DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE SKRIFTER, BIND VI, NR. 4

OBSERVATIONS ON DINOFLAGELLATES

BY

OVE PAULSEN †

Edited by

JUL. GRØNTVED

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1949

Det Kongelige Danske Videnskabernes Selskabs publikationer i 8vo:

Oversigt over selskabets virksomhed,
Historisk-filologiske Meddelelser,
Arkæologisk-kunsthistoriske Meddelelser,
Filosofiske Meddelelser,
Matematisk-fysiske Meddelelser,
Biologiske Meddelelser.

Selskabet udgiver desuden efter behov i 4to »Skrifter« med samme underinddeling som i »Meddelelser«.

Selskabets adresse: Dantes plads 35, København V.

Selskabets kommissionær: *Ejnar Munksgaard,* Nørregade 6, København K.

DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE SKRIFTER, BIND VI, NR. 4

OBSERVATIONS ON DINOFLAGELLATES

BY

OVE PAULSEN †

Edited by

JUL. GRØNTVED

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1949

CONTENTS

PRINTED IN DENMARK
BIANCO LUNOS BOGTRYKKERI

Shortly before his death in the spring of 1947 Professor PAULSEN expressed to me the desire that I should see to the publication of the following work in the event of his succumbing to his illness.

When he died, the manuscript lay ready in draft form, and, beyond editorial corrections, I have made no change or addition in the text; the original text-figures now printed were in the form of pencil sketches, some of them indistinct or lacking in detail; and as I have had to complete these, I am co-responsible for a number of the figures. Among Professor PAULSEN's figure sketches I have removed a few which I was sure he himself would have regarded as superfluous had he been able to make a final revision of the illustration material. The copies inserted have been chosen in accordance with the context of the manuscript.

The genus *Ceratium* is not dealt with in this work; however, among Professor PAULSEN's papers there is a considerable number of sketches and notes for a monographic treatment of the northern forms of that genus. There is no doubt that it was his original intention to subject the *Ceratium* species to a study in the same manner as the Dinoflagellates in the following; when the state of his health deteriorated during the past few years, he probably decided to omit *Ceratium* in order to concentrate on concluding the other part of the work.

The departure of Professor PAULSEN has meant the loss of a scientist with a profound knowledge of the taxonomy of the Dinoflagellates; his works within this branch of science will guarantee his name from descending into oblivion for many years to come; to us who knew him personally his illness and death were the source of deep sorrow. We preserve his memory in grateful recollection.

JUL. GRØNTVED

I. On the Taxonomy of the Dinoflagellates in General.

During the past twenty years or so our knowledge of the Dinoflagellates has been increased considerably. Some of the more imporatnt works to appear in these years are:

Marie V. Lebour, The Dinoflagellates of Northern Seas. 1925.
C. A. Kofoid and T. Skogsberg, The Dinophysoidae. 1928.
E. Lindemann, Peridineae (in Engler und Prantl). 1928.
M. Lefèvre, Monographie des espèces d'eau douce du genre Peridinium. 1928.
J. Schiller, Dinoflagellatae (in Rabenhorst's Kryptogamenflora). 1933—37.

Lebour, Lindemann and Schiller cover the entire section, in general and in detail, whereas Kofoid & Skogsberg and Lefèvre monograph smaller groups and, as far as possible, clarify the problems occurring within them, especially the many difficult questions of species-separation. I shall revert to this later.

The general view obtainable over the Dinoflagellates from the use of each of these comprehensive works is very variable, at any rate when we take Lebour on the one hand and Lindemann and Schiller on the other.

Lebour's book is the smallest; it comprises only the Dinoflagellates of the northern seas, and its lay-out is more that of a classification book than of a monograph. The taxonomic sub-groups are relatively few; the species are listed under the following ten families:

Prorocentridae	*Pouchetiidae*
Pronoctilucidae	*Blastodiniidae*
Gymnodiniidae	*Dinophysidae*
Polykrikidae	*Glenodiniidae*
Noctilucidae	*Peridiniidae*

This is a clear and perspicuous classification; each family has its own distinct characters, materially different organisms are separated from one another, and nothing related is divided, except perhaps that e. g. the close relationship between *Gymnodiniidae* and *Pouchetiidae* might have been expressed in some way or another.

LINDEMANN's work is an organization and generic monograph; it is the natural history of the Dinoflagellates; all that is known of it is carefully treated and clearly presented. But, with all the admiration one feels for a work of this kind, it is regrettable that taxonomic perspicuity has been lost.

LINDEMANN builds up a large taxonomic structure of subdivisions, orders and quite small families, and in many cases has separated what Sections belong together; sometimes he also seems to have grouped together organisms which are not closely related. An example of the latter is presumably his Class *Kolkwitziellales* and under it the family *Kolkwitziellaceae* (p. 71), whose four genera seem to be inadequately known and have merely this in common that the theca is not composed of plates (I wonder if *Lissaïella* and *Kolkwitziella* are not young forms).

Splitting up into many small families is carried through especially in the Order *Peridiniales*, which in LINDEMANN contains the following 14 families:

Glenodiniaceae	*Heterodiniaceae*
Protoceratiaceae	*Pyrophacaceae*
Dinosphaeraceae	*Ostreopsiaceae*
Gonyaulacaceae	*Oxytoxaceae*
Peridiniaceae	*Ceratocoryaceae*
Ceratiaceae	*Cladopyxiaceae*
Goniodomaceae	*Podolampaceae*

Of these 14 families, seven have only one genus, four have two genera, while *Glenodiniaceae* and *Peridiniaceae* have three and *Gonyaulacaceae* have five. Unfortunately, from this series of families one receives a false impression of uniformly separated, so to say parallel families, whereas the truth seems to be that while some of the families are well characterized, e. g. *Ceratiaceae*, *Podolampaceae*, *Cladopyxiaceae*, *Oxytoxaceae* and *Heterodiniaceae*, others approach one another so closely that it seems reasonable to place them together in one group. This applies for example to *Protoceratiaceae*, characterized by LINDEMANN mainly by the heavy reticulation concealing the plate arrangement, and *Dinosphaeraceae*, which comprises a single species which, in its plate arrangement, closely approaches *Gonyaulax* and was originally described as such by LEMMERMANN. From it KOFOID & MICHENER have set up a genus, *Dinosphaera*, and from this LINDEMANN a new family, though its deviation from *Gonyaulax* is not greater than the differences to be found within LINDEMANN's *Gonyaulacaceae*. Nor does the setting up of this latter family — as of *Goniodomaceae* — seem to involve any scientific or practical gain. For the sake of perspicuity they ought to remain in the family *Peridiniaceae*, with whose other genera they have main features in common. And to me the same seems to apply to *Glenodiniaceae*.

There are no rules for the setting up of families and their mutual boundaries; but it is surely desirable that the families in a large group should be separated one from another by character differences which everywhere are of the same size or importance.

SCHILLER's impressively large two-volume work: *Dinoflagellatae (Peridineae)* in monographischer Behandlung, in RABENHORST's Kryptogamenflora von Deutschland, Österreich und der Schweiz, 2. Aufl. 10. Bd. 3. Abt., is a taxonomic monograph; for, unlike LINDEMANN in his taxonomic section, it does not stop at grouping the genera but also includes all known species.

It was not before time that a work of this kind appeared and we must be grateful to Professor Jos. SCHILLER for writing it; the material had gradually acquired such a large compass that it was sorely in need of summarization, examination and criticism; the mere collecting of the enormous material and presenting it in arranged form is meritorious; here one can find all references to what has been published on the Dinoflagellates; the author shunned no trouble to ensure that everything was included, and he gave his work abundant illustration by reproducing the figures of the various researchers; no wonder he confused them occasionally or mistook them; more pains might have been taken in this.[1]

In respect to the main classification of the whole of this large group SCHILLER has followed PASCHER, the Dinoflagellates being divided into two series: *Desmokontae* and *Dinophyceae*. The former have the flagella at one end of the cell, the wall of which is divided into two by a seam. To these he places i. a. *Prorocentraceae* and the Class *Dinophysiales* with the families *Dinophysiaceae*, *Amphisoleniceae*, *Ornithocercaceae*, *Citharistaceae*; the last two families were set up by KOFOID & SKOGSBERG and seem to be very similar.

Dinophyceae, the second series, does not contain *Dinophysiales*, which seems somewhat confusing. Its Orders are *Gymnodiniales* with six families, *Blastodiniales* with six families, and *Peridiniales* with sixteen families, which are:

Ptychodiscaceae	*Centrodinium*
Glenodiniopsidaceae	*Goniodomaceae*
Glenodiniaceae	*Ceratocorys*
Peridiniaceae	*Oxytoxaceae*
Goniaulacaceae	*Cladopyxiaceae*
Congruentidiaceae	*Ostreopsiaceae*
Protoceratiaceae	*Podolampaceae*
Heterodiniaceae	*Lissodiniaceae*

SCHILLER's family *Ptychodiscaceae*, corresponding to LINDEMANN's Class *Kolkwitziellales*, consists of the following, mostly insufficiently known genera: *Ptychodiscus*, *Kolkwitziella*, *Lophodinium* and *Berghiella*, whilst *Lissaiella*, which LINDEMANN includes in this company, is now left out as a "fragliches *Amphidinium*" and with an interrogation mark is placed to the genus mentioned. Do not *Kolkwitziella*, *Lopho-*

[1] The same applies to the bibliography, where e. g. the author's own works are not all included, and the index (Inhaltsübersicht). In the latter, for example in the second volume, it is surprising to see which families are shown under the Order *Peridiniales*: the last four, Nos. 17—20, belong to other Classes, whose names have been forgotten in the index.

dinium and *Berghiella* also need a question mark, I wonder? As to *Ptychodiscus*, this genus is not well clarified either; at any rate, the two figures from MURRAY & WHITTING which SCHILLER reproduces (*Peridinium ovatum?*) scarcely belong to *Ptychodiscus noctiluca* STEIN. Instead of setting up a provisional family of inadequately known genera, it would perhaps be better to place them under "incertae sedis".

SCHILLER's second and third families, *Glenodiniopsidaceae* and *Glenodiniaceae*, are not separated by any important character at all. The reason for their separation is apparently SCHILLER's effort to discover primitive characters, as is suggested by the following sentence (SCHILLER 1937, p. 80): "Bei manchen Gattungen (of *Glenodiniopsidaceae*) besitzen die Platten eine auffällig unregelmässige oder polygonale Umgrenzung, die man als Ausdruck einer niedrigen Entwicklungsstufe ansehen darf, da auch ihre eigentümliche Anordnung Ähnlichkeit mit der Felderung mancher genauer untersuchter Gymnodinien erkennen lässt." It must be admitted that in its shape and arrangement of plates the genus *Glenodiniopsis* bears some likeness to forms described as *Gymnodinium*; but there is no such likeness for *Sphaerodinium*, whose epitheca plates in fact resemble those of *Peridinium*.—To this family SCHILLER also places *Pyrophacus* side by side with *Hemidinium!* The former differs so much from other Dinoflagellates that it surely deserves to have its own family, *Pyrophacaceae* LINDEMANN, whereas *Hemidinium* is a *Glenodiniaceae*—if this family is to be maintained. SCHILLER states about this family: "Wir stellen die Formen mit weniger als zwei Interkalarplatten in die Gattung *Glenodinium*" 1937, p. 130); it consists chiefly of the genus *Glenodinium* alone, a somewhat heterogeneous genus, to which *Dinosphaera palustris* is also placed. On this species LINDEMANN built up a new family (see above), whereas SCHILLER goes so far as to reject the genus and place the species to *Glenodinium;* originally it was described by LEMMERMANN as a *Gonyaulax*! Would it not be the more reasonable to allow the genus *Dinosphaera* to stand and to place it under *Gonyaulacaceae*? The characters of its plates seem to justify it.

SCHILLER also places *Diplopsalis* under *Glenodinium*, though *Diplopsalis* otherwise is regarded as coming near to *Peridinium* and was almost classified there by PAULSEN (1907, p. 9). Therefore, if the relationship *Peridinium—Diplopsalis* is close, and if on the other hand (according to SCHILLER) *Diplopsalis* may even be placed to the genus *Glenodinium*, the consequence must be that there is no biological basis for separating the two families *Peridiniaceae* and *Glenodiniaceae*, let alone *Glenodiniopsidaceae*. They should be put together as *Peridiniaceae*.

Objection might also be raised to SCHILLER's placing of *Ceratium* under *Heterodiniaceae* (although he does not even mention the genus *Ceratium* in the description of the family. 1937, p. 327), whereas *Centrodinium* (the genus name) is shown as a separate family. In LINDEMANN *Centrodinium* is placed to the family *Ceratiaceae*, whereas *Heterodinium* represents a new family.

Without going into further detail I must say that the taxonomic surveys of this group published by these two modern authors, LINDEMANN and SCHILLER, taken together create confusion, if anything, and that the old, simple division with few

families fitted better in with the imperfect knowledge of the Dinoflagellates with which we must rest content as yet.

On the subject of SCHILLER's general remarks I take the liberty—with qualifications based upon some knowledge of northern plankton—of differing with him as to the variability of the Dinoflagellates. SCHILLER's qualifications are Mediterranean, and it cannot but do good to discuss the different opinions which have been arrived at. To my mind, SCHILLER takes much too theoretical a view of the question. He seems to believe that what has once been demonstrated with regard to one or more Dinoflagellates must thereafter have validity for all. For example (1937, pp. 128—129) he points out that among the Protophytes the absorption of dissolved food takes place through the entire surface of the cell, and the larger this surface is, the more rapid and complete must absorption be: "Nun haben gerade die Bewohner des an Nahrung ärmsten Warmwassers in den Tropenmeeren die grösste Oberflächenentwicklung. Es ist daher naheliegend, die plasmagefüllten Fortsätze der Zellen (Hörner) als physiologische Einrichtungen im Dienste der Nahrungsaufnahme anzusehen." And with this he compares the Phanerogams, whose root system is more strongly developed in oligotrophic than in eutrophic soil, a fertile idea which in the main is doubtless correct. Here SCHILLER is thinking of PETERS' (1932) demonstration that in the Atlantic *Ceratium* has the shorter horns and more thickly-walled theca the more nutritive the water is—and vice versa. This, however, is contested by STEEMANN NIELSEN (1934), who in the Pacific found that the length of the horns does not depend upon the quantity of nutrition but upon the temperature and neritic influence, as low temperature and neritic influence cause longer horns and vice versa. SCHILLER also mentions this elsewhere (1937, p. 353). On p. 129 he goes farther and points out that families like *Ornithocercus*, *Histioneis*, *Ceratocorys* and *Ceratium* are much differentiated warm water types and that the most long-horned species of *Peridinium*, e. g. *P. Murrayi*, *P. grande*, *P. elegans*, *P. fatulipes*, live exclusively in warm water. To this, however, I would point out that *P. oceanicum*, perhaps the most long-horned *Peridinium* known to us, has been recorded in Davis Strait (by VANHÖFFEN), and although it or closely related forms are also known in warmer seas, the Mediterranean for instance, it is observed most frequently in the North Atlantic.

The two examples to which I have referred seem to show that the matter is not so simple as SCHILLER seems to believe, but that the question of the cause of long or short horns—indeed of the variation of the Dinoflagellates—has not yet been settled.

As regards the fresh water species, LEFÈVRE's fine "Monographie des espèces d'eau douce du genre *Peridinium*" (1928) contains handsome examples of variation. Take *P. gatunense* NYGAARD (p. 94) for example. LEFÈVRE lists the following variants:

(1) *α collineatum* and *γ travectum*, apparently small, purely phenotypical differences.
(2) var. *zonatum* (PLAYF.), almost globular, no apical spines, epitheca larger than hypotheca, tabulation as on the main species, but the plates are not areolated but provided with a few wavy lines. Found only in Australia.

(3) var. *madagascariensis* (LEF.). Ornamentation consisting of pronounced, parallel longitudinal ribs. Found only in Madagascar.
(4) f. *globosum*. The plates convex so that the cell is almost globular. France. Presumably another phenotypical deviation.
(5) f. *majus*. No hyaline lists at the transversal furrow. Reticular plates. Madagascar.
(6) f. *ornatum*. Ornamentation consists of thick lists in no definite order or direction. Madagascar.

How shall we rightly regard such a form circle, spread as it is almost all over the world (Panama, France, the Cameroons, Madagascar)? The question of how it has obtained such a world-wide distribution cannot, I suppose, have its answer in birds? or, as WESENBERG-LUND thinks, the very high geological age of many freshwater organisms? Whatever it may be, it is improbable that for instance the population in Lake Gatun in Panama and that in Madagascar have much mutual intercourse; the more or less isolated populations must have been left chiefly to themselves and they have varied independently.

The fact that LEFÈVRE describes some as varieties, others as *formae*, is explained by the purpose of his work (p. 5): „Le présent travail a en effet pour objet une étude systematique du genre, mais une étude que je me suis efforcé de baser sur la connaissance des variations, de façon à pouvoir rapprocher des espèces qu'on croyait autrefois très éloignées. J'ai pu ainsi réduire le nombre des types en introduisant les espèces déchues en variétés des premières. On se rend de cette façon beaucoup mieux compte de la parenté des espèces de leur "possibilités", de leur évolution." And SCHILLER had a similar intention with his work.

Now as we know, "species" is a difficult concept. Among the higher plants the best definition is perhaps: Species is the name given to two forms that are mutually sterile; or better: whose mutual offspring are sterile. But as the Dinoflagellates are asexual (as far as we know) and moreover variable, we cannot actually speak of their species. Accordingly, we might ask the question: Which deviations from a main form are merely phenotypic, which are genotypic? Or, in other words, are the forms and varieties of—in this case *Peridinium gatunense*—direct results of exterior influences, or may some of them be due to a genotypic change in the nature of the organism, possibly induced by exterior conditions but now constant and thus now a new biotype? I am inclined to think that the latter is probable as regards *zonatum* and *madagascariensis* (which also are "espèces déchues"), both because they deviate more from the main form than "the forms" and because they occur in particularly remote populations. This is true especially of *zonatum*, as no other *gatunense* forms are known in Australia, whereas f. *majus*, which is very like the main form, also occurs in Madagascar and therefore perhaps reduces the value of this assumption.

But if *zonatum* and *madagascariensis* are biotypes whose characters are genotypic, then they are what is usually called "species", regardless of their relationship

to *gatunense* and no matter whether we call them "species" or "variety"; they have a taxonomic and biological independence and are not phenotypic "forms."

To return to the marine Dinoflagellates. It is evident that the Dinoflagellates possess a great capacity for variation, but there are differences; some species or groups are more variable than others. With regard to tabulation, DANGEARD (1927 c, p. 2) said that in some species we find "des modifications fortuites et très rares," in others, e. g. *Peridinium oblongum* and *P. ovatum* "des variations normales et fixées," all concerning the intercalary plate 2a on the dorsal side of the epitheca. Let us turn to *P. ovatum*. This species is a fairly constant one in the North Atlantic, easily recognizable by the depressed shape, the short apical horn, right-handed girdle and two small, narrow-winged or unwinged spines close behind the end of the longitudinal furrow. As such it is depicted e. g. by GRAN 1902 (fig. 11), FAURÉ-FREMIET (1908, Pl. 15, fig. 5) (*P. lenticulatum*), by PAULSEN (1908, fig. 54) and by LEBOUR (1925, Pl. 26, fig. 1). MANGIN (1911, fig. 1) from La Manche shows "individus dextres et senestres" of this species in almost equal numbers, *i. e.* he considers there are almost equally many right-handed and left-handed individuals. I wonder if MANGIN has not been dealing with dead cells, or has treated his material with too strong a reagent and then (as already assumed by PETERS, 1928, p. 114) drawn their ventral sides whether they were turned downwards or upwards. About half of them in that case would be reversions of the actual pictures.[1]

Peridinium ovatum is very common in the northern Atlantic. There are some individuals there which lack the two spines. As a rule the tabulation is Meta quadra; DANGEARD (1926, fig. 12 F. G.) figures an Ortho quadra from the coast of France, but does not say it is an Ortho. LEBOUR (1925, p. 110) found the species Meta penta in many localities, sometimes all individuals, sometimes mixed with Meta quadra. DANGEARD (1927 c, p. 4) for those which are Meta penta set up the variety var. *asymmetricum*, which was rare in the Atlantic west of France but dominant elsewhere. RICHARD BIEBL (1936), too, from the North Atlantic figured the normal quadra form and "the variation form," which is penta (fig. 3). Finally, I myself in plankton from North Icelandic waters have examined the tabulation of 20 *P. ovatum:* they were all Meta, 12 of them were quadra, 6 penta and 2 intermediates, for 2a was in contact with 3'' only at one point.

In tropical Atlantic waters west of Africa *P. ovatum* is replaced by a larger, asymmetrical form which has no spines and lacks supporting spines in the girdle lists. At first DANGEARD (1927 c) called it var. *major*, but in 1927 b (p. 360) he elevated it to a "species" after having verified the constancy of the characters. He called it "espèce cantonnée dans la région chaude," whereas both forms of *P. ovatum* are found in temperate waters separately or mixed. To *P. ovatum* DANG. must also be reckoned *P. ovatum* v. *inarmata* MATZ. (1933, p. 476), which is sometimes

[1] MANGIN did the same in another place: his *Peridinium sphaeroideum* (1922, fig. 24, II) is drawn from ventral and dorsal sides—the same cell—and the ventral view is an inversion, *i. e.* it turned downwards when drawn.

quadra and sometimes penta; furthermore, *P. simulum* PAULS. should also be placed under it.

I should consider it probable that *P. majus* (not named by SCHILLER) should be regarded as a separate warm-water "species", a biotype, whereas *asymmetricum* and *symmetricum* must be forms or phenotypes. For the diagnosis of "species" we should therefore require not only the morphological description but also as far as possible its occurrence, the kind of water in which it is found; because the fact that it is not found together with a related species is one of the reasons why we regard it as foreign to it.

SCHILLER (1937, p. 186) regards *P. ovatum* as a variety of *P. globulus* STEIN, and under the latter places quite a number of different forms, which I shall discuss and judge in the following.

First the main species, *P. globulus* STEIN, of which its author reproduces three drawings and a fourth with spines, which later becomes *P. quarnerense*. The three drawings depict a globular species with short, "affixed" apical horns, the girdle strongly right-handed (displaced as much as the width of the girdle or more), the longitudinal furrow slightly curved. Almost "planozone". Two of the figures show clearly that on the ventral side the plates have a Meta arrangement; the third, which is seen from the dorsal side, shows a 2a that is hexa, not angular but almost regularly elliptic. No such cell has been found since, or at any rate published. Moreover, Meta hexa is a rare combination ("bisher in der Natur nicht festgestellt" (PETERS)), though I shall revert to this below; and whereas all specimens which later have been described as *P. globulus* are Meta, the dorsal side seems to be variable; BROCH (1910a, fig. 2) has quadra, DANGEARD (1927b, p. 361, fig. 27, 1927c, fig. 8) penta and MATZENAUER (1933, fig. 63a, b) likewise penta. On this subject DANGEARD says (1927c, p. 13): "Par conséquent le cas du *P. globulus* se pose de la façon suivante: ou bien il existe trois races tabulaires différant entre elles par la disposition de la plaque médio-dorsale δ, (l'une correspondant aux dessins de STEIN et du type "para"[1], l'autre à ceux de BROCH et du type "*divergens*", le troisième à notre description et du type "*pyriformia*"), ou bien il y a eu confusion par les autres (should doubtless read "auteurs") entre plusieurs espèces distinctes.

Nous croyons, jusqu'à nouvel ordre, que cette dernière hypothèse doit être rejetée et qu'il s'agit bien partout de la même espèce, et il est d'autre part difficile de croire à une erreur dans le description des plaques, étant données les figures si nettes qui en ont été données.

Il y a donc lieu de croire, jusqu'à plus ample informé, à l'existence pour le *P. globulus* de plusieures lignées de tabulation différente, comparables à celles qui viennent d'être reconnues pour le *P. ovatum* et le *P. oblongum*". In a footnote he adds: "Nous ferons remarquer cependant que certaines figures de BROCH pour le *P. globulus* pourraient résulter à la rigueur d'une confusion avec un *P. ovatum* globuleux et dépourvu d'épines antapicales."

[1] *I. e.* what we call Meta, hexa.

At the present moment I have nothing better to put in place of this statement of DANGEARD's; I also agree with him regarding his reservation concerning BROCH's *P. globulus*; I am not certain that BROCH's figures belong together, or that the forms illustrated are rightly placed here. In 1930 (p. 60) I voiced the assumption that the *P. spheroides* described by DANGEARD represents the true *P. globulus* STEIN, and I still assume that this is probable or possible; it cannot be proved, however, and therefore it is best to retain DANGEARD's name.

To this certainly insufficiently known species, *P. globulus* STEIN, SCHILLER places as "varieties" *P. ovatum* (POUCH.) SCHÜTT and *P. quarnerense* (STEIN) SCHRÖDER, which generally have been regarded as species, and a few more that are mentioned below.

What does SCHILLER understand by "variety"? He writes: (1937, p. 186) "*Peridinium globulus* und seine Variation kenne ich aus der Adria durch vieljährige Beobachtungen," and: "In der Adria treten die kugeligen wie querovalen Formen ohne Bindung an Zeit und Ort auf. Ebenso nach MATZENAUER im Indischen Ozean. Aber eine gewisse Bindung der Körperform and die Grösse ist offenbar." It seems to emerge from this that SCHILLER regards these "varieties" as results of a fortuitous variation (modification) of a genotypically homogeneous material. This is what in taxonomy is usually called by the name of "forma." To me the word "variety" seems inapplicable to these asexual organisms, of the causes of whose variation we know practically nothing; it is difficult enough to distinguish between "forma": phenotype, and "species": biotype.

However, the fact that *P. globulus*, *P. ovatum* and *P. quarnerense* occur together in the Adriatic need not signify that they are specifically associated. STEEMANN NIELSEN (1941) has shown that whereas closely related species of sexed organisms cannot occur together, because if they did they would cross, whereby the boundary between them would be obliterated, it is common for closely related species of asexual organisms to have the same distribution because they often have the same life requirements and there is no crossing. *P. ovatum* is a eurythermic species and common in the northern Atlantic, both the others are more stenothermic and are rarely or never seen in northern waters, but are common in the Mediterranean and other warm waters. For this reason alone *P. ovatum* differs from *P. globulus*, but morphologically too *P. ovatum* and *P. globulus* are so different that it is not permissible to unite them.

(1) The form: *P. globulus* is globular, *P. ovatum* lenticular. It was asserted by BROCH (1910) that the *Peridinium* cell may change its form through the growth of the intercalary striae and from being globular when young become lenticular. PETERS (1928, p. 104) holds, on the other hand, that the *Peridinium*—theca "äusserst formgetreu zu wachsen pflegt[1]."

Moreover, *P. ovatum* has a gradually rising apical horn, whereas on *P. globulus*

[1] SCHILLER (1937, p. 187) considers that the present writer has construed "einen in dem Masse gar nicht bestehenden" difference between BROCH and PETERS and says that PETERS' excellent studies have confirmed BROCH's results. However, PETERS himself declares (l. c.) "zu dieser Auffassung von BROCH stehen meine Ergebnisse im Gegensatz."

the apical horn is "affixed." *P. ovatum* has two antapical spines (which are rarely lacking in northern seas), whereas *P. globulus* is inermis.

(2) Arrangement of plates. Here we must differentiate between *P. spheroides* DANG. (which SCHILLER also incorporates in *P. globulus*) and *P. globulus* DANGEARD and BROCH. Like *P. ovatum*, *P. spheroides* is Meta. The four apical plates are very characteristic, 3′ being quite small and foursided. The accessory plates are of unequal sizes; 2a is the largest and it is hexa, or strictly hepta, as it borders upon seven neighbouring plates (*i. e.* 2′ in addition to the usual six, as 1a does not border upon 3′), and it lies obliquely left of the apical plate 1′; in this form it is drawn unanimously by DANGEARD (1927 a, fig. 3), PAULSEN (1930, fig. 31) and MATZENAUER (1933, fig. 62 b). Without doubt *P. spheroides* DANG. is a separate species.

The *Peridinium* which DANGEARD (1927 c) describes and figures as "*P. globulus* STEIN" must belong to another species than *P. spheroides*; it is Meta penta, but nevertheless its arrangement of plates is more symmetrical than that of *P. spheroides*; 3′ is larger, and the three accessory plates are of almost equal size. The longitudinal furrow is short, and there are no spines; it should not be grouped together with others from which it differs, even if its arrangement of plates is like that of *P. ovatum;* further observations of it may perhaps provide more information of the entire form-circle of "*P. globulus*".—*P. globosum* DANGEARD may possibly be an abnormal *P. spheroides*; of its accessory plates, 3a is the largest, 2a is very small, which might perhaps explain why the girdle has become circular. But it is Ortho and has no "bouton apical". The sides of the longitudinal furrow converge below and the girdle has very narrow lists. It has only been found once and, as SCHILLER says, must be allowed to lie until further investigations have been made.

Peridinium quarnerense, which SCHRÖDER first described as a variety of *P. globulus* with reference to STEIN's pl. 9, fig. 8 (1883), was "promoted" by BROCH (1910 a, fig. 3) to a species, but SCHILLER (1937, p. 184) again lists it as a variety of *P. globulus*, though regarding it as "eine bestachelte Form"; in that case it should surely have been called a forma, it has nothing to do with *P. spheroides*, but is possibly a *P. globulus* furnished with spines; it is insufficiently known, however. SCHÜTT's pl. 15, fig. 48 (1895) corresponds exactly to STEIN's fundamental figure (pl. 9, fig. 8); both are almost globular with "affixed" apical horn, girdle strongly right-handed, curved longitudinal furrow and two long spines without fins. Neither of these figures, however, shows the arrangement of the epithecal plates. No doubt it is the same form as that shown by BROCH (1910 a, fig. 3); his two specimens are (calculated) 35 and 53 μ long and Meta quadra. *P. quarnerense* (SCHRÖDER) SCHILLER (1929, fig. 18), is also Meta quadra; it is 62 μ long (calculated). DANGEARD (1927 c, fig. 9) from the tropical sea west of Africa describes a similar form about 60 μ long which is Meta penta, and, despite this deviation, he is inclined to place it to *P. quarnerense*, because in all other respects is has the morphological characters of that species. PAULSEN (1930, fig. 32) illustrates a similar penta form from the Alboran Sea; MATZENAUER (1933, p. 476) found it to be common in the Indian Ocean. He records distinct differ-

ences in size and also in shape: the small specimens are chiefly globular, the larger ones mostly somewhat flattened, "Stachel wohl immer ausgebildet"; his forms, too, are penta ("dorsale Interkalare unsymmetrisch").

In my opinion, the two forms, quadra and penta, should be regarded as one species, *P. quarnerense*, and this species should be kept separate from *P. globulus*, for the present at any rate; the presence or absence of antapical spines would then be the more correct mark of distinction.

The other forms referred by SCHILLER to *P. globulus* var. *quarnerense* are: *P. cerasus*, PAULS., *P. patens* DANG. and *P. subpyriforme* DANG.

P. cerasus was described in 1907 (p. 12) from the southern part of the North Sea. The cell is almost globular, it has a distinct and fairly long apical horn, the girdle is slightly right-handed and there are two antapical spines, not at the margin of the longitudinal furrow but unsymmetrically at a distance from it. Meta quadra. Length (without spines) 40 μ; from the east coast of Greenland PAULSEN published a drawing (1911, p. 307) and a measurement: 36 μ. With a mark of interrogation MEUNIER (1910, p. 37, pl. 2, figs. 27—29) published three figures from the Barents Sea which seem to be of the same form, except that he drew it as Ortho. (As a matter of fact, MEUNIER often drew the plate arrangements inaccurately.[1])

PAVILLARD (1916, p. 34) considered that *P. quarnerense* and *P. cerasus* are distinctly specifically different and published a figure (without plates) which undoubtedly was *P. cerasus*, calculated length 43 μ; in the Gulf of Lyon the species was found on rare occasions in the cold water of spring. BÖHM (1933, fig. 2) draws a specimen from the Adriatic (calculated length about 54 μ). He saw the species only once in winter. "Wahrscheinlich allogen." PETERS (1928, p. 45), who found the species in the Mediterranean, published four good figures and remarks that the left margin of the longitudinal furrow is always more distinct than the right, and that the theca is always strongly punctate or pored. The tabulation is very constant; a feature that is particularly characteristic is that the precingular 1″ is very small in contrast to the large 7″; but he adds that both the apical horn and the antapical spines may be longer or shorter. "Wieweit *P. cerasus* mit *P. quarnerense* SCHRÖDER verwandt ist, müssen erst Variationsuntersuchungen zeigen." Naturally, they are related, but scarcely identical. The *P. cerasus* drawn by LEBOUR (1925, pl. 27, fig. 1) and by DANGEARD (1927b, p. 358), WAILES (1928, pl. 1, figs. 30—31) and PETERS (1930, fig. 40E) has a short or almost no apical horn (moreover, DANGEARD's form is hexa), for which reason I am almost inclined to rule them out, because the species, where I have seen it, seems to be constant as regards its apical horn; however, PETERS has seen something different, and therefore the question must remain open.

MATZENAUER's *P. sinaicum* (1933, p. 459) from three stations in the Indian

[1] MEUNIER adds: Qui nous dira que notre rapprochement est fondé? Tant il est vrai que dans ce domaine d'organismes très petits, très simples et fort similaires au fond, la moindre incorrection du dessin fausse complètement la physionomie des objets représentés!

L'identification tentée ici ne va pas sans beaucoup de bonne volonté; mais nous ne la ménageons pas, dans le but de réduire la synonymie.

Ocean agrees in form and size (length 28—31 μ) exactly with *P. cerasus*, the apical horn especially being the same; the arrangenemt of plates is not given, however.

P. patens DANGEARD (1927 b, p. 372), which SCHILLER also lists as a synonym of *P. quarnerense*, is a globular form with two short antapical spines; it is Meta hexa (an uncommon combination[1]), slightly right-handed. DANGEARD places it to Sect. *Paraperidinium*. It resembles *P. sphaeroidea* ABÉ (which is quadra), but has shorter spines and narrower lists along the longitudinal furrow; the apical horn is a small "bouton apical". DANGEARD gives the length as 60 μ. CANDEIAS (1930, p. 26, pl. 2, figs. 47—48) illustrates from Sesimbra, Portugal, exactly the same Meta hexa form, whose length I have calculated at about 67 μ. CANDEIAS places it with some doubt to *P. patens* and thinks that perhaps it might be a deformed *Paraperidinium*, because, as far as I understand, PETERS (1928) denied that the combination Meta hexa should exist in nature. As this same form has been described similarly by two different authors, there is reason for regarding it as an independent species.

P. subpyriforme DANG., also classified as *P. quarnerense* by SCHILLER, was described from the Mediterranean (1927 b, p. 358, fig. 21 d—e; it was also figured 1932, p. 342, fig. V a, b). The shape of the cell is "ovalaire ou elliptique," but according to the figures it is more globular; it is Meta penta with a very short "affixed" apical horn, slightly right-handed; the longitudinal furrow is narrow and there are two short antapical spines, the right one with a small subspine. Length 50—55 μ. MATZENAUER (1933, p. 460) and ABÉ (1936 b, figs. 30—37) agree in their description of the same form; in particular, ABÉ's beautiful figures show the left list of the longitudinal furrow borne by the left antapical spine, whereas the right spine is some distance from the furrow.—This species differs from *P. patens* by the shape of the cell and by being penta; nevertheless, they seem to be so closely related that one feels inclined to unite them in one species, though this would scarcely be correct without further study. And when one views the species established by ABÉ (1936 b): *P. solitarium*, which is very like *P. subpyriforme*, and *P. ventralis*, which comes close to *P. quarnerense*, one is fascinated by the multitude of forms and by doubt as to the possibility of rightly comprehending it.

P. spitzbergense BROCH (1910 b, p. 49, fig. 24) must also be mentioned here for the sake of completeness, as SCHILLER also shows it with a ? as a synonym of *P. globulus*. Shape globular, girdle right-handed. A small antapical spine at the right margin of the longitudinal furrow, a well-developed list on its left margin. The four plates 1′, 2′, 1″ and 2″ meet at one point.

This species should perhaps be placed to the form-rich group "incertae sedis".

Other examples of "microspecies" that may be instanced are *P. crassipes* and *P. curtipes*.

P. crassipes was described in 1907 by KOFOID (p. 309, pl. 31, fig. 46, 47) from the neritic plankton of the Pacific off South California (St. Diego). In the same year

[1] The following species are also Meta hexa: *P. asperum* WAILES, *P. dakariensis* DANG. and *P. hirobis* ABÉ.

PAULSEN (p. 17, fig. 24) to this species placed a form which previously had been called *P. divergens* and which is said to be oceanic and to be of no uncommon occurrence in the North Sea and the Skagerak. There is no denying that these two peridinians are very much alike; compare, for example, KOFOID's fig. 46 with PAULSEN's fig. 24 b.

In 1912 E. JØRGENSEN wrote (p. 8) " . . . *P. crassipes* PAULSEN anbelangend, scheint es mir — jedenfalls vorläufig — nicht praktisch, diesen Namen einer gemeinen Warmwasserart ohne weiteres auf unser gelbe *P. crassipes* PAULSEN überzuführen[1] . . Bei der Warmwasserart ist die linke Partie an der ventralen Seite sehr hervortretend und die Querfurche selbst rasch und deutlich aufsteigend, was durch die erwähnte Asymmetrie der Querfurchenregion noch stärker augenfallend ist," and suggested the name of *P. curtipes* for the northern species (at the same time renaming PAULSEN's *P. divergens P. speciosum*),

The reasonableness of not uniting a cold-water and a warm-water form under the same specific name, together with JØRGENSEN's reputation as a keen-sighted taxonomist, had the result that many plankton students kept the northern *P. curtipes* and the sub-tropical *P. crassipes* separate: DANGEARD (1932) speaks of "cette distinction fort utile et très justifiée" (p. 344), whereas others put them together on account of the great mutual similarity. SCHILLER (1937, p. 225) has no doubt: "Ich wage es nicht einmal, *curtipes* als forma zu *crassipes* zu stellen," as both colour and other alleged signs of separation are variable, and "wollte man analog wie hier diese Querfurchenpartie bei anderen Arten verwenden, so kämen neue Arten und damit ebensolche Verwirrung heraus wie hier."

It must be admitted that the question of how these two species should be designated is difficult. It is tempting—and also easy for future workers who are to determine plankton—to place them together; but if they can be kept apart it should be done, because for the purpose of our research it is more important to separate than to mix together. We do not know how far the variability goes; but, speaking generally, we see that the warm-water forms are left-handed, whereas those from cold and temperate seas have almost a circular girdle, and therefore to me it seems most correct that, until typical forms of both are found together, intermixed, they should be kept apart. At Banyuls-sur-Mer DANGEARD (1932) found *P. crassipes* exclusively, and he contests (wrongly, I consider) BROCH's record of the circular-girdled form from Rovigno.

Most of the published figures of the *P. crassipes-curtipes* complex can easily be identified as the one or the other of the two forms. The drawings reproduced by SCHILLER (fig. 220, p. 224) are all of *P. curtipes* except a, k, and j, which are *P. crassipes* (o and l perhaps are doubtful). Below I shall go through all known figures in order to throw further light on the question.

P. crassipes: KOFOID 1907, pl. 31, figs. 46—47 (from the tropical Pacific) (SCHILLER fig. 220 a)—ABÉ 1927, fig. 26, 27 (from the Sea of Japan).—DANGEARD 1927 b, fig. 32 c

[1] JØRGENSEN's remark about the colour (l. c.) is quite misleading; as far as I know (PAULSEN 1908), both species have yellow chromatophores and often contain red oil.

(from the tropical Atlantic).—PAULSEN 1930, fig. 36 (Mediterranean) (SCHILLER fig. 220j). —DANGEARD 1932, fig. VII (Banyuls-sur-Mer).—MATZENAUER 1933, fig. 50 ("*P. crassipes*") and fig. 52 ("*P. curtipes*") (from the tropical Indian Ocean). MATZENAUER makes the distinction between the two species that *P. crassipes* has straighter sides (conical-concave), whereas *P. curtipes* has more concave sides, the epitheca tapering rather suddenly into a conical antapical horn. Moreover, *P. crassipes* has antapical horns of unequal length, the right being the longer (this feature was also pointed out by DANGEARD and by PAULSEN), whereas *P. curtipes* tends to have a longer left horn. From both species MATZENAUER sets up a "f. *asymmetrica.*"—I consider that both are *P. crassipes* and that the differences pointed out are irrelevant: for *P. crassipes* the conical and the concave outline were already drawn by PAULSEN 1907. Both MATZENAUER's forms are from tropical seas. BÖHM (1933, fig. 4a—g) examined and figured *P. crassipes* from the Adriatic; he did not see the other species, *P. curtipes.* His seven figures express well the variability of the species, but they are all distinctly *P. crassipes.* Its habitus is very variable, writes BÖHM: concave, almost straight or broken ("geknickt") lateral contours, the displacement of the girdle varies, one furrow width or twice that. The antapical horns are rarely hollow at the tip, which is often drawn out into a spine of varying length. The theca is thick, punctate or finely reticulate; length 84—124 μ, breadth 75—108 μ.—By means of measurements of the species BÖHM shows that it is the intercalary striae that grow in width and increase the size of the cell. A remarkable feature, however, is the occurrence of a few giant forms with no intercalary striae at all.

P. curtipes PAULSEN 1907 fig. 24a—f; 1908, fig. 73a—f ("*P. crassipes*") (from Iceland and the Murman coast); the latter (fig. d) deviates by having concave epitheca sides. LINDEMANN 1923, figs. 80—86 (from the Bosporus) ("*P. crassipes*").—DANGEARD 1926, fig. 12 ("*P. crassipes*") (from the western part of the Channel).—PETERS 1928, fig. 11 ("*P. crassipes*") (from the Weddell Sea); two of the figures are penta or, as PETERS says, have asymmetrical "Täfelung." PETERS does not consider JØRGENSEN's separation of the two species as justified; the difference in the girdle, he considers, is a variable character.

The following figures seem doubtful to me: BROCH 1910b, Spitzbergen, fig. 27 under the name *P. crassipes.* The figure is reproduced by LEBOUR (1925, fig. 39); it is not seen straight from the ventral side.—DANGEARD 1927b, fig. 32b ("*P. curtipes*") is drawn from the dorsal side and can hardly be determined. DANGEARD acknowledges the difference between *P. crassipes* and *P. curtipes;* from the western part of the Channel he has only *P. crassipes,* but from the "Sylvana" cruise the same author has both *P. crassipes* and *P. curtipes;* he doubts that *P. curtipes* can be a northern species. And if we check with the station map we find that "*P. curtipes*" has been found mostly down off the coast of Guinea, whereas "*P. crassipes*" has been demonstrated from Cape Finisterre to approximately lat. 20° N.

Other examples are *P. pallidum* OSTF. and *P. Schilleri* PAULS.; the former is a common northern species, the latter from the Mediterranean. SCHILLER (1937,

p. 211) regards the latter as a variety of the former. By this he no doubt means that it is different from *P. pallidum*, which it resembles. But it is either a "forma," conditioned by external factors, a modification which in some generation or other may turn back to the main form, or it is conditioned genotypically, in which case it must be regarded as a "species"; and having regard to the distance dividing *P. Schilleri* from *P. pallidum*, it is probable that these two are different "specifically."

Thereafter I would say quite briefly that SCHILLER's reference of *P. oviforme* DANG. (SCHILLER 1937, p. 195, fig. 191 h—n) to *P. pyriforme* seems quite unjustified, as I imagine anyone can see on viewing the figures—"c'est surtout à la physionomie cellulaire qu'il faudra appel pour fixer l'espèce" (LEFÈVRE 1928, p. 64). Likewise the incorporation (SCHILLER l. c., p. 199, fig. 194 e—i) of SCHILLER's *P. styliferum* in *P. breve* PAULSEN.

For the rest, all matters of detail to which a discussion of such a large work might call for will not be touched upon here (some I shall mention in the latter part of the present work); but I shall try to submit some general remarks on the Algae group that is of interest to us at the moment.

SCHILLER's taxonomic analysis of the Dinoflagellates has as its background the impression of chaos caused by the many described forms, and as its object an effort to bring order into this chaos. He says, *inter alia*, that it is so difficult to describe Dinoflagellates correctly that analysts of plankton samples become apt to describe the forms they find as new species, because this is easier than looking for the correct name in the great and much scattered literature.

In what precedes I have tried to show that SCHILLER has not always been felicitous in his efforts to diminish the number of recognized species by listing a number of described species as synonyms. As the chief example I took *P. globulus* STEIN, a species to which several others are placed as synonyms: *P. spheroides* DANG., *P. simulum* PAULS., *P. quarnerense* (SCHRÖD.) BROCH, *P. cerasus* PAULS., *P. patens* DANG., *P. subpyriforme* DANG., *P. ovatum* (POUCH.) SCHÜTT, of which seven species none, in the opinion of the present writer, belong to *P. globulus*; most of them should be regarded as good species. And if we can say with SCHILLER that there is chaos, it is not taxonomy but nature that it is chaotic, and it is of nature that we must try to to give a picture. To produce that picture, however, the oft-mentioned variability of the Dinoflagellates must be combined with their geographical distribution.

As regards this variability of the Dinoflagellates, we must first realise that these organisms (as far as we know) are asexual. If this is true, it provides us with the assurance that no hybrids arise between the different forms. SCHILLER remarks (1937, p. 74): "Die Gattungen *Peridinium*, *Ceratium* sind wie *Rosa*, *Rubus* u. v. a. Musterbeispiele dafür, dass Arten im Sinne der klassischen Systematik in der Natur gar nicht existieren, sondern ein (allerdings unentbehrliches) Ergebnis des Ordnungstriebes der Menschen sind," and he is quite right. It may be observed, however, that both *Rosa* and *Rubus* are sexed and that the multiplicity of forms of these genera

is comprehensible as hybrid complexes—which is precluded as far as *Peridinium* and *Ceratium* are concerned. As a matter of fact, however, there are different and determinable forms of species of sexed organisms. For example, ornithologists describe races of bird species, the same species differing in appearance in different regions: *e. g.* a Greenland, a Scandinavian and a North Siberian race. In typical cases these races are easy to distinguish, but they run one into the other, presumably by crossing, because the different races are mutually fertile. We find a similar phenomenon among plants. Many phanerogams vary, in that in various parts of the same country, Skåne for example, varieties have arisen in the course of time, so-called ecotypes, which do not cross because they are geographically separated and which therefore remain distinct taxonomically as well. But if separated ecotypes are brought together, they cross and form transitions (Turesson, 1922).

Taraxacum, for example, is asexual and polymorphous; there are more than a hundred species of *Taraxacum* in Denmark, over two hundred in Sweden, and it has been shown that Iceland has a *Taraxacum* flora that is quite different from Denmark's and that several parts of Europe again have entirely different species (see Christiansen, 1941; Sørensen, 1941).

Accordingly, as regards variability *Taraxacum* provides a picture similar to *Peridinium*: both are apomictic genera divided up into numerous "microspecies". These "microspecies" in *Taraxacum* are on the whole constant when cultivated through several generations; a few per cent of them segregate new biotypes which are thought to arise by alteration of somatic cells. And, naturally, closely related "microspecies" often occur together; they cannot cross-pollinate one another. Furthermore, as new biotypes may constantly occur, it is also natural that the *Taraxacum* floras of the different countries prove on examination to differ one from the other, even if perhaps they are all ordinary *Taraxacum vulgare* (*officinale*) to the casual glance. The plant geographer, who studies plant associations and their ecology, may simply record "*Taraxacum vulgare*," but a florist or a student of genetics must go deeper and try to analyse the *Taraxacum* populations occurring in nature; this he can do only by cultivation experiments. These experiments have led to the result that the *Taraxacum* species form a "chaos," which, however, it has been possible to straighten out to some extent by diligence and insight.

It is probable that genetically the genera of the Dinoflagellates, e. g. *Peridinium*, have a history similar to that of *Taraxacum*; but two circumstances make their study very difficult. The first is that they become mixed together by the movements of the water, and the second—and more important—that they refuse to be cultivated; at any rate it has hitherto been impossible to cultivate them.[1]

For these reasons we cannot yet decide which forms are biotypes and which

[1] Of late years scientists studying at Professor Braarud's Laboratory in Oslo have succeeded in cultivating a number of species of the Dinoflagellates, *e. g. Ceratium fusus, Goniaulax polyedra, G. tamarensis, Peridinium triquetrum, P. trochoideum, Protoceratium reticulatum*.—J. Gr.

are phenotypes, modifications engendered by external factors. SCHILLER attaches importance to the latter, being of opinion that fluctuating variation lies at the bottom of the multiplicity of forms.

It is no doubt probable that fluctuating variation plays some rôle, but just as probable that mutation takes place, whereby new, constant biotypes are segregated. Indeed, we may say that if SCHILLER is right in building his system upon a line of evolution from primitive to more highly developed forms, it is probable that this evolution is still in process and that new forms consequently must always be in process of creation; for why should evolution suddenly have completed its course? Evolution is always taking place, species are probably never static; indeed, there are writers who hold that a species is "the momentary realisation of a line of evolution, this latter being the fundamental unit" (FÆGRI, 1937).

In the course of such an evolution some characters must have become fixed, for instance the difference in the tabulation between *Goniaulax* and *Peridinium*. Others perhaps are doubtful, such as the distinction between *Archaeperidinium* JØRGENSEN, which has but two intercalary plates in the epitheca, and *Veroperidinium* PAULS., which has three, while others again seem to be quite uncertain, such as the various forms of the 2a-intercalary plate (quadra or penta) in *Peridinium ovatum*. The same applies to every other possible character. We can now regard and describe all occurring forms as species; this has the advantage that we acquire a survey, an inventory, of everything. On this SCHILLER says (1937, p. 125): "Dieser in der jungen Systematik aller Organismengruppen zu beobachtende Vorgang hat bei den Dinoflagellaten seine Berechtigung nunmehr verloren, da wir die überaus grosse Variabilität und glücklicherweise auch bereits deren Ursache und Richtung erkennen können." It is going rather far to say that we know the cause and direction of variability. Presumably SCHILLER was thinking of the freshwater *Peridineae*, which generally are more variable than the marine and whose character is said to change with the physical and chemical properties of the water, so that they become different from one pond to another, and from lake to lake: for instance, a species that is usually spineless acquires spines, and is regarded as a "*forma armata*".

Let us grant that this may be true and apply to freshwater Dinoflagellates (but see above, p. 9—10). But it is dangerous to generalize. "Tel caractère qui nous parait relativement fixe dans un groupe nous semble au contraire très variable dans un autre" (LEFÈVRE 1928, p. 64). Therefore, if the presence or absence of spines is a variable character among the freshwater species (or some of them), it need not be so among the marine species; at any rate it is not so always, as has been indicated regarding *Peridinium ovatum*, whose few spineless individuals must be regarded as deformations.

On the whole, it is impossible to say definitely what characters are fixed; all are valid, but none can decide whether a taxonomic unit is a *species* or a *forma*.

Species and *forma*, these are the two categories which perhaps we should employ. SCHILLER also used *varietas*, but he does not tell how he distinguishes his categories;

one gets the impression that a small deviation from the specific characters is called a *varietas* and a smaller deviation is called a *forma*—quite subjectively.

HUSTEDT (1937, p. 186) defines a variety thus: "Kleine Einheiten, die sich von den Arten, zu deren Formenkreis sie gehören, nur durch ein oder wenige, nach unseren Begriffen geringfügige, aber erblich bedingte Merkmale unterscheiden. Sie sind daher im erbbiologischem Sinne konstant . . . Demgegenüber ist die "*forma*" keine geschlossene Einheit, sie ist nicht erblich bedingt . . . durch lückenlose Übergänge mit der Art verbunden und praktisch nicht von ihr zu trennen." To this clear formulation I would say that when a species is distinguishable from the variety by the latter's deviating in "small, in our conception insignificant, but genetically conditioned characters," then the question may be asked what are insignificant characters; and the answer is that no constant characters are insignificant, and that variety, rationally speaking, is thus the same as species.

But as in dealing with the Dinoflagellates we do not know what characters are constant and what are variable, we must (and this applies on the whole to taxonomy) regard species as a practical concept; here I shall quote HUSTEDT again (l. c., p. 471—472): "Nahe verwandte Formen, die regelmässig unter den gleichen ökologischen Bedingungen nebeneinander vorkommen ohne lückenlose Übergänge zu bilden, sind wahrscheinlich verschiedene Arten, jedenfalls als solche zu behandeln, bis eine etwaige Zusammengehörigkeit einwandfrei nachgewiesen werden kann.—Differente Formen, die durch konvergente Reihen scheinbar mit einander verbunden sind, aber in geographisch voneinander getrennten Gebieten leben, sind wahrscheinlich ebenfalls verschiedene Arten."

In conjunction with what has been said above it may perhaps be permissible to suggest as a probability: The variability of the Dinoflagellates is of two kinds, (1) modifications, possibly governed by external factors, which lead to phenotypes that are not constant but capable of varying in different directions; the resulting differences should be called "*forma*"; (2) genotypic changes, possibly mutations, which produce new biotypes or what we may call "*species.*"

Whether a given taxonomic group is a *forma* or a *species* cannot be decided; but we shall be working in the right direction if, when classifying organisms that are much alike but capable of being distinguished morphologically, we regard them as *species* if they occur constantly separate in different seas, but as *formae* if they are found together and are connected by transitions.

II. Division of the Genus *Peridinium* into Sections.

The original sections were set up by JØRGENSEN in 1913; PAVILLARD 1916, PETERS 1928, PAULSEN 1930, and SCHILLER 1937 all altered them a little, but on the whole we still have JØRGENSEN's sections (or groups, as ABÉ calls them); however, if only we could adhere to the purely schematic classification according to the tabu-

lation, especially as suggested by PETERS, we should have something more tangible to work with. Actually, however, the Peridinians are too variable for classification in that manner, and the dorsal area is more variable than the ventral (see DANGEARD's paper 1927 c, referred to above p. 11). In his latest work (1936 a), which SCHILLER had not seen, ABÉ points out that the four (—five) plates of the longitudinal furrow provide better characters for species and "groups" than the plates on the epitheca, and he brings beautiful and undoubtedly very careful drawings accompanied by detailed descriptions of a number of species. "The ventral area," he says (1936a, p. 641), "exhibits wide diversity in structure and is to be regarded as the most highly specialized, and functionally, morphologically and genetically important part of the skeleton," it having "direct relations with the motile organ". ABÉ was unable to describe the structure of the ventral area of all the species which he deals with; its analysis is very difficult because it is complex, composed as it is of tiny plates which are apt to adhere together.

I think it is justifiable to express some doubt as to whether we have any real main criterion. For on comparing ABÉ's figures (1936a) of the species *Peridinium abéi*, *P. clavus*, *P. Thorianum*, which are grouped among the Avellana, with *P. constricta*, which is placed to the Monovela (which two groups are held to be separable by the structure of the ventral area), we find that there is no great difference between the ventral plates of these species, but merely that *P. constricta* has a flagellar fin and its anterior plate extends a little beyond the girdle up upon the epitheca. These of course are differences that are worth noting, but I scarcely think they are so weighty as ABÉ believes. Naturally, it is a very difficult and time-consuming job to elucidate these matters, so that unless someone with unlimited time and energy undertakes to go through the entire genus *Peridinium* for that purpose, we shall scarcely ever get a new taxonomy built up on the ventral area. For the present, at any rate, we shall be compelled to adhere to the old one.

On turning over the pages of SCHILLER's book where he deals with *Peridinium*, and examining his illustrations, one gains the definite impression that there is something wrong with his section Tabulata. In the first place, it contains all the freshwater species (which LEFÈVRE divided into a number of groups), and also many marine species; the latter are split up into three sub-sections called a, b and c. a comprises marine species with three intercalaries and includes *P. hangoei* SCHILL. and *P. trochoideum* (STEIN) LEMM. as well as *P. adense* MATZ. and *P. subsalsum* OSTF. These I consider may rightly be placed to Tabulata. Then there are seven species set up by MEUNIER (*P. elongatum*, *P. fimbriatum*, *P. hyalinum*, *P. nudum*, *P. robustum*, *P. verrucosum*, *P. bulla*) which, as MEUNIER almost on principle draws all *Peridinium* with Ortho arrangement, must be so doubtful that they may be called incertae sedis. Finally, SCHILLER reckons *P. globosum* DANG. as belonging to Tabulata, but it is quite alien in this company and moreover has only been seen once; it is referred to on p. 14 and must be labelled as unplaced.

SCHILLER's second Tabulata sub-division, b, comprises marine species with two intercalaries and with a symmetrical dorsal plate pattern. This is Section Avellana PAULS., characterized (1930) by two intercalaries and symmetrical epitheca, but which SCHILLER has abolished; I consider it should be retained. ABÉ (1936a, p. 647) acknowledges it as a "group," and I quote the following from his description: "The body is globular, rounded polyhedral or elongated biconical, with circular or oval girdle section and no antapical horn or spine. The deeply concave descending girdle (*i. e.* left-handed girdle) has a corrugated wall. In most cases there is at the apex of the epitheca a peculiar elongated, dorso-ventral furrow, sometimes extending dorsally and indenting the dorsal apical plate 3′ . . . . . The apical pore lies in its median part or close to its ventral end." ABÉ then gives a detailed description of the ventral area, to which I refer.

To his sub-section b SCHILLER also places *P. colombense* MATZ.(?), *P. orbiculare* PAULS. (which does not belong there, it being a *Diplopsalis*; in my opinion *Diplopsalis* should be regarded as a genus (see p. 8); cf. LINDEMANN 1928) and *P. minutum* KOF. (= *P. monospinum* PAULS.?). The latter ABÉ (1936a, p. 670) places to a new Section, Monovela ABÉ, "characterized by flat ventral area, by having the flagellar fin as sole extension of the thecal surface . . . The apical horn may be present or absent . . . The anterior plate of the ventral area indents the epitheca deeply. The plate formula as 4′, 2—3a, 7″, 5‴, 2⁗. When there are two intercalary plates they may be equal or subequal, and when there are three they are asymmetrical and lie more on the left side of the body. The midventral apical plate (1′) is asymmetrical in shape and somewhat oblique in position. The apical pore is prolonged ventrally or dorsally into the apical furrow or slit . . ." To this section he places the species *P. monispinum* PAULS., *P. minutum* KOF., *P. asymmetrica* (ABÉ) ABÉ (*Sphaerodinium asymmetrica* ABÉ 1927), *P. mutsuensis* ABÉ, *P. monovelum* ABÉ, *P. constricta* ABÉ.

In the words of ABÉ (l. c., p.670), this section is "most closely related genetically to the Avellana group"; the only characters of it that are easily observable are the ventral fin or velum and the indentation of the epitheca. It might perhaps be bracketed together with Avellana, but it is doubtless more correct to retain it.

SCHILLER's third sub-section of Tabulata, "marine Arten mit zwei Interkalaren und symmetrischem dorsalen Plattenmuster" comprises *P. excentricum* PAULS., *P. grenlandicum* WOLOSZ. and *P. triquetrum* (EHRENBERG) LEBOUR. A remarkable company! In 1930 (p. 43) PAULSEN set up Sect. Excentrica, containing the two first-named species, and they are (as ABÉ, 1936a, p. 680, also demonstrated as regards *P. excentricum*) so different from the other species of *Peridinium* that there is every possible reason for retaining that Section. *Heterocapsa triquetra* ought to retain its own generic name; as LINDEMANN has also pointed out, it differs from *Peridinium*. SCHILLER considers that LINDEMANN's arguments are without significance, but I certainly think that absence of an apical pore and the extension of the longitudinal furrow upon the epitheca, and the numerous small brown chromatophores together

provide characteristics enough for the genus *Heterocapsa*. No doubt *P. balticum* (LEVANDER) should also be placed to Excentrica.

As regards these Sections Avellana, Monovela and Excentrica, according to earlier interpretation they would belong to the subgenus Archaeperidinium JØRGENSEN (Properidinium MEUNIER). SCHILLER (1937, p. 130) remarks—justly, I think—that the presence of a small number of plates cannot be regarded as a primitive character, rather the reverse; the prefixes *archae-* and *pro-* are therefore devoid of meaning, and the subgenera Archaeperidinium and Properidinium ought to be abolished, as SCHILLER already has done; likewise Veroperidinium PAULS. (1930, p. 54); ABÉ has also shown (1936a, p. 670) that of closely related species in Monovela, one may have two, the other three intercalaries.

According to the considerations above, the species which SCHILLER lists under Section Tabulata should be distributed among the following sections: Tabulata, Avellana, Monovela and Excentrica.

Section Tabulata JØRGENSEN.

Rounded cells without horns and without or with small antapical spines. Girdle left-handed (or circular). No apical furrow or groove including the apical pore. Tabulation: Ortho, penta, quadra or hexa; three, rarely two, intercalaries. Under this heading come all fresh-water species and of the marine the following:

P. adense MAYZ. Insufficiently known quadra species from Aden.
P. hangoei SCHILLER (= *P. novascotiense* GRAN & BRAARUD). Penta species from Finnish waters and the Gulf of Maine.
P. subsalsum OSTF. Brackish-water species. Illustrated by OSTENFELD with two and by LEMMERMANN with three intercalaries (penta).
P. trochoideum (STEIN) LEMM. (= *P. faeröense* PAULS.). Decidedly neritic hexa species from European coastal waters.
? *P. americanum* GRAN & BRAARUD. Four intercalaries.
? *P. delicatissimum* BRAARUD. Insufficiently known.
? *P. deficiens* MEUN.

Three of these species occur in more or less brackish water and may perhaps for that reason by included among the freshwater species. In any case, Section Tabulata consists chiefly of freshwater species.

Section Avellana PAULS.

Rounded cells without horns and without or with small antapical spines. Girdle left-handed. A dorso-ventral furrow or groove includes the apical pore. Tabulation: Ortho: two intercalaries. Includes the following species:

Cells much longer than broad: *P. ventricum* ABÉ, *P. abéi* (ABÉ) PAULS.
Cells almost globular: over 50 μ in diameter: *P. Thorianum* PAULS.; smaller are *P. avellana* MEUN., *P. nux* SCHILLER (= *P. Levanderi* ABÉ), *P. Hidemitii* n. nom. (= *P. rotundata* ABÉ, 1936a, non KARSTEN 1907), *P. Pietschmanni* BÖHM.
Cells depressed: *P. denticulatum* GRAN & BRAARUD, *P. hemisphaericum* ABÉ, *P. clavus* ABÉ. The two latter are presumably identical.

Under this heading mention may also be made of *P. laticeps* GRØNTVED (1938), a species recalling *P. Granii* but with only two dorsal intercalaries.

Section Monovela ABÉ.

Rounded cells without horns and spines, but with a conspicuous flagellar fin as the sole extension of the thecal surface. Girdle circular. The anterior plate of the ventral area indents the epitheca deeply. Tabulation: Ortho; mostly two, but sometimes three intercalaries; symmetric or more or less unsymmetric. To this section belong: *P. asymmetricum* (ABÉ) ABÉ (= *Sphaerodinium asymmetrica* ABÉ), *P. monovelum* ABÉ (three intercalaries), *P. mutsuensis* ABÉ, *P. minutum* KOF. (= *P. monospinum* PAULS.), *P. constricta* ABÉ (= *P. minutum*?).

Section Excentrica PAULS.

Depressed or globular cells without spines; girdle circular or left-handed. Tabulation: Ortho, two intercalaries, one of them much bigger than the other. The section comprises:

P. excentricum PAULS. with ventrally displaced apical horn, and perhaps two species without apical horn: *P. balticum* (LEVANDER) LEMM., *P. grenlandicum* WOLOSZ.

Sections Humilia JØRGENSEN and Piriformia JØRGENSEN. These two sections (both Meta) were separated by JØRGENSEN by the fact that the former is quadra, the second penta. It has since been shown, *i. a.* by BARROWS and by LEBOUR, that species under these headings may sometimes be quadra, sometimes penta, for example *P. ovatum* (see above p. 11). It would therefore be best to unite these two sections into one:

Section Humili-piriformia.

Species without hollow antapical horn. The shape of the cell is depressed, *i. e.* flattened from above downwards, globular or pear-shaped; girdle right-handed; often, but not always, with two antapical spines. Tabulation: always Meta, dorsally penta, quadra or hexa.

I shall not divide this large section into sub-sections but quite practically try to set up some groups.

(1) Globular species without antapical spines, apical horn hardly apparent or very short and "affixed." *P. globulus* STEIN (penta), *P. spheroides* DANG. (hepta, see p. 14), *P. Joubini* DANG. (penta).

(2) Cells flattened from above downwards. *P. ovatum* (POUCH.) SCHÜTT (quadra or penta) (= *P. marukawai* ABÉ), *P. subcurvipes* LEB. (quadra), *P. monacanthus* BROCH (quadra), all with antapical spines; *P. majus* DANG. (= *P. simulum* PAULS.) (penta), spineless like *P. decipiens* JØRGS. (= *P. dubium* BROCH)?, which species may belong here.

(3) Globular or pear-shaped cells with two antapical spines.

(a) Globular cells whose apical horn is not plainly "affixed": *P. Braarudi* SCHILL. (penta), *P. gibbosum* MATZ. (penta), *P. patens* DANG. (hexa), *P. quarnerense* (SCHRÖDER) BROCH (penta or quadra), *P. solitarium* ABÉ (penta), *P. subpyriforme* DANG. (penta), *P. truncus* ABÉ (penta), *P. ventralis* ABÉ (quadra).

(b) Pear-shaped cells with semiglobular hypotheca and more or less cuneate epitheca: *P. asperum* WAILES (hexa), *P. breve* PAULS. (quadra), *P. brevipes* PAULS. (= *P. varicans* PAULS.) (quadra), *P. gracile* GRAN & BRAARUD, *P. latispinum* MANGIN (? = *Sylvanae* DANG.; ? = *africanoides* DANG.) (penta), *P. micrapium* MEUN. (quadra?), *P. oviforme* DANG. (penta), *P. piriforme* PAULS. (penta), *P. roseum* PAULS. (quadra or penta; see this paper p. 53), *P. Steinii* JØRGS. (penta), *P. styliferum* SCHILL., *P. Wiesneri* SCHILL. (quadra).

(c) Somewhat depressed cells, hypotheca ending in two broad rudimentary hollow horns each bearing a spine: *P. Granii* OSTF. (quadra or penta), *P. mite* PAVILL., *P. finlandicum* PAULS. (?) (penta). These species have some resemblance to the right-handed *Divergentia* species.—*P. laticeps* GRØNTVED (1938) was found in single specimens west of Greenland. It calls to mind *P. Granii*, but has only two dorsal intercalaries. Hence it ought to be ascribed to Sect. Avellana, but in shape and characters it differs widely from other species of that Section. The true *P. Granii* is also found in Davis Strait.

(d) Pear-shaped cells with distinct ("affixed") long apical horn: *P. cerasus* PAULS. (quadra), *P. longicollum* PAV. (penta), *P. tenuissimum* KOF. (hexa).

In the above list are included some few species Meta hexa, viz. the following: *P. asperum* WAILES, *P. patens* DANG., *P. tenuissimum* KOF. They all seem to fit easily into this Section. *P. globulus*, which STEIN drew hexa, I referred to above p. 12. *P. dakariense* DANG., also hexa, is ascribed to Divergentia (see below).

P. minusculum PAV. (1905, p. 57), in 1917 further elucidated by the same author as to its tabulation and listed by SCHILLER under Pyriformia, differs so much from *Peridinium* in both tabulation and its whole appearance that I—like LEBOUR—prefer to regard it as a separate genus, in which case it should have the name *Minuscula bipes* (PAULS.) LEBOUR. It seems to have a very wide area, occurring off Iceland, Greenland, in the Barents Sea, the Baltic, the English Channel, off Vancouver, in the Gulf of Maine, the Mediterranean (Etang de Thau, abondant en février).

Section Pellucida Jørgensen.

Species without hollow antapical horns. Cell mostly ovoid and pointed or acuminate at the top, but rarely with an "affixed" apical horn. Girdle right-handed, two antapical spines, often a third on the left side as a continuation of the left edge of the longitudinal furrow. Tabulation: Para, usually hexa, rarely quadra or penta; exceptions: Matzenauer (1933, fig. 42) has a *P. pellucidum*, Meta; Mangin (1912, fig. 18), a *P. macrospinum*, Ortho; Meunier also has some Orthos.

The species ascribed to this section are listed under three items.

(1) Pear-shaped cells: *P. curvipes* Ostf. (= *P. variegatum* Peters) (hexa; Peters has penta, rarely quadra) see Lebour 1925, pl. 29, fig. 1); *P. diabolus* Cleve (= *P. macrospinum* Mangin 1912; *P. formosum* Pavillard 1909) (penta; Dangeard 1927 b has hexa), *P. longipes* Karsten (tabulation unknown); *P. Okamurai* Abé (hexa), *P. pallidum* Ostf. (hexa or quadra), *P. Paulseni* Pav. (tabulation unknown), *P. pedunculatum* Schütt (tabulation unknown), *P. pellucidum* (Bergh) Schütt (hexa, see below), *P. Schilleri* Pauls. (hexa), *P. tenuissimum* Kof. (? better: Humilipiriformia), *P. tristylum* Stein (Br. Schröder (1900) has quadra for "var. *ovata*"; Dangeard (1927 b) hexa for a similar form; Stein figures the main species quadra, but it seems rather schematic).

(2) Globular or ovoid cells: *P. heteracanthum* Dang. (hexa), *P. hirobis* Abé (?, is Meta hexa), *P. nipponicum* Abé (hexa), *P. ovum* Schiller (*P. ellipsoideum* Dang. non Mangin, *P. ellipsoides* Dang. (hexa), *P. rectum* Pav., non Kof. (hexa)); *P. sphaericum* Okamura (*spheroidea* Abé) (quadra ?).

(3) Depressed cells: *P. islandicum* Pauls. (see this paper p. 55).

As to *P. pellucidum*, Matzenauer (1933, p. 461) says that its systematic position is dubious; he has found the species Meta, and Abé the same (1927, p. 401). The species being widely ranging and very variable, it is probable that a closer study of it will lead to its division; Broch (1910 b) has already set up three varieties, differing with regard to the fins on the spines.

Section Conica Jørgensen.

Species mostly with hollow antapical horns, cell ventrally seen quadrangular or nearly so, hence no apical horn, girdle left-handed or circular. Tabulation: Ortho, mostly hexa, but penta and quadra also occur. The species are listed under two items:

(1) With hollow antapical horns: *P. conicoides* Pauls. (hexa); *P. conicum* Gran (hexa) incl. f. *bilobata* Meun. (= *P. intermedium* Candeias 1938), and f. *Asamushi* Abé 1927 (four intercalaries), not Gran & Braarud 1935 (two intercalaries), not f. *islandica* Braarud 1935, which is right-handed; *P. divaricatum* Meun. (hexa); *P. Gainii* Dang. (hexa); *P. latissimum* Kof. (hexa); *P. leonis* Pav. (hexa, but Dangeard has figured a specimen penta, if the identification be correct?), incl. *P. excavatum*

MARTIN 1929; *P. Marielebourae* PAULS. (quadra), incl. *P. obtusum* FAURÉ-FREMIET 1908, non KARSTEN; *P. obtusum* KARSTEN incl. *P. leonis* MATZ. non PAVILL.; *P. pentagonum* GRAN (hexa).

(2) Cells without hollow antapical horns: *P. achromaticum* LEVANDER (OSTENFELD from the Aral Sea (1908) has drawn it with only two intercalaries) (hexa); *P. Anthonyi* FAURÉ-FREMIET (hexa); *P. biconicum* DANG. non ABÉ (hexa); *P. punctulatum* PAULS. (penta, see this paper p. 54), *P. subinerme* PAULS. (hexa, see this paper p. 54), *P. turbinatum* MANG. (= *P. inaequale* PETERS, non FAURÉ-FREMIET) (hexa ?).

Section Oceanica JØRGENSEN.

Hollow antapical horns. Epitheca with concave sides, tapering into a long or short apical horn. Girdle left-handed, forming an oblique angle with the longitudinal axis. Tabulation: Ortho, mostly quadra, but also penta and hexa occur. (Exceptions: MANGIN (1911, 1913) figured *P. oceanicum* and *P. depressum* as right-handed; but, as already stated p. 11, he sometimes draws the under side of the cell. KARSTEN (1907, pl. 52, fig. 5a—b) drew *P. pustulatum* Meta, but does not mention it in the description p. 417; BARROWS (1919, pl. 20 fig. 7-8) drew a *P. oceanicum* (or more closely related to a race of *P. depressum* BAIL. ?) as Para; and DANGEARD (1927 c, fig. 1) a "*P. depressum*" (if this species ?) Para.

P. grande, *P. elegans*, *P. fatulipes* and *P. tumidum* are Meta and are here ascribed to Sect. Divergentia.

In my opinion the species belonging to this section are:

(1) Depressed cells, girdle very oblique to the longitudinal axis: *P. depressum* BAIL. 1855 (incl. *P. parallelum* BROCH, (this paper p. 59). *P. marinum* LINDEM. 1925, p. 98) (quadra), a very variable species (see PETERS 1928, SCHILLER 1937). Related or perhaps identical are: *P. antarcticum* SCHIMPER (KARSTEN 1907, pl. 19, figs. 1—4), ? = *P. complanatum* KARSTEN, ? = *P. pustulatum* KARSTEN and *P. saltans* MEUN. (1910, pl. 1 bis, figs. 9—14).

(2) Cells not depressed.

(a) Cell nearly as broad as long, antapical horns thick of unequal length: *P. claudicans* PAULS. (vix CARISSO 1911, pl. 2, figs. 14—15, vix LINDEMANN 1924, p. 228) (quadra, penta or hexa. See SCHILLER 1937, fig. 250, c—g).

(b) Cell ovate, much longer than broad, antapical horns of equal length: *P. oblongum* (AURIVILL.) CLEVE; AURIVILLIUS (1898) in his description refers to BERGH 1881, figs. 39, 40 (= *P. oceanicum* var. *parvulum* MANG. 1913, ? = *P. venustum* MATZENAUER 1933, p. 464). See SCHILLER 1937, fig. 257, c, d, g, j, k.

(c) Cell with long, thin antapical horns and elongated apical horn: *P. oceanicum* VANHÖFFEN 1897, pl. 5, fig. 2; the most typical apart from the original seems to be in SCHILLER 1937 fig. 257a—b. *P. Murrayi* KOF. is a related species with distended antapical horns.

This seems to be a natural section; its species are closely related, and, as SCHILLER points out, the long-horned are mostly oceanic, the short-horned neritic, *e. g. P. oblongum* and perhaps still more *P. claudicans* are native to eutrophic waters; but it is a long way from there to bracketing the species together, as SCHILLER has done to some extent. The above species seem to me to be easy to classify, despite their variability.

Section Divergentia JØRGENSEN (incl. Paradivergentia PAULS.).

Species with hollow antapical horns; there is often a deep indentation between them. The epitheca usually conical and only faintly tapering to an insignificant apical horn, or not at all. Tabulation: Meta, hexa or quadra. One group is Para and was ascribed to Sect. Paradivergentia PAULS. It is now taken back to Divergentia for two reasons. Firstly, various authors: MEUNIER 1910, BARROWS 1918, LINDEMANN 1924, have described and illustrated specimens of "*P. divergens*" with Para tabulation. PETERS (1928, p. 113) says of this that no such irregular variation in the ventral tabulation is known elsewhere and that, for *P. divergens*, it is probably a matter of different species. Another thing is that Paradivergentia (which to my mind is only one species) has a right-handed girdle. But in addition, there are also some Meta species that are right-handed like the Para species. The direction of the girdle seems generally to be constant, like the ventral tabulation; but if we were to set up sections with reference to both these characters we should have three sections instead of the original section Divergentia; and as all the species otherwise as regards general structure are closely related, I prefer to divide the section Divergentia into three groups as follows:

(1) Meta species with left-handed girdle: *P. crassipes* KOF. (quadra, see SCHILLER 1937, fig. 220j); *P. curtipes* JØRGENSEN (quadra or penta, PETERS 1928, fig. 11; see SCHILLER fig. 220i); the relation between these two species is mentioned on p. 16—18 of this paper; *P. divergens* EHBG. (= *P. speciosum* JØRGENSEN (quadra, see LEBOUR 1925, pl. 26, fig. 2)); a related form or species is *P. remotum* KARST.;[1] *P. elegans* CLEVE (= *P. grande* DANG. 1927 b, PAULSEN 1930) (quadra); *P. fatulipes* KOF. (quadra); *P. grande* KOF. (quadra); *P. tumidum* OKAMURA (quadra).

(2) Meta species with right-handed girdle: *P. acutipes* DANG. (quadra); *P. angustum* DANG. (? = *P. breve* DANG. 1927, p. 366, non PAULSEN) (quadra); *P. Brochi* KOF. & SW. (= *P. adriaticum* BROCH 1910) (quadra or hexa, DANGEARD 1932, p. 343); *P. dakariense* DANG. (hexa); *P. inflatum* OKAM. 1912 (= *P. crassum* DANG. 1927 b, *P. divergens*, "abweichende Form," LINDEMANN 1924, fig. 78).

(3) Para species with right-handed girdle (Paradivergentia): *P. solidicorne* MANG. 1922 (= *P. aerolatum* PETERS, = *P. spiniferum* SCHILLER) (quadra, PETERS 1928, SCHILLER 1929; hexa, DANGEARD 1927 b, MATZENAUER 1933, SCHILLER 1937,).

[1] SCHILLER 1937 has *P. remotum* in two places: first (p. 227) as "eine grosse Form" of *P. divergens*; next (p. 262) as a species under Sect. Oceanica.

It may be that the three species described ought to be kept separate, or that new species might be pointed out. But with our present knowledge it seems natural to keep them united.

III. Icelandic Dinoflagellates.

1. On Northern Dinophysis and Phalacroma species.

A. *Dinophysis arctica* Mereschk. and its relatives.

The species from The White Sea was described 1879, p. 177 and figured Tab. 11, fig. 19; a copy of the drawing is here annexed (fig. 1a). "Diese Art unterscheidet sich der Form nach gar nicht oder nur sehr wenig von den nahestehenden Arten insbesondere *D. laevis*. Doch existiert ein Unterschied in der Sculptur der Oberfläche: Bei *D. laevis* ist dieselbe ganz glatt, während sie bei der Art des Weissen Meeres chagrin-artig und mit sehr feinen und regelmässig geordneten Pünktchen bedeckt ist . . . Auch ist der Seitenfortsatz von etwas anderer Form und grösser als bei *D. laevis*, von welcher letzterer unsere Art auch durch ihre geringere Grösse abweicht. Ihre Länge nämlich übertrifft nicht 0,036 mm, während bei *D. laevis* sie 0,05‴ ausmacht . . .".

What, first, is *D. laevis*? It was described by Claparède et Lachmann 1859 and figured Tab. 20, fig. 13, later by Jørgensen (1899, p. 32) given variety rank under *D. rotundata*, now *Phalacroma rotundatum*, to which it no doubt belongs. Hence the comparison is not very good, since Mereschkowsky's figure shows a rather long ovoid body, the posterior part broadest.

About this species, *D. arctica* Mereschk., there has been great confusion.[1] A *Dinophysis* corresponding exactly to the original *D. arctica* has not been published. Nearest to it come 2 figures, one by Pouchet (see fig. 1b) and one by Levander (see fig. 1c). Pouchet (1883, Tab. 18—19, fig. 6) has under the name of *D. laevis* (but not Clap. & Lachm.) figured a form whose shape is similar to that of *D. arctica*.

Levander (1894, Tab. 2, fig. 26) has another similar form from Finnish waters, but its surface is coarsely poroid. Length 45—46 μ. Hence it is bigger than *D. arctica* and has a different surface, but that should be no serious objection in uniting this form with *D. arctica*?

Next comes *D. granulata* Cleve (1899, pl. 4, fig. 7) (see fig. 1d). It was described from Spitzbergen in these few words: "A very small form remarkable for its coarse structure. It seems to belong to the arctic neritic plankton." The figure given is rather coarse, it is reproduced in Paulsen 1908 and in Lebour 1925. (The calculated length

[1] To make things worse, Schiller (1933, p. 119, fig. 112b) has published a figure said to be reproduced after Mereschkowsky, but which seems to be a bad copy of Cleve's *D. granulata*. Schiller's description: "Körper im Seitenansicht ± breit elliptisch . . . am tiefsten in der Mitte;" does not correspond to the original figure, nor to *D. granulata* Cleve.

of the cell is 30 μ). The shape is ovoid, with a long, longitudinal list, and the upper girdle list is almost vertical. *D. granulata* is by PAULSEN (1908) and by SCHILLER (1933) regarded as a synonym of *D. arctica*, and LEBOUR (1925) reproduces CLEVE's drawing without mentioning *D. granulata*. It might be right to unite these two small species, on account of their ovoid form and vertical girdle list, but both surface and longitudinal lists are different,—hence the union cannot be said to be quite convincing.

JØRGENSEN (1912, p. 10) says about *D. granulata*: "Sie ist eine der wichtigsten *Dinophysis*arten, da sie eine ausgesprochene Kaltwasserform zu sein scheint. Es gibt aber hier mehrere Formen[1], die unter einander relativ verschieden sind. Einige derselben treten als arktische oder boreale ozeanische Formen auf, andere scheinen

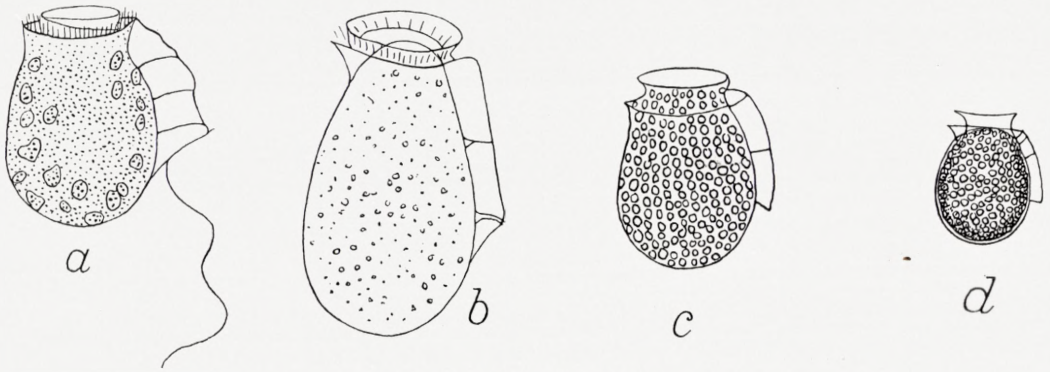

Fig. 1. *Dinophysis arctica* MERESCHK.
a, from MERESCHKOWSKY 1879. — *b*, from POUCHET 1883 (*D. laevis*). × 500. — *c*, from LEVANDER 1894 (*D. rotundata* CLAP. & LACHM.). × 520. — *d*, from CLEVE 1899 (*D. granulata* CL.). × 500.

neritisch zu sein." JØRGENSEN found the species both in the Skagerak, the Kattegat, and in the inner Baltic. (OSTENFELD (1913) has it not from Danish waters, nor has PAULSEN (1907)).

JØRGENSEN's record of *D. granulata* from the Baltic induces KOFOID & SKOGSBERG (1928, p. 229) to ask whether *D. granulata* JØRGS. is not identical with *D. baltica* (PAULS.) KOF. & SKOGSBERG, figured (as *D. ovum*?) by LEVANDER (1900) from the Baltic, the two species being "strikingly similar." In my opinion they are distinct, *D. baltica* being bigger, and more pointed upwards.

On the other hand, the *Dinophysis* found in the Baltic by JØRGENSEN may be identical with the "*Dinophysis arctica*" figured by WOLOSZYNSKA (1929, Tab. 5, fig. 4—5, 10—12), and perhaps with *D. Paulseni* WOLOSZ. (ibid. Tab. 4, fig. 2). These forms agree in outline and in porulation with CLEVE's *D. granulata*, but they are big, their length being given as 42 μ (but calculated from the drawings they are more than 50 μ long). In my opinion they are to be regarded provisionally as related species, until a closer examination of the northern *D. arctica* (*granulata*) permits a comparison of it to WOLOSZYNSKA's beautiful figures. These agree well with the *D. arctica* sketched by BRAARUD (1935, fig. 22) from the Denmark Strait, 45 and 51 μ long.

[1] Had JØRGENSEN only drawn some of them!

D. arctica MERESCHK. (= *D. granulata* CLEVE) might then be regarded as an insufficiently known arctic species, represented in the Baltic by related or identical forms. It should be characterised by its small size, ovoid body and narrow girdle lists. Two forms should be excluded from it, viz. *D. Granii* and *D. subcircularis* to be discussed below.

Dinophysis Granii n. nom. *D. granulata* GRAN (1902, p. 183, fig. 9), non CLEVE. *D. arctica* HJ. BROCH (1910, fig. 1, II), non MERESCHK.

The two quoted drawings, here reproduced (fig. 2a, b), represent a characteristic form, whose body is short, regularly ellipsoid and antapically rounded. The surface is described by BROCH as finely punctate poroid. The girdle lists are narrow, the foremost not erect (as it is in *D. sphaerica*). Longitudinal list in GRAN's figure short (newly divided cell?), in BROCH's long with 3 spines. Length (calculated) 40, 41 μ. Known from the Norwegian Sea (GRAN), and from Spitzbergen (BROCH). It seems to be different from *D. arctica* in its elliptic and not oval outline, and perhaps in its finely poroid surface. It cannot belong to *D. sphaerica* because of its shorter body and narrow girdle list[1].

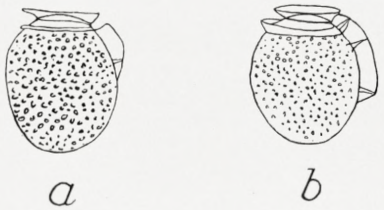

Fig. 2. *Dinophysis Granii* n. nom. *a*, from GRAN 1902 (*D granulata*). × 450. — *b*, from BROCH 1910 (*D. arctica*). × 420.

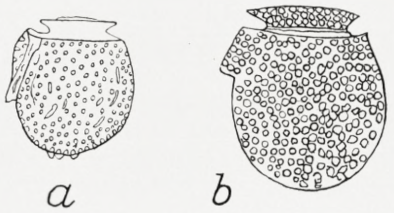

Fig 3. *Dinophysis subcircularis* n. nom. *a*, from PAULSEN 1911 (*D. arctica*). × ca. 375. — *b*, from JØRGENSEN 1900 (*D. acuminata* v. *granulata*). × 580.

D. subcircularis n. nom. *D. acuminata* var. *granulata* JØRGENSEN (1900, p. 19, Tab. 3, fig. 33), non CLAP. & LACHM., nec CLEVE; *D. arctica* PAULSEN (1911, p. 305, fig. 1), non MERESCHK.

This species (fig. 3) is characteristic by its nearly circular outline when seen laterally, by its narrow girdle lists over which the epitheca is hardly seen, by its short and narrow longitudinal list, and by its coarse poroid surface structure. Small antapical protuberances may be present. Length 42 μ (JØRGENSEN), 36—42 μ (PAULSEN).

JØRGENSEN says (l. c. p. 19): "Weicht von der Hauptform durch gröbere Areolierung, breitere Gestalt und Ermangelung deutlicher Höcker am hinteren Ende

[1] Is *D. sphaerica* STEIN well identified, and is it found in Northern waters? Neither PAULSEN (1908) nor LEBOUR (1925) give original drawings of this species, nor does AURIVILLIUS, who has it from Spitzbergen. —A comparison between STEIN's figures (t. 20, fig. 3 & 4) and KOFOID & SKOGSBERG's fig. 31, 3 & 4 (p. 243) arouses a suspicion that the latter is not identical with the former, especially regarding the anterior girdle list.

ab. Häufig jedoch ein einzelner stachelähnlicher Höcker ventral hinten . . . Diese ganz kleine Form ist der Hauptart ziemlich unähnlich, weshalb sie vielleicht eine eigene Art bildet."

It bears some resemblance to *D. micropterygia* DANGEARD (1927b, p. 381, fig. 44e, and 1927a, p. 13, fig. 8E), which was found at a single station in the tropical Atlantic. It has about the same shape of the body, the same coarse structure and the same narrow girdle lists. But it is bigger, its diameter being 50—60 μ, and it lacks protuberances. Being a tropical form it is probably specifically different from the arctic *D. subcircularis*.

B. *Dinophysis norvegica* CLAP. & LACHM. and its relatives.

D. norvegica was first described by CLAPARÈDE & LACHMANN (1859, p. 407, pl. 20, fig. 20) in these words: "Chagrin de la carapace très-grossier. Moitié postérieure réduite à l'état d'une simple plaque concave. Corps comprimé, bordé par une limbe strié. . . . Elle présente toujours son maximum de largeur en son milieu, et sa moitié antérieure (le fond du pot) se termine en faîte pointu . . . Le chagrin . . . varie beaucoup de grosseur . . . Le limbe qui entoure le corps du pot sur son arête de compression, est moins large du côté qui porte l'anse que du côté opposé. Souvent il est dentelé sur son bord . . . Longueur d'environ 0,06 mm. . . . Bergen, Glesnæsholm (Sartorøe)."

While in the description the authors refer to fig. 20, in the "explication des planches," *D. norvegica* is said to be represented by fig. 18, but in reality it must be fig. 19, as only this drawing shows the "limbe strié" (striate border) by which the species is characterized. It is also this fig. 19 which is quoted by JØRGENSEN (1899) and reproduced (bad copy) by SCHILLER (1933).

The first to take up this species was E. JØRGENSEN (1899, p. 29). From his description the following sentences are quoted: "Hinterkörper ungefähr an oder wenig hinter der Mitte am breitesten, in einer breiten stumpfen, nicht oder nur wenig ventralwärts geschobenen Spitze endigend. Die Rückencontour meistens uneben, mehr oder weniger wellenförmig (oder wie unregelmässig stumpf gezähnt). Diese Unebenheit ist zumal am Hinterende gewöhnlich sehr deutlich. Die linke Flügelleiste . . . deutlich areoliert . . . Contourleisten meistens bedeutend breiter (than in *D. acuta*). Körperoberfläche gröber areoliert . . . Wie die Figuren T. I, fig. 3—6 zeigen, variirt diese Art nicht unbedeutend . . . Der Name *Dinophysis norvegica* lässt sich nach meiner Ansicht ungezwungen auf diese in den Figuren T. I, fig. 3—6 dargestellte Art überführen." JØRGENSEN quotes as synonyms: *D. acuta* R. BERGH (1881, Tab. 15, fig. 49—50) (see fig. 5A, B); *D. acuta* STEIN (1883, Tab. 20, fig. 20).

Still it is doubtful if the *Dinophysis* described by JØRGENSEN from the Norwegian Sea really is the same as CLAPARÈDE & LACHMANN's species from the same waters. But at any rate, the figures of the last named authors being perhaps somewhat schematic, JØRGENSEN is the first to give a clear idea of what we now call *D. norvegica*,

and hence he may be said to be its real author. His drawings are here (fig. 4) reproduced; the length of the cells is calculated at 60—68 μ (JØRGENSEN has given no measures). As compared to BERGH's figures quoted from the Danish waters (fig. 5 A, B), JØRGENSEN's forms are more robust, broader and more blunt antapically, and they are not, as BERGH's forms are, characterised by the concavity of the antapical

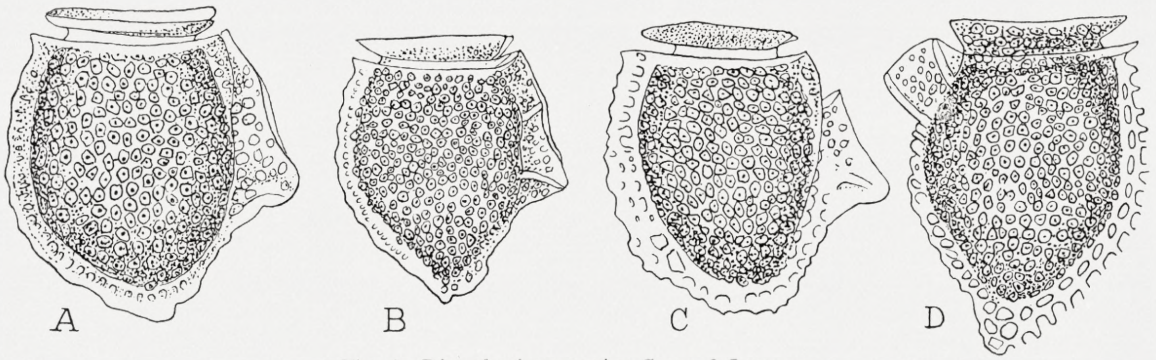

Fig. 4. *Dinophysis norvegica* CLAP. & LACHM.
From JØRGENSEN 1899 (t. 1, fig. 3—6). A, C, D, × 600; B, × 500.

part of the ventral outline. The same concavity is seen on BERGH's fig. 11—12 from 1887, and in LEBOUR's (1925) fig. 21 a[1]. These two forms, the robust one from the Northern Atlantic, and the slender one from the Baltic and its outlets were in 1907 by PAULSEN distinguished as "geographical races", named respectively, f. *crassior*, and f. *debilior* (figured by PAULSEN 1908, fig. 12 a—b, and reproduced by SCHILLER 1933, fig. 122, l—m), (see fig. 5 C, D).

HJ. BROCH's figure from Spitzbergen (1910, fig. 1, I) represents as it were an intermediate form nearest to f. *crassior*, calculated length 62 μ (see fig. 5 E).—MEUNIER's *D. norvegica* (1910, Tab. 3, fig. 38—40) from the arctic seas hardly belongs to this species, and the same must apply to the organism figured by DANGEARD (1926, fig. 15 D) from French waters.

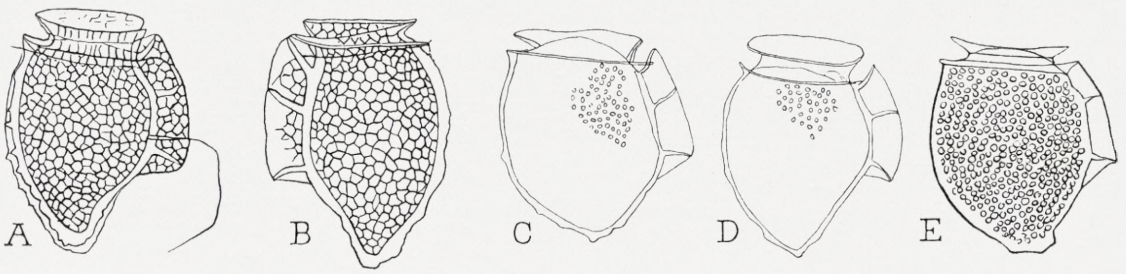

Fig. 5. *Dinophysis norvegica* CLAP. & LACHM.
A, B, from BERGH 1881 (*D. acuta*). — C, D, from PAULSEN 1908 (C: f. *crassior*; D: f. *debilior*). × 460. — E, from BROCH 1910. × 420.

[1] Said to be copied after PAULSEN, which it is not.

Woloszynska in her memoir on Dinoflagellates from the Polish Baltic (1929, p. 252, Tab. 6) writes on *D. norvegica*:" Zellen seitlich zusammengedrückt, in Schalenansicht eiförmig, ca. 50—70 μ lang, ca. 38—50 μ breit. Grösste Breite in der Mitte. Hypovalva vorn breit, hinten stark verschmälert, dorsal bogenförmig gekrümmt, ventral konkav, gerade oder seltener konvex. Form und Breite der Schalen sehr variabel. Skulptur der Schalen stark areoliert; Areolen rund oder eckig, mit Poren. Membran der Schalen dick. Schalennaht grob gezähnt. Hypovalva mit breiten, unregelmässigen, grob gestreiften Säumen, hinten mit einigen Höckerchen versehen; seltener Hinterende ohne Höckerchen. Neritische Form. Littoralplankton."—Woloszynska gives no less than 13 drawings of *D. norvegica*. Of these I would refer fig. 11—12 to *D. borealis* (see this paper p. 46); the others all belong to f. *crassior*, which form was not hitherto known from the Baltic.

In their great work on The Dinophysoidae (1928) Kofoid & Skogsberg (p. 256) tentatively refer a specimen found in the Panama area to this species, with the remark that it is strikingly similar to Broch's figure from Spitzbergen. The specimen figured (p. 243, fig. 31, 8) has some antapical protuberances but in other respects it does not recall any published figure of *D. norvegica*, and it must be excluded from that species (length 44.5 μ).

Schiller (1933, p. 129) reproduces no less than 16 figures of *D. norvegica*, a sign that he finds the species difficult to delimitate. Several remarks could be made on this group of figures, first that *a* and *b* do not belong here, next that his reference to var. *crassior* and var. *debilior* is false: *d* designated as var. *crassior* is v. *debilior*, *l* a *crassior*, is named v. *debilior*; indeed this drawing is the type of v. *crassior*[1].

The distinctive character for *D. norvegica* sens. lat. noted by most authors is that the cell is irregularly bordered along the suture of the hypotheca and, next, its more or less pointed shape. In my opinion the most characteristic feature is the strongly curved dorsal outline and the ventral-antapical flatness or concavity. The suture-border with its irregular indentations is not always present.

How are the two "geographical races" to be understood? There is no sense in terming them varieties (p. 13); either they must be regarded as *formae* or as *species*. And as they are fairly easy to recognize and are geographically separated, we will consider them as two separate species, thus:

Dinophysis norvegica (Clap. & Lachm.) Jørgs.

Clap. & Lachm. 1859, p. 407, Tab. 20, fig. 19; Jørgensen 1899, p. 29, Tab. 1, fig. 3—6; Paulsen 1907, p. 5, fig. 1a; 1908, p. 14, fig. 12a; Broch 1910b, fig. 1, IA—B.—This paper p. 34. seqq.

A coarse form, short and broad. Dorsal outline strongly curved, antapical ventral outline straight and more rarely a little concave, ending in an obtuse angle (90° or a little more), rounded towards the apical-ventral part, where the spines

[1] Several of the figures are very badly copied, and figs. i—k are not from Paulsen, as stated, but from Meunier. Fig. p is not *D. ventricosa* Clap. & Lachm., but *D. norvegica*.

are. Dorsal suture as a rule strongly bordered, ventral-antapical suture sometimes too. Unbordered forms occur. Surface as a rule strongly sculptured by large poroids or by meanderings.

Length: in Patreksfjord (see fig. 6) (60—)62—65(—72) μ; in Norvegian waters, calculated from JØRGENSEN's figures, 60—68 μ; inner Baltic, from WOLOSZYNSKA 50(?)—70 μ.

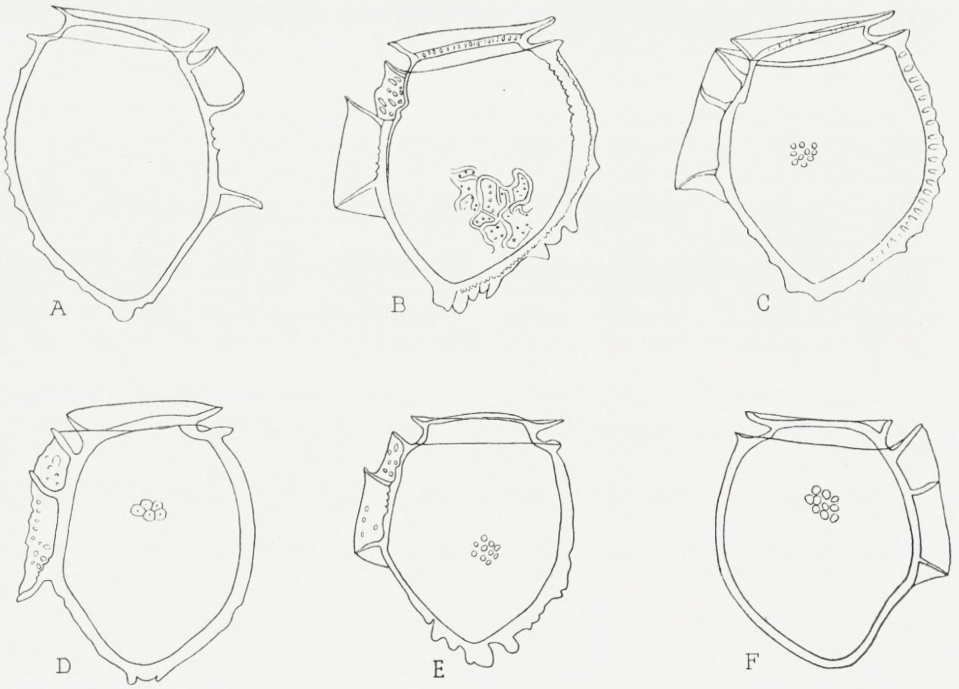

Fig. 6. *Dinophysis norvegica* (CLAP. & LACHM.) JØRGS. From "Dana"-Station 4457 (65° 34.7′ N. Lat., 23° 58′ W. L.) Patreks Fjord, NW-Iceland, 20/7—32.
Length of the cells: A = 72 μ, B = 67 μ, C = 67 μ, D = 60 μ, E = 62 μ, F = 62 μ.

Width: in Patreksfjord 47—55 μ.

Ratio $\frac{\text{length}}{\text{width}}$: ca. 1.1—1.5.

Neritic, boreal or arctic.

Dinophysis debilior (PAULSEN) emend.

D. norvegica var. *debilior* PAULSEN 1907, p. 5, fig. 1b; 1908, p. 14, fig. 12b; *D. acuta* BERGH 1881, p. 218, Tab. 15, fig. 49—52; 1887, fig. 11—12.

Narrower, pointed antapically. Dorsal outline regularly curved, antapical-ventral outline concave, ending in a sharp angle below 90°. Dorsal suture as a rule narrowly bordered, ventral-antapical suture sometimes, too. Surface sculptured.

Length 57—64 μ.

Width 39—45 μ, all dimensions from BERGH.

Ratio $\frac{\text{length}}{\text{width}}$: 1.4—1.7.

Neritic temperate form, known from Danish waters.

Dinophysis islandica n. sp.

An interesting plankton population was encountered at station 4457 in Patreks Fjord, NW-Iceland, July 20th, 1932. The plankton was taken with a Nansen net, vertical haul 50—0 m. The main species of the sample were *Chaetoceros debilis, C. constrictus, C. compressus, Rhizosolenia semispina, Rh. alata,*—few *Ceratium longipes* and few animals, several *Peridinium ovatum, P. subinerme, P. pallidum.* Of *Dinophysis* the sample contained *D. acuta,* rather few but typical, *D. norvegica* vera, i. e. what I consider the true *D. norvegica* (*crassior,* see above), and numerous other *Dinophysis* of smaller size. Between these latter, I distinguished three forms and named them provisionally: (1) "*pointed norvegica*", an antapically pointed form calling to mind *D. norvegica,* (2) "*obtusa*", a rounded form, and (3) "*obtusa verrucosa*" with same oultine as (2) but verrucose along the suture, especially antapically. Soon I became aware that these three forms were not easy to distinguish, the pointed and the rounded form being connected by numerous transitions of warts and thus being very variable.

Hence, in order to have some numerical difference I measured length and width of a number of cells, in all 211. In every one of these specimens was measured: the length of the cell, girdle lists not included, and the width of the cell, from the hindmost spine parallel to the girdle. The magnification was ×800. I noted only the number of the dividing lines of the micrometer covered by the cells; each dividing line meaning 2.5 μ.

The measurements, plotted together in fig. 7—8 seem to show with a fair amount of certainty:

(1) *D. acuta* is the biggest, but the curve of *D.* "*norvegica vera*" overlaps that of *D. acuta.* Of this norvegica 6 cells are here figured (fig. 6), they are somewhat different but have the same shape of the body. The walls are more or less sculptured by poroids, sometimes they also have meanderings. As a rule the dorsal suture is irregularly dentate, but also smooth forms occur (fig. 6F) and these are mainly by their dimensions (length 62—72 μ) separated from the forms of "*pointed norvegica*". I assume this form to be the true *D. norvegica* and to be identical with JØRGENSEN's figures from 1899; this form has a calculated length of 60—68 μ.

(2) "*Pointed norvegica*" in this locality or in this population has no connection with "*norvegica vera*", and therefore is not to be considered a local relative of it.

(3) "*Obtusa*" and "*obtusa verrucosa*" go always together and in almost equal number, they might be given the common name "*obtusa sens. lat.*".

(4) "*Obtusa sens. lat.*" and "*pointed norvegica*" are not duly separated by the measures; their curves overlap, and "*pointed norvegica*" is the smaller of the two.

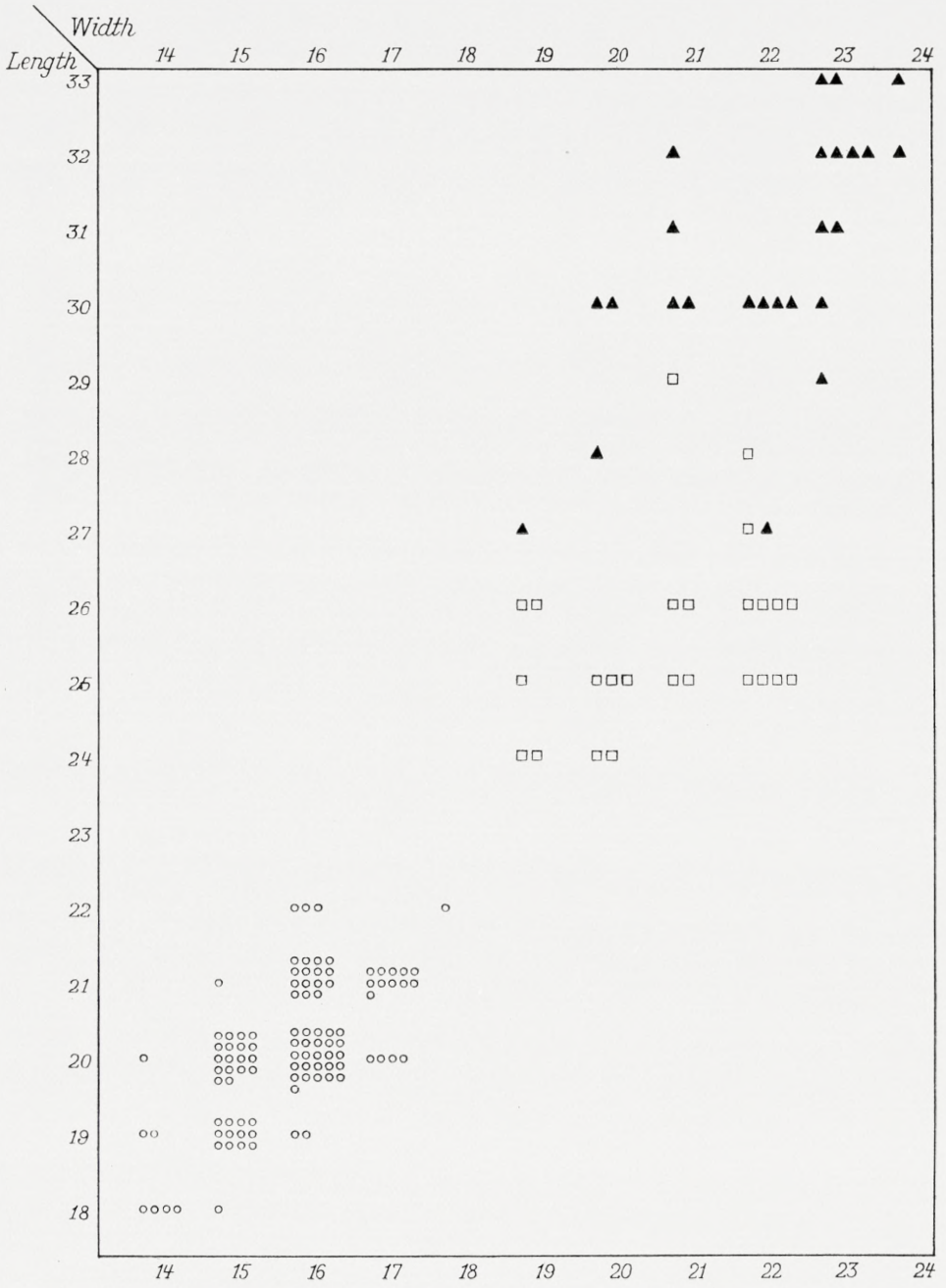

Fig. 7. Measurements of *Dinophysis*-cells from "Dana"-station 4457 (65° 34.7′ N. Lat., 23° 58′ W. L.) Patreks Fjord NW-Iceland, 20/7—32. Measuring-units = 2.5 μ.
▲ = *D. acuta*. □ = *D. "norvegica vera."* ○ = *D. "pointed norvegica"* (*D. islandica* f. *angulata*; see text p. 38 and fig. 11 A—H).

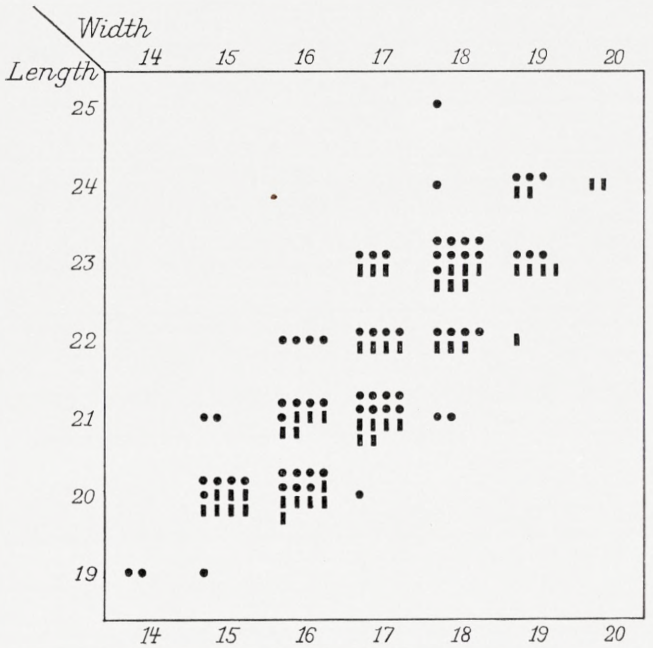

Fig. 8. Measurements of *Dinophysis*-cells from "Dana"-Station 4457 (65°34.7′ N. Lat., 23°58′ W. L.) Patreks Fjord NW-Iceland, 20/7—32. Measuring-units = 2.5 μ.
▮ = *D. "obtusa"*. ● = *D. "obtusa verrucosa"* (Those two forms are united in one: *D. islandica* f. *obtusa*; see text below and fig. 11 I—T).

By plotting the length alone, or the width alone of all three forms together we get rather regular curves of the whole population (figs. 9a and 10a). But in plotting them separately the result is very irregular curves (figs. 9b and 10b). Hence I am inclined to conclude that these three forms "*pointed norvegica*", "*obtusa*" and "*obtusa verrucosa*" belong together in one species, which we shall call *Dinophysis islandica* n. sp.

In figs. 11A—T are represented some of the numerous cells studied. A—H I would call *forma angulata*; this is the "*pointed norvegica*" of my earlier provisional nomenclature and a rather characteristic form whose pointed hypotheca and flat ventral-antapical line make it easily recognizable. Antapical protuberances are often found, but not always. Length 45—55 μ. Width 35—45 μ. This form really calls to mind *D. norvegica* as described by JØRGENSEN. As shown by the measurements it seems not to be akin to the *norvegica* present in this population, but possibly it might be a descendent from another population of relative forms.

The figures show transition between f. *angulata* and f. *obtusa*. Many more drawings might have been reproduced.

Fig. D shows a specimen whose two theca-halves are not equal, the small right one being 45×35 μ, the bigger left one 50×42 μ; the longitudinal list is broken.

For figs. I—T the name *Dinophysis islandica* f. *obtusa* is proposed. The figures

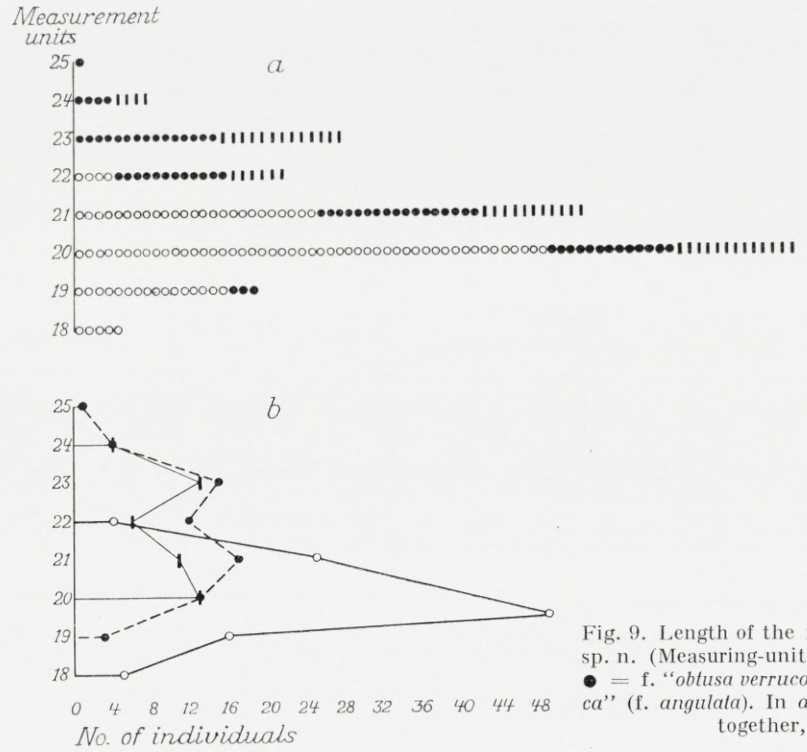

Fig. 9. Length of the forms of *Dinophysis islandica* sp. n. (Measuring-units = 2.5 μ). ▮ = f. "*obtusa*". ● = f. "*obtusa verrucosa*". ○ = f. "*pointed norvegica*" (f. *angulata*). In *a* the three forms are plotted together, in *b* separately.

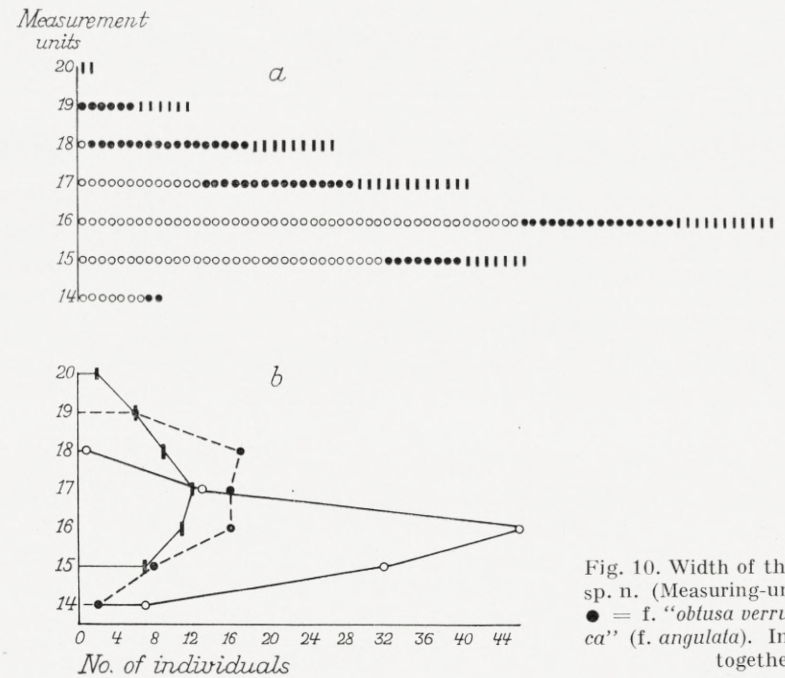

Fig. 10. Width of the forms of *Dinophysis islandica* sp. n. (Measuring-units = 2.5 μ). ▮ = f. "*obtusa*". ● = f. "*obtusa verrucosa*". ○ = f. "*pointed norvegica*" (f. *angulata*). In *a* the three forms are plotted together, in *b* separately.

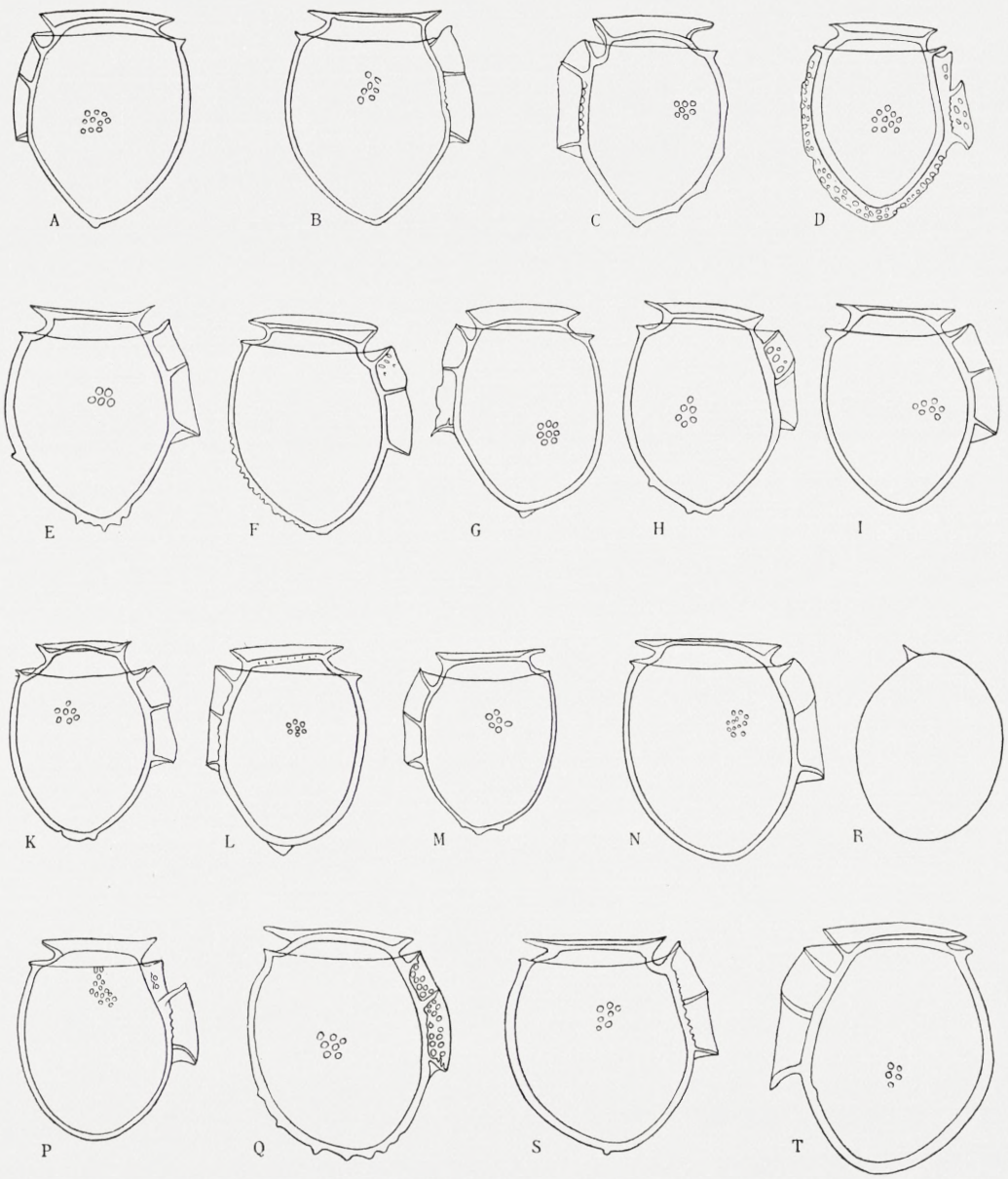

Fig. 11. *Dinophysis islandica* sp. n. From "Dana"-Station 4457 (65° 34.7′ N. Lat., 23° 58′ W. L.) Patreks Fjord NW-Iceland, 20/7—32. A—H. *D. islandica* f. *angulata* (*"pointed norvegica"* see text pp. 39—40). I—T. *D. islandica* f. *obtusa*. (All figures × 520).

are rather different, some being verrucose, some not, and broad froms like T call to mind *D. acuta*. T is 60 μ long, but the smallest *D. acuta* in this population is 68 μ.

Length of f. *obtusa*: 48—62 μ, width: 35—47 μ.

Still two *Dinophysis*-forms were found in this population of Patreks Fjord. One is a specimen of *D. borealis* n. sp., described below (p. 46). It is 42 μ long, 30 μ broad, its more rounded from and specially its more protracted shape anteriorly distinguish it from *D. islandica* (fig. 12, A). The second is a small *Dinophysis* of which I have seen but two specimens. It is a delicate species with an ovoid body, broadest before the middle, and with a rather coarse sculpture. We might call it *Dinophysis amygdalus* n. sp. It is represented in fig. 12 B—D. Length 37 μ, width 24 μ.

Tentatively I have tried to separate the specimens of *Dinophysis* occurring

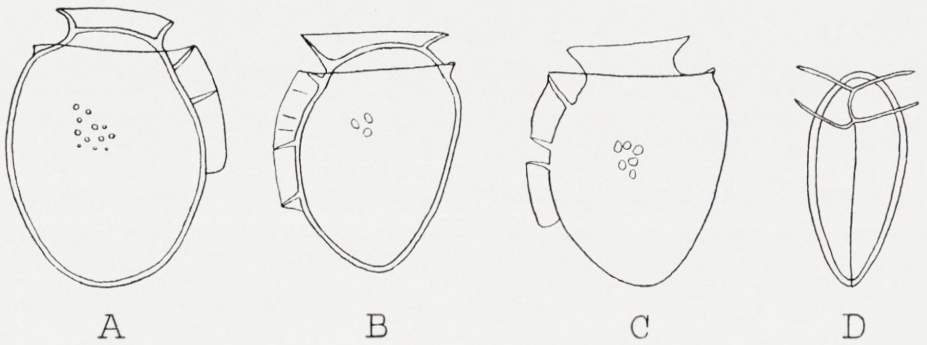

Fig. 12. *Dinophysis*-species from "Dana"-Station 4457 (65° 34.7′ N. Lat., 23° 58′ W. L.) Patreks Fjord, NW-Iceland, 20/7—32. A. *Dinophysis borealis* sp. n. (see fig. 14 K—U); Length 42 μ, width 30 μ. B—D. *Dinophysis amygdalus* sp. n.; length 37 μ, width 24 μ.

together in Patreks Fjord. But I am not sure I have found the right limits or have brought things together that really belong together. Let the whole be a view or picture of a *Dinophysis*-population from an Icelandic Fjord, where some individuals may have been born or have been stationary for a while, whereas others perhaps may have been brought in from the open sea lately.

A clever systematist might perhaps create a whole series of new species. I have tried to proceed cautiously, being content to represent the variability in *Dinophysis*.

C. *Dinophysis acuminata* Clap. & Lachm. and its relatives.

Original diagnosis: Chagrin de la carapace très-fin. Moitié postérieure réduite à l'état d'une simple plaque concave. Pas de limbe. Sommet de la moitié antérieure armé d'une dent.—Chez cette espèce, le bord ventral, c'est-à-dire celui qui porte l'anse, est beaucoup moins bombé que le bord dorsal, et la moitié anterieur (le corps du pot), au lieu de se terminer en un faîte pointu situé dans l'axe du corps, est arrondie à son sommet, mais munie d'une dent qui est plus raprochée de la région ventrale que de la région dorsale. En outre, la moitié postérieure ou rudimentaire

est beaucoup plus étroite que chez les espèces précédentes.[1]—Près de Glesnæs. Longueur environ 0 mm·044.

A copy of CLAPARÈDE & LACHMANN's drawing of this species is annexed (fig. 13 A). It may be permitted to suspect that the figures drawn by CLAPARÈDE (without camera lucida) are not quite exact. R. S. BERGH (1881, p. 185) says "die Zeichnungen welche Claparède beigegeben hat, sind auch mehr schön als naturtreu zu bezeichnen."

Of all figures published under the name of *D. acuminata* but few come near to CLAPARÈDE's drawing. The form figured by JØRGENSEN (1923, p. 20, fig. 25) has the same distal-ventral protuberance (there may be two or more in succession, says JØRGENSEN), the body is somewhat ovoid (posteriorly broader) and the dorsal outline is more rounded than the ventral one. Calculated length 50 μ.

Also the *D. acuminata* ascribed and figured from Polish waters by WOLOSZYNSKA (1929, p. 252, Tab. 4, fig. 5—8; Tab. 5, fig. 1) may belong to this species, being

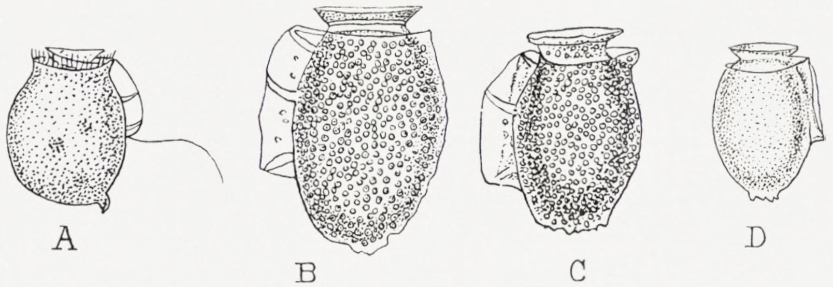

Fig. 13. *Dinophysis acuminata* CLAP. & LACHM. A, from CLAPARÈDE & LACHMANN 1859 (t. 20, fig. 17), × 300 à 350. B, C, D, from JØRGENSEN 1899 (t. 1, fig. 7—9), B × 600, C × 500, D × 400.

ovoid, 42—45 μ long and coarsely areolated, distant protuberances as a rule present. Also the "*Dinophysis baltica*" WOLOSZ. (non PAULS.) seems to me to be a true *D. acuminata*.[2]

Apart from the above-named forms, a *Dinophysis* like that figured by CLAPARÈDE & LACHMANN seems not to have been published. But authors, especially JØRGENSEN himself, have given the name of *D. acuminata* to more slender ellipsoid forms provided with one or more protuberances at the antapical end. JØRGENSEN's drawings (1899, p. 30, Tab. 1, fig. 7—9) are here reproduced (fig. 13 B, C, D); length 47—49 μ (calculated). JØRGENSEN writes about them: "Es ist mir zumal aus vier Gründen sehr wahrscheinlich, dass meine Art dieselbe wie *D. acuminata* CLAP. & LACHM. ist. Erstens wegen des hinten abgerundeten Hinterkörpers, zweitens wegen des auffallend kleinen Kopftrichters, drittens wegen der schmalen Flügelleiste und viertens wegen der kleinen Grösse. Auch die Körperareolierung stimmt sehr wohl." Later JØRGENSEN (1912, p. 10), when he describes the occurrence of the species from the Skagerak to the

[1] *I. e. D. ventricosa.*

[2] *D. Levanderi* WOLOSZ. (ibid. Tab. 4, fig. 1) and *D. cassubica* WOLOSZ. (ibid. Tab. 5, fig. 2) may(?) represent a true *D. baltica* (PAULSEN), characterised by its ovoid form and by its pointed hollow-sided epitheca on which the girdle-lists sit like a small hat on a big head.

Baltic, says: "Die Art ist sehr vielgestaltig; ausser den bei JØRGENSEN 1899 abgebildeten Formen gibt es auch an der norwegischen Westküste eine, die viel besser und ziemlich genau mit der bei CLAPARÈDE und LACHMANN abgebildeten übereinstimmt."—It had been a good thing if JØRGENSEN had published a sketch of this form.[1]

The same or similar forms have been described and figured by the following authors: PAULSEN 1908, p. 15, fig. 13 (two of JØRGENSEN's 1899-figures); LINDEMANN 1924, fig. 8—9, two different forms from the Bosporus ("sehr variabel"); LEBOUR 1925, p. 80, Tab. 12, fig. 2b, vix 2a (widely distributed, chiefly in the North. Length 38—51 μ); DANGEARD 1926, p. 328, fig. 15E, from the west coast of France; G. W. MARTIN 1928, Tab. 2, fig. 8—9, Tab. 8, fig. 6, from the coast of New Jersey (length 43—45 μ); SCHILLER 1933, p. 120, fig. 113, reproducing JØRGENSEN, LEBOUR, KOFOID (*D. ellipsoides*), CLEVE; GRAN & BRAARUD 1935, p. 372, fig. 47a—i, k (length 31—41 μ). CLEVE's figure from 1900 (Tab. 8, fig. 3) may also belong here; he calls it *D. Vanhöffenii*; about this name see below.— That all the figures quoted should be identical, is not certain, they are entered here as relative forms. All are more or less provided with antapical protuberances, but it should be emphasized that this character cannot be regarded as specifical; above it has been shown that *D. norvegica* and *D. islandica* very often have antapical protuberances and the same is the case of *D. sacculus* STEIN, *D. ellipsoides* KOF., *D. tuberculata* MANG.[2]

To sum up: under the name of *D. acuminata* at least two different forms are known, one the original species of CLAPARÈDE & LACHMANN, with an ovoid body, another the ellipsoidal form described by JØRGENSEN. KOFOID and SKOGSBERG (1928, p. 228) put in these words:

"*Dinophysis acuminata* CLAPARÈDE and LACHMANN was described from the west coast of Norway. The type, as figured, is characterized especially by being much broader posteriorly than anteriorly and by having a small, triangular antapical protuberance somewhat ventrally to the midline of the body. Under this name JØRGENSEN (1899) gave a short description and fairly good figures of a form which he had found in hundreds of specimens on the west coast of Norway; the three specimens figured, however, (1899, Pl. 1, fig. 7—9) differ strikingly from the type as figured by CLAPARÈDE and LACHMANN (1858, Pl. 20, fig. 17); they are about as wide anteriorly as posteriorly or even slightly narrower posteriorly than anteriorly, and they have some small, rounded protuberances in the middle of the postmargin of the body. In a later paper JØRGENSEN (1912) points out that *D. acuminata* is very variable and that on the west coast of Norway there is a form that agrees fairly well ("viel besser und ziemlich genau") with the type specimen. PAULSEN (1912, p. 261) considers it possible that it will prove necessary to divide *D. acuminata* in two or more species.

[1] I have written to Bergens Museum and asked if there were any drawings or papers left after JØRGENSEN, but without result.

[2] The antarctic "*D. acuminata*" mentioned and figured by BÖHM (1933a, p. 16, fig. 3) seems to deserve a special name, being more slender, pointed at both ends, and possessing a high and rather vertical anterior girdle list. It may provisionally bear the name *Dinophysis Böhmii* n. nom.

These facts seem to indicate, first, that *D. acuminata* at the present time is a collective species, and, second, that the form described and figured by JØRGENSEN (1899, pl. 1, fig. 7—9) is specifically distinct from the type. The last circumstance is the more confusing since many modern investigators evidently have treated JØRGENSEN's (1899) figures as if they had been drawn from the cotypes."

In what follows a *Dinophysis*-population will be presented which may perhaps elucidate the question. It dates from the station 4252, taken in July 1931 at 66° 17′ N, 20° 16′ W, at the north coast of Iceland, ab. 9 miles off Skagi. The plankton on the whole was poor in animals (*Evadne*, *Teneura*, *Calanus*) but rich in microplankton, consisting of both diatoms (*Chaetoceros densus*, *C. debilis*, *Rhizosolenia styliformis*) and of Dinoflagellates of which *Ceratium longipes*, *C. arcticum*, *C. fusus*, *Peridinium depressum*, *P. ovatum* and *Dinophysis acuminata* were common. Smaller *Dinophysis* specimens of the *acuminata*-type were also found. The different forms were drawn by *camera lucida*. 36 cells were drawn. Some of them are reproduced in fig. 14.

The variation is rather great, but unfortunately the number of measured cells was too small to permit any construction of variation-curves.

In this material it seems reasonable to distinguish 3 species, here named *Dinophysis Lachmanni* (figs. A—H), *D. borealis* (figs. K—U), and *D. Skagi* (fig. X) and all of them are or may be "acuminated", *i. e.* have antapical protuberances.

Fig. 14A—H in my opinion represent JØRGENSEN's 1899-form. The body has an ellipsoid form, broadest near the middle; they are more or less "acuminate". Length 50—52 μ. Ratio $\frac{\text{Length}}{\text{Width}} = 1.40—1.50$. In several of them the longitudinal list is incomplete, because the cell has divided itself lately. The sculpture is poroid; For this form I will propose the name

Dinophysis Lachmanni n. nom.

Syn. *D. acuminata* JØRGENSEN 1899, p. 30, Tab. 1, fig. 7—9 (length 47—48 μ, width 31—33 μ, non CLAP. & LACHM.; ? LINDEMANN 1924, fig. 8—9 ("sehr variabel", from Bosporus, no measures); LEBOUR 1925, Tab. 12, fig. 2b; ? DANGEARD 1926, p. 328, fig. 15E (from the west coast of France, no measures); G. W. MARTIN 1928, Tab. 2, fig. 8—9 (length 43—45 μ, from the coast of New Jersey);—non BÖHM 1933a (see above), nec. *D. Vanhøffenii* CLEVE 1900.

D. Lachmanni is known from the North Atlantic, from British, French(?) and American waters and from the coast of Norway and Iceland.

Dinophysis borealis n. sp.

The organisms represented by fig. 14K—U which are here named *D. borealis* are certainly related to *D. Lachmanni*, but they are shorter and broader, the ratio $\frac{\text{Length}}{\text{Width}}$ mostly being between 1.3 and 1.4 .Length 42—52 μ. Antapical protuberance present or absent, but as a whole less than in *D. Lachmanni*; the body is narrowed apically (the neck is slender), the dorsal outline bending inwards at the girdle.—

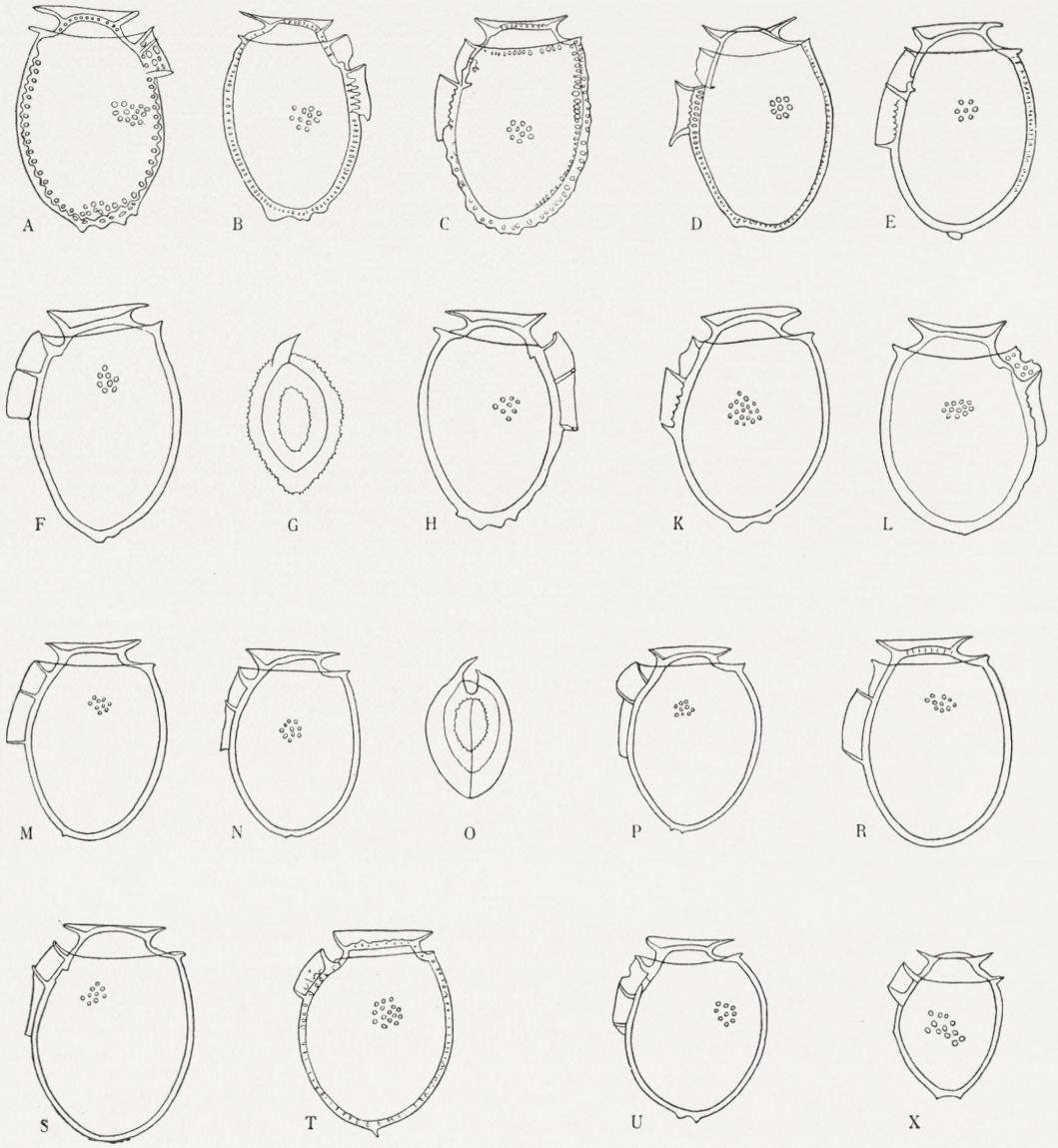

Fig. 14. *Dinophysis*-species from "Dana"-Station 4252 (66° 17′ N. Lat., 20° 16′ W. L.) off Skagi, N-Iceland, July 1931. A—H. *D. Lachmanni* nom. n. K—U. *D. borealis* sp. n. (T and U, f. *latior*). X, *D. Skagi* sp. n. (All figures × 520).

Figs. T and U (length 47 and 42 μ) are somewhat shorter and broader than the rest, and indeed they may represent a separate species. Of this "*forma latior*" as we may call it, I have seen only the two figured specimens.

Closely related to *Dinophysis borealis* or identical with it are the following previously published figures:

D. acuminata LEBOUR 1925, Tab. 12, fig. 2a; GRAN & BRAARUD 1935, p. 371, fig. 47; WOLOSZYNSKA 1929, Tab. 6, fig. 11—12; this paper fig. 12A. GRAN & BRAARUD give the following description: "The specimens which we have referred to *acuminata* vary in the shape of the body, the form of the anterior cingular lists and, like all the *Dinophysis* species, in the thickness and the structure of the cell wall. The form of the cell is egg-shaped, the greatest depth in the middle of the cell[1], with the posterior part of the hypotheca varying from being globular to more or less conical. The epitheca has a flattened to concave part on the dorsal side, just below the apex. Most of the specimens do not have any uneven contour at the antapex, but the very thick-walled specimens have small protuberances, and these specimens also have lists which are areolated, while most of the specimens do not have any conspicuous structure in the lists.—The length of the left sulcal list is from 0.4 to 0.5 of the length of the body. Length of the cell: 33 to 51 μ."

I think that these forms drawn and described by GRAN & BRAARUD agree fairly well with the Icelandic form here mentioned. Yet the variation, also in size, is greater in the Gulf of Maine material, but that may be accounted for by the fact that this material has been collected under different conditions and in three different stations, whereas my material dates from one station only.

D. borealis, as here delimited, is known from N. Iceland, from British waters, from the Baltic and from the east coast of U. S. A.

Dinophysis Skagi n. sp.

Finally the third form to be distinguished in the *Dinophysis* of station 4252 is represented in fig. 14X. It is a small form, length 35 μ, width 25 μ, broadest in the middle, with the ventral outline more sharply rounded than the dorsal one, and with distinct protuberances at the antapical end. The third spine of the longitudinal list is not to be seen.—I have seen but two specimens of this form, but on account of its characteristic outline I venture to describe it as a new species.

D. Synopsis of "acuminate" *Dinophysis*-species.

On the preceding pages have been mentioned the *Dinophysis*-species which are "acuminate", *i. e.* have antapical protuberances, and it appears that several species have these ornaments. In order to make it easy to distinguish these species, they are here represented side by side with a series of somewhat schematic figures, fig. 15.

E. What is *Dinophysis Vanhöffenii* OSTF.?

OSTENFELD (1899, p. 58, without illustration) gives this name to a heavily sculptured form, short and rounded in outline and with protuberances at the antapical

[1] If it is broadest at the middle of the body it is not egg-shaped, an egg having its greatest depth near one end of the body.

end. He quotes VANHÖFFEN (1897, Tab. 5, fig. 7), who has figured the form under the name "*D. ovata* CLAP. & LACHM.," but, OSTENFELD adds, this must be an error, CLAPARÈDE & LACHMANN having named a similar form "*D. ovalis*", but not mentioned any "*D. ovata*". "According to their figures (CLAP. & LACHM. Tab. 20, fig. 14—15) and text (p. 409) it cannot be this species as the drawing clearly shows an apical part reaching up over the girdle lists, and this is not the case in VANHÖFFEN's drawing nor in the specimens seen by me. I therefore propose to name this species *D. Vanhöffenii* nom. nov. VANHÖFFEN having been the first to observe it, and as I should

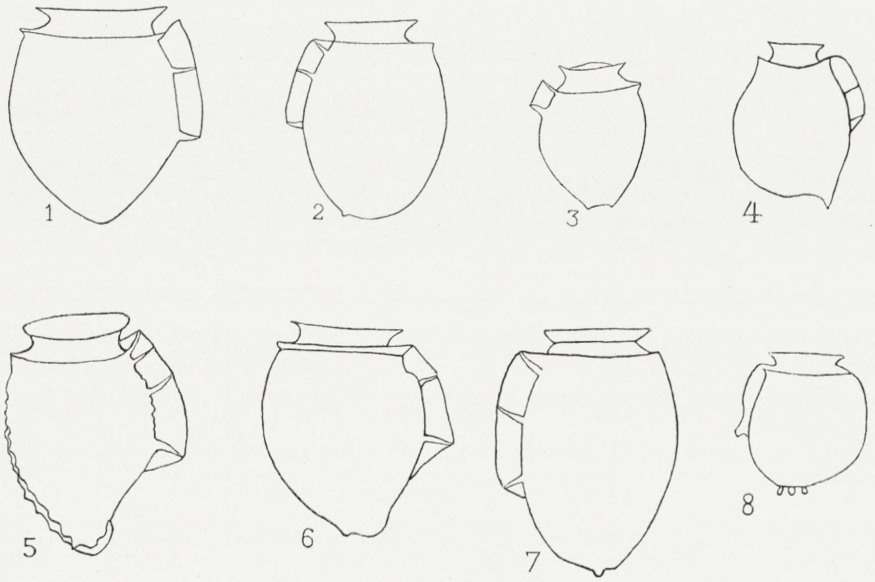

Fig. 15. Somewhat schematic figures of "acuminate" *Dinophysis*-species. 1. *islandica*; 2. *borealis*; 3. *Skagi*; 4. *acuminata*; 5. *debilior*; 6. *norvegica*; 7. *Lachmanni*; 8. *subcircularis*.

not like to name it *D. ovata* VANH., because this name is due to an error." (Translated from Danish).—But it was OSTENFELD who was in error: CLAPARÈDE & LACHMANN's name was *D. ovata* and not *D. ovalis*. As to VANHÖFFEN's drawing it is very small; its epitheca is rather low, surpassed by the anterior girdle list. Its rounded body, like that of *D. ovata* CLAP. & LACHM. (also as drawn by JØRGENSEN 1923, fig. 3) cannot refer it to *D. acuminata* (PAULS. 1908, p. 15), but it must belong to VANHÖFFEN's *D. ovata*, renamed by JØRGENSEN (1923, p. 6) *Phalacroma ovatum*. JØRGENSEN says that it is common in West Norwegian fjords, and found sparingly in the Mediterranean.

Hence, *D. Vanhöffenii* OSTF. is to be regarded as a synonym of *Phalacroma ovatum* (CLAP. & LACHM.) JØRGENSEN, as already suggested by KOFOID & SKOGSBERG (1928, p. 228).

The name given by OSTENFELD has been misused by CLEVE (1900a, p. 16), who applies it partly to a rounded form (*D. sphaerica*?), partly to an *acuminata*-

like form (see SCHILLER 1933, p. 118, 119). Also OKAMURA has misunderstood "*D. Vanhöffenii*"; his form has been (partly) named by KOFOID & SKOGSBERG as *D. Okamurai*.

F. *Dinophysis dens* PAVILLARD.

PAVILLARD 1916, p. 57, Tab. 3, fig. 1; JØRGENSEN 1923, fig. 23; KOFOID & SKOGSBERG 1928, p. 230; SCHILLER, 1933, p. 130; ?*D. vermiculata* POUCHET 1894, fig. 17 c.

The specimens figured (fig. 16) were found at station 4447 in Denmark Strait ab. 170 miles W. of Snæfellsnes, in the month of July 1932; 5 specimens were seen, length 42, 45, 55, 56, 57 μ; PAVILLARD has 50—55 μ, JØRGENSEN 51 μ. I think the

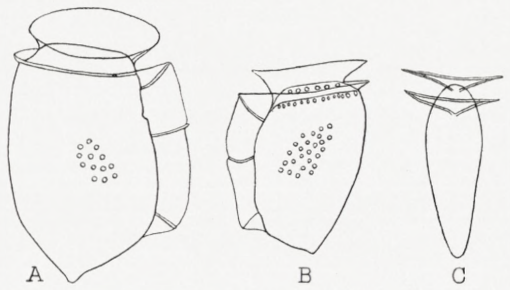

Fig. 16. *Dinophysis dens* PAV. From "Dana"-Station 4447 (64° 38′ N. Lat., 30° 10′ W. L.) ab. 170 miles off Snæfellsnes, July 1932. (× 520).

identification is correct, the broad anterior end and the oblique antapical end of the body being very characteristic. *D. vermiculata* described by POUCHET from "Voyage de "La Manche"" may be the same species, a little different in outline and with vermiculate, not poroid walls. Otherwise the species was previously only known from the Mediterranean.

G. *Dinophysis acuta* EHBG.

Four drawings here reproduced (fig. 17) show some variations of this species; one of them a specimen in bipartition.

Of three populations large enough to permit statistics, one from the Faeroes and two from Iceland, a number of specimens have been measured (length without girdle, width from the base of the hindmost spine parallel to the girdle); measuring-unity: micrometer-graduation mark, each valuing 2.5 μ. The result is given in Tables 1—3. It shows that the Faeroe specimens are on an average bigger than the Icelandic ones, although there is some overlapping.

Table 1. *Dinophysis acuta*. "Dana"-St. 4400. W. of the Faeroes (62° 21′ N; 11°00′ W), $^{24}/_{6}$ 32. (Measure-units of 2.5 μ).

Length \ Width	20	21	22	23	24	25	26	27	Total
29.....	1	2	1	..	..	..	..	..	4
30.....	..	1	2	2	..	..	..	..	5
31.....	..	2	7	8	2	..	..	..	19
32.....	..	1	3	9	14	3	..	..	30
33.....	..	..	1	9	9	10	..	..	29
34.....	..	1	..	3	5	8	1	1	19
35.....	..	..	..	..	3	..	..	..	3
Total.....	1	7	14	31	33	21	1	1	

Table 2. *Dinophysis acuta*. "Dana"-St. 4452. Faxafloi, W. of Iceland (64°08′ N; 22° 46′ W) $^{18}/_{7}$ 32. (Measure-units of 2.5 μ).

Length \ Width	20	21	22	23	24	25	Total
27.....	1	..	..	..	..	..	1
28.....	1	..	1	..	..	..	2
29.....	..	4	4	2	..	..	10
30.....	..	6	11	3	1	..	21
31.....	..	1	4	5	1	..	11
32.....	..	..	..	..	4	1	5
33.....	..	..	..	..	..	1	1
34.....	..		..	..	..	1	1
Total.....	2	11	20	10	6	3	

Table 3. *Dinophysis acuta*. "Dana"-St. 4402. 100 km S. of Ingolfs Höfdi, Iceland (62°23′ N; 16°05′ W), $^{25}/_{6}$ 32. (Measure-units of 2.5 μ).

Length \ Width	20	21	22	23	24	25	26	Total
29.....	1	..	2	..	..	..	..	3
30.....	2	6	3	..	..	..	..	11
31.....	..	3	5	6	..	..	..	14
32.....	..	2	7	15	9	..	..	33
33.....	..	..	1	6	5	1	1	14
34.....	..	..	..	..	1	2	..	3
35.....	..	..	..	..	..	..	1	1
Total.....	3	11	18	27	15	3	2	

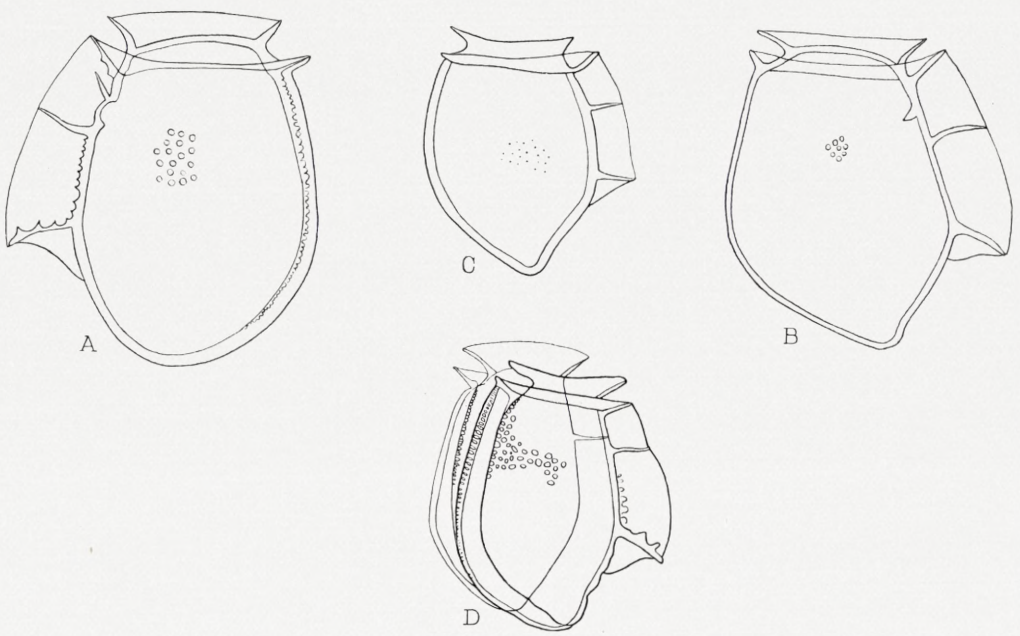

Fig. 17. *Dinophysis acuta* EHBG. A, from "Dana"-Station 4447 (64° 38′ N. Lat., 30° 10′ W. L.), July 1932. B and C, from "Dana"-Station 4457 (65° 34.7′ N. Lat., 23° 58′ W. L.), July 1932. D, from "Dana"-Station 4258 (66° 32′ N. Lat., 15° 45′ W. L.), August 1931. (A, B, C × 520; D × 300).

H. *Phalacroma irregulare* LEBOUR.

Lebour 1925, p. 78, Tab. 11, fig. 4 a—c.

The three drawings annexed (fig. 18) may show this species, whose specificity is perhaps dubious, *Ph. rotundatum* being, as JØRGENSEN (1923, p. 5) says, a variable species, or perhaps a group of species—According to LEBOUR's drawings *Ph. rotundatum* has the ratio $\frac{\text{length}}{\text{width}} = 1.0—1.1$, *Ph. irregulare* 1.23. Of the specimens here figured, A

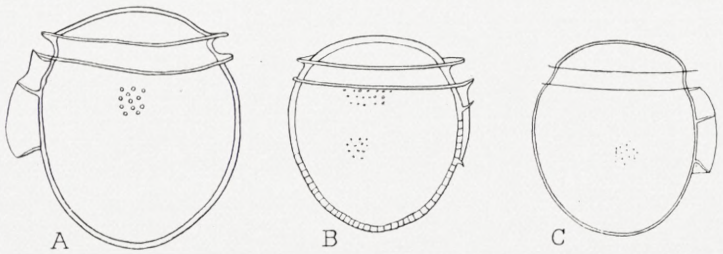

Fig. 18. *Phalacroma irregulare* LEBOUR. A. (57 μ long) from "Dana"-Station 4478 (65° 18′ N. Lat., 13° 53′ W. L.), 29/7-32. B. (60 μ long) from "Dana"-Station 4252 (66° 17′ N. Lat., 20° 16′ W. L.), July 1931. C. (49 μ long) from "Dana"-Station 4457 (65° 34.7′ N. Lat., 23° 58′ W. L.), 20/7-32.

has the ratio 1.2, B 1.16, C 1.2. I have not observed whether the poroids contain pores—a character given by LEBOUR for *Ph. irregulare* in contradiction to *Ph. rotundatum*. C is a curious form, constricted at the girdle; its walls are very delicate, the sculpture barely visible.

2. Icelandic *Peridinia, Ptychodiscus,* and *Goniaulax.*

A. *Peridinium roseum* Paulsen.

Paulsen 1904, p. 23, fig. 9; Meunier 1910, Tab. 2, fig. 10—11 (sed false delineata: ortho!); Jørgensen 1912, p. 7; Lebour 1925, p. 130, fig. 41 a; Pavillard 1931, Tab. 2, fig. 10 A, 10 B.

This species is insufficiently known, on account of its original description; the plate-arrangement as drawn there cannot be true; the figures d, e, f, represent the species more truly than a, b, c.

In plankton-samples from Iceland waters the species has been seen now and then in recent years. The figures annexed (fig. 19) may give some idea of it. It is, as

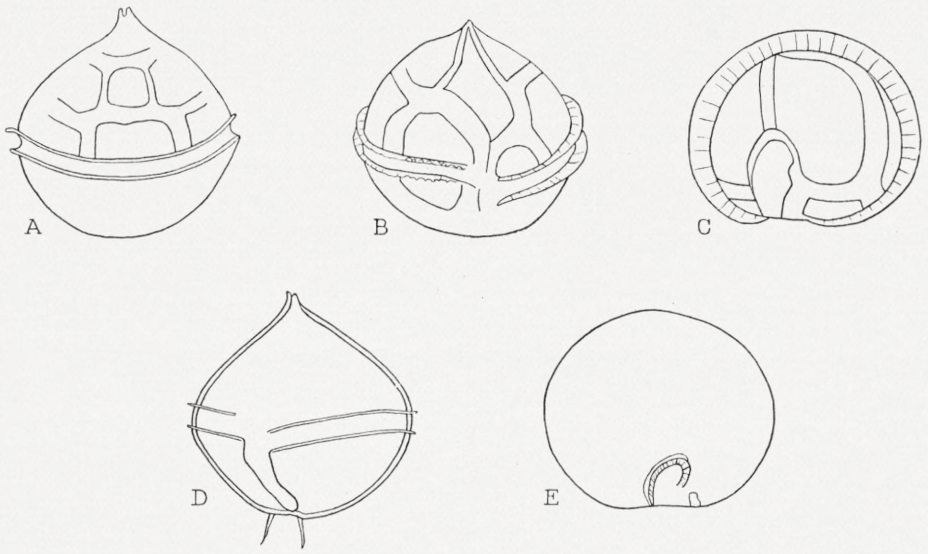

Fig. 19. *Peridinium roseum* Paulsen.
A, B, C, from "Dana"-Station 4407 (63° 30.5′ N. Lat., 20° 04.5′ N. W. L.), 27/6—32. (All figures × 520).

delineated by Pavillard, Meta quadra (a single specimen penta) and therefore is ascribed to the section Humili-Piriformia.

P. distans Mangin (1912, fig. 21, 1) from the coast of France has some resemblance to *P. roseum* but is different by its circular girdle.

P. roseum has been found along the North and East coast of Iceland, in the Denmark Strait, in the Kara and Barents Seas. Pavillard (1931) has it from numerous stations of the "Princesse Alice" from 61° N. along the Norwegian coast, and particularly from many places at Spitzbergen; North of 78° N, he says, the *Ceratia* have disappeared, and "*Peridinium pallidum* pullule ça et la, avec le *P. roseum*". Hence *P. roseum* must be characterised as a cold water species, and neritic. Still it has also

been recorded from Danish and Scottish waters. JØRGENSEN (1912, p. 7) says a related form (var. *aciculatum* JØRGS.) occurs in the Skagerak and the Great Belt, but he has not figured it.

B. *Peridinium punctulatum* PAULSEN and *P. subinerme* PAULSEN.

The *Peridinium* represented in fig. 20 belongs to *P. punctulatum*. It has a conical epitheca; its hypotheca is rounded with but a shallow depression and no antapical horns. The girdle is circular, the left edge of the longitudinal furrow ends in one or two small fins or lists. Tabulation: Ortho, hexa. The whole surface is covered by tiny spines connected by fine lines. Length 50—57 μ, width 57—60 μ. Found at the Faeroes, in the Nolsø Fjord near Thorshavn.

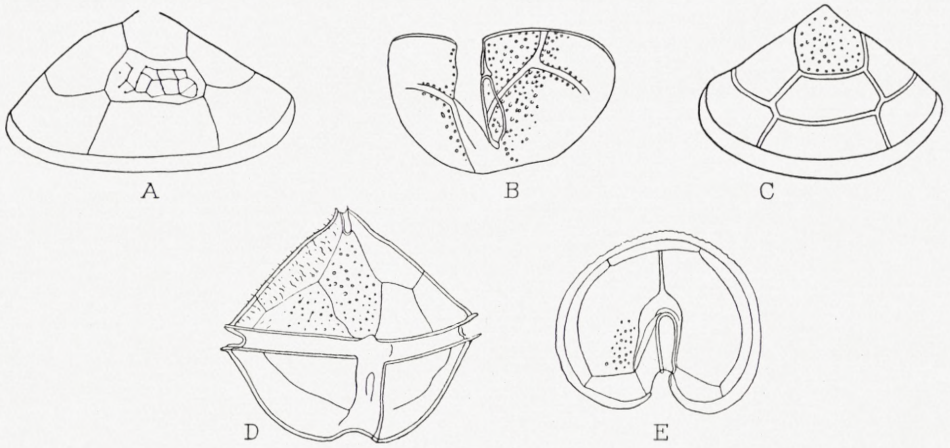

Fig. 20. *Peridinium punctulatum* PAULSEN.
From "Dana"-Station 4496 (62° 04.5′ N. Lat., 6° 46′ W. L.), 2/8-32. (× 520).

The relation of *P. punctulatum* to *P. subinerme* has been discussed by some authors. The dorsal intercalary 2a is in *P. punctulatum* usually penta, thus in the figures of PAULSEN 1907, fig. 28, 1908, fig. 79; MEUNIER 1919, Tab. 17, fig. 32—35; DANGEARD 1927 b, fig. 20e, f, as distinct from *P. subinerme*, where it is hexa.

JØRGENSEN (1912) and PETERS (1928) have united the two species into one under the name *P. subinerme*. MEUNIER (1919) keeps them distinct, and also LEBOUR (1925) gives both species, *P. subinerme* under Sect. Conica and *P. punctulatum* under Sect. Tabulata, thus separating them at the symmetric or unsymmetric 2a. MATZENAUER (1933) has found related species in tropical waters (if the same?) and recognizes both species, adding that they are alike and that *P. punctulatum* has been found with 2a both penta and hexa ("dorsale Lappenzusammensetzung vom Typus Conica oder auch "Tabulata""). SCHILLER (1937, p. 245, figs. 244—245) regards *P. punctulatum* as a variety of *P. subinerme* distinguished by "eine etwas niedrigere

und breitere Gestalt, die meist schmälere Längsfurche und durch das schärfere Hervortreten der äquatorialen Partie . . . 2a ist meist fünfseitig, also unsymmetrisch."

To this I would remark that there can be no doubt that the specimens here figured are *P. punctulatum*, and not *P. subinerme*, and that the identification has been easy wherever I have seen these two species. It appears from SCHILLER's treatment, that also he is able to distinguish the two forms,—if then they are regarded as varieties or as species is irrelevant.

PETERS (1928) denies the right to distinguish species by symmetry or asymmetry, and perhaps he is right in respect of the dorsal symmetry (but the distinction between Ortho, Meta, and Para is more stable).

Still, of the organisms drawn by PETERS as *P. subinerme*, none is *P. punctulatum*, and I wonder if he has ever seen a true *P. punctulatum*.

The main differences between the two species are: *P. punctulatum* has a lower epitheca, as a rule 2a penta, and a rounded hypotheca without spines, whereas *P. subinerme* has a higher epitheca, 2a as a rule hexa and an angular hypotheca with two small spines.—Both of them belong to the Section Conica.

It is not important if in this case there are two species or only one, but I would emphasize that in principle it is better to keep apart than to unite.

The spiny cover of the cells here mentioned (Fig. 20) is new for *P. punctulatum*, a parallel to *P. pentagonum* var. *spinulosum* MANGIN (1912, p. 29, fig. 17, Tab. 1, fig. 11) and to *P. crassipes* var. *spinulosa* DANGEARD (1926, p. 324, fig. 12D, E). Our organism might then be named *spinulosa*, too, but if it be true that such characters as reticulation, punctulation, or spinosity are not reliable species-characters but change according to conditions, not as a variety but as a *forma*. This is a protest against SCHILLER's saying (1937, p. 246: "Die Punktierung der Hülle und die kleinen Stacheln am Ende der Längsfurchenränder sind natürlich als akzessorische Bildungen nicht einmal zur Unterscheidung einer *forma* geeignet." Why "natürlich"? nobody can be sure. As ordinarily used, "*forma*" is just a designation for a small deviation from the normal form, owing to local conditions.

C. *Peridinium islandicum* PAULSEN.

This species was described by PAULSEN (1904, p. 23). It is characterised by its depressed oblique form, by its small size (length 56—64 μ, diameter 68 μ); antapically the cell has two wingless spines, perhaps also a third with a narrow wing. Its tabulation is: Para hexa.—The species has been studied by BROCH (1910 b, p. 46), who gives some drawings of its plates, but not the shape of the cell. Next MEUNIER (1910, Pl. I, fig. 10—13, p. 27) mentions and figures it, but the drawing shows a *Metaperidinium*. Finally SCHILLER (1937, p. 206) describes the species, reproducing PAULSEN's figures, and adds: "Ungenügend bekannte und wenig charakteristische Art." In contrast to this, MEUNIER (l. c.) begins the description of *P. is-*

landicum by these words: "Espèce à caractères bien distincts, dont la vue latérale (fig. 13) est la plus suggestive, car elle montre bien l'obliquité de l'axe polaire sur la ceinture."

The annexed figures (fig. 21) show the species in question and its tabulation.

As already stated in 1904, this species is found along the North and East coasts of Iceland, in greater quantities in the month of July. It has also been seen in samples

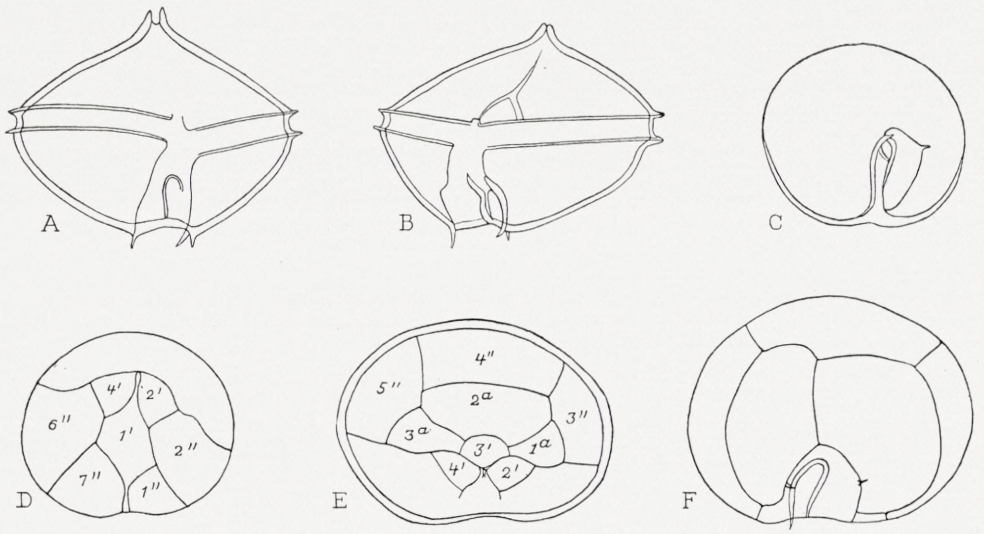

Fig. 21. *Peridinium islandicum* Paulsen. A. from "Dana"-Station 4474 (66° 22′ N. Lat., 14° 27′ W. L.), 26/7-32. (× 520). B, D, E, F, from "Dana"-Station 4478 (65° 18′ N. Lat., 13° 53′ W. L.), 29/7-32. (× 520). C, from "Dana"-Station 4262 (65° 55′ N. Lat., 14° 33′ W. L.), 2/8-32. (× 300).

from the near Greenland East coast and in single specimens from S. Iceland and from W. of the Faeroes. Meunier has it from the West coast of Novaya Zemlya, and Broch from the Icefjord in Spitzbergen. Broch (l. c. p. 26) terms it an arctic-neritic species, to which I agree.

D. *Peridinium piriforme* Paulsen.

Paulsen 1907, p. 13; 1908, p. 46, fig. 57; Meunier 1910, Pl. I, fig. 14—18, pl. II, fig. 18—19 (tabulation in error); Paulsen 1911, p. 310, fig. 8; Lebour 1925, p. 126, fig. 38; Peters 1928, p. 51, fig. 14; Schiller 1937, p. 194, fig. 191 a—g, not cet. fig.; non Abé 1936 b, fig. 43—47, nec Schiller 1929, fig. 20 (*oviforme!*); *P. Steinii* f. *pyriformis* Paulsen 1905, fig. 3 d—e.—? *P. africanoides* Dangeard 1927, p. 357.

The drawings here reproduced (fig. 22) show the Iceland form, which is the original one, first described. It is characteristic by its clumsy shape, the epitheca being conical, almost rectilinear in outline. The tabulation is Meta penta.—The sutures are often very broad. They may be both striate and reticulate, the reticulation

extending out over the striate surface. There are pores in the plate-areoles but none on the areoles of the sutures. Length 63—75 μ.

SCHILLER has united to this species the *P. oviforme* DANG., it being also Meta penta, but in my opinion he is not right in doing so, *P. oviforme* being very different in shape of body.

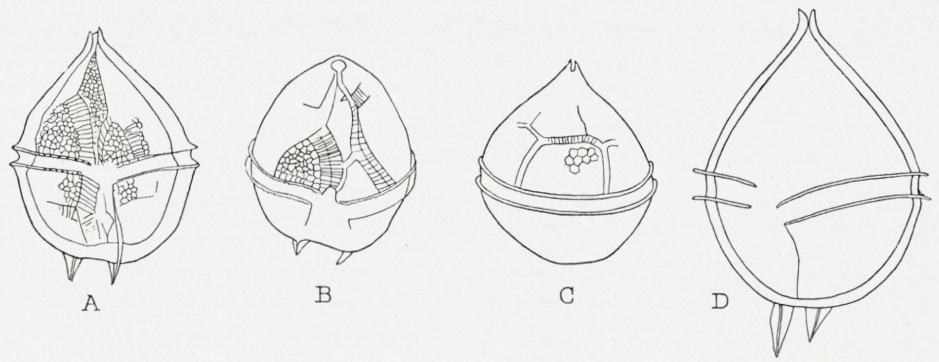

Fig. 22. *Peridinium piriforme* PAULSEN. A, from "Dana"-Station 4264 (65° 19.5′ N. Lat., 13° 34′ W. L.), 4/8-31. (Length 72 μ). B, from "Dana"-Station 4260 (66° 25′ N. Lat., 15° 04′ W. L.), 2/8-31. (Length 68 μ). C, from "Dana"-Station 4264 (65° 19.5′ N. Lat., 13° 34′ W. L.), 4/8-31. D. from "Dana"-Station 4202 (47° 36′ N. Lat., 28° 39′ W. L.), 29/6-31. (× 520).

Related to *P. piriforme* is *P. breve* PAULSEN. It has the same clumsy shape but is shorter, and *P. breve* might indeed be a *forma* of *P. piriforme*. BROCH (1910 b) has found a similar form at Spitzbergen and called it *P. breve*; it is Meta quadra and seems to be identical with *P. sphaeroideum* MANGIN (1922, p. 81, fig. 24, II) (the first figure is drawn from the under side) from antarctic waters; BROCH's figure may not be the true *P. breve*. Of the other forms put together by SCHILLER (1937, p. 198, fig. 194)

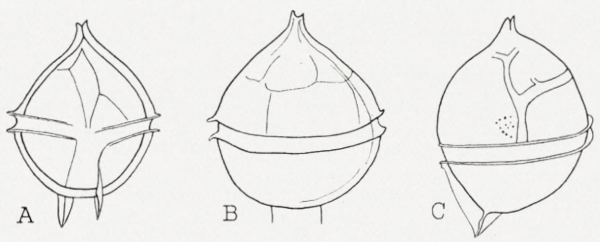

Fig. 23. *Peridinium pyriforme* (ABÉ 1936b)?
A—C from "Dana"-Station 4255 (66° 30′ N. Lat., 17° 17′ W. L.), 2/8-31. (× 520).

under the name of *P. breve*, e—h (*P. pedunculatum* SCHILLER 1929) and i (*P. styliferum* SCHILLER 1929), are both Meta, but seem in other respects to approach Sect. Pellucida.

The organisms represented in fig. 23 seem identical with *P. pyriforme* ABÉ 1936b, fig. 43—47, a relative form, but pear-shaped, with acuminate epitheca; it comes near to *P. Steinii* JØRGS.

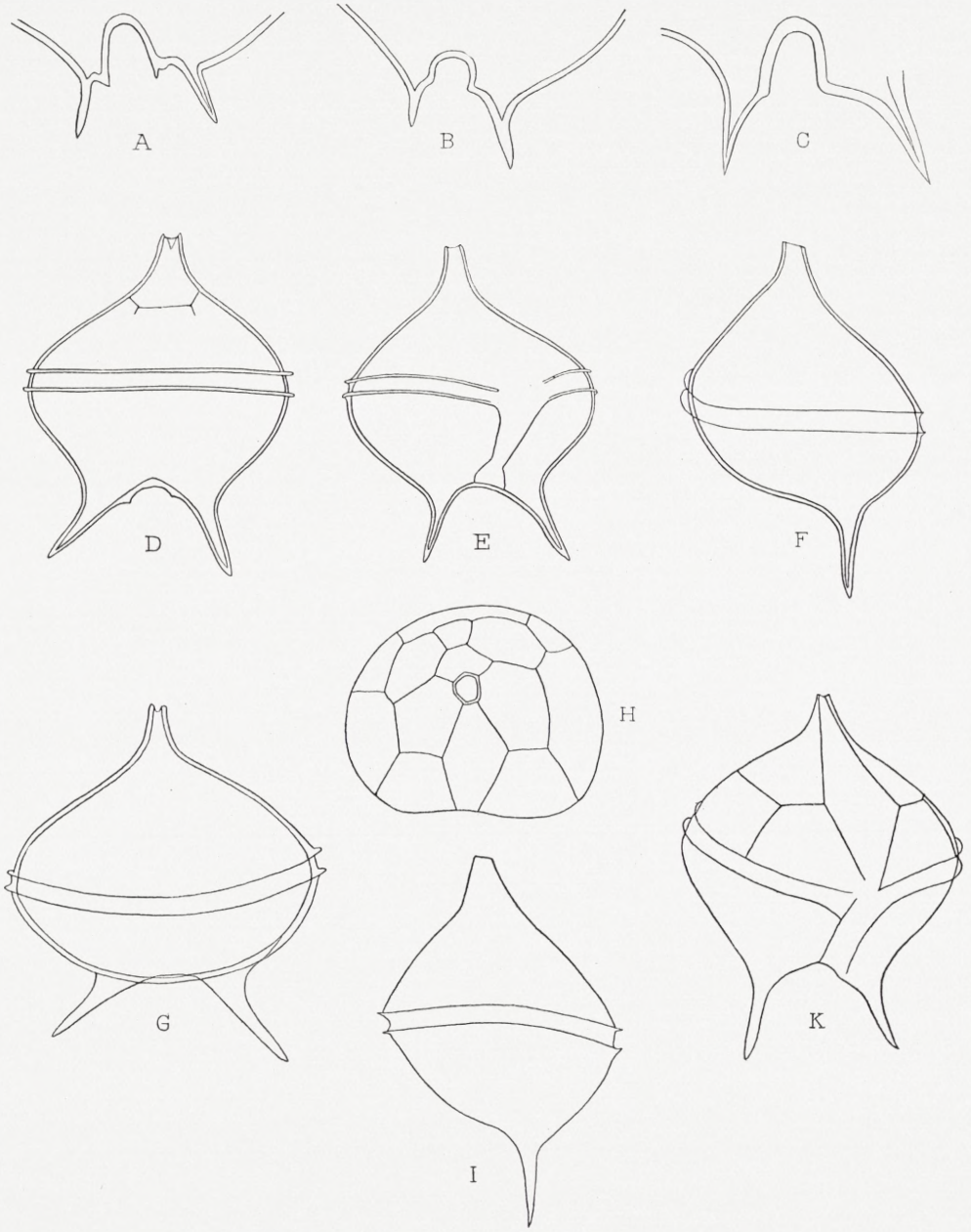

Fig. 24. A—C, The antapical horns of *Peridinium depressum* (see figs. 25—28). D—H, *Peridinium saltans* MEUNIER from "Dana"-Station 4413 (63° 34′ N. Lat., 22° 23′ W. L.), 28/6-32. (× 520). I—K, *Peridinium depressum forma* from "Dana"-Station 4413. (× 520).

E. *Peridinium depressum* Bail.

On the subject of the great variability of this species Peters (1928) published splendid and convincing investigations, and I regret that I overlooked them while working with *P. depressum*. Candeias (1934) has contributed a valuable supplement to Peters' work.

Through my researches I have come to the same conclusion as Peters with regard to *P. parallelum* Broch, namely that the hollowness or solidity of the antapical horns cannot serve as a specific character. The figures (24 A—C) demonstrate this. But it is not in all populations of *P. depressum* that we find solid antapical horns; in some they are completely absent, in others they dominate, and in others again we find both kinds of antapical horns together in about equal numbers. The four curves (figs. 25—28) show firstly the variation in the transdiameter measured in divisions of 2.5 μ; next the position as regards the antapical horns, hs meaning: right horn hollow, left solid, ss: both solid, hh: both hollow. The determination of whether a horn is "solid" or "hollow" is not always certain, as there are many transitions; but in every case it was made on the same principles.

Of the four "Dana"-stations, all of which were taken in June 1932, No. 4402 lies rather far out to sea and remote from the other three, all of which were taken near the southwest coast of Iceland.

It will be seen that the population from Station 4402 consists of individuals

Measure-units	
36.....	ss ss
37.....	ss ss ss ss
38.....	ss ss ss ss ss ss ss ss ss ss ss ss
39.....	ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss hh
40.....	ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss hh
41.....	ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss
42.....	ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss hh
43.....	ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss ss hh hh hh
44.....	ss ss ss ss ss ss ss ss ss ss ss ss ss hh
45.....	ss ss ss ss ss ss ss ss ss ss ss ss ss ss
46.....	ss ss ss ss ss ss ss ss ss ss ss hh
47.....	ss ss ss ss ss ss ss
48.....	ss ss ss ss
49.....	ss ss ss hh
50.....	ss ss ss
51.....	ss ss ss ss
52.....	
53.....	ss
54.....	
55.....	
56.....	ss

Fig. 25. *Peridinium depressum* s. lat. Transdiameters (in units of 2.5 μ). St. 4402. 62° 23′ N., 16° 05′ W., ab. 100 miles S. of Ingolfs Høfdi. 26/6-32.—Transdiameter: 90—140 μ. (hs: see text).

Measure-units	
36	hh hh
37	
38	hh hh
39	hh hh
40	hh hh hh hh hh hh hh hh hh
41	hh hh hh hh hh hh hh hh hh hh hh hh hh
42	hh hh hh hh hh hh hh hh
43	hh hh hh hh hh hh hh hh hh hh hh hh hh hh hh hh hh
44	hh hh hh hh hh hh hh hh hh hh hh hh hh hh hh hh hh hh hh hh
45	hh hh hh hh hh hh hh hh hh hh hh hs
46	hh hh hh hh hh hh hh hh
47	hh hh hh hh hh hh
48	hh hh
49	hh hh hh
50	hh hh hh hh
51	hh hh

Fig. 26. *Peridinium depressum* s. lat. Transdiameters (in units of 2.5 μ). St. 4411. 63° 49′ N., 22° 11′ W., near Westmann Islands. 28/6-32.—Transdiameter: 90—127 μ. (hs: see text).

Measure-units	
33	ss ss ss
34	hs hs hs hs hs ss
35	hh hs hs hs hs hs hs hs hs hs ss ss ss ss ss ss ss ss
36	hh hh hh hh hh hs hs hs hs hs hs hs hs hs hs hs hs hs ss ss ss ss ss ss ss
37	hh hh hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs ss ss ss ss ss ss
38	hh hh hh hh hs hs hs hs hs hs hs hs hs hs hs hs hs s hs hs hs hs hs hs ss ss ss ss ss ss ss
39	hh hh hh hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs ss ss ss ss ss ss ss ss ss ss
40	hh hh hh hh hh hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs ss ss ss ss ss ss ss ss ss ss
41	hh hh hh hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs hs ss ss ss ss ss ss ss ss ss
42	hh hh hh hh hh hh hh hh hh hh hs hs hs hs hs hs hs hs ss
43	hh hs hs hs hs hs hs hs hs ss ss ss
44	hh hh hh hh hh hh hs hs hs hs ss ss
45	hh hs hs hs hs hs hs hs hs hs hs ss
46	hh hs hs hs hs ss ss ss
47	hh hs hs hs ss
48	hh hs hs hs hs ss ss ss ss
49	hs hs ss ss ss ss
50	hs hs
51	hs hs ss ss
52	hs
53	hs
54	hs
55	hs ss
56	
57	hs

Fig. 27. *Peridinium depressum* s. lat. Transdiameters (in units of 2.5 μ). St. 4413. 63° 34′ N., 22° 23′ W., ab. 25 miles S. of Reykjanes. 28/6-32.—Transdiameter: 82—142 μ. (hs: see text).

Measure-units	
46.....	hh hh hh hh hh hh hh hh hs
37.....	hh
38.....	hh
39.....	hh hh hh
40.....	hh hh hh hh hh hh
41.....	hh hh hh hh
42.....	hh hh hh hh
43.....	hh hh hh hh hh hh
44.....	hh hh hh hh hh hh
45.....	hh hh hh hh hh hh
46.....	hh hh hh hh hh hh hh hh hs
47.....	hh hh hh hh
48.....	hh hh hh hh hs
49.....	hh hh hh hs
50.....	hh hh hh hh
51.....	hh hh hh
52.....	hh hh hh
53.....	hh
54.....	hh
55.....	hh

Fig. 28. *Peridinium depressum* s. lat. Transdiameters (in units of 2.5 μ). St. 4415. 64° 14′ N., 22° 13′ W Faxa Fjord near Reykjavik. 29/6-32.—Transdiameter: 92—137 μ′. (hs: see text).

with solid antapical horns, with a very few hh. The opposite is the case with 4411 and 4415, where the horns are hollow and only a few individuals have a solid left antapical horn. Finally, 4413, of which the greater part consists of individuals with the right horn hollow, left solid, whereas both hh and ss also occur.

The organisms represented in fig. 24 D—H call to mind *P. saltans* MEUNIER, a species recognized by LEBOUR but rejected by SCHILLER. MEUNIER (1910, p. 26) distinguishes it from *P. depressum* (his *P. divergens*) by its small size and by the divergent antapical horns. His specimens have a (calculated) length of ab. 72 μ and a transdiameter of ab. 62 μ,—mine are 85—90 μ long and have a transdiameter of 65—75 μ; the antapical horns are shorter and hardly so widely divergent as those figured by MEUNIER. The apical tabulation of my specimens is figured (24 H); the 2a is much smaller than that drawn by MEUNIER.

I doubt if it would be right to maintain *P. saltans* as more than a *forma* of *P. depressum*. In the same station (in Faxa Floi) where this dubious *P. saltans* was found, also another small *P. depressum* was observed, it is figured (fig. 24J- K) and shows relatively long antapical horns which are only slightly divergent, and this must be the same thing.

F. *Ptychodiscus inflatus* Pavillard.

Pavillard 1916, p. 12, pl. I, fig. 3a, 3b.

On station 4488, North of the Faeroes (62° 42′ N., 8° 40′ W.) the organisms here figured (fig. 29) were taken in a haul 50—0 m and are ascribed to the species named above. It is mainly characterised by its two unequal halves separated by a girdle, and by the narrow keel on the smaller half, which is somewhat concave. On the bigger convex half, under the end of the keel, is a longitudinal furrow, with lists on either side. Therefore the bigger half must be the hypotheca and the carinated smaller half the epitheca (in contradistinction to Pavillard and Schiller, who both regard the keel-half as the hypotheca). The cell-content is granulated, the walls without

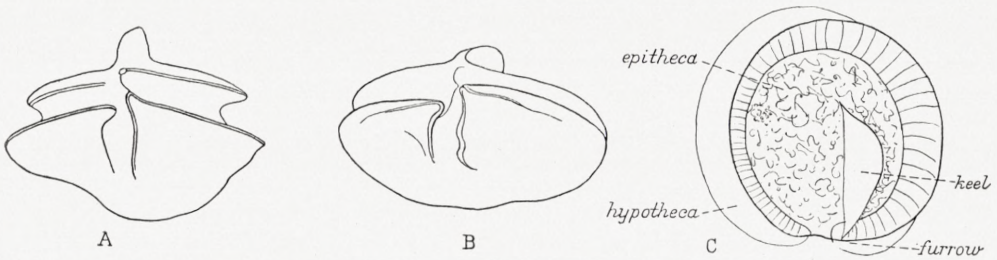

Fig. 29. *Ptychodiscus inflatus* Pav.
A—C, from "Dana"-Station 4488 (62° 42′ N. Lat., 8° 40′ W. L.), 30/7-32.

sutures and visible sculpture. There is a hole where the girdle and the keel meet. Greatest width 75—100 μ, length (keel incl.) 30 μ, keel 17 μ.

I would suggest, that the "Stabplatte" figured in *Ptychodiscus noctiluca* Stein is a keel like that described by Kofoid and by Pavillard and in the present treatise, and next that the organism figured by Murray and Whitting (1899, Tab. 27, fig. 5a, 5b, 5c) is not a *Ptychodiscus*, but some *Peridinium* or *Diplopsalis*. The family of *Ptychodiscaceae* Lemm. in my opinion ought not to have been created, firstly because its members are not sufficiently known, and, secondly, because in the conception of Schiller (1937), it embraces forms not relatively but very different from one another. But it is the trend now to create new small families, see also Lindemann's treatise 1928 in "Die natürlichen Pflanzenfamilien."

G. *Goniaulax Ostenfeldii* (Paulsen) Emend.

Goniodoma Ostenfeldii Paulsen 1904, p. 20, fig. 2; Lebour 1925, p. 90, fig. 27; Woloszynska 1929, p. 257, Tab. 15, fig. 11—13; Schiller 1937, p. 440, fig. 481.

This species was described from Icelandic waters. Its membrane being very delicate, it is difficult to make out its tabulation, and Lebour (l. c.) rightly said that "This species had not had its plates worked out sufficiently to characterise it." Hence in refinding it in Icelandic plankton I have tried to make out its plates, using potassic hydrate, which makes the cell-wall burst and the plates show themselves. The figures

(30 C—E) show the result, and the species as suggested by LEBOUR, must be classed among *Goniaulax*. It has 4 apicals and 6 precingulars; the girdle plates have not been made out; 6 postcingulars, 1 intercalary plate (p), 1 antapical plate and 4 plates of the ventral area. Hence it seems to be well characterised as a *Goniaulax*. LEBOUR

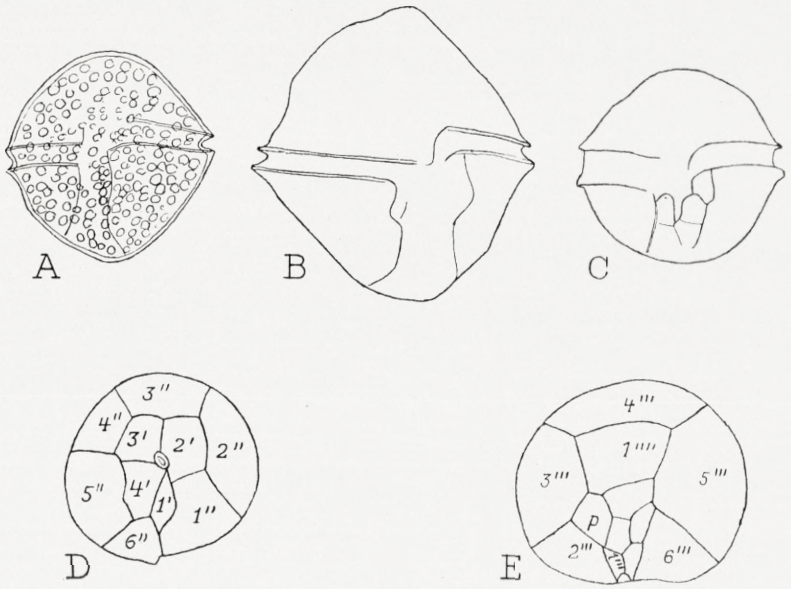

Fig. 30. *Goniaulax Ostenfeldii* (PAULS.) emend. B, from "Dana"-Station 4249 (66° 30′ N. Lat., 23° 00′ W. L.), 31/7-31. C, from "Dana"-Station 4217 (65° 42′ N. Lat., 25° 32′ W. L.) 15/7-31. A, 40 μ long; B, 63 μ long; C, 40 μ long. D—E, schematic drawings.

thinks it is related to *G. orientalis* LINDEMANN (1924, p. 221), but the tabulation seems different; f. inst. *G. orientalis* has but three apicals. *G. Ostenfeldii* seems to be identical with *G. tamarensis* LEBOUR (GRAN & BRAARUD 1935, p. 376), which species provisionally may be regarded as a synonym, but its tabulation is not sufficiently known.

G. Ostenfeldii is often found abundantly along the coasts of Iceland. It is also known from the Baltic.

IV. Bibliography.

Abé, T. H. 1927. Notes on the Protozoan Fauna of Mutsu Bay. I. Peridiniales.—The sci. rep. of the Tohoku Imp. Univ. 4. Ser., biol. II, No. 4. Sendai.

— 1936a. II. Genus Peridinium: Subgenus Archaeperidinium.—Ibid. X, Nr. 4.

— 1936b. III. Subgenus Protoperidinium: Genus Peridinium.—Ibid. XI, No. 1.

Aurivillius, C. W. S. 1898. Vergl. tiergeogr. Untersuch. über die Plankton Fauna des Skageraks in den Jahren 1893—1897.—Kgl. Svenska Vet. Akad. Handl. 30. Stockholm.

Barrows, A. L. 1918. The significance of skeletal variations in the genus Peridinium.—Univ. of California publ. in Zoology 18, No. 15. Berkeley.

Bergh, R. S. 1881. Der Organismus der Cilioflagellaten.—Morphol. Jahrb. 7. Leipzig.

— 1887. Über den Teilungsvorgang bei den Dinoflagellaten.—Zool. Jahrbücher. II. Jena.

Biebl, R. 1936. Beobachtungen an Planktonfängen zwischen Wesermünde und Island.—Oesterr. bot. Zeitschr. 85. Wien.

Broch, H. 1910a. Die Peridinium-Arten des Nordhafens (Val di Bora) bei Rovigno im Jahre 1909.—Arch. f. Protistenk. 20. Jena.

— 1910b. Das Plankton. Zool. Ergebn. der schwedischen Exp. Spitzbergen 1908.—Kgl. Svenska Vet. Akad. Handl. 45. Stockholm.

Braarud, Trygve. 1935. The "Øst"-Expedition to the Denmark Strait 1929. II. The Phytoplankton and its conditions of growth.—Hvalrådets Skrifter, Nr. 10. Oslo.

Böhm, A. 1933. Beobachtungen an adriatischen Peridinium-Arten.—Arch. f. Protistenkunde. 80. Jena.

— 1933a. Zur Kenntnis der antarktischen Dinophysiaceae.—Intern. Rev. Hydrogr. & Hydrobiol. 29. Leipzig.

Candeias, A. 1930. Estudos de Plancton na Baia de Sesimbra.— Bull. Soc. Portugaise des Sciences Naturelles. XI, No. 3.

— 1934. Contrebuïção para o conhecimento da variação em Peridinium depressum Bayley.—Memórias e Estudos do Museu Zoológico Univ. Coimbra. Sér. I, No. 76. Coimbra.

— 1938. Microplancton da Região da Foz do Douro.—Bol. Soc. Broteriana. XIII.

Carrisso, L. W. 1911. Materiaes para o estudo do plancton na costa Portuguêsa. Fasc. I.—Diss. Coimbra.

Christiansen, M. P. 1941. Er de danske Mælkebøtter Kosmopoliter?—Bot. Tidsskrift 45. København.

Claparède, E. et Lachmann, J. 1859. Études sur les Infusoires et les Rhizopodes.—Mém. Inst. Nat. Genevois, 5, 6, 7, Genève.

Cleve, P. T. 1899. Plankton collected by the Swedish Exped. to Spitzbergen in 1898.—Kgl. Svenska Vet. Akad. Handl. 32. Stockholm.

— 1900. Report on the Plankton collected by the Swedish Exped. to Greenland in 1899.—Ibid. 34. Stockholm.

Cleve, P. T. 1900a. Notes on some Atlantic Plankton-organisms.—Ibid. 34. Stockholm.
Dangeard, P. 1926. Description des Péridiniens testacés recueillis par la mission Charcot pendant le mois d'Août 1924.—Ann. Inst. Océanogr. N. S. 3. Paris.
— 1927a. (Avril). Péridiniens nouveaux ou peu connus de la croisière du "Sylvana."—Bull. Inst. Océanogr. No. 491. Monaco.
— 1927b. Phytoplancton de la croisière du "Sylvana" (Fév.—Juin 1913).—Ann. Inst. Océanogr. N. S. 4. Paris.
— 1927c. (Dec.). Notes sur la variation dans le genre Peridinium.—Bull. Inst. Océanogr. No. 507. Monaco.
— 1932. Phytoplancton recueilli à Banyuls-sur-Mer.—Arch. de Zool. expér. et gén. 74. Paris.
Fauré-Fremiet. 1908. Études descriptives des Péridiniens et des Infusoires ciliés.—Ann. sc. nat. Zool. 9. Paris.
Fægri, K. 1937. Problems of Taxonomy and Phylogenetics.—Bot. Review, 3.
Gran, H. H. 1902. Das Plankton des norwegischen Nordmeeres.—Report on Norwegian Fishery- and Marine-Investigations, 2, No. 5. Bergen.
Gran, H. H. and Braarud, Trygve. 1935. A quantitative study of the Phytoplankton in the Bay of Fundy and the Gulf of Maine.—Journ. biol. Board of Canada. 1, No. 5. Toronto.
Grøntved, Jul. and Seidenfaden, Gunnar, 1938. The Phytoplankton of the Waters West of Greenland. The "Godthaab"-Exped. 1928.—Meddelelser om Grønland 82, No. 5. København.
Guðmundsson, Finn. 1937. Rannsóknir á íslenzku sjávarsvifi.—Náttúrufræðingnum, VII, 2. Reykjavik.
Hermann, Frede and Thomsen, Helge, 1946. Drift-bottle experiments in the Northern North Atlantic.—Medd. Komm. for Danmarks Fiskeri- og Havundersøgelser. Ser. Hydrografi. III. Nr. 4. København.
Hustedt, Fr. 1937. Zur Systematik der Diatomeen.—Ber. d. deutsch. bot. Ges. 55. Berlin.
Jørgensen, E. 1899. Protophyten und Protozoën im Plankton aus der norwegischen Westküste.—Bergens Museums Aarbog No. VI. Bergen.
— 1900. Protistenplankton aus dem Nordmeere in den Jahren 1897—1900.—Bergens Museums Aarbog No. VI. Bergen.
— 1911. Peridiniales: Ceratium. Résumé sur le Plancton.—Bull. Conseil Perm. Internat. Expl. de la Mer. 7. Copenhague.
— 1912. Bericht über die von der schwedischen hydr.-biol. Komm. in den schwedischen Gewässern in den Jahren 1909—10 eingesammelten Planktonproben. Göteborg.
— 1923. Mediterranean Dinophysiaceae.—Report Danish ocean. Exped. 2. København.
Karsten, G. 1905—07. Das Phytoplankton des Antarktischen Meeres nach dem Material der deutschen Tiefsee-Expedition 1898—1899. Jena.
Kofoid, Ch. A. 1907. Dinoflagellata of the San Diego region, III. Descriptions of new species.—Univ. of California Publ. in Zool. 3, No. 15. Berkeley.
Kofoid, Ch. A. and Skogsberg, T. 1928. The Dinoflagellata: The Dinophysoidae.—Mem. Mus. Comp. Zool. 51. Cambridge. U. S. A.
Lebour, Marie V. 1923. Plymouth Peridinians. IV. The plate arrangement of some Peridinium species.—Journ. Mar. Biol. Assoc. XIII. No. 1. Plymouth.
— 1925. The Dinoflagellates of Northern Seas.—Plymouth.
Lefèvre, M. 1928. Monographie des espèces d'eau douce du genre Peridinium Ehrb.—Arch. de Bot. II. Caen.
Levander, K. M. 1894. Materialien zur Kenntnis der Wasserfauna in der Umgebung v. Helsingfors.—Acta Soc. Flora Fauna Fennica. XII. Nr. 2. Helsingfors.
— 1900. Über das Herbst- und Winter-Plankton im finnischen Meerbusen und in der Ålands-See 1898.—Ibid. XII. Nr. 5.

LINDEMANN, E. 1924. Peridineen aus dem goldenen Horn und d. Bosporus.—Bot. Archiv. 5. Leipzig.
— 1925. Neubeobachtungen an den Winterperidineen des Golfes von Neapel.—Ibid. 9.
— 1928. Peridineae in "ENGLER: Die natürlichen Pflanzenfam." II. Leipzig.
MANGIN, L. 1911. Modifications de la cuirasse chez quelques Péridiniens.—Intern. Revue ges. Hydrob. u. Hydrogr. IV. Leipzig.
— 1911. Sur l'existence d'individus dextres et senestres chez certains Péridiniens.—Comptes rendus Ac. Sc. 153. Paris.
— 1912. Phytoplancton de la croisière du *René* dans l'Atlantique.—Ann. Inst. Océanogr. IV. fasc. 1. Paris.
— 1913. Sur la flore planctonique de la rade de St.-Vaast-la-Hougue 1908—1912.—Nouv. Arch. du Muséum d'historie nat. V. Sér. Paris.
— 1922. Phytoplancton antarctique (Expédition antarctique de la "Scotia" 1902—1904).—Mém. Acad. Sci. de l'Institut de France. 57. Paris.
MARTIN, G. W. 1929. Dinoflagellates from marine and brackish waters of New Jersey.—Univ. of Iowa Studies in Nat. Hist. XII, No. 9. Iowa.
MATZENAUER, LOTHAR. 1933. Die Dinoflagellaten des Indischen Ozeans (Mit Ausnahme der Gattung Ceratium).—Bot. Archiv. 35. Leipzig.
MERESCHKOWSKY, C. 1879. Studien über Protozoen des nördlichen Russlands.— Arch. f. mikrosk. Anatomie. 16. Bonn.
MEUNIER, ALPH. 1910. Mikroplankton de mers de Barents et de Kara.—Duc d'Orléans camp. arctique de 1907. Bruxelles.
— 1919. Mikroplankton de la Mer Flamande, III. Les Péridiniens.—Mém. Mus. d'hist. nat. Belgique. 8. Bruxelles.
MURRAY, G. and WHITTING, F. G. 1899. New Peridiniaceae from the Atlantic.—Trans. Linn. Søc. Ser. II. Bot. 5. London.
OKAMURA, K. 1912. Plankton-organisms from Bonito fishing grounds.—Rep. Imp. Bur. of Fisheries. Scient. investigations. 1. Japan.
OSTENFELD, C. H. 1899. In: KNUDSEN & OSTENFELD: Iagttagelser over Overfladevandets Temp., Saltholdighed og Plankton paa islandske og grønlandske Skibsrouter i 1898.—København.
— 1908. The Phytoplankton of the Aral Sea and its affluents, with an enumeration of the Algae observed.—Wiss. Ergebnisse der Aralsee-Expedition Lief. 8. St. Petersburg.
— 1913. De danske Farvandes Plankton i Aarene 1898—1900.—Kgl. Danske Vid. Selsk. Skrifter, 7. Række. Naturv. og Mathem. Afd. IX, 2. København.
OSTENFELD, C. H. and PAULSEN, OVE. 1911. Marine Plankton from the East-Greenland Sea.—Medd. om Grønland. 43. København.
PAULSEN, OVE. 1904. Plankton-investigations in the waters round Iceland in 1903.— Medd. Komm. f. Havundersøgelser. Ser. Plankton. I. København.
— 1905. On some Peridineae and Plankton-diatoms.—Ibid. I. København.
— 1907. The Peridiniales of the Danish Waters.—Ibid. I. København.
— 1908. Peridiniales.—Nordisches Plankton. 18. Kiel.
— 1911. Marine Plankton from the East-Greenland Sea. III. Peridiniales.— Medd. om Grønland. 43. København.
— 1912. Perìdiniales ceteræ, — Bull. trimestr. Rés. des observ. sur le Plankton 1902—08. 3me partie. Copenhague.
— 1930. Études sur le microplancton de la mer d'Alboran.—Trab. inst. españ. oceanografia. 4. Madrid.
PAVILLARD, J. 1905. Recherches sur la flore pélagique (Phytoplankton) de l'Étang de Thau.—Trav. l'inst. Bot. l'univ. Montpellier.
— 1909. Sur les Péridiniens du Golfe du Lion.—Bull. Soc. Bot. France. 56. Paris.

PAVILLARD, J. 1916. Recherches sur les Péridiniens du Golfe du Lion.—Trav. inst. bot. univ. Montpellier. Sér. mixte. 4. Cette.

— 1917. Protistes nouveaux ou peu connus du plankton méditerranéen.—C. R. Ac. Paris. 164.

— 1931. Phytoplankton (Diatomées, Péridiniens) provenant des campagnes scientif. du Prince Albert I de Monaco.—Résult. des camp. sci. 82. Monaco.

PETERS, NICOLAUS. 1928. Die Peridineenbevölkerung der Weddellsee mit besonderer Berücksichtigung der Wachstums- und Variationsformen.—Intern. Rev. d. ges. Hydrobiol. u. Hydrographie. 21. Leipzig.

— 1930. Peridinea.—Die Tierwelt der Nord- und Ostsee. I, 1. Leipzig.

— 1932. Die Bevölkerung des Südatlantischen Ozeans mit Ceratien.—Wiss. Ergebn. d. "Meteor"-Exped. 1925—1927. Biol. Sonderunters. I. Berlin u. Leipzig.

POUCHET, G. 1883. Contribution à l'histoire des cilio-flagellés.—Journ. de l'anatomie et de la physiologie. Paris.

— 1894. "Histoire Naturelle." In "Voyage de "La Manche" à l'île Jan Mayen et au Spitzberg."—Nouv. Arch. Missions Sci. et Lit. 5.

SCHILLER, Jos. 1929. Über eine biol. u. hydrogr. Untersuchung des Oberflächenwassers im westlichen Mittelmeer im Aug. 1928.—Bot. Archiv. 27. Leipzig.

— 1933, 1937. Dinoflagellatae (Peridineae) in monographischer Behandlung I—II.—Rabenhorst's Kryptogamenflora. 10. Leipzig.

SCHRÖDER, BR. 1900. Das Phytoplankton des Golfes von Neapel.—Mitt. aus der zool. Stat. zu Neapel. 14.

SCHÜTT, FR. 1895. Die Peridineen der Plankton-Expedition.—Ergebnisse der Plankton-Exped. 4. Kiel und Leipzig.

STEEMANN NIELSEN, E. 1934. Untersuchungen über die Verbreitung, Biologie und Variation der Ceratien im südl. Stillen Ozean.—Dana-Report, No. 4. Copenhagen & London.

— 1941. Über das Verhältnis zwischen Verwandtschaft und Verbreitung von Organismen in Beziehung zu ökologischen Studien auf Grundlage der Verbreitung.—Kgl. Danske Vid. Selsk. Biol. Medd. 16. København.

STEIN, F. R. v. 1883. Der Organismus der Infusionsthiere. III. 2. Leipzig.

SØRENSEN, THORV. 1941. Experimental investigations on "species" formation in Taraxacum.—Bot. Tidsskrift. 45. København.

TURESSON, G. 1922. The genotypical response of the plant species to the habitat.—Hereditas. III. Lund.

USSATSCHEW, P. I. 1935. Die Zusammensetzung und Verteilung des Phytoplanktons des Barents-Meeres im Sommer 1931. (In Russian).—Transactions of the arctic Inst. of the U. S. S. R. Leningrad.

VANHÖFFEN, E. 1897. Die Fauna und Flora Grønlands.—Grønl. Exped. d. Gesellsch. für Erdkunde zu Berlin. 2. Berlin.

WAILES, G. H. 1928. Dinoflagellates and Protozoa from British Columbia.—Vancouver Museum, Notes 3.

WOLOSZYNSKA, J. 1928. Dinoflagellatae der polnischen Ostsee sowie der an Piaśnica gelegenen Sümpfe.—Arch. d'Hydrobiologie et d'Ichtyologie. III, Nr. 3—4. Warszawa.

Indleveret til selskabet den 20. december 1948.
Færdig fra trykkeriet den 5. oktober 1949.

DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB

BIOLOGISKE SKRIFTER

BIND II (KR. 61.00):

kr. ø.

1. BÖCHER, TYGE W.: Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. I. Über die Flechtenheiden und Dünen der Insel Läsö. 1941 ..... 4.00
2. SØRENSEN, THORVALD: Untersuchungen über die Therophytengesellschaften auf den isländischen Lehmflächen (»*Flags*«). 1942 ..... 3.00
3. ORLA-JENSEN, S.: The Lactic Acid Bacteria. Die echten Milchsäurebakterien. Ergänzungsband. 1943 ..... 18.00
4. WESTERGAARD, M.: Cyto-Taxonomical Studies on *Calamagrostis Epigeios* (L.) Roth, *Ammophila Arenaria* (L.) Link, and their Hybrids (*Ammophila Baltica* (Flügge) Link). 1943 ..... 8.00
5. NIELSEN, K. BRÜNNICH: The Asteroids of the Senonian and Danian Deposits of Denmark. *Opus posthumum* edited by TH. MORTENSEN and ALFRED ROSENKRANTZ. 1943 ..... 9.50
6. ROSENVINGE, L. KOLDERUP and LUND, SØREN: The Marine Algæ of Denmark. Contributions to their Natural History. Vol. II. Phæophyceæ. II. Corynophlaeaceæ, Chordariaceæ, Acrothrichaceæ, Spermatochnaceæ, Sporochnaceæ, Desmarestiaceæ, Arthrocladiaceæ. With supplementary Comments on Elachistaceæ. 1943 6.00
7. BÖCHER, TYGE W.: Studies on the Plant Geography of the North-Atlantic Heath Formation. II. Danish Dwarf Shrub Communities in Relation to those of Northern Europe. 1943 ..... 12.50

BIND III (KR. 60.50):

1. OLSEN, SIGURD: Danish Charophyta. Chorological, Ecological and Biological Investigations. 1944 ..... 22.00
2. JESSEN, KNUD and HELBÆK, HANS: Cereals in Great Britain and Ireland in Prehistoric and Early Historic Times. 1944 ..... 8.50
3. GRAM, K., JØRGENSEN, C. A. og KØIE, M.: De jydske Egekrat og deres Flora. 1944 26.00
4. ORLA-JENSEN, S., OLSEN, ERIK and GEILL, TORBEN: Senility and Intestinal Flora. A Reexamination of Metchnikoff's Hypothesis. 1945 ..... 4.00

BIND IV (KR. 72.00):

1. BÖCHER, TYGE W.: Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. II. Über die Waldsaum- und Graskrautgesellschaften trockener und halbtrockener Böden der Insel Seeland mit besonderer Berücksichtigung der Strandabhänge und Strandebenen. 1945 ..... 20.00
2. SØRENSEN, THORVALD and GUÐJÓNSSON, GUÐNI: Spontaneous Chromosome-Aberrants in Apomictic Taraxaca. Morphological and Cyto-Genetical Investigations. 1946 ..... 10.00
3. BÖCHER, TYGE W., CHRISTENSEN, TYGE and CHRISTIANSEN, M. SKYTTE: Slope and Dune Vegetation of North Jutland. I. Himmerland. 1946 ..... 12.00

kr. ø.

4. Böcher, Tyge W.: *Dichothrix gelatinosa* sp. n. Its Structure and Resting Organs. 1946 ..... 2.00
5. Rosenvinge, L. Kolderup and Lund, Søren: The Marine Algæ of Denmark. Contributions to their Natural History. Vol. II. Phæophyceæ. III. Encoeliaceæ, Myriotrichiaceæ, Giraudiaceæ, Striariaceæ, Dictyosiphonaceæ, Chordaceæ, and Laminariaceæ. 1947 ..... 14.00
6. Ravn, J. P. J.: Om Nyker-Omraadets Kridtaflejringer. 1946 ..... 4.00
7. Knisely, Melvin H., Bloch, Edward H., and Warner, Louise: Selective Phagocytosis. I. Microscopic Observations concerning the Regulation of the Blood Flow through the Liver and other Organs and the Mechanism and Rate of Phagocytic Removal of Particles from the Blood. 1948 ..... 10.00

Bind V (kr. 82.50):

1. Nielsen, Anker: Postembryonic Development and Biology of the Hydroptilidæ. A Contribution to the Phylogeny of the Caddis Flies and to the Question of the Origin of the Case-Building Instinct. 1948 ..... 30.00
2. Jørgensen, Erik G.: Diatom Communities in Some Danish Lakes and Ponds. 1948 ..... 18.00
3. Lemche, Henning: Northern and Arctic Tectibranch Gastropods. I. The Larval Shells. II. A Revision of the Cephalaspid Species. 1948 ..... 18.00
4. Sørensen, Thorvald: A Method of Establishing Groups of Equal Amplitude in Plant Sociology Based on Similarity of Species Content and its Application to Analyses of the Vegetation on Danish Commons. 1948 ..... 7.50
5. Nilsson, Tage: On the Application of the Scanian Post-Glacial Zone System to Danish Pollen-Diagrams. 1948 ..... 9.00

Bind VI (under pressen):

1. Orla-Jensen, S., Orla-Jensen, Anna D. and Snog-Kjær, Agnete: Biological Researches on the Silage Process. 1948 ..... 2.00
3. Tuxen, S. L.: Über den Lebenszyklus und die postembryonale Entwicklung zweier dänischer Proturengattungen. 1949 ..... 10.00
4. Paulsen, Ove: Observations on Dinoflagellates. Edited by Jul. Grøntved. 1949. 9.00

Ny uforandret Udgave.

Orla-Jensen, S.: The Lactic Acid Bacteria. Skrifter, naturv. og math. Afd. 8. V. 2. 1919. Second Edition 1942 ..... 30.00

PRINTED IN DENMARK
BIANCO LUNOS BOGTRYKKERI