

OBSERVATIONS AND RECOMMENDATIONS ON THE FOSSIL DINOCYST
GENERA *CTENIDODINIUM*, *DICHADOGONYAULAX*,
AND *KORYSTOCYSTA*

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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 inter-

calary paraplates are present in *D. culmula*.

Korystocysta, erected by Woollam in 1983, has a *Ctenidodinium* style epicystal 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 epicystal archeophyles 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-

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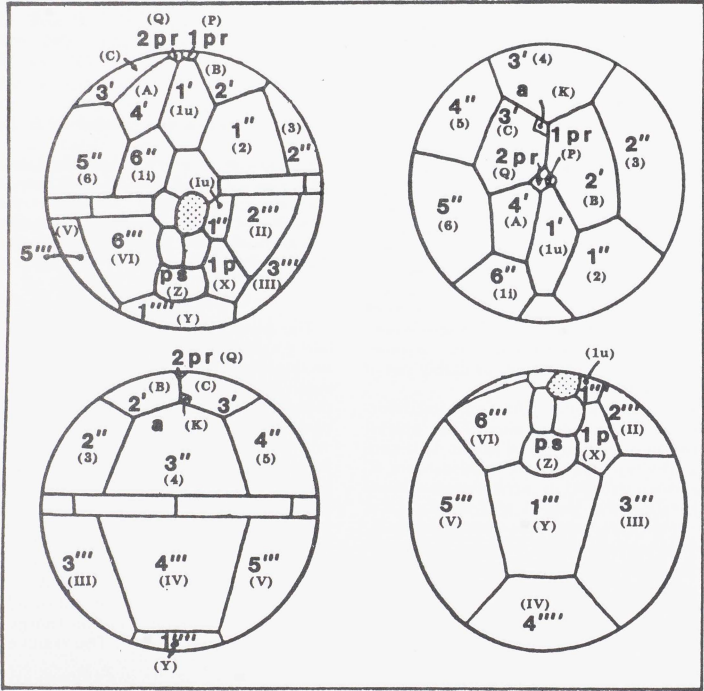
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velopment of ornamentation on the anterior and posterior paracingular margins is a variable feature, virtually impossible to discern in highly compressed specimens, and seems to me to be not the sort of morphologic feature that should be utilized to 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'' (Woolam, 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 Kodoidian notation. Text figure 1 provides a comparison of major plate series using Kodoidian 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 1pr, 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 fourth apical 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 displace-

TABLE I

MORPHOLOGIC FEATURE GENUS	PREAPICAL PARAPLATE(S)	APICAL PARAPLATE TOPOLOGY	ANTERIOR INTERCALARY PARAPLATES	PARACINGULAR ASYMMETRY	ACCESSORY RIDGES	APICAL HORN
<i>Ctenidodinium</i>	1-2 Paraplates	2' & 4' Separated By Preapicals	1-2 Paraplates	Generally Yes, But Variable	Not Generally Present	No
<i>Dichadogonyaulax</i>	0-1 Displaced Posteroventrally	2' & 4' In Contact	Absent	Generally Not, But Variable	No	No
<i>Korystocysta</i>	1-2 Paraplates	2' & 4' Separated By Preapicals	1-2 Paraplates	No Asymmetry In Documented Forms	Yes	Yes Size Varies

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. schizoblattum* 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 *schizoblattum* in the genus *Ctenidodinium*.

The hypocystal 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) (Woollam, 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 *Cribroperidinium*. 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 PALYNOLOGY

Class DINOPHYCEAE Fritsch 1929

Order PERIDINIALES Haeckel 1894

PLATE 1

Figures

- 1, 2. *Ctenidodinium combazii*, Photomicrograph and camera lucida drawing illustrating the anterior intercalary paraplate and the central position of the preapical paraplate. Bar equals 20 μm . P41126A02 S8, R14.4/+5.2, Upper Bathonian, The Fleet, Dorset, England.
3. *Korystocysta kettonensis* (?), Photomicrograph of detached epicyst (operculum) illustrating the paraplate topology. Note the central location of the preapical paraplate and the two anterior intercalary paraplates. Bar equals 20 μm . DNB80/19 Ketton, R12.8/+3.3, Bathonian, Ketton Cement Quarry, England.
- 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.
- 8, 9. *Dichadogonyaulax* sp. B, Intact specimen, epicyst (interior view) and hypocyst of a complexly ornamented form. 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, Pallasioides Zone, Littleton Brick Pit, Wheatley, England.
- 11, 12. *Korystocysta pachyderma*, Lateral views illustrating the two anterior intercalary paraplates and the slightly elongate 1p paraplate. Bar equals 20 μm . P41135B09, R26.9/+22.3, Lower Bathonian, Burton Cliff, England.

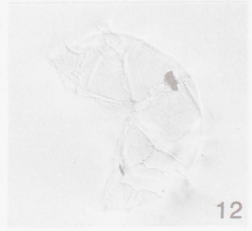
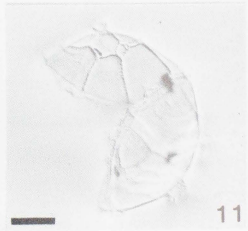
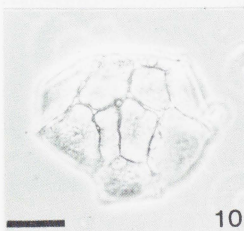
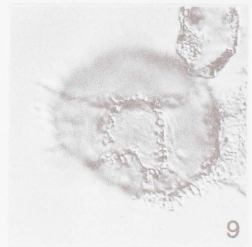
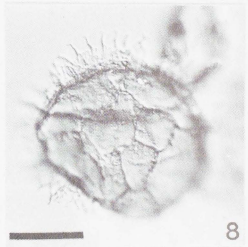
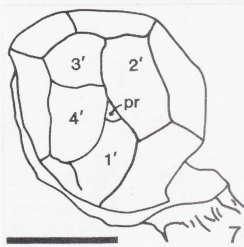
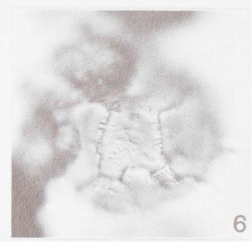
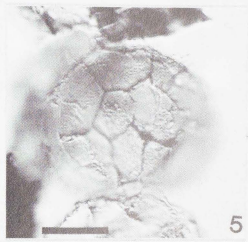
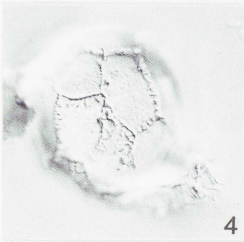
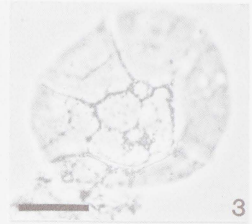
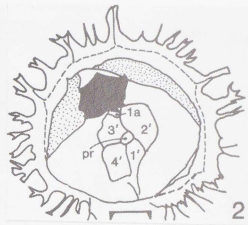
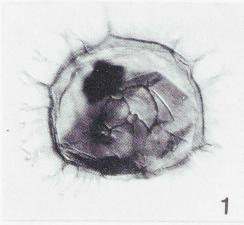


PLATE 1

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. Combination (epicystal, trptAtItP, 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. selluwoodii - (Sarjeant, 1975) Stover and Evitt 1978

C. tenellum - Deflandre 1938

PLATE 2

Figures

1. *Ctenidodinium chondrum*, Detached epicyst illustrating the paraplate topology. Bar equals 20 μm . P1018C61A, R10/+18.9, Upper Jurassic subsurface, Atlantic Coast offshore, U.S.
2. *Ctenidodinium continuum*, Detached epicyst illustrating the paraplate topology. Bar equals 20 μm . B41135B09, R8.6/+16.5, Lower Bathonian, Burton Cliff, England.
3. *Ctenidodinium tenellum*, Detached epicyst illustrating the paraplate topology. Bar equals 20 μm . P41126A02 S8, R14.5/+16.2, Upper Bathonian, The Fleet, Dorset, England.
4. *Ctenidodinium* cf. *combazii*, Antapical paraplate illustrating accessory parasutural ridges ("growth bands") similar to those described by Gocht (1984). Bar equals 20 μm . P41126A05 S8, R7.3/+13.3, Upper Bathonian, The Fleet, Dorset, England.
- 5, 6. *Dichadogonyaulax irregulare*, n. sp., Holotype. Hypocyst and epicyst (interior view) of an intact specimen. Note large size of the antapical paraplate and the interrupted parasutural crests. Bar equals 20 μm . P320C66A, R15.7/+9.7, Lower Cretaceous, north Louisiana subsurface, U.S.A.
7. Paratype. An intact, compressed specimen illustrating the large antapical paraplate. Bar equals 20 μm . P280C52A, R19.1/+5.3, Lower Cretaceous, north Louisiana subsurface, U.S.A.
8. Bar equals 20 μm . 64X A33-8, Lower Cretaceous, eastern Louisiana subsurface, U.S.A.
9. Paratype. An intact specimen illustrating the extreme variation in parasutural ornamentation and dissection. Bar equals 20 μm . P280C52A, R15.7/+8.6, Lower Cretaceous, north Louisiana subsurface, U.S.A.
10. Paratype. Interior view of epicyst. Bar equals 20 μm . P280C44A R6.2/+7, Lower Cretaceous, north 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.
12. Hypocyst. Note highly dissected parasutural ornamentation. Bar equals 20 μm . P317C29A R1.7/+9.7, Lower Cretaceous, north Louisiana subsurface, U.S.A.

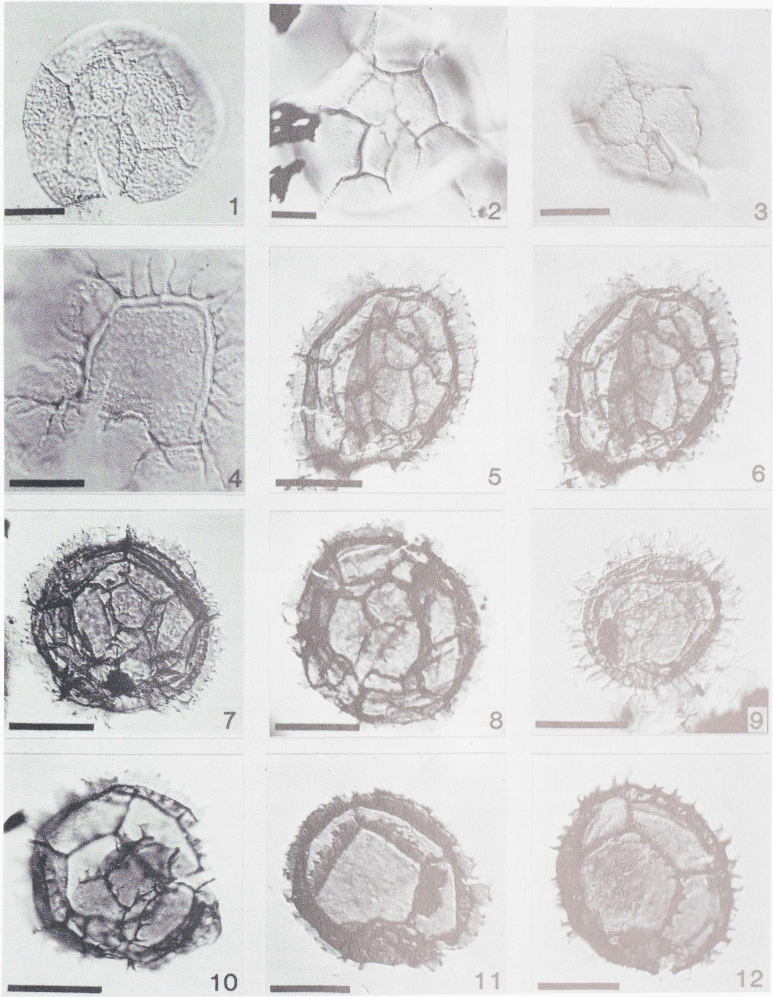


PLATE 2

Provisionally accepted species:

Generally these are species about which questions exist concerning the epicystal paratabulation.

C.? *mosaicum* - Dodekova 1975

C.? *rotundum* - Dodekova 1975

C.? *schizoblattum* - (Norris 1965) Lentin and Williams 1973

C.? *scissum* - McIntyre and Brideaux 1980

C.? *stauromatos* - (Sarjeant, 1976) Stover and Eviitt 1978. If the number of anterior intercalary paraplates reported 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", x-6c, 6"', 1p, 1"', x-6s, indicated by parasutural crests, ridges, or rows of processes, crests 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) archeophyle 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) archeophyle and processes similar to those of *Spiniferites* Mantell. However, Duxbury (1977) reports that *Al-*

vellodinium 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 epicystal paratabulation and in lacking accessory ridges and apical horn; from *Energlynia* in lacking an antapical horn and possessing an epicyst and hypocyst of nearly equal size.

Accepted species:

D. culmula - (Norris 1965) Sarjeant 1966

D. pannea - (Norris 1965) Sarjeant 1966

D. irregularis - 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 1975 to *Ctenidodinium*
D. stauromatos - Sarjeant 1975 to *Ctenidodinium* (?)

PLATE 3

Figures

- 1, 2. *Dichadogonyaulax culmula*, Detached epicyst (interior view). The arrow indicates the apparent position of the preapical paraplate. Bar equals 20 μ m. 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 μ m. P61060A09 R11.2/+18.7, Tithonian, Cherty Series, Portland Beds, Worbarrow Bay, Dorset, England.

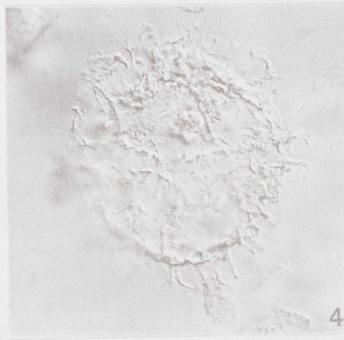
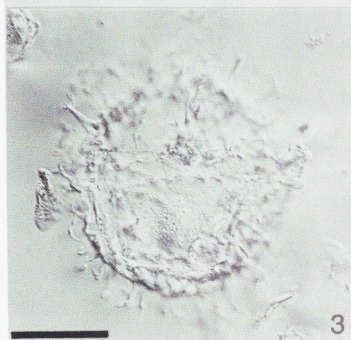
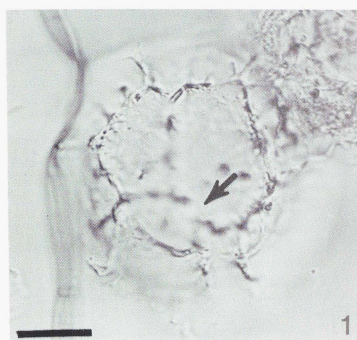


PLATE 3

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: 1pr, 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 posterovertrally. 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. irregularis* is most similar to *D. parnea* but differs by being slightly smaller, having parasutural crests that are discontinuous in distribution, and by having higher crest ornamentation on the epicyst. *D. irregularis* 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. irregularis* 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 abbreviate apical horn. Paratabulation formula: 1-3pr, 4', 1-2a, x-6c, 6''', 1p, 1''', x-6s, indicated by parasutural ridges, which may or may not be or-

namented 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 archeopyles 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. kettonense* - (Sarjeant 1966) Woollam 1983. Type species (see comments above)*K. pachyderma* - (Deflandre 1938) Woollam 1983.*Note*: *K. norrisii* (Pocock 1972) Woollam 1983 is considered herein to be a junior synonym of *K. pachyderma*.

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REVIEW

THE MAMMOTH HUNTERS, a novel by Jean M. Auel. Published by Crown Publishers, Inc., New York, 1985, x + 645 pp., casebound, \$19.95

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.