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ON THE SKELETAL MORPHOLOGY OF *GONYAULAX CATENATA* (LEVANDER)

BY

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Through the kindness of Dr. K. M. Levander of the University of Helsingfors, Finland, I have been enabled to make an examination of abundant material of his *Peridinium catenatum* (see Levander, 1894a), and to compare its skeletal structure with that of *Gonyaulax* described in the preceding paper (*Univ. Calif. Publ. Zool.*, vol. 8, no. 4). The material placed at my disposal is a collection made in the Gulf of Finland, May 26, 1900, from 20 meters to the surface. It abounds in isolated individuals and in chains of 2, 4, 6, or even 10 individuals. With this abundant material, apparently in a similar phase of thecal condition, I have been enabled to analyze the plates and thus to clear up some uncertainties regarding the skeletal structure of the organism and to demonstrate its close relationship to the genus *Gonyaulax*, so close indeed that it seems best to include it herein. My most cordial thanks are extended to Dr. Levander for his courtesy and to Mrs. Josephine Rigden Michener for the carefully made drawings which illustrate this paper.

In Levander's (1894a) account of the species he relates his analysis of the plates and concludes that the organism on that

basis is most nearly related to *Peridinium*. In reaching this conclusion he was evidently influenced by the presence of a narrow midventral plate in the epitheca, apical *1′* of my nomenclature (pl. 18, fig. 2) and *r* of his (pl. 18, fig. 6), the homologue of the rhomb plate of *Peridinium*, and by the fact that the total number of plates in both his form and in *Peridinium* was apparently the same. Although he explicitly notes the general resemblance of the hypotheca to that of *Gonyaulax* he still concludes that "sowohl nach der Gestalt der Schale wie auch der *Zusammensetzung* derselben aus Tafeln schliesst unsere Art am meisten an die Gattung *Peridinium* an, in welche ich sie auch deshalb angereiht habe."

The diagrams of the plates of his *Peridinium catenatum* in an apical view of the epitheca and a view of the hypotheca from above looking toward the antapex are reproduced in plate 18, figures 6 and 7. The results of my analysis are shown in figures 1 and 2. The numbers and general relations of the plates in the epitheca are essentially similar in his diagram and my own, the differences being mainly in the relative dimensions of the plates and directions of the bounding sutures portrayed in the two diagrams.

In the analysis of the hypotheca, however, there are two differences between the two diagrams (figs. 2 and 7) which have an important bearing on the relationships of the species in question. Levander figures the hypotheca as composed of six postcingular plates (his "post-äquatorialen Felder" I, I′–V′), a midventral furrow plate, and a pentagonal antapical plate which in his figure is deeply invaded by an elliptical area (unlabeled) bearing the posterior point of connection with the adjacent member of the chain. As determined by me the hypotheca (pl. 18, fig. 1) consists of six postcingular *1‴–6‴* one posterior intercalary *1ᵖ* one antapical *1⁗*, and the ventral area composed of several intermediate plates (*int. pl.*) and a widely expanded posterior plate (*post. pl.*) bearing the posterior attachment pore (*post. att. po.*). This plate is not deeply indented into the antapical. The hypotheca as thus analysed corresponds plate for plate with that of *Gonyaulax*, not of *Peridinium*.

Levander seems to have represented the relations of the antapical and posterior furrow plate in different fashion from that portrayed in my figure.

The plate formula for *Peridinium steini* as determined by me (1909) and that of *Gonyaulax spinifera* and *G. polyedra* and of Levander's *Peridinium catenatum* are given below.

Table of Plate Formulas

	Apicals	Anterior intercalaries	Precingulars	Girdle	Postcingulars	Posterior intercalary	Antapicals
Peridinium steini	4′	3ª	7″	3	5‴	0ᵖ	2⁗
P. catenatum	4′	4ª	6″	6	6‴	1ᵖ	1⁗
Gonyaulax spinifera	3′	0ª	6″	6	6‴	1ᵖ	1⁗
G. polyedra	4′	2ª	6″	6	6‴	1ᵖ	1⁗

The essential likeness of *P. catenatum* to *Gonyaulax* and its dissimilarity to *Peridinium* is at once apparent in the table. A detailed examination only serves to emphasize these conclusions, as follows:

The apical plates of *Peridinium* show marked uniformity and bilateral symmetry (See Stein, 1883, pls. 9–11, and Kofoid, 1909, pl. 2, fig. 1) while those of *Gonyaulax* (see preceding paper, pls. 9–17) usually show marked irregularities in size and position and also decided bilateral asymmetry which is usually more marked in the dorsal region and left face. This is also true of Levander's species. Apical *1′* is not a subsymmetrical rhomb plate as in *Peridinium* but an asymmetrical narrow plate strikingly like that in *Gonyaulax*, running from the anterior margin of the anterior plate of the ventral area to the apex where it is connected with a small closing platelet (*cl. pl.*, pl. 18, fig. 2) just as in *Gonyaulax*. Again in *Peridinium* the anterior intercalaries are symmetrically placed mid-dorsal plates two or three in number, and of approximately equal size, or placed in nearly a bilaterally balanced relation. In Levander's species they (*1ª–4ª*) are irregular in size and lie somewhat upon the right dorsal shoulder, again just as in *Gonyaulax*, especially *G. polyedra* (see preceding paper, pl. 12, fig. 20.).

There are six precingulars (*1″–6″*) in Levander's species and in all species of *Gonyaulax*, and seven in *Peridinium*. Moreover

in the latter genus plate *1″* is triangular or pentagonal and usually small. In *Gonyaulax* and in Levander's species *1″* is quadrangular and large.

The girdle plates (*1–6*) in *Gonyaulax* and in Levander's species are six in number with sutures approximately those of the two adjacent series in location. In *Peridinium* there are three with no dorsal sutures.

There are six postcingulars (*1‴–6‴*) in *Gonyaulax* and in Levander's species, and but five in *Peridinium*. Postcingular *1‴* in *Gonyaulax* is a very small plate, in *Peridinium* it is relatively much larger. In Levander's species it is relatively smaller than in any species of *Peridinium*, though still unusually large for *Gonyaulax*.

In Levander's species and in *Gonyaulax* there is always present a posterior intercalary plate, *1ᵖ*. This is absent in *Peridinium*, though possibly represented by the left antapical.

In *Peridinium* there are two nearly symmetrically placed antapical plates, in *Gonyaulax* and in Levander's species there is but a single median one *1⁗*.

The *ventral area* of both *Peridinium* and *Gonyaulax* consists of an anterior and posterior plate, with several intermediate plates between. These plates in Levander's species much resemble those in those species of *Gonyaulax* in which the ventral area is wide and nearly straight as in *G. polyedra* and *G. triacantha*. The anterior plate is deeply notched by the flagellar pore (pl. 18, fig. 5) and the ventral area widens into the posterior plate as in *G. triacantha*. This plate is, however, relatively much wider in Levander's species than in any other species of *Gonyaulax*. *Peridinium* usually has a ventral notch at the apex while this is not found in any species of *Gonyaulax* nor in Levander's species. The ventral pore so generally present in *Gonyaulax* is not found in *Peridinium* and appears to be lacking in Levander's species, in which, however, the general porulation is greatly reduced.

From the facts detailed above I conclude that this interesting species of Levander's belongs in the genus *Gonyaulax* rather than in *Peridinium*. A brief description is here appended.

Gonyaulax catenata (Levander) Kofoid

Pl. 18, figs. 1–7.

Glenodinium cinctum, Pouchet (1883), p. 441, pl. 20/21, fig. 36, *fide* Cleve (1901a), p. 256.

Peridinium catenatum Levander (1894), pp. 1–19, pl. —, figs. 1–10.

P. catenatum, Van Höffen (1897), p. 267, pl. 5, fig. 5.

Amylax catenata, Meunier (1910), p. 52, pl. 1bis, figs. 46, 47; pl. 3, figs. 28–34.

Diagnosis: A minute species with the general form of a *Peridinium* but the plates of *Gonyaulax*. Plate formula *4′*, *4ᵃ*, *6″*, *6*, *6‴*, *1ᵖ*, *1⁗*. Posterior plate of ventral area exceeding 0.5 transdiameter in width. Several antapical spines present. Ring shaped starch grains. Fission with chain formation.

Description: *Body* rounded, flattened dorso-ventrally, length 0.85–0.95 transdiameter, dorso-ventral diameter (between levels of extremes) 0.75 transdiameter, in middorsal line about 0.5 transdiameter. Cross-section at girdle reinform. *Epitheca* slightly exceeds hypotheca, its right shoulder convex, its left slightly concave, its altitude 0.47 transdiameter, contracted distally to a low apical horn scarcely differentiated, with apex attaining a girdle with across and guarded laterally by two spine-like extensions of the apical plates (pl. 18, fig. 4). *Hypotheca* low and wide with concave postmargin 0.6 transdiameter across, its altitude 0.4 transdiameter, deeply excavated ventrally.

Girdle equatorial, descending, displaced distally 1 girdle width, without overhang, often constricted middorsally (pl. 18, fig. 4) near the fission line (between girdle plates *3* and *4*). The furrow is deeply impressed, with scarcely salient ridges, and no fins. The *ventral area* is exceptionally open, very slightly indenting the epitheca and expanding posteriorly to a width of 0.6 transdiameter and reaching the postmargin. Its width at the distal posterior girdle ridge equals or exceeds that of the girdle.

The *plate formula* is *4′*, *4ᵃ*, *6″*, *6*, *6‴*, *1ᵖ*, *1⁗* (pl. 18, figs. 1, 2). *Apical 1′* is very slender, about 0.3 girdle width across, *2′* and *4′* are elongated in the longitudinal and *3′* in the transverse direction. The *anterior intercalaries* *1ᵃ–4ᵃ* are very uneven in size, *1ᵃ* and *4ᵃ* on the left and right shoulders, and *2ᵃ* superposed (anteriorly) upon *3ᵃ* near the middorsal line. *Precingular 6″* is quadrangular and *postcingular 1‴* nearly square, 1 girdle width across and 1.5 long. *Posterior intercalary 1ᵖ* is much wider than long. The anterior plate of the ventral area (pl. 18, fig. 5), is deeply notched on its posterior margin by the flagellar pore and a small extension meets apical *1′*. Two intermediate plates (*int. pl.*, pl. 18, fig. 1) of nearly equal size are plainly discernible and the wide posterior plate (*post. pl.*) reaches the postmargin and extends from the left antapical spine to the right face somewhat above the right spine.

The *surface* is marked by faint salient lines and a delicate tracery which rarely attains the condition of a meshwork. Several prominent pores are found along the girdle and several on the apical plates. No ventral pore could be with certainty distinguished. A delicate fin guards the left margin of the ventral area and two tapering antapical spines rise nearly 0.5 transdiameter apart from the antapical plate. They are 0.5 to 0.75 girdle width in length. The left one is sometimes double (fig. 5). Two or three accessory antapicals arise from the margins of the ventral area. Fins are scarcely developed upon any of the spines.

The individuals both isolated and in chain exhibit very clearly the attachment pores through which the protoplasmic continuity of sister cells in chain is maintained. The anterior pore (*ant. att. po.*, pl. 18, fig. 2) lies just dorsal to the apex in the upper edge of apical *3′*, not in the apex itself. The posterior pore (*post. att. po.*, pl. 18, fig. 1) is on the right side of the posterior plate of the ventral area. The apex and anterior attachment pore of *Ceratium* (see Kofoid, 1909) coincide. This fact raises the question as to the homology of the apex of *Ceratium* and that of *Gonyaulax*.

The plasma in the two individuals in chain (pl. 18, fig. 3) contained constricted nuclei (pl. 18, fig. 3); and all in the collection were crowded with globular, ring-shaped and occasional comma-shaped starch granules.

Chain formation was exceedingly common and chains of even ten individuals were noted.

Dimensions: Length, 30μ; transdiameter, 33μ; dorso-ventral diameter, 16–22μ; width of girdle, 3–5μ; length of antapical spine, 2–4μ.

Synonomy: Cleve (1901a) is probably correct in regarding *Glenodinium cinctum* of Pouchet (1883) as Levander's (1894) *Peridinium catenatum*. Mennier (1910) includes this species in his new genus *Amylax*, a genus based on the presence of starch grains. On the basis of skeletal morphology this species is, however, a *Gonyaulax*, and I therefore reject his assignment. He has not analyzed the skeletal morphology of any species of his newly created genus.

Comparisons: Resembles *G. series* Kofoid in the fact that it forms chains but not in the method of their formation. In the presence of numerous antapical spines, wide ventral area, and especially wide posterior plate, this species is nearest *Gonyaulax triacantha*. It also approaches this species in having four anterior intercalaries in the right dorsal region. *G. triacantha* has two, while none, or but one, in the right ventral region is the usual arrangement. This species is perhaps worthy of subgeneric distinction.

Distribution: Known from the Baltic, and North Sea, the North Atlantic and waters about Greenland.

Described by Levander (1894a, b) from the winter and spring plankton of the Gulf of Finland with maximum in May; reported from the Baltic by Cleve (1897), Apstein (1908), Driver (1908), Kraefft (1900), and Lohmann (1908), and by various observers of the International Commission for the Investigation of the Sea (see Ostenfeld, 1906, 1909); from the coastal waters of Greenland by Van Höffen (1897); as rare in the North Atlantic, 66° to 69° N, 53° to 55° W, by Ostenfeld (1899) and by Ostenfeld and Paulsen (1904) as *Peridinium* sp., aff. *P. catenatum* as rare at ten stations in the North Atlantic, 59° to 60° N, 13° to 49° W.

It is plainly a boreal species with preference for neritic, brackish, waters, but occasionally oceanic.

For papers cited see bibliography of preceding paper.

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EXPLANATION OF PLATE 18

Gonyaulax catenata (Levander) Kofoid

All figures magnified 1400 diameters

Fig. 1. Antapical view of hypotheca, showing plates.

Fig. 2. Apical view of epitheca, showing plates.

Fig. 3. Two individuals in chain, showing cell contents, nucleus and starch grains.

Fig. 4. Dorsal view of theca, showing surface structure.

Fig. 5. Ventral view of same.

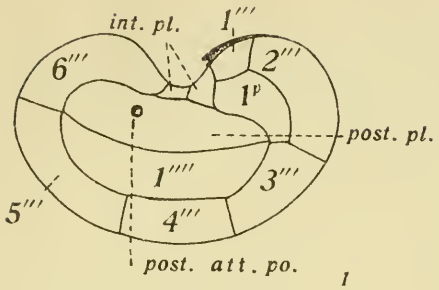
Fig. 6. Diagram of epitheca in apical view, with Levander's (1894) nomenclature. After Levander (1894) text figure 3.

Fig. 7. Same of hypotheca from above. After Levander (1894) text figure 4.

ABBREVIATIONS

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

Figures drawn by Mrs. Josephine Rigden Michener.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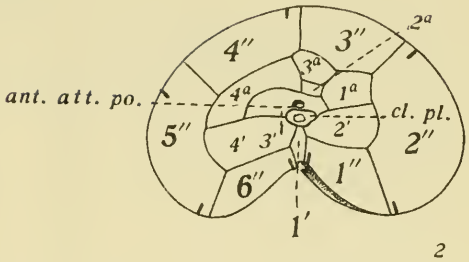
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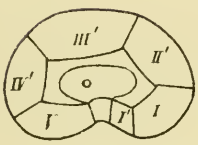
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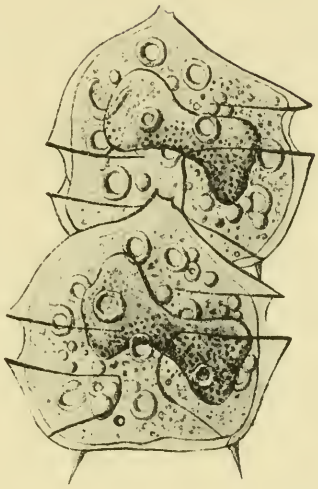

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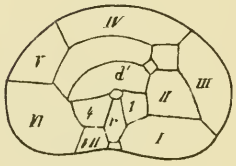
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