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REPORTS ON THE SCIENTIFIC RESULTS OF THE EXPEDITION TO THE EASTERN TROPICAL PACIFIC, IN CHARGE OF ALEXANDER AGASSIZ, BY THE U. S. FISH COMMISSION STEAMER "ALBATROSS," FROM OCTOBER, 1904, TO MARCH, 1905, LIEUT. COMMANDER L. M. GARRETT, U. S. N., COMMANDING.

XX.

MUTATIONS IN CERATIUM.

By Charles Atwood Kofoid.

With Four Plates.

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W. McM. WOODWORTH. The Annelids.

[1] Bull. M. C. Z., Vol. XLVI., No. 4, April, 1905, 22 pp.
[2] Bull. M. C. Z., Vol. XLVI., No. 6, July, 1905, 4 pp., 1 pl.
[3] Bull. M. C. Z., Vol. XLVI., No. 9, September, 1905, 5 pp., 1 pl.
[4] Bull. M. C. Z., Vol. XLVI., No. 13, January, 1906, 22 pp., 3 pls.
[5] Mem. M. C. Z., Vol. XXXIII., January, 1906, 90 pp., 96 pls.
[6] Bull. M. C. Z., Vol. L., No. 3, August, 1906, 14 pp., 10 pls.
[7] Bull. M. C. Z., Vol. L., No. 4, November, 1906, 26 pp., 4 pls.
[8] Mem. M. C. Z., Vol. XXXV., No. 1, February, 1907, 20 pp., 15 pls.
[9] Bull. M. C. Z., Vol. L., No. 6, February, 1907, 48 pp., 18 pls.
[10] Mem. M. C. Z., Vol. XXXV., No. 2, August, 1907, 56 pp., 9 pls.
[11] Bull. M. C. Z., Vol. LI., No. 6, November, 1907, 22 pp., 1 pl.
[12] Bull. M. C. Z., Vol. LII., No. 1, June, 1908, 14 pp., 1 pl.
[13] Bull. M. C. Z., Vol. LII., No. 2, July, 1908, 8 pp., 5 pls.
[14] Bull. M. C. Z., Vol. XLIII., No. 6, October, 1908, 285 pp., 22 pls.
[15] Bull. M. C. Z., Vol. LII., No. 5, October, 1908, 11 pp., 2 pls.
[16] Mem. M. C. Z., Vol. XXXVII., February, 1909, 243 pp., 48 pls.
[17] Mem. M. C. Z., Vol. XXXVIII., No. 1, June, 1909, 172 pp., 5 pls., 3 maps.
[18] Bull. M. C. Z., Vol. LII., No. 9, June, 1909, 26 pp., 8 pls.
[19] Bull. M. C. Z., Vol. LII., No. 11, August, 1909, 10 pp., 3 pls.
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BY CHARLES ATWOOD KOFOID.

WITH FOUR PLATES.

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Mutations in Ceratium. By CHARLES ATWOOD KOFOID.

CONTENTS.

NORMAL SCHIZOGONY IN CERATIUM.

Throughout the genus Ceratium asexual reproduction occurs, in so far as is known, exclusively by schizogony. Multiple spore formation such as is seen in some other genera of dinoflagellates, as for example in Pyrophacus, is, as yet, entirely unknown. This schizogony takes the form of an oblique fission of the entire organism whereby not only the nucleus and cell plasma are divided but the parental skeleton as well.

Division of Ancestral Skeleton.

This skeleton is made up of a definite number of plates with a typical arrangement throughout all the species of the genus. It is parted at schizogony along existing sutures between the plates by the fission plane which is oblique to the major axis, passing at an angle of approximately 45° from the right anterior shoulder of the midbody to the left posterior region at the outer side of the base of the left antapical horn. By this process the ancestral skeleton is parted (see plates **1** and **2**) so that the anterior schizont receives apical plates 1′–4′, precingulars 1″ and 2″, the two girdle plates between the proximal end of the girdle and a point near the middorsal line, and postcingular plates 1‴–3‴, in all 9 plates together with the proximal half of the girdle and anterior moiety of the so-called ventral plate. The posterior schizont receives precingulars 3″–4″, the two girdle plates between its middorsal gap and its distal end, postcingulars 4‴ and 5‴ and antapicals 1⁗ and 2⁗; in all 6 plates, the distal half of the girdle and the posterior moiety of the ventral "plate." The ventral plate, as Lauterborn (1895) has shown, is divided between the two schizonts by a more or less oblique line, which passes from the flagellar pore at the proximal end of the girdle to the attachment area at its distal end. The position of the fission plane with reference to the skeletal plates was correctly given by Bütschli (1885) and Bergh (1886). but the number and position of the plates are not completely or correctly given by either author. The plates composing the skeleton and the nomenclature here used were described by me in a recent paper (1907 b).

Formation of New Skeletal Parts.

As the schizonts diverge after nuclear division, their exposed plasma adjacent to the fission plane is moulded into the form of the completed epitheca and hypotheca and is coincidently reclothed with a thin hyaline pellicle, which in a short time shows the pores and arrangement of suture lines and plates characteristic of the species. The newly formed skeletal parts, as I have shown elsewhere (1908), take on the facies of the parental individual; that is, if the parental skeleton was of a coarse-ribbed and rugose type or of a more delicate and hyaline cast, the newly formed plates of the daughter schizont are speedily thickened and their surface diversified to a degree corresponding to that of the parental skeleton by a sort of compensatory growth. The whole process is a relatively rapid one, with the exception that the prolongation of the apical horn to the full length normal to the isolated individual is often delayed as in all the individuals, save the anterior one only, in a chain of *C. vultur* shown in plate 4, fig. 7. The result of this normal process of schizogony is the formation of schizonts which are, in all essential details, of similar form and structure. An illustration of this phenomenon is seen in this chain of *C. vultur*, where a series of schizonts of at least the fifth generation are seen still in chain. All exhibit the same form of midbody, essentially similar spread of horns with like major flexures near their bases. The cell wall even of the youngest skeletons is thickened to a like extent and in homologous regions, and all of the anterior horns have lateral lists, as does the ancestral skeleton seen in the epitheca of the anterior schizont.

Similarity of Normal Schizonts in Chain.

The differences between the cells in a normal chain consist of varying lengths of the apical horn (though this is often surprisingly uniform); differences in the length of the antapicals, which in the case of very long-horned species, such as *C. carriense*, are often considerable; differences in the major flexures or spread of the antapical horns resulting possibly from juxtaposition in chain formation, and slight differences in the texture of the skeleton and the degree of development of ribs and lists upon its surface arising during the rapid process of compensatory growth. Most, if not indeed all, of these differences fall either in the category of growth or age differences or individual fluctuating variations. When measured and plotted, their dimensions form a normal frequency of error curve. I have made such measurements and plots for a number of the species of Ceratium on ten to a thousand individuals, and find that these differences conform typically to the so-called fluctuating type of variation.

The chain of *C. vultur* (plate 4, fig. 7) is a fair representative of the usual degree of variation. I have found as high as twenty individuals in chain of this species, which is one prone to chain formation, with no greater variation than that shown here. Extremes of variation in individuals in chain are to be seen in Pouchet's (1894, p. 171, fig. 13) figures of chains of 3 and 4 schizonts, but even here the differences are strictly of the kinds above mentioned.

In sharp contrast with most Protozoa (notable exceptions appear in linear arrangement of recent schizonts of Spirochaeta and Trypanosoma) and even most of the dinoflagellates, the schizonts of Ceratium have a tendency, more or less pronounced, to adhere in chain for some time after schizogony. This tendency is more marked in some species than in others. For example, in the subgenus Euceratium Gran in the species *C. vultur*, *C. schranki*, *C. carriense*, and *C. palmatum*, chains of 4–20 individuals are not unusual, while in *C. furca*, *C. fusus*, *C. biceps*, and other representatives of the subgenera Biceratium and Amphiceratium rarely more than two individuals (except in *C. candelabrum*) are seen in chain and chains are relatively infrequent. Chain formation is most readily found in collections made in the night or in the early morning. In my own experience at San Diego (latitude 32° 40′) they are most abundant in collections made between 3 and 7 o'clock in the morning, cell division seeming to be favored by the conditions of illumination and possibly by the falling temperature prevailing during the night. The schizonts part company shortly after the completion of schizogony and skeletal formation, and chains are absent or relatively rare in collections made later in the day.

The morphology of chain formation is correlated with the presence of an apical pore at the end of an apical horn. As the new skeletal moieties are formed respectively on the posterior and anterior regions of the diverging schizonts, the plasma of the posterior member is drawn out in a long strand which becomes the apical horn. Its tip rests immediately upon the distal end of the newly forming girdle (plate **1**), at which point the plasma of the two individuals remains in continuity without interference by the forming skeleton. As the newly forming skeletons are completed, the apical pore of the posterior schizont is set under the anterior shelf or list of the distal end of the girdle at the margin of the ventral plate (plate **1**) of the anterior schizont. The posterior list of the girdle is not formed at this point, and the apical horn as it passes posteriorly lies in a channel or depression on the ventral face of the midbody along the right margin of the ventral plate. The place of junction on the anterior schizont I designate as the attachment area (att. a.) and the depression as the chain channel (ch. ch.). The anterior end of the apical horn is also modified, its ventral side being prolonged in a short lobe, giving to the apical pore an irregularly oblique opening (Entz, 1905), a condition found in individuals in chain and also in those but recently released from chain formation. In most free individuals the apical pore is transverse, as in the anterior parental skeleton of the schizont I_3 in the chain shown in plate **1**.

In the course of my investigations upon the dinoflagellates of the Pacific conducted for the past eight years at the San Diego station and upon the collections of the "Albatross" in the tropical Pacific and elsewhere, many instances of chain formation have come under my observation. They have always been of interest and have received close inspection, and many are recorded in my unpublished sketches, especially those having any bearing on the question of variation in Ceratium. Hundreds of such chains have been inspected by myself or my assistant, Miss Rigden. With the exception of three instances noted later these chains have been of the normal type described above. The material examined from San Diego covers all seasons of the year and depths from 0–500 fathoms, and that from the "Albatross" includes collections from Alaska waters, the coast of California, and from the Expedition to the Eastern Tropical Pacific extending southward to Easter Island in the South Pacific, and from depths of 0–800 fathoms. My material is therefore fairly representative of Ceratium in its oceanic and neritic environments within the range of conditions of the normal distribution of the genus.

The literature of the subject prior to 1908 contains but few references to chain formation beyond those of Michaelis (1830), Allman (1855), Murray (1882), Pouchet (1883, 1885, and 1894), Bütschli (1885), Bergh (1886), Schütt (1895, 1896), Karsten (1905, 1906, 1907), and Entz (1907). In all these cases the type of chain formation is the normal one above described.

THE GENUS CERATIUM.

The genus Ceratium is a large one of wide distribution in the plankton of fresh water and the sea. Most of the species are also of wide distribution and some are cosmopolitan. They exhibit a wide range of variation in many cases, especially in length and differentiation of the horns, their principal organs of flotation, in adaptation to varying conditions of life. No less than 290 different names have been given in this genus in recognition of the species, subspecies, and other subordinate categories in which the forms have been classified. In the opinion of the writer probably not less than two thirds of these are based upon growth, age, or temperature characters, while the remaining third are well founded; but even so, the degree to which the biological process of speciation has progressed in this genus is, in comparison with other dinoflagellates, except Peridinium, relatively great, a fact of possible significance in connection with the phenomenon of mutation herein described. All of the species of the genus, with the possible exception of a few numerically rare and structurally widely divergent species, fall into five sharply defined subgenera as follows: —

Tripoceratium, subgen. nov.

Antapical horns subequal, reflected anteriorly, their tips symmetrically pointed closed. Apical horn differentiated abruptly from the rotund midbody. Postmargin rounded, no postindentation. Over 25 species. C. *tripos*, *C. arcuatum* (fig. A).

Macroceratium, subgen. nov.

Antapical horns, subequal, reflected anteriorly, their tips truncate, open, or contracted or rounded, but usually with terminal pore. Apical horn differentiated abruptly from more or less rotund midbody. Bases of the antapicals projected more or less posteriorly beyond midbody forming a postindentation. Over 25 species. *C. macroceros, C. gallicum* (fig. B), *C. vultur* (plate **4**, fig. 7).

Biceratium Vanhöffen.

Antapical horns more or less unequal, deflected posteriorly, their tips pointed, closed. Apical horn differentiated or tapering from the midbody. Deep postindentation. Over 10 species. *C. furca*, *C. pentagonum* (fig. C), *C. californiense* (plates **1–3**, plate **4**, fig. 4).

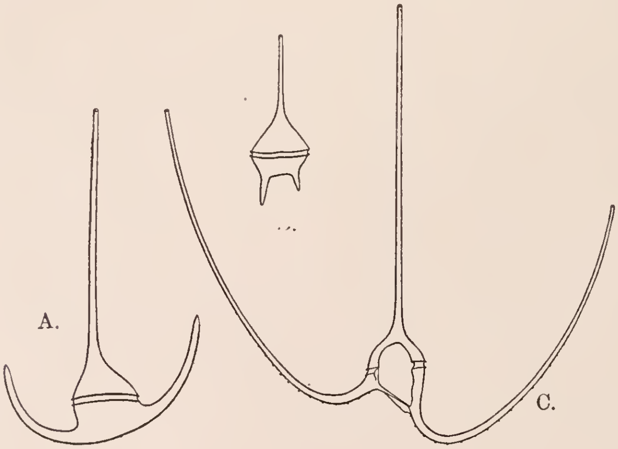


Fig. A. *Ceratium arcuatum*, dorsal view. × 155.
Fig. B. *C. gallicum*, ventral view. × 155.
Fig. C. *C. pentagonum*, dorsal view. × 155.

Amphiceratium Vanhöffen.

Antapical horns directed posteriorly, their tips pointed, closed; the right minute or suppressed, the left and the apical greatly elongated. Midbody usually gradually merging into the apical horn. Several species. *C. fusus.*

Poroceratium Vanhöffen.

Antapical horns subequal, directed posteriorly. Midbody extends to apical pore. Apical horn not differentiated. A few species. *C. gravidum.*

The subgenera Tripoceratium and Macroceratium together form the group designated by Gran (1902) as the subgenus Euceratium, but it seems best to recognize as subgenera the two large natural groups of species contained therein and easily separable on fundamental structural characters. The *C. tripos* and *C. macroceros* sections have been recognized in various ways, though not hitherto as subgenera, by recent systematists, as, for example, by Ostenfeld (1903), Pavillard (1907), Karsten (1907), and Paulsen (1908).

The number and relation of the skeletal plates are similar in all the subgenera. I have therefore (1907 b) considered this fact as the justification for keeping this large genus intact, since skeletal plates constitute generic characters throughout the family Peridinidae, to which Ceratium belongs. Amphiceratium and Poroceratium are more aberrant subgenera in which the tripartite form of the skeleton prominent in the others is considerably obscured by specializations for flotation. The other three subgenera, Tripoceratium, Macroceratium, and Biceratium, are less divergent and not so aberrant. They contain the simpler and presumably more primitive species. These also contain the greater part of the species in the genus and are separated from one another by fundamental structural features, such as the direction and curvature of the antapical horns and the forms of their distal ends, which are not so patently adaptive modifications. Should these characters alone be used as a basis for the subdivision of the genus, it would necessitate the inclusion of Amphiceratium and Poroceratium in the subgenus Biceratium. The morphological basis upon which these three principal subgenera rest is thus of general import throughout the genus.

The mutations discussed in this paper connect the three fundamental subgenera, Tripoceratium, Macroceratium, and Biceratium. *Ceratium* (*Tripoceratium*) *tripos* mutates to *C.* (*Biceratium*) *californiense*, and

C. (*Biceratium*) *californiense* is found in chain with *C.* (*Macroceratium*) *ostenfeldi.* Both the amplitude and the direction taken in these abrupt changes in form are of great interest, and are, I believe, of profound significance in their bearing upon the question of the method of organic evolution in nature.

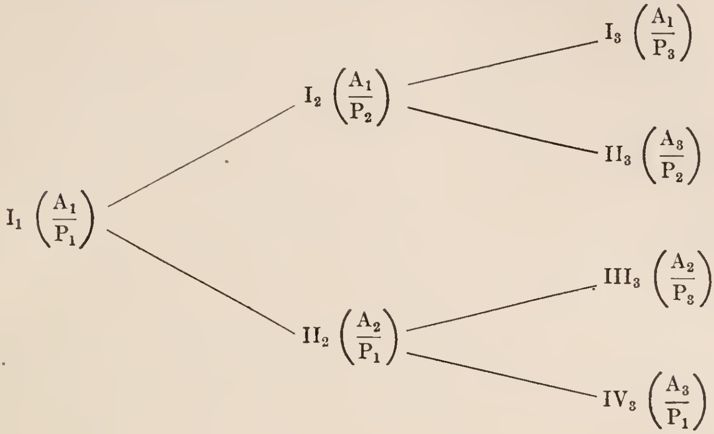
The species in or between which these mutations occur are well-established species of the genus, have a wide distribution in the sea, and in the main, excluding questions of synonymy, a general recognition in the literature of the subject. The evidence of this abrupt change in form, this mutation, or perhaps we may even say transmutation, of species seems unequivocal. The facts upon which these conclusions rest are as follows.

THE MUTATION OF CERATIUM TRIPOS TO C. CALIFORNIENSE.

The chain exhibiting this change (plates **1–3**) was taken at 8 A. M. Jan. 24, 1905, at Sta. 4737, 19° 57′ 30″ S., 127° 20′ 18″ W., on our line between the Galapagos Islands and Manga Reva in an intermediate haul from 300 fathoms to the surface. It consists of four individuals in a chain which has resulted from two succeeding cell divisions. The four individuals are in the third generation, that is, are granddaughter cells of an original grandparent cell. The original skeleton of the grandparent cell is now widely severed, its anterior moiety forming the forward armor of the foremost (uppermost in the plates) individual, and its posterior moiety the rearward shell of the hindmost (lowermost in the plates) in the chain.

Chronology and Nomenclature of Skeletal Parts of Chain.

An analysis of the chronology of skeletal formation and the distribution in the present chain of the skeletal parts formed in the three generations is illustrated in the accompanying diagram in which A_1 A_2 A_3 and P_1 P_2 P_3 represent the anterior and posterior moieties of the skeletons formed on the first, second, and third generations respectively. For convenience in referring to the individuals in the following discussion they are numbered from the anterior end posteriorly, with the distinguishing number of the generation added as subscript; thus the individual I_3 is the first (foremost) individual in the third generation, and its skeleton $\frac{A_1}{P_3}$ consists of the anterior moiety of the grandparent cell of the chain and a posterior moiety formed at the latest division. It is patent that each individual possesses one moiety of the latest generation, while the other has descended from some antecedent one.



An inspection of the figures on plates **1–3** and a comparison of the skeletal conditions there presented makes it evident that the present chain reveals, by virtue of the existence of fixed skeletal parts passed by "down inheritance," the skeletal morphology for three generations. The chains of Ceratium offer thus a unique opportunity for the study of pedigree cultures in relatively simple organisms. The species characters in Ceratium lie mainly in the skeletal parts, and these are so preserved in later generations that the skeletal morphology of a line of descent may be traced with a degree of certainty unsurpassed in other organisms. The genetic connection of the members of the chain is insured beyond all question, a condition difficult to realize where the schizonts are separated at the close of cell division. Furthermore there can be no possibility of accidental contamination of a culture from air-borne spores or encysted forms such as must always attend pedigree culture work with most flagellates and ciliates.

Genuineness of the Chain.

This is, beyond all question, a genuine chain of genetically related Ceratium formed by schizogony with skeletal and plasmatic continuity, as is usual in chain formation. It is not a chance assemblage of individuals, jostled together in the crowded collection. Neither is the posterior member of the series accidentally attached to a chain of unrelated origin. The following facts sustain this assertion: —

(1) The chain has held together not only during the more or less violent disturbances involved in making a plankton haul with a silk net from a vessel at sea, but also during the microscopical examination in the course of which it has been rotated several times in freeing it from entangling organisms and in securing dorsal and ventral views. It has also survived the changes of fluid incident to the staining process and a final transfer from a 4 per cent solution of formalin in sea water through alcohol grades to glycerine, made by passing the fluids through beneath the cover glass. In the course of these changes it has been subjected to some bending and strains, but has not parted except as shown (plate 3) in the figure of the cell contents, where the junction of cells II_3 and III_3 is slightly disconnected.

(2) The connections between the apical horns of II_3, III_3, IV_3, and the attachment area at the distal ends of the girdles of I_3, II_3, and III_3, respectively, are both normal and typical. I have studied with especial care under the oil immersion lens the details of the most important connection, namely, that between the apical horn of IV_3 (*Ceratium tripos* representative) and the cell ($III_3 =$ *C. californiense*) to which it is attached anteriorly. This is in all respects perfectly typical, even the protoplasmic bridge appearing to be still intact.

(3) The apices of all the horns, save the ancestral one, which is on the anterior skeletal moiety of I_3, exhibit the flaring, slightly lobed margin about the apical pore, described by Entz (1905), which is characteristic of this part of recently formed anterior horns. These are the conditions to be expected in a normal chain of four individuals.

(4) Contrasts in the hyalinity and porulation of the anterior and posterior moieties of the skeletal wall of the several individuals are indicative of recent normal chain formation. These differences are due to the fact that the skeletal wall grows darker with age and its pores are more easily seen. This is plainly noticeable in the case of III_3 and IV_3, upon whose recent separation by division the whole point of this communication rests. The anterior skeletal moiety of IV_3 in the original specimen is very plainly of a more delicate texture than the posterior one, barring only the right antapical region which has apparently recently exuviated or is undergoing resolution. The posterior moiety of III_3 is likewise of a lighter texture than the anterior one of that individual, though the difference between them was less striking than in the case of the two regions of the skeleton of IV_3. These contrasts are just such as would appear if III_3 and IV_3 had recently originated by the division of the posterior member of a chain of two schizonts. Differences of similar im-

port can also be detected between the older and newer skeletal parts on the two sides of the line of fission in the anterior pair, I_3 and II_3, of the chain.

(5) Finally, the nuclear conditions within the cell body (plate **3**) in all four individuals are prophetic of another division. It was not possible in the unsectioned preparation to make out finer cytoplasmic structures within the skeletal wall, but the nuclei have either completely divided (IV_3) or nearly so (III_3) or are plainly in the process of division (II_3 and I_3). The division stages here shown are similar to those which Lauterborn (1895) has found in *C. hirundinella*, a fresh-water species, and are in all respects of the normal type. There is an apparent progression in the stage of mitosis from the anterior schizont posteriorly.[1]

No structural feature is apparent in the individual cells to which this difference in mitotic activity can be traced. There is, for example, no corresponding series of differences in volume of the cell mass, or in ratio of nucleus and cytoplasm. It is possibly of interest in this connection to note that division has progressed farthest in the posterior cells of the chain, those which in normal locomotion are bathed in water which receives the waste products of the more anteriorly located members of the chain. Locomotion occurs in chains of Ceratium even during division, for the flagella persists during the process of schizogony (see Lauterborn, 1895). I have myself seen chains in locomotion with active flagella in recently collected plankton, quite contrary to the observations of Murray and Tizard (1882).

Completeness of the Chain.

Not only is this a genuine chain, but it is in all probability a complete chain. The presence of a long anterior horn with squarely truncate tip upon the foremost cell of the chain is conclusive evidence that the chain is complete in that region, that is, that no schizonts have cut loose from the chain at this end during the present cycle of schizogony. The tip of all young apical horns is peculiarly asymmetrical in adaptation to chain

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[1] In view of the many discussions over the direction of the plane of division among flagellates, especially in parasitic forms such as Spirochaeta and Trypanosoma, it is of interest to note here that during the process of mitosis the equatorial plane or cleft between the parting chromatin masses shifts from approximately a longitudinal position to one at 45° to the major axis. The seemingly oblique division of the dinoflagellates is thus in its relation to the position of the nucleus prior to mitosis, a *longitudinal* one. It is, however, oblique in the skeleton and also in the plasma, unless the latter shifts with the nucleus.

formation. The fact that the antapical horns of the hindmost member of the chain have undergone autotomy is also suggestive that this end of the chain is likewise complete. As I have shown elsewhere (1908), autotomy occurs not infrequently in isolated Ceratium in the plankton, but I have never seen it in Ceratium in chain. Autotomy possibly occurs only under conditions unfavorable to normal cell division. Because of this autotomy and the characters of the posterior skeletal moiety P_2, I regard the posterior end also of the chain as complete.

It is a fact, which I have frequently observed in crowded plankton collections, that the dinoflagellates, Ceratium among them, often tend to cell division (often abortive) under the adverse conditions presumably prevailing in such collections. It seems improbable, however, that this division approaching in the chain shown in plates **1–3** was brought on by the treatment to which they were subjected in the process of collection, for it is far advanced in division, and moreover it was our custom on the "Albatross" Expedition to fix the catches of the fine silk nets very shortly after they were brought aboard, after a brief preliminary treatment with chloretone.

Evidence of Mutation.

Turning now to a detailed consideration of the data afforded by the chain shown in plates **1–3**, we find that it consists of four individuals, the rearmost of which (IV_3) is *Ceratium tripos* or a closely related species belonging to the subgenus Tripoceratium, while the other three belong to the subgenus Biceratium, to a species which I have recently (1907 c), described as *C. californiense.* The characters which determine the species in question lie in the main in the posterior part of the organism. The anterior moiety of the skeleton contains here no easily recognizable specific characters. It is impossible to determine with certainty the species of the rearmost member of the chain, since its antapical horns have undergone autotomy, the right horn having been severed by a section plane close to the midbody and the left at a distance of 0.5 of a transdiameter (at the girdle) from the midbody. This entire or partial removal of the antapical horns obscures in this individual the species characters which in the subgenus Tripoceratium are largely found in the curvature and position of these horns. There is no doubt, however, that the posterior moiety of the skeleton of the rearmost cell (IV_8) is that of the Tripoceratium type. The species was probably one with broadly evenly curved horns such as *C. arcuatum, C. schranki,* if not indeed *C. tripos* (*s. str*) itself. It will suffice for present purposes to designate it as *C. tripos.*

The other three members of the chain are of a different type. The differences lie in the following characters: (1) The antapicals are unequal, (2) posteriorly directed with some lateral curvature, and (3) the apices except in II_3 taper to sharp tips. (4) There results from the posterior direction of the horns a deep postindentation with sharply defined rectilinear postmargin. In *C. tripos* (cf. Fig. A), on the other hand, antapicals are curved anteriorly to a direction subparallel to the apical and their tips are abruptly pointed. There is no postindentation, and the postmargin is broadly curved with no sharp limits. The differences between the two types are profound and coincide with the distinctions between the subgenera Tripoceratium and Biceratium. The three forward members of the chain I_3, II_3, and III_3 belong to the species *C. californiense.* In cell II_3 the antapicals are distally curved outwardly a little more than in I_3 and III_3, and the tip of the right is bluntly rounded and that of the left abruptly pointed, but not in the *C. tripos* fashion with a median symmetrical point, but with a sharp point at the *outer* margin, a feature found in many other species of the subgenera Biceratium and Amphiceratium, but not in those of Tripoceratium.

The species *Ceratium californiense* was originally described by me (1907) from the waters of the Pacific off San Diego. It occurs throughout the eastern tropical Pacific in the material of the "Albatross" Expedition. It has also been recorded from the Indian Ocean by Karsten (1907). It is in my own experience a relatively rare species, occurring sparingly in the plankton. There are many such species in the different subgenera of Ceratium. The species *C. tripos* and *C. ostenfeldi* are, however, common species of wide distribution in all seas save polar waters.

Progressive Perfection of the Mutant.

The form of individual II_3 is of great interest and possibly of considerable significance. The wider spread of the horns and the absence of the tapering tip bring this individual somewhat nearer than I_3 and III_3 to the ancestral type, though neither curvature nor tip is like that of *C. tripos.* It looks as though there were some subtile ancestral influence which at the first division (I_1 to $\frac{I_2}{II_2}$) tended, though unsuccessfully on the whole, to prevent the complete saltation from *C. tripos* to *C. californiense.* Two generations (asexual!) are here required to perfect the mutation.

The relations of this phenomenon are best understood when one reconstructs the two antecedent generations from their skeletal parts distributed in the third. This can readily be done by a comparison of the formula on p. 221 and plates **1** and **2**. The ancestral individual of the chain was a *C. tripos* with skeletal parts A_1 and P_1 now on individuals I_3 and IV_3. Its daughter cells were I_2 and II_2, the first with skeletal parts A_1 and P_2, the second with A_2 and P_1. Thus the anterior member (I_2) of the chain with two individuals had the anterior moiety (A_1) of the original *C. tripos* skeleton and a new posterior moiety (P_2) which was fundamentally of the Biceratium type, but the newly formed skeletal parts were still subject to a lingering influence that shows unmistakable relations to the ancestral Tripoceratium type. In the next division, in which I_2 forms $\frac{I_3}{II_3}$, and II_2 forms $\frac{III_3}{IV_3}$, the newly formed posterior moieties (P_3 in I_3 and III_3) attain the typical form of *C. californiense* while P_2 is passed to II_3. The posterior skeletal moieties containing the most clearly defined subgeneric and specific characters P_1, P_2, and P_3 thus form a *short* series with the most abrupt change between P_1 and P_2 and record a complete transformation in the short space of three generations (two cell divisions), from the species *C. tripos* to the species *C. californiense*, and from the subgenus Tripoceratium to the subgenus Biceratium.

The chain shown in plates **1–3** was discovered in material preserved in formalin. Its further development had been stopped in the very act of a third division. What might have resulted from this division cannot be told. The fact that three of the four daughter cells are of the type of *C. californiense* and that the two generations show a movement in the direction of the perfection of that type suggests its probable continuance.

Significance of Autotomy and Resolution of the C. tripos Skeleton.

The condition of the skeleton of the *C. tripos* cell, especially of its posterior moiety P_1, is also most suggestive. Not only have the horns undergone autotomy, but there is evidence that the skeleton is being further modified. The wall of the left antapical horn and that of the right antapical region (Plate 2) is exceedingly thin and tenuous, and the pores are scarcely visible, as though the wall had been thinned down by a process of solution. This condition is in sharp contrast to that of the unmodified ancestral skeleton in the rest of the posterior skeletal moiety P_1. This has a heavier, less hyaline wall whose pores become gradually fainter in the more distal parts. It thus appears that the ancestral skeletal moiety, *i. e.* of *C. tripos*, of this posterior member of the chain is gradually disappearing. In all other structural features and in the process of cell division this member of the chain appears to be a normal cell. The question naturally arises, will this process continue until the old skeleton is entirely lost and will a new skeleton of the *C. californiense* type be formed in its place? This cell IV_3 is a sister cell of a *C. californiense* III_3. Is not its inherited skeleton of the *C. tripos* type, and are its nucleus and plasma now, and perhaps since the first division, of the *C. californiense* type? Only pedigree cultures can give a decisive answer to these interesting questions.

THE MUTATION BETWEEN CERATIUM CALIFORNIENSE AND C. OSTENFELDI.

PLATE 4, FIG. 4.

Another chain was taken in the intermediate haul from 800 fathoms to the surface at 8 A. M. on December 31, 1904, at station 4711, 7° 47′ 30″ S., 94° 5′ 30″ W., on our line between Easter Island and the Galapagos Islands. The chain consists of two individuals only. The anterior member of the chain is a *Ceratium ostenfeldi*, the posterior is *C. californiense.* The anterior member has the antapical horns recurved anteriorly with truncated open tips. Their bases are also projected posteriorly, forming a deep postindentation and a long straight postmargin. These are characters of the subgenus Macroceratium. The posterior member has the antapical horns projected posteriorly, with slight outward curvature, a characteristic of the species (*C. californiense*), with tapering pointed tips and deeper postindentation, characteristics of the subgenus Biceratium. The mutation here involves the two species *C. ostenfeldi* and *C. californiense*, belonging to two of the important subgenera of the genus, Macroceratium and Biceratium. The anterior cell of this chain has the characteristically open tips of the subgenus Macroceratium. The extruding plasma (plate **4**, fig. 5) leaves no doubt on this point. The typical proportions of the three horns and the general habitus of the cell suggest that it is a normal cell, not an autotomized one. Owing to the state of development in which the relatively short horns of the anterior member of this chain appear, its specific identity is somewhat obscured. I have referred the cell to the species *C. ostenfeldi* rather than to *C. macroceros*, because of the distance to which the major flexures in the bases of the antapicals are projected posteriorly. This is much greater in *C. macroceros* and much less in

C. intermedium, especially in the left horn, than it is in *C. ostenfeldi*. Compare on this point the original figure of *C. macroceros* (Claparède et Lachmann (1858–1861, plate 19, fig. 1), Ostenfeld's (1903, p. 584, figs. 136–139) figures of *C. intermedium*, and Kofoid's (1907 c, plate 26, figs. 22–25) of *C. ostenfeldi*. The three species here named form a group of closely related but clearly separable species, much confused in the earlier and some of the recent literature (see Paulsen, 1908, for the synonymy of the first two, and Kofoid, 1907, for that of *C. ostenfeldi*).

Evidences of Genuineness and Completeness.

The internal evidence is conclusive that this is a genuine chain and not a chance union. The connection is in every way typical. On the other hand, it is not certain that the whole of the chain is here represented. The relatively short apical horn of the anterior member is indicative alike of the recent formation of the chain and of this part of the skeleton; that is, it is not A_1 but A_{1+x}. A comparison of this chain with the one previously discussed and that of *C. vultur*, shown in plate **4**, fig. 7, will tend to confirm this conclusion. Again, it is also uncertain whether or not the posterior member of the original chain is here represented by the rear cell. I can find no internal evidence that is absolutely conclusive in either direction. The chain may therefore be comparable with $\frac{\mathrm{III}_3}{\mathrm{IV}_3}$ or with $\frac{\mathrm{II}_3}{\mathrm{III}_3}$ of the chain shown on plates **1–3**, or in more general terms with $\frac{(\mathrm{I}+x)_y}{(\mathrm{II}+x)_y}$, in which x represents the number of these individuals in the chain beyond the first, and y the number of the generation to which they belong. It is, however, to my mind more probable that the pair was not terminal $\left(\frac{\mathrm{III}_3}{\mathrm{IV}_3}\right)$ but intermediate $\left(\frac{\mathrm{II}_3}{\mathrm{III}_2}\right)$ in position, in such a relation as exists in the case of $\frac{\mathrm{II}_3}{\mathrm{III}_3}$ in the chain on plates **1–3**; that is, the present cells were not separated in the last schizogony, and consequently the anterior skeletal moiety of the foremost cell and the posterior of the rear one were not joined in the skeleton of any parent cell. They are not sister cells, but cousins of indeterminate degree of nearness or remoteness. The grounds upon which this conjecture rests are: (1) the forward cell is 20 per cent wider at the girdle than the rearward one; (2) the lengths of the sides of the plates along the fission lines differ so in the two cells that they cannot be joined without considerable change in their length.[1] We are therefore left in doubt, and perhaps in total ignorance, of the form of the ancestral skeleton. We can only say with certainty that these two very diverse cells, these two species of Ceratium, have descended from an ancestral cell similar to one of the two or possibly totally different from either. In view of the limited number of cells usually found in Ceratium chains, the short time in which chain formation, as a rule, continues and the youth (relative shortness of the apical horns) of both cells, the inference may be made that generations which separate them from the ancestral form are few rather than many, and that the relationship between the two cells is near rather than remote.

In the case of the mutation of *C. tripos* to *C. californiense* there was evidence in the chain (plates **1–3**) that the change was to a slight degree graduated, that is, that the second division produced a more pronounced type of *C. californiense* than the first. In the case of *C. ostenfeldi* and *C. californiense* the chain is too short to yield any evidence. I have found, however, in the plankton of the Pacific several individuals of *C. californiense* which exhibit structural features which tend toward but do not attain the characteristics of subgenus Macroceratium. For example, the following have been recorded: individuals with the lateral curvature of the antapical horns slightly more pronounced than in the normal individual, and again, with one or both antapical tips squarish (plate **4**, fig. 6), but still closed, and one case with one tip plainly open (autotomy?). These observations lead me to surmise that the phenomenon of abruptly transitional forms exists also here between the two types involved in this mutation. In the one mutation, and possibly in both, however, the changes, in comparison with the variations of the fluctuating type are: (1) less frequent in occurrence; (2) more extreme in their amplitude; and (3) involve at the same time a whole complex of fundamental characters.

Earlier Observations on Mutations in Protista.

Mutations in Diatoms.

A phenomenon similar in some respects to the mutations in Ceratium has been found by Müller (1903, 1904, 1906) in the colonies of Melosira, a fresh-water diatom in which the cells are normally found joined together in linear filaments or chains. In the same filament Müller found cells,

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[1] The fact that in the chain shown in plate **1** two sister cells, the third and the fourth, have apparently unequal transdiameters, is due to the obliquity of the position of III_3 when sketched. In plate **3** the real dimensions are better shown.

with thick walls and coarse pores, and those with thin walls and fine pores in a different pattern of arrangement. In such chains cells were also found with the two valves different, one of them of the heavy, the other of the lighter type. The cells of the two types were, however, of the same form and size. He concluded in his first interpretation (1903, 1904) that he was dealing with instances of "Sprungweise Mutation." These mutations occurred in several species. Later (1906), following the publication of Gran's paper (1904) and Karsten's (1904) critique upon his own and Gran's interpretation, he changed his conclusion to accord with that of Gran, that is, that these were cases of polymorphism.

In the Arctic plankton Gran (1904) found *Rhizosolenia semispina*, a species with thin walls, long intermediate bands and slender pointed tips with a thin terminal bristle, a species abundant in spring and summer. Within its range of distribution occurs also *R. hebetata*, a winter species of about the same size, with thick walls, short intermediate bands, and blunt rounded tips. Chains are not found in these species, but Gran found single individuals in which one half of the skeleton was that of *R. hebetata* and the other that of *R. semispina*, indicating a sudden change from the former to the latter. A similar connection between two species was found by Gran in chains containing *Chaetoceras criophilum* and *C. boreale*, in which the former has suddenly given rise to the latter. It is, perhaps, significant that these mutating chains were taken "aus relativ warmen Wasser ausserhalb des nördlichen Norwegens," while the Rhizosolenia in which evidences of mutation were found occurred in "Planktonmaterial von der Grenze des Treibeises." These are both regions where environmental contrasts were strongly marked, where factors exist which might call forth mutations.

Gran's interpretation is best given in his own words: "Wenn um die Rhizosolenien als Beispiel zu nehmen — *R. hebetata* sich in *R. semispina* verwandeln kann, aber *R. semispina* niemals oder nur ausnahmsweise in *R. hebetata* übergeht, dann können wir von einer Mutation sprechen. Wenn aber die beiden Formen unter dem Einfluss von wechselnden äusseren Faktoren regelmässig ineinander übergehen können, dann haben wir eigentlich nur eine Art, und die Veränderungen sind Aeusserungen eines gesetzmässigen Dimorphismus." He adds thereto the idea that in the two species with practically similar areas of distribution *Rhizosolenia hebetata* is adapted to winter and Arctic conditions with slow reproduction, and *R. semispina* to those of spring and summer with more rapid multiplication and greater competition. He notes also the points of structure in which the winter form *R. hebetata* approaches a diatom resting spore, a phenomenon not without a parallel in the case of the Ceratium mutant *C. californiense.* But in neither case are the mutants typical resting spores.

In his critique Karsten (1904) concurs in Gran's interpretation, and adds thereto the suggestion that the polymorphism is an adaptation to flotation.

The correctness of Gran's interpretation rests fundamentally upon two hypotheses: (1) that mutations are not reversible, and (2) that such sudden changes in form called forth by environmental conditions cannot be regarded as mutations but must be regarded as dimorphism (polymorphism). Added thereto is the secondary question as to the numbers of the mutants of the organisms mutating. That is, does *Rhizosolenia hebetata* have its origin *solely* by mutation regularly each recurring season from *R. semispina?*

The process of mutation is undoubtedly reversible in some cases. Mutants of *Oenothera lamarckiana* have given rise in turn to the parent form (MacDougal, Vail, and Shull, 1907). Herpetomonas forms give rise to Trypanosoma forms and *vice versa.*

Mutants arise, in some cases at least, in response to known stimuli (Tower, 1906, MacDougal, Vail, and Shull, 1907), and it seems reasonable to believe that abrupt hydrographic changes in the environment of the plankton may serve as stimuli. The mutations found by Gran and those in Ceratium have occurred in regions or times of environmental contrasts. The number of instances of mutation, or the coefficient of mutability, has been proved to be variable (MacDougal, Vail, and Shull, 1907). There is apparently no necessity that it should always be low or remain at the same level. This coefficient is probably a function at a given time of the number of individuals in a physiological state in which stimuli producing mutation become effective. In the case of asexually produced functional individuals of the protists we may reasonably expect that the observed numbers of mutants would be larger, and possibly, also, that the coefficient would be higher, than in the sexually produced (Huxleyan) individuals of the Metazoa and Metaphyta. We may still correctly designate the process as mutation, though the numbers of mutants be large. On the other hand, should mutations be of necessity rare and Gran's objection to applying the term mutation to the phenomenon hold good, there is as yet no basis in observation for concluding, in so far as can be determined from Gran's data, that the actual changes of *Rhizosolenia hebetata* to *R. semispina* and *vice versa* are coincident in number and in extent of distribution with the phenomenon which he designates as a seasonal dimorphism of one species, *R. hebetata*, with a winter form, f. *hiemale*, which changes to a summer one, f. *semispina*, and *vice versa.*

With our present knowledge another interpretation is, I believe, certainly possible, namely, that *R. hebetata* and *R. semispina* are two distinct species with separate seasonal (predominant) distribution, and that under the stimulus of certain environmental factors they mutate with a coefficient at present unknown, the one to the other. The fact that the actual change (mutation) from Gran's winter form (*hebetata*) to the summer one (*semispina*) was observed by him in plankton taken in February in the middle of the Arctic winter does not particularly favor the seasonal dimorphism interpretation.

Mutations in Desmids.

Desmids eaten by Daphnia and Cypris continue to divide in the digestive tract. This has been observed by Cushman (1904) in the three genera Cosmarium, Euastrum, and Micrasterias. The newly forming semi-cells are, however, unlike the parent cell, being of bizarre and contorted form, possibly as a result of the stimulus of the secretions of the digestive tract.

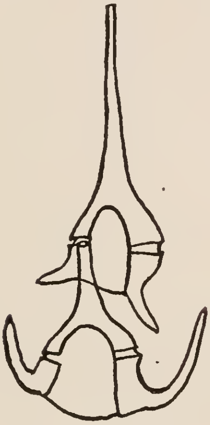
The occurrence in nature in the plankton of Loch Morar of desmids one semi-cell of which has the structure of *Xanthidium subhastiferum* and the other of its var. *murrayi* has been noted by W. and G. S. West (1903). This phenomenon is similar to that in diatoms and dinoflagellates and presumably originates in like fashion.

Mutations in Ciliates.

In pure cultures of *Paramecium caudatum* Calkins (1906) found among the daughter cells arising by the early divisions of an exconjugant a strain of *P. aurelia* which continued to exhibit the characters of this species, to wit, two micronuclei, and smaller size, for about three months through forty divisions, when the culture reverted to *P. caudatum.* Calkins is inclined to doubt the validity of a number of the characters previously used to separate the two species and is inclined to combine them as one. In my opinion the phenomenon with which he was dealing is similar in all important phases to that in Ceratium, and may be regarded as a process of mutation, occurring in the course of asexual reproduction and producing a weak species, *P. aurelia.*

Mutations in Ceratium.

Ceratium chains showing phenomena similar to those here described have been observed by Lohmann (1908) in the marine plankton at Kiel: "Bei Versuchen Plankton in grossen Glashäfen zu kultivieren fand ich bei der täglichen Untersuchung kleiner Wasserproben durch Zentrifugieren und Filtrieren zahlreiche Ketten von *Ceratium tripos*, die bisher in der Ostsee nicht gefunden waren. Später zeigte sich bei der Untersuchung der Netzfänge, dass in diesen keine einzige Kette zu finden war, während die Filterfänge solche enthielten. Es müssen also die Individuen einer Kette bei der Netzfiltration in der Ostsee sich von einander lösen, während sie im Nordsee-und Ozeanwasser so fest miteinander verbunden sind, dass sie auch in den Netzfängen erhalten bleiben. An diesen Ketten liess sich nun leicht der Nachweis führen, dass alle Jugendformen Hensens besondere Formen von *Ceratium tripos balticum* sind und in den Entwickelungsgang dieser einen Art gehören. Es besteht hier also ein ausserordentlich reicher Polymorphismus, der aber nur in ganz bestimmten Perioden des Jahreskreislaufes hervortritt und also unter den Begriff der Temporalvariationen fällt. Ausser den von Hensen beschriebenen Formen kommen noch



D.

E.

Fig. D. Mutating chain of *Ceratium tripos balticum* after Lohmann (1908, p. 270, fig. 21, II a) "Temporalvariationen von *Ceratium tripos balticum* II. a. forma *lata*, Kette von forma *typica* und forma *lata*."

Fig. E. The same after Lohmann (fig. 21, III b). "Kette von forma *truncata* und *lineata*."

einige andere vor." The fact that chains were not found in the collections made at Kiel in the Baltic, but were found in the North Sea and Atlantic, is possibly due to the times of the day at which collections were made in the two regions.

Lohmann unfortunately gives us no clue to the relative abundance of the heteromorphic chains observed by him, but the inference one is led to make from his discussion and conclusion is that they were not uncommon, perhaps were numerous. He figures but two chains, and these only in outline sketches which are here reproduced in figures D (his figure 21, II a) and E (his figure 21, III b); the first represents a chain of two individuals, the posterior schizont being a normal *Ceratium tripos balticum* Schütt[1] and the anterior a Ceratium of different type called by Lohmann *C. tripos balticum* forma *lata*. This anterior member is similar in some particulars to the second cell (II_3) of the chain figured by me on plates **1–3** and also to the cell (I_2) of the previous generation which may be reconstructed from the skeletal parts A_1 and P_2, the homologue of the anterior cell in Lohmann's chain.[2]

Judging from the length of the apical horn, this chain is complete anteriorly, possibly also posteriorly, though the antapical horns of the posterior member of the chain are relatively short. In any event, whether the two cells are sister schizonts or not, they are of different types. The posterior is *C. tripos balticum*, belonging to the subgenus Tripoceratium, and the anterior is *C. minus*, belonging to the subgenus Biceratium, but still showing in the lateral deflection of its antapical horns a slight tendency toward the Tripoceratium type of skeleton.

[1] Schütt (1893, p. 70) applies this name to both the Baltic and Atlantic forms of *C. tripos*, forms which Ostenfeld (1903) later separates as *C. tripos* var. *subsalsa* (Baltic form) and *C. tripos* var. *atlantica*, and Paulsen (1908) in his monograph of the Peridiniales in Nordische Plankton follows the usage of Ostenfeld.

[2] A young Ceratium with undeveloped apical horn and very short diverging antapicals which has many points of resemblance to Lohmann's f. *lata* was described as *Ceratium minus* by Gourret (1883) from Marseilles. Another Ceratium of somewhat similar form as regards the shape of the midbody, the shortness and direction of the antapical horns, was figured by Bergh (1881), from Baltic waters as a variety of *C. furca*. This form was designated later by Lemmermann (1899, p. 347) as *C. furca* var. *divergens*. Lemmermann included in this variety Bergh's figures 14–17, but figure 17 is *C. lineatum* Ehrbg., and only figures 14–16 should be assigned to a relationship to Lohmann's forma *lata*. The indications are that Bergh (1881), Gourret (1883), and Lohmann (1908) were all dealing with the same form and that Gourret's, the older name, should be used for it. There is also a possibility that *C. californiense* is the tropical representative of this northern form. A more extensive study of both northern and southern forms is needed for a final settlement of the question.

The second chain figured by Lohmann (fig. E) consists also of two individuals. The rear cell is designated by him as *C. tripos balticum* forma *truncata,* and the forward cell as *C. tripos balticum* forma *lineata.* As I have elsewhere (Kofoid, 1908) shown, autotomy is of wide occurrence in the genus Ceratium. It is a degeneration phenomenon taking place in adverse conditions which, in plankton sinking to deeper and colder waters, is correlated with flotation and assumes an adaptive significance. The posterior member is an autotomized individual of *C. tripos balticum.* The anterior member resembles the species described by Ehrenberg from the northern waters as *C. lineatum* and appearing often in the literature of recent years as *C. furca balticum* Moebius, a spurious name, for Moebius never described such a species.

Lohmann's forma *lineata* as seen in the anterior cell (heteromorph) of his figure III b has certain structural features in which it resembles his f. *lata;* such as the form and proportions of the midbody, the shape of the ventral plate, the divergence of the right horn, and the dimensions of the cell. It differs in its tapering posteriorly directed left antapical horn. This difference may be partially accounted for by the seeming obliquity of the view shown in Lohmann's figure III b. In it the left side of both cells is relatively expanded and the right foreshortened, and the left horn may be so placed that any divergence is obscured by the angle of vision. A close relationship between the heteromorphs of the two chains figured by Lohmann is, in the light of these considerations, not improbable.

The cells of this chain are representatives of the two subgenera Tripoceratium and Biceratium. By reason of the considerable length of the apical horn of the anterior schizont and the autotomy of the antapicals of the posterior one, the chain may be regarded as complete or entire, the result of a single schizogony, in which occurs a complete saltation from *C. tripos balticum* to a form resembling *C. lineatum,* with less apparent tendency to produce an intermediate condition such as is manifested in the other chain Lohmann figures (fig. D) or in that shown in plates **1–3**.

SIGNIFICANCE OF THE PHENOMENON.

The fact of supreme importance in the phenomena recorded by Lohmann (1908) and observed by myself in greater diversity, is the abrupt and complete change in form in a line of descent in a single, or at the most in two generations of organisms asexually reproduced. The change is recorded in immovable skeletal parts which reveal with unmistakable clearness the transmutation in form while the accessory phenomenon of chain formation renders possible a rigorous certainty in determining the line of descent. These changes give rise, not to new types, hitherto unknown, but old well-known types give rise suddenly to others old and well known or at least previously known. The particular category to which these types are referred, species, subspecies, varieties, or forms, is a subordinate matter. For convenience in discussion and also as an expression of my own opinion I have regarded them in the preceding pages as species and shall continue to do so in those that follow. The importance of the change in form is, however, not removed by a change in the category to which they are assigned. The fact here remains that like gives rise to unlike, that the descendents differ profoundly from the ancestral type.

Unknown Factors.

What, then, is the biological significance of these abrupt changes? No conclusive answer at present can be given to the question, for there are so many deficiencies in our knowledge of dinoflagellates in general, of the conditions of life in the sea, and of the prevalent causes and consequences of these phenomena of sudden change, that all conclusions must contain a large element of uncertainty owing to this relatively narrow basis of fact. For example, we know as yet nothing of sexual reproduction in the marine dinoflagellates beyond the occurrence of resting spores that possibly have a sexual origin. Are special gametes formed, or are all schizonts capable of conjugation? We have as yet no adequate quantitative studies of the extent and character of variation in the species of the genus nor correlation of these changes with the physical factors of the environment such as the temperature, salinity, and molecular friction. Ostwald's (1903) theoretical formulas regarding specific surface and molecular friction are yet to be put to the test of a practical application in Ceratium. Are species with different specific surfaces and individuals within the species having different surfaces distributed in the sea at such seasons and in such places as to conform to Ostwald's computations? Will Entz's (1905) conjectures as to the existence of universal intergradations of species in the genus Ceratium bear the test of an intensive study by the statistical method? Will Lohmann's (1908) suggestion of a widespread seasonal polymorphism in the genus find confirmation in pedigree cultures?

Beyond the instances here recorded we know nothing of the extent to which these changes occur in nature, nothing of their seasonal and geographical distribution. Do they occur in all seas and at all seasons, or only at certain times of the year or of the life cycle of the organisms, or only in certain localities or under certain conditions? Are other species in the genus also produced in the same way? Are certain rare and aberrant species produced in this way? For example, are *Ceratium reflexum* and *C. paradoxides*, which are always found singly, and seem to be structurally ill-adapted to flotation and unable because of their defects ever to establish themselves, — are these defective species continually produced and maintained by repeated mutations? In what proportion of schizogonies do these sudden changes occur? What would a complete genealogy of all the descendants from one pair of gametes of Ceratium reveal as to constancy in form?

Again we have no conclusive evidence as to the factors which cause or bring about these sudden changes. Are they due to internal phenomena proper to the cell itself, to abrupt changes in ratio of nucleus and cytoplasm, or in the morphology and functional activity of the chromatin substance, to heterotypical rather than typical mitoses? Or are they due to the shock of modification in external factors such as changes in temperature, salinity, or the chemical composition of the sea water, or to the interaction between these external forces and the substances and processes of the cell?

The consequences of these sudden changes in form are also wholly unknown. There is as yet no evidence as to the fate of the newly formed mutants. Do they continue to produce their own kind by schizogony? Do these schizonts conjugate, and are the descendants of the resulting zygote similar to the gametes or to their heteromorphic ancestor? Do they revert to ancestral types, remain constant, or possibly form other and different species of Ceratium? Is there a normal, usual cycle of changes or are such changes sporadic and exceptional?

Could an answer be given to any of these queries, much light would be shed upon the meaning of this phenomenon, its relation to life processes of the organism, and its significance for the theories as to the origin of species and the process of evolution in general.

Four different interpretations may be given to the phenomenon.

Seasonal Polymorphism (*Gran and Lohmann*).

These changes are seasonal, temporal variations. This is the interpretation of Lohmann (1908), who has followed in the main the conclusions of Gran (1904) regarding a similar phenomenon in diatoms. He regards the heteromorphic schizonts, the anterior members of his chain (see figs.

D and E) as summer forms of *C. tripos balticum*, the one (fig. D) as forma *lata* and the other as forma *lineata*. He subsequently introduces the second or gamete hypothesis, which will be discussed later, but favors the first interpretation, however, for he revises the nomenclature of these species of Ceratium, and throughout his paper refers to *Ceratium "lineatum"* (anterior schizont in fig. E) as *C. tripos balticum* forma *lineatum* and to *C. minus* Gourret (anterior schizont in fig. D) as *C. tripos baltica* forma *lata* f. nov. From the discussion and treatment of these forms in his tables he evidently regards all *C. lineatum* and *C. minus* which were found in his plankton collections from the Baltic as well as those found in heteromorphic chains as summer forms of *C. tripos* var. *balticum*, and gives figures of a number of isolated individuals of typical *C. lineatum* Ehrbg., which he also designates as such forms of *C. tripos.*

It is difficult, with merely the outline figures of Lohmann to examine, to pass critical judgment upon the specific identity of the forms he figures. Certain differences, however, between the anterior heteromorphic schizont of his chain (III b) (fig. E) and the typical *C. lineatum* shown in his figures III c, d, f, and g of detached schizonts lead me to doubt the specific identity and genetic continuity of the two forms. (His figure IV g is reversed ; that is, it represents the dorsal side seen from the ventral face.) *Ceratium lineatum* has a midbody of different proportions from the heteromorph. The following table of proportionate measurements, using the transdiameter of the individual as the unit of measurement, expresses these differences:

		Ceratium lineatum, Lohmann's figures III c, d, f, g, extremes and averages.	
	Heteromorph.	Extremes.	Averages.
Length of midbody	1.4	(1.6–1.9)	1.75
Distance from girdle to Postmargin in axial region	.5	(.60–.65)	.63
Length of left antapical	.82	(.75–1.2)	1.0
Length of right antapical	.43	(.43–70)	.62
Transdiameter of figure in millimeters	11.	(7.5–9.)	8.1
Ratio of two horns	1:1.9	1:1.6	

The midbody of *C. lineatum* is absolutely smaller, relatively narrower and longer, and tapers more gradually into the apical horn. Its two antapical horns are not so unequal in length. Lohmann states that the volume of the smallest individuals of f. *lineatum* is only one tenth of that of *C. tripos balticum*. The possibility of a confusion here by Lohmann of *C. lineatum* and Ehrenberg's minute species *C. eugrammum*, of similar habitus but smaller size, is not wholly excluded. The chain of two individuals of forma *lineata* (Lohmann, fig. III c) resembles the heteromorph in the more rotund midbody and has its proportions, though of smaller size. While the possibility of a complete transition from the heteromorph cell (fig. E) to *C. lineatum* is certainly open, it hardly seems to me that Lohmann's published data are adequate to establish this derivation or the conclusion that *C. lineatum* of Baltic summer plankton owes its origin to heteromorphic divisions of *C. tripos.*

Included in Lohmann's figures of *C. tripos balticum* f. *lata* are two isolated individuals (II c and d) which have the rotund midbody of the other figures of f. *lata* and also of the heteromorph of his figure III b. They have, however, a different facies. They are smaller than f. *lata,* have a greater disproportion in the antapical horns, and the apical horn is short, displaced to the right, and its axis is oblique to that of the midbody. I have never seen this species with a long apical horn. This is *Ceratium ehrenbergi*, described by me (1907) from the Eastern Tropical Pacific, where it is widely distributed though relatively rare. It does not there intergrade with any Ceratium similar to Lohmann's f. *lata* (= *Ceratium minus* Gourret).

In addition to the internal evidence in Lohmann's figures for holding in abeyance his interpretation of these heteromorphic schizonts as seasonal forms of *C. tripos*, there are certain other considerations which weigh against this conclusion.

(1) The changes between *C. tripos balticum* and the heteromorphs in Lohmann's chains and those observable in the chains found by me are not of the type to be expected in seasonal variations in *C. tripos* and in the subgenus Tripoceratium. In general, in warm seas long-horned species of Ceratium, occur and in colder water the shorter-horned ones (see Schütt, 1898, Chun, 1905, and Karsten, 1907). My own observations on the plankton of the Pacific at San Diego and in the collections of the "Albatross" confirm this, and also show that the same species grow longer horns in warmer than in colder waters at the same or in different localities. Minkiewitsch (1900) and Entz (1905) have noted a similar difference in Ceratium in the Black and Adriatic seas between such summer and winter forms. Changes are brought about by mere lengthening of the horns. Usually all three share proportionally in the process, though there are some species in which the apical horn is the one most modified. Beyond this lengthening and some attendant changes in the calibre and flexibility of the horns and in some cases changes in size, which may or may not be a part of this adaptive process, these seasonal

(temperature) variations leave the general facies or habitus of the organism unchanged, and are not of the abrupt type seen in these heteromorphic chains where the whole form of the organism is suddenly recast in another entirely distinct mould or pattern. These seasonal changes belong rather to the fluctuating type of variations, while those of the heteromorphic chains are saltatory in character.

The physical conditions prevalent at the time of the greatest increase (September 7–28) in numbers of these smaller individuals (see Lohmann's table, p. 242–243) give a constant index of molecular friction (64.5 to 65). It is also a period of falling temperatures. Lohmann's conclusions and tables require that in the face of this *C. tripos balticum* should give rise (on September 28) to 53.5 short-horned individuals to 100 of the type, individuals moreover of much smaller size and therefore of greatly increased specific surface. The volumes of *C. tripos balticum*, its f. *lineata* and f. *lata* are given in Tabelle B (Lohmann) as 100,000, 8,000, and 10,000 cubic micromillimeters respectively. (The volumes of the two forms are stated on p. 271 to be 1/8 and 1/10, respectively, of that of the type.) This means at least a doubling of the specific surface of the organism in the "seasonal change." With constant molecular friction and *falling* temperature it seems incredible that *Ceratium tripos* should suddenly give rise to considerable numbers of smaller forms, "seasonal variations," in which the specific surface of the organism is doubled, an adaptation to *rising* temperature and falling molecular friction! This is an additional reason for believing that these *smaller* forms do not lie in the genetic cycle of *C. tripos balticum*, but are independent species included incorrectly in Lohmann's tables, and that their sudden increase in the plankton of Kiel was due to other causes than seasonal variation of *C. tripos.*

(2) The known distribution of *Ceratium lineatum* (*sensu latu*), *C. californiense*, and *C. minus* affords no satisfactory basis for regarding them elsewhere as seasonal forms of *C. tripos*. The former species (*sensu latu*) (Cleve, 1900, 1902) has a wide range of distribution in colder and warmer seas, as has also *C. tripos* (*sensu latu*). In the seasonal and geographical distribution of *C. lineatum* (*sensu latu*) and *C. minus* and forms resembling it in the Pacific Ocean, I have found no indications which suggest that the two form a part of the genetic cycle of *Ceratium tripos* with seasonal limitations.

(3) The numerical proportions of *Ceratium tripos balticum* and the f. *lineata* (Ehrbg.) Lohmann and *lata* Lohmann are hardly those that would be expected if the latter are seasonal forms of the first. We would

expect in typical seasonal changes in Ceratium that a larger proportion of the individuals would be affected by the general climatic factors which underlie such modifications. As the following table, taken from Lohmann's paper, shows, the total numbers of all the short-horned "forms" constitute but a small portion of the numbers of the type *C. tripos balticum*, not exceeding 1 per 100 in 7 of the 15 collections between August 24 and November 29 and rising above 12 in but one instance, while only between September 21 and October 4 do the totals of the "forms" rise above one eighth of the numbers of the typical *C. tripos balticum.*

Their increase in numbers is (see table) preceded and accompanied by considerable fluctuations in the temperature, salinity, and specific gravity of the sea water. The conditions on August 24 represent the cessation of a rapid fall in temperature, 3° in a fortnight, increase in salinity (1.415 to 1.669), and specific gravity (9.26 to 11.79), with a less rapid increase in deeper (15 m.) waters (1.936 to 2.043). During the period August 24 to September 28 surface waters cool slowly to 13.9°, but deeper waters rise to 15.4° on August 31 and fall slowly during the following month. These changes are possibly the result of the Baltic circulation, and in comparison with other conditions at other seasons in the table are unusual. Change is indicated in the character of the water. Lohmann's tables therefore exhibit to an unknown extent the effect of this circulation, and the changes in numbers of the organisms under discussion may in part (how large can only be conjectured) be due to the inflow of water of higher salinity and a different plankton content. A hydrographic factor introducing a different plankton rather than merely a seasonal one modifying an existing plankton is suggested by these physical data as operative in producing the changes shown in the relative numbers of the organisms listed in Lohmann's statistical tables.

The same hydrographic causes probably underlie the occurrence in the winter plankton of the Baltic of *Ceratium tripos balticum* forma *pendula* and f. *penduloides* Lohmann (=C. *tripos* f. *hiemale* Paulsen). This is a long-horned *C. tripos*, probably entering the Baltic in winter, as Lohmann suggests, with the invasion of waters of higher salinity (Gulf Stream ?). Though it has a seasonal occurrence in the Baltic, it is probably not everywhere a "seasonal" form, as Paulsen's name and Lohmann's discussion seem to indicate, but an invader from warmer seas, where it is not uncommon. In Baltic waters abnormal conditions (see Lohmann's figure 21 I g, h) arise in the horns as the result of the changes to which it is subjected as the invading waters mingle with those of lower salinity.

MEMBERS[1] OF CERATIUM TRIPOS BALTICUM AND CHANGES IN ENVIRONMENTAL FACTORS.

(Compiled from LOHMANN, 1908, p. 276, and Table A.)

Dates of Collection.	August, 1905.		September.			
	24.	31.	7.	14.	21.	28.
Typical C. tripos balticum	680,000	240,000	200,000	185,000	280,000	160,000
Total short-horned forms	170	580	1,990	13,900	33,000	85,800
(*a*) f. lata	170	....	180	5,600	30,000	66,000
(*b*) f. truncata	....	120	310	3,600	1,700	16,000
(*c*) f. lineata	....	460	1,500	4,700	1,300	3,800
(*d*) To 100 of the type	0.02	0.2	1.0	7.5	12.0	53.5
Molecular friction after Ostwald	68.	64.	64.5	65.	65.	65.
Temperature (C.°) at surface	15.9	15.8	15.8	15.	14.4	13.9
Temperature (C.°) at 15 m.	13.0	15.4	15.2	14.4	14.2	14.4
Salinity (%) of the water, 0 m.	1.669	1.604	1.472	1.526	1.546	1.640
Salinity (%)of the water, 15 m.	2.043	1.730	1.655	1.795	1.748	1.748
Specific gravity of the water, 0 m.	11.79	11.32	10.32	10.84	11.84	11.66
Specific gravity of the water, 15 m.	15.19	12.44	11.82	13.04	12.71	12.68

October.				November.				
4.	12.	19.	26.	1.	8.	17.	24.	29.
180,000	44,000	110,000	110,000	590,000	250,000	55,000	44,000	47,000
21,900	2,810	4,620	420	8,900	2,170	310	413	....
14,000	1,800	420	130	1,100	270	140	....	....
2,600	250	1,700	90	400	600	....	83	....
5,300	760	2,500	200	7,400	1,300	170	330	....
12.0	6.5	4.0	0.4	1.5	0.8	0.5	0.9	....
66.5	71.5	75.	80.	78.	77.	84.5	84.	84.5
12.0	10.7	9.2	7.6	7.7	7.4	5.7	4.6	5.0
....	11.2	9.6	7.4	8.4	8.5	5.5	5.7	5.5
1.530	1.498	1.499	1.505	1.499	1.487	1.490	1.429	1.438
1.781	1.572	1.523	1.512	1.617	1.617	1.517	1.483	1.449
11.40	11.38	11.54	11.73	11.69	11.66	11.83	11.41	11.42
13.09	11.82	11.67	11.82	12.54	12.52	12.05	11.78	11.51

[1] Per 100 meters.

We conclude, then, from an examination of Lohmann's hypothesis of seasonal forms, that the heteromorphs are not of the character to be expected in seasonal changes, that the evidence of any genetic connection between them and the *C. lineatum* and *C. ehrenbergi* of his figures is inconclusive, and that his tables of seasonal distribution of his seasonal forms probably include other species than the heteromorphs and in part illustrate the changing population due to circulation of the Baltic.

Gamete Hypothesis.

As a corollary to the first hypothesis of seasonal variation, Lohmann proposes a second, to wit, that the two forms, f. *lata* and f. *lineata*, are stages of *C. tripos* which conjugate; that is, they are gametes. The reduction in size which he believes occurs in the descendants of the heteromorphs of the chains he regards as an adaptation to greater ease of movement on the part of the gametes facilitating conjugation. He calls attention to the occurrence of these so-called gametes immediately after the culmination of the greatest numbers of *C. tripos balticum*, a period when gametes and sexual reproduction would naturally be expected.

While not accepting his interpretation that all f. *lata* and f. *lineata* in his figures and tables are heteromorphs or their derivatives, I believe that the hypothesis that the heteromorphs themselves and their derivative may be gametes must certainly be held open until the actual process of sexual reproduction in some marine species of Ceratium is known. But certain considerations militate against this hypothesis.

(1) Lohmann lays emphasis upon the reduction in size which he finds in his seasonal forms. The isolated individuals of *C. tripos balticum* f. *lineata* are (fide Lohmann) but one tenth and f. *lata* but one eighth of the volume of *C. tripos balticum.* The heteromorphs in his chains (fig. II a and III b) show no such reduction in size. I have given above my reasons for doubting the conclusion that all of the isolated individuals showing this reduction belong in the cycle initiated by heteromorphs. I deem it probable that *C. lineatum*, *C. eugrammum*, and *C. ehrenbergi* have been included by Lohmann and are the cause of a part, at least, of the seeming reduction he has found. Decrease in volume, other things being equal, results in increased specific surface, and is, it seems, an adaptation to higher temperatures and decreased molecular friction in the sea water, and may therefore facilitate locomotion. My contention is only that Lohmann's evidence is inconclusive that the smaller individuals which exhibit this "reduction" lie in the

same genetic cycle with the larger *C. tripos* and are therefore to be regarded as gametes of that species.

(2) Both *C. tripos* and *C. ostenfeldi* (plate 1 and plate 4, fig. 4) have been found by me in chain with the same type of heteromorph. There is, as I have shown (p. 228), some difficulty in determining what the ancestral cell was in the heteromorphic chain containing *C. ostenfeldi* and *C. californiense*. In any event it seems improbable that we should find the same type of skeleton-bearing gamete for the two species *C. tripos* and *C. ostenfeldi*, or that *C. californiense*, being a gamete of *C. tripos*, should give rise to *C. ostenfeldi* by schizogony. Any interpretation of this chain in accord with the gamete theory is, with our present knowledge, beset with difficulties.

(3) The known cases of conjugation in Ceratium do not lend support to the view that special gametes marked by a sudden change in form from the parent type are produced prior to conjugation. Zederbauer's (1904) and Entz's (1907) description of conjugation in *C. hirundinella*, a fresh water species, shows the union of normal forms of that species. Pouchet (1885) figures two cases of the union of two individuals of *C. fusus* in ventral apposition with extruded (?) plasma in one case, and another instance of conjugation (?) of *C. biceps* has come under my observation. In all three instances presumably of conjugation, the gametes are *normal* individuals of the species.

If these heteromorphs are neither seasonal forms nor gametes, what is their biological significance? I have two alternative hypotheses to make, both provisional in view of our imperfect knowledge of the process and its results with which we are dealing, hypotheses, moreover, which are perhaps not mutually exclusive but merely two aspects of, or methods of approach to, a common phenomenon.

Degeneration or Atavism Hypothesis.

The heteromorphs are degenerate or atavistic forms of dominant thriving species called forth by the impact of new and perhaps adverse conditions to which they are subjected by the circulation of the sea or their own active or passive movements principally in the vertical direction. The exceedingly great sensitiveness of pelagic organisms to even slight changes in their environment is quickly impressed upon one who works with living plankton or traces their vertical and horizontal distribution. For example, certain species of dinoflagellates rarely appear in the plankton taken near shore at San Diego or Naples, but only at a distance of several kilometers. A similar phenomenon appears also in the vertical distribution of certain species. Yet the differences in the environing factors attending these changes in distribution may be very slight. The pelagic fauna is attuned to environmental changes of smaller amplitude than that to which the shore and land fauna are subjected, and presumably is in turn profoundly affected by changes in these factors of an amplitude which has little or no influence upon organisms of a fauna with more varied environment.

My grounds for proposing this interpretation are twofold: —

1. The occurrence of degeneration forms in flagellates under culture in media different from their normal habitat. Küster (1908) finds that *Gymnodinium fucorum* when cultivated in 1–2 per cent salt solution or in sugar solutions gives rise to heteromorphic cysts of irregular forms which may be designated as degeneration stages, in the narrow sense of the word, since the forms are irregular and of various shape and the cultures often die out. Amœboid forms arise in agar and in gelatine cultures. Zumstein (1900) was able to cultivate *Euglena gracilis* on solid media and produce a heteromorphosis to Palmella-like groups of organisms.

The most striking instances, however, of heteromorphic changes are those called forth in Trypanosoma under culture in blood agar. A summary from the biological point of view of the recent results of work in this line will be found in Doflein (1909). Trypanosoma in such cultures takes on the form of Herpetomonas, an intestinal parasite of Diptera, a transformation which involves a considerable change in the position and relations of the flagella. The process is, moreover, reversible, for the Herpetomonas forms reintroduced into the blood are changed again to Trypanosoma. The heteromorphoses here induced by the modified environment are significant of the probable path of evolution of the parasitic Trypanosoma and might be regarded as an atavistic reversion. These reversions and the degeneration of Trypanosoma arising in other cultures may be regarded as stages in the operation of the same heteromorphic process in which the organism takes on another, and perhaps in some instances an ancestral, type of structure.

The heteromorphic chains of Ceratium may then represent a similar biological process. There is in *C. californiense* and in the heteromorphs figured by Lohmann a reduction in the extent of the horns. The parent cell in some cases also undergoes autotomy which may be likewise regarded as a degeneration phenomenon arising, as I have elsewhere suggested (1908), in response to the change involved in the sinking of the organism to deeper, colder waters. The heteromorphs possibly represent the first steps in a process whose last stages, judging from conditions in other organisms, would unquestionably be called degeneration. There is also a probability that the short-horned heteromorphs approach the ancestral type in form, for the species of the subgenus Biceratium are unquestionably more like the other genera of the Peridinidae, for example, like Peridinium and Gonyaulax, than are the long-horned species of Macroceratium and Tripoceratium. *Ceratium minus* or *C. californiense* affords a plausible starting point for the derivation of the other species of the genus, and their occurrence in heteromorphic chains might well be regarded as an atavistic reversion.

2. Another reason for suggesting that the production of heteromorphs is a degeneration phenomenon lies in the peculiarly hyaline character of the skeleton of *C. californiense.* It resembles in this respect to some extent the wall of what are probably the cysts of dinoflagellates for which Pouchet (1894) established the genus Sphaerosperma. There are other species in the genus, notably *C. teres* and possibly *C. inclinatum* and *C. tenuissimum,* all of which are relatively small forms, and have to some degree this peculiar hyaline aspect. Sutures are still present in these species, but are often exceedingly difficult to detect. Cysts of dinoflagellates have, in so far as they are known, no sutures and are peculiarly hyaline. I have often noted cyst formation (gelatinous or pellicular) in moribund dinoflagellates, and Küster (1908) finds it in his degenerating cultures of Gymnodinium. This resemblance to cysts on the part of the heteromorph, *C. californiense,* may be interpreted as an indication of degenerative phenomena, while its appearance in the other species named raises an interesting question as to their possible origin by a process like that which gives rise to *C. californiense,* involving, perhaps, certain other dominant and larger species of Ceratium which they more or less resemble.

Mutation Hypothesis.

The heteromorphs are mutants, the result of the process of mutation occurring in nature. The considerations which support this view are as follows: —

1. The change is saltatory. It is accomplished in a single schizogony or generation or at the most in two. It is not a process of the slow accumulation of minute variations or a gradual decline in structural characters. In the suddenness of its appearance and the completeness of the transformation the result in Ceratium is comparable with that obtained by DeVries (1905) in Oenothera, Tower (1906) in Leptinotarsa, and Calkins (1906) in Paramecium.

2. The instances of its occurrence appear to be rare. This is true in general of the elementary species mutating from *Oenothera lamarckiana*. With the single exception of an outbreak of *Leptinotarsa pallida* (in the field) the numbers of heteromorphic individuals obtained in the pedigree studies of Tower (1906) were small. The mutation of *Paramecium caudatum* to *P. aurelia* was observed but once by Calkins (1906) in his many cultures of this protozoan.

It is obviously no necessary criterion of a mutant that it should be rare. It is conceivable, indeed quite probable, that under certain suitable conditions in nature mutations might be called forth in great numbers at one time. The fact is merely stated that mutations have been seen in but relatively few instances among many of normal reproduction observed in Ceratium, and that this coincides with observations on mutation elsewhere. In this connection it is well to note that in view of the relative simplicity of their structural features, rapidity of reproductive processes, and the ease under favorable conditions with which great numbers of individuals can be assembled and examined, the Protozoa present unique opportunities for attack upon the problem of mutation. It is possible, for example, in a few days to pass in critical review more Ceratium than fishes, birds, or mammals in a lifetime.

3. The instances of its occurrence suggest the action of environmental factors in producing the mutations. In one at least of Lohmann's instances and in one of my own the parent cell had undergone autotomy. The distribution of autotomized Ceratium in the plankton of the sea suggests, as I have elsewhere (1908) shown, the action of environmental changes, possibly those resulting from the sinking of the organism or the vertical circulation of the water. Autotomized individuals of *C. tripos balticum* (forma *truncata* Lohmann) were rather common in the Baltic plankton at the time when the heteromorphic chains were found by Lohmann in aquaria stocked from the Baltic. As I have elsewhere noted, Lohmann's seasonal tables of physical data indicate a considerable change in the Baltic in temperature and salinity, suggestive of an unusual amount of circulation prior to and during the time when the heteromorphic chains appeared. Chains, however, were found only in aquaria where naturally the conditions as to illumination, movement of the water, and extent and character of temperature changes differ from those in the sea. It is possible that some of these changes were potent in stimulating Ceratium to mutation here.

The two cases of mutation found by me occurred about 1500 miles apart in the eastern tropical Pacific, but both in localities with certain hydrographic factors in common. They were both taken in regions where hydrographic contrasts were noticeable.

The heteromorphic chain shown in plates **1–3** was taken at Station 4737, 500 miles N. E. of Manga Reva in the southern margin of the great eddy that lies in the angle between the South Equatorial and the Humboldt current. The station was located over the depression between the Albatross Plateau and that from which the Paumotu Archipelago rises, a depression blocked to an unknown extent to the south by Pitcairn and other scattered islets. (See Mr. Agassiz's (1906) Report of the Expedition, plates 1 and 2.) Across this gap as the "Albatross" approached Manga Reva there was a rapid decline in surface temperatures from 81.5° to 77.5°. The distribution of surface temperatures elsewhere in this region suggests the existence (see Agassiz, 1906, plate 3 a) of a belt extending eastward from Manga Reva and skirting the southern edge of the Albatross Plateau in which there is a change in surface temperature, 4.5° in 4° of latitude, which is relatively rapid as compared with those in the region of the adjacent eddy. An area of higher specific gravity (1.0260 as compared with 1.0252–1.0256. See Agassiz, 1906, plate 3 b) extends in a similar direction. The specific gravity of the water at this station is higher than that upon either side for some distance. Temperature sections at adjacent stations (see Agassiz, 1906, plate 5) to a depth of 800 fathoms show noticeable irregularities but no extreme conditions. An unusually large amount of dead and moribund material (see Agassiz, 1906, p. 18) occurred in the plankton of this locality. The possibility of an upwelling from deeper layers in the neighborhood is thus suggested in view of the configuration of the bottom and the hydrographic conditions above noted. We may conclude that this heteromorphic chain occurred in a region offering possibilities of environmental contrasts.

The second heteromorphic chain (plate **4**, fig. 4) was taken at Station 4711, about 500 miles S. W. of Chatham Island and near the outer edge of the great Humboldt Current as it turns westward in the South Equatorial. The temperature conditions at this and an adjacent Station, 4713, were extraordinary (see Agassiz, 1906, p. 21, plate 8) in the rapidity with which the water became colder within the short distance of 50 fathoms from the surface. The temperatures at this station at the surface, 25, 50, 100, 200, 300, 400, 600, and 800 fathoms, were 75.3°, 73.8°, 59.5°, 54.9°, 51.1°, 45.6°, 43.4°, 39.2°, and 37.4°, a decrease in the first 50 fathoms of 15.8°, and in 100 fathoms of 20.4.° The change is most rapid between 25 and 50 fathoms, where it amounts to a difference of 13.3° in 25 fathoms. This is without exception the most rapid change in temperature recorded at any of the twenty-seven stations at which serial temperatures were taken on the expedition. It occurs, moreover, within the strata of water which normally is abundantly inhabited by Ceratium, and in amplitude it corresponds to changes in surface temperatures to be found only within 30 or 40 degrees of latitude.

The contrast in specific gravity of surface waters at this station (1.0256) and that (1.0252) of the adjacent one (4712) farther in the Humboldt Current is also extreme, though similar to the change found elsewhere along the western and southwestern edge of the current.

No less striking than the rapidity in change in temperature and density is the character of the plankton in this region (see Agassiz, 1906, p. 18). There was an unusual proportion of dead and moribund material, and the debris of plankton organisms, skeletons of dinoflagellates, diatoms, radiolarians, and fragments of copepods. The explanation of this rise of the isothermobath of 60° on the western margin of the current (see Agassiz, 1906, plate 8) and the accompanying moribund nature of much of the plankton is possibly to be sought in some phase of vertical circulation within the strata affected by the currents, such as an aspiration zone or an upward compensation movement at the edge of the current due to the piling up of water on its left margin as a result of the earth's rotation (see Nathanson, 1906, 1906 a), or to an upward suction between local diverging branches of the current (see Schott, 1903).

The location of this station with reference to the current and to the distribution of temperatures in the vertical direction is thus unique in the extremes of the environmental conditions afforded within relatively narrow limits in the zone inhabited by the phytoplankton.

That the shock of environmental changes upon the organism at the time of reproduction is potent in producing changes in form or mutations has been shown experimentally by Tower (1906) for Leptinotarsa. The changes noted by Calkins (1906) for Paramecium followed the isolation of a conjugating pair of individuals which doubtless involved some environmental change. The experiments of MacDougal, Vail, and Shull (1907) upon Oenothera indicate the potency of external agencies in producing mutations in plants.

The occurrence of these heteromorphic chains in regions where they may have been subjected to unusual environmental conditions is, I believe, one consideration for regarding them as mutants called forth by the shock of environmental contrasts. The autotomy of the horns in certain instances of heteromorphic chains is perhaps indicative of adverse conditions, such as sinking to a zone of low temperature. The return of such an individual to the upper levels by the vertical movement of the water might afford the occasion for renewed growth and reproduction for cells in suitable physiological stages. The schizogony which ensues results at once in a mutation, and with the new generation the line of descent passes into a new or different stage of equilibrium.

These heteromorphic changes in Ceratium occur in the course of asexual reproduction. There is no evidence that the parent cell is a zygote or one of a recently conjugated pair of gametes. If the idea of the individual is conceived in the Huxleyan sense, these mutants and those of the diatoms belong in the same category as bud sports and are to be regarded as isolated apical cells which have abruptly assumed new or different specific characters. Will the next sexual reproduction in the line of descent be followed by a reversion to the old form? Certain studies on bud sports (see MacDougal, Vail, Shull, 1907) indicate the permanence of the change.

The occurrence of mutations in the asexually reproduced individuals of Ceratium bring additional confirmation to the idea that mutations are not necessarily dependent upon sexual reproduction for their appearance, but are a manifestation of a fundamental property of protoplasm of plants and animals alike, a property which is variously manifested in the mutations of sexually produced organisms, as in the elementary species of Oenothera, in the results of the hybridization including those which follow the Mendelian formulae, in those in which asexual reproduction occurs, as in bud sports and in these heteromorphs of Ceratium, and perhaps, also, in many types of neoplasms and abnormalities. They are a manifestation of unit systems (see Ritter, 1907) changing under stimulus in kaleidoscopic fashion from one stage of equilibrium to another.

The seeming reversion in these mutants of Ceratium to old and fundamental subgeneric types, the occasional reversibility of mutations elsewhere, and the limitations in the range and number of mutant types appearing generally in nature and under culture, suggest that the chemical nature of living substances and the ever fleeting organization of these substances in equilibriums of living structures which we call organisms, place certain rather definite restrictions upon the number and amplitude of the departures which mutants make from their sources. From the point of view of mutation the relation which exists among the members of a group of elementary species, or perhaps among the species of a genus, presents a striking analogy to that which has been found to exist among the various radio-active substances or members of a chemical series of related organic substances. Such a view tends to bring the organization of the living world into closer agreement with the organization of matter as it is seen elsewhere.

BIBLIOGRAPHY.

Agassiz, Alexander.

1906. Reports on the Scientific Results of the Expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross," from October, 1904, to March, 1905, Lieut.-Commander L. M. Garrett, U. S. N., commanding. V. General Report of the Expedition. Mem. Museum Comp. Zoöl., Vol. 33, p. i–xiii, 1–75, 96 pls., 8 figs. in text.

Allman, G. J.

1855. Observations on *Aphanizomenon flos-aquae*, and a species of Peridinínea. Quart. J. micr. Sci., Vol. 3, p. 21–25, pl. 3, figs. 1–17.

Bergh, R. S.

1881. Der Organismus der Cilioflagellaten. Eine phylogenetische Studie. Morph. Jahrb., Bd. 7, p. 177–288, Taf. 12–14.

1886. Ueber den Theilungsvorgang bei den Dinoflagellaten. Zoöl. Jahrb., Bd. 2, p. 73–86, Taf. 5.

Būtschli, O.

1883–1887. Protozoa, II Abth. Mastigophora. Bronn's Klassen u. Ordn., Bd. 1, p. 617–1097, Taf. 39–55.

Calkins, G. N.

1906. *Paramecium aurelia* and *Paramecium caudatum.* Biol. Studies by the Pupils of W. T. Sedgwick, p. 1–10, pl. 1.

Chun, C.

1903. Aus den Tiefen des Weltmeeres. Schilderungen von der deutschen Tiefsee-Expedition. Zweite Auflage, 592 pp., 46 Taf.

Claparède, E., et Lachmann, J.

1858–1861. Études sur les Infusoires et les Rhizopodes. Mem. Inst. Genev., T. 5, Mem. 3, p. 1–260; T. 1, 13, 1858; T. 6, Mem. 1 (un), p. 261–482; T. 14–24, 1859; T. 7, Mem. 1, p. 1–291; T. 1–12, 1861.

Cleve, P. T.

1900. The seasonal distribution of Atlantic plankton organisms. Göteborg. 368 pp. Also in Göteborg's Vetensk. Handl., 4 Folge, Vol. 3, p. 1–368.

1902. Additional notes on the seasonal distribution of Atlantic plankton organisms. Göteborg. 51 pp. Göteborg's Vetensk. Handl., 4 Folge, Vol. 4, p. 1–51.

Cushman, J. A.

1904. Division in Desmids under pathologic conditions. Rhodora, Vol. 6, p. 234.

DeVries, H.

1905. Species and varieties: their origin by mutation. Lectures delivered at the University of California. Edited by D. T. MacDougal. Chicago. 18, 847 pp.

Doflein, F.

1909. Die Protozoen als Parasiten und Krankheitserreger nach biologischen Gesichtspunkten dargestellt. Zweite Auflage. München.

Entz, G. jun.

1905. Beitrage zur Kenntnis der Peridineen. I. Die Peridineen des Quarnero und das Variieren mariner Ceratien. II. Homologie des Panzers und der Teilung der Phalacromeen und Ceratien. Math. naturw. Ber. Ungarn. Berlin and Budapest, Bd. 20, p. 96–144, figs. 1–47, 1–66.

1907. A Peridineak Szervczetérol. Allattani Kozlem. Vol. 6, p. 11–30, p. 2–4. German abstract, p. 49–50.

Gourret, P.

1883. Sur les Peridiniens du Golfe de Marseille. Ann. Mus. Marseille, T. 1, No. 8, 114 pp., 4 pls.

Gran, H. H.

1902. Das Plankton des norwegischen Nordmeeres von biologischen und hydrographischen Gesichtspunkten behandelt. Rept. on Norwegian fishery and marine investigation, Vol. 2, No. 5, 222 pp., 1 pl., 15 figs.

1904. Die Diatomeen der arktischer Meere. I Teil. Die Diatomeen des Planktons. Fauna Arctica, Bd. 3, p. 509–556, Taf. 17. Mit 6 Figs. im Text.

Karsten, G.

1904. Review of Müller (1903, 1904) and Gran (1904). Bot. Zeit., Bd. 62; II, p. 337–341.

1905. Das Phytoplankton des Antarktischen Meeres nach dem Material der deutschen Tiefsee-Expedition, 1898–1899. Wiss. Ergebn. d. deutsch. Tiefsee Exp., B. 2, Teil 2, p. 1–136.

1906. Das Phytoplankton des Atlantischen Oceans. Wis. Ergebn. d. deutsch. Tiefsee Exp., B. 2, Teil 2, p. 137–219, Taf. 20–34.

1907. Das Indische Phytoplankton. Wis. Ergebn. d. deutsch. Tiefsee Exp., B. 2, Tiel 2, p. 220–548, Taf. 35–54.

Kofoid, C. A.

1907 a. Reports on the Scientific Results of the Expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross," from October, 1904, to March, 1905, Lieut.-Commander L. M. Garrett, U. S. N., commanding. IX. New species of Dinoflagellates. Bull. Mus. Comp. Zoöl., Vol. 50, p. 163–207, pls. 1–17.

1907 b. The plates of Ceratium with a note on the unity of the genus. Zool. Anz., Bd. 32, p. 177–183, 8 figs.

1907 c. Dinoflagellata of the San Diego region. III. Description of new species. Univ. Calif. Publ. Zool., Vol. 3, p. 299–340, pls. 22–33.

1908. Exuviation, autotomy, and regeneration in Ceratium. Univ. Calif. Publ. Zool., Vol. 4, p. 345–386, 33 figs. in text.

Küster, Ernst.

1908. Eine kultivierbare Peridinee. Arch. f. Protistenkunde, Bd. 2, p. 357–368, 4 figs. im Text.

Lauterborn, R.

1895. Protozoenstudien I. Kern und Zelthulung von *Ceratium hirundinella* O. F. M. Zeitsch. f. wiss. Zool., Bd. 59, p. 167–190, pls. 12–13.

Lemmermann, E.

1899. Ergebnisse einer Reise nach dem Pacific. (H. Schauinsland, 1896–1897.) Planktonalgen. Abh. Ver. Bremen, Bd. 16, p. 313–398, pls. 1–3.

Lohmann, H.

1908. Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. Wiss. Meeres untersuch. Abth. Kiel., N. F., Bd. 10, p. 129–370, Taf. 1–17. Tabeln A und B und 22 Textfiguren.

MacDougal, D. T., Vail, A. M., and Shull, G. H.

1907. Mutations, variations, and relationships of the Oenotheras. Publ. Carnegie Inst. No. 81. 92 pp., 22 pls., 73 figs. in text.

Michaelis, G. U.

1830. Ueber das Leuchten der Ostsee nach eigenen Beobachtungen, nebst einigen Bemerkungen uber diese Erscheinung in andern Meeren. Hamburg. 52 pp., 2 pls.

Minkiewitsch, R.

1900. Sur la biologie des Protozoaires de la Mer Noire. Bull. Lab. Biol. St. Petersb., Vol. 4, No. 3, p. 7–11, pl. 1. In Russian.

Müller, O.

1903. Sprungweise Mutation bei Melosireen. Ber. deutsch. bot. Ges., Bd. 21, p. 326–333, Taf. 17.

1904. Berichte uber die botanischen Ergebnisse der Nyassa-See und Kinga-Gebirgs-Expedition der Hermann- und Elise-geb. Heckmann-Wentzel-Stiftung. VII. Bacillariaceen aus dem Nyassalande und einigen benachbarten Gebieten. Engler's Bot. Jahrb., Bd. 34, p. 256–301, Taf. 3–4.

1906. Pleomorphismus. Auxosporen und Danersporen bei Melosira-Arten. Jahrb. f. wiss. Bot., Bd. 34, p. 49–87, Taf. 1–2.

Murray, John, and Tizard, Thos. H.

1882. Exploration of the Faroes Channel during the Summer of 1880 in H. M.'s hired ship "Knight Errant." Proc. Roy. Soc., Edinburgh, Vol. 11, p. 638–677.

Nathanson, A.

1906. Ueber die Bedeutung vertikaler Wasserbewegungen fur die Produktion des Planktons im Meere. Abh. Sachs. Ges., Bd. 29, p. 355–433. Mit 1 Karte.

Ostenfield, C. H.

1903. Phytoplankton from the sea around the Faeröes. Botany of the Faeröes, Vol. 2, p. 558–611, figs. 119–144.

Ostwald, W.

1903. Theoretische Planktonstudien. I. Ueber die Beziehungen des Planktons zu dem Gehalte des Wassers an gelosten Stoffen. Zool. Jahrb. Syst., Bd. 18, 62 pp., 4 Taf.

Paulsen, O.

1908. Peridiniales. Nordisches Plankton von Brandt u. Apstein. XVIII. p. 1–124. Mit 155 Textfiguren.

Pavillard, J.

1905. Recherches sur la flore pélagique (phytoplankton) de l'étang de Thau. Travail de l'Institut Bot. de l'Université de Montpellier et de la Stat. Zool. de Cette, Serie Mixte, Mem. No. 2, 116 pp., 1 carte, 3 pls.

Pouchet, G.

1883. Contribution a l'histoire des cilio-flagelles. J. Anat. Physiol., T. 19, p. 399–455, pls. 18–21, 50 figs in text.

1885. Nouvelle contribution à l'histoire des Péridiniens marins. J. Anat. Physiol., T. 21, p. 28–88, pls. 2–4.

1894. Histoire naturelle, in Voyage de "la Manche" l'ile Jan Mayen et au Spitzberg. Jouillet-Aout, 1892. Nouv. Arch. Miss. Sci., T. 5, p. 154–217, pl. 22.

Ritter, W. E.

1907. Syllabus of a course of lectures on organic evolution. San Diego. 20 pp.

Schott, G.

1905. Uebersicht der Meeresstromung und Dampferwege in einer Weltkarte. Ann. Hydrog. u. Mar. Meteor., Bd. 33, p. 397–407, Taf. 13.

Schutt, F.

1893. Das Pflanzenleben der Hochsee. 75 pp., 35 figs. im Text. 1 Karte Kiel und Leipzig. Also in Ergebn. Plankton Exped., Bd. 1 A, p. 243–314, figs. 57–92.

1895. Die Peridineen der Plankton-Expedition. Ergebn Plankton-Expedition, Bd. 4, M. a. A., 170 pp., 27 pls.

1896. Peridiniales. Engler u. Prantl. Nat. Pflanzenfamilien, Teil I, Abt. 1, 30 pp., 43 figs.

Tower, W. L.
1906. An investigation of evolution in chrysomelid beetles of the genus Leptinotarsa. Publ. Carnegie Inst., No. 48. 320 pp., 31 Text figures, 30 pls.

West, W., and G. S.
1903. Scottish freshwater plankton, No. 1. Journ. Linnean Society, London. (Botany.) Vol. 35, p. 519–556.

Zederbauer, I. E.
1904. Geschlechtliche und ungeschlechtliche Fortpflanzung von *Ceratium hirundinella.* Ber. deutsch. Bot. Ges., Berlin., Bd. 22, p. 1–8, pl. 1.

Zumstein, H.
1900. Zur Morphologie und Physiologie der *Euglena gracilis* Klebs. Jahrb. f. wiss. Bot., Bd. 34, p. 149–198, Taf. 6.