

**A revision of the marine peridinioid genera (Pyrrhophyta)  
utilizing hypothecal-cingular plate relationships  
as a taxonomic guideline**

Stephen R. INDELICATO and Alfred R. LOEBLICH III

*University of Houston Marine Science Program, 4700 Avenue U  
Galveston, Texas 77550-9199 USA*

INDELICATO, S.R. and LOEBLICH III, A.R. 1986. A revision of the marine peridinioid genera (Pyrrhophyta) utilizing hypothecal-cingular plate relationships as a taxonomic guideline. Jap. J. Phycol. 34: 153-162.

The cingulum of peridinioid dinoflagellates is compared and the most probable thecal plate homologies are indicated for these plates in the genera *Ensiculifera*, *Pentapharsodinium* gen. nov., *Peridinium*, *Proto-peridinium* and *Scrippsiella*. The newly proposed cingular plate homologies in addition to cyst type and thecal morphology are used as criteria to establish the new genus *Pentapharsodinium*. *Ensiculifera*, originally invalidly described, was not validated but placed in the synonymy of *Scrippsiella* because there are insufficient thecal differences between the type species of the two genera to warrant separate generic status. Three new marine orthoperidinioid species are described. Mutually exclusive criteria that define each of the above four validly described genera are proposed.

*Key Index Words:* Calciodinellaceae; dinoflagellates; *Pentapharsodinium* gen. nov.; taxonomy; theca.

Traditionally, thecate dinoflagellates are classified according to the number and arrangement of the "major" thecal plates, i.e. the plates of the epitheca and hypotheca. However, more recently, the marine *Peridinium* species have been subdivided into several genera based upon "minor" thecal plate differences; specifically the number of cingular plates.

BALECH (1959), who considered the number of plates in the cingulum and the arrangement of the sulcal plates of prime importance in distinguishing the orthoperidinioid dinoflagellate genera, utilized these characters as the basis for the description of the genus *Scrippsiella* BALECH ex LOEBLICH 1965. The sulcal and cingular areas were accorded prime importance by him as they are "connected with the most dynamic parts of the cell", and therefore were considered by him to be less subject to evolutionary change. BALECH (1967) subsequently described the

dinoflagellate genus *Ensiculifera*, emphasizing these same thecal regions. According to BALECH, the type species of both of these marine peridinioid genera have identical thecal plate tabulations differing only in the number of cingular plates; six for *Scrippsiella* and five for *Ensiculifera*, and several other minor morphological differences. These two genera are distinctly different from that of many marine *Peridinium* Ehrenberg species, which are now referred to *Proto-peridinium* BERGH (LOEBLICH 1968, 1970, BALECH 1974).

More recently, cyst morphology, although mostly used in palynology, has been emphasized as being an important criterion for the taxonomy of the extant peridinioids primarily due to its presumed conservative nature (DALE 1977, 1978). Since 1967, the morphological characteristics used to distinguish the genera *Ensiculifera*, *Scrippsiella* and *Peridinium* have been considered and

analyzed by several authors with varying interpretations (BOURRELLY 1968, COX and ARNOTT 1971, BALECH 1974, FINE and LOEBLICH 1976, DALE 1977, STEIDINGER and BALECH 1977). In spite of the number of studies of these genera a set of characteristics that would allow unambiguous assignment of these species to these genera has never been universally accepted. To this day, these marine orthoperidinioid dinoflagellates remain poorly defined.

Even when using both cyst morphology and cingular plate numbers to classify these organisms some problems remain. For example, DALE (1977) isolated a dinoflagellate from marine waters which he identified as "*Peridinium faeroense*". This isolate formed resting cysts composed of organic material similar to the freshwater *Peridinium* spp. yet had a thecal tabulation identical to *Ensiculifera*. Prior to this, the species *P. faeroense* had been placed in the genus *Scrippsiella* by BALECH and SOARES (1966). In spite of sufficient descriptive knowledge such as the type of cyst, thecal tabulation, and general morphology necessary to separate the organisms into species, little emphasis has been given to developing generic diagnoses that are mutually exclusive for these orthoperidinioid dinoflagellates. When each species was described, the descriptions of the species were made sequentially without adequate reference to previously described species or without clear concept of generic diagnoses.

LOEBLICH and LOEBLICH (1979) utilized thecal plate overlap as well as the concept of "homologous plates" to distinguish evolutionary trends within the gonyaulacoid and peridinioid lineages. [See LOEBLICH and LOEBLICH (1985) for a discussion of the methodology we employ to determine thecal plate homologies.] The peridinioid dinoflagellates all have a typical hypothecal plate tabulation of five postcingulars and two antapicals. Fossil records of dinoflagellate cysts show that this hypothecal tabulation dates from the early Jurassic (BUJAK and DAVIES 1983).

We find the relationship between the position of the sutures separating adjacent hypothecal plates and the position of the sutures separating adjacent cingular plates to be useful in assigning these species to genera. For peridinioid species we detect two collinear sutures (X and Y sutures, see Fig. 1) among the hypothecal and cingular series. The consistent occurrence of these collinear sutures in peridinioids is considered a conserved feature of their theca. This suggests to us its usefulness in peridinioid systematics.

In this paper we propose the incorporation of the above detected relationship as a character of value in the generic descriptions. In conjunction with cyst morphology and several other morphological characteristics, these plate relationships can serve as a means of assigning peridinioid species to individual genera. We will also attempt to resolve some inconsistencies in the literature pertaining to these species as well as to propose some revisions in the taxonomy of these peridinioid species.

### Hypothecal-cingular Plate Relationships

When the hypothecal plates of the peridinioids are viewed from the antapical with the cingular plates attached, several distinct patterns can be seen (Fig. 1). A "transitional" or small 1c plate is only present in the marine species. This characteristic plate is never seen in the fresh water *Peridinium sensu stricto* (s.s.) (i.e. *Peridinium cinctum*).

There are two sutures of the cingular series which we consider to be "homologous" in a variety of species because they are found in the same position on all fresh water and marine peridinioids whose cingular plates have been studied. One of these is collinear or nearly collinear with the suture between the 4<sup>th</sup> and 5<sup>th</sup> plates (labeled X in Fig. 1) and the other is collinear or nearly collinear with the suture between the 1<sup>st</sup> and 2<sup>nd</sup> plates (labeled Y). There are two cingular plates which lie ventral to

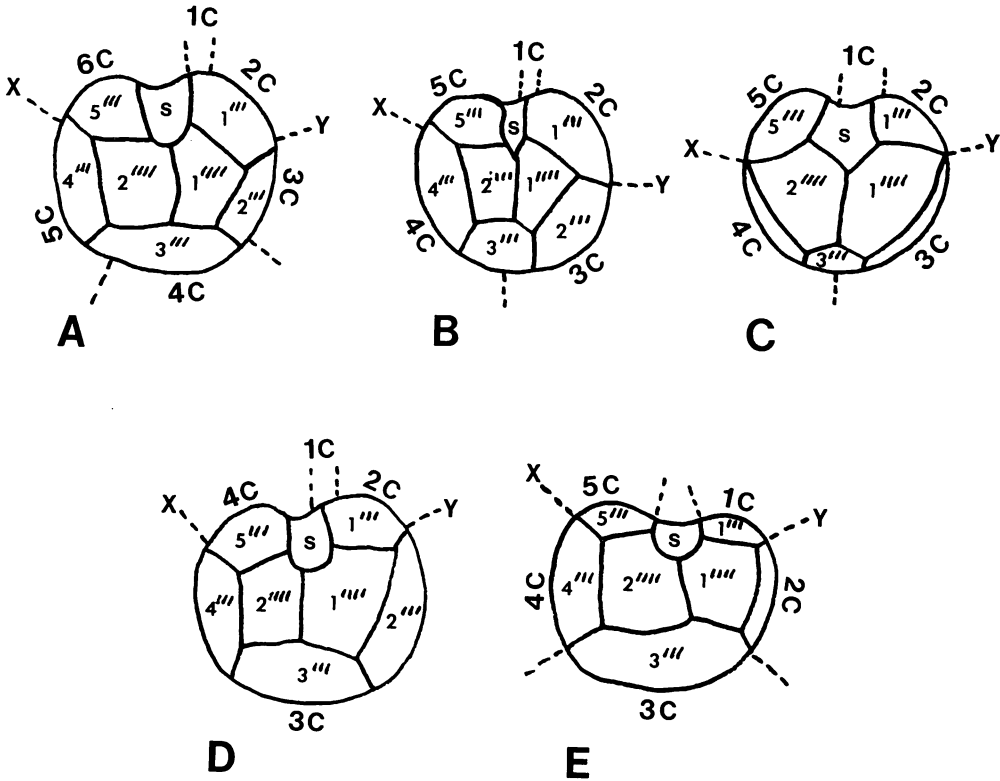


Fig. 1. Diagrams of hypothetical plates in antapical view of several peridinoid dinoflagellate species showing the relationships of the hypothetical plates to the cingular plates. a) *Scrippsiella tinctoria*, b) *Pentapharsodinium trachodium* sp. nov., c) *Pentapharsodinium dalei* sp. nov., d) *Protoperidinium* sp., and e) *Peridinium cinctum*.

these homologous sutures (excluding the transitional plate) in all species studied. In *Peridinium* s.s. these are labeled as the 1c and 5c plates, in *Scrippsiella* as the 2c and 6c, in *Protoperidinium* as the 2c and 4c, and in *Pentapharsodinium* gen. nov. (see below) as the 2c and 5c. Generally these cingular plates run along the complete length of the 1''' and 5''' plates, being slightly displaced along the 1''' plate only if a transitional plate is present.

Major differences in the cingular plate series of these genera occur dorsal to the sutures that are interpreted as being homologous in these species (termed sutures X and Y). In *Peridinium* s.s., there are three cingular plates dorsal to these sutures (2c, 3c, and 4c). Because the sutures separating the hypothetical plates in this genus are collinear with the sutures of the cingular

series, there is one cingular plate associated with each hypothetical plate. Members of the genus *Peridinium* which do not have this configuration of cingular plates should be carefully studied for possible reassignment to different genera.

Members of the genus *Scrippsiella* also have three cingular plates dorsal to the two homologous sutures (3c, 4c, and 5c). This can easily be seen in the recently described *S. tinctoria* (INDELICATO and LOEBLICH, 1985). However, the presence of the transitional plate in members of this genus along with their marine habitat would clearly separate them from *Peridinium* s.s.

The protoperidinioids (*Protoperidinium* and *Diplopsalis*), are noted for the absence of any cingular sutures dorsal to the homologous collinear sutures. The characteristic 3c plate in these genera begins at the 1'''-2'''

suture and completely wraps around the organism to the 4"-5" suture.

The genus, *Pentapharsodinium* gen. nov., was created because the cingular plate configuration does not resemble the *Peridinium* s. s., *Scrippsiella*, or protoperidinioid configurations (Fig. 1). Members of the genus *Pentapharsodinium* also have five cingular plates as does *Peridinium* s. s., however, the position of the sutures in the cingulum of these two genera are fundamentally different. In *Pentapharsodinium*, only one cingular suture is found dorsal to the two homologous sutures to form the plates 3c and 4c. This suture arises from the center of the 3" plate. In *Peridinium* s. s., there are three cingular plates dorsal to sutures X and Y (2c, 3c, and 4c) and all of the sutures are collinear with the sutures of the hypothecal plates. Even though *Pentapharsodinium* and *Peridinium* s. s. each have five cingular plates, they are easily

separable because these cingular plates border different hypothecal plates. Although both genera have five cingular plates they differ from each other in that *Pentapharsodinium* has a transitional plate, and *Peridinium* s. s. has three cingular plates lying dorsal to sutures X and Y rather than two.

These cingular plate configurations can be better visualized using the following suggested simple notation. Members of the genus *Scrippsiella* have a "5+t" cingular plate tabulation (five larger plates and one transitional); *Pentapharsodinium* a "4+t"; protoperidinioids a "3+t"; and *Peridinium* s. s. a "5+0" (Table 1). We prefer to consider the small 1c plate as a transitional plate rather than the first cingular plate in light of our belief that the X and Y sutures (Fig. 1A-D) separate homologous plates in all peridinioid species. Thus the 1c plate of *Peridinium* s. s. is the homolog of the 2c plate in the marine peridinioid species.

Table 1. Summary of the characters useful in separating peridinioid dinoflagellates.

Genus "	Habitat	Cingular Plates	Cyst Type	Photosynthesis	Apical Pore
<i>Scrippsiella</i>	M	6(5+t)	Calcareous Acapsulate	+	+
<i>Pentapharsodinium</i>	M	5(4+t)	Organic Acapsulate	+	+
<i>Protoperidinium</i>	M	4(3+t)	Organic Acapsulate	-	+
<i>Peridinium</i> s. s.	F	5(5+0)	Organic Capsulate	+	+ -

M=marine, F=freshwater, t=transition plate, +=present, -=absent, +- =variable, found in some but not all species.

### Taxonomic Revisions

The confusion regarding the taxonomy of the dinoflagellate genera *Scrippsiella* and *Ensiculifera* can be traced to much of the previous literature which contains inconsistencies, misinterpretations, inadequate descriptions, and lack of suitable documentation e.g. photomicrographs. Some of these taxonomic problems are addressed below.

Division **Pyrrhophyta** PASCHER, 1914

Order **Peridinales** HAECKEL, 1894

Family **Calciadinellaceae** DEFLANDRE, 1947

### *Pentapharsodinium* INDELICATO et LOE-

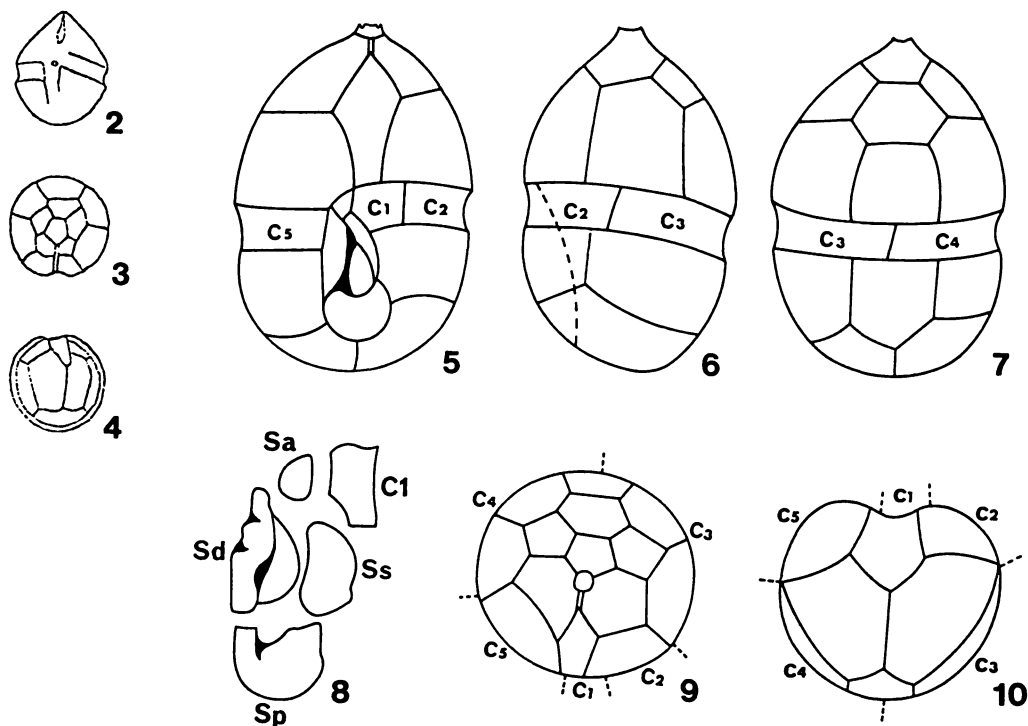
BLICH, **gen. nov.** Cellulae photosynthetici.

Formula laminarum: pp, pr, 4', 3a, 7", 5c [4+t], 4s, 5"', 2"', dispositione orthoperidinioidea. Cysta sphaerica, membrana organica, acapsulata. Habitus: in aqua marina.

Type species: *Pentapharsodinium dalei* sp. nov.

Etymology: the name refers to the five part cingular series on a rotating dinoflagellate. Taken from Greek: *penta*, for five; *pharsos*, for part; *dinos*, for whirling or rotation.

DALE (1977) made observations on dino-



Figs. 2-4. Paulsen's (1905, his fig. 5) original drawings of *Peridinium faeroense*. 2, cell in ventral view; 3, epithecal view (anterior); 4, hypothecal view (posterior). Figs. 5-10. Dale's (1977, his figs. 1-5, and 7) original drawings of "*Peridinium faeroense*". 5, Ventral view; 6, lateral left view; 7, dorsal view; 8, sulcal plates; 9, apical view of epitheca; and 10, antapical view of hypotheca.

flagellate cultures derived from the germination of two dissimilar cysts collected from Cape Cod Bay and Norwegian fjord sediments. The first type, "spiny" cysts, gave rise to cells which he identified as *Scrippsiella trochoidea* (STEIN) LOEBLICH. The second type bore bifurcated spines and gave rise to cultures which he identified as "*Peridinium faeroense*". Dale's drawings (Figs. 5-10) and photomicrographs of the thecate stage of the organisms derived from the bifurcated spiny cysts, however, do not resemble Paulsen's original line drawing of *P. faeroense* (Figs. 2-4). Differences include the overall shape of the cell, the width and shape of the 1' plate, the relative width of the 3''' plate and the differences in relative sizes of the 1'' and 7''' plates. Even though Paulsen's (1905) illustrations would be considered inadequate for the description of a new species by modern taxonomists, the

differences are great enough to indicate that Dale's specimens are not conspecific with Paulsen's. Dale's drawings of "*P. faeroense*" also differ significantly from the drawings of *S. faeroense* by BALECH and SOARES (1966). BALECH and SOARES' *S. faeroense* more closely resembles Paulsen's original drawing than Dale's, particularly in reference to the cell shape and narrow 1' plate. We believe the organism Dale identified as "*P. faeroense*" is not the *P. faeroense* that Paulsen originally described, but is in fact a previously undescribed species.

SCHILLER (1935) placed *P. faeroense* in the synonymy of *Peridinium trochoideum*. LATER PAULSEN (1949) considered his *P. faeroense* to be synonymous with *P. trochoideum* in agreement with Schiller. This conclusion is further supported by the scanning electron micrographic studies of Fine and LOEBLICH (1976) and the light micro-

scopic observations STEIDINGER and BALECH (1977). In the absence of material fitting the description of Paulsen's *P. faeroense* that shows any demonstrable differences from *S. trochoidea* we concur with SCHILLER, PAULSEN, FINE and LOEBLICH, and STEIDINGER and BALECH in considering *Peridinium faeroense* a subjective synonym of *S. trochoidea*.

Dale's isolate of "*P. faeroense*" possesses five cingular plates and an organic walled "non-capsulate" cyst. These two characteristics differ from the six cingular plates and calcareous walled cysts formed by *Scrippsiella* species. This prompted Dale to consider this organism as a marine member of the genus *Peridinium* s. s. whose type species, *P. cinctum*, is a freshwater organism. The cingular plates of Dale's marine isolate and *P. cinctum* are not homologous to each other. Dale's isolate possesses a small 1c plate which is homologous to the transitional (1c) plate of the scrippsielloids. *Peridinium cinctum*, however, possesses no such transitional plate (BOURRELLY 1968). The 1c plate of *P. cinctum* lines adjacent to the 1" and 1'" plates, and appears to be the homolog of the two plates, 1c and 2c of Dale's isolate. All of the sutures of the cingular series in *P. cinctum* are collinear with sutures in the precingular and postcingular series, whereas Dale's isolate possesses no such cingular sutural relationship.

*Peridinium cinctum* also produces a double walled organic "capsulate" cyst (DURR 1979) in contrast to the non-capsulate bifurcated spine bearing organic walled cyst of Dale's isolate. If cyst morphology and plate homologies have any systematic value in determining relationships then these characteristics would argue against the placement of Dale's "*faeroense*" isolate within the genus *Peridinium*. Dale himself suggests the need for further subdivisions of the genus *Peridinium* (DALE 1978). [See BUJAK and DAVIES (1983) for a discussion of the evolutionary lineages of the family Peridiniaceae with regard to cyst morphology.] The vegetative cell of Dale's isolate differs

from members of another marine peridinioid genus, *Proto-peridinium*, BERGH in that Dale's isolate is photosynthetic and lacks the characteristic 3c plate which in *Proto-peridinium* nearly encircles the entire cell (GRAHAM 1942). Morphologically, Dale's isolate resembles, but has fundamental thecal differences from *Scrippsiella*, the only well-recognized extant genus of the family Calciodinellaceae. Consequently, we placed it in a new genus, *Pentapharsodinium*, and include it in the family Calciodinellaceae. This assignment is made in spite of the absence of a calcified cyst being present. Since all extant members of this family have not been tested for the presence of a calcareous cyst, it is unknown whether this trait should be used as a familial character. Two species are included in *Pentapharsodinium* gen. nov.

***Pentapharsodinium dalei* INDELICATO et LOEBLICH, sp. nov.**

Synonymy:

*Peridinium faeroense* (non PAULSEN 1905), DALE 1977, p. 244, figs. 1-5, 7-8.

*Peridinium faeroense* (non PAULSEN 1905), DODGE 1983, p. 162, figs. 18 n-p, Pl. III e-f.

Epitheca conica ad rotundatam, hypotheca rotundata. Epitheca poro apicali eminente praedita. Hypotheca dorso-ventraliter compressa et longitudine epithecae quasi aequa. Cingulum latum cavazoniforme, descendens, per 1/2 partis latitudinis dispositum, sine laciniis. Sulcus latus profundusque, ad antapicem attingens. Collara sulcaria angusta interdum adsunt. Formula laminarum: pp, pr, 4', 3a, 7'', 5c, 4s, 5''', 2''''', dispositione orthoperidinioidea. Cellula 18-35  $\mu\text{m}$  long., 15-29  $\mu\text{m}$  transdiametro. Nucleus 15-20  $\times$  12-18  $\mu\text{m}$ , medius, sphericus ad ovoideum. Flagellum longitudinale longitudini cellulae aequum. Cysta sphaerica, membrana organica spinas bifurcatas in eius superficie ferente.

Habitus: In aqua marina, in loco Langviksbukta, Oslofjord, Norway dicto. Holotypus: figura inter verba 5.

Etymology: The *dalei* is a patronmic for

Mr. Barrie Dale who first discovered this species.

***Pentapharsodinium trachodinum*** INDELICATO et LOEBLICH, **sp. nov.**

Synonymy:

*Ensiculifera loeblichii* COX et ARNOTT 1971, pp. 125-135, figs. 1-34. Invalid ICBN Art. 43.1 [*Ensiculifera* invalid (Art. 36.2) therefore included species are invalid.].

*Peridinium loeblichii* (COX et ARNOTT) DALE 1977, pp. 244-247, figs. 6, 9, 12, 20, 22, 26. Invalid ICBN Art. 43.1 (basonym invalid).

Latin diagnosis of *Pentapharsodinium trachodium* sp. nov.: see COX and ARNOTT (1971, p. 124).

Habitus: in aqua marina, in loco Salton Sea, California dicto. Holotypus: figura 26 in COX and ARNOTT (1971, p. 130).

Etymology: The epithet refers to the rough surface ornamentation of the thecal plates; *trachodes* taken from Greek meaning of rough nature.

The second described species in the genus *Ensiculifera*, *E. loeblichii*, was proposed by COX and ARNOTT (1971) and was later transferred to *Peridinium* by DALE (1977). *Ensiculifera loeblichii* possesses a plate tabulation similar to *Pentapharsodinium dalei*, differing only in the shape and relative sizes of the sulcal plates, especially the posterior sulcal (DALE 1977). Noted similarities include identical major plate tabulations (4', 7", 5c, 4s, 5"', 2'''), cingular plate homologies, and overall size and shape of the cell. Cysts from *E. loeblichii* are as yet unknown.

As mentioned above, the genus *Ensiculifera* is invalid (ICBN Art. 36.2) and thus the species *E. loeblichii* is invalid as the genus in which it was described was never validly described. The type species of *Ensiculifera* was reinterpreted by us to be a member of the genus *Scrippsiella*. *Ensiculifera loeblichii* of COX and ANOTT however, differs in the number and basic homologies of cingular plates from the type species *Scrippsiella sweeneyae* (BALECH 1959).

With respect to the cingular tabulation it more closely resembles the new species we describe as *Pentapharsodinium dalei*. Conclusions reached by an analysis of the cingular plate number and homologies supports placement of *E. loeblichii* into the genus *Pentapharsodinium*. We validly describe this species and place it the new genus *Pentapharsodinium* as *P. trachodium* sp. nov.

***Scrippsiella*** BALECH ex LOEBLICH, 1965

***Scrippsiella mexicana*** INDELICATO et LOEBLICH, **sp. nov.**

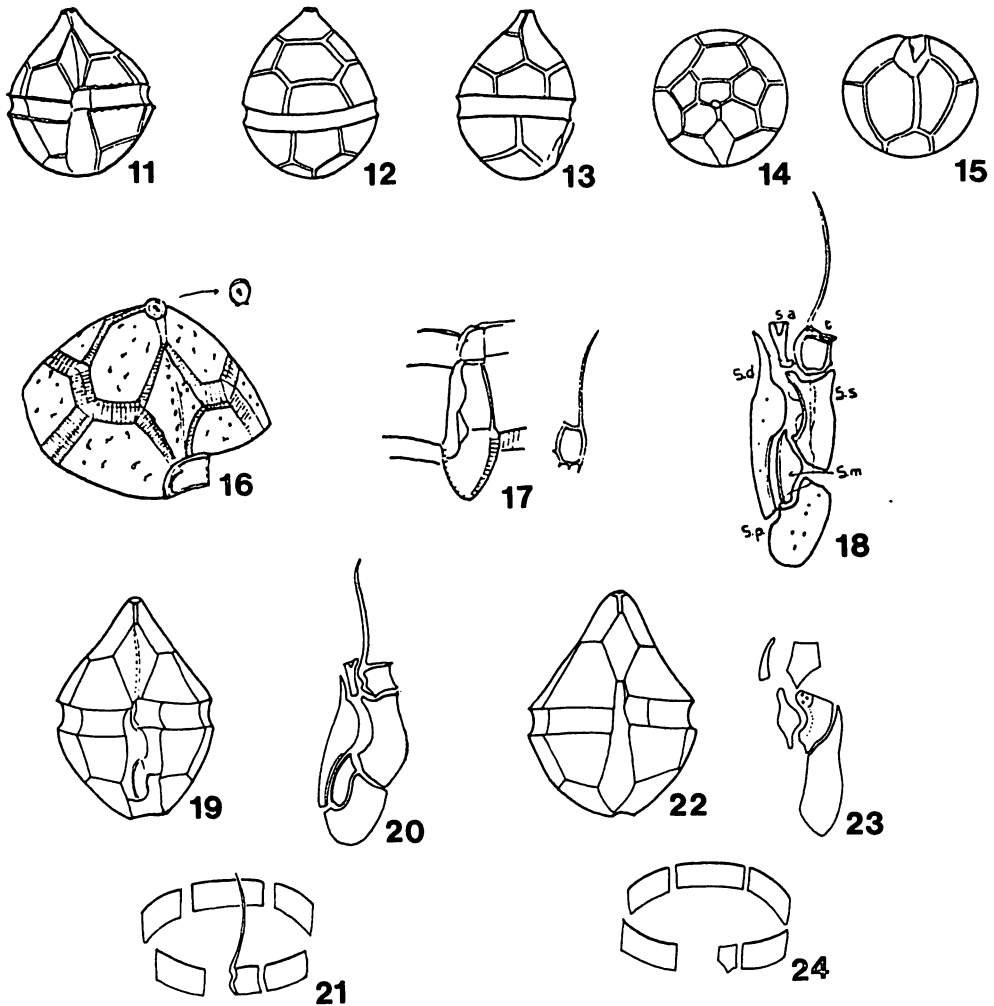
Synonymy:

*Ensiculifera mexicana* BALECH, 1967, p. 120-122, plate 9, figs. 136-144. Invalid ICBN Art. 36.2.

Epitheca conica, hypotheca rotundata, sine cornibus projectionibus. Cingulum centrale descendes per 1/2 latitudinis in regione sulcali depositum. Poro apicali elevato. Formula laminarum: pp, pr, 4', 3a, 7", 6c (5+t), 5s, 5"' et 2''', dispositione orthoperidinioidea. Laminarum t cum spina majora. Cellulae 42-45  $\mu$ m longa, 35-36  $\mu$ m lata. Organismus photosyntheticus. Habitus: in aqua marina, in loco Gulf of Mexico (26° 23'N, 90°44'W) dicto. Holotypus: figura inter verba 11.

Etymology: *mexicana* refers to the Gulf of Mexico type locality of the species.

BALECH (1967) described, from plankton collected March 1, 1965 in the Gulf of Mexico, the monotypic genus *Ensiculifera* of which the type species, *E. mexicana*, differed from the type species of *Scrippsiella* in three basic characteristics: the arrangement and shape of the sulcal plates; the possession of a long "knife"-like process on the 1c (transitional) plate; and *E. mexicana* was originally thought to possess five cingular plates as opposed to four for *Proto-peridinium* species and six for *Scrippsiella* species. In that monograph, BALECH's drawings (Figs. 11-18) of *Ensiculifera mexicana* were sketchy and the placement of the cingular plates was not consistent with the description in his text. His drawings indicated a sutural disposition that is



Figs. 11-18. Balech's (1967, his figs. 136-144) original drawings of *Ensiculifera mexicana*. 11, ventral view; 12, dorsal view; 13, right lateral view; 14, epitheca; 15, hypotheca; 16, ventral view of the epitheca with pore plate; 17, ventral area and first cingular or "transitional" plate; and 18, sulcal series and the "transitional" plate. Figs. 19-24. Balech's (1974, his figs. 4-8) original drawings of *Ensiculifera* (Figs. 19-21) and *Scrippsiella* (Figs. 22-24). 19, ventral view; 20, sulcal series and "transitional" plate; 21, cingular series; 22, ventral view; 23, sulcal series and "transitional" plate; and 24, cingular series.

consistent with four cingular plates, much in the same arrangement as those found in *Protopteridinium* (GRAHAM 1942). In a later paper (1974), Balech again presented a line drawing (Figs. 19-21) of *E. mexicana*, this time clearly with six cingular plates, arranged identically to those found in *Scrippsiella* (Figs. 22-24). In the absence of unequivocal data (i.e. photomicrographs) on the correct number of cingular plates in

*E. mexicana*, we are left to justify the separation of this genus from *Scrippsiella* on Balech's remaining two characteristics.

Variations in sulcal plate sizes and arrangements have been noted among members of *Scrippsiella*, i.e. *S. subsalsa* (STEIDINGER and BALECH 1977), and *S. sweeneyae* (BALECH 1959). The sulcal plate disposition of *S. mexicana* does not differ significantly from other *Scrippsiella* species and should



not warrant the separation of a new genus. The presence of a spine on the 1c plate of *S. mexicana* is Balech's strongest argument for the formation of the genus *Ensiculifera* (hence the name "ensiculifera"). However, differences in thecal processes or cell body projections within a particular dinoflagellate genus are not unusual, e.g. the presence or absence of antapical spines in freshwater *Peridinium* species or the variations in antapical extensions of the cell exhibited by different species of *Protoperidinium* (GRAHAM 1942). In the past this has not led to the formation of new genera nor should it now.

WALL *et al.* (1970) reported that *E. mexicana* produces a calcareous cyst. This would strongly support the placement of this species in the genus *Scrippsiella* over the genus *Pentapharsodinium* gen. nov. In addition, the genus *Ensiculifera* and species *E. mexicana* are not validly published since no Latin description or diagnosis accompanied the description of this taxon. BALECH (1967, p. 122) used the botanical suffix for the family Peridiniaceae, therefore the reader is left with the conclusion that he considered *E. mexicana* a plant and a Latin diagnosis was required as stated in the International Code of Botanical Nomenclature (Art. 36.2).

In summary to date with the changes proposed in this paper there are two species referable to *Pentapharsodinium* gen. nov.: *P. dalei* sp. nov. and *P. trachodium* sp. nov. In addition, there are seven species referable to *Scrippsiella*: *S. gregaria* (LOMBARD et CAPON) LOEBLICH, SHERLEY et SCHMIDT 1979, *S. mexicana* sp. nov., *S. saladense* BALECH 1963, *S. subsalsa* (OSTENFELD) STEIDINGER et BALECH 1977, *S. sweeneyae* BALECH ex LOEBLICH 1965, *S. tinctoria* INDELICATO et LOEBLICH, 1985, and *S. trochoidea* (STEIN) LOEBLICH 1976.

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インデリカート, S. R.・レーブリッヒ III, A.R.: 分類学的ガイドラインとして  
下殻の横溝板関係を用いた海産ペリジニウム類 (橙藻植物門) の属の改訂

海産の渦鞭毛藻のペリジニウムグループの横溝板を相互に比較し, *Ensiculifera*, *Pentapharsodinium* gen. nov., *Peridinium*, *Protoperidinium*, *Scrippsiella* の各属間の最も妥当と思われる鋸板の homology を明らかにした。シストの形態と鋸板の形態に加えて, 新しく提案した横溝板 homology を新属 *Pentapharsodinium* の設立のための基準形質に使用した。 *Ensiculifera* は設立時において不当であったが, これを正当化せず, *Scrippsiella* の異名に落した。それは, 独立の属とするに足る十分な鋸板の違いがこの二つの属のタイプ種に見当らないからである。Orthoperidinioid の 3 新種の記載を行い, また, 上述の正当に記載した 4 新属を識別する基準形質について述べた。