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DINOFLAGELLATA OF THE SAN DIEGO REGION, IV. THE GENUS *GONYAULAX*, WITH NOTES ON ITS SKELETAL MORPHOLOGY AND A DISCUSSION OF ITS GENERIC AND SPECIFIC CHARACTERS

BY

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(Contributions from the Laboratory of the Marine Biological Association of San Diego)

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A. INTRODUCTION

The genus *Gonyaulax* is one of the most widely represented of the dinoflagellates, occurring in boreal, temperate and tropical seas and in both brackish and fresh waters. It is also at times exceedingly abundant in coastal waters, appearing in numbers so great as to discolor the sea. *Gonyaulax polyedra* is the cause of periodical outbreaks of "red water" along the coasts of southern California in middle and late summer which are accompanied by remarkable displays of phosphorescence. The outbreaks occasion the destruction of great numbers of the fish of the shal-

low waters and of the invertebrates such as the holothurians, annelids, sipunculids, and some of the mollusks [see Torrey (1902)]. It is cast upon the sands along shore by the breakers and its decay there, together with that of the animals killed by its abundance, causes a stench which suggests that of the Nile which in Hebrew writings is recorded as having turned to blood. It is not improbable that the phosphorescence and red water reported by Darwin (1871) off the coast of South America and by Streets (1878) in the Gulf of California, was caused by this species or some related dinoflagellate.

Present Status

Although widely distributed and at times abundantly represented in the plankton, this genus has remained in a state of imperfect definition and has been a great source of uncertainty and a cause of oft recurring confusion in the matter of its characters and its limits. Very few of the species assigned to it, even in recent years, have been accurately defined in the matter of their skeletal morphology, and a number of older species of the genus have been variously interpreted by later writers with the result that it has become increasingly difficult to determine with what species an author is dealing, unless his work is accompanied by figures and in some cases not even these relieve the confusion which reigns in this genus. Another and very fundamental reason for this confusion lies in the fact that a wide range of material is often necessary to determine the limits of variation within the species of the genus. This wide range in variation coupled with the very dissimilar appearances which even the same individual may present from different points of view, make the interpretation of the older literature, and some of the more recent, exceedingly difficult, and usually force the investigator to a re-examination of pertinent material before he can come to any conclusion that does not rest all too much upon conjecture.

B. MATERIAL

This paper is based primarily upon the examination of the plankton collected off the coast of southern California by the San

Diego Marine Biological Station during the past ten years, and upon certain collections made in Alaska in the summer of 1905 by the U. S. Bureau of Fisheries Str. "Albatross." Permission to use the data from the latter source has been kindly granted by Hon. Geo. M. Bowers, U. S. Commissioner of Fisheries.

Grateful acknowledgments are here made to the San Diego Marine Biological Association for its continuous interest in and support of this work, to the Smithsonian Institution for the privileges of their research table at the Naples Zoological Station in 1908, and to Mr. R. W. Harvey, Miss Ethel Abeel, and especially to Mrs. Josephine R. Michener for drawings.

The plankton from the coast of California at my disposal is primarily oceanic, but this is supplemented by neritic collections from San Diego Bay, San Pedro Harbor, and from San Francisco Harbor, while that in the collection from Alaska is primarily neritic. The southern oceanic plankton taken off San Diego from deeper levels (50-100 fathoms) contains considerable moribund plankton of northern (Alaskan) facies.

In addition to the material above noted the writer has had at his disposal, but not included in the scope of the present paper, the very extensive collections of the expeditions of the Str. "Albatross" to the Eastern Tropical Pacific of 1904-1905 and to the Northern Pacific in 1905-1906, as well as numerous collections from European waters made during his tour of the biological stations of Europe in 1908-1909. The material upon which this study is based is therefore both extensive and representative. My especial thanks are tendered to Dr. Andrew Scott of Piel-in-Barrow, for a collection rich in Dinoflagellata, from the Faeroes Channel.

The collections of plankton made during the past ten years mainly at San Diego and San Pedro and in the California Current off these ports are distributed through all seasons of the year, but more especially during the summer and in mid-winter. Nearly every collection contains one or more species of *Gonyaulax*.

In all fourteen species have been recorded. Of these four are new, *G. alaskensis*, *G. diegensis*, *G. sphaeroidea* and *G. scrippsae*.

Four are at times fairly common, *Gonyaulax polyedra, G. digitale, G. diegensis* and *G. polygramma;* of the remainder, *G. alaskensis, G. kofoidi, G. pacifica, G. scrippsae, G. spinifera, G. triacantha,* and *G. turbynei* are rare, and *G. fragilis, G. birostris* and *G. sphaeroidea* very rare. The winter plankton of tropical facies brings *G. birostris, G. pacifica, G. kofoidi, G. sphaeroidea, G. polygramma* and *G. turbynei* to the coasts of southern California. *G. alaskensis* is a northern form drifting southward in the deeper plankton. *G. scrippsae* and *G. diegensis* were found in the neritic plankton, the remainder in both neritic and oceanic plankton. *Gonyaulax triacantha* has thus far been found only in neritic plankton from Alaska, and the distribution of *G. spinifera* (*sensu stricto*) is imperfectly known at present, not having been distinguished from *G. digitale* during the progress of the work.

C. GENERAL DISCUSSION OF THE GENUS

I. Generic Characters

1. HISTORICAL DISCUSSION

The genus *Gonyaulax* was first defined by Diesing (1866) for the single species (*Peridinium spiniferum*) which Claparède and Lachmann (1858-1861) had previously assigned to the genus *Peridinium*, but in their description placing special emphasis upon the helicoidal form of the transverse furrow. No mention is made by them of an extension of the longitudinal furrow to the apex upon the epitheca. Diesing's generic diagnosis is likewise based upon the marked displacement of the girdle which results in the helicoidal form of the transverse furrow and he has embodied the idea in his generic name *Gonyaulax* (γόνυ [knee] αὖλαξ [furrow]). Diesing's diagnosis which follows contains no reference to the extension of the longitudinal furrow upon the apex.

Gonyaulax Diesing

Peridinii spec. Claparède

"Animalcula solitaria libera symmetrica. Corpus immutabile, ovatum, ecaudatum, ciliatum, lorica, tabulata, sulco, hiante transversali in pagina dorsali obliquo in pagina ventrali bis geniculato et altero longitudinali, ab

anfractu anteriore sulci transversalis ad extremitatem anticam excurrente, tripartita inclusum, ciliis e sulcis prominentibus. Os terminale. Flagellum unum pone os. Anus . . . . Ocellus nullus. Partitio ignota. Maricolae."

In Stein's (1883) great monograph, the text for which was unfortunately never completed, he notes (p. 12) his observation at Kiel of "*Perid. spiniferum* Cl. Lach., auf welches bereits Diesing eine neue Gatt. *Gonyaulax* gegründet hat, die wohl berechtigt ist, aber ganz anders characterisirt werden muss." The modifications which Stein made were (1) a correct orientation with the pointed end anterior, (2) designation of a narrow area from the proximal end of the girdle to the apex as an extension of the longitudinal furrow, (3) an analysis of the thecal plates in two species, with three apicals (Frontalien), five precingulars (Basalien), five postcingulars (Basalien) and two "Endplatten" one of which is the antapical and the other the posterior accessory.

Later monographers, Bütschli (1885b), Schütt (1896), and Paulsen (1908), all follow Stein in his interpretation of an extension of the longitudinal furrow anteriorly to the apex. Bütschli finds six precingulars (in *Gonyaulax polyedra*) and later discoveries of new species have necessitated some modifications in the range in form of body and number of apical plates found in the genus. In essential particulars Stein's diagnosis has stood with but minor additions to the present time.

2. MODIFICATIONS RESULTING FROM NEW DATA

As a result of my investigations on this genus certain fundamental modifications are necessary in the generic diagnosis of *Gonyaulax*.

(1) The form of the body is exceedingly varied and affords no basis for diagnosis. It ranges from an almost perfectly spherical form such as is seen in *G. sphaeroidea*, to polyhedral species such as *G. polyedra* and *G. ceratocoroides*, and to elongated types such as *G. birostris* and *G. jolliffei*. In the development of spines, we find conditions ranging from the smooth, spine-free *G. sphaeroidea* to the spinous *G. triacantha*, and to *G. ceratocoroides* with its long processes resembling those of *Ceratocorys*. In like manner no particular type of surface markings is prevalent. The surface

may be smooth or reticulate, and the mesh may be predominantly linear, vermiculate, polygonal or irregular. None of these features affords any satisfactory criterion for a genuine diagnosis.

(2) The displacement of the girdle in a descending spiral with the distal end one or more girdle widths posterior to the proximal occurs in all species of the genus. It is this character primarily which distinguishes *Gonyaulax* from *Amphidoma* in which the displacement is at the most but slight.

(3) The longitudinal furrow should not be considered as extending, as Stein (1883) supposed, anteriorly upon the epitheca to the apex. There is no basis in the skeletal morphology for this interpretation, and there is no suggestion of such an extension of the furrow in the external appearance in a number of species which belong in this genus. The midventral apical plate (*1'* fig. A) in *Gonyaulax* which is homologous with the diamond-shaped "Rautenplatte" of *Peridinium*, extends from the apex posteriorly until it meets an anterior extension of the ventral area (*v. a.*, figs. A and B) and thus separates the precingular series in the midventral line between precingulars *1''* and *6''*. In most but not all species of *Gonyaulax* this ventral apical *1'* is a narrow plate. When suture lines are marked by thickenings of the wall, as for example in *G. ceratocoroides* [see Murray and Whitting (1899, pl. 30, fig. 6)] this plate, in consequence of these thickenings, lies at the bottom of a depression between elevated ridges. This, however, does not occur in all species and the trough thus formed is not a part of the furrow in which the longitudinal flagellum lies any more than are similar depressions between ridges elsewhere on the thecal wall. (See Murray and Whitting's figures).

(4) There is no trace of evidence whatever that this so-called anterior extension of the longitudinal furrow to the apex ever functions as a longitudinal furrow; that is, that it serves as a trough for the longitudinal flagellum, whose normal position is in the furrow running posteriorly from the flagellar pore.

To regard this plate as a part of the longitudinal furrow is thus to assign to it a function which it does not have, and to obscure its morphological relations. Furthermore, to make this

mistaken interpretation the basis of generic diagnosis as Stein and his followers have done is to exclude from the genus species, such as *G. sphaeroidea*, whose skeletal morphology would otherwise compel their inclusion in the genus. It is therefore necessary to eliminate this interpretation, and to confine the designation of longitudinal furrow (or the more widely applicable term, "ventral area," which seems desirable on account of conditions in *Ceratium*) to that part of the theeal wall in which the flagellum is found extending posteriorly between the two ends of the girdle. This term ventral area was proposed by me (1909) for this region in *Peridinium* and appears to be widely applieable in other genera.

(5) The plates of the genus (Figs. A and B) are not as heretofore described, but, in all species which I have thus far examined they are as follows: apicals, 3 to 6; anterior intercalaries, 0 to 3; precingulars, 6; girdle, 6; postcingulars, 6; posterior intercalary, 1; antapical, 1. The ventral area contains one anterior plate indenting the epitheca, in the posterior margin of which lies the flagellar pore, a group of about four small intermediate plates and a large posterior plate.

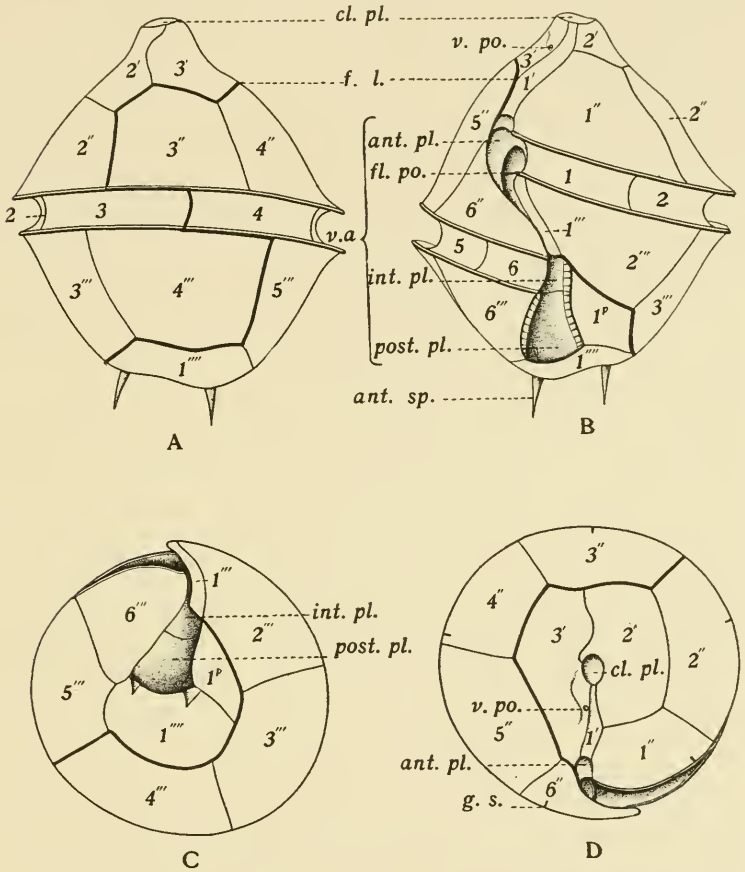
3. SKELETAL PLATES OF *GONYAULAX*

The *apical plates* (*1'-6'*) are those in contact with the apex. This *does not have an open pore* as sometimes indicated, but is closed by a minute closing platelet (*cl. pl.*, fig. A) which often adheres to the top of apical *1'* and covers the truncate apex. The number of the apicals varies from three to six in different species. At least three have been found in all species analyzed. It is probable that plate *1'* has been overlooked in cases where two apicals have been reported. Bifurcated and trifurcated apices such as Murray and Whitting (1899, pl. 30, figs. 1-3) have described in their inverted figures are due to the parting of the apicals, a phenomenon very commonly observed in many species of the genus, preparatory to ecdysis or the escape of the contents.

In some cases as in *G. apiculata* and *G. polyedra* one or more of the plates in the apical region are crowded away from contact with the apex. Such plates I have designated as *anterior inter-*

calaries (1^a–3^a), as well as other plates lying between the apical and precingular series.

The *precingular plates* (*1″–6″*, fig. A) are invariably six in number in the species which I have examined. Stein (1883)



Figs. A-D. Plates of thecal skeleton of *Gonyaulax spinifera* (Clap. et Lach.) Diesing × 1000. A, dorsal view; B, ventral view; C, antapical view; D, apical view. *1–6*, girdle series of plates; *1′–3′*, apical series; *1″–6″*, precingular series; *1‴–6‴*, antapical series; 1^p posterior intercalary; *1⁗*, antapical plate; *ant. pl.*, anterior plate of ventral area; *ant. sp.*, antapical spine; *cl. pl.*, closing platelet of apex; *f. l.*, fission line along which skeleton parts in cell division; *fl. po.*, flagellar pore; *int. pl.*, intermediate plates (usually four in number, hidden in constricted region of ventral area); *post. pl.*, posterior plate of ventral area; *v. a.*, ventral area (''longitudinal furrow'' of other writers in part); *v. po.*, ventral pore.

reported five and though Bütschli (1885b) later reported six in *G. polyedra*, no one has presumed to question the accuracy of Stein's observations, so great has been the confidence placed in his work which as a rule is extremely detailed and reliable. Lemmermann (1907) figures and describes six precingular (Praeaequatorialplatten) in *Gonyaulax palustris*.

The *girdle plates* (*1-6*) are six in number and may be disarticulated from one another with comparative ease.

The *postcingular plates* (1‴–6‴, fig. B) are invariably six in number, plate *1‴* of the series lying immediately adjacent to the ventral area (on its left edge) as a slender linear structure. This plate has hitherto been overlooked, though Entz (1904, fig. 4a, f) delineates it but does not otherwise note its presence or significance. Paulson (1904) indicates it in his figure of *G. triacantha* but does not otherwise note its presence. Lemmermann (1907) figures six postcingulars in *G. palustris* (in his fig. 5) but states that there are five "Postaequatorialplatten," no one of which can, however, be homologized with the narrow postcingular *1'* of my nomenclature.

The *posterior intercalary* (*1ᵖ*) and *antapical* (*1⁗*, fig. B) are invariably present without change in number in the different species and the latter constitutes the most ready means of separation of this genus from most of the genera of the Peridinidae.

II. Generic Diagnosis

Gonyaulax Diesing emend.

Body variously shaped, spheroidal, polyhedral, broadly fusiform, elongated with stout apical and antapical prolongations, or dorso-ventrally flattened. Apex rounded or truncate symmetrically or asymmetrically, never acutely symmetrically pointed. Antapex rounded, flattened, or pointed symmetrically or asymmetrically. Girdle usually equatorial, descending, displaced distally one to seven times its own width, and sometimes with slight overhang. Transverse furrow impressed or not; longitudinal furrow usually slightly indenting the epitheca, often flaring distally, well developed, reaching to or approaching the

antapex. Thecal wall (text figs. A-D) consisting of one to six apical plates (*1′–6′*), none to three anterior intercalaries (*1ª–3ª*), six precingulars (*1″–6″*), six girdle plates (*1–6*), six postcingulars, (*1‴–6‴*), one posterior intercalary (*1ᵖ*), and one (*1⁗*) antapical. The longitudinal furrow occupies the whole of the ventral area (*v. a.*) which slightly indents the epitheca and consists of one anterior, about four intermediate and one posterior plate. The midventral plate (*1′*) of the apical series is usually a narrow plate extending posteriorly to a junction with the anterior plate of the ventral area, thus parting precingulars *1″* and *6″*. When guarded by lateral ridges it simulates an anterior extension of the longitudinal furrow. It bears at its apex a delicate extension, the closing platelet which covers the apical region.

Surface smooth or rugose with major thickenings along suture lines and minor ones on plates forming a regular or irregular polygonal mesh of varying size, often with vermiculate, longitudinal elements predominating, sometimes spinulate. Furrows with or without lists which in many species are ribbed or spinulate. One or more antapical spines sometimes present, rarely with sheathed spines of the *Ceratocorys* type. Plates porulate, with pores in centers, angles or nodes of the mesh. A peculiar large ventral pore (*v. po.*) occurs to the right of the midventral line usually near the suture between apical *1′* and the plate to its right. Theca divided obliquely in fission. Ecdysis frequently seen. Chromatophores yellow to dark brown, often dense. In fresh, brackish and marine waters from boreal to tropical regions.

III. Comparisons With Other Genera

The presence in *Gonyaulax* of a single large antapical plate separates this genus at once from *Pyrophacus* and *Podolampas* (4 antapicals), *Goniodoma*, *Protoceratium*, and *Blepharocysta* (3 antapicals), and from *Diplopsalis* and *Peridinium* (2 antapicals). The hypotheca of *Gonyaulax* is identical with that of *Steiniella* and *Ceratocorys* [see Kofoid 1910] in its skeletal elements. The epitheca of the latter genus is distinguished by having five instead of six precingulars as in *Gonyaulax*.

Steiniella, however, has its epitheca also of the same skeletal constitution as that of *Gonyaulax* and should on this ground be included therein. The fact that the apex (region of the closing platelet) is carried over on the dorsal face scarcely suffices as a generic character, as it is almost realized in some species of *Gonyaulax*, as for example in *G. alaskensis* and *G. hyalina*, and the gap between the two genera is practically obliterated. Recognizing the fundamental identity of the skeletal formula in these two genera and finding it difficult to apply consistently any set of morphological distinctions between the two as the number of species ascribed to them has increased, I feel constrained to include *Steiniella* Schütt (1895) in the older genus *Gonyaulax*, according it therein only a subgeneric status.

The differences between the valid species of *Steiniella* (*S. fragilis*, *S. mitra*, and *S. inflata*) and *Gonyaulax* are no greater, if indeed as great, as those now found between species within *Gonyaulax* itself. A marked tendency to fall to pieces on the part of the theca, the predominance of vermiculate-linear markings, and an elongated apex overlapping the dorsal edge of the anterior end of the body are the only available characters upon which to found the genus *Steiniella*, and no one of them affords an adequate basis for separation since they are all to be found in varying degrees within *Gonyaulax* itself. They are, moreover, purely superficial characters such as are subject to great modifications in many of the larger genera of the dinoflagellates.

The species of *Steiniella* thus far described which should be transferred to *Gonyaulax* are the following:

Gonyaulax (*Steiniella*) *fragilis* Schütt. See Schütt (1895).

G. (*Steiniella*) *mitra* (Schütt). See Schütt (1895).

G. (*Steiniella*) *inflata* (Kofoid). See Kofoid (1907a).

Certain other species have been described in the genus *Steiniella* which have previously been otherwise assigned. *Steiniella*(?) *punctata* described by Cleve (1900a) was assigned by me (1907a) to the new genus *Murrayella*, while Cleve's (1903) *Steiniella* (?) *complanata* was in the same paper referred by me to another new genus *Centrodinium*. *Steiniella cornuta* described by Karsten (1907) is identical with the larger forms of

Gonyaulax pacifica described by me in the same year (April 13, 1907), but prior to the publication of Karsten's paper (December, 1907). It may therefore be dismissed as a synonym of *G. pacifica*.

A homonym (in botanical nomenclature) of *Steiniella* Schütt was established by Bernard (1908) for a single species, *S. Gravenitzii* (*Protococcaceae*) for the reception of which I here propose the generic name *Steinedesmus* nom. nov.

The relations of *Amphidoma* and *Murrayella* to *Gonyaulax* are intimate, but our present knowledge of their skeletal morphology is insufficient for final conclusions as to their standing. In so far as our data go they are both generically distinct. The apical and antapical regions in both are difficult of analysis on account of the small size of the plates and their firm adhesion one to another. *Amphidoma* is distinguished from *Gonyaulax* by six apicals and no precingulars, by the form of the apices, by the feebly developed longitudinal furrow, equatorial, and non-displaced, horizontal girdle; *Murrayella* by its five postcingulars, the absence of a truncate apex, and by the form of the longitudinal furrow.

The genus *Ceratocorys* is distinguished by its five precingulars, three apicals and one anterior intercalary and by the anteriorly located girdle.

The genus *Spiraulax* Kofoid founded on *Gonyaulax jolliffei* Murray and Whitting differs from *Gonyaulax* in the shortened apical *1′* (rhomb plate of various authors), the junction of precingular *1″* and anterior intercalary *1ª* across the midventral line, in the presence of a ventral notch in apical *1′*, and in the absence of a ventral pore. See Kofoid (1911c).

IV. Skeletal Fission

Cell division in the genus *Gonyaulax* may take place in thecate individuals and in this case it involves the division of the enveloping theca. Fission of the cell mass which has rid itself of its skeleton by ecdysis is possible especially in such species as *G. polyedra* where this phenomenon is often seen, but no conclusive evidence of cell division in the naked stage has

thus far been observed by me. In the fission of thecate individuals the parental skeleton parts along uniformly definite sutures as in *Ceratium* (see Kofoid, 1909a) in an irregular plane at approximately right angles to the major axis of the spindle of the dividing cell. This plane parts the antero-sinistral moiety from the postero-dextral one. Chain formation occurs in conjunction with thecal fission, in so far as my own observations and the literature indicate, only in *Gonyaulax catenata* (Levander) Kofoid, and in *G. series*, as I have elsewhere shown (1911c). Chain formation of the plasma mass followed by skeletal formation *de novo* occurs in *Gonyaulax series* (see Kofoid, 1911a).

The anterior moiety (see text-figures A–D and pl. 10, figs. 9, 10) receives from the ancestral skeleton all of the apical series, and interior intercalaries when these are present, precingulars *1″* and *2″*, girdle plates *1–3*, and postcingulars *1‴–4‴*. The posterior moiety receives precingulars *3″–6″*, girdle plates *4–6*, postcingulars *5‴–6‴*, posterior intercalary 1^p, and the antapical *1⁗*. The fission line appears to pass through the flagellar pore and the greater part, if not the whole, of the ventral area goes with the posterior moiety. The path of the fission plane along the sutures is clearly shown in text figures A–D. The precise location of the fission line in the ventral area has not been accurately determined as yet. The figure of Entz (1905, fig. 58) suggests that this line passes through the flagellar pore and separates the anterior plate of the ventral area from the intermediates. Since he does not distinguish the subdivisions of this area, or indeed in his figures the other plates of the thecal wall, he has left the matter still in some uncertainty.

V. Subgenera and Species of Gonyaulax

For convenience the species of *Gonyaulax* may be grouped in three subgenera based upon the general form of the body. It is somewhat difficult to define these groups in such a way as to make the assignment of every known species to one of the three perfectly evident. A few aberrant species are in consequence included in the larger subgenera. As a result of my examination of extensive material of this genus and of a critical review

of the literature the following species are recognized as valid and are grouped as follows. Pertinent bibliographical references are appended in each case.

1. Subgenus **Gonyaulax** (Diesing) Kofoid subgen. nov.

Body spheroidal or polyhedral, not greatly elongated, apical closing platelet not carried over upon the dorsal side. This includes the non-fusiform species of the genus as heretofore defined. Here belong:

Gonyaulax apiculata (Penard) Entz (1904), p. 11, fig. 4a–i.
Syn. *Peridinium apiculatum* Penard (1891), p. 51, pl. 3, figs. 3–13.
G. clevei Ostenfeld (1901), p. 133, fig. 2.
G. apiculata var. *clevei* Ostenfeld (1908), p. 164, pl. 5, figs. 59, 60.
G. catenata (Levander) Kofoid (1911b). Described as *Peridinium catenatum* by Levander (1894a), pp. 1–18, pl. —, figs. 1–11.
G. diegensis, sp. nov. See p. 217.
G. digitale (Pouchet) (1883), p. 433, pl. 18/19, fig. 14 as *Protoperidinium digitale*. See p. 214 of this paper.
G. kofoidi Pavillard (1909), p. 278, fig. 1, A, B.
G. pacifica Kofoid (1907b), p. 308, pl. 30, figs. 37–39.
G. palustris Lemmermann (1907), pp. 296–297, figs. 1–5.
G. polyedra Stein (1883), pl. 4, figs. 7–9.
G. polygramma Stein (1883), pl. 4, fig. 15. See *G. steini* Lemmermann, in list of indeterminate species on p. 203 for the remainder of Stein's figures.
G. scrippsae, sp. nov. See p. 228.
G. series Kofoid (1911a), pp. —, pls. 1–2, figs. 1–6. (In press.)
G. sphaeroidea, sp. nov. See p. 206.
G. spinifera (Claparède et Lachmann) Diesing (1886), p. 96. Originally described by Claparède and Lachmann (1858–1859), p. 405, pl. 20 figs. 4, 5, as *Peridinium spiniferum*.
G. triacantha Jörgensen (1899), p. 35. See Kofoid (1906b), pp. 102–105, figs. 1–3.
G. turbynei Murray and Whitting (1889), p. 323, pl. 28, figs. 4a, b.

2. Subgenus **Fusigonyaulax**, subgen. nov.

Body elongated, usually fusiform, often with an elongated apical and antapical horn. Here belong:

Gonyaulax birostris Stein (1883), p. 4, fig. 20.
G. glyptorhynchus Murray and Whitting (1899), p. 324, pl. 28, fig. 3a–c.
G. highleii Murray and Whitting (1899), p. 324, pl. 28, fig. 2a, b.

G. jolliffei Murray and Whitting (1899), p. 324, pl. 28, figs. 1a, b, which might be placed here, is described by me (1911c) as in a new genus, *Spiraulax*.

3. Subgenus **Steiniella** (Schütt) Kofoid, subgen. nov.

Body rounded, spheroidal or subpolyhedral, exceedingly fragile, closing platelet of apex carried over upon dorsal side. Surface markings tending to longitudinal direction.

Gonyaulax alaskensis, sp. nov. See p. 249.

Gonyaulax hyalina Ostenfeld og Schmidt (1901), p. 172, figs. 24 a-d.

Gonyaulax fragilis (Schütt), described as *Steiniella fragilis* by Schütt (1895), p. 6, figs. 26_{1-14}.

Gonyaulax inflata (Kofoid). Described as *Steiniella inflata* by Kofoid (1907a), pp. 168–169, pl. 2, fig. 15.

Gonyaulax mitra (Schütt). Described as *Steiniella mitra* by Schütt (1895), pl. 7, figs. 27_{1-3}. Possibly not a *Steiniella*.

4. Subgenus **Acanthogonyaulax** subgen. nov.

Characterized by spines upon the hypotheca with axial cores similar to those of *Ceratocorys*. Girdle premedian. Plates of apical region numerous (6 in *G. ceratocoroides*). Contains one species *G. ceratocoroides* (Murr. and Whitt.) Kofoid (1910, p. 182).

For convenience in reference I append herewith (1) a list of species of *Gonyaulax* regarded by me as synonyms, (2) a list of described species which I regard as indeterminable and therefore invalid, (3) a list of species originally described in other genera which are here included in the genus *Gonyaulax*, and (4) species referred to *Gonyaulax* but belonging to other genera.

VI. Annotated List of Species of Gonyaulax Regarded Here as Synonyms

Gonyaulax apiculata var. *clevei* Ostenfeld (1908), p. 164, pl. 5, figs. 59, 60 = *G. apiculata* (Penard) Entz.

G. clevei Ostenfeld (1901), p. 133, fig. 2 = *G. apiculata* (Penard) Entz (1904), p. 14, fig. 4.

G. grani Henckel (1909), p. 118, pl. 30, figs. 1–16 = *G. digitale* (Pouchet) Kofoid.

G. globosa Stüwe (1909), p. 275, pl. 2, fig. 7 = *G. kofoidi* Pavillard (1909), p. 278, fig. 1 A, B. Doubtfully listed here.

G. levanderi (Lemmermann) Paulsen (1907), p. 8, fig. 8 = *G. spinifera* (Clap. et Lachm.) Diesing. See p. 213 of this paper.

G. mangini Fauré-Fremiet (1908), p. 230, fig. 16, pl. 16, fig. 19 = *G. spinifera* (Clap. et Lachm.) Diesing.

VII. Indeterminate Species, Names Which Should be Regarded as Applied to Unrecognizable Species

Gonyaulax caspicus Henckel (1909), pl. 29, figs. 6–15. No description published. On p. 187 as *G. caspicum.*

G. obliqua (Gourret) Lemmermann (1899), p. 368. Figure and description of *Roulea obliqua* Gourret (1883), p. 87, pl. 2, figs. 39, 39a, too indefinite to permit reidentification. Possibly a synonym of *G. spinifera.*

G. polygramma var. Stein (1883), pl. 4, figs. 16, 17.

G. schuetti Lemmermann (1899, p. 367), based on *G. polygramma* Stein var. of Schütt (1895), pl. 8, figs. 33b $_{1\text{-}3}$ Probably an early stage in the reformation of the theca following ecdysis in some indeterminable species.

G. steini Lemmermann (1907), p. 298, based on part (pl. 4, figs. 16, 17) of Stein's (1883) *G. polygramma.* ("Eine Varietät mit zugespitzer Endplatte.") This is plainly different from Stein's figure 15, which is a typical *G. polygramma,* but the "variety" has been figured in such oblique positions as to render reidentification wholly conjectural.

Roulea spinifera Gourret (1883), pp. 86–87. Assigned by Lemmermann (1907), p. 298, to synonomy of *G. spinifera.* Specific relations indeterminable.

VIII. Species of *Gonyaulax* Described in Other Genera, or Assigned to Species in Other Genera, Which Belong in *Gonyaulax*

Amylax lata Meunier (1910), pp. 51–52, pl. 3, figs. 24–27 = *Gonyaulax triacantha* Jörg. (1899), p. 35.

Amylax nivicola Meunier (1910), p. 53, pl. 3, figs. 35, 36. Probably *Gonyaulax.* Generic and specific status problematical.

Amylax perpusilla Meunier (1910), p. 53, pl. 3, fig. 37. Probably *Gonyaulax.* Generic and specific status problematical.

Amylax catenata Meunier (1910), p. 52, pl. 1 bis, figs. 46, 47; pl. 3, figs. 28–34 = *Gonyaulax catenata* (Levander) Kofoid (1911b), pp. 287–294, pl. 18.

Ceratium hyperboreum Cleve (1900a), p. 14, pl. 8, fig. 14 = *Gonyaulax triacantha* Jörgensen (1899), p. 35. Quoted by Lemmermann (1907), p. 298, as *Ceratium hyperboreum* and by Linko (1907), pl. 91, as *Geratium hyperboreum.*

Ceratocorys spinifera Murray and Whitting (1899), p. 329, pl. 30, figs. 6a, b, e = *G. ceratocoroides* Kofoid (1910), p. 182. The remaining figures, 6c, d, are of *Ceratocorys.*

C. [*cratocorrys!*] *spinifera,* Schröder (1906), p. 329 = *Gonyaulax spinifera.* Lapsus.

Goniodoma milneri Murray and Whitting (1899), p. 325, pl. 27, figs. 2a–d = *Gonyaulax milneri* (Murr. and Whitt.) Kofoid.

Heterodinium triacantha (Jörgensen) Kofoid (1906a), p. 354 = *Gonyaulax triacantha.* See Kofoid (1906b), p. 102.

Peridinium apiculatum Penard (1891), p. 51, pl. 3, figs. 3–13 = *Gonyaulax apiculata* (Penard) Entz (1904), p. 11, figs. 4a–i.

Peridinium catenatum Levander (1894a), pp. 1–18, pl. figs. 1–11 = *Gonyaulax catenata* (Levander) Kofoid (1911b), pp. 287–294, pl. 18.

Peridinium digitale, Lemmermann (1899), p. 369 = *Gonyaulax digitale* (Pouchet) Kofoid. See p. 214 of this paper.

Peridinium levanderi Lemmermann (1900), p. 120, based on Levander's (1894a), p. 50, pl. 2, fig. 21, of *Peridinium sp.* = *G. spinifera.*

Peridinium pyrophorum, Lemmermann (1899), p. 369 = *Gonyaulax polygramma* Stein.

Peridinium spiniferum Claparède et Lachmann (1858-1859), p. 405, pl. 20, fig. 4, 5 = *G. spinifera* (Clap. et Lachm.) Diesing (1866), p. 96.

Protoperidinium digitale Pouchet (1883), p. 433, pl. 18/19, fig. 14 = *G. digitale* (Pouchet) Kofoid. See p. 214 of this paper.

Protoperidinium pyrophorum Ehrbg. See Pouchet (1883), p. 433, pl. 18/19, fig. 15 = *G. polygramma* Stein (1883), pl. 4, fig. 15. Pouchet's form is not that of Ehrenberg (1838), p. 133, pl. 1, fig. 1, which is fossil.

Roulea obliqua Gourret (1883), p. 87, pl. 2, figs. 39, 39a = *G. obliqua* (Gourret) Lemmermann (1899), p. 368. Indeterminable.

Roulea spinifera Gourret (1883), pp. 86–87, pl. 2, fig. 43. Assigned by Lemmermann (1907), p. 298, to synonomy of *G. spinifera.* Indeterminable.

Steiniella cornuta Karsten (1907), pp. 348, 420, pl. 53, figs. 7a-c = *Gonyaulax pacifica* Kofoid (1907b), p. 308, pl. 30, figs. 37–39.

Steiniella fragilis Schütt (1905), pl. 6, figs. 26_{1-14} = *G. fragilis* (Schütt) Kofoid.

Steiniella inflata (Kofoid) (1907a), pp. 168-169, pl. 2, fig. 15 = *G. inflata* (Kofoid).

Steiniella mitra Schütt (1905), pl. 7, figs. 27_{1-3} = *G. mitra* (Schütt) Kofoid.

IX. Described or Cited Species of *Gonyaulax* Which Belong in Other Genera

Gonyaulax fimbriatum Murr. and Whitt. See Schröder (1906), p. 329, lapsus (?) for *Goniodoma fimbriatum* = *Ceratocorys armatum* (Schütt) Kofoid (1910), p. 181.

D. SPECIES OF *GONYAULAX* FROM THE COAST OF CALIFORNIA

The species of *Gonyaulax* included in the following key have been found along the Pacific coast between southern Alaska and

San Diego. Skeletons or moribund individuals of Alaskan species may be expected in the deeper plankton (ca. 50-100 fathoms) as far south as San Diego and are therefore included in this key. It is to be expected that the further examination of the plankton of subtropical facies occurring at San Diego during late autumn and early winter will bring to light additional species normal to warmer seas. No fresh-water species has as yet been reported from California.

I. Key to Species of *Gonyaulax* in California Waters

1. Body elongated, fusiform, length 1.5 transdiameters or more 2
1. Body not elongated, length less than 1.5 transdiameters 3
2. Antapex decidedly asymmetrical 4
4. Very large, length over 100μ, body deeply excavated, antapex in ventral view broadly rounded ..... **pacifica**
4. Large, length less than 100μ, not so deeply excavated, antapex obliquely truncate ..... **kofoidi**
2. Antapex nearly symmetrical 5
5. Length less than 2 transdiameters ..... **Spiraulax jolliffei** gen. nov.
5. Length more than 2 transdiameters ..... **G. birostris**
3. Apex extended over to dorsal face 6
3. Apex not extended on to dorsal face 7
6. Body elongated, surface vermiculate ..... **G. fragilis**
6. Body rotund, surface reticulate ..... **G. alaskensis**
7. Body spheroidal ..... **G. sphaeroidea**
7. Body not decidedly spheroidal 8
8. Antapical spines not present 9
8. With one or more antapical spines 10
9. Body polyhedral, surface reticulate ..... **G. polyedra**
9. Body ellipsoidal, with longitudinal striae predominant 11
11. Girdle with considerable displacement and overhang ..... **G. scrippsae**
11. Girdle with little displacement and overhang ..... **G. turbynei**
10. Apical horn 0.4 transdiameter, 5 antapical spines ..... **G. triacantha**
10. Apical horn not so well differentiated, fewer antapical spines 12
12. Surface with longitudinal striae predominant ..... **G. polygramma**
12. Surface with polygonal recticulations 13
13. Large species, length 60–100μ, apical horn moderately differentiated ..... **G. diegensis**
13. Medium-sized species, 40–50μ, apical slightly differentiated ..... **G. digitale**
13. Small species, 30–40μ, apical scarcely differentiated ..... **G. spinifera**[1]

[1] Sometimes without antapical spines.

II. Descriptions of Species of *Gonyaulax* Diesing, With Notes on Synonomy, Variation, and Distribution

1. Subgenus **Gonyaulax** subgen. nov.

The California representatives of this subgenus fall into several groups of species of unequal coherence and content; to wit, the *spinifera*, *polygramma*, *polyedra*, and *sphaeroidea* groups. The *spinifera* group consists of four species, *G. spinifera*, *G. digitale*, *G. diegensis* and *G. triacantha*. The first three form a series of increasing size, of closely related species, from which the fourth differs widely in form of body, surface markings and distribution of the antapical spines, the possession of which forms the main character linking it to this group.

a). The *Sphaeroidea* Group

Characterized by spheroidal form, smooth or feebly reticulated surface, girdle and ventral area scarcely impressed.

Here belong *Gonyaulax sphaeroidea* sp. nov. and *G. palustris* Lemm.

1. **Gonyaulax sphaeroidea** sp. nov.

Pl. 16, figs. 41, 42

Diagnosis—A medium-sized species with spheroidal body, no apical horn or with one which is but slightly differentiated, girdle displaced 1.5 to 2 times its width, anterior intercalary plate present, surface smooth or faintly reticulate, rather sparingly punctate. Hyaline lists on both sides of longitudinal furrow.

Description: *Body* spheroidal, major axis slightly exceeding equatorial (1.12 transdiameters), no apical horn differentiated in specimen figured. *Epitheca* slightly exceeding hypotheca, each nearly hemispherical. Section at girdle with only a trace of flattening on ventral face.

The *girdle* is equatorial, slightly postmedian, descending, displaced distally 1.5 to 2 girdle widths, and has an overhang of less than 0.5 girdle width. It is not impressed and has low hyaline, non-ribbed lists.

The *ventral area* or longitudinal furrow is slightly curved to the left opposite the distal end of the girdle, and flares posteriorly to more than a girdle width. It is guarded on either side by salient membranous, non-ribbed lists which increase in height posteriorly. Anteriorly the ventral area slightly indents the epitheca.

The *plate formula* is *3′*, *1ª*, *6″*, *6*, *6‴*, *1ᵖ*, *1⁗*. The *apical* plates, *1′* to *3′* surround the apex. Apical *1′* is a slender plate reaching to the ventral area, separating plates *1″* and *6″* of the precingular series and bearing at its apex the elliptical closing platelet, a thin scale-like structure which covers the so-called apical pore, and when the plates are parted often remains attached to the slender midventral apical plate *1′*. Plates *2′* and *3′* are nearly bilateral and placed saddle fashion upon the anterior end. The *anterior intercalary* is a small plate not touching the apical region and lying to the right (of body, left of figure) of apical *1′*, and between the apical and precingular series. It bears on its median margin a conspicuous pore, which is present throughout the genus *Gonyaulax*, and has not been noted heretofore, which I call the ventral pore. The six *precingulars 1″–6″* are all prominent plates, *6″* being quadrangular. It is triangular in most species which have widely displaced girdles. The girdle plates are normally six in *Gonyaulax* but were not separated in this species as the material at command was limited. The six *postcingulars* are typical; postcingular *1′* being, as usual, a narrow plate partially hidden on the left margin of the longitudinal furrow. The *posterior intercalary 1ᵖ* is a wide plate at the left of the longitudinal furrow, touching neither the girdle nor the antapex. The single *antapical 1⁗*, is a large pentagonal plate whose ventral margin is slightly indented by the ventral area.

The *ventral area* includes those plates of the thecal wall which are involved in the longitudinal furrow. There are as many as six of these in some species of *Gonyaulax*. Only the most anterior one is to be seen in the figure.

The *surface* of the San Diego specimen was perfectly smooth and was sparsely porulate with rather large scattered pores. There were no surface markings or reticulations and the lists along the furrows were without ribs.

Cell contents unknown.

Dimensions: Length, 43μ; transdiameter, 38μ; dorsoventral diameter the same; girdle width, 4.5μ.

Comparisons: Its spherical form and smooth surface at once distinguish it from all described species of the genus.

Described from an empty theca taken in surface plankton off San Diego, November 26, 1904. The composition of the plankton in this collection indicates its oceanic and subtropical origin as shown by the presence of such species as *Pyrophacus horologicum*, *Ceratocorys armatum*, *C. horrida*, *Gonyaulax turbynei*, *Ceratium reticulatum* and *Podolampas palmipes*.

b). The *Spinifera* Group

A group of rotund species characterized by the presence of one or more antapical spines, more or less widely displaced

girdle and slightly differentiated apical horn. Plate formula *3′* (or *4′*), *0* (or *2*)^{a}, *6″*, *6‴*, *1*^{p}, *1⁗*. No longitudinal striae.

One of the most puzzling cases of confusion which exists among the Peridinidae is that which involves *Gonyaulax spinifera*, due, in my opinion, to the defective figure of Claparède and Lachmann (1858-1859) who originally described the species as *Peridinium spiniferum*, to Stein's (1883) error in failing to distinguish between the form he described as *G. spinifera* and that of Claparède and Lachmann, and to the non-acceptance by subsequent writers of Pouchet's (1883) *Protoperidinium digitale* as distinct from the species originally described as *spiniferum*. The acceptance on the part of later workers of the application of the name *spinifera* to Stein's species has led to the re-description of the minute original form as a new species by Paulsen (1907), Fauré-Fremiet (1908), Henckel (1909) and possibly to repeated appearance of *Gonyaulax* spp. in the plankton records of the International Commission for the Investigation of the Sea. See Ostenfeld (1906, 1909).

The examination of a wide range of material, and an inspection of all published figures have convinced me that there are two somewhat similar forms but distinct species of *Gonyaulax* widely distributed in the neritic and in the oceanic plankton to some extent. These are, (1) the minute form with widely displaced, overhanging girdle and usually two, rarely several, small antapical spines, and (2) a larger form with less displacement and overhang and two larger spines. This first is the original *G. spinifera*, the type species of the genus, known in later literature as *G. levanderi* (Lemmermann) Paulsen, *G. mangini* Fauré-Fremiet, and possibly *G. caspica* Henckel. Doubtless it has sometimes been confused with and often combined with the other common species, *G. digitale* (Pouchet) (described as *Protoperidinium digitale*).

The other species is the larger and, it seems from all the evidence obtainable, is the more abundant one, has less displacement and less overhang of the girdle, is often more rugose, and has two prominent antapical spines. It was first described, as above stated, by Pouchet (1883, July-August) and several

months later referred by Stein (1883, November) to *G. spinifera* (Clap. et Lachm.) Diesing, a reference widely followed by subsequent workers. The date of publication of Stein's (1883) monograph is stated in a letter to me from the publisher to have been the latter part of November.

To these two forms I here add a third and still larger species *G. diegensis*, distinguished by its still larger size, widely displaced but not much overhanging girdle, usually three antapical spines, by its wide intercalary bands, and by the presence of four apical plates.

These three species form a series of increasing size comparable with that formed in the *polygramma* group by *G. turbynei*, *G. scrippsae*, *G. polygramma*, *G. kofoidi*, and *G. pacifica*, and as in the case of that series, showing more or less intergradation.

The possibility that they form merely a growth series is excluded by their distribution, for in the case of the *polygramma* series, *G. kofoidi* and *G. pacifica* are tropical and oceanic, and the other two do not occur together with them in such numbers as the growth relation demands. The possibility that they are geographical (temperature) species or "races" is suggested by the present incomplete data of their distribution, but it is by no means conclusively determined. All three, *spinifera*, *digitale*, *diegensis*, occur, perhaps together, in the San Diego region. Their predominant centers of distribution must be determined to solve this problem. In my opinion from data at present available they are distinct species.

The inclusion of *G. triacantha* in the *spinifera* group is an arbitrary assignment, based primarily on the presence of several antapical spines. Here also may be placed *G. apiculata* (Penard) Entz, and its variety *clevei* (Ostenfeld).

2. **Gonyaulax spinifera** (Claparède et Lachmann) Diesing

Pl. 10, figs. 8–10; pl. 16, fig. 39, and text figs. A–D.

Peridinium spiniferum Claparède et Lachmann (1858–1859), p. 405, pl. 20, figs. 4, 5.

Gonyaulax spinifera (Clap. et Lachm.) Diesing (1866), p. 96.

Peridinium sp. Levander (1894b), p. 50, pl. 2, fig. 21.

Peridinium vexans Murray and Whitting (1899), p. 327, pl. 29, figs. 7a, b. See discussion of synonomy below.

P. levanderi Lemmermann (1900), p. 120.
Gonyaulax sp. Van Breeman (1905), p. 42.
C. [*eratocorys*] *spinifera*, Schröder (1906), p. 329. Lapsus.
Gonyaulax levanderi, Paulsen (1907), p. 8, fig. 8.
G. levanderi, Ostenfeld (1908), p. 165, pl. 5, figs. 54–58.
G. levanderi, Paulsen (1908), p. 30, fig. 38.
G. mangini, Fauré-Fremiet (1908), pp. 213, 230; fig. 6, pl. 16, fig. 19.

Diagnosis: A minute rotund species somewhat elongated anteriorly, with relatively wide oblique girdle with considerable overhang; epitheca with convex sides, with or without two or more small antapical spines. Longitudinal furrow not flaring much posteriorly, often abruptly widened opposite distal end of girdle. Line joining ends of girdle makes an angle of 27°-40° with major axis. Surface lightly marked. Length 24-50μ.

Description: *Body* small, length, excluding spine 1.14–1.25 transdiameters; rotund, girdle section subcircular. *Epitheca*, subconical, more rotund than in *G. digitale*, apex subsquarely truncate, nearly a girdle width across; apical horn not much differentiated or barely suggested; sides slightly convex, greatest altitude, 0.6 to 0.7 transdiameter. *Hypotheca* subhemispherical, greatest altitude, 0.6 transdiameter, antapex broadly rounded or sub-truncate between spines, with one, two or more usually short antapical spines, rarely with none. The spines shown in plate 10, figures 9 and 10, are exceptionally long.

The *girdle* is the most striking characteristic of this species. It is relatively very wide, one-sixth of the transdiameter across, descending, displaced twice its width (2.2–3) or more, with an overhang of 1 to 2 girdle widths. It is deeply indented, with low ridges, sometimes salient, and without lists.

The *ventral area* (*v.a.*, text fig. B.) is very oblique anteriorly, slightly indents the epitheca, is laterally compressed almost to closure between the overhanging ends of the girdle and is nearly straight posteriorly with a slight deflection to the left side of the body. It is not expanded posteriorly as in *G. digitale* (Pouchet), its distal end being about 1.4 wider than at the distal posterior girdle ridge. The most marked and fairly constant feature is its abrupt almost rectangular expansion to the left just opposite to the distal end of the girdle, a feature not prominent in *G. digitale* or *G. diegensis*. This expansion is better shown in plate 10, figure 10, than in plate 16, figure 39.

Plate formula is *3′*, *0ª*, *6″*, *6*, *6‴*, *1ᵖ*, *1⁗*. Apical *1′* is curved with large ovate or elliptical closing platelet (*cl. pl.*, pl. 10, figs. 8, 9). Apical *3′* bears a faint trace (pl. 16, fig. 39, and text fig. B) of a curved marking resembling a suture line which marks off the apical-median part of the plate in somewhat the same fashion in which apical *4′* is delimited in *G. diegensis*. I have not been able to separate this as a plate in *G. spinifera* and the marking is often absent. Ventral pore (*v. po.*) is on median edge of apical *3′*, about one-half of the distance from the apex to the

apical-precingular suture. *Precingular 1″* is vertically displaced anteriorly the whole length of 6″, separated by ventral area from plate 6″, which is nearly triangular (pl. 10, fig. 10). *Posteingular 1‴* is very small, linear, overhanging oblique part of ventral area. *Posterior intercalary* is 1 to 1.3 girdle widths across.

The plates of the *ventral area* (*v. a.*, pl. 10, fig. 8) are much obscured by the obliquity and overhang of the girdle. The anterior plate (*ant. pl.*) slightly indents the epitheca, is not crossed by the anterior girdle ridge and bears on its postmargin the anterior edge of the flagellar pore. The intermediate plates (*int. pl.*, pl. 10, fig. 10) must be small as they are more or less hidden in the oblique part of the longitudinal furrow. The posterior plate (*post. pl.*) is large and extends anteriorly almost to the level of the distal end of the posterior girdle ridge. Its posterior end roundly indents the antapical plate.

The *surface* is smooth, sparingly porulate with large pores, especially near suture lines which are marked by faint lines. A faint reticulum about the pores is sometimes developed. Ridges along girdle and ventral area heavier, continued on either side in short spinules which are rather nearer together than in *G. digitale*, being about 1.5 girdle widths apart. Often but a single spine, the right one, is present, and sometimes none at all is found. In the brackish water form of this species described as *G. levanderi*, Paulsen (1907, fig. 8a), has figured these spines as posterodorsal to the end of the ventral area and also finds several small accessory spinules. The two spines in our material are located near the points where the ventral area indents the antapical, a position which the antapical spines often occupy in this genus. Lists on the spines are rare in this species. Chromatophores often dark yellowish brown. *Contents* dense, occasionally pale and translucent.

Dimensions: Length, 24 to 50μ, generally 35 to 40μ; transdiameter, 21 to 33μ. In the Aral Sea Ostenfeld (1908) records forms referable tentatively to this species, 40 to 50μ in length and 32 to 44μ wide. A few of our marine forms approaching this size have been found by me.

The following table of measurements gives the range in dimensions observed in San Diego material and recorded elsewhere.

Measurements of *Gonyaulax spinifera*
(Dimensions in Microns)

Locality	Date	Length	Transdiameter
San Pedro Harbor, Calif.,	May 31, 1901	44	35
San Pedro Harbor, Calif.,	May 31, 1901	35	31
San Pedro Harbor, Calif.,	May 31, 1901	40	35
San Pedro Harbor, Calif.,	May 31, 1901	45	39
Off San Diego, Calif.,	June 28, 1904	48	37
Off San Diego, Calif.,	June 28, 1904	41	23

Locality	Date	Length	Trans-diameter
Off San Diego, Calif., June 28, 1904		40	30
Off San Diego, Calif., Dec. 2, 1904		38	30
Off San Diego, Calif., Dec. 2, 1904		38	35
Loring, Alaska, Sept. 15, 1905		40	34
Loring, Alaska, Sept. 15, 1905		45	40
Claparède and Lachmann (1858–1859), p. 405, pl. 20, fig. 4.		30–40	20–26(?)
Murray and Whitting (1899), pl. 29, fig. 7a.		39	33
Fauré-Fremiet (1908), p. 230, pl. 16, fig. 19.		40	33
Ostenfeld (1908), pl. 5, figs. 54–58.		40–50	32–44

Variation: Quite variable in amount of overhang (1 to 2 girdle widths) and displacement of the girdle (2.2–3 girdle widths), number and development of antapical spines, from none to two main ones with accessory spinules, and in development of surface markings.

Comparisons: Most like *G. digitale* with which it has been more or less confused and not with certainty always separable from it. In material from the Faeroes, Irish Sea, Naples, and Alaska which I have examined there seem to be fairly constant differences between the two species which, however, are in some cases difficult to apply.

From *G. diegensis* it is distinguished at once by its much smaller size, absence of intercalary striae, and its smaller antapical spines. The table below summarizes the important points of difference in the three species.

Species Characters in *Spinifera* Group

	Spinifera	*Digitale*	*Diegensis*
Length	24–50μ	45–75μ	60–100μ
Width	20–37μ	34–50μ	45–82
Antapical spines	0–2, small	2 (4)	1–3, usually 3
Angle made with major axis by line joining ends of girdle	27°–40°	5°–18° (26°)	0°–8° (15°)
Displacement of girdle in girdle widths	2.3–3	1.5–2.5	3–5
Overhang of girdle ends, in girdle widths	1.5–2	0.5–1.25	0–1
Form of longitudinal furrow	Widens abruptly opposite distal end of girdle	Not abruptly widened	Not abruptly widened
Apical 4′	Not separated	Not separated	Separated

Synonomy: The species originally described by Claparède and Lachmann (1858–1859) as *Peridinium spiniferum* was clearly a small one (40μ) with widely displaced overhanging girdle, as is evident in both the figures and description. This Diesing (1866) made the type (only species) of his genus *Gonyaulax*. It is equally evident that Stein's (1883) figure is of a form with less displacement and overhang and probably (exact magnifications are not given) of larger size. An examination of extensive material from tropical and northern waters from the Atlantic, Pacific and Mediterranean has convinced me that there are two distinct and separable forms confused more or less under the name *G. spinifera*. Others have evidently labored under the same opinion and have sought to escape from it by renaming either the smaller or larger form according as the name *spinifera* was applied to Stein's or the original describer's figures. Pouchet (1883), who had Claparède and Lachmann's paper (1858-1859) at hand distinguished the larger form which Stein (1883) a few months later published as *G. spinifera*, as *Protoperidinium digitale*. Later workers finding the smaller form with oblique and overhanging girdle have recognized its distinctness from the *G. spinifera* of Stein (1883). Levander (1894b) called it *Peridinium* sp. Lemmermann named it *P. levanderi;* Van Breeman (1905) recognized its distinctness from *G. spinifera* of Stein and left it unnamed and Paulsen (1907, 1908) and Ostenfeld (1908) have called it *G. levanderi*, while retaining Stein's name for the larger form, and Fauré-Fremiet names it *G. mangini*. The distinctions between the two forms have evidently been widely recognized though Paulsen cautiously says of *G. levanderi* "Vielleicht eine Hungerform von *G. spinifera*."

There can be no doubt of the fact that if the two forms are distinct the older name *spinifera* should remain with the small form originally described by Claparède and Lachmann and that the larger form figured by Stein should bear another name. Pouchet's (1883) name *digitale* is the proper one for the larger species. It is quite probable that Murray and Whitting's *Peridinium vexans* is *Gonyaulax spinifera*, for it agrees with it in size and

structural features in so far as represented in their figures. The only disturbing feature in this interpretation is the overrun of the apex upon the dorsal side, perhaps the result of the oblique view suggested by curvature of girdle and occlusion of spines in their figure. It is plainly a *Gonyaulax* and evidently close to *G. spinifera* as shown by the size (40μ), overhang and displacement of girdle, and flare of longitudinal furrow opposite distal end of girdle. The fins on the antapical spines are unusual.

Distribution: Any discussion of the distribution of this species in the present confused state of records of occurrence is futile. Statements of occurrences can be based only on figures which are plainly *G. spinifera sensu stricto* or upon records of *G. levanderi*. Its distribution in California waters is not as yet fully determined since all of our earlier records include *G. digitale* and to some extent *G. diegensis* under the single caption of *G. spinifera*.

It is known to occur in San Pedro Harbor, May 31, 1901 (No. 505); in collections made off San Diego, June 28 (Nos. 130, 133) and December 2 (No. 342), 1904; and at Loring, Alaska, September 15, 1905. Claparède and Lachmann (1858-1859) describe it from the western coast of Norway. It is reported as *Peridinium* sp. from the Gulf of Finland by Levander (1894) and by Van Breeman (1905) as *Gonyaulax* sp. from the Zuider Sea. It is reported by Paulsen (1907) from the eastern Baltic and Iceland, and by Ostenfeld (1908) from the Aral Sea. It is described by Fauré-Fremiet (1908) as *G. mangini* from the Baie de la Hougue on the northern coast of France.

Evidently neritic, and predominantly in northern and temperate waters.

3. **Gonyaulax digitale** (Pouchet) Kofoid

Pl. 9, figs. 1–5.

Protoperidinium digitale, Pouchet (1883), p. 443, pls. 18–19, fig. 14.
Gonyaulax spinifera, Stein (1883), pp. 13, 16, pl. 4, figs. 10–14.
G. spinifera, Schütt (1887), pp. 366–367, pl. 18, figs. 7–11; (1895), pl. 9, figs. 34 $_{1-2}$.
Peridinium digitale, Lemmermann (1899), p. 369.
Gonyaulax spinifera, Van Breeman (1905), pp. 41–42, figs. 10 a-b.

G. spinifera, Entz (1907), pp. 11–19, pl. 2, figs. 5–6; (1909), pp. 247–256, pl. 8, figs. 5–6.

G. spinifera, Paulsen (1907), pp. 7–8, fig. 6; (1908), pp. 28–29, fig. 37.

G. Granii, Henckel (1909), p. 118, pl. 30, figs. 1–16.

Diagnosis: Larger than *G. spinifera*, less rotund, with less overhang. Epitheca subconical, shoulders often slightly angled, generally two stout antapical spines. Line joining ends of girdle makes an angle of 13°–18° with major axis; longitudinal furrow not abruptly widened opposite distal end of girdle; surface usually heavily reticulated.

Description: Based largely on material from the Faeroes. *Body* subrotund, sometimes subangular at precingular suture, with short, stout apical horn one to two girdle widths in length and 1 to 1.5 widths at apex, rising from slightly angled shoulders of the subconical epitheca; its length 1.1–1.17 (in Stein's figure 12, 1.5) transdiameters. Little if any convexity in sides of epitheca, except at approaching fission(?), its greatest altitude 1.45 transdiameters. Altitude of the *hypotheca* 0.55 transdiameter. The latter more rotund than epitheca, contracted to a broad antapex somewhat less than 0.5 transdiameter across.

Girdle equatorial, descending, displaced 2 to 2.5, with an overhang of 1 to 1.25 girdle widths. Furrow deeply impressed with stout marginal ridges bearing a low ribbed fin. Longitudinal furrow slightly sigmoid, laterally compressed nearly to closure between girdle ends, oblique to the major axis in this region 13°–18°, rarely 26°, expanding posteriorly. This expansion is more apparent than real for the left side of the middle part of the furrow is encroached upon by the thickened reticulate fin (*f.*, pl. 9, fig. 5) arising from the median margin of the posterior intercalary plate *1p*), which simulates the thecal wall in its structure and gives the longitudinal furrow of heavily reticulated thecae an appearance of constriction anteriorly or expansion posteriorly which is not found in less heavily reticulated individuals such as those from Southern Alaska waters (pl. 9, fig. 4). The *ventral area* slightly indents the epitheca in a small angular area. The longitudinal furrow of this species lacks the markedly abrupt expansion immediately opposite the distal end of the girdle which characterizes *G. spinifera*.

The *plate formula* is *3′*, *0ª*, *6″*, *6*, *6‴*, *1p*, *1⁗*. *Apical 1′* (pl. 9, fig. 5) is very slender with a slight median expansion to the left and bears a large closing platelet at its apex. Apical *3′* bears the ventral pore (*v. po.*) on its median margin toward the base of the apical horn. *Precingular 6″* is almost triangular. *Postcingular 1‴* is very narrow and is curved over into the longitudinal furrow. The *antapical 1⁗* is large, and is barely indented by the ventral area. The plates of the *ventral area* (pl. 9, fig. 5) are an anterior plate (*ant. pl.*) crossed by the anterior girdle ridge, a large posterior one (*post. pl.*) reaching to the level of the pos-

terior girdle ridge and several intermediate (*int. pl.*) ones hidden in the compressed longitudinal furrow.

The *surface* of northern forms (Faeroes, pl. 9, figs. 1–3, 5) is deeply and coarsely reticulate with central pores in the mesh, 4 to 6 meshes on the side of a precingular plate. Ribs are faintly or strongly marked along sutures and those adjacent to both furrows bear lists which along the girdle are ribbed. Two stout subequal antapical spines 1 to 1.5 girdle widths in length and about 2 apart are often provided with fins which may bear accessory spinules. In some cases these (pl. 9, fig. 4) become as large as the two main spines. In exceedingly rugose individuals (pl. 9, fig. 5), the fin and spines (*ant. sp.*) are converted into a recticulate structure resembling the thecal wall.

Dimensions: Length (37) 50–75μ; transdiameter, 34–50μ; width of girdle, 5μ; length of antapical spines, 3 to 10μ.

Table of Measurements of *Gonyaulax digitale*

Locality	Date	Length in microns excluding spines	Width
Faeroe Channel	August, 1907	42	35
Faeroe Channel	August, 1907	57	48
Faeroe Channel	August, 1907	68	48
Faeroe Channel	August, 1907	52	43
Faeroe Channel	August, 1907	37	30
Faeroe Channel	August, 1907	40	37
Faeroe Channel	August, 1907	53	45
Faeroe Channel	August, 1907	56	48
Faeroe Channel	August, 1907	54	44
Faeroe Channel	August, 1907	67	60
Bay of Naples	April 4, 1909	60	48
Off San Diego	June 22, 1905	60	50
Loring, Alaska	Sept. 15, 1905	42	35
Loring, Alaska	Sept. 15, 1905	43	35
Loring, Alaska	Sept. 15, 1905	40	35

Variation: Varies principally in surface markings from excessively rugose to nearly smooth forms, in the overhang and displacement of the girdle, and overgrowth of the longitudinal furrow by its lateral walls which is much greater in rugose specimens, in the development of spines and fins, and in size (37–75μ).

Comparisons: See *G. spinifera*. The wide heavy form (compare pl. 9, fig. 2) figured by Van Breeman (1905, fig. 10b) probably represents a condition brought about by an expansion at the apical-precingular sutures possibly preparatory to fission.

Alaskan forms (pl. 9, fig. 4) are smaller, more rotund and less rugose than those from the Faeroes.

Synonomy: See *G. spinifera*. It is highly probable that *G. spinifera* of many writers is in reality *G. digitale* as here defined. The possibility also of the inclusion of *G. spinifera* as above defined, together with *G. digitale*, is excluded only in case of those writers, e.g., Paulsen, who have noted the distinctness of *G. levanderi*, or in those papers accompanied by diagnostic figures. The sketches published by Henckel (1909) of *G. grani* from the Caspian Sea seem to be referable to *G. digitale*. In any event this supposed new species from the Caspian Sea requires a more critical diagnosis before its distinctness from *G. digitale* can be recognized.

Distribution: This species occurred rather frequently in plankton taken in the harbor at Loring, Alaska (55° 40′ N, 131° 35′ W), September 15, 1905 (see pl. 9, fig. 4), and a few specimens have been recognized in the plankton of the San Diego region taken in early summer (No. 919, June 22, 1905), which seem to be referable to this species. They are possibly of northern origin, carried southward in the California current. Full data as to the occurrence of this species in the San Diego region are not available since the species was not distinguished from *G. spinifera* during the examination of most of the collections. Essentially a northern species but not confined to neritic plankton though favoring coastal region, Faeroes, Iceland, North Sea, Concarneau, Naples, Caspian Sea, coasts of Alaska and California. In the absence of figures it is wholly conjectural to base reports of the occurrence of this species upon records of *G. spinifera*, as upon those of Cleve (1901a), though it is extremely probable that many records of the aforesaid species are, especially in northern waters, in reality referable to *G. digitale* wholly or in part.

4. **Gonyaulax diegensis** sp. nov.

Pl. 13, figs. 21–24; pl. 16, fig. 40.

Gonyaulax spinifera, Schütt (1895), pl. 9, figs. 34_{1-2}. Reference here problematical.

G. spinifera, Wright (1907), p. 5, pl. 1, fig. 14.

G. polygramma, Meunier (1910), pp. 54–55, pl. 3, figs. 5–13.

Diagnosis: A large robust species with short stout apical horn, elongated apex, two or three antapical horns, widely dis-

placed (3 to 6 girdle widths) girdle with little overhang, longitudinal furrow not abruptly widened opposite distal end of girdle. Apical *4'* separable. Reticulate surface with wide reticulate intercalary bands.

Description: *Body* elongate-spheroidal, its length nearly 1.2 transdiameters, slightly flattened on ventral face. *Epitheca* exceeds hypotheca. Epitheca contracted to stout apical horn 2 to 4 girdle widths in height and 3 to 4 across at the base and 1.1 to 2 at the apex, with broadly and regularly rounded shoulders, its greatest altitude 0.85 transdiameter, flaring a little at the girdle. *Hypotheca* also flaring at girdle, its greatest altitude 0.6 transdiameters, antapex wide but very broadly rounded bearing two or three short, stout, close-set spines.

The *girdle* is equatorial, descending, displaced distally 3 to 6 girdle widths, and with rarely more than 1 of overhang. Furrow very deeply impressed with salient heavy ridges of thecal wall. In ventral view both portions appear curved, the distal one sweeping in a regular curve (pl. 13, fig. 24) from the margin posteriorly so that its distal end lies nearly midway between the proximal end and the antapex. It is thus one of the most widely displaced girdles in the whole genus.

The *ventral area* or longitudinal furrow is spoon-shaped with slight irregularities in its course. It is nearly closed by lateral compression between girdle ends and flares posteriorly to a maximum width of four girdle widths, rounding at the postmargin which indents the antapical slightly. It is guarded by fins on either side, each at times (pl. 13, fig. 24) with a few heavy ribs. There is no marked expansion as in *G. spinifera* opposite the distal end of the girdle. Anteriorly the ventral area indents the epitheca for a distance of about three girdle widths ending in a rounded margin, a girdle width across, which abuts directly against the posterior end of the midventral apical *1'*.

Plate formula 4', 0ª, 6'', 6, 6''', 1ᵖ, 1''''. The *apical* series consists of a midventral apical *1'*, a very slender plate with sinuous sides to whose apex is attached a much elongated, curved, concave, elliptical closing platelet (pl. 13, fig. 22, and *cf. pl.*, figs. 23 and 24). This platelet extends a trifle beyond the apex upon the dorsal side as in the subgenus *Steiniella* and is marked with a marginal row of pores. Plate *2'* has the upper end carried around to the right beyond the middorsal line as in many other species (*G. triacantha, pacifica, digitale*) of this genus. The third plate, *3'*, just barely touches the apex in a point adjacent to *2'*, the remaining part of the apical margin being occupied by a small plate, *4'* (pl. 13, fig. 23), apparently cut out of the top of plate *3'* by a curved suture. This suture line is not prominent and separates with difficulty as do also the other sutures on this shoulder of the theca. It has been separated, however, several times in my material. A region similar to plate *4'* is suggested by surface markings in *G. spinifera* and is marked off in several other species, for example, in *G. polygramma*, but it is not separable in them. The median margins of plates *3'* and *4'* are in contact with plate *1'* and the anterior angle of the former bears the ventral pore

(*v. po.*, pl. 13, fig. 23) which in this species is quite large and often elongated. The *precingular* plates are all large, except plate *6″*, which is small and triangular in form. In a few cases observed its apex is truncated but the length of the fourth side thus formed is not over a girdle width. *Postcingular* plate *1‴* is about 1 girdle width across and 3 to 5 in length. The *posterior intercalary*, *1p*, is an elongated pentagonal plate to the left of the furrow. The single *antapical*, *1⁗*, is relatively small, and is not deeply indented by the ventral area.

The anterior plate (*ant. pl.*, pl. 13, fig. 23) of the *ventral area* is greatly elongated in this species (4 girdle widths), expands anteriorly and is deeply notched at its postmargin by the flagellar pore (*fl. po.*) The intermediate plates (*int. pls.*, pl. 13, fig. 21) are obscured in the depths of the longitudinal furrow between girdle ends. The posterior plate (*post. pl.*) is a rounded quadrilateral reaching anteriorly nearly to the level of the distal end of the girdle.

The *surface* of this species is most characteristic, its whole area usually being reticulate with subregular polygonal mesh but not uniformly so. Polygonal areas in each of the precingular and postcingular plates contiguous on one side to the girdle are more heavily marked (pl. 16, fig. 40). The more lightly marked margins bear the some relation to the plates that intercalary bands do, and they are probably of this nature. These intercalary bands vary in width in different individuals and the contrasted markings vary greatly in relative distinctness and in degree of development in different individuals. In the more heavily marked forms (pl. 13, fig. 24) the central reticulations are coarse and heavy and are less sharply delimited from the lighter margins. In more lightly marked forms the intercalary bands are very sharply marked off from the more densely pitted or reticulate central regions. In some cases (pl. 16, fig. 40) the intercalary bands are quite free from all but the faintest reticulations. The pores are large, sparsely distributed over the more reticulated central parts of the plates and located in the nodes of the mesh rather than in the center of the enclosed areas. There are no girdle lists, but those of the longitudinal furrow on plates *1‴* and *1p* are heavily ribbed. The spines on the antapex arise near the middle of the antapical plate and not from the nodes of the sutures. They are usually two, occasionally but one, and quite often three, the third being on the right side. The spines are usually finned. The girdle is heavily reticulate except where crossed by intercalary bands.

The contents are prone to escape through the parted apicals as in *G. polygramma* and *G. polyedra*. There is a centrally located ellipsoidal nucleus with moniliform chromatin network. The irregular chromatophores are of a yellowish brown color. The plasma is not especially dense.

Dimensions: Length (60) 75 to 100μ; transdiameter (45) 70 to 82μ; width of girdle 4.5 to 5μ. The following measurements apply to material from the San Diego region, and to figures referable to the species.

Measurements of *Gonyaulax diegensis*

Locality	No. collection	Date	Length in microns excluding spines	Trans-diameter
Schütt (1905) Naples(?)		.....	65	43
Wright (1907) Grand River, Gulf of St. Lawrence		....	75	45
Off San Diego, Calif.	62	June 8, 1904	60	43
Off San Diego, Calif.	73	June 8, 1904	82	65
Off San Diego, Calif.	73	June 8, 1904	95	74
Off San Diego, Calif.	120	June 23, 1904	90	75
Off San Diego, Calif.	120	June 23, 1904	60	43
Off San Diego, Calif.	128	June 23, 1904	65	45
Off San Diego, Calif.	141	June 30, 1904	98	78
Off San Diego, Calif.	141	June 30, 1904	74	55

Ten individuals taken in surface plankton June 27, 1905, off San Diego, were respectively 70, 75, 75, 80, 80, 83, 87, 90, 92, and 100μ in length.

Variation: This species varies greatly in size, in girdle displacement (3 to 6 girdle widths) and overhang (0 to 1.5), in the degree to which reticulations are developed and thickened, and in the widths of the intercalary bands and the distinctness with which they are marked out. In all individuals which I have examined, however, the bands are definitely discernible. The smaller forms (60 by 45μ) are found in the same collections with the largest ones and seems to represent merely the extremes in variation, though the most of the individuals are 75μ or more in length.

Synonomy: It seems possible but by no means certain that the form figured by Schütt (1895) is this species, since it has the size, the general form, the color and the three antapicals characteristic of it. Wright's (1907) figure is open to a similar interpretation. Neither has, however, indicated the intercalary bands usually apparent on the less heavily marked specimens of the species.

Meunier (1910) figures as *G. polygramma* a form which is not even remotely like that species, though he comments upon the resemblance to *G. spinifera*. His magnification is unfortunately not given. In proportions, girdle, and surface markings his form is so remarkably like *G. diegensis* that I am constrained to include it in the synonomy of that species. This is the only species which he refers to *Gonyaulax*.

Comparisons: This species is a member of the *G. spinifera* group, related to *G. digitale* (Pouchet), differing from it in its size, in its more pronounced rotundity, its broad intercalary bands, and in having few pores located sparingly in the nodes of the fine reticulum instead of many centrally located in the openings of the mesh, and in three finned antapical spines, whereas *G. spinifera* usually has two spines, without fins. It differs from *G. spinifera* in much greater size, less overhang of girdle, and absence of expansion of longitudinal furrow opposite the distal end of the girdle.

Distribution: In neritic plankton of spring and summer at San Diego. Less abundant in oceanic plankton. Many empty thecae were taken in plankton off kelp zone in 1904 with *Gonyaulax spinifera*, *G. polyedra*, *Dinophysis homunculus* and *Ceratium pentagonum*. The abundance of empty thecae in this region may be due to the discharge of skeletons in faeces of the abundant sessile plankton-feeding fauna of the kelp zone, or to adverse local conditions about this zone leading to ecdysis.

5. **Gonyaulax triacantha** Jörgensen

Pl. 11, figs. 11–15.

Gonyaulax(?) triacantha Jörgensen (1899), no. 6, p. 35.
Ceratium(?) hyperboreum Cleve (1900a), 1, pp. 14–15, pl. 18, fig. 14.
Ceratium(?) hyperboreum Cleve (1901a), p. 223.
Gonyaulax hyperborea (Cleve) Paulsen (1903), p. 90.
Gonyaulax triacantha, Paulson (1904), pp. 21–22, fig. 5a-d.
Heterodinium triacantha (Jörg.) Kofoid (1906a), p. 354.
Gonyaulax triacantha, Kofoid (1906b), pp. 102–105, figs. 1-3.
Ceratium hyperboreum, Lemmermann (1907), p. 298.
Geratium hyperboreum, Linko (1907), p. 91.
Amylax lata Meunier (1910), pp. 51–52, pl. 3, figs. 24–27.

Diagnosis: A small species (50μ) with rotund hypotheca, epitheca with concave faces, and obliquely truncated apex. Girdle slightly displaced, ventral area spreading posteriorly to the right, five to seven spreading antapical spines, surface finely reticulate. Northern neritic species.

Description: *Body* rotund posteriorly, concave anteriorly, flattened ventrally, girdle postmedian. The length (excluding spines) 1.16 to 1.20 transdiameters, dorso-ventral diameter 0.5 to 0.6 transdiameter, girdle section reniform (pl. 11, figs. 11, 12) of empty thecae. The usual form is more rotund (see Paulson, 1904, fig. 5d). *Epitheca* flaring at the

base into the spreading girdle, its altitude 0.75 transdiameters, its sides contracted in a sweeping concave curve into the well-developed apical horn with a slight hump at the apical-precingular suture. Apical horn 0.35 transdiameters in height, very obliquely truncated with acute termination on its right margin. *Hypotheca* broadly rounded posteriorly, its altitude nearly 0.4 transdiameter, excavated ventrally. *Girdle* postmedian, descending, displaced distally one furrow width. Furrow deeply impressed with stout ridges of body wall. *Ventral area* is exceptionally wide in this species: it indents the epitheca about a furrow width, flaring posteriorly to the left immediately behind the girdle to 2 and at the slightly convex post margin to 3.8 furrow widths.

Plate formula, *3′*, *2ª*, *6″*, *6*, *6‴*, *1ᵖ*, *1⁗*. *Apical* region (pl. 11, figs. 11–15) consists of a midventral apical (Rautenplatte) *1′* widened in its middle to the left to nearly two girdle widths, a short plate on the left dorsal face of the apical horn which cuts off the two anterior intercalaries (*1ª*, *2ª*) from contact with the apex, and the right ventral apical *3′*. The circular closing platelet (*cl. pl.*, pl. 11, fig. 12) is attached to apical *1′*. *Precingular 6″* is quadrilateral and is separated by apical *1′* and the anterior plate of the ventral area (*ant. pl.*) from precingular *1′*. *Postcingular 1‴* is a narrow and sometimes very short plate on the left of the longitudinal furrow; postcingular *3‴* is narrower than other members of the series. *Posterior intercalary 1ᵖ* is concave on its right margin, expanding posteriorly. *Antapical 1⁗* is 0.75 transdiameter from right to left but narrow dorso-ventrally. The *ventral area* (*v. a.*, pl. 11, figs. 11–13) is composed of a triangular anterior plate (*ant. pl.*) crossed in the middle by the anterior girdle ridge and notched posteriorly by the flagellar pore (*fl. po.*, fig. 13). Behind this lie four intermediate plates (*int. pl.*) and the spreading posterior plate (*post. pl.*).

The *surface* is minutely and quite regularly reticulated with a mesh which sometimes shows a tendency toward a quadrilateral pattern. Pores not demonstrated. Ventral pore (*v. po.*) near apex on right margin of plate *4′*. Girdle without hyaline lists, a very wide (1–1.5 furrow widths) hyaline, faintly reticulated, list on left side of ventral area (pl. 11, fig. 13), arising from suture along posterior intercalary, decurrent posteriorly, with an antapical spine (*a*) on the node where this suture joins the antapical suture. The largest antapical spine (*f*), 0.33 transdiameter in length, arises from the right antapex from the surface of the antapical plate, and a somewhat shorter one (*e*) from the left antapex. Three or four additional spines (*b*, *d*, *c*) arise at or near the nodes of the antapical suture. The areolation of the surface of the plates extends for a short distance upon the base of the spines. They are, however, solid.

Contents exceedingly dense, obscuring thecal structure; chromatophores thickly packed.

Dimensions: Length, excluding spines, 58 to 60μ; transdiameter, 34 to 35μ; dorso-ventral diameter, 20μ (diameters measured on empty theca, those with contents are less flattened);

length of longest spine 12 to 15μ; width of furrow, 4μ; Paulsen (1908) gives length (without spine ?) as 72 to 84μ. Cleve's (1900) figure is 70μ without spines. Alaskan specimens appear to be smaller than those of European waters.

Variation: This species varies in the number of spines. Five can usually be found, and as many as seven sometimes appear. The surface markings are more pronounced in some individuals than in others and linear striae are sometimes more evident than in the individual figured (pl. 11, fig. 13). Postcingular *1‴* is subject to considerable variation in length.

Comparisons: *Gonyaulax triacantha* is one of the best defined and most isolated species in the genus. It is remarkable both in form and in the development of the antapical spines as well as in the character of the surface markings. It is not structurally nearly related to any other species and its inclusion in the *spinifera* group is justified mainly on the ground of its antapical spines. Two dorsal intercalaries still further distinguish it.

Synonomy: First described but without figures by Jörgensen (1899) who questionably referred it to the genus *Gonyaulax* and later by Cleve (1900) as *Ceratium hyperboreum*. It was first figured by Paulsen (1904) who analysed the plates incompletely but verified Jörgensen's conjecture that it belonged in *Gonyaulax*. It was later referred by me (1906a) to my new genus *Heterodinium* on account of certain structural features found in Paulsen's incomplete figures, but this error on my part was corrected a few months later (1906b) upon examination of material from Alaska, which enabled me to extend the analysis of the thecal plates. A fuller knowledge of the genus enables me in the present paper to correct and supplement certain interpretations and deficiences in my earlier analysis. These are the correct analysis of the apical region showing 3 apicals (*1′*, *2′*, *3′*) and two dorsal intercalaries (*1ª*, *2ª*) instead of 3 apicals (Kofoid, 1906b, fig. 1, pls. 1, 2, 3); six precingulars (*1″–6″*) instead of 5 (*1–8*), and 6 postcingulars (*1‴–6‴*), instead of 5 (*9–13*). Paulsen's figure (1904, fig. 5a) was correct in suggesting the presence of the small plate, my postcingular 1‴, though it was not delimited therein from the posterior intercalary.

Judging from the obliquity of the ventral area (longitudinal furrow plate) and the location of the small posteingular *3'''*, Paulsen's (1904) figure 5d is evidently not an "antapical view" of the hypotheca as stated, at least not *from* the antapex but rather from the direction of the apical pole. He shows five postcingulars and a furrow plate, but does not represent in this figure the small posteingular *1'''* (of my nomenclature). It is also evident that the two plates on the ventral side to the right of the doubled suture line (in his figure *d*) both belong to the ventral area and that the direction of their boundaries should be somewhat modified. In other respects this figure harmonizes with my findings. His double suture line is evidently the fission line, as will be seen on comparing his figure, as interpreted above by me, with the fission line of text figures A-D.

Meunier (1910) has created a new genus, *Amylax*, for this species and certain other inadequately defined forms, basing the genus solely upon the presence of starch grains in the cytoplasm. He includes in this genus a species which he calls *A. lata*, which is, however, undoubtedly *Gonyaulax triacantha* Jörg. I cannot agree that the species he figures is not *triacantha*. In girdle, spines, surface markings, and dorso-ventral compression it is a typical representative of the species. The outline of the epitheca of the specimens he figures is more convex than in my figures, which are of a skeleton from which cell contents had escaped, and hence its sides are more concave than in his figures. The generic basis he proposes is also, in my opinion, quite inadequate, and might lead to endless confusion if followed. In skeletal structure his *A. catenata* (= *Gonyaulax catenata* (Levander) Kofoid) is also referable to the genus *Gonyaulax*. Since skeletal structure has been generally utilized in generic characters in the dinoflagellates, it seems logical and advisable to follow it in this instance. I therefore reject his genus *Amylax* and refer the species in it to *Gonyaulax*.

Distribution: Fairly abundant in plankton from Alaska, Yes Bay and Loring (55° 40′ N, 131° 35′ W) taken by U. S. Steamer "Albatross" of the Bureau of Fisheries, September 15, 1905. It is to be expected in coastal plankton drifting southward in deeper levels, along the coast of California.

Reported by Jörgensen (1899) from Herlö fiord, by Cleve (1900a) from Spitzbergen, by Paulsen (1904) as abundant in fiords in Iceland, from Shetland and the Faeroes, and by Paulsen (1907) as rare in the North Sea, Skagarak and Cattegat. It is plainly a neritic northern species. It appears in the records of the International Commission for the Investigation of the Sea (see Ostenfeld, 1906, 1909), from the North Atlantic, North and Baltic Seas, and the Gulfs of Bothnia and Finland as present in small numbers.

c). The *Polygramma* Group.

This group is represented in the plankton of the San Diego region by five species, *G. turbynei* Murr. and Whitt., *scrippsae* sp. nov., *polygramma* Stein, *kofoidi* Pavillard, and *pacifica* Kofoid, which form a series of increasing size, characterized by linear markings with a predominantly longitudinal direction. In the order named the species represent stages in increase in size, elongation of body and increase in antapical asymmetry. Owing to the considerable variability in proportions and in surface markings, a wide range of material and a large series of carefully executed drawings are desirable for a critical comparison of the species in this group. Plate formula *3′*, *0ª*, *6″*, *6*, *6‴*, *1ᵖ*, *1⁗* .

6. **Gonyaulax turbynei** Murray and Whitting

Pl. 17. fig. 44

Gonyaulax Turbynei Murray and Whitting (1899), pp. 323–324, pl. 28, figs. 4a, b.

G. polygramma Stein (1883), in part, pl. 4, fig. 19 only.

G. Turbinei, Schröder (1906), pp. 329, 340.

Glenodinium ovatum Fauré-Fremiet (1908), p. 214–5, pl. 15, fig. 2. Provisionally referred here.

Diagnosis: A small ovoid species, with equatorial girdle displaced 1 to 1.5 girdle widths, without marked overhang, with linear markings more or less well developed.

Description: *Body* ovoid, length 1.16 transdiameters, girdle section circular. Epitheca and hypotheca subequal. *Epitheca* a low cone with somewhat convex sides, its altitude 0.6 transdiameter. No apical horn, apical region elliptical, flattened, sloping ventrally. *Hypotheca* subhemispherical with very slight ventral depression.

Girdle equatorial, descending, displaced distally 1 to 1.5 girdle widths, with very little if any overhang, deeply impressed, without lists or prominent ridges.

Ventral area does not indent the epitheca, its anterior part much restricted, the middle region very narrow, and the posterior part elliptical, the whole having the shape of a short-handled spoon with a sigmoid handle. The narrow apical *1′* appears to continue the ventral area to the apical region.

The *plate formula* is *3′*, *0ᵘ*, *6″*, *6*, *6‴*, *1ᵖ*, *1⁗*. The ventral *apical 1′* is very slender about 0.3 girdle width across, bent to the right in the middle of its course. It bears a median line of pores and carries at its apex an elliptical closing platelet. The ventral pore is an elliptical structure on the median margin of plate *3′*. Plates *2′* and *3′* are almost bilaterally arranged upon the left and right sides of the apex. *Precingular 6″* is displaced posteriorly nearly to the level of the proximal end of the anterior girdle list and is plainly quadrilateral in form. *Postcingular 1‴* is very short, scarcely a girdle width in length. *Posterior intercalary 1ᵖ* widens posteriorly to nearly two girdle widths. *Antapical 1⁗* is deeply indented by the ventral area. The anterior plate of the *ventral area* is small, not indenting the epitheca and bearing the flagellar pore on its posterior margin. The intermediate plates are hidden in the constricted part of the area. The posterior plate is elliptical with a group of pores at its posterior part.

The *surface*, in well-developed thecae, is rather strongly marked by prominent longitudinal striae which stand out from the minor mesh work most clearly in the precingular series of plates, and less so in the apical region and the distal part of the postcingular zone. About ten major lines may be counted across the ventral face. Between these lines a minor network breaks up the surface into irregular polygons, or areoles in a few of which pores of irregular sizes may be detected. The number of pores is ten to fifteen in each major plate of the precingular and postcingular series. The girdle plates are coarsely and unevenly porulate. Faint traces of intercalary bands may sometimes be detected. There are no spines or lists on this species, as a rule.

Dimensions: Length, 47μ; transdiameter, 37μ; width of girdle 5μ. Murray and Whitting (1899, pl. 28, fig. 4) figure an individual 35 by 28μ.

Variation: Varies considerably in the development of surface markings, in the width of precingular 6″, and somewhat in the development of an apical elevation, all features tending toward *G. polygramma*, the next member of the series in this group.

Comparisons: The linear markings and absence of apical horn and of antapical spines distinguish it from members of the *G. spinifera* group, and the last two characteristics and its smaller size serve to separate it from *G. polygramma*. The absence of overhang separates it from *G. scrippsae*.

Synonomy: The form described by Fauré-Fremiet (1908)

from St. Vaast as *Glenodinium ovatum* is quite similar in form, proportions and size to this species but lacks wholly both sutures and surface markings. It possibly bears the same relation to this species that Schütt's (1895, pl. 8, figs. $33b_{1-3}$) *G. polygramma* Stein var. (= *G. schuetti* Lemm.) does to *G. polygramma*, that is, it is the result of recent ecdysis, only taken at an earlier stage in the growth of the theca.

The status of the small form with hyaline finely and abundantly striate theca figured by Stein (1883, pl. 4, fig. 19) as a "Panzer eines sehr jungen Individuums noch ohne Spur von Täfelung und Sculptur" is still somewhat problematical. I find it at times in the summer plankton at San Diego. It is uniformly smaller than *G. polygramma*. It differs from *G. schuetti* Lemm. (= *G. polygramma* var. Schütt) in the presence of numerous fine striae and in smaller size. In fact *G. schuetti* appears to be only a *G. polygramma* which has recently shed the thecal wall by ecdysis, and has acquired an early phase of a new theca. It differs decidedly from *G. scrippsae* in its but slightly displaced not overhanging girdle. If not an immature or early phase in thecal development following ecdysis it is possibly some as yet unknown type of sporulation, in *turbynei* or some related species. It may be designated as forma *longistriata* forma nova.

It is obvious that the apical horn in this form is more developed than in the typical *G. turbynei* (compare Stein's pl. 4, fig. 19, and my pl. 17, fig. 44). This feature is, however, characteristic in the thin theca following ecdysis in *G. spinifera* and *G. polygramma* (See Stein 1883, pl. 4, figs. 11 and 13, and Schütt 1895, pl. 8, fig. 33b, pl. 9, fig. 34) and might therefore be expected to find some expression also in the corresponding stage in the more rotund *G. turbynei*.

Distribution: Taken in surface plankton July 12, 1904, in California current off San Diego. Probably common but escaping readily through the meshes of the plankton net. Occurrence in other collections of San Diego material not yet determined. Reported as yet only by Murray and Whitting (1899) from the tropical Atlantic in 16°–44° N and 19°–69° W at temperatures of 55°–80°, and by Schröder (1906) from the Indian Ocean south of Ceylon.

7. **Gonyaulax scrippsae** sp. nov.

Diagnosis: A small very rotund species with small apical horn, much displaced girdle, surface with fine striations principally in the longitudinal direction.

Description: *Body* subspheroidal, its length 1.12–1.15 transdiameters. Dorso-ventral diameter equal to transdiameter. *Epitheca* subhemispherical, contracted abruptly at the apex to a short apical horn whose altitude and diameter are each less than a girdle width, with an oblique apex tilted toward the ventral face. Its greatest altitude is 0.6 to 0.7 transdiameters. Its sides are regularly convex without trace of angulation at the shoulders. The *hypotheca* is nearly hemispherical, its greatest altitude is about 0.6 transdiameter. There is no angulation at the antapex.

The *girdle* is equatorial, descending, displaced 2 to 3 girdle widths with an overhang of 0.1 to 1 girdle width. The *furrow* is deeply indented with marginal ridges scarcely elevated above the body contour and without lists. The *ventral area* or longitudinal furrow is sigmoid, rather narrow. The ventral area makes a shallow rounded indentation into the epitheca, is compressed almost to closure in its oblique course between the girdle ends and widens beyond the girdle to 1.4 girdle widths. Its posterior end is rounded and barely indents the antapical plate.

The *plate formula* is *3′, 0ª, 6″, 6, 6‴, 1ᵖ, 1⁗*. *Apical 1′* is a slender plate expanded toward the apex at the apical-precingular suture and bears at the apex the elliptical closing platelet (*cl. pl.*, pl. 13 fig. 27). Apical *3′* bears the ventral pore (*v. po.*) very near the apex. *Precingular 6″* is triangular and postcingular *1‴* almost linear in form. *Posterior intercalary 1ᵖ* is a relatively small plate in this species. The plates of the *ventral area* in the intermediate region are obscured in the narrow furrow. The anterior plate (*ant. pl.*) is partially crossed by the anterior girdle ridge and notched in its left ventral edge by the flagellar pore (*fl. po.*). There are suggestions of several intermediate plates (*int. pl.*) and a well-defined posterior plate (*post. pl.*) some distance behind the distal end of the girdle.

The *surface* is very characteristically marked with fine subparallel lines which are mainly longitudinal but in some places are parallel to the intercalary bands which are formed in all specimens I have seen along the sutures. In cases of lightly marked specimens these lines are regularly punctate (pl. 13, figs. 26, 27). In other cases the markings are more of the vermiculate-reticulate type of heavier pattern though still of delicate tracery and with more of a mesh work developed, especially distally and on the hypotheca (pl. 16, fig. 38). Pores are not evident except two marginal rows of minute ones just within the girdle ridges. Sutures are very faint, marked by intercalary bands. No lists or fins have been seen though in some cases two minute spinules (pl. 16, fig. 38) appear on the antapex at junction points of the ventral area and antapical plate. The girdle is abundantly marked by numerous parallel ribs which connect the pores on its two sides.

Dimensions: Length, 29 to 39μ; transdiameter, 27 to 34μ; dorsoventral diameter the same; width of girdle, 4 to 5μ.

Variation: Varies in surface markings and in girdle displacement and overhang as above stated.

Comparisons: Its small size and peculiar markings combined with its considerable displacement serve adequately to characterize this species. It might be easily confused when full of contents with *G. spinifera*, in young stages with small spines, but is more rotund with characteristic surface markings. It is also somewhat similar to *G. turbynei* but has greater displacement of the girdle and much finer markings.

Distribution: Found thus far mainly as empty thecae in neritic summer plankton at San Pedro and San Diego, California.

Named for Miss Ellen B. Scripps whose interest in marine biology has made possible the foundation of the San Diego Marine Biological Station.

8. **Gonyaulax polygramma** Stein

Pl. 10, figs. 6, 7; pl. 17, fig. 47

Protoperidinium pyrophorum Pouchet (1883), p. 433, pl. 18/19, fig. 15. In explanation of plates (p. 455) as *P. prophorum*. This is not *Peridinium pyrophorum* (also as *Peridinium ?* (*Glenodinium ?*) *pyrophorum* in explanation of plates) of Ehrenberg (1836), p. 133, pl. 1, fig. 1, iv; (1854), p. 17, pl. 37, vii, figs. 3, 4.

Gonyaulax polygramma Stein (1883), pl. 4, fig. 15. It is possible that figs. 16 and 17 (= *G. polygramma* var. Stein = *G. steini* Lemmermann 1907) represent another and indeterminable species.

G. polygramma Stein var. Schütt (1895), fig. 33 $_{1-3}$.

G. polygramma Stein var. Schütt (1895), fig. 33 $_{1-3}$.

G. polygramma, Delage et Hérouard (1896), p. 383, fig. 662.

Peridinium pyrophorum, Lemmermann (1889), p. 369. "Ob zu *Gonyaulax* gehörend!"

Gonyaulax Schuettii Lemmermann (1899), p. 367, based on Schütt (1895), pl. 8, fig. 33.

G. polygramma, Entz (1905), pp. 110, 138–142, figs. 58–59; (1907), pp. 11–22, pl. 3, figs. 1–3, 5–6; (1909), pp. 247–260, pls. 9, figs. 1–3, 5–6.

G. polygramma, Paulsen (1907), pp. 7–8, fig. 7; (1908), pp. 28–29, fig. 36.

G. polygramma, Okamura (1907), p. 132, pl. 13, figs. 13a–d.

Diagnosis: A medium-sized species of slightly elongated form, symmetrically rounded hypotheca, girdle displaced posteriorly a little more than its width, narrow ventral apical, spread-

ing longitudinal furrow, usually with two or more short unequal antapical spines, rarely but one or none; theca with three apicals and no intercalary and ten to fifteen longitudinal striae.

Description: *Body* elongated, its length 1.5 to 2 transdiameters, subcircular in cross-section at the girdle, flattened ventrally. Epitheca exceeds hypotheca. *Epitheca* subconical, broadly angled at apical-precingular suture, its altitude 0.6 to 0.95 transdiameters, contracted to a stout apical horn one girdle width across and one to two in height. *Hypotheca* broadly and symmetrically rounded, its altitude 0.5–0.6 transdiameters. *Girdle* postmedian, descending, displaced distally 0.1 to 1.5, or even 2, girdle widths, with very little overhang if any; furrow deeply impressed with stout ridges, rarely with very low lists. *Ventral area* on longitudinal furrow widening on the right distally to 2 girdle widths, very narrow between girdle ends. The anterior plate (*ant. pl.*, pl. 10, fig. 7) of the ventral area indents the epitheca somewhat more than a girdle width, and is squarely truncate anteriorly.

The *plate formula* is *3′*, *0ᵃ*, *6″*, *6*, *6‴*, *1ᵖ*, *1⁗*. The ventral *apical, 1′*, is slender, widening posteriorly on the left, slightly excavated. It is attached to the elliptical closing platelet (*cl. pl.*, pl. 10, fig. 7), which contains an elongated hyaline area. Apicals *2′* and *3′* are wide plates, the anterior dorsal angle of *2′* being continued in a small point to the right (pl. 10, fig. 6). The upper end of apical *3′* sometimes has a small pore-free area set off from the rest of the plate by a well-marked oblique curved rib, as in *G. spinifera*. The area thus enclosed corresponds in position and relationships to a larger area in *G. areolata* and to the small separable apical plate in *G. diegensis*. It is not in our experience, separable in *G. polygramma*. It might be regarded as an incipient plate, the separation of which in *G. polyedra* and *G. diegensis* is fully realized. There is no ventral notch, but the ventral pore (*v. po.*) can usually be found on the median margin of *3′* a short distance above the apical-precingular suture. It is sometimes a mere notch in the margin of the plate. *Precingular 6″* is quadrangular, its anterior face being nearly two girdle widths across. *Postcingular 1‴* is very narrow, overhanging the furrow. The *posterior intercalary* is very large, two girdle widths across, and the *antapical 1⁗* relatively small, and indented by the rounded end of the *ventral area*. This area has its anterior plate (*ant. pl.*) deeply notched for the flagellar pore and its posterior plate broadly rounded posteriorly. Between the two the four or five narrow subdivisions of the intermediate plate (*int. pl.*, pl. 10, fig. 7) can be made out in some specimens.

The *surface* of the theca is very characteristically marked by a series of 10–15 linear ridges with subparallel longitudinal arrangement, continued from one plate through the next and across the girdle from epitheca into hypotheca with more or less continuity. The ventral area and the posterior intercalary plate are not thus marked. Lemmermann's (1907) statement that in his *G. steini* (=*G. polygramma* var. Stein) "Zwischenplatten zahlreich" is doubtless based upon a misconception of the relation of these striae to suture lines. The intermediate

regions between the striae are freely areolated or sometimes reticulated, with scattered pores with a tendency to linear grouping along the ribs. The ribs lie on suture lines in some cases, but several ribs may appear on one plate. The ventral area is sparingly porulate. The girdle ridges may be faintly armed with lists, and low denticulate lists may guard the longitudinal furrow. At its posterior end the denticulations become finned antapical spines sometimes 1.5 girdle widths in length and 1–3 in number. There is often none, and the single one or the largest where several are present is at the left. The suture lines are sometimes marked by narrow intercalary bands.

Contents dense, chromatophores crowded, yellowish to dark brown, elliptical or sausage-shaped, sometimes linear and radiating from the center of the cell mass. The theca is frequently opened by parting of the apical plates and the contents escape in a membranous envelope which is soon differentiated into a new theca. In this stage it is faintly and abundantly striate longitudinally and has been designated by Lemmermann (1899) as *G. schuetti* on the basis of Schütt's (1895) figures.

Dimensions: Length, 42–75μ; transdiameter, 38–48μ; length of longest antapical spine, 2–8μ; width of girdle, 4–5μ.

Variation: This widely distributed species varies toward both *G. turbynei*, the next smaller member of the series, and toward *G. kofoidi* and *G. pacifica*, the larger ones. This variation is expressed in a shorter or longer apical region, in suppression or extension of the antapical spines, and in increasing development of the left antapical spine. There is also great variation in the development of surface markings. In highly striated forms the number of major lines seems to be fairly constant and in the main the species is one of the most easily recognized ones in the genus.

Synonomy: Originally described by Stein (1883) from the Atlantic and Pacific. Prior to the appearance of Stein's paper (November, 1883), Pouchet (July–August, 1883) published a figure of a *Gonyaulax* which is undoubtedly *G. polygramma* under the name of *Protoperidinium pyrophorum* and indicated in his discussion that it was provisionally regarded as identical with Ehrenberg's (1836) fossil *Peridinium* (?) *Glenodinium* (?) *pyrophorum*. It is, however, wholly different and Stein's name becomes applicable. Lemmermann's (1899) designation, as a distinct species, of the thin-shelled sutureless forms following ecdysis figured by Schütt (1895), should be dismissed, but his later (1907) designation of Stein's figures 16 and 17 as *G. steini*

on the ground of the difference in proportions and antapex should be accepted in so far as the removal of the two figures from the species *polygramma* is concerned. Stein's two figures are, however, so drawn that no one has ever recognized this "Varietät" in material. Lemmermann's (1907) statement that *G. steini* is from the "Pacific" is not verifiable in Stein's work. The figures are oblique views, lack critical details and are not diagnostic. This "variety" possibly represents extreme variants either of *G. polygramma* or *G. kofoidi* and it is impossible to determine which. It should be relegated along with Lemmermann's name to the category of indeterminate species. His recognition of Pouchet's *Protoperidinium pyrophorum* as a valid species of *Peridinium* may also be dismissed as a synonym of *Gonyaulax polygramma*.

Comparisons: This common species and *G. turbynei* are at once distinguished from all others except *kofoidi* and *pacifica* by their linear markings. From *G. turbynei* it is distinguished by its better developed apical horn, and presence of antapical spines. The three species with antapical spines may be distinguished readily by the following complexes of characters:

Comparisons of Species

Species	*polygramma*	*kofoidi*	*pacifica*
Length	42–75μ	77–110μ	106–179μ
Axial ratio	1.25–1.5	1.5–2	1.5–1.75
Girdle section	Circular	Circular	Obliquely reniform
Antapex	Symmetrically rounded	Obliquely asymmetrical	Asymmetrically rounded
Width of posterior intercalary in transdiameters	0.22	0.148	0.08

It is also more pronounced in its linear markings and generally more rugose than these other species.

Stein's (1883) figure 15 is somewhat more angular and has a less sloping epitheca than is usually found in the species, while that of Delage and Hérouard (1896) constructed after Schütt has certain obvious defects. Paulsen's (1907–1908) figure is evidently from a tilted specimen and does not show the typical linear markings in full.

Distribution: This species occurs in the coastal and oceanic plankton of the San Diego region, but never in numbers. Its

periods of greatest relative abundance appear to coincide with that of the plankton of semi-tropical facies in November-January. It is also sparingly present in June–September, especially at times of outbreaks of red water.

Judging from the reported occurrences of this species it is generally rare but widely distributed in tropical waters. It is reported from the Atlantic by Murray and Whitting (1899), and found occasionally, according to Cleve (1901a) as far north as 60° N. It is also reported by Cleve (1901b), and by Karsten (1907) from the Indian Ocean, by Schröder (1900) from Naples, by Entz (1902) from the Adriatic, by Ostenfeld and Schmidt (1901) from the Red Sea, and by Schmidt (1901) from the Gulf of Siam, by Nishikawa (1901) and Okamura (1907) from Japanese waters, and by Zacharias (1906) from the South Pacific off Antofagasta, Chili.

9. **Gonyaulax kofoidi** Pavillard

Pl. 14, fig. 30

Gonyaulax kofoidi Pavillard (1909), p. 278, fig. 1.

G. globosa Stüwe (1909), p. 275, pl. 2, fig. 7. Doubtfully assigned here.

Diagnosis: A large species with elongated body, tapering apical horn, asymmetrical antapex and prominent left antapical spine, with coarsely porulate longitudinally striate surface.

Description: Body elongated, length, excluding spine, 1.65 transdiameters, girdle section subcircular, flattened ventrally. *Epitheca* exceeds hypotheca its altitude 0.9 to 1.1 transdiameter, conical, with slight angulation on left shoulder, and abruptly changing to a tapering apical horn 0.4 to 0.5 transdiameter in length, 2 to 2.5 girdle widths wide at the base and 1.5 at the truncate apex. *Hypotheca* with nearly straight sides and obliquely truncate antapex. The oblique postmargin is 0.3 transdiameter in length; altitude of hypotheca 0.75 transdiameter.

Girdle descending, displaced distally 2 to 2.25 girdle widths, its ends lacking at least 0.5 of a girdle width of completing the circuit. Both proximal and distal ends curve posteriorly. It is deeply impressed, with salient heavy ridges of thecal wall. The anterior plate of the *ventral area* (pl. 14, fig. 30) indents the epitheca for 1.5 girdle widths, ending in an obliquely truncate margin. The region of the intermediate plates is almost completely buried between the girdle ends. The ventral area curves to the right and in its distal half flares widely, mainly to the right to 3 girdle widths, the wide porulate posterior plate reaching the postmargin. It is guarded on the right side anterior to the distal end of the girdle and on the left, posterior to its proximal end, by a hyaline fin or list, passing posteriorly to the base of the single antapical spine.

The *plate formula* is *3′*, *0ᵃ*, *6″*, *6*, *6‴*, *1ᵖ*, *1⁗*. *Apical 1′* is a slender ribbon-like plate bearing the elliptical closing platelet at its apex and passing posteriorly to junction with the oblique margin of the anterior plate of the ventral area, thus parting precingulars *1″* and *6″*. Apical *2′* bears an apical lobe to the right resting in a terminal excavation in apical *3′*, which bears near its posterior end on the median margin the circular ventral pore. *Precingular 6″* is quadrangular. *Postcingular 1″* is minute, 1 girdle width wide and 2 in length, and *posterior intercalary 1ᵖ* is a large plate 2 to 3 girdle widths wide and 0.5 to 0.6 transdiameter in length. *Antapical 1⁗* is wholly exposed on the dorsal face.

The *surface* is coarsely, regularly and heavily porulate and sparingly marked with heavy longitudinal striae, about seven in dorsal view on the precingular plates and a like number on the postcingular, and four on the apicals. In ventral view the striae are less regular. There are seven on the hypotheca and five or six on the epitheca. The girdle bears two rows of marginal pores and is crossed by irregular striae. The antapical spine is 1.5 to 2 girdle widths in length, finned on both sides and bears a basal reticulation.

Dimensions: Length, excluding spine, 100 to 110μ; transdiameter, 62 to 65μ; dorso-ventral diameter about the same; length of antapical spine, 8 to 10μ.

Variation: Varies in extension of apical horn, length of apical spine, obliquity of postmargin, and development of fins, and prominence of the pores.

Synonomy: About the same time that Pavillard (1909) described *G. kofoidi* Stüwe (1909) published a brief diagnosis and a simple figure of a form he calls *G. globosa*. In his description he distinctly specifies an absence of parallel markings. These characterize *G. kofoidi*. In size, however, it approaches *G. kofoidi*, and in outline in ventral view *G. pacifica*, but is much smaller than the latter and has a conical instead of a flattened epitheca and thus approaches *G. kofoidi*. It occurred in several collections in the North Atlantic. It is possible that it is only a smooth form of *G. kofoidi*, and if so, it falls into the synonomy of that species. Stüwe's figures and descriptions are not sufficiently diagnostic to be of much assistance. It has not been possible as yet to determine the exact dates of publication of Pavillard's and Stüwe's papers and thus settle the matter of priority. I provisionally adopt Pavillard's name, as certainly applying to the species here described, and probably having priority.

Comparisons: See *G. polygramma* (p. 229). Distinguished readily from *G. polygramma* by its larger size, greater antapical asymmetry and elongation of apical region; from *G. pacifica* by its smaller size, greater rotundity at girdle and oblique antapex.

Distribution: Taken at San Diego, November 12, 1904, in surface plankton seven miles WNW of Point Loma. This collection contained also *G. pacifica*, *Ceratium trichoceros* and *Ceratocorys armatum*, all tropical species. Reported by Pavillard (1909) in the winter plankton of the Gulf of Lyons.

10. **Gonyaulax pacifica** Kofoid

Pl. 15, fig. 35

Gonyaulax pacifica Kofoid (1907), p. 308, pl. 30, figs. 37–39.
Steiniella cornuta Karsten (1907), pp. 348, 420, pl. 53, fig. 7.

Diagnosis: An exceedingly large species, resembling *G. polygramma* Stein, asymmetrically flattened and excavated on the ventral face, in ventral view more rounded especially on post margin than in *G. kofoidi* Pavillard, linear markings less regular and usually less developed than in *G. polygramma*, posterior intercalary very narrow, its length five to seven times its width. Proximal end of girdle curved posteriorly.

Description: The largest known species of the genus, its outline varying greatly with the point of view. Seen in ventral view the body resembles *G. polygramma* and *G. kofoidi* but is usually more rotund posteriorly, the sides of both epitheca and hypotheca being convex, with some contraction near the apex. Occasional specimens have straight or concave or even slightly angled slopes of the epitheca. The striking feature of the species is the broad, deep asymmetrical excavation of the ventral face, principally upon its right side, which extends posteriorly to the thin postmargin giving almost the shape of a scoop to deeply excavated individuals and an asymmetrically reinform cross-section at the girdle, as well as a much modified lateral profile. Because of this asymmetry it is rather difficult to get strictly ventral or lateral views of the theca, our figure (pl. 15, fig. 35) giving an obliquely ventral view with greater exposure of the left face. *G. polygramma* and *G. kofoidi* approach more nearly to a circular cross-section at the girdle. In this species the dorso-ventral diameter is from 0.6 to 0.75 of the transdiameter.

The length, excluding spine, is 1.6 to 2 transdiameters (used in this description for the greatest diameter at the girdle which is somewhat oblique to the true transdiameter). The *epitheca* is contracted distally to a short, scarcely differentiated apical horn about two girdle widths in length and obliquely truncated. It is deeply and abruptly concave above the girdle on the ventral face. Its altitude is from 0.78 to 1.16

transdiameters. The *hypotheca* has, in ventral view, a broadly rounded postmargin whose even contour is interrupted by the asymmetry adjacent to the base of the antapical spine. In lateral view it is a rather abruptly contracted cone, especially on the ventral face. Its altitude is 0.6 to 0.8 transdiameters.

The *girdle* is postmedian, descending, displaced distally 1.5 to 3 girdle widths, with a sharply curved proximal end, far more than in either *G. polygramma* or *G. pacifica,* without overhang. Furrow relatively very narrow, its width 0.1 to 0.05 transdiameters, very deeply impressed and with projecting shelf-like ridges of thecal wall, which occasionally bear very low lists. The *ventral area* or longitudinal furrow somewhat obscured by asymmetrical ventral excavation in which it lies, is relatively wide, gradually spreading posteriorly to four girdle widths. The *ventral area* indents the epitheca with a slender extension of the anterior plate with oblique end, and posteriorly the wide posterior plate broadly invades the antapical plate. In some cases this end of the ventral area is at the postmargin of the body. In others it lies somewhat anterior to it so that the antapical plate is exposed in the ventral view as in our figure.

The *plate formula* is *3′, 0ª, 6″, 6, 6‴, 1ᵖ, 1⁗*. Ventral *apical 1′* is very slender and is attached at the apex to a closing platelet. Apical *2′* is asymmetrically extended in the apical region in an apical lobe which crowds in between the apex and the top of apical *3′*. There is no apical notch as in *Spiraulax jolliffei* and the small inconspicuous ventral pore is borne at the posterior corner of apical *3′*. *Precingular 6″* is quadrilateral its anterior margin being convex and about four girdle widths long. *Postcingular 1‴* is very small, and the *posterior intercalary* very long and narrow. The plates were not correctly interpreted in my earlier (1907) description. The *ventral area* consists of a narrow anterior plate against the lower half of which the furrow abuts, which is deeply notched posteriorly by the flagellar pore. The large posterior plate has a broadly rounded postmargin. Between these two plates there are at least three plainly marked off intermediate plates, the anterior one of which is notched by the flagellar pore.

The *surface* is marked by striae which follow longitudinal suture lines and occasionally transverse ones also, in bands of one to four closely set parallel elements. They are better developed on the pre- and postcingular plates, are often incomplete and show a tendency to follow lines of pores. Intercalary bands of varying width may follow the main suture lines. The wall is generally rather thin and hyaline with minute, sparsely distributed pores in rather vague lines. We have not seen coarsely or heavily reticulated individuals, though faint reticulations are sometimes present (pl. 15, fig. 35). The furrow is often heavily ribbed. There are sometimes very low hyaline girdle lists and low denticulate lists with abundant spinules arise from the sutures between the posterior intercalary *1ᵖ* and the ventral area, and between the latter and the antapical. The solid antapical spine is relatively short, from 1 to 3 girdle widths in length. It is tapering, sometimes finned on both sides and arises from the left angle of the antapical plate.

Dimensions: Length, excluding spine, 148 to 167μ; greatest diameter, 72 to 88μ; dorso-ventral (oblique), 53 to 76μ; length of antapical, 4 to 18μ; width of furrow, 5 to 8μ.

Variation: An exceedingly variable species in size, shape of epitheca, development of surface markings, especially in number and extent of longitudinal striae, width of intercalary bands, and finer surface markings. This added to the change in outline and proportions with change in orientation, and an adequate description becomes exceedingly difficult.

Synonomy: Karsten (1907, December), has described as *Steiniella cornuta* an organism which exhibits the form, proportions, linear markings, and ventral excavation characteristic of this species (Kofoid, 1907, April 11, 13).

Comparisons: See *G. polygramma* (p. 229). The earlier figures (see Kofoid, 1907b, pl. 30, figs. 37–39) of this species are of a more rugose specimen which, owing to escape of contents, is somewhat collapsed and it therefore fails adequately to show the typical rotundity of this species, or its usual delicacy of surface markings. It varies towards *G. kofoidi* Pavillard, but is separable by the proximal curvature of the girdle, the ventral excavation and the more rounded antapical outline. It is not in our experience merely an accumulation of extreme variants of the *polygramma-kofoidi* series, but a well-established species with relatively few individuals which exhibit intergradations.

Distribution: Sparingly present in the autumn (October to January) in oceanic plankton of semitropical facies. Associated with *Ceratium reticulatum*, *C. trichoceros* and *Ornithocercus magnificus*. Reported by Pavillard (1909) in the winter plankton of the Gulf of Lyons, where it has its maximum in January. Reported also by Karsten (1907) as *Steiniella cornuta*, from the Indian Ocean, 9° 6′ N, 53° 41′ E in catch from 200 m.

d). The *Polyedra* Group

Characterized by polyhedral form, with angled sutures, rugose surface, without longitudinal striae. No apical horn. Plate formula *4′*, *2ª*, (or *5′*, *0ª*), *6″*, *6*, *6‴*, *1ᵖ*, *1⁗*.

Here belong *Gonyaulax polyedra* Stein and *G. milneri* (Murray and Whitting) Kofoid, originally described by Murray and

Whitting (1899) as *Goniodoma milneri*. It has, however, a plate formula identical with that of *Gonyaulax polyedra* and does not exhibit the three antapicals characteristic of the genus *Goniodoma*. *Gonyaulax ceratocoroides* is closely related in plating to this group, but because of its peculiar antapical spines is placed in the subgenus *Acanthogonyaulax*.

11. **Gonyaulax polyedra** Stein

Pl. 12, figs. 16–20; pl. 14, figs. 28, 29, 31; pl. 17, fig. 43.

Blepharocysta splendor maris Ehrenberg (1873), in part, pp. 3–4 (of reprint), pl. 1, figs. 11, 12 only.

Gonyaulax polyedra Stein (1883), p. 13, pl. 4, figs. 7–9.

G. polyedra Bütschli (1885a), p. 545, pl. 26, figs. 20, 21; (1885b), pp. 932–933, 950–953, 1020, pl. 52, figs. 3a, b.

G. polyedra, Schütt (1896), p. 21, fig. 29.

Gonyaulax sp., Torrey (1902), pp. 187–192, figs. 1–3.

G. polyedra, Okamura (1907), p. 132, pl. 5, figs. 35a–c (= *Goniodoma acuminatum* Stein).

G. polyedra, Paulsen (1907), pp. 7–8, fig. 5; (1908), pp. 28, 31, 33, fig. 40.

Diagnosis: A small, angular, polyhedral species, with ridges along sutures, equatorial girdle displaced 1–2 girdle widths, regularly pitted, rugose surface, four apical and two intercalary plates, the right apical *4′* minute.

Description: *Body* polyhedral, subconical anteriorly, truncated posteriorly, its length 1.15 transdiameters, the ventral face scarcely excavated. The *epitheca* has both shoulders angled at the apical-precingular suture; its greatest altitude is about 0.6 transdiameters. There is no distinct apical horn. The *hypotheca* is more angular, sides straight or nearly so, contracted regularly to a broadly truncated antapex 0.4 transdiameter in width, its greatest altitude almost 0.5 transdiameter. The girdle section is nearly circular.

The *girdle* is nearly equatorial descending, displaced distally 1 to 2 girdle widths, without overhang, and in some cases even parted 0.5 girdle width, deeply impressed, guarded by low ridges with coarsely and abundantly ribbed lists. Its ends are sometimes slightly curved posteriorly in some individuals.

The *ventral area* or longitudinal furrow is broad, not deeply excavated, widening posteriorly to 1.5 girdle widths, its rounded posterior margin slightly indenting the antapex. It is nearly straight.

The *plate formula* is *4′*, *2ᵃ*, *6″*, *6*, *6‴*, *1ᵖ*, *1⁗*. The formula here given for the *apical* region differs from that given by Bütschli (1885a, 1885b), Torrey (1902), and Paulsen (1907, 1908), in that here as in other species of *Gonyaulax* and Peridinidae generally we designate as apicals (see Kofoid 1909b) only those plates which reach the apex and as inter-

calaries those between these plates and the precingulars; and also in the fact that two additional plates are here defined for the apical region for the first time. A minute but perfectly distinct plate, *4p*, lies between the two intercalaries, *1a*, *2a*, and the apex. This plate appears in the figures of Bütschli (1885b) and Torrey (1902) but is not treated as a separate plate by them. When the structure of the apical region of *G. polyedra* is considered in the light of that of other species of the genus, the homologies of the parts are clearly as follows: the so-called anterior extension of the longitudinal furrow is a ventral apical *1'*, homologous with the diamond-shaped plate of *Peridinium*. The *intercalary* region of the right shoulder contains two plates instead of one as in *Spiraulax jolliffei*. *Gonyaulax sphaeroidea* and *G. apiculata*, the adjacent apical region is greatly reduced in size and the territory which is occupied by apical *3'* in such species as *G. polygramma*, a typical *Gonyaulax* with three apicals, is subdivided into two plates, one of which, *3'*, on the right dorsal shoulder is of some size while the other, *4'*, is the minute plate in question. It is quite probable that the extra intercalary, *1a*, adjacent to apical *4'* has been split off from its lower edge and also belongs in the territory of apical *3'* of several species of the *polygramma* and *spinifera* groups, where its presence is suggested by the surface markings indicative of an incipient suture. The position and relations of the two large plates on the right shoulder are those of the intercalaries and the small plate is plainly one of the apical series. The disposition of the plates here proposed enables us to homologize the plates of the apical region of *polyedra* with those of other species of the genus.

There is some variation in size of apical *4'* (compare plate 14, figure 28, and plate 12, figure 20), which gives rise to certain modifications of the relations of the plates to the elliptical apical area which contains the closing platelet (*cl. pl.*, pl. 12, fig. 20). Ordinarily the plate designated as anterior intercalary *2a* does not come into contact with this apical region (pl. 12, figs. 18 and 20). In one case (pl. 14, fig. 29) of a reduced apical *4'* this intercalary impinges upon the apical region.

In another instance a third right dorsal anterior intercalary plate (*x*, pl. 14, fig. 28) appears as an extra plate which seems to have developed at the expense of the equatorial ends of apical *3'* and intercalary *1a*. This is the only instance thus far detected in any species of the genus *Gonyaulax* of a variation in the number of plates. The genus exhibits a noteworthy rigidity in this respect.

Apical 1' is much wider than figured by Stein (1883) and is somewhat irregular in outline, widening at the apical-intercalary suture (pl. 12, fig. 20). An apical notch has not been found but the ventral pore (*v. po.*) in the right margin of apical *1'* opposite the middle of intercalary *2a* was noted. At its apical end plate *1'* appears to include the region designated in other species as the closing platelet (*cl. pl.*, pl. 12, fig. 20). It contains a minute hyaline oblong area. Apical *2'* is large, covering the left apex. *Precingulars 1"* and *6"* are parted by the ventral area and apical *1'* which are joined in the midventral line. *Precingular 6"* is pentagonal. *Postcingular 1"'* is a very slender plate at the edge of the ventral area and has been overlooked in all previous accounts of the species. The

posterior intercalary, 1p, is a rather large quadrangular plate and the *antapical 1""*, a subregular pentagonal plate indented at the midventral angle by the rounded margin of the ventral area (pl. 12, fig. 19).

The *ventral area* (pl. 17, fig. 43) indents the epitheca for half a girdle width, the anterior plate being squarely truncate anteriorly and deeply notched posteriorly by the flagellar pore (*fl. po.*). The posterior plate is exceptionally large, extending anteriorly well toward the distal end of the girdle. Three intermediate plates in addition to the hyaline scale of the pore region have been isolated.

The *surface* is uniformly but not closely porulate with rather large pores about which on a high focus a coarse reticulation may be seen. In some cases the reticulum is finer than the porulation and some meshes have no pores (pl. 14, fig. 31). In some cases no reticulum is visible or merely a faint areolation. A regular line of pores follows each margin of the girdle plates and in reticulate thecae the reticulum between these resembles a columnar arcade. The ventral area in young specimens (pl. 17, fig. 43) is also porulate in its peripheral parts only. On the whole, the large size of the pores and feebly developed reticulum gives the impression of a porulate rather than a reticulate type of theca in this species. There are no free spines or lists other than those about the girdle, which are low with stout denticulations rising from the basal ridge. The theca of this species is rather fragile and is easily and quickly shed, in fact ecdysis seems to be normal and frequent, judging by the number of empty thecae and isolated plates found in the plankton wherever the species is abundant. It also occurs very frequently in crowded or moribund plankton collections. A thin pellicle surrounds the cell body within the theca, the apical and precingular plates spread apart along the longitudinal sutures, especially those in the sagittal plane, and the *Gymnodinium*-like cell body escapes and presumably its thin pellicle is differentiated into a new theca.

The *cell contents* are very dark orange-brown and the chromatophores are densely packed together. When present in great numbers, as they often are, they give the sea a reddish color, and cause magnificent displays of phosphorescence at night. Oil droplets abound in the cytoplasm and it gives off a rank odor upon decay.

Dimensions: Length, 50 (43 to 54)μ; transdiameter, 45.6 (37 to 53)μ; dorso-ventral diameter about the same; width of girdle, 4 to 5μ. Ten individuals measured.

Variation: There is considerable variation in size, in angularity, in porulation, development of reticulum and girdle lists. The displacement of the girdle varies from one to nearly two girdle widths. The adjustment of apical plates to each other also exhibits some irregularities in the lengths of the different lines. Apical *4'* varies considerably in size and one instance of three anterior intercalaries has been recorded (pl. 14, fig. 28).

Comparisons: *Gonyaulax polyedra* is quite distinct from all other species of the genus except *G. milneri*, in the character of its apical plates and in the presence of two anterior intercalaries. The absence of linear markings and the four apical plates distinguish it at once from *G. polygramma*, its common associate in subtropical waters, and the absence of antapical spines and shorter, more angular epitheca, as well as four apicals, mark it off from the *G. spinifera* group, with species of which it is often found. The other species (*ceratocoroides*, *milneri*), with four or more apicals, either have no anterior intercalary, or at the most but one.

Synonomy: This species is so well marked that it has rarely been confused with others. Okamura's (1907) figure assigned to this species is *Goniodoma acuminatum* Stein.

Ehrenberg (1859) described as *Peridinium splendor maris*, a highly phosphorescent dinoflagellate from the plankton in August at Naples and later (1873, pl. 1, figs. 7–18) figured it, and in the explanation of the plate suggested the new generic name *Blepharocysta* for this organism. The description and the figures in both cases are entirely inadequate for certain reidentification. Stein (1883) admirably figures an organism which he assigns to Ehrenberg's "*Blepharocysta splendor maris* (z. Theil)" noting particularly in his brief text "Ehrenberg warf damit noch andere unklare Formen zusammen." Stein does not, however, state which of the several forms figured by Ehrenberg he regards as the part of the agglomeration equivalent to *B. splendor maris*. Jörgensen (1899) criticizes Stein's procedure on the ground that Ehrenberg's figures show an impressed girdle while the *B. splendor maris* of Stein's figures entirely lacks impression of the girdle into the contour of the body. He further notes the fact that two of Ehrenberg's figures (figs. 11 and 12) evidently belong to *Gonyaulax polyedra*, to which I agree. However, I see no ground, beyond the *statement* in the original description and in the explanation of Ehrenberg's plate that there are three end plates in each half of the theca, for accepting Jörgensen's suggestion that Ehrenberg's figures 7 to 10 are possibly referable to *Goniodoma acuminatum* Stein. No one of these figures *shows*

the angular body, or three "Endplatten" characteristic of the genus *Goniodoma*. Jörgensen seems to have overlooked the fact that Stein assigns only a part of Ehrenberg's complex to his emended *Blepharocysta splendor maris*. While Ehrenberg's figures 11 and 12 are in all probability *Gonyaulax polyedra*, the other figures are unmistakably not *Goniodoma* and might better be crudely drawn *Blepharocysta* than *Gonyaulax polyedra*. It seems best, therefore, in the absence of any valid criterion for determining what Ehrenberg actually had, to accept *Blepharocysta splendor maris* Ehrbg. in part (figs. 11, 12) as a synonym of *Gonyaulax polyedra* and to allow Stein's emended *Blepharocysta splendor maris* to stand for the well-figured organism to which he attached the name proposed by Ehrenberg, and therefore to leave the name also attached to the plainly unrecognizable figures 7–10, 15–18, of Ehrenberg's original delineation of the species.

Distribution: Very abundant in the San Diego region in the summer plankton, July–September, when it causes local outbreaks of "red water" which extend along the coast of Southern and Lower California. The northern limit of the region of excessive abundance is approximately Santa Barbara and the southern one is at present unknown, though inadequate data (Darwin, 1871, Streets, 1878), suggest at least local outbreaks along South American coasts and in the Gulf of California. Torrey (1902) records reports of an outbreak off Tomales Bay, north of San Francisco, about forty years ago.

The seaward extension of the discolored areas is quite irregular, ranging from one-half to three miles. The local distribution within the "red water" itself, as seen from the mast head or from Mt. Soledad (elevation 822 feet), near La Jolla, is exceedingly irregular, areas of deeply discolored water of varying size and intensity being interspersed with areas of clearer water. In the early part of August, 1907, with the University of California dredging party in the launch "Elsie," I ran by night from San Diego to San Pedro, a distance of about one hundred miles, through the discolored coastal zone. The depth of discoloration, the brightness of the phosphorescenee by night, varied greatly

at different points along the coast, being especially marked off La Jolla, Point San Juan, Newport, and San Pedro. This irregularity may be due to the configuration of the coast and of the bottom, especially to the sunken valleys which may serve as conduits for upwelling waters. It is quite possible that the local and periodical enrichment of coastal waters by the nitrogen-bearing waters from the depths along the coasts of California, is one of the primary causes for the occurrence of these outbreaks of "red water" and in part for the irregularities of their appearance and inequalities in their local distribution.

This species upon stimulation by the movement of the water as in the breakers along shore, or in the path of a moving fish, gives forth a brilliant greenish-blue flash of phosphorescence of an instant's duration, which bathes the breakers or white caps in a foam of fire, and outlines the path of fishes, seals and porpoises or the wake of a steamer with a luminous trail which lingers for some seconds, or even minutes, as the motion of the water dies down.

The decay of countless millions of these organisms in the water and upon the beaches where they are continually stranded by the receding waves, creates a nauseous and penetrating stench of most disagreeable nature. The products of decay (and metabolism ?) of these organisms are toxic to many marine organisms, which die in great numbers (see text figure E) and are cast up by the tide upon the beaches.

Not all organisms are equally affected (See Torrey, 1902), by these adverse conditions but mainly bottom forms which cannot retreat into places of safety, such as the holothurians, sipunculids and bottom-feeding fish, such as the sting ray (*Urolophus halleri*) and guitar fish (*Rhinobatis productus*) and littoral crustaceans, such as *Hippa analoga* and *Cancer antennarius*. The organisms of the plankton, both large and small, and the widely ranging fishes, seem not to be affected adversely, at least to a fatal degree. It is obvious that the bottom-dwelling forms would be overwhelmed by the accumulation upon the bottom in shallower waters of organic debris from the excessive development of the plankton of the "red water," principally *Gonyaulax poly-*

edra, and this localization of a region of fermentation is doubtless the immediate cause of the destruction of the large numbers of the representatives of the bottom fauna.

Fig. E. Shore at East San Pedro, California, in August, 1907, during an outbreak of red water, showing dead fishes and invertebrates stranded on the shore at low tide. Photograph by Professor W. R. Coe.

This species is the most abundant dinoflagellate of the San Diego region during summer months and is found in small numbers throughout the year in both oceanic and neritic plankton. It is found at least as far north as San Francisco along the coast of California.

It is widely distributed in temperate and subtropical waters of coastal regions, but apparently is not common in the more strictly oceanic plankton. The extensive records of Cleve (1901a, 1902) for the Atlantic do not contain this species, and it appears in the many collections of the International Commission for the Investigation of the Sea (see Ostenfeld, 1906, 1909) only

(unless it be as *Gonyaulax* sp.) from Danish waters where Aurivillus (1898), Cleve (1900b) and also Paulsen (1907) report it. Jörgensen (1899, 1905) reports it rare in Norwegian fiords and Ostenfeld (1899, 1900, 1903) from the neritic plankton at the Faeroes, in adjacent waters north of Scotland (60° N, and 4°–6° W) and in the North Atlantic at about 60° N, 31° W. Later Ostenfeld and Paulsen (1904) report other occurrences along the route of Danish steamers going to Greenland in the North Atlantic along the parallel of 60° N at 1°, 13° and 27° W, and in all cases as rare. Stein (1883), Bütschli (1885) and others have found it at Kiel, Schröder (1900) at Naples, Entz (1902) in the Adriatic at Quarnero, and Pavillard (1905) in the Gulf of Lyons, Whitelegge (1891) reports it at Port Jackson, Australia, during an outbreak of discolored water which he attributes mainly to *Glenodinium rubrum*, a new species which he describes from the red water. This form looks suspiciously like the contents of *Gonyaulax polyedra* after ecdysis. Okamura's (1907) record of this species from Japanese waters is to be rejected, since his figure is plainly that of *Goniodoma acuminatum*. Karsten (1906) reports it once in the Valdivia Collections from Station 55, 2° 36′ N, 3° 27′ E, in the Gulf of Guinea, in a locality which is perhaps within the reach of neritic influences.

The species exhibits as a whole marked preferences for a neritic distribution, with rare occurrences in territory invaded by oceanic currents which may carry occasional individuals away from neritic regions, as in the case of records in the North Atlantic and Gulf of Guinea. Both in local distribution and relative numbers it is remarkably erratic, varying, in seemingly similar regions where other cosmopolitan dinoflagellates occur with greater regularity and uniformity, from an entire absence of all records of occurrence up to overwhelming numbers, which completely mask the other dinoflagellates, and in fact all the microplankton and even exterminate the bottom fauna. The indications are that *Gonyaulax polyedra* is a species in a peculiarly susceptible physiological condition in which the reproductive and growth processes may be more than usually sensitive to stimulus by favorable conditions in the environment.

2. Subgenus **Fusigonyaulax** subgen. nov.

Sectio *Fusiformes*, Lemmermann (1907), p. 299.

Body elongated, fusiform, with centrally located well differentiated apical and antapical horns. Girdle not displaced more than 3 furrow widths. Usually three (rarely two or four) apicals and no (rarely one) anterior intercalary. Usually from tropical or warm temperate waters.

This subgenus may be divided for convenience in treatment into two groups, the *birostris* group with elongation exceeding two transdiameters, and the *acuta* group, with elongation less than two transdiameters and therefore containing the stouter, more robust members of the subgenus.

e). The *birostris* Group

Characterized by a length exceeding two transdiameters, an apical horn equaling or exceeding a transdiameter in length, and a finned central antapical spine of nearly equal length and by a subglobular or ellipsoidal midbody. Surface pitted or areolated.

This group contains *Gonyaulax birostris* Stein, *G. highleii* Murray and Whitting, and *G. glyptorhynchus* Murray and Whitting. This group of species is in need of careful revision, for it is desirable that distinctions between the species be more clearly defined.

Represented at San Diego by *G. birostris* Stein.

12. **Gonyaulax birostris** Stein

Gonyaulax birostris Stein (1883), pl. 4, fig. 20

Diagnosis: Body elongated fusiform, with abruptly swollen midbody, girdle displaced 1.5 furrow widths, apical precingular suture oblique. Apical *1′* very narrow. Antapical spine equaling transdiameter in length.

A single individual referable to this rare species was taken in surface collection (No. 679) made September 24, 1904, ten miles WNW of Point Loma. It was somewhat shorter than the specimen shown in Stein's (1883) figure and had the areola-

tions on the surface well developed. Neither drawing nor full description was obtained.

This species was described by Stein (1883) from the Pacific and has since been reported by Murray and Whitting (1899) from the temperate and tropical Atlantic between 4° and 42° N and 20° to 66° W; by Zacharias (1906) from the Gulf of Naples, by Entz (1907) from Quarnero, and by Karsten (1907) from the northwestern part (9° N, 54° E) of the Indian Ocean. It is apparently a rare oceanic species of the warmer seas.

3. Subgenus **Acanthogonyaulax** subgen. nov.

Represented by *Gonyaulax ceratocoroides* Kofoid, a tropical species described by Murray and Whitting as *Ceratocorys spinifera*. See Kofoid (1910). Not as yet found at San Diego, but to be expected in the winter plankton.

4. Subgenus **Steiniella** (Schütt) Kofoid

Steiniella Schütt (1895, p. 151, pl. 6, fig. 26; 1896, p. 19, fig. 26. Not *Steiniella* Bernard (Protococcaceae) (1908, p. 189).

Characterized by a laterally compressed apex which is carried over on to the dorsal face of the epitheca. Large rotund body with very fragile theca, often faintly marked with longitudinal vermiculations. Three or four apicals and no anterior intercalary. Ventral pore sometimes absent (?).

This subgenus falls into three groups of unequal content: the *fragilis* group, rotund, without constriction behind girdle, the *bispinosa* group, with marked constriction, containing *G. bispinosa* Kofoid and Michener, and the *mitra* group, greatly elongated and laterally compressed, containing *G. mitra* (Schütt) Kofoid. Only representatives of the first named group have as yet been discovered in the San Diego region.

g). The *Fragilis* Group

Characterized by rotund form of body, with no differentiated apical horn, no constriction immediately behind the girdle, and predominantly longitudinal markings.

Here belong *G. fragilis* (Schütt), *G. hyalina* Ostenfeld and Schmidt, and *G. alaskensis* sp. nov.

13. **Gonylaulax fragilis** (Schütt)

Pl. 15, figs. 33, 34, 36, 37; pl. 13, fig. 25.
Steiniella fragilis Schütt (1895), pl. 6, figs. 26_{1-14}.

Diagnosis: Length, 1.14 to 1.35 transdiameters. Epitheca conical, hypotheca asymmetrically rounded, girdle displaced 3 girdle widths. No spines.

Description: *Body* rotund, somewhat elongated, slightly flattened on ventral face. Epitheca and hypotheca subequal. *Epitheca* a low cone, 0.66 transdiameters in middorsal altitude, its sides slightly convex. No apical horn. Apical region extending a short distance on dorsal face. *Hypotheca* sac-like, its middorsal altitude 0.72 transdiameter, abruptly and asymmetrically rounded at antapex, the left side being a trifle the fuller. *Girdle* slightly premedian, descending, displaced distally 3 girdle widths, without overhang, proximal end curved posteriorly, furrow not deeply impressed, with scarcely any salient ridges and no lists. Ventral area indenting the epitheca scarcely a girdle width, widening posteriorly to the right and then to the left.

Plate formula 3′, 0^a, 6″, 6, 6‴, 1^p, 1⁗. *Apical 1′* slender, about 0.5 girdle width across, slightly sigmoid, with elongated closing platelet which extends upon the dorsal face at its anterior end. It joins the anterior plate of the ventral area posteriorly. Apicals *2′* and *3′* surround the apex in saddle fashion. *Precingular 6″* triangular. *Postcingular* 1‴ long and slender, expanding anteriorly less than a girdle width across. *Posterior intercalary* 1^p, two girdle widths across. *Antapical 1⁗* deeply indented by the posterior end of the ventral area. The *ventral area* is about 0.5 girdle width across between girdle ends, flaring asymmetrically posteriorly to at least 3 girdle widths and carried well under the antapex into the antapical plate, and usually without lists. The surface is nearly smooth, with feeble or more pronounced vermiculations running in short, sinuous longitudinal lines. They run posteriorly from the pores about which they take their origin. (See Schütt, 1895, pl. 6, fig. 26_2.) Often two originate from the same pore. Suture bands are finely areolated. The arrangement of surface markings, of pores and of chromatophores all give the organism an appearance of longitudinal striation. In some specimens the vermiculations coalesce (pl. 13, fig. 25) to form a semi-striate meshwork with pores at the nodes. *Chromatophores* ellipsoidal, irregular, or linear, in peripheral or radial arrangement, several large anteriorly located pusules and posteriorly located ellipsoidal nucleus.

Dimensions: Length, 82–105μ; transdiameter, 65–80μ; dorso-ventral diameter, 60–65μ; width of furrow, 5μ.

Variation: I have noted some variation in form of antapex, surface markings, and shape of ventral area, which is usually not so wide as figured by Schütt (1895).

Comparisons: Distinguished from *G. alaskensis* by its more elongated body, more linear markings and absence of antapical spines. From *G. hyalina* it differs in its less rotundity and less pronounced linear markings. In this species the length and transdiameter are about equal. From *G. inflata* it differs in its less expanded girdle region, less sloping hypotheca and smaller size.

Synonomy: Originally described by Schütt (1895) in his new genus *Steiniella*, but in all skeletal characters a typical *Gonyaulax*.

Distribution: Taken sparingly in the plankton of the inner harbor, at San Pedro, Calif. (No. 505), May 31, 1901; evidently carried in by tidal currents with the oceanic plankton from the outside.

Reported by Ostenfeld (1900) as very rare in Gulf Stream waters north of Scotland 59° N, 2°–9° W, and by Cleve (1901a) from the Atlantic 29°–47° N and 9°–23° W. Also by Schröder (1900) from Naples and by Entz (1902) from Quarnero on the Adriatic.

14. **Gonyaulax alaskensis** sp. nov.

Pl. 17, figs. 45, 46; pl. 14, fig. 32.

Diagnosis: A very large polyhedral species with much displaced (4 girdle widths) girdle, apex dorsally extended, coarse reticulations often of predominantly longitudinal elements with scattered pores at the nodes. Longitudinal furrow flaring widely at antapex; two short antapical spines. The ventral area reaches nearly half the distance from girdle towards apex.

Description: *Body* polyhedral with rounded angles, its length 1.05–1.12 transdiameters, nearly circular in equatorial cross-section with some flattening on ventral face of hypotheca. *Epitheca* approximately equal to hypotheca, low, conical, its greatest altitude 0.66 transdiameter, slightly angled at the apical-precingular sutures. No apical horn, apex small, elongated, extending dorsally beyond the summit, less than a girdle width across and 2.5 in length, sloping obliquely toward the ventral face. *Hypotheca* subhemispherical, its altitude 0.6 transdiameter with convex sides swelling at the girdle, contracted to a proportionally small antapex less than 0.3 transdiameter across, bearing two small, stout, widely separated spines.

The *girdle* is equatorial, descending with little (0.5 to 1.5 girdle widths) overhang, but relatively great displacement (4 girdle widths).

The two ends are both sometimes curved posteriorly and the distal end declines steadily in a long slope from the right side of the body. The furrow is relatively narrow, very deeply impressed with salient ridges bearing low, abundantly ribbed fins of 0.5 girdle width in height. The anterior plate (*ant. pl.*, pl. 14, fig. 32) of the ventral area indents the epitheca nearly half way to the apex. The *ventral area* or longitudinal furrow is much compressed laterally between the ends of the girdle where it makes an angle of 25° with the major axis. The salient right mid-ventral region with the distal end of the furrow crowds the furrow to the left and (pl. 17, fig. 45) overhangs it. Posteriorly it flares very abruptly to the right side to 3 girdle widths at the postmargin.

The *plate formula* is *3′*, *0ᵃ*, *6″*, *6*, *6‴*, *1ᵖ*, *1⁗*. *Apical 1′* is a short plate 0.2 transdiameters in length and 0.5 to 0.8 girdle width across bearing at its apex the elongated elliptical closing platelet (*cl. pl.*, pl. 14, fig. 32). Apical *3′* bears in its median margin less than a girdle width below the apex the conspicuous ventral pore (*v. po.*). *Precingular 6″* is quadrangular. *Postcingular 1‴* relatively broad, 1 to 2 girdle widths across; *posterior intercalary* very wide; *antapical 1⁗* rather widely and deeply invaded by posterior plate of ventral area. *Ventral area* with long, slender anterior plate (*ant. pl.*, pl. 14, fig. 32) nearly 3 girdle widths in length, partially crossed by the anterior girdle ridge, with a shallow notch at its postmargin for flagellar pore. Intermediate plates obscured. Posterior plate beginning about two girdle widths behind the distal end of girdle and flaring rapidly and principally to the right side, expanding from one girdle width anteriorly to three at the postmargin.

The *surface* is very characteristically marked with a light tracery of delicate meshwork made up predominantly of longitudinal or semi-detached vermiculate elements with which transverse or irregular bars form an incomplete mesh. In some specimens the mesh work is predominantly polygonal, especially on the hypotheca and near sutures. On others the longitudinal pattern predominates especially on pre- and postcingular plates and along suture lines (pl. 17, figs. 45, 46). The low fin on the girdle lists is very abundantly ribbed as are also the low fins on plates *1‴*, *6‴*, and *1ᵖ* which overhang the longitudinal furrow. The low fin between the two antapical spines is likewise minutely and abundantly ribbed. In fact the fins throughout are all low and abundantly ribbed, the distance between the thickenings in their substance corresponding remarkably well with the diameter of the polygonal meshwork upon the shell, suggesting the action of a similar physical factor determining both. The only fin showing an unusual development is the one on plate *1‴*. In most species of *Gonyaulax* no fin appears here or at the most it is a very low list. In this species it almost completely covers over the furrow. In one specimen (pl. 17, fig. 46) the girdle lists are lacking and there is no fin on the postmargin between the antapical spines. The two antapical spines are short (0.6 girdle width), stout, and finned on both sides, or entirely lacking fins.

The pores are sparingly distributed, in rows along sutures, in the girdle where the two rows are joined by vertical ribs as in *G. scrippsae*,

and in certain nodes of the meshwork on the plates. They are of small size and inconspicuous.

The *cell contents* are not dense. In addition to the ellipsoidal nucleus there is in some individuals a very large dense yellowish chromosphere, nearly 0.4 transdiameters across similar to those often seen in *Oxytoxum*.

Dimensions: Length, 65 to 77μ (4 measured); transdiameter, 65 to 74μ; girdle width, 4μ; antapical spines, 3 to 4μ.

Variation: Varies in size, fin development, and degree to which the linear type of markings is realized.

Comparisons: Belongs to the subgenus *Steinidla*. The characters in which it resembles *Steinidla fragilis* are (1) the surface markings which are slightly of the linear-vermiculate type so well developed in that species, (2) the overrun of the apex upon the dorsal side, and the elongation of the closing platelet and (3) the fragility of the theca. In none of these characters, however, does it attain the degree realized in other species of the subgenus *Steinidla*. It may be distinguished from other members of the *G. fragilis* group by its two antapical spines.

It is a very well defined species easily recognizable by reason of its elongated anterior plate of the ventral area; its wide postcingular *1'''*, its widely separated antapical spines, and by its characteristic surface markings.

Distribution: Taken thus far but twice at San Diego, first on June 9, 1904 (No. 65) in a haul from 75 fathoms several miles off San Diego, and a second time in a vertical haul from 170 fathoms, about ten miles off San Diego on June 23, 1904 (No. 120). A number of specimens have been observed in a surface collection made in the evening (7 p.m.) at Loring, Alaska, September 15, 1905, by Mr. F. M. Chamberlain of the U. S. Bureau of Fisheries, S.S. "Albatross." Permission to use this material has been kindly granted by Hon. Geo. M. Bowers, Commissioner, U. S. Bureau of Fisheries.

E. GENERAL DISCUSSION OF GENERIC AND SPECIFIC CHARACTERS IN *GONYAULAX*

The oft repeated and long continued close scrutiny of numerous groups of individuals of related species such as has been

the basis of the preparation of this paper affords an exceptional opportunity not only for the appreciation and detection of minute details of structural differences upon which the concept of species is customarily built, but also for an ever growing realization that other phases of the organism which may be designated broadly as physiological or functional, rather than structural, are just as profoundly and truly characteristic of species as are those other concrete indications of activity of the living substance which are recorded in more or less permanent expression in form. It may be useful to sum up here both the morphological and functional data and to give the impressions which this study has made upon me with reference to the nature and relations of both generic and specific characters.

The generic characters of *Gonyaulax* are the displacement of the girdle and the constant number of skeletal elements in the hypotheca, girdle, and precingular series of plates, in all a constancy in not less than twenty of the twenty-three to twenty-six skeletal elements characteristic of the different species, and the form and relations of apical *1'*. If we divide the skeleton into zones or belts of plates, as follows (a) apicals, three to five; (b) anterior intercalary (incomplete), none to two; (3) precingulars, six; (4) postcingulars, six; (5) posterior intercalary (incomplete), one; (6) antapical, one, we discover that the posterior half of the skeleton, the girdle, and precingular belt are constant, while the plates of apical region and adjacent intercalary region are variable in number and position. The generic characters thus inhere in the skeleton in and adjacent to the girdle and longitudinal furrow (ventral area of this paper), structural features moulded by the two flagella, the prime ordinal characters of the Dinoflagellata. They thus express, in so far at least as the maintenance of constant number is concerned, conservative ancestral tendencies in the organism, and are directly related to the regions of major activity.

These characters are maintained with remarkable constancy amidst a great diversity of external form, ranging from the spherical as seen in *G. sphaeroidea* (pl. 16, figs. 41, 42), to the greatly elongated seen in *G. birostris*, or the polyhedral in *G. polyedra* (pl. 17, fig. 43).

The ventral pore is also found throughout the genus, but this is present, though not hitherto described, in other genera, such as *Amphidoma*, *Goniodoma*, *Pyrophacus*, and *Centrodinium*. It therefore can not be regarded as a generic character.

I. SPECIES CHARACTERS

1. The Extent of Differences between Species

The specific characters which differentiate the thirty-six or more species of this genus are of greatest variety and affect, in one species or another, practically all the structural elements which make up the organism (see Kofoid, 1906c). Not only is this true for the genus as a whole, but it is also true to a large degree for each species as a unit. It differs from its congeners not merely in certain easily detected and quickly defined structural features which strike the eye at once, but in manifold minor details which are less easily comprehended and can only be described by a mass of minutiae and often accurately expressed only by statistics of proportional measurements. These become evident as one works over the material, in spite of increasing evidences of variation, which on the novice too often leave the impression of inextricable confusion. Just as in the case of the Gadidae, where Williamson (1910) has so clearly demonstrated that the species are profoundly differentiated not only in surface characters such as scalation and fin rays, but by internal visceral and skeletal structures as well, so also in the Dinoflagellata specific characters extend throughout the organism but are more easily comprehended in the less labile skeletal structures. To this the work of Schmidt (1905, 1906) upon the young stages of the various species of cod in the North Atlantic and North Sea has added equally striking evidence of the specific distinctness of the eggs and fry, differences in dimensions, oil drops, pigmentation, and the like, which the experienced eye soon learns to utilize as an infallible guide to the separation of these organisms in the early stages of their development. In a like direction the work of the various divisions of the International Commission for the Investigation of the Sea has brought to light the fact that sharply defined differences based on salini-

ties, temperature, and currents delimit the seasons and spawning territories of the adults of the various species of the Gadidae.

Distinguishing characters of a type not unlike in essential nature to that found among the Gadidae may also be demonstrated between the various species of *Gonyaulax*. It will suffice for illustration to compare two common species, *G. spinifera* and *G. polygramma* (compare figs. A-D, pl. 16, fig. 39 and pl. 17, fig. 47), species of about the same size, often found in the same waters. They differ in size, proportions, in displacement, overhang and margins of girdle; in proportions, shape and markings of the ventral area; in shape of apical region; in size, number, and symmetry of antapical spines; in location of ventral pore; in shape of plates *1′*, *3′*, *6″*, *6‴*, *1ᵖ*, and *1⁗*; in surface markings which are predominantly linear in *polygramma*, and reticulate in *spinifera*. Finally in numbers and distribution there are indications (precise information is lacking on account of confusion in literature as to the synonomy and specific limits of *G. spinifera*) that *G. spinifera* has more of a neritic distribution in colder waters and *G. polygramma* oceanic in warmer waters.

The number of characters separating species would be somewhat lessened if the comparison should, for example, be made between those of the *polygramma* series, as for example *G. turbynei* (pl. 17, fig. 44), *G. polygramma* (pl. 17, fig. 47), *G. kofoidi* (pl. 14, fig. 30), and *G. pacifica* (pl. 16, fig. 35), but even here the characters found in common in all or certain members of the series such as linear markings, antapical spines, antapical asymmetry, or apical horn, differ between several members of the series in the degree and manner of their expression in qualitative and quantitative fashion.

II. Characters of Value in Distinguishing Species

1. Structural Characters

Those structural characteristics which have proved to be of greatest value in the analysis of species in *Gonyaulax* fall naturally into two groups, (1) those affecting fundamental features such as number of plates, form of the body, displacement of the girdle, and form of the ventral area; and (2) superficial char-

acters such as surface markings, and outgrowths such as spines, lists, and fins.

The *types of bodily form* may all be traced back to modifications of a sphere, a type realized almost perfectly in *G. sphaeroidea* and *G. palustris*, less so in *G. scrippsae* and *G. turbynei*. This sphericity is retained in the posterior part of the body, in the more conservative hypotheca in *G. apiculata*, *G. fragilis*, *G. digitale*, *G. scrippsae*, *G. diegensis*, *G. triacantha*, and *G. hyalina*.

Elongation of the body is apparent in the whole body in *G. apiculata* and *G. fragilis;* in the apical region only in *G. spinifera*, *G. digitale*, *G. diegensis*, and *G. ceratocoroides*, and especially in *G. mitra*. Elongation of the epitheca as a whole is seen in the large numbers of the *polygramma* group, *G. polygramma*, *G. kofoidi*, and *G. pacifica*. Elongation of the hypotheca in excess of that of the epitheca is noticeable in *G. mitra*, in *G. milneri*, and *G. ceratocoroides*. Elongation with marked accompanying attenuation of both halves is seen in the subgenus *Fusigonyaulax* in its species *birostris*, *glyptorhynchus*, and *highleii*. The polyhedral form of body is found in *G. polyedra*, *G. milneri*, and *G. ceratocoroides*. In these the sutures are somewhat salient and the plates flattened rather than convex.

The most fundamental and characteristic structure in the genus *Gonyaulax*, and for that matter in the Dinoflagellata, is the girdle, the trough in which the ribbon-like protoplasmic sheet called the transverse flagellum lies. Throughout all species of *Gonyaulax* this girdle is wound in a descending spiral about the body, the amount of descent varying from one to seven girdle widths in different species. The amount of displacement is characteristic for the species, subject however to some variation within the species. An abrupt proximal curvature is distinctive of some species, as for example of *G. pacifica* (pl. 15, fig. 35) and *G. triancantha* (pl. 11, fig. 13) and a sweeping distal one of *G. diegensis* (pl. 13, fig. 24). In *G. spinifera* (pl. 16, fig. 39) and *G. digitale* (pl. 9, fig. 3) the girdle makes more than a complete circuit of the body, the overhang of the two ends being several girdle widths.

The actual width of the girdle is fairly constant in all species,

being about five microns, possibly in correlation with a constancy in the size of the flagellum or range of its field of action.

The manner in which the furrow is formed varies in different species. In one, *G. sphaeroidea* (pl. 16; fig. 41), it is not at all impressed into the body wall, in several (*G. ceratocoroides*, *G. milneri*) the surface is merely flattened, in others (*G. palustris*, *G. scrippsae*, pl. 16, fig. 38, and in the subgenus *Fusigonyaulax*) it is slightly impressed, while in the great majority of species, as in *G. spinifera* (pl. 16, fig. 39), *G. polygramma* (pl. 17, fig. 47), it is quite deeply set into the body wall.

The sides of the furrow are variously constructed. In non-impressed and shallow types the sides are formed by high membranous lists either without (*G. sphaeroidea*) or with (*G. milneri*, *G. ceratocoroides*, *G. birostris*, *G. glyptorhynchus*) ribs. In nearly all of the deeply impressed types there are no membranous lists, the edges of the furrow being formed by thick scarcely salient shelves of thecal wall, as in *G. polygramma*, *G. triacantha*, and *G. diegensis*. In a few cases, as in *G. spinifera* (all?) these edges may bear low fins with short ribs.

The form of the longitudinal furrow or ventral area also differs in different species, largely in correlation with the form of the girdle. The overhang and displacement give it a marked sigmoid curvature in *G. spinifera* (pl. 16, fig. 39), *G. digitale* (pl. 9, fig. 3), and *G. scrippsae* (pl. 16, fig. 38). In species with displaced girdle, such as *G. diegensis* (pl. 13, fig. 24), a narrow constricted region extends between the two ends of the girdle. In polyhedral forms, *G. polyedra* (pl. 17, fig. 43), *G. milneri*, and *G. ceratocoroides*, and especially in *G. catenata*, this area is a widely expanded, vertical, straight tract within which the minor skeletal elements, six in number, which compose it, can be readily determined. In all except the *polyedra* and *sphaeroidea* groups the ventral area is widened posteriorly, enormously so in *G. triacantha* (pl. 11, fig. 13) and *G. catenata*, and considerably in the *polygramma* series (pl. 17, fig. 47). In the subgenus *Steiniella* (except in *G. mitra*) the distal enlargement is considerable and rather abrupt (pl. 17, fig. 45) and in the *G. spinifera* series it is often spoon-shaped (pl. 16, fig. 39). The degree

to which the armature of fins and spines is developed on the sides of this area is to a considerable extent a species character, as is also the extent of the indentation which it makes in the terminal antapical plate.

The *constituent plates of the theca* are subject to diversifications in the various species only in the apical and anterior intercalary regions, *those parts of the organism directed forward in locomotion and therefore most subject to the impact of the environment.*

The total number of plates in the apical-intercalary region is usually 3 (20 cases), occasionally 4 (6 cases), rarely 5 (2 cases), or 6 (2 cases) or even 8 (1 case). The distribution of these plates between the apical and intercalary regions varies. I arbitrarily distinguish all those plates in contact with the apex as apicals, and all others anterior to the precingulars as anterior intercalaries. The following table indicates the distribution of the several types of plating among the species of the genus.

Apical Plates in Species of Gonyaulax

Species	Total plates	Number of Apicals	Number of anterior intercalaries	Position of anterior intercalaries
G. alaskensis, birostris, digitale, fragilis, glyptorhynchus, inflata, kofoidi, pacifica, polygramma, scrippsae, spinifera, turbynei	3	3	0	
G. apiculata(?), sphaeroidea	4	3	1	right ventral
G. diegensis, hyalina(?)	4	4	0	
G. triacantha	5	3	2	dorsal
G. jolliffei (= Spiraulax jolliffei)	5	4	1	right ventral
G. milneri	5	5	0	
G. polyedra	6	4	2	right ventral
G. ceratocoroides	6	6	0	
G. catenata	8	4	4	dorsal
G. highleii, mitra, palustris(?), serics	?	?	?	

An inspection of the table shows at once the predominance of the $3'$–0^a combination and also that there is no marked tendency for the deviations from this to conform to the lines

which separate the subgenera and groups which I have recognized. In the discussion of the species, especially of those with the *3′–0ª* combination I have repeatedly called attention to an incipient suture in apical *3′*, which if realized would give rise to a *3′–1ª* or a *4′–0ª* arrangement. It may be noted in passing that in the individualized plates of the theca of the Dinoflagellata we come about as close to a realization of unit characters in these so-called lower and supposedly simple organisms as we do anywhere in the organic world. This exhibition in *Gonyaulax* of a tendency on the part of plate *3′* to divide into two elements and its apparent realization in certain species (e.g. in *G. diegensis*) is strongly suggestive of a gradual rather than an abrupt transition from a three-unit to a four-unit phase in this region of the skeleton.

The differentiation in form and in position of ends of girdle and in form of ventral area modify certain plates of the thecal wall to an unusual degree. These plates are apical *1′*, anterior intercalary *1ª*, precingular *6″*, the anterior plate of the ventral area, postcingular *1‴*, and the posterior intercalary *1ᵖ*. Three significant relations of these plates appear to be correlated with their relatively greater degree of diversification.

In the first place they are, with two exceptions (apical *1′* and anterior intercalary *1ª*) immediately in contact with the region of protoplasmic motion, the furrows in which the two flagella are active, during the time of thecal formation; in the second place they are all in immediate contact with the line along which the theca is parted in cell division, and thus in a region of constantly repeated liberation along one margin, from restraining contacts with other plates.

It should, however, be noted in this connection that the girdle plates *1–6* are absolutely constant in number and exhibit few modifications in the genus, and that other plates along the fission line (see text figs. A-D, p. 195) do not manifest an equal amount of diversification within the genus. In a third particular, however, the plates named, together with the whole ventral area which is quite variable, do occupy a unique relation among the elements of the theca. They all lie in the midventral region adjacent to the flagellar pore precisely in the region where the spiral move-

ments of the two flagella bring a current of water sweeping over the surfaces of these plates. In other words they constitute a region of maximum contact with the environment. The direct action of the environment as a potent modifying agent in the process of speciation is thus strongly suggested.

The surface of the thecal wall of *Gonyaulax* exhibits nearly all of the modifications found in the whole order of Dinoflagellata ranging from the smooth almost undifferentiated spineless and finless *G. scrippsae* to the exceedingly rugose *G. milneri* and the long-spined *G. ceratocoroides*. Minute quadrangular areolations are seen in *G. triacantha* (pl. 11, fig. 13), pits which pass over into a coarse mesh work in *G. polyedra* (pl. 14, fig. 31), linear striae in the *polygramma* (pl. 17, fig. 47) group, and vermiculate in certain species of the subgenus *Steiniella* (pl. 17, fig. 46), while in many instances a reticular meshwork, usually quite characteristic of the species is found. These surface markings are peripheral characters in immediate contact with the environing medium and more than any other feature of skeletal organization exhibit variation in respect to age of the theca, but especially with reference to temperature, salinity and perhaps to more subtile chemical modifications in the water in which they are found. The proof of this statement lies in the fact that most of the individuals taken at one time in a given locality will bear a characteristic facies, expressed in *Gonyaulax* in surface markings, and this may differ in greater or less degree from the same species taken elsewhere, or at the same locality at another season.

The marked asymmetry expressed in the inequality of the two posterior horns in *Peridinium* and *Ceratium* is hinted at in the tendency toward antapical asymmetry seen in the larger members of the *polygramma* series, as for example in *G. pacifica*. It is perhaps to be correlated in all instances with the proximity of this region to the posteriorly extending flagellum with the current of water it produces sweeping backward in the immediate neighborhood of the left antapical region.

Physiological Characters

In the matter of *size* each species has its characteristic limitations, the range in size increasing with the amount and geographi-

cal distribution of the material, in which, however, the greater part of the individuals are grouped about a mean. Thus five are very small (22–40μ), *G. catenata, palustris, scrippsae, series* and *spinifera;* four are small (40–60μ), *G. polyedra, sphaeroidea, triacantha* and *turbynei;* five are of medium size (60–80μ), *G. alaskensis, apiculata, digitale, milneri* and *polygramma;* five are large (80–100μ), *G. ceratocoroides, diegensis, fragilis* and *hyalina;* four are very large (100-120μ), *G. birostris, glyptorhynchus, highleii,* and *kofoidi;* and three are giants (130–250μ), *G. inflata, mitra* and *pacifica.*

In *type of asexual reproduction* two species exhibit very distinct features which set them off from all others. In *G. catenata* Levander (1894a) has described a type of chain formation with accompanying skeletal fission, while in *G. series* I (1911a) have found chain formation with accompanying reduction in size of the terminal members of the series and what appears to be skeletal formation in entirety *de novo* after chain formation. In no other species has chain formation been noted, though normal binary fission of cell body and skeleton alike occur in a large number and possibly in all of them.

The *distribution* of the species is characteristic. Two only are known from fresh water, *G. apiculata* and *G. palustris;* one, *G. catenata,* from the brackish water of the Baltic, and one, *G. triacantha,* appears to be a northern circumpolar neritic form. By far the greater part of the species are primarily tropical or of the warm temperate zone; here belong *G. birostris, ceratocoroides, fragilis, glyptorhynchus, highleii, hyalina, inflata, kofoidi, milneri, mitra, pacifica, polygramma, sphaeroidea,* and *turbynei.* Many of these invade temperate and even far northern or far southern waters sparingly with currents from equatorial regions. The species which appear to have a predominantly temperate distribution are *G. alaskensis, diegensis, digitale, polyedra, scrippsae* and *spinifera,* though these also invade tropical and circumpolar regions to some extent. The *marked increase in speciation in waters of higher temperature is noteworthy.*

Nothing is known yet of their vertical distribution.

The relative numbers in which the species occurs is also a

characteristic. In *G. polyedra* we have a species which may occur sporadically in overwhelming numbers, others, such as *G. digitale*, *polygramma*, *spinifera*, *pacifica*, *catenata*, *diegensis* and *triacantha* may be locally common, or have a wide distribution, while others, as in the case of most of the tropical species, have been met with in small numbers and rarely, in a few cases only, singly as yet.

Fragility of the shell is another physiological feature of *Gonyaulax* which is noticeable in the genus as a whole, but with wide divergencies among the species. It is very rarely, for example, that one finds an intact theca of *G. fragilis*, or its relatives in the subgenus *Steiniella*. Likewise *G. catenata* is excessively fragile, while *G. polyedra* and members of the *birostris* group are prone to part in the apical region. On the other hand in most species the sutures on the right shoulder of the theca and of the ventral area posterior to its anterior plate are separated with great difficulty, if at all.

The habit of ecdysis is allied to this proneness to disintegrate on the part of the thecal wall. In *G. polyedra*, *G. polygramma*, *G. spinifera* and perhaps in others members of the group to which these belong, the ecdysis is frequently seen, and it is no unusual thing to find empty thecae of many of the species with dorsal apical plates torn loose or missing, in the plankton.

F. SUMMARY

1. The genus is redefined on the basis of its skeletal morphology. The skeleton consists of three (three to six) apicals, no or one (none to four) anterior intercalaries, six precingulars, six girdle plates, six postcingulars, the posterior intercalary, one antapical and the plates of the ventral area.

2. The so-called "longitudinal furrow" extending to the apex is not in any morphological or functional meaning a furrow, but merely the narrow apical plate *1'*, the homologue of the rhomb plate of *Peridinium*.

3. There is always a minute closing platelet in the apex and a ventral pore (with several exceptions) on the right ventral

apical or anterior intercalary plate to the right of the mid-ventral line.

4. The ventral area or true longitudinal furrow consists of an anterior plate indenting the epitheca and bearing on its post-margin the flagellar pore; and an intermediate region of two to four small plates, and a large posterior plate.

5. The fission line in dividing thecae is described.

6. The genus is revised, twenty-five species being recognized, fourteen recorded from coasts of California, and four new ones, *G. alaskensis, G. diegensis, G. scrippsae, G. sphaeroidea* described. The synonomy, variation and distribution of each is discussed.

7. The all-pervading character of specific differences in both morphological and physiological details is described.

8. The apical region and ventral area, regions coming most in contact with the environment are most subject to diversification.

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EXPLANATION OF PLATES

PLATE 9

Gonyaulax digitale (Pouchet) Kofoid

Fig. 1. Ventral view of theca showing plates. Specimen from Loring, Alaska, September 15, 1905. × 1000.

Fig. 2. Ventral view of heavy theca possibly approaching fission. From 0–5 m., August, 1907, Faeroes Channel. × 1000.

Fig. 3. Ventral view, showing surface markings, from same collection as specimen in figure 2. × 1000.

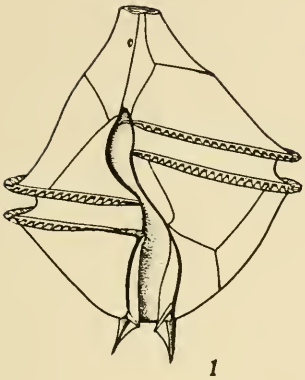
Fig. 4. Ventral view of heavily finned type. Loring, Alaska, September 15, 1905. × 1000.

Fig. 5. Ventral view of very rugose form with reticulations replacing spines in antapical fins. Surface reticulations shown only on plates *6″*, *1ᵖ*, and *1⁗*. From same collection as specimen shown in figure 2. × 1000.

ABBREVIATIONS

1–6—girdle plates.
1′–3′—apical plate.
1″–6″—precingular plates.
1‴–6‴—postcingular plates.
1ᵖ—posterior intercalary.
1⁗—antapical plate.
ant. pl.—anterior plate of ventral area.
ant. sp.—antapical spine.
cl. pl.—closing platelet.
f.—fin of ventral area.
fl. po.—flagellar pore.
int. pl.—intermediate plates of ventral area.
post. pl.—posterior plate of ventral area.
v. po.—ventral pore.

Figures 1, 2, 4, 5, drawn by Mrs. Josephine Rigden Michener, figure 3 by Miss Ethel Abeel.



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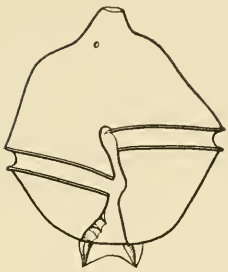

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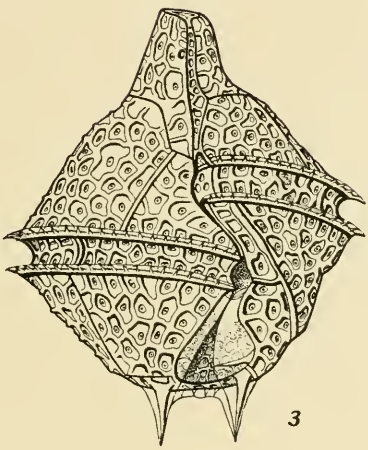

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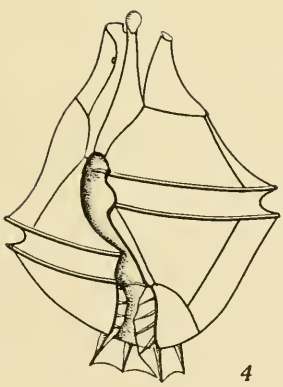

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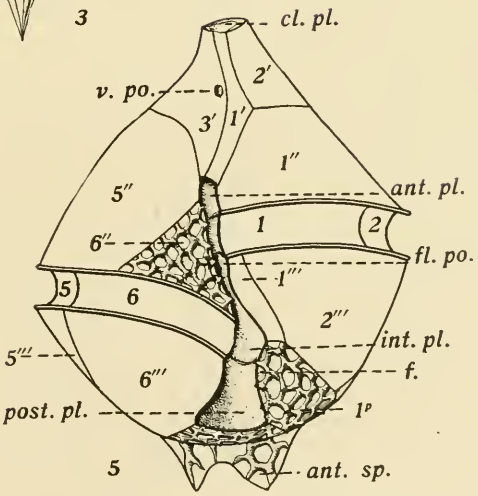

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PLATE 10

Fig. 6. Dorsal view of theca of *Gonyaulax polygramma* Stein, showing plates. San Diego, December 12, 1904. × 1000.

Fig. 7. Ventral view of same. The specimen figured shows an unusual number of antapical spines. × 1000.

Fig. 8. Ventral view of theca of *Gonyaulax spinifera* (Clap. et Lach.) Diesing *sensu stricta*. San Pedro Harbor, May 31, 1901.

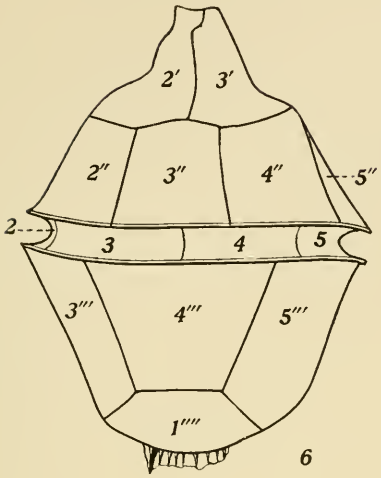
Fig. 9. Dorsal view of another individual from same collection, showing theca after recent fission. The newer moiety is smooth, the older reticulate. × 1000.

Fig. 10. Ventral view of same. × 1000.

ABBREVIATIONS

1–6—girdle series of plates.
1′–3′—apical series.
1″–6″—precingular series.
1‴–6‴—postcingular series.
1ᵖ—posterior intercalary plate.
1⁗—antapical plate.
ant. pl.—anterior plate of ventral area.
ant. sp.—antapical spine.
cl. pl.—closing platelet of apical region.
f. l.—fission line.
fl. po.—flagellar pore.
int. pl.—intermediate plates of ventral area.
post. pl.—posterior plate of same.
v. po.—ventral pore.

Figures 6–8 drawn by Mrs. Josephine Rigden Michener; figures 9 and 10 by C. A. Kofoid and Mr. R. W. Harvey.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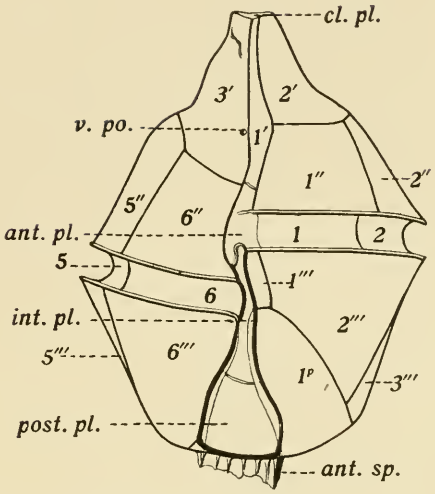
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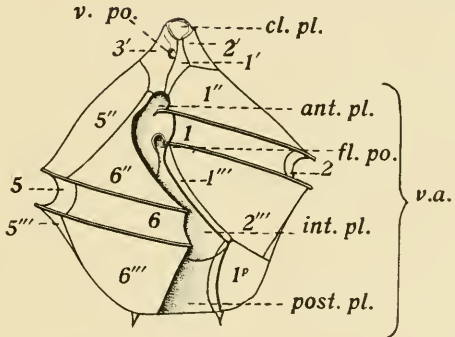
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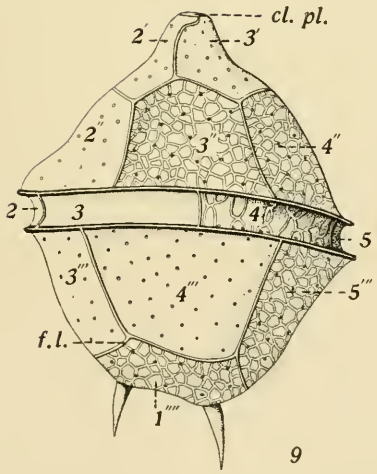
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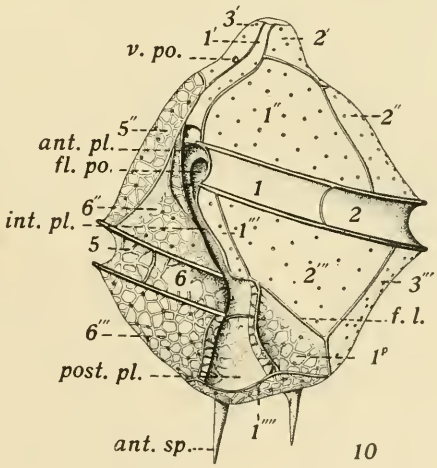
9


3′
1′
2′
v. po.
1″
2″
5″
ant. pl.
fl. po.
1
6″
2
int. pl.
1‴
5
6
2‴
3‴
f. l.
6‴
1ᵖ
post. pl.
1⁗
ant. sp.

10

PLATE 11

Gonyaulax triacantha Jörg.

All from specimens from Loring, Alaska, September 15, 1905.

Fig. 11. Antapical view of hypotheca. × 1000.

Fig. 12. Diagram of apical view of epitheca. × 1000.

Fig. 13. Ventral view of theca, with plates and surface markings. From an empty theca. × 1000.

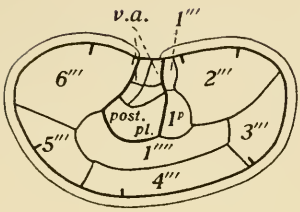
Fig. 14. Lateral view of same. × 1000.

Fig. 15. Dorsal view of same, showing plates and thickness of wall. Note solid antapical spines. × 1000.

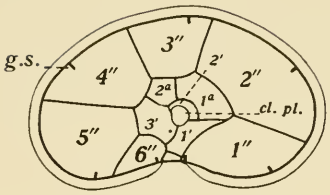
ABBREVIATIONS

1–6—girdle plates.
1′–4′—apical plates.
1ª–3ª—anterior dorsal intercalaries.
1″–6″—precingulars.
1‴–6‴—posteingulars.
1ᵖ—posterior intercalary.
1⁗—antapical.
a. sp.—antapical spines.
ant. pl.—anterior plates of ventral area.
cl. pl.—closing platelet.
f.—fin on margin of ventral area.
fl. po.—flagellar pore.
int. pl.—intermediate plates of ventral area.
l.—list of ventral area.
post. pl.—posterior plate of ventral area.
v. a.—ventral area.
v. po.—ventral pore.

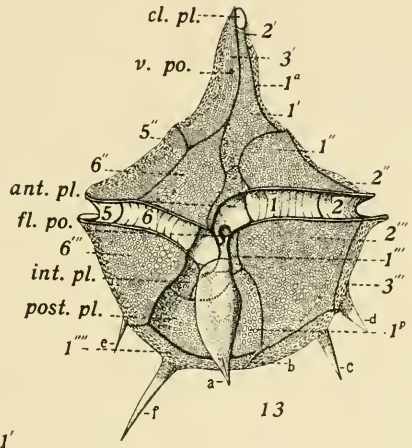
Figures drawn by C. A. Kofoid, R. W. Harvey and Mrs. Josephine Rigden Michener.


v.a.
1'''
6'''
2'''
post. pl.
1^p
5'''
3'''
1''''
4'''

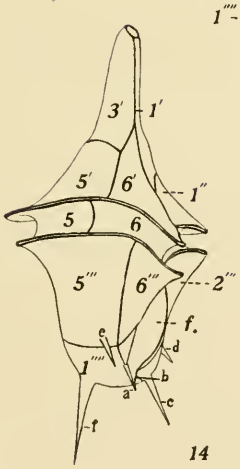
11


g.s.
3''
2'
4''
2^a
2''
1^a
cl. pl.
5''
3'
1'
6''
1''

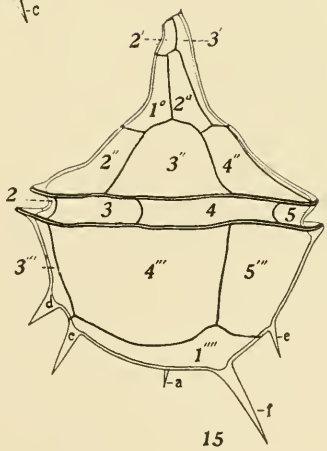
12


cl. pl.
2'
v. po.
3'
1^a
1'
5''
1''
6''
2''
ant. pl.
1
2
fl. po.
5
6
2'''
6'''
1'''
int. pl.
3'''
post. pl.
d
1^p
1''''
e
a
b
c
f

13


3'
1'
5'
6'
1''
5
6
5'''
6'''
2'''
f.
e
d
1''''
b
a
c
f

14


2'
3'
1^a
2^a
2''
3''
4''
2
3
4
5
3'''
4'''
5'''
d
c
1''''
e
a
f

15

PLATE 12

Gonyaulax polyedra Stein

All specimens from San Diego, June, 1904.

Fig. 16. Dorsal view of theca showing plates. × 1000.

Fig. 17. Ventral view of same. × 1000.

Fig. 18. Ventral view of recently divided theca, showing unmarked anterior moiety and porulate posterior one and the fission line (*f. l.*) × 1000.

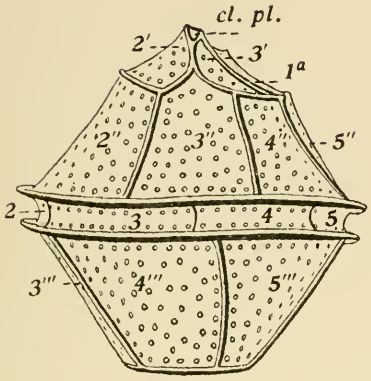
Fig. 19. Antapical view of hypotheca. ×1000.

Fig. 20. Apical view of epitheca with normal type of apical plates. × 1000.

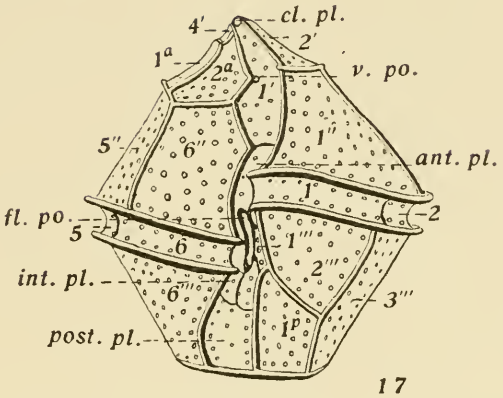
ABBREVIATIONS

1–6—girdle series of plates.
1′–4′—apical series.
1ª–2ª—anterior intercalary plates.
1″–6″—precingular series.
1‴–6‴—postcingular series.
1ᵖ—posterior intercalary plate.
1⁗—antapical plate.
ant. pl.—anterior plate of ventral area.
cl. pl.—closing platelet of apex.
f. l.—fission line.
fl. po.—flagellar pore.
int. pl.—intermediate plate of ventral area.
post. pl.—posterior plate of same.
v. po.—ventral pore.

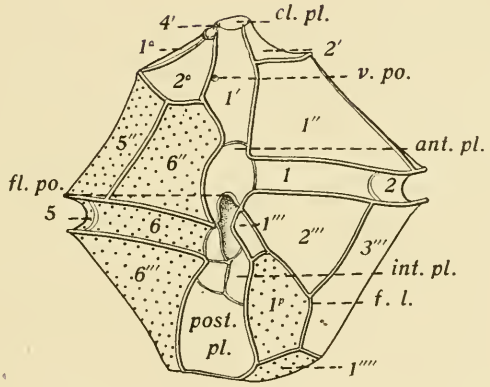
Figures 16, 17, 19, and 20 drawn by Mr. D. B. Billinghurst, figure 18 by Mrs. Josephine Rigden Michener.


cl. pl.
2'
3'
1a
2''
3''
4''
5''
2
3
4
5
3'''
4'''
5'''

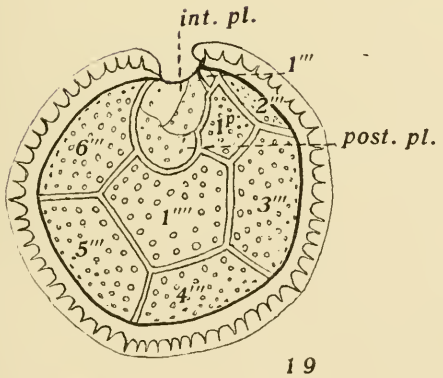
16


4'
cl. pl.
2'
1a
2a
v. po.
1'
1''
5''
6''
ant. pl.
1
2
fl. po.
5
6
1'''
2'''
int. pl.
6'''
3''''
1p
post. pl.

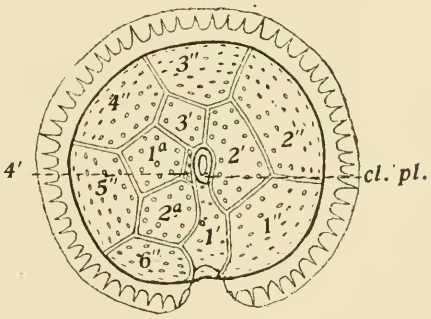
17


4'
cl. pl.
1a
2'
2a
v. po.
1'
1''
ant. pl.
5''
6''
1
2
fl. po.
5
6
1'''
2'''
3'''
int. pl.
6'''
1p
f. l.
post.
pl.
1''''

18


int. pl.
1'''
2'''
1p
post. pl.
6'''
1''''
3'''
5'''
4''''

19


3''
4''
3'
1a
2'
2''
4'
cl. pl.
5''
2a
1'
1''
6''

20

PLATE 13

Fig. 21. Diagram of plates of hypotheca of *Gonyaulax diegensis* sp. nov. in antapical view. × 500.

Fig. 22. Surface view of apical closing platelet of same. × 1000.

Fig. 23. Diagram of plates of epitheca of same in apical view. × 500.

Fig. 24. Ventral view of theca of rugose specimen with wide intercalary bands. Figures 21–24 all from specimens taken June 21, 1904, on the "New Cod Ground," off San Diego, California.

Fig. 25. A precingular plate of *Gonyaulax* (*Steiniella*) *fragilis* (Schütt) showing surface markings. Note nodal pores and partial submergence of linear markings. San Pedro Harbor, California, May 31, 1901. × 1000.

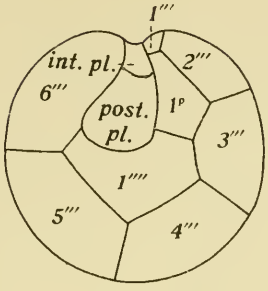
Fig. 26. Antero-dorsal view of theca of *Gonyaulax scrippsae* sp. nov. Channel, San Pedro Harbor, California, May 29, 1901. × 1000.

Fig. 27. Ventral view of theca of same. × 1000.

ABBREVIATIONS

1′–4′—apical series of plates.
1″–6″—precingular series.
1‴–6‴—postcingular series.
1p—posterior intercalary plate.
1⁗—antapical plate.
ant. pl.—anterior plate of ventral area.
cl. pl.—closing platelet of apex.
fl. po.—flagellar pore.
int. pl.—intermediate plates of ventral area.
post. pl.—posterior plate of same.
v. po.—ventral pore.

Figures 21–25 drawn by Mrs. Josephine Rigden Michener; figures 26, 27 by Mr. R. W. Harvey.



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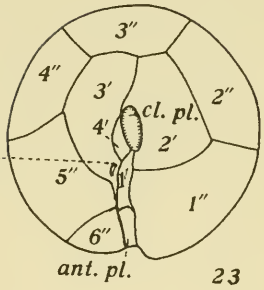

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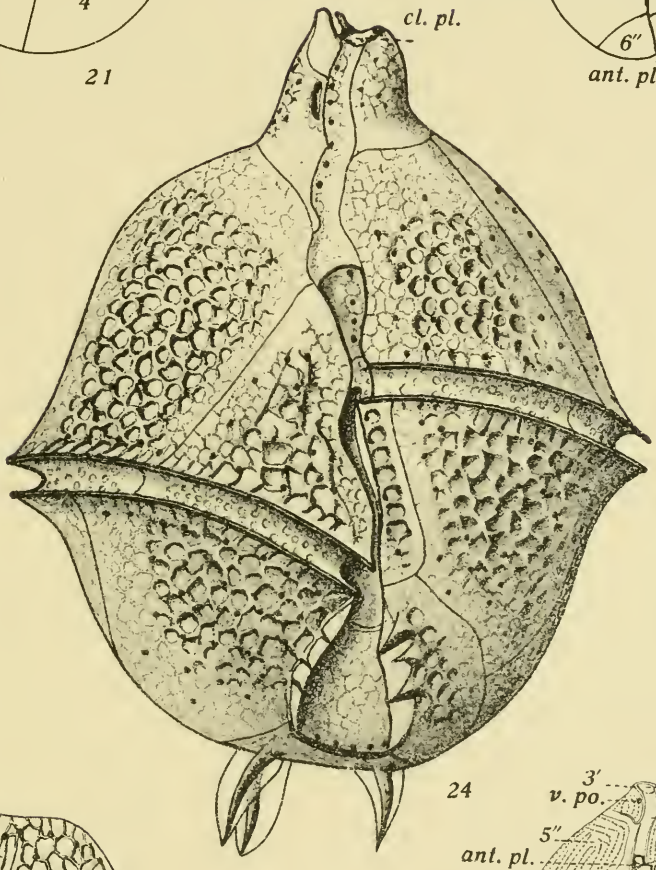

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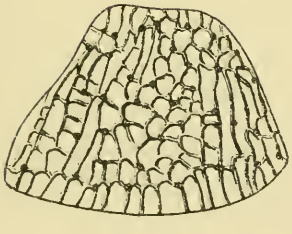

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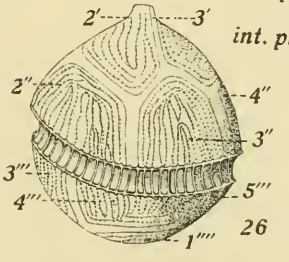

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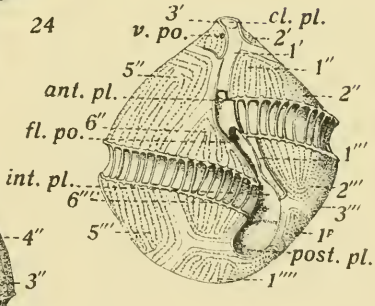


27

PLATE 14

Fig. 28. Diagram of plates of epitheca of *Gonyaulax polyedra* Stein in apical view, showing an extra anterior dorsal intercalary. San Diego, California, July, 1904. × 1000.

Fig. 29. Same of another and much larger individual, showing contact of anterior intercalary 2^a with the apical region (*cl. pl.*). San Diego, California, July, 1904. × 1000.

Fig. 30. Ventral view of theca of *Gonyaulax kofoidi* Pavillard, showing parted apex, and surface markings. Seven miles WNW Point Loma, California, November 12, 1904. × 1000.

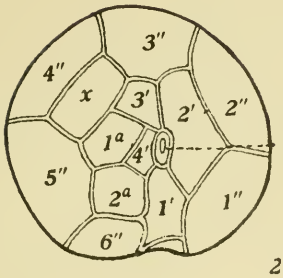
Fig. 31. Midventral region of theca of *Gonyaulax polyedra* Stein, showing markings, pores, and plates of ventral area. San Diego, July, 1904. × 1000.

Fig. 32. Apical view of epitheca of *Gonyaulax* (*Steiniella*) *alaskensis* sp. nov., showing plates. Loring, Alaska, September 15, 1904. × 1000.

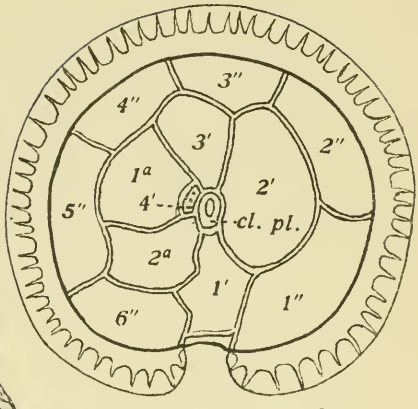
ABBREVIATIONS

$1'$–$4'$—apical series of plates.
1^a–2^a—intercalary plates.
$1''$–$6''$—precingular series.
ant. pl.—anterior plate of ventral area.
cl. pl.—closing platelet of apex.
fl. po.—flagellar pore.
g. s.—girdle suture.
int. pls.—intermediate plates of ventral area.
post. pl.—posterior plate of same.
v. po.—ventral pore.
x.—extra anterior intercalary plate.

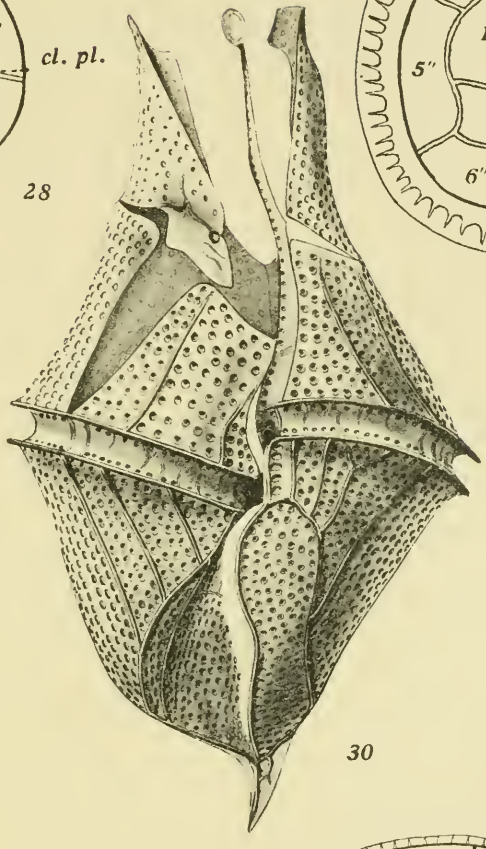
Figures 28, 29, and 31 drawn by Mr. B. D. Billinghurst; figures 30 and 32 by Mrs. Josephine Rigden Michener.


3″
4″
x
3′
2′
2″
1ª
4′
cl. pl.
5″
2ª
1′
1″
6″

28


3″
4″
3′
2″
1ª
2′
5″
4′
cl. pl.
2ª
1′
1″
6″

29



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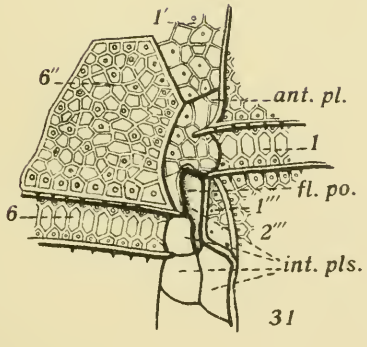
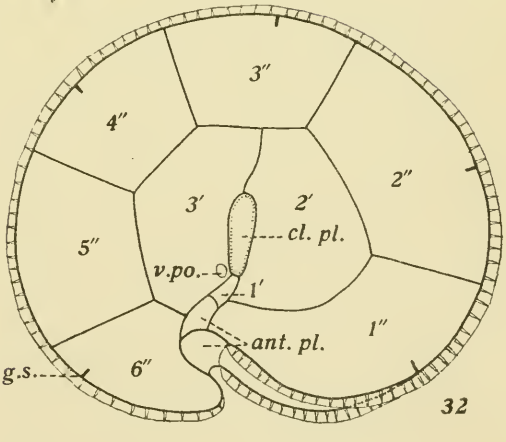

1′
6″
ant. pl.
1
fl. po.
1‴
6
2‴
int. pls.

31


3″
4″
2″
3′
2′
cl. pl.
5″
v.po.
1′
1″
ant. pl.
g.s.
6″

32

PLATE 15

Fig. 33. Antapical view of hypotheca of *Gonyaulax* (*Steiniella*) *fragilis* (Schütt), showing plates. San Pedro Harbor, California, May 31, 1901. × ca. 500.

Fig. 34. Apical view of epitheca of same, showing plates, girdle, and ventral area. Anterior plate, and plate *1′* stippled. × ca. 500.

Fig. 35. Oblique ventral view of *Gonyaulax pacifica* Kofoid with apicals parted. Seven miles WNW Point Loma, California, November 12, 1904. × 1000.

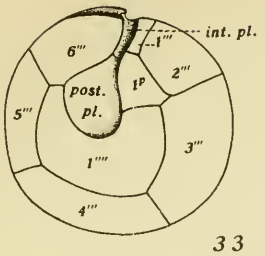
Fig. 36. Dorsal view of theca of *Gonyaulax fragilis* Schütt, showing plates. Same individual as figure 33. × ca. 500.

Fig. 37. Ventral view of same, showing plates, except subdivisions of intermediate region of ventral area. Girdle and ventral area stippled. × ca. 500.

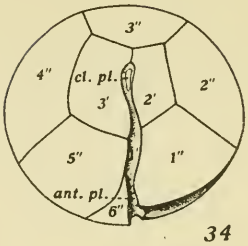
ABBREVIATIONS

1–6—girdle series of plates.
1′–3′—apical series.
1″–6″—precingular series.
1‴–6‴—postcingular series.
1ᵖ—posterior intercalary plate.
ant. pl.—anterior plate of ventral area.
1⁗—antapical plate.
cl. pl.—closing platelet of apex.
fl. po.—flagellar pore.
int. pl.—intermediate plates of ventral area.
post. pl.—posterior plate of same.

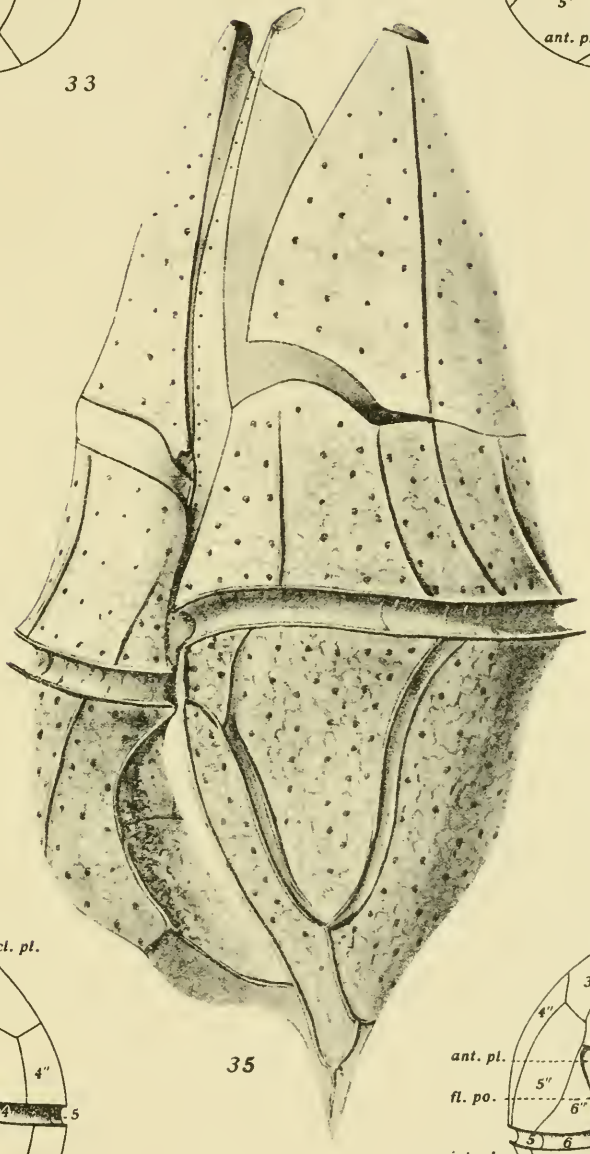
Figures drawn by Mrs. Josephine Rigden Michener.


int. pl.
6‴
1‴
2‴
1ᵖ
post. pl.
5‴
3‴
1⁗
4‴

33


3″
4″
cl. pl.
2″
3′
2′
5″
1″
ant. pl.
6″

34



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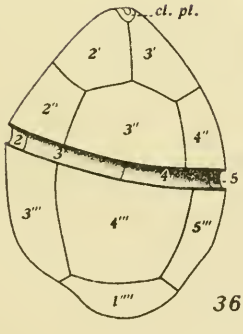
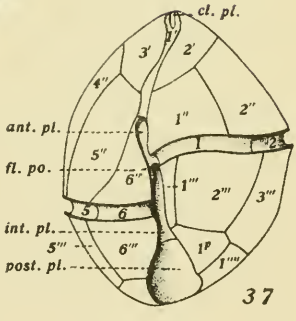

cl. pl.
2′
3′
2″
3″
4″
1
2
3
4
5
3‴
4‴
5‴
1⁗

36


cl. pl.
1′
3′
2′
4″
1″
2″
ant. pl.
5″
fl. po.
6″
1‴
2‴
3‴
5
6
int. pl.
5‴
6‴
1ᵖ
post. pl.
1⁗

37

PLATE 16

Fig. 38. Ventral view of *Gonyaulax scrippsae* sp. nov., showing surface markings. Channel, San Pedro Harbor, California, May 29, 1901. × 1000.

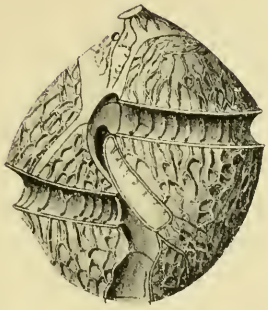
Fig. 39. Ventral view of *Gonyaulax spinifera* (Clap. et Lach.) Diesing *sensu strictu*. Loring, Alaska, September 15, 1904. × 1000.

Fig. 40. Ventral view of lightly reticulated individual of *Gonyaulax diegensis* sp. nov. with wide intercalary bands. New Cod Grounds, San Diego, California, June 23, 1904. × 1000.

Fig. 41. Postero-dorsal view of theca of *Gonyaulax sphaeroidea* sp. nov., showing surface structure. Nine miles WSW Point Loma, California, surface, November 26, 1904. × 1000.

Fig. 42. Ventral view of same.

Figure 38 drawn by Miss Ethel Abeel, figures 39–42 by Mrs. Josephine Michener.



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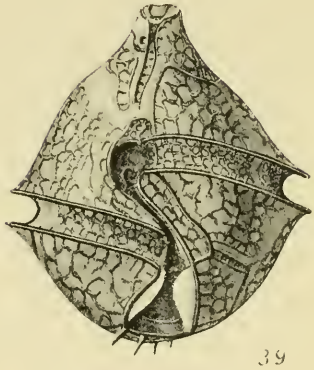

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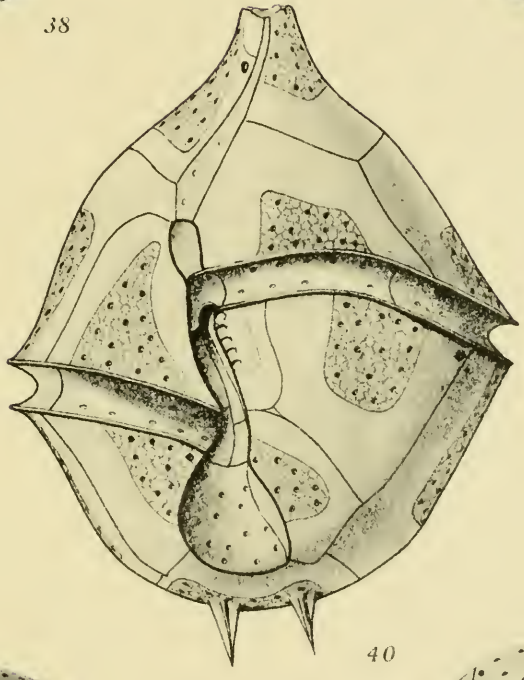

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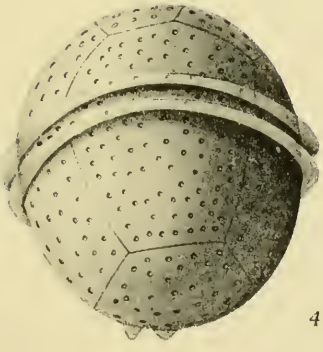

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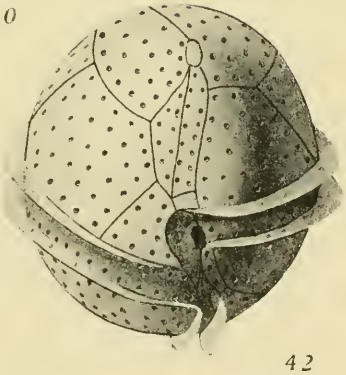

42

PLATE 17

Fig. 43. Ventral view of theca of *Gonyaulax polyedra* Stein, showing surface structure and plates. San Diego, California, June 23, 1904. × 1000.

Fig. 44. Ventral view of *Gonyaulax turbynei* Murray and Whitting, showing surface structure. San Diego, California, July 12, 1904. × 1000.

Fig. 45. Ventral view of theca of *Gonyaulax* (*Steiniella*) *alaskensis* sp. nov., showing plates and surface structure. Loring, Alaska, September 15, 1904. × 1000.

Fig. 46. Dorsal view of same. × 1000.

Fig. 47. Ventral view of theca of *Gonyaulax polygramma* Stein, showing surface structure. San Diego, California, November 12, 1904. × 1000.

Figures 43, 44, 46, 47 drawn by Mrs. Josephine Rigden Michener. figure 45 by Miss Ethel Abeel.