the peristomal area into the function of the mouth, are the conditions described by MacLennan et Connell 1931 in *Eupoterion pernix*. In this species, the kineties 2 and 3 form an additional loop besides the loop of the adoral kineties, and the kineties n and $n-1$ are shortened and densely covered with kinetosomes (Fig. 9).

Nevertheless more characteristic is the formation by some groups of the kineties of the general ciliature of the persitomal infundibulum, in a manner which corresponds to the phenomena occurring in typical *Trichostomata* (Fig. 9). Such a ciliated infundibulum is in *Conchophthiridae*, or exactly in *Conchophthirus*,

and in *Thigmophryidae*. In the representatives of the genus *Conchophthirus* this phenomenon occurs in variable intensity: the ciliature of infundibulum is formed by several kineties of the left part of ciliature. They encroach from behind to the infundibulum, describe its walls and penetrate outside backwards. They produce a more or less distinct eaves over the anterior part of peristome. In *Myxophyllum* those are also kineties of the left part of ciliature, which encroach upon the plate of infundibulum, run over its walls and continue subsequently on the body surface, till they reach the anterior suture (R a a b e 1936). In *Thigmophrya* (R a a b e 1936, F e n c h e l 1965) those are kineties belonging to the left part of the system and behaving similarly as in *Myxophyllum* i.e. they continue their course from the posterior to the anterior suture. It is very characteristic that in all the forms which have a ciliated infundibulum, the adoral kineties are small, highly reduced and concealed in the estuary of the peristomal funnel; in *Myxophyllum* they are possibly atrophied. All those forms have a dense and abundant general ciliature.

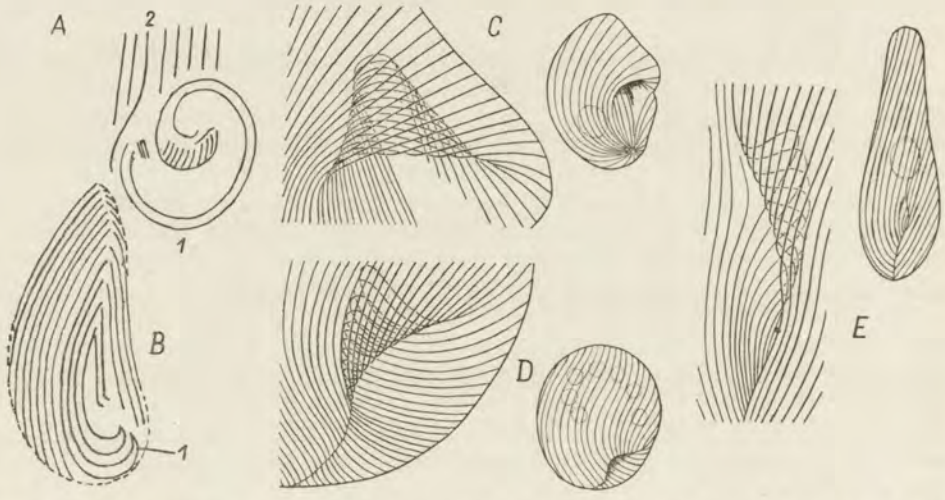

Fig. 9. The kineties of the general ciliature angaged into the service of the mouth: A — kinety 2 accompanies the adoral kineties in *Boveria subcylindrica* Stev., B — additional kineties in *Eupoterion pernix* MacLennan and Connell, C — infundibulum in *Conchophthirus anodontae* (Stein), D — in *Myxophyllum steenstrupi* (Stein), E — in *Thigmophrya macomae* Ch. Lw. After Chatton et Lwoff, MacLennan and Connell, and from Raabe

The general ciliature disappears or at least tends to disappear in *Ancistrocomidae* and *Sphenophryidae*. It may be accepted after C h a t t o n et L w o f f 1949 that in such forms as *Ancistrocoma, Holocoma* or *Hypocomagalma,* it remains besides the thigmotactic ciliature so that nearly the whole body is covered with cilia. Exception is made for an elongated naked field, which corresponds (in my interpretation) to the naked peristomal area of *Ancistrinae*. The nearly full ciliature of *Goniocoma macomae* (Chatton et Lwoff) should be interpreted separately. Here the relations are exactly inverse as in the former genera, especially in *Hypocomagalma dreissenae* Jar. et Raabe, and the disposition

of kineties cannot be adapted to the scheme of *Ancistrinae* (Fig 11). It could be only accepted that the ciliature coating the body of *Goniocoma* is not the retained general ciliature but the thigmotactic ciliature expanded secondarily over the whole body (R a a b e 1938, 1959).

Thigmotactic zone

The ciliary thigmotactism in ciliates may be achieved only by the movements of a definite part of ciliature with no perceptible morphological aspects. So it occurs — no doubt — in numerous free-living ciliates e.g. in *Paramecium*. In *Thigmotricha*, beginning with the forms which seem to differ less than the others from their free-living ancestors — a certain morphological expression of thigmotactism is the densification of kinetosomes in kineties and crowding of kineties in the anterior part of the left body side. This is the situation in many *Hemispeiridae — Ancistrinae*, in *Conchophthiridae* and in *Thigmophryidae*. In all those forms, there is no distinct morphological separation of the thigmotactic area from the remaining ciliated body surface and no limitation of the general ciliature from the thigmotactic one.

In some *Conchophthiridae* the thigmotactic area becomes concave and differentiates in this way from the remaining ciliature. It concernes sometimes the

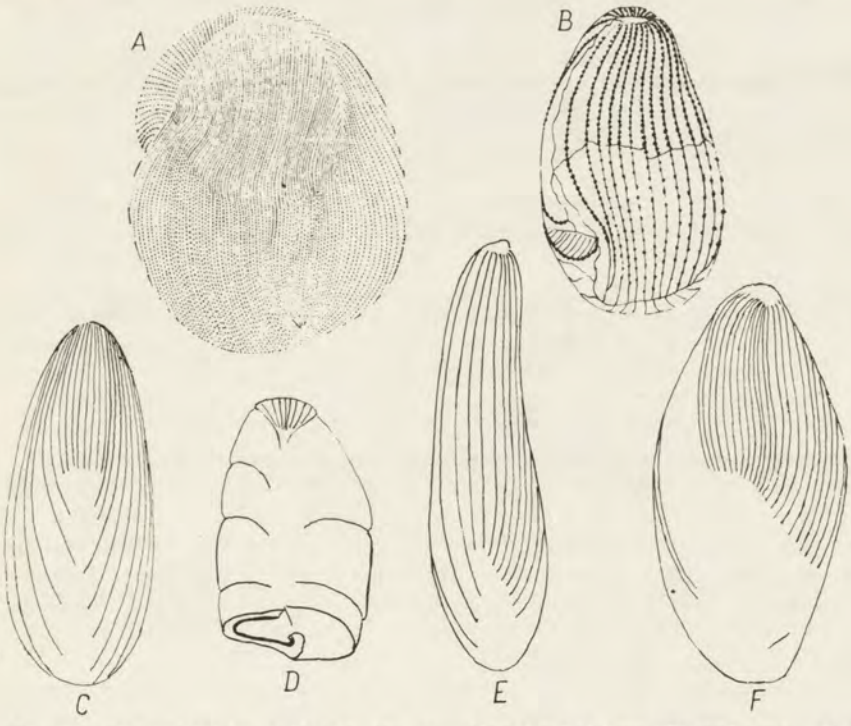

Fig. 10. The thigmotactic ciliature in: A — *Conchophthirus discophorus* Mermod, B — *Ancistrumina limnica* (Raabe), C — *Ancistrospira veneris* Ch. Lw. — système secant, D — *Hemispeira asteriasi* Fauré-Frem., E — *Ancistrocoma pelseneeri* Ch. Lw., F — *Hypocomides modiolariae* Ch. Lw. From Raabe, Chatton et Lwoff and Fenchel

whole left body side as e.g. in *Conchophthirus klimentinus* Raabe, in the other species of this genus it appears only in its anterior part. *C. discophorus* Mermod has a well delimited thigmotactic area embraced by a high margin (Fig. 10 A).

Among *Hemispeiridae*, two directions of development of the thigmotactic area and its ciliature are marked. They have been well distinguished and studied by Chatton et Lwoff 1949, 1950. One of them is the already mentioned development of this area in *Ancistrinae* (= *Protophryinae*), concerning only some densification of kinetosomes in the anterior sectors of the left body side kineties. Another line of development is represented by the members of the subfamily *Hemispeirinae* and consists in a differentiation of rather dorsal rows of kineties which fail to reach the posterior suture, break approx. in the middle of the body length. They are arched and closed as if by parentheses by the nearest kineties of the general ciliature (système secant).

The differences between those two evolutionary paths within *Hemispeiridae* become clear when two possibly primitive forms of both subfamilies are compared i.e. such forms which do not show any high retrogradation and spiralization of the adoral kineties. As such forms may be considered: *Ancistrumina* from *Ancistrinae* and *Ancistrospira* from *Hemispeirinae* (Fig. 10 B, C). In some forms of the subfamily *Ancistrinae* e.g. *Boveria* which are more advanced as to the behaviour of the adoral kineties, the situation of the thigmotactic area remains not altered. In the parallel forms of the subfamily *Hemispeirinae* — as e.g. in *Hemispeira* — the thigmotactic area is shifted to the apical pole (Fig. 10 D). Its kineties remain dense although the kineties of the general ciliature are much reduced and rarified. In this way, a quite different body form arises and appears different orientation in movement: *Hemispeira* moves along the substrate with its bundle of thigmotactic ciliature on its apex, whereas its adoral target is pushed off.

This duality of the evolutionary paths of the thigmotactic zone seems to be retained in *Ancistrocomidae* although the inclination to reduce the general and adoral ciliatures leaving only the thigmotactic one in the anterior body part — is characteristic for the whole family. In such forms as *Hypocomides* or *Hypocomella*, the evolutionary line of *Ancistrinae* is continued, whereas in genera like *Ancistrocoma* — rather a line originating from *Ancistrospira* with its thigmotactic ciliature as système secant seems to be more probable (Fig. 10 E, F). It could be postulated, that *Ancistrocomidae* derive generally from *Hemispeiridae*, i.e. equally from *Ancistrinae* as *Hemispeirinae*. Although Chatton et Lwoff 1949, 1950 are inclined to derive them only from *Hemisperinae*. Really, the preservation of the thigmotactic zone of *Ancistrospira* type in *Ancistrocoma* is unusual, but it takes place only in *Ancistrocoma* and *Holocoma*, perhaps in *Hypocomagalma*, i.e. in forms which retain the general ciliature as well. Other forms approach rather *Ancistrinae* which was already mentioned before (Raabe 1959). The comparison of the thigmotactic zone in *Proboveria* or *Boveria* with that in *Insignicoma* seems very interesting since the last form retained "vestige de la frange adorale" and even the topography of separate parts of ciliature is very similar.

The thigmotactic zone of *Ancistrocomidae*, namely those of the structure type of *Hypocomides* or *Hypocomella* with no general ciliature, differentiated very distinctly. But what is it like in the forms with a nearly full body ciliature as are *Ancistrocoma*, *Holocoma*, *Hypocomagalma* and at last *Goniocoma*?

The ciliature of *Hypocomagalma dreissenae* Jar. et Raabe, similarly as that

of *Ancistrocoma* or *Holocoma* may be looked upon as a retained general ciliature, and a thigmotactic ciliature closed in a "système secant". The right kinety of this ciliature lies closely to the naked surface, behind it lies the first kinety of the general ciliature which is shifted slightly backwards, further on, lies the second kinety etc. The naked areas may be compared to the naked peristomal area of *Hemispeiridae*. However in *Goniocoma macomae* (Chatton et Lwoff), the conditions are quite reverse! Here the "système secant" of the thigmotactic ciliature is not limited on the right side but gradually passes into a kineties system which covers the whole body. The interval marking the beginning of the kineties complex which reach nearly vertically the kineties of the real thigmotactic area — are located on its left side! Therefore I am inclined to interprete this situation in this way, that the ancestors of *Goniocoma* have completely lost the general ciliature retaining only the thigmotactic one, but afterwards the whole body of the ciliate became covered by this ciliature, which appeared as a secondary process (R a a b e 1938) (comp. Fig. 11 and pp. 16, 17).

Some of the *Ancistrocomidae* show another evolutionary tendency bound with the thigmotactic ciliature: an inclination for closing its zone. This appears

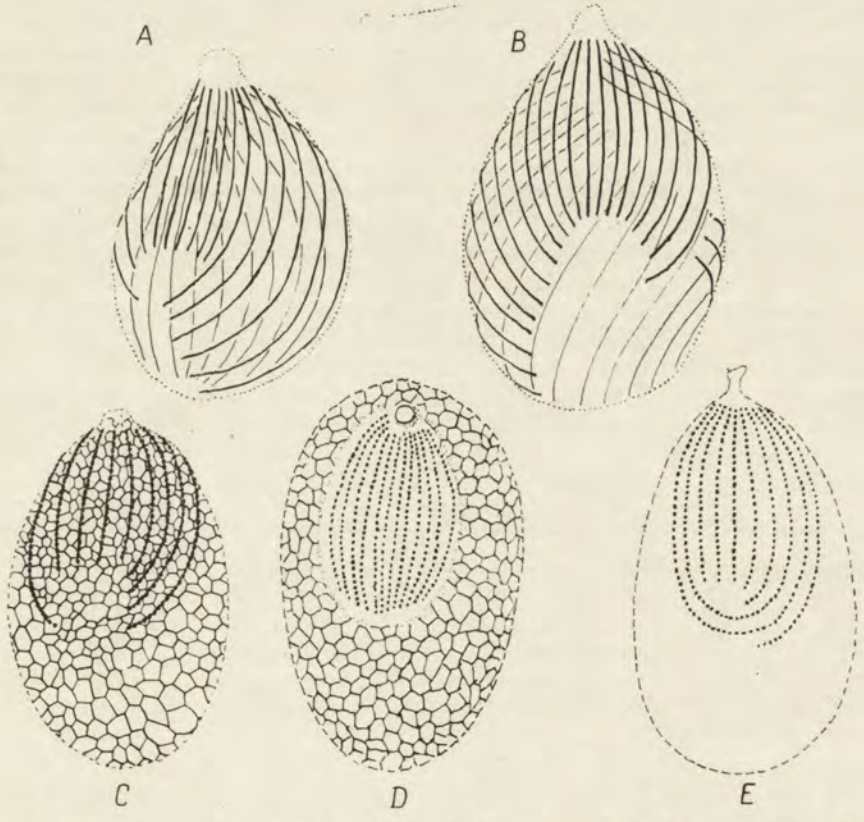

Fig. 11. The thigmotactic ciliature in: A — *Hypocomagalma dreissenae* Jar. Raabe, B — *Goniocoma macomae* Ch. Lw., C — *Hypocomella* sp. from *Bithynia* from Balaton, D — *Hypocomina patellarum* (Licht.), E — *Colligocineta furax* Kozloff. From Raabe and Kozloff

already in *Hypocomella* and in some other similar genera, their marginal kineties which are arched in opposite directions, approach by their ends to one another. This is very distinctly marked in *Hypocomina patellarum* (Licht.), although (against the opinion of Lichtenstein 1921) Chatton et Lwoff 1950 stated that those kineties are however "bipolaires comme celles de tous les Thigmotriches" [1]. This is supported by my own results. It is characteristic that the thigmotactic zone of *H. patellarum* is distinctly concave and surrounded by a thickening, but in fact all the kineties are bipolar. That it is not a categorical feature of *Ancistrocomidae* was proved by the findings of Kozloff 1965 that in his *Colligocineta furax*, the marginal kineties of the right side of the thigmotactic area join in the posterior part the marginal kineties of the left side i.e. their continuation and a real closure of the thigmotactic ciliature occurs (Fig. 11).

In the representatives of the family *Sphenophryidae* which derive from *Ancistrocomidae*, thigmotactism assumes another form. In tomits it is effected by the sucking snout and the ciliary adhesive areas, similarly as in *Ancistrocomidae*. In *Gargarius*, in the clinging function seems to participate the folded surface of the body besides the snout, and in the other *Sphenophryidae* also the foot; Chatton et Lwoff 1950 are inclined to accept the foot as derived from suçoir. The thigmotactic ciliature remains at least in the tomits. Even in the trophonts of *Lwoffia cilifera* Kozloff it has presumably another signification. In all the tomits the ciliature consists of two parts, namely: 2+2 (or 3) kineties on one side and 5—7 kineties on the other, being consistent with the ciliature of *Hypocomatidium sphaerii* Jar. et. Raabe. The same system of cilia-less kineties remains also in the trophonts of *Sphenophryidae*. Raabe 1949 and Dobrzańska 1961 indicated this coincidence or similitude of the kineties system in *Sphenophryidae* to the situation in *Hypocomatidium*. Their observations were correct. They suggested even on the ground of those observations the monophylety of *Sphenophryidae*, independently of the various shape of their trophic forms (comp. Fig. 5, and pp. 9, 10).

It may be summarized that in *Sphenophryidae*, the thigmotactic kineties loose their functions in the trophic forms in favour of adhesive role of the snout

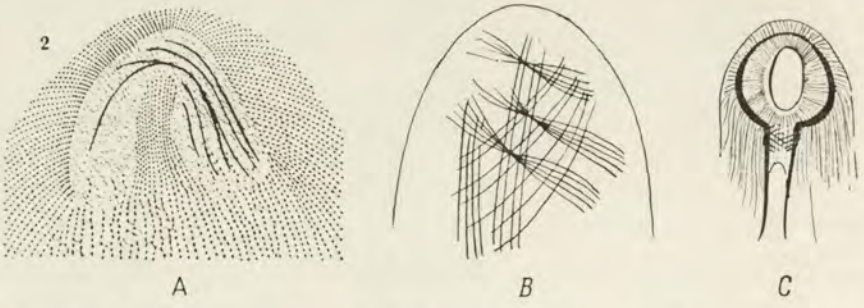

Fig. 12. The thigmotactic apparatus in *Hysterocinetidae*: A — *Hysterocineta paludinarum* (Stein), B — *Ptychostomum ohridanum* Puyt., C — *Cotylothigma rhynchelmis* (Heidenr.). From Raabe, de Puytorac and Heidenreich

[1] Fig. XXI, page 430 in the work Chatton et Lwoff 1950 does not represent surely *H. patellarum!*

or of the foot. It occur here a rather typical substitution of organs and function. Nevertheless the development of the thigmotactic ciliature in the families *Hemispeiridae, Ancistrocomidae* and *Sphenophryidae* constitutes a distinct range which begins by the differentiation of the thigmotactic zone, is continued by its development up to its isolation and disappearence in favour of another adhesive system.

Another different way of development of the thigmotactic ciliary zone, localized in the left anterior body part, is that which leads to *Hysterocinetidae* and ramifies among them in different — but rather similar — directions (Fig. 12). This way may provide perhaps some connections to *Astomata.*

A primitive form of the family *Hysterocinetidae — Protoptychostomum simplex* (André, 1918) Raabe 1949, is perhaps the exit form of this family and represents a primitive form of the thigmotactic system as well. It is essentially the same zone which occurs e.g. in *Conchophthirus* limited in front by a narrow naked stripe of the broadened anterior suture. In its posterior part it joins gradually the general ciliature. However this zone initially narrow, grows up so as to form a horse-shoe with increasingly large branches which press together kineties, penetrating between them from behind. This state is represented in the genus *Hysterocineta.* As a complicated clinging apparatus act here: a naked zone lying closely to the anterior suture, being in the process of transformation into the sucker, and a small channel inside in which run the kineties. Their cilia play a role of prepulsation, driving water out of the channel and causing adhesion of the sucker. The naked area of the sucker is strengthened by fibrils which are able to contract. The fibrils run more or less parallel to the anterior suture. The subsequent development of the thigmotactic apparatus occurs according to several tendencies acting together or separately. Those are: 1. closing the sucker from behind by the outgrowth of the naked area and by breaking the kineties which encroach into the channel, 2. formation of lobes in the posterior part of the sucker which encroach upon one another, and 3. formation of skeletal and support elements of the sucker.

The posterior closing of the sucker may be followed well in the series *Protoptychostomum → Hysterocineta → Ptychostomum.* In this range the arms of the sucker grow consecutively, cut across the kinety entering from behind its furrow. This phylogenetic process may be proved well in the morphogenesis of the sucker of opisthe in division (R a a b e 1938, 1949). As result, the sucker open from behind, occurs in the representatives of genera *Protoptychostomum, Hysterocineta, Elliptothigma,* whereas the closed form appeares in *Cotylothigma, Kysthothigma* (not exactly examined), *Ptychostomum, Craticuloscuta* and *Epicharocotyle.*

The pellicular lobes which encroach upon one another behind the sucker and cause the formation of the channel which makes the sucker furrow longer, occur in *Cotylothigma.* It is striking that they appear in the representatives of the only genus which has the stifft skeletal ring of its sucker. Possibly those plasmatic lobes give to it some plasticity in action again.

The supporting elements on the territory of the sucker in *Hysterocinetidae* seem to have a double character: elastic-contractil and skeletal. Those are fibers running in *Protoptychostomum* and *Hysterocineta* and in some representatives of the genus *Ptychostomum* more or less parallel to one another and to the anterior margin of the sucker. In many species of *Ptychostomum* this system is complicated and fibrils of different character arise, situated in different

planes. Exact details are to be discussed in the chapter devoted to *Hysterocinetidae*.

At last, some other solutions concerning the thigmotactic systems or simply clinging ones, may be found in some — at least — *Astomata* providad that its origin could be suggested from some *Thigmotricha*. Here the evolution followed the direction of formation a skeletal apparatus with external elements in form of spines which serve for anchorage upon the host's body, or of producing powerful suckers. This problem will be discussed in the chapter on the eventual relations between *Thigmotricha* and *Astomata*.

Buccal apparatus and adoral kineties

As it was intended to present in the general chapter, the plesiomorphic *Thigmotricha* represent this type of structure in which the cytostome was shifted backwards along the ventral body margin and the adoral kineties had been engaged into its service. They are at first long, running from the anterior suture as far as to embrace the cytostome with their ends.

In many ciliates such kineties become shortened and their kinetosomes are densified, producing undulating membrane (UM), undergoing spiralization or far-leading transformations which result in formation of adoral zone of membranells (AZM). The relation of UM to the accompanying AZM may be various in the quantitative aspect as well. In the classical case of *Tetrahymenidae* it has the formula 1 UM+3 AZM, in *Spirotricha* — 1 UM+*n* AZM, *n* — expressing extremely various and sometimes very high values. For embracing in one term all the possible systems UM+*n* AZM I suggested (Raabe 1963) the term ambihymenium.

In *Thigmotricha*, Chatton et Lwoff 1949, 1950 accepted the determination of adoral kineties by the name: kinety 1 or stomatogenic kinety (corresponding to UM), and kinety B, or more precisely, kinety A+B+C, or the prostomic kinety (corresponding to AZM). In the trophic stages, the prostomic kinety has never a character of a row of transverse membranelles — it is a continuous kinety, sometimes slightly fragmented into several segments (A, B, C — according to Chatton et Lwoff). The character of AZM may have the anlage of the prostomic kinety in time of its formation or divisional reorganization, before all in the opisthe. Chatton et Lwoff 1949 suggest that in the trophic stages this kinety is a polykinety. This seems not to be correct as a general phenomenon (see later).

As an exit form for *Thigmotricha*, the form of adoral kineties represented by *Ancistrum* or *Ancistrumina* was assumed. Those are two kineties running nearly along the whole body from the anterior apical suture, far backwards where they twist left (especialy the stomatogenic kinety) around the cytostome. This form corresponds to the structure of adoral kineties in the hypothetical ancestor of *Thigmotricha*, resembling *Pleuronematidae* by its structure. In *Hemispeiridae* the adoral kineties may undergo changes which were determined by Raabe 1959 as realizing different degree of advancement and different combinations of two tendencies: retrogradation and spiralization on the posterior body pole (Fig. 4).

The division processes in the forms of a minor retrogradation as e.g. in *Proboveria loripedis* Chatton et Lwoff, according to the studies of those authors (Chatton et Lwoff 1936) — speak in favour of the fact that the extension of adoral kineties along the body length, parallel to the general ciliature is

the plesiomorphic exit form. Here in the pre-division stage the kineties elongate and shift forewards so that the division furrow divides them equally as it does with the kineties of the general ciliature.

The tendency to retrogradation and spiralization (and sometimes to abbreviation of the adoral kineties) occurs in *Hemispeiridae* in various ways and reaches a different degree. It is interesting that in both subfamilies: *Ancistrinae* and *Hemispeirinae* there arise ranges parallel with this regard, which caught attention of Chatton et Lwoff 1949. Their table is presented below.

La Famille des *Hemispeiridae*

La cinétie stomatogène prend naissance:	Aire thigmotactique constituée par:	
	les segments antérieurs des cinéties générales de longueur normale. Pas de systèmes sécants.	des cinéties réduites à leur segment antérieur et encadrées de systèmes sécants.
	Protophryinae	*Hemispeirinae*
sur le tiers antérieur du mèridien ventral	*Protophrya* *Ancistrum*	*Ancistrospira*
à l'équateur	*Proboveria*	*Plagiospira*
sur le tiers postérieur du méridien ventral	*Ancistrella*	
au niveau du pôle postérieur	*Boveria*	*Cheissinia* *Hemispeira*

In *Hemispeiridae,* besides the changes in the disposition of the adoral kineties, an inclination appears to involve the nearest kineties of the general ciliature into the function of the peristomal apparatus. This problem was discussed in the preceding chapter. As already said above, mostly the kinety 2 is engaged but sometimes the kinety *n* and *n*—1, and the kinety 3 as well. This tendency is especially strongly marked in *Eupoterion pernix* in the description of MacLennan and Connell 1931. Although the results of those authors failed to be supported by anybody, and Chatton et Lwoff 1949 recognized *Eupoterion* as a "typical *Ancistrum*", those data however are suggestive because they reveal a final — as if expected — result of common tendencies (Fig. 9).

The structure of adoral kineties in *Hemispeiridae,* and consequently in the representatives of other families of *Thigmotricha,* remains still not thoroughly elucidated. Chatton et Lwoff 1949 try to represent this structure in a manner which would connect it clearly with tetrahymenium, and other authors followed this concept. Chatton et Lwoff show (especially very convincingly in schematic drawings) that the stomatogenic kinety is haplokinety which changes its feature only in the division reorganization when it acts really as a stomatogenic one. The prostomal kinety (A+B+C) is — according to those authors — a polykinety or rather a diplokinety. It is divided into 3 segments:

the short initial segment A, the longer median base segment B, and the final one C rolled around the mouth. The course of stomatogenesis really justifies such an interpretation. The number of initial membranelles of the type AZM which give then origin to the prostomal kinety, is however higher than 3 (R a a b e 1963). This will be discussed more extensively in the chapter on morphogenesis of *Thigmotricha*. In the trophic conditions however disappears generally the diplokinetism of the prostomal kinety as well as its division into the segments A, B, and C; the kinety becomes haplokinety. Sometimes it seems to be a polykinety which is evoked by the zigzag arrangement of its kinetosomes on the kinetodesme. Sometimes it seems that it is really a polykinety.

The apparent controversy or difference of the fundamental features of adoral kineties organization, is in reality not a controversy. Possibly in time of formation of the stomatogenic kinety, the prostomal kinety arises as a row of oblique membranelles of the AZM type i.e. polykinetic ones. In the subsequent stomatogenesis, its fate may be various depending on its dimensions, compactness and destination. It may remain a fragmented polykinety, a uniform polykinety or it may systematize the complex of kinetosomes and become a haplokinety. The data concerning the structure of both adoral kineties will be given with discussion on separate families of *Thigmotricha*.

The problem of the cytostomal apparatus itself in *Hemispeiridae*, and consequently also in the other *Thigmotricha* possessing a mouth, has not been fully elucidated either. Possibly the situation in various families may be different.

In *Hemispeiridae* and *Conchophthiridae* the oral apparatus is constructed similarly as in *Pleuronematidae*. Several or more parallel fibrils run from the final twisting of the stomatogenic kinety towards the end of the prostomal kinety. Those fibrils are deprived of kinetosomes, they are rather supporting fibrils, perhaps keeping the cytostome open. Their role and significance are not known even in the free-living ciliates. C a n e l l a et R o c c h i C a n e l l a 1964 define this structure as "pseudomembranula radialmente striata", not trying to define its significance either.

The fundamental type of the structure of adoral kineties in *Thigmotricha* — as described above — holds true for *Hemispeiridae*, as well *Ancistrinae* as *Hemispeirinae*, diverging only because of some evolutionary tendencies, before all retrogradation and spiralization. In the forms of both subfamilies, which are the most advanced in this regard, the final effect may be various: in *Boveria* on its posterior pole arises a full circle of the adoral spiral and in *Hemispeira* only a half of it (Fig. 4).

Among *Conchophthiridae*, in the representatives of the genus *Conchophthirus* the adoral kineties are quite homological to those kineties in *Hemispeiridae* as it was remarked by R a a b e 1936 and supported by C h a t t o n et L w o f f 1949. This homology was ascertained by the study of R a a b e 1963 on stomatogenesis in *Conchophthirus* (Fig. 13 A). Among *Thigmophryidae*, the conditions found by F e n c h e l 1964 in *Thigmophrya* allow to homologize their adoral kineties with the described type of structure. It seems (although the matter has not been thoroughly investigated) similar situation exists in *Cochliophilus* according the study of K o z l o f f 1945. The adoral apparatus of *Myxophyllum* is quite unknown; if it would be found that the adoral kineties fail to occur here at all, this genus should eventually find another position in taxonomy. Similarly unknown are the conditions in *Conchophyllum caryoclada*

(Kidder, 1933) Raabe, 1936. It should be added that in *Conchophthiridae* (*Conchophthirus, Conchoscutum*) as well as in *Thigmophryidae* (*Myxophyllum, Thigmophrya*), the adoral ciliary apparatus is enriched by penetration into the infundibulum of a certain number of kineties of the general ciliature which produce here a ciliated funnel or channel.

The structure and disposition of adoral kineties in two families requires some interpretation. Those two families had been created for single species because of their distinctness — among others — in the structure of adoral kineties. These are: family *Peniculistomatidae* with one species *Peniculistoma mytili* (De Morgan) Jankowski, connected surely to *Conchophthiridae* and the family *Thigmocomidae* with one species *Thigmocoma acuminata* Kazubski approaching rather the *Hemispeiridae*. It is amazing that the adoral kineties are disposed in both groups in a rather similar way. This fact should rather be looked upon as convergency. In the interpretation of K a z u b s k i 1958 concerning *Thigmocoma*, the kinety 1 is slightly shifted backwards and forms a loop round the cytostome. Kinety ABC is situated more in front and is distinctly displaced to the left side. In *Peniculistoma* it may be ascertained (according to data of K i d d e r 1933) that the kinety 1 describes a large loop and the kinety AB is also deflected left of it. It seems that the short bundles of cilia continuing the arch of the kinety 1, may be looked upon as a part C of the prostomal kinety in the interpretation of C h a t t o n et L w o f f. F e n c h e l 1965 present the structure of the adoral kineties in *Peniculistoma* in a slightly different way. It may be supposed that in this case he had to deal with a not fully developed system. (Fig. 13 B, C).

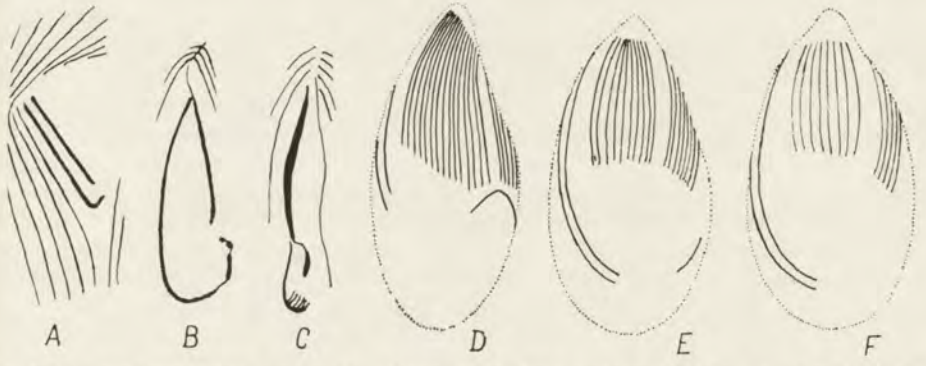

Fig. 13. The adoral kineties in: A — *Conchophthirus unionis* Raabe, B — *Peniculistoma mytili* (De Morgan), C — *Thigmocoma acuminata* Kazubski, D — *Hypocomides musculus* Fenchel, E — *Insignicoma venusta* Ch. Lw., F — *Raabella helensis* Ch. Lw. From Raabe, Kidder, Kazubski, Fenchel, Kozloff and Raabe

In the representatives of the family *Hysterocinetidae*, the adoral kineties penetrate into the peristomal funnel describing spirals around its wall. The picture of this spiralization reminds those occurring in *Peritricha*, although here only convergency may be actual. A serious difficulty presents the composition of the adoral apparatus in *Hysterocinetidae*. It is composed of three parallel kineties: two of them on the left side of the peristomal zone, and one on its right side. Or, considering the topography: two kineties nearer the anterior body margin and one kinety nearer the posterior one.

The study of morphogenetic stages help rather little to interprete such a system, because — as it seems to be quite common — the peristomes of both daughter individuals and at any rate the peristome of the opisthe arise de novo and not by transformation of the parental peristome. As a working concept, a supposition may be put forward that the adoral kineties of *Hysterocinetidae* correspond to two adoral kineties of *Hemispeiridae* and of other *Thigmotricha* with addition of the kinety 2 which is here fully adapted. A final solution of this problem is very difficult because the course of the kineties of the general ciliature in the posterior part of the body of *Hysterocinetidae* is disturbed.

The groups of *Thigmotricha* which were discussed above, namely *Hemispeiridae, Thigmocomidae, Conchophthiridae, Thigmophryidae, Peniculistomatidae, Hysterocinetidae* and *Protanoplophrya,* although show some modifications, keep their adoral kineties which are in service of the primary cytostome shifted generally to the posterior body end. In *Ancistrocomidae* and *Sphenophryidae* (and in the family *Hypocomidae* s. str. which is, as it seems, not connected with the above groups), the primary cytostome disappears and its function is performed by another structures: in the first family by the sucking snout (suçoir), and in the second one by a more extensive area of food-uptake.

Since the cytostome disappears in the posterior body end, and the snout appears on its anterior pole, the adoral kineties are deprived of their function and atrophy, remaining only in some forms as rudiments. Presence of such remnants in *Ancistrocomidae* would speak in favour of their origin from *Hemispeiridae.*

May be for this reason Chatton et Lwoff in their short comunications before the II world war, introduced the term "frange adorale" and "cinétie prostomienne vestigiale" for the differentiating kineties which are not included exactly to the assembly of thigmotactic kineties of some *Ancistrocomidae.* In the second part of their monography (1950) those authors perform a revision and show a general retreat from the former positions stating that: "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 considerer comme l'equivalent de la ciliature prostomienne des *Hemispeiridae*". In consequence, the differentiated kinety with longer cilia the authors call in 1950 only "cinétie vestigiale". It should be reminded that as well the "frange adorale" as "cinétie prostomienne vestigiale" or "cinétie vestigiale" are in the meaning of Chatton et Lwoff not any kinety running from the apical body end backwards, but a short segment located more or less in the middle part of the body, sometimes even vertically to the kineties of the thigmotactic ciliature.

In my opinion, the retreat of Chatton et Lwoff from their former position was at least too early. The argument which follows from the considerations of those authors that this "cinétie vestigiale" does not repeat the morphogenetic stages of the adoral kineties of *Hemispeiridae* and cannot therefore be recognized as their homologous structure, seems to be not justified and decisive. I think that there is no absolute rule of recapitulation, and that such a recapitulation would not be valid in the cases of vestigial systems, being however preserved in the descendants of forms which possessed them as functioning systems.

In my opinon (Raabe 1938) the concept of preservation the vestigial adoral

kineties in *Ancistrocomidae* is fully acceptable but only in this case when two whole kineties running to the right of the thigmotactic ciliature were recognized as such ones. Such kineties occur in some representatives of the family *Ancistrocomidae* namely in *Hypocomides, Anisocomides, Insignicoma, Raabella, Hypocomatidium.* The marginal of those kineties could be comparable with the stomatogenic kinety and the more median with the prostomal kinety. As prolongation of one of those kineties, rather of that marginal one, may be recognized the short segment of kinetosomes, oriented obliquely or even vertically to the kineties of the thigmotactic ciliature, occurring in e.g. *Insignicoma, Anisocomides, Hypocomides.* Presumably it is the only way of elucidation the genesis of this mysterious segment (Fig. 13 D, E, F).

For finding the exit form of such a system, *Proboveria* or *Boveria* should be examined in which the spiralled ends of adoral kineties take also a vertical position to the thigmotactic ciliature. Such forms may be put side by side with *Anisocomides* or *Hypocomides* and especially with *Insignicoma.* It may be imagined that the course of the right from two long kineties was complemented so that it became joint by a short arched segment. This kinety — as mentioned above — could be recognized in this concept as a former stometogenic kinety. The more central kinety would be the preserved prostomal one. In *Isocomides* this system undergoes further modifications, in the others as *Raabella* or *Hypocomatidium* remain only the arched segments of former adoral kineties, the "frange adorale" disappears at all.

Independently of the way of interpretetion concerning the vestigial adoral kineties in *Ancistrocomidae,* this family is characterized by the atrophy of the mouth, and formation of a suçoir instead of it, which is formed according to the opinion of Chatton et Lwoff distinctly from the bouton adhesif of *Ancistrinae.* The substitution of organs occurs. From this new mouth runs inside the cytoplasm a more or less marked cytopharynx. In *Sphenophryidae* even this mouth atrophies or undergoes further transformations. It remains in *Gargarius* and extends as a clinging-absorbing area in some representatives of other genera before all in *Spenophrya* sp. sp. The manner of absorbing food by this area is not clear but the most probable seems to be pinocytosis. At any rate, any structures of adoral apparatus are absent.

The internal systems

The internal organelles of *Thigmotricha* fail to represent forms which would deviate in a high degree from the commonly encountered models characteristic for ciliates — at least — for all the *Holotricha.* Besides, they did not attract the attention of scientists except in some cases.

The nuclear apparatus presents here the most common type. It consists of a big solid macronucleus and usually only one micronucleus. The ratio of Ma: Mi volume is variable. Sometimes [*Conchophthirus curtus* Englm., *Protoptychostomum simplex* (André), *Peniculistoma mytili* (De Morgan)], besides a single Ma occur two Mi. In one only case, in *Myxophyllum steenstrupi* (Stein) occur 7 Ma and only one Mi. The shape of Ma is usually ovoid, ellipsoidal or spherical. In elongated forms (e.g. *Protanoplophya,* some *Hysterocinetidae)* especially in those which reproduce by means of the posterior budding, Ma is also much elongated and Mi is located on its end instead in the median part.

The division processes of the nuclear apparatus had been often observed: Kidder in *Peniculistoma* (1933), *Ancistrum* (1933), *Conchophthirus* (1934); Rossolimo und Jakimovitsch 1929, in *Myxophyllum*; Beers 1963 in *Conchophthirus*. In *Myxophyllum* the macronuclei do not accumulate into one division Ma as it takes place in e.g. multinucleated *Hypotricha (Urostyla* in the study of H. Raabe 1947) but divide synchronously independently one of another.

The osmoregulation-excretory apparatus occurs in *Thigmotricha* mostly in the form of one contractile vacuole. In some more elongated forms, several vacuoles may appear (2 in *Protoptychostomum),* and even a higher number of them (*Elliptothigma, Protanoplophrya*). It is characteristic that the multiplication of vacuoles occurs in intestinal parasites and in such ones which approach with other regards to *Astomata*. Presumably this may be recognized as an adaptative convergency not deciding about the eventual relationship of some *Thigmotricha* with — at least — some groups of the still polyphyletic "order" *Astomata*.

The alimentary system of *Thigmotricha* begins with the cytostome which is initially placed on the body surface. It penetrates secondarily into the bottom of the peristome as a funnel-shaped structure. Into the cytostome encroach distal segments of the adoral kineties (*Hystorocinetidae*) or the kineties of the general ciliature which form a ciliated infundibulum. A short or long cytopharynx runs from the cytostome, sometimes inside the cytoplasm in some species (e.g. *Ancistrocoma*) and reaches nearly the posterior body end, opposite to the sucking snout. Food vacuoles occur generally as single structures, arising consecutively and migrating so along the cytoplasm. Only in the intestinal parasites, *Hysterocinetidae,* they do not migrate separately in cytoplasm but accumulate in some distinctly outlined spaces of an shape which is characteristic for separate genera and species. Those are either rounded sacculous spaces or zones which push forwards one or two arms embracing the nuclear apparatus and the pulsatile vacuole. Those zones remind somewhat of similar structures occurring in some *Peritricha* or the endoplasmatic saccules of *Entodiniomorpha*; however the individuality of separate vacuole is kept.

In a certain connection with the alimentary system are the specific vacuoles which appear in the posterior body part of some *Ancistrocomidae*. These are vacuoles containing some stainable or unstainable concrements flowing in a liquid substance. Those concrements seem to be non indigested food particles or a deposit of not excreted metabolites. They are comparable to some described, among others by Dogiel 1929 in the ciliates living in the cattle rumen, "Konkrementenvacuolen" to which author ascribed the role of statocysts. Really, in a ciliate living in a stream flowing along the mantle cavity of the host — such an explanation of the role of this organellum would be quite acceptable. The observation of living material reveals that the bodies in the vacuoles perform vibrations which may eventually sygnalize the retention of the current and a possibility of changing the place by the ciliate.

Another intracellular elements derived, as it seems, from the cortical system, are the fibrillar structures as well the contractile ones as the elastic as, at last, the stiff skeletal elements. Among *Thigmotricha* they were studied and described only in the representatives of the family *Hysterocinetidae*. Here they appear before all in the thigmotactic non-ciliary apparatus i.e. on the territory of the sucker. In the more plesiomorphic forms (with this regard as

well as in all the others) they are fibrils parallel to the anterior margin of the sucker i.e. to the anterior suture of the ciliary system, and are disposed in one plane just beneath the pellicle (*Protoptychostomum, Hysterocineta*). In the representatives of the genus *Ptychostomum* their number increases, their system is distributed in many planes and has a very different composition. At last in the genus *Cotylothigma* arises a skeletal ring supporting the sucker, not closed in its posterior part, and two strong fibers which support the ciliated channel (comp. Fig. 12). Those details will be discussed more extensively in the characteristic of the family *Hysterocinetidae*.

There is still one element occurring in *Sphenophryidae* which is not known as concern its structure and function, this is the so-called "corps enigmatiques" (Chatton et Lwoff 1922, 1950). It appears in the cytoplasm of the trophic forms in the time of budding and, according to Chatton et Lwoff 1950 passes on the bud and gives the base for formation of the adhesive sole of the new individual. Those problems concerning only one family will be discussed more exactly in the chapter on *Sphenophryidae*.

Cytological study of cytoplasm and granules and structures contained in it, were not carried out on the material of *Thigmotricha*. A certain analysis of the endoplasmic granules in *Conchophthirus curtus* Englm. was performed by Beers 1962. He stated in the granuloplasm of this ciliate some osmiophilic grains of a secretion character and qualified them as Golgi bodies or Golgi material. The author considers them as "muciferous granules" and postulates their role in thigmotactism. If it was proved on another material is would constitute an interesting contribution to elucidation of the functioning of the thigmotactic zones. It should be stressed that similar granulations appear under the surface of the sucker in *Hysterocinetidae*.

General characteristic of *Thigmotricha*

The evolutionary trends within *Thigmotricha* — as presented here — are so very much diverging that a question arises whether it possible to give a short concise. characteristic of this whole order. Not a static characteristic would be desired which would define only the range of features, but a dynamic one establishing and registrating rather the evolutive tendencies within the order. The attempt of a such characteristic follows.

Ordo *Thigmotricha* Chatton et Lwoff, 1922, emend

Ciliata — *Holotricha* living as commensals or parasites on the body covering or respiratory areas of aquatic molluscs or other aquatic invertebrates as well as in the posterior segment of the intestine and exceptionally in the renal system of molluscs and annelides.

In the less modified forms, the body is — as a rule — flattened laterally, covered with a more or less uniform ciliature. Kineties are bound together with two sutures: the anterior one which runs along the anterior body margin, and the posterior — on the posterior margin of the body. In this way, the system of kineties is divided into two parts, the right and the left which correspond initially to two body sides. In the more apomorphic forms, the ciliature may

be densified (polymerization of kineties) or it may be reduced as to its complete loss.

Thigmotricha are characterized by a well expressed thigmotactism which is served by: thigmotactic ciliature of the left anterior body side more or less distinctly differentiated from the general ciliature, suckers formed on this territory or unciliated adhesive areas in the sedentary forms. The adoral ciliature of more plesiomorphic forms (standing nearer the exit forms, possibly of the feature of *Pleuronematidae*) is constituted of two kineties, more or less parallel and lying along the ventral margin of the body, between the left and right part of the general ciliature. Those are: the stomatogenic kinety defined by Chatton et Lwoff as the 1 and the oral kinety defined by them as the prostomal kinety or A+B+C. The first one has in the trophic stages the structure of the haplokinety (UM), the second one — of a haplokinety or polykinety and in its development posses the form of AZM. The adoral kineties which were initially more or less parallel to the adjacent kineties of the general ciliature — run along the body forming a loop around the cytostome in the posterior body part. From that form on, the adoral system differentiates according to 3 fundamental tendencies: retrogradation, spiralization on the posterior body pole, and reduction. There exist a tendency to include into the adoral system also the nearest adjacent kineties of the general ciliature, or to penetrate into the infundibulum of a number of kineties of the general ciliature. In the cases of reduction of the adoral kineties and of shifting the buccal apparatus backwards, a new different apparatus of foodtaking from the body of the host may arise. It has a shape of a sucking snout on the anterior body pole, or a more extensive adhesive-sucking surface.

The nuclear apparatus conserves its normal feature: 1 big Ma and 1 small Mi. Only exceptionally several of those elements occur. The osmoregulative--excretion system is also simple (1 C.V.). In the intestinal forms a tendency appears to multiply it. In some forms arise accumulations of food vacuoles.

The body shape shows a graet variability reflecting the kind and degree of adaptation to the specific life conditions. From the exit form which is a slightly laterally flatened ovoid, it tends to shorten and to flatten the body in forms living on the respiratory surfaces, to modify completely the body in branchial sedentary forms and to elongate it in many intestinal parasites.

Reproduction of the plesiomorphic forms occurs by an equal transverse division. In this process the adoral apparatus undergoes considerable transformations. In the sedentary forms, often deprived of cilia in the trophic stages, occurs budding of the ciliated tomits and in some elongated intestinal forms — a posterior budding and even catenulation. Conjugation was observed in some species of different families.

In the above diagnosis of the order as distinctive features which undergo more or less distinct evolutionary changes, all three groups of ciliature were accepted, namely: the general ciliature, the thigmotactic ciliature and the adoral ciliature i.e. the adoral kineties. The analysis which is to characterize the evolution paths among *Thigmotricha* and to motivate the distinctness of single families of this order, should be based on the following criteria:

1. Situation and character of the general ciliature, accepting the system of equal meridional kineties as its exit form. The general ciliature may show an

inclination to polymerization or — in contrast — to reduction especially in the posterior part of the body.

2. Situation and character of the thigmotactic ciliature. As its exit form should be recognized the anterior part of the left side of the body ciliature which is not differentiated morphologically but only functionally. This ciliature tends to differentiate and to persist even in the case of atrophy of the general ciliature or to recede in favour of the adhesive apparatus — suckers or the adhesive-absorptive areas which act more effectively.

3. Situation and character of the adoral kineties for which two long kineties running nearly along the whole body on the ventral margin should be accepted as the exit form. Those kineties may undergo retrogradation or spiralization, or both tendencies simultaneously or, at last, reduction till their complete atrophy. In the last case an apparatus develops for taking food instead of the atrophied cytostome.

Evidently those tendencies of those features do not appear simultaneously in separate families of *Thigmotricha*. Some species, genera or families represent plesiomorphic feature of e.g. the general ciliature but may be characterized as well by the apomorphic form of e.g. adoral ciliature etc. This mosaic character in the state and intensity of the evolutive tendencies of different parts of the ciliary system, permits a total, very general but significant characteristic of separate families of *Thigmotricha*.

Not cleaming for strictness and not trying to establish the phylogenetic connections of separate families, those tendencies are represented in the diagram (Fig. 14). The circles which encroach one upon another represent: 1. tendency to reduction of the general ciliature (although really the evolutionary process proceeded as well towards its polymerization as reduction). 2. tendency to reduction of the thigmotactic ciliature and to formation of other

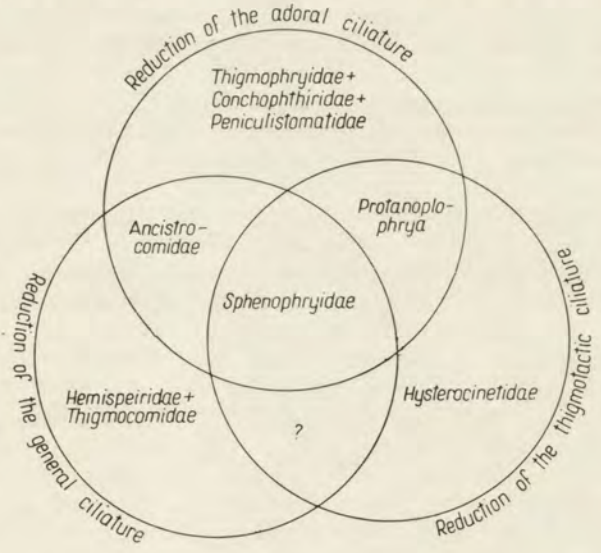

Fig. 14. The evolutionary tendencies in ciliary apparatus in *Thigmotricha*. Oryg.

adhesive apparata instead of it and 3. tendency to the reduction of the adoral ciliature.

In the concept as represented in this diagram, the families *Thigmophryidae, Conchophthiridae* and *Peniculistomatidae* found themselves in the same compartment. This is not strange nor striking. After the discovery by Fenchel 1964 the adoral kineties in *Thigmophrya,* the essential — as it seemed — difference between *Thigmophryidae* and *Conchophthidae* had been effaced. Only the problem of adoral kineties in *Myxophyllum* remains not elucidated. The genus *Peniculistoma* created by Jankowski 1964 for *"Conchophthirus" mytili* De Morgan,, was quite arbitrary excluded by Fenchal 1965 from *Conchophthiridae* and included to a separate family. In fact, the families *Thigmophryidae, Conchophthiridae* and *Peniculistomatidae* are rather near one another and could be even recognized as the subfamilies of one family — according to the rules of prioritate the family *Thigmophryidae.*

A separate position among the families of a dense ciliature occupy *Hysterocinetidae* as a well defined group of distinct evolutionary tendencies. A separate position is also that of the genus *Protanoplophrya* which represents a specific way of evolution. As it seems it should not to be included into the family *Conchophthiridae* as suggested by Corliss 1961, but rather a separate family — *Protanoplophryidae* should be created which would as yet, embrace this genus only[2].

From those families of a dense ciliature, differentiate the others with a scarce general ciliature and with a tendency to its reduction. Those families constitute the evolutive chain established by Chatton et Lwoff. It leads from *Hemispeiridae* by *Ancistrocomidae* to *Sphenophryidae.*

In the same compartment of the diagram are found the families *Hemispeiridae* (with two subfamilies: *Hemispeirinae* and *Ancistrinae*) and *Thigmocomidae.* In fact the differences between them are not very essential and their evolutionary trends are rather converging. It should be reminded that Kazubski 1963, distinguishing the family *Thigmocomidae* recognized the differences between *Hemispeirinae* and *Ancistrinae* (= *Protophryinae*) so essential that they would allow to raise those subfamilies to the range of families equivalent to *Thigmocomidae.* Consequently there would exist an inverse possibility to recognize those three groups as subfamilies of one family *Hemispeiridae.*

According to the former discussion and to the situation visualized in the diagram, the families *Ancistrocomidae* and *Sphenophryidae,* both fail to differ so strikingly from other families of *Thigmotricha* as it was found by Chatton et Lwoff 1939, 1949, 1950. The French authors joint those families (together with *Hypocomidae*) into a separate suborder *Rhynchodea* as an opposite suborder to *Stomodea* which embraced the families with a preserved cytostome and the adoral apparatus. i.e. *Conchophthiridae, Thigmophryidae* and *Hemispeiridae.* Although the link between *Ancistrocomidae* and *Sphenophryidae* is very strong, equally strong and direct seem to be the connections of *Ancistrocomidae* and *Hemispeiridae.* That is to say *Sphenophryidae, Ancistrocomidae* and *Hemispeiridae* have more of common than the latter ones and e.g. *Conchophthiridae* or, the more so, *Hysterocinetidae.*

[2] More exact diagnoses will be presented in the subsequent parts of this work in the chapters in which these families and subfamilies are to be discussed.

For that reason I do not follow Chatton et Lwoff, 1949, 1950 in their division of *Thigmotricha* into the subordes *Rhynchodea* and *Stomodea (Archynchoidina* and *Rhynchodina* in Corliss 1961).

The family *Ancistrocomidae* — as mentioned before — is distinctly differentiated and presumably not uniform. Three groups of species are well distinguishable in it., which differ from one another in the features of three complexes of ciliature: the general ciliature, the thigmotactic one and the remnants of the adoral kineties. I suggest to consider those groups as subfamilies, namely: 1. subfamilia *Hypocomidinae* sf. n., its representatives preserve the remnants of their adoral kineties, with the type-genus *Hypocomides* Ch. Lw., 2. subfamilia *Ancistrocominae* sf.n., with the general ciliature but with no remnants of the adoral kineties, with the type-genus *Ancistrocoma* Ch. Lw. and 3. subfamilia *Hypocomellinae* sf.n., keeping only the thigmotactic ciliature with the type-genus *Hypocomella* Ch. Lw.

At last, the family *Sphenophryidae* which represents the highest point of tendencies to reduction of all three parts of the ciliary system. This group is compact and presumably strictly monophyletic. As mentioned above, no place for the family *Hypocomidae* s.str. is seen in this system. It seems to be connected with quite different places in the system of ciliates.

In the subsequent parts of my monograph I shall apply this system suggested below because it indicates best the differences and similitudes, the phylogenetic connections and the range of different groups of *Thigmotricha:*

Fam. *Hemispeiridae* König, 1894, Chatton et Lwoff, 1949 emend.
- subfam. *Hemispeirinae* König, 1894, Chatton et Lwoff, 1949 emend.
- subfam. *Ancistrinae* Issel, 1903 (= *Protophryinae* Cépède, 1910, Chatton et Lwoff emend.)
- subfam. *Thigmocominae* Kazubski, 1958

Fam. *Ancistrocomidae* Chatton et Lwoff, 1939
- subfam. *Ancistrocominae* subfam. nova
- subfam. *Hypocomidinae* subfam. nova
- subfam. *Hypocomellinae* subfam. nova

Fam. *Sphenophryidae* Chatton et Lwoff, 1921

Fam. *Thigmophryidae* Chatton et Lwoff, 1923. emend.
- subfam. *Thigmophryinae* Chatton et Lwoff, 1923
- subfam. *Conchophthirinae* Kahl, 1931, 1934
- subfam. *Peniculistomatinae* Fenchel, 1965

Fam. *Hysterocinetidae* Diesing, 1866

Fam. *Protanoplophryidae* fam. nova

In my considerations, especially when morphology, morphogenesis and phylogenesis of *Thigmotricha* are concerned, I intend to pay a special attention to the cortical systems i.e. in the first place to the structures of the ciliary system. I feel it dispensable to explain that this system in ciliates reacts most intensely to any evolutionary adaptive changes and is their excelent index on one, and shows considerable features of conservatism — at least in its general scheme — on the other hand. Consequently this system reveals as well the plesiomorphic characters which are specific for the exit forms of the given group, as the apomorphic characters which reflect its development and specialization.

As it has been discussed above, I attribute a great importance to the character of the general thigmotactic and adoral ciliature, to their progressive and regressive changes which permits to situate side by side the groups — the families of the order *Thigmotricha*. The structure of the ciliary system will serve also for the diagnoses of genera and species since the ciliature shows a great stability within the species whereas the body shape may undergo considerable variability. At last the transformations of the ciliary system are the most valuable element of the ciliates morphogenesis. This element had been studied extensively in the considerations on other ciliates.

Of course, any considerations of a comparative character present an essential value only in this case when in the detailed study the same methods of preparation and of description have been applied. The present tendency recommended by the international conventions, to base on the silver and gold impregnation methods may possibly overcome many difficulties in future. Nevertheless the descriptions of earlier authors are presently not reliable, and even in the contemporary studies some of those methods prove to be insufficient.

I still consider the classical dry silver impregnation method of Bruno Klein to be the most effective for revealing the details of the structure of the ciliary system (together with the so called infraciliature) in *Holotricha*. A certain flattening of the body in the course of drying may be easily interpreted. The objection as to the failure of this method when applied to the marine material is essential. However in my own experience it gave satisfactory and even good results with this material as well. The adventage of the Klein's method is that it presents a unique way to visualize as well kinetosomes as fibers which bind kineties, as — at last — the fibers producing the network in the places deprived of ciliature.

Other methods as the moist method of Chatton et Lwoff and all the protargol methods are effective only to a certain degree despite their great advantages. Possibly because of their conservation and mordantage procedure they reveal as a rule — only the kinetosomes and fail to reflect the course of the connective fibers and of the network coating the body. They are valuable only for revealing the invaginated ciliary systems as e.g. the infundibular kineties and only in those instances I shall take advantage of them or refer to the results of other authors.

Of course, besides the cortical systems, I shall also discuss the other internal systems, however only at a moderate degree because *Thigmotricha* have been rarely investigated in this aspect. May be I shall have the opportunity to discuss the results of the electron microscopy applied to this subject if the planned investigations would be realized.

Summary

The paper constitutes the first introductory part of the planned monographic work on *Thigmotricha*. It contains a short historical outline of the research on this group as well as general morpho-comparative considerations on its representatives. Those considerations concern in the first place the structure of the ciliary system. This part of the work has been concluded by the discussion on the mutual relation of separate *Thigmotricha* families and by the proposed system of this order which is modified when compared with the systems of Kahl, of Chatton et Lwoff and of Corliss.

STRESZCZENIE

Praca stanowi pierwszą, wstępną część zamierzonego monograficznego opracowania *Thigmotricha*. Zawiera krótki zarys historyczny badań nad grupą oraz ogólne rozważania morfologiczno-porównawcze nad jej przedstawicielami. Rozważania te odnoszą się przede wszystkim do budowy układu rzęskowego. Część zostaje zamknięta omówieniem wzajemnego stosunku poszczególnych rodzin *Thigmotricha* i proponowanym systemem tego rzędu, zmodyfikowanym w porównaniu z systemami Kahl'a, Chatton et Lwoff i Corliss'a.

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Study on the growth of skeletal elements in *Trichodina pediculus* Ehrbg.

Badania nad wzrostem elementów szkieletowych u *Trichodina pediculus* Ehrbg.

The question of variability of trichodina, and first of all the variability of the shape of the denticles, was treated by the author on the example of *Trichodina pediculus* Ehrenberg, 1838, in the report for Second International Conference on Protozoology, London 1965 (Kazubski, 1965). In this report I stated the appearance in *Trichodina pediculus* this kind of the variability of denticles which might be the evidence of the growth of those elements. At the same time the growth of the inner rays has been considered as that indicating to the age of trichodina. This regularity is quite obvious, because the individual structures begin with smaller size and then grow to reach the size characteristic for adult specimens. It has become quite obvious after having looked over a great number of the microphotographs of the species of trichodina examined in the same magnification. It has been clearly shown and proved on photograms included in the previous work of the author (Kazubski, 1965). But in that report the author has used a sentence: "Simultaneously the diameter of the skeletal ring enlarges", which needs more detailed grouding. It is necessary, because after the binary fission of trichodina appears a great reconstruction of the adhesive disc, relying on formation "de novo" of the skeletal ring of the daughter individual. One can easily imagine the situation, when all the structures appear at once in suitable places and no growth of the diameter of the elements of the adhesive disc is necessary.

First of all the author wants to consider some aspects of the division of the adhesive disc the trichodina.

During the division the adhesive disc of the parent specimen with the denticulate ring in diameter R breaks into two halves, which close. In consequence a daughter individual arises with a number of the denticles equal, more or less, to the half of the total number of the denticles in the parent specimen and with the skeletal ring r in in the diameter, one half less than that of the denticulate ring of the parent individual, because:

$$1/2\ 2\pi R = 2\pi r \qquad \text{and so:}$$
$$1/2\ R = r$$

Then a complete reorganisation of the adhesive disc starts, resulting in the return to the situation which has existed before the division; among others it results in formation of a new skeletal ring of the size and number of the links

characteristic for given species. The elements of the new denticulate ring appear and the old ring is gradually resorbed. The new denticles appear outside of the old skeletal ring in some distances from the outer ends of the blades of the old denticles. In *T. pediculus* and several other species of *Trichodina,* examined by the author, this distance is 1 μ approx.

Formation of the new denticles begins with the appearance of the diagonal slats, which will appear at the basis of the blades and which will connect them to the central part of the denticles. Next, the central part of the denticles, coming into one another, are built up as wel as the centrifugal blades and centripetal rays (Fig. 1, Pl. I, II).

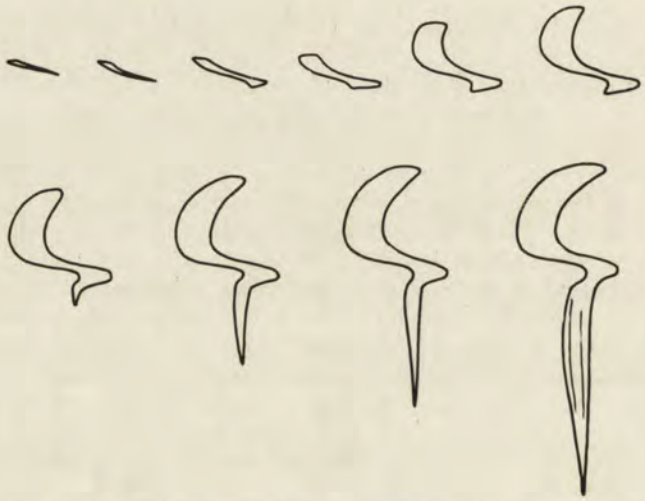

Fig. 1. Scheme of growth of denticle of *Trichodina pediculus,* succesive developmental stages

Simultaneously with the formation of the denticles, new radial pins of the adhesive disc are being formed. They appear between the old ones and from the very beginning they are visible as thin streaks only in silver impregnated preparations after Klein. Their width gradually increases and after some time they resemble the streaks already existing.

When measuring the newly formed skeletal ring one must draw attention to the following phenomenon. The diameter of the denticulate ring is being measured more or less in the half of the width of the central part of the denticle. The first elements of the new skeletal ring are, as it has been already mentioned, the diagonal slats of blades, the parts of the denticle situated centrifugally to the central part of the denticle. As a result of this, the diameter of the first outline of the denticulate ring is larger than in fact the later one, in the same specimen. These slats grow also centripetally, at the same time the old denticulate ring being gradually resorbed; thus relatively considerable differences between diameter of the original outline and the proper diameter of the denticulate ring of the young specimen occur (Table 1).

The main purpose of this study is the analysis of the size variations which take place in the adhesive disc in *T. pediculus* already after its regeneration.

The lenght of ray of the denticle and the diameter of the denticulate ring

Table 1

Dimensions of the elements of adhesive disc in post-division specimens of *Trichodina pediculus* from different hosts and in different stages of development

Host	Diameter of adhesive disc in μ	New denticulate ring				Old denticulate ring			
		number of denticles	diameter of denticulate ring in μ	length of denticles in μ	length of rays in μ	number of denticles	diameter of denticulate ring in μ	length of denticles in μ	length of rays in μ
Pelmatohydra oligactis	32.2	27	26.0	1.0	—	13	15.6	10.2	5.2
	31.2	—	25.0	1.0	—	15	15.6	9.4	4.2
	36.4	27	23.9	4.2	—	13	—	7.3	6.2
Rutilus rutilus fry	40.6	30	30.2	1.0	—	15	17.7	13.3	7.2
	35.4	—	30.2	1.0	—	14	17.7	11.4	6.2
	37.4	27	26.0	3.1	—	14	17.7	10.4	6.2
Coregonus albula fry	39.5	31	31.6	1.5	—	14	18.2	13.3	7.8
	38.4	—	31.6	1.5	—	15	18.8	13.3	7.8
	40.6	28	27.4	4.7	—	14	17.3	11.8	7.8
	40.6	28	27.4	4.7	—	12	18.0	10.2	6.3
	40.6	29	25.9	5.5	1.0	14	18.3	10.2	7.6
	40.0	31	28.2	5.5	—	15	17.5	9.4	5.5

are considered as the leading features. As the author has mentioned before, the length of ray may be treated as the measure of the relative age of trichodina. But the diameter of the denticulate ring may be regarded as that representing all the diameters of the adhesive disc, because no considerable differences in the proportions of the adhesive disc have been noticed. The method of measuring is shown on Fig. 2. For measuring one of the largest denticles was chosen.

In Figs. 3 and 4 several diagrams show correlation between the dimensions of the detailed parts of the denticles and their number in the denticulate ring, and diameter of the skeletal ring. Only the diagrams 1 and 2, concerning *Trichodina pediculus* from *Pelmatohydra oligactis*, are collective, and the examined specimens of ciliates were found on five host individuals and gathered from 10th till 20th July, 1964. All of those hydras came, however, from the same pond in Kortowo, near Olsztyn. In all other cases the material to the particular series of diagram has been taken from one host specimen — a fish — and all

the examined ciliates have been fixed at the same time and in the same way. Those populations descended from the fry of *Rutilus rutilus* (20th May, 1961) diagrams 3, 4, 9, and 10), from the fry of *Coregonus albula* (22nd May, 1964) (diagrams 5, 6, 11 and 12) and the fry of *Alburnus alburnus* (27th June, 1964) (diagrams 7 and 8). The two last populations have been obtained by experimental infection.

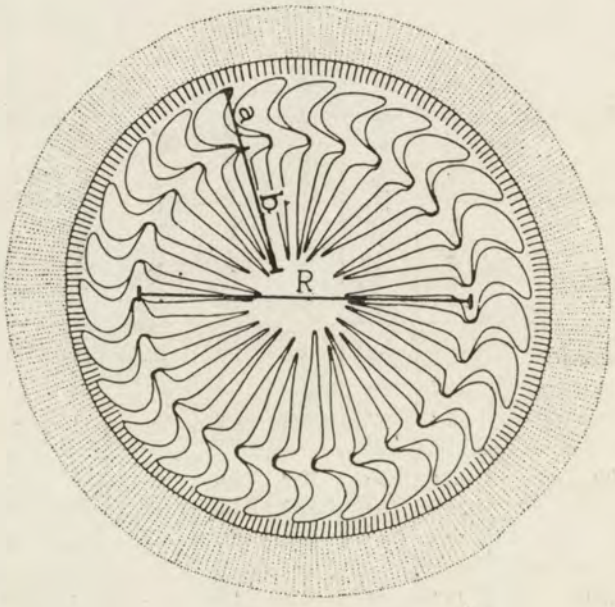

Fig. 2. Scheme of measurement of skeletal elements in trichodina: R — diameter of denticulate ring, a — length of outer blade, b — length of inner ray

The diagrams 1, 3, 5 and 7 show the correlation between the length of the inner ray and the diameter of the skeletal ring. In all those four diagrams a relatively great range of variability in both the examined qualities is visible. The great range of the variability of the ray lenght has been expected, because its growth can be observed directly. However, such a great range of variability in diameter of the skeletal ring has been rather surprising. In the examined cases the diameter of the denticulate ring has grown up from 10.5 to 15 μ, and the radius has increased in length from 5 — 7.5 μ, respectively. These data concern the extreme values, of course. Considering the possible morphological variability of the specimens of the same age, observed increase would be less pronounced.

The enlargement of the diameter of the denticulate ring can be pointed out in the other way too, quite independently. In the Table 1 the data concerning the already divided specimens are presented, grouped according to their hosts and the stage of the regeneration. As an example, I want to consider the material from *Coregonus albula,* as the most representative with regard to the number of specimens examined. This comparison shows that the diameter of the old denticulate ring is rather similar in all the individuals being 17.3 — 18.8 μ.

On this ground we can calculate that the parent individuals which posses the denticulate ring with the circumference of double length, should have been in diameter of the denticulate ring 34.5 — 37.5 μ (the radius 17.2 — 18.8 μ). In fact, these dimensions are probably a little smaller, because some pushing apart of the denticles during the break of the skeletal ring should be taken into consideration. In spite of that, the dividing individuals of *T. pediculus* belong, no doubt, to the largest group in population.

The new denticulate ring in the specimens of the examined population is 26 — 28 μ in diameter (the radius 13 — 14 μ) (Table 1.). In comparison with the already established measurements of the dividing specimens, the diameter of the skeletal ring increases about 8.5 — 9.5 μ, and the length of radius about 4.2 — 4.8 μ, respectively. These latter data are approximately the same as those presented in the diagram 3., particularly if we consider the previous objections, according to which the growth taken from the diagram is a little greater, because the differences in the dimensions of the specimens at the same age was not taken in account. Thus, the enlargement of the diameter of the skeletal ring can be proved.

In all those examined diagrams (1, 3, 5, and 7) the existence of a very high positive correlation between the two considered dimensions could be shown. This correlation between the length of the ray and the diameter of the skeletal ring, and so indirectly, the other diameters of the adhesive disc can be regarded as additional argument for the growth of trichodina and all the elements of the adhesive disc during the life of the ciliate. There is in this case unanimous and correlated enlargement of all the elements.

Another evidence in favour of the growth of trichodina is the fact that the young specimens with the denticle ray not shaped yet, and with visible process of the binary fission of the radial pins (these two phenomena occur paralelly and end, according to my direct observations on *T. pediculus*, almost simultaneously), group together on one pole of the correlation dispersion field (Pl. I 1, 2, II 5—7). Of course, the border line between these two groups of individuals is never distinct, as it is shown in the diagrams. This fact is justified, if we take into consideration the difficulty in deciding whether the dentical ray has been completely developed (moreover, it grows later too), or if the old and new radial pins of the adhesive disc have been developed in the same way, and whether there are the same spaces between them.

Considering these two processes representing the growth, it seems to the author that the second way, i. e. the observation of the radial pins of the adhesive disc, would be more convenient for determination of process of aging in trichodina. Besides, defining developmental stages of the centripetal rays of the denticles in the species characterised by small dimensions of those elements (in *T. pediculus* the inner rays of the denticles are very large and of comparatively complex shape) can meet with difficulty.

Since it could be expected that the dimensions of the denticulate ring may depend on the number of the denticles. The author examined for each population the correlation between the diameter of the denticulate ring and the number of the denticles in a ring (diagrams 2, 4, 6 and 8). It has been proved, that in all examined populations the correlation coefficient is almost zero. Thus, it is evident that there is no dependence between the number of the denticles and the diameter of the denticulate ring. Moreover, the estimation of the dispersion of the points in correlation diagrams and the negative values of the

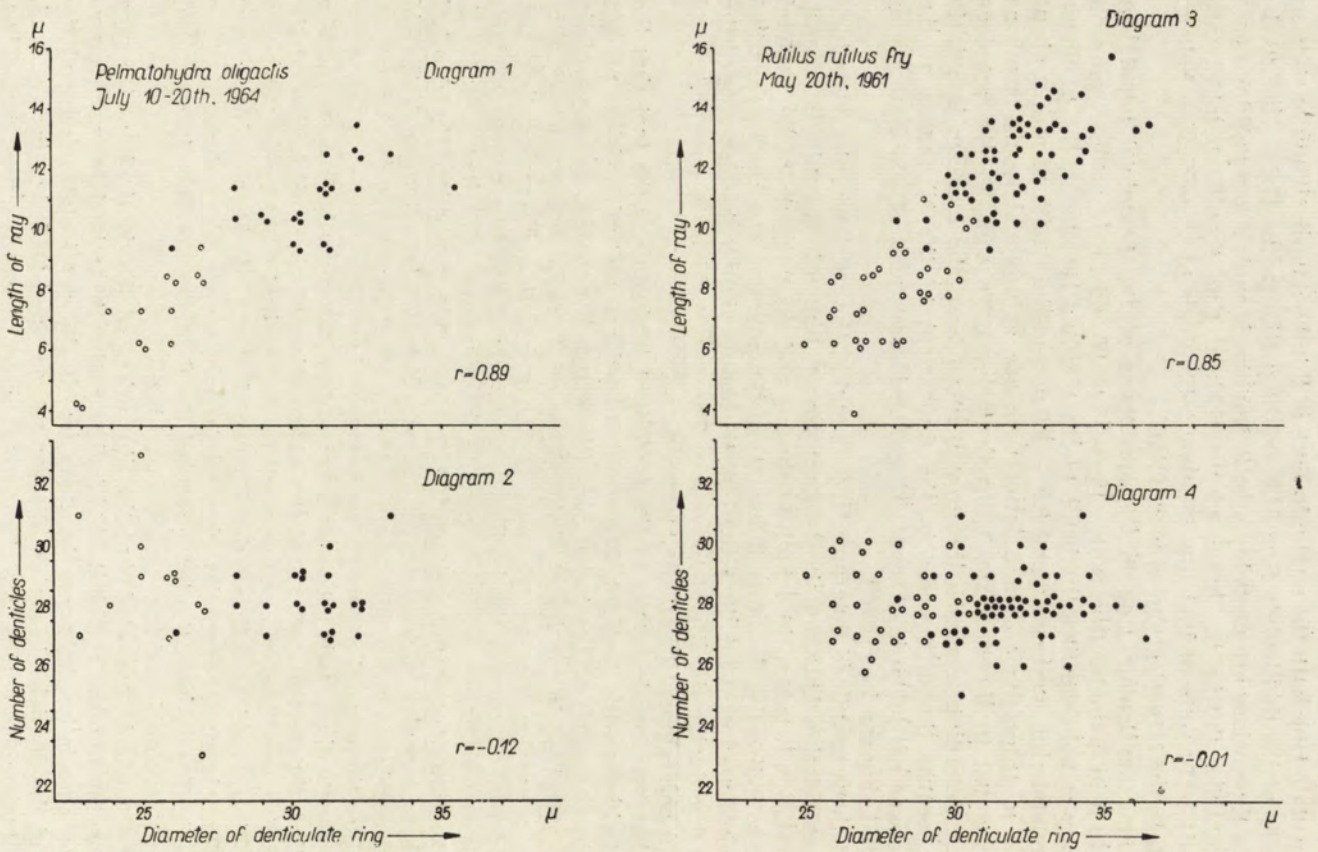

Fig. 3. Diagrams of correlation between length of rays and diameter of denticulate ring and between number of denticles and diameter of denticulate ring in examined populations of *Trichodina pediculus*, r — correlation coefficient, the white circles show the young specimens, the black the adult ones. The same in Fig. 4 and 5

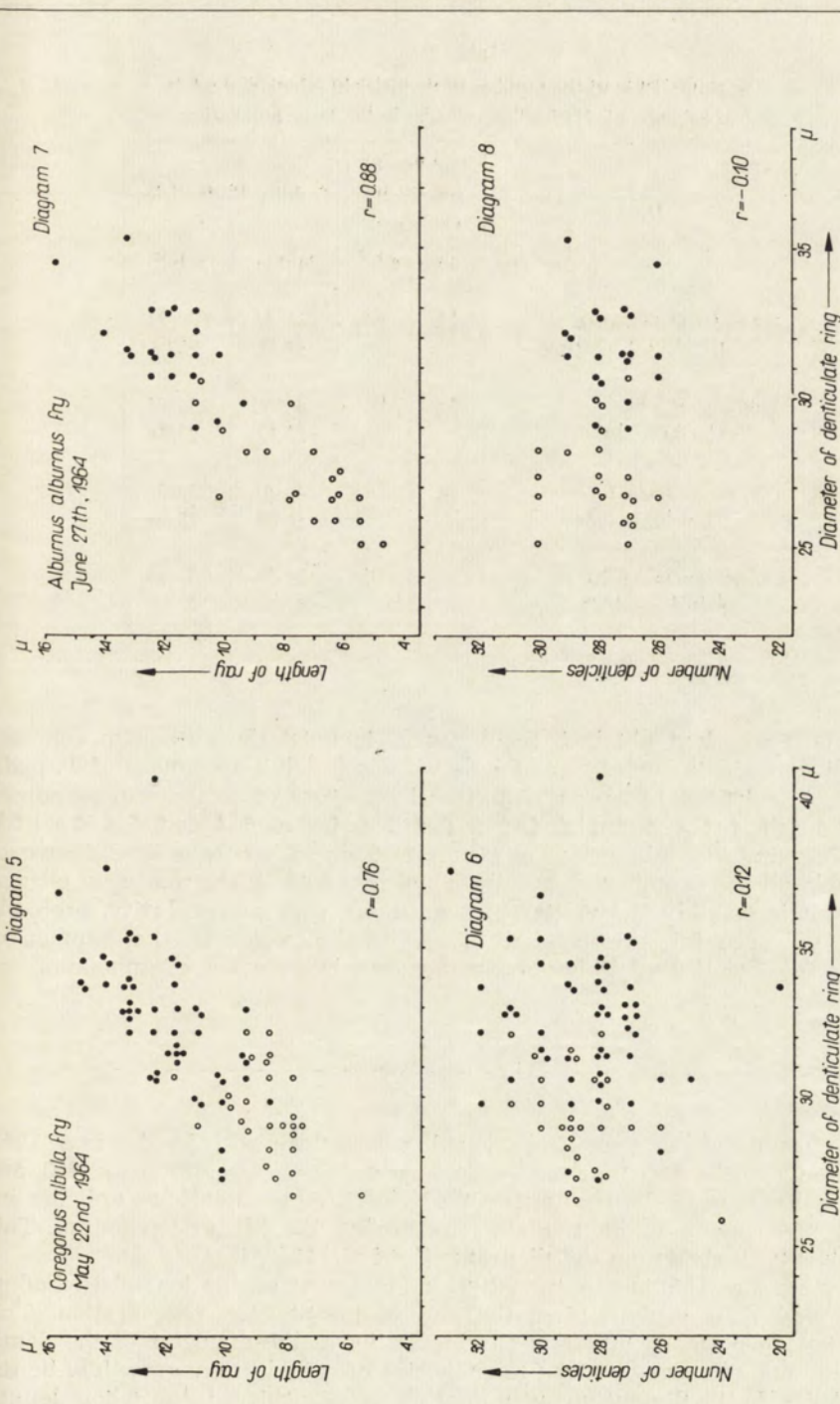

Fig. 4. Diagrams of correlation between length of rays and diameter of denticulate ring and between number of denticles and diameter of denticulate ring in examined populations of *Trichodina pediculus*, r — correlacion coefficient

Table 2

Comparision of the number of denticles in young and adult specimens of *Trichodina pediculus* in the same population

Host	Number of specimens examined		Number of denticles	
	young	adult	young	adult
Pelmatohydra oligactis 10—20th July, 1964	13	24	23—33 28.54	27—31* 28.08**
Rutilus rutilus fry 21st May, 1961	34	64	26—30 28.12	25—31 27.94
Coregonus albula fry 22nd May, 1964	28	54	24—31 28.68	22—33 28.50
Alburnus alburnus fry 27th June, 1964	21	20	26—30 27.95	26—29 27.55

* — the range of variation
** — the mean

correlation coefficient obtained many times, inclined the author to compare the number of the denticles in young as well as in adult specimens of *T. pediculus*. Those calculations have shown, that in the case of all the four examined populations the average number of the denticles in young specimens is a little higher than that in adult specimens (Table 2). This difference is small, however it occurs in all the examined populations and it cannot be the matter of chance. This result is possibly the matter of some more general regularity, probably it gives evidence for existence of the seasonal changes in the number of denticles in *T. pediculus*. This phenomenon requires further examination.

Discussion

The question of the growth of trichodina was dealt with by Laird 1953. He carried out the research on *Trichodina parabranchicola* Laird, 1953 and *T. multidens* Laird, 1953. He noticed the growth of the denticles and the increasing of diameter of denticulate ring during the life of trichodina. This growth has been shown on the diagrams (Laird 1953, text-fig. 2).

The studies carried out by the author on different populations of trichodina have proved their growth after the end of postdivision regeneration. This growth is shown among others in the increasing of the diameter of the denticulate ring and other elements of the adhesive disc, and in the growth of denticles. Besides, if the dimensions of a denticle are considered, the whole length or the length of its separate elements can be used. The author thinks the most representative would be measuring of the inner ray, because it is a linear ele-

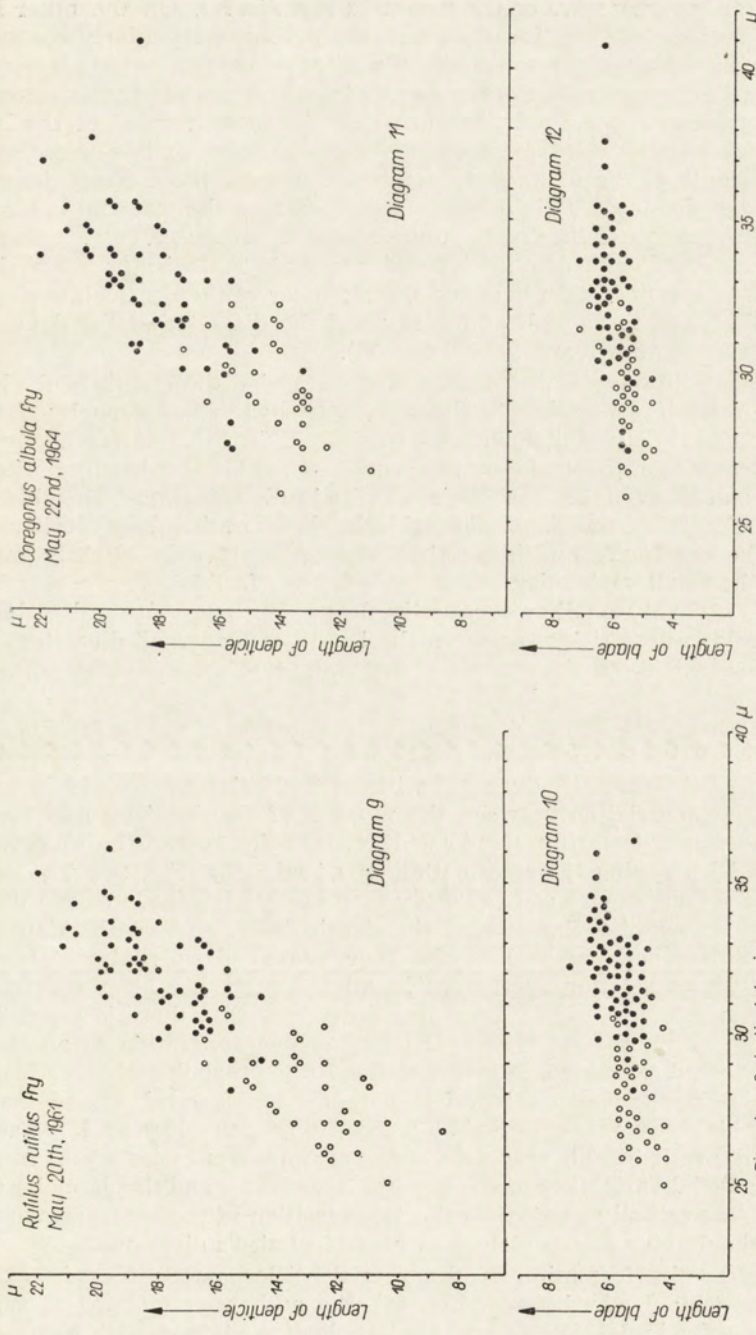

Fig. 5. Diagrams of correlation between whole length of denticle and diameter of denticulate ring and between length of blade and diameter of denticulate ring in two examined populations of *Trichodina pediculus*

ment and grows slowly and continually. Moreover, this measurement proved to be useful in the present work on the growth of *T. pediculus*. On the other hand, the author realises that this measurement has become particularly convenient in *T. pediculus*, which is characterised by well developed, very long inner rays. However, in the case of many other species in which the rays are shorter this method may prove less suitable. In such case the measurement of the length of the whole denticle would be recommended. Analysis of this measurement and of the length of the blade and correlation both of those dimensions with the diameter of the denticulate ring has been shown on the material taken from the two most numerous examined populations of *T. pediculus*. (Fig. 5, diagrams 9 — 12). As we see there are no distinct differences in *T. pediculus* in correlation between the length of the denticle and the diameter of the denticulate ring and correlation between the length of the ray and the diameter of the denticulate ring (compare diagrams 3 and 9, or 5 and 11).

At the same time the author thinks that measuring the length of the blade, as one of the factors pointing to the age of trichodina, as done by Laird (1953), is comparatively of little value. This part of denticle is formed relatively early and is very soon finished. Further growth of the blade is hardly noticeable. It can be stated even on the basis of Laird's diagrams in which the correlation dispersion for *T. parabranchicola* shows rather high positive correlation, whereas in *T. multidens* this correlation is only slightly marked because of the small variability of the blade length. In this case the correlation coefficient is probably small or eventually close to zero. The autor also obtained a small correlation coefficient between the length of blade and diameter of the adhesive disc in both of the examined populations of *T. pediculus* (diagrams 10 and 12).

Quite another matter to be discussed is the question of the variability of the number of denticles in trichodina. Laird 1953 pronounces on the possibility of formation of the denticles during the life of trichodina as it could be proved by the positive correlation between the number of the denticles and the diameter of the denticulate ring (Laird 1953, text-fig. 1). and the observations of such denticles during their formation (Laird 1953, Fig. 97). The results obtained by the author are contradictory to those got by Laird. No positive correlation between the diameter of the denticulate ring and the number of the denticles has been noticed in the four examined populations. In these populations the correlation coefficient in all the cases has been approximate to zero (digrams 2, 4, 6 and 8). But some data show that there is a possibility of increasing the number of the denticles from one generation to another, at least in the period examined. It seems to the author that this observation, if it would be confirmed, may explain Laird's diagram. Laird stated that the material for his study, was collected by him within the whole year. If we assume that Laird availed in his diagrams of the samples from whole year material and if the seasonal variability of the number of denticles and the diameter of the denticulate ring actually exist, then the juxtaposition of the measurements and characters should give such a picture as found in Laird's diagrams.

As concerns the formation of the new denticles among already existing ones, observed by Laird (1953, Fig. 97), the authors is inclined to suppose the following. Laird 1953 has observed trichodina stained with hematoxilin which does not give good picture of the adhesive disc and does not show many details in the structure of the denticles. In his study the author applied silver

impregnation method after Klein. This technique enables to obtain very good and distinct picture of the adhesive disc of trichodina, with their details visible very well. Lots of specimens have been photographed. The author has never observed formation of the new denticle in the already existing ring in several hundreds of the *T. pediculus* examined. As concerns the dividing denticles, observed by the author in other species of trichodina for several times, they should be considered as teratological cases. Those anomalies must have come into being during the formation of the denticulate ring after division. This has been pointed out, among others, in the study on ultrastructure of trichodina, specially in the paper of Favard, Carasso et Fauré-Fremiet 1963 in which the enormous complexity of the structure, particularly that of the adhesive disc, has been shown. The author thinks that in connection with this, such an important reconstruction of part of trichodina body which must have appeared in consequence of the formation of a new denticle, is impossible under normal conditions. There are no reasons to suppose that there is a possibility of increase of the denticle number during the individual life of trichodina.

On the basis of the already given data one can draw the following conclusions:

In *T. pediculus* a distinct individual growth is marked, which is seen among others in the growth of the denticles (considerable, visible increase of their length) and in the elongation of the diameter of the denticulate ring and the adhesive disc itself. This growth may be comparatively large. That is why the author would like to support his previously expressed opinion (Kazubski 1965), saying that if we want to obtain maximum comparative description of the species for taxonomy purposes, we must base our studies on adult specimens only. Young individuals with underdeveloped inner rays or with not completed reconstruction of radial pins of adhesive disc should be eliminated.

In the examined populations the lack of the positive correlation between the size of the adhesive disc and the denticulate ring and the number of denticles has been observed. That points out that the increase in the denticle number does not appear during the individual life of trichodina. Now, obtaining the negative correlation in several cases and stating that the average number of the denticles in the young specimens is a little higher than that in the adult specimens in all the populations examined suggests the existence of the periodic tendency to increase the number of the denticles from one generation to another (cyclomorphosis?).

Summary

On the example of *T. pediculus* the author evolves the previously expressed idea about the appearance of the growth of the elements of the adhesive disc in trichodina. Diuring the growth of trichodina not only the length of the denticle increases (particularly the length of the denticle ray) but also diameter of the denticulate ring and that of the adhesive disc. But the increase in the number of denticles has not been noticed during the individual life of trichodina. On the other hand some facts point out the possibility of the periodical increase in the number of denticles from one generation to another (cyclomorphosis?).

STRESZCZENIE

Autor rozwija, na przykładzie *Trichodina pediculus*, wyrażony poprzednio (Kazubski 1965), pogląd o występowaniu wzrostu elementów tarczy czepnej u trichodin. W czasie wzrostu trichodiny zwiększa się nie tylko wysokość haka (szczególnie długość promienia haka) ale także średnica wieńca haków oraz średnica tarczy czepnej. Nie stwierdzono natomiast zwiększenia się liczby haków w czasie indywidualnego życia trichodiny. Z drugiej strony pewne dane wskazują na możliwość okresowego zwiększania się liczby haków z pokolenia na pokolenie (cyklomorfoza?).

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EXPLANATIONS OF PLATES I—II

Trichodina pediculus (Ehrenberg) growth of elements of adhesive disc

Population from *Rutilus rutilus*

1—2: young individuals

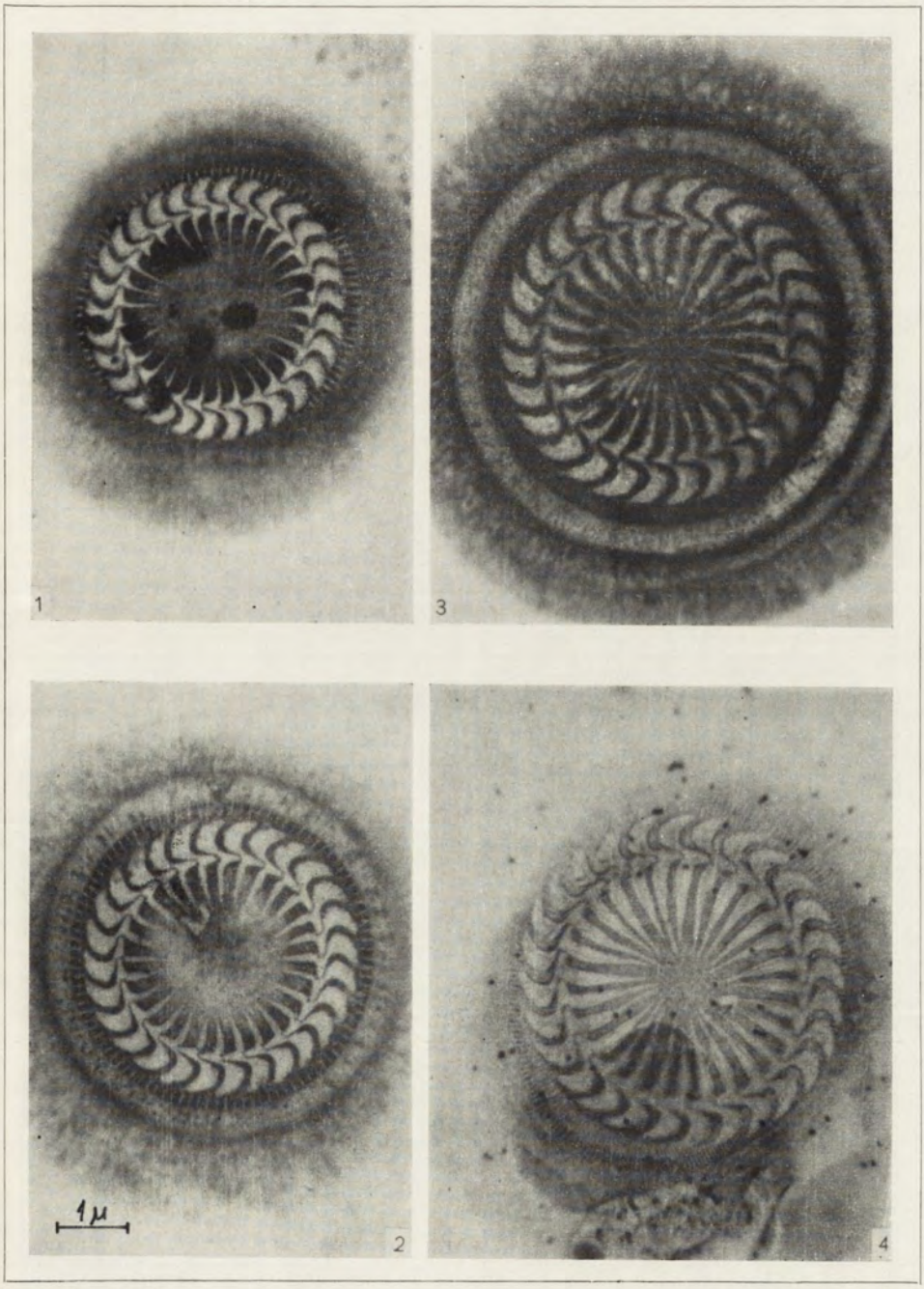
3—4: adult individuals; on phot. 4 the details of structure of inner rays are visible

Population from *Coregonus albula*

5—7: young individuals, succesive stages; doubling of radial pins is visible

8—9: adult individuals

All microphotographs in the same magnification (1000×)



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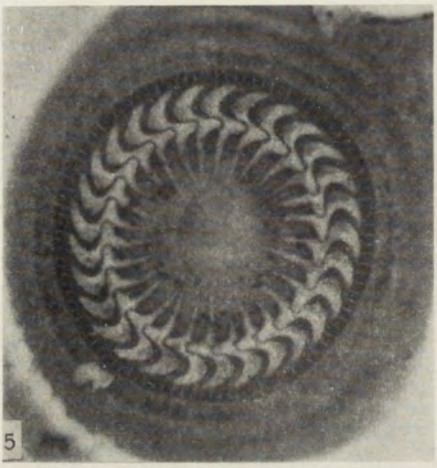

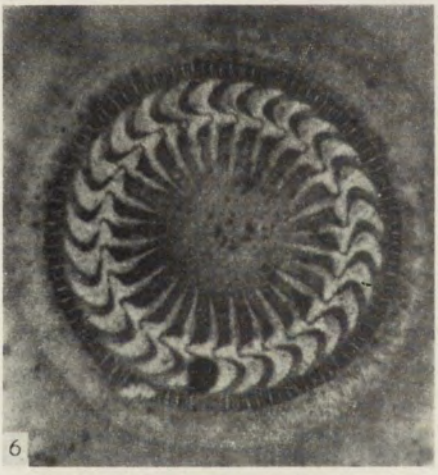

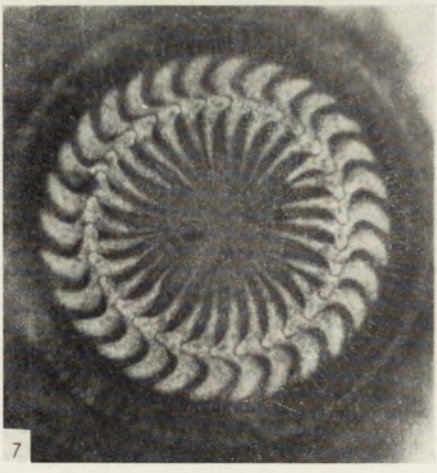

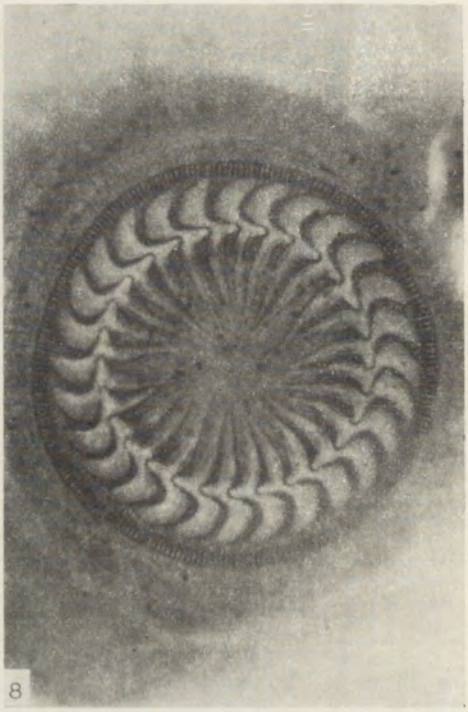

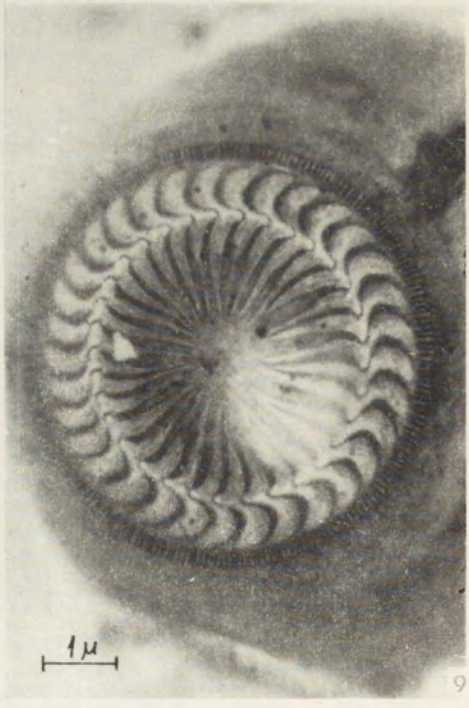

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Ядерный аппарат и некоторые структуры цитоплазмы *Helicoprorodon gigas* (*Holotricha, Gymnostomatida*)

The nuclear apparatus and some cytoplasmic structures of *Helicoprorodon gigas (Holotricha, Gymnostomatida)*

Крупная морская инфузория *Helicoprorodon gigas* (Kahl) — один из наиболее характерных представителей интерстициальной фауны литорального песка. Эта форма была впервые описана Калем (Kahl 1933, 1935) под названием *Chaenea gigas*, а позже выделена Форе-Фремье (Fauré-Fremiet 1950) в самостоятельный род *Helicoprorodon*. Морфологические описания этого вида приводятся также Боком (Bock 1952), Фьельдом (Fjeld 1955), Дражеско (Dragesco 1960) и Райковым (1960).

Географическое распространение *H. gigas* очень широкое, по-видимому, космополитное. Этот вид отмечен, в частности, в Балтийском и Северном морях (Kahl 1933, 1935; Bock 1952; Fjeld 1955), в Баренцовом и Белом морях (Райков 1960, 1962), на Атлантическом побережье Франции (Fauré-Fremiet 1950; Dragesco 1960) и на противоположной стороне Атлантики — на восточном побережье США (Fauré-Fremiet 1951), в Средиземном (Nobili 1957) и Черном (Ковалева 1966) морях, а также в тропической Атлантике (Мавритания — Dragesco 1965). Найден он и в бассейне Тихого океана — в Японском море (Райков 1963).

Несмотря на хорошую изученность внешней морфологии *H. gigas*, цитологические исследования этой формы еще никем не проводились. Задача настоящей работы — заполнить этот пробел.

Материал и методика

При выполнении данной работы мы располагали материалом из следующих районов:

1. Баренцово море, Дальнезеленецкая бухта (сборы 1958 и 1960 г.),
2. Белое море, Кандалакшский залив (сборы 1961 г.),
3. Японское море, Уссурийский залив (сборы 1962 г.),
4. Черное море, Крымский полуостров (сборы 1963 и 1964 гг.).[1]

[1] Материал по черноморским *H. gigas* собран В. Г. Ковалевой, которой автор искренне благодарен также и за помощь в обработке всего материала.

Использовались как тотальные препараты, так и срезы толщиной 5 мк (заливка в парафин). Для изготовления тотальных препаратов инфузории фиксировались смесью Ниссенбаума (Nissenbaum 1953); для срезов материал фиксировался сулемой с уксусной кислотой, смесями Ценнкера (с уксусной кислотой или с формалином), Буэна, Санфеличе, Шампи или Бенда.

Тотальные препараты окрашивались чаще всего по Фельгену или гемалауном; применялась также импрегнация протеинатом серебра (протарголом) по Бодиану в модификации Дражеско (Dragesco 1962). Срезы окрашивались: на ДНК — по Фельгену, на РНК — метиловым зеленым-пиронином или галлоцианином (из контрольных препаратов РНК удалялась рибонуклеазой или 1 N HCl при 60° в течение 10 мин.), на белок — сулемовым раствором бромфенолового синего. Кроме того, применялось окрашивание срезов железным гематоксилином, особенно после осмиевых фиксаторов и смеси Буэна.

Форма и число ядер

Helicoprorodon gigas имеет, как правило, один макронуклеус в виде длинной цепочки узелков, и несколько микронуклеусов. Однако, детальный анализ показывает значительную изменчивость ядерного аппарата даже в пределах одной популяции.

Форма макронуклеуса. Наиболее часто встречающаяся форма макронуклеуса — это одна непрерывная цепочка веретенообразных узелков, соединенных тонкими перемычками (Табл. I 1,2, II 5). Как правило, цепочка не вытянута в одну линию вдоль тела даже у вытянувшихся особей, а у фиксированных (сократившихся примерно в 2 раза) она всегда образует многочисленные петли и изгибы, так что ход цепочки иногда весьма запутан (Табл. I 1, 2, II 5). Реже (приблизительно у 10% особей) цепочка макронуклеуса не сплошная. а разделена на 2—4 не связанных друг с другом участка (Табл. II 6).

Размеры узелков макронуклеуса также бывают различными. Чаще встречаются особи с относительно небольшими узелками (Табл. I 1 и 3, II 4—6). Реже узелки длинные, колбасовидные (Табл. I 2). Возможно, что форма макронуклеуса с крупными узелками появляется незадолго до деления особи. Однако, поскольку в нашем материале делящихся особей не встретилось, мы не можем утверждать этого с достоверностью.

Обычно цепочка макронуклеуса занимает более или менее центральное положение в цитоплазме (Табл. I 1,2, II 5,6). Однако, вся цепочка может быть смещена к переднему (Табл. I 3) или, напротив, к заднему (Табл. II 4) концу тела.

Число узелков макронуклеуса у *H. gigas* сильно варьирует. Во всем изученном материале минимальное число узелков — 8, максимальное — 62. В отдельно взятых географических районах размах изменчивости следующий (в скобках указан модальный класс):

Баренцово море — от 8 до 24 узелков (Mo = 11—15),
Белое море — от 11 до 34 узелков (Mo = 21—25),
Японское море — от 17 до 27 узелков (Mo = 16—20),
Черное море — от 11 до 62 узелков (Mo = 31—35).

Таким образом, если *H. gigas* из Баренцова, Белого и Японского морей более или менее сходны по числу узелков макронуклеуса, то инфузории из Черного моря отличаются от них гораздо большей изменчивостью этого признака в сторону высоких значений. Модальное число узелков макронуклеуса у черноморских форм также заметно выше, чем в других районах.

Интересно сравнить эти данные с имеющимися в литературе. У *H. gigas* из

Кильской бухты 18—23 узелка макронуклеуса (Bock 1952), у формы из Ла-Манша — 15—30 узелков (Dragesco 1960). Следовательно, обе эти формы сходны по числу узелков с *H. gigas* из Баренцова, Белого и Японского морей. Однако, *H. gigas* из Осло-фиорда (Fjeld 1955) имеет 38—100 узелков макронуклеуса, т. е. больше напоминает черноморскую форму. Во всяком случае, еще преждевременно придавать этим различиям значение географической изменчивости.

Микронуклеусы *Helicoprorodon gigas* свободно рассеяны по цитоплазме (Табл. I 1—3, II 4). Число микронуклеусов варьирует в материале из Баренцова моря от 20 до 40, в беломорском от 16 до 35, в дальневосточном от 18 до 30 и в черноморском от 11 до 35, т. е. в целом по всем районам от 11 до 40 (модальный класс — от 16 до 20). Таким образом, по числу микронуклеусов инфузории из Черного моря не отличаются от других популяций так, как они отличаются по числу узелков макронуклеуса. Литературных данных по числу микронуклеусов у *H. gigas* нет.

Наряду с обычными экземплярами, в сборах из Баренцова, Белого и Черного морей встретились и безмикронуклеусные особи (Табл. II 5,6). Частота их встречаемости среди особей, изученных в этих районах, составила на Баренцовом море 6% (5 экземпляров из 82), на Белом — 4% (3 экз. из 71), на Черном — 12% (2 экз. из 16), а в среднем по всему материалу около 6%.

Микронуклеусы

Цитохимические особенности. Микронуклеусы *H. gigas* довольно крупные, овальной формы, длиной около 4 мк (Табл. III 7, IV 16, V 21—23). По Фельгену они окрашиваются очень ярко и вполне гомогенно (Табл. III 7, IV 16). Метиловым зеленым-пиронином они красятся в равномерно зеленый цвет, т. е. связывают только метиловый зеленый (Табл. V 21). После рибонуклеазы окрашиваемость микронуклеусов не изменяется. Интенсивная окрашиваемость микронуклеусов галлоцианином также не меняется ни после обработки срезов рибонуклеазой, ни после экстракции соляной кислотой. Отсюда следует вывод, что микронуклеусы содержат ДНК, но лишены РНК. Окрашивание микронуклеусов на белок — умеренной интенсивности (Табл. V 22, 23); этим методом хорошо выявляется оболочка микронуклеуса, плотно прилегающая к хроматину.

Митозы микронуклеусов протекают у *H. gigas* совершенно несинхронно и не связаны с делением цитоплазмы. Число одновременно делящихся микронуклеусов в одной особи обычно не превосходит 2—3, т. е. около 10% от общего числа микронуклеусов. Асинхрония митозов микронуклеусов, несомненно, является причиной широкой изменчивости числа микронуклеусов у особей одной популяции.

Ход митоза довольно своеобразен. В ранней профазе оболочка микронуклеуса вздувается, а хроматин приобретает узловато-сетчатое строение (Табл. III 8). Позже хромосомы микронуклеуса становятся более толстыми и гладкими и располагаются внутри ядра в виде дугообразно изогнутых пучков (Табл. III 9). Весьма вероятно, что на самом деле это один пучок хромосом, сложным образом скрученный внутри микронуклеуса. На следующей стадии хромосомы укорачиваются еще больше, и появляются два „полюса" под ядерной оболочкой, к которым сходятся концы хромосом. Поскольку эти „полюсы" еще не находятся на диаметрально противоположных концах микронуклеуса, хромосомы, проходя от одного полюса до другого, описывают внутри ядра сложные петли

(Табл. III 10). Затем „полюсы" расходятся на противоположные концы ядра, и весь микронуклеус становится веретенообразным. Хромосомы укорачиваются еще сильнее и приобретают вид прямых нитей или слабо изогнутых дуг, соединяющих оба полюса (Табл. III 11). К концу профазы происходит продольное расщепление хромосом (Табл. III 12).

В метафазе двойные хромосомы максимально укорачиваются, собираясь в экваториальной зоне веретена. Концы хромосом соединены с полюсами тонкими ахроматиновыми фибриллами (Табл. III 13).

В анафазе две группы дочерних хромосом расходятся к полюсам, а веретено начинает перешнуровываться. На этой стадии хромосомы в дочерних пластинках одинарные (следовательно, хроматиды метафазных хромосом разошлись — Табл. III 14). Наконец, в телофазе интерзональная область веретена вытягивается в длинный фибриллярный тяж, соединяющий дочерние микронуклеусы (Табл. III 15).

Оболочка микронуклеуса во время митоза не растворяется, как и обычно у инфузорий (обзор: Райков 1967).

Интерпретация этого типа митоза затруднительна. По-видимому, „полюсы", появляющиеся в профазе, соответствуют внутриядерным центросомам, хотя никаких гранул в них различить не удается. Продольное расщепление хромосом в поздней профазе происходит в соответствии с классической схемой митоза, но вот механизм разделения хроматид и расхождения их в дочерние ядра понять очень трудно. Хромосомы все время ориентированы вдоль оси веретена, что несовместимо с представлением о наличии у них локализованных центромеров. Неоднократно предполагалось, что при митозах этого типа происходит скольжение одной хроматиды относительно другой в противоположные стороны (*Gastrostyla* — Weyer 1930, *Conchophthirius* — Kidder 1934, *Urostyla* — Raabe 1946). Однако, это означало бы, что сестринские хроматиды движутся к полюсам негомологичными концами вперед.

Девиде и Гейтлер (Devidé und Geitler 1947, Devidé 1951) показали, что у ряда инфузорий (*Colpidium, Euplotes, Chilodon*) при митозе микронуклеуса истинные хромосомы не видны, а наблюдаемые палочковидные образования суть агрегаты многих хромосом. Такие агрегаты делятся, по данным этих авторов, поперек, а число их непостоянно. Насколько это объяснение приложимо к микронуклеусам с отчетливым продольным расщеплением хромосом (*Gastrostyla, Conchophthirius, Urostyla, Helicoprorodon*) — еще совершенно не ясно.

Макронуклеус

Хроматиновые элементы. Хроматин макронуклеуса *H. gigas* обычно выглядит гомогенным или мелкозернистым. По Фельгену он чаще всего окрашивается равномерно и очень интенсивно; не красятся лишь ячейки, в которых располагаются нуклеолы (Табл. IV 16, 17). Перемычки между узелками макронуклеуса также дают положительную реакцию, хотя и менее яркую, чем сами узелки.

Однако, у особей с крупными, длинными узелками макронуклеуса (Табл. I 2) строение хроматина иное. В центре каждого узелка появляется крупная полость, очень слабо красящаяся по Фельгену. В периферической зоне узелка становятся отчетливо видны хроматиновые нити, толщиной около 0,5 мк и длиной до 4—5 мк, ориентированные в узелки преимущественно радиально (Табл. IV 18). Поскольку такие картины удается изучать только на срезах, фактическая дли-

на нитей может быть гораздо больше. В перемычках между узелками хроматин остается гомогенным.

На тонких тангенциальных срезах таких макронуклеусов хроматиновые нити видны особенно хорошо (Табл. IV 19). Некоторые нити прослеживаются здесь на значительном протяжении. Среди нитей видны Фельген-отрицательные нуклеолы.

Наконец, встречаются особи, хроматиновые нити макронуклеуса которых имеют не равномерную толщину, а состоят из овальных элементов, соединенных друг с другом в длинные цепочки. Очень часто такие цепочки лежат попарно, причем элементы парных цепочек располагаются строго друг против друга (Табл. IV 20). Создается впечатление, что парные цепочки — сестринские, получившиеся в результате удвоения одной хроматиновой нити.

Толкование таких картин представляет известные трудности. Логичнее всего предположить, что хроматиновые нити макронуклеуса суть хромосомы, проходящие на определенной стадии клеточного цикла редупликацию. Аналогичные хроматиновые нити, часто располагающиеся попарно, описывались в полиплоидных макронуклеусах *Paramecium* (Schwartz 1958; Saito and Sato 1961), *Tetrahymena* (Sato and Saito 1959), *Vorticella* (Müggе 1957), *Bursaria* (Ruthmann und Heckmann 1961) и других инфузорий.

Однако, генетические данные показывают, что в полиплоидном макронуклеусе хромосомы должны быть объединены в геномы; иначе трудно понять механизм деления полиплоидного макронуклеуса (см. обзоры: Grell 1964, Райков 1967). Грель (Grell 1953, 1964) предположил, что хромосомы каждого генома макронуклеуса соединены в виде цепочек в сборные хромосомы. Такие цепочки из палочковидных элементов (хромосом?) были действительно найдены Рутманном (Ruthmann 1963) в макронуклеусе *Loxophyllum meleagris*.

Картины цепочек из мелких хроматиновых элементов, встречающиеся у *H. gigas* (Табл. IV 20), очень напоминают сборные хромосомы макронуклеуса *Loxophyllum*. Поэтому можно думать, что мелкие элементы этих цепочек и есть истинные хромосомы, а сами цепочки — сборные хромосомы, расщепляющиеся продольно без распадения на свои составные элементы. Границы между истинными хромосомами видны только на некоторых стадиях цикла редупликации; остальное время хроматиновые нити (сборные хромосомы?) кажутся сплошными или не видны вовсе.

Эта точка зрения, теоретически наиболее вероятная, наталкивается, правда, на некоторые трудности. Главная из них — это несоответствие размеров хроматиновых элементов, входящих в состав цепочек в макронуклеусе (Табл. IV 20), и размеров митотических хромосом микронуклеуса (Табл. III 11—14). Последние намного длиннее при более или менее одинаковой толщине. Хромосомы микронуклеуса не соответствуют и целым цепочкам в макронуклеусе: те, по-видимому, могут быть еще намного длиннее, чем хромосомы микронуклеуса. Может быть, это несоответствие вызвано тем, что хромосомы микронуклеуса тоже не одиночные, а сборные, как это предполагали Девиде и Гейтлер (Devidé und Geitler 1947, Devidé 1951). Может быть также, что хромосомы микронуклеуса политенные и потому крупнее мелких хроматиновых элементов (одиночных хромосом?) макронуклеуса.

Хроматин макронуклеуса содержит, наряду с ДНК, также рибонуклеиновую кислоту (РНК), но в небольшом количестве. Метиловый зеленый — пиронин красит хроматин в голубой цвет (Табл. V 21), а после обработки рибо-

нуклеазой — в чисто зеленый. Хроматин дает интенсивную реакцию на белок (Табл. V 22). В макронуклеусах с радиальными хроматиновыми нитями белок хроматина концентрируется главным образом в этих нитях. Центральная полость таких макронуклеусов белка не содержит или содержит очень мало (Табл. V 23).

Нуклеолы. Нуклеолы макронуклеуса фельген-отрицательные, обычно мелкие, многочисленные (Табл. IV 16). Реже нуклеолы более крупные, полиморфные (Табл. IV 17). Нуклеолы имеются только в узелках четковидного макронуклеуса, а в перемычках между узелками их никогда не бывает (Табл. IV 16, 17, V 21, 22).

Нуклеолы, как обычно, богаты РНК: они ярко красятся пиронином (Табл. V 21) и галлоцианином; их базофилия снимается действием рибонуклеазы. В нуклеолах очень высокая концентрация белков (Табл. V 22). Нуклеолы имеются и в макронуклеусах с нитчатым строением хроматина, но отсутствуют в их центральной полости (Табл. V 23).

Оболочка макронуклеуса одевает как его узелки, так и перемычки между ними. Цитохимически в ней обнаруживаются белки (Табл. V 22, 23).

Некоторые структуры цитоплазмы

Цитоплазма *H. gigas* сильно вакуолизирована, богата РНК (Табл. V 21). После окраски железным гематоксилином, а также сулемовым раствором бромфенолового синего в ней выявляются овальные или палочковидные митохондрии (Табл. V 22, 23).

У *H. gigas* цитоплазма богата различными фибриллами. На переднем конце тела располагается трубчатая глотка, окруженная длинными трихитами. Последние образуют настоящий палочковый аппарат, как у типичных *Cyrtophorina* (Табл. VI 24). На поперечных срезах видно, что трихиты располагаются двумя концентрическими венчиками, приблизительно по 30 трихитов в каждом. Кроме того, в окологлоточной цитоплазме видны более тонкие фибриллы, поддерживающие палочковый аппарат (Табл. VI 24).

Пучки трихитов, похожих на окологлоточные, имеются и в цитоплазме. Они располагаются в эндоплазме, ориентированы беспорядочно и достигают значительной длины. Упаковка трихитов в пучках довольно рыхлая (в отличие от глоточных трихитов). Трихиты особенно хорошо выявляются после серебрения протарголом и имеют вид прямых или слегка извилистых нитей (Табл. VI 26, 27). Как глоточные, так и цитоплазматические трихиты дают четко положительную реакцию на белок (Табл. V 23). РНК они не содержат.

Кроме того, протаргол выявляет в цитоплазме многочисленные короткие изогнутые нити неизвестной природы (Табл. VI 26, 27).

Серебрение протарголом четко обнаруживает также и кинетосомы (Табл. VI 25). У *H. gigas* кинетосомы одинарные, располагаются в рядах очень тесно друг к другу. Ресничные ряды проходят по телу спирально, число их около 40.

Резюме

Морская инфузория *Helicoprorodon gigas* (Kahl) имеет один четковидный макронуклеус и от 11 до 40 микронуклеусов. Число узелков макронуклеуса варьирует от 8 до 62. Около 6% всех особей оказались безмикронуклеусными. Микронуклеусы содержат ДНК и умеренное количество белков. РНК в них отсутствует. Митозы микронуклеусов несинхронны и не связаны с делением

цитоплазмы. Во время митоза хромосомы длинные, нитевидные, ориентированы вдоль веретена, расщепляются продольно. Оболочка микронуклеуса при митозе сохраняется. Хроматин макронуклеуса содержит ДНК, небольшое количество РНК и много белков. В известные периоды клеточного цикла в нем выявляются многочисленные хроматиновые нити, иногда состоящие из парных цепочек мелких овальных элементов. Возможна интерпретация нитей как сборных хромосом, а мелких элементов — как истинных хромосом. Нуклеолы макронуклеуса многочисленные, богатые РНК и белком. Кратко описаны глоточные и цитоплазматические трихиты, а также кинетосомы после серебрения протарголом.

SUMMARY

The typical marine sand dwelling ciliate *Helicoprorodon gigas* (Kahl) has been studied using collections from the Barentz, White, Black and Japan seas. This species has one moniliform macronucleus and 11 to 40 micronuclei (Pl. I 1—3, II 4). About 6 per cent of individuals are amicronucleate (Pl. II 5, 6). The macronuclear chain is always wound and folded, and sometimes even fragmented into a number of pieces (Pl. II 6). The number of macronuclear nodes varies from 8 to 62; the Black sea infusorians differ from other populations by their especially wide range of variation of this number. Numbers of macronuclear nodes above 34 are present in Black sea material only.

The micronuclei are large, compact, and strongly Feulgen-positive (Pl. III 7, IV 16). They contain no RNA (Pl. V 21) and a moderate quantity of proteins (Pl. V 22, 23).

Mitoses of the micronuclei are completely asynchronous and independent from cytokinesis. In prophase long wound chromosomes are seen (Pl. III 8—10), which become then oriented along the nucleus and longitudinally split (Pl. III 11—12). At metaphase they shorten (Pl. III 13). The mode of anaphase chromatid separation is not clear; gliding of chromatids in opposite directions is not excluded. The nuclear membrane remains intact throughout the mitosis. It is not clear whether micronuclear chromosomes are single or composite in the sense of Devidé and Geitler (1947).

The chromatin of the macronucleus looks usually homogeneous (Pl. IV 16—17), but in specimens with large macronuclear nodes (before division?) it becomes fibrous (Pl. IV 18—19). The centers of such nodes are hollow (Pl. IV 18, V 23). The chromatin threads can become double and subdivided into small elements connected in a chain-like manner (Pl. IV 20). The interpretation of these chains as composite chromosomes, the small elements being true chromosomes, is possible. The macronuclear chromatin contains little RNA (Pl. V 21) and much protein (Pl. V 22, 23).

Macronuclear nucleoli are numerous, rich in RNA (Pl. V 21) and protein (Pl. V 22, 23).

Some cytoplasmic structures are briefly described: mitochondria (Pl. V 22, 23), buccal trichites (Pl. VI 24), cytoplasmic bundles of trichites (Pl. VI 26, 27), and kinetosomes (Pl. VI 25), the latter two after Protargol impregnation.

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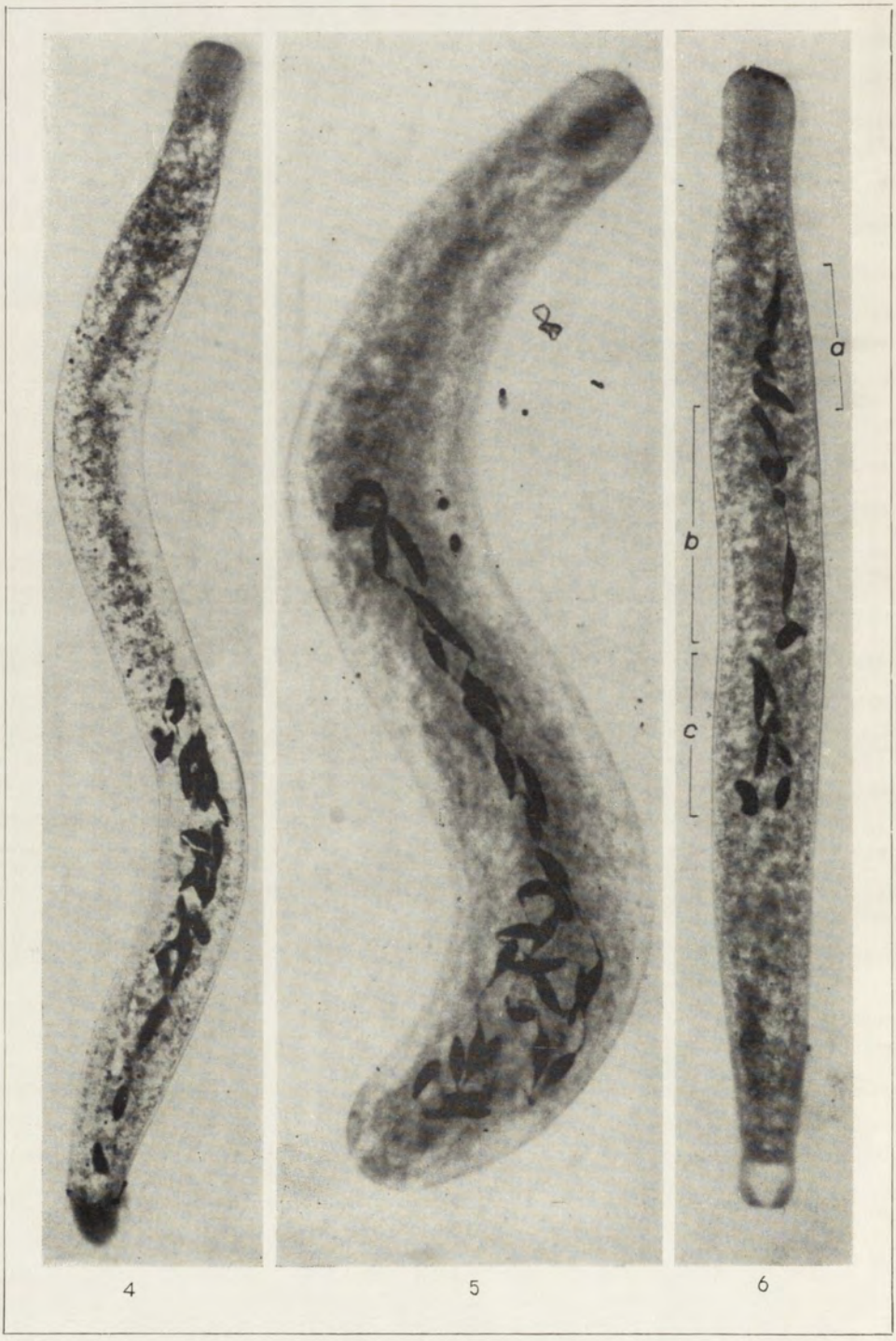

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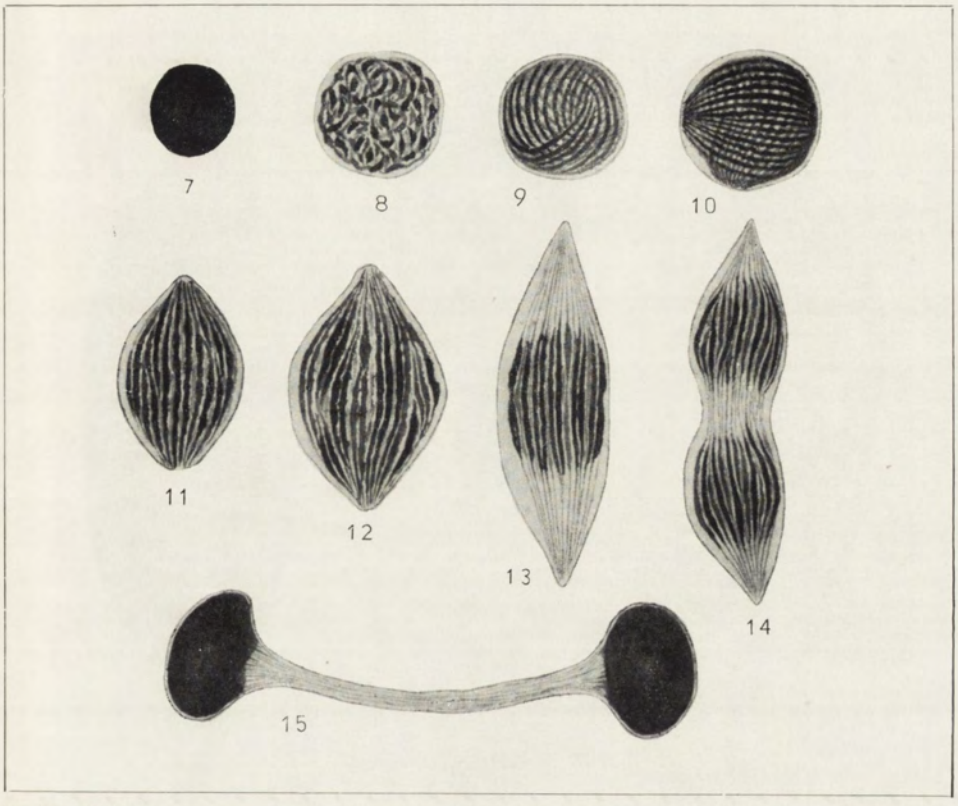

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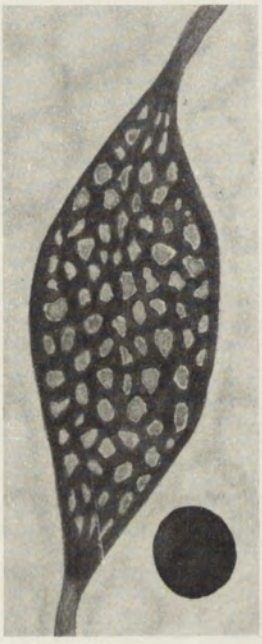

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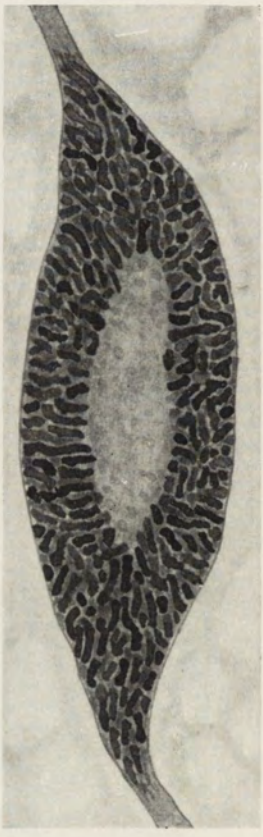

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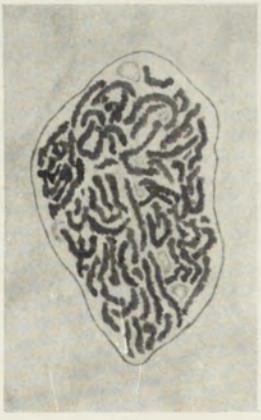

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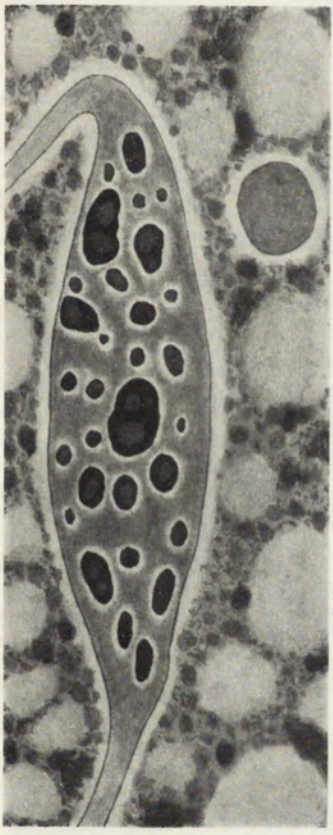

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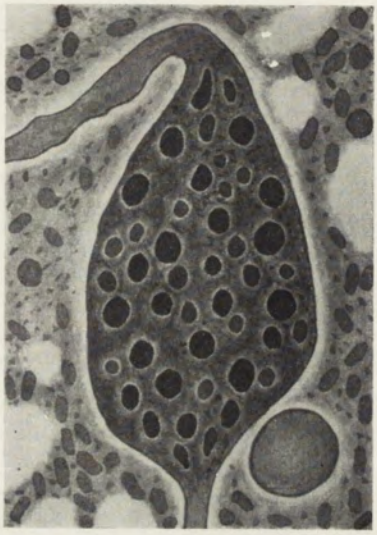

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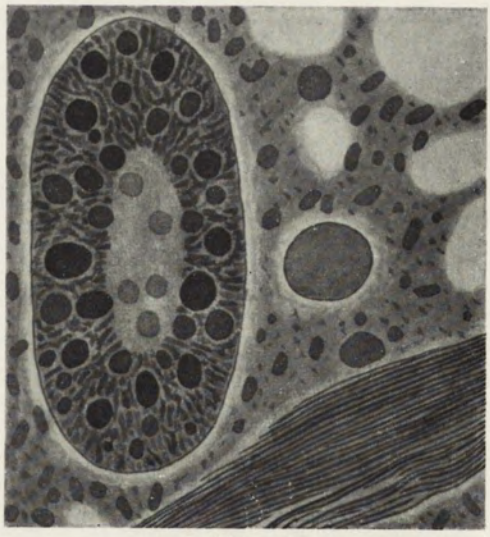

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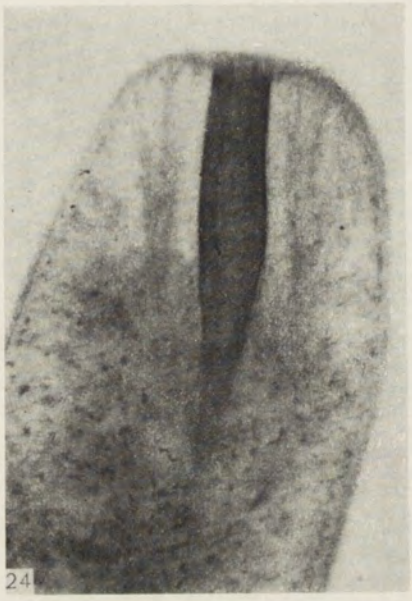

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ОБЪЯСНЕНИЕ ТАБЛИЦ I—VI

Тотальные препараты *Helicoprorodon gigas* (Kahl)

1: Макронуклеус в виде сплошной цепочки с мелкими узелками; много микронуклеусов; железный гематоксилин, 240×
2: Макронуклеус в виде сплошной цепочки с крупными узелками; много микронуклеусов; железный гематоксилин, 300×
3: Макронуклеус в переднем конце тела; много микронуклеусов; гемалаун, 170×
4: Макронуклеус в заднем конце тела; много микронуклеусов; гемалаун, 155×
5: Макронуклеус в виде сплошной цепочки; безмикронуклеусная особь; гемалаун, 300×
6: Макронуклеус из трех независимых участков (*a*, *b*, *c*); безмикронуклеусная особь; гемалаун, 200×

Митоз микронуклеуса. Рисунки со срезов. Фельген — лихтгрюн, 3200×

7: Покоющийся микронуклеус
8: Ранняя профаза
9, 10: Средняя профаза
11: Поздняя профаза с одинарными хромосомами
12: Удвоение хромосом в конце профазы
13: Метафаза
14: Анафаза
15: Телофаза

Строение макронуклеуса (всюду изображен только один его узелок). Рисунки со срезов. Фельген — лихтгрюн, 3200×

16: Узелок макронуклеуса с мелкими нуклеолами; справа внизу микронуклеус
17: Узелок макронуклеуса с крупными полиморфными нуклеолами
18: Крупный узелок макронуклеуса с центральной полостью и нитчатым хроматином
19: Тангенциальный срез макронуклеуса, видны хроматиновые нити
20: То же, видны двойные цепочки хроматиновых элементов

Цитохимия ядер. Рисунки со срезов, 3200×

21: Узелок макронуклеуса и микронуклеус (справа); метиловый зеленый — пиронин
22: Узелок макронуклеуса и микронуклеус (справа внизу); сулема — бромфеноловый синий
23: Узелок макронуклеуса (с нитчатым хроматином и центральной полостью) и микронуклеус (правее центра); справа снизу — пучок цитоплазматических трихитов; сулема — бромфеноловый синий

Структуры цитоплазмы

24: Передний конец тела (тотальный препарат); виден палочковый аппарат глотки; железный гематоксилин, 1000×
25: Кинетосомы в спиральных рядах (виден край тела); тотальный препарат, серебрение протарголом, 1850×
26, 27: Пучки цитоплазматических трихитов; тотальные препараты, серебрение протарголом, 1850×

EXPLANATION OF PLATES I—VI

Whole mounts of *Helicoprorodon gigas* (Kahl)

1: Moniliform macronucleus with small nodes, many micronuclei; iron haematoxylin, 240×
2: Moniliform macronucleus with large nodes, many micronuclei; iron haematoxylin, 300×
3: Macronucleus in the anterior body end, many micronuclei; haemalum, 170×
4: Macronucleus in the posterior body end; many micronuclei; haemalum, 155×
5: Macronucleus moniliform, no micronuclei; haemalum, 300×
6: Macronuclear chain divided into three sections (*a*, *b*, *c*); no micronuclei; haemalum, 200×

Micronuclear mitosis. Drawings from sections, Feulgen — Light green, 3200×

7: Resting micronucleus
8: Early prophase
9, 10: Middle prophase
11: Late prophase (chromosomes single)
12: Doubling of chromosomes by the end of prophase
13: Metaphase
14: Anaphase
15: Telophase

Macronuclear structure (only one node shown in each figure). Drawings from sections, Feulgen — Light green, 3200×

16: Macronuclear node with small nucleoli; micronucleus at lower right
17: Macronuclear node with large polymorphous nucleoli
18: Large hollow macronuclear node with fibrous chromatin
19: Tangential section of a macronuclear node showing chromatin threads
20: The same, but showing double chains of chromatin elements

Cytochemistry of nuclei. Drawings from section, 3200×

21: Marconuclear node and a micronucleus (at upper right); Methyl green — pyronin
22: Macronuclear node and a micronucleus (at lower right); Mercuric Bromphenol blue
23: Macronuclear node (with fibrous chromatin and central cavity); micronucleus at right center; bundle of cytoplasmic trichites at lower right; Mercuric Bromphenol blue

Cytoplasmic structures

24: Anterior body end showing pharyngeal trichites; whole mount, iron haematoxylin, 1000×
25: Kinetosomes in spiral rows at body margin; whole mount, Protargol, 1850×
26, 27: Bundles of cytoplasmic trichites; whole mounts, Protargol, 1850×

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Traumatic disturbance of cell division and regeneration of fragments derived from dividing individuals *Urostyla*

Zakłócenia traumatyczne podziału i regeneracja fragmentów z osobników dzielących się *Urostyla*

The process of division in *Ciliata* may be manifested as consecutive phases of changes in the nuclear apparatus and in the superficial structures. The nuclear apparatus may divide into a double number of components in a simple manner as e.g. in *Tetrahymena, Myxophyllum* or, in the case of forms with a dispersed nuclear apparatus, (*Stentor, Urostyla, Dileptus*) the division of Ma is preceded by condensation of the nuclear material.

The formation of the daughter cells preceded by appearing of new oral primordia for the opisthe (*Tetrahymena, Stentor*), or as in the case of *Hypotricha* by formation of new sets of the oral and somatic ciliature, and by resorption of the old paternal ciliature.

In the litterature, a number of factors had been reported which may involve disturbances in the normal course either of the nuclear apparatus division (temperature, poisons), or in formation of the ciliature primordia (temperature, poisons, operation) or — at last — in formation of the division furow (temperature, operations etc). These problems have been recently studied by Frankel 1960, 1964 b, 1965, Gavin 1965, Gavin and Frankel 1966, Tartar 1961, 1966, Hashimoto 1961, Eberhardt 1962, Wise 1965 a, Golińska 1966 and oth.

Numerous investigations indicate that the two different division processes as formation of primordia and constriction may occur independently of each other, e.g. hampering of the oral primordia formation should not obligatory inhibit simultaneously the constriction between the daughter individuals which leads to formation of astomatic individuals (Frankel 1961, 1964 a), whereas the arrest of constriction without impairing the primordia leads to formation of doublets (Fauré-Frèmiet 1948, Totwen-Nowakowska 1965).

In *Hypotricha,* the inhibition of the primordia development occurs only in the very early division stages when only the primordium of AZM of opisthe has been formed and the primordia of the somatic cirri are absent (Hashimoto 1961, Wise 1966 a). In more advanced stages, the impairment of primordia by operation or by the UV irradiation fails to interrupt their development and the damage is repaired in the post-division regeneration (Dembowska 1925) or in the course of the subsequent division (Wise 1965 a).

The aim of the present research was to study in what manner occurs the

regeneration of fragments originating from dividing individuals and — on the other hand — what is the efect of traumatic impairments on the course of the division process. Three species: *Urostyla grandis* Ehrenberg, 1838, *U. weissei* Stein, 1858 and *U. cristata* Jerka-Dziadosz, 1965 were the object of study. Since those species differ from one another in the localization of division primordia, (Jerka-Dziadosz 1963, 1964, 1965 b), it was anticipated to obtain differences in the traumatic disturbances of division. This would provide a possibility of finding out some species specifities as well as some more general features which might have a character of more extensive regularities.

Materials and methods

The methods of culture of *Urostyla grandis, U. cristata* and *U. wessei* were reported in the previous papers (Jerka-Dziadosz 1963, 1964, 1965 b). For experiments dividing individuals were used. Ciliates were operated at three different division stages: 1. at early stage prior to the condensation of Ma, 2. at the stage with the condensed Ma and 3. after the fission of Ma when the division furrow is already well developed. Definite body parts of the ciliate were cut off: a fragment of proter, fragment of opisthe or fragments as well of proter as of opisthe simultaneously. The operation line ran nearer the furrow or nearer the distal parts of the individual. All three operation types were performed on all three species. Every operation type was repeated 25—30 times.

Operations were carried out manually under the stereoscopic microscope at 100 × magnification, by means of a suitably sharpened needle. The operated individuals were transferred from the culture upon a cover slide and observed in a suspended drop under the microscope. No immobilization treatment ether chemical nor mecanical was applied during observation.

In fixed preparations, the nuclear apparatus was stained with the Feulgen's method and the ciliary apparatus with the iron hematoxyline after Parducz.

Results

The morphogenetic processes occurring in time of division and regeneration in the three species studied had been described in the previous articles of Jerka-Dziadosz 1963, 1964 a, 1965 b. In all three species, the whole ciliature arises during division and regeneration. In both processes, the localization of morphogenetic areas, the sequence of formation and of separation of primordia are very similar.

In *Urostyla grandis* all the categories of cirri and the oral ciliature of the opisthe arise in the middle of the ventral body surface (Fig. 1 A_1). The oral ciliature of the opisthe and all the categories of somatic cirri of proter and opisthe differentiate of this initially uniform mass of cilia (Jerka-Dziadosz 1963). In *Urostyla cristata* each cirri category arises at another spot of the cell (Fig. 1 B_1). At first the primordium of AZM of opisthe is formed, then in three various places of every offspring arise: in the middle — the primordia of the frontal, ventral and transversal (FVT) cirri and on the sides, the primordia of the marginal ones (Jerka-Dziadosz 1964). The pattern of the division morphogenesis in *U. weissei* is very similar to that in *U. cristata*. Here various categories of cirri arise also in three places of the cell (Fig. 1 C_1).

The macronucleus of all three species condenses in division as to form one mass and subsequently divides itself into a double number of components for the offsprings. At this time Mi divides as well (R a a b e 1946, 1947).

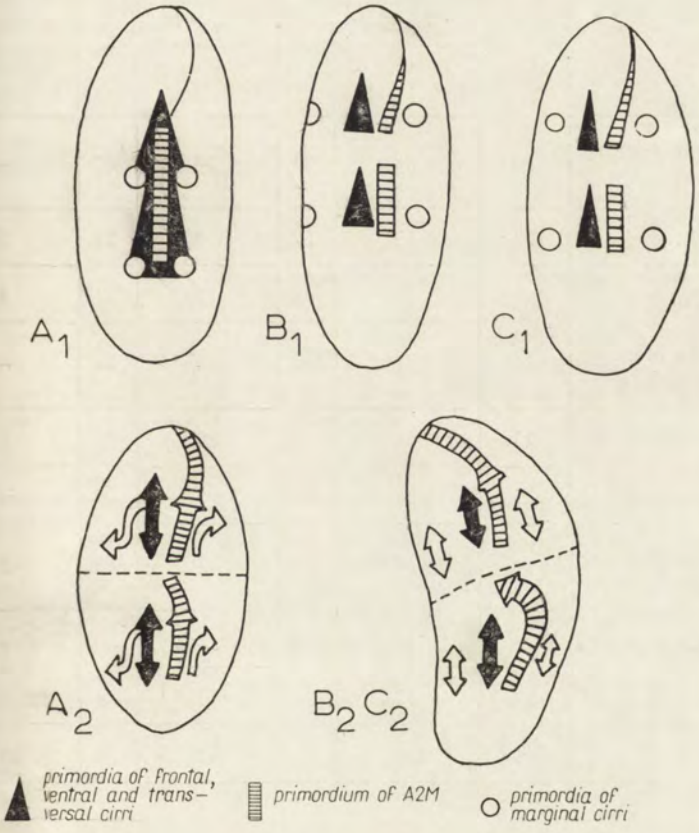

Fig. 1. Scheme of disposition of new ciliature primordia during division in *Urostyla grandis* (A), *U. cristata* (B) and *U. weissei* (C); directions of dispersion of primordia and course of the division furrow — *U. grandis* (A), *U. cristata* and *U. weissei* — (B_2, C_2), (description in text)

Urostyla cristata

The division stages of this ciliate are rather easily discernable owing to the characteristic changes of shape. The nuclear apparatus may be observed in the living material which simplifies very much the recognition of the division stage. The results of experiments are presented in the Table 1. Out of 244 operated individuals 65% divided normally after the same elapse of time as separate the unimpaired individuals. 3—5 hrs. from the moment of fission, in the individuals with the traumatic disturbances begin to arise the primordia of the new regeneration ciliature.

Table 1
Results of dividing individuals of *Urostyla cristata*

Type of operation		Number of operations	Results of operation					
			separation of speciments		single resorption		multiple resorption	
			number of individuals	%	number of individuals	%	number of individuals	%
Proter damaged	Ma prior to condensation	24	8	33	16	67	—	—
	Ma condensed	33	19	57	9	27	5	15
	Ma separated	49	30	61	15	31	4	8
Opisthe damaged	Ma prior to condensation	21	21	100	—	—	—	—
	Ma condensed	25	15	60	9	36	1	4
	Ma separated	26	21	81	5	19	—	—
Proter and opisthe damaged	Ma prior to condensation	19	14	74	3	16	2	10
	Ma condensed	18	13	72	5	28	—	—
	Ma separated	29	17	59	11	38	1	3
Total		244	158	65	73	30	13	5

About 35% (86 individuals) failed to divide. In those cases separation was inhibited and the dividing individual returned to the single form.

The section line runs from left to right across the anterior individual (Fig. 3 A)

The fragment of proter which has been cut off (dashed) is regulating its shape. The primordia of division ciliature which are present on it grow up and migrate occupying this place on the fragment which corresponds to their position in the unimpaired individual. The old paternal ciliature becomes resorbed. When the fragment contains the nuclear aparatus, the primordia of the new regeneration ciliature appear about 6 hrs. after operation. The position of those primordia corresponds to the position of the regeneration promordia on the morphostatic individual which has undergone the regulation of its shape. In the middle of the fragment arises the AZM primordium, near it on the right, the promordia of FVT cirri, on its left — the primordia of the left marginal cirri. However the promordia of the right marginal cirri arise on the right body

side. The course of development of the primordia is the same as in the fragments from the morphostatic individuals (J e r k a - D z i a d o s z 1965 a).

An impaired division individual in which a part of the proter has been cut off may: 1. divide into the opisthe and a fragment of the proter or, 2. the constriction becomes stopped and in this case the fragment of proter becomes resorbed by the opisthe (Fig. 2). In the first case, the proter fragment which has been separated by the constriction, regulates the shape and later on develops the regeneration primordia in about 6 hrs. after the operation i.e. within the same time in which the cut off fragment of the proter — which was discussed above — develops such primordia.

The unimpaired opistor concludes its division processes by resorption of the ciliature and returns to its morphostatic form.

When the constriction has been retained (Fig. 3 A), the shape regulation process in proter being summarized with the morphogenetic movements of the

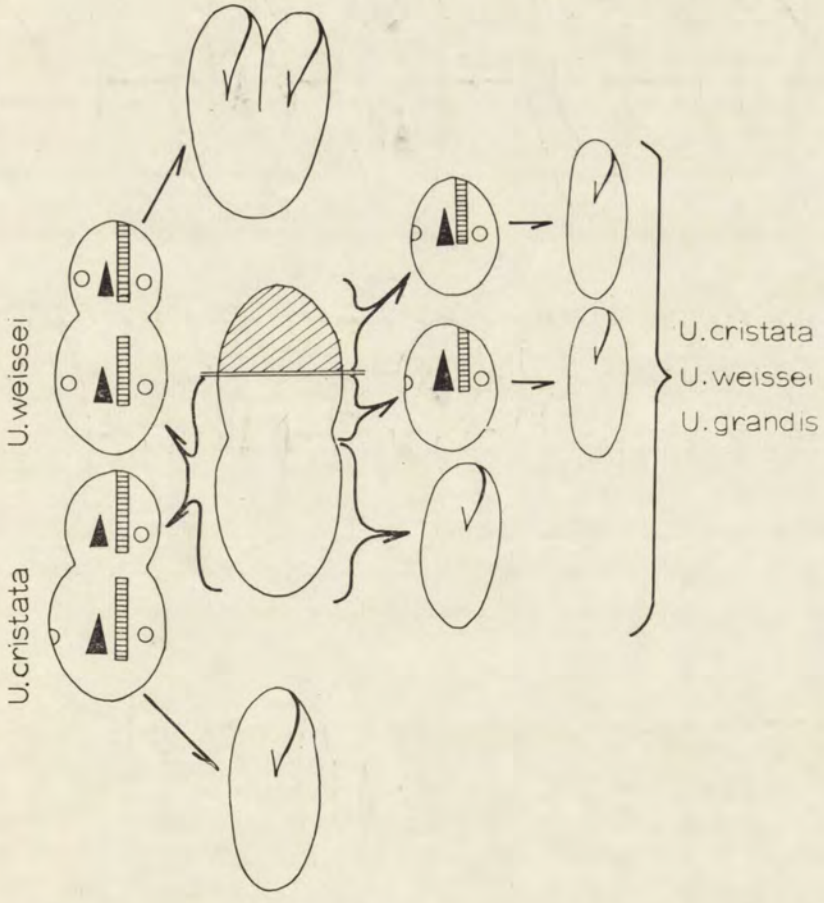

Fig. 2. Scheme demonstrating the behaviour of fragments originating from dividing individuals of *Urostyla grandis*, *U. cristata* and *U. weissei* (description in text).

opisthe primordia, brings about that the proter fragment clings to the anterior part of the opisthe with its right margin (Pl. I 1). The traumatic damage of the anterior individual stimulates it to formation of the regeneration primordia. This process in turn induces the formation of regeneration primordia in the posterior unimpared individual as well. The regeneration and reorganization primordia arise about 6 hrs. after operation i.e. 4 hrs. after completion of the division processes. Since the right body side of the proter fragment is blocked as adhering to the opisthe, it fails to produce the right marginal cirri. During resorption of the old ciliature, the opisthe AZM occupies somehow a part of the proter approaching it and fusing often with its AZM. Such an individual undergoes subsequently a new reorganization in which only one assembly of ciliature is formed and distributed over the whole cell teritory. The unit reorganized in this way returns to its morphostatic form.

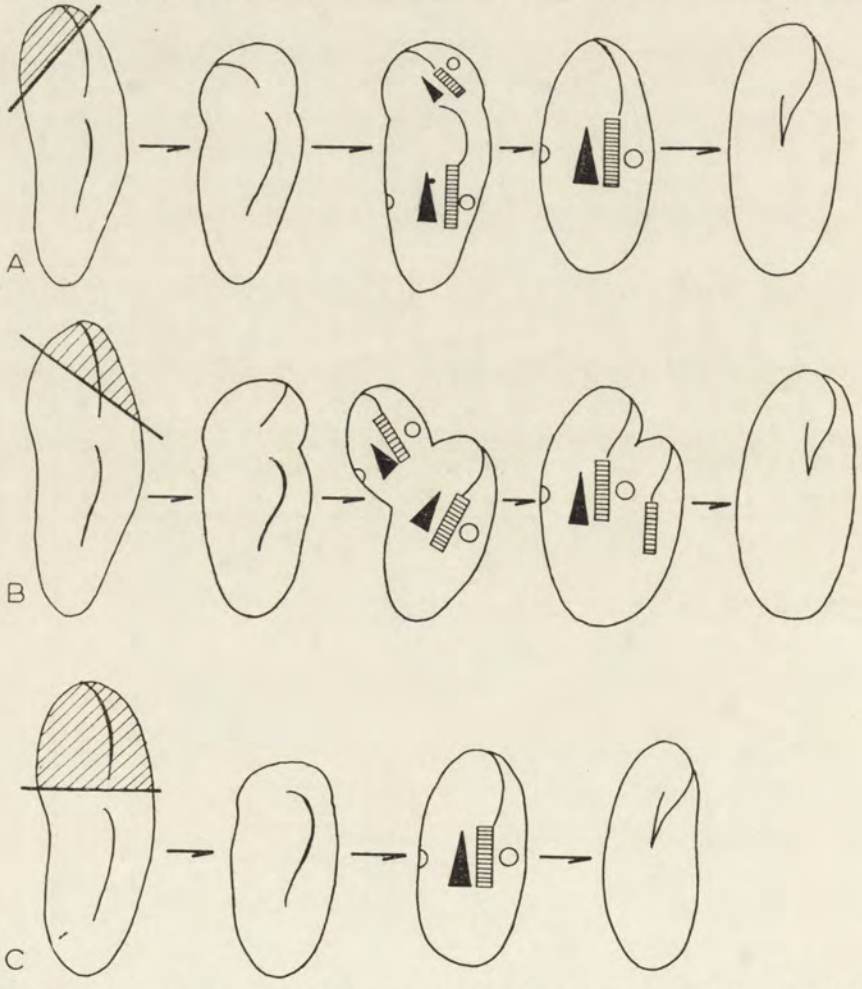

Fig. 3. Scheme of regeneration of dividing individuals of *Urostyla cristata* in which the constriction was arrested The cut off fragment is dashed. Lettering as in Fig. 1

The section line runs obliquely from the right to left across the anterior individual (Fig. 3 B)

The proter fragment which has been cut off behaves similarly as the corresponding fragment obtained in the preciding experiment. It produces the primordia of the regeneration ciliature about 6 hrs. after operation. In a similar way regenerates the second proter fragment separated from the opisthe by the furrow.

If, as result of the operation, the separation is inhibited, the constraction of the wound in the proter fragment as well as the morphostatic movements in the opisthe, involve shifting of the proter to the r i g h t side of the opisthe.

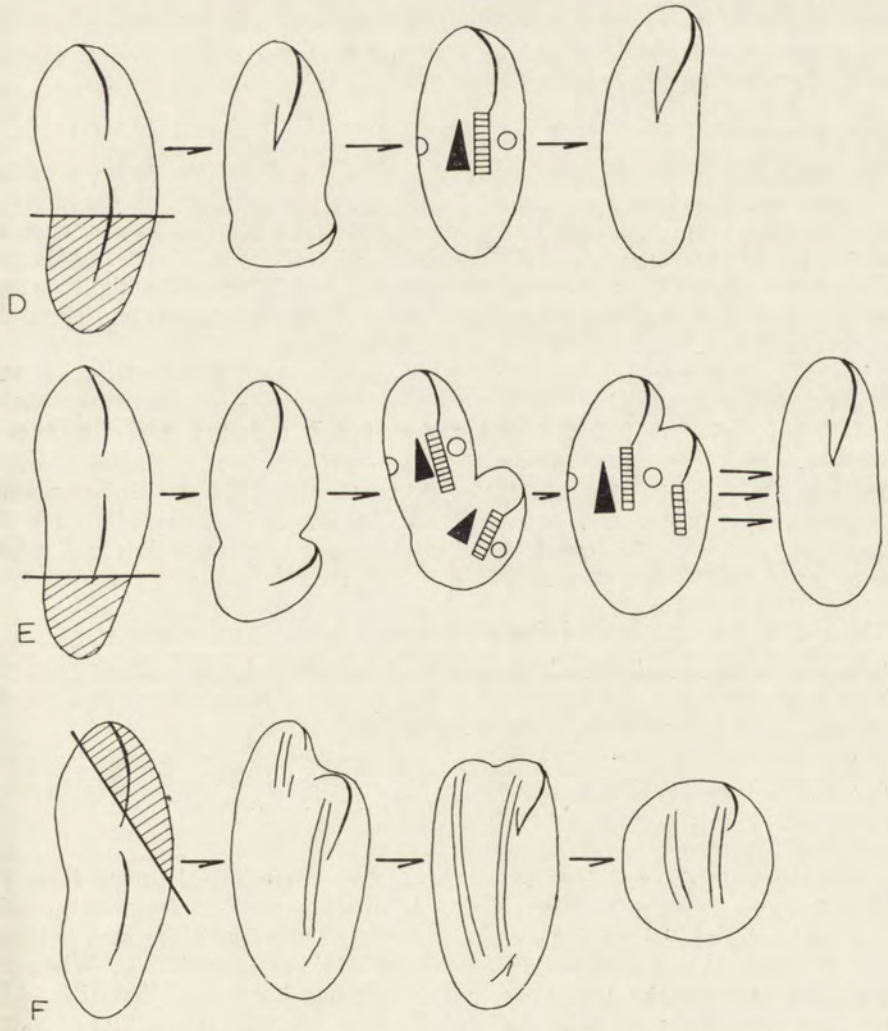

Fig. 4. Scheme of regeneration of dividing individuals of *Urostyla cristata* in which the constriction was arrested. The cut off fragment is dashed. Lettering as in Fig. 1

The posterior individual is connected with the proter fragment in a place in which normally the primordia of the marginal cirri arise (Pl. I 2, 3, 4). The process of regeneration of the proter induces the reorganization in opisthe which fails to produce the right marginal cirri. In this way a pseudo--doublet, constituted of two forms grown together by their sides arises. The right component of such a doublet (Pl. I 5) — the reorganized proter — has its complete ciliature, whereas the left component has no right marginal cirri. The right individual still undergoes the reorganization several (4—5) times, spreading its primordia further and further over the neighbour territory each time. In the left individual, a reorganization is also induced but it concerns only the AZM. In this way, after several reorganizations the left individual is resorbed by the right one. So as a result of such operation, provided that the division has been inhibited, the impaires proter resorbs the unimpaired opistor assuming transitionally the form of a pseudo-doublet. After several reorganizations it returns to the single morphostatic from.

The section line crosses the proter near the division furrow (Fig. 3 C)

The cut off fragment of proter, after having regulated its shape, produces new regeneration primordia about 6 hrs. after the operation, if the division primordia have been damaged. In the more advanced division stages, such an operation might not damage the division primordia of the ciliature. In this case they separate normally, and after their shape regulation, take their proper places on the territory which has been reduced by the operation. Then the regeneration primordia are no more produced.

The remaining part of the division individual may divide what in this species occurs rather rarely. The separated fragment — if sufficiently big — regenerates the ciliature within the normal time. If it is too small however it assumes a spherical form and dies in several hours.

If the constriction has been inhibited (Fig. 3 C), the AZM of opisthe occupies the remainder of the proter. After the distribution of its primordia over the territory of the proter fragment, opisthe undergoes reorganization and subsequently returns to its morphostatic form.

The section line crosses opisthe near the division furrow (Fig. 4 D)

The fragment of opistor which has been cut off uder conditions that the division primordia remain unimpaired, regulates its shape distributes its division primordia and returns to the morphostatic form.

If the division primordia have been impaired, such an opisthe fragment produces new regeneration primordia of ciliature about 6 hrs. after operation, and after their distribution and resorption of the old ciliature it returns to its morphostatic form.

Similarly as in the previous experiment, the separation of proter from the opisthe fragment occurs rather rarely. A small separated fragment of the opisthe — if of a sufficient size — produces the primordia of the new ciliature within the some time as other fragments of dividing individuals. When the constriction between the offspring individuals has been inhibited (Fig. 4 D), then proter resorbs the remainder of opisthe together with its portion of paternal ciliature. After resoprtion, the reorganization of ciliature occurs again and involves the return to the morphostatic form of the individual.

The section line is parallel or oblique to the furrow at the level of the middle of the opisthe body (Fig. 4 E)

The opisthe fragment which has been cut off regenerates in the same manner as all others fragments of dividing individuals which are sufficiently big and possess the nuclear apparatus, as described previously.

In the case when the division furrow has separated proter from the opisthe fragment, the latter regenerates within the some time as the cut off fragment.

If the constriction has been inhibited, the opisthe fragment shifts owing to the morphogenetic movements and grows with its right margin fast to proter (Fig. 4 E). The traumatic stimulus involves the formation of new regeneration primordia of ciliature on the damaged opisthe (about 6 hrs. after operation). This process — in turn — induces the formation of reorganization primordia in the unimpaired proter. Since the right body margin of the opisthe has been blocked, the marginal cirri fail to appear. The place of this ciliature becomes occupied by a part of the left marginal cirri of proter and a pseudo-doublet form arises in this way. The extension of the territory occupied by the cirri of proter causes a new reorganization of the ciliary apparatus which — in turn — induces an incomplete reorganization of the opisthe. After several consecutive reorganizations, opisthe is fully resorbed by proter. The result of this experiment resembles to the results obtained after a traumatic section of the proter.

Two operations were executed simultaneously: proter and opisthe were cut at different levels. The cut off fragments, if sufficiently big and with the nuclear apparatus, after the shape regulation, separation of the division primordia and resorption of the old ciliature — produce new regeneration primordia. After their distribution and resorption of the former ciliature those fragments assume their morphostatic form.

Fragments of the offspring individuals separated by the division furrow, regenerated within the same time as the cut off fragments. If the constriction between the damaged individuals has been inhibited, then — depending on their reciprocal disposition and on the size of both fragments — resorption of one of the fragments occurs, either by means of a single or twice repeated reorganization, or by formation of a transitory pseudo-doublet.

The section line runs obliquely from the right side margin of proter to the left margin of opisthe (Fig. 4 F)

The posterior fragment containing the major part of the unimpaired opisthe and a small part of proter, was observed. Such individual may divide into two fragments which after completion of the division processes, initiate regeneration. The division constriction may be stopped (Fig. 4 F), then two fragments remain joined together. A small part of AZM, the primordia of the fronto-ventro--transversal cirri and an insignificant part of primordia of the right marginal cirri, remain in the fragment of proter. As a result of simultaneous occurrence of such processes like shape regulation and morphogenetic movements of division primordia — the remainder of proter AZM growes together with the AZM of opisthe cirri of FVT of proter lay parallel to the FVT cirri of opisthe. The final form has one oral apparatus, one contractile vacuole and two assemblies of FVT cirri. Such an individual feeds and lives for about 48 hrs., it attains even higher dimensions then the dividing individuals, subsequently it begins to degenerate assuming a spherical shape and dies after two days without any signs of reorganization.

Urostyla weissei

Similary as in *U. cristata* division stages in *U. weissei* may be easily recognized by the changes in the body shape and in the nuclear apparatus, which is distinctly seen in the living material. The same operations were executed as in *U. cristata*. The summary observations results are represented in Table 2. 241 operated individuals were analyzed out, of which 65% divided normally, 35% failed to divide. The division may be retracted by means of resorption of a fragment from one of the offsprings (17%) similiarly as it occurred in the case of *U. cristata* or doublets may be produced (about 17%) which return to the single form by means of seperation of the components.

Table 2
Results of operation of dividing individuals of *Urostyla weissei*

Type of operation		Number of operations	Results of operation					
			separation of speciments		single resorption		doublets	
			number of individuals	%	number of individuals	%	number of individuals	%
Proter damaged	Ma prior to condensation	32	12	37	15	47	5	16
	Ma condensed	35	17	49	12	34	6	17
	Ma separated	44	33	75	4	9	7	16
Opisthe damaged	Ma prior to condensation	21	15	72	3	14	3	14
	Ma condensed	24	23	96	1	4	—	—
	Ma separated	23	21	91	—	—	2	9
Proter and opisthe damaged	Ma prior to condensation	21	11	52	1	5	9	43
	Ma condensed	22	11	50	6	27	5	23
	Ma separated	19	13	69	1	5	5	26
Total		241	156	65	43	18	42	17

The section line runs parallel or obliquely to the division forrow more or less in the middle of the proter body.

Most frequently the cut off fragment contains no nuclear apparatus and dies in this case. If the section line runs nearer the furrow, the fragment may contain the nucleus and them, after completion of the division processes and after the resorption of the parental ciliature, it produces the regeneration pri-

mordia of the new ciliature about 5—6 hrs. after operation (Fig. 2). The position of the regeneration primordia resembles to the position of the division primordia except that similarly as in *U. cristata,* only one assembly of primordia arises in fragments.

The second fragment of the dividing individual which was operated in the above described manner, namely the fragment separated by the furrow, regenerates within the same period of time as the cut off fragment. If the constriction has been inhibited, then the opisthe concludes the distribution of the division primordia in a normal way, and resorbs the paternal ciliature. In the fragment of proter which is fused with opisthe healing of the wound and the shape regulation occurs. Owing to the obligue course of the division furrow and to the precess of shape regulation, proter becomes shifted to the right margin of opistor (Pl. II 6). About 6 hrs. after operation, the formation of the regeneration primordia in the proter fragment begins, and this process — in turn — induces the formation of the reorganization primordia in opisthe. Both individuals produce a complete ciliature and fuse together by their sides. In this way arises a homopolar flat doublet consistng of two individuals fused together by their lateral body margins (Fig. 5 A, Pl. II 7).

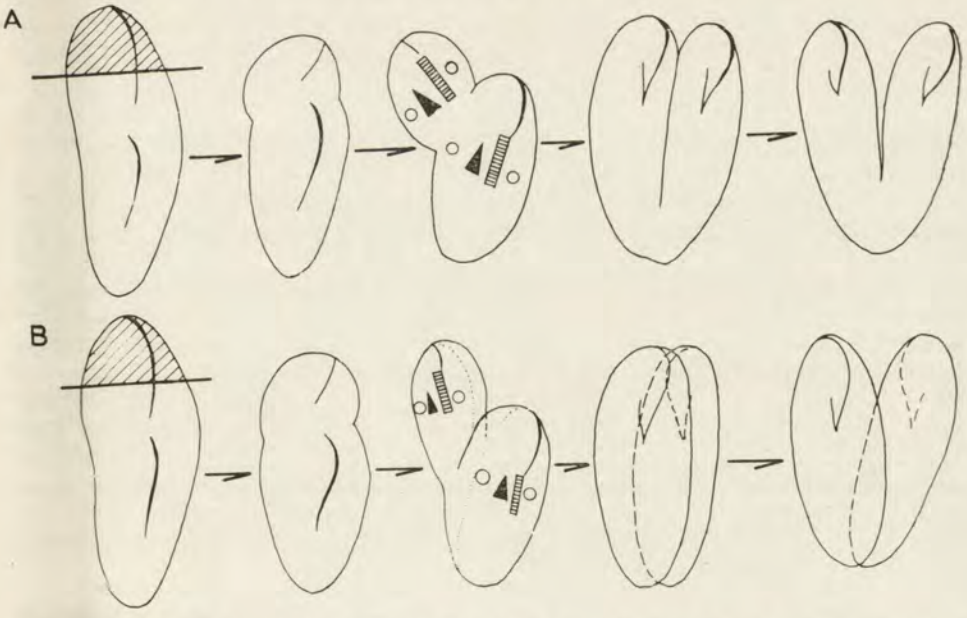

Fig. 5. Scheme of formation of doublets after operation during division in *Urostyla weissei.* A — formation of a flat doublet, B — formation of spherical doublet. The cut off fragment is dashed. Lettering as in Fig. 1

The process of contraction and the morphogenetic movements may lead to groving together of two individuals by their dorsal body sides (Pl. II 8). In this way spherical doublets arise (Fig. 5 B).

The return of the doublet to single forms occurs by detaching of the doublet components which begins in its anterior part. In the final stage the individuals adhere to each other by their posterior ends (Pl. II 9).

The section line crosses proter near the division furrow parallel or obliquely to the furrow

The results of these operations are similar to those obtained after corresponding operatios of *U. cristata*. The cut off fragment of proter regenerates normally providet that it contains the nuclear apparatus and its division primordia are impaired. Similar is the behaviour of the second fragment which is separated from the first one by the the furrow.

If the separation of the individual has been stopped, the opisthe AZM encroaches upon the teritory of the damaged proter. After the distribution of the division primordia of the opisthe over the whole enlarged teritory, a new reorganization of the opisthe follows which leads to a morphostatic form (compare *U. cristata* Fig. 3 C).

The section line crosses opisthe parallel or obliquely near the divison furrow

The cut off fragment regenerates normally. Separation of proter and the very small fragment of the opisthe occurs rather rarely. After such separation, the opisthe fragment — if not too small for regeneration — produces the primordia of the new ciliature 5—6 hrs. after operation.

In the case of inhibition of the constriction, the proter resorbs the fragment of the opisthe together with the corresponding share of the parental ciliature and subsequently undergoes the reorganization of ciliature (compare in *U. cristata* Fig. 4 D).

Resorption of the injured individual does not mean the resorption of its nuclear apparatus. Inhibition of condensation and division of Ma was never observed. The separated Ma of the injured offspring takes same position as in a normal unimpaired individual. Two nuclei are situated one behind the other. All the individuals obtained after resorption of proter or opisthe fragments proved to be nuclear doublets. A single individual contains most frequently 4 Ma after the resorption of a fragment. One case was observed in which in the subsequent division, 4 Ma condensate into one mass and in the course of the subsequent two nuclear divisions separate into 4 parts, two for each offspring individual. Condensation of Ma in the division of the nuclear doublet is not the only form of return to the norm for the nuclear apparatus. Nuclear doublets were observed initially with 4 Ma then 5, 6 and even 8 Ma which would indicate the dispersion of the nuclear material. However detailed studies on the nuclear apparatus were not carried out and the above data should be considered as an additional finding. It may be only stated that during the resorption of the impaired individual, the atrophy of its nuclear apparatus and of its surface structures do not occur simultaneously.

The section line crosses opisthe in the middle of length parallel or obliquely to the division furrow

After this operation phenomena occur similar to those observed after an analogical section of proter. The cut off opisthe fragment regulates its shape and — if the nuclear apparatus is present in it — begins to regenerate its ciliature 5—6 hrs. after the section.

The remaining part of the division individual may divide. The fragment of the opisthe which has been separated by the furrow produces the primordia of the new ciliature and after their distribution and after the resorption of the ciliature which arose in the course of division, returns to the morphostatic form.

In the case of inhibition of the constriction between proter and the fragment of opisthe, in both parts joint together, the morphogenetic processes of division become concluded. In the fragment of opisthe occurs the contraction of the wound and shape regulation as well. Those processes together with the morphogenetic movements which cause an oblique course of the division furrow, give as a result the shift of proter and its growing closely to the right side of the opisthe. The traumatic stimulus evokes in the opisthe fragment the formation of new regeneration primordia of ciliature, and this process —in turn — induces the reorganization of proter. After separation of primordia in both joint individuals, a doublet arises composed of two complete individuals grown together with their lateral or dorsal sides. They are the same as forms obtained when a part of proter has been cut off.

Urostyla grandis

The experiments were complicated by the fact that in *U. grandis* the early division stages are not distinguishable in the ciliates in culture and when the morphogenetic changes become discernable in the living ciliates, it is difficult to recognize whether the process observed is division or physiological reorganization. In the moment when the division furrow becomes visible, division is already much advanced. The only securation was sampling the experimental ciliates from the cultures in very good condition in which the percentage of individuals in reorganization is negligible.

This ciliate — in contrast to the other species under study — shows a very low percentage of post-traumatic division disturbances. After 85 operations only 7 cases of inhibition of constriction were stated. Hampering of separation of the offspring individuals occurred only after the operation in which the section line ran very near the division furrow. In this case, a remaining small fragment of proter or opistor might be resorbed together with the paternal ciliature. However in the majority of cases, very small fragments were separated as well.

If the section line ran somewhat farther from the division furrow, the individual continued to divide normally. Similarly as in the species described previously, formation of primordia of the new ciliature begins not earlier than 5—6 hrs. after operation and 4 hrs. after the separation of the offspring individuals.

Discussion

Dembowska (1925) stated that in the moment of formation of two division areas in *Stylonychia,* although the division furrow is not yet visible, both future individuals constitute already independant units. According to Reynolds (1932) the physiological individuality of the future offsprings in *Oxytricha fallax* manifests already 5 hrs. prior to their separation i.e. at least 2 hrs. before the primordia are formed. Eberhardt (1962) stated in the regeneration processes in *Blepharisma* that the injury in the individuals approaching division becomes compensated by the division processes, and the regeneration processes fail to occur in this case. Contrary conclusions were postulated by Fauré-Fremiet (1910) based on experiments with operations executed on dividing

individuals of *Urostyla grandis*. According to this author, the differentiation of two individuals occurs only at a certain — rather early — stage of primordia development. However this interpretation is not precisely clear and as yet has not been confirmed. It seems difficult to understand at which degree the process of inhibition of the division furrow is concerned and at which the resorption of the ciliature primordia occurs.

It may be assumed — accepting the conclusions of Dembowska and of Reynolds — that in the moment of formation of the division areas, both future offsprings individuals are independant units. This would suggest that prior to the formation of primordia reorganization of two individuals into units capable to produce their own ciliature primordia must occur.

The results cited above indicate that a long time before appearance of division symptoms, distinct signs of physiological delimitation of offsprings are present. The process leading to this delimitation is often called the individualization (Tartar 1961). Uhling (1960) understrands this definition as a transformation of an original single surface gradient into two ones, for two offspring cells.

The division individualization occurs presumably in the majority of ciliates. The effect of this process is the size regulation of the anterior oral apparatus in the forms which produce new primordia only for the posterior individual e.g. in *Glaucoma* (Frankel 1960), or in *Stentor* (Tartar 1961). In *Hypotricha*, the anterior oral apparatus does not possibly arise de novo and is only regulated to the size of proter. No one of the authors has described the anterior AZM primordium as such one. Dembowska found that in *Stylonchia* the membranelles of the anterior AZM become exchanged in situ. A similar conclusion seems to follow from the publications concerning *Euplotes* (Chatton et Seguela 1940, Bonner 1954, Yow 1958, Wise 1965 b; Hashimoto 1961).

The present studies seem also to indicate only the regulation of the anterior AZM. In all three species of *Urostyla*, no primirdium of a new AZM in proter was found, however the symptoms of AZM reorganization occurring in proter are rather distinct (Jerka-Dziadosz 1963, 1964, 1965 b).

Factors involving the onset of individualization process prior to the division, or factors of initiation the division are as yet unknown. The causes of this phenomenon are looked for in the plasmo-nuclear ratio (Hertwig 1903), in the threshold size of the organism, in senescence of the cell etc. On the other hand, some factors which delay the moment of division onset in the normal life cycle are known. To those factors belong: UV irradiation, the action of higher temperature or of the metabolic inhibitors (Giese and Reed 1940, Giese and Lusignan 1961 a, 1961 b, Giese and McCow 1963 a, 1963 b, Giese, McCow and Cornell 1963, Giese, Richter and Berry 1963, Frankel 1960, 1964 b, Gavin 1965, Wise 1965 a, Gavin and Frankel 1966). The operation injuries delay the initiation of division as well (Reynolds 1932).

In a normal undisturbed division process, two individuals become separated by the division furrow. The processes which control the formation and persistence of the division furrow are till now not elucidated. Many facts indicate however that formation of the furrow should be included rather to the processes of form regulation of the new individuals than to formation of ciliary primordia.

It follows from the studies on *Urostyla*, that damaging of the primordia may

inhibit the formation of the division furrow (Fig. 2) but this effect is not obligatory. In two of the species under study: *U. cristata* and *U. weissei*, 65% of individuals operated in different manner in the course of division, separate into offspring individuals independently of the distinguished division stages as well as of the type of operation. The only difference which may be noticed, is an insignificant rise of number of separating individuals in the groups which were operated at more advanced stages of divison when the furrow is seen well (Table 1 and 2). In the remaining 35%, the arrest of constriction between the offsprings was obtained. T a r t a r (1966) studying the effect of removal of the oral primordium in *Stentor* ascertained that in $^1/_3$ of operated individuals fission becomes inhibited. In *Stentor* the furrow is developed i.e. the discontinuity of kineties is seen but the constriction is absent.

In *Urostyla grandis* the constriction was arrested only in 8% of cases and only after the sections running near the furrow. In this species neither permanent nor transitory double forms were obtained. The differences in the traumatic disturbances of division in the three *Urostyla* species under study may be accounted for by the differences in the density of cytoplasm along the course of the division furrow. In *Urostyla grandis* the cytoplasm is dense and stiff (after operation no outflow of cytoplasm is observed) and the pellicle is stiffened by fibers which initiate at the base of cirri (unpublished) and by very numerous protrichocysts. In *Urostyla cristata* and *U. weissei* the cytoplasm is more liquid and less compact and the irregular deepening of the furrow and its oblique course support the mutual translocation of the offspring individuals after operation (Fig. 1 A_2, B_2, C_2).

The study on regeneration in course of division in *Urostyla* provides the possibility to analyze the experimental cases when the furrow separates an individual from fragments of different kind, or when the furrow runs between two fragments.

The case when the division furrow separates two individuals occurs not only in the normal division of *Urostyla*. If a part of one of the offspring individuals is cut off in such a manner, that the primordia of the division cirri remain unimpaired, then despite cutting off, a comparatively big part of the body, the regeneration primordia are not produced. It is important in this phenomenon that the division cirri in the course of development and spreading to their final places, occupy other loci at the cell surface than those which they would occupy in the unimpaired individual. It follows from the above fact — which was stressed by W i s e (1965 b), as well as by D o r o s z e w s k i i R a a b e (1966) — that the development of primordia depends on the epigenetic factors.

Another important statement is the fact that the reduction of the area which is to be occupied by the primordia, fails to involve disturbance of equilibrium which would be sufficient to initiate a new reorganization. Presumably spreading of division primordia and growth of ciliature become inhibited in the moment when the proportion characteristic for the species has been attained.

In the case when the furrow has separated the offspring individual from the fragment with the impaired ciliature primordia, the fragment concludes the division processes after its separation, resorbes the old ciliature and produces the primordia of new regeneration ciliature. There is a striking fact that the cut off fragment and the remaining part of the individual which has been separated by the division constriction regenerates in the same time. Besides, the time after which the regeneration of fragments of dividing individuals

begins, is much longer than the regeneration time of fragments from the morphostatic individuals. A supposition arises that during the division, the substances which might be important for morphogenesis are exhausted. They are indispensable for the formation primordia and only when the young individual is grown up it becomes able to produce new primordia. It seems to be connected with the fact that the macronucleus in *U. cristata* looses its nucleoli which contain RNA, during the stage of reorganization band and condensation of Ma in division. The new nucleoli appear in Ma only 1.5—2 hrs. after division.

These postulations are supported by the study on the nuclear apparatus of *Euplotes*. The autoradiographic studies of Gall (1959) and Prescott and Kimball (1961) showed that during the transition of the reorganization band, DNA and histones are synthetized whereas RNA becomes free, and a part of its content passes to cytoplasm. H. Raabe (1946) stated that in *Urostyla grandis* the "oxygranules" containing RNA disappear during the pre-division reorganization and macronuclei condense in division. Such a considerable delay of regeneration in the fragments of division individuals — when compared to the fragments of morphostatic individuals was stated only in *Hypotricha*. This seems to be connected with the fact that in this group of ciliates, the whole ciliature arises de novo during division and regeneration. In the other groups of *Protozoa*, the regeneration of fragments of dividing individuals fails to differ so much from that in the morphostatic individuals. Golińska (1966) stated that in *Dileptus* the damaged proter begins its regeneration soon after the operation. If the operation has carried out at an early stage of division then — in the moment of separation — regenerated proter may not differ from the unimpaired opisthe.

In the other *Protozoa* e.g. *Spirostomum* the division promordia become resorbed after the operation of dividing individual and are replaced by reorganization primordia, or division primordia may serve as regeneration primordia (Eberhadt 1962). In *Spirostomum* like in *Dileptus*, regeneration may occur prior to the conclusion of the division process.

Although factors controlling the formation and persistence of the division furrow are still not elucidated, the consequence of inhibiting the separation of the offspring individuals may be analyzed as well as the mutual influence when they are joined as: two individuals, individual with a fragment or two fragments.

The inhibition of constriction between two individuals occurs rather rarely. In this case different types of doublets may arise, composed of offspring individuals joined together. In *U. grandis* cultures spontaneous occurrence of star-shaped doublets and in *U. cristata* — chain-like doublets was ascertained. Frankel (1964 a) obtained chain-like doublets in *Tetrahymena pyriformis* after a prolonged action of high temperature. Totwen-Nowakowska (1964, 1965) described three types of doublets of *Stylonychia mytilus* obtained after disturbances of conjugation and after the action of thermic shock on dividing individuals. Fauré-Fremiet (1945, 1948) obtained doublets of *Urostyla weissei* and *U. trichogaster* after the action diluted formalin on dividing individuals.

In all the cases cited above, different kinds of multiplied forms arise as individuals. Such multiplied forms may also arise after impairing one or both effect of inhibition of the division furrow and of mutual shifting of the offspring or by arresting the fission of fragments.

In the litterature not many data have been sygnalized concerning the inhibition of the furrow development by means of a traumatic stimulus. Numerous studies concerned the action of high and low temperature as well as of the hydrostatic pressure (Marsland 1938, 1959, 1960, Frankel 1964 a, 1964 b). Operation and also UV irradiation are the only stimuli — known as yet — which may inhibit the constriction without impairing directly the region of the division furrow. This fact seems to support the postulation that the division furrow is rather connected with the shape-producing processes.

When one of the offspring individuals has been damaged, it develops its division primordia like the unimpaired individual with which it is joined, then regenerates its ciliature and induces simultaneously the reorganization in the unimpared individual.

Induction of primordia in the morphostatic partner may be compared with the same phenomena occurring in the homopolar graft of *Stentor* obtained by Tartar (1961). After the reorganization of both joined individuals of *Urostyla weissei,* two types of doublets may arise: flat ones, and others grown together by their dorsal sides, resembling to the double form of *Stylonychia.* They were described by Tchang Tso-Run, Shi Xin-Bai and Pang Yan-Bin (1964) and Tchang Tso-Run and Pang Yan-Bin (1965) after an operation impairing the division. Similar results after the action of raised temperature sygnalized Totwen-Nowakowska (1965). The doublets of *Stylonychia* are able to divide and to form offspring doublets. They also regenerate in a double form after transection (Totwen-Nowakowska, personal comunication). The second type of doublet in *U. weissei* obtained after retaining the fission of fragments is the form constituted of two individuals grown together by their dorsal side. Such a double form of this species has been described by Fauré-Fremiet (1948), in *Stylonychia* by Totwen-Nowakowska (1965), in *Oxytricha* by Dawson (1920) and in *Euplotes* by Kimball (1941).

In *Urostyla cristata* occurs a particular — as yet not reported in the literature — consequence of inhibition of the division furrow between the individual and the fragment. The fragment may shift in relation to the individual owing to the morphogenetic movements. In the case when — as result of translocations of the offsprings — the right margin of the ciliate has been blocked (the surface of body on which normally the primordia of the marginal cirri arise), this coalescence excludes the formation of new marginal cirri. The places of those cirri become occupied by a part of marginal cirri of the neighbour, for which the extension of the area occupied by its own primordia seems to be a stimulus for the subsequent reorganization. An evidence supporting this view is the fact that although primordia may be "adjusted" when they are too big for the area they occupy, they must be replaced by new ones when they are too small. In populations of *Tetrahymena* Williams (1958, 1960, 1961) detected the occurence of two forms: "macrostoma" with a large mouth and "microstoma" with a small mouth. He stated that "macrostoma" can produce in division two offspring individuals with small mouth i.e. in proter the large mouth becomes small, while the form with small mouth may be transformed into one with a large mouth only after a reorganization in the cyst. Similarly enlarging of the surface and of volume of one the components of the pseudo-doublet in *Urostyla cristata* is a stimulus for the subsequent reorganization. This process is repeated as many times till the fragment becomes fully resorbed. The resorption of one of the components of the pseudo-doublet indicates that in the multiplied form

only those components may be preserved in which the coalescence is not blocking the place of the cirri formation (e.g. *Urostyla weissei*).

If the furrow between the two fragments is blocked, in the case of *U. weissei* a regular flat or spherical doublet may be produced by them what was discussed above. Nowever in the case of *U. cristata* a fragment in which all places of primordium formation are free — resorbs the fragment joined with it in which the area of marginal primordium formation has been blocked. Besides resorption makes possible a occupation of a limetid fragment portion and when the fragment is big, the resorption is repeated till the whole fragment becomes engulfed.

In *Urostyla cristata* an interesting case of a double form was found in which both marginal areas were blicked as a result of shifting. This form was unable to produce any own primordia. Only growth and shifting of the division primordia was observed.

Neither inhibition of development nor resorption of division primordia was observed after operations of dividing *Urostyla* individuals. It is an amazing result because the other factors which exert influence upon division as temperature, UV irradiation, metabolic poisons, inhibit the development of primordia before all. As to the effect of operation, only H a s h i m o t o (1961) ascertained the resorption of AZM primordium in *Oxytricha fallax* after traumatic damage of the cell beyond the primordium at its very early stage of development. Presumably in *Urostyla* the possiblity of inhibiting the development of the AZM primordium at the first stage exists as well. The experiments however were not carried out at this stage because the ciliates with the AZM primordium only and with no cirri primordia are not easy to distinguish among the morphostatic cells in the culture. The dividing cells damaged by operation at later stages show no disturbances in regulation of fibrillar structures and develop normally.

Conclusions

After the traumatic damage of dividing individuals of *Urostyla grandis*, *U. cristata* and *U. weissei*, only the separation of the offspring individuals may be inhibited. In all the cut off fragments, separated or joined in the place of the division furrow, the morphogenetic processes as: dispersion of primordia and resorption of the paternal ciliature continue to occur with no interruption. Only after their conclusion and growing up of the offspring individuals, the primordia of new regeneration or reorganization ciliature are produced.

Inhibition of the separation process of the offspring individuals involves resorption of one the those individuals or formation of doublets. This resorption may occur in the course of one (*U. weissei*, *U. grandis*), two or several (*U. cristata*) reorganization. depending on the size of the resorbed individual or fragment.

Inhibition of constriction does not depend on the division stage. This process occurs as well at the early as at the later division stages. This inhibition exerts no influence upon the course of development of the division primordia.

In different fragments of the same individual regeneration occurs synchronically and not earlier than 5 hrs. after the operation.

In the fragments originating dividing individuals in which the division primordia have not been impaired, no process of formation of new regeneration ciliature occurs. The division cirii occupy places indicated by the process of

shape regulation which occurs simultaneously. As a result these places may be different from those which would be occupied by the division cirri in a normal unimpaired individual.

Summary

Dividing individuals of *Urostyla grandis, U. weissei* and *U. cristata* were operated at three different stages of division. It was ascertained that regeneration of fragments of dividing individuals initiates about 3 hrs. later than regeneration of fragments of morphostatic individuals. Formation of regeneration primordia sets on only after completion of such division processes as: dispersion of primordia, separation by the furrow and resorption of old cirri. Operation evokes no disturbances in the normal development of primordia and in resorption of the old ciliature.

In 35% of cases the constriction of the offspring individuals of *U. cristata* and *U. wessei* was arrested. As resultt of this either the fragment of the individual is resorbed or double forms arise (*U. weissei*). In *U. grandis* inhibition of the constriction occurs very rarely and in this case the fragments is resorbed by the unimpaired individual. In all three species no regeneration ciliature is produced when the operation fails to damage the division primordia.

STRESZCZENIE

Operowano osobniki dzielące się *Urostyla grandis, U. weissei* i *U. cristata* znajdujące się w trzech różnych stadiach podziałowych. Stwierdzono, że regeneracja fragmentów z osobników dzielących się rozpoczyna się około 3 godziny później niż regeneracja fragmentów z osobników morfostatycznych. Wytwarzanie zawiązków regeneracyjnych rozpoczyna się dopiero po dokończeniu takich procesów podziałowych jak: rozchodzenie się zawiązków, rozdzielenie bruzdą i resorbowanie starych cirri. Operacja nie powoduje zaburzeń w normalnym rozwoju zawiązków i resorpcji starego orzęsienia.

W 35% przypadków otrzymano zatrzymanie przewężania osobników potomnych *U. cristata* i *U. weissei*. W wyniku tego fragment osobnika może zostać zresorbowany, lub też tworzą się formy podwójne (*U. weissei*). U *U. grandis* hamowanie przewężania występuje bardzo rzadko i w tym wypadku fragment zostaje zresorbowany przez osobnika nieuszkodzonego. U wszystkich trzech gatunków nie wytwarzane jest orzęsienie regeneracyjne, jeżeli operacja nie uszkadza zawiązków podziałowych.

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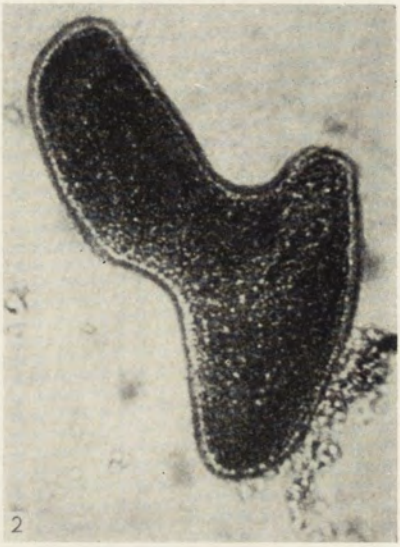
EXPLANATION OF PLATES I—II

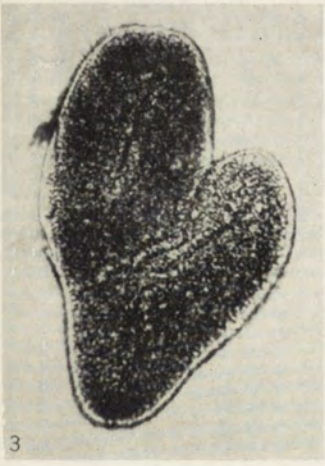
Post-traumatic disturbances of division in *Urostyla cristata*

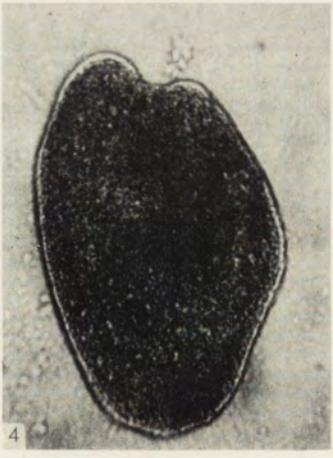
1: Fragment of proter grown together by its side to opisthe (10×25)
2: Fragment of proter shifted to the right side of opisthe (10×25)
3: Regeneration of proter and reorganization of opisthe (10×25)
4: Incomplete doublet, both individuals grown together by their sides (10×25)
1—4 photograms of living material (phase contrast)
5: Ventral ciliature of a incomplete doublet. Staining after method of Parducz (10×25)

Post-traumatic disturbances of division in *Urostyla weissei*

6: Proter grown together to the lateral margin of the opisthe (10×25)
7: Flat doublet constituted of two individuals grown together by their sides (10×25)
8: Spherical doublet constituted of two individuals grown together by dorsal sides (10×25)
9: Desintegrating doublet, two individuals grown together by their posterior body ends (10×25)
6—9 photograms of living material







M. Jerka-Dziadosz auctor phot.

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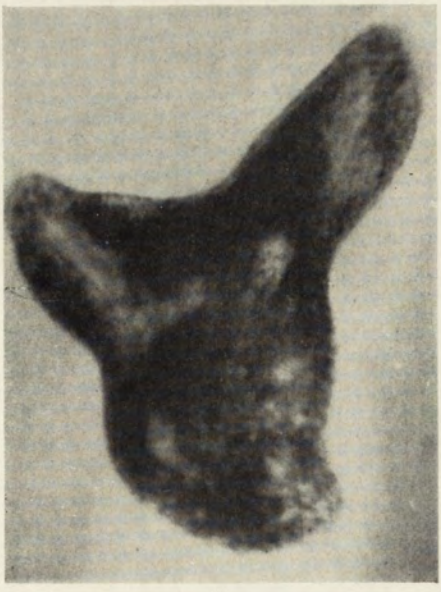

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Новые данные по фауне инфузорий мезопсаммона Баренцова моря

New data on the infusorian fauna of the mesopsammon of the Barentz Sea

Видовой состав псаммофильных инфузорий и характер их распространения на песчаной литорали Дальнезеленецкой бухты Баренцова моря были в основных чертах изучены И. Б. Райковым (1960). Более детальное исследование этой фауны, однако, представлялось весьма желательным. Наша работа выполнена летом 1966 года в Мурманском морском биологическом институте. Обработав собранный материал, мы смогли значительно дополнить список видов, приведённый Райковым в своей статье (1960).

Пробы песка брались в основном в восточной, мало заилённой части песчаной литорали Дальнего пляжа Дальнезеленецкой бухты, а также частично в губе Ярнышной, где заиление значительно и поэтому фауна интерстициальных инфузорий там сильно обеднена. Сбор и обработка материала проводились обычными методами, используемыми исследователями псаммона (Fauré-Fremiet 1950, Dragesco 1960, Raikov 1962).

Видовой состав фауны

В составе интерстициальной фауны восточной части Дальнего пляжа Дальнезеленецкой бухты нами было обнаружено 37 видов инфузорий. Сопоставив наши данные с данными Райкова (1960), мы смогли составить общий список видов, в который включены 50 видов псаммофильных инфузорий, принадлежащих к 26 родам. Одной звёздочкой (*) обозначены виды, впервые указываемые нами для фауны Баренцова моря, т. е. не отмеченные Райковым (1960). Двумя звёздочками (**) обозначены виды, найденные как Райковым, так и нами. Без обозначения оставлены формы, отмеченные только Райковым.

Отряд *Holotricha*

Семейство *Holophryidae*

1. *Pseudoprorodon arenicola* Kahl **
2. *Helicoprorodon gigas* Kahl **

3.	*H. orientalis* Raikov	*
4.	*Prorodon* sp.	
5.	*Lacrymaria lagenula* Cl. et L.	**
6.	*L. olor* var. *marina* Kahl	*
7.	*Trachelocerca coronata* (De Morgan)	
8.	*Tracheloraphis phoenicopterus* Cohn.	**
9.	*Tr. prenanti* Dragesco	*
10.	*Tr. drachi* Dragesco	*
11.	*Tr. drachi* f. *bimicronucleata* Raikov	*
12.	*Tr. striatus* Raikov	*
13.	*Tr. discolor* Raikov	*
14.	*Tr. vermiformis* Raikov	*
15.	*Tr. stephani* Dragesco	*
16.	*Tr. dogieli* Raikov	**

Семейство *Colepidae*

17.	*Coleps pulcher* Spiegel	
18.	*C. tesselatus* Kahl	

Семейство *Amphileptidae*

19.	*Litonotus pictus* var. *binucleatus* Kahl	**
20.	*Loxophyllum setigerum* Quenn.	*
21.	*L. laevigatum* Sauerbrey	*
22.	*L. undulatum* Sauerbrey	*

Семейство *Loxodidae*

23.	*Remanella granulosa* Kahl	**
24.	*R. rugosa* Kahl	
25.	*Kentrophoros latum* Raikov [1]	**

Семейство *Chlamydodontidae*

26.	*Chlamydodon triquetrus* O.F.M.	

Семейство *Geleiidae*

27.	*Geleia murmanica* Raikov [2]	**
28.	*G. orbis* Fauré-Fremiet	*
29.	*G. nigriceps* Kahl	**
30.	*G. fossata* Kahl	
31.	*G. decolor* Kahl	

Семейство *Frontoniidae*

32.	*Frontonia arenaria* Kahl	**
33.	*Fr. marina* Fab.-Dom.	*
34.	*Uronema marinum* Dujardin	**

[1] В статье Райкова (1960) эта форма обозначена как *Centrophorella grandis*. В более поздней статье Райков (1962) выделил её в самостоятельный вид *Kentrophoros* (syn. *Centrophorella*) *latum*.

[2] В статье Райкова (1960) эта форма обозначена как *Geleia orbis*. Позже Райков (1962) выделил её в самостоятельный вид *G. murmanica*. Настоящая же *G. orbis* указывается нами для Баренцова моря впервые.

Отряд *Spirotricha*

Подотряд *Heterotricha*

Семейство *Spirostomatidae*

35. *Blepharisma clarissimum* Anigstein **
36. *Blepharisma clarissimum* f. *arenicola* Kahl **
37. *Gruberia lanceolata* (Gruber)
38. *G. uninucleata* Kahl *
39. *Condylostoma remanei* Spiegel **
40. *C. arenarium* Spiegel **

Подотряд *Oligotricha*

Семейство *Halteriidae*

41. *Strombidium sauerbreyae* Kahl

Подотряд *Hypotricha*

Семейство *Oxytrichidae*

42. *Keronopsis rubra* (Ehrenberg) **
43. *Trachelostyla caudata* Kahl **
44. *Oxytricha discifera* Kahl **

Семейство *Euplotidae*

45. *Euplotes harpa* Stein
46. *E. cristatus* Kahl
47. *Diophrys scutum* Dujardin **
48. *Diophrys* sp. *
49. *Uronychia transfuga* O.F.M. **

Семейство *Aspidiscidae*

50. *Aspidisca* sp.

Краткое описание некоторых видов

Tracheloraphis prenanti Dragesco, 1960 (Рис. 1 А, В)

Исследования, проведённые Дражеско (Dragesco, 1960) на побережьях Франции, Райковым (1962, 1963) на Белом и Японском морях, Агамалиевым (1966) на Каспийском море, а также на Чёрном море (Ковалёва 1966), показали, что этот вид обладает большим полиморфизмом и, возможно, заслуживает подразделения на группу близких видов. Пока это не сделано, целесообразно в каждом случае нахождения *Tr. prenanti* давать описание обнаруженной формы. Нам встретилась одна из разновидностей *Tr. prenanti*, описанная Дражеско (Dragesco 1960) — а именно разновидность с 16 ресничными рядами. Эта форма имеет одно сложное ядро с 2 микронуклеусами и 4—6 макронуклеусами (Рис. 1 В).

Тело инфузории удлинённо-веретенообразное, спереди плавно переходит в гибкую шейку, заканчивающуюся утолщенной головкой (Рис. 1 А). Рот терминальный, имеет вид простой воронки.

Задний конец тела заострён и образует короткий „хвостик".

Характерная для этого вида широкая безресничная зона равна примерно 5—6 ресничным рядам.

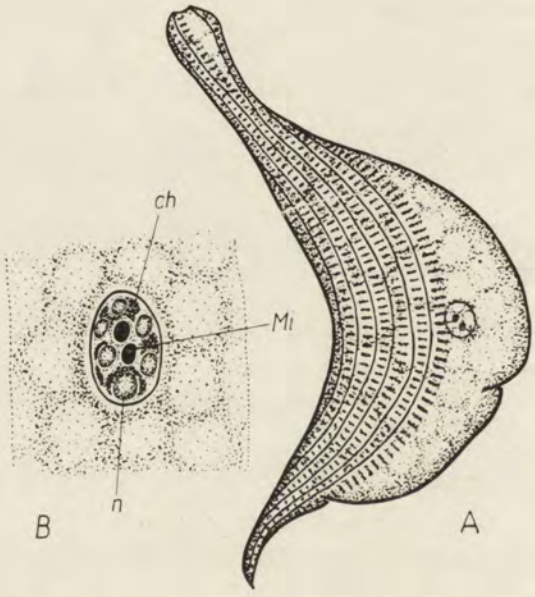

Рис. 1. *Tracheloraphis prenanti* Dragesco. А — общий вид (тотальный препарат, реакция Фёльгена); В — сложное ядро (тотальный препарат, реакция Фёльгена): *Mi* — микронуклеус, *n* — нуклеола, *ch* — хроматиновые гранулы

Fig. 1. *Tracheloraphis prenanti* Dragesco. A — general view (whole mount, Feulgen reaction); B — complex nucleus (whole mount, Feulgen reaction); *Mi* — micronucleus, *n* — nucleolus, *ch* — chromatin granules

Размер нашей формы не превышает 600 мк, в то время как у Дражеско размер *Tr. prenanti* варьирует от 400 до 2000 мк.

Эта же разновидность была обнаружена Дражеско в районе Баньюльса (Франция), Райковым на Белом и Японском морях, Агамалиевым на Каспийском море, Ковалёвой на Чёрном море.

Tracheloraphis vermiformis Raikov, 1962 (Рис. 2 А—С)

Подробное описание *Tr. vermiformis* даётся Райковым (Raikov 1962), впервые встретившим эту форму в псаммоне Белого моря. Так как Райков обнаружил и изучил этот вид только на фиксированном материале, мы приводим рисунок, сделанный прижизненно (Рис. 2 А).

Форма тела этой инфузории цилиндрическая, червеобразная. У живых особей имеется довольно длинная, гибкая шейка. Головка четко не выражена. Рот воронкообразный, окружён длинными ресничками.

Число ресничных рядов у найденных нами экземпляров не превышает 55, в то время как беломорские *Tr. vermiformis*, описанные Райковым, имеют около 70 ресничных рядов. Между ресничными рядами располагаются округлые, бесцветные протрихоцисты (Рис. 2 C). Очень узкая голая полоска прижизненно не видна.

Задний конец тела инфузории заострён и образует короткий „хвостик".

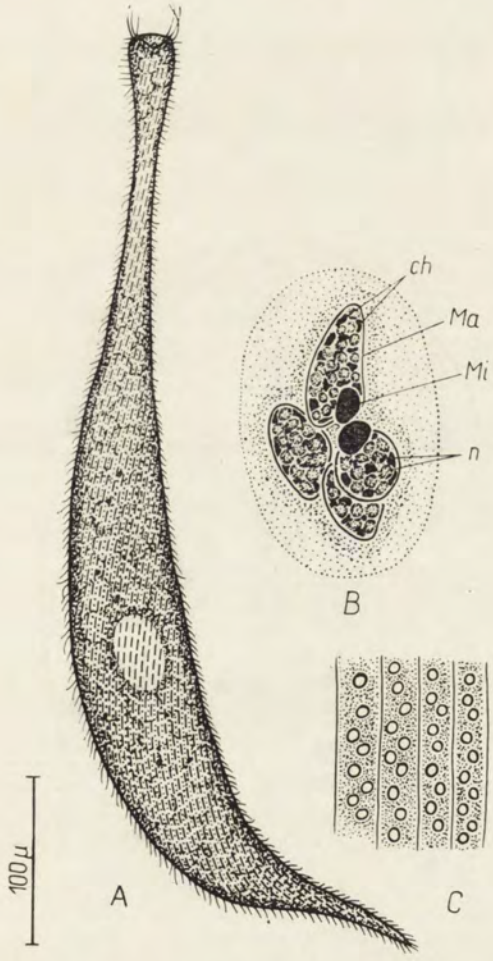

Рис. 2. *Tracheloraphis vermiformis* Raikov. A — общий вид (прижизненно); B — ядерный аппарат (тотальный препарат, метиловый зелёный-пиронин); C — протрихоцисты (прижизненно): *Ma* — макронуклеус, *Mi* — микронуклеус, *n* — нуклеола, *ch* — хроматиновые гранулы

Fig. 2. *Tracheloraphis vermiformis* Raikov. A — general view (living specimen); B — nuclear apparatus (whole mount, methyl green-pyronin); C — protrichocysts (from living specimen). *Ma* — macronucleus, *Mi* — micronucleus, *n* — nucleolus, *ch* — chromatin granules

Ядерный аппарат представлен 4 макронуклеусами и 2 микронуклеусами (Рис. 2 В). Нам не удалось наблюдать, однако, толстых, аностомозирующих тяжей хроматина в макронуклеусе *Tr. vermiformis*, которые наблюдались в материале Райкова. Хроматиновый материал в макронуклеусах нашей формы имеет вид мелких гранул, разбросанных среди многочисленных нуклеол. Микронуклеусы крупные, резко фёльген-положительные.

Окраска живых инфузорий в падающем свете белая.

Размер живых особей варьирует от 600 до 1000 мк.

Diophrys sp. (Рис. 3)

На тотальных препаратах, окрашенных протарголом, среди многочисленных типичных *Diophrys scutum*, нам встретился один экземпляр, у которого отчётливо были окрашены основания шести трансверсальных цирр (у *D. scutum*

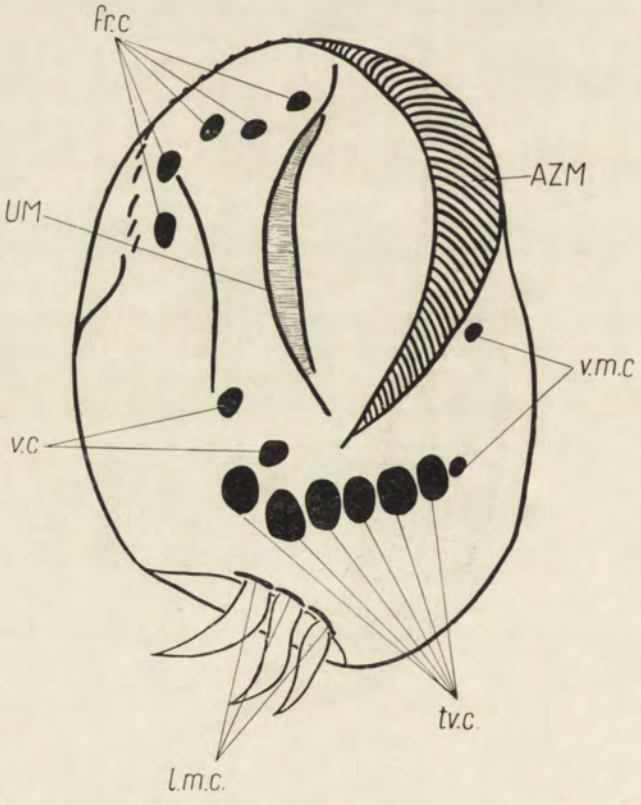

Рис. 3. *Diophrys* sp. (тотальный препарат, протаргол); *fr.c.* — франтальные цифры; *r.m.c.* — правые маргинальные; *l.m.c.* — левые маргинальные; *v.c.* — вентральные; *tv.c.* — трансверсальные; *AZM* — адоральная зона мембранелл; *UM* — ундулирующая мембрана

Fig. 3. *Diophrys* sp. (whole mount, protargol); *fr.c.* — frontal cirri; *r.m.c.* — right marginal cirri; *l.m.c.* — left marginal cirri; *v.c.* — ventral cirri; *tv.c.* — transversal cirri; *AZM* — adoral zone of membranelles; *UM* — undulating membrane

их обычно пять). По всем остальным систематическим признакам эта форма аналогична *D. scutum*. На препаратах, окрашенных протеинатом серебра (протарголом), четко видны адоральная зона мембранелл, ундулирующая мембрана и основания 5 фронтальных, 2 вентральных, 3 левых маргинальных, 2 правых маргинальных, 6 трансверсальных цирр (Рис. 3).

Пока ещё неясно, представляет ли эта форма новый вид, близкий к *D. scutum*, или это просто аномальный экземпляр.

Обсуждение

Анализ списка видов показывает, что основной состав фауны псаммофильных инфузорий Баренцова моря тот же, что и Белого и Японского морей. Из 47 точно определённых видов фауны Баренцова моря общих с Белым морем оказалось 36, с Японским — 29. В частности в Баренцовом море отмечены следующие виды, впервые найденные в Белом море (Raikov 1962): *Tracheloraphis striatus* Raikov, *Tr. drachi* f. *bimicronucleata* Raikov, *Tr. discolor* Raikov, *Tr. vermiformis* Raikov, а также *Helicoprorodon orientalis* Raikov, до сих пор известный только из Японского моря (Райков 1963). Кроме того, интерес представляет нахождение *Tracheloraphis stephani* Dragesco — вида, впервые найденного (Dragesco 1965) в морском песке у побережья Мавритании.

Чтобы получить более четкое представление о сходстве и различии сравниваемых фаун, были вычислены коэффициенты общности по формуле, предложенной Райковым (1963) $K = \sqrt{\frac{2C}{A+B}}$, где C — число общих видов или родов, а A и B — числа видов или родов в двух районах. Так, коэффициент общности по числу видов с Белым морем равен 0.68, по числу родов — 0.85, с Японским соответственно — 0.51 и 0.66. Такие довольно высокие коэффициенты общности являются дополнительным аргументом, говорящим в пользу гипотезы Форе-Фремье о космополитном характере распространения псаммофильных видов морских инфузорий.

Выводы

На песчаной литорали Баренцова моря обнаружено 50 видов псаммофильных инфузорий, список которых приводится в статье.

Даются краткие описания трёх видов: *Tracheloraphis prenanti* Dragesco (одной из разновидностей этого вида), *Tracheloraphis vermiformis* Raikov и *Diophrys* sp.

Для сравнения фаун интерстициальных инфузорий изученных районов Баренцова, Белого и Японского морей вычисляются коэффициенты общности.

SUMMARY

A list of 50 species of interstitial ciliates inhabiting the sandy littoral of the Barentz Sea is given. Three species are shortly described:

1. One of the varieties of the highly polymorphous species *Tracheloraphis prenanti* Dragesco. Our form has 16 kineties and one complex nucleus containing two micronuclei and six macronuclei.

2. *Tracheloraphis vermiformis* Raikov, originally described by Raikov (1962) from fixed material only. A drawing of a living specimen is given. The number of kineties of the Barentz Sea form of this species is about 55. The nuclear group consists of two micronuclei and 4 macronuclei. The non-ciliated dorsal zone is very narrow and visible in fixed material only (whole mounts).

3. *Diophrys* sp. This form is analogous to *Diophrys scutum* according to all characters except the number of transversal cirri. *D. scutum* has 5 such cirri, while our form has 6.

A comparison of the specific composition of the sand dwelling fauna of ciliates of the Barentz Sea, on one hand, and of the White and Japan Seas, on the other hand, shows a high degree of community of all the three faunas. This argues in favor of the hypothesis by Fauré-Fremiet supposing cosmopolitan geographical distribution of the psammophilous species of marine ciliates.

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Pileocephalus astaurovi sp. n., a gregarine parasite of *Baicalina spinosa* (Mart.) (*Trichoptera*) from Baical Lake

Pileocephalus astaurovi sp. n., pasożytnicza gregaryna z *Baicalina spinosa* (*Mart.*) (*Trichoptera*) z Bajkału

The fauna of the Baical Lake is extremely interesting due to its unusual endemic character. However, the knowledge of gregarines parasitic in various invertebrates in Baical Lake is limited only to one species known from turbellarians (Swartzewsky 1910) and to two species from gammarids (Zwetkow 1928).

In April of 1966 I had the opportunity of working in the Biological Station of the Biological-Geographical Scientific Institute of the Irkutsk Univesity in Bolshiye Koty at Baical Lake. During that time I examined a number of invertebrates obtained for me through the facilities of the Station.

Special thanks are expressed to Professor M. M. Kozhov, Rector P. F. Bočkarov and Messrs. N. Rezinkov and V. Kaplin for generous help during my work at Baical Lake and Irkutsk. The travel grant obtained from the Polish Academy of Sciences and the Academy of Sciences of the U.S.S.R. is acknowledged.

Results of studies on microsporidian infections of gammarids were recently published (Lipa 1967 a) and on gregarines are just prepared for publications (Lipa 1967 b).

Materials and methods

Larvae of *Baicalina spinosa* (Mart.) for this study were collected on April 6 and 7 of 1966 at the shore of Baical Lake close to Biological Station at Bolshiye Koty.

The larvae were collected about 100 meters from the coast on the depth of 3 to 4 meters. As Baical Lake was covered at that time with the ice 60 do 80 cm. thick, the air holes were made and the sea diver Mr. N. S. Rezinkov was going down to the bottom.

Collected larvae were immediately brought to laboratory, identified and examined by me under the microscope. The insects were dissected and their tissues as well as gut contents were used to prepare microscopic slides. Photographs were taken by Mr. Vitali Kaplin and myself.

Results

Pileocephalus astaurovi species nova

Host species: *Baicalina spinosa* (Mart.)
Site of infection: digestive tract.
Type locality: Baical Lake close to Bolshiye Koty, Soviet Union.
Derivation of name: After Academician Boris Lvovič Astaurov, Director of the Filatov's Laboratory of Experimental Embryology, The Severtzov's Institute of Animal Morphology, Academy of Sciences of the U.S.S.R., Moscow, to whom the author is indebted for generous help.

Morphology: Cephalins up to 230 μ. Gamonts solitary up to 774 μ long and 341 μ wide. Ratio LP : TL = 1 : 2.7 to 4.1; WP : WD = 1 : 1.1 to 1.4. In cephalines these ratios are slightly different. Measurements of eleven gamonts and of three cephalins are given in Table 1.

Table 1

Measurements of gamonts and cephalins of *Pileocephalus astaurovi* sp. n..(in microns)

LP	LD	WP	WD	TL	LP : TL	WP : WD
			Gamonts			
206	568	128	149	774	1 : 3.7	1 : 1.1
175	546	263	330	721	1 : 4.1	1 : 1.2
165	525	237	288	690	1 : 4.1	1 : 1.2
165	515	278	340	680	1 : 4.1	1 : 1.2
165	474	227	268	639	1 : 3.8	1 : 1.2
206	419	263	341	625	1 : 3.0	1 : 1.3
213	412	206	270	625	1 : 2.9	1 : 1.0
220	376	270	291	595	1 : 2.7	1 : 1.1
149	390	227	327	539	1 : 3.6	1 : 1.4
123	412	227	237	535	1 : 4.3	1 : 1.1
118	319	149	175	438	1 : 3.7	1 : 1.2
			Cephalins			
74	156	57	71	230	1 : 1.3	1 : 1.2
78	149	96	106	227	1 : 2.8	1 : 1.1
25	78	37	71	103	1 : 4.5	1 : 1.9

Legends: LP — Length of protomerite; LD — Length of deutomerite; WP — Width of protomerite; WD — Width of deutomerite; TL — Total length

Protomerite broadly rounded, usually wider than long. Deep constriction at septum and the septum itself well seen (Pl. I 1, 2). At the apex of protomerite the basis of the epimerite, that was lost, is well seen (Pl. I 2). Epicyte is well seen as thin translucent layer around the body. Endocyte is dense and black. Deutomerite widest at shoulder and ending in an acute point. Epicyte and endocyte similar to that of protomerite. However, in many cases endocyte at acute point is transparent (Pl. I 2).

Nucleus with diameter up to 50 μ poorly seen as white spot in black endocyte, located in the front part of deutomerite. Number of karyosomes has not been determined.

Cysts spherical up to 500 μ in diameter; cyst dehiscence by simple rupture.

Host parasitization: Eight larvae and two pupae of *Baicalina spinosa* were examined. Four larvae out of eight were infected with gregarines. Two examined pupae were free from the parasite. The intensity of infection was moderate and up to 10 gregarines were observed in the midgut and hindgut.

Systematic position: Type of epimerite and other morphological features indicate that the studied gregarine belongs to the genus *Pileocephalus* whose members parasitize in *Trichoptera* (W a t s o n 1916). This is the first record of a gregarine infection of *Baicalina spinosa* and apparently new species is involved.

While examining the literature on members of *Pileocephalus* genus I have not found any species that might eventually be identified with the studied species. All of them differ in morphology and infect other hosts.

The view that gregarine found in *Baicalina spinosa* is a new species is strongly supported by the fact that the insect host is an endemic inhabitant of Baical Lake. Therefore I consider that the gregarine found in *Baicalina spinosa* has not been previously described and accordingly I propose for it name *Pileocephalus astaurovi* sp. n.

Summary

A new gregarine *Pileocephalus astaurovi* sp. n. is described from the digestive tract of *Baicalina spinosa* (Mart.) (*Trichoptera*) from Baical Lake. Gamonts are solitary and up to 774 μ long. Four out of eight larvae were infected with the parasite; two pupae were free from infection.

STRESZCZENIE

Opisano nowy gatunek gregaryny *Pileocephalus astaurovi* sp. n. z przewodu pokarmowego larw chruścika *Baicalina spinosa* (Mart.) (*Trichoptera*) z jeziora Bajkał. Gamonty są pojedyńcze a ich długość sięga 774 μ. Z ośmiu badanych larw, cztery były zarażone przez pasożyta; dwie badane poczwarki były zdrowe.

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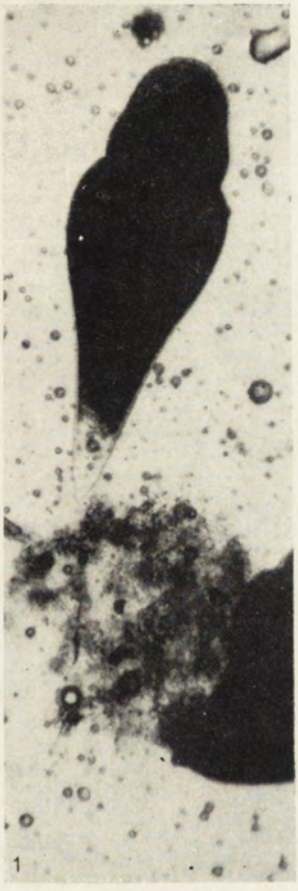
EXPLANATION OF PLATE I

Gamonts of *Pileocephalus astaurovi* sp. n., from *Baicalina spinosa* (Mart.)
Magnification: 1—120×, 2—170×



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Nosema kozhovi sp. n., a new microsporidian parasite of *Brandtia lata lata* (*Crustacea, Gammaridae*) of Baical Lake

Nosema kozhovi sp. n. (*Microsporidia*), nowy pasożyt *Brandtia lata lata* (*Crustacea, Gammaridae*) z Bajkału

In April 1966, by the arrangement between Polish Academy of Sciences and the Academy of Sciences of the U.S.S.R., I had the opportunity of working at Baical Lake that is famous of its unic faunistic features (Kozhov 1965).

Special thanks are expressed to Professor M. M. Kozhov, Rector of the University — Professor P. F. Bočkarov, Mrs. Galina S. Kaplin, and to Messrs. Nokolai Rezinkov, Vitali Kaplin and Nikolai Kulagin for generous help during my work at Baical Lake and Irkutsk. The travel grant obtained from the Polish Academy of Sciences and the Academy of Sciences of the U.S.S.R. is acknowledged.

The aim of this work was to obtain information on protozoans parasitic in Baical invertebrates, especially of gammarids. So far there are only records of gregarine infections of turbellarians (Svartzevski 1910 a, b), trichopterans (Lipa 1967 a) and gammarids (Zwetkow 1928; Lipa 1967 b) in Baical Lake.

Material and methods

Larvae and adults of *Brandtia lata lata* (Dybowski) for this study were collected on April 6 and 7, 1966 at the shore of the Baical Lake close to Biological Station of the Biological-Geographical Scientific Institute of the Irkutsk University at Bolshiye Koty.

The gammarids were collected about 100 meters from the coast on the depth from 3 to 4 meters. As Baical Lake was covered at that time with the ice about 60—80 centimeters thick, the air holes were made and the sea diver Mr. Nikolai S. Rezinkov was going down to the bottom.

The collected gammarids were immediately brougth to laboratory, identified by Mrs. Galina S. Kaplin and later examined by me under the microscope.

The gammarids were dissected and their gut and other tissues were used to prepare microscopic slides. The tissue smears were fixed in methanol and stained with 0.5% Giemsa's solution. Studies of the life cycle were completed at my Poznań laboratory.

Results

Nosema kozhovi species nova

Host species: *Brandtia lata lata* (Dybowski)
Host tissue involved: General infection; especially gut epithelium.
Type locality: Baical Lake close to Bolshiye Koty, Soviet Union, April 7, 1966.
Derivation of name: After Professor Mikhail Mikhailovic Kozhov, Head of the Department of Zoology, Irkutsk University, whose kind help made this study possible.

Schizogony and sporogony: The development of the studied microsporidian is typical for the genus *Nosema*. Schizonts are up to 5 microns in diameter. Uni- and binucleated schizonts were observed. The nuclei of schizonts are bright red and the cytoplasm deeply blue. Sporonts are elongated, binucleated and are up to 6 microns long. They stain with Giemsa's solution less intensive than schizogonic stages. Since the sporonts give rise to one spore the microsporidian under investigation belongs to the genus *Nosema*.

Spore: Oval, living spores are 3.3 to 3.9 microns long by 2.1 to 2.2 microns wide (Pl. I 1). Fixed and stained spores are 2.5 to 4.0 by 1.8 to 2.1 microns. Results of measurements of 50 fresh and 50 stained spores are given in Table 1.

Table 1
Frequency distribution of the length of two samples of 50 spores each of microsporidian *Nosema kozhovi* sp. n.

Sample	Dimensionable groups in microns			
	2.1—2.5	2.6—3.0	3.1—3.5	3.6—4.0
Fresh spores	—	—	41	9
Fixed and stained spores	1	41	7	1

Attempts to extrude polar filaments using spores stored for three months in water at room temperature failed, although the spore wall was easily broken applying pressure on cover glass (Pl. I 2, 3).

Young spores stained with Giemsa's solution have large bright red nucleus and deep blue cytoplasm (Pl. I 4). Many stained spores show presence of the glycogen granule that is red in color and located at one end of the spore. Mature spores stain weaker; their cytoplasm and vacuole are stained light blue and their nuclei are faint red (Pl. I 5).

Host parasitization and pathology: *Brandtia lata lata* is a common inhabitant at the shore bottom of Baical Lake. During the course of this study 11 larvae and 4 adults were examined. Out of this number only one larva was found to be infected by the parasite.

The infected larva had the abnormal appearance; it was milky white and showed very low mobility comparing with the healthy ones. After dissection water become whitish due to enormous number of released spores. All tissues were infected but especially heavily the gut epithelium, fat body and muscles were destroyed.

Systematic position: As it was mentioned above the microsporidian infecting *Brandtia lata lata* belongs to the genus *Nosema* since the sporont gives rise to one spore. As this is a first record of a microsporidian infection of *Brandtia*

and the studied species is quite different from the other microsporidians known from gammarids (Table 2), I consider it to be a new species. Accordingly a name *Nosema kozhovi* sp. n. is proposed.

Discussion

The microsporidian infections of crustaceans, especially of gammarids, are imperfectly known. In the literature available to me I have found only few records (Table 2). One of it refers to *Nosema gammari* van Ryckeghen and others to members of the genus *Thelohania.*

Tabele 2

A record of microsporidian infections of gammarids *(Crustacea, Gammaridae)*

Microsporidian	Host	Infected tissues	Spore size in microns	References
Baccillidium niphargi (Poisson) (= *Mrazekia niphargi* Poisson)	*Niphargus stygius* Schiödte	not mentioned	8—9 by 3	Poisson (1924), Jirovec (1936)
Nosema gammari van Ryckeghem	*Gammarus pulex* L.	body cavity	1.5 by 0.75	van Ryckeghem (1930)
Nosema kozhovi sp. n.	*Brandtia lata lata* (Dybowski)	gut epithelium. fat body. muscules	Fresh: 3.3—3.9 by 2.1—2.2 Stained: 2.5—4.0 by 1.8—2.1	Lipa (present paper)
Ostosporea gammari van Ryckeghem	*Gammarus pulex* L.	circulatory system and heart epithelium	4—6 by 1.2—2	van Ryckeghem (1930)
Thelohania giraudi Léger (= *Plistophora blochmanni Zwolfer* = *Glugea mülleri* Pfeiffer pro parte)	*Gammarus pulex* L. *G. locusta* L.	muscules	5.5	Léger (1909), Léger et Hesse (1917) Pfeiffer van Ryckeghe (1930), Georgevitch (1929)
Thelohania mülleri (Pfeiffer)	*Gammarus pulex* L.	muscules	4—5 by 2	Pfeiffer (1895), Stempell (1902), Kudo (1924)
Thelohania mülleri minuta van Ryckeghem	*Gammarus pulex* L.	muscules	5 by 3	von Ryckehgem (1930)
Thelohania vandeli Poisson	*Niphargus stygius* Schiödte	not mentioned	6—6.5 by 3	Poisson (1924)

Spore of *Nosema gammari,* that infects *Gammarus pulex* L., are very small and measure 1.5 by 0.75 microns as compared with large spores of *Nosema kozhovi* sp. n.

Members of *Thelohania* genus cannot be taken under consideration at the taxonomic discussion of *Nosema kozhovi* sp. n. as their sporogony is quite different than of members of *Nosema genus.*

Statement that the studied *Nosema* is a new species is strongly supported by the fact that *Brandtia lata lata* is an endemic inhabitant of Baical Lake and the same probably refers to its parasite *Nosema kozhovi* sp. n.

This is the first record of microsporidian infection of the Baical invertebrates.

Summary

Nosema kozhovi sp. n., parasitic in *Brandtia lata lata* (Dybowski) is described. Spores are oval and measure 3.3 to 3.9 by 2.1 to 2.2 microns when alive;

fixed and stained spores are 2.5 to 4.0 by 1.8 to 2.1 microns. The main tissue attacked is gut epithelium; fat body and muscles are also involved. This is the first record of microsporidian infection of invertebrates in Baical Lake. A list of microsporidians recorded from gammarids is given.

STRESZCZENIE

Nosema kozhovi sp. n., pasożytującą w kiełżu *Brandtia lata lata* (Dybowski) (*Crustacea, Gammaridae*) opisano w jeziorze Bajkał. Spory są owalne i mierzą: świeże od 3.3 do 3.9 mikronów długości i 2.1 do 2.2 mikronów szerokości; spory barwione mierzą 2.5—4.0 mikronów długości i 1.8—2.1 mikronów szerokości. Pasożyt atakuje głównie nabłonek jelita, mieśnie i ciało tłuszczowe. Jest to pierwszy przypadek mikrosporydiozy bezkręgowców w jeziorze Bajkał. Podano listę *Microspridia* opisanych z kiełżów.

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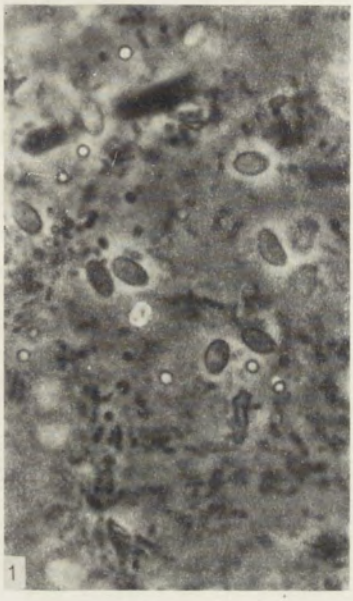
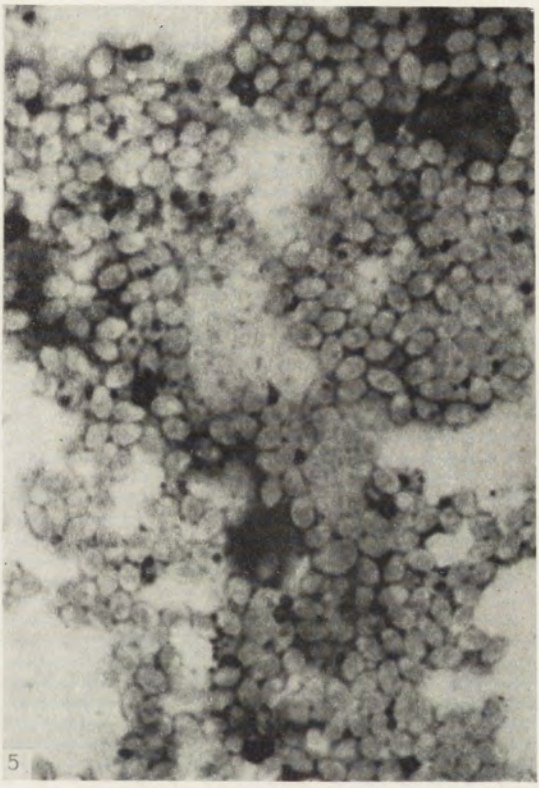
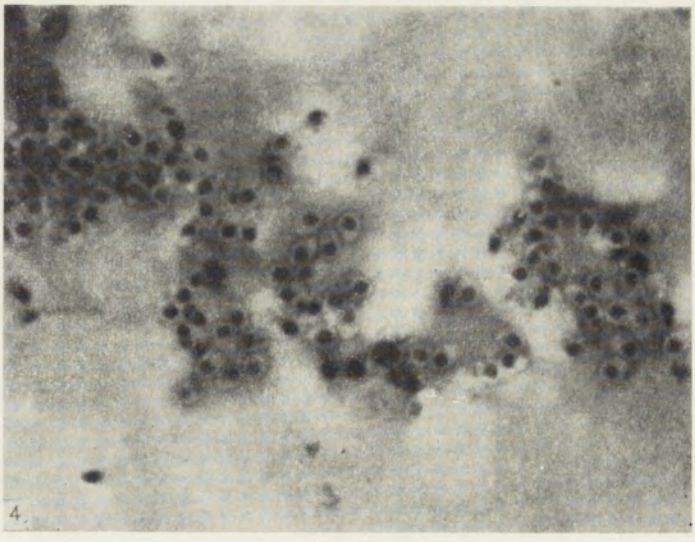
EXPLANATION OF PLATE I

Nosema kozhovi sp. n. from *Brandtia lata lata* (Dybowski)

1: Fresh spores as seen in the host tissue
2—3: Spores with broken walls due to applying pressure
4—5: Spores stained with Giemsa's solution







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