Advances in
MORPHOGENESIS

VOLUME 2

Advances in MORPHOGENESIS

Edited by

M. ABERCROMBIE

Department of Anatomy
University College
London, England

JEAN BRACHET

Faculté des Sciences
Université Libre de Bruxelles
Belgium

VOLUME 2

1962
ACADEMIC PRESS
New York and London

ACADEMIC PRESS INC.
111 Fifth Avenue
New York 3, New York

U.K. Edition, Published by
ACADEMIC PRESS INC. (LONDON) LTD.
Berkeley Square House
Berkeley Square, London, W.1

Library of Congress Catalog Card Number: 60–16981

Printed in Great Britain by Robert MacLehose and Co. Ltd, Glasgow

CONTRIBUTORS TO VOLUME 2

J. CLAVERT, *Professor of the Faculty of Medicine, Strasbourg, France.*

GERHARD KRAUSE, *Zoologisches Institut der Universität Würzburg, Germany.*

TH. LENDER, *Université de Paris. Faculté des Sciences, Centre d'Orsay, Laboratoire de Biologie animale, S.P.C.N., France.*

J. MILAIRE, *Laboratoire d'Anatomie et d'Embryologie humaines de la Faculté de Médecine, Université de Bruxelles, Belgium.*

SILVIO RANZI, *Zoology Department, State University, Milan, Italy.*

Z. RYCHTER, *Department of Anatomy, Charles University, Prague, Czechoslovakia.*

KLAUS SANDER, *Zoologisches Institut der Universität Würzburg, Germany.*

B. M. SHAFFER, *Department of Zoology, Cambridge University, England.*

VANCE TARTAR, *Department of Zoology, University of Washington, Seattle, U.S.A.*

ENRICO URBANI, *Department of Zoology and Comparative Anatomy, University of Camerino, Italy.*

CONTENTS

CONTRIBUTORS TO VOLUME 2 v

Morphogenesis in Stentor

VANCE TARTAR

I. Introduction 1
II. Development of New Individuals in *Stentor* 2
A. The Normal Form 2
B. Origin of Two Stentors from One in Division 3
C. Reorganization of an Individual 4
D. Regeneration 4
III. Adjustment of Proportionality and Arrangement of Parts 7
IV. Relation of Cell Elaborations to the Cortical Pattern 9
A. Induction of Membranellar Bands 9
B. Induction of Mouthparts Formation 11
V. Activation and Inhibition of Primordium Formation in Development 12
VI. Upper and Lower Limits to Size of Organizational Mass 14
A. Lower Limits 14
B. Upper Limits 15
VII. Reconstitution of Minced *Stentor* 17
VIII. Nucleocytoplasmic Interaction 18
A. Cytoplasmic Differentiation without Nuclear Differentiation 18
B. Necessity of the Nucleus for Primordium Formation and Development 19
C. Nuclear Behaviour Governed by the Cytoplasm 20
D. Chimeras 21
IX. Conclusions 22
References 25

Symmetrization of the Egg of Vertebrates

J. CLAVERT

I. Introduction 27
II. Determination of Bilateral Symmetry in Amphibians 28
A. *Rana fusca* 28
B. Other Amphibians 37
C. Conclusions 38
III. Determination of Bilateral Symmetry in Birds 39
A. Structure of the Egg 39
B. Formation of the Egg 41
C. Relation between Position of the Embryo and Direction of Coiling of the Chalazae 42

D. Relation between Egg Position in the Uterus and Embryo Orientation 43
E. The Critical Phase during Symmetrization of the Uterine Egg 47
F. Conclusions 49
IV. Determination of Bilateral Symmetry in Reptiles 49
V. Determination of Bilateral Symmetry in Fish 51
A. Chondrostei (*Acipenser sturio, A. ruthenus, A. huso*) 51
B. Selachii (*Scylliorhinus canicula*) 53
C. Teleostei 54
VI. Discussion and Interpretation of Results 55
VII. Summary 59
References 59

Comparative Biochemical Studies on Amphibian and Invertebrate Development

ENRICO URBANI

I. Introduction 61
II. Embryonic Development and Metamorphosis of Amphibians 63
A. Proteolytic Enzymes 67
B. Ribonucleic Acid and Phosphates 76
C. Amylases 79
D. Lipases 82
E. Energy Sources 84
III. Biochemical Considerations on the Development of some Invertebrates 91
A. *Artemia salina* Leach 92
B. *Bombyx mori* L. 94
C. *Musca domestica* L. 96
IV. Results and Conclusions 97
References 102

The Acrasina

B. M. SHAFFER

I. Introduction 109
A. Deviations from the Mean 109
B. The Pseudoplasmodium 111
II. The Non-Social Phase 113
A. The Cells 113
B. Organization 116
III. The Onset of the Social Phase 118
A. Food Shortage 118
B. The Initiators 119
C. The Founders 129
D. Sexuality 131
IV. The Aggregation 134
A. The Cells 134

B. Organization 138
C. Acrasin 154
D. The Nature of Intercellular Bonding 157
V. The Grex 160
A. The Cells 160
B. The Whole 171
References 179

Histochemical Aspects of Limb Morphogenesis in Vertebrates

J. MILAIRE

I. Introduction 183
II. Experimental Data 184
III. Histochemical and Morphological Data 185
A. Methods 186
B. Observations 186
IV. Conclusions 204
References 208

The Proteins in Embryonic and Larval Development

SILVIO RANZI

I. Introduction 211
II. Studies on Differentiation 211
A. Sea Urchins 212
B. Amphibians 219
C. Attempt at Comparison 225
III. Studies on Determination 227
A. Alterations in Early Determination 227
B. Differences in Proteins from Embryos Showing Different Malformations 231
C. Animalizing Agents Denaturing Proteins 238
D. Protein Denaturation and Developmental Processes 239
E. Action of Vegetalizing Agents 241
F. Differences in Resistance to Breakdown of Proteins from Embryos Showing Different Malformations 244
G. Predisposition to and Inhibition of Protoplasmic Structural Breakdown 248
H. Embryonic Proteins and the Nature of the Denaturation induced by Animalizing Agents 249
I. Evidence from the Research of Other Authors 251
J. Conclusion 253
References 255

Ooplasmic Reaction Systems in Insect Embryogenesis

GERHARD KRAUSE and KLAUS SANDER

I. Introduction 259
II. Natural and Experimental Conditions Influencing Development 260
A. External Factors 260
B. Internal Factors 261
III. Preformed Prerequisites in the Ooplasm 262
A. Egg Dimorphism 263
B. Control Substances 265
C. Control Centres 268
D. Types of Egg Architecture 272
IV. Superficial Cleavage 274
A. Synchronous Mitoses and Collective Migration of Energids 275
B. Vitellophags 277
C. Cleavage in the Future Thorax Region 277
V. Activation 279
A. A Type of Reaction Sequence 280
B. Autonomous Ooplasmic Processes 283
C. Nucleocytoplasmic Interactions 286
VI. Morphogenetic Movements 287
A. Germ Anlage Formation 288
B. Anatrepsis 290
VII. Metameric Organization 291
A. Organ Pattern in the Periplasm 291
B. Antagonistic Polar Prerequisites 294
C. Initial Concentration of Potentialities 297
Acknowledgements 299
References 299

Factors in Morphogenesis of Regenerating Fresh-Water Planaria

TH. LENDER

I. Introduction 305
II. The Neoblasts of Fresh-Water Planaria 306
A. Cytological Study of the Neoblasts 306
B. Neoblasts of the Regeneration Blastema 308
C. Planarian Neoblasts with Limited Regeneration Capacity 311
III. Differentiation Factors 312
A. Determination of the Blastema 312
B. Organ Differentiation in Regeneration 313
IV. Conclusion 326
References 329

Experimental Morphology of the Aortic Arches and the Heart Loop in Chick Embryos

Z. RYCHTER

I. Methods Relating to the Problem of Local Intervention 333
II. Experimental Morphology of the Aortic Arches 336
A. Suppression of One Aortic Arch 337
B. Simultaneous Suppression of Two or Three Aortic Arches 339
C. Simultaneous Suppression of Four or Five Aortic Arches 347
D. Some Vascular Anomalies Resulting from Experiments on Aortic Arches 348
E. Position of the Recurrent Nerve in Various Aortic Arch Patterns 354
III. Experimental Morphology of the Heart Loop 355
A. Conditions Governing the Form and Location of Ventricular Septal Defects 355
B. Experimental Heart Ectopia 357
C. Haemodynamic Effects of Suppressing Development of the Atrium and their Morphogenetic Significance 358
D. Transposition of the Aorta into the Right Ventricle 360
E. Influence of the Blood Stream on the Proximal Bulbar Cushions 362
IV. Simultaneous Experiments on the Heart Loop and Aortic Arches 364
A. Relation of the Incumbent and Transposed Aorta 364
B. Dependence of the Critical Period on Experimental Procedure 365
V. Theory of the Teratogenetic Meaning of Local Damage to the Heart Loop and Aortic Arches 367
References 369

AUTHOR INDEX 373

SUBJECT INDEX 383

MORPHOGENESIS IN STENTOR

VANCE TARTAR†

Department of Zoology, University of Washington, Seattle, U.S.A.

I. Introduction 1
II. Development of New Individuals in *Stentor* 2
A. The Normal Form 2
B. Origin of Two Stentors from One in Division 3
C. Reorganization of an Individual 4
D. Regeneration 4
III. Adjustment of Proportionality and Arrangement of Parts 7
IV. Relation of Cell Elaborations to the Cortical Pattern 9
A. Induction of Membranellar Bands 9
B. Induction of Mouthparts Formation 11
V. Activation and Inhibition of Primordium Formation in Development 12
VI. Upper and Lower Limits to Size of Organizational Mass 14
A. Lower Limits 14
B. Upper Limits 15
VII. Reconstitution of Minced *Stentor* 17
VIII. Nucleocytoplasmic Interaction 18
A. Cytoplasmic Differentiation without Nuclear Differentiation 18
B. Necessity of the Nucleus for Primordium Formation and Development 19
C. Nuclear Behaviour Governed by the Cytoplasm 20
D. Chimeras 21
IX. Conclusions 22
References 25

I. Introduction

Ciliate protozoa of the genus *Stentor* have proved to be the most operable of all cells. We can now perform many of the classical experiments of grafting, transplantation, and transposition on a unicellular organism whose form should be completely definable and capable of total surveillance in any experimental situation. The mode of morphogenesis, analysable by such interferences, will be simple and specialized because it involves neither cellularization nor intercellular relationships; but since the problem of the development of form is still so much a mystery we should look for clues in any direction. Whether by contrast or comparison, ciliate studies may supply such hints. Using as our example the large and exquisite species *S. coeruleus*, we shall describe the form and

† This investigation was supported by research grant C-3637 from the National Cancer Institute, U.S. Public Health Service.

morphogenetic behaviour of this animal and indicate resemblances with other types of development.

II. Development of New Individuals in *Stentor*

A. The Normal Form

Form may be described as a set of specific parts integrated in certain geometric and proportionate relations to each other. The shape of *Stentor* is roughly that of a cone. On the sides of the cone, running from base to apex, are about 100 pigmented stripes of graded widths alternating with rows of body cilia associated with contractile fibres (Fig. 1*a*).

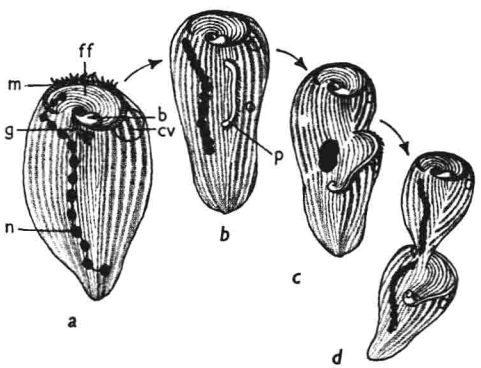

FIG. 1. Morphology of *S. coeruleus* and its transformation into two individuals at division. (*a*) Form in morphostasis. n—chain macronucleus; g—coiled gullet; m—membranellar band with membranelles drawn on far side only; ff—frontal field; b—buccal pouch; cv—contractile vacuole. (*b*) Early division stage, with lateral oral primordium p, nuclear nodes coalescing, and new contractile vacuole appearing. (*c*) Later stage, with anlage cut into the posterior daughter by the fission line, primordium coiling inward to form the mouthparts, and nucleus clumped in one compact mass. (*d*) Incipient separation of daughter cells, with renodulation and division of the macronucleus. Original striping in anterior daughter shows herringbone pattern from cutting out and shifting posteriorly of the anlage; constriction forms new tail pole. Original and multiplied striping within curve of the primordium is carried forward to form new frontal field for the posterior daughter.

A whorl of similar concentric stripes covers the broad end. It has been found that cell shape is largely a function of the cortical pattern, for when this pattern is disarranged the relaxed cell shape is correspondingly abnormal (e.g. Fig. 10*b*). At the apex of the cone where the posterior ends of the stripes converge the holdfast is formed; this is a temporary pseudopodial organelle which can be taken down as the animal detaches itself and swims away. Located at the broad end are the feeding organelles: these consist of a nearly complete circle of ciliary membranelles terminating in a set of mouthparts consisting of buccal pouch, coiled

gullet, and cytostome. The contractile vacuole is invariably found to the left of the gullet and an anal pore lies nearby. The macronucleus is a string of nodes lying underneath the ectoplasm and is located with great regularity as shown in the sketch (Fig. 1*a*). Numerous micronuclei lie along the macronuclear chain but they are entirely dispensable for all cell functions except conjugation (Schwartz, 1935). For brevity we can simply refer to the macronucleus as the nucleus, mindful that it originates in conjugation from chromosomal micronuclei.

Electron microscopy has revealed an extraordinary fine structure in the parts enumerated. For example, in the related *S. polymorphus* each of the 250 membranelles consists of three rows of from 20 to 25 cilia, each cilium arising from a kinetosome which also gives off a fibre to the interior, all these ciliary rootlets being neatly packed together to form a fan terminating in a stalk which is connected with the stalks of adjacent membranelles (Randall and Jackson, 1958). Like other highly complex ciliates and flagellates, *Stentor* is notable for the variety and number of organelles within a single cell.

B. Origin of Two Stentors from One in Division

Stentors reproduce by converting one form and individuality into two which are then separated by cell division (Fig. 1*b–d*). The original feeding organelles and contractile vacuole pass to the anterior daughter, the tail pole and holdfast remaining as part of the posterior offspring. This direct inheritance makes for a certain disproportion in the progeny which is soon adjusted by subtle changes (Morgan, 1901; Weisz, 1951). The posterior daughter acquires a new contractile vacuole and set of feeding organelles. As the oral primordium develops it cuts off an area of lateral striping which is carried forward as the new broad end or frontal field of the posterior daughter, and most of this striping is newly developed within the curvature of the anlage. For the anterior daughter a new tail pole is produced by constriction of the division furrow which, in proceeding forward around the primordium, cuts out a section of lateral stripes so that when the anterior stripes come together they form a herringbone pattern contributing to the conical shape. The cortical structure which forms the lateral striping is therefore simply cut across by the fission line and divided between the two daughters. During this process the beads of the macronucleus coalesce into a ball which then extends into a sausage-shaped organ and is cut in two by the cell constriction, the separate parts renodulating, each to about the original number of nuclear beads.

Sub-cortically, granular carbohydrate reserves located toward the posterior end of the cell are also divided equally between the two daughters (Weisz, 1949a). Half the granules stream forward and the

posterior boundary of this anterior mass defines precisely the future division furrow which thus separates this mass into the anterior cell (Tartar, 1959a). The precise translocation of this material reminds one of the migration of granules and polar plasm in early development of certain eggs.

In the production of new individuals, therefore, as much as possible of the old is passed on directly, with new parts formed only when unavoidable, and this is generally true for ciliates and flagellates. There is a direct inheritance of parts which go to make up the form, different for each of the two daughter cells, together with a true epigenesis or elaboration of new parts, notably in the development of the oral primordium for the posterior cell.

C. Reorganization of an Individual

Occasionally stentors produce a new set of feeding organelles replacing the mouthparts and adjacent membranelles of the original set which are then resorbed. Although there may be other causes, this replacement occurs if for any reason the original feeding organelles are too small in proportion to the cell though perfect in their construction, for these organelles apparently never increase *in situ* but only through primordium formation and development. Alternatively, reorganization may occur if the nucleus is too small, as when all but one or two of the nodes are excised; for oddly enough the nucleus is unable to undergo compensatory hypertrophy except as an accompaniment of primordium formation (Schwartz, 1935). 'Reorganization' is therefore something of a misnomer because there is no widespread re-organization; nor is there good evidence that this process is to replace worn-out ingestive structures, as was once thought. Rather should we note that it quickly registers whether any of the parts which make up the total form are disproportionate; reorganization is one of the means for correcting disproportionality, of which others will be discussed later.

D. Regeneration

Regeneration in *Stentor* is of wide range. Excised holdfasts are replaced in about one hour, even without benefit of the nucleus. This is understandable because according to Andrews (1945) the holdfast is merely a modification of the posterior ends of the lateral stripes and therefore should not demand synthesis of new parts, which apparently requires the presence of the nucleus. It has also been found that new posterior poles and holdfasts can arise in a novel way, seldom if ever occurring in nature (Tartar, 1956b). Aboral halves, produced by cutting the cell in two longitudinally, fold upon themselves to heal. The striping is rather sharply bent at the fold (Fig. 2). If this configuration is main-

tained, in which original anterior and posterior polar regions are now adjacent, then the striping is cut across at the bend by a fission line, and the cut ends are gathered together as a new posterior pole where a holdfast develops. This process is therefore like that by which a new 'tail'

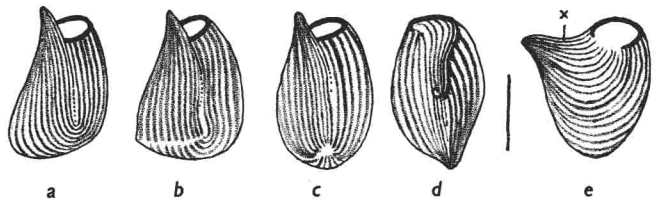

FIG. 2. Unusual manner of tail-pole formation in folded longitudinal halves. (a) Half-cell folds on itself to cover wound surface, bringing head and tail poles together. (b) Striping cut by fission line along the bend. (c) Gathering of cut ends to form new tail pole. (d) New pole formed, old tail pole regresses and feeding organelles in process of regenerating. (e) Commoner occurrence, in which original polarization is preserved and head and tail poles separate by growth between them of new striping (x). (After Tartar, 1956b.)

is produced for the anterior daughter in division, except that the striping of the posterior half also participates, regardless of the fact that its original polarity is 'incorrect' for this formation. However, this is not the only way of resolving the morphological dilemma. Usually new stripes grow between the head and tail remnants which are therefore moved apart until they become polar opposites again (Fig. 2*e*).

Lateral striping can be slashed through repeatedly and indiscriminately without provoking the formation of an oral regeneration primordium. Cut edges of the ectoplasm simply come together and heal, and the ciliary rows and pigment bands realign and join. Feeding organelles can also be cut through the region of the mouthparts or the membranellar band and they simply heal together; but if the parts are far displaced so they cannot join, or if all or any portion is entirely removed, then a new set is regenerated through primordium formation which largely replaces the old, though an aboral portion of the old membranelles, if present, may remain intact and join with the new. The more of the original feeding organelles left intact, the more delayed the regeneration. This indicates that all portions of these organelles participate in an inhibition of primordium formation; yet the inhibition is apparently not a simple chemical one since, when cut and displaced, all parts of the feeding organelles are present yet regeneration eventually occurs because the parts are no longer joined in their proper relationships.

Calkins' (1933) distinction between basic and derived parts of the protozoan cell may be useful in the present connection. The lateral striping with its ciliary rows or kineties is apparently basic, i.e. never regenerating *de novo*, passed on by direct inheritance to daughter cells,

and increasing only by growth in length and by multiplicative replication of new stripes. Formation of new pigment bands by splitting of the old ones indicates this and can be observed. Another indication is that nucleated endoplasmic spheres, deprived of the entire cortex with its lateral striping, persist for two or more days without disintegration but never regenerate, being unable to produce striping (and kinetosomes?) *de novo* (Tartar, 1956c). Other parts are derived from the lateral striping. The holdfast is clearly such an elaboration of posterior stripe-ends. Feeding organelles are the most conspicuous elaboration, arising from a primordium appearing within the lateral striping and intimately correlated with its pattern, as we shall see. In the related *Fabrea* (Villeneuve-Brachon, 1940) silver staining indicates that the ciliary basal bodies of the anlagen originate from multiplication of these kinetosomes in the adjacent lateral ciliary rows. Hence there is genuine epigenesis of the derived structures, while the fundamental organization grows only from its like.

The macronucleus is also a derived structure, originating from products of the micronuclear syncaryon after conjugation. The micronucleus is basic, new ones arising only by replication of the old. (Chromosomes as a *set* are basic parts of a nucleus, for if one type of chromosome is lost it cannot be regenerated from the remainder.) Yet in the vegetative life of *Stentor* the macronucleus behaves as a basic part. Theoretically it should be replaceable from the scattered micronuclei; but surprisingly enough emacronucleated stentors never do this, remaining functionally enucleate (because the micronuclei are ineffective in vegetative life) and die in a week. After partial enucleation, the macronuclear chain is regenerated only if at least one node is left. Regeneration is by growth from the remainder, for if the node is pre-labelled with radioactive phosphorus, activity is uniformly distributed throughout the regenerated chain (de Terra, 1958). This compensatory nuclear increase occurs only after primordium formation in regeneration or reorganization.

Even tiny nucleated fragments only $\frac{1}{123}$ the size of the largest specimens can regenerate feeding organelles and tail poles in proportion to their size. Here we may speak of a complete individualization in which a small part becomes a whole, for the accomplishment is even greater than in cell reproduction. The fragment heals and thus survives because it maintains the cell type of organization. It retains that portion of the original striping which it bears and which undoubtedly determines the polarity of the regenerant as well as producing the derived organelles. A normal *Stentor* therefore potentially can form about 125 individuals, presuming each cut fragment can be supplied with a nuclear node. And in some ciliates like *Ichthyoptherius* (Mugard, 1948) multiple division occurs in which the lateral striping is autonomously broken into tiny

patches which become separate cells and individualities. In either case, the part becomes a whole when it is no longer in intimate structural relation with other parts.

III. Adjustment of Proportionality and Arrangement of Parts

Lateral striping is prevented from becoming abnormally long by the onset of fission in which the stripes are cut in two, and if there are too few stripes new ones are added by rapid stripe multiplication. A small fragment begins with short stripes far less in number than the normal complement of about 200 but the stripes then multiply at the line of healing and increase in length as the tiny *Stentor* grows until a fully normal complement is restored. Similarly, longitudinal halves of stentors, with half the normal number of stripes do not remain permanently narrow, for compensatory stripe multiplication occurs; but this increase stops when the normal number is achieved. Evidently there is some means for controlling the upper limit, and such a control is inferred from the finding that of several salts tested lithium chloride alone produces an increase in the number of stripes above normal, the treated cell becoming extraordinarily broad and even transforming into a doublet stentor (Tartar, 1957a). It is of course most interesting that the lithium ion has enduring morphogenetic effects on stentors as well as on embryos.

Stentors are capable of many other minor adjustments, always tending toward the normal form. Morgan (1901) found that when stentors are cut in two transversely, the too-large feeding organelles of the anterior fragment somehow decrease in size, as does the disproportionate tail of the posterior piece. Much more striking is the behaviour of excised, nucleated heads (Fig. 3). These discs fold to cover the exposed endo-

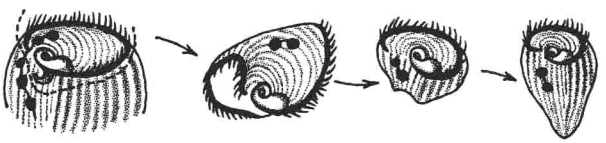

FIG. 3. Reconstruction in an excised, nucleated head. Feeding organelles and frontal field excised as indicated. Head folds on itself to heal. Membranellar band gradually reduces in length and mouthparts in size as lateral striping grows out, producing a perfect tiny stentor of normally proportionate parts.

plasm and in the course of several days the enormously disproportionate feeding organelles are gradually reduced to proper size, resorbed parts apparently furnishing the material for outgrowth of lateral striping to produce the normal tail and cell shape (Tartar, 1960a). By a remarkable morphollaxis the bizarre fragment is thus remodelled as a tiny normal *Stentor*.

In grafts of two animals, or when extra heads or tails are transplanted on to a single individual, the duplicate parts usually fuse together; and just those portions of the membranellar band or of the cortical striping between the duplicated tails are resorbed as is required for unification. In doublet stentors the normal form is often begun by resorption of one set of mouthparts. If the head is circumscribed and merely rotated through 180°, healing is very neat and feeding continues. Only the pattern of the cell is changed in a subtle way, yet the mistake is eventually corrected (Fig. 4). Mouthparts become detached from the membranellar band,

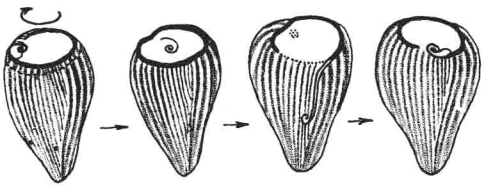

FIG. 4. Response to minor alteration of the cell pattern. Head is circumscribed and rotated through 180°. Ends of the membranellar band meet and fuse, with mouthparts separating into the frontal field. Old mouthparts resorbed as primordium forms in proper location and part of peristome is resorbed to permit new parts to enter the frontal field, restoring the normal pattern and relation of parts.

move into the frontal field and are resorbed, whereupon an oral primordium appears on the opposite side in the normal primordium site and a section of the old band is dissolved to permit entrance of a new set of mouthparts, now in the proper location (Tartar, 1960a). Departures from the normal form and pattern generally elicit appropriate means for their correction.

Cell pattern can also be disarranged by circumscribing a *Stentor* and rotating the anterior half through 180° on the posterior portion. Again we have a subtle alteration which does not appear to interfere with normal functions yet is never tolerated. When the incision is at the mid-level of the axis or somewhat forward and regeneration is induced, the cortical structures of the anterior part are resorbed as those of the posterior part extend and take over (Tartar, 1956a). When the cut is made posterior to the mid-line, it is the posterior stripes which disappear (Uhlig, 1959). When the cut is made in the middle and regeneration is not induced, certain stripes in each half penetrate through those of the other and a doublet stentor is produced, yet this doublet will eventually revert to the single form (Tartar, 1959b). Whether directly by resorption or by the circuitous route of doublet formation, these specimens eventually return to the normal pattern.

In spite of these remarkable tendencies to revert to normal, extreme abnormalities of form develop in some strains of *S. coeruleus* without