I. ABSTRACT
The fossil dinocyst genus Dichadogonyaulax, erected by Sargeant in 1966, has proven to be very controversial. It has been synonymized with Ctenidodinium at least twice and resurrected at least twice. The separation of the two genera was based on the equal development of paracingular ornamentation in Dichadogonyaulax and the unequal development of those features in Ctenidodinium. This paracingular differentiation is a somewhat variable feature and probably not of generic significance.

There is, however, a fundamental difference in the paratabulation of the epicyst between representatives of the two genera. The type species of Ctenidodinium, C. ornatum, exhibits a preapical paraplate separating the second and fourth apical paraplates and also possesses anterior intercalary paraplate(s); whereas the type of Dichadogonyaulax, D. culmula, either has no preapical paraplate or it is reduced and displaced toward the ventral surface, thus allowing contact between the second and fourth apical paraplates. No anterior intercalary paraplates are present in D. culmula.

Korystocysta, erected by Woollam in 1983, has a Ctenidodinium style epicyst paratabulation and differs from Ctenidodinium in having an abbreviated apical horn and accessory parasutural ("growth bands") ridges.

II. INTRODUCTION
The generic differentiation of paratabulate gonyaulacoid dinocysts with epicyst archaeophyles has proved to be troublesome for many palynologists. In fact, the differentiation of species within this complex is frequently easier than deciding in which genus the species fits. This situation is a result of the two principal genera, Ctenidodinium and Dichadogonyaulax, being separated on the unequal versus equal development of paracingular ornamentation. This feature has been regarded as not having generic significance by some workers (Lentin and Williams, 1973; Stover and Evitt, 1978) and by others as the major generic criterion (Sargeant, 1966, 1975; Woollam, 1983). The relative de-
Development of ornamentation on the anterior and posterior paracingular margins is a variable feature, virtually impossible to discern in highly compressed specimens, and seems to me to be not the sort of morphologic feature that should be utilized to separate dinocysts at the generic level.

The paratabulation of the various species in this complex generally has been accurately recorded in the literature, if not by the first worker, then by further study and/or emendation. Upon initial examination, it emerges that both Ctenidodinium and Dichadogonyaulax, as currently circumscribed exhibit as paratabulation of: 0-3pr, 4', 0-2a, 6', 6c, x-6s, 6'', 1p, 1'' (Woollam, 1983). Further study of numerous specimens, however, has demonstrated that a means of separating Ctenidodinium and Dichadogonyaulax exists, that being the epicystal paratabulation. It is the intent of this paper to demonstrate the evidence to support the utilization of epicystal paratabulation as a means of separating the two previously mentioned genera and to briefly discuss and emend Korystocysta.

The principal sources for the dinocysts illustrated herein are core and cutting samples of wells from the Gulf and Atlantic coastal plain. In addition, some outcrop

Text Fig. 1 Diagrammatic representation of a gonyaulacoid dinocyst in: A) ventral view, B) apical view, C) Dorsal view, and D) antapical view comparing Kofoidian paraplate notation (boldface) of major paraplate series with the Taylor (1980) notation (parentheses).
samples from classic British and European localities were examined. The type material for *Ctenidodinium chondrum* was supplied to the author by Warren Drugg. The type material for *C. scissum* (McIntyre and Brideaux, 1980) was supplied by the I.S.P.G. of Calgary. Their assistance in this study is gratefully acknowledged. Illustrated specimens are stored at Amoco Production Company in New Orleans, Louisiana (U.S.). Specimens are located by reference to the lower left corner of the coverslip, with label at observer's left, in millimeters to the right (R) and away (+) from the observer.

### III. ACKNOWLEDGMENTS

The author would like to thank Amoco Production Company for permission to publish this work. The assistance of Sue Evans for drafting and Jim Truehart for photographic work was invaluable. Thanks also go to Jeff Stein and Sue Duffield who read earlier versions of the manuscript. In addition, informal discussions with Dan Beju and David Wall were helpful in consolidating the thoughts expressed herein, although the views expressed are the author's alone.

### IV. DISCUSSION

All paratabulation information in this paper uses Kodoidal notation. Text figure 1 provides a comparison of major plate series using Kodoidal notation with the newer notation of Taylor (1980) being used by some authors.

The dinocysts comprising the *Ctenidodinium* "complex" are gonyaulacoid cysts, which exhibit differences in epicystal paratabulation. The epicystal paratabulation of *C. ornatum*, the type species, and its close relative *C. combazii* is lpr, 4', 1-2a, 6" (Pl. 1, figs. 1, 2). The paraplate topologic arrangement is also significant when comparing those forms in the *Ctenidodinium* "complex." The preapical paraplate is located at the apex, thus separating the second and apical fourth paraplates (Pl. 1, figs. 1, 2; Pl. 2, figs. 1-3). This arrangement also exists in the species assigned to *Korystocysta* (Pl. 1, figs. 3, 11, 12).

Examination of the epicystal paratabulation of the type species of *Dichadogonyaulax*, *D. culmula* (Pl. 3, fig. 1) reveals a paratabulation of 1pr, 4', 0-a, 6". In addition to the absence of the anterior intercalary paraplates, the location of the preapical paraplate is significant. The preapical paraplate is displaced posteroventrally, thereby allowing contact between the second and fourth apical paraplates (Pl. 3, fig. 1). The displacement of the preapical paraplate, which appears to be a result of shortening the first apical paraplate, is also seen in *D. pannea* (Pl. 1, fig. 10), *D. cf. D. culmula* (Pl. 1, figs. 4 and 7), and *Dichadogonyaulax* sp. B (Pl. 1, figs. 5-9).

I, therefore, propose to separate *Dichadogonyaulax* from *Ctenidodinium* on the basis of the posteroventral displacement.

### TABLE I

<table>
<thead>
<tr>
<th>MORPHOLOGIC FEATURE</th>
<th>PREAPICAL PARAPLATE(S)</th>
<th>APICAL PARAPLATE TOPOLOGY</th>
<th>ANTERIOR INTERCALARY PARAPLATES</th>
<th>PARACINGULAR ASYMMETRY</th>
<th>ACCESSORY RIDGES</th>
<th>APICAL HORN</th>
</tr>
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<tbody>
<tr>
<td>Ctenidodinium</td>
<td>1-2</td>
<td>2' &amp; 4' Separated By Preapicals</td>
<td>1-2 Paraplates</td>
<td>Generally Not</td>
<td>Not</td>
<td>No</td>
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<td></td>
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</tr>
</tbody>
</table>

A summary of the key morphologic features for generic separation of *Ctenidodinium*, *Dichadogonyaulax*, and *Korystocysta*.
ment of the preapical paraplate, which allows contact between the second and fourth apical paraplates. Although D. culmula and D. pannea have no anterior intercalary paraplate, the figure of C. schizoblatum by Norris (1965, Fig. 4A) indicates the presence of a single paraplate (3' of Norris) in that position. The figure also illustrates the contact of the second and fourth apical paraplates and a thickened parasuture in the same position as the preapical paraplate in D. culmula. Until the type material can be re-examined it appears preferable to retain schizoblatum in the genus Ctenidodinium.

The hypocystral paratabulation of Ctenidodinium, Dichadogonyaulax, and Korystocysta is the same in terms of the number of paraplates and topology with minor variations in paraplate shape. The posterior intercalary paraplate is somewhat elongate in Korystocysta (Pl. 1, fig. 12) (Wooliam, 1983). The antapical paraplate of Dichadogonyaulax and Ctenido-
dinium is slightly asymmetric with the long side pointing toward the sixth postcingular paraplate (Pl. 1, figs. 6, 9; Pl. 2, fig. 4).

The recent study by Helenes-Escamilla (1984) demonstrated strong asymmetry of the antapical paraplate in Cri-broperidinium. The epicystal arrangement in that genus shows the displacement of the preapical paraplate (“P” of Helenes-Escamilla) in a posteroventral direction, i.e., a situation identical to that in Dichadogonyaulax. Dichadogonyaulax exhibits a unique combination of morphologic features that serve to distinguish it from its other relatives in the Ctenidodinium “complex.”

Table I summarizes the key morphologic features I propose to utilize to separate Ctenidodinium, Dichadogonyaulax and Korystocysta.

V. SYSTEMATIC PALYNOTOLOGY
Class DINOPHYCEAE Fritsch 1929
Order PERIDINIALES Haeckel 1894

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PLATE 1

Figures
4. 7. Dichadogonyaulax cf. D. culmula, Photomicrograph and camera lucida drawing illustrating the posteroventral displacement of the preapical paraplate and the resulting contact of paraplates 2' and 4'. Compare with pl. 3, figs. 1, 2. Bar equals 20 μm. P1018C54A, R14.3/+15.8, Upper Jurassic subsurface, Atlantic Coast offshore, U.S.
5. 6. Dichadogonyaulax sp. B, Intact specimen, epicyst and hypocyst (interior view) of a lightly ornamented form. Note the slight asymmetry of the antapical paraplate in Fig. 5. Bar equals 20 μm. Upper Jurassic, C.O.S.T. B-3, Atlantic Coast offshore, U.S.
10. Dichadogonyaulax pannea, Detached epicyst (interior view) showing the contact between paraplates 2' and 4'. Bar equals 20 μm. PL2330/1; R2.7/+14.6, Middle Tithonian, Pallasioresides Zone, Littleton Brick Pit, Wheatley, England.
Genus CTENIDODINIUM Deflandre 1938 emend.
Synonym: Brotzenia Horowitz 1975
Type species: C. ornatum (Eisenack 1935) Deflandre 1938

Emended Description: Proximochorate dinoflagellate cysts constructed of an autophragm, subspherical to ellipsoidal in shape, lacking an apical horn. Paratabulation formula: 1-3pr, 4', 1-2a, 6', x-6c, 6'', 1p, 1'', x-6s, indicated by parasutural ridges, crests or septa which are generally ornamented with spines. Accessory ridges ("growth bands") generally absent. Combina- tion (epicystal, tptAtITP, henceforth referred to as Type E) archeopyle, operculum separating from the hypocyst along the posterior margin of the precingular paraplates. Parasutural features on the paracingulum may or may not be reduced on the anterior margin as compared with the posterior margin.

Comparison: Ctenidodinium differs from Dichadogonyaulax in possessing one or more preapical paraplates positioned at the apex and anterior intercalary paraplates, from Korystocysta in generally lacking accessory parasutural ridges (although see Gocht, 1984, and Pl. 2, fig. 4) and an apical horn, and from Energlynia in lacking an antapical horn and having an epicyst and hypocyst of nearly equal size.

Accepted Species:
- C. chondrum - Drugg 1978
- C. combazii - Dupin 1968
- C. continuum - Gocht 1970
- C. elegantulum - Millioud 1969
- C. ornatum - (Eisenack, 1935) Deflandre 1938
- C. sellwoodii - (Sarjeant, 1975) Stover and Evitt 1978
- C. tenellum - Deflandre 1938

PLATE 2

Figures
8. Bar equals 20 μm. 64X A33-8, Lower Cretaceous, eastern Louisiana subsurface, U.S.A.
11. Hypocyst. Note dissected parasutural crests and large size of the antapical paraplate. Bar equals 20 μm. 64X A33-6, Lower Cretaceous, eastern Louisiana subsurface, U.S.A.
Generally these are species about which questions exist concerning the epicystal paratabulation.

C.? mosaicum - Dodekova 1975
C.? rotondum - Dodekova 1975
C.? schizoblatum - (Norris 1965) Lentin and Williams 1973
C.? scissum - McIntyre and Brideaux 1980

If the number of anterior intercalary paraplates repeated by Sarjeant is correct, then this species warrants a new genus.

Genus DICHADOGONYAULAX Sarjeant 1966 emend.

Type species: Dichadogonyaulax culmula (Norris 1965) Loeblich and Loeblich 1968.

Emended Description: Proximochorate dinoflagellate cysts constructed of an autophragm only. Subspherical in shape, lacking an apical horn. Paratabulation formula: 1pr, 4', 0a, 6'', 1p, 1'', x-6s, indicated by parasutural crests, ridges, or rows of processes, cysts generally ornamented with spines. Accessory ridges absent. Paraplates of the anterior intercalary series absent. Preapical paraplate reduced in size and displaced posteroventrally, resulting in contact between paraplates 2' and 4'. Combination (epicystal, type E) archeopyle separating from the hypocyst along the posterior margin of the precingular paraplates. Parasutural features on the paracingulum may or may not be reduced on the anterior margin as compared with the posterior margin.

Comparison: The transfer of D. culmula to Alvellodinium Duxbury by Davey (1982) is herein rejected. A. falsificum and D. culmula resemble each other in having an epicystal (type E) archeopyle and processes similar to those of Spiniferites Mantell. However, Duxbury (1977) reports that Alvellodinium has three apical paraplates, and makes no reference to the presence of a preapical paraplate or its position, thus allowing differentiation of the two genera.

Dichadogonyaulax is separated from Ctenidodinium by possessing a type of epicystal paratabulation that lacks anterior intercalary paraplates and allows the 2' and 4' to be in contact. Dichadogonyaulax differs from Korystocysta in its epicyst paratabulation and in lacking accessory ridges and apical horn; from Energylnia in lacking an antapical horn and possessing an epicyst and hypocyst of nearly equal size.

Accepted species:
D. culmula - (Norris 1965) Sarjeant 1966
D. pannera - (Norris 1965) Sarjeant 1966
D. irregulare - n. sp. herein

Reattributed species:
D. rotunda - (Dodekova 1975) Woollam 1983 to Ctenidodinium (?)
D. schizoblata - (Norris 1965) Sarjeant 1966 to Ctenidodinium (?). This form may represent an intermediate type between Ctenidodinium and Dichadogonyaulax. The illustration by Norris (1965, fig. 4) of specimen 416/2 shows an anterior intercalary and an apparent preapical area that is displaced posteroventrally allowing 2' and 4' to contact. Additional specimens are necessary to determine the consistency of this relationship in this species.

D. sellwoodii - Sarjeant 1973 to Ctenidodinium
D. stauromatos - Sarjeant 1973 to Ctenidodinium (?)

Figures
1, 2. Dichadogonyaulax culmula. Detached epicyst (interior view). The arrow indicates the apparent position of the preapical paraplate. Bar equals 20 µm. P61059A09; R14.9/+ 0.8, Tithonian, Cherty Series, Portland Beds, Worbarrow Bay, Dorset, England.

3-6. Intact specimen, Figs. 3-5. L. lateral, optical section and R. lateral (interior) views respectively. Note well-developed paratabulation and relatively long processes. Fig. 6, process detail. Bar equals 20 µm. P61060A09 R11.2/+ 18.7, Tithonian, Cherty Series, Portland Beds, Worbarrow Bay, Dorset, England.

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PLATE 3
No. 4

Observations on Fossil Dinocysts

PLATE 3
DICHADOGONYAULAX IRREGULARE n. sp.

Plate 2, figs. 5-12

Holotype: Sample P320C66A; R15.7+/+ 9.7, Pl. 2, figs. 5, 6.

Type locality: Hosston Formation, Amoco No. 1, Crown-Zellerbach; Section 10, T13N, R1W, Winn Parish, Louisiana.

Description: Gonyaulacoid dinocyst with epicystal (type E) archeopyle, operculum generally free. Paratabulation formula: lpr, 4′, 0a, 6′, xc, 1p, 6′′, 1′′′, xs, expressed by discontinuous parasutural crests which are ornamented with acuminate spines of varying lengths. Paraplates 2′ and 4′ in contact, preapical paraplate displaced posteroventrally. Antapical paraplate only slightly asymmetric and very large (Pl. 2, figs. 11, 12). Cyst surface chagrenate to microreticulate.

Dimensions: Holotype: 49 μm in diameter. Range: 43 (48.5) 51 μm in diameter (20 specimens).

Comments: Most specimens are encountered as isolated epicysts or hypocysts. The discontinuous nature of the parasutural crests is distinctive and exhibits no repetitive pattern that could be distinguished in several hundred observations.

Comparison with similar species: D. irregulare is most similar to D. pannea but differs by being slightly smaller, having parasutural crests that are discontinuous in distribution, and by having higher crest ornamentation on the epicyst. D. irregulare differs from D. culmula in having acuminate terminations on the crest spines rather than bifid terminations as in D. culmula. In addition, the parasutural crests of D. irregulare do not exhibit the basal perforations that are present in D. culmula. The antapical paraplate is larger than in other species of Dichadogonyaulax, generally being about half the diameter of the hypocyst.

Occurrence: Lower Cretaceous, Neocomian, north Louisiana subsurface, Atlantic coast offshore subsurface, U.S.A.

Genus KORYSTOCYSTA Woollam 1983 emend.

Type species: Korystocysta kettonensis (Sarjeant 1976) Woollam 1983

Emended Description: Proximate dinocysts constructed of an autophragm. Subspherical to ellipsoidal in shape generally bearing an abbreviated apical horn. Paratabulation formula: l-3pr, 4′, 1-2a, x-6c, 6′′, 1p, 1′′′, x-6s, indicated by parasutural ridges, which may or may not be ornamented with short spines or denticles. Accessory ridges (“growth bands”) invariably present, expressed as denticulate or non-denticulate ridges. Combination (epicystal, type E) archeopyle separating along the posterior margin of the precingular paraplates. Operculum free or attached at parasulcus.

Comparison: Korystocysta differs from other genera with epicystal archeopyleys by having accessory ridges paralleling its parasutural ornamentation (i.e., “growth bands”), and by possessing an apical horn. The accessory parasutural features readily allow separation of this genus from other related forms, although they may be difficult to discern on poorly preserved specimens (Pl. 1, figs. 3, 11, 12).

Comments: Recently, Gocht (1984) demonstrated “growth bands” on specimens otherwise attributable to C. combazii and I have observed similar features on the same species (Pl. 2, fig. 4). If this condition is observed on other species of Ctenidodinium, Korystocysta may prove to be a superfluous genus. The emendation also restricts the genus to those forms having preapical and anterior intercalary paraplates and allows the operculum be free or attached. It is the author’s experience that epicysts are commonly observed separate from hypocysts and that only in areas of poor preservation are the preapical and anterior intercalary paraplates not evident.

Accepted Species:

K. gochtii - (Sarjeant 1966) Woollam 1983. It is possible that this species may be a junior synonym of K. kettonensis and a result of an artifact of preservation. I concur with Woollam’s (1983) comment on the difficulty of differentiating these species.

K. kettonensis - (Sarjeant 1966) Woollam 1983. Type species (see comments above)


Note: K. norrisii (Pocock 1972) Woollam 1983 is considered herein to be a junior synonym of K. pachyderma.

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IDENTIFICATION AND ORIGIN OF DINOFLAGELATE CYSTS FROM SOME WESTERN EUROPEAN LOWER CRETACEOUS DEPOSITS

DEFLANDRE, G., 1938, Micr o p la n cton des DODEKOVA, DUPIN, DRUGG,

GOCHT, DUXBURY, S., GOCHT, LOEBLICH,

HOROWITZ,

THE


This is the third in the readable series of novels published by the author treating of life in prehistoric times. It is a continuation of the life of Ayla, the young girl from The Clan of the Cave Bear and The Valley of Horses. It will be welcomed by those who enjoyed the previous volumes.

---H.C.S.

December 5, 1985

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Surv. Denmark, Ser. B; No. 6.


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