

The cyst and theca of *Gonyaulax verior* SOURNIA (Dinophyceae) and their implication for the systematics of the genus *Gonyaulax*

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On the basis of unialgal cultures established from living cysts recovered from surface sediments, thecate and encysted forms of the dinoflagellate *Gonyaulax verior* SOURNIA are described from Japan and the United States. The cyst is ovoidal to ellipsoidal, lacks ornamentation, and is sometimes surrounded by mucilaginous material. The thecal plate formula of this species is identical to that of the *Spinifera* group of the genus *Gonyaulax*, but the cyst is distinctly different in shape, lacks ornamentation, and has a different archeopyle features from them. These observations emphasize the need for re-examinations of the systematics of the genus *Gonyaulax*, with due consideration of both the cyst and motile stage morphology.

Key Index Words: *Gonyaulax verior*—Dinophyceae—cyst-theca relationship—taxonomy.

Some species of the dinoflagellate genus *Gonyaulax* are known to produce fossilizable resting cysts during their life cycle (e.g. WALL & DALE 1968, DALE 1983). Most of these species belonging to the *Spinifera* and *Polyedra* groups of the subgenus *Gonyaulax* as defined by KOFOID (1911) showed the morphological differences between their cysts. Therefore, they have been divided into more than six cyst genera with twelve species by paleontologists (e.g. DALE 1983). This extraordinary circumstance was recognized and discussed as a heterosporous problem by WALL (1971, 1975). Its significance in dinoflagellate phylogeny and evolution, however, has not yet been resolved.

Recently DOBEL and TAYLOR (1981)

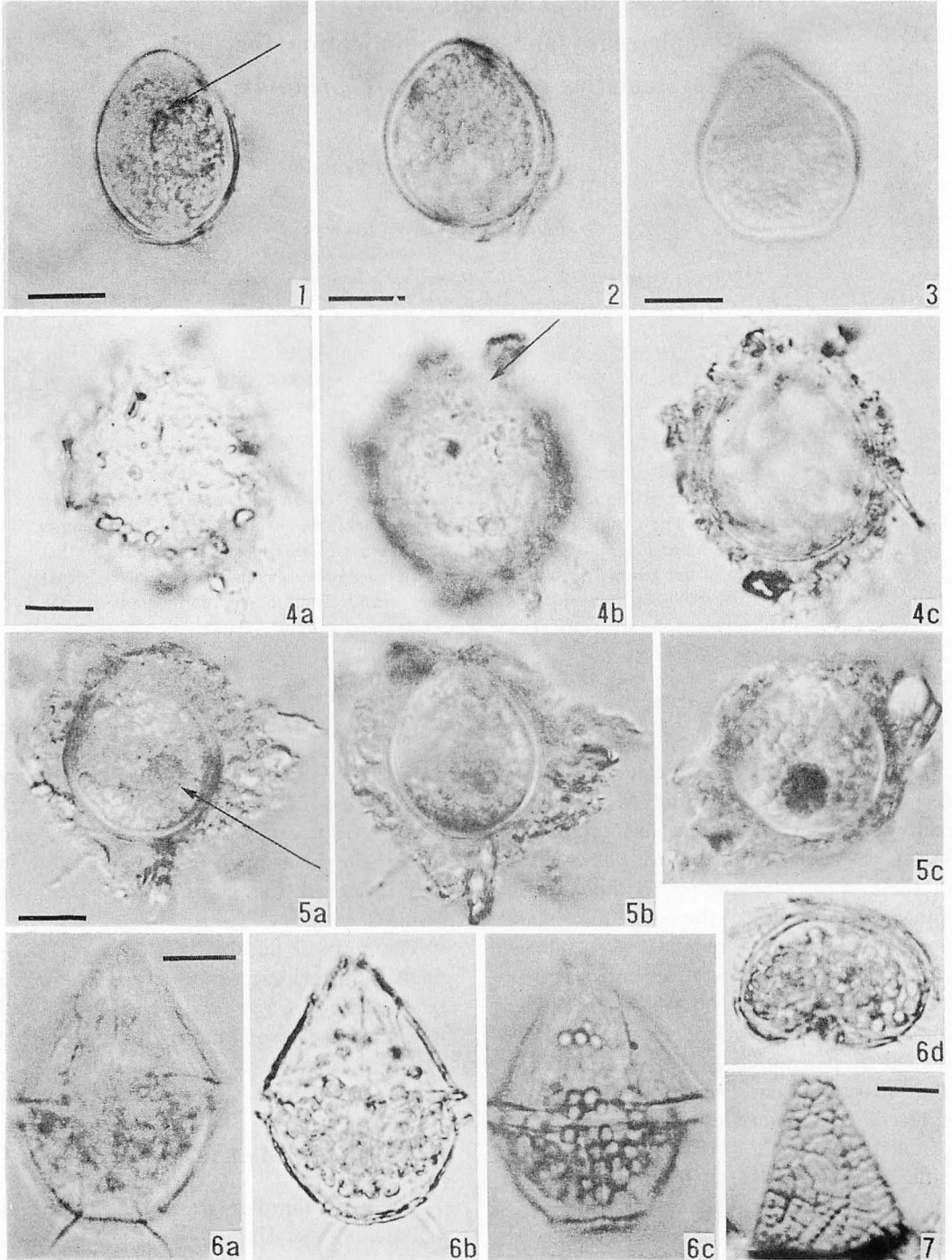
documented two rather unusual cyst-theca relationships in *Steiniella*, another subgenus of the *Gonyaulax*. Their results did not clarify the heterosporous problem, but in fact increased the complexity within the genus *Gonyaulax*.

The purpose of this report is to document the previously undescribed cyst-theca relationship of *Gonyaulax verior* SOURNIA and to discuss the taxonomic significance of the cyst with respect to the systematics of the genus *Gonyaulax*.

Material and Methods

Sediment samples were collected from Japan and the United States. In Japan, surface sediments from Hiroshima and Hakata Bays and the Yatsushiro Sea were collected by a simple gravity TFO (University of Tokyo, Fisheries Oceanography

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Laboratory) corer. The upper two centimeters of these cores were cut and stored at approximately 4°C in a refrigerator for several months before processing. The stored sediment was sieved through 125 μm and 20 μm stainless steel screens after sonication for about ten seconds in order to disaggregate detritus. Living cysts were isolated by a capillary pipet and inoculated individually in tissue culture wells containing 1 ml of filtered seawater. Samples from the United States were collected from Perch Pond, Falmouth MA using a hand-held coring device. The top several cm of sediment were removed and stored at 4°C until processing, a procedure similar to that described above except that different sieves were used to collect the 20–80 μm size fraction.

Germination was monitored for individual cysts in tissue culture wells, viewed from below with an inverted microscope. Excysted specimens were then removed and taken photomicrographs under higher magnification on a light microscope (Zeiss IM-35) and an interference microscope (Olympus BH).

For detailed observation of thecate forms from Japan, net haul material containing numerous *Gonyaulax verior* cells was collected from Lake Hamana in August 1984 by Mr. OKAMOTO of the Fisheries Laboratory, Faculty of Agriculture, University of Tokyo. These specimens were observed under a scanning electron microscope (JSM-T200).

Observation

Cyst form

The cyst of *Gonyaulax verior* is ovoidal to

ellipsoidal (31–38 μm by 26–35 μm ; Figs. 1–2) without distinctive projections except for one or two rarely observed very small antapical nodes (Fig. 3). The post equatorial zone is the widest (Figs. 2, 3, 5). The cyst wall consists of two transparent layers, the relatively thick endophragm and thin periphragm without any ornamentation and sculpture (Fig. 3). The archeopyle is formed at one of the poles, typically the apex, and is possibly a chasmic type (simple slit). There is no paratabulation.

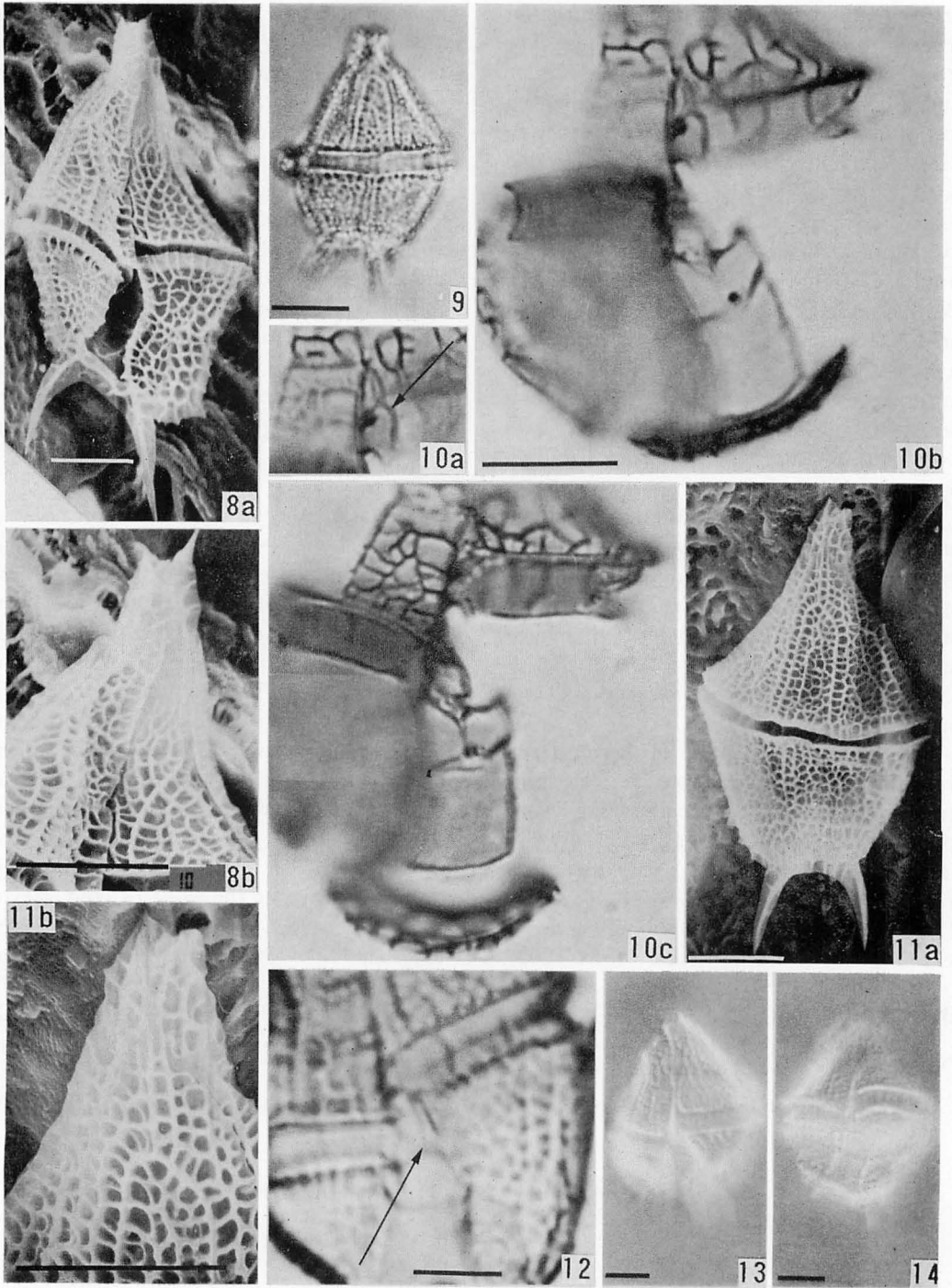
The living cyst always contains one to two red pigmented bodies (Figs. 1, 5a), and is sometimes surrounded by gelatinous material containing many small sedimentary and siliceous biogenic particles (Figs. 4, 5).

Thecate form

Numerous thecate cells were germinated from the living cysts described above from both Japan and the United States. These cells are 30–34 μm in length, 26–32 μm width and 15–20 μm in thickness, brownish yellow in color, and moderately compressed dorso-ventrally (Fig. 6d). The epitheca is triangular with a slightly concave outline in dorso-ventral view, with a broad apical horn (Figs. 6b, 9). The hypotheca is roundly trapezoidal with two conspicuous antapical spines which project from the theca (Figs. 6a, 8a). The cingulum is deeply concave at the equator and laevorotary in its own width at the sulcus (Figs. 8a, 10c, 11a). It slightly overlaps antero-posteriorly. The sulcus is triangular in equatorial view, with the anterior half being very narrow and barely protruding into the epitheca (Fig. 12). The posterior half broadens towards the base. The right

Figs. 1–14. *Gonyaulax verior* SOURNIA and scale bar is 10 μm (scale bar in Fig. 7 is 2.5 μm).

Figs. 1 & 2. Living ellipsoidal cysts (Perch Pond), showing a red body (arrow in Fig. 1). Fig. 3. Living ovoidal cyst (Perch Pond), showing very small antapical bosses (arrow). Fig. 4. Empty cyst after excystment (Hakata Bay) a; Lateral view, b; Archeopyle (arrow), c; Optical cross section of lateral view. Fig. 5. Living cyst before germination (Hiroshima Bay). a; Dorso-ventral view showing a red body (arrow), b; Optical cross section of dorso-ventral view, showing a thick endophragm, c; Optical cross section of polar view. Fig. 6. Thecate cell germinated from the cyst shown in Fig. 4. (Hakata Bay). a; Dorsal view, b; Optical cross section of dorso-ventral view, c; Dorsal view, d; Optical cross section of polar view. Fig. 7. Thecal plate showing a reticulate structure (Perch pond).



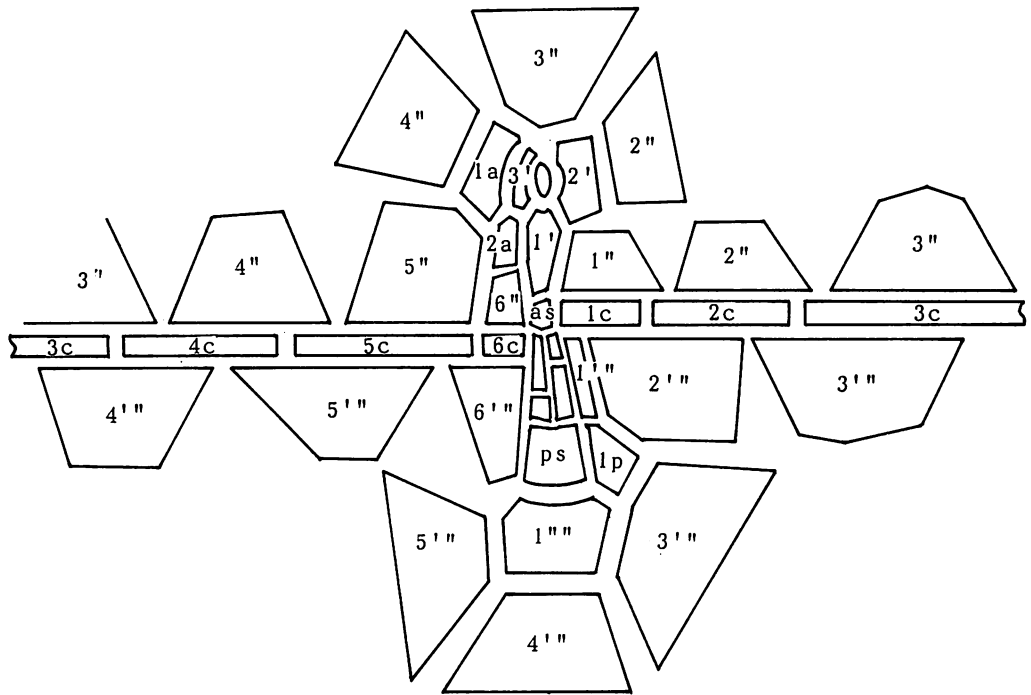


Fig. 16. Diagrammatic illustration of the thecal plate tabulation of *Gonyaulax verior* Sournia

Table 1 Cyst formation and archeopyle types of the genus *Gonyaulax* and its related genera. C.P.: Combination precingular archeopyle, P: Precingular archeopyle, S: Chasmic (slit-like) archeopyle.

Genus	Subgenus	Group	Cyst formation	Archeopyle type
<i>Gonyaulax</i>	<i>Gonyaulax</i>	Polyedra	+	C. P. (2"~5" or 2"~5"+1a~2a)
		Polygramma	-	
		Spheroidea	-	
		Spinifera	+	P (3") C. P. (3"+4" or 2"+3") S
	<i>Acanthogonyaulax</i>		-	
	<i>Fusigonyaulax</i>		-	
	<i>Steiniella</i>		-	
<i>Protoceratium</i>			+	P (3")
<i>Protogonyaulax</i>			+	S
<i>Goniodoma</i>			+	S

shape with two short and two long plate boundaries (Figs. 6a, 8b). Plate 2' is nearly pentagonal. The 3' plate is the smallest in this series, nearly rectangular and contacting the apical pore (Fig. 11b). These are two anterior intercalary plates which differ in size and shape from each other (Fig. 8b).

Plate 1a is larger than the 2a in size and similar to the 2' in size and shape. Plate 2a is small, pentagonal and contacts the 1', 3', 1a, 5" and 6" plates (Fig. 8b). There are no ventral pores in any plate. The precingular series has six plates. Two of them, the 3" and 5" plates, are pentagonal while

the others are trapezoidal in shape (Figs. 13–14). The 6" plate is the lowest vertically (Fig. 13), but the others are higher and nearly equal in height (Fig. 11a). There are six postcingular plates. The 1" plate is very narrow, rectangular in shape, and is mostly situated within the sulcus (Fig. 12). The 3" plate is nearly pentagonal while the others are basically trapezoidal in shape (Fig. 11a). The suture between the 3" and 4" is not shifted towards the right (Fig. 11a). The posterior intercalary plate is relatively large, and contacts the 1", 2", 3", 1" and the posterior sulcal plates (Fig. 8a). The antapical plate is nearly quadrangular, but has two additional short sutures. These major plates have a coarse reticulated structure, resembling an irregular mesh (Figs. 7, 11b).

The cingulum contains six rectangular plates with weak longitudinal striations (Figs. 10b, 12). The sulcus consists of six platelets. The posterior sulcal platelet is the largest and trapezoidal in shape (Fig. 10c). The anterior sulcal platelet has an inverted U-shape (Fig. 10b). Additionally, four small platelets are distributed in this area. All sulcal platelets have a smooth surface (Fig. 10c).

Discussion

Comparison of the cyst forms between species examined and related ones

Several species of both peridinialean and gymnodinialean dinoflagellates are known to produce a simple cyst which lacks any characteristic ornamentation. These include *Gonyaulax monilata* (WALKER and STEIDINGER 1979), *Protogonyaulax affinis* (FUKUYO *et al.* 1985), *Protogonyaulax catenella* (FUKUYO 1980, 1985), *Protogonyaulax tamarensis* (DALE 1977, ANDERSON and WALL 1978), *Gyrodinium instriatum* (FUKUYO 1982b, MATSUOKA 1985), and *Gyrodinium uncatenum* (TYLER *et al.* 1982). Their cysts are also covered with adhesive and transparent material (=mucilaginous layer termed by ANDERSON and WALL 1978), and lack a dis-

tinctive archeopyle which reflects simple or compound paraplates.

The cyst of *Gonyaulax verior* also lacks any spinous ornament and clear archeolye structure, and is surrounded by adhesive and transparent substance, sometimes with many small sediment and siliceous biogenic particles. This cyst is different from *Gonyaulax monilata*, *P. affinis*, *P. catenella*, *P. tamarensis*, and *Gyrodinium uncatenum* in mostly having an ovoidal cyst body. The cyst of *Gonyaulax verior* also differs from *Gyrodinium instriatum* by lacking a tremic (hole-like) archeopyle. However, it is very difficult to distinguish closely one from the others following normal palynological processing, because all of these cysts are simply spherical, lack characteristic ornamentation, and are surrounded by a thin wall which is easily deformed after germination.

Sousa E. SILVA (1962) found two different types of resting cysts in unialgal culture of *Gonyaulax diacantha* (= *G. verior*). One of them had a relatively thick and smooth cyst wall and the other was covered with many short conical spines. The present cyst resembles the former except that it has a mucilaginous layer which SOUSA E. SILVA (1962) did not describe.

Comparison of the thecate forms among other species of Gonyaulax

Some species of *Gonyaulax* have one or more conspicuous antapical spines on their thecate stages. These species include *Gonyaulax monocantha*, *Gonyaulax triacantha*, *Gonyaulax longispina* and *Gonyaulax verior*.

Gonyaulax verior is clearly different from *G. monocantha* and *G. triacantha* in having two rather than one or three antapical horns and has coarsely reticulated plates. *G. verior* is similar and related to *G. longispina* in thecal outline of dorso-ventral view and in having two antapical horns. DODGE (1982) considered *G. longispina* to be a junior synonym of *G. verior*, because the cell length and forms of the antapical spines could greatly vary within a single strain. However, we feel that these are two independ-

ent species, because *G. verior* has a broader sulcus and a shorter apical horn and the antapical horns lacking a wing ornament or flange.

Taxonomic position of Gonyaulax verior

KOFOD (1911) divided the genus *Gonyaulax* into four subgenera; *Gonyaulax*, *Fusigonyaulax*, *Steiniella* and *Acanthogonyaulax*, and the subgenus *Gonyaulax* into four groups; *Sphaeroidea*, *Spinifera*, *Polygramma* and *Polyedra*. Some species of *Spinifera* and *Polyedra* produce fossilizable resting cysts (WALL and DALE, 1968). Several cysts in the *Spinifera* group are distinctively different from each other in shape and ornamentation. They have consequently been assigned into several paleontological cyst genera. These cysts, however, have one common characteristic—a precingular archeopyle—, although a few have a combination precingular archeopyle {i.e. *Bitectatodinium tepikiense* and *Spiniferites* sp. 1 (= *Gonyaulax* cf. *alaskensis* of DOBELL and TAYLOR, 1981)}.

The cyst-theca relationship of two species of *Gonyaulax* which are similar to *G. alaskensis* was reported by DOBELL and TAYLOR (1981). Although these thecae were attributed to the subgenus *Steiniella* by KOFOD (1911), the cysts generally resemble those of the *Spinifera* group in having furcate processes and precingular archeopyle. Their examination also showed that they differ from the *Spinifera* group and the fossil genus *Spiniferites* in having a precingular archeopyle consisting of two free opercula (2P, 3"-4").

The cyst of *Gonyaulax verior* is clearly different from cysts of the *Spinifera* group, because it has neither simple nor a combination precingular archeopyle, and has no reflected tabulation.

TAYLOR (1975), BALECH (1977) and DODGE (1985) proposed similar reassessments of the genus *Gonyaulax* based on differences in the thecal plate tabulation. For example, DODGE (1985) suggested *Gonyaulax polyedra* should be separated from the genus *Gonyaulax* and provisionally proposed the

fossil genus *Lingulodinium* for this thecate species. *Gonyaulax tamarensis* has already been transferred into the genus *Protogonyaulax* by TAYLOR (1979), the genus *Alexandrium* by BALECH (1985) and *Gessnerium* by LOEBLICH and LOEBLICH (1979). Based on cyst morphology, those two species differ from the cysts of *Gonyaulax spinifera*, the type species of *Gonyaulax*, in both ornamentation and archeopyle type. Thus the cyst morphology supports the need for a reassessment of *Gonyaulax* as presented by TAYLOR (1975), BALECH (1977) and DODGE (1985).

All cyst forms belonging to the genus *Gonyaulax* possess a precingular archeopyle and a relatively thick peri- and endophragm. The cyst of *Gonyaulax verior* that we described here has a distinctively different cyst from all other known *Gonyaulax* (s.s.) cysts. This species has never been attributed to any subgenus and group of *Gonyaulax*. Its thecal morphology differs from the *Spinifera* group in having no ventral pore, less cingular displacement and a nearly straight sulcus without any overhang of the cingulum. Consequently, we believe that it should be assigned to a new group and probably new subgenus in the genus *Gonyaulax* in the future, based on its thecal tabulation similar to *Gonyaulax*, but its cyst morphology differing from the other species of this genus. We need further evaluations of the cyst morphology of *Gonyaulax verior*, since other closely related species in different genera also have simple ovoidal to spherical cysts without distinct archeopyles.

The above discussion argues that both thecal and cyst morphology are primarily contributed to the systematics of the genus *Gonyaulax*.

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松岡数充*・福代康夫**・Donatd M. Anaerson*** : *Gonyaulax verior* SOURNIA の
シストと有殻細胞および *Gonyaulax* 属の分類学的意義

日本及び北米の海底表層堆積物から採取された *Gonyaulax verior* SOURNIA の生シストの単種培養株を用いた観察結果に基づき、本種の有殻細胞及びシストの形態を記載した。シストは卵型稀に楕円形で、表面に装飾物を欠き、時には粘着物で覆われる。本種は有殻細胞の鍍板配列では *Gonyaulax* 属・*Spinifera* グループと同様であるが、シストでは外形、装飾物の有無、発芽孔の形態などが異なっている。これらの観察結果から、遊泳・有殻期及びシスト期の細胞形態にもとづいて *Gonyaulax* 属全体の系統・分類を再考する必要性が示唆される。(*852 長崎市文教町1-14 長崎大学・教養部・地学教室, **113 東京都文京区弥生1-1-1 東京大学・農学部・水産学

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新 刊 紹 介

BIRD, K.T. and BENSON, P.H. (Ed.): Seaweed Cultivation for Renewable Resources. Developments in Aquaculture and Fisheries Science, vol. 16. xiii+381 pp. Elsevier. Amsterdam, Oxford, New York, Tokyo (1987). 邦貨 約20,500円。

日本、中国、韓国及びフィリピンでは食用として、また海藻多糖類（寒天、アルギン酸、カラギナン）の生産のための大規模な海藻養殖が行なわれ、海藻資源の開発がされている。一方、第一次大戦中にドイツから海藻灰の輸入の停止、第二次大戦中の日本からの寒天の輸入が途絶えて、米国ははじめ戦争相手国が痛手を受けて、その開発に努力が払われました。また、1970年代初頭に世界中がオイルショックに見舞われた非産油国はその代替えエネルギーとして海洋生物資源（海藻）から燃料（メタンガス）を生産する研究が進められました。

本書は、新資源としての大型海藻を増産するための養殖技術及びそれよりメタンガスを生産するための開発技術を紹介したもので、14章からなり、各専門家が最近の研究をレビューしたものです。各章を要約すると、第1章は、世界の海藻の利用と養殖の歴史、特に米国のジャイアントケルプ (*Macrocystis pyrifera*) 増産プロジェクトの歴史的経過について；第2～4章は、米国太平洋海岸沖に生育する海洋バイオマスの最重要種とされるジャイアントケルプの養殖の基礎的研究（生態、生長、採苗、施肥、病害、育種）について；第5～6章は、中国及び日本のコンブ養殖の現状、さ

らに中国及び日本の技術を応用した米国のコンブ養殖と一部はオゴノリ養殖の現状について；第7章は、熱帯及び亜熱帯海域で養殖する場合の地理的、物理的及び生物的環境要因、その海藻の生理・生態及び主要有用海藻の種類・成分・用途について；第8章は、米国フロリダ州西海岸でメタンガス生産のための、主としてオゴノリの、他にホンダワラ、アオノリ、アオサ等の養殖の基礎的研究について；第9章は、有用海藻（コンブ、アマノリ、ホンダワラ、アオノリ）の組織培養のバイオテクノロジーの最新の研究について；第10章は、海藻生育地及び海藻上に着生する窒素固定細菌及び藍藻が海藻の主栄養素である窒素源の供給に大きい役割を果していることについて；第11～12章は、大型海藻からメタンガス生産の生物学的特性とその多糖類の生物分解過程について；第13章は、経済的側面からみた養殖場の選択、その面積、養殖筏の構造、メタンガス転換コストについて；第14章は、米国ワシントン州 Puget Sound で、日本の技術導入をしたノリ養殖の開発について、それぞれ総説したものである。

以上のように、本書は主として米国において企業としての大型海藻の大規模養殖の技術と、それよりメタンガス生産のための技術開発の研究の現状を紹介したものである。これはまた、将来日本の海藻資源開発の際に多くの示唆を与えてくれるものと思う。また、各章には、多くの引用文献が掲載されており、その詳細を知ろうとする人に役立つものといえる。

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