NOMENCLATURE AND HOMOLOGY IN PERIDINIALEAN DINOFLAGELLATE PLATE PATTERNS

by GEOFFREY L. EATON

ABSTRACT. The apical and antapical series of peridinialean dinoflagellate thecal plates are redefined relative to the cingulum. They are then compatible with the Kofoidian pre- and postcingular series, and the need to recognize anterior and posterior intercalary series is removed. The concept of apical closing and antapical closing series is introduced. Homologous and corresponding plates are recognized in fifteen selected modern and fossil dinoflagellates by comparing interseries relationships with respect to a model plate pattern. The differences between the selected patterns are due to three variable effects. First, the reduction in plate number through simplification, where one plate in one pattern corresponds to two or more plates in another pattern. This critically affects interseries relationships. Secondly, the primary development of fewer plates without affecting interseries relationships. Thirdly, the variation in the relative size of certain plates. The interaction of these three effects resulted in the comparatively independent evolution of epithecae and hypothecae. Reduction in over-all plate number, particularly through the primary development of fewer plates, may well represent a fundamental trend in the evolution of peridinialean plate patterns.

THE dinoflagellates of the Order Peridiniales Haeckel 1894 are often informally described as 'armoured'. They are so called because their cell covering includes a layer of rigid, polygonal, suturally united, cellulosic plates, termed the theca. Text-fig. 1 shows thecal morphology and nomenclature in two typical peridinialean dinoflagellates, *Protoperidinium depressum* (Bailey) Balech 1974 and *Gonyaulax spinifera* (Claparède and Lachmann) Diesing 1866. The theca is divided into two parts, epitheca (anterior) and hypotheca (posterior), which are separated by an equatorial groove termed the cingulum. The two ends of the cingulum are separated on the ventral surface by a more or less longitudinal groove termed the sulcus. Motility is achieved by the beating of two flagella (not shown in text-fig. 1) which originate from the sulcus. The transverse flagellum lies within the cingulum, while the longitudinal flagellum lies within, and extends posteriorly beyond, the sulcus. The thecal plates are arranged in roughly parallel transverse series. Differences in tabulation; that is the number, shape, and arrangement (plate pattern) of the thecal plates, have long been used as the main criterion for taxonomic separation within the Peridiniales. The accepted system of thecal plate nomenclature was defined by Kofoid (1907, 1909, 1911).

The fossil peridinialean dinoflagellate record ranges back at least 200 million years into the Late Triassic period. However, in terms of representing the absolute geological history of the Peridiniales, this record has only limited effectiveness. This is because all fossilized dinoflagellates attributed to the Peridiniales are non-motile cysts rather than motile thecae, and modern studies show that only a very small proportion of living peridinialeans produce potentially fossilizable cysts. Comparisons between modern thecae and fossil cysts show that not all modern plate patterns have been recognized in the fossil record, and some fossil plate patterns are unknown in modern dinoflagellates. Accepting the limitations of the fossil record, and the fact that cysts only rarely show full details of their parent thecal tabulation, it is still possible that the relative distribution of the different plate patterns through geological time may provide some evidence of trends in plate pattern evolution. The recognition of such trends is dependent on the critical assessment of the similarities and differences between different plate patterns. Such an assessment will involve the recognition of homologous plates in different patterns. In my own studies on fossil dinoflagellates I have found that a strict application of Kofoid's

plate nomenclature often results in apparently homologous plates in different patterns, being assigned to different transverse plate series. I believe that compatibility between nomenclature and homology is essential for the recognition of evolutionary trends, and that it can only be achieved by modifying certain aspects of Kofoid's system. Discussion of the need for this modification and a way of effecting it, forms the basis of this paper.

According to Evitt *et al.* (1976) fossil cyst plate patterns should be discussed in terms of their paratabulatory nomenclature (paraplates, parasutures, etc.). However, in this paper on modern
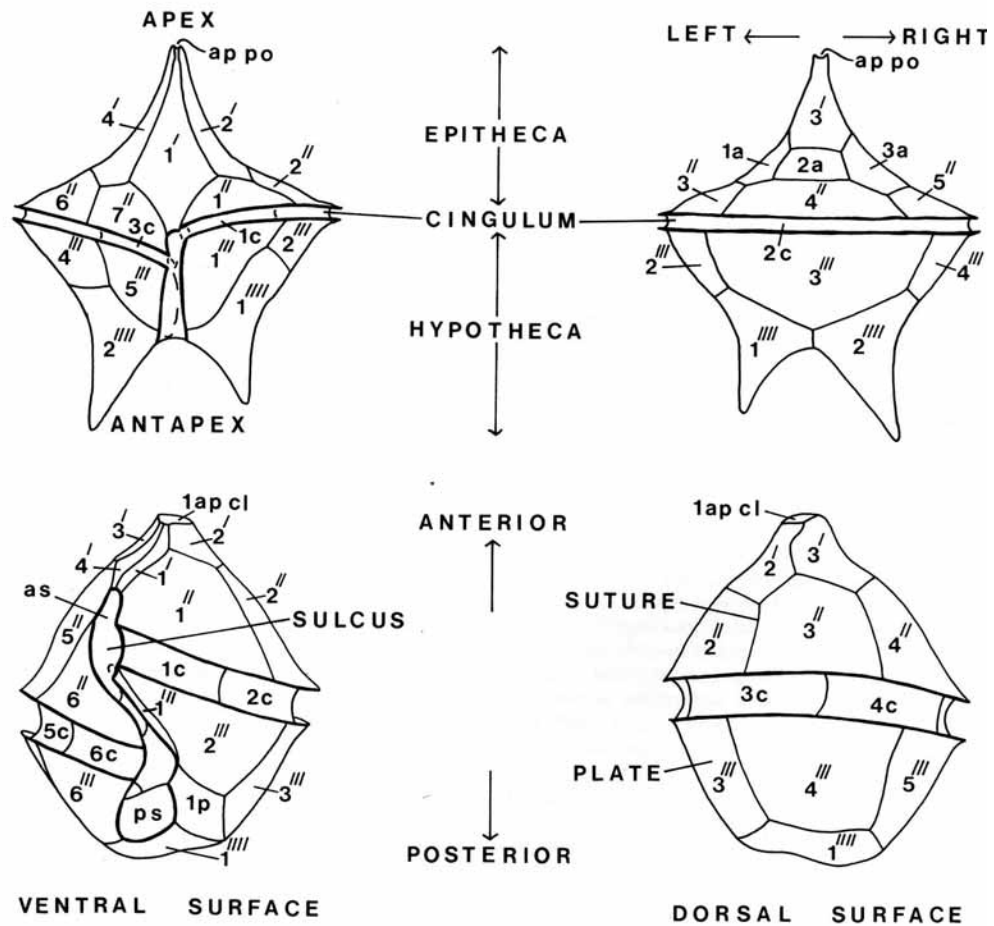
TEXT-FIG. 1. Thecal morphology of two modern peridinialean dinoflagellates. Upper, *Protoperidinium depressum* (Bailey) Balech 1974. Lower, *Gonyaulax spinifera* (Claparède and Lachmann) Diesing 1866. Interpretation of the transverse plate series is conventional Kofoidian. The distribution and number of cingular and sulcal plates in *P. depressum* is assumed to be typical of the genus. In *G. spinifera* only the anterior (a.s.) and posterior (p.s.) sulcal plates are annotated.

thecae and fossil cysts I wish to avoid the use of a dual 'tabulation/paratabulation' nomenclature. Therefore I assume that the fossil cyst paraplate patterns are a fair representation of their parent thecal plate patterns, and treat them all, modern and fossil, simply as plate patterns.

ORIGIN AND DEVELOPMENT OF THE KOFOID SYSTEM OF THECAL PLATE NOMENCLATURE

Although the system of peridinialean thecal plate nomenclature which has been generally used for the past seventy years is attributed to Kofoid, it should be remembered that he was clearly influenced by several nomenclatural systems proposed by earlier workers, e.g. Stein, Bütschli, Schütt, Paulsen, Fauré-Fremiet (see Kofoid 1909, p. 44). All these earlier workers recognized that thecal plates are arranged in transverse rows, and that there are four major plate series, two anterior to the equator and two posterior to the equator. Various names had been applied to these series (see Kofoid 1909, p. 44), but those used by Bütschli (1885) were closest to Kofoid's subsequent terminology. Bütschli described the most anteriorly positioned series as apical, and the most posteriorly positioned as antapical. The two intervening series were termed pre-equatorial (anterior) and post-equatorial (posterior).

Kofoid recognized seven transverse plate series, comprising the four major series plus the cingular series and two incomplete intercalary series. Each series was designated by superscript acute accent marks, figures or letters, or simply by letters. The series were named from apex to antapex as: apical ($'$), anterior intercalary (a), precingular ($''$), cingular (c), postcingular ($'''$), posterior intercalary (p), antapical ($''''$). The plates in each series were numbered in sequence, anticlockwise (in apical view) from the ventral surface. Additional plates at the extreme apex or within the sulcus were individually designated, e.g. apical closing plate (cl. pl.). During subsequent use, Kofoid's system has remained unchanged except for the designation of the sulcal plates (s) and the use of various abbreviations to designate additional individual plates. The typical application of Kofoid's nomenclature to *P. depressum* and *G. spinifera* is shown in text-fig. 1. These two forms together illustrate all seven of Kofoid's transverse plate series. Their respective tabulation formulae are: $4'$, 3a, $7''$, 3c, $5'''$, Op, $2''''$, 6–7s, and 1 ap. cl., $4'$, Oa, $6''$, 6c, $6'''$, 1p, $1''''$, 5s.

The most extensive discussion of thecal plate nomenclature is given in Kofoid (1909, pp. 40–45), but definitions of the various plate series are also found in Kofoid (1907, 1911).

Kofoid (1907, p. 179) defined the four major plate series with reference to modern *Ceratium* Schrank 1793. Kofoid stated: 'I shall use the term apical for the anterior series of plates only, and shall designate the series anterior to and contiguous to the girdle [cingulum] as precingular (prec.), and that posterior to and contiguous to it as postcingular (postc.) and the posterior ones as antapicals (antap.).'

Kofoid (1909, pp. 26–28) next applied his nomenclature to modern peridiniacean dinoflagellates, using *P. steini* (Jörgensen) as an example. His nomenclatural interpretation of *P. steini* is equally applicable to *P. depressum* (text-fig. 1). Kofoid interpreted the apical plates as 'those whose apical ends border the apical pore' (ap. po. in text-fig. 1). The combination of this interpretation of the apicals and Kofoid's earlier interpretation of the precingulars leaves three plates unaccounted for on the dorsal surface. These plates 'intercalate' between the apicals and precingulars and were referred to the anterior intercalary series (1a–3a), a term Kofoid had previously used in his original description of *Heterodinium* Kofoid 1906.

In his studies on modern *Gonyaulax* Diesing 1866, Kofoid (1911, p. 194) interpreted the apical plates as 'those in contact with the apex'. He recognized that in this genus the apex does not have an open pore, but is occupied by a small apical closing plate (1 ap. cl. in text-fig. 1). Kofoid designated as anterior intercalary those plates anterior to the precingular series but not in contact with the apex. This series was not recognized in all species of *Gonyaulax*. Kofoid also introduced the concept of a posterior intercalary series with reference to *Gonyaulax*. The single plate (1p) assigned to this series lies posterior to postcingulars $1'''$ and $2'''$, and anterior to antapical $1''''$ which occupies the antapex.

Kofoid realized that thecal plates are arranged in rows roughly parallel to the cingulum. This led him to use the cingulum rather than the geometric equator as a basis for defining transverse plate series. This approach recognized the fundamental importance of the structure which divides the theca into epitheca and hypotheca. Kofoid (1909, p. 43) believed that his recognition of transverse series throughout the theca clarified the confused situation that had previously existed over the nomenclature of plates anterior to the precingulars. His beliefs would seem to have been justified by the subsequent application of his nomenclature to modern dinoflagellates and to fossil forms ranging back to the Triassic period.
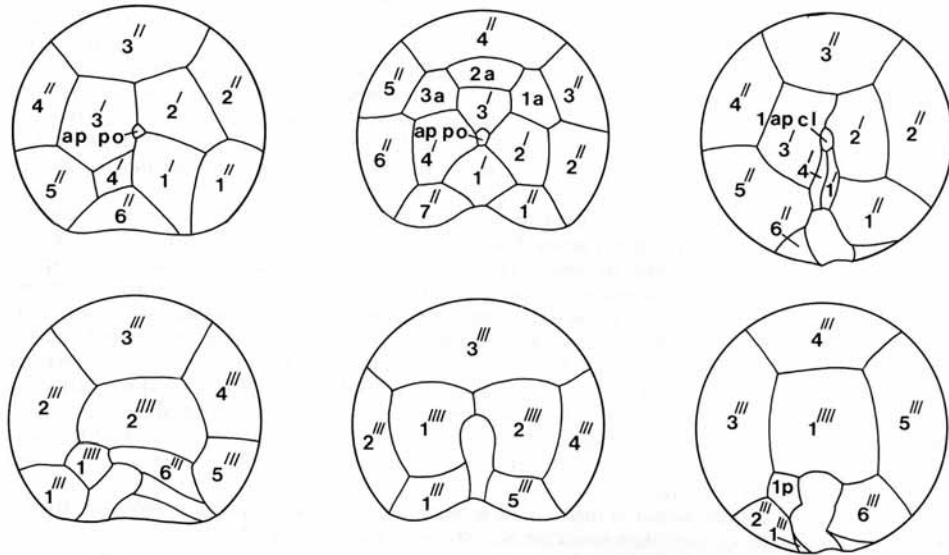
C. HIRUNDINELLA   P. DEPRESSUM   G. SPINIFERA

TEXT-FIG. 2. Conventional Kofoidian interpretation of tabulation in polar views of *Ceratium hirundinella* (Müller) Schrank 1793, *Protoperidinium depressum* (Bailey) Balech 1974, *Gonyaulax spinifera* (Claparède and Lachmann) Diesing 1866. Upper, epithecae. Lower, hypothecae.

A problem in designating apparently homologous plates

Although Kofoid did not recognize any intercalary plates in *Ceratium*, a case can sometimes be made for a single anterior intercalary in *Ceratium hirundinella* (Müller) Schrank 1793 (text-fig. 2). In a particular form of this species, Wall and Evitt (1975, p. 21) designated as apical 4′ a plate which does not reach the tip of the apical horn. They admitted that strictly speaking this plate should be designated anterior intercalary, but to do so would only lead to confusion. They argued that since the homology of this plate and the fourth apical of other species of *Ceratium* is so obvious, it is better to consider this plate as a shortened apical. In this particular case Wall and Evitt considered the recognition of 'obvious' homology to be more important than the strict application of a definition or rule.

This approach can also be applied to other dinoflagellates, for instance, the fossil taxon *Hystrichogonyaulax cladophora* (Deflandre) Stover and Evitt 1978 and certain species of fossil

Ctenidodinium Deflandre 1938. In some well-preserved specimens of *H. cladophora* (text-fig. 3) a plate can be recognized anterior and adjacent to 3″ and 4″. This plate does not touch the apical closing plate (1 ap. cl.) and is therefore designated anterior intercalary 1a. Two such plates are recognizable in *Ctenidodinium pachydermum* (Deflandre) Gocht (1970, pl. 29, fig. 5) and *Ctenidodinium* sp. (text-fig. 3), and 2a in this pattern appears to be homologous with 1a in *H. cladophora*. Also, 2a in *Ctenidodinium* sp. and 1a in *H. cladophora* appear to be homologous with apical 3′ in *Gonyaulax polyedra* Stein 1883 (text-fig. 3). If this interpretation of homology is correct, then this particular anterior intercalary plate in the two fossil taxa could be interpreted as a shortened apical.
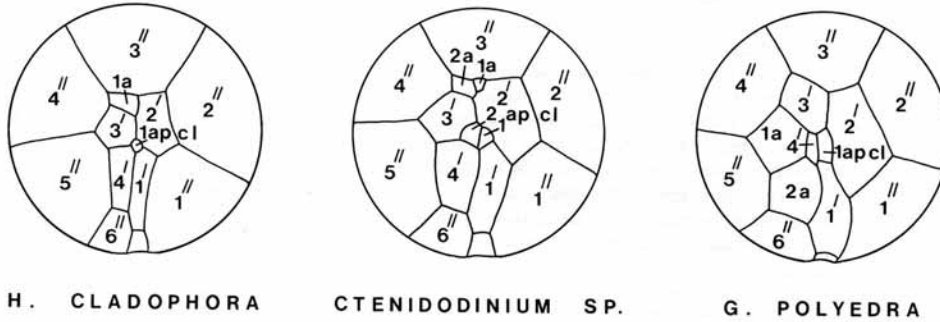
TEXT-FIG. 3. Conventional Kofoidian interpretation of epithecal tabulation in *Hystrichogonyaulax cladophora* (Deflandre) Stover and Evitt 1978, *Ctenidodinium* Deflandre 1938 sp., *Gonyaulax polyedra* Stein 1883.

Kofoid's (1911, pp. 194–195) own comments on the anterior intercalaries in gonyaulacacean dinoflagellates are significant here. Kofoid designated as anterior intercalary, plates in the apical region which are 'crowded away from contact with the apex . . . as well as other plates lying between the apical and precingular series'. He also considered the two anterior intercalaries lying laterally and ventrally to the right of the greatly reduced apical 4′ in *G. polyedra* (text-fig. 3) to be plates which had been 'crowded away' from the apex. Kofoid remarked further (Kofoid 1911, p. 239) that the area of 1a had probably 'split off' from the edge of apical 4′, and he also illustrated one specimen of *G. polyedra* (Kofoid 1911, pl. 14, fig. 29) in which intercalary 2a actually touches the apical closing plate. There is no doubt that Kofoid considered intercalaries 1a and 2a in *G. polyedra* to be territorially apical, but their spatial relationship with the extreme apex required their designation as anterior intercalary.

The anterior intercalary plates in *H. cladophora* and *Ctenidodinium* sp. seem to be apicals which have been shortened and crowded away from the apex, and according to Kofoid's comments on *G. polyedra* their designation as intercalary is entirely justified. Also, it can be argued that Wall and Evitt should have adopted this approach with *C. hirundinella*. Apical 4′ could be interpreted as being crowded away from the apex to occupy an anterior intercalary position, and this plate could then be designated 1a. This would not lead to the confusion Wall and Evitt suggested. It would simply reflect the strict application of a universally recognized rule, and any discussion of homologous relationships with the apical plates of other taxa would be of secondary importance. However, against this it can be argued that the recognition of homologous plates in different dinoflagellates is in fact of primary importance, and is critical to the understanding of the evolution of thecal plate patterns. Therefore, since the Kofoid rules require that apparently homologous plates in different taxa are assigned to different plate series, Kofoid's method of defining these series should be re-evaluated.

An inconsistency in plate series definition

The foregoing comments are specifically concerned with the anterior intercalary and apical series in gonyaulacacean epithecae. More important is the concept of these series in peridiniacean dino-flagellates. The partially developed anterior intercalary series is a characteristic feature of the peridiniacean plate pattern, and there can be little doubt that Kofoid considered these intercalaries to be additional plates between the precingulars and apicals. However, a polar view of the peridiniacean epitheca does not support this interpretation. In *Protoperidinium depressum* (text-fig. 2) for instance, the three anterior intercalaries 1a–3a and apicals 1′, 2′, and 4′ form a perfect ring of plates, effectively concentric with the precingular series. The interpretation of these six plates as the apical series would leave only Kofoidian apical 3′ unaccounted for. Thus Kofoid's concept of the anterior intercalary series seems to be an artificial one which resulted directly from his interpretation of the apical series in peridiniacean dinoflagellates.

I can only speculate on the reasons why Kofoid defined the apical series in the way he did. He may simply have believed that the apical plates should occupy or at least touch the morphological apex. He may have been influenced by the fact that his concept of the apical series resulted in the recognition of four apical plates in *Ceratium*, peridiniacean taxa, and certain species of *Gonyaulax*, and this consistency might be significant. Whatever reason is suggested, one major criticism is inescapable: Kofoid's concept of the apical series in peridiniacean dinoflagellates is incompatible with his basic statement on plate series definition. That is, since the division of the theca into epitheca and hypotheca is of such fundamental importance, the intervening cingulum should be used as the basis for defining the transverse plate series (Kofoid 1909, pp. 41, 43).

For consistency, after the precingular series had been defined as the plates anterior to and contiguous to the cingulum, the next series should have been defined as the plates anterior to and contiguous to the precingulars. This consistent definition of the apical series would not have affected Kofoid's interpretation of *Ceratium*, but it would have greatly affected his interpretation of the peridiniacean plate pattern. In *P. depressum* there would be six apicals rather than four, a residue of one plate at the apex (Kofoid's apical 3′), and no anterior intercalaries. In species of *Gonyaulax* such as *G. polyedra* there would be five apicals (Kofoid's 1′–3′, 1a, 2a) rather than four, a residue of two plates at the apex (1 ap. cl. and Kofoid's apical 4′), and again no anterior intercalaries. In *H. clado-phora* there would be five apicals, in *Ctenidodinium* sp. there would be six, and the conventional intercalary plate in both patterns previously suggested to be homologous with apical 3′ in *G. polyedra* would now be designated apical. Also, apical 4′ in *C. hirundinella* would be designated apical, independent of its relationship with the morphological apex.

A similar argument can be made against Kofoid's interpretation of the antapical series in *Gonyaulax* and his resulting concept of a posterior intercalary series. After the postcingular series had been defined as the plates posterior to and contiguous to the cingulum, the next series should have been defined as the plates posterior to and contiguous to the postcingulars. This consistent definition of the antapical series would not have affected Kofoid's interpretation of *Ceratium* or the basic peridiniacean plate pattern, but it would have affected his interpretation of *Gonyaulax*. In the latter genus, the plate conventionally designated posterior intercalary 1p would become first antapical 1‴″, conventional 1‴″ would become 2‴″, and there would be no posterior intercalaries.

Thus initially on the grounds of consistency in plate series definition and some limited evidence of plate homology, redefinition of the apical and antapical series is justified.

MODIFICATION OF KOFOID'S SYSTEM OF PLATE SERIES NOMENCLATURE

Definition of all the transverse plate series relative to the cingulum generally results in the recognition of two major plate series on both the epitheca and hypotheca. Any remaining plates occur at or near the poles of the theca and can be accommodated in a third epithecal or hypothecal series. Although this approach differs from Kofoid's concept of transverse plate series, only the apical and antapical series need to be redefined. Also, almost all of Kofoid's terms are still applicable and there is only one completely new plate series.

I would emphasize here that the following definitions are only intended to be broad guides to the recognition

of the various plate series and the designation of individual plates. I do not believe that such definitions should be rigidly applied. Subjective interpretation is unavoidable, and interplate relationships must be considered for each plate pattern before individual plates can be assigned to the various plate series.

Definition of the transverse series

Three transverse series are recognized on the epitheca: precingular, apical, apical closing; and three are also recognized on the hypotheca: postcingular, antapical, antapical closing.

The precingular series ('') was satisfactorily defined by Kofoid (1907, p. 179) as the row of plates anterior to and contiguous to the cingulum. This definition is retained here.

The apical series (') is redefined as the row of plates anterior to and contiguous to the precingular series. Also included is the plate (or plates) anterior to and contiguous to the sulcal area, as suggested by Kofoid. The apical series may be interrupted by a posterior extension of the apical series and in certain circumstances apical plates may touch the cingulum (e.g. *Helgolandinium subglobosum*, text-fig. 7).

The apical closing series (ap. cl.) is defined as the plates anterior to and contiguous to the apical series. The concept of apical closing plates was discussed by Kofoid (1911, p. 194) with respect to the small plate occupying the extreme apex of *Gonyaulax*. My idea of the apical closing series includes this and any other plates anterior and contiguous to the apical series, with the term 'closing' being used in a geometric rather than a biologically functional sense. This series may be represented by a distinct row of plates, and in certain circumstances apical closing plates may interrupt the apical series and touch the precingular series (e.g. *Shublikodinium arcticum*, text-fig. 8).

The postcingular series (''') was satisfactorily defined by Kofoid (1907, p. 179) as the row of plates posterior to and contiguous to the cingulum. This definition is retained here.

The antapical series ('''') is redefined as the plates posterior to and contiguous to the postcingular series.

The antapical closing series (an. cl.) is proposed as a new series, and is defined as the plates posterior to and contiguous to the antapical series. Again, 'closing' is used in a purely geometric sense. So far this series has been recognized only in *S. arcticum* and *Rhaetogonyaulax rhaetica* (both text-fig. 8).

Application to selected modern and fossil dinoflagellate plate patterns

The plate patterns of five modern and ten fossil dinoflagellates are illustrated in text-figs. 4–8 as diagrammatic polar (epithecal and hypothecal) views, in which I have tried to retain true interplate relationships with minimum distortion of observed plate geometry. This type of illustration is used rather than conventional ventral and dorsal views (text-fig. 1) because it allows a better appreciation of the geometric relationship between individual plates or groups of plates. Hypothecae are illustrated with the sulcus to the south rather than the conventional north, to emphasize certain similarities with epithecae. The plates are numbered in terms of the modified plate series nomenclature, and the direction of numbering is conventional. Individual cingular and sulcal plates are not indicated.

The listed data for each pattern include the specific name with its authorship, geological age (where relevant), the source of the plate pattern, and the modified tabulation formula. The formula is expressed in terms of the epithecal (E) and hypothecal (H) transverse series only. Changes in plate designation are indicated, with the reinterpreted designation first, followed by the conventional Kofoidian designation in parentheses. Where necessary, changes in dinoflagellate cyst archaeopyle nomenclature are indicated for the fossil taxa, in terms of the notation previously discussed by Evitt (1967) and Stover and Evitt (1978).

Gonyaulax spinifera (Claparède and Lachmann) Diesing 1866, Recent, text-fig. 4.

From: Kofoid (1911, text-figs. A–D) and Wall and Dale (1970, text-figs. 19–22).
Modified tabulation formula, E: 1 ap. cl., 4', 6''; H: 6''', 2''''.
Changes in plate designation: 1'''' (1p), 2'''' (1'''').

Gonyaulax polyedra Stein 1883, Recent, text-fig. 4.

From: Kofoid (1911, pl. 12, figs. 16–20).
Modified tabulation formula, E: 2 ap. cl., 5', 6''; H: 6''', 2''''.
Changes in plate designation: 2 ap. cl. (4'), 4', 5' (1a, 2a), 1'''' (1p), 2'''' (1'''').

Hystrichogonyaulax cladophora (Deflandre) Stover and Evitt 1978, Late Jurassic, text-fig. 4.

From: Deflandre (1938, text-figs. 5, 6) and my own observations.
Modified tabulation formula, E: 1 ap. cl., 5', 6''; H: 6''', 2''''.
Changes in plate designation: 3' (1a), 4', 5', (3', 4'), 1'''' (1p), 2'''' (1'''').

Ctenidodinium Deflandre 1938 sp., Middle Jurassic, text-fig. 5.

From: my own observations.
Modified tabulation formula, E: 2 ap. cl., 6′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 3′, 4′ (1a, 2a), 5′, 6′ (3′, 4′), 1⁗ (1p), 2⁗ (1‴′).

Paragonyaulacysta Johnson and Hills 1973 *s.l.*, Middle Jurassic, text-fig. 5.

From: Johnson and Hills (1973, text-fig. 9) and my own observations.
Modified tabulation formula, E: 1 ap. cl., 5′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 3′–5′ (1a–3a), 1⁗ (1p), 2⁗ (1‴′).
Cyst archaeopyle type: dorsal apical, type A, 2A or 3A (conventionally intercalary, type I, 2I or 3I).

Luehndea spinosa Morgenroth 1970, Early Jurassic, text-fig. 5.

From: Morgenroth (1970, pl. 9, figs. 1–4), Evitt (unpublished data).
Modified tabulation formula, E: 1 ap. cl., 6′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 1 ap. cl. (3′), 3′–5′ (1a–3a), 6′ (4′), 1⁗ (1p), 2⁗ (1‴′).

Canninginopsis denticulata Cookson and Eisenack 1962, Mid Cretaceous, text-fig. 6.

From: Cookson and Eisenack (1962, text-fig. 2), Wall and Evitt (1975, text-fig. 11).
Modified tabulation formula, E: 1 ap. cl., 4′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 1⁗ (1p), 2⁗ (1‴′).

G. SPINIFERA   G. POLYEDRA   H. CLADOPHORA
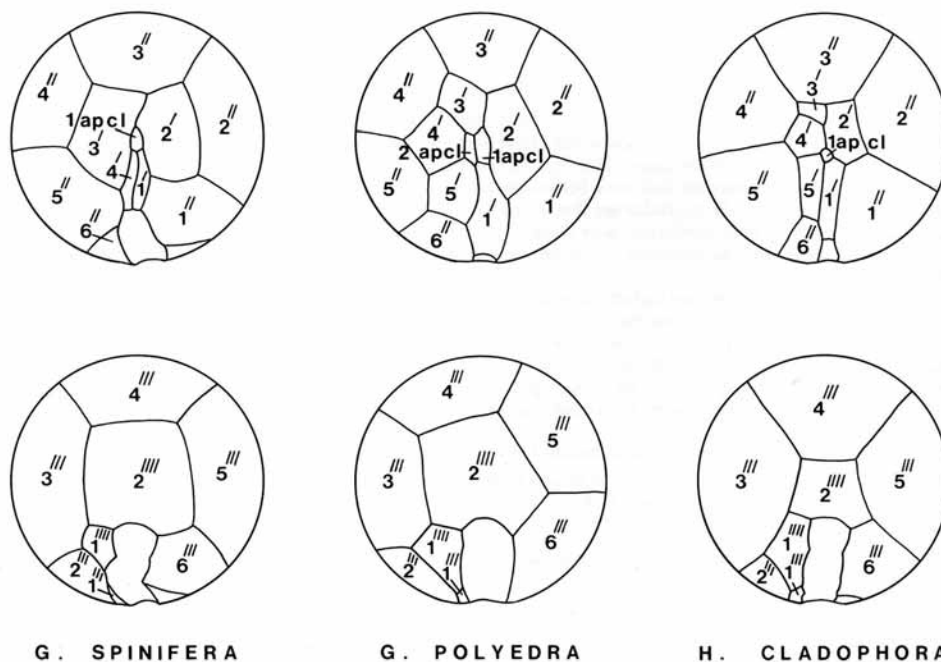
TEXT-FIG. 4. Modified interpretation of tabulation in polar views of *Gonyaulax spinifera* (Claparède and Lachmann) Diesing 1866, *Gonyaulax polyedra* Stein 1883, *Hystrichogonyaulax cladophora* (Deflandre) Stover and Evitt 1978. Upper, epithecae. Lower, hypothecae.

Ceratium hirundinella (Müller) Schrank 1793, Recent, text-fig. 6.

From: Wall and Evitt (1975, text-figs. 5, 6).
Modified tabulation formula, E: 4′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 1⁗ (1p), 2⁗ (1⁗), relative to Wall and Evitt (1975).

Thalassiphora delicata Williams and Downie 1966, Eocene, text-fig. 6.

From: Eaton (1976, text-figs. 18, 20).
Modified tabulation formula, E: 1 ap. cl., 4′, 6″; H: 6‴, 2⁗.
Changes in plate designation: 1 ap. cl. (4′), 4′ (1a), 2⁗ (1p). Also, the sixth pre- and postcingulars are now recognized.

Protoperidinium depressum (Bailey) Balech 1974, Recent, text-fig. 7.

From: Gocht and Netzel (1974, text-fig. 1).
Modified tabulation formula, E: 1 ap. cl., 6′, 7″; H: 5‴, 2⁗.
Changes in plate designation: 1 ap. cl. (3′), 3′–5′ (1a–3a), 6′ (4′).

Phthanoperidinium tritonium Eaton 1976, Eocene, text-fig. 7.

From: Eaton (1976, text-fig. 24).
Modified tabulation formula, E: 1 ap. cl., 6′, 7″; H: 5‴, 2⁗.
Changes in plate designation: 1 ap. cl. (3′), 3′–5′ (1a–3a), 6′ (4′).
Cyst archaeopyle type: dorsal apical, type A (conventionally intercalary, type I).
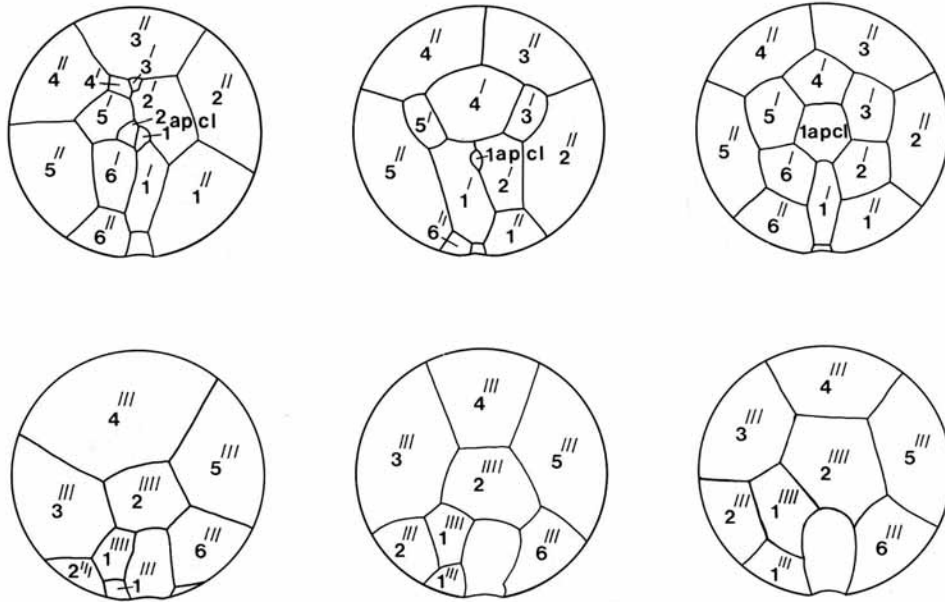
CTENIDODINIUM SP.   PARAGONYAULACYSTA S.L.   L. SPINOSA

TEXT-FIG. 5. Modified interpretation of tabulation in polar views of *Ctenidodinium* Deflandre 1938 sp., *Paragonyaulacysta* Johnson and Hills 1973 s.l., *Luehndea spinosa* Morgenroth 1970. Upper, epithecae. Lower, hypothecae.

Helgolandinium subglobosum von Stosch 1969, Recent, text-fig. 7.

From: von Stosch (1969, text-fig. 3).
Modified tabulation formula, E: 5′, 7″; H: 7‴, 3⁗.
Changes in plate designation: 1′ (1″), 2′–5′ (1′–4′), 1″–7″ (2″–8″).

The very small plate designated 9″ by von Stosch (1969, text-fig. 3*f*) which lies anterior to the anterior sulcal plate and touches the first cingular plate is here referred to the sulcus as a second anterior sulcal plate, 2 a.s. A similarly positioned plate can sometimes be recognized in *Paragonyaulacysta s.l.*

Dapcodinium priscum Evitt 1961, Early Jurassic, text-fig. 8.

From: Evitt (1961, text-figs. 1–20).
Modified tabulation formula, E: 1 ap. cl., 7′, 7″; H: 7‴, 3⁗.
Changes in plate designation: 1 ap. cl. (3′), 3′–6′ (1a–4a), 7′ (4′), 2‴–7‴ (1‴–6‴), 1⁗, 2⁗ (1p, 2p), 3⁗ (1‴‴).

On the hypotheca, Evitt originally recognized only six postcingulars, but several of his drawings (Evitt 1961, text-figs. 5–10, 15–17, 19) show an undesignated plate comparable in position to the reduced first postcingular of *Gonyaulax*. This plate is designated 1‴ here, and the number of postcingulars is increased from six to seven.

Shublikodinium arcticum Wiggins 1973, Late Triassic, text-fig. 8.

From: Wiggins (1973, text-fig. 3).
Modified tabulation formula, E: 6 ap. cl., 6′, 7″; H: 7‴, 3⁗, 1 an. cl.
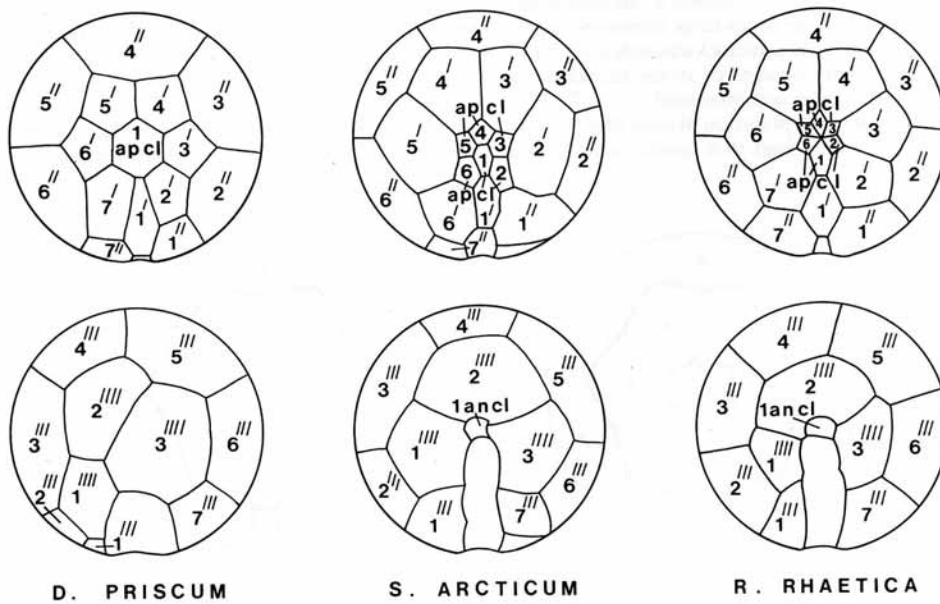Changes in plate designation: 1 ap. cl. (va. cl.), 2–6 ap. cl. (2′–6′), 2′–6′ (1a–5a), 1 an. cl. (ppl).
Cyst archaeopyle type: combination apical closing-apical, type t͟A͟C͟L͟ tA (conventionally combination apical-intercalary, type tA tI).

C. DENTICULATA   C. HIRUNDINELLA   T. DELICATA
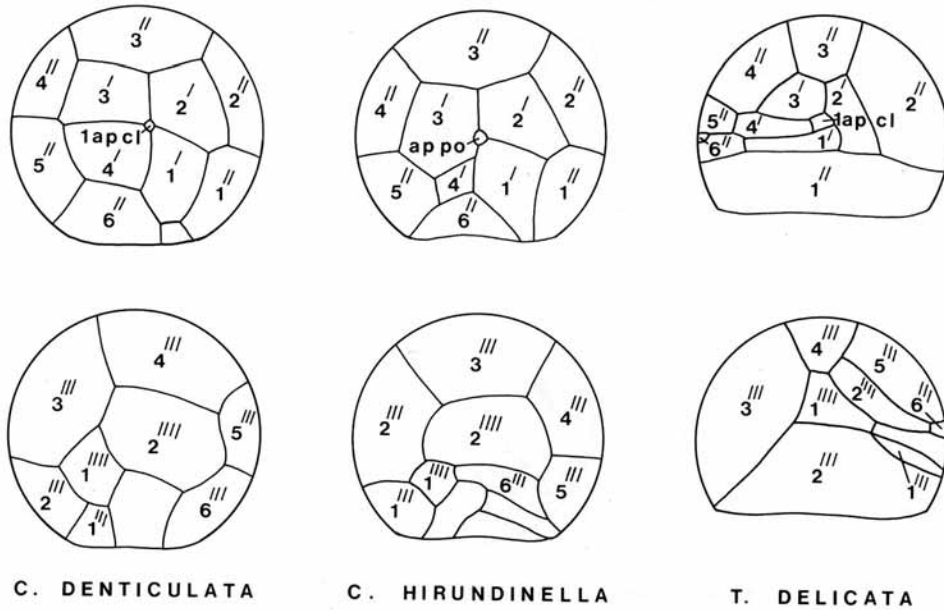
TEXT-FIG. 6. Modified interpretation of tabulation in polar views of *Canninginopsis denticulata* Cookson and Eisenack 1962, *Ceratium hirundinella* (Müller) Schrank 1793, *Thalassiphora delicata* Williams and Downie 1966. Upper, epithecae. Lower, hypothecae.

P. DEPRESSUM   P. TRITONIUM   H. SUBGLOBOSUM
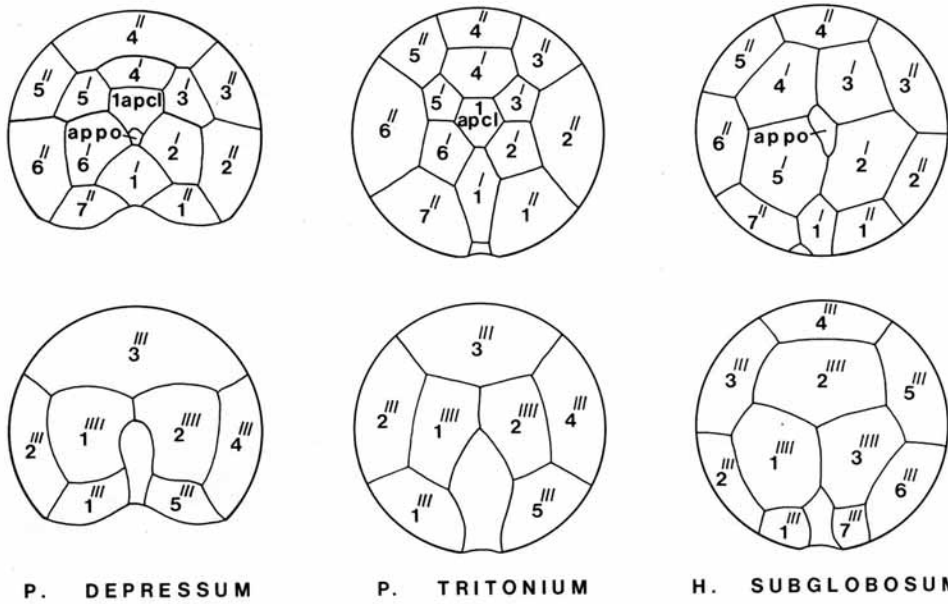
TEXT-FIG. 7. Modified interpretation of tabulation in polar views of *Protoperidinium depressum* (Bailey) Balech 1974, *Phthanoperidinium tritonium* Eaton 1976, *Helgolandinium subglobosum* von Stosch 1969. Upper, epithecae. Lower, hypothecae.

D. PRISCUM   S. ARCTICUM   R. RHAETICA

TEXT-FIG. 8. Modified interpretation of tabulation in polar views of *Dapcodinium priscum* Evitt 1961, *Shublikodinium arcticum* Wiggins 1973, *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich 1968. Upper, epithecae. Lower, hypothecae.

Rhaetogonyaulax rhaetica (Sarjeant) Loeblich and Loeblich 1968, Late Triassic, text-fig. 8.

From: Harland, Morbey and Sarjeant (1975, text-fig. 2).

Modified tabulation formula, E: 6 ap. cl., 7', 7''; H: 7''', 3'''', 1 an. cl.

Changes in plate designation: 1–6 ap. cl. (1'–6'), 1' (a.v.), 2'–7' (1a–6a), 1'''', (1p), 1 an. cl. (1''''').

Cyst archaeopyle type: combination apical closing-apical, type $\overline{tACL}$ tA (conventionally combination apical-intercalary, type $\overline{tA}$ tI).

## HOMOLOGOUS AND CORRESPONDING PLATES IN SELECTED DINOFLAGELLATE PLATE PATTERNS

Method

The method used here for recognizing homologous and corresponding plates in different plate patterns involves critical comparisons of their interplate relationships. These comparisons are made with respect to a model plate pattern (text-fig. 9) whose epitheca and hypotheca both show a very high degree of radial symmetry and plate regularity. The model plate series are interpreted in terms of the modified nomenclature, but to emphasize the model nature of the pattern, the Kofoidian style notation is not applied. Instead, the series are referred to as 'ap.' (apical), 'prec.' (precingular), 'postc.' (postcingular) and 'antap.' (antapical). Also, the plates in each series are simply numbered consecutively 1, 2, 3 etc., and referred to as ap. 1, postc. 3, etc. The idea of this model plate pattern is based on the following observations.

In the fifteen epithecal patterns illustrated in text-figs. 4–8, the maximum number of plates in any of the transverse series is seven (7', e.g. *D. priscum*; 7'', e.g. *P. depressum*). Also, the most regular interseries relationship involves groups of three plates (3-plate relationship) with one plate in one series touching two plates in an adjacent series. This relationship is fully developed between the precingular and apical series in *L. spinosa* and *D. priscum* for instance, and between six of the apicals (2'–7') and five of the apical closing plates (2–6 ap. cl.) in *R. rhaetica*.

The model epitheca shows a full development of the 3-plate interseries relationship in a pattern with seven plates in all three transverse series. The direction of numbering the epithecal plates is conventional, i.e. anticlockwise relative to the apical pole. When an observed epithecal pattern does not show counterparts of all the model plates, it is the highest numbered model plates which are considered to be unrepresented.

A similar interpretation of such observations on the fifteen hypothecal patterns illustrated in text-figs. 4–8 would lead to a model pattern closely comparable to *S. arcticum* and *R. rhaetica*. The
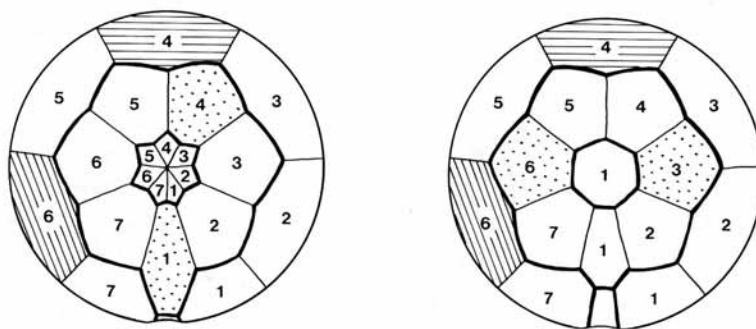

TEXT-FIG. 9. The model plate pattern. Left, epitheca, E: 7 ap. cl., 7 ap., 7 prec. Right, hypotheca, H: 7 postc., 7 antap., 1 an. cl.

maximum number of plates in any of the transverse series is again seven, but this maximum only occurs in the postcingular series (e.g. *H. subglobosum*). The maximum number of antapicals is only three (e.g. *D. priscum*), with a single antapical closing plate developed only in *S. arcticum* and *R. rhaetica*. All four patterns with seven postcingulars and three antapicals (*H. subglobosum*, *D. priscum*, *S. arcticum*, *R. rhaetica*) show a constant relationship between these two series. This involves groups of four plates (4-plate relationship) with one antapical touching three postcingulars. However, this arrangement can be interpreted in terms of the fundamental 3-plate relationship (fully developed in the model epitheca), if each of the three antapicals is treated as two plates, and the intervening mid-ventral area is also considered to be an antapical plate.

Thus the model hypotheca shows a full development of the 3-plate relationship between the postcingulars and antapicals, with seven plates in both series. The model hypothecal plates are numbered anticlockwise relative to the antapical pole. This is the reverse of convention, but is more convenient for the discussion of observed hypothecal patterns which do not show counterparts of all the model plates. As with the epithecae, it is the highest numbered model plates which are considered to be unrepresented.

In text-fig. 9, four plates on both the epitheca and hypotheca are ornamented. I consider these to be key reference plates in the discussion of homologous plate relationships and the comparison of different plate patterns.

For ease of comparison with the model pattern, the epithecae and hypothecae of the selected modern and fossil dinoflagellates are discussed and illustrated separately (text-figs. 10–12). The modified system of plate series nomenclature is applied throughout with a Kofoidian style notation.
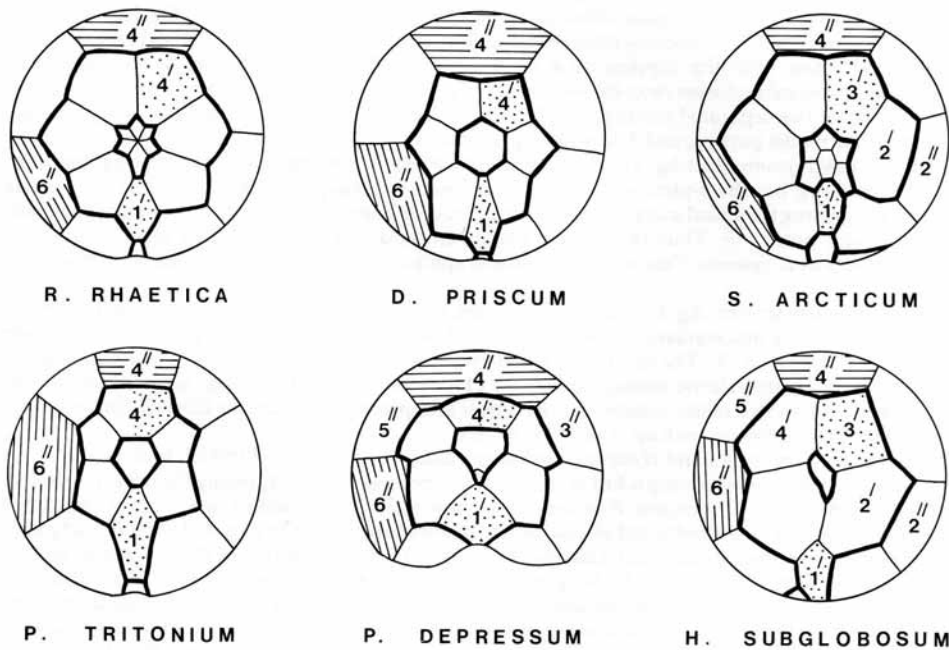
TEXT-FIG. 10. Epithecal plate patterns of six selected dinoflagellate taxa. The key reference areas are ornamented.

The direction of numbering the plates is conventional. In the text-figures the interseries boundaries are thickened for emphasis, and only those plates critical to the discussion are numbered. A maximum of four such plates on both the epitheca and hypotheca are also ornamented, either in full or in part. Each ornamented area corresponds to one key plate in the model pattern.

Epithecal plate patterns (text-figs. 9, 10, 11)

The model epithecal pattern (text-fig. 9) has twenty-one plates arranged in three series (7 ap. cl., 7 ap., 7 prec.). This discussion is primarily concerned with the apical and precingular series in which the key reference plates are ap. 1, ap. 4 (stippled), and prec. 4, prec. 6 (shaded).

Rhaetogonyaulax rhaetica and *Dapcodinium priscum* (text-fig. 10) both have a 7', 7'' pattern, and also show a full development of the 3-plate relationship. Because of this, the seven apicals and seven precingulars in both patterns are considered to be respectively homologous with ap. 1–7 and prec. 1–7.

In *Shublikodinium arcticum* (text-fig. 10) which has a 6' 7'' pattern, the 3-plate relationship is lost in the vicinity of precingular 2'' which is touched by only one apical, 2'. Compared with the model pattern, plate 2' occupies the position of two plates, ap. 2 and ap. 3. Thus apical 2' in *S. arcticum* corresponds to two plates in the model pattern, and as a result, apical 3' in *S. arcticum* is homologous with key ap. 4. The interruption of the apical series in *S. arcticum* by a posterior extension of the apical closing series between 1' and 2', does not affect the over-all interpretation of the 3-plate relationship. *Phthanoperidinium tritonium* (text-fig. 10) also has a 6', 7'' pattern, but the 3-plate relationship is lost in the vicinity of 4''. Thus apical 4' corresponds to two plates in the model pattern, and only its stippled area corresponds to key ap. 4. In the 6', 7'' pattern of *Protoperidinium depressum* (text-fig. 10), the 3-plate relationship is lost in the vicinity of three consecutive precingulars, 3''–5''. Even so, I still consider that only apical 4' corresponds to two plates in the model pattern, and this accounts for the loss of the 3-plate relationship between the apical series and 4''. The further loss in the vicinity of 3'' and 5'' is due to a relative lateral displacement of the two intra-apical sutures which border 4'. Thus only the stippled area of 4' in *P. depressum* corresponds to key ap. 4. In *Helgolandinium subglobosum* (text-fig. 10) which has a 5', 7'' pattern, the 3-plate relationship is lost in the vicinity of two separated precingulars, 2'' and 5''. Thus apicals 2' and 4' each correspond to two plates in the model pattern, and 3' is homologous with key ap. 4.

In *Luehndea spinosa* (text-fig. 11) there are only six plates in both the apical and precingular series (6', 6'' pattern), but the 3-plate relationship is maintained throughout. Because of this the twelve plates comprising the apical and precingular series are considered to be respectively homologous with ap. 1–6 and prec. 1–6. Thus the highest numbered model plates, ap. 7 and prec. 7, have no counterparts in *L. spinosa*. This last comment also applies to the eight remaining patterns discussed here.

Ctenidodinium sp. (text-fig. 11) has a 6', 6'' pattern, but the 3-plate relationship is lost in the vicinity of two consecutive precingulars, 2'' and 3''. Plate 2'' has one apical touching it, 2', while 3'' has three apicals touching it, 2'–4'. The loss of the 3-plate relationship is due to the critical shortening of 3', accompanied by the relative enlargement of 2'. Plate 4' is also shortened, but not critically. As in *L. spinosa*, the twelve plates comprising the apical and precingular series in *Ctenidodinium* sp. are respectively homologous with ap. 1–6 and prec. 1–6.

In *Gonyaulax polyedra* and *Hystrichogonyaulax cladophora* (text-fig. 11) which both have a 5', 6'' pattern, the 3-plate relationship is lost in the vicinity of precingular 2''. Applying the principle used in the interpretation of *S. arcticum*, *P. tritonium* etc., apical 2' corresponds to two plates in the model pattern. Thus 3' in *G. polyedra* and *H. cladophora* is homologous with key ap. 4. The shortening of 3' in *H. cladophora* is not critical, and is comparable to 4' in *Ctenidodinium* sp. In *Paragonyaulacysta s.l.* (text-fig. 11) which also has a 5', 6'' pattern, the 3-plate relationship is lost in the vicinity of precingular 6''. Thus only the stippled area of 1' corresponds to key ap. 1, and the unornamented area of 1' corresponds to ap. 6. The shortening of apicals 3'–5' in *Paragonyaulacysta s.l.* is not critical.
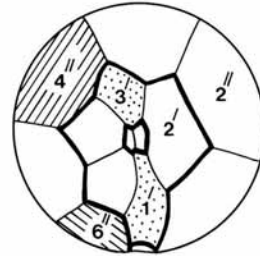
Gonyaulax spinifera, *Canninginopsis denticulata*, and *Ceratium hirundinella* (text-fig. 11) all have a 4', 6'' pattern and identical homologous and corresponding plate relationships. Loss of the 3-plate
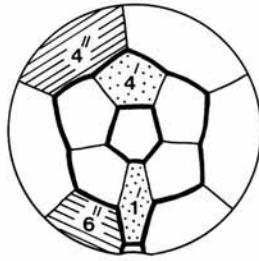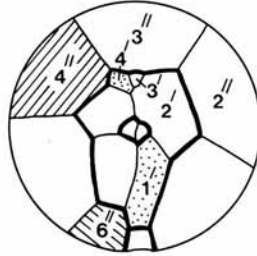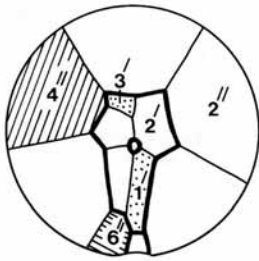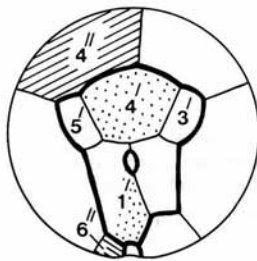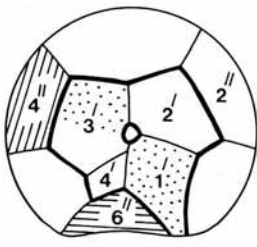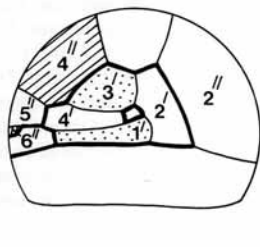
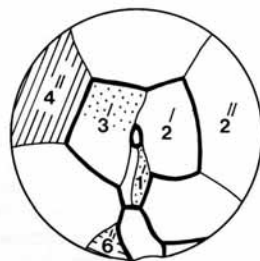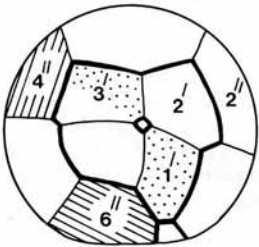TEXT-FIG. 11. Epithecal plate patterns of a further nine selected dinoflagellate taxa. The key reference areas are ornamented.

relationship occurs in the vicinity of precingulars 2″ and 4″. Thus 2′ and 3′ each correspond to two plates in the model pattern, and therefore the stippled area of 3′ corresponds to key ap. 4. The further loss of the 3-plate relationship in *G. spinifera* is due to the critical shortening of 6″. The shortening of 4′ in *C. hirundinella* is not critical.

In *Thalassiphora delicata* (text-fig. 11) which also has a 4′, 6″ pattern, the 3-plate relationship is lost in the vicinity of three precingulars, 2″, 5″, and 6″. Thus 2′ and 4′ each correspond to two plates in the model pattern, and 3′ is homologous with key ap. 4. Plate 6″ is critically shortened and is not touched by any of the apical series.

Only limited comments can be made on possible homologous relationships in the apical closing series, because of the great variation in its development. It is reasonable to suggest that 1 ap. cl. in *R. rhaetica* and *S. arcticum* corresponds to the first and seventh apical closing plates in the model pattern, and that the five remaining plates in all three patterns are respectively homologous. Also that the large single apical closing plate in *D. priscum*, *L. spinosa*, *P. tritonium*, and *P. depressum* corresponds to all seven apical closing plates in the model pattern. However, the relationship between these two extremes of development, and the apical closing plates in *G. spinifera* and *Ctenidodinium* sp. for instance, is undetermined.

Hypothecal plate patterns (text-figs. 9, 12)

The model hypothecal pattern (text-fig. 9) has fifteen plates arranged in three series (7 postc., 7 antap., 1 an. cl.). This discussion is only concerned with the postcingular and antapical series in which the key reference plates are postc. 4, postc. 6 (shaded) and antap. 3, antap. 6 (stippled). The fifteen selected hypothecae do not show the same range of variation as their epithecae, and can be discussed in terms of only eight patterns.

The 'rhaetogonyaulacacean' type (*Rhaetogonyaulax rhaetica*, *Shublikodinium arcticum*), *Helgolandinium subglobosum*, and *Dapcodinium priscum* (text-fig. 12) all have a 7‴, 3⁗ pattern. The seven postcingulars in these patterns and the model pattern are respectively homologous. The antapical-postcingular interseries relationship is constant, with each antapical touching three postcingulars. As stated earlier, each antapical corresponds to two plates in the model pattern. Since 1⁗–3⁗ occupy the position of antap. 2–7, 1⁗ corresponds to antap. 6–7, 2⁗ to antap. 4–5, and 3⁗ to antap. 2–3. Thus, only the stippled area of 3⁗ corresponds to key antap. 3, and only the stippled area of 1⁗ corresponds to key antap. 6.

Although no counterpart of antap. 1 is shown in the 7‴, 3⁗ patterns, it may be represented by the posterior area of the sulcus. However, in fossil dinoflagellates the individual sulcal plates are often very poorly defined, and it is by no means certain that all areas designated posterior sulcal (p.s.) are respectively homologous. Consequently this relationship is only questionably applied to the fifteen selected patterns (Table 1).

A significant feature of *D. priscum* is the anticlockwise rotation of its plate pattern relative to the model pattern, and the associated reduction of 2‴ and 1‴. These reduced plates correspond to the highest numbered model postcingulars, postc. 6, postc. 7, and this influenced my earlier statement that when a hypothecal pattern does not show counterparts of all the model plates, it is the highest numbered model plates which are unrepresented. Consequently it is convenient to discuss the plate relationships of the five remaining patterns in an anticlockwise direction, i.e. in terms of 6‴–1‴ and 2⁗–1⁗.

In *Luehndea spinosa* there are only six postcingulars and two antapicals (6‴, 2⁗ pattern). Plates 6‴–1‴ are respectively homologous with postc. 1–6, and there is no counterpart of postc. 7. Thus 3‴ is homologous with key postc. 4, and 1‴ is homologous with key postc. 6. Antapical 2⁗ touches four postcingulars and therefore corresponds with three plates in the model pattern, antap. 2–4. Thus only the stippled area of 2⁗ corresponds to key antap. 3. Plate 1⁗ touches three postcingulars and therefore corresponds to two plates in the model pattern, antap. 5, 6. Thus only the stippled area of 1⁗ corresponds to key antap. 6, and there is no counterpart of antap. 7.

In the 'peridiniacean' type pattern (*Protoperidinium depressum* and *Phthanoperidinium tritonium*) there are only five postcingulars and two antapicals (5‴, 2⁗ pattern). Plates 5‴–1‴ are respectively

TEXT-FIG. 12. Eight hypothecal plate patterns representative of the fifteen selected dinoflagellate taxa. The key reference areas are ornamented.

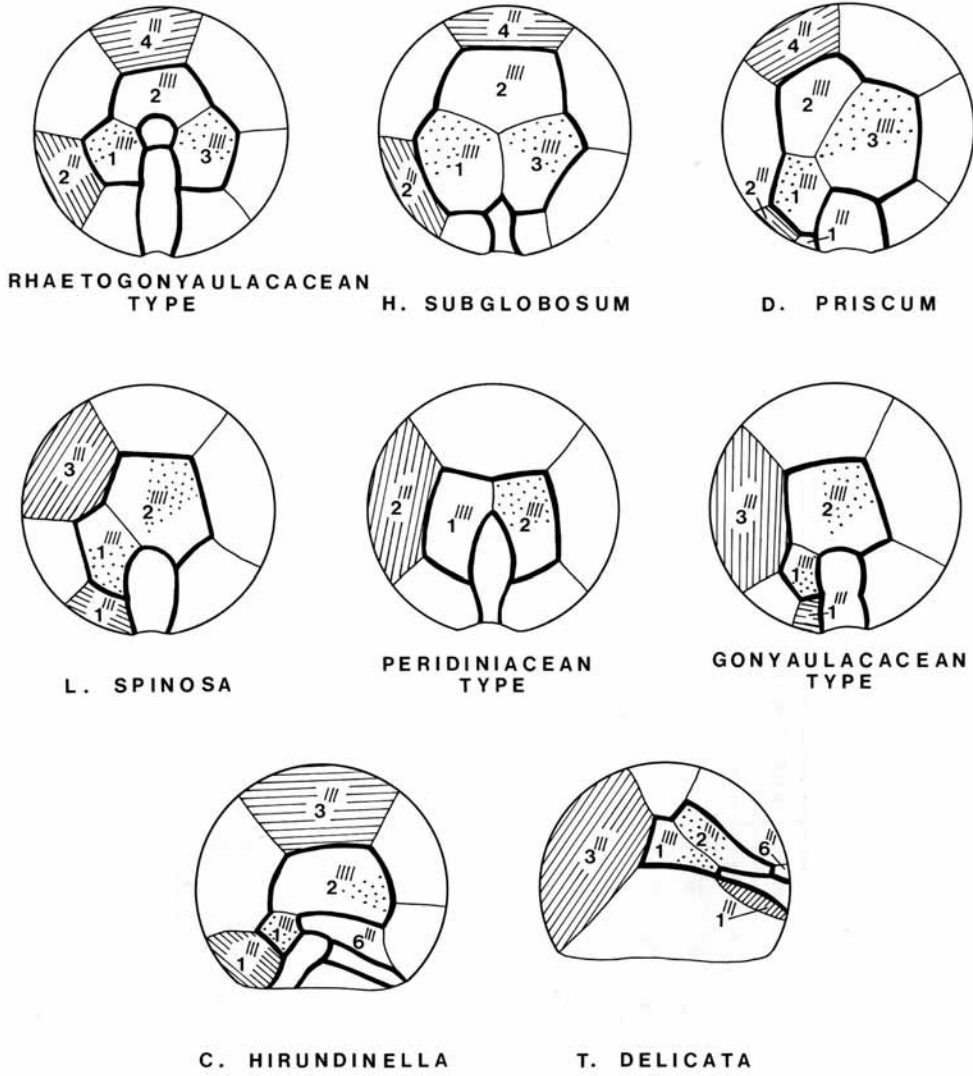| PLATE SERIES	MODEL PATTERN	R. RHAETICA	D. PRISCUM	S. ARCTICUM	H. SUBGLOBOSUM	P. TRITONIUM	P. DEPRESSUM	L. SPINOSA	PARAGONYAULACYSTA s.l.	CTENIDODINIUM sp.	G. POLYEDRA	H. CLADOPHORA	G. SPINIFERA	C. DENTICULATA	C. HIRUNDINELLA	T. DELICATA
APICAL	1	1	1	1	1	1	1	1	1(pt)	1	1	1	1	1	1	1
	2	2*	2	}2*	2	2	2	2	2	2	}2	2	2	2	2	2
	3	3*	3*		2	3*	3*	3*	3*	3*		2	2	2	2	2
	4	4*	4*	3*	3	}4*	4*	4*	4*	4*	3	3*	3	3	3	3
	5	5*	5*	4*	}4		5*	5*	5	4*	4	}3	3	3		}4
	6	6*	6*	5*		5*	5*	6	1(pt)	6	5*	5	4	4	4	
	7	7*	7	6*	5	6	6	–	–	–	–	–	–	–	–	–
PREC.	1	1	———————————————————————————→													1
	↓	↓														↓
	6	6	———————————————————————————→													6
	7	7	——————→		7	–	–	–	–	–	–	–	–	–	–	–
POSTCINGULAR	1	7	7	7	7	5	5	6	——————————————————————→						6(?pt)	6
	2	6	6	6	6	4	4	5	——————————————————————→							5
	3	5	5	5	5	3	3	4	——————————————————————→							4
	4	4	4	4	4	2	2	3	——————————————————————→							3
	5	3	3	3	3	1	1	2	——————————————————————→							2
	6	2	2	2	2	–	–	1	——————————————————————→							1
	7	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–
ANTAPICAL	1	←————————————— ?p.s. —————————————→														?6‴(pt)
	2	}3	3	3	3	2	2	}2	——————————————→					2		}2*
	3															}2
	4	}2	2*	2	2	1	1									
	5							}1*	——————————————→					1*		}1
	6	}1*	1*	1	1	–	–								1*	}1*
	7					–	–	–	–	–	–	–	–	–	–	–

TABLE 1. Homologous and corresponding plates in the fifteen selected plate patterns and the model pattern. The modified interpretation of transverse series is applied throughout. Plates with an asterisk would be designated intercalary using the conventional Kofoidian system.

homologous with postc. 1–5 and there are no counterparts of postc. 6, 7. Thus 2‴ is homologous with key postc. 4. Antapicals 2‴‴ and 1‴‴ each touch three postcingulars and therefore each corresponds to two plates in the model pattern. Thus only the stippled area of 2‴‴ corresponds to key antap. 3, and there are no counterparts of antap. 6, 7.

The 'gonyaulacacean' type pattern (*Gonyaulax spinifera*, *G. polyedra*, *Hystrichogonyaulax cladophora*, *Ctenidodinium* sp., *Canninginopsis denticulata*, *Paragonyaulacysta s.l.*) with six postcingulars and two antapicals (6‴, 2‴‴ pattern) differs from *L. spinosa* only in showing considerable reduction of 1‴, 2‴, and 1‴‴. The interseries relationships of the gonyaulacacean pattern are directly comparable with *L. spinosa*. Thus 3‴ is homologous with key postc. 4, and 1‴ is homologous with key postc. 6. Also, only the stippled area of 2‴‴ corresponds to key antap. 3 and only the stippled area of 1‴‴ corresponds to key antap. 6.

Ceratium hirundinella also has a 6‴, 2‴‴ pattern, but is unusual in that postcingular 6‴ touches 1‴‴ as well as 2‴‴. A possible explanation of this relationship is that 6‴ in *C. hirundinella* actually represents two plates, 6‴ *s.s.* and the conventional posterior sulcal plate (p.s. in text-fig. 1). The latter plate has not been precisely identified in *C. hirundinella*, although it must be admitted that the sulcal area of *Ceratium* in general is poorly known (Wall and Evitt 1975, p. 19). Plates 5‴–1‴ are respectively homologous with postc. 2–6, and there is no counterpart of postc. 7. Thus 3‴ is homologous with key postc. 4, and 1‴ is homologous with key postc. 6. Antapical 2‴‴ touches five postcingulars and therefore corresponds to four plates in the model pattern, antap. 2–5. Thus only the stippled area of 2‴‴ corresponds to key antap. 3. Plate 1‴‴ touches 1‴ and 2‴ and is therefore homologous with key antap. 6. There is no counterpart of antap. 7.

Thalassiphora delicata also has a 6‴, 2‴‴ pattern, but its interseries relationships effectively represent a lateral reversal of the gonyaulacacean arrangement. This affects the antapicals, where 2‴‴ only touches three postcingulars and therefore corresponds to two plates in the model pattern, and 1‴‴ touches four postcingulars and therefore corresponds to three plates in the model pattern. Thus only the stippled area of 2‴‴ corresponds to key antap. 3, and only the stippled area of 1‴‴ corresponds to key antap. 6.

The interpreted homologous and corresponding plate relationships of the fifteen selected plate patterns and the model pattern (excluding the apical closing, cingular and antapical closing series) are summarized in Table 1. This emphasizes the fact that plates conventionally designated intercalary (*) in one pattern, are homologous with or partially correspond to conventional apical or antapical plates in another pattern. Examples include apical 4′ (conventional 2a) in *Protoperidinium depressum* homologous with apical 3′ in *Gonyaulax spinifera*, and antapical 1‴‴ (conventional 1p) in *G. spinifera* which partially corresponds to part of antapical 1‴‴ in *Helgolandinium subglobosum*. This table also shows that when a series is represented by the same number of plates in different patterns, the plates need not all be respectively homologous. Examples include the four apicals in *G. spinifera* and *T. delicata*, and the two antapicals in *G. spinifera*, *T. delicata*, and *P. depressum*.

DISCUSSION

The differences between the fifteen selected plate patterns (text-figs. 10–12) reflect an over-all trend of reduction in the total number of plates. This reduction is effected in two particular ways. There may be simplification through the development of a single plate in one pattern which spatially corresponds with two or more plates in another pattern. This critically affects interseries relationships. Alternatively there may be a primary development of fewer plates in particular series, without affecting interseries relationships. These two styles of reduction may occur independently or together. They may also be accompanied by variation in the relative size of certain plates which may affect interseries relationships through critical shortening or lateral reduction.

Reduction through simplification affects the apical closing, apical and antapical series. The development of a single large apical closing plate in *D. priscum* for instance, represents simplification of the six-plate arrangement in *R. rhaetica* and *S. arcticum*. In the apical series, simplification occurs

in specific areas, e.g. mid-ventral (1') in *Paragonyaulacysta s.l.*; left lateral (2') in *S. arcticum*; mid-dorsal (4') in *P. tritonium*; left and right lateral, (2', 3') in *G. spinifera*, (2', 4') in *T. delicata*; left ventral and right lateral (2', 4') in *H. subglobosum*. In the antapical series, simplification is best defined with reference to the model antapicals, antap. 2–7. For instance, the three antapicals in *H. subglobosum* reflect simplification of antap. 2–7 in the form 2–3, 4–5, 6–7. In the patterns with only two antapicals this simplification takes several forms, e.g. 2–3, 4–5 (peridiniacean type), 2–4, 5–6 (gonyaulacacean type), 2–5, 6 (*C. hirundinella*), 2–3, 4–6 (*T. delicata*).

Reduction through the primary development of fewer plates is best defined with reference to the position of plates which are homologous with or in part correspond to model key reference plates.

In the six epithecae in text-fig. 10 (*R. rhaetica* etc.) the position of these plates is virtually constant. In particular, the equivalent of key prec. 4. is invariably mid-dorsal. A similar constancy is shown by eight of the epithecae in text-fig. 11 (*L. spinosa* etc., but not *T. delicata*). However, in these patterns the equivalent of key prec. 4 is invariably right dorso-lateral in position. Compared with *R. rhaetica* etc. (text-fig. 10), this represents a rotation of the epithecal pattern, anticlockwise relative to the apical pole. This accommodates the primary development of one less apical and one less precingular plate (i.e. no counterparts of ap. 7, prec. 7).

In the eight hypothecae in text-fig. 12 there is considerable variation in the position of the key reference areas. In particular, the equivalent of key postc. 4 rotates from mid-dorsal in the rhaetogonyaulacacean type and *H. subglobosum*, through left dorso-lateral in *D. priscum* and *L. spinosa*, to left lateral in the gonyaulacacean and peridiniacean types. This rotation, which affects the over-all hypothecal pattern, is anticlockwise relative to the antapical pole. This accommodates the primary development of fewer postcingulars and antapicals (i.e. no counterparts of two or more of postc. 6, 7, antap. 6, 7).

The effect of variation in the relative size of certain plates is well shown by the epithecae of *Ctenidodinium* sp., *H. cladophora*, *Paragonyaulacysta s.l.* and *G. spinifera* (text-fig. 11), in which there is enlargement of the lateral and left ventral precingulars (compared with *L. spinosa*). This is at the expense of the apical series which becomes longitudinally aligned, and 6″ which is reduced. In the somewhat bizarre pattern of *T. delicata* (text-figs. 11, 12) the considerable enlargement of 1″ and 2‴, 3‴ is accommodated by the displacement of the sulcus, 1′, 4′, 1‴, 6‴ and 1‴′, 2‴′ to a right lateral position. There is also reduction of 5″ and 6‴, and 6″ is critically shortened. Other examples of critical shortening include 3′ in *Ctenidodinium* sp. and 6″ in *G. spinifera*, while 4′ in *P. depressum* is critically reduced laterally.

Reduction in the total number of thecal plates may well represent a fundamental trend in the evolution of peridinialean plate patterns. If this is so, then available evidence from the fossil record suggests that primary development of fewer plates was the most important means of achieving this reduction. This evidence is provided for epithecae by the appearance in the Late Triassic of patterns with counterparts of ap. 7, prec. 7 (*R. rhaetica*, *S. arcticum*), followed in the Jurassic by the appearance of patterns without counterparts of these two plates (e.g. *L. spinosa*, *Ctenidodinium* sp.). The hypothecal evidence is provided by the successive appearance of the rhaetogonyaulacacean type (Late Triassic), *D. priscum* and *L. spinosa* (Early Jurassic), gonyaulacacean type (Middle Jurassic) and the peridiniacean type (Late Jurassic). The great range of variation shown by Late Triassic and younger plate patterns resulted from the effects of reduction through simplification, and variation in relative plate size, being superimposed on the effect of primary reduction. The interaction of these three variables resulted in epithecae and hypothecae evolving comparatively independently and this is emphasized by the way in which the epitheca and hypotheca accommodated the effects of primary reduction. In both, rotation is anticlockwise relative to their respective pole, and therefore the hypotheca rotates in the opposite direction to the epitheca relative to the polar axis of the theca. The model plate pattern appears to represent an evolutionary base to which all Late Triassic and younger peridinialeans of the selected type are related. This type is characterized by having up to seven plates in each of its epithecal and hypothecal transverse series. In view of this relationship, the complex model pattern could be representative of a pre-Late Triassic ancestral peridinialean.

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