

# THE PHYSIOLOGICAL REGENERATION (REORGANIZATION) OF THE ORAL APPARATUS IN THE COLPIDIUM KLEINI (CILIATA, TETRAHYMENIDAE)

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## Synopsis

The physiological regeneration of the oral apparatus of *Colpidium kleini* has been investigated and, in connection with this, some atypical phenomena are described. As first sign of the physiological regeneration a narrow-meshed network of the silver-line system shows itself at the posterior end of the oral apparatus. Subsequently the new oral basal bodies appear at the junctions of the network which develops continuously. The new basal bodies originate, *de novo*, from the substance of the silver-line system. At the end of the process, the basal bodies, initially irregularly arranged, will be organized to the final basal bodies of the new membranelles. Parallel with this, the original oral apparatus is absorbed. At that time the newly formed oral apparatus begins to wander in anterior direction and, having reached the original oral region, its invagination will be accomplished. All these processes lead to the physiological regeneration of the oral apparatus. Several problems of the physiological regeneration are discussed. Between the morphogenesis of the new oral apparatus and the silver-line system an intimate relation has been revealed.

## Introduction

In the literature, there are few precise data about the physiological regeneration (reorganization) of *Ciliata*. It seems, at present, that the alterations in the silver-line system need, in the first place, a more profound investigation. As for the well investigated species of the *Colpidium* — *Glaucoma* — *Leucophrys* — *Tetrahymena* group (C—G—L—T group) [3], there have performed no thorough investigations on these processes. Some information can be found in the works of KLEIN [24, 25, 28] concerning *Colpidium campylum*, in those of GELEI [17] (on *Glaucoma scintillans*), CHATTON, LWOFF, LWOFF and MONOD [1] (on *Glaucoma*), CORLISS [3] (on *Tetrahymena pyriformis*) and FRANKEL [15] (on *Glaucoma chattoni*). FOISSNER [13] and TOTWEN-NOWAKOWSKA [39] have described the physiological regeneration and some spontaneous dividing-malformations on *Colpidium kleini* and on *Stylonychia mytilus*, respectively. Many authors have mentioned, in connection with other investigations, the physiological regeneration (reorganization) [6, 16, 19, 21, 29, 33, 35, 38]. The most intensive investigations of these phenomena were performed by SCHWARTZ [34] on *Stentor coeruleus* reviewed by GRELL [18].

This study reports on investigations concerning the physiological regeneration of the oral apparatus of *C. kleini* with special regard to the involved morphogenetical changes of the silver-line system. Besides, various atypical phenomena are described.

## Material and method

Mass-cultures of *Colpidium kleini* [10], *C. campylum* STOCKES, *C. colpoda* EHRBG., *Glaucoma scintillans* and *Tetrahymena pyriformis* have been studied. The physiological regeneration of the oral apparatus shows many similarities in these species. For this reason, a more precise description of this phenomenon seems to be sufficient only in one species, namely in *C. kleini*. As culture medium hay or lettuce-leaf extracts were used (no axenic cultures were set up).

The animals were silverized by using the author's "dry" modification of the original method of KLEIN [9, 23]. As it is documented by the photos, this method is apt for the visualization of the silver-line system of KLEIN. Its essential advantage is that one can obtain, by using it, well-silverized animals in 80 to 90%.

The terminology is in accordance with that used by KLEIN [28] and CORLISS [4].

## Results

In like manner as in our study on the morphogenesis of *C. kleini* [14], the description of the physiological regeneration of the oral apparatus will be here divided into different stages. Each of these stages will be determined by special alterations in the silver-line system.

In an earlier work [10] we already have performed a detailed investigation of the silver-line system (Figs 1 and 2) and the oral apparatus. The oral apparatus of *C. kleini* has the same typical architecture as described by CORLISS [5] for the family of *Tetrahymenidae*; namely, it consists of three adoral membranelles and an undulating membrane. Fig. 3 shows the fine structure of the oral apparatus of *C. kleini*.

### *The normal physiological regeneration of the oral apparatus*

**Stage I.** Fig. 4 shows a very early regeneration stage. In all probability, it starts with the formation of a narrow-meshed silver-line system along the "Richtungsmeridian" [17] (stomatogenetic kintety [30]). In direct connection with the cell-mouth the silver-line system begins to show alteration. The outgrowing silver-lines form anastomoses with the protrichocyst-fibrils situated on the left side of the direction-meridian ("Richtungsmeridian"). As it is shown in Fig. 5 (a magnified part of Fig. 4), the formed narrow-meshed network contains no accumulated argyrophil substance (compare with Fig. 6). The connection of this network with the oral apparatus is very conspicuous.

In this stage the oral apparatus begins to degenerate, namely, the three adoral membranelles and the undulating membrane will be resorbed. In some other animals, however, structures of the oral apparatus could be better identified than in Figs 4 and 5.

**Stage II.** It is similar to Stage I differing, however, by that in junctions of the narrow-meshed network numerous grain-like accumulations of argyrophil substance occur (see e.g. the arrow). These represent, without doubt, the basal bodies of the prospective oral apparatus. The small sizes of these accumulations

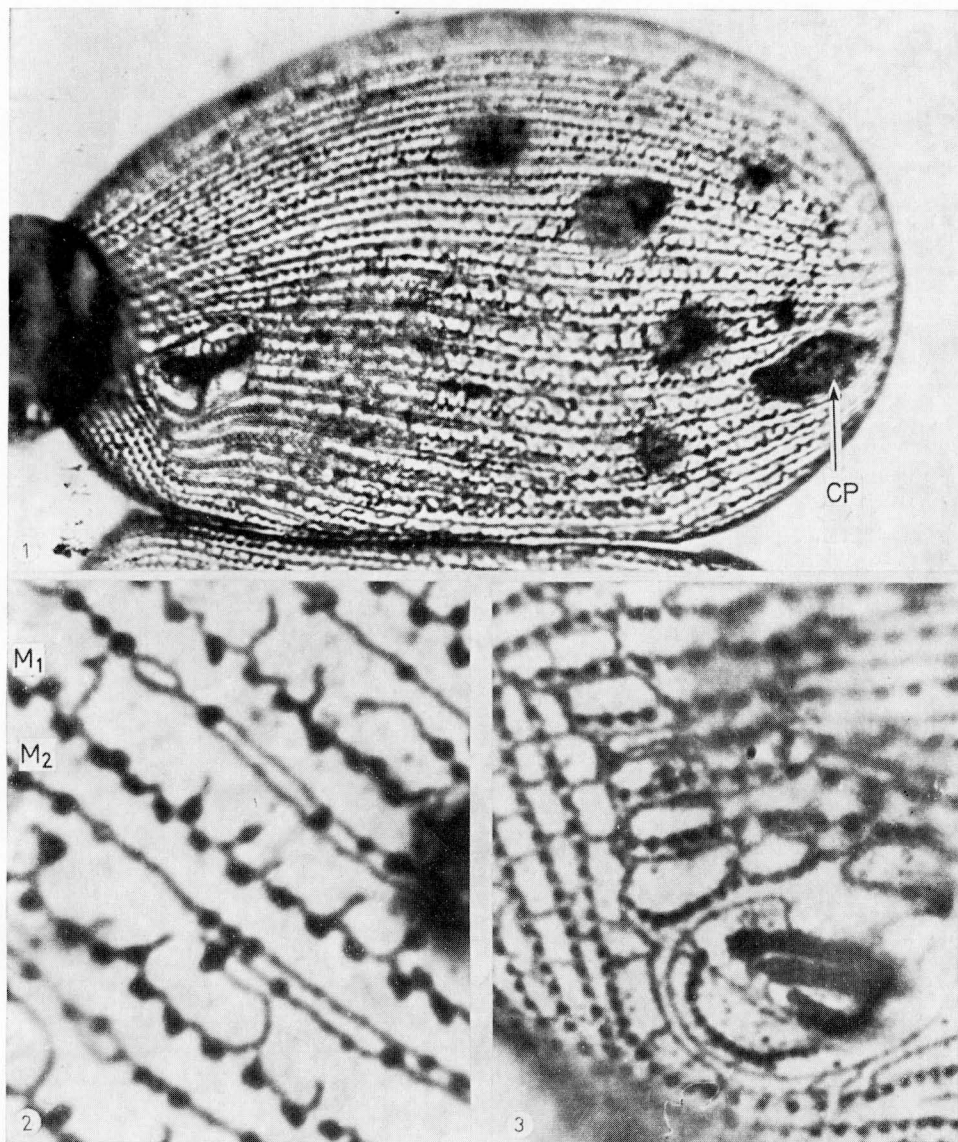


Fig. 1. *C. kleini*, ventral view with oral apparatus and cytopygge (CP). The faecal ball must have been pushed out immediately before shrinkage as shown by the cytopygge being in an early stage of regeneration. Approx.  $\times 1,300$

Fig. 2. *C. kleini*, view on part of the dorsal side. First-order meridians ( $M_1$ ) with joined basal bodies and second-order meridians ( $M_2$ ) with joined protrichocyst are well-distinguishable. The majority of the protrichocysts have been pushed out, most probably in response to the stimulus of shrinkage. Note the initial regeneration appearing in the silver-line system at the site where division of second-order meridians (in two fibrils running parallel) is seen. Approx.  $\times 6,000$

Fig. 3. *C. kleini*. Architecture of the oral apparatus. Note tetrahymenid organization (three adoral membranelles and an undulant membrane). Approx.  $\times 4,000$



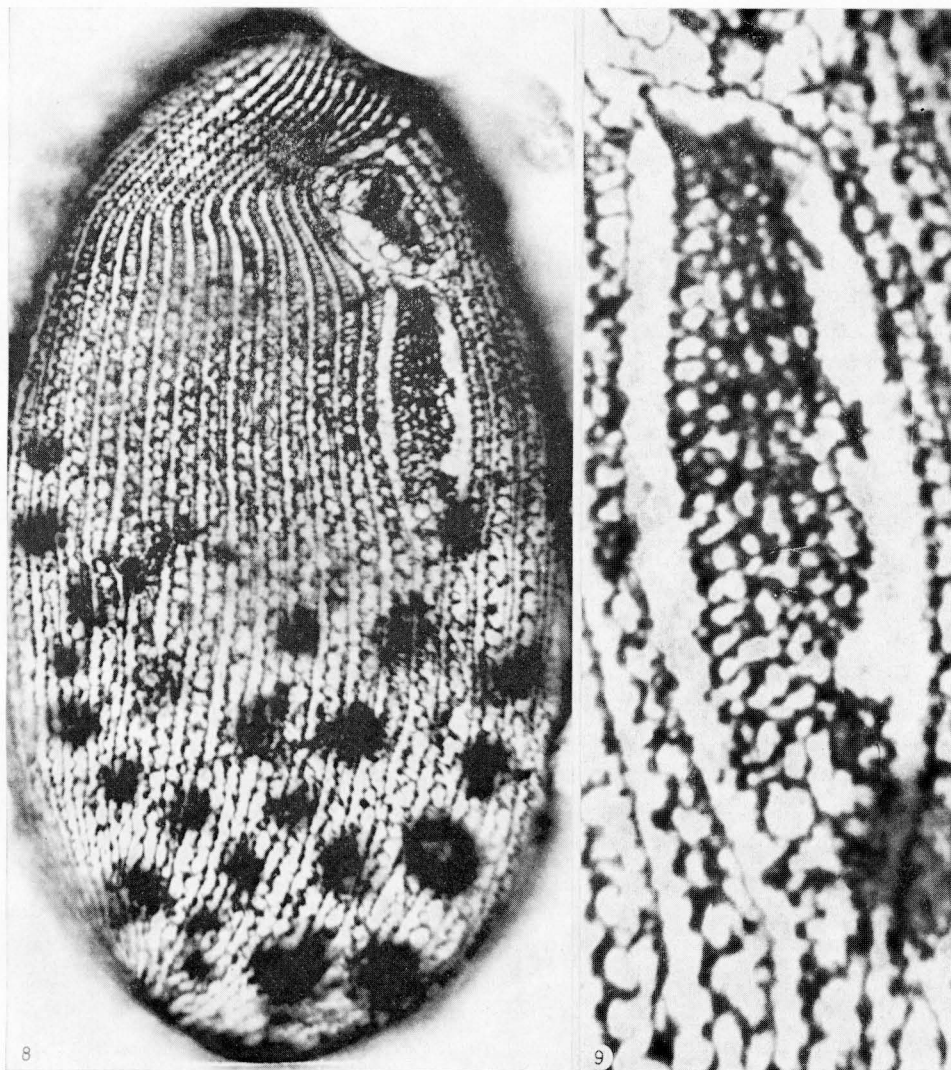


Figs 4 and 5. *C. kleini*, initial stage of the physiological regeneration of the oral apparatus. Close beneath the oral apparatus a narrow-meshed silver-line system begins to be formed (Fig. 5). Approx.  $\times 1,250$ ;  $\times 5,500$

Fig. 6. *C. kleini*, physiological regeneration. In the narrow-meshed network seen in Fig. 5, *de novo* formed basal bodies of the future oral apparatus are appearing; initially as small argyrophyl substance in the junctions of the narrow-meshed network (arrow); soon thereafter they reach the size of normal basal bodies. Approx.  $\times 5,800$

Fig. 7. *C. kleini*, physiological regeneration. The narrow-meshed area beneath the oral apparatus has significantly enlarged. Note the numerous newly-formed basal bodies in the junctions of the narrow-meshed network and the completely degenerated structures of the old oral apparatus. Invagination is retrograde. Approx.  $\times 4,500$





Figs 8 and 9. *C. kleini*, physiological regeneration. A well-pronounced narrow-meshed silver-line system is developing adjacent to the old, completely degenerated, oral apparatus. Note the newly-formed basal bodies of the future oral apparatus inside the system. Approx.  $\times 1,600$ ;  $\times 4,500$

points to that the basal bodies are not yet fully developed. It is very probable that they will be formed *de novo* in the silver-lines of the narrow-meshed network.

*Stage III.* A further enlargement of the narrow-meshed silver-line system is to be found under the oral apparatus. At the junctions of this network numerous newly-formed basal bodies are situated.

In this stage, the original oral apparatus is remarkable. Its triangular form is still well-recognizable, however, the specific oral structures are totally degenerated. At the original oral region an undifferentiated mass of argyrophil substance is merely to be found, expanding itself directly above the cytostome entry. It is to be noted, further on, that the invagination will be retrograde. The oral groove (Oralgrube), in which the cytostome is located, disappears and the oral region seems quite flat.

*Stage IV.* The new oral-anlage has continued to develop significantly. The narrow-meshed network reaches as far as about the cell-centre and then does not continue to grow. The posterior end is situated about the site where the stomatogenesis starts at the division [14]. In the course of the whole process, this network remains connected with the direction-meridian (Richtungsmeridian) and the original oral region (Fig. 9). In this stage, no organization of the basal bodies can be observed within the narrow-meshed network (Fig. 9). The old oral apparatus seems to be totally degenerated preserving still, however, its normal size.

*Stage V.* In this stage, there begins the orientation of the basal bodies situated within the narrow-meshed network of the new oral-anlage. The future adoral membranelles are well observable by having an extraordinary size. The membranelles are by about a third longer than those of the normal animal. The undulating membrane (see at the arrow) is not yet developed conspicuously. Its basal bodies are still irregularly arranged within the narrow-meshed network. From the fully developed adoral membranelles solitary silver-lines travel to the undulating membrane just developing.

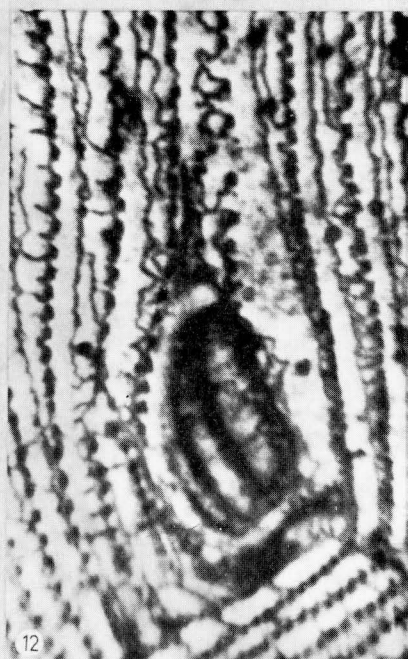
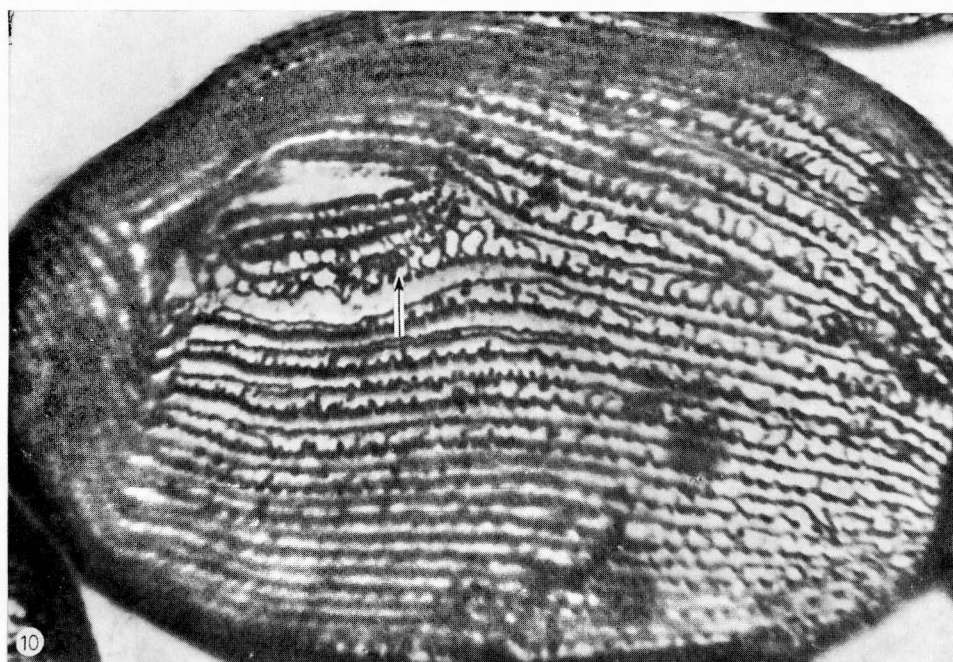
The old oral region seems to be very small. The specific oral structures have been totally absorbed.

*Stage VI.* The membranelles having newly formed in stage V have displaced themselves anteriorly to the original oral region. There starts the invagination of the new oral structures, which already have their definitive pattern (compare Fig. 11 with Fig. 3). At the posterior end of the new oral apparatus some rests of the narrow-meshed network activated for development are still visible. Obviously the membranelles have become somewhat shorter (compare with stage V), but grown in width.

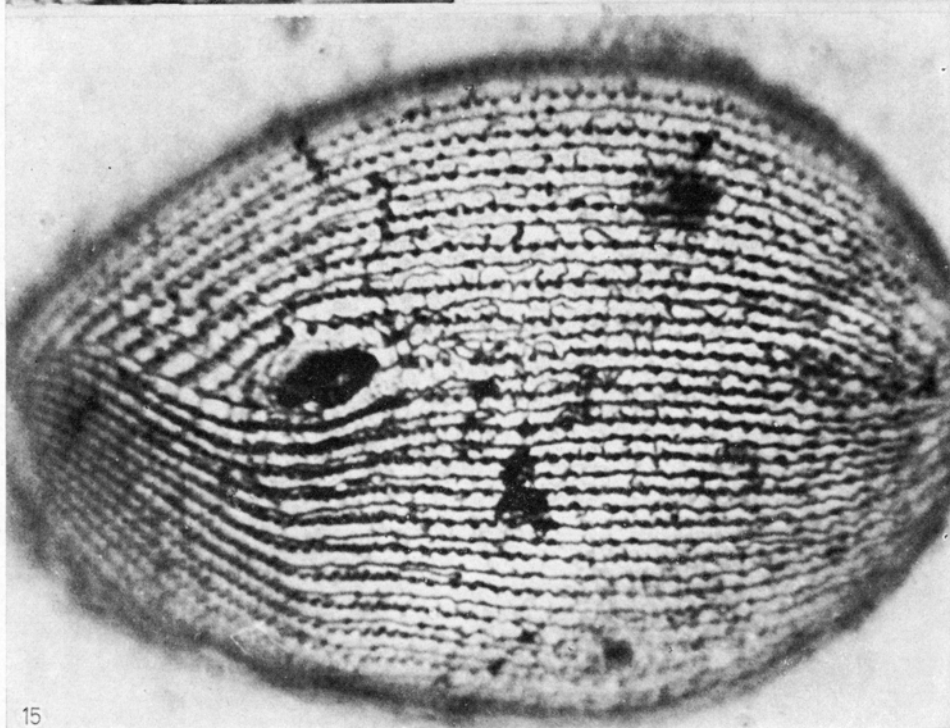
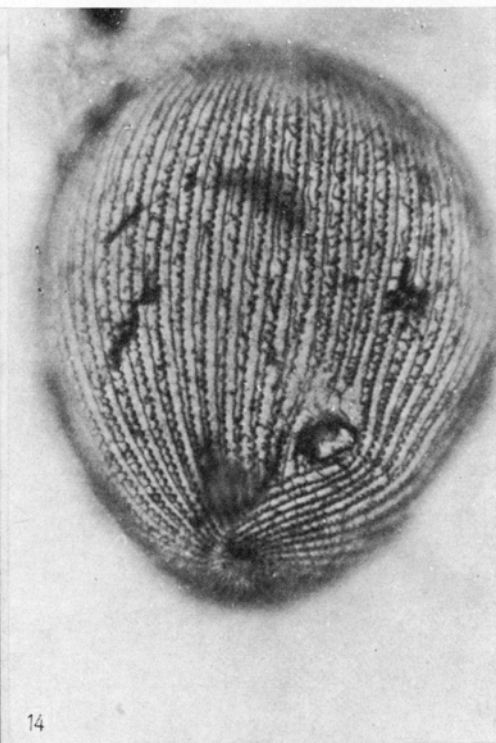
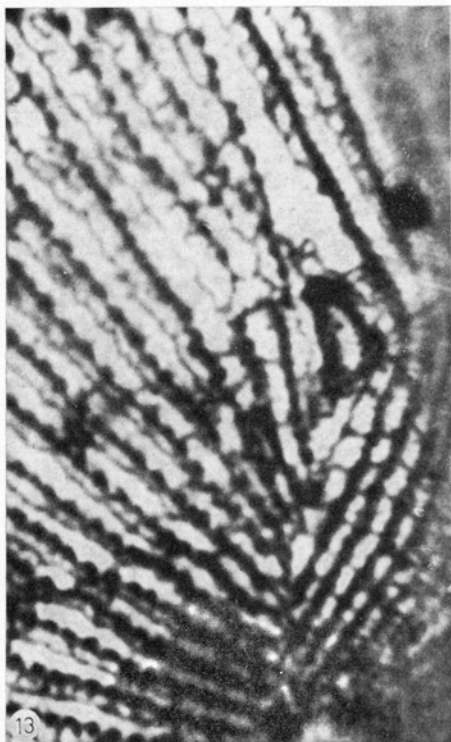
*Fig. 10. C. kleini*, physiological regeneration. The initially irregularly arranged basal bodies in the narrow-meshed network are turning into the basal bodies of membranelles. The three basal adoral membranelles are already well visible. The undulant membrane is still incomplete. The bodies are loosely scattered in the narrow-meshed network. The old oral structures appear small and degenerated. Approx.  $\times 1,300$

*Fig. 11. C. kleini*, final stage of the physiological regeneration of the oral apparatus. The new oral structures are already in the original oral region and begin to be invaginated. Approx.  $\times 1,000$

*Fig. 12.* Defective regeneration. Approx.  $\times 3,600$







### *Atypical phenomena*

*Defective regeneration.* In a single case an anomalous reorganization of the oral apparatus was observed (Fig. 12). That here a real regeneration of the oral apparatus had occurred is shown by the direction-meridian (Richtungs-meridian). It still shows those typical features which are observable after regeneration: a slight breaking up and interlacement of the silver-lines immediately under the oral apparatus. This defective regeneration is characterized by the lack of the undulating membrane and the cytostome-entry. The adoral membranelles are, nevertheless, well observable. These oral structures show no signs of invagination.

*Degeneration without regeneration.* In certain cases degeneration of the oral apparatus could be observed without any sign of regeneration. The probable phases of the absorption-process are shown in Figs 13, 14 and 15. The membranelles, the cytostome as well as the silverizable fibrils of the silver-line system disappear gradually. Finally, at the oral region, an undifferentiated mass of argyrophil substance can merely be found (Fig. 15). Animals without this accumulation could never be observed. This process of degeneration resembles, in principle, that observed in the normal physiological regeneration (see page 360). Signs of any regeneration are obviously lacking. A similar phenomenon has been described by FRANKEL [15].

Occasionally, a narrow-meshed silver-line system appeared to extend above the oral region.

### **Discussion**

#### *Cause and biological significance of the physiological regeneration*

KLEIN [24], who was the first to describe the close relation of the physiological regeneration to the morphological alterations of the silver-line system, has supposed that regeneration must take place because, due to the successive dividing of an individual, the senescent oral apparatus of the parent animal will be used up. IVANIC [19], based on various observations, suggests that the development of the resting-stage in *Chilodonella uncinatus* is induced by the using up during the vegetative period and an injury of the locomotory and nutritive organelles; these organelles are decomposed during the resting-stage and rebuilt immediately before excystation. According to GARNJOBST [16] the physiological regeneration in hypotrichous *Ciliata* opens a way towards a fundamental reorganization of the cell; this must be preceded by an elimination of the accumulated metabolic products. Similar observations were published by

TOTWEN-NOWAKOWSKA [39]. CORLISS [3] considers the differentiation of the old oral apparatus an occasion for regeneration. The conclusions drawn by DEMBROWSKA [6] and SCHWARTZ [34] are principally different from the views cited above. They attribute the phenomena to a disproportionation of the biological system. It has been emphasized most definitely by SCHWARTZ that physiological regeneration does not serve as a substitution of the organelles which need to be renewed after having been used for a long period of time, for pushed-out membranelles of *Stentor* could be substituted by formations originated in basal structures that had remained in the cytoplasm. This may occur after experimental injury as well as after prolonged use. Experiments on *C. kleini* have clearly shown that injured oral structures and lost somatic cilia can be substituted by basal structures that have remained in the cortex [11, 12]. At the same time no considerable changes occur in the silver-line system. In some *Ciliata*, on the other hand, partial injury of the oral apparatus, or of the individual is followed by total regeneration [21, 38]. *Paramecium* is absolutely incapable of substituting an experimentally injured oral apparatus, a phenomenon suggestive of the great variability of reorganization potency.

According to the majority of the authors [6, 16, 19, 21, 22, 33, 35, 39] the term physiological regeneration comprehends more or less the whole animal. Especially the experiments of JERKA-DZIADOSZ [20, 21, 22] have proved that the absorption process of the ciliary apparatus of hypotrichous *Ciliata* is an "all or none" reaction [21]. MAC LENNAN [29] and SCHWARTZ [34], on the other hand, believe that physiological regeneration comprehends but especially highly organized organelles and those incapable of accreting (oral structures, macronucleus, membranelle band and a quantity of micronuclei). This belief is due to a misinterpretation (the physiological regeneration of the somatic ciliature is, naturally, much more difficult to observe) and to a too narrow definition of the term physiological regeneration. In *C. kleini*, too, a regeneration of the somatic ciliature may occur simultaneously with that of the oral apparatus. The same however cannot be observed directly because of the lack of considerable changes in the silver-line system.

The cause of the physiological regeneration in *C. kleini* is absolutely unclear. Even the very acceptable ideas of SCHWARTZ [34] are not valid for *C. kleini*. It has been proved experimentally that partially injured oral structures may proceed without any visible regenerative process in the silver-line system [11, 12].

The significance of the physiological regeneration in *C. kleini*, on the other hand, appears to be clear. All the authors cited above in connection with this question agree in that it leads to a reorganization of the entire organism.

The relation between physiological regeneration and some changes, especially reorganization processes, in the macro- and micronucleus is still unclear. Several authors [6, 33, 34] have described reorganization of the nuclear appa-



ratus occurring simultaneously with that of the cortical structures. It is still questionable whether here a reorganization of the nuclear apparatus is induced by that of the cortical structures or *vice versa*. It is quite unlikely that the two processes run independent of each other. Investigations into these processes are in progress.

### *Genesis of the new basal bodies*

The genesis of the new basal bodies in the course of the physiological regeneration of *C. kleini* has already been clarified. There is no doubt that they arise *de novo*, viz. from the substance of the silver-lines (Figs 7 and 9). Further development of the basal bodies takes place in the junctions of the narrow-meshed network activated for regeneration. No division of these organelles could ever be observed. The basal bodies arise in the same way in the course of morphogenesis as well [14]. It is supposed by numerous authors that the basal bodies originate in the silver-lines [e.g., 8, 14, 28, 29], others assume that they are capable of dividing [2, 7, 37]. Electronmicroscope findings are most consistent with the view of PITEKKA and CHILD [31], who suggest that the kinetosomes arise by a sudden polymerization from fibrous structures in a predetermined molecular milieu. This view appears to be consistent with the present findings. The fibrous structures may belong to the silver-line system [12], whereas the well-defined molecular milieu may come about in the course of the morphogenesis from the junctions of the silver-line system.

### *Silver-line system, and morphogenesis of the new oral apparatus*

KLEIN [25], MAC LENNAN [29] and TAYLOR and GARNJOBST [35] were the first to demonstrate the close relationship between silver-line system and physiological regeneration. They postulated an organizing function of the silver-line system. The experiments on *C. kleini* support this view. All parts of the new oral apparatus come about in close relation to morphological changes in the silver-line system. The orientation of the new basal bodies, having arisen in the silver-line system, might be attributed to that system, considering that, while basal bodies are turning into the basal bodies of membranelles, visible changes appear in the configuration of the narrow-meshed network of the silver-line system (Figs 11, 13, 14 and 16). FRANKEL's [15] suggestion that the arise of the oral opening and the formation of the membranelles are controlled by different mechanisms is, in view of the present results and of the processes observed during stomatogenesis unlikely [14]. More probably both the physiological regeneration and the stomatogenesis are continuously progressive processes a determining factor of which may be represented by the silver-line system. This is supported by the fact that the silver-line system is the

first, still absolutely undifferentiated, sign of physiological regeneration and stomatogenesis. New silver-lines are always the first to be built up, and new basal bodies appear thereafter. Consequently, a leading function of the basal bodies in various morphological processes, as is generally assumed today [2, 7, 31, 37], is unlikely. Appearing first after the formation of the silver-lines, they should be regarded in the morphogenesis as "secondary" organelles which are unlikely to introduce morphogenesis or play any leading role. KLEIN [28] already has referred to this fact.

The similarity between the regeneration of the oral apparatus of *C. kleini* and the stomatogenesis was striking [for comparison see 14]. Both processes are identical in detail, although, due to environmental differences, fine dissimilarities can be demonstrated. It would be of great interest to reveal whether the period of the formation of the oral apparatus during physiological regeneration is equal to that during morphogenesis. CORLISS [3] firmly states that there is no difference in duration between the two phenomena, but does not support his conclusion with exact data. The question whether and how the physiological regeneration in *C. kleini* proceeds under experimental conditions has remained open. DEMBROWSKA [6] has several times observed spontaneous regeneration in fasting *Stylonychia*. Since physiological regeneration may become fulfilled during division [26, 33] in the cyst [19], following experimental injury [37] as also in the interphases either before or after division, it should be assumed that this process is regulated by a well-defined mechanism which may be activated at any time. Spontaneous malformations of division showed a complete autonomy of the physiological regeneration from both stomatogenesis and nuclear division [13]. Both processes may occur in the same animal at the same time in different developmental stages [13].

#### REFERENCES

1. CHATTON, E., LWOFF, A., LWOFF, M., MONOD, J. (1931) La formation de l'ébauche buccale postérieure chez les ciliés en division et ses relations de continuité topographique avec la bouche antérieure. *Compt. rend. soc. biol.*, **107**, 540—544.
2. CHATTON, E., SEGUELA, J. (1940) La continuité génétique des formations ciliaires chez les ciliés hypotriches. Le cinétome et l'argyrome au cours de la division. *Bull. biol. France Belg.*, **74**, 349—442.
3. CORLISS, J. O. (1953) Comparative studies on holotrichous ciliates in the Colpidium-Glaucoma-Leucophrys-Tetrahymena group. II. Morphology, life cycles and systematic status of strains in pure culture. *Parasitology*, **43**, 49—84.
4. CORLISS, J. O. (1959) An illustrated key to the higher groups of the ciliated protozoa, with definition of terms. *J. Protozool.*, **6**, 265—281.
5. CORLISS, J. O. (1961) The ciliated protozoa. Pergamon Press.
6. DEMBROWSKA, W. S. (1938) Körperreorganisation von *Stylonychia mytilus* beim Hungern. *Arch. Protistenk.*, **91**, 89—106.
7. EVANS, F. R., CORLISS, J. O. (1964) Morphogenesis in the hymenostome Ciliate *Pseudocohnilembus persalinus* and its taxonomic and phylogenetic implications. *J. Protozool.*, **11**, 353—370.
8. FAURE-FREMIET, E. (1961) Cils vibratiles et flagelles. *Biol. Rev.*, **36**, 364—536.
9. FOISSNER, W. (1967) Wimpertiere im Silberpräparat. Ein verbessertes "trockenes" Verfahren zur Darstellung des Silberliniensystems. *Mikrokosmos*, **4**, 122—126.

10. FOISSNER, W. (1969) Eine neue Art aus der Gattung *Colpidium* (Stein 1860): *Colpidium kleini*. *Acta Protozool.*, **7**, 17–23.
11. FOISSNER, W. (1970) Reaktionen des Silberliniensystems der Ciliaten auf mechanische Insulte. I. Teil. *Protoplasma*, **68**, 23–45.
12. FOISSNER, W. (1970) Reaktionen des Silberliniensystems der Ciliaten auf mechanische Insulte. II. Teil. *Protoplasma*, **68**, 433–456.
13. FOISSNER, W. (1970) Spontane Teilungsmißbildungen bei *Colpidium kleini* (Ciliata, Holotricha). *Arch. Protistenk.*, **112**, 99–105.
14. FOISSNER, W. (1970) Corticale Morphogenese bei *Colpidium kleini* (Ciliata, Holotricha). *Acta Protozool.*, [In press]
15. FRANKEL, J. (1960) Morphogenesis in *Glaucoma chattoni*. *J. Protozool.*, **7**, 362–376.
16. GARNJOBST, L. (1937) A comparative study of protoplasmic reorganization in two hypotrichous Ciliates *Stylonethes sterkii* and *Euplotes taylori* with special reference to cystment. *Arch. Protistenk.*, **89**, 318–380.
17. GELEI, J. v. (1935) Der Richtungsmeridian und die Neubildung des Mundes während und außerhalb der Teilung bei den Ciliaten. *Biol. Zbl.*, **55**, 436–445.
18. GRELL, K. G. (1968) Protozoologie, 2. Auflage, Springer, Berlin.
19. IVANIC, M. (1936) Zur Kenntnis der Vermehrungsruhestadien bei *Chilodon uncinatus*. *EHRBG. Arch. Protistenk.*, **87**, 159–171.
20. JERKA-DZIADOSZ, M. (1964) Localization of the organization area in course of regeneration of *Urostyla grandis* EHRBG. *Acta Protozool.*, **2**, 129–136.
21. JERKA-DZIADOSZ, M. (1965) Morphogenesis of ciliature in the physiological and traumatic regeneration of *Urostyla cristata* JERKA-DZIADOSZ 1964. *Acta Protozool.*, **3**, 133–141.
22. JERKA-DZIADOSZ, M. (1967) Traumatic disturbance of cell division and regeneration of fragments derived from dividing individuals *Urostyla*. *Acta Protozool.*, **5**, 59–78.
23. KLEIN, B. M. (1926) Über eine neue Eigentümlichkeit der Pellicula von *Chilodon uncinatus* EHRBG. *Zoolog. Anz.*, **67**, 1–2.
24. KLEIN, B. M. (1928) Die Silberliniensysteme der Ciliaten. Weitere Resultate. *Arch. Protistenk.*, **62**, 163–246.
25. KLEIN, B. M. (1929) Weitere Beiträge zur Kenntniss des Silberliniensystems der Ciliaten. *Arch. Protistenk.*, **65**, 183–258.
26. KLEIN, B. M. (1936) Beziehungen zwischen Maschenweite und Bildungsvorgängen im Silberliniensystem der Ciliaten. *Arch. Protistenk.*, **88**, 1–22.
27. KLEIN, B. M. (1939) Das Silberliniensystem und Cytopygentätigkeit. *Arch. Protistenk.*, **92**, 401–407.
28. KLEIN, B. M. (1942) Silberlinien- oder neuroformative System der Ciliaten. *Ann. Naturhist. Museums Wien*, **53**, 156–336.
29. MAC LENNAN, R. F. (1935) Dedifferentiation and redifferentiation in *Ichthyophthirius*. I. Neuromotor system. *Arch. Protistenk.*, **86**, 191–210.
30. NANNEY, D. L. (1966) Corticotypic technics in *Tetrahymena* taxonomy. *J. Protozool.*, **13**, 483–490.
31. PITELKA, D. R., CHILD, F. M. (1964) The locomotor apparatus of Ciliata and Flagellata: Relations between structure and function. In HUTNER, S. H. *Biochemistry and Physiology of protozoa*. Academic Press, N.Y.
32. RAABE, Z. (1934) Weitere Untersuchungen an einigen Arten des Genus *Conchophthirus* STEIN. *Ex. Mem. Polon.*, 222–235.
33. SCHMÄHL, O. (1926) Die Neubildung des Peristoms bei der Teilung von *Bursaria truncatella*. *Arch. Protistenk.*, **54**, 360–429.
34. SCHWARTZ, V. (1935) Versuche über Regeneration und Kerndimorphismus bei *Stentor coeruleus* EHRBG. *Arch. Protistenk.*, **85**, 10–138.
35. TAYLOR, C. V., GARNJOBST, L. (1939) Reorganization of the "silverline system" in the reproductive cysts of *Colpoda duodenaria*. *Arch. Protistenk.*, **92**, 74–90.
36. TARTAR, V. (1954) Anomalies in regeneration of *Paramecium*. *J. Protozool.*, **1**, 11–17.
37. TARTAR, V. (1956) Pattern and substance in *Stentor*. In: *Cellular mechanisms in differentiation and growth*, **4**, 73–100.
38. TARTAR, V. (1957) Deletion experiments on the oral primordium of *Stentor coeruleus*. *J. exp. Zool.*, **136**, 53–73.
39. TOTWEN-NOWAKOWSKA, I. (1964) Doublets in a clone of *Stylonychia mytilus* (O.F.M.). *Acta Protozool.*, **2**, 137–146.
40. WISE, B. N. (1965) Effects of ultraviolet microbeam irradiation of morphogenesis in *Euplotes*. *J. exp. Zool.*, **159**, 241–268.

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