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DINOFLAGELLATE CYST TERMINOLOGY

W.R. EVITT, J.K. LENTIN, M.E. MILLIOUD,
L.E. STOVER, AND G.L. WILLIAMS



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DINOFLAGELLATE CYST TERMINOLOGY

Abstract

Recent advances in our knowledge of fossil dinoflagellates and fuller awareness of the distinction between cyst and theca have led to the development of a "cyst terminology" distinct from a "thecal terminology". This paper thus proposes modifications, based on a few key terms, prefixes and suffixes, to the somewhat imprecise cyst terminology currently in use.

Résumé

Des progrès récents dans la connaissance que nous avons des dinoflagellés et une meilleure compréhension de la distinction à faire entre "cystes" et thèques ont permis de mettre au point une terminologie des "cystes" distincte de celle des thèques. Cette étude propose donc des modifications, fondées sur quelques termes principaux, des préfixes et des suffixes, à la terminologie des "cystes" quelque peu imprécise actuellement utilisée.

INTRODUCTION

The descriptive terminology applied to modern dinoflagellate thecae has understandably been used for fossil dinoflagellates which originally were thought to be thecae. The realisation that fossil dinoflagellates are cysts and differ markedly from the thecate stage, has resulted in two major changes to our vocabulary. Firstly, as the great diversity of morphologic features displayed by fossil dinoflagellates has become apparent, the descriptive terminology applied to them has expanded. Secondly, the morphologic differences between dinoflagellate resting cysts and dinoflagellate thecae have necessitated the development of a "cyst terminology", as distinct from a "thecal terminology". Notwithstanding the already extensive vocabulary collated by Williams, Sarjeant, and Kidson (1973), we recommend further modifications in the terminology of fossil dinoflagellates, in the hope that they will make morphologic descriptions more lucid. Terms are presented in italics where first introduced.

THE TERMS EPICYST AND HYPOCYST

The theca of a motile dinoflagellate consists of an anterior epitheca (including the apical pole or apex) and a posterior hypotheca (including the antapical pole or antapex) separated by a more or less prominent and frequently equatorial, transverse flagellar furrow. Formerly epitheca and hypotheca were used to describe the equivalent areas in fossil dinoflagellates, but Downie and Sarjeant (1966) argued that it was incorrect to apply these terms to fossil dinoflagellates, since the latter were known to be cysts. Downie and Sarjeant proposed the terms epittract and hypottract, which have since been widely used. Drugg and Loeblich, 1967 (p. 182) introduced the term tract for the whole cyst. As the name for the container of the protoplast in its resting stage, tract is synonymous with cyst and, therefore, superfluous. Tract (from Latin *tractus* = area) is also etymologically inappropriate for a three-dimensional structure composed of one or more walls, where no connotation of area or region exists.

Lister (1970) proposed the terms epicyst and hypocyst for acritarchs, noting that they correspond to the terms epittract and hypottract in dinoflagellate cysts. We recommend that Lister's terms also be applied to the dinoflagellate cyst in place of epittract and hypottract. The parallel notion of the theca being divided into epitheca and hypotheca and the cyst being divided into epicyst and hypocyst have commendable consistency, clarity and simplicity.

Adoption of the term epicyst in place of epittract requires that archeopyles previously referred to as epittractal be renamed. We propose the term epicystal archeopyle. Examples of genera having epicystal archeopyles are *Ctenidodinium* Deflandre, 1938 emend. Sarjeant, 1966 and *Callaiosphaeridium* Davey and Williams, 1966.

USAGE OF THE PREFIX "PARA" IN CYST TERMINOLOGY (Fig. 1)

We recommend use of the prefix "para" (Greek: near, beside) in conjunction with features of the cyst which have, in the past, been described as "corresponding to", "reflecting", or being the "equivalent of" certain features of the theca, but to which have been applied the very same terms used for the thecal features cingulum, plate, sulcus, suture and tabulation.

PARACINGULUM; Adjectival form, paracingular:

Definition: Any feature or combination of features on the cyst, regardless of its exact morphological expression, corresponding to the cingulum (= transverse flagellar furrow, or girdle) of the theca.

Discussion: The paracingulum may be a pronounced furrow as in *Dinogymnium* Evitt, Clarke and Verdier, 1967, a narrow zone bounded by parallel septa and crossed by several short septa of similar structures as in *Leptodinium* Klement, 1960, emend. Sarjeant, 1969 and marked by a series of six isolated processes as in *Hystrichosphaeridium* Deflandre, 1937, emend. Davey and Williams, 1966b, or indicated by an equatorial zone devoid of processes as in *Oligosphaeridium* Davey and Williams, 1966b.

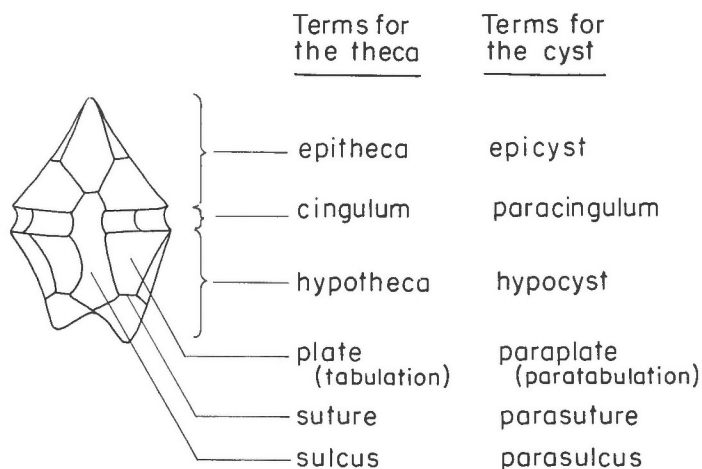


Figure 1. Major divisions of the theca and cyst, and terms employing the prefix "para-".

PARAPLATE; Adjectival form, paraplate:

Definition: That portion of a cyst corresponding in position and extent to a thecal plate.

Discussion: Paraplates may be delineated by ridges or septa along their boundaries, as in *Gonyaulacysta* Deflandre, 1964, ex Norris and Sarjeant, 1965, and *Leptodinium*. They may also be expressed by single or grouped features covering a portion (small or large) of the paraplate. Examples of the latter are the relatively isolated intratabular processes of *Hystrichosphaeridium*, the proximally expanded and inflated processes of *Hystrichokolpoma cinctum* Klumpp, 1953, the arcuate to circular process-bearing ridges of *Areoligera* Lejeune-Carpentier, 1938, emend. Williams and Downie, 1966c, and of *Systematophora* Deflandre and Cookson, 1955, and the clusters of granules or short projections in some species of *Deflandrea* Eisenack (s. l.) and *Wetzeliella* Eisenack (s. l.). Although a theca is divided by sutures into its full complement of thecal plates and the sutures may be made visible by chemical means (e. g., treatment with javelle water) even if not discernible when the theca is intact, a cyst is not necessarily resolvable into its full complement of constituent paraplates. The paracingulum in *Oligosphaeridium* is indicated by an equatorial zone devoid of processes and individual paraplates are not normally discernible. In some species of *Deflandrea* only one paraplate may be visible, the mid-dorsal intercalary paraplate, which is delineated by the archeopyle suture.

PARASULCUS; Adjectival form, parasulcal:

Definition: Any feature or combination of features on the cyst, regardless of its exact morphological expression, corresponding to the sulcus (= longitudinal flagellar furrow) of the theca.

Discussion: A ventral interruption in the paracingulum or a ventral longitudinal concavity (especially in the hypocyst) often are the only evidence of the parasulcus. In some species of *Leptodinium* and *Gonyaulacysta* the parasulcus is delineated by ridges or septa, and may be divided into paraplates.

In *Hystrichokolpoma* Klumpp, 1953, the parasulcus is typically marked by a group of distinctively slender processes. The anterior extremity of the parasulcus in species with an apical archeopyle is commonly indicated by a depression in the margin of the archeopyle, the parasulcal notch, and a corresponding parasulcal tongue extending from the margin of the operculum. Similarly in some genera having a 2A + 6P combination archeopyle (for example *Homotryblum* Davey and Williams, 1966) the parasulcal tongue is present as a short projection extending above the archeopyle margin.

PARASUTURE; Adjectival form, parasutural:

Definition: Any feature or combination of features on the cyst, regardless of its exact morphological expression, corresponding to a thecal suture, i. e. one of the major discontinuities by which the theca is divided into a number of separate thecal plates.

Discussion: Parasutures may be expressed by more or less continuous ridges; by septa or grooves, with or without projections extending from them, as in *Gonyaulacysta*, *Leptodinium* and *Spiniferites* Mantell, 1850, emend. Sarjeant, 1970; by rows of projections such as granules or spines; or by interruptions in an otherwise more or less evenly distributed ornamentation. The true sutures, or archeopyle sutures, on the cyst usually correspond to the sutures between plates on the theca. According to the definition above, therefore, archeopyle sutures are usually parasutures. This may seem a contradiction in terms until it is realised that "parasuture" does not necessarily mean "not a suture", but means "a cyst feature in the relative position of a thecal suture". Except for the archeopyle suture, parasutures are usually not expressed as sutures (i. e., cuts through the cyst wall).

PARATABULATION; Adjectival form, paratabulate:

Definition: The sum of those characteristics of the evident paraplates that pertain to their number, size, shape, and mutual relationships.

Discussion: The paratabulation of the cyst is analogous to the tabulation of the theca and most cysts are in some measure paratabulate, with some of the paraplates being evident. When all of the paraplates of a cyst are not visible, the paratabulation is less complete than the inferred tabulation of the theca within which the cyst formed.

Paratabulation is, in part, synonymous with pseudotabulation, which we recommend be suppressed. Pseudotabulation was introduced by Balech (1967) for a pattern of structures on the cyst "... which mimics that of *Gonyaulax*...". Although later used by Wall (1971), pseudotabulation has not found wide acceptance and we believe paratabulation is etymologically preferable. The features on the cyst are no more pseudothecal features than vice versa. The prefix "para-" conveys a sense of comparability, without suggesting the mimicry implied by "pseudo-".

The clarity and completeness of the paratabulation varies greatly. The only evidence for it in some taxa may be the distinctive shape of an archeopyle or traces of a paracingulum. Alternatively, the paratabulation

may be expressed as clearly and completely as the thecal tabulation. Examples of fully expressed paratabulation are the theca-like patterns of polygonal paraplates outlined by parasutural ridges or septa in *Leptodinium* and *Gonyaulacysta* and the somewhat less obvious low-relief surface pattern in *Palaeoperidinium pyrophorum* (Ehrenberg, 1838) Sarjeant, 1967. Paratabulation that is fully expressed but not obviously similar to a pattern of polygonal plates is the arrangement of single intratabular processes in *Hystrichosphaeridium tubiferum* (Ehrenberg, 1838) Deflandre, 1937b emend Davey and Williams, 1966b.

Although the archeopyle usually provides a clear indication of some of the paratabulation, in no known species does it indicate the complete paratabulation and in most instances the opening involves only one or a small number of paraplates.

PARATABULATION FORMULA AND RELATED DEFINITIONS

Paratabulation Formula

Selected information about the paratabulation can be expressed as the paratabulation formula, comparable to the tabulation formula for the theca. A paratabulation formula gives the number of evident paraplates in each series, but it does not include information on the morphological expression or on the size and mutual relationships of the evident paraplates. For recording paratabulation formulae we propose to use, with minor exceptions, the plan and symbols suggested for tabulation formulae by Kofoid (1909). These were first applied to fossil dinoflagellates by Deflandre (1938) and have been used widely in palynological publications since then. The system we recommend is as follows:

(a) The symbols suggested by Kofoid be used to identify the several series of paraplates, except that we recommend use of *pr* for preapicals as proposed by Loeblich III (1970) instead of the *acl* for apical closing plate used by Kofoid. When discussing paraplates of a series, the adjectival terms, apical etc., are used. Thus in a paracingulum with six paraplates, one would refer to paraplate 3c, as the third cingular paraplate.

(b) A single numeral without query (?) indicates confidence that the number of paraplates has been determined reliably for the series specified; e.g. - 4', 3a, 7".....

(c) A numeral preceded by a query (?) indicates that individual paraplates have been recognised in the series specified, but that their exact number is in doubt; e.g. - 4', ?2a, 7"..... or 4', ?2-3a, 7".....

(d) A query (?) without a numeral indicates doubt that paraplates of the series specified occur in the cyst; e.g. - 4', a?, 6".....

(e) Two hyphenated numerals indicate variation in the taxon being discussed; e.g. - 4', 0-4a, 6".....

(f) (New Proposal). An "X" indicates that some structure (i. e. , not just an absence of features present elsewhere on the cyst) represents the series of paraplates specified, but that individual paraplates are not distinguishable. Example: 4', 3a, 7", Xc, 5"..... which might pertain to a specimen in which some feature (e. g. , a bulge, or pair of parasutural lines, or a single prominent septum) marks the position of the paracingulum but gives no indication of its subdivision into paraplates.

(g) A zero is an explicit statement that paraplates of the specified series are not themselves marked by any distinctive structures, although their general location may be evident from the distribution of features in adjacent areas; thus 4', 0a, 6"....., means that no anterior intercalary paraplates are differentiated and 4', 6", 0c, 5"....., means that no cingular paraplates are represented, as in the equatorial zone devoid of processes in *Oligosphaeridium*.

(h) Failure to refer to particular paraplate series does not necessarily imply that they are absent. An acceptable formula for paratabulate peridiniacean species would be 4', 3a, 7", 5"', 2"', although it could be expressed more explicitly as pr?, 4', 3a, 7", Xc, 5"', 0p, 2"', Xs.

The paratabulation formula for a cyst is a statement of the number of observable paraplates and their disposition. The tabulation formula for a theca expresses the total number of thecal plates. Consequently the two formulae (for cyst paratabulation and for thecal tabulation) derived from the analysis of structures produced by the same organism will be identical only when the number of paraplates apparent on the cyst represents the full complement of thecal plates. The number of paraplates is not always equal to the number of plates of the equivalent theca and often the evidence for paraplates on the cyst is incomplete. The only paraplate clearly delineated in *Tectatodinium* Wall, 1967, is the single precingular paraplate (3") whose loss results in the archeopyle. A paratabulation formula recording this information would read: 0pr, 0a, 1", 0c, 0"', 0p, 0"', 0s, where 1" refers to the presence of a single paraplate and not specifically the first precingular. In contrast, the paratabulation formula for *Leptodinium mirabile* Klement, 1960 (incorporating unpublished observations by Evitt) can be stated: 2pr, 4', 2a, 6", 6c, 6"', 1p, 1"', 5s.

Most formulae published with descriptions of fossil dinoflagellates appear under such headings as "plate formula", "tabulation formula", "process formula", "tabulation", and "cyst formula" are paratabulation formulae in the sense proposed here.

Process Formula

Paratabulation is also expressed by the process formula, which is based on the distribution of intratabular processes or process groups. The term has been used for dinoflagellate cysts (Stover, 1975) as well as for acritarchs (Lister, 1970). In some species

the process formula for the cyst corresponds exactly to the paratabulation formula. However, there will be differences between those formulae when parasutural features indicate a greater number of paraplates than do the processes. V. D. Wiggins and D. W. Engelhardt (personal communications) have observed parasutural lines on the periplasm of some Lower Cretaceous *Oligosphaeridium* specimens from Alaska. These lines delineate six cingular paraplates, devoid of processes as in all species of this genus. The process formula for these forms would refer to 0c, whereas the paratabulation formula would refer to 6c. Eaton (1971) observed only five precingular, and no anterior sulcal processes in *Areosphaeridium multicornutum* Eaton, 1971, although parasutures on the archeopyle margin indicate six precingular paraplates and one anterior sulcal, paraplate. Here the process formula would refer to 5", whereas the paratabulation formula would indicate 6" + as.

Inferred Tabulation Formula

A paratabulation formula is a statement of features observed on the cyst. To a degree it is interpretative, for it depends upon an analysis of morphological features. But it should not be an inference or an extrapolation as to what the organization of plates on the parent theca may have been like. A formula presenting such an inference is an inferred tabulation formula.

A single tabulation formula may reasonably be inferred from fossils with different paratabulation formulae. For example, an inferred tabulation formula of 1pr, 4', 0a, 6", 6c, 6"', 1p, 1"', 5s, as in *Gonyaulax* Diesing, 1866, and some other modern genera, may be inferred from many fossil dinoflagellates whose paratabulation formulae differ, including the three species noted in Table 1.

Certain paraplates, such as those of the paracingulum and parasulcus may be undefined by surface markings or other features on the cyst. Similarly the paraplate representing the small first postcingular plate of the *Gonyaulax*-type of tabulation frequently is not discernible.

SUMMARY OF TERMINOLOGY RELATING TO TABULATION AND PARATABULATION

Thecae of dinoflagellates of the Order Peridinales are divided into several series of more or less polygonal units, the plates. The lines of separation between plates are sutures, and the sum of the characteristics of the plates (i. e., their number, size, arrangement into series, shape, mutual contacts) constitutes the tabulation. Certain aspects of the tabulation (number of plates in each series) may be abbreviated in a tabulation formula (or plate formula) using the form and symbols suggested by Kofoid.

An unit area on the cyst corresponding to a thecal plate is a paraplate. Paraplates are delineated by parasutures (i. e., linear features which correspond

in position to thecal sutures), or by non-parasutural features (e. g., intratabular processes or process groups) that are positioned in areas corresponding to the more central parts of the thecal plates. The sum of the characteristics of the paraplates constitutes the paratabulation. The numbers of evident paraplates and their organization into several series may be abbreviated in a paratabulation formula, using the form and system suggested by Kofoid for thecal tabulation. A paratabulation determined from the distribution of intratabular processes or process groups, may be abbreviated in a process formula.

The tabulation of a theca is inherently complete, since the entire theca is divided by sutures into plates. The paratabulation of a cyst may be either complete, or more commonly incomplete, since small or large portions of the cyst may bear no markings that permit recognition of paraplates. The paratabulation formula records any degree of incompleteness in the paratabulation by indicating only those paraplates which are apparent from special features on the cyst. This distinguishes the paratabulation formula from the inferred tabulation formula, which is an interpretation of what the tabulation of the supposed corresponding theca may have been.

Table 1
Paratabulation formulae in three types
of gonyaulacacean cysts.

FORMULA	MANIFESTATION
<i>Hystrichosphaeridium tubiferum</i> (Ehrenberg) 1pr, 4', 0a, 6", 6c, 6"', 1p, 1"', 5s	"complete" suite of paraplates, each paraplate indicated by a single intratabular process.
<i>Oligosphaeridium complex</i> (White) 0pr, 4', 0a, 6", 0c, 5"', 0p, 1"', 1s	each paraplate indicated by single intratabular process, but none present for the paracingulum, for the first postcingular paraplate, or for any sulcal paraplates except the posterior one.
<i>Spiniferites pseudofurcatus</i> (Klumpp) 0pr, 3', 0a, 5", 5c, 5"', 0p, 1"', 0s	Paraplates outlined by process-bearing parasutural ridges. Failure of certain parasutural lines to develop results in certain paraplates being undefined. In this case "missing" boundaries are between the areas representing thecal plates as follows: 1' and 4', 6c and 6", 6" and the sulcus, 1"' and the sulcus, and 1s-5s (i. e., all the sulcal plates).

Table 2

Wall, body and cavity terminology in dinoflagellate cysts.

PREFIX	MEANING	COMBINATION	DEFINITION	STEM	MEANING	COMBINATION	DEFINITION
auto-	single	autophragm	single wall	-phragm	wall	autophragm	single wall
		autocyst	single body			endophragm	inner wall
		autocoel	single cavity			mesophragm	middle wall
endo-	inner	endophragm	inner wall	-cyst	body	periphragm	outer wall
		endocyst	inner body			ectophragm	extreme outer wall
		endocoel	inner cavity			autocyst	single body
meso-	middle	mesophragm	middle wall	-coel	cavity	endocyst	inner body
		mesocyst	middle body			mesocyst	middle body
		mesocoel	middle cavity			pericyst	outer body
peri-	outer	periphragm	outer wall	-coel	cavity	ectocyst	extreme outer body
		pericyst	outer body			autocoel	single cavity
		pericoel	outer cavity			endocoel	inner cavity
ecto-	extreme outer	ectophragm	extreme outer wall	-coel	cavity	mesocoel	middle cavity
		ectocyst	extreme outer body			pericoel	outer cavity
		ectocoel	extreme outer cavity			ectocoel	extreme outer cavity

TERMS BASED ON A
COMBINATION OF STEMS AND PREFIXES

The use of a coordinated system of word stems and prefixes is proposed for certain features of dinoflagellate cysts. The prefixes endo-, meso-, peri-, and ecto-, in conjunction with the stems -phragm and -coel have previously been used to define wall layers, and cavities within or between them (Davey *et al.*, 1966; Evitt, 1969). The following paragraphs and tables present further systematic combinations of these word elements, and propose some new terms.

Pertaining to Cyst Wall Structure (Fig. 2)

We advocate using the five prefixes and three stems listed in Table 2, for naming the layers of the cyst wall, the three-dimensional bodies formed by them, and the spaces or cavities within or between them. They provide a total of fifteen terms. The potential wall layers are autophragm, endophragm, mesophragm, periphragm and ectophragm. The stem -cyst is recommended to replace -blast (Evitt, 1969) and -corpus (Norris and McAndrews, 1970) for the three-dimensional body formed by one wall layer. Thus we refer to the autocyst, endocyst, mesocyst, pericyst and ectocyst. The potential cavities recognised are autocoel, endocoel, mesocoel, pericoel and ectocoel.

Procedure for Identifying Wall Layers

A procedure is outlined for identifying the various wall layers (Table 3), which is based on the recognition of regular structures (Fig. 3). Such structures are processes, septa, or other features distributed in an organized way and similar in form, number and distribution. They are never absent from specimens of a given species, being among its most essential

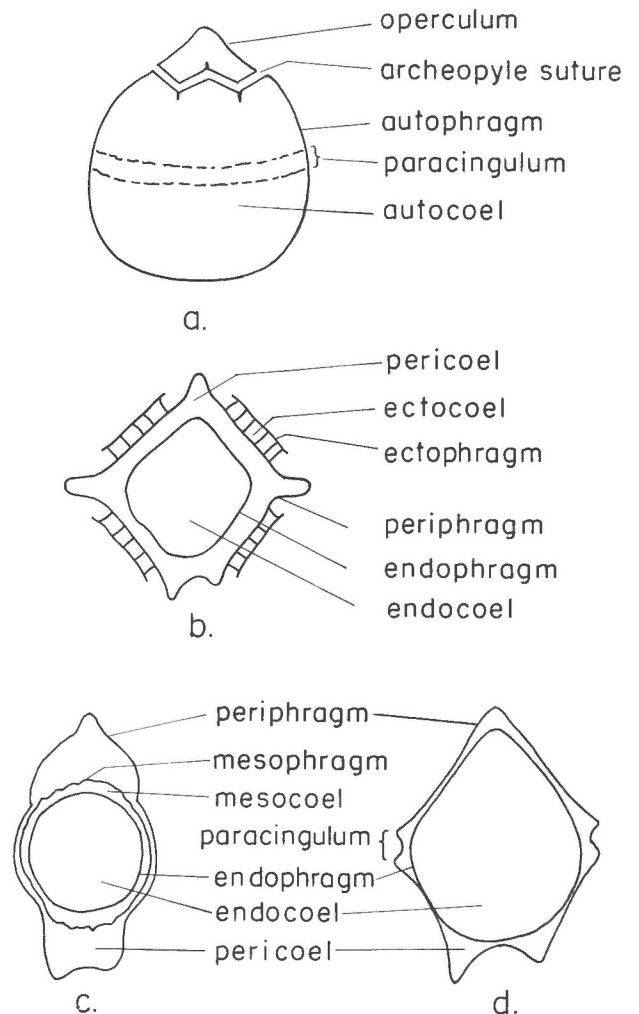


Figure 2. Wall layers, bodies, and spaces, as in -
a. *Chytroeisphaeridia*
b. *Wetzeliella coleothrypta*
c, d. *Deflandrea* (s.l.) spp.

Table 3

Identification of wall layers in a dinoflagellate cyst.

Number of wall layers	Regular processes, etc. interconnect the layers	Identification of layers	Examples
one	---	autophragm	<i>Chytroeisphaeridia</i> , <i>Cyclonephelium</i> , <i>Pseudoceratium</i> , <i>Tenua</i>
two	no	endophragm and periphragm	<i>Deflandrea</i> (most), <i>Endoceratium</i> , <i>Hystrichosphaeridium</i> , <i>Senoniasphaera</i> , <i>Spiniferites</i> , <i>Thalassiphora</i> , <i>Triblastula</i> , <i>Wetzeliella</i> species such as <i>W. articulata</i>
two	yes	autophragm and ectophragm	<i>Aptea</i> , <i>Cannosphaeriosis</i> , <i>Chlamydothrella</i> , <i>Gardodinium</i> , <i>Samlandia</i>
three	no	endophragm, mesophragm, and periphragm	<i>Deflandrea</i> (a few species)
three	yes, with respect to the outer two layers	endophragm, periphragm, and ectophragm	<i>Nematosphaeropsis</i> , <i>Wetzeliella</i> species such as <i>W. coleothrypta</i> and <i>W. tenuivirgula</i>

characteristics. Processes commonly are regular structures. However, constant presence of processes or other structures does not alone suffice to make them regular. Structures that are not regular vary greatly in numbers and position from specimen to specimen within one species, and may be absent from some specimens. Such structures appear to be incidental, or even accidental, attributes of the specimens in which they occur. The individual wall layers are discussed below.

Ectophragm: The ectophragm is the thin outermost wall layer and is supported by projections from the underlying layer (periphragm or autophragm). The projections appear to be continuations of the ectophragm. The ectophragm bears no projecting sutures on its outer surface. It is rarely in contact with the underlying layer and may be continuous or incomplete. It may be reduced to an interrupted membrane, to a highly perforate membrane, to small patches of material at the tips of supporting processes, or to a system of rod-like trabeculae or ribbon-like structures.

Periphragm: The periphragm is a very variable layer, ranging from a thin, clear, and nearly featureless membrane to an elaborately structured layer from which processes arise. As a membrane it may be continuous or locally perforate or absent. It may bear processes, septa, less easily named structures, or a combination of any of these. Such projections are regular. Species possessing a periphragm also have a distinguishable, underlying layer, the endophragm, although in some specimens the endophragm is absent (either through failure to develop before fossilization or through mechanical separation and loss during transport or sample preparation). The periphragm

may be widely separated from the endophragm, or appressed to it locally, or everywhere except at the bases of projections or at abrupt changes in the curvature of the endophragm (as at the apex, antapex, or paracingulum). The periphragm is rarely supported by structures projecting from the endophragm, in contrast to the common relationship between periphragm (or autophragm) and ectophragm. When such structures are present between endophragm and periphragm, they are not regular in that they usually are few in number and vary in number and position from specimen to specimen.

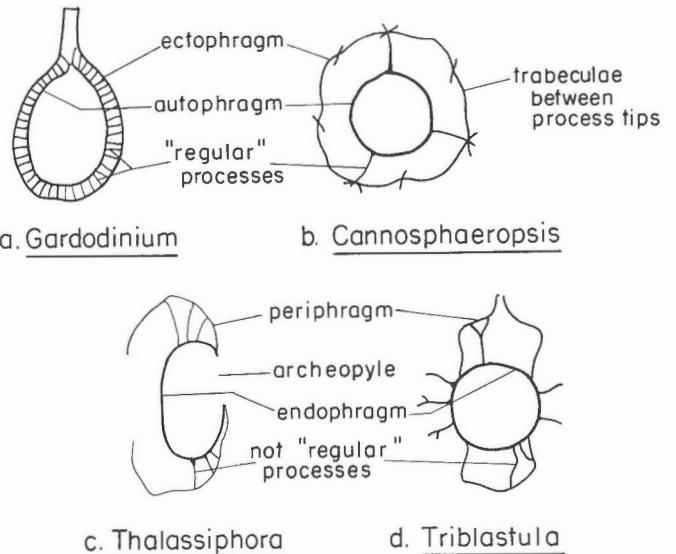


Figure 3. "Regular" and other processes.

Mesophragm: The mesophragm is a rarely developed wall layer located between the periphragm and endophragm. It consists of a membrane which may be separated from or in contact with the other layers, and it neither bears, nor is supported by, processes or septa.

Endophragm: The endophragm is the innermost wall layer when a periphragm is recognizable. Its thickness varies but is usually greater than that of the periphragm, and its inner surface is usually smooth, although fine internal corrugations and parasutural grooves may occur. Its outer surface may be smooth or may bear various features of low relief such as ridges, granules or tubercles. It does not bear regular projections that are continuous with the periphragm. The endophragm is normally continuous, except for the archeopyle, and lacks perforations.

Autophragm: This term is appropriate in any of three cases: 1) where the wall is known to be composed of only one layer; 2) where small size, a thin wall, or poor preservation prevents recognition of endophragm or periphragm, although these may be present and appressed; 3) to denote the inner of two layers where the outer layer is supported by projections from the inner layer, as the ectophragm is supported by the periphragm. In the last case, the inner layer represents indistinguishable endophragm and periphragm. Like the endophragm, the autophragm is normally smooth on the inner surface, continuous and without openings except for the archeopyle. The only known exception is the genus *Dinogymnium*, in which the autophragm is penetrated by many minute pores.

Other Terms from Wall-Layer Prefixes (Figs. 4, 5)

To specify the wall layer in which a particular feature occurs, the appropriate wall-layer prefix as shown in Table 2 may be combined with the term for the feature in question to make a short and unambiguous compound term. Some of the terms that might be used

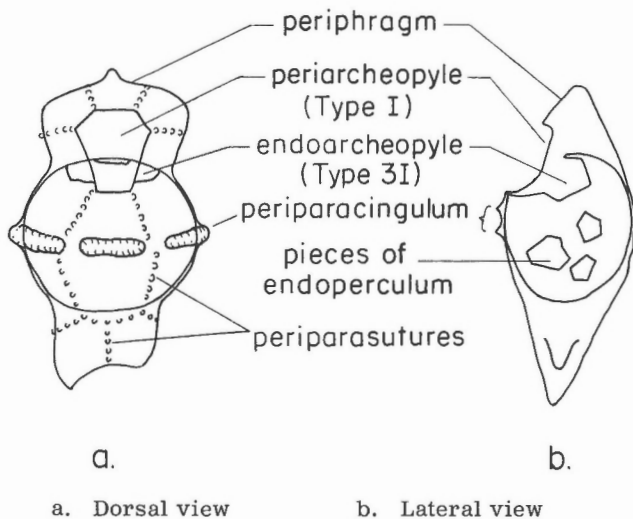


Figure 4. Some additional terms using wall-layer prefixes applied to features in two species of *Deflandrea* (s. l.) type.

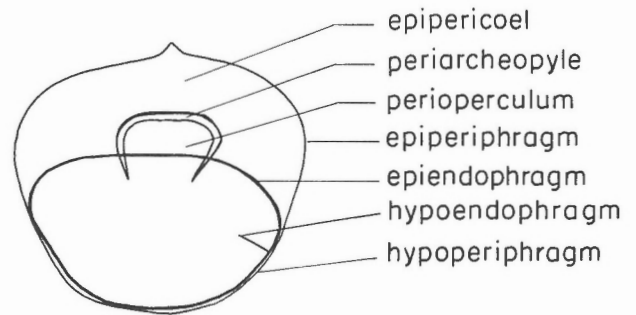


Figure 5. Some additional terms with prefixes "epi-", "hypo-", and "peri-" applied to *Nelsoniella* sp.

appropriately as stems for such compounds would be archeopyle, operculum, paracingulum, paraplate, parasulcus, parasuture, and paratabulation.

Not all the possible combinations will prove useful but some will be helpful when describing cysts in which the wall layers are separated sufficiently for a feature to be expressed independently in two or more layers. Such terms make it possible, for example, to indicate that the periarcheopyle is Type I, whereas the endoarcheopyle is Type 3I with an endoperculum composed of three separate pieces. One may also say that in *Peridinium limbatum* (Evitt and Wall, 1968), the periparatabulation is incompletely indicated by parasutural rows of granules or spines, whereas a complete endoparatabulation is indicated by endoparasutures which are grooves in the endophragm.

Terms with Prefixes "Epi" and "Hypo" (Fig. 5)

The prefixes epi- and hypo- can be used for formulating terms to specify the location of a feature in the anterior (apical) or posterior (antapical) part of the cyst. Epicyst and hypocyst have been discussed in previous pages. Other suggested compound terms are epiparatabulation, hypoparatabulation, hypopericoel, hypoperiphragm, hypoendophragm, epipericoel, epiperiphragm and epiendophragm, which might be used as in the following examples. The archeopyle sutures in *Hemicystodinium* Wall (1967) delineate an almost complete epiparatabulation, whereas there is no indication of a hypoparatabulation. In *Nelsoniella* Cookson and Eisenack, 1960, the hypoperiphragm and hypoendophragm are appressed, without intervening hypopericoel, but a large epipericoel separates the epiperiphragm from the epiendophragm.

THE TERMS PENITABULAR AND PANDASUTURAL (Fig. 6)

Wall and Dale (1968) suggested peritabular to describe "Ornamentation which originates immediately interior to the margins of reflected plate-areas ...". Since the prefix peri- has been used in this paper and elsewhere, to mean outer, we propose the term penitabular (Latin: *penitus* within), to replace peritabular as defined by Wall and Dale (*op cit.*).

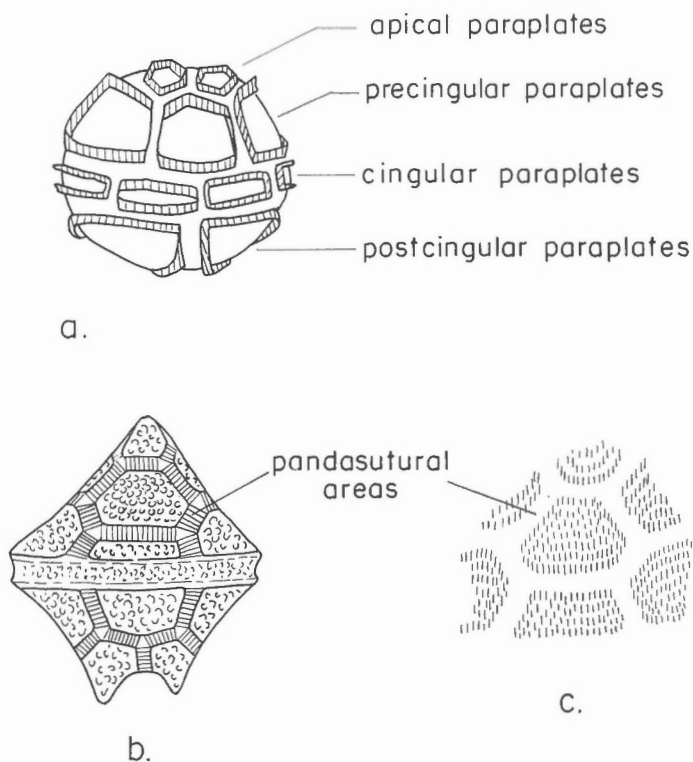


Figure 6. Schematic drawings to illustrate -
 a. Penitabular septa as in *Eisenackia circumtabulata*
 b, c. Pandasutural areas as in *Palaeoperidinium* sp. and *Deflandrea phosphoritica*.

Penitabular refers to linear features (e.g., ridges, septa, rows of granules) which lie immediately within the margin of a paraplata, whether that margin is marked by a parasutural line or is inferred from the distribution of other features (Fig. 6). Penitabular features of adjacent paraplata are at least in part subparallel and are separated by a narrow, essentially parasutural band of the wall surface. The septa which clearly define the paraplata in *Eisenackia circumtabulata* Drugg, 1967, are penitabular features, as are the lines of contact between periphragm and endophragm around the inflated bases of processes in *Hystrichokolpoma cinctum*. Penitabular and intratabular features may intergrade, as the former become successively more restricted to central portions of the paraplata.

The term pandasutural (Latin: *pando* spread) is proposed for the peripheral zone of a paraplata, which is distinguished from the remaining area of the paraplata by contrasting surface features. Pandasutural bands are not necessarily separated from the remainder of the paraplata by penitabular features. In *Palaeoperidinium pyrophorum* transversely striate pandasutural areas separate finely reticulate polygonal areas of the paraplata (Fig. 6b). Certain species of *Deflandrea Eisenack* (s.l.) possess pandasutural areas devoid of surface features which separate polygonal areas of ornamentation (Fig. 6c). Pandasutural areas on the cyst sometimes appear to represent the bands of

incremental plate growth recorded on thecal plates by somewhat analogous differences in surface markings (e.g., striate, non-porate bands along the sutures, which contrast with reticulate-porate central parts of the thecal plates). Like these growth zones, pandasutural bands on cysts may vary markedly in width and clarity within a single species or even on a single specimen.

Comment on Usage of the Term Cyst

In the foregoing pages we have recommended three different uses of cyst: in one sense as an independent word and in two senses as a word stem in combination with prefixes. In the hope of avoiding confusion these uses are summarized here. Cyst used independently, refers to the whole structure (whether composed of one or more layers) which contained the protoplast of the resting cell. It thus replaces the terms tract, test and shell. As a stem combined with a variety of prefixes -cyst in one sense refers to the entire three-dimensional body formed by one wall layer. Examples are such terms as endocyst, pericyst, and autocyst. In these usages -cyst replaces -blast and -corpus of certain recent authors. In a second sense -cyst may refer to a major portion of the wall lying either toward the apex or toward the antapex from the paracingulum. In the examples epicyst and hypocyst, -cyst replaces -tract.

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ADDENDUM

The term "plate" is so firmly entrenched in the English descriptive literature on dinoflagellates that we are suggesting "paraplate" for the corresponding feature on the cyst. The linguistically hybrid character of this term may make it unattractive or unacceptable in languages other than English. An equivalent term based on entirely classic roots would be "paratabula" (pl. "paratabulae"), and we recommend this as a synonymous alternative to "paraplate".

