

THE ARMoured DINOFLAGELLATA: II. PROROCENTRIDAE AND DINOPHYSIDAE (A)

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With 2 Text-figures and 2 Diagrams

Many elaborate or voluminous monographic works of armoured dinoflagellates have been presented, leaving, however, some or other important taxonomical problems almost or entirely unsolved. It may be fruitless to carry on taxonomical studies on any groups of dinoflagellates, putting undue stress upon structural features, morphologically distinct but taxonomically insignificant. Within several years after the present author commenced his morphological study of this group of dinoflagellates, he gradually learned that almost every former investigator had failed in estimating all of the available morphological features for the purpose to find in them some significance taxonomically very important. This was mentioned, though very briefly, in one (1936) of his previous papers in regard to the genus *Peridinium*. GRAHAM (1942), paying due consideration to this, stated that "The ventral area was almost unknown in the Peridiniales when this investigation was started. Since then, however, ABÉ (1936) has begun a reclassification of the genus *Peridinium* on the bases of the structures of this regions, and TAI and SKOGSBERG (1934) have demonstrated the importance of this feature in the Dinophysiales." In regard to Dinophysidea, which corresponds to KOFOID and SKOGSBERG's (1928) Dinophysoidae, the present author found a structural feature which is in the closest connection with the ventral area and regarded as of the most taxonomical importance, although TAI and SKOGSBERG had overlooked it. This paper was written, focussing his considerations on his own observations on one hand and on the review of all available literature on the other hand, in hopes of further advancement of the studies of this animal group.

The material upon which this work was based was a small fraction of the collections made in the years 1926-1940 from various parts of the coastal waters of Japan, principally from Mutsu Bay, near the Misaki Marine Biological Laboratory and the Shimoda Marine Biological Laboratory, both facing Suruga Bay, and from the Inland Sea of Japan.

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Family Prorocentridae KOFOID

Prorocentridae KOFOID 1907: KOFOID & SWEZY 1921: LEBOUR 1925.

Syn.: Prorocentraceae SCHÜTT 1896: PAULSEN 1906: LEMMERMANN 1913: LINDEMANN 1928: SCHILLER 1928, 1931. Prorocentrinea POCHE 1913.

Of the four genera, *Prorocentrum*, *Exuviaella*, *Cenchridium* and *Porella*, the last two are well defined, while the first two have been dealt with as highly variable genera. They have been variously characterized by different authors, and moreover there have been recorded many intermediate forms which can be allocated to either of them. The present author agrees to JÖRGENSEN'S (1923) opinion that their generic distinction is arbitrary. It seems highly justifiable and at the same time practically convenient to unite them under the name of *Prorocentrum*.

BERG (1881), ascertaining the thecal wall to comprise two valves only, described that "Der Weg vom *Prorocentrum* an den Peridiniden und Gymnodiniden geht durch *Dinophysis*". And a little later, BÜTSCHLI (1887, p. 920) ingeniously observed that "Etwas in der Mitte des vorderen Randes findet sich zwischen den beiden Klappen eine rundlich Oeffnung, durch welche die Geisseln ihren Austritt nehmen. Gewöhnlich scheint diese Oeffnung etwas auf die rechte Seite verschoben und die rechte Klappe besitzt dementsprechend eine muldenförmig Ausbuchtung," These structural relationships were confirmed by WOŁOSZYNSKA (1928) and also by LEBOUR (1922) who established, so far as he is aware, closer affinities between Prorocentridae and Dinophysidae than ever suggested as referred to in later paragraphs.

Genus *Prorocentrum* EHRENBERG

Prorocentrum EHRENBERG 1833: KENT 1880-81: SCHÜTT 1896: BERG 1902: LEBOUR 1925: LINDEMANN 1928: SCHILLER 1928, 1931.

Syn.: *Exuviaella* CIENKOWSKI 1881: SCHÜTT 1895: BÜTSCHLI 1889: LEBOUR 1922, 1925: LINDEMANN 1928: SCHILLER 1928, 1931: BRAARUD, MARKALI & NORLI 1958. *Postprorocentrum* GOURRET 1883.

Since BERG (1881), the apical spine, collar or triangular extension has been assigned as belonging to the two valves. Basing on morphological analyses carried out by the present author, he was led to conclude that any of the apical extension belongs to the apical plate represented by the flagellar pore plate but not to the valves. The taxonomic demarcation of *Prorocentrum* and *Exuviaella* had not been well established since CIENKOWSKI and EHRENBERG, and later many new species were reported by various authors and allocated arbitrarily to either of them, because of very incomplete characterizations of the two genera; this brought forth taxonomic confusions, which made in turn the definition of respective genera more and more difficult. So far as the present author's analysis suggests, there could not be found any significant basic characteristics available to separate these genera from each other, because many intermediate forms and also many incompletely explored aberrant ones are recorded.

Prorocentrum micans EHRENBERG

Fig. 1 a-k.

Prorocentrum micans, BERG, 1881, p. 260, Figs. 56-59; STEIN, 1883, Pl. 1, Figs. 1-12; POUCHET, 1885, Pl. 26, Fig. 6 a-f; BÜTSCHLI, 1885, Fig. 19; OKAMURA, 1907, p. 134, Fig. 28; FAURÉ-FREMIET, 1908, p. 213, Fig. 1; LEBOUR, 1925, p. 16, Fig. 5; SCHILLER, 1928, p. 57, Fig. 17 a-e; 1931, p. 35; MARTIN, 1929, p. 11, Pl. 3, Figs. 10-13, Pl. 8, Fig. 3; BRAARUD & ROSSAVIK, 1951, p. 14, Figs. 2-4.

The thecal wall of *Prorocentrum micans* consists invariably of the two subequal bilateral valves and a small but distinct elliptical apical plate which is inlaid largely

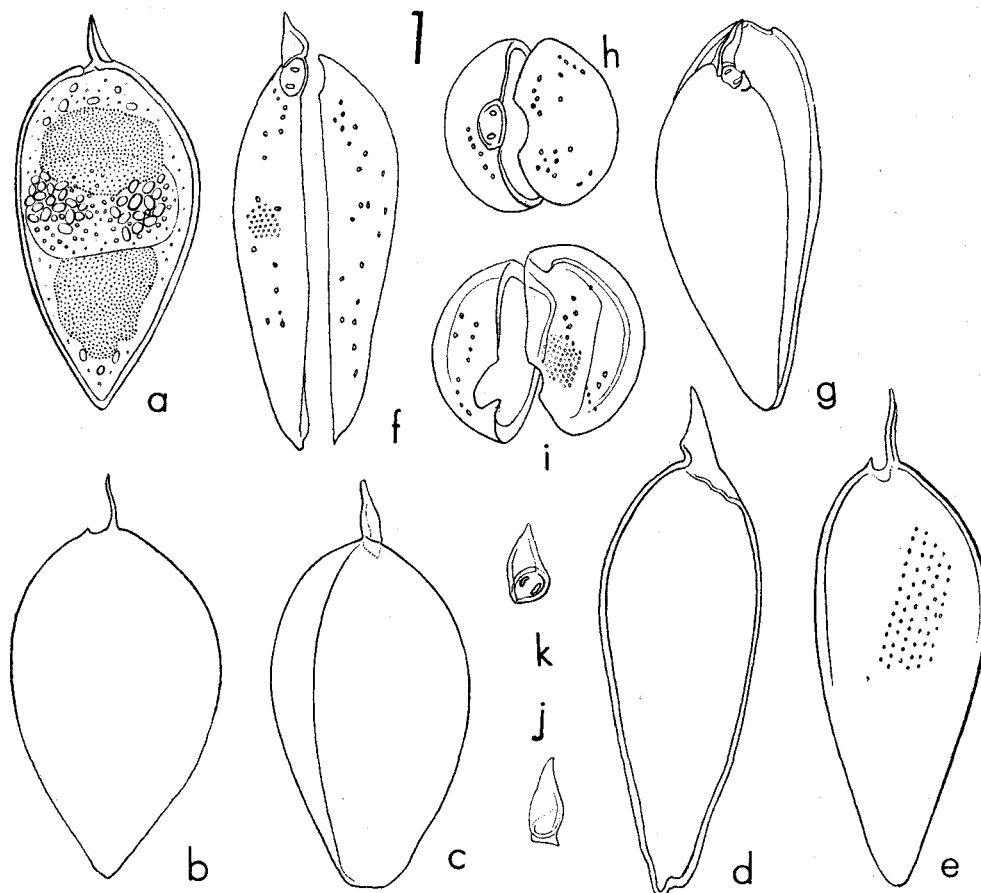


Fig. 1. *Prorocentrum micans* EHRENBERG. a-b, Side views of rather shorter specimens. c, Oblique ventral view of another shorter but more rotund specimen. d-e, Side views of rather elongated specimens. f, Ventral view of a longer specimen, split along the sagittal suture. g, Oblique ventral view of a partially split specimen, showing the apical plate furnished with a longer dorsal and a shorter triangular fins. h, Apical view of a partially split specimen with the apical plate being held within the right valve. i, Apical view of partially separated two valves, deprived of the apical plate. j-k, Ventral and oblique anterior views of isolated apical plate. In f-h and k are illustrated partially the distributions of minute pores more or less regularly arranged.

in the corresponding indentation of the right valve and partly in a smaller concavity of the other valve. The way in which this apical plate lies across the sagittal suture can clearly be seen in Fig. 1 *f* and *i*. Usually one can see a small but distinct triangular fin standing along one end of this platelet, lying nearer to or across the fission suture. This structure had been misinterpreted as a spine. Closer examination will reveal the existence of a similar but much smaller fin standing along the other end of the platelet (Fig. 1, *g*) and lying entirely within the right thecal valve. But in the majority of literature, this smaller one has been overlooked. In addition, this platelet is perforated with two tiny pores arranged along its greater dimension, that is, slantwise across the sagittal suture. It may be better avoided to name it simply as a pore plate. Oblique anterior and ventral views of this isolated platelet, together with its triangular surface extension, are illustrated in Fig. 1, *j* and *k*.

The shape and dimensions of this species seem to be highly variable as partly illustrated here and also done by BRAARUD (1951) who recorded some of its aberrant forms which resemble in some or other points *Prorocentrum micans* var. *undulatum* BOHM, *Pr. adriaticum* SCHILLER, *Pr. arcuatum* ISSEL and *Pr. gibbosum* (SCHILLER). It is a neritic species of a cosmopolitan distribution with exceptions of the Arctic and the Antarctic regions. It occurs usually in estuaries and polluted coastal regions and was often reported to be a predominant member of the phytoplankton in the coastal waters (ALLEN 1922-33, FOX 1929, BIGELOW and LESLIE 1930 and CUPP 1930), and in some years it is so numerous to form the "red water" (ALLEN 1928, 1933). It may be interesting in this regard to note that the highest figure of its density recorded in Oslo harbour was 125 480 cells per litre in 1935 and similar values were repeated there also in 1936 and 1937 (BRAARUD 1945, BRAARUD and ROSASVIK 1951).

Dimensions: Length, 48-59 μ . Bilateral dimension, 20-28 μ . Dorsoventral dimension, 16-25 μ .

Prorocentrum compressum (OSTENFELD)

Fig. 2 a-e.

Syn.: *Exuviaella compressa* OSTENFELD, 1889, p. 59; LEBOUR 1925, p. 13, pl. 1, Fig. 2; SCHILLER 1931, p. 17, Fig. 11 a-d; WOOD 1953, p. 178, Fig. 2.

Exuviaella marina SCHÜTT 1895, Pl. 1, Fig. 1; 1896, p. 8, Fig. 11.

Dinophysis compressa STEIN 1883, Pl. 1, Fig. 34.

Prorocentrum bidens SCHILLER 1928, p. 61, Fig. 21.

The body in side view is broadly ovate with the greatest dimension at premedian, median or postmedian, and its bilateral dimension is about one half of its length in specimens without any trace of the megacytic growth, but about three-fourths in the majority of the megacytic forms. The megacytic zone may often be unequal in breadth between the opposite sides of the body separated by the sagittal suture. The

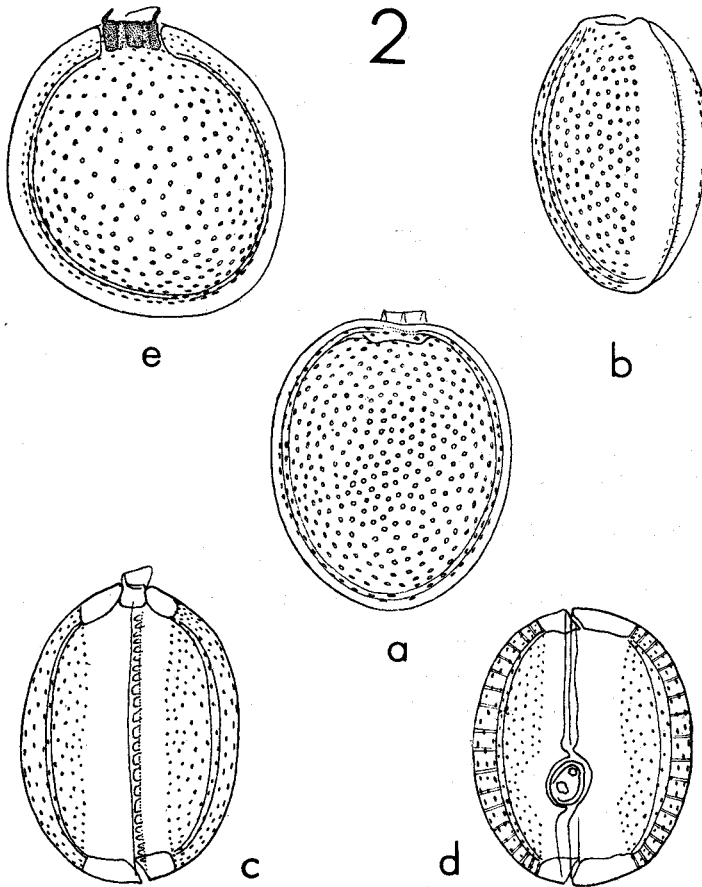


Fig. 2. *Prorocentrum compressum* (OSTENFELD). a, Side view of a symmetrically shaped specimen. b, Oblique ventral view of the same specimen showing the non-perforated growth zone. c, Dorsal view of a somewhat grown specimen, showing the subsagittal growth zone along which the thecae are thickened and the slanting inter faces between the two valves. Faces of contact are serrated. The apical fin is shown in optical section as continuous to the apical plate. d, Apical view of the specimen c with the grown zones unequally built along the suture. Minute canalicules are shown passing through the entire thickness of the thecae. e, Side view of a somewhat irregularly shaped specimen, showing an optical section of the apical plate perforated by two minute pores and with the apical collar-like structure.

apical end of body is rounded or slightly concaved. The apical plate lies largely within the right valve, extending somewhat aslant (Fig. 2 d). It has two tiny pores obliquely arranged for passage of the flagella and collar-like extensions around the plate. The structural unity of the platelet and its collar-like structures is shown in Fig. 2 c and e.

Distribution: Suruga Bay. It is regarded as an oceanic species, recorded from the subtropical and the warm-temperate waters of the Pacific, the Atlantic, the Mediterranean and the Adriatic Seas.

Dimensions: Length, 35–45 μ . Bilateral dimension, 16–18 μ . Dorsoventral dimension, 23–37 μ .

Family Dinophysidae KOFOID

- Dinophysidae KOFOID, 1906, 1907: LANKESTER, 1909: DOFLEIN, 1909, 1911, 1916, 1926, 1952: KOFOID & MICHENER, 1911: LEBOUR, 1925: PETERS, 1930.
 Syn.: Dinophysida BERG, 1882: STEIN, 1883: BÜTSCHLI, 1885: SEDGWICK, 1896.
 Dinophyseae SCHÜTT, 1896: PAULSEN, 1908.
 Dinophysiaceae PAVILLARD, 1916: JÖRGENSEN, 1923: SCHILLER, 1931.
 Dinophysoidae KOFOID, 1916: KOFOID & SKOGSBERG, 1928.
 Dinophysiales LINDEMANN, 1928: SCHILLER, 1931.
 Dinophysines CHATTON, 1952.

There have been proposed different systems of the classification of this group of dinoflagellates by various authors, putting stress in diagnosing species and genera on similarity or dissimilarity of the body shape and its surface extensions such as lists, ribs and spines as a whole, but without paying due considerations to morphological features which bear in reality much more fundamental taxonomical significance than ever been esteemed. TAI and SKOGSBERG (1934) were the first who carried out far-reaching morphological studies about the number and arrangement of the thecal plates on some genera and concluded that "in all these genera, the number of plates is constant." This conclusion is correct in the main but for one case so far as the present author is aware.

The present author commenced his morphological studies of this group of dinoflagellates in 1925 basing on the material collected from the Japanese waters, chiefly for the purpose of revealing the detailed thecal morphology as accurately as possible. Then, he has come here to the stage of presenting a new system of classification of the group, which is inconsistent with any of the previous authors'. This new system is based on the morphological features which have never been properly appreciated, but are so significant that every genus involved in this group can be characterized by them and the interrelation among genera can be defined more clearly.

A genus, *Thecadinium*, was established and assigned, though with some uncertainty, to Dinophysidea by KOFOID and SKOGSBERG (1928) to comprise two species of *Phalacroma ebriola* HERDMAN and *Phalacroma Kofoidi* HERDMAN, both of which had been dealt with by LEBOUR (1925) as *Phalacroma* species. SCHILLER (1931) followed KOFOID and SKOGSBERG's opinion. Describing four new species of *Thecadinium*, BALECH (1956) re-assigned *ebriolum* of HERDMAN to the genus *Sinophysis* which was established by NIE and WANG (1944), though with incomplete characterizations. So far as BALECH's thecal analysis reveals, although it is far from complete, only *Sino-*

physis ebriolum is to be allocated to Dinophysidae, because its theca consists of two similarly shaped bilateral valves. But judging from its extremely small epitheca, its subterminal cingulum and especially its larger posterior sulcal plate attaining half as long as the body (BALECH, 1956, p. 32, Figs. 9-22), it cannot be allocated to any known genera of Dinophysidae. No further details were illustrated by him. Moreover, the present author could not examine NIE and WANG's original paper. For these reasons, the present author cannot judge whether or not BALECH's generic allocation is correct. His considerations were paid only to BALECH's drawings, particularly to Figs. 9-13.

The thecal plates

It was TAI and SKOGSBERG (1934) who described and figured for the first time two sets of the ventral epithecal and hypothecal plates in some of Dinophysidae. Some years prior to this, the present author noticed the existence of these two sets of the paired ventral plates and of the two types of their arrangement, particularly in the hypotheca, one longitudinal and the other bilateral. As seen later, the present author found bilaterally arranged ventral hypothecal plates in *Amphisolenia* and was captured by a keen interest to uncover any of hidden phylogenetic relationships between this genus and the other genera of Dinophysidae with differently arranged ventral hypothecal plates. Those relationships might support the present author's supposition that two quite different arrangements are the results of the evolutionary divergence into two branches within the Family Dinophysidae. His morphological analyses were, then, concentrated to reveal the arrangement and the relative or total length of the ventral hypothecal plates, because it was found that the ventral epithecal plates take without exception the bilateral arrangement so far as the author's analyses uncovered. Not so far ago, it was found that the bases of the first, the second (fission), and the third ribs of the left sulcal list exactly correspond respectively to the anterior ends of the two moieties of the paired ventral hypothecal plates and the posterior or dorsal end of the posterior moiety of the paired plates in *Dinophysis* and allied genera. In other words, these three ribs consist each of longitudinally conjoined paired elements, respectively belonging to two adjacent thecal plates. After this discovery, it has become very easy to measure the accurate relative or total length of the two ventral hypothecal plates in the lateral view of specimens basing on the published figures in literature so far the ribs are shown clearly. In no case, the left sulcal list terminates in front of the posteriormost end of the paired hypothecal plates. It was at this level of the present author's achievement, that TAI and SKOGSBERG's (1934) work was published. Their work became a great support to the present author's view, as if afforded some examples of missing links by which the interrelation between the two typical types of the arrangement, longitudinal and bilateral, of the ventral hypothecal plates became recognizable to a certain degree.

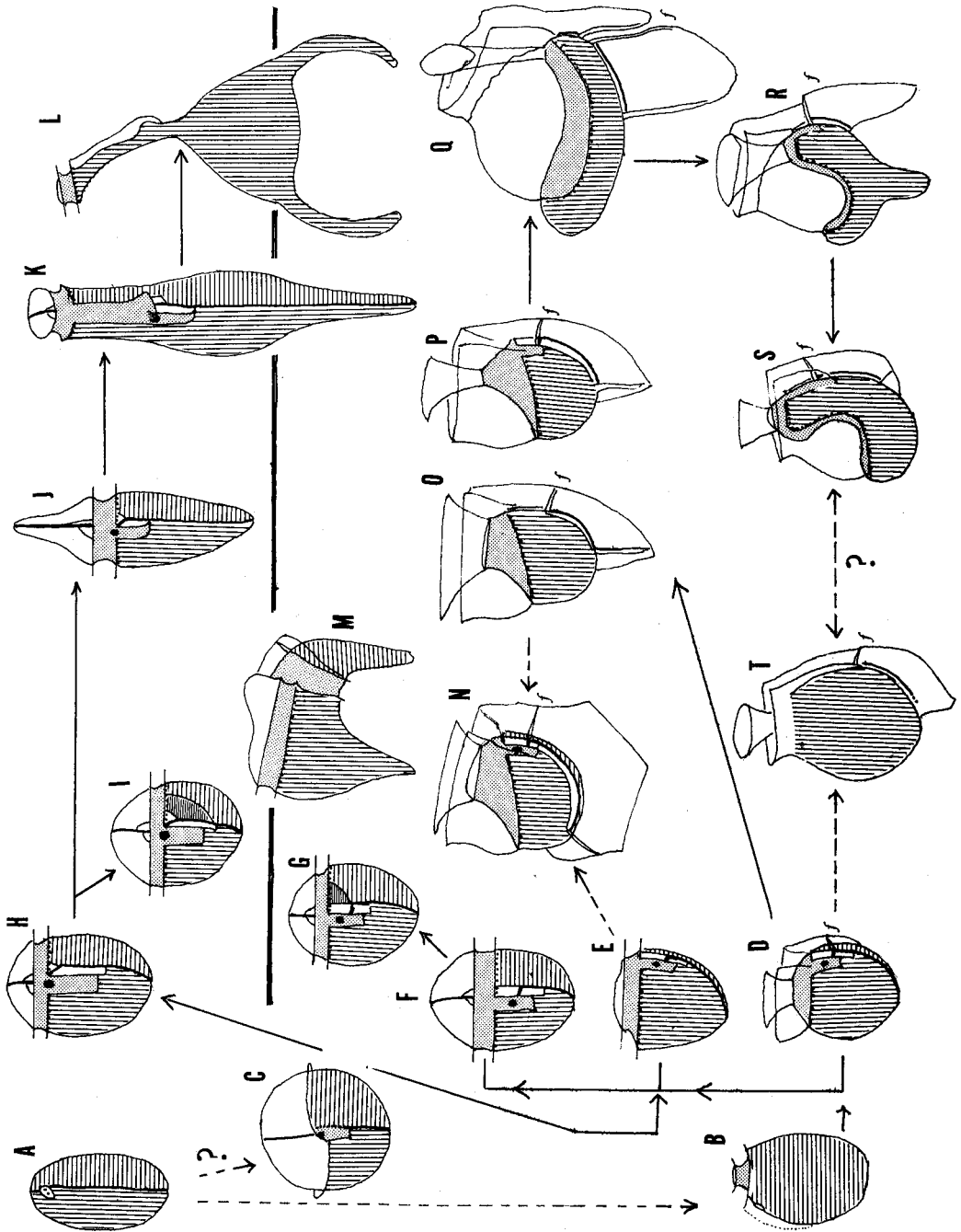


Diagram A.

Basing largely on the present author's own analytical observations and partly on TAI and SKOGSBERG's illustration which is partly misdrawn, he contrived to re-examine every species and genus found in any literature available at hand. Thus, his work has been extended to the survey of the whole field of the Family Dinophysidae from the view-points of both classification and taxonomy.

The number and arrangement of the thecal plate are still uncertain as to *Sinophysis*, *Palaeophalacroma* and *Dinofurcula*. It was ascertained, however, that the epitheca consists of two paired smaller midventral and much larger dorsal plates in *Dinophysis* (= *Phalacroma*), *Metaphalacroma*, *Heteroschisma*, *Proheteroschisma*, *Ornithocercus*, *Oxyphysis*, *Amphisolenia* and in all probability in *Tripsolemia* so far as certified or suggested by TAI and SKOGSBERG and also by the present author. Further, it can be said with little doubt that the same is true about *Histiophysis*, *Parahistioneis*, *Histioneis* and *Citharistes*. All these genera have invariably a minute epitheca, the structure of which has never been analysed into its constituent plates, presumably because of its too smaller size.

Two smaller ventral and two larger dorsal cingular plates have been confirmed in the *Dinophysis*—*Amphisolenia* group, but not yet in the *Histiophysis*—*Citharistes* group. In the latter, however, a line indicative of the suture separating the right dorsal cingular plate from the right ventral is illustrated by KOFOID and SKOGSBERG (1928) in both *Histioneis pacifica* (Pl. 20, Fig. 8) and *Histioneis elongata* (Pl. 11, Fig. 7). This seems to afford a support to the view that the cingular wall consists, in all the genera involved in the latter group, of four plates just as in the other group.

The major portion of the hypotheca, outside the ventral area, is covered with two smaller ventromedian and other two much larger dorsolateral plates in all genera excepting *Heteroschisma* and *Proheteroschisma*, in which "a postcingular plate" was recorded by KOFOID & SKOGSBERG (1928) and TAI & SKOGSBERG (1934). It may be interesting to note in this respect that the former authors wholly overlooked both of the paired ventromedian plates, while the latter authors described and figured the anterior moiety of the paired ventral hypothecal plates and the postcingular plate misinterpreting to form an unified single plate. The present author is still in doubt whether or not these two genera are worthy to be in a distinct generic status, partly because of

Diagram A. Diagrammatical illustrations of genera involved in Dinophysidae.

Longitudinally striped region represents the right valve in A or the right hypothecal plate in others. Transversely striated region represents the left valve in A or the left or left dorsal hypothecal plate in others. More finely striated region in G and I represents the so-called "postcingular plate". Finely-dotted region is the cingulum-sulcus system. White area without any marking in hypotheca represents the ventral paired hypothecal plates.

Abbreviations: A, Prorocentridae. B, *Sinophysis* (reconstructed from BALECH's). C, *Palaeophalacroma* (after SCHILLER, somewhat modified). D-F, *Dinophysis* (original). G., *Proheteroschisma* (after TAI & SKOGSBERG, somewhat modified). H, *Metaphalacroma* (after TAI & SKOGSBERG). I, *Heteroschisma* (after KOFOID & SKOGSBERG, somewhat modified). J, *Oxyphysis* (after TAI & SKOGSBERG, somewhat modified). K, *Amphisolenia* (original). L, *Tripsolemia* (original). M, *Dinofurcula* (after KOFOID & SKOGSBERG). N, *Ornithocercus* (original). O-P, *Parahistioneis* (after KOFOID & SKOGSBERG and SCHILLER, somewhat modified). Q-R, *Histioneis* (partly original, partly after SCHILLER). S, *Citharistes* (after SCHILLER, somewhat modified). T, *Histiophysis* (after KOFOID & SKOGSBERG). *f* represents the fission rib.

their extreme scarcity of the specimens examined, partly of their extreme rarity, and of feasibility of their characters not being fixed, or of their mutability or variability.

As shown in Diagram A, disregarding the three incompletely known genera, *Palaeophalacroma*, *Sinophysis*, and *Dinofurcula*, all other genera can be distributed into two groups, in one the ventral hypothecal plates longitudinally arranged and in the other with the bilaterally arranged. To the former are allocated *Dinophysis* (= *Phalacroma*), *Proheteroschisma*, *Histiophysis*, *Ornithocercus*, *Parahistioneis*, *Histioneis* and *Citharistes*, and to the latter belong *Metaphalacroma*, *Heteroschisma*, *Oxyphysis*, *Amphisolenia* and *Triposolenia*. The first three genera of the latter group agree with one another, according to TAI and SKOGSBERG's (1934) and the present author's new interpretation, in that the longer plate of the ventral hypothecal ones lies along the left side of the sulcus while the other much smaller triangular plate borders anteriorly on the cingulum. The ventral hypothecal plates in these genera are liable then to take an antero-posterior arrangement. Comparing *Oxyphysis* with *Amphisolenia*, one will notice that the ventral area of *Oxyphysis*, covered largely by the posterior sulcal plate, coincides with the some plate of *Amphisolenia*, not only in its shape but also in the structural relationships to the fission suture and the longer right ventral hypothecal plate (Diagram B_{C-D}). This suggests clearly a close phylogenetic affinity between them. The two ventral hypothecal plates in *Amphisolenia* take undoubtedly the bilateral arrangement. Basing on these, it seems most highly justifiable to regard *Metaphalacroma* as representing a primitive feature of the typically bilateral arrangement.

In all genera belonging to the *Dinophysis*—*Citharistes* group, the two ventral hypothecal plates take the longitudinal or antero-posterior arrangement, and these two plates show some variations in their relative or total length, by such differences in length respective genera are characterized. In *Dinophysis* (= *Phalacroma*)—*Proheteroschisma* (Diagram A_{D-E-F-G}) group, the total length of these paired ventral hypothecal plates is subequal with or a little greater than that of the sulcus, occupying anterior one-half or a little more of the hypotheca, but infrequently attaining the entire length of the hypotheca as in the case of *Dinophysis truncata*. The posterior moiety of the paired ventral hypothecal plates is subequal with or a little greater in length than the anterior moiety. In *Parahistioneis* (Diagram A_{O-P}), these seriated plates extend posteriorly to the middle of the hypotheca or more generally to the antapex of the body, and the posterior moiety is much longer than the anterior.

In *Histiophysis* (Diagram A_T), judging from the figure given by KOFOID and SKOGSBERG (1928, Pl. 5, Fig. 5), the anterior moiety of the seriated plates appears to extend posteriorly as far as the sulcus, shortly beyond the middle of the hypotheca, and the posterior moiety seems to terminate on the ventral of the antapex. In *Ornithocercus*, the seriated plates extend at least to the antapex, in major cases even onto the dorsal side beyond it and thus covering about three-fourths of the circumferential dorsoventral length of the hypotheca; the anterior moiety extends along about

anterior one-third of the ventral side of the hypotheca (Diagram A_N). So far as concerned with the illustrations found in literature, the total length of the paired plates in *Histioneis* (Diagram A_{R-B}) seems to vary greatly in different species, occupying a little or much less than the ventral half of the circumferential length of the hypotheca, and the anterior moiety appears to be very short. In *Citharistes* (Diagram A_S), the plates lie along the major ventral length of the hypotheca, so far as judged from the published figures.

Looking through Diagram A, one may become aware of the peculiarities exhibited respectively in the *Metaphalacroma*—*Tripsolemia* group and the *Dinophysis*—*Citharistes* group. In the former group, the cingulum keeps a fairly uniform width all around the body which is elongated antero-posteriorly in *Oxyphysis* or so only posteriorly in *Amphisolenia* and *Tripsolemia*, while in the latter group quite variable modifications are seen. In many species of *Dinophysis*, it is noticed that the cingulum keeps its subequal width all around the body, while the cingular bottom-wall is more strongly slanting on the dorsal side than in the midventral portion. As a result, the bottom-wall of the cingulum comes broader, though very slightly, from the midventral towards the mid-dorsal. This dorsoventral difference in breadth of the cingular wall becomes increasingly pronounced so distinctly in some of advanced genera in the order of *Ornithocercus*, *Parahistioneis* and *Histioneis*. Roughly in parallel with this, there can be seen a trend towards the reduction of the epitheca and also towards the antero-posterior flattening of the hypotheca; the latter results in many cases in the dorsoventral elongation of the body as schematically illustrated in the order from Fig. E to Fig. Q. In some species of *Histioneis* (Fig. R), the body outline from lateral is remarkably bent down posterodorsally, superficially presenting a transitional form connecting the typical *Histioneis* (Fig. Q) with *Citharistes* which is distinguishable from the aberrant forms of *Histioneis* by its greater body length as is the case of *Histiophysis*. As to only the body shape, the form similar to *Histiophysis* may be found in some typical species of *Dinophysis*. On the other hand, *Histiophysis* is closely related to *Citharistes* in regard to their greatly elongated ventral hypothecal plates and also to their body length not so much reduced. The peculiar and characteristic features of *Citharistes* can be induced by the dorso-posterior elongation of the cingulum at the sacrifice of the corresponding part of the hypotheca.

The cingular and sulcal lists

Both of the cingular and the sulcal lists are built less remarkably in all species and genera of the *Metaphalacroma*—*Tripsolemia* group and in some of the least differentiated forms of the *Dinophysis*—*Citharistes* group, while they are much broad or stoutly formed in some of the highly differentiated genera of the latter group. In any case, however, it is to be reminded that the anterior cingular list consists of the

marginal extensions of the four epithecal plates, while the posterior cingular list and the right sulcal list are marginal extensions of the larger dorsal hypothecal plates, whereas the left sulcal list consists of usually three and not infrequently two components of different origins: the anterior standing along the anterior or median margin of the lateral or anterior moiety of the paired ventral hypothecal plates, the middle along the median margin of the posterior moiety of the paired plates, and the posterior or the dorsalmost, if present, standing along the median margin of the right dorsal hypothecal plate. In *Amphisolenia* and *Tripsoleonia*, however, the most part of the left sulcal list is nothing but the posterior continuation of the posterior cingular list, standing along the ventral anteromedian margin of the left dorsal hypothecal plate, while the marginal free extensions of the paired ventral hypothecal plates form only the posteriormost small portion of the left sulcal list. In any case, however, the fission rib stands invariably within the span of the sulcus, because the sagittal fission suture passes through the sulcus.

Presumably owing to the great difficulties of analysing the morphological details of the encrusting thecal wall of these organisms, in diagnosing genera and species, apparently undue stress has been put on the shape, size, extent and the structural differentiation of the cingular and the sulcal lists, but without paying efforts in advance to inquire into the property, nature, and the construction of these and further into the limit, degree, and the direction of their structural differentiation. The details of variations of these lists must be given, not only as a whole but also in respect to their different constitutional elements. So far as revealed by the morphological analyses of the present author, the most distinct structural variations of the lists in regard to the genus *Ornithocercus* are centered in the posteromedian portion of the left sulcal list, built along the entire length of the posterior ventral hypothecal plate. In this regard, it is necessary to take the following facts into account. This part of the list acts simply as a sail, rudder or a keel, while other portions of the same list and other lists bear invariably more or less important relationship to either of buoyancy of body or activities of the transverse and the trailing flagella; some sorts of deficiency or abnormality beyond a certain limit in the latter portions of the lists, may be fatal to the organism. Of all genera of Dinophysidae, *Ornithocercus* is the one that occurs most frequently in the surface water subjected to the frequent changes in light intensity, salinity, and temperature caused respectively by solar radiation, storms, precipitations, and mixing of the sea water with the coastal, river, or upwelling water. These surface extensions of the thecae are re-built at every binary fission, though partly, outside the body by temporally extruded extramembraneous cytoplasm. For these reasons, it is very probable that the structural variations will occur most feasibly in those thecal portions extending out from the body surface into the ambient water and being subjected to its everchanging physico-chemical environmental conditions. Similar variations or the structural differentiation may occur in some parts of these lists in genera other than *Ornithocercus*, although such variations

are scarcely recorded. No further descriptions are given here about the lists of the species and general with highly specialized cingular and sulcal lists, which are not yet examined actually in detail by the present author. But, here it is very noticeable that, contrary to many authors' observations, the anterior cingular list is closed in the midventral portion in every species or genus while the posterior cingular list is invariably interrupted in the midventral by the sulcus, and that the ventral margins of the right and the left sulcal lists are never attached to each other to form a canalicular structure closed ventrally and opening only at both the anterior and posterior ends as misinterpreted in *Parahistioneis* or *Histioneis* in KOFOID and SKOGSBERG's (1928) voluminous monographic work. That work seems to comprise imaginations and erroneously or carelessly made misdescriptions in some places, at least in the part regarding the structural relations of the cingular and sulcal lists. Consequently, only the drawings given or cited by KOFOID and SKOGSBERG (1928) or SCHILLER (1931) are referred to and availed in discussing the structural relations of the broad and well developed cingular and sulcal lists seen in the highly specialised forms of Dinophysidae.

The ventral area or sulcus

TAI and SKOGSBERG (1934) described that the sulcus of Dinophysidae consists of four sulcal plates. The present author also reached the same conclusion in regard to the number and arrangement of the sulcal plates in *Dinophysis* (= *Phalacrocoma*), *Ornithocercus* and *Amphisolenia*. Although nothing has been recorded on the structural differentiation of the sulcus in *Dinofurcula*, *Histiophysis*, *Parahistioneis*, *Histioneis* and *Citharistes*, it seems very likely that these five genera agree to *Dinophysis* or *Ornithocercus* in the structural relations of the sulcus, because the sulcus in these genera does not show any distinctive peculiarities or irregularity in its extent and lateral expansion, but retains a subequal width throughout its length and the flagellar pore seems to lie in front of or posterior to the fission rib of the left sulcal list just as in other genera. In this regard, it is to be emphasized that all genera of Dinophysidae exclusive of *Amphisolenia* and *Triposolenia* agree to one another in the structure of the sulcus or rather the ventral area which is keeping a subequal width throughout its entire length and truncated at the posterior end. In the arrangement of the four sulcal plates, all bordering directly the flagellar pore, all genera of Dinophysidae agree to *Peridinium* and its allied genera (ABÉ 1936-41). In the *Peridinium* group, however, the ventral area exhibits a fairly great variation in its size, extent and shape in accordance with the expansion or elongation of respective sulcal plates. It is very interesting that in *Amphisolenia* and *Triposolenia* the posterior sulcal plate comes out of the longitudinal furrow or the sulcus which is nothing but a surface groove specially differentiated to guard the proximal parts of the flagella. This feature, together with the sulcal quartet, can not be of a morphological or taxonomical significance, because the

similar features are ascertained in the Family Podolampidae (ABÉ, 1966) and in the genus *Peridinium* and its allies (ABÉ 1936-41) too, all these are taxonomically very distinct and of course to be assigned respectively to quite different evolutionary lines.

The interrelation between the sulcus, the sagittal suture and the megacytic zone was described and figured for the first time by TAI and SKOGSBERG (1934, p. 397-), though with some uncertainty. Finding four constituent plates in the sulcus, the authors advocated to classify them, though only for convenience' sake, into two pairs. The arrangement of these four plates was confirmed also by the present author in many species described in this paper. It is very peculiar that the arrangement coincides with that of the genus *Peridinium* (ABÉ 1936-41) and its allies. In Podolampidae (ABÉ 1966), however, the arrangement is somewhat modified, presumably in close association with the entire lack of the cingulum. In Dinophysidae, the posterior sulcal plate covers mostly the entire breadth of the posterior portion of the ventral area posterior to the flagellar pore, as schematically illustrated in four figures of Diagram B.

Theoretically and practically, four types of the plate arrangement can be defined in the anterior half of the sulcus: (1) the left sulcal extends to or slightly beyond the posterior cingular ridge of the same side, while the anterior and the right sulcals extend anteriorly to the epitheca as represented in Fig. A of Diagram B; (2) all of the anterior, the right and the left sulcal plates reach the epitheca (Fig. B); (3) the left sulcal is much reduced (Fig. C) and (4) both of the right and the left sulcals extend anteriorly shortly beyond the posterior cingular ridge, while the anterior sulcal only reaches the epitheca (Fig. D). Nearly all species of *Peridinium* and its allied genera have the ventral area of Type A, and this type of the arrangement was ascertained so far as analyzed by the present author himself, in the species and genera with the ventral hypothecal plates arranged antero-posteriorly. The Type C was illustrated by TAI and SKOGSBERG (1934, Fig. 14 H) in *Oxyphysis*, and the Type D was ascertained by the present author in *Amphisolenia* and some species of *Dinophysis*. The Type B may be the case of TAI and SKOGSBERG's *Metaphalacroma skogsbergi* and (*Pseudophalacroma*) *nasutum*, for the latter of which the American authors illustrated two different subtypes: in one subtype the left sulcal borders directly the flagellar pore (Fig. 14 K), while in the other (Fig. 14 B) the same plate is lying along the entire span of the left ventral end of the cingulum, but separated from the flagellar pore. So far as the present author's observations are concerned, the latter subtype (Fig. 14 B) has never been ascertained in nature, or theoretically it is not the configuration thought of normally.

The megacytic or growth zone

In all species and genera including *Dinophysis* and others so far analyzed, the megacytic zone on the ventral side of the body disappears invariably at the level of the fission rib of the left sulcal list. However, none has been reported about the

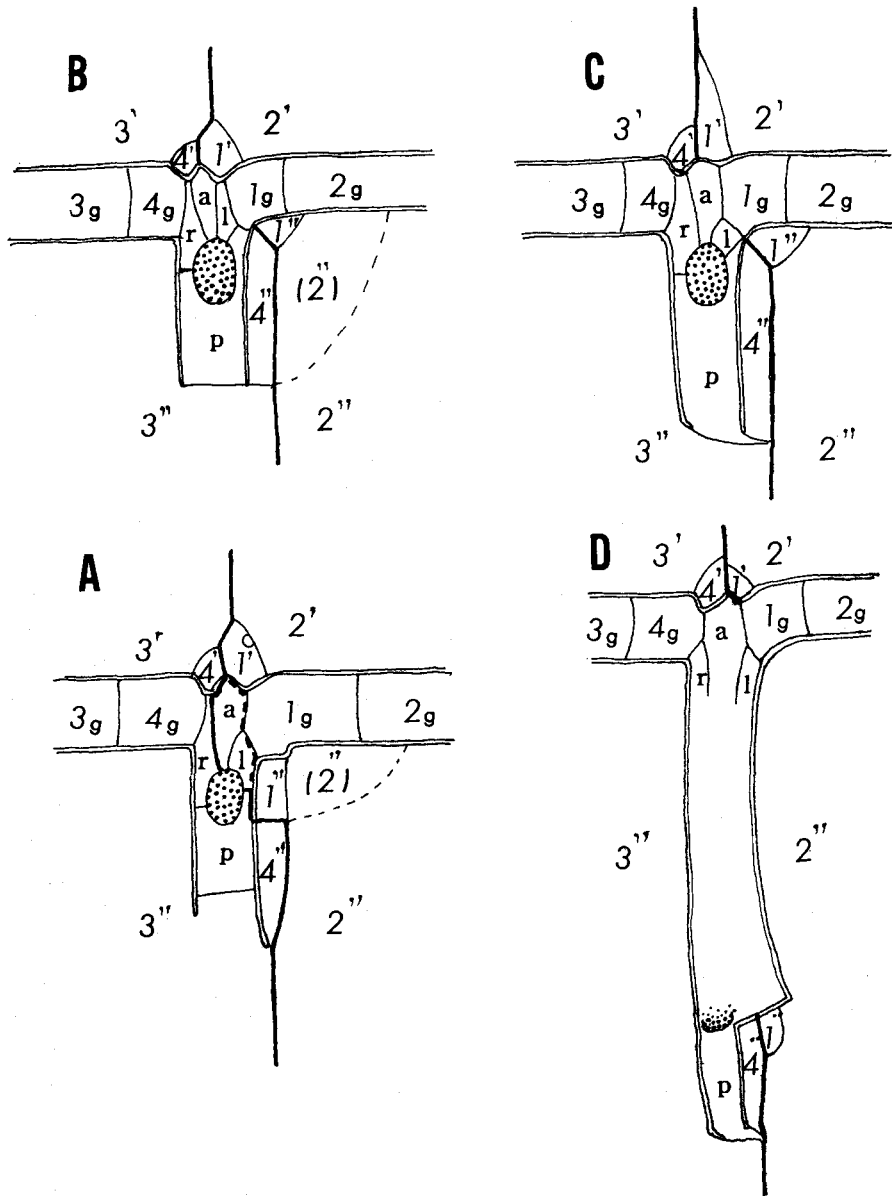


Diagram B. Plate pattern in and around the sulcus. 1'-4' represent epithelial plates. 1_g-4_g represent the cingular plates. 1''-4'' represent hypothetical plates, the so-called postcingular plate is represented with (2''). a, r, l, p represent respectively the anterior sulcal, the right sulcal, the left sulcal and the posterior sulcal plate. A thicker solid line passing between 1'' and 4'' posteriorly and between 4', 3' and 1', 2' anteriorly is the fission suture along which the megacytic or growth zone is formed. A thicker broken line within the sulcus of fig. A represents the route along which is built the overgrown megacytic zone. The *Dinophysis*-*Citharistes* group may be represented by the Type A, *Heteroschisma* by the Type B, *Oxyphysis* by the Type C and *Amphisolenia* and *Triposolenia* by the Type D.

relation between the growth in breadth of the megacytic zone and variations in shape and size of the body. Growth of the thecal wall occurs only along the sagittal sutural zone both in Prorocentridae and Dinophysidae. In the former, the breadth of the growth zone is equal or subequal all around the body and the relative structure of the apical plate to the sutural line is little affected by the formation of the growth-zone. In the latter, however, breadth of the growth zone is invariably kept at the minimum in the midventral region of the cingulum, irrespective of the sagittal suture passing through the small anterior portion, the anterior half or the entire length of the sulcus. In the epitheca, the megacytic zone regularly becomes broader towards the dorsal. In the hypotheca, which is somewhat irregular and variable in the lateral outline in major cases, the greatest breadth of the megacytic zone is found either in the antapex or on the dorsal of it. On the ventral side, the zone becomes narrower towards the fission rib or further towards the cingulum, but on the dorsal side the zone becomes narrower towards the cingulum or keeps its subequal breadth throughout its anterior major length.

Here, two types of the megacytic zone formation are distinguished. In most of the species in which the bilateral thecal valves meet each other posteriorly along the suture in a sharp-wedge-shape, the megacytic zone on either side is broadened in conformity to the original surface convexity of the hypothecal plate. In such cases, the shape and length of the body in lateral outline comes to vary according to differential growth of the megacytic zone. There can be found another type of the megacytic zone growth quite different from this. In the hypotheca of *Dinophysis mitra*, the present author ascertained that the broad megacytic zone is formed in the bilateral direction, bending more or less sharply along the original outer margin of the dorsal hypothecal plate. Consequently, the triangular hypotheca of younger specimens becomes quadrangular in dorsoventral view in overgrown stages, although in the epitheca the megacytic zone is built in conformity to the original surface of the epithelial plates, keeping as a whole a broad triangular contour in dorsoventral view throughout the growing stages of the megacytic zone. The present author found some intermediate forms connecting these two extreme cases and also observed some cases in which the megacytic zone was flattened in the epitheca and hull-shaped in the hypotheca or the wedge-shaped antapex was more and more rounded with the increase of the megacytic zone in breadth. In this respect, it is noteworthy that SCHILLER (1931) presented an extremely megacytic form in his Fig. 59 *b* under the name of *Phalacroma rudgei*, in which the megacytic zone is strongly flattened all around the body. At any rate, on these findings, the present author attained the conclusion that it is very important in diagnosing rather smaller species of *Dinophysis* to be careful not to put undue stress on small variations of body shape and size, unless inquiring into detailed morphological features of the megacytic zone formation, as the zone will bring about fairly distinct variations of body shape and size in those species.

In ordinary cases, the megacytic zone is formed equally on either side of the

sagittal suture. Not rarely, however, the breadth of the zone will show slight differences between the right and left sides of the suture. In extremely asymmetrical forms, the megacytic zone is formed broadly only along one side of the sagittal suture in both the epitheca and the hypotheca (Fig. 24). Though it is uncertain whether or not such irregularities are due to the environmental conditions, it seems that the breadth of the megacytic zone does not increase continuously but intermittently. The rather broader megacytic zone is usually marked on the surface with reticulation similar to that on the general hypothecal plate, and the reticulation in each bilateral half of the megacytic zone is often divided into more than two parallel stripes according to the grade of clearness of meshworks, which are most pronounced in the stripe along the outer margin of the original thecal plate, but most faint in the stripe directly along the suture. On the other hand, the present author happened to observe a few specimens with an extremely broad megacytic zone. In some of these specimens, the megacytic zone is clearly distinguished from the original extent of the thecal plate by a distinctly formed ridge which indicates clearly some intermittent stages of the formation of meshworks and in some others such a demarcation is vanished completely, suggesting occurrence of reorganization of the meshwork along the thecal surface.

The megacytic zone of Dinophysidae corresponds to the sutural zone of *Peridinium* and its allied genera, in which the sutural zone is distributed all over the body surface yielding to body growth. That of the Dinophysidae is characterized by the complicated structural differentiation of the faces of contact between the two thecal valves. In surface view, the sagittal suture appears to consist of a zigzag line, but closer observations reveal that the narrow band including this zigzag line within it is divided into bilateral subequal halves by a very faint and straight line running on the outermost surface of the band. By pressing apart the two adjoining thecal plates, one can discern that the face of contact of these plates is ornamented with alternately arranged conical indentations and corresponding conical processes, showing as a whole a regularly serrated margin. The basal halves of the processes are covered by a narrow lamella extending from the outermost surface of the thecal wall. In the natural and intact state, the conical processes of one plate are tightly held in the corresponding indentations of the opposite plate so that the distal margins of the narrow outermost lamellae come to contact with each other as illustrated in Fig. 21 on *Dinophysis cuneus*. In none of other sutures, any trace of such a serrated structural differentiation has been ascertained. The fact that the two valves are liable to be separated along this sagittal suture and the growing of the thecal plates is allowed only along the same suture, are apparently due to that the two valves are kept mechanically with each other only by this complicatedly differentiated structure, while the other sutures in general are very simple in structure, presumably fixedly combined with one another by some chemical or physical means.

Although the double foldings of the left sulcal list at the level of the fission rib had not been properly elucidated before TAI and SKOGSBERG (1934), this peculiarity was often figured, particularly clearly by KOFOID and SKOGSBERG (1928). This double folding is really due to the leftwards displacement of the anterior moiety of the paired ventral hypothecal plate together with the anterior or left element of the conjoined fission rib, and complementally new formation of a transverse list connecting the separated elements of the fission rib. Within the sulcal area, the growth zone is arranged, according to TAI and SKOGSBERG (1934, p. II, fig. 2), anteriorwards from the transversely formed list to the midventral end of the sagittal epithecal suture by passing across the flagellar pore. Their conclusion seems correct and reasonable in the main, though far from complete to show all the facts. So far as uncovered by the present author, there are two distinctly different types or routes of the zone formation. In the type regarded as ordinary one, the anterior and the left sulcals and the right and the posterior sulcals are separated to different daughter specimens as surmised from Fig. 10 *m*; this agrees in the main with TAI and SKOGSBERG's observation.

It is, however, questionable whether or not the growth zone is formed in the portions imaginarily illustrated by them. Fig. 17 *f* is the ventral view of a partially dissociated specimen of *Dinophysis porodyctyum*. It is noteworthy that the lateral dimension of the right sulcal plate is increased greatly, but the breadth of the anterior and the left sulcal plates is increased only slightly and that the actual route of the sagittal growth zones along the lateral sides of these plates can be suggested by the serrated feature along the plate edges, which is unique for the sagittal fission suture. In addition, the development of a broad and distinct growth zone along the median margin of the anterior ventral hypothecal plate and that of the right ventral cingular plate cannot be overlooked. The above mentioned plates are not originally the sulcal elements, but the medianward extensions of the extrasulcal ventral hypothecal and ventral cingular plates. It is interesting in this regard that the ventral pore in this case is deformed to be somewhat elongated towards the proximal end of the girdle, presumably in conformity to the obliquely extended proximal portion of the transverse flagellum. In extremely pronounced megacytic forms of *Dinophysis mitra*, one can distinguish a different type (Fig. 18 *p*) in which, though the anterior sulcal plate was lost during the present author's treatment, the right and left sulcal plates are nearly unchanged in shape and size, nevertheless the distinct broad megacytic zones, structurally continuous to the anterior ventral hypothecal and the left ventral cingular plates, are formed longitudinally along the left side of the three ordinary anterior sulcal plates to connect the intra-fission-rib megacytic zone directly with the zone at the ventral end of the epitheca. Then, Fig. 18 *q* is peculiar in this respect. The figure represents the right valve only and clearly shows the right sulcal plate of the type of Fig. 17 *f*, thus suggesting the occurrence of two different types of the megacytic growth within a single species. In the former type, the fission suture, accompanied

with the sutural grown zone, passes across the flagellar pore even partially, but in the latter type the conclusive feature is not similar.

There is another example which seems most suitable for inquiring into the property or the nature of the megacytic zone. KOFOID and SKOGSBERG (1928) presented the ventral view (Pl. I, Fig. 7) of an extreme megacytic specimen of *Heteroschisma aequale*, which exhibits unusual structural relations between the sulcus and the megacytic zone. This had been left unaccounted for before TAI and SKOGSBERG (1934) reported the morphological details of *Metaphalacroma* which was characterized by its extremely small anterolateral moiety of the paired ventral hypothecal plates. This small anterolateral hypothecal plate is considered theoretically as dislocated laterally from the sulcus by the development of the megacytic zone running along almost the entire length of outside the sulcus and forming anteriorly a unified continuous zone across the midventral portion of the cingulum, but keeping the closest contact with the larger left dorsal hypothecal plate. The corresponding structural features were shown in KOFOID and SKOGSBERG's figure, in which are shown a minute triangular structure, suggestive of the anterolateral moiety of the ventral hypothecal plates, lying along the left side of the megacytic zone and along the posterior cingular ridge, and the longitudinal sagittal suture running along the middle of the broad megacytic zone and without any connection with the flagellar pore.

Considering these facts, it is proposed here to distinguish 'the growth zone' from 'the megacytic zone.' The former, here proposed newly, represents the younger growing stages of the sagittal sutural zone and bears the capability to bring forth the binary fission of the body as the result of the further growth of this zone, whereas the latter represents the extremely overgrown stages of the same structure, which is now so arranged and forfeited the reproductive ability to bring forth the binary fission. In this respect, it is very interesting to note that such overgrown specimens not only of *Dinophysis* but also of *Peridinium* which bears an encysted body within the overgrown empty theca were observed most frequently in Mutsu Bay which is comparatively shallow throughout and scarcely affected by the oceanic inflows because of its narrow mouth. On the contrary, not a single one of such overgrown specimens has been seen in Suruga Bay. The record of the extreme megacytic specimen of *Heteroschisma* was ever made by KOFOID and SKOGSBERG also at a coastal station in the vicinity of Callao in the East Pacific.

Interrelations between genera

It has been accepted generally that the taxonomy of armoured dinoflagellates is to be based upon the number and the arrangement of the thecal plates. It was TAI and SKOGSBERG (1934) who established for the first time that the number of the thecal plates is constant in some species and genera of Dinophysidae. Basing on his own

observations and also reviewing literature, the present author is going to prove in the following that, with the exception of *Heteroschisma* and *Proheteroschisma*, the number of the thecal plates is constant throughout the Family Dinophysidae, and that all genera involved in the family, are divided into two groups in regard to the arrangement of the paired ventral hypothecal plates. Incompletely known *Palaeophalacroma*, *Dinofurcula* and *Sinophysis* are left out of consideration in both cases.

It is very questionable which of the bilateral and the anteroposterior arrangements of the paired ventral hypothecal plates is more primitive. Judging from the facts that the bilateral symmetry is fairly well maintained throughout the structural features of the body as a whole and the paired ventral epithecal plates keep unexceptionally the bilateral arrangement, it seems highly justifiable to regard the bilateral arrangement of the ventral hypothecal plates as more primitive. The two groups of genera thus divided exhibit respectively different trends of the morphological differentiation as given in Diagram A.

KOFOID and SKOGSBERG (1928, p. 30-31) assumed, though with some uncertainty, that the equatorial position of the cingulum is the sign of the most primitive feature in this group of dinoflagellates. Their assumption was based on the facts that in the majority of highly specialized forms the cingulum is in the main anterior subterminal and that highly morphological differentiations can be seen solely in the larger hypotheca. If this assumption is to be accepted, then what is the situation of *Sinophysis*? This genus resembles much closer some of *Dinophysis* than the highly advanced genera.

Other knotty problems in that assumption are that any of the primitive species of Dinophysidae is more closely related in essential morphological features to Prorocentridae than to any of the unarmoured dinoflagellates and that it seems more expedient and reasonable to place the first emergence of the cingulum or its precursor in the earliest stages of the evolutionary tract of dinoflagellates to the area surrounding the apical plate or the flagellar pore than to imagine the first appearance of the much elongated cingular structure around the largest portion of the body, far posterior to the old apical plate or the flagellar pore. The preceding assumption presented by the present author seems to be more easily accepted to understand the diversified evolutionary tracts of the Dinophysidae, including on one hand some forms in which the increase of size and the structural differentiation are seen mainly in the hypotheca and on the other hand some others in which the increase of size occurs in both the epitheca and the hypotheca.

Taking the above-mentioned facts together with variously developed morphological features of the epitheca, the cingulum, the sulcus, the hypotheca, the cingular and the sulcal lists, and the arrangement of the paired ventral hypothecal plates into account separately or in combinations, the present author proposes here a new system of classification of the Family Dinophysidae, leaving *Sinophysis*, *Palaeophalacroma* and *Dinofurcula* as uncertain genera, the exact situations of which are not yet confirmed.

Classification

Family Dinophysidae

- Genus *Sinophysis* BALECH
Palaeophalacroma SCHILLER
Metaphalacroma TAI & SKOGSBERG
Heteroschisma KOFOID & SKOGSBERG
Oxyphysis KOFOID
Amphisolenia STEIN
Tripisolenia KOFOID
Dinophysis EHRENBERG
Proheteroschisma TAI & SKOGSBERG
Histiophysis KOFOID & SKOGSBERG
Dinofurcula KOFOID & SKOGSBERG
Ornithocercus STEIN
Parahistioneis KOFOID & SKOGSBERG
Histioneis STEIN
Citharistes STEIN

In the systematic account to be given in the forthcoming papers, the group of genera with the anteroposterior arrangement of the ventral hypothecal plates will be dealt with first, because its occurrence is more general than that of the group with the bilateral arrangement of the plates, and it may be understood more easily.