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## I. FACTORS IN THE EVOLUTION OF THE PELAGIC CILIATA, THE TINTINNOINEA

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The façade of the Prussian Marine Biological Station on the Island of Heligoland bears in enduring mosaic this inscription from Goethe's *Faust*:

Alles ist aus dem Wasser entsprungen,  
 Alles wird durch das Wasser erhalten.  
 Ocean gönn uns Dein ewiges Walten.

As biochemists, physiologists, botanists, and zoölogists, each of us might wish, in the interests of scientific accuracy, to reduce the sweeping comprehensiveness of the first two propositions of this motto by some limiting modifications. On the other hand, as biologists we all gladly recognize the imperial sway of the sea and join the procession seaward. We shall find ourselves in illustrious company, with Aristotle, with Darwin and Huxley, with Balfour and Van Beneden, with Haeckel and Dohrn, with Agassiz and Brooks, with Murray and Hjort, and with Whitman and Jordan.

All these and many other inquiring minds have been inducted into the charm and mystery of life in the sea and have sought the solutions of its many inviting problems in the study of its varied and manifold organic types and of their marvelously adaptive structures and functions.

It is fitting, perhaps it is even inevitable, that biologists should thus turn to the sea and that they should find there both adequate material for investigation and the intellectual satisfaction resulting from its analysis. The reasons for this are many and varied. Some are obvious, others are too subtle for analysis, too little comprehended for statement, or too elusive for expression. Perhaps an enumeration of some of the more obvious ones will serve to introduce my theme for this evening.

The sea is the oldest ecologic niche on the globe, provided the hypothesis of the permanence of the ocean basins is correct. Its changes in temperature and salinity, if any considerable ones have occurred since Pre-Cambrian times, must have been slight and in any event very gradually made. Time for the progress of evolution has thus been available longer in the sea than on land and certain important environing factors have remained more uniform in the sea than on the land.

The sea is also the largest arena on the globe in which the struggle for existence has been enacted and life in many of its varied forms has waxed and waned. Mere size of the environment in itself has, it is true, little direct biological significance to the individual, but indirectly it makes possible the increase and maintenance of great numbers of individuals in

which evolution proceeds and thus provides the quantitative background for diversification of the race.

The sea also has always presented a wide geographical range from equatorial to polar conditions, thus affording the complete range in temperature and in light. There has also been the great vertical range in depth, with its extreme conditions of temperature, light, and pressure. Not the least important among the geographical factors operating in the evolution of life is the seashore, with its tidal amplitude and its alternating contrasts of exposure and submergence, its mechanical shocks of breakers and of eroding currents. The varied forms of substrate from the beach to the edge of the continental shelf afford the stage for the evolution of attached and burrowing forms of life. The tributary rivers with their burdens of silt, their diluent effects upon the salinity, and their varying contributions of chemical substances in solution, present new problems for adaptation and a grouping of environmental factors different from those of the land, as do also the land-locked brine-pools with their increasing salinity.

The sea also presents an aspect in all of these major factors of temperature, light, pressure, salinity, movement, and substrate, of gradual and regular change as over against the more abrupt and more strikingly irregular changes so characteristic of the environments of life upon land. Temperatures change slowly from latitude to latitude, from surface downward, and between noon and midnight. There are few submarine forests to interrupt the penetration of light, and pressure accumulates downward with little interruption by other factors as compared with that due to atmospheric conditions on land. The movements of the water, except at the immediate surface and in the breakers and tidal rips, are leisurely as compared with those of streams on land.

In consonance with these equable aspects of the marine environment we find the life of the sea delicately attuned to small environmental changes. Vertical migrations adjust the vertical distribution to changing conditions of illumination. Changes in the sizes and content of hydrostatic vacuoles, and adaptive modifications in the relative surfaces of the floating organisms of the plankton make adjustments in adaptation to the varying problems of flotation that arise with modifications in viscosity of the water following upon changes in temperature.

The well-known delicacy of pelagic organisms and the consequent difficulties of keeping them under laboratory conditions illustrate practically the narrow limits of this attunement of pelagic life to its environment as compared with that of the littoral fauna. To the pelagic organisms the shock of such sudden changes is unknown, but to the inhabitants of the littoral zone, and especially of the land, adaptation to extreme changes is the secret of survival.

The sea has been the stage whereon has been enacted the greater part of the drama of emergent animal life. The arthropods and higher vertebrates are the only outstanding exceptions to this limitation, and even these contain striking examples of elaborate adaptive flares among groups which have reverted to the marine environment, as for example seals, whales, petrels, and albatrosses.

The fundamental patterns of animal structure as represented in the main phyla have all had their origin in the sea. Some greatly diversified groups such as Radiolaria, Dinoflagellata, Foraminifera, sponges, corals, siphonophores, Copepoda, Trilobita, Brachiopoda, Cephalopoda, and Ophiuroidea have gone through their evolutionary flare in the sea.

The investigator may therefore approach the sea with confidence that it will throw light upon problems of the evolution of life.

It will be of interest to turn our attention this evening to a survey of the results of this evolutionary process in a single group of typical pelagic organisms, the Tintinnoinea, pelagic marine ciliates, which have had almost their entire evolution in the sea. These animals belong to the Protozoa, the most primitive phylum, and also belong to the more highly differentiated *Heterotrichida*.

This suborder Tintinnoinea is represented in a revision just completed (see Kofoid and Campbell, 1929) by 12 families, 51 genera, and 705 species. Of these genera only 3 have entered the fresh-water habitat, and only 8 valid species have been recognized therein. Their main area of evolution has thus been the sea. Not only is this true, but they have evolved principally in the high seas, only about ten per cent of the species appearing to be restricted to coastal regions. They therefore represent typical pelagic evolutionary results.

The material upon which our presentation is based is that of the Agassiz (1906) Expedition to the Eastern Tropical Pacific of 1904-1905 of the U.S.S. "Albatross," supplemented by the plankton collections of the same vessel in San Francisco Bay and in other Californian and Alaskan waters, by my own collections in a traverse of the North Pacific and Indian Oceans from Seattle to Colombo, Ceylon, and by the plankton collections off San Diego by the Scripps Institution.

A systematic revision of the entire group has recently been completed (Kofoid and Campbell, 1929) in the course of which the entire literature has been examined and the all-too-often conflicting and complicated systematic accounts of genera and species have been put in order. A better understanding of the mode of formation of the lorica or house in which the animal lives (see Campbell, 1926, 1927) which is the basis of classification, has made possible a clearer differentiation between modifications due to excess or lack of lorica-forming substance and those structural features of genetic significance.

Owing to previous lack of precision in generic distinctions and to varying concepts of species limits, a bewildering permutation of generic and subgeneric allocations of various species has often been made by different or even by the same investigator. One species may appear in five or six different genera, and not only trinomial but even quadrimomial usages in nomenclature have emerged.

Our own extensive material has made possible a clearer understanding of generic characters and of specific limits. In the light of these we have revised the entire group, combining under one specific name mere form variants of the species resulting from the amount of material available for the lorica or arising from the effect of temperature upon size. We have given specific status to all categories having valid structural characteristics, eliminating wholly all varieties and subspecies.

The absence of sharply defined barriers and the cosmopolitan, or, perhaps one should say, cosmo-thalassic, distribution of pelagic organisms in all seas of comparable environmental nature make the recognition of geographical races or subspecies so arbitrary a procedure within the Tintinnoinea that we exclude their recognition entirely. For example, *Tintinnus birictus* in the warmer parts of its area of distribution has smaller loricae than those in the colder parts, but these extremes in size intergrade. It is also possible that there may be an intergradation vertically in size between loricae formed in the upper and warmer and those formed in the deeper and colder levels of distribution.

In order that comparisons both within and between species may be made, many thousands of drawings have been prepared to provide a basis for measurement and analysis of both inter- and intra-specific differences. All species in all genera have also been drawn to the same scale of magnification and grouped together in order to bring out the interrelations of species within the genus, and to represent visibly the known results of speciation within each genus.

The results are published by the permission of Hon. Henry O'Malley, United States Commissioner of Fisheries, and of Dr. Thomas Barbour, Curator of the Museum of Comparative Zoölogy of Harvard University. Acknowledgments are made to the Board of Research of the University of California for grants in aid.

The Tintinnoinea are trumpet-shaped *Heterotrichida* with a leiotropic, spiral membranelle zone of highly developed cilia used in locomotion, in capture and selection of food, and in shaping up the secretion which forms the lorica.

The accompanying figure exhibits the details of structure. Note should be made of the relatively large size of these motor organelles and of their location and reach with reference to the size and structure of the lorica or house.

Since the entire classification of the Tintinnoinea is based upon the structure of the lorica, its mode of formation is of interest. No account of the actual formation of an entire lorica has been published, and only scattered observations on parts of the process are available. These leave many lacunae in our knowledge and we are obliged to build up our picture of the process from incomplete data.

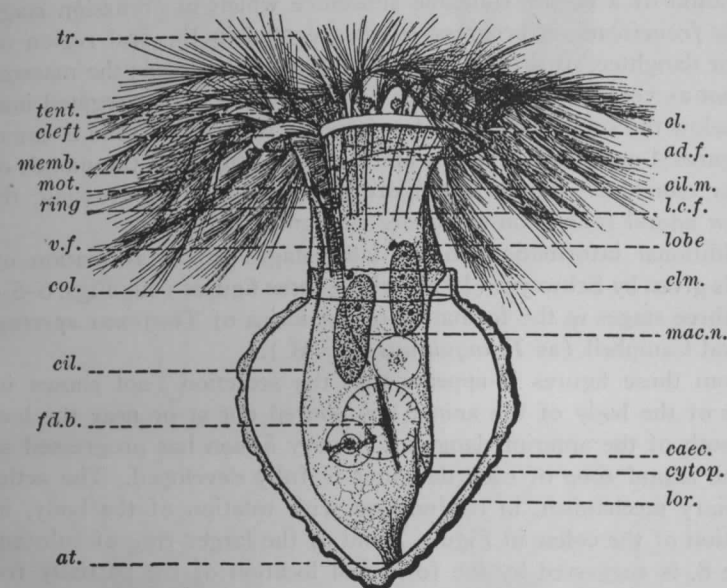


FIG. 1.—Semi-diagrammatic figure of *Tintinnopsis* showing the general morphology of the cytostome. *ad.f.*, adoral fiber of the neuromotor apparatus; *at.*, attachment to the lorica; *caec.*, caecum; *cil.*, somatic cilia; *cil.m.*, ciliary membrane; *cl.*, peristomal collar; *clm.*, column; *cleft*, cleft in the peristomal margin; *col.*, lorical collar; *cytop.*, cytopyge; *fd.b.*, food body; *lobe*, lateral column lobe used in shell-building; *lor.*, outlines of the lorica; *l.c.f.*, lateral ciliary field; *mac.n.*, macronucleus; *memb.*, membranelle; *mot.*, neuromotorium; *ring*, circumoesophageal ring; *tent.*, tentaculoid; *tr.*, trichocysts; *v.f.*, ventral fiber of the neuromotor apparatus.  $\times 850$ . After Campbell (1926, p. 189, Fig. B).

All Tintinnoinea build a lorica or house in which they live permanently, although they will detach their adhesive stalk and leave the lorica in adverse conditions. The available evidence indicates that a new lorica is formed only at binary fission and only for the anterior daughter, the old house being retained by the posterior daughter.

The lorica is formed from a substance secreted by the parent and stored up in granules in the cytoplasm in its anterior end near the mouth. This substance is extruded from the mouth of the anterior daughter in the late stages of plasmotomy following upon the divisions of the macro- and



miconuclei and the formation of a new adoral zone for the posterior daughter. Possibly this is preceded by the division of the neuromotorium and the posterior migration of its posterior moiety to the side of the parent body. About this as a center the new adoral zone forms laterally and later becomes the anterior end of the posterior daughter.

The accompanying figures (Figs. 2-5) show the accumulation and localization of a deeply stainable substance which in pre-fission stages of *Favella franciscana* is progressively segregated in the oral region of the anterior daughter. In Figure 2 the secretion is dispersed; the macronuclei have not as yet divided. In Figure 3 the granules are segregated immediately below the surface on the side where the new adoral zone is emerging. In Figures 4 and 5 the granules are massed adjacent to the mouth of the anterior daughter. In the last figure plasmotomy is progressing, though the new adoral zone is on the under side and not figured.

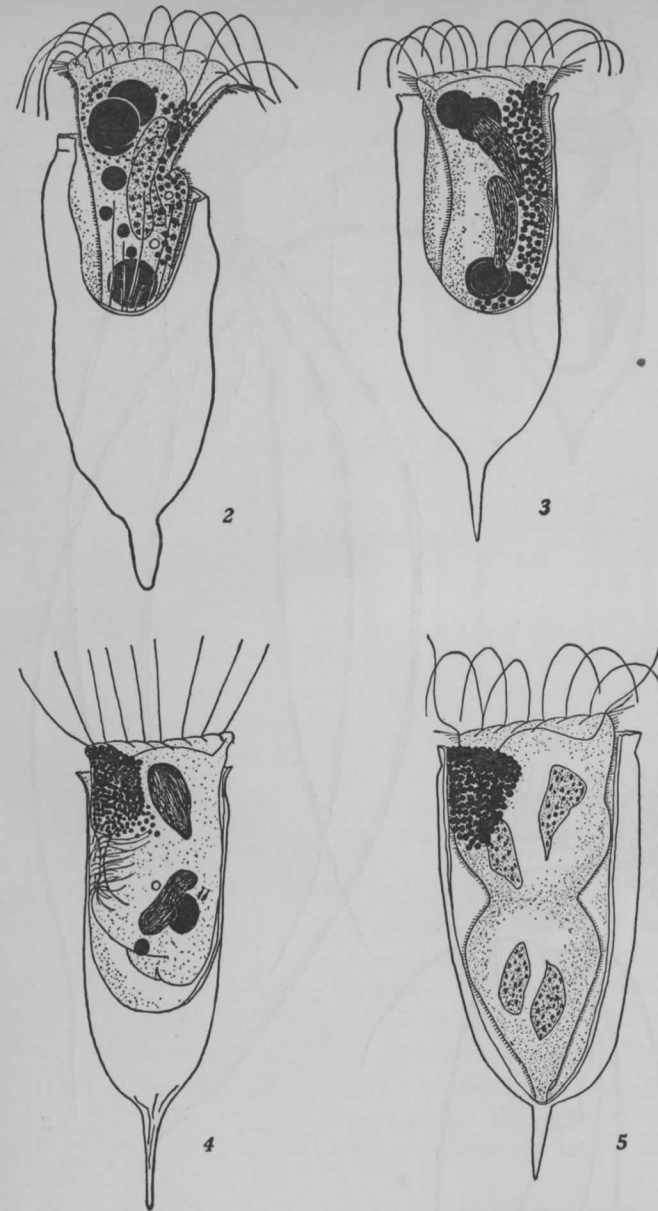
Additional information on the later stages in the formation of the lorica is given by Schweyer (1909) whose three figures (our Figs. 6-8, p. 8) show three stages in the formation of the lorica of *Tintinnus apertus* Koid and Campbell (as *T. inquilinus* O.F.M.).

From these figures it appears that the secretion (not shown in the figures of the body of the animal) is poured out at or near the level of the mouth of the anterior daughter. Binary fission has progressed so far that the adoral zone of each daughter is fully developed. The action of the ciliary mechanism, in conjunction with rotation of the body, in the formation of the collar in Figure 7 and of the larger ring of substance in Figure 8, is suggested by the form and location of the partially formed lorica. In Figure 6 the secretion immediately surrounds the anterior adoral zone as a cap or lies in concentric shell-like fragments above as though molded by the successive rotations of the adoral zone and hardened *in situ*. It is significant that even these fragmentary and imperfect formations have taken on the same alveolar structure as that of the parent lorica.

From the imperfect knowledge of the actual process of the formation of the lorica and from the comparative study of the various patterns of loricae formed in the Tintinnoinea we can arrive at certain conclusions regarding the lorica and its systematic evolutionary significance.

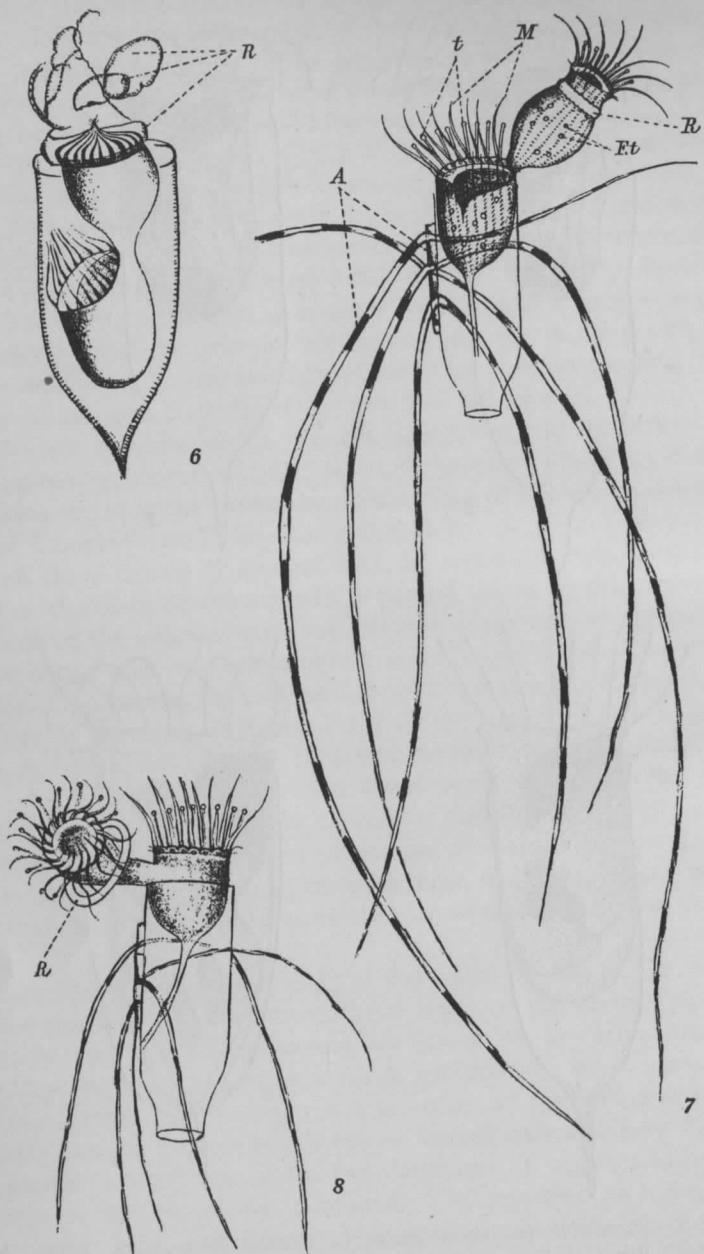
The substance of the lorica is a secretion of the parent animal prior to binary fission. Loricae are therefore formed only at binary fission and only for the anterior one of the two daughters. It appears to be formed but once in the life of the individual. The secretion of lorica-forming substance has been observed only in animals in which the preparations for binary fission are also apparent.

The substance is chitin, or chitinoid in nature, swells up rapidly on contact with sea water, and hardens quickly with the formation of pri-



FIGS. 2-5.—Successive pre-fission stages in *Favella franciscana*  $\times 200$ . After Campbell (1927, Fig. C, 1, 5, 6, and 7).





FIGS. 6-8.—Binary fission and formation of the lorica in *Tintinnus apertus* Kofoid and Campbell. After Schweyer (1909, Pl. 10, Figs. 4, 6, and 8). The lorica in Figs. 7 and 8 is attached to the frustule of a pelagic diatom *Chaetoceros*. *A*, bristle of *Chaetoceros*; *Ft.*, fat droplet; *M*, membranelle; *R*, ring, or other anlage of lorica; *t*, tentacle.

primary, secondary, and tertiary reticular or alveolar structure of varying degrees of fineness in the different genera. There is often formed a distinct outer and inner lamella between which the secondary and tertiary alveoles are arranged in prismatic fashion.

There are very great differences in both the coarser and finer patterning of the substance which suggest a wide range of chemical and physical properties of the lorica-forming substances among the different genera. Thus in *Tintinnidium* (Fig. 29, 4\*) and in *Tintinnopsis* (Fig. 12) the

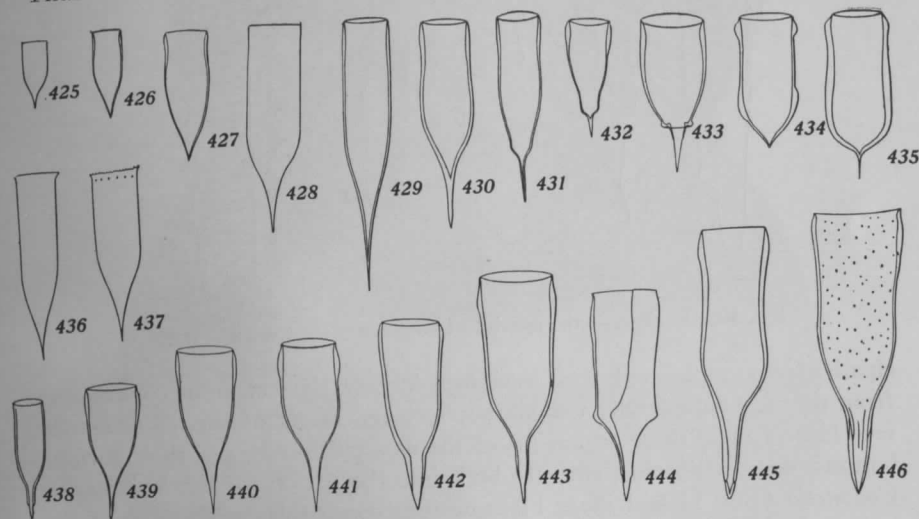


FIG. 9.—Loricae of the species of *Parundella*. 425-446.  $\times 200$ . (The numbers, such as 425-446, in this and other figures, are those of Kofoid and Campbell, 1929.)

lorica often carries a ragged coat of surplus blobs of alveolar substance and the shape in patterning is more or less chaotic. In *Brandtiella*, on the other hand, there are two regions, an inner one of definite shape and an outer more amorphous mantle. In genera such as *Parundella* (Fig. 9) the wall is homogeneous, bilamellate, translucent, and shows scarcely any trace of visible alveolar structure. In *Climacocylis* (Fig. 10, p. 10) the secondary alveoles are very coarse, rather loosely aggregated, very delicate in consistency, and extraordinarily transparent. The physical nature of the substance of the lorica appears to be a generic or family character, in some instances at least.

The lorica is not always entirely composed of the secreted substance but may incorporate foreign objects within its substance as an enveloping matrix. These seem to be derived from two sources, primarily and prin-

\* See p. 35. This number and others thus cited are as in Kofoid and Campbell, 1929, Literature Cited, p. 38.

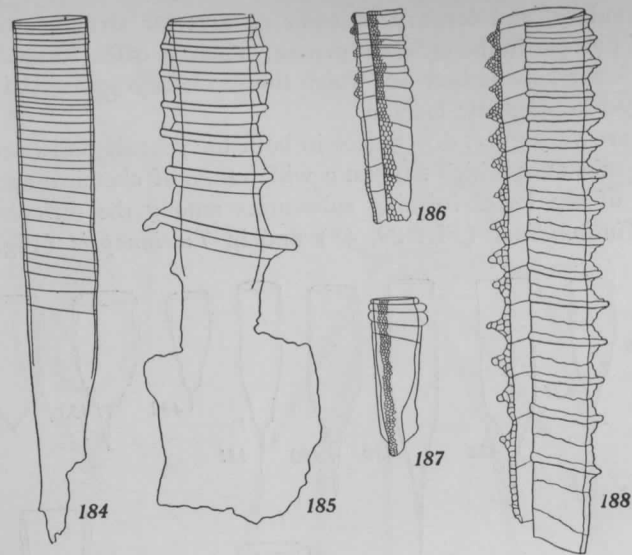


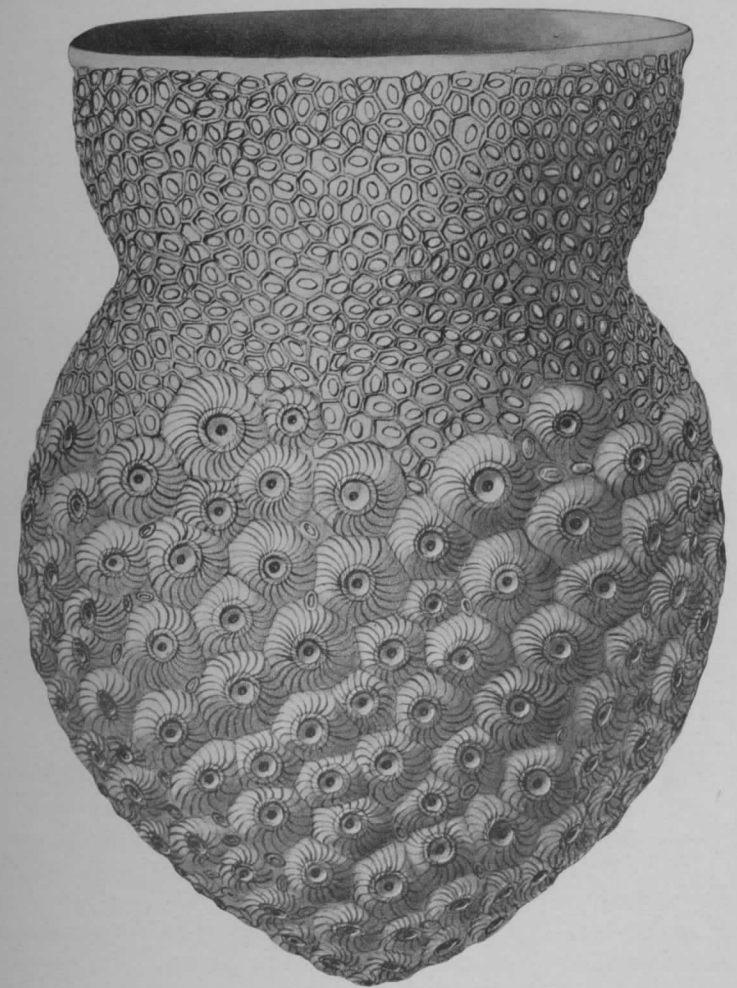
FIG. 10.—Loricae of the species of *Climacocylis*. 184–188.  $\times 200$ .

cipally from undigested fecal residues, largely the calcareous coccoliths from the flagellate family Coccolithophoridae. Many of the Tintinnoinea feed largely upon these organisms of the nannoplankton, and their curious buttons, disks, ellipsoids, etc., are built into the pattern of the lorica as in *Codonella* (Fig. 11 and Plate I) in designs comparable with those of the houses of fresh-water rhizopods which utilize the frustules of diatoms in their houses, except that the coccoliths are even more distinctly built into the wall of the lorica than are the diatoms in that of the rhizopod house.

In other cases, especially in fresh-water and neritic species growing in silt-laden waters, the lorica tends to agglomerate to itself, possibly only during its formative period, not only blobs of lorica substance but also minute particles of foreign matter, which assist in giving the ragged appearance to the loricae of such a neritic genus as *Tintinnopsis* (Fig. 12, p. 12). The extent to which fecal residues and foreign agglomerates are utilized in the formation of the lorica and the manner in which they are utilized also appears to be something of a generic character. Genera with homogeneous substance, such as *Proplectella* (Fig. 13, p. 13) and *Undella* (Fig. 14, p. 13) use neither coccoliths nor agglomerates, while genera with patterned loricae such as *Codonella* (Fig. 11) and *Dictyocysta* (Fig. 15, p. 14) contain species which habitually make extensive use of coccoliths in the wall of the lorica.

The lorica of each species is the resultant of two factors, namely, the chemical and physical nature of the secreted substance and the stereotyped

## PLATE I



Lorica of *Codonella acuta* Kofoid and Campbell, from Station 4666 in the Peruvian Current.  $\times 1440$ .

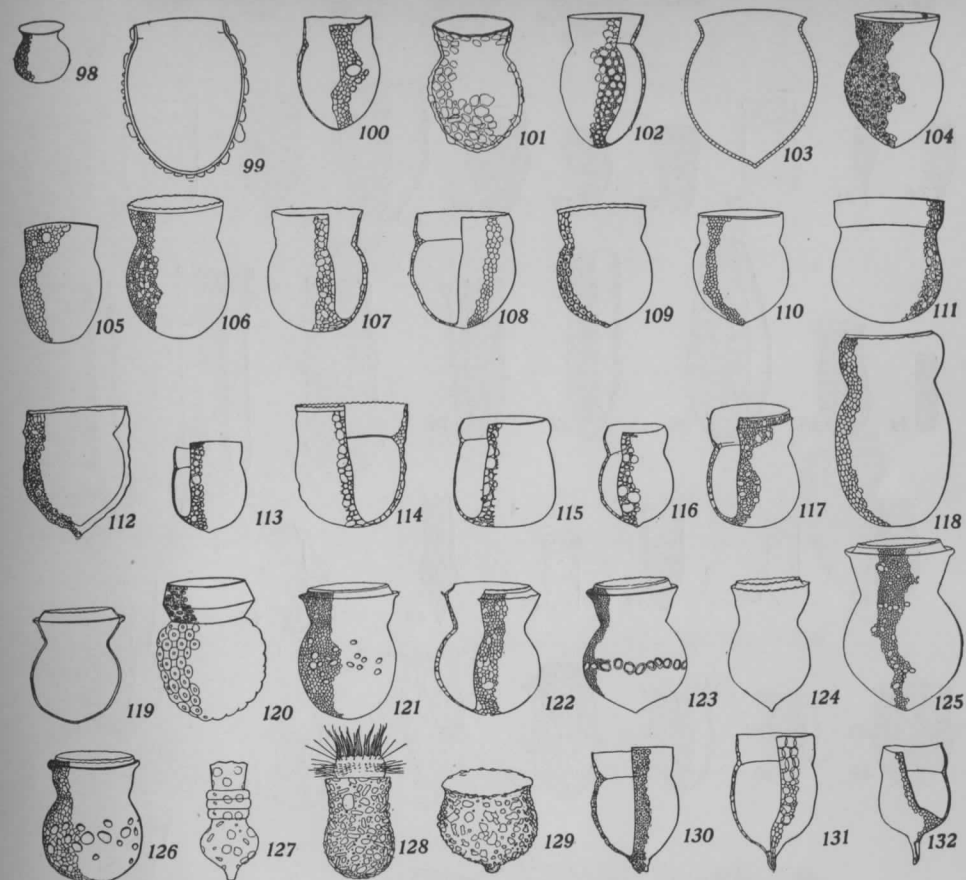


FIG. 11.—Loricae of the species of *Codonella*. 98-132.  $\times 200$ .

behavior of the organism in the very brief period of the molding and hardening of this substance in the newly forming lorica.

This brings us to the most difficult and perplexing part of the problem in the analysis of the formation of the lorica, namely: Is the new lorica formed in entirety by the anterior daughter which occupies it, or do both daughters share in this function? If the former supposition is true, how can the anteriorly located membranelles shape up the elaborately differentiated aboral end of the lorica into a pedicel, knob, skirt, and lance in such species as those of *Xystonellopsis* (Fig. 16, p. 15), and how are spiral striae which cover the entire lorica developed? If the latter is the case, we are confronted by the extraordinary fact that the most conspicuous character of the species, namely, the patterning of the lorica, is the result of the stereotyped behavior of the *two* daughter individuals. Moreover, this



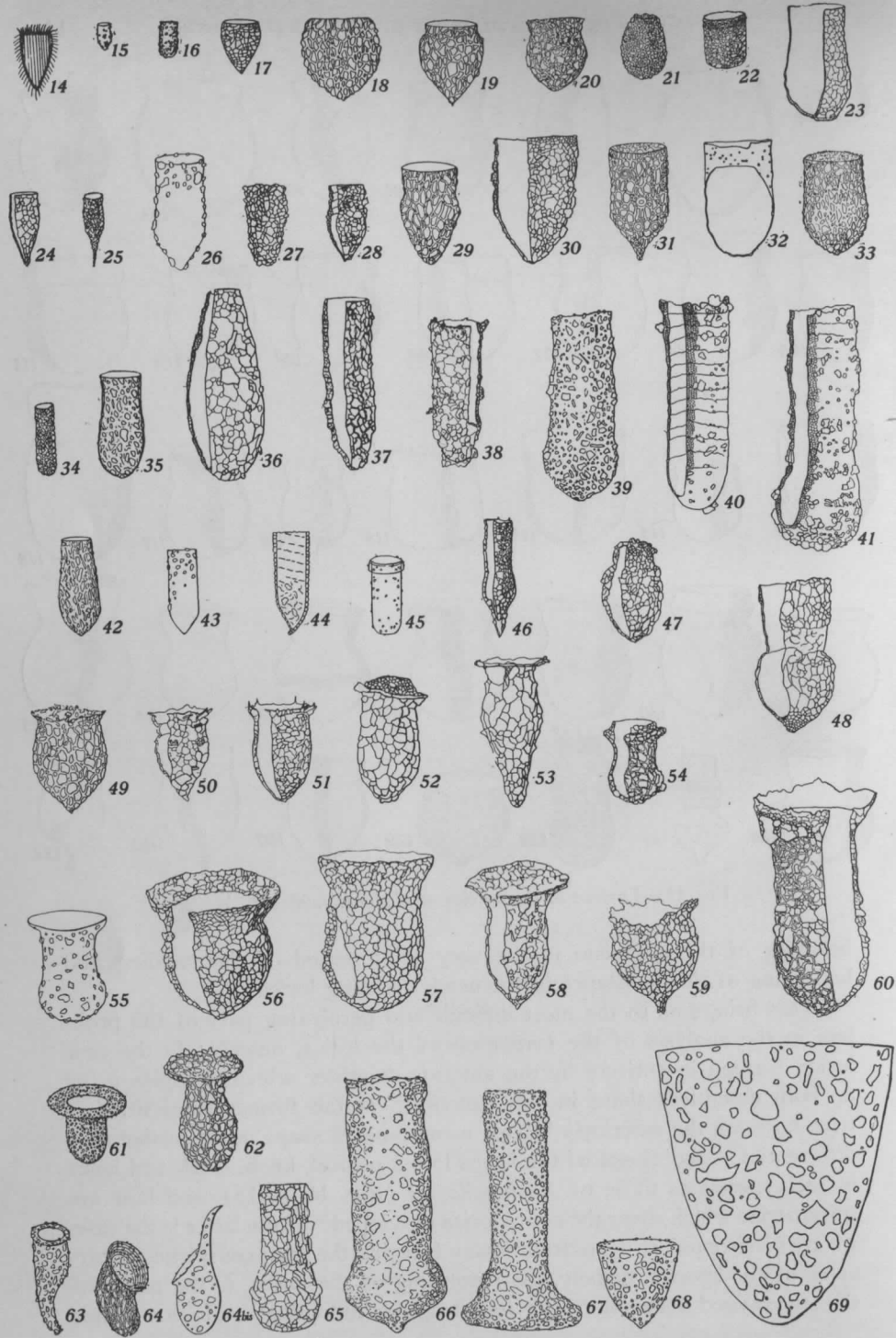


FIG. 12.—Loricae of species of *Tintinnopsis*. 14-69.  $\times 200$ .

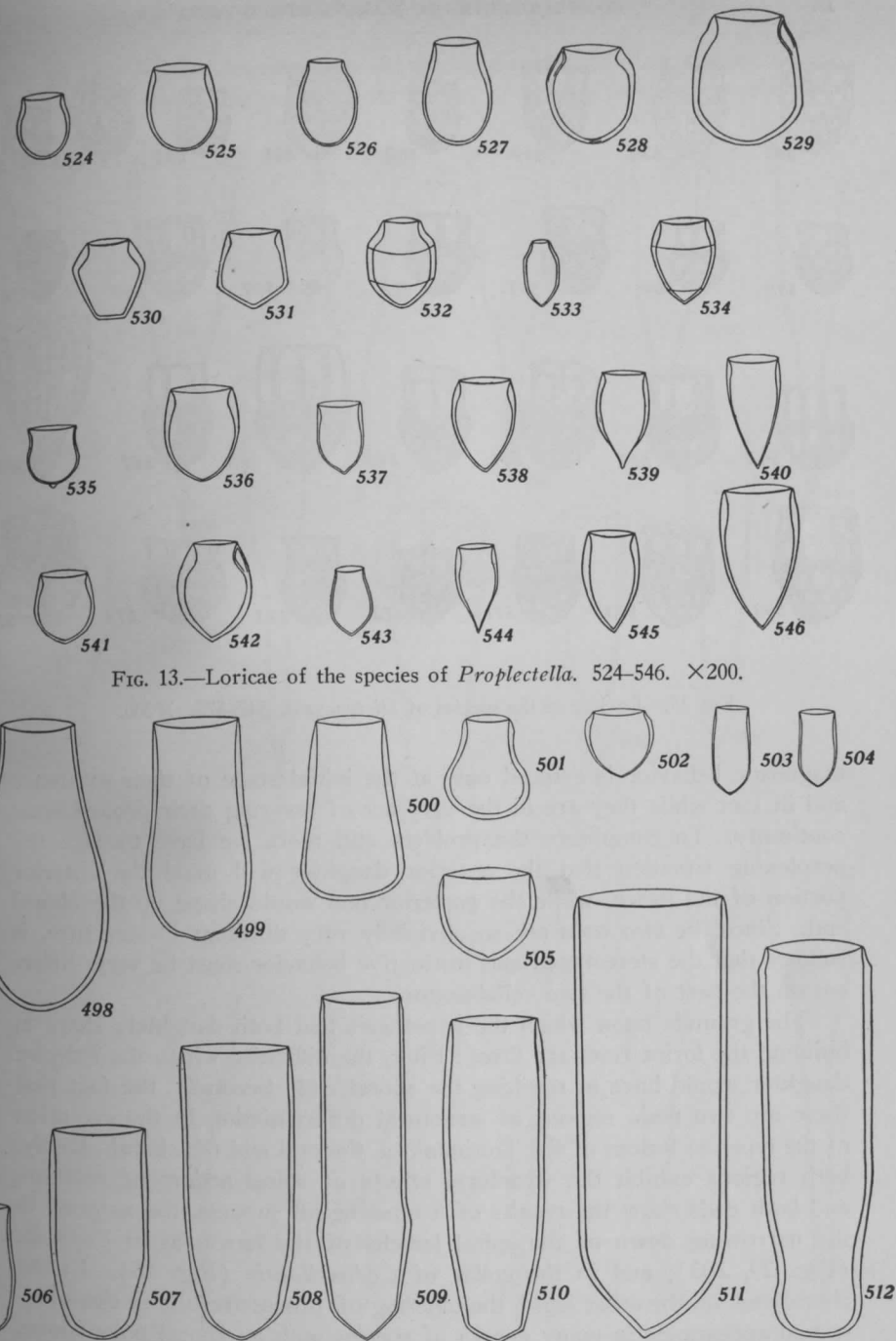


FIG. 13.—Loricae of the species of *Proplectella*. 524-546.  $\times 200$ .

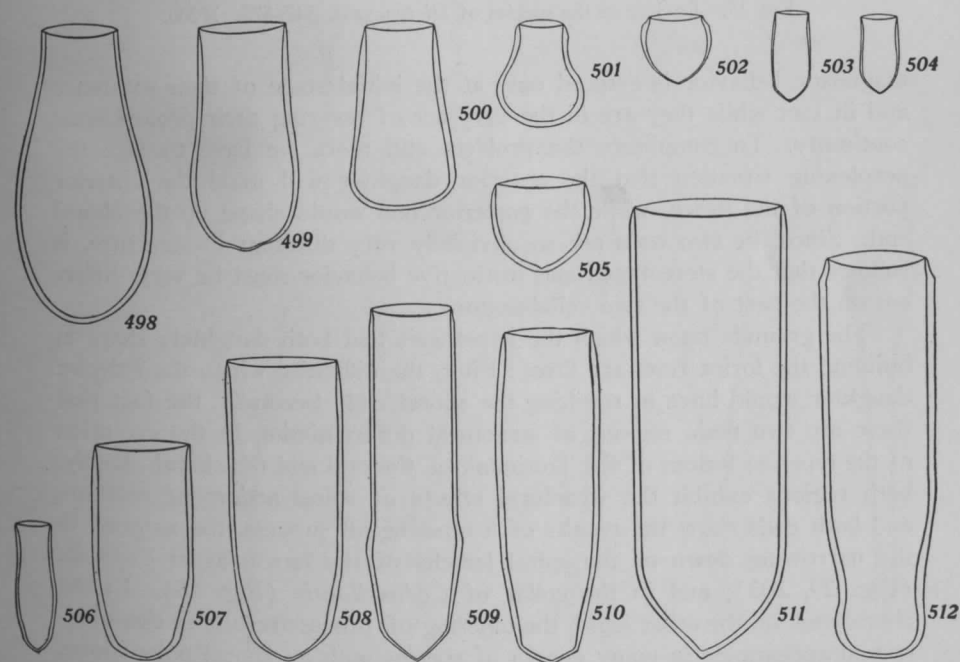


FIG. 14.—Loricae of the species of *Undella*. 498-512.  $\times 200$ .

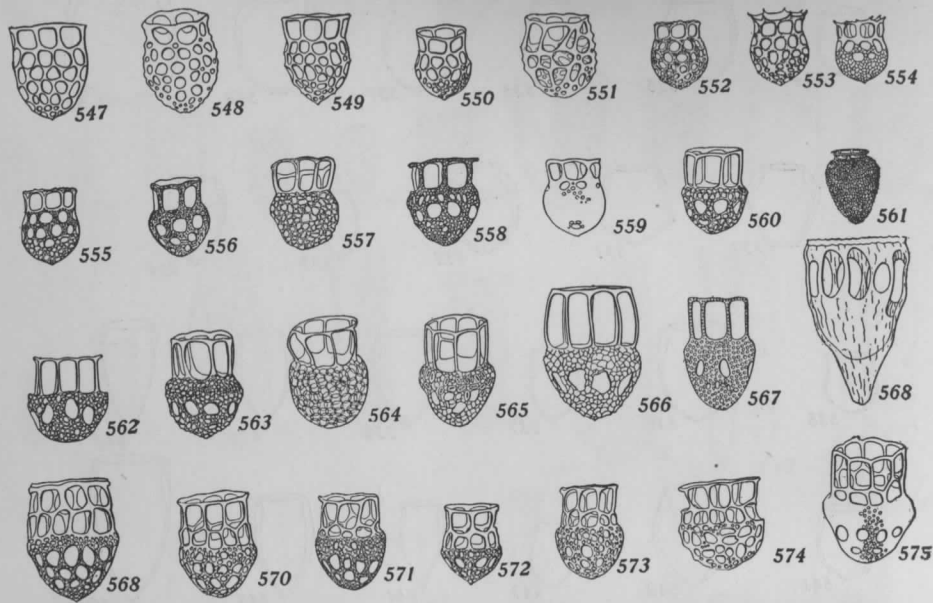


FIG. 15.—Loricae of the species of *Dictyocysta*. 547–575.  $\times 200$ .

diagnostic behavior is evinced only at the initial stage of their existence and in fact while they are in the very act of severing their protoplasmic continuity. To complicate the problem still more we have to face the perplexing situation that the anterior daughter will mold the anterior portion of the lorica, while the posterior one would shape up the aboral end. Since the two ends are so obviously very different in structure, it follows that the stereotyped and instinctive behavior must be very different on the part of the two collaborators.

The grounds upon which the hypothesis that both daughters share in building the lorica rests are three: First, the difficulty which the anterior daughter would have in reaching the aboral end. Secondly, the fact that there are two main regions of structural differentiation in the evolution of the types of loricae of the Tintinnoinea, the oral and the aboral. Lastly, both regions exhibit the structural effects of spiral action, of rotation, and both ends show the results of a tapering-off process, the anterior in the narrowing down of the spiral lamella of the lorica, as in *Coxiella* (Fig. 29, 203), and in the collar of *Codonellopsis* (Fig. 18). In the aboral end, on the other hand, the tapering-off process results in the wide-spread appearance in many genera of species with an aboral point, horn, or lance, as in *Xystonellopsis* (Fig. 16).

In this connection attention should be directed to observations on the behavior of the living animal in its house. It is attached by a more or less

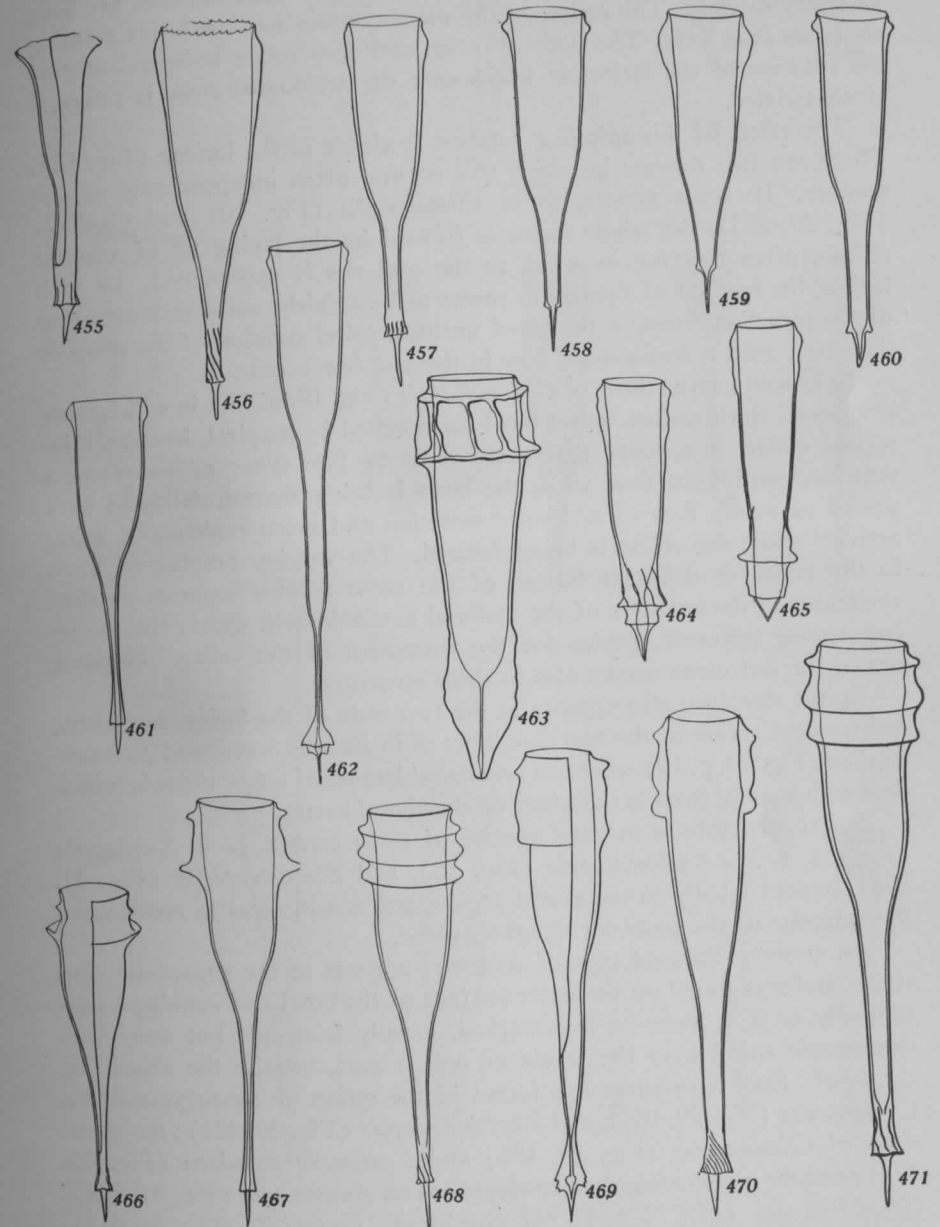


FIG. 16.—Loricae of the species of *Xystonellopsis*. 455–471.  $\times 200$ .

slender pedicel with an adhesive, spreading, terminal foot adherent to the bottom or side of the lorica. The body can be greatly elongated and extended beyond the oral rim of the lorica. The membranelles are long and very flexible. The action of the membranelles sets the lorica rotating about its long axis. The body also can and does rotate independently of the rotation of the lorica, in which case the attenuated stalk is progressively twisted.

The effect of this spiraling rotation is visible in the loricae (Fig. 17). There are two regions in which this occurs, often independently of one another. In some genera, as in *Climacocylis* (Fig. 10) and *Coxiella* (Fig. 29, 203), the whole lorica is formed by the laying up of a spiral ribbon, often tapering in width as the oral rim is approached. In such loricae the method of formation seems to be a fairly uniform outpouring of the secretion during a period of uniform spiral rotation of the anterior daughter, with a diminishing flow in the last few turns.

In loricae such as those of *Codonellopsis* (Fig. 18, p. 18), in which there is a dense, thick-walled, spiral bowl surmounted by a spiral, hyaline, thin-walled collar, it appears that there must be two types of secretion, a massive, continuous flow while the bowl is being shaped, followed by a period of scanty flow of a thinner secretion and more evidence of spiral activity while the collar is being formed. The varying number of turns in the collar in different loricae of the same species suggests marked variations in the amounts of the material available both within the species and among different species for the formation of the collar. Thinning out of the last turns occurs also in these structures.

Spiral structure also appears at the two ends of the lorica, suggesting independent action of the two daughters as in *Favella brevis* and *F. helgolandica* (Fig. 19, p. 19) where an oral spiral lamina of a few turns is coincident with a spiral twist to the wings on the aboral horn.

Spiral structure is in most species of some genera, as in *Salpingella* (Fig. 31, 673), *Xystonellopsis* (Fig. 16), and *Steenstrupiella* (Fig. 31, 593), limited wholly to the aboral region, and would seem to result from the behavior of the posterior daughter alone.

An entirely different type of structure appears in the superficial ribs, striae, and fins found on the outer surface of the bowl and running longitudinally or in a more or less marked, usually leiotropic but sometimes dextrotropic spiral over the whole or only a part, usually the aboral, of the bowl. Such structures are found in the striae of *Protocymatocylis*, *Cymatocylis* (Fig. 29, 188), and *Rhabdonellopsis* (Fig. 30, 421); the spiral shelf of *Climacocylis* (Fig. 29, 188) and *Xystonella scandens* (Fig. 30, 454); and the more or less fin-like elevations on *Amphorella* (Fig. 31, 592), *Amphorellopsis* (Fig. 31, 594), *Odontophorella*, *Dadayiella* (Fig. 31, 613), *Ormosella* (Fig. 31, 633), *Stelidiella* (Fig. 31, 627), *Daturella* (Fig. 31,

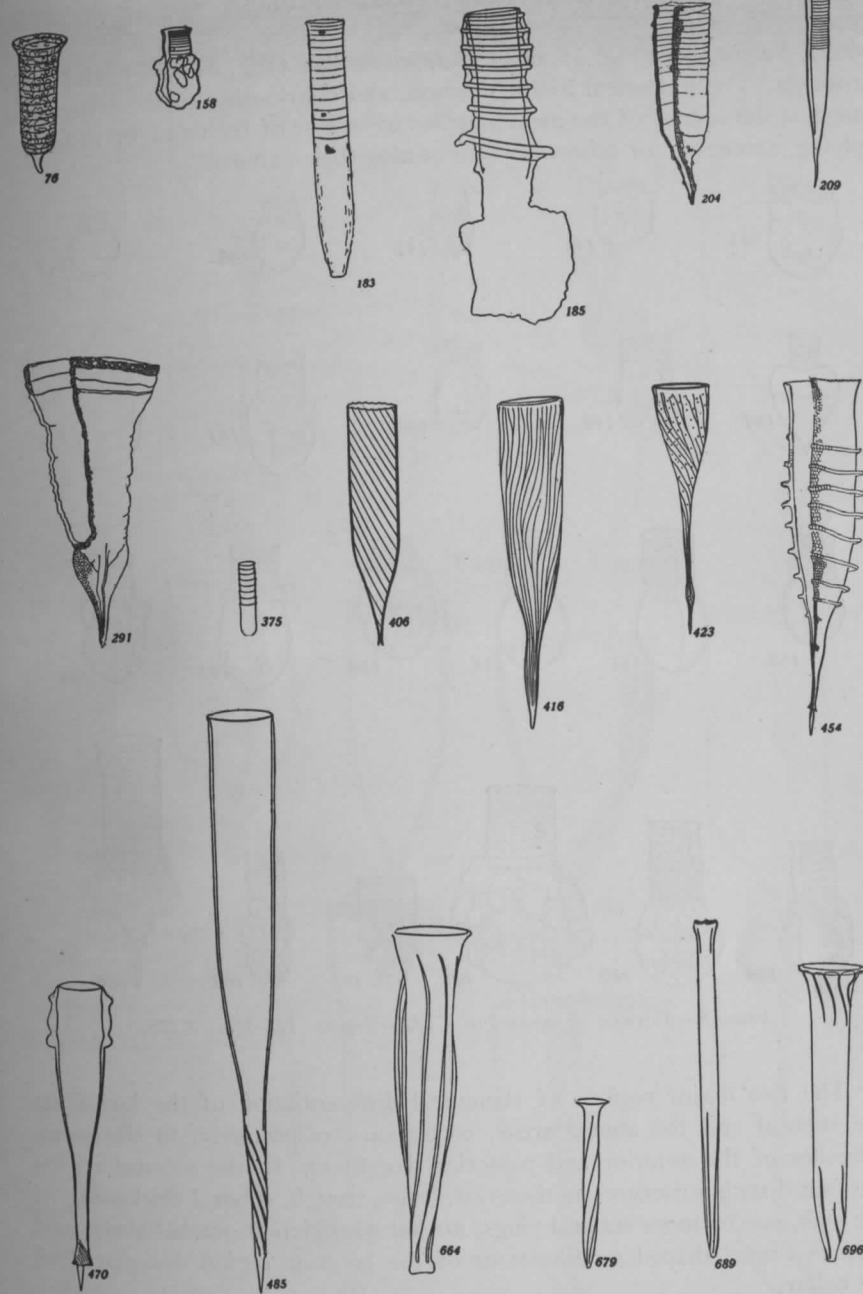


FIG. 17.—Spiral structure in the loricae of the Tintinnoinea.  $\times 125$ . 76, *Tintinnopsis cincta*; 158, *Codonellopsis indica*; 183, *Laackmanniella prolongata*; 185, *Climacocylis scalaria*; 204, *Coxiella helix*; 209, *Helicostomella subulata*; 291, *Favella helgolandica*; 375, *Metacylis annulata*; 406, *Rhabdonella anadyomene*; 416, *Rhabdonella lohmanni*; 423, *Rhabdonellopsis minima*; 454, *Xystonella scandens*; 470, *Xystonellopsis torta*; 485, *Xystonellopsis krämeri*; 664, *Daturella stramonium*; 679, *Salpingella altiplicata*; 689, *Salpingacantha ampla*; 696, *Epicranella bella*.



662), *Salpingella* (Fig. 31, 673), *Salpingacantha* (Fig. 31, 695), and *Epicranella*. The numerical limits, position, and distribution of the structures suggest the agency of the membranelles of one or of both daughters in applying, arranging, or otherwise determining their pattern.

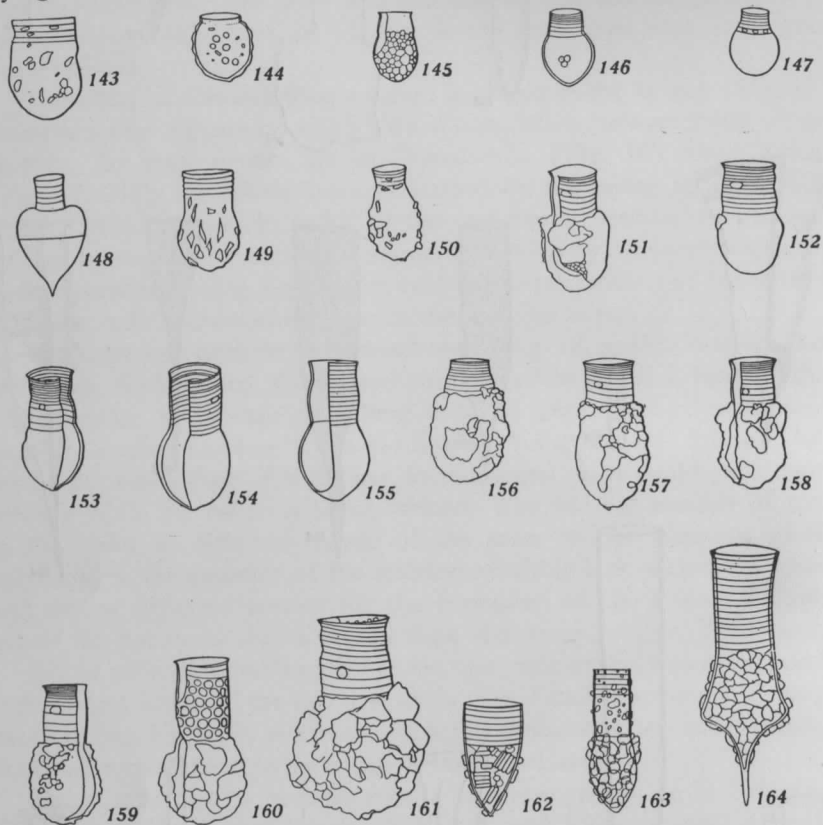


FIG. 18.—Loricae of species of *Codonellopsis*. 143–164.  $\times 200$ .

The two major regions of structural differentiation of the lorica are the suboral and the aboral areas, contiguous, respectively, to the membranelles of the anterior and posterior daughters. In the suboral region are found such structures as the crest, ledge, trough, suboral thickening of the wall, one or more suboral rings, nuchal constriction, nuchal shelf, and various funnel-shaped modifications of the anterior region designated as the collar.

In the aboral region are to be found, below the bowl, the pedicel, knob, skirt, aboral horn or lance, and various additions to these in the form of striae or fins. It seems more probable that the membranelles and oral

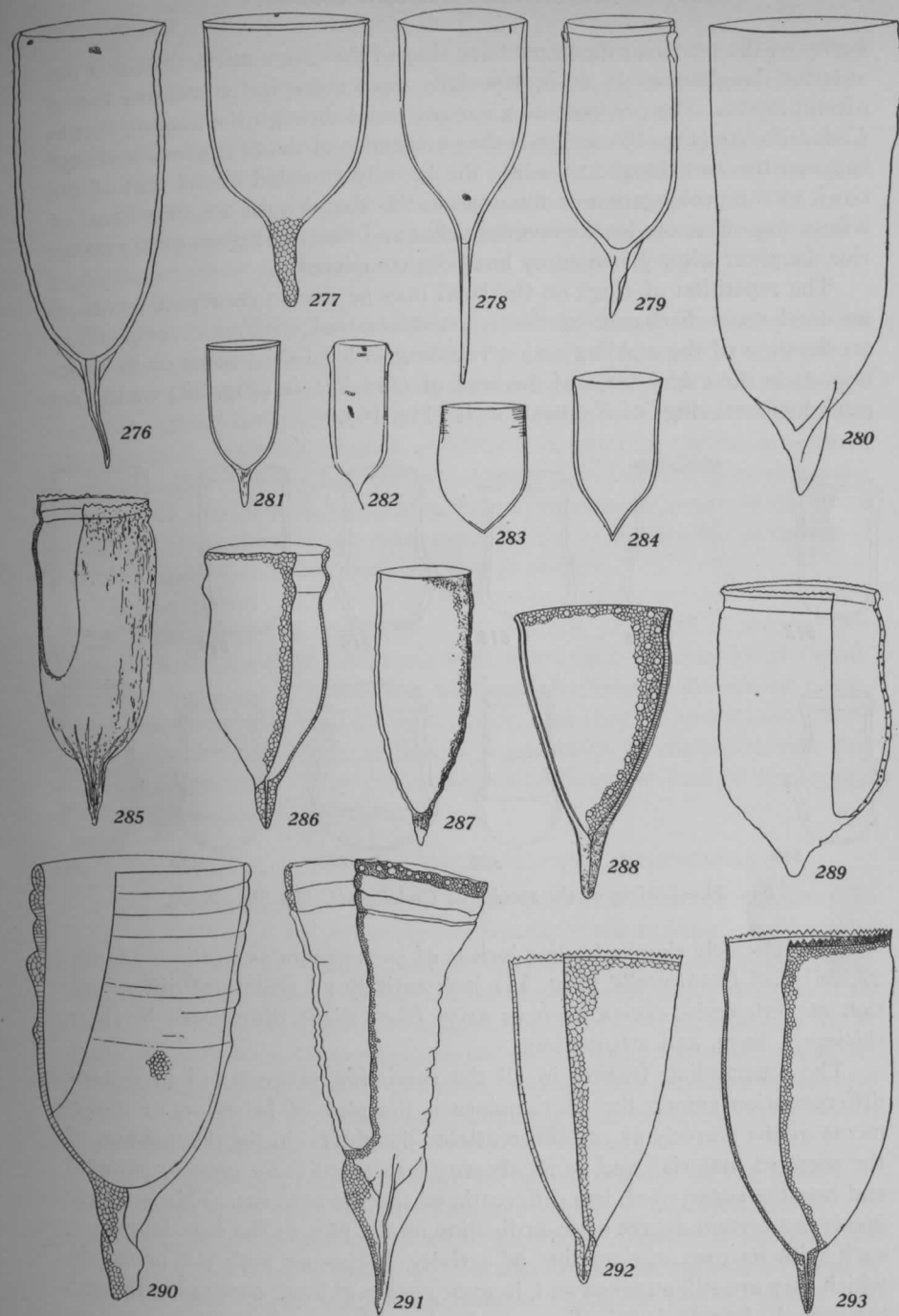


FIG. 19.—Loricae of the species of *Favella*. 276–293.  $\times 200$ .

cavity of the posterior daughter have shaped these structures than that the anterior daughter could do it, especially since the spiral structures are so often present. The presence of a narrow canal through the aboral horn in *Codonellopsis* (Fig. 18) suggests the persistence of the protoplasmic strand between the two daughters, while the broadly rounded aboral end of the bowl, or the prolongation of the bowl in the aboral horn are suggestive of a finishing-off action by the membranelles and the oral region of the posterior daughter after plasmotomy has been completed.

The repetition of rings on the bowl may be due to recurrent waves of an accelerated discharge of the secreted material without corresponding acceleration of the molding action resulting in local thickening or in buckling, as in the undulations of the wall of *Undellopsis* (Fig. 20) or the repeated suboral rings of *Xystonellopsis* (Fig. 16).

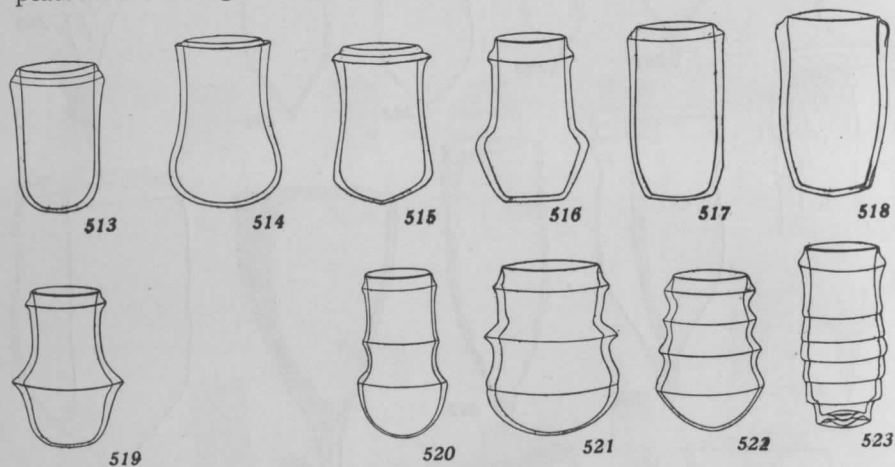


FIG. 20.—Loricae of the species of *Undellopsis*. 513-523.  $\times 200$ .

The relatively simple, hyaline loricae of such genera as *Tintinnus* (Figs. 27, 28) and *Proplectella* (Fig. 13) lack entirely all structural differentiation at both ends, except such as arise from slight differences in slope, thickness, flare, and attenuation.

The outstanding feature in all the speciating process and in generic differentiation among the Tintinnoinea is the play of behavior, of movements of the scarcely as yet differentiated daughters, in the distribution of the secreted material, and in its shaping into the diverse generic patterns and into the superposed, less differentiated specific patterns. This behavior involves a certain degree of co-ordination on the part of the two daughters, each with its own distinct line of activity, beginning with the period in which they are still attached and, in most genera at least, continuing beyond the period of protoplasmic discontinuity for at least a short time.

The function of the lorica or house of the Tintinnoinea is problematical in the extreme. Two major uses suggest themselves, protection and flotation. Protection against most of their carnivorous foes seems futile in the light of the fact that many plankton feeders, such as *Salpa*, take their catch with little selection, straining all organisms from the water within certain limiting dimensions, and making no choice among them. The locomotor powers of the housed ciliate are also very considerable and would facilitate a certain degree of escape from animals seeking to capture particular species as food.

Flotation, on the other hand, is a common necessity of all plankton organisms and is generally facilitated by increase of specific surface, or by hydrostatic vacuoles. In the ciliates the locomotor activities necessitate a certain density and continuity of the cytoplasm which militates against the latter method, while the absence of internal or external skeletal structures is unfavorable to extensions of the surface. The house within which the animal lives affords an increase in surface without modification of the shape of the body or change in the consistency of the cytoplasm for purposes of flotation, and this without much increase in volume.

The aboral end is forward in locomotion, and its pointed or rounded shape facilitates the morphologically backward progression, so that the house does not materially interfere with locomotion. It may be of significance that there are relatively few non-housed ciliates in the marine plankton as compared with that of fresh water, and that the evolutionary flare of the housed Tintinnoinea in the sea is enormous as compared with that of ciliates elsewhere. They constitute nearly forty per cent of the known ciliates, marine and fresh-water.

#### FACTORS IN THE EVOLUTION OF THE TINTINNOINEA

Any consideration of these complex problems must of necessity be highly speculative. Our objective data consist of the existing fauna, a total of 51 genera and 705 species, with structural groupings and geographical distribution which are the visible results of the evolutionary process. This array of evidence suffices to incite some comment on their relations to the various factors with which the orthodox evolutionist expresses his analysis of the process of speciation or evolution. Among these are isolation, natural selection, action of the environment, mutation, hybridization, orthogenesis, and, we may add, quanta.

The geographical distribution of the known species of the genera of the Tintinnoinea in the Eastern Tropical Pacific is characterized by the coincident occurrence of two or more species of a genus at many of the collecting stations. The same feature appears in the records of Brandt (1907) in the Atlantic and of Laackmann (1909) in the Antarctic. For example, in our records at Station 4724 in the South Equatorial Drift the





Structures such as these are sometimes present in all members of a genus, and specific differences are more often made up of very minor modifications in size, proportions, angles, slopes, and the like. Their character and range are such that, if the interspecific differences have survival value, it is beyond comprehension why intergrading individuals should be eliminated or why one species differs in survival value from others in the same genus. All seem to lie within the dead-line of survival value, and so might many other mutant types. It is difficult to find satisfactory evidence for the differentiating survival value of the type of differences between the species. To say that these varied differences are all linked with unseen ones that do have such values is of no great assistance in the problem.

On the other side of the question there is the fact that only a relatively few of the 705 species are individually numerous. Many are very rare, as though lacking in reproductive vigor, though the house may exhibit no signs of the decrepitude of its maker.

In the matter of generic distinctions there is considerable evidence of marked differences in the nature of the lorica-forming substances. The substance within each genus is fairly uniform. In some, as in genera of the Undellidae, the substance is homogeneous, does not form patterns, and the loricae are relatively free from structural differentiations of all kinds except rings, bulges, and pointed aboral ends.

In other genera, such as *Dictyocysta* (Fig. 15), *Epiplocylix* (Fig. 22), *Petalotricha* (Fig. 23), and *Ptychocylix* (Fig. 24, p. 26), there is in each a characteristic patterning of the surface with lines or reticulations suggestive of patternings directly referable to the chemical and physical natures of the differing colloidal substances. Differences such as these can hardly be regarded as brought about by natural selection or as incident thereto. They are the expression of definite chemical and physical differences, and their origin and pattern rest on chemical and physical laws.

The generic distinctions in the main in the Tintinnoinea usually involve these differences in the lorica-forming substance and are rather sharply marked. There is usually but little difficulty when one has all of the species before him in making satisfactory generic allocations of most species. In a few instances, as between *Tintinnopsis* and *Stenosemella*, the intergradation is close. Some large genera, such as *Codonella* and *Xystonellopsis*, are less coherent than others, such as *Dictyocysta*.

The possibility of hybridization is suggested by certain curious "cross-overs" of generic characters between quite distinct genera in the case of single species in one of the two genera concerned.

Thus *Xystonella scandens* (Fig. 25, 434, p. 26) is the only species in the genus *Xystonella* which has a spiral shelf. In all other features the lorica is that of a typical *Xystonella*. This shelf is the outstanding generic char-

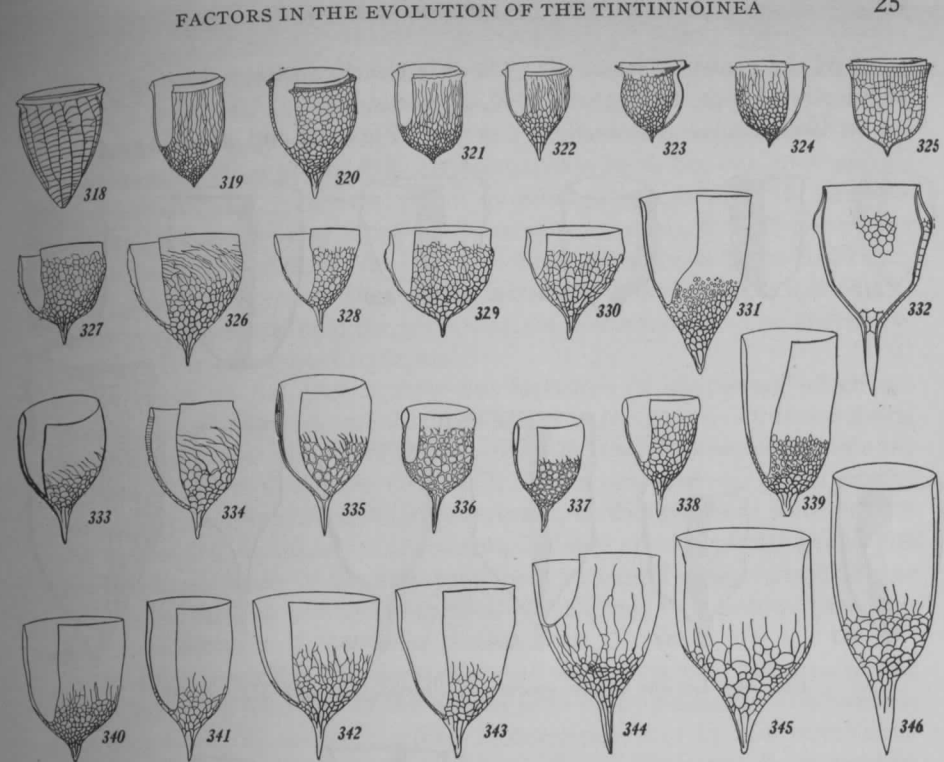


FIG. 22.—Loricae of the species of *Epiplocylix*. 318–346.  $\times 200$ .

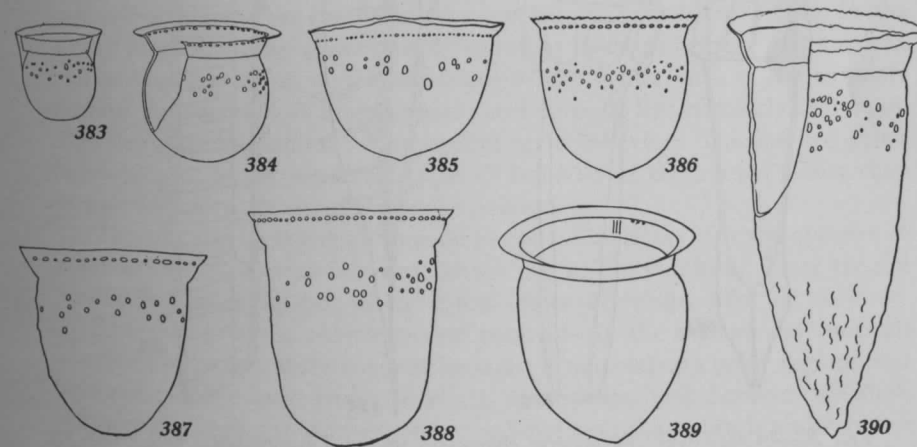


FIG. 23.—Loricae of the species of *Petalotricha*. 383–390.  $\times 200$ .

acter of the genus *Climacocylis*. There is clearly an intermingling of the characters of these two genera in *X. scandens*.

In like manner *Xystonellopsis ornata* (Figs. 16 and 25, 463) of the

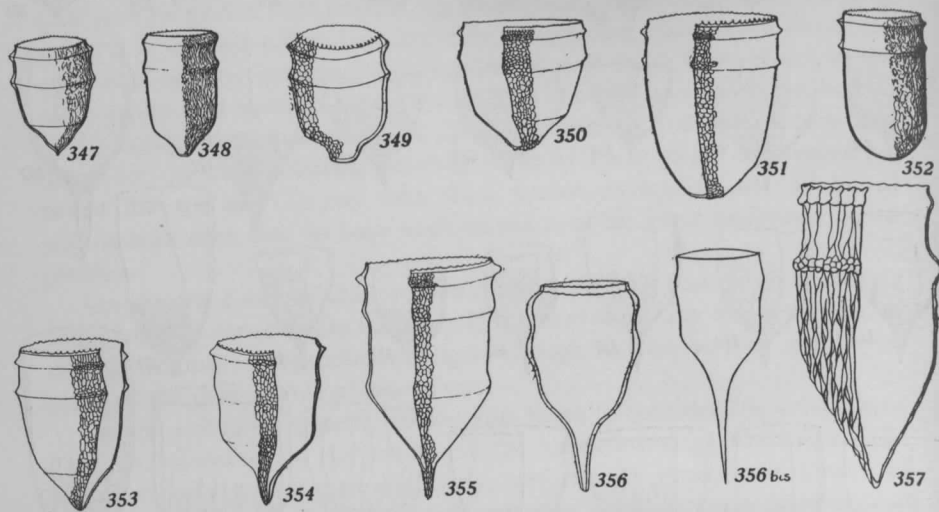


FIG. 24.—Loricæ of the species of *Ptychocylis*. 347-357.  $\times 200$ .

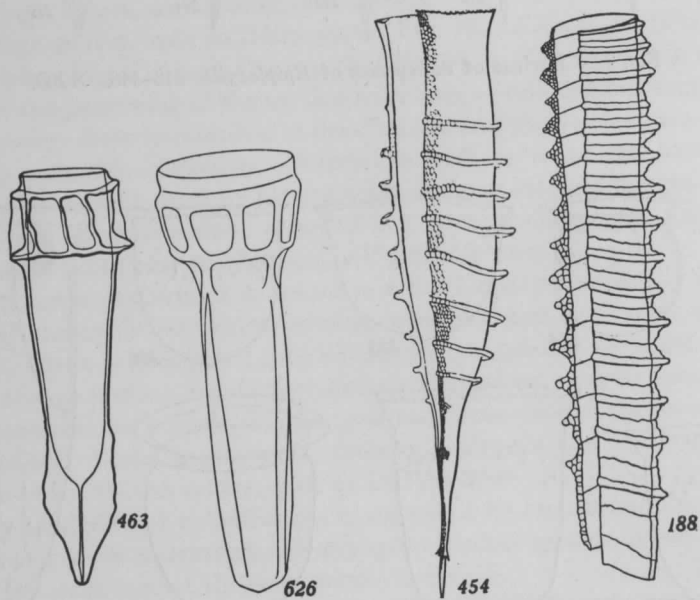


FIG. 25.—"Cross-over" of generic characters in the Tintinnoinea. 463, lorica of *Xystonellopsis ornata*; 626, lorica of *Stelidiella fenestrata*; 454, lorica of *Xystonella scandens*; 188, lorica of *Climacocylis elongata*.

family Xystonellidae differs from all other species in its genus in having vertical bars between the two suboral rings. In this respect it resembles the remote genus *Stelidiella* of the family Tintinnidae, the species of which have a rather stout aboral end. As compared with all but one other species in *Xystonellopsis*, *X. ornata* has an unusually stout aboral end. There is thus in this species also a curious admixture of characters of two rather widely separated genera. An origin of these admixtures by hybridization is suggested. There are some other instances of such admixtures of less striking character among the genera of the Tintinnoinea. The alternative hypothesis is convergent mutation.

In many of the genera there are instances of characters which are present in some species and absent in others in the genus. Thus the aboral horn or point is present in some and absent in other species in *Tintinnopsis* (Fig. 12) and in *Codonella* (Fig. 11). The aboral flare occurs in similar fashion in *Tintinnopsis* and *Leprotintinnus*, as though there were present the expression of recessive characters in some species of the genus and not in others. Many of the most prominent structural characteristics of the loricae are shuffled among the species of the genus in a fashion very suggestive of the play of Mendelian combinations.

In this connection the dependence of such structural features of the lorica upon the behavior of the animal is to be emphasized. The lorica is not an anatomical structure arising in development or by redifferentiation in the ciliate after conjugation or binary fission. It is the direct product of the mode of behavior of the animal at the particular moment of the formation of the lorica. An example of such differential behavior between species or genera is seen in the differences between the homogeneous structure, the spiral structure, and the annulate pattern of the lorica. In the non-spiral pattern the behavior does not lead to spiral lamination; in the spiral pattern the behavior during secretion leads to a continuous spiral, ribbon-like deposition of the substance of the lorica; and in the annulate pattern the secretion is intermittently and more or less regularly increased. The structure in each case is dependent upon behavior. The shuffled genes in such cases as this represent types of behavior of the animal rather than morphological patterns of structure primarily.

The relation of the environment to the evolutionary process appears to have certain rather striking correlations in the Tintinnoinea. They are not limited to this group but more or less affect all pelagic life.

The two greatest environmental contrasts in the marine environment are those of temperature contrast between equatorial and polar regions and between surface and deeper levels in the tropics, and between the high seas and the neritic area in matters of salinity and of amplitude and rapidity of the changes in chemical content, temperature, and movement of the water.

The structure of the lorica reflects the influence of these contrasted regions. The influence is evident both in generic groups and within the individual species. Temperature through its relations to viscosity of the water affects the buoyant action of the lorica. It also affects directly the velocity of all chemical reactions, and thus influences growth, reproduction, secretion, and possibly also the rate of formation of the lorica. Even a casual inspection of the dimensions of the loricae of genera limited, respectively, to polar and tropical seas reveals the fact that genera limited to polar seas such as *Cymatocylis* and *Parafavella* have a very much larger proportion of species of larger sizes than of smaller ones, and that tropical genera, as for example *Amplectella* and *Proplectella* (Fig. 26), are either wholly made up of small species or have very few large species.

A quantitative study of the dimensions of 1,000 individuals of *Tintinnus tenue* in the area explored by the Agassiz Expedition to the Eastern Tropical Pacific shows the loricae of this species taken in the Peruvian Current at stations of lower surface temperatures (66° to 74°F.) are predominantly larger than those taken elsewhere at stations where this temperature was 75° to 83°F. There is thus a parallelism between the type of modifications of the individual regarded as fluctuating and directly correlated with the action of the environment upon the individual, and those differences in size between species which we are wont to regard as hereditary and genetic. The correlation is with the same aspects of temperature in both types of differences, individual and genetic.

In one other important particular the evolution of the Tintinnoinea exhibits a correlation with the environment, namely, in the relation of temperature to the number of species. More species are found in equatorial regions than in polar ones. In our revision of the suborder we list 705 species. Of these, 8 are from fresh water, 59 are restricted to Arctic waters, over 40 to the Antarctic, and 515 to warm temperate and tropical regions. As a general rule the number of species taken by any one haul of the plankton net in circumpolar seas is small, but the number of individuals may be very great. On the other hand, in tropical seas the reversed relation exists. The species are numerous and the individuals of each are few, at least of the great majority of them.

The total of known species in polar waters is 101, and in the tropics 515. The polar faunas are not as well known as those of the tropics. These crude figures, however, give a ratio of 1 to 5 between the respective numbers of species in these contrasted regions. If the difference between the extremes of temperature in these two contrasted regions approximates 20°C. Van 't Hoff's Law calls for a quadrupling of the rate of chemical reactions and of biological processes, or a ratio of 1 to 4. In accordance with this law and the resultant higher rate of chemical changes within the living substance in warm seas we may expect an increase in the oppor-

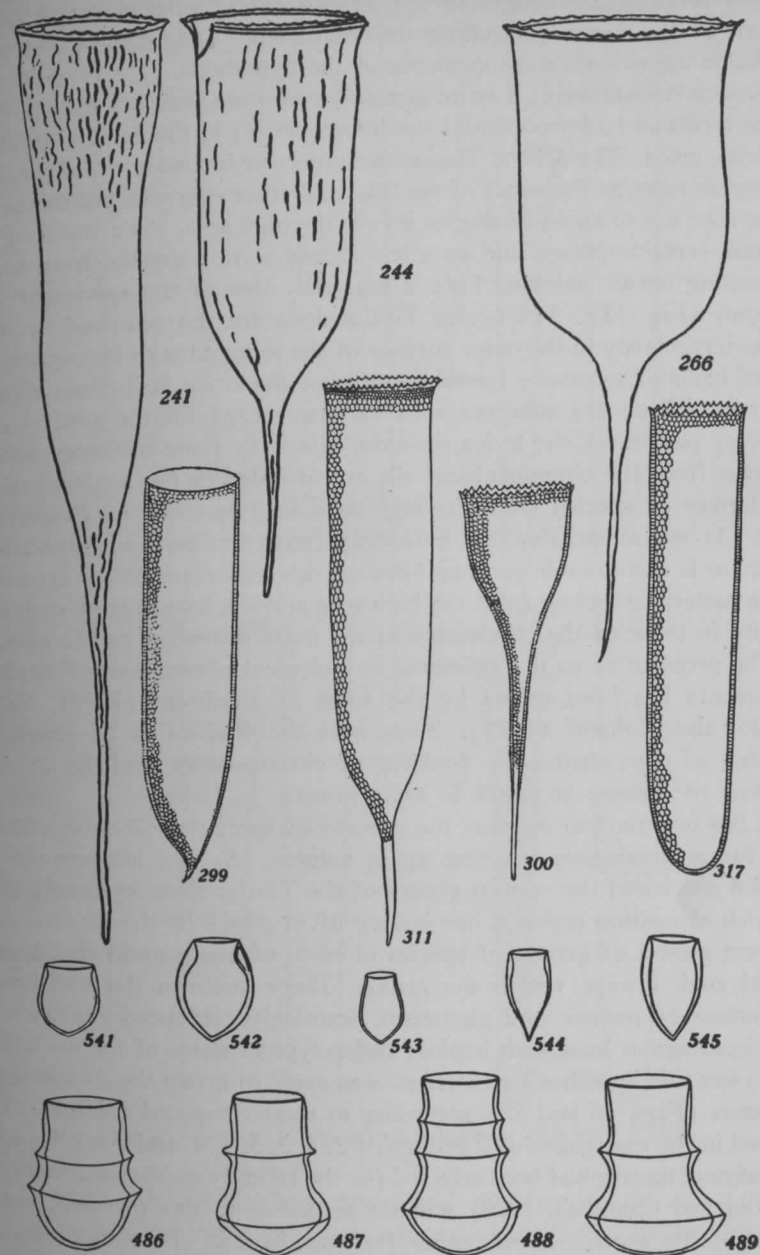


FIG. 26.—Comparison of loricae of genera from polar and from tropical seas. *Cymatocylis*, 241, 244, 266, from the Antarctic, and *Parafavella*, 299, 300, 311, 317, from northern seas. *Proplectella*, 541-545, from the tropical Pacific; and *Amplectella*, 486-489, also from the tropical Pacific.  $\times 200$ .



tunities for mutant changes in the lorica-forming substance and in the pattern of the genes controlling differentiation. The observed facts of speciation approximate the demands of the hypothesis.

A second instance of a more general correlation between the structure of the lorica and environmental conditions occurs in the genera restricted to neritic areas. The pelagic Tintinnoinea more or less invade and permeate the neritic zone, as the result of the tidal and other currents, but the neritic fauna does not to an equal degree invade the high seas. As a result of this contrast certain species, and to a less extent certain genera, have a predominating neritic habitat. This is especially true of the species of *Tintinnopsis* (Fig. 12). The neritic Tintinnoinea are characterized by more or less irregularity in the outer surface of the lorica, due to the agglomeration of blobs of substance resembling that of the lorica in its finer alveolar structure. These are adherent with varying regard for the general symmetry or pattern of the lorica, in most cases. In some instances foreign particles from the circumambient silt are included in the agglomerations. The loricae of species from the high seas such as those of *Proplectella* (Fig. 13) are remarkably and uniformly free from such agglomerations, and there is a noticeable contrast between this adherence to the symmetry of the pattern in loricae from the high seas and the looseness of such conformity in those of the inhabitants of the more disturbed neritic area.

The problem as to the existence in biological phenomena of anything like quanta has been raised by the work of Przibram (1929), Szttern (1914), and Koltzoff (1928). They note the duplication of genes, the doubling of gene chains, the doubling of chromosomes, and the step-like doubling of volume at moult in some insects.

It has occurred to me that the process of speciation likewise offers a field for an analogous stepping up in volume. As one inspects the assembled species of the various genera of the Tintinnoinea, especially those in which elongation prevails, one is very often struck by the recurrence in different genera of groups of species in each, of one general size, and of several such groups within the genus. There are also the well-known phenomena of nanism and gigantism, seemingly correlated elsewhere in some instances at least with haploid and polyploid states of the nucleus.

To test this hypothesis an attempt was made to group the 29 species of *Tintinnus* (Figs. 26 and 27) according to their computed volumes. This resulted in the emergence of 7 groups of 2, 5, 5, 5, 4, 4, and 4 species each. The original figures had been selected for the recently published conspectus (Kofoid and Campbell, 1929) without reference to this problem, but as typical of the species, among other features, in size. They therefore are not widely divergent from the modes of the species represented. In computing the step-up from one group to the next the assumption is made that the volume of the lorica would be doubled at each step.

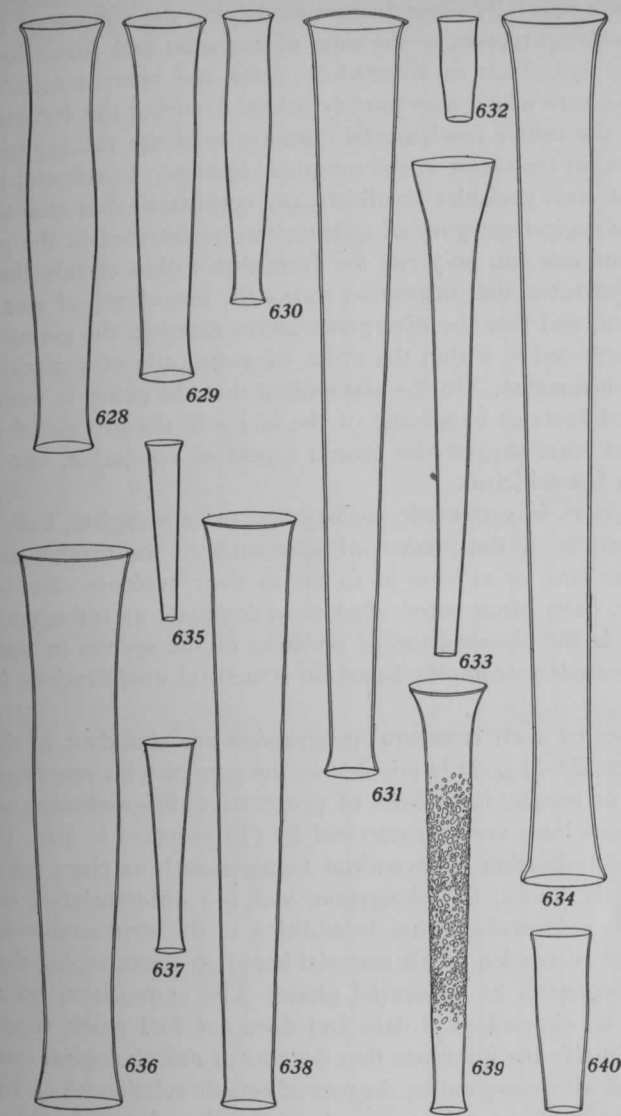


FIG. 27.—Loricae of species of *Tintinnus*. 628-640.  $\times 200$ .

Starting with the smallest group and stepping up the seven to the largest, we find the computed mean volumes of the loricae of the species of the several groups depart from the expected ones by +14.9, -3.6, +20, -8.3,  $\pm 0$ , and -26 per cent, respectively, and that the average departure is  $\pm 11$  per cent.

There are naturally other factors modifying the volume of the loricae, such as the temperatures at the time of secretion and formation, the volume of the cytoplasm as affected by prior and current metabolism, the unknown factors which may modify behavior during the formation of the lorica, and the rather fundamental question as to the validity of including the void within the lorica in the computed volume. In rebuttal to the suggestion that such variables invalidate any conclusion that quanta phenomena, or a biological category of quanta, can be detected in the phenomena of speciation, one can only cite the facts that within certain limits size is a species character, that inspection shows the prevalence of size groups in many genera, and that the divergence above noted in the genus *Tintinnus* from the expected is within the order of magnitude of variation in other biological phenomena. On the assumption that the genus is monophyletic, the observed facts as to volume of the lorica in the groups of species of *Tintinnus* at least suggest the quanta aspect of speciation, but still leave much room for criticism.

Investigators in systematic zoölogy and paleontologists, both of whom view the results of the process of speciation in the groups under their inspection *in toto*, or at least in so far as their evidence affords such an opportunity, have often noted what they designate as orthogenesis. Concretely this is the phenomenon of seriation of the species in one or more lines from simple to complex based on structural modifications in definite directions.

Evidences of such structural progression are abundant in the Tintinnoinea (Figs. 29-31). It is possible in the genera with numerous species to find one or usually more lines of progressive differentiation among the species. These lines are characterized by (1) increase in size, (2) duplication or multiplication of structural features such as rings, spiral turns, striae, pedicels, knobs, (3) elongation, and (4) differentiation of surface pattern. The paleontologist has in addition to the structural evidence the chronological succession of his material based on stratigraphic data, which give to orthogenesis its sequential phase. The systematist, on the other hand, lacks all chronological data and does not find much support from genetics to justify the inference that degrees of morphological resemblance are evidences of corresponding degrees of genetic relationships. In the suborder Tintinnoinea the only approach to the time factor in the evolution of the group is to be found in the very large body of evidence that evolution has progressed most rapidly, as shown in multiplication of species and diversification of genera, in the tropical seas. Here the operation of Van 't Hoff's Law in accelerating life processes has so increased the speed of living that more evolution has happened here than in the colder polar regions within the same period.

In Figures 29-31 the simplest and the most highly specialized species

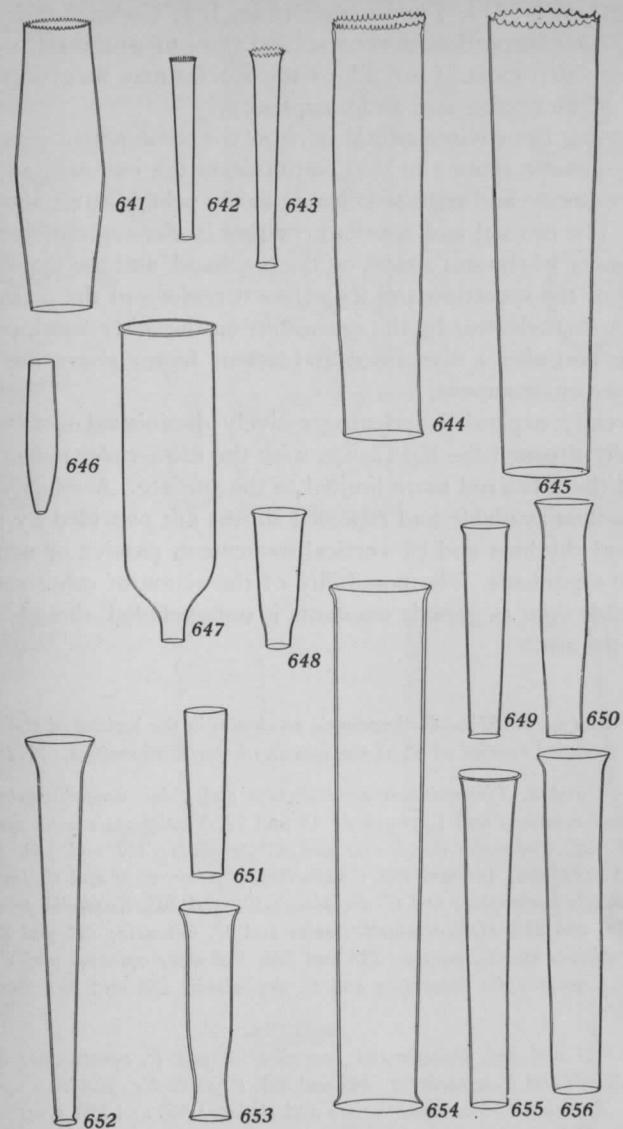


FIG. 28.—Loricae of the species of *Tintinnus*. 641-656.  $\times 200$ .

in each of 46 genera of the Tintinnoinea are represented in pairs. These paired figures represent the ends of the single or of the main series of species if there is more than one series, in each of the genera. They exhibit the beginnings and ends of one or more of the types of structural progressions enumerated above. In some of the genera, such for example

as *Codonella* (Fig. 11), *Tintinnopsis* (Fig. 12), *Codonellopsis* (Fig. 22), it is possible on inspection to note several lines of progressive differentiation within which most, if not all, of the species may be grouped in series of species of increasing size and complexity.

In scanning the environmental horizon for some potent agency capable of inciting genetic change in the Tintinnoinea the one outstanding factor subject to extreme and repeated change in the pelagic environment is solar radiation. The diurnal and seasonal changes in the angle of incidence and in the intensity of the sun's rays, on the one hand, and the vertical selective absorption of the spectrum and its adjacent regions of the octaves of electromagnetic disturbances by the sea water, on the other hand, present both a changing and also a diversified and potent factor above the light floor in the marine environment.

The greatly expanded and progressively diminished spectrum is thus flashed daily through the light zone, with the ultra-violet penetrating most deeply and the infra-red more limited to the surface. A selective action of the light is thus available and repeated shocks are provided by the diurnal and seasonal rhythms and by vertical movement, passive or active, on the part of the organisms. The possibility of the action of other sections than that of visible light as genetic excitants is not excluded, though evidence is lacking in the sea.

FIGS. 29-31 (pp. 35-37).—Orthogenesis as shown in the loricae of the simplest and most highly modified species of 45 of the genera of the Tintinnoinea.  $\times 125$ .

FIG. 29.—4 and 8, *Tintinnidium semiciliatum* and *Tdm. neapolitanum*; 9 and 10, *Leprotintinnus neriticus* and *L. simplex*; 15 and 77, *Tintinnopsis nana* and *Tps. urniger*; 99 and 125, *Codonella brevicollis* and *C. cistellula*; 137 and 140, *Stenosemella inflata* and *S. expansa*; 144 and 180, *Codonellopsis tuberculata* and *C. longa*; 187 and 188, *Climacocylis scalaroides* and *C. decipiens*; 190 and 203, *Coxliella pelagica* and *C. decipiens*; 206 and 210, *Helicostomella longa* and *H. kiliensis*; 211 and 222, *Cyttarocylis eucecryphalus* and *C. magna*; 223 and 226, *Poroecus apicatus* and *P. annulatus*; 235 and 262, *Cymatocylis antarctica* and *C. drygalskii*; 284 and 290, *Favella azorica* and *F. brevis*.

FIG. 30.—304 and 314, *Parafavella greenlandica* and *P. ventricosa*; 321 and 332, *Epiplocylis healdi* and *E. acuminata*; 348 and 355, *Ptychocylis cylindrica* and *P. urmula*; 358 and 364, *Acanthostomella minutissima* and *A. lata*; 366 and 370, *Craterella torulata* and *C. acuta*; 372 and 382, *Metacyclis lucasensis* and *M. rossica*; 383 and 390, *Petalotricha entzi* and *P. foli*; 392 and 395, *Protorhabdonella striatura* and *P. simplex*; 398 and 418, *Rhabdonella amor* and *R. conica*; 419 and 421, *Rhabdonellopsis longicaulis* and *R. composita*; 425 and 446, *Parundella minor* and *P. attenuata*; 449 and 454, *Xystonella lanceolata* and *X. scandens*; 463 and 475, *Xystonellopsis ornata* and *X. pinnata*; 486 and 492, *Amplectella insignis* and *A. quadricollaria*; 493 and 494, *Amplectellopsis angularis* and *A. biedermanni*; 496 and 497, *Cricundella tridivisa* and *C. quadridivisa*; 503 and 512, *Undella clevei* and *U. bulla*; 513 and 523, *Undellopsis pacifica* and *U. umbilicata*; 524 and 529, *Proplectella perpusilla* and *P. ovata*.

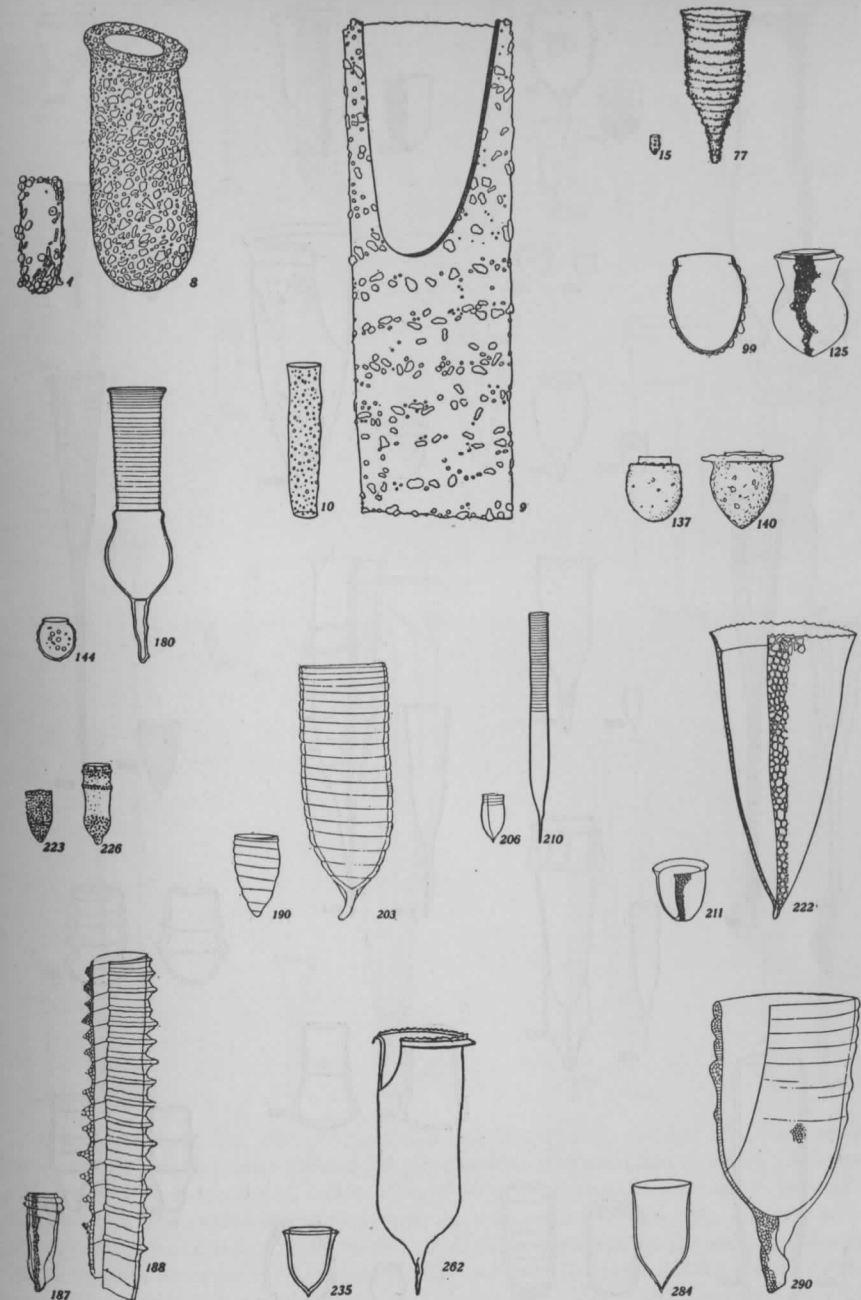


FIG. 29

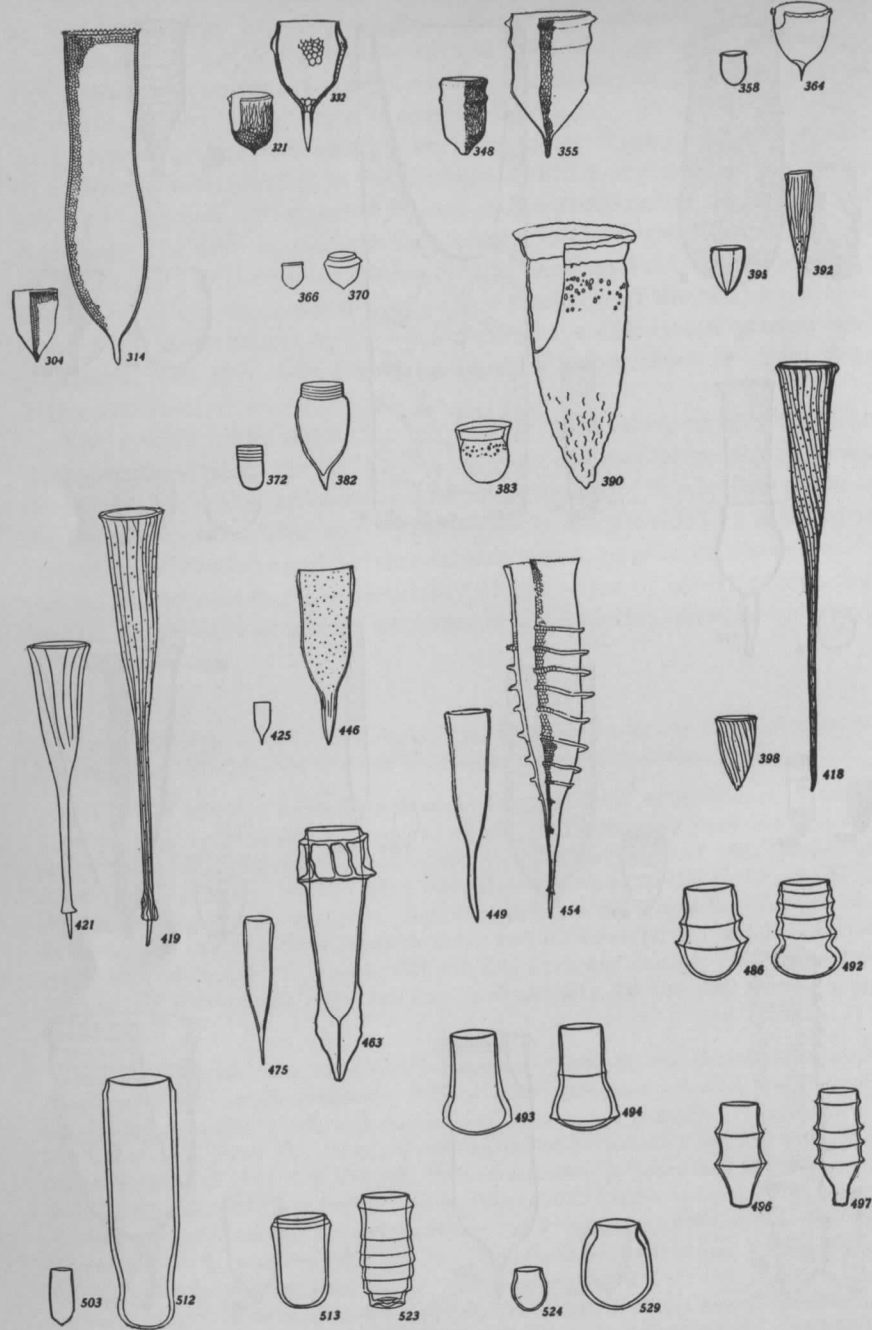


FIG. 30

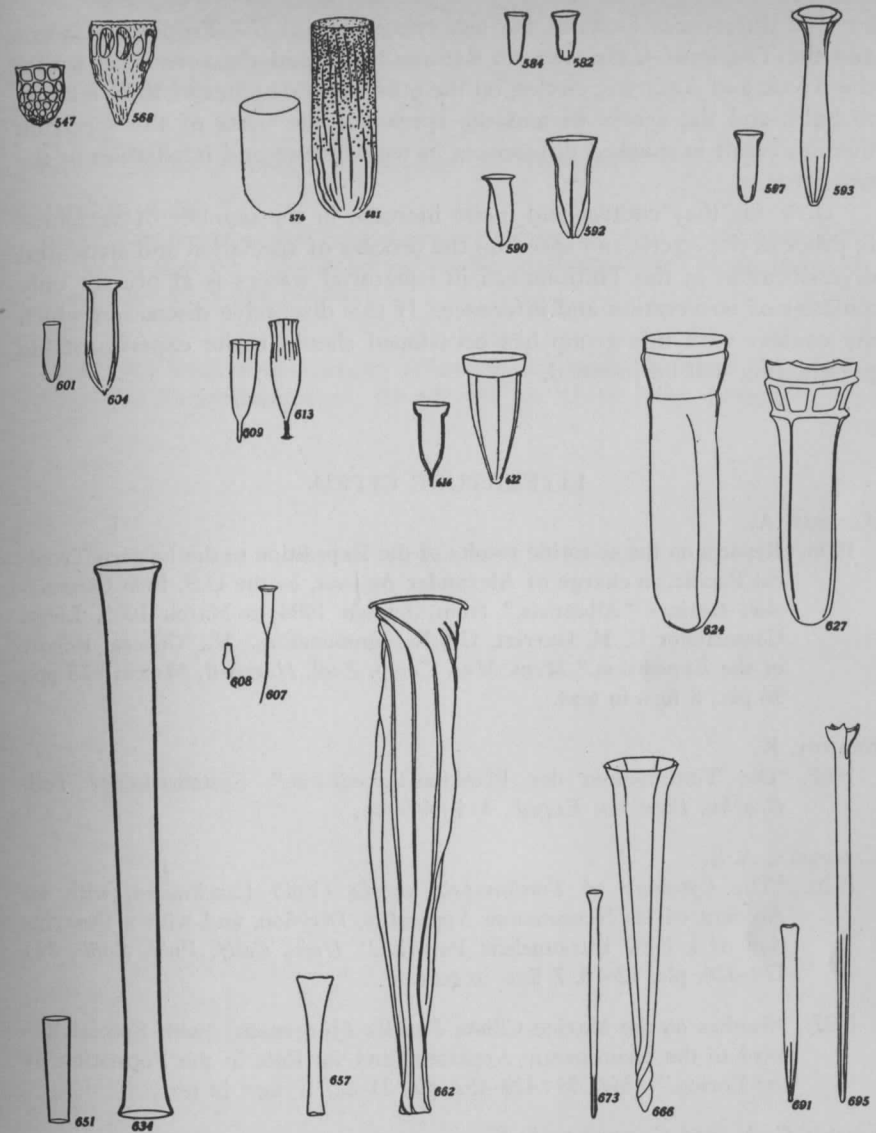


FIG. 31.—547 and 568, *Dictyocysta obtusa* and *D. apiculata*; 576 and 581, *Bursaopsis vitrea* and *B. punctostriata*; 582 and 584, *Canthariella septinaria* and *C. brevis*; 590 and 592, *Amphorella minor* and *A. calida*; 593 and 597, *Steenstrupiella entzi* and *S. gracilis*; 601 and 604, *Amphorellopsis tropica* and *A. tetragona*; 607 and 608, *Albatrossiella filigera* and *A. minutissima*; 609 and 613, *Dadayiella acuta* and *D. jørgenseni*; 616 and 622, *Ormosella bresslaui* and *O. schmidtii*; 624 and 627, *Stelidiella phialia* and *S. stelidium*; 634 and 651, *Tintinnus birictus* and *T. tubulosus*; 657 and 662, *Daturella angusta* and *D. magna*; 666 and 673, *Salpingella octogenata* and *S. acuminatoides*; 691 and 695, *Salpingacantha simplex* and *S. undata*.



The differences between the belt lying betwixt the Tropic of Cancer and the Tropic of Capricorn, on the one hand, and the polar seas within the Arctic and Antarctic circles, on the other, in the matter of their relation to light, and the access of and the spread of the parts of the spectrum therein, result in marked differences in temperature and irradiation in the two areas.

How far they control and incite increase in the number of vertebrae in fishes in the Arctic and speed up the process of speciation and structural diversification in the Tintinnoinea in equatorial waters is at present only a matter of observation and inference. If this discursive discussion which my contact with this group has occasioned should invite experiment, its presentation will be justified.

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