The Genus *Alexandrium* Halim (Dinoflagellata)

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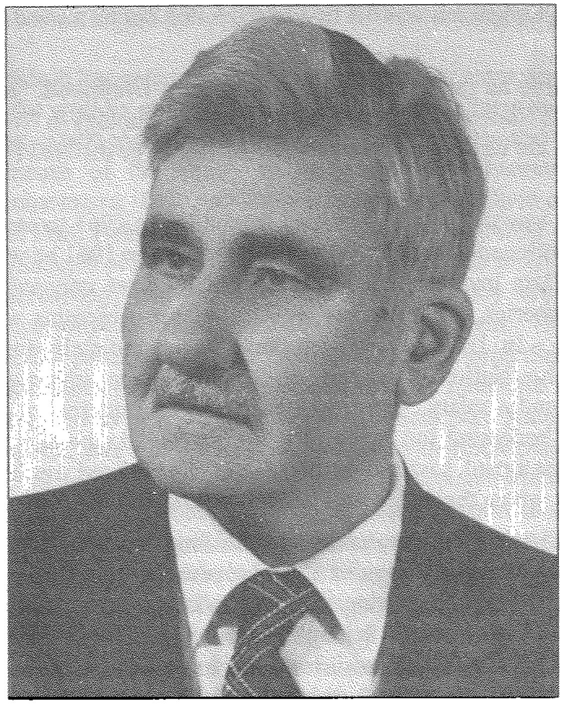

Enrique Balech

Going through life I have always been impressed and influenced by people having humility, kindness and understanding. I have been fortunate in meeting many that fit into that mould. However, there are few that I can say have also been geniuses in their field. One such person came to Sherkin in 1989 when we invited scientists from around the world to participate in a workshop "The Problems of Toxic Dinoflagellate Blooms in Aquaculture". He was a 79-year-old Argentinian - Prof. Enrique Balech.

It was at this workshop that I learned that Prof. Balech was finalizing this manuscript and would like to have it published. I offered to do it for him and so following discussions with Dr. Karen Steidinger, who also participated in the workshop, things were put in train to realize Prof. Balech's dream.

One morning at around 6 o'clock, as the two of us had breakfast in my kitchen, he talked to me of his life. It shows one does not need money and expensive equipment to undertake research.

As a student he had decided to study bats but he became enthusiastic about the microscope and this began his life-long love for phytoplankton. This was away back in 1934 in the Museum of National Science in Negutica, Argentina.

Freshwater phytoplankton was his first introduction but he moved on to marine in a short time.

At the same time he taught in a high school for a livelihood. In 1941 he was appointed to the National Council of Science and Technology in Negutica. In 1947 Peron changed the director and the new person in charge disliked Prof. Balech and fired him.

He returned to teaching in a high school from 1947 to 1961 to earn a salary. All this time he continued with this phytoplankton work. In 1961 he was appointed to the Mar Del Plata Institute which was created by three universities for marine biology and fisheries. This was the only institute in Argentina with money and research posts. In 1962 he resigned and was immediately appointed by the President to the National Council of Science as an investigator with full independence and a salary. He retired in 1981 as a principal investigator as he found himself becoming too much of a bureaucrat. As he said, he became an amateur scientist again! Listening to him talking I wondered was he ever anything but an amateur, given the difficulties he had earning a salary.

I asked him had he a modern microscope? Smiling, he said: "I still use the same one for over 50 years, but I do need a good typewriter; the one I have is not very good." He said that when looking at phytoplankton he draws much as drawings give you time to look at detail; with photographs one misses a lot. He made his own camera lucida from string, a mirror, a can and pieces of timber. As he spoke I started to think of the many scientists worldwide who, yet working on microscopes costing thousands and thousands of pounds, have to send their specimens to him for the final identification.

In our hours of talking this great man never once bemoaned the fact that he had so little of the material things in life. One thing is sure, he had an abundance of contentment and happiness. As he talked I mentally compared him with some of those scientists in his field who were so convinced of their own greatness. A number of whom I have met and may God deliver me from their arrogance. What time will, of course, show is that Prof. Balech's work will survive.

I believe present and future "red tide" scientists should be encouraged to keep ploughing their own furrow even when they find difficulty in obtaining the funds to carry out their research. When they feel alone and frustrated I pray they will remember the difficulties that Prof. Balech overcame throughout his long life.

It was fascinating to meet this wonderful man who knew the true value of life.

Matt Murphy, Director,
Sherkin Island Marine Station,
Co. Cork, Ireland.

A TRIBUTE

Prof. Enrique Balech has spent much of his professional career studying plankton collected from the world's oceans. His study of dinoflagellates over five decades has made him an expert and leader in this field. His work has and continues to be exceptional because of his ability to recognize and illustrate conservative morphological characters. Using a simple monocular brightfield microscope and a camera lucida, Prof. Balech has been able to see and accurately portray species without the advantages of modern optical aids such as differential interference of fluoresence microscopy, and yet his detail and accuracy are beyond most descriptions employing these and more advanced equipment. He increased the value of using plate patterns and their tabulations for armored dinoflagellates by showing the importance of the small sulcal and cingular plates for identifying and separating genera and even species. His use of apical pore plates, position and shape of the 1' plate, shape of the anterior and posterior sulcal plates, presence of a ventral pore, size of the 6" plate, and other plate characteristics of *Alexandrium* species has provided other taxonomists with the essential tools to separate closely related species. No biological species is without morphological variation, and Prof. Balech has also studied this variation in dinoflagellate species to document the degree of variation in what was considered conservative characters. He is a skilled scientist who willingly shares his knowledge and time to explain how to look for and recognize the smallest detail. He is careful and meticulous in his approach and technique, and most importantly he is a teacher. He recognizes that we will always be students and need to continually learn.

I have known Prof. Balech for 25 years, the first 15 through correspondence. I did not actually meet Enrique until 1985 when we travelled together to a toxic dinoflagellate conference in Canada. I had always thought of him as "the" dinoflagellate expert and my mentor. During the trip, I learned about the man. Enrique Balech is much more than a dinoflagellate taxonomist, he is an historian and is versed in world events. He has a wonderful sense of humor and a compassion for mankind; as he does with dinoflagellates, he sees beyond the obvious.

Dr. Karen Steidinger,
Florida Department of Environmental Protection,
Florida, U.S.A.

TRANSLATION OF MANUSCRIPT

Several people contributed to the process by which Prof. Balech's original Spanish manuscript was translated into English. Dr. Karen Steidinger, an internationally known dinoflagellate taxonomist and a long-time admirer of Prof. Balech and his work, employed Paloma Rodriguez to do the original translation, which was then word processed by Julie Garrett, an assistant of Dr. Steidinger's at the Florida Department of Environmental Protection. Beverly Roberts, a colleague of Dr. Steidinger's since 1972, worked with Iliana Quintero-Hunter, a Spanish-speaking co-worker, to proof the English version against the original manuscript. Ms. Roberts rewrote the English manuscript as required and corresponded with Prof. Balech about questions that neither she nor Dr. Steidinger could resolve. Ms. Roberts, who has had the pleasure of meeting Prof. Balech, was pleased to have the first-hand opportunity to learn more about taxonomy from Prof. Balech himself.

This manuscript has been translated from the original Spanish in such a way as to preserve Prof. Balech's style. It also uses uncomplicated sentence structure because of the expected non-native English reading audiences. Therefore, in places material is duplicated, but completely re-writing these places would have damaged the style. The book is presented as the Professor wished.

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ABSTRACT

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A historical account of the genus *Alexandrium* is presented. Of those species that are now considered to belong to *Alexandrium*, the oldest one was originally described as *Goniodoma ostenfeldii* in 1904 by Paulsen who transferred the species to *Gonyaulax* in 1949. In 1925, Lebour described the second species under the name *Gonyaulax tamarensis*. Since then, several species have been added to these atypical *Gonyaulax* but, not until the 1970's, were they recognized as a special group within the genus *Gonyaulax*, the so-called "*Gonyaulax* of the *tamarensis* or *catenella* group".

In 1960, Halim discovered a small dinoflagellate for which he created the new genus *Alexandrium*. In 1967, he established another genus, *Gessnerium*, for a species that he inadvertently thought was a new one, not realizing that it was already published by Howell as *Gonyaulax monilata*.

Several authors recognized that species in the "*tamarensis* group" were very similar to each of the species in Halim's genera. The conviction soon grew that these dinoflagellates should be in a genus separate from *Gonyaulax*. Therefore, at least one of Halim's genera should be adopted for this so-called group of *Gonyaulax*. Because *Alexandrium* has priority over *Gessnerium*, the former name must be adopted for this complex of species that formerly was referred to *Gonyaulax*. The use of *Alexandrium* is also supported by my recent re-description of its type species, *A. minutum*. Because the 1' in *A. minutum* is connected to the Po, the genus *Protogonyaulax* Taylor is invalidated because it was based solely upon the supposed disconnection of both plates in *A. minutum*.

All the species studied here share the same structural features in the hypotheca, cingulum, sulcus, and even the epithecal region with the exception of the 1' plate. Therefore, my opinion is that they should be incorporated into a single genus. However, the differences in 1' seem to justify a subdivision of the genus. Therefore, *Gessnerium* is here retained as a discrete subgenus containing the species in which the 1' is not rhomboidal and does not have any contact with the Po.

The completion of this monograph was preceded by a long quest for material from many places around the world. These places and the people who sent material or gave some other assistance are listed in "Materials, Methods, and Acknowledgements". This abundant material came from almost all the places where the genus has been recorded and, therefore, offers an exceptional opportunity for a critical review of the genus and the intraspecific variations.

The thecal characteristics of the genus are detailed. For the thecal formula, the Kofoidian system is used as modified and detailed by Balech (1980) and Balech and Tangen (1985). The formula accepted for the genus is Po, 4', 6", 5"', 2"", 6c, and 9-10s. All the plates and their variations are described in detail. Structures observed in the Po are explained: 1) the centrally or not quite centrally located aperture called either the foramen or comma, 2) the callus or thickening of the ventral half of the comma's right margin, 3) the canopy, which is a very thin membrane covering most of the foramen as a diaphragm, 4) the rather large connecting pore or pores that are located dorsally or to the right of the comma, and 5) the small marginal pores.

The 2"" plate has two main types: type A, which is elongated dorsoventrally or longitudinally, and type B, which has its transversal axis longer than the longitudinal one.

In the most typical *Alexandrium*, 1' is rhomboidal and connected to the Po. Its longer right margin is frequently interrupted by an indentation forming, in whole thecae, a "ventral pore". The presence or absence of a ventral pore is a specific character. In many individuals of some *Alexandrium* species (among them the type species), the 1' appears to be disconnected from the Po in whole thecae, but dissections demonstrate that both plates are connected by a thin thread-like projection of the vertex of 1'. However, in some other species, exemplified by "*Gonyaulax monilata* Howell", the 1' is completely separated from the Po, and its shape is greatly changed.

In most of the species, the theca is smooth except for some small pores, generally in the center of minute bumps. In a few species (e.g., *A. foedum*), the pores are bigger and more densely arranged. In some plates of *A. minutum*, areolation is faint but discernible. In *A. balechii*, the hypotheca has more or less conspicuous ridges partially closed in reticula. In *A. insuetum* and an undetermined species obtained in the Gulf of Mexico, the reticulation is well-formed over the whole theca. Nonetheless, sculptured species are exceptional in this genus.

All the species have a slightly descending cingulum. The displacement of the right end is generally about one cingulum height. Conspicuous cingular lists are not present.

The sutures are never prominent and the sulcal lists are poorly developed.

The taxonomic value of the thecal features are analyzed.

Taking into account all the thecal characteristics, a subdivision is proposed. Two subgenera are accepted: *Alexandrium* (= *Protogonyaulax*), type species *A. minutum* Halim, and *Gessnerium*, type species *A.* (*Gessnerium*) *monilatum* (Howell). The only deciding differences between the subgenera are the shape of the 1' and its connection with the Po. In the subgenus *Alexandrium*, these two plates are connected either directly or indirectly by a thread. In *Gessnerium*, they are totally disconnected and the shape of 1' is very different. Because the other thecal components do not show marked differences, a taxonomic division higher than subgenus is not necessary.

The subgenus *Gessnerium* is a transitional step toward *Goniodoma*. The distinction between *Goniodoma* and *Gessnerium* is stressed.

In the subgenus *Alexandrium*, several discrete groups are formed: *minutum* group, *ostenfeldii* group, *catenella* group, *fraterculus* group, *tamarense* group, and *kutnerae* group. They are not given formal taxonomic status.

Species of the *minutum* group are characterized by their small size, irregularly oval shape, very narrow 6", and shape of the S.p. The following species are in this group: *A. minutum*, *A. lusitanicum*, *A. angustitabulatum*, and *A. andersoni*.

The *ostenfeldii* group is formed by globose species of medium to large size. Their thecal walls are particularly thin and collapsible. The 1' is narrow and has a large ventral pore. Two species are well-studied: *A. ostenfeldii* (= *Pyrodinium phoneus* ?) and *A. peruvianum*. The species *Gonyaulax dimorpha* is somewhat dubious.

The *kutnerae* group is formed by large globose species. The 1' is rather wide with a very small ventral pore that is often located inside the plate. Two species are in this group: *A. kutnerae* and *A. leei*.

The *tamarense* group is not easily defined. It is formed by species that 1) do not form chains, 2) are generally of medium size, 3) have a Po, 1', and 1" of medium width, 4) may or may not have a small ventral pore, and 5) have an S.p. that is longer than wide with well-projected ventral corners. Four species are in this group: *A. tamarense*, *A. fundyense*, *A. acatenella*, and *A. tropicale*. The first two have been the subject of many studies because of their importance in connection with the production of Paralyzing Shellfish Poison (PSP). One species found in Thailand is presented as *Alexandrium* sp. cf. *tamarense*. Two dubious species (*Alexandrium* spp. II and III), which are listed as *incertae sedis*, may belong in this group.

The *catenella* group is formed by two species that are compressed anterior-posteriorly and form chains: *A. catenella* and *A. compressum*. They do not have a ventral pore.

The *fraterculus* group is composed of four species that are also chain formers but are not anterior-posteriorly compressed. The ventral pore is present. The species within this group are *A. fraterculus*, *A. cohorticula*, *A. affine*, and *A. tamiyavanichi*.

As *incertae sedis*, four taxa are presented. The first is a species quite different from the others, with uncertain relationships: *A. concavum*. The second one, *Alexandrium* sp. I, is a taxon that is certainly new but is not completely studied (only one short chain has been found in the Gulf of Mexico). It has a somewhat compressed theca, a 1' connected to the Po, and a reticulation that covers the whole theca. This reticulation of the whole theca and some tabular features make it different from any other species in the subgenus.

The third and fourth *incertae sedis* species (*Alexandrium* spp. II and III) are related to *A. fundyense* but differ from it in several details. Study of more material is needed to establish their taxonomic status with some certainty. One was found in Pacific waters off Mexico and the other in south Australian waters.

In the subgenus *Gessnerium*, nine species are recognized. They are *A. monilatum*, *A. balechii*, *A. foedum*, *A. pseudogoniaulax*, *A. taylori*, *A. margalefi*, *A. insuetum*, *A. hiranoi*, and *A. satoanum*.

In total, 28 duly published species (excludes numbered species and species *inquirendae*) are accepted in the genus *Alexandrium*, but the undoubtedly new, reticulated species (*A.* sp. I) found in the Gulf of Mexico should be added.

As species *inquirendae*, I list some taxa that I have not seen and that are unlikely to be recognized now. They are *Alexandrium depressum*, *Gonyaulax dimorpha*, *G. lebourae*, *G. conjuncta*, *G. catenella sec* Postek and Cox (most probably *A. tamarense*), and *Pyrodinium phoneus*. Clearly, all of them are *Alexandrium*.

All the species, except the *inquirendae* and two others (*A. hiranoi* and *A. satoanum*) that were recently described by Japanese specialists, are described in detail. *Alexandrium lusitanicum*, *A. leei*, *A. fundyense*, and *A. insuetum* were already published in 1985 with a very short diagnosis. In this monograph, they are given a detailed description and discussion. Concise descriptions of *A. tamiyavanichi*, *A. taylori*, and *A. margalefi* are published elsewhere (Balech, 1994) and are complemented in this monograph. Both F. J. R. Taylor and I had intended to introduce a new species at the 1985 Conference on Toxic Dinoflagellates; it was announced using Taylor's name of *Protogonyaulax angustitabulata* although I recommended that the name be changed to *Alexandrium angustitabulatum*. Neither name has been appropriately published. F.J.R. Taylor has agreed that his species name combined with *Alexandrium* could be published as a new species in this monograph.

The Genus *Alexandrium* Halim

INTRODUCTION AND HISTORY

For a long time, scientists expressed doubts about several aspects of the complex genus *Gonyaulax* Diesing. They questioned its real limits, its relationships with other genera, and even its orthography because it is sometimes written as *Goniaulax* (probably etymologically more accurate). The genus evolved rather chaotically until Kofoid's (1911) first attempt at revision.

Undoubtedly, Kofoid's effort was successful with the principal species, because with excellent drawings, he clarified and defined some structural features. However, he also made several errors in determining tabulation, and he subdivided the genus inappropriately. He divided it into four subgenera, based mainly on shape and to some extent on sculpture; the result is a strange, completely artificial division. One of his subgenera is *Steiniella*, created by Schutt as a genus. Also, Kofoid incorporated the genus *Amylax* Meunier into *Gonyaulax*. However, the same year, he separated *G. jolliffei* Murray and Whitting from *Gonyaulax* and created a new genus *Spiraulax* for it. I want to stress that although *Spiraulax jolliffei* is completely separate from *Gonyaulax*, it is probably not the species published by Murray and Whitting.

A new species, *Gonyaulax tamarensis*, was described by Lebour (1925). It is distinguished by its simple shape. It lacks an apical horn or conspicuous spines. It has a thin theca with four apical plates but no intercalary plates.

After Lebour's description, Whedon and Kofoid (1936) described two species with the same tabular formula: *G. acatenella* and *G. catenella*. The latter forms chains and has been studied extensively since the late 1930's when it caused Paralyzing Shellfish Poisoning (PSP) in humans who consumed certain bivalve mollusks. Because this toxic species is distributed worldwide, it has become the most famous of those *Gonyaulax* species having four apicals and no intercalary plates. *Gonyaulax acatenella* did not have the same fortune. It is seldom mentioned and its description is inadequate.

Other similar species were grouped with these three and as a whole were identified as the "tamarensis group" or sometimes as the "catenella group" without a formal taxonomic status. Subsequently, Balech and Tangen (1985) reported that Lebour's species was not, as believed, the first known of this particular group of *Gonyaulax*. Instead, 20 years before, Paulsen (1904) described a species that he erroneously placed in the genus *Goniodoma* and called *Goniodoma ostenfeldii*. Paulsen (1949) rectified the error by changing the genus to *Gonyaulax*, but the new description in his posthumous work does not correspond with his original illustration.

On the other hand, *Gonyaulax orientalis* Lindemann 1924, similar to some of these species, belongs to *Goniodoma* (Balech, 1979a). Its maintenance in *Gonyaulax* by Schiller and others is because they relied, not on the original publication, but on the drawings and description of Lebour (1925), which undoubtedly correspond to another taxon. Therefore, she described only two species that could be related to the "tamarensis group", i.e., *G. tamarensis* and *Goniodoma ostenfeldii*.

This confusion and hesitation between the genera *Goniodoma* and *Gonyaulax*, which began with the century, increased in the following years. This became evident in Gaarder's (1954) Atlantic Deep-Sea Expedition study on dinoflagellates in which her *Goniodoma concavum* and *G. depressum* have "*Gonyaulax* from *tamarensis* group" characteristics. However, this investigator clearly perceived that the two genera could be easily confused, and I believe she was the first to emphasize (p. 30) that the apparently clear differences between both are the result of the arbitrary assignment of similar plates to different series. Interestingly, one of these species, *G. concavum* or a similar form, was later found inside cysts of *Pyrocystis*.

Woloszynska and Conrad (1939) described a dinoflagellate that caused red tides and toxicity in Belgian waters. They called it *Pyrodinium phoneus*. Clearly, it belongs to the group that has four apicals but no intercalaries. Steidinger (1973) confirmed its affinity and added that *P. phoneus* and *G. tamarensis* var. *excavata* were the same taxon. Loeblich and Loeblich (1975) transferred *P. phoneus* to *Gonyaulax* but rejected the synonymy proposed by Steidinger.

Howell (1953) described a new species, *Gonyaulax monilata*, that is anterior-posteriorly compressed, forms chains, causes red tides and fish kills, but has one particularity: 1' does not connect with the Po.

Halim (1960) created the genus *Alexandrium* with only one species: *A. minutum*, a small dinoflagellate that produced a red tide in Alexandria Harbor, Egypt. The theca of *A. minutum* was almost isodiametric and somewhat elongated. The variably shaped, slightly conic epitheca had no spines or horns, a rather large oval Po, and four apicals of which 1' was disconnected from the Po almost as in the Howell species. The hypotheca was variably shaped, hemispheric to not quite conic, and rather flattened on the antapex. The sulcus was large. The descending cingulum was deeply excavated, without a curtain fin. Halim assigned the following formula to the genus: 4', 0a, 6", 7c, 5"', 2p, and 1"". The plate that he called the first cingular is now considered the S.a.

Halim (1967) established another monospecific genus, *Gessnerium*, with the species *mochimaensis*, which was found in the Bay of Mochima, eastern Venezuela. The following formula was assigned: Po, 3', 0a, 7", 5"', 2p, 1"", 7c, and 6s. Following the plate nomenclature that I use in this monograph, his 1"" is clearly the S.p., his C_1 is the S.a., and his left sulcal (S.s.a. according to my modifications of Kofoid's definition) is what Kofoid called 1"'. Although displaced from the Po, Halim's first precingular is homologous to the 1' of other species, as he noted in *Alexandrium*. With the tabulation corrected in this way, this species' formula would be Po, 4' (3'+1' as proposed by Taylor [1976]), 6", 6c, 6"' (per Kofoidian nomenclature), 1"" and 1p (2"" per Balech [1980]), and 7s. This formula corresponds to the *tamarensis* group of *Gonyaulax* and to *Pyrodinium*. Also, all characteristics of *G. mochimaensis* correspond to those of *Gonyaulax monilata*. Probably, Halim was unaware of the Howell publication. Since then, the *tamarensis* group has been integrated into two subgroups: one in which 1' has clear contact (direct or indirect) with the Po and one in which this contact is lost. Later, this variable character caused confusion when placing species in appropriate genera.

Gran and Braarud (1935) studied an abundant *Gonyaulax* in the Bay of Fundy (Atlantic coast of North America). They identified it as *G. tamarensis*. The identification was confirmed by Lebour who studied material gathered by Canadian investigators (see Medcof et al., 1947). In the 1940's, Braarud maintained the first "*tamarensis*" clonal cultures, started from Norwegian material, that had the same characteristics as the species he had studied in the Bay of Fundy.

He noted that two clones maintained some constant differences and, based on these differences, he created two varieties: *excavata* and *globosa* (Braarud, 1945). Balech (1971) considered it suitable to change them to species: *G. excavata* and *G. globosa*. Simultaneously, he described specimens obtained in the equatorial Atlantic that he hesitatingly referred to *excavata*. However, Loeblich and Loeblich (1975) believed that the Atlantic organism was a different taxon, and the difference was later confirmed.

Several other species were added to the group by different authors (Biecheler, Wood, Balech and Mendiola, Balech, Steidinger, Inoue and Fukuyo, Kita and Fukuyo, and Fukuyo and others). Balech and Tangen (1985) redescribed Braarud's two varieties and demonstrated that *globosa* is synonymous with *Goniodoma ostenfeldii* Paulsen.

Tamarensis-group taxonomy became more and more complicated due to these additions and to the differing opinions of subsequent investigators, with respect not only to species, but also to genus. At the specific level, a single species from the same location has been given different names (e.g., *G. tamarensis* and *G. excavata* in Japan, *G. tamarensis excavata* and *G. excavata* in the Gulf of Maine and the Bay of Fundy), or two different species have received the same name. At the generic level, this group now contains members that have previously been assigned to *Gonyaulax*, *Goniodoma*, *Pyrodinium*, *Alexandrium*, *Gessnerium*, *Protogonyaulax* and possibly *Glenodinium* (almost certainly, *Glenodinium* sp. Lindemann, 1924, p. 218, fig. 3 is an *Alexandrium*, and its "kleineform", fig. 2, could be *A. minutum*).

Steidinger (1971) was the first to note formally that these species should be put into another genus. She provisionally placed her new species *Gonyaulax balechii* in the genus *Gonyaulax* and said that later it might be necessary to create a new genus for this species "once the *catenella* group has been removed from *Gonyaulax sensu stricto*". She commented that if the tabular formula of *Alexandrium minutum* were modified, *A. minutum* would belong in this group of *Gonyaulax*. Besides providing a good description of the new and rather aberrant species, this work is noteworthy for three reasons: the first commentary on separating the whole *tamarensis* (or *catenella*) group from *Gonyaulax*, the recognition that *Alexandrium* was part of this group, and the first formal tabular characterization of the group as follows: Po, 4', 0a, 6", 6c, 6"', 1p, 1"", and 7-8s.

Simultaneously, Balech (1971) noted the existence of a special *Gonyaulax* group and suggested that it be separated as a subgenus using the name of *Alexandrium* or *Gessnerium*. Consequently, during the seventies, the idea matured that the *tamaresis* group was a well-characterized systematic unit that deserved its own serious designation.

Today, Steidinger's and Balech's partial proposals about the generic separation of the group are generally accepted. If the group is not located in the oldest genera named, such as *Goniodoma*, *Pyrodinium*, or even *Glenodinium*, with which it has no affinity, only two generic names are admissible for these dinoflagellates: *Alexandrium* and *Gessnerium*. If all species of this group are congeneric, the proper name to adopt is the former because it is older. As this is the premise I follow, this revision carries the title of *Alexandrium*.

MATERIALS, METHODS, AND ACKNOWLEDGEMENTS

In order to accomplish this work, I tried to get material from the most diverse sources including the type locale whenever possible. This required a long and patient correspondence that sometimes was not successful because of various circumstances: the colleagues that were consulted did not have samples of these organisms and often did not know them; at the moment, nobody was working on the re-collection and study of dinoflagellates in the area of concern; the water where the species was originally located is now so polluted that these organisms and others that prospered there some decades ago can no longer survive (as in Bruges canal or Brugge in Belgium with *P. phoneus*); the brackish water bodies where the species was obtained no longer exist (type locations for *G. dimorpha* Biecheler); the investigator had moved to another area or country or had just left these studies; and others did not answer.

The lack of both material and references from three countries with very extensive coasts is noticeable: mainland China, India, and Pakistan. Also, toxicity reports and sample material from continental Asia have come from only three countries: Korea, Thailand, and Russia. It is unlikely that species of *Alexandrium* actually do not exist in other Asian countries. Therefore, they are virgin fields for study.

This re-collection campaign, although slow, was successful. I send my warmest gratitude to the many colleagues that generously contributed. This work could not have been accomplished without their help. I am grateful to anyone who sent me information and references or tried to obtain them. I apologize if, by negligence or accident, someone is omitted.

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Individual cells were isolated with micropipettes, oriented, measured, and drawn using a camera lucida. Afterwards, their thecae were disintegrated with sodium hypochlorite and the plates were examined with the oil immersion objective and phase contrast. Iodine dye and Brilliant Cresil Blue were sometimes used to improve the examination. All measurement bars in the figured Plates represent 10µm. A bar applies only to the closest figure unless otherwise noted in the plate description.

All cell dimensions are expressed in µm, therefore, this unit measurement is usually omitted. L (Latin, *longitudo*) stands for longitude; A (Latin, *amplitudo*) indicates the maximum width measured between the lateral extremes of the cingular flange (Fig. A); and Trd stands for transdiameter or transverse diameter (differentiated from A because it indicates width measured at the cingulum bottom; the difference A - Trd corresponds to twice the cingulum depression). DV indicates the dorsoventral diameter or thickness (depth) of the cell. The difference A - DV shows the degree of dorsoventral flatness of the theca, i.e., the larger the difference, then the flatter the cell.

The cingulum is always descending because the right end is lower or more posterior than the left one. The direction of the transverse flagellum is left to right. I place a number between parentheses after the word "descending" that indicates the displacement of one cingulum end with respect to the other, expressed as cingulum height; hence, (1) indicates that the displacement is one cingulum height and (1.75) that it is one and three-quarter times the cingular height.

MORPHOLOGICAL CHARACTERISTICS OF THE THECA

The theca of *Alexandrium* (Fig. A) is characterized not only by the tabular formula but also by general morphology and structure. The tabular formula is as follows: Po, 4' (3'+1'), 6", 5"', 2"", 6c, and 9-10s. I use Kofoidian notation, with modifications that are explained below.

A new notation was presented by Taylor (1977) in 1974 at the Marine Plankton and Sediments Conference in Kiel and was completely developed later (Taylor, 1979). Eaton (1980) also proposed that the Kofoidian system be abandoned and replaced by the one he outlined. In my opinion, their systems reveal more clearly the real affinity of Peridinian dinoflagellates. In addition, Taylor separated what he calls Gonyaulacoidea from them.

Undoubtedly, the Kofoidian system is not perfect and some of his formulas for very similar genera are considerably different. These misleading formulas are due to an arbitrary or subjective assignmemt of certain plates to various series, such as occurs when a plate may be classed as either 1' or 1" or when some plates may be assigned to either sulcal or hypothecal series.

Balech (1967, 1971) brought attention to the difficulty of adjudicating whether the Gonyaulacoid plate that Kofoid called 1"' belonged to the sulcal region or to the postcingular series. Balech (1980) again discussed the subject and proposed, not a new nomenclature, but criteria to assign some plates to different series reliably. These proposals had been presented earlier at the 1978 Penrose Conference on dinoflagellates where I affirmed the unquestionable homology of the *Goniodoma* S.s.a. with the *Gonyaulax* 1"', Kofoid's 3"" in *Goniodoma* with the S.p. in *Gonyaulax*, and the 1"" of *Goniodoma* with the p plate of the other genus. Loeblich and Loeblich (1979) presented an argument about *Gonyaulax* tabulation and drew the same conclusions. Because they did not mention my proposals, apparently, their conclusions were derived independently.

In fact, my studies show that the decision to locate Kofoid's 1"' either in the sulcus or in the postcingular series is still rather uncertain. Taylor's proposal could eliminate the problem, but because I have not studied his system thoroughly and, moreover, have not applied it to different cases, I am not sure that it does not introduce some other inconvenience. Therefore, I use Kofoid's old notation because it is generally easy and practical to use except for these instances that we are discussing. Nevertheless, a system of parallel tabular series that eliminates or erases the sulcal unit would hide the peculiarity and structural importance of this area.

The controversial 1"' of Kofoid appears in some species to be a 1"', but in other species, even within the same genus, it clearly has sulcal or transitional characteristics. Given careful observation with light microscopy, this plate in some *Alexandrium* species is more or less hidden within the sulcus and partially covered by a narrow membrane attached to the plate on its left: this membrane is the anterior part of the left sulcal list. Taylor (1979) notes that, in the closely related genus *Pyrodinium*, scanning electron microscopy shows that the plate generally called 1"', which he called Is, is completely in the sulcal depression and is covered by the left sulcal list. In other *Alexandrium* species, this plate is large, is sometimes relatively wide (*A. balechii*), and is outside the sulcal depression. In several species, the sulcal membrane cannot be seen on the adjacent plate: either it does not exist or it is very reduced on that plate. Evidently, Kofoid's 1"' plate shows the evolutionary transition between both series. However, I classify it as the left anterior sulcal (S.s.a.).

Another problem is presented by 1'. In most *Alexandrium* species, it is clearly and sometimes extensively connected with the Po (Fig. B2a). At other times, it is clearly separated from the Po (Fig. B2c) and may even be far away and twisted obliquely as in *Goniodoma*[1] where the edge that is usually in the upper right position becomes plainly anterior. Between both extremes are species in which the 1' keeps the usual rhomboidal shape, but in whole thecae, the 1' appears to be disconnected from the Po. However, dissection shows that almost always the two plates are indirectly connected by a filiform prolongation of 1' (Fig. B2b) as in *A. minutum*, the type species. *Alexandrium minutum*, *A. kutnerae*, *A. fraterculus*, and some other species include members with either direct or indirect contact.

The taxonomic implications of the possible connection between the Po and the 1' will be discussed later. When assigning a plate to one of the epithecal series, Eaton gives priority to contact with the cingulum rather than with the Po. However, Eaton does not assign the controversial 1' to a series based on its relationship to the cingulum, because he considers the sulcus to be an interruption of the cingulum. If we, instead, consider the girdle as a whole, i.e., the cingulum combined with the area that I call "cruciform" (where the cingulum and sulcus intersect), this controversial plate is considered precingular. As a consequence, the resulting epithecal formulas (Fig. C2) are quite different from the formulas derived by strictly applying Kofoid's definitions (Fig. C1). In Fig. C1, the two epithecae correspond to the two types that occur in *Alexandrium*, and their tabular formulas differ as follows: Po, 4', and 6" for the left figure; Po, 3', and 7" for the right one. Such differing formulas appear to indicate a rather important tabular difference that would justify establishing two different genera. The difference completely obscures the obvious homologies, which were first asserted by Howell (1953), between 1' of the left figure and 1" of the right figure. Fig. C2 shows the same epithecal types but with plate formulas established according to the modified Eaton notation. Now the formulas are identical (Po, 3', and 7"), thus suggesting the same genus.

Let us examine some of the tabular details of *Alexandrium* (Fig. A). The extreme anterior plate or Po (Fig. B1) is always large and predominantly oval with its narrower end directed ventrally or left ventrally because the main axis of the pore plate is almost always oblique, i.e., directed from the dorsal right to the ventral left side. However, the shape may be more angular as in *A. fraterculus*. The Po of *Alexandrium* has a cavity (aperture) that I call a comma or foramen that is large, comma-shaped (sometimes oval), and centrally or not quite centrally located. The comma is covered by a membrane or canopy that is narrower than the comma. The callus or thickening of the ventral half of the right margin of the comma contributes to the support of the canopy. Frequently, small marginal pores occur outside the comma. One or two rather large pores may be located dorsally or on the right side of the comma. They are called secondary or connecting pores because they are mainly found in chain-forming species (the anterior member of the chain sometimes lacks them). There seems to be some protoplasmic continuity through them.

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[1] The name of this genus is controversial. Several authors for different reasons proposed to replace it, but the replacements were too similar or were less acceptable than the original. Because the original is very well known, I use it until the problem is solved.

The border between plate 1' and the Po is short and usually oblique. Sometimes, the connection is by an acute vertex that may elongate into a filament. In these cases in whole thecae, 1' seems totally disconnected from the Po and the connecting filament is only viewed by dissection.

When compared with the 1' of *Gonyaulax s. str.*, the 1' of *Alexandrium* is relatively wide (Fig. B2). In most of the species, it is rhomboidal and laterally asymmetric. Nearly always, the posterior-left and the anterior-right margins are clearly larger than the other two sides. The anterior and posterior corners are frequently briefly truncated. The anterior-right side is usually concave and in most species is interrupted by a small notch that, in combination with the left margin of 4', delineates a special pore of unknown function, called the "ventral pore". A notch in plate 4' may also be associated with this pore; rarely, the pore is formed only or almost only by the 4'. However, in some species, the pore may be enclosed within the right margin of the 1' and may even be displaced to the plate interior (mainly, *A. leei* and some theca of *A. kutnerae*) The ventral pore is large in species of the *ostenfeldii* group. Some species like *A. catenella* and *A. fundyense* lack a ventral pore. It is important to emphasize that when the ventral pore is small, it is difficult to detect, especially in a whole theca with protoplasm.

The main, longitudinal axis of 1' is usually clearly oblique from the left dorsal to the right ventral. The intersection of this axis with the main axis of the Po forms an obtuse angle open to the right. In *A. tropicale*, the axes of the two plates form an almost straight line along the cell's sagittal plane.

When the Po and 1' are connected, either directly in one case or indirectly by a filament in the second case, differences are more apparent than real because both situations may be displayed within one species. In both cases, the 1' maintains its typical, elongated, and rhomboidal shape. A third case deserves more attention because the two plates are totally disconnected and, when compared to the 1' of the previous two groups, the plate is shorter and shaped differently because the margin that is homologous to the anterior right margin of 1' in the previous two groups becomes shortened and tends to be horizontally directed. The shape of 1' becomes pentagonal, either almost symmetrical (*A. monilata*) or very asymmetrical because the margin with 2' is greatly reduced (*A. balechii*). In *A. margalefi*, this margin with 2' does not exist and the plate is trapezoidal or almost square. The latter species represents the culmination of an evolutionary process that began with species in which this plate (1') is unquestionably apical and ended with species in which the same plate has precingular characteristics. Only a comparative study shows that they are homologous. In the third case described above (Fig. D), the ventral pore may be absent (e.g., *A. monilata*, *A. balechii*, *A. foedum*), present in the usual anterior-right location although the margin has been converted to a more anterior position (e.g., *A. insuetum*, *A. pseudogoniaulax*, and *A. hiranoi*), or located in the left end of the margin (e.g., *A. taylori* and *A. margalefi*). The ventral pore of *A. taylori* is not actually notched into the 1' plate but into the 4' plate with some 2' participation.

The heptagonal 2' is the largest apical and the only one with a dorsoventral development. 3' is more regular, hexagonal, almost always wider than tall, and asymmetric because the anterior left border with 2' is longer than the anterior right border with 4'. Depending on the species, this asymmetry varies from small to quite pronounced. 4' is the most irregular of the apicals. Its shape is similar to 2' or 2' inverted and may be pentagonal or a rather shorter hexagonal. Its margin with 6" is often the shortest but may be relatively long or non-existent, e.g., *A. balechii* lacks a common margin between 4' and 6".

Of the six precingular plates, 6" is the most interesting because of its variations. It is often pentagonal with two very distinct left margins. Whereas the anterior left margin (connected with the posterior right margin of 1') is more or less straight and rather oblique, the posterior left margin is reinforced, often a little concave, and almost vertical to join with the S.a. However, in species such as *A. ostenfeldii* and *A. taylori*, this posterior left margin is straight and notably oblique (inversely oblique to the anterior margin). In only one species, *A. balechii*, 6" is very small and triangular and has no common margins with 1' or 4'.

In the postcingular series, 1"' (or Kofoidian 2"') is trapezoidal, wider than it is long, and longer on the left side. Its oblique posterior margin is joined with the anterior margin of the 1"". Its short and generally somewhat concave border with the sulcal area is usually reinforced and sometimes supports a small or very narrow sulcal list.

The last postcingular, 5"', is rather long and usually almost triangular (trapezoid if the posterior margin is very oblique). The plate may have a sulcal list that is supported by the reinforced plate margin bordering the sulcal area. The list is very narrow in some species and rather developed in other species.

Both antapicals are very different from each other because of their position and shape. 1"" is vertically or obliquely elongated, and often it is more advanced toward the cingulum than is the second. It is sharp-ended anteriorly and its sulcal border, which supports a more or less developed list, constitutes most of the sulcus' left margin. This sulcal list may project below the antapex as a false spine.

2"" is clearly posterior or posterior-dorsal; its major axis varies from transverse to dorsoventral (longitudinal). Its shape is pentagonal and more or less asymmetrical with two usually very distinct ventral margins. The ventral margin that borders with the S.p. is larger than the other, is concave, and is generally directed obliquely to the ventral and left side of the cell. The ventral margin that is connected with 1"" is shorter, straight, and horizontal or oblique. Rarely, both ventral margins are almost equal (*A. ostenfeldii*). For convenience, those 2"" with a transverse main axis will be called type B (Fig. E2), while those with a dorsoventral main axis will be called type A (Fig. E1). 2"" is positioned almost laterally with respect to the S.p. in *A. pseudogoniaulax* and *A. foedum*.

Concerning general plate (excludes cingular and sulcal plates) sculpture (relief and depressions), most of the thecae of this genus are characterized by tenuous or absent thecal detail. Consequently, most thecae are rather homogeneously featureless. However, all of them have small, usually irregularly scattered pores that sometimes are perforations of rather inconspicuous protuberances. Large, unequal-sized, and numerous pores are found on the epithecae of a few species (*A. balechii* and *A. foedum*). Irregular poroids or a beginning of alveolation can be seen in *A. minutum*, and these ornamentations are more or less conspicuous depending on where the material comes from. Another degree in the complexity of thecal ornamentation, as seen in the hypotheca of *A. balechii*, is the pattern produced by irregular, branching crests that form a more or less incomplete reticulation without enclosed spaces or well-formed alveoli. The most complex thecal ornamentation is a well-formed reticulation that occurs in *A. insuetum* and another species from the Gulf of Mexico (described in this monograph as *A.* sp. 1 because of its incomplete study).

The cingulum is generally deeply excavated and always descending. Cingulum displacement in most species is approximately one cingulum height, without overlap. Cingular lists are absent or very narrow (up to 2.8 µm wide). Frequently, a thin vertical membrane can be seen.

It is a continuation of the outermost thecal layer that extends between both cingular margins or ends of its lists ("curtain fin", Fig. A1). Cingular plates lack much detail: neither large differences in size nor conspicuous pores, except in the aberrant *A. balechii.*

The sulcus is composed of several plates or plate pairs (Fig. F1) among which are one anterior sulcal plate (S.a.) and one posterior (S.p.). Two lateral pairs are present: one posterior pair composed of the left posterior sulcal plate (S.s.p.) and the right posterior one (S.d.p.) and one anterior pair composed of the S.s.a. and the S.d.a. Two small median plates are located in the space between the two anterior lateral sulcal plates and are arranged on the sulcal axis, one anterior to the other: S.m.a and S.m.p. An anterior accessory plate (S.ac.a.) is located above the S.d.a.'s internal oblique margin. The accessory plate continues the S.a.'s unciform apophysis (Fig. F2) and is usually triangularly shaped. The posterior accessory plate (S.ac.p.) is located below the posterior internal corner of the S.d.a. and is generally in a small notch that occurs in the anterior part of the S.d.p.'s internal margin. Thus, the whole sulcus may be formed by 10 plates, but it is not certain that all of them exist in all the species, although they probably do.

Fukuyo (personal communication) says that at least some of the species have eleven sulcal plates. However, I could not confirm the existence of an eleventh plate despite careful and repeated examinations. Sometimes, a protuberance on the internal margin of the S.a. gives the impression of an eleventh plate. However, this protuberance, which is caused by a crease in the plate, is not separable from the S.a. and, therefore, is not a distinct plate. Even without the possibility of an eleventh plate, the sulcus is very complex.

The S.a. plate always has a posterior armhole or "posterior sinus" (Fig. F2) that is rather large and round, usually with a thickened margin. The posterior margin of the "left branch" is also reinforced, is straight or irregular, and articulates with the S.s.a. plate. The "right branch" constitutes an often curved, sometimes very oblique, thin apophysis that I call "unciform apophysis". The anterior margin of the plate can be straight, irregular, concave, or convex. It may be a truncated tip that always articulates with 1'. In *A. foedum*, it is interrupted by a small anterior notch. Because most of the plate is usually sunk with respect to the anterior cingulum margin and the 1' base, the anterior portion is quite bent towards the ventral face, forming an oblique groove or fold that is quite noticeable in several theca. In most species, the anterior margin of the S.a. continues with the anterior left margin of the cingulum or goes a little onto the epitheca. However, in a few species (e.g., *A. cohorticula*, *A. kutnerae*), a transverse thickness crosses the anterior portion of the plate; it is a continuation of the anterior left cingular flange. The precingular part (p.pr., Fig. F2) of the S.a. that is above the thickening protrudes into the epitheca. Usually, the S.a. is longer than it is wide or is approximately isodiametric, but in some species it is wider than it is long. Sometimes the unciform apophysis is projected posteriorly in a narrow membranous flange.

The most common type of S.p. (Fig. G1) almost always has pointed anterior edges that enclose a "V"-shaped area. This area contains a membranous portion, which is sunk below the plane of the S.p., that supports both the S.d.p. and the S.s.p. Usually, this plate type is clearly longer than wide. It frequently has a small or relatively large pore that is almost always closer to the right (or anterior-right) plate border and is connected to the border by a narrow canal or sometimes only by a narrow groove (Fig. G2). In some cases (Fig. G3 and G4), the plate is rhomboid, is as wide as it is long, and has a ventral edge that is wide and truncated.

In the *minutum* group, the S.p. is very different (Fig. G9 and G10). The plate is short, is wider than it is long, and has no prominent anterior projections. It has a non-membranous, large anterior margin that is usually concave but may have irregularities. The plate body in this type is not conspicuously sunk below the plane of the thecal surface.

Similar to this type are S.p. plates (Fig. G11 and 12) that are also wider than they are long, are a little or not curved, and are without a marked ventral-anterior indentation. They are characterized by their extreme asymmetry. They have two right margins; the anterior right margin is very oblique and the posterior right is very much shorter than the left margin, e.g., in *A. ostenfeldii.*

Some species have S.p. plates that do not correspond to any of these types. However, they can be considered as extreme variations of the first type. In *A. taylori* (Fig. G7), the plate is long and twisted to the left, and the anterior margin is very oblique. In *A. margalefi* (Fig. G6), the anterior margin is oblique and separated into two concavities that are both limited by tips. *Alexandrium pseudogoniaulax* (Fig. G8) has a similar S.p., but the left tip has a greater development and forms an arm or apophysis that is briefly truncated.

In chain-forming species, the S.p. plate has an orifice or connecting pore that is usually large and round but may be oval or irregular. This pore is centrally located or slightly displaced to the right. It is evidently a connection site between individuals of the chain, and in chain-forming species, another connecting pore is located in the Po plate. However, this pore in the S.p. can be present in species that do not form chains, in which case, it is almost always small and notably eccentric; probably it functions in cell division before the protoplasm has separated. Sometimes, only a notch appears in the right margin or only the groove is evident.

The S.s.p. is pentagonal and asymmetrical. Its two lateral borders are long. The interior or right one has a weak reinforcement that supports an anterior projection in some species. The two anterior margins form an open angle towards the posterior; the external anterior margin that borders the S.s.a. is longer than the internal anterior margin that borders the S.m.p.

The S.d.p. is usually a little longer than the S.s.p. and frequently narrower. It is essentially quadrangular. The anterior and posterior margins are short and usually oblique. The posterior margin is sometimes divided into two segments that form a more or less noticeable angle. The interior margin is slightly shorter than the exterior margin and is usually straight, while the exterior is generally convex. The anterior-internal corner is sometimes briefly truncated, which results in a notch in which the S.ac.p. is located.

Resting anteriorly on the S.d.p. is the S.d.a., which extends the right edge of the cingulum. It has a more or less triangular shape. Its anterior or anterior-internal margin is oblique, reinforced, and almost always somewhat sinuous or softly convex. The right or exterior margin is usually concave. The posterior-exterior corner is frequently briefly truncated and is connected by this small truncated site to the anterior-internal corner of 5"'.

The S.s.a. is very variable. It corresponds with 1"' in the most common nomenclature used previously. Because it usually sinks obliquely into the sulcal depression in complete thecae, it appears to be narrower than it really is. On some occasions, it supports on its right margin a very narrow and small membrane that is not part of the cingular posterior list, as it is in *Goniodoma*, possibly because when the membrane exists in *Alexandrium*, it is only rudimentary. Anterior and right margins may be somewhat reinforced. The shape of the plate can be irregularly oval or rather pentagonal with the left posterior margin bordering the anterior margin of the 1"" and the right posterior margin bordering the S.s.p. In a few species, it is completely above the level of the sulcus (e.g., *A. foedum* and *A. balechii*). In this latter, aberrant species, it is also transversely extended and wider than it is long.

The two median sulcal plates articulate with the right margin of the S.s.a. The S.m.p. is usually pentagonal-shaped, anterior-posteriorly elongated, and almost completely supported by the anterior right margin of the S.s.p. The S.m.a. is often shorter but wider, sometimes clearly elongated in the transverse and oblique direction. It closes the S.a. posterior sinus almost completely.

I call the last two sulcal plates accessory plates because of their small size, which makes them very difficult to detect. The anterior accessory sulcal plate, S.ac.a., is located above the oblique or longer margin of the S.d.a. and immediately below the unciform apophysis of the S.a. It is usually triangular and small, but it may be quite large in some species: *A. pseudogoniaulax*, *A. foedum*, *A. balechii*, and *A. taylori*. The S.ac.p. plate is normally the smallest. In several species, it is really tiny, less than or equal to 1 µm. In *A. taylori*, it is pentagonal and relatively conspicuous. In *A. ostenfeldii*, the S.ac.p. is rather large but very narrow . It was not observed in several species and may or may not exist in all of them; therefore, the tabular formula for *Alexandrium* is read 9-10 s.

TAXONOMIC CHARACTERS AND CRITERIA

Except for a few species with some very peculiar characteristics, the genus *Alexandrium* is notably homogeneous and lacks those conspicuous elements, frequent in other genera such as *Gonyaulax s. str.*, that help to distinguish among species (e.g., apical horns, spines, notable structures, and differences in size or tabular details). Therefore, it is necessary to carry the observations to an extreme and look at small details that would be considered unimportant in other dinoflagellates. The general characters used are size, shape, chain formation, cingular and sulcal excavation, sulcal list development, Po, 1', 6", and all the sulcal plates, especially the S.p., S.a., and S.s.a.

Size is a secondary characteristic, as evidenced by the large variations within certain species. One possible cause for these within-species variations is gamete and zygote formation. Although these reproductive stages have been investigated, they are rarely applied to taxonomic issues. Zygotes usually have notably larger size than the majority of the vegetative cells, while some of the cells that act as gametes (microgametes) are smaller. Sousa e Silva (1965, 1971) also reported dinoflagellate dwarfish cells. In spite of this, some species are differentiated by their normally small size (e.g., species from the *minutum* group and *A. tropicale*) and some by their large size (e.g., *A. kutnerae* and *A. concavum*). Most species are between both extremes and the average length is between 30 and 40 µm.

Shape can be considerably altered by environmental conditions, especially in cultures, and somewhat altered by sexual reproductive stages such as zygotes. Shape, especially of the posterior region, will appear to vary when even small changes in position of the specimen occur. In addition, appearance may be altered by coverslip pressure and adherence of the specimen to the glass. Nevertheless, shape is an important taxonomic character. Some species are more or less anterior-posteriorly flattened (*A. catenella*, *A. compressum*) or are somewhat deformed (*A. monilatum*). Others are spheroidal (*A. kutnerae*) or somewhat elongated, usually because of a long epitheca (*A. acatenella*). The principal characteristic of *A. concavum* is its pentagonal, almost biconical, shape, which is totally different from all its congenera.

Some species are usually chain formers. Long chains can be formed by several dozens of individuals linked by the S.p. plate of one cell to the Po plate of the following cell. Generally, an individual is somewhat rotated with respect to the next cell on the chain in such a way that if the first of seven cells is in perfect ventral view, then the fifth, sixth, or seventh cell has a perfect lateral view. The connection is loose and, therefore, each individual has some freedom of movement. It is also a weak connection and the chains are easily fragmented. Chain-forming species are *A. catenella*, *A. fraterculus*, *A. cohorticula*, *A. compressum*, *A. monilatum*, *A. tamiyavanichi*, *A. affine*, and *A.* sp I. The majority of their congenera do not usually have connected individuals. However, when they are connected, they usually form pairs or, rarely, aggregates of four or six.

Although the Po plate is rather similar for most species within the genus, it may have some characters that conspicuously differentiate it from other Po plates, as Fukuyo (1985) stated. In *A. fraterculus*, the irregular Po plate has a ventral and a dorsal prolongation. *Alexandrium affine* typically has a narrow Po plate that has almost parallel lateral margins, a small, ventral foramen, and a dorsal connecting pore. On the other hand, the Po plate of *A. compressum* is very wide, has a comma very displaced to the left, and has a large connecting pore.

Probably, of the epithecal plates, the 1' has the most taxonomic value because of its visible and distinguishing characteristics. The most important characteristic is its position in relation to the Po: disconnected or connected. In most species, the 1' is connected to the Po directly or indirectly by a filiform prolongation and is asymmetric, rhomboidal, and elongated. When the Po and 1' are connected, the margin between 1' and 4' is usually in a right-anterior location; when the Po and 1' are disconnected, that margin is shorter and clearly anterior. Another consideration is the alignment of the Po with the 1': whether the two align along a straight line or at an angle that is more or less open towards the right. Another important taxonomic characteristic is the presence or absence of a ventral pore. Studies of clonal cultures and of dense, homogeneous natural populations demonstrated the taxonomic value of this detail. Also, its size and location are useful differentiating features. Experience indicates that the ventral pore exists in most *Alexandrium* species but that, frequently, it is unnoticed. Early investigators such as Lebour, Braarud, and others did not mention it. However, Braarud, in his unpublished notes (see Balech and Tangen, 1985), showed it prominently in his "*tamarensis* var. *globosa*" (= *A. ostenfeldii*). Likewise, in the original description of *A. minutum*, the ventral pore is not mentioned, but later studies proved its constant presence.

Differences among the other epithecal plates are less important, except the 3' for which symmetry or asymmetry has some differential value and the 6" that is wide in *A. ostenfeldii* and very narrow in the *minutum* group. Also, in the 6" of most species, the angle formed between the two left margins is very open; however, in *A. andersoni*, it is clearly more closed because of the strong obliquity of the posterior left margin. In this species, the major plate width is located at the middle of the plate instead of along the posterior margin.

The hypothecal plates that provide valuable information to the taxonomist are the two antapical pl In the 1"", useful differences occur in plate size, relative width, the right margin, and the left sulcal list. The 2"" plate, in some species, is very short in the dorsoventral or longitudinal direction. In some other species, it is elongated in this direction. Although these characters vary too much to have taxonomic importance in some species (e.g., in *A. tamarense*), they are quite fixed in others and, therefore, acquire some diagnostic value.

As mentioned, all sulcal plates have taxonomic value. Along with the Po, 1', and 6", the sulcal plates of *Alexandrium* provide the greatest support for the separation of this group as a genus. Perhaps, the most distinctive characters are found in the S.p. and the S.a. plates (Fukuyo [1985] emphasized the differences in the S.p., but omitted those of the S.a., which have greater taxonomic value). Size, location, and shape of the connecting pore in the S.p. are quite constant, but its presence or absence is not consistent because in species that normally do not form chains, it may be present or absent. Other characteristics of this plate and the S.a. were mentioned with some detail in the preceding section.

Most *Alexandrium* species do not have thecal sculpture (with the exception of pores and frequently very small protuberances in which the pores are located), and the theca can be described as practically smooth. However, some species have either the beginning of irregular sculpture (*A. minutum*), a more accentuated sculpture (*A. balechii* and *A. foedum*), or an elaborate, reticulated ornamentation (*A. insuetum* and *A.* sp. 1). These sculptures were previously considered to be constant. However, in *A. minutum*, the degree of reticulation is variable. Although external factors such as environmental conditions may influence the degree of reticulation, thecal sculpture still has diagnostic value.

In the past, taxonomy was based on thecal characters. However, in recent years, some attempts have been made to introduce different criteria such as dinocysts (resistant forms) or chemical differences. Unfortunately for the hopes of those wishing to give cysts a systematic preeminence, using cysts has yielded poor results. Also, a practical reason not to give emphasis to cysts is that those who work with plankton samples do not find them. However, the second taxonomic criterion has more promise. Cembella and Taylor (1985) and Hayhome et al. (1989) used electrophoresis of soluble enzymes and fluorometric analyses for measuring DNA with some promising results but still no conclusions. Scholin and Anderson (1993) used sequence analysis of ribosomal subunits as molecular markers, not to modify the taxonomical basis, but to ascertain the origins and relationships among different *Alexandrium* strains. These studies provide very interesting complementary information. Although I think that chemical procedures are auxiliary tools for the taxonomist, at the moment and probably for a long time, taxonomy must be based on thecal morphology.

SUBDIVISION OF THE GENUS

As I have stated, most of the species are morphologically very similar, and for this reason, those species comprising *Alexandrium* should be treated as a whole unit. However, within this unit, certain characteristics are common to some species but establish differences among others.

Taylor (1979) thought that those species in which the Po and 1' plates are connected should probably be separated from those in which these two plates are disconnected. He also thought it was advisable to give generic status to both groups; he reserved the name *Alexandrium* for the species in which 1' does not touch the Po and created the genus *Protogonyaulax* for the others. Later studies showed that in the type species of *Alexandrium*, the two plates are connected either directly or indirectly (Balech, 1988). Therefore, Taylor's genus is synonymous with Halim's.

Alexandrium minutum, *A. kutnerae*, and *A. fraterculus* have individuals in which the Po and 1' plates appear to be disconnected; however, the 1' plate always maintains the typical rhomboidal shape and even in the area of apparent disconnection with the Po, all the epithecal structure remains unaltered. However, some species have a very different type of 1'. In these species, it becomes almost rectangular or, sometimes, pentagonal. Also, the margin, which in other species is the long anterior right margin, is largely shortened and becomes almost horizontal, causing complete loss of contact with the Po. If we accept Taylor's assertion that the lack of contact between the 1' and Po is of taxonomic value, this could only be applied to those species in which the disconnection is real (not true for *A. minutum*) and constant. This group then would also have a 1' plate that has a very different shape and is, in truth, typically precingular.

In this group with the disconnected 1', the species that was first described is the one that Howell called *Gonyaulax monilata* and later Halim called *Gessnerium mochimaense*. This peculiar group is similar to *Goniodoma* (I use this classic generic name, even though it has been replaced in recent years, because the replacement names have been unacceptable for one reason or another), and, in some of the *Alexandrium* species, 1' is an exact copy of the *Goniodoma* 1'. However, *Goniodoma* has two important tabular differences (Fig. H1): 1) the main axis of the Po, which is of a different type than *Alexandrium*, is definitely transversal and the suture that begins at the plate's acute, left pole is laterally directed instead of being more or less longitudinally directed as in *Alexandrium* (*Gessnerium*) (Fig. H2), and 2) 1' (1" in the figure) does not touch 2'. In *Gessnerium*, the Po has a typical central or not quite central foramen, and its main axis is more longitudinally oblique than transversal; 1' almost always touches 2'. However, the species *A. margalefi* is an exception with respect to this last character. In this species, as in *Goniodoma*, 1' does not touch 2'; however, the orientation of the Po and 1' and of the suture between them is still the same as in the other congenera.

Considering these special characteristics, it would be possible to separate *Gessnerium*, but it does not seem suitable to give it generic status because, with the exception of the epithecal characters, tabular characteristics from all remaining areas (cingulum, sulcus, and hypotheca) are the same and do not allow us to differentiate this group from *Alexandrium*. Therefore, I support the suggestion of Loeblich and Loeblich (1979): maintain this very similar group of species as a generic unit and subdivide it into two subgenera (they talk about possible sections).

Consequently, with some doubts, I accept *Gessnerium* as a subgenus of *Alexandrium* because it allows us a species grouping that facilitates taxonomic handling. Interestingly, in none of the species of this subgenus has the production of an appreciable amount of PSP been confirmed.

Gessnerium is a more heterogeneous group than is *Alexandrium* because the former is composed of distinctly different species. For example, *A.* (*G.*) *monilatum* has a very characteristic type of S.p., and *A.* (*G.*) *insuetum* is the only one with a strong reticulation. *Alexandrium* (*G.*) *balechii* has a very reduced 6", its two left lateral sulcal plates and S.p. are totally different from the other known species, and it is somewhat reticulated on the hypotheca. Another strongly scultured species is *A. foedum*, which has a very different tabulation. In this subgenus, four more species are very distinct. Due to their lack of sculpture, prominent ventral pore, and elongated and oblique S.p., they are more similar to each other than to the other species in this group. These species are *A.* (*G.*) *pseudogoniaulax*, *A.* (*G.*) *taylori*, *A.* (*G.*) *margalefi*, and *A.* (*G.*) *hiranoi.*

In the subgenus *Alexandrium*, some species can be grouped by narrow affinities (to which I do not consider it advisable to assign formal categories), but some species do not form definite groups. On the other hand, species may have characteristics indicating affinity with two or more groupings. For instance, preference might be given to chain formation or to the presence or absence of ventral pores or to a certain type of S.a. The species that cannot at this time be assigned to one of the informal groups are *A. concavum*, which has a unique shape, and *Alexandrium* sp. I from the Gulf of Mexico, which is the only one of this subgenus that has a well-reticulated theca and which has some plates of a special type.

Best defined are the *minutum* and *ostenfeldii* groups. The former is composed of four small species with two distinctive tabular characteristics: 6" is very narrow, and the S.p. is flat, wider than long, and specially shaped. The latter group contains globular or not quite globular species that are medium to large in size and have a very narrow 1' and a large ventral pore. Species in this latter group also have an S.p. that is wider than long but, because the S.p. is very asymmetric, it is very different from the S.p. noted in the *minutum* group. The *ostenfeldii* group is composed of two acknowledged species and one doubtful species.

The *catenella* group is well-characterized by cells that are rather flattened anterior-posteriorly and form chains. The 1' lacks a ventral pore. Two species are included.

The *fraterculus* group also forms chains, but cells are not flattened and the 1' has a ventral pore. The group contains four species.

The *kutnerae* group is formed by two rather large species that are not chain-formers, are rather globose, and have a small ventral pore that is frequently enclosed within the right portion of 1'.

The *tamarense* group is formed by small- to medium-sized species that are either not flattened or scarcely anterior-posterior flattened and may or may not have a ventral pore. Their shape is irregular with a more or less marked antapical concavity. They have an S.p. that I call *tamarense*-type. It is longer than wide, is curved, and has a ventrally directed projection at each end of the anterior margin. The group is composed of six species, two of which (*Alexandrium* spp. II and III) are dubious.

As a whole, the subgenus includes 20 species that seem well-established (including *A. concavum* and *A.* sp. I) and some doubtful species.

TEXT FIGURES

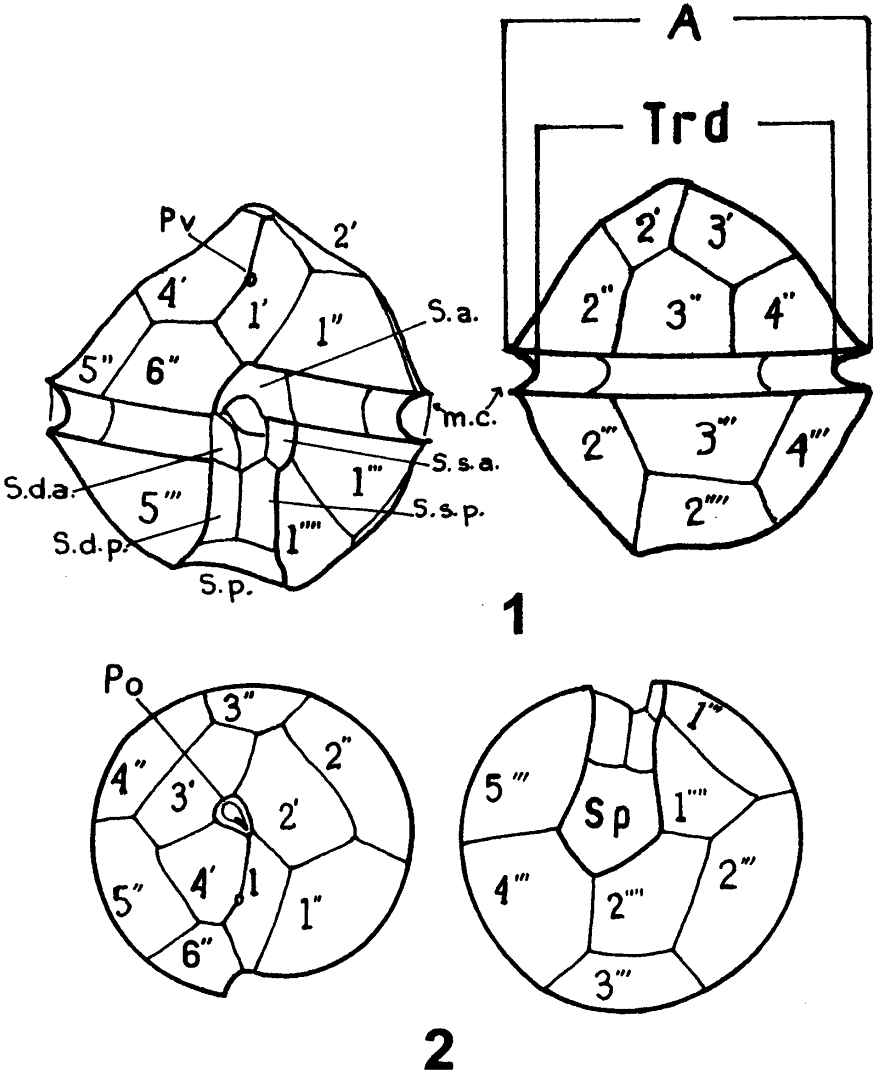

Figure A. Thecal plates. 1) whole theca: ventral view (left), dorsal view (right); 2) polar views: apical view (left), antapical view (right). Pv = ventral pore; m.c. = curtain fin; A (amplitude) = maximum cingular width; Trd (transdiameter) = minimum cingular width.

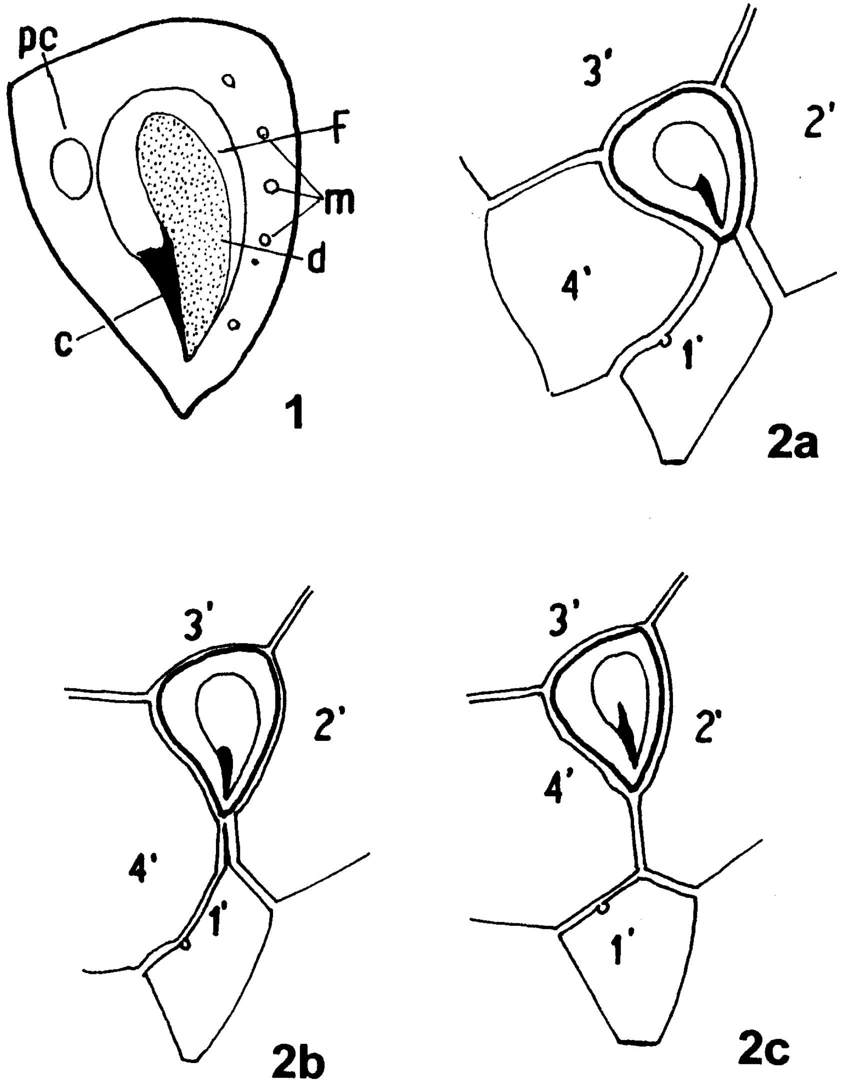

Figure B. Structure and connections of the Po plate. 1) parts of the Po: pc = connecting or conjunction pore, F = foramen or comma, d = canopy, c = callus, m = marginal pores; 2) relationships of Po and 1': direct connection of Po and 1' (2a), indirect connection by a threadlike projection of 1' (2b), and disconnection (*Gessnerium* type) (2c).

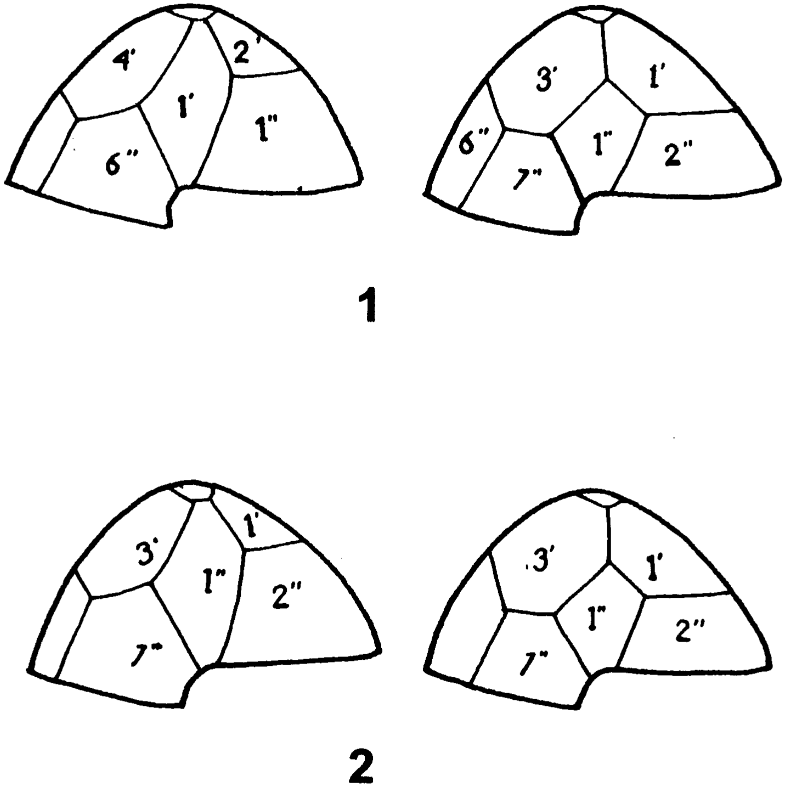

Figure C. Different criteria for the notation of the middle ventral plate: 1) notation strictly following Kofoid's criterion (i.e., defining the apical plates as those connected to Po and neglecting evident homologies); 2) the same plates giving priority to contact of the plates with the cingulum and with the "cruciform" area (i.e., the region formed by the cingulum and the sulcus).

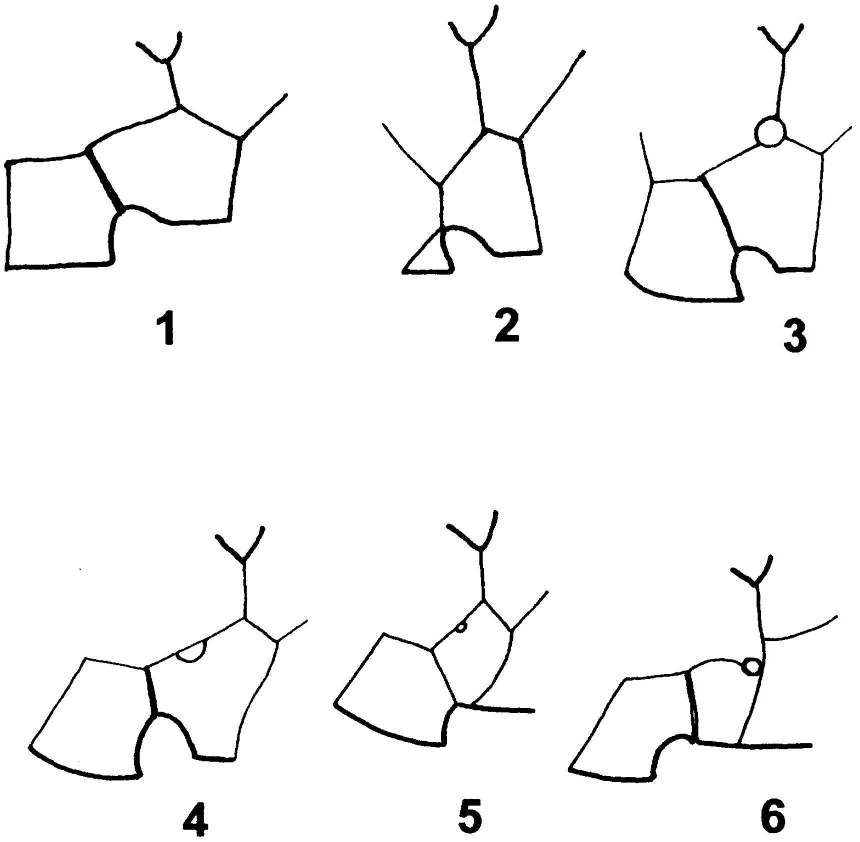

Figure D. Shapes and connection of 1' in *Gessnerium*: 1) *A.* (*G.*) *monilatum* 2) *A.* (*G.*) *balechii* 3) *A.* (*G.*) *taylori* 4) *A.* (*G.*) *pseudogoniaulax* 5) *A.* (*G.*) *insuetum* 6) *A.* (*G.*) *margalefi*.

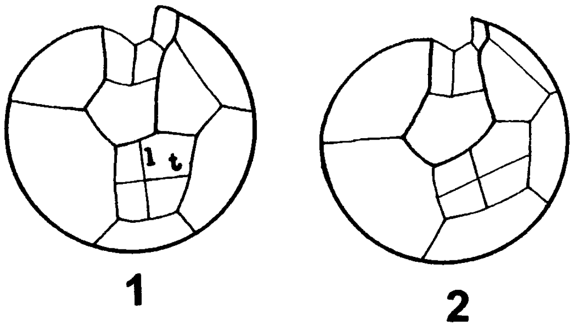

Figure E. Types of 2"" plates: 1) type A; 2) type B.

NOTE: l = longitudinal axis extending from the center of the border between 2"" and S.p. to the center of the dorsal border; t = transversal axis from the center of the right margin to the center of the left margin.

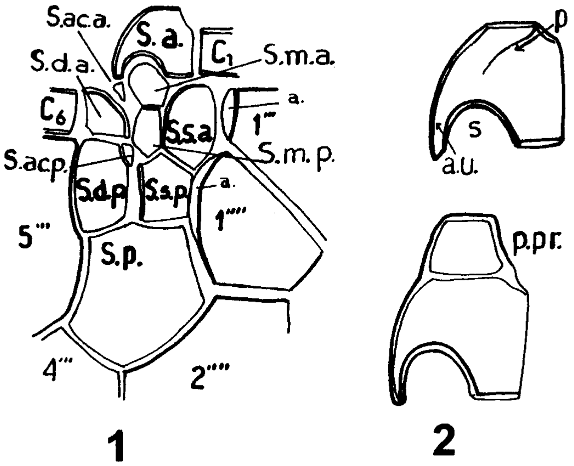

Figure F. The sulcal plates: 1) names and placement of sulcal plates: S.a. = anterior plate, S.p. = posterior plate, S.s.a. = left anterior lateral plate, S.s.p. = left posterior lateral plate, S.d.a. = right anterior lateral plate, S.d.p. = right posterior lateral plate, S.m.a. = anterior median plate, S.m.p. = posterior median plate, S.ac.a. = anterior accessory plate, S.ac.p. = posterior accessory plate, a = list; 2) two types of anterior sulcal plates: one (top) without a precingular part and the other (bottom) with a precingular part (p.pr.); P = fold or "plica", S = posterior sinus, and a.u. = unciform apophysis.

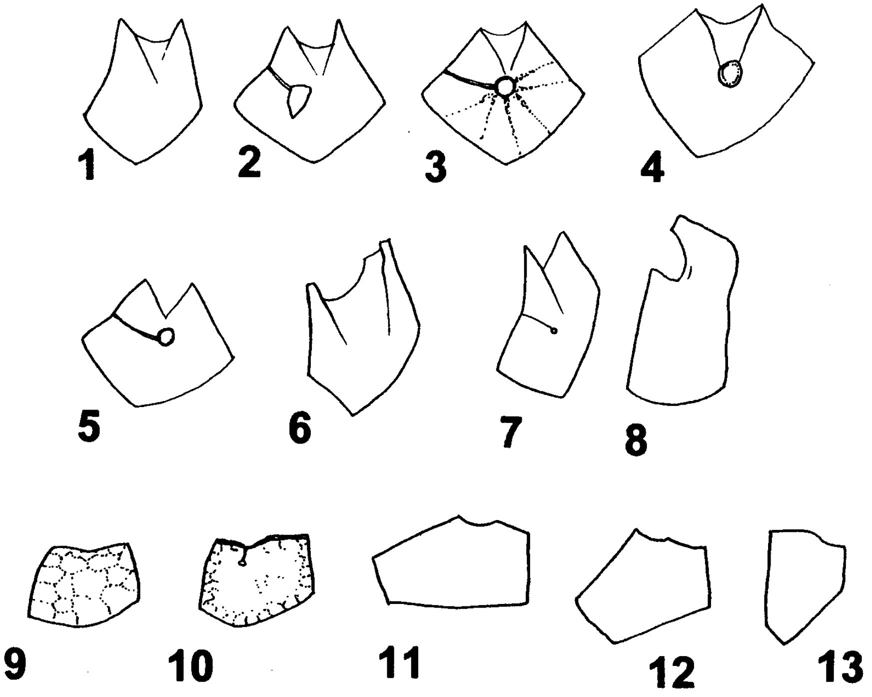

Figure G. S.p. plates: 1) *A. tamarense*; 2) *A. catenella*; 3) *A. monilatum*; 4) *A. compressum*; 5) *A. fraterculus*; 6) *A. margalefi*; 7) *A. taylori*; 8) *A. pseudogoniaulax*; 9) *A. insuetum*; 10) *A. minutum*; 11) *A. ostenfeldii*; 12) *A. peruvianum*; 13) *A. balechii*.

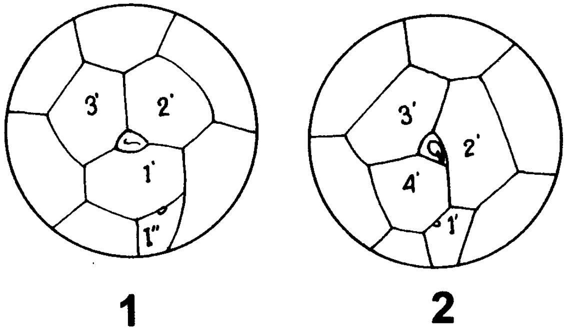

Figure H. Comparison of *Goniodoma* and *Alexandrium* (*Gessnerium*): 1) apical view of *Goniodoma* 2) apical view of *Gessnerium*.

Genus *Alexandrium* Halim

Gonyaulax Diesing partim, auct.

Goniodoma Stein partim; Paulsen (1904); Biecheler (1952); Gaarder (1954)

Gessnerium Halim (1967)

Pyrodinium Plate, partim, *sec* Taylor (1976)

Protogonyaulax Taylor (1979)

Gonyaulacidae with the following tabular formula: Po, 4', 6", 5"', 2"", 6c, and 9-10s. 1"" always much anterior to 2"". Cingulum generally well-excavated, descending usually 1 width, without overlap, and without or with only small lists. Without horns or spines. Theca rarely sculptured. Chloroplasts. Transversely elongated nucleus.

Subgenus *Alexandrium*

Plate 1' linked to Po, connected either directly and visibly or indirectly by an elongated and narrow prolongation, more or less filiform.

Group *minutum*

Small species, L usually less than 30 µm. General shape predominantly oval. 6" very narrow. S.p. short, wider than long, not quite symmetric, with long and irregular anterior margin that is more or less subdivided into two parts. Group composed of *A. minutum* (genotype), *A. angustitabulatum*, *A. lusitanicum*, and *A. andersoni.*

Alexandrium minutum Halim

Plate I, fig. 1-50

Alexandrium minutum Halim (1960: 101, fig. I a-g); Balech (1989)

Alexandrium ibericum Balech (1985b: 37, fig. 15)

Cell is small, oval to elliptical in ventral view, and somewhat dorsoventrally flattened. Cingulum is well-excavated, without lists, and descending (usually 1 but sometimes <1). Hypotheca is hemi-elliptical, sometimes somewhat antapically flattened, and scarcely sloping.

Po is oval, somewhat irregular, more or less concave to the right, and rather narrow. Callus is very reduced. 1' is narrow, contacting the Po directly or, more often, indirectly by a thread-like prolongation that can be rather long and not easily observed unless the theca is dissected. Ventral pore is small and always very close to the posterior extreme of the anterior right margin.

S.a. is approximately as long as it is wide with a straight or almost straight anterior margin and a slightly deep posterior sinus. S.s.a. is very narrow and rhomboidal. S.s.p. is almost always rather short. S.d.p. has an almost horizontal anterior margin and a convex and oblique posterior margin that is more often subdivided into two almost straight portions with opposite obliquity. S.d.a. is triangular and narrow. Accessory sulcal plates are very small. S.p. is almost always symmetrical.

Theca frequently has an irregular areolation that is barely visible, diffuse, and seen mainly in the 1' and even more in the S.p. However, thecae from some locations have an incipient reticulation in the hypotheca.

Dimensions: L 15.5-29, the majority 21-26. A equals L, sometimes a little larger but, more often, somewhat smaller. Trd is always smaller than L and 4 to 6 µm less than A. Halim noted L 16-23.2, A 13-20.3 (possibly he was referring to the transdiameter).

The present description, based on material from the type location in Egypt, is brief because the information has been published in detail (Balech, 1989). However, before the 1989 re-description, I studied material obtained from other sites and countries and published a very brief diagnosis of this species as *A. ibericum.* In this monograph, I include some complementary observations.

In material from sources other than from Egypt, a little morphological diversity is observed. The hypotheca varies from almost hemispherical to almost conical, but the posterior flattening, when it occurs, is not very marked and is scarcely oblique. When the theca is positioned obliquely, the sulcal lists appear to be projected a little posteriorly. In this case, the left list almost always emerges a little.

The Po has an inconspicuous comma and the callus is barely noticeable. Almost always, the small marginal pores are somewhat more remarkable than in the Egyptian material. The height of 6" is 1.5 to 2 times larger than its width measured along the posterior margin. The smaller ratio is due to the existence of a spur that can prolong the left posterior corner of the plate. The left margin contacts the S.a., is somewhat arched and almost always vertical, but is sometimes oblique to the right and backwards.

The 1"" is pentagonal. The margin that borders the S.p. is well reinforced and supports a narrow sulcal list, which is a little bit wider in its anterior half. The shape of this border is variable, but in most of the thecae, it is rather regular and slightly convex or almost straight.

The two anterior margins of the S.s.p. that touch the S.s.a and S.m.p. form a corner that may be very emphasized or scarcely noticeable. The S.s.a. is a narrow rhomboid in which the height of the somewhat asymmetric posterior triangle is about 0.3 - 0.5 of the height of the anterior triangle.

Thecae from Egypt (Alexandria) have very little sculpture, with pores that are very difficult to see. In thecae with thicker walls, the pores may be in the center of very small protuberances.

Thecae from Spain (Pontevedra) have rather large and numerous pores that sometimes, especially in the 1', are transformed into a kind of large areolation. Also, 2"" is usually rather areolate. The S.p. almost always has at least short grooves that are almost perpendicular to its margins and represent a beginning reticulation. Such sculpture remains to a lesser degree in specimens from a different location in Spain (Vigo), France (Bretagne), Portugal, and the U.S.A. In Australian specimens, it is almost always very difficult to see (as in those from

Alexandria). In the Italian specimens from the Gulf of Naples, however, the hypotheca has a strong and true reticulation that is barely perceptible in the epitheca.

In most specimens, even the smallest, intercalary bands occur, either as simple or double bands.

Cell dimensions of specimens collected from these other locations agree with those measured from the type location although the smallest sizes were not observed: L 22-28.5, A 18-27.5, Trd 15-22.

Interestingly, this species retains all of its characteristics even though it is widely distributed. The only exception is the peculiar thecal sculpture that is exaggerated in Italy, reduced in Egypt and Australia, but is essentially the same pattern in all of them.

Distribution: Egypt (Alexandria Harbor), Spain (Pontevedra, Barcelona, and the Ria de Vigo), France (Vilaine Bay in Bretagne), Portugal (Obidos Lagoon), Italy (Bay of Naples), U.S.A. (Mineola in New York State), Australia (Port River near Adelaide), and Turkey (Bay of Izmir).

Alexandrium lusitanicum Balech

Plate II, fig. 1-15

Alexandrium lusitanicum Balech (1985b: 37, fig. 16)

It is very similar to *A. minutum* because of its general shape, size, 6", and S.p. type. Therefore, I will only mention the distinguishing characteristics.

The 1' is almost always regularly truncated on the anterior and posterior. In almost all the thecae, it is directly linked to the Po; however, in some thecae, the connection is made by a short projection. Its anterior right margin is rather concave or rather flexuous at the position of the small ventral pore, but in some, the margin is almost straight. The 1' of *A. lusitanicum* is almost always wider than that of *A. minutum*.

The Po is quite wide whereas the Po of the type species is rather narrow. The comma head and callus are scantly differentiated.

The S.a. is the plate that primarily distinguishes this species from *A. minutum* because the plate is notably wider than long. The S.d.p. usually is narrower on the posterior and its interior margin is more open anteriorly towards the S.m.p. The S.p. usually has the right half of its anterior margin more angular, coinciding with the angular posterior margin of the S.d.p. The 2"" seems to be predominantly type B; *A. minutum* is predominantly type A.

Dimensions: L 17.5-27.5, A 16-24.5.

The differences with *A. minutum* are so small that the species' independence is doubtful. The observed differences in some of the plates (Po, 1', 2"", S.d.p., and some others) and in sculpture are scarcely important and not absolute. Therefore, the only truly distinguishing characteristic is the width of S.a. Thus, study of this plate should be emphasized.

It has been found only along the Iberian Peninsula: Portugal (Obidos Lagoon) and Spain (Galicia). The specific name refers to the region of Portugal.

Alexandrium angustitabulatum F.J.R. Taylor n. sp.

Plate II, fig. 16-30

Alexandrium sp. Balech (1985b: 36, fig. 14a-b)

Alexandrium angustitabulatam (Taylor and Cassie) Balech (*nomen nudum*, ms name).

This species is similar to *A. minutum*. It usually has a well-marked and symmetric antapical concavity that does not slope, which is unlike the two previous species in which the concavity is almost always inconspicuous and, when it exists, slopes. However, the truly distinctive character is the shape of the 1' plate. Its larger margins are parallel, are almost always straight, and have a greater difference in length than the two smaller margins. While the posterior right margin is rather long in the two previous species, it is very short in this one. There is no ventral pore. The anterior corner can be truncated for a clear connection with the Po or sharply pointed or extended by a thin and very short prolongation, although this latter possibility is rare. Another quite notable characteristic is the almost always equal length of the posterior right margin and the posterior truncation that borders with the S.a.; these two margins form an angle that is clearly more open than in the other species.

The Po has a well-developed callus and, very often, small marginal pores.

The 2"" is almost always wider than long (type B).

The S.a. is approximately as wide as it is long. It has convex lateral margins, especially the left margin, which contrasts with *A. minutum* in which this margin is always straight. Compared with those of *A. minutum*, the other sulcal plates are similar; however, the two left lateral plates and the S.d.p. of *A. angustitabulatum* are frequently proportionally wider and the S.p. usually is clearly longer.

Dimensions: L 17.5-24, A 17.5-24. Although, some specimens are somewhat longer than wide, the majority are approximately isodiametric as in the other two species.

The plate that differentiates the species best is 1'. In the *minutum* group, *Alexandrium angustitabulatum* is the only known species that lacks a ventral pore. Another distinguishing characteristic is the posterior right margin that is much shorter than in other species. It approaches a horizontal direction and almost equals the length of the short posterior border that connects with S.a.

Until now, this species has been found only in New Zealand where it can produce red tides and toxicity.

Alexandrium andersoni Balech

Plate II, fig. 31-41

Alexandrium andersoni Balech (1990: 394, figs. 34-50)

I describe this species briefly. Because a detailed description was recently published, I am providing only some complementary details and giving emphasis to the more important characteristics of the species.

It is rather small, wide, and oval to elliptic, although on the average, it is somewhat larger than the preceding species. The cingulum is less excavated and is descending (<1). Antapical flattening either does not occur or is scarcely marked and somewhat oblique.

The Po is oval to triangular and has a straight, very oblique dorsal margin. As in *A. minutum*, it contains a slightly emphasized comma and rudimentary callus.

The 1' is rather narrow. Its posterior end is truncated and its sharp anterior is often prolonged in a short filament that connects it with the Po. A small ventral pore is generally located at the midpoint of the anterior right margin.

The 2' is relatively short and wide with the dorsal margin longer than in the majority of its congenera. The 3' is usually almost symmetric. The 2"" is longer than wide (type A).

As in other species of the *minutum* group, the S.p. is wider than long, but it is more asymmetrical because it is clearly shorter on its left side. Another characteristic is that the S.s.a. is wider, similar to the type found in the *tamarense* group. The S.ac.p. is relatively large and elongated, contrasting with the very small size of the pebble-shaped plate in the other three species.

Protoplasm is scarcely pigmented.

Dimensions: L 21-35, A 18-33.

It is clearly differentiated from the other species of the *minutum* group because of its 6" and S.a. plates. The 6" is narrow, mostly in the posterior. It has two straight left margins with approximately the same length that, from the vertex that links them, are obliquely directed to the right. Therefore, the middle portion of the plate is much wider than the anterior portion or, especially, the posterior portion. The width as measured along the posterior margin may be as little as one-sixth of the maximum width of this plate.

The marked obliquity of the posterior left margin of the 6" corresponds to the inclined right margin of the S.a. This sulcal plate is markedly trapezoid-shaped, with all its sides straight except, of course, the one that contains the posterior sinus, which is large but not very deep. The two lateral margins are oblique, especially the right one. Due to this pronounced obliquity, the anterior width of the plate is less than one-third of the posterior width.

This species does not produce PSP (Anderson, et al., 1990).

Presently, it has been found only along the east coast of the U.S.A. (Cape Cod).

Group *ostenfeldii*

Cell globe-shaped, medium- to large-sized. Theca thin-walled, easily collapsed. Sulcus scarcely excavated. 1' narrow and very oblique, with a large ventral pore.

Two species are well-studied: *A. ostenfeldii* and *A. peruvianum*. Another species is still not well defined and, thus, has not been formally transferred to *Alexandrium*: *Gonyaulax dimorpha* Biecheler.

Alexandrium ostenfeldii (Paulsen) Balech and Tangen

Plate III, fig. 1-24

Goniodoma ostenfeldii Paulsen (1904: 20, fig. 2)

Goniaulax tamarensis Lebour var. *globosa* Braarud (1945: 12, fig. 5Band Pl. III)

Goniaulax ostenfeldii (Paulsen) Paulsen (1949: 62, not fig. 30

Heteraulacus ostenfeldii (Paulsen) Loeblich (1970: 904)

Gonyaulax globosa (Braarud) Balech (1971: 29, not *Gonyaulax globosa* Stuve, 1909)

Gonyaulax trygvei Parke (1976: in Parke and Dodge, 1976)

Protogonyaulax globosa (Braarud) Taylor (1979: 52)

Gessnerium ostenfeldii (Paulsen) Loeblich and Loeblich (1979: 44)

? *Pyrodinium phoneus* Woloszynska and Conrad (1939: 1-5, fig. 1-12)

Triadinium ostenfeldii (Paulsen) Dodge (1981:279)

Alexandrium ostenfeldii (Paulsen) Balech and Tangen (1985: 338, fig. 3-5)

The cell is relatively large and not quite spherical. The epitheca is somewhat conic-convex, with regularly curved sides; the apical area either does not project or has a very slight relief. The hypotheca is hemispheric and approximately the same height as the epitheca; the antapical area may be somewhat obliquely flattened.

The cingulum is either not excavated or only scarcely so and is descending (<1). The sulcus is slightly depressed and, therefore, almost not noticeable.

As this species was described in detail by Balech and Tangen (1985), I will only give some complementary details, mostly based on the material from Spain (Galicia). In these specimens, the cingulum only descends about 0.3 cingulum height and has very narrow (1 µm wide) lists (1985 description specifies without lists). In some places, the lists have basal granules that represent incipient ribs (or radii of the lists).

The S.s.p. is always wider anteriorly than posteriorly. It is more variable than the S.d.p. and frequently has an oblique longitudinal fold that can in part explain the plate variation. Also, the S.s.a. sometimes shows an oblique fold that crosses it.

The largest specimens (L up to 56) usually have meagerly developed sutural bands. However, in the U.S.A. (Dockton, Washington), some very large specimens had wide sutural bands; these specimens were more elongated than the usual (the greatest measured L 71, A 64.5, Trd 57, DV 51).

Alexandrium ostenfeldii is presumably found along all of the western European coast because it was obtained in Norway and Spain (Vigo and Pontevedra) and, if the synonymy with *Pyrodinium phoneus* is confirmed, in Belgium, too. Furthermore, it was found in the U.S.A. (near Tacoma, Washington), Egypt (Alexandria Harbor), Iceland, the Faeroes, and East Asiatic Russia (along the Kamchatka Peninsula).

Alexandrium peruvianum (Balech and Mendiola) Balech and Tangen

Plate IV, fig. 1-19

Gonyaulax peruviana Balech and Mendiola (1977: 49, fig. 1-12)

Alexandrium peruvianum (Balech and Mendiola) Balech and Tangen (1985:342)

Although very similar to the preceding species, this one is usually smaller. Balech and Mendiola (1977) gave a detailed description; therefore, I only add some complementary data. The cell is always a little bit wider than long and sometimes has a small apical protuberance. The Po is oval and longer than wide and has a somewhat flattened dorsal margin. The comma has a very emphasized shape and a conspicuous head. On the other hand, the callus is very weak but sometimes is projected towards the dorsal area. The canopy is fully visible. The Po almost always has marginal pores on the left side. Usually one or two, seldom more, marginal pores occur on the right and may be somewhat larger than the others. This plate has a truncated ventral pole, but sometimes the angle by which it is connected with 1' is so oblique that the ventral margin almost joins with the left margin and then this posterior portion appears sharp.

The 6" usually is a little bit wider than long. The cingular concavity is smooth. The hypotheca usually shows a slight posterior and oblique flattening.

The 1"" is rather wide, but this characteristic is variable. It has two margins bordering the sulcus. The portion that connects with the S.s.a. and S.s.p. is longer than that connected to the S.p., slightly reinforced, and more or less long italic S-shaped. The segment touching the S.s.a. is not quite horizontal and is straight or somewhat convex. The longer portion touching the S.s.p. is almost vertical and almost always slightly concave. The margin bordering the S.p. is outwardly oblique, shorter, non-reinforced, and straight or almost straight. Apparently, there are no sulcal lists.

The 2"" is longer in the dorsoventral direction than wide (type A). In very few theca, its width equals its length.

The S.a. is approximately as long as wide, or a little wider when the size of the posterior sinus increases the distance between the two posterior projections. The anterior margin is very short, generally one-fifth or less of the plate's maximum width. Sometimes, it is so oblique that the plate becomes sharply pointed anteriorly (in this case, 1' appears posteriorly sharp). The unciform apophysis can be almost as wide as the left posterior branch and its posterior tip is roughly folded inward. The posterior sinus is wide and low.

The S.s.a. is quite wide, but its length/width relationship varies considerably, ranging between 1.15 and 1.44 but occurring most frequently between 1.25 and 1.30.

The S.p. is irregularly pentagonal. The margin that touches other sulcal plates is somewhat oblique and generally slightly concave. It is subdivided into two portions; each portion borders a posterior lateral sulcal plate. The two right margins vary in length. Generally, but not always, the anterior right margin that borders the 5"'is longer than the posterior right margin that borders the 4"'. The posterior margin that adjoins 2"" is rather inclined forward and to the left.

The left margin is short. Once only, I saw a small connecting pore very close to the anterior right margin.

The S.d.p. is exceptionally thin and has an indentation on the anterior third or fourth part of the internal margin where the very narrow but quite long S.ac.p. is located. The S.d.a. is very oblique, to the point that a great part of its anterior-internal margin (hypotenuse of the triangle) becomes almost vertical. It supports a very small S.ac.a. The S.s.p. is rather longer than wide and narrows posteriorly.

Dimensions: Peruvian material: L 25-40, Trd 29-41; a dwarf specimen L 20, Trd 19. North American material: L 33-44, A 33-44, in more than a few specimens A is somewhat greater than L.

The close relationship of this species with *A. ostenfeldii* and *Gonyaulax dimorpha* is evident. According to Balech and Tangen (1985) the anterior right margin of 1' in *A. peruvianum* is clearly curved; whereas that of Paulsen's *A. ostenfeldii* is differently arranged in two straight segments. Examination of more material showed that this difference exists in most of the thecae, but not in all of them. In *A. ostenfeldii*, the S.s.a. is almost always wider, and both the 6" and the S.d.a are wider. However, the two species can be distinguished by the distinctively different shape of the S.a.

On the other hand, it is more difficult to differentiate *A. peruvianum* from *G. dimorpha* because Biecheler's description of *Gonyaulax dimorpha*, although very good for its time, is insufficient today because nothing is known about its sulcal plates. It is also doubtful that the two forms included in her species are truly conspecific. However, the long form could possibly be individuals that are extremely elongated and enlarged. As observed in *A. ostenfeldii*, some thecae of *G. dimorpha* with wide sutural bands are clearly elongated. At the moment, a few general criteria seem to indicate that *Gonyaulax dimorpha* is different from both *A. peruvianum* and *A. ostenfeldii*. It is differentiated from them by its definite antapical concavity, by the apparently narrower S.s.a, and by the strong asymmetry of the 3' and the 2"" that, according to the French investigator's figures, should have a very different shape than the 2"" in *A. ostenfeldii* and *A. peruvianum*. Perhaps more importantly, the S.a. in all of her figures, while appearing to be more similar to the S.a. of *A. peruvianum* than to the S.a. of *A. ostenfeldii*, penetrates high into the epitheca. This penetration does not occur in *A. peruvianum* from Peru. However, in some *A. peruvianum* from the U.S.A., the plate indents the epitheca slightly and obliquely. The taxonomic importance, if any, of this character will only be ascertained when material is obtained from some brackish lagoons, which are similar to the original (but no longer available) site, in the south of France.

Distribution: It has been reported from the type location in Peru (Callao) and from the U.S.A. (New York).

Group *kutnerae*

Cell large, globose or not quite globose. Hypotheca sometimes with an obscure posterior lobulation. Sulcus large and shallow. 1’ rather wide with a very small ventral pore that is more or less enclosed and is frequently located far away from the plate margin. S.a. longer than wide.

Two species have been described: *A. kutnerae* and *A. leei*. In the former, a portion of the S.a. is precingular and the hypotheca is not posteriorly lobed. In the latter, the S.a. does not extend beyond the cingulum and the left hypothecal area is somewhat lobed.

Alexandrium kutnerae (Balech) Balech

Plate V, fig. 14-26

Gonyaulax kutnerae Balech (1979b: 61, Illust. 3, fig. 1-11)

Alexandrium kutnerae (Balech) Balech (1985b: 37, fig. 8A-C)

The epitheca is hemielliptic to conic-convex with a rounded and sometimes slightly flattened vortex. The hypotheca is almost always hemispheric with a very slight posterior flattening. The cingulum is excavated and descending (1, sometimes slightly >1). Sulcus is ample and slightly depressed.

Po is oval. The plate has a slightly marked callus on the main foramen and has small marginal pores.

The 1’ is of medium width and may be directly or indirectly linked to the Po. The anterior right margin is straight or somewhat curved. A small ventral pore is enclosed below the middle of this margin and, occasionally, is located somewhat far away from the edge. The 3’ is rather long.

Sulcal lists are rather developed, but they do not extend beyond the posterior border of the theca.

In the sulcus, the most characteristic plate is the long S.a. with a precingular part that extends above the cingulum. The anterior edge of this extension is pointed, rounded, or obliquely truncated; its posterior delineation is a somewhat flexuous crest. The S.s.a. is of moderate width. The S.d.p. is narrow and rather longer than the S.s.p. The S.p. may or may not have a connecting pore, although I never saw chains.

The theca is weak and easily collapsed. Pores are small and numerous.

Dimensions: L 51-65, A 49-64, Trd 41-57

Balech (1979b) and Balech et al.(1984) describe this species in more detail.

This species has been found from southern Brazil to 38°S in Argentina, always scarce.

Alexandrium leei Balech

Plate IV, fig. 20-28; Plate V, fig. 1-13

Alexandrium leei Balech (1985b: 37, fig. 9A-C)

This species is rather large and does not form chains. The epitheca is very regularly conic-convex, somewhat shorter than the hypotheca. The hypotheca is also conic-convex but has a slight antapical indentation that is asymmetric and sloping and delimits a lobule on the left. This left lobule is obtuse and large. The right lobule is short and almost indistinguishable. If the theca is positioned obliquely with the epitheca slightly lifted, this posterior lobulation is more apparent.

The cingulum is descending (usually >1, up to 1.5) and is concave but not very deep. It is clearly delimited by flanges but lacks true lists. A thin membrane ("curtain fin" of Kofoid), extending between the anterior and posterior margins, covers the cingulum. The sulcus is rather short and not very deep. Sulcal margins are reinforced. Where the S.s.a. is located, the left sulcal margin is displaced to the left.

In lateral view, the theca shows a slight dorsoventral flattening and the longitudinal axis clearly slopes ventrally from the anterior part.

Because of their peculiar characteristics, two epithecal plates are important: Po and 1’. The Po, which slightly alters the regularity of the epithecal vertex, is long and rather narrow. Its margin is very marked and perforated by some very small and irregularly distributed pores. A notch almost always abruptly interrupts the right margin at its midpoint. Sometimes, however, a true notch is not formed and only a deviation of the external margin is seen. The central aperture has a very long comma shape. The callus is rather short but very strong. The canopy is very narrow, almost lanceolate. Sometimes the middle of the plate shows some twist to the right.

The 1’ is rather wide and usually connected with the Po. The posterior third or fourth portion of the anterior right margin slants more obliquely to the right. A ventral pore does not occur at the point where the slant begins, but a groove connects the margin with the pore. The small- to medium-sized pore is circular to elliptic. It is surrounded by a barely conspicuous reinforcement and is always located more or less far from the plate margin. The shortest distance between the pore and the margin is shown in Pl. IV, fig. 27 (center). The posterior right margin is relatively long. The plate posterior is truncated; the anterior is also usually truncated. The 2’ and 4’ plates are rather wide. The 3’ has the usual hexagonal shape and is almost symmetrical.

In the precingular series, 6" is of medium width.

In the hypotheca, the most interesting feature is the large size of the two antapical plates. 1"" is wide and has a reinforced internal margin with almost no lists (in some specimens, a rudimentary list can be detected along the margin’s midpoint). This margin is somewhat sinuous, concave in its middle part and somewhat convex at both extremes. 2"" is large. Its dorsoventral axis is as long or longer than the transversal axis.

1"' is wide, with its internal and posterior margins fully oblique. There are no lists on this plate or the opposite plate, 5"'.

In the sulcus, the S.a. is somewhat longer than wide. The unciform apophysis is scantly curved. In situ and without crushing the plate, the unciform apophysis looks thin, but it is prolonged inward as a flat surface. The anterior margin is more or less straight.

The S.p. is rather short and wider than long. Its longitudinal axis is somewhat oblique to the right. Its anterior margin has irregularities and sinuosities. Both edges of this margin form projections that are more or less pointed; the wide middle portion is shorter than either end and may be pointed or rounded. Minor irregularities in the margin may occur. This plate lacks a connecting pore. To fit against the anterior margin of the S.p., the posterior margin of each posterior lateral plate has either a convexity or a centric or eccentric angle, rather variable among specimens.

The small anterior margin of the S.d.p. slopes and is thickened. The right margin is clearly convex. The posterior is subdivided into two equal or unequal parts and, in this case, either one may be the longer. Approximately, the anterior third or fourth of the left margin is somewhat thickened and a little bit indented. An elongated but very small S.ac.p. plate is located in the indentation.

The posterior margin of the S.d.a. rests upon the S.d.p.'s anterior margin and has the accustomed curvilinear, triangular shape. Its hypotenuse or anterior-internal margin is convex and rather regular, is reinforced, and supports a very small and triangular S.ac.a. The S.d.a. is connected with the 5"' by a short, truncated posterior right border.

The S.s.p. is relatively wide. As always with this plate, the anterior margin is composed of two halves. The external half is longer and connects with the S.s.a., whereas, the internal half connects with the S.m.p. These two segments form an angle that is more open than usual, mostly because the external half slopes less and is more horizontal than in most of its congenera. The internal margin is scarcely concave and is thinly reinforced. The posterior margin is usually subdivided into two segments or it may be somewhat convex.

The S.s.a. is more than twice as long as it is wide. The anterior margin is very short, reinforced, and a little sloped or rounded. The external margin is convex and forms an angle that may, exceptionally, be located near the midpoint but is usually located more posteriorly at the beginning of the last third of the margin. The internal margin is somewhat sinuous with slight anterior and posterior convexities.

Both median sulcal plates are large, especially the anterior one. The S.m.p. is longer than wide. It is irregularly pentagonal, as is the S.m.a. which is somewhat shorter and much wider. The right margins and, sometimes, the anterior margin of the S.m.a. are reinforced.

The theca is thin-walled and rather easily collapsed. Pores, generally very fine, are irregularly dispersed.

The fixed protoplasm does not seem contracted. It is dark brown and full of inclusions (starch ?) that are ellipsoidal in shape and about 2.5 - 2.8 µm long.

The usual banana-shaped nucleus is transversely located; its two ends project ventrally. Frequently, an end may also bend posteriorly. Perhaps, this curve is caused by the large, spherical body located in the hypotheca. Although I do not know the function and composition of this body, I saw it in most of the specimens.

Dimensions: L 44-58, A 44-53.5 (usually equal to L, but sometimes smaller), Trd 39-51. DV is 3-4 µm smaller than Trd. In well-oriented specimens, the epitheca is 4-5 µm shorter than the hypotheca.

Distribution: A sample collected with a Van Dorn bottle on November 21, 1982, in Korea (Jinhae Bay) contained a few specimens. It was reported from the Gulf of Thailand (Kodama et al., 1982) and the Philippines (Bay of Manila).

Discussion: This species is part of a group characterized by relatively large size, spheroid or wide ellipsoid shapes, and no angularities. Some species within this group have a very narrow and oblique 1' and a large ventral pore. They are similar to the *ostenfeldii* group as represented by *A. ostenfeldii*. However, the present species is well-differentiated from the *ostenfeldii* group by having a wider 1' and a smaller ventral pore. Because of these two features, it is closer to *A. kutnerae*, which may also have this pore located somewhat far from the margin. However, it differs from *A. kutnerae* by its lack of sulcal lists, the shape of 1"', its characteristic left posterior lobule, its Po, and all of its sulcal plates, especially the S.a. Additionally, the S.s.a is different from all its congenera.

I dedicated this species to my Korean friend Dr. Byung Lee, marine biologist and planktologist, who prominently influenced the development of marine biology in his country.

Group *tamarense*

Not chain-forming. Shape more or less obscurely pentagonal, almost isodiametric. Po medium wide without corner projections. 6" medium wide. S.p. longer than wide, with both anterior corners projected. Size almost always medium.

Four species are included: *A. tamarense*, *A. fundyense*, *A. acatenella*, and *A. tropicale*. Also described is one taxon that is doubtfully referred to *A. tamarense*. The first three species are very similar. However, *A. tropicale* has several characters that differentiate it.

Alexandrium tamarense (Lebour) Balech

Plate VI, fig. 1-40, Plate VII, fig. 1-9

Gonyaulax tamarensis Lebour (1925: 95, Illust. 14 (1a-1d))

Gonyaulax tamarensis var. *excavata* Braarud (1945: 10-12 and 14, Pl. 2, fig. 5A)

Gonyaulax excavata (Braarud) Balech (1971: 20 (*non* fig. 119-124))

Gessnerium tamarensis (Lebour) Loeblich and Loeblich (1979: 45)

Protogonyaulax tamarensis (Lebour) Taylor (1979: 51)

Alexandrium excavatum (Braarud) Balech and Tangen (1985: 334, Fig. 1 (A-L) and Fig. 2)

Cell is small- to relatively large-sized and is somewhat isodiametric. In ventral view, the shape is irregularly pentagonal and convex. The cell frequently has one or two shoulders that may or may not be very noticeable. The hypotheca is irregularly trapezoidal with convex and sometimes irregular sides. A concavity may be located on the left side of the hypotheca; sometimes a protuberance is above it. This concavity is not deep, but it is noticeable. The posterior margin is very often asymmetric, sloped forwards and to the right.

The descending (1) cingulum is excavated and has a very narrow list. The sulcus is variably deep and has moderately developed lists.

The Po is often very wide and markedly angular. Its dorsal margin is relatively extensive and is more often straight or nearly straight, but it is sometimes regular or irregularly convex. Commonly, the right margin is composed of two segments. The dorsal segment is usually straight or almost straight but is sometimes regularly or irregularly convex and parallel to the major axis of the plate. The ventral segment is sloped inward and is straight or rather concave. The ventral end is almost always fully truncated and forms a clear connection with 1'. Rarely, a Po is found that has a laterally located connecting pore that is almost always small (several were found in material from Norway [Oslo]). Small marginal pores were detected in the Po of thecae from England (Cornwall) and Korea.

The 1' has a relatively variable width. Usually, the anterior angle and, especially, the posterior angle are rather extensively truncated. The anterior right margin is often rather concave. Sometimes, the margin is abruptly angled at the location of the ventral pore. Occasionally, the two larger margins are straight. The ventral pore is small and always exists. Both its position on the margin and the degree of its indentation on the plate may vary. For example, the notch frequently occurs mostly within the suture region and penetrates only a little or not at all onto the plate. In other cases, the pore may be formed by two conjugated notches, one in 1' and the other in 4'. In some individuals, the notch is in the 4' plate, completely or almost completely. In this latter circumstance, the pore would be missed if the observer examined only the 1'.

3' is always clearly asymmetrical, but the degree of asymmetry varies.

1"" is somewhat narrow. The most variable feature is the development of the left sulcal list, which is rather wide in some cases and rather narrow in others. The right sulcal list, supported by the 5"' plate, is usually barely conspicuous.

2"" is variable. It is transversely extended in some thecae (type B) or dorsoventrally in others (type A), with some in transition. Type B is dominant and is the type represented in Lebour's description. However, the transition forms occur frequently.

The sulcal plates also vary. The S.a. is always narrow, is generally a little longer than wide, and has a deep posterior sinus. The anterior margin is more or less straight, wide, and situated at or a little above the level of the anterior left margin of the cingulum. In Lebour's figure, the anterior margin clearly intrudes onto the epitheca. From the left side of this margin, a short and oblique groove is directed to the right and down. Frequently, a portion of this margin, usually the right part but sometimes the left part, is lifted more or less abruptly and penetrates into the epitheca, sometimes quite deeply. This may be a frequent and rather noticeable characteristic in cultured specimens, but it is rare in field specimens.

The S.p. may or may not have a connecting pore that is small, clearly displaced to the right, and connected to the edge by a groove. Sometimes, a groove occurs without a pore; many thecae have neither, as is the case for most of those from the Argentine Sea. The length/width relation of this plate is somewhat variable.

Of the remaining sulcal plates, the most variable one is the S.s.a. It may be relatively wide or rather more narrow, but its essential characteristics are retained. Sulcal plates were described in detail in Balech (1977) and in Balech and Tangen (1985) as *A. excavatum*.

Interestingly, the very irregular epithecae and the more rounded ones with the sometimes slightly flattened apex are found in clonal cultures.

The symmetry of the hypotheca and the degree of excavation of the antapical concavity are also rather variable. In the Norwegian material, symmetric thecae were found almost as frequently as asymmetric ones. The Argentinian material was almost always asymmetrical.

This is now one of the two or three better known species that produce PSP. If this species truly encompasses such a wide range of morphological variation, and I accept now that it does, then the causes that make it nontoxic in the type locale but toxic in most of the other locations should be thoroughly investigated.

Distribution: southeastern and southern England, Great Britain (northeast coast), Norway, Spain, Portugal, U.S.A. (both coasts, especially the northern regions), Canada (west coast), Japan, Korea, and in the Argentinian littoral from Buenos Aires to the Gulf of San Jorge in Patagonia. Probably, it occurs along the Atlantic coast of Europe and the coasts of other countries such as the former Soviet Union and China.

Dimensions: L 22-51, A 22-50, Trd 17.5-44. A is usually almost equal to L but may be a little larger or smaller. The largest specimens were reported from Norway and southern England;

the smallest were from Argentina (Patagonia). The majority of theca that have been measured varied in length from 28 to 35; however, in other material from some countries, the length of the majority was between 35 and 44.

Variations and Discussion: This species is widely distributed and, therefore, its characteristics are more variable. The length of the largest specimen can be more than twice that of the smallest. Also, although the majority in all size ranges are approximately isodiametric, the relationship between length and width changes with the populations.

Lebour's description is very concise and her drawings are very schematic. The fact that her figure 1c shows the epitheca in interior view is somewhat irrelevant. The only dimension that she recorded was L 36, which can be considered common to the species. Her figures show a regular, wide, and oval shape without a posterior concavity and a 1' without a ventral pore. The absence of the pore should not count as a specific characteristic, because it is not easily observed in whole thecae, especially if they contain protoplasm. Sometimes, investigators that saw the pore omitted it from their publications. For example, Braarud noted the ventral pore in "var. *globosa* Braarud" and drew it in his notes, but he did not include it in his published drawings. Failure to see the pore in *tamarensis* is understandable because the pore is very small. Nonetheless, it is now certain that this species has a pore, because the pore was found in material from the Tamar River estuary in England by later authors (Loeblich and Loeblich, 1975; Balech, 1977). Loeblich and Loeblich studied two cultures from the Tamar River, one with a pore and the other without it. They chose the one with a ventral pore (culture 173) as the type. This would be the valid designation of the type. The material from the southeast of England sent by Dodge also has a ventral pore.

Braarud found a similar form in Norway. Although it had a "clearly different shape, with a strong antapical depression", he believed that it was a variety of the Lebour species and named it var. *excavata*. Later, I found a warm-water form that resembled Braarud's variety more closely than it did any other taxa known at that time. Because the warm-water specimen was certainly shorter than *G. tamarensis* and was clearly different from Lebour's species, I elevated Braarud's variety to species without studying Norwegian material (Balech, 1971). However, I was still doubtful about ascribing the equatorial Atlantic form to *excavata* and reported it as *excavata* with a "?". Later, it was evident that this taxon from the equatorial Atlantic did not correspond with the Norwegian taxon, and it was renamed *A. tropicale*.

Later, when material from both the Tamar River and the Fjord of Oslo were studied, characteristics of both forms were delineated more precisely. Specimens from the Tamar River had a more regular shape, a more rounded apex, and an almost rounded antapex. However, even in the almost certainly monospecific material that I examined from the Tamar River, some specimens had a clear posterior concavity. Furthermore, whether the observer perceives a round hypotheca or one with a posterior depression depends largely on the position of the observed specimen. If the hypotheca is somewhat elevated towards the observer, it looks round. However, if the hypotheca is tilted downward, it looks concave.

As more material was studied, differentiating between *tamarense* and *excavatum* became more difficult. Material from southeastern England (Cornwall), which is near the site of the *tamarense* type, is not morphologically distinct from *excavatum*. In Spanish samples that I studied, representatives of this group were scarce. However, when they were present, the individuals could be similar either to Braarud's variety or to the Tamar River material or show transitional characteristics. Some Argentinian populations have the typical characteristics of *excavatum* and they are identical to individuals in photographs published by the Japanese.

The variations noted in the abundant material from different sources indicated that the apparent differences between *tamarense* and *excavata* were not valid.

Over time, this steady acquisition of more detailed knowledge finally led to a change in the thinking of certain taxonomists including myself. For example, Loeblich and Loeblich (1975) said (p. 220), "we do not consider it [*excavatum*] to be conspecific with typical *G. tamarensis*", but Loeblich and Loeblich (1979) stated without discussion that *excavata* was a synonym of *tamarensis*. Taylor (1979) noted the same conclusion. In the past, I thought that the two taxa should be maintained separately and did so in Balech (1985b). Balech and Tangen (1985) also kept them separate. However, in that paper, we had the opportunity to discuss why this was done. We clarified that our purpose was not to resolve the synonymy of *excavatum* but to provide, for the first time, a modern and detailed study of the Norwegian material. We hoped that such description would provide an adequate base for knowledgeable discussion. Now, along with other researchers including Fukuyo, I accept the synonymy of these two taxa.

However, everything is not resolved, and some questions still persist. For instance, according to the Loeblich's (1975), typical forms of *tamarense* have important biological characteristics that are different from those ascribed to *excavatum*; typical *tamarense* do not produce PSP, are not bioluminescent, and have a slightly different thermal tolerance than does the so-called *excavatum* that is toxic and bioluminescent. Boyer et al. (1985) also concluded that typical *tamarense* do not produce PSP.

Based on the above, the recommendation of Tangen and myself that material from the type locality and nearby areas should be re-examined is still valid. A detailed study by the English specialists would be very useful and should include thorough plate analysis, ultrastructure documentation, and biological evaluation of the different morphotypes, especially those differentiated by the presence or absence of the ventral pore. Comparisons could then be made between the English material and the material from other locations around the world. For example, how does the English material compare with the material from Argentina, which has a pore, is also toxic and luminescent, and has chloroplasts?

As with some other taxa, the largest variations are found in cultures, mainly in those that are old or in bad physiological condition. The above observations refer only to individuals that are not aberrant.

The taxon that is described next is perhaps a variety of the above. If so, the ecological boundary of *A. tamarense* will be greatly extended because warm water populations will be included, whereas those forms presently assigned to Lebour's species occur only in cold to cold-temperate waters.

Alexandrium sp. cf. *tamarense*

Plate VII, fig. 10-22

Plankton samples from Thailand contained some individuals that were a small, almost isodiametric species. The cells either lacked shoulders or had scarcely noticeable ones.

1' is almost always wide. The anterior right margin and the posterior left margin are almost the same length. Usually, both are almost straight, but occasionally, the anterior right one is slightly concave. The small ventral pore is usually enclosed by a filamentous projection of the margin.

1"" is somewhat narrow and almost triangular although its external corner is truncated and forms a generally short margin. The internal margin has a slight concavity in the middle that is limited by the convex ends. The margin is weakly reinforced, except posteriorly, and supports a very narrow list. 2"" is transversely elongated (type B).

Dimensions: L 22-28.5, A 23-29.5, Trd 17.5-24.

Comparisons: These specimens may or may not belong to *A. tamarense.* On the average, they are smaller than European *tamarense* but larger than Argentinian ones. Their shape is more regular than the typical *A. tamarense*, sulcal lists are more reduced, and 1' is wider with generally straight margins. The S.a. is somewhat wider with a rather long and straight anterior margin. The S.p. is a little shorter. The S.s.a. is wider and angular. Perhaps the most striking feature is the lack of reinforcement on the posterior portion of the internal margin of 1"".

Small differences among populations may be phenotypic and, therefore, lack taxonomic significance. However, one feels some uncertainty in accepting this warm water material into the same taxon as *A. tamarense*, which so far has only been reported as a cold or cold-temperate species. Perhaps, it could be considered as a subspecies, but at the moment, I do not hazard an opinion.

The absence of evident abnormalities in the cultures from Thailand and the similarity of the thecae coming from two different locations in Thailand indicate that the observed characteristics in this culture are normal in this taxon.

It was studied by Kodama et al. (1988) and Fukuyo et al. (1988), who reported it simply as *A. tamarense*.

The studied material came from the northern Gulf of Thailand (Pranburi and Ban Leam). According to Japanese determinations, it does not produce PSP.

Alexandrium fundyense Balech

Plate VII, fig. 23-32, Plate VIII, fig. 1-19

Alexandrium fundyense Balech (1985b: 93, fig. 18)

By its shape and size, it cannot be distinguished from *A. tamarense.* Therefore, instead of providing a detailed description, I will note only its variations and its differences from the last species.

Most specimens that are not obviously collapsed are as wide or wider than they are long. The L/A ratio is almost always less than unity, in the range from 0.87-1 but usually between 0.93-0.98. The length of most individuals is between 27 and 37 µm, but some may occasionally be larger, between 39 and 50 µm. Interestingly, these larger specimens usually have a rather different shape. They are somewhat elongated and the L/A ratio in almost all of them is equal to or greater than one. Indeed, most of them range between 1.01 and 1.09, averaging approximately 1.04. Additionally, their hypothecae are more regularly convex.

The primary difference from *A. tamarense* is the lack of a ventral pore, which hardly seems enough to separate them as species. However, I believe that the proven constancy of this character justifies separation of *A. fundyense* from the Lebour species. Clonal cultures of each species have been consistent as demonstrated with several clones (429 ca of Loeblich [1979] and several isolated stocks maintained by White and Anderson).

Some other small differences occur, but they are not consistent. For instance in *fundyense*, the Po is usually less wide, less angular, and almost oval. Also, the anterior portion of S.a. is usually rather elevated and penetrates into the epitheca. However, this character seems to be enhanced in culture. For example, in the majority of the *tamarense* from natural populations, the S.a. has a more or less straight anterior margin that is at the same level as the left anterior cingular margin; however, in cultured *A. tamarense*, the S.a. may project into the epitheca. While almost all of the *fundyense* that I studied were cultured, that is not the case for *A. tamarense.* In the two plankton samples of *A. fundyense* that I studied, the S.a. looked more like the S.a. of *tamarense.* However, if only cultures of the two species are compared, then specimens of *A. fundyense* with an S.a. that indents the epitheca occur more often than do individuals of *A. tamarense* with an elevated S.a. Finally, in most of the *fundyense* studied, 2"" is type A, while in most *tamarense*, it is type B or intermediate.

Distribution: Type locale is the Bay of Fundy on the Atlantic coast of North America between Canada and the U.S.A. It is also found on the northeast coast of the U.S.A. from Maine to Massachusetts; its most southern distribution was reported at 40°40'N in New York State. *Alexandrium tamarense* has not been found in the type locale and tends to be distributed more in the southern part of this northeast Atlantic region. So far, *A. fundyense* has not been reported anywhere else.

This species is toxic and occurs in cold water.

Alexandrium acatenella (Whedon and Kofoid) Balech

Plate VIII, fig. 20-31, Plate IX, fig. 1-10

Gonyaulax acatenella Whedon and Kofoid (1936: 31, fig. 8-13)

Alexandrium acatenella (Whedon and Kofoid) Balech (1985b: 37, fig. 19)

Cell is longer than it is wide and is faintly heptagonal to octagonal. Epitheca length is equal to or longer than the length of the hypotheca plus the cingulum. The epitheca has straight or slightly convex flanks that are slightly oblique in the lower two-thirds. The angle that this lower portion forms with the vertical ranges between 20 and 30°, usually 25° but occasionally 18°. In the upper one-third of the epitheca, there is a marked and abrupt change in direction. The angle that this portion forms with the horizontal ranges between 20 and 28° in most typical specimens. The apical region is sometimes somewhat protuberant.

Cingulum is well-excavated, descending (1). It has narrow but fully perceivable cingular lists that are about 1.5-2 μm wide. A curtain fin that extends across the cingulum converts it into a tube.

Hypotheca has a shallow antapical concavity, limited on the left by the sulcal list, which is projected posteriorly. The right flank of the hypotheca is straight or softly convex, rather sloping. The upper two-thirds of the left one is slightly oblique, straight or rather concave. The posterior third is strongly slanted inward.

Po is irregularly oval and relatively narrow; sometimes it has a short dorsal flattening. The callus is somewhat developed. 1' contacts the Po and has a small ventral pore that is located almost always at or slightly below the midpoint of the anterior right margin. Frequently, the pore indents the 4' more than it does the 1'. 3' is very asymmetric. 6" is medium wide.

1"' has a strong, irregularly concave reinforcement on the internal margin. 5"' is rather narrow and almost always has strong crests on the internal margin.

1"" is of variable width but is generally rather narrow. Its internal border is well reinforced and sinuous and has a well-developed list. 2"" is type B and wider than long.

S.a. is as long as it is wide or longer. Its anterior margin is irregular, shallowly concave, and reinforced. Sometimes, this reinforcement is so thick and bulky that the concavity projects on each side into tips. The posterior sinus is rather deep. The plate is curved: the anterior portion curves inwardly and both sides curve inwardly. These curvatures change the aspect and the relative plate height depending on how flattened the plate is when it is being observed. Furthermore, these curvatures produce a horizontal or somewhat oblique fold in the anterior portion of the plate.

The S.p. is the *tamarense*-type but is wider. In the Japanese material, it almost always has a round connecting pore that is located rather far away from the right margin but is connected to the margin by a groove.

The S.d.p. is medium wide. Its anterior margin slopes strongly. Its posterior margin is usually convex or subdivided into two almost straight segments, although sometimes, the margin is almost straight and slopes in the direction opposite that of the anterior margin.

The S.s.p. has the usual shape, is of relatively short or medium length, and shares a long border with the 1"". The S.s.a. is longer than wide, usually rather narrow. The S.d.a. has the usual shape. It is irregular, triangular, about as wide as long, and rather rough.

The median sulcal plates are well-developed and about equally long. The accessory sulcal plates are small and rather delicate.

The theca is sculptured due to large and small pores occurring in small protuberances. In some of the Japanese material, an extensive but very delicate reticulation is present, formed by almost invisible lines that link the protuberances.

Chloroplasts are elongated and arranged irradiately. The nucleus is C-shaped.

Dimensions: L 35-51 (most are between 40 and 46), A 33-44 (only one was larger than 40), Trd 26.5-35.

Discussion: The description is based on culture material from Japan (Kagawa Prefecture). I also found a few specimens in plankton from Argentina (Gulf of San Matias); these differ somewhat from the Japanese ones. The shape of the Argentinian specimens is a little more elliptical because angles are less pronounced. The epitheca is usually a little longer. The hypotheca is sometimes more rounded and sometimes lacks an antapical concavity. When the antapical region is rounded, the sulcal list is not projected posteriorly. The list is most likely to be observed, but only slightly, when the specimens are flattened posteriorly or have a shallow concavity. The S.a. does not have the strongly concave left margin that is usually observed in the Japanese specimens. The S.p. is more narrow, is clearly longer than wide, and lacks a connecting pore. Reticulation is not present, but the variably sized pores and protuberances are noticeable. Some of these differences between Japanese and Argentinian material, such as the oddly shaped S.a. and the presence of a connecting pore in Japanese theca, may be the result of culture conditions. The dimensions, however, are very similar; Argentinian specimens measured L 36-51 (mostly 41-45), A 40-42, and Trd 29-38 (only one larger than 36). However, few specimens were measured. Whedon and Kofoid note the following dimensions: L 36-44 and A 38-45, but this appears to be a mistake because in the three figures of whole specimens in ventral view, L is clearly greater than A.

This is another questionable species that is very similar to *A. tamarense*. However, some seemingly valid differences include an epitheca that is clearly longer than the hypotheca, its general shape, a wider S.p., and thecal sculpture. It is toxic.

Distribution: U.S.A. (northern Pacific coast), Canada (Pacific coast), Japan, Argentina (northern Patagonia). Guzman and Campodonico (1978) mention a personal communication from Manuela Pintos who reported this species from northern Chile (Arica). This identification should be confirmed.

Alexandrium tropicale Balech

Plate IX, fig. 11-27

Gonyaulax excavata (Braarud) Balech (1971: 28, fig. 119-124, non *Gonyaulax tamarensis* var. *excavata* Braarud; non *Gonyaulax excavata (Braarud) Balech, 1971)*

Alexandrium tropicale Balech (1985b: 37, fig. 7)

Cell is small, is a little wider than long, and has a rather regular and rounded pentagonal shape. Epitheca is conic convex and usually lacks shoulders, although barely noticeable ones may occasionally occur. Hypotheca is symmetric and has a slight antapical depression. Cingulum is well-excavated, has strongly reinforced margins, and is descending (somewhat <1). Sulcus is also deep and has strong margins.

The Po is oval and has a straight or somewhat concave right margin. The comma is rather wide with an average or well-thickened callus; peripheral pores are noticeable on the left side. The direction of this plate's longitudinal axis is almost the same as that of the cell's sagittal plane. The dorsal margin is round to rather flat; the ventral end is pointed.

The 1' is rather narrow and is shaped like an irregular and asymmetric rhomboid. The plate is sharp anteriorly and generally somewhat truncated posteriorly. It is almost always connected to the Po by a sharp apical prolongation. This plate is slightly oblique (almost vertical) with a rather large ventral pore. The posterior right margin is long, sometimes longer than the anterior right margin.

2' is rather short. 3' usually is clearly asymmetrical. Its length/width relation is rather variable, but the plate tends to be relatively narrow and long.

6" is relatively wide. Its posterior left margin is fully concave and reinforced.

1"" is usually rather narrow. 2"" is narrow and elongated in the dorsoventral direction (type A).

The S.a. is narrow. Its anterior margin is reinforced and usually irregular. The ends of this margin may project as two tips of which the left is often more elevated. The unciform apophysis is rather oblique and abruptly folded in its extreme. The posterior sinus is rounded and of medium depth.

The S.p. is the common *tamarensis*-type, rather curved to the right. The S.d.p. has very sloping anterior and posterior margins. The posterior-right corner is sometimes truncated to produce a very short margin that is sloped in the opposite direction of the posterior margin. The S.d.a. is rather elongated transversely. The small S.ac.a. is located above the S.d.a. and just below the unciform apophysis. The S.s.p. is variable; it may be relatively short and wide in some specimens but long and rather narrow in others. The S.s.a. is narrow and rather long and has a regularly curved internal margin. The median sulcal plates are moderately developed. Although their height is similar, the S.m.p. is narrow while the S.m.a. is much wider.

The epithecal and hypothecal plates and, frequently, the S.p. have noticeable pores that perforate small and slightly projecting bumps. These pores are irregularly located, except near the precingular margins where they are rather densely and regularly distributed. In the cingular plates, there are two rows of marginal pores that are very thin and only visible when the plate is flattened because they are otherwise covered by the lists.

Chloroplasts are numerous and irregularly oval in shape. The sausage-shaped nucleus is very thick.

Dimensions: L 24.5-30.5, A 25.5-33, Trd 20.5-28. Very little dorsoventral flattening occurs.

When I first described the species (Balech, 1971), I doubtfully attributed it to *Gonyaulax excavata* (= var. *excavata* created by Braarud for *G. tamarensis*). However, using material of the variety from his country, I carefully studied the taxon of the Norwegian specialist and concluded that the specimens that I described in 1971 were a different species. This confirmed the opinion of Loeblich and Loeblich (1975). Therefore, I later reported the species with a new name (Balech, 1985b).

It is apparently a warm water, oceanic species. Most specimens were obtained in the equatorial Atlantic where temperatures were greater than 27°C. Later, two or three specimens, which were slightly different but maintained the species' fundamental characteristics, were found in the southwestern Atlantic off the mouth of the Rio de la Plata. Loeblich and Loeblich (1975) reported that Steidinger and Williams collected it near the U.S.A. (Florida), but this identification is uncertain.

Group *catenella*

Clearly flattened anterior-posteriorly, although some abnormal specimens almost isodiametric. Wide or very wide Po, connected directly to 1’. No ventral pore. S.p. almost as wide as long, almost rhombic, with the ventral edge replaced by a rather moderate depression. Connecting pores well-developed in the Po and the S.p. Sulcal lists barely developed. This group contains two species: *A. catenella* and *A. compressum.*

Alexandrium catenella (Whedon and Kofoid) Balech

Plate X, fig. 1-31 and Plate XI, fig. 1-12

Gonyaulax catenella Whedon and Kofoid (1936: 125, fig 1-7)

Gessnerium acatenellum (Whedon and Kofoid) Loeblich and Loeblich (1979: 44)

Protogonyaulax acatenella (Whedon and Kofoid) Taylor (1979: 51)

Alexandrium catenella (Whedon and Kofoid) Balech (1985b: 37, fig. 2a-c)

Cell is small- to medium-sized, somewhat flattened anterior-posteriorly. This species usually forms curved chains. Epitheca has more or less noticeable shoulders and a rather upraised apical region. Cingulum is very excavated, descending (1, sometimes a little more). It generally has an overlapping membrane or curtain fin that extends from the projecting flange on the epitheca to the corresponding flange on the hypotheca. Sulcus is rather deep, abruptly widened on the posterior. Sulcal membranes are moderate, but sometimes they project slightly toward the posterior region and look like one or two small spines. On some occasions, the antapical left lobule is a little longer and rounder than the right one.

Po is wide with a dorsal margin that is oblique and almost straight. The left margin is regular or irregularly convex. The right one is sinuous, almost always straight or slightly convex in its dorsal half and concave in its ventral half. The ventral portion of the plate is usually clearly and obliquely truncated, which provides extensive contact with 1’. The comma has a large head that is close to the left margin and has a thick callus. The canopy is narrow and translucent. A connecting pore that is medium-sized and elliptically shaped is located near the comma head to its right. Frequently, accessory pores are present, especially a more ventral one.

1’ does not have a ventral pore and directly contacts the Po. It is asymmetrically rhomboidal (each pair of long and short sides is parallel). Usually, the anterior right margin is clearly concave. The anterior and posterior corners are more or less extensively truncated.

Plates 2’, 3’, and 4’ have raised flanges that support the Po and are frequently denticulated, especially 2’. 2’ is the largest apical plate and is usually connected with 3’ by a sinuous margin that is mostly concave. 3’ is hexagonal and clearly asymmetrical with the anterior left side up to twice as long as the anterior right side. 4’ is relatively short and wide.

In the precingular series, only 6" is noteworthy. It is medium wide. Its internal margin borders with the S.a. and has a barely pronounced concavity.

In the hypotheca, 5"' is wide and has a somewhat reinforced internal margin that is slightly S-shaped and supports a narrow list. Its anterior-internal corner is usually briefly truncated and reinforced.

1"" is rather narrow, long, and very oblique. Its sulcal list is moderately wide, wider anteriorly than posteriorly. 2"" is transversely elongated (type B).

In the sulcus, the S.a. is longer than wide or as long as wide. It does not extend above the anterior-left margin of the cingulum. A deep posterior sinus is present. The anterior margin is wide and almost straight. A fold may be obliquely directed from the left anterior to the right posterior of the plate, usually ending before it reaches the notch.

The S.p. is asymmetric, rhombic, and almost as wide as long. The margin that borders S.s.p. and S.d.p. is scooped. The margins that border the 1"" and 5"' are almost straight. Where they join with the curved ventral margin, two crests are formed. These crests are directed posteriorly then diminish before reaching the plate midpoint. The two dorsal margins are usually rather convex and are distinct from each other because the left one is longer. A large, irregularly shaped connecting pore is located a little to the right of plate center. The pore is dorsoventrally elongated and either quadrangular or triangular with more or less obtuse vertices. It is linked by a small channel to the ventral right margin.

The S.s.a. deflects the left sulcal margin outward in a rather pronounced way. It is relatively wide, rather shallowly set in the sulcus, and irregularly oval-shaped. Its two posterior margins form a rather obvious angle.

The S.s.p. is trapezoid-shaped. Its anterior left margin adjoins the S.s.a. and is rather long and very oblique. The anterior internal corner is truncated, which forms a short anterior right margin. This margin supports a relatively wide and short S.m.p. whose internal margin is scarcely concave and slightly reinforced. The posterior left margin of the S.s.p. is short but only a little longer than the anterior left margin. As a whole, this plate is relatively wide.

The S.d.p. is rather short and relatively wide and has a smoothly convex right margin. The posterior margin is very oblique. The anterior margin is clearly divided in two by an angularity. A very short and oblique fold is sometimes directed towards the anterior from the left margin. The S.d.a is triangular and almost as long as wide and has a sinuous and reinforced anterior-internal margin. The median sulcal plates have an average development and are rather short. The accessory plates are small, especially the S.ac.p., which is very small.

Thecal walls have perforated granules, more or less visible depending on the thecae. In some hypothecal plates, especially in 2"", vermiform folds may be present. Sometimes, longer folds occur in 4"'. Occasionally, 1"" has a short transversal fold that originates near the internal reinforced margin. Actually, any of the hypothecal plates can have long irregular crests or a series of short crests that sometimes occur on all the thecal plates.

Dimensions: They are rather variable. L 20-39.5 (exceptions), (<24 and >34 are exceptions), A 22-44, Trd 17.5-37. The L/A relation also varies. This species usually is wider than long, and the anterior-posterior flattening is often rather conspicuous. Nonetheless, in some specimens, the length equals the width (width measured more often as Trd rather than as A). Both the absolute and relative dimensions change according to the population. For example, Australian specimens that I studied were usually smaller than those from either South America or the northwestern U.S.A. Cultures from southern California contained the smallest cells, but this could have been due to special conditions of the medium. Examples of variable L/A relationships are as follows: L 24, Trd 22; L 29, A 39, Trd 35; L 28.5, A 28.5, Trd 22.5.

Discussion: Among the species that form more or less long chains, *A. catenella* is usually differentiated quite easily because it is anterior-posteriorly flattened, it lacks a ventral pore on 1', and the 1' is connected to the Po. The last characteristic differentiates it clearly from *A. monilatum*. *A. compressum* is more flattened than *A. catenella* is, but the former has a very regular shape, it has a completely different Po, it is much wider, and it has a large, almost circular connecting pore. *Alexandrium fraterculus* and *A. cohorticula* have a clearly different shape, are generally longer than wide, and have a ventral pore. The Po of *A. fraterculus* is characterized by its irregular shape, its pointed ends, and the presence of a dorsal connecting pore. *Alexandrium cohorticula* has an S.a. with a well-delimited precingular portion. *Alexandrium tamiyavanichi* is similar to *A. catenella* because both are a little wider than long. However, *A. tamiyavanichi* is easily differentiated because of its S.a. with a noticeable precingular part and because of the *tamarensis*-type S.p. that contrasts with the S.p. of *A. catenella*, which is wide and almost rhombic. *Alexandrium affine* is distinguished by its unmistakable Po that is narrow and has a large, circular connecting pore that is dorsally located.

Therefore, *A. catenella* is easily differentiated from the other concatenated species. Its anterior-posterior flattening is rather characteristic; however, this characteristic alone is not sufficient to distinguish it from all *Alexandrium* species. As Taylor (1984) and I observed, some specimens are isodiametric and, therefore, are difficult to differentiate from *A. tamarense* and related species. The absence of a ventral pore distinguishes it well from the Lebour species. However, in the *tamarensis* group, *A. fundyense* lacks this pore and also is wider than long. However, this latter species does not form chains and has a different S.p. that is more irregular and elongated. Also it usually has a rather distinct Po and S.a.

L. Nishitani (personal communication) observed that, along the Pacific coast of the U.S.A. (Washington state: the area of the Strait of San Juan de Fuca and Puget Sound), a number of individuals were parasitized by *Amoebophrya*; these theca were elongated. Elongation was also observed in some isolated individuals that were not parasitized. I suppose that these non-parasitized individuals could be zygotes.

Neglecting certain structural details, however, has frequently led to mistaken identification of this species. For example, the *G. catenella* of Postek and Cox (1976) does not have a Po of the same shape and type as in *A. catenella* Also, in the former, 1' has a ventral pore (see discussion in species *inquirendae*).

Alexandrium catenella is essentially a cold water species that is seldom found in water temperatures >12°C and usually does not reproduce at temperatures >16°C. It has a wide distribution in these cold waters. It was first identified along the western U.S.A. (in California [near San Francisco] and in Oregon). Later, it was found more northwards along the Pacific coast of Canada and the U.S.A. (Alaska). Carried by the California Current, it has extended southward as well to southern California where its population has apparently increased (B.C. Abbott, personal communication). In South America, it was found in southern Chile and southern Argentina. It has also been observed in South Africa, Australia (including Tasmania), and Japan. It is probably in some other places such as the cold Pacific. Interestingly, it does not seem to be creditably reported in the cold Atlantic, except for some poorly documented observations in the Argentinian part of the big island of Tierra del Fuego. Furthermore, some reports contradict the above assertion that this is a cold water species because it has been collected from waters off Japan and Australia in which temperatures were about 20°C.

Alexandrium compressum
(Fukuyo, Yoshida, and Inoue) n. comb.

Plate XII, fig. 1-9

Protogonyaulax sp. Fukuyo (1981: 35, fig. 1-5)

Protogonyaulax compressa Fukuyo, Yoshida, and Inoue (1985: 30, fig. 3d-f and 30-33)

This species forms chains. The theca is anterior-posteriorly flattened. The epitheca is regularly convex and has an apical protuberance that is relatively conspicuous. The sides of the epitheca are low and regular. The antapical concavity is very wide and is surrounded by moderately developed lists. The cingulum is descending (1) and very excavated. The sulcus is very wide posteriorly and has narrow sulcal lists.

The Po is ovoid and very wide with a slight tendency to be curvilinearly triangular except its right margin, which is straight or almost straight. The ventral point is scarcely truncated. A notch is located at the junction of the dorsal margin with the right margin, which is also the location of the suture between apical plates 3' and 4'. A long, narrow comma is located to the left; callus is slightly noticeable. A large connecting pore is located at the right of the comma's head and is wide and elliptically shaped.

The 1' is directly connected with the Po and is of medium width. The anterior right margin is oblique and somewhat concave. No ventral pore is present. The 3' is wide, short, and asymmetric. 6" is rather wide.

Postcingular plates are large. 1"" is medium wide with a narrow list. 2"" is wide but very short, almost completely located in the left half of the hypotheca.

S.a. is somewhat wider than long and has a posterior sinus that is rounded, reinforced, and deep. The anterior margin is sinuous and somewhat more elevated to the left.

S.p. is very big. Its shape is almost a square except that the ventral corner is truncated and borders with the lateral posterior sulcal plates. The connecting pore is large, not quite circular, located almost in the middle of the plate, and linked by a small channel to the anterior right margin.

The other sulcal plates were poorly studied. The S.d.p. is medium wide. The S.d.a. is transversely elongated and has a right-anterior portion that is delimited by a peculiar fold. The average-sized S.ac.a. is located above the S.d.a. The S.s.a. is rather narrow.

It has numerous, easily seen, but irregularly distributed pores. In the specimens I studied, all the hypothecal plates had long, irregular, transversal crests composed of short, vermiform segments.

Dimensions: L 35.5, A 47.5, Trd 33. The Japanese noted L 36-40.

In April 1958, I found a chain of this species in waters off of southern California at station CALCOFI I37-40. It was recorded as *Gonyaulax* cf. *catenella* based on some rapid, rough sketches done at the time. Later, it was found again in small numbers in Japan (north and south) and described as a new species (Fukuyo et al., 1985).

Group *fraterculus*

Thecae from somewhat longer than wide to isodiametric. Chain forming. With ventral pore. Fully developed sulcal lists, except in *A. affine*. It has four species: *A. fraterculus*, *A. cohorticula*, *A. affine*, and *A. tamiyavanichi*. Two of the species (*A. tamiyavanichi* and *A. cohorticula*) have an S.a. with a precingular part. The other two have a special type of Po.

Alexandrium fraterculus (Balech) Balech

Plate XII, fig. 10-26

Gonyaulax fratercula Balech (1964: 31, Pl. IV, fig. 47-58)

Gessnerium fraterculum (Balech) Loeblich and Loeblich (1979: 44)

Protogonyaulax fratercula (Balech) Taylor (1979: 51)

Alexandrium fraterculus (Balech) Balech (1985b: 37, fig. 4)

Cell is medium-sized and forms chains. Theca is pentagonal, irregular, and either isodiametric or somewhat longer than wide. Cingulum is descending (1 or a little more) and deeply excavated and has very narrow membranes and a thin curtain fin. Epitheca is conic and truncated and has rather marked shoulders. Hypotheca is trapezoidal and has a wide, short, and symmetric antapical concavity. Sulcal lists are fully developed. Usually, they are slightly projected posteriorly when the theca is in ventral view, although, sometimes, only one of the lists is projected posteriorly.

The Po is very characteristic, quite narrow and very irregular. The left margin is regular or irregularly convex. The dorsal portion of the left margin is briefly concave, which forms a dorsal point. The right margin is irregular and generally divided into 3 or 4 straight or concave segments, of which the ventral segment is clearly concave and oblique. The plate's ventral end is also sharp-pointed. The comma is relatively small, especially narrow, and very displaced to the left. The callus is barely noticeable. A connecting pore that is circular and large is located to the right of the comma's head. Marginal secondary pores are present, especially on the left side.

1' is medium-wide. A small ventral pore is usually located at about the midpoint of the anterior right margin. The plate's anterior end may be briefly truncated, which allows a direct connection with the Po. However, more frequently, the end is sharp-pointed and very often prolonged by a short filiform extension that produces an indirect connection with the Po. 2' is rather narrow and has extensive contact with 1". 3' is very asymmetric. 4' is rather narrow. 6" is moderately wide.

1"' is rather long with a concave internal margin that is reinforced and has a narrow sulcal list. 5"' is long and trapezoid-shaped and has a rather long and wide sulcal list.

1"" is long and narrow with very short posterior margins. The sulcal or internal margin is regularly convex and supports a sulcal list that is well-developed ventrally. The 2"" plate is very short and transversely elongated (type B).

Sulcus is wide in the posterior and deep. The S.a. is usually longer than wide, sometimes isodiametric with a deep posterior sinus that is narrow and reinforced. The unciform apophysis is thin. The plate's anterior margin is frequently divided into a right segment that is generally somewhat reinforced and a left segment that is longer and oblique.

The S.p. is wide, approximately as wide as long. It has a V-shaped ventral border. The connecting pore is circular or not quite circular and is centrally located. A narrow channel connects the pore with the anterior portion of the right margin.

The S.s.p. is longer than wide, is narrow anteriorly, and has a very oblique anterior left margin. The S.s.a. is rhomboidal, medium-wide, and sharp-pointed anteriorly. The internal margin is convex, somewhat reinforced, and obscurely subdivided into two portions that border the two median sulcal plates. It has two straight posterior margins of which the external posterior one is shorter than the internal posterior one.

The S.d.p. is medium-wide and has straight anterior and posterior margins. The posterior margin has an articulate fringe. The S.d.a. is triangular, approximately as wide as long. Its anterior-internal margin is well reinforced.

The median sulcal plates are almost the same size and are pentagonal. The anterior plate has an oblique major axis, whereas, the posterior plate has a longitudinal major axis. The S.ac.a. is oblique, triangular, and averagely developed. The S.ac.p. is very small.

General plates (the main epithecal and hypothecal plates) have pores that are irregular in both size and distribution.

Dimensions: L 32-49.5 (most were 35-41), A 29-47 (predominantly, A = L), Trd 26-37.5.

This species forms very labile chains. Nevertheless, when the chains are undisturbed by stirring or other agitation, they may consist of more than 60 cells.

As Fukuyo (1981) noted, its Po is very distinct, which definitely separates it from other concatenated species, such as *A. cohorticula*, *A. affine*, *A. compressum*, and *A. catenella*.

It is a warm-water species that is found in the Atlantic between southern Brazil and the northern Argentinian littoral. It is sometimes found in the oceanic environment of the Brazil Current. In the Pacific Ocean, it is reported from Ecuador, Japan, Korea (Han and Yoo, 1983), the Gulf of Thailand, and the Gulf of Manila in the Philippines.

The designations "fratercula" and "fraterculum" are incorrect. Because it is a substantive in apposition, it should be written *fraterculus* in any genera in which it is located.

According to Noguchi et al. (1985), it did not produce PSP. However, in Uruguay, its presence coincided with outbreaks of toxic mollusks at a time when no other suspect organisms were observed in the plankton.

Alexandrium cohorticula (Balech) Balech

Plate XI, fig. 24-33

Gonyaulax cohorticula Balech (1967: 111, fig. 117-122)

Gessnerium cohorticula (Balech) Loeblich and Loeblich (1979: 44)

Protogonyaulax cohorticula (Balech) Taylor (1979: 51)

Alexandrium cohorticula (Balech) Balech (1985b: 37, fig. 5)

This species is similar to *A. fraterculus* in shape, size and chain formation. It is described in Balech (1967), therefore, I will only give complementary and differential details.

The epitheca is more regular and rounded than in *A. fraterculus* and does not have well-marked shoulders. The sulcal lists are well developed and project posteriorly when the thecae are observed in perfect ventral view.

The Po is much more regular than in *A. fraterculus*. The plate has a straight dorsal margin, although sometimes the dorsal-left corner is somewhat pointed. The ventral end is truncated and directly contacts the 1'. The connecting pore is large and elongated. 1' has a ventral pore that is clearly located in the posterior portion of the anterior right margin. The 2' margin with 1" is much shorter than the one in *A. fraterculus*. 3' is also asymmetrical but is more regular.

1"" is wider and has longer external margins than the 1"" in *A. fraterculus*. The large sulcal list is characterized by an abrupt narrowing in its lower third.

Almost all the sulcal plates are different from those in *A. fraterculus*, especially the S.a., which has a well-developed precingular part that is square or trapezoid-shaped. The S.p. is narrower and its connecting pore is irregular, oval, and longitudinally elongated.

The S.s.a. has a rather oblique anterior margin instead of a point, and its posterior external margin is always longer than the one in *A. fraterculus*. The S.s.p. is wider, sometimes narrowed a little in the posterior.

The S.d.p. frequently has thin grooves. The S.d.a is rather wider than it is in *A. fraterculus*. The median sulcal plates and the accessory plates are a little bit larger.

Sculpture consists of generally small, densely distributed pores. Pores are also found in some of the sulcal plates. Sometimes, very small pores are irregularly distributed in the cingular plates but are mainly concentrated near the margins.

Nucleus is rather narrow and sometimes rather twisted.

Dimensions: L 48-55, A 48-57 (equal or rather larger than L).

The most similar species is *A. tamiyavanichi*. The differences between the two are reported in the description of *A. tamiyavanichi*.

This is a warm-water species. Until now, it has only been found in the Gulf of Mexico and, apparently, in the Gulf of California.

Alexandrium affine (Inoue and Fukuyo) Balech

Plate XIII, fig. 20-36

Protogonyaulax sp. Fukuyo (1981: 14, fig. 1-5 and 35, fig. 1-5)

Protogonyaulax affine Inoue and Fukuyo (in Fukuyo et al., 1985: 30, fig. 1E, 3A-C and 24-29)

Alexandrium fukuyoi Balech (1985b, fig. 6(a,c), *nomen nudum*)

Alexandrium affine (Fukuyo) Balech (1985b: 38)

Cell is medium-sized, almost isodiametric, generally a little longer than wide, and convex-pentagonal. The epitheca is longer than the hypotheca and is conic-convex. It sometimes has a slight indication of shoulders, usually only on one side. The hypotheca is short and has an asymmetrical notch or antapical concavity that is noticeable and wide. This concavity is limited on the left by a small projection of the sulcal list. This species forms chains.

The Po is narrow, long, and fundamentally bullet-shaped. The dorsal margin is straight, short, and perpendicular to the lateral margins. The lateral margins are almost parallel in the dorsal two-thirds of the plate. Along this dorsal part, the left margin is slightly convex; the right one is straight or rather irregular but may occasionally be slightly concave. This dorsal section is generally followed by a short oblique ventral section. The ventral extreme may be acute but is more often briefly truncated. The main foramen does not form a true comma because it is oval and relatively small; it is located in the ventral half of the plate. The callus is short but well-developed. A connecting pore is located in the dorsal half of the plate and is large and almost circular. Frequently, a small notch replaces the right dorsal corner of the plate.

1' is directly connected with the Po and has a small ventral pore at about half height. The posterior end of the plate is straight. 3' is slightly to completely asymmetrical. 6" is medium wide. Its posterior left margin is reinforced, long, and concave. The anterior left margin is short and straight. The anterior margin, which borders with 4', is almost always concave.

1"' is trapezoidal and has a reinforced and concave internal margin. 1"" is narrow and has a list that is rather developed anteriorly but which narrows abruptly posteriorly. 2"" (type B) is narrow dorsoventrally, wide transversely, and boomerang-shaped.

The cingulum is descending (1) and quite excavated. The sulcus is excavated and does not penetrate into the epitheca.

The S.a. is somewhat longer than wide, has a rather regular shape, and is not very much wider posteriorly than anteriorly. The anterior margin is straight or almost straight, although it may be somewhat sunk in the center, and has a fold that is almost always short and oblique to the right. The right margin is moderately convex.

The S.p. is *tamarense*-type but wider. It has an obvious, round pore that is linked to the right margin by a small, well-marked channel.

The S.d.p. has a right margin that is smooth and regularly convex. The anterior and posterior margins are oblique. The internal margin is straight, but frequently both extremes are somewhat indented. The elongated S.ac.p. is located in the anterior-internal depression.

The S.d.a. has the accustomed triangular shape. Its length is approximately equal to its width. A fully developed S.ac.a. is located above its oblique anterior margin.

The S.s.p. is usually rather narrow though variable. The S.s.a. is moderately wide with a rather curved internal margin.

The median sulcal plates are about the same size.

The general plates have scattered pores that may sometimes be rather large.

The protoplasm is usually full of thick refracting bodies. The nucleus is located somewhat above the cingular level and has very thick and noticeable strands. In ventral view of the ends of the nucleus, approximately 34 strands may be counted.

Dimensions: In my material, the length fluctuates between 26.5 and 44. Measurements larger than 35 are exceptional. The largest specimens are almost imperceptibly wider than long. Width (A) varies between 24.5 and 44. Trd is 4 to 6.5 less than A. Cells are slightly flattened dorsoventrally. Fukuyo's L is 26-38.

The most distinguishing characteristic of this species is the shape of the Po, which differentiates it from all other species of this genus.

It was first reported by Fukuyo (1981), who published clear pictures of its Po and presented it as *Protogonyaulax* sp. Afterwards, when I found it in Korean material, I had no doubt about either its synonymy with Fukuyo's species or its taxonomic novelty.

I decided then to dedicate this new species to its discoverer and present it at the Third Conference on Toxic Dinoflagellates (Balech, 1985b). However, a little before the meeting, I learned that Inoue and Fukuyo would present it at the same time as *Protogonyaulax affinis* n. sp. Therefore, at the end of my manuscript, I reported *A. affine* as a new combination. However, the name *fukuyoi* was not eliminated from the key or the figure and becomes, therefore, an invalid name without proper diagnosis or publication.

Distribution: It is found in Japan (the Sea of Okhotosk, rarely the Bay of Mutsu, and the interior Sea of Seto). It is also found in Korea (Bay of Jinhae), Spain (Vigo), Portugal (culture 268 from Sousa e Silva), the Gulf of Thailand, and the Philippines (Bay of Manila).

Alexandrium tamiyavanichi Balech

Plate XIII, fig. 1-19

Protogonyaulax cohorticula (Balech) Taylor, *sec* Kodama et al., (1988); non *Gonyaulax cohorticula* Balech (1967)

Alexandrium tamiyavanichi Balech (1994)

Cell is medium-sized, isodiametric or a little wider than long. In ventral view, its contour is rather regular. This species forms chains.

The epitheca is short and is either somewhat cone-shaped or the equivalent of about one-third of a sphere. In some individuals, one or both sides may have more or less marked shoulders.

The hypotheca is a little longer than the epitheca. In ventral view, the right flank is more or less regularly convex. The left flank, however, usually shows an inflection at half height. The sulcus penetrates into the epitheca forming a concavity. The lists are fully developed and are projected a little posteriorly at the antapex. The descending (1) cingulum is deeply excavated and has a curtain fin.

The Po is irregularly oval and wide. The right margin is usually straight or a little concave, but sometimes it is a little convex. The central comma is large with a strong callus that is projected somewhat dorsally. Several small marginal pores occur along the left margin. The connecting pore is medium-sized and is located near the right margin of the comma's head. Two or three minor pores are located more ventrally, close to the callus.

1' is rather wide and has extensive contact with the Po. A small ventral pore is generally located in the posterior portion of the anterior right margin. The posterior margin of this plate is very peculiar because its border with the S.a. forms a reinforced, short, irregularly concave, and very oblique margin.

3' is asymmetrical. Sometimes, it shows some thin, vertical grooves that begin at the posterior margin. 4' is rather wide. Sometimes, it has a small notch that contributes to the formation of the ventral pore. 6" is rather wide.

5"' has a reinforced internal margin that supports a conspicuous list. 1"" is narrow with a reinforced internal margin that is irregularly undulated. It sometimes has an anterior and a posterior convexity separated by a middle concavity; otherwise, only an anterior convexity continues with an almost straight posterior half. The sulcal list is convex. It is wide anteriorly but narrows posteriorly. 2"" is wide (type B).

The S.a. is typical. It is long and composed of two parts. The posterior or more typical part of the plate has a long and sharp-pointed unciform apophysis. It is separated from the anterior part by a transversal bar that almost always forms an anterior concavity. The anterior or precingular part usually forms a triangle but occasionally forms a trapezoid. The left side is frequently somewhat concave.

The S.p. is *tamarense*-type. Its posterior attachment pore is not quite central and varies in size and shape, sometimes almost circular but more frequently irregular or elliptical. A narrow furrow connects it to the right margin of the plate.

The S.s.a is rhomboidal and medium-wide. Its anterior-internal margin is frequently strongly reinforced. The S.s.p. is typically shaped and quite short.

The S.d.p. is relatively long in most of the thecae. The anterior margin is oblique and reinforced. Its external corner is sometimes rather projected. The posterior margin is convex or angular. The S.d.a. is visibly wider than long.

Both median sulcal plates are pentagonal and fully developed. The S.m.p. is elongated and much more narrow than the S.m.a., which is approximately as wide as it is long.

The S.ac.a. is well-developed. It is usually triangular and sharp-pointed at the posterior. The S.ac.p. is very small and granulated.

The general plates are densely perforated by pores. Old thecae have small perforated bumps. Between the bumps are smaller pores with margins that are not thick. Sometimes, all the thecal surface has irregularities that tend to appear reticulated.

The protoplasm is dark. The nucleus is at cingulum level. It is transversely elongated and banana-shaped.

Dimensions: L 31-41.5, A 31-41.5, Trd 26.5-35.5. Although the extreme dimensions indicate cells as wide as they are long, more frequently the width (A) exceeds the length by 2-3 µm.

Discussion: This species shares with *A. kutnerae* and *A. cohorticula*, a very distinctive character: the S.a. has a well-developed precingular region bordered posteriorly by a transversal bar or rib. However, *A. kutnerae* is much larger and has a very different globose shape. In *A. kutnerae*, 1' is narrower and frequently is connected with the Po indirectly. Its ventral pore is almost always enclosed within the 1' plate and, sometimes, is even displaced inward and separated from the margin. The 1'''' of *A. kutnerae* is wider and more regular. 2'''' is more regular and not clearly transversely elongated. It does not form chains. Its S.p. is narrower, almost never with a connecting pore. The S.d.a is approximately as long as it is wide.

The most similar species to *A. tamiyavanichi* is *A. cohorticula*, so much so, that it was presented as *A. cohorticula* by Japanese researchers (see synonymy). Both are chain formers and their sizes are equivalent. However, *A. cohorticula* has a more irregular shape and an epitheca that is longer than wide. Its Po is comparably longer and more sharp-pointed. The comma is not central but is somewhat displaced ventrally and, therefore, leaves a wider dorsal margin. 1' is narrower and more irregular and has a straight and more or less horizontal posterior margin that contrasts with the curvature and large obliquity of the corresponding margin in *A. tamiyavanichi*. The left sulcal list of *A. cohorticula* is exceptionally wide anteriorly and it abruptly lessens posteriorly. The S.p. has a connecting pore that is larger and oval. The S.a. of *A. cohorticula* has a precingular portion that is longer and square, limited posteriorly by a very strong and straight or almost straight bar. Its S.s.a. is longer and has a different shape. Its S.d.a. is not wider than long. Its S.d.p. is generally more robust and it does not have such an oblique anterior margin.

In perfect ventral view of an *A. cohorticula* theca, the hypotheca appears shortened, which results in the right margin of 1'''' and the posterior margin of 5''' being located more posteriorly. This posterior location combined with the increased width of the sulcal lists projects these lists behind the hypotheca, in a degree that is unique in the genus. This does not happen in *A. tamiyavanichi*. In summary, the differences in the posterior margin of 1', in the Po, in the S.d.a., in the S.a., and in the list of 1'''' seem to offer valid characters for the specific separation of this species. It can be supposed, however, that some other cited differences are phenotypical.

The studied material was from a culture established from material collected from the northern part of the Gulf of Thailand (Ang Sila). Afterwards, the species was observed in the Philippines (Bay of Manila) and, apparently, it is also found somewhat southwest of Thailand (Andaman Sea).

As suggested by Dr. Piyankarnchana, I devoted this species to Prof. Suthichai Tamiyavanich, a pioneer of research concerning red tides and intoxication by dinoflagellates in Thailand. He died in an accident while collecting material for these studies.

INCERTAE SEDIS

This section is composed of those taxa that cannot be integrated into defined groups, those that are similar to known species but are not clearly related, and species that are evidently independent but were insufficiently studied and cannot be presented as new.

Alexandrium concavum (Gaarder) Balech

Plate XVII, fig. 24-29

Goniodoma concavum Gaarder (1954: 27, fig. 32 (a-f))

Gonyaulax concava (Gaarder) Balech (1967: 108, Pl. VI (108-116))

Alexandrium concavum (Gaarder) Balech (1985b: 37, fig. 17 (a-b))

In ventral view, the cell is pentagonal, somewhat longer than wide. The epitheca is conic, truncated, and rounded on the apex. Its flanks are rather undulated. The hypotheca is as long or somewhat longer than the epitheca and has smoothly concave flanks. In perfect ventral view, an antapical concavity either does not exist or is barely evident. When the antapex is somewhat raised, it appears to be flat or slightly convex. The cingulum is strongly excavated and descending (1). It has rudimentary lists. The sulcus is rather deep and is narrow anteriorly.

1' has the typical shape for *Alexandrium*. It is rather oblique-rhomboidal and sharp-ended anteriorly. It either contacts the Po directly or is connected by a short filament. The ventral pore is small but easily perceived and is located a little below the midpoint of the anterior right plate margin.

Postcingular plates are long. 1'''' is long and narrow. It has an undulated internal margin that is not very reinforced and supports a narrow left sulcal list. 2'''' is narrow, oblique, and transversely elongated (type B).

The S.a. is rather wider than long with a strong posterior sinus that is rounded and reinforced. The unciform apophysis is curved. A transversal fold, which is somewhat concave, crosses the plate near the convex anterior margin. The S.p. is the most frequent type, sometimes with a notch in the right margin. The S.d.p. is long. The S.s.p. is long and narrow, especially posteriorly. The S.s.a. is medium-wide. The S.d.a. has a triangular shape and is rather wider than long. The median sulcal plates are fully developed. The accessory plates are small.

All the general plates have small pores that are rather densely and very irregularly distributed. Sometimes, sutural bands are present.

Protoplasm is clear. Chloroplasts are very pale, elongated, and rather sinuously shaped. They radiate from the center where the nucleus is located. The nucleus is medium-sized. It is transversely elongated, but less so than in the other species, and in some individuals, is almost spheroid.

Dimensions: L 51-80, Trd 45-64.5.

The species is poorly studied because it is rare. In spite of its size (the largest of the genus), its tabulation is scarcely discernable because of its delicate thecal walls. Therefore, many tabular details still need to be revealed.

Unlike most of its congenera, this species is oceanic, a characteristic that contributes to its rarity. Gaarder (1954) obtained it in several oceanic Atlantic stations. I studied it in water samples that were collected in the Gulf of Mexico and Caribbean Sea far offshore (Balech, 1967) and in one sample off Brazil (Balech, unpublished data).

Another reason for its uncertain position is that it differs in shape from all other *Alexandrium*. Instead, it may be confused with *Protoperidinium*.

The apparent lack of contact between 1' and the Po explains why its discoverer assigned it to the genus *Goniodoma*.

Karsten (1907, Pl. 54, fig. 7) reported a spherical, planktonic cyst that contained two dinoflagellates with *Protoperidinium* aspects; they were called "*Peridinium* sp." They did not have visible tabulation and were presented in a more or less lateral view. I reported a similar discovery (Balech, 1962) for which I could partially determine epithecal tabulation that corresponded to *Alexandrium* and could only be similar to the Gaarder species. Interestingly, Karsten's discovery was from the Indian Ocean while mine was from the tropical Pacific, approximately half way between Central America and Hawaii. Taylor (1973) found these "cysts" again in the Indian Ocean.

Taylor (1972) reported Michener's unpublished observations of this species from Pacific samples. Michener's drawings are the most complete that have been done for this peculiar Peridinioidea; her drawings are very interesting and detailed, and thus are very important.

From all this, Taylor deduced that the "*Peridinium*", which were similar to *Gonyaulax*, found in the transparent spheres from the Pacific and Indian oceans and the free forms from the Atlantic studied by Gaarder and myself were the same organism: a thecal stage of the genus *Pyrocystis*. Meunier and Swift (1977) supported the conclusions of Taylor.

Two elements in these affirmations are disputable: the specific identity and the generic assignment. Regarding the former, I believe that the only studies with enough tabular detail are Michener's for the "cyst" forms (I believe that the observations and drawings should be attributed only to her) and Gaarder's and mine for the free forms. Given these studies, the specific identity of the Indian and Pacific forms is very doubtful. On the other hand, the Atlantic forms have not been found, so far, inside of spherical bladders. Although similarities exist, discrepancies are also evident. According to Michener's drawings, a very peculiar ventral pore occurs in her specimens near the posterior end of 1'. Whereas, in the Atlantic specimens, the type and location of this pore are normal. In the Atlantic specimens, the Po is longer and is fully visible in anterior-dorsal view. Its comma is more ventrally located. The S.s.a is rather wider in Michener's drawings (in Taylor, 1972) and the antapical plates look very different. Because of the above, the synonymy of all these forms is not only rather doubtful but also unlikely.

Loeblich and Loeblich (1979) did a lucid analysis of Taylor's suppositions and concluded as I did above. They said 1) that the *?Goniodoma concavum* that I presented in 1962 is not the same organism that I described in 1967 as *Gonyaulax concavum* and 2) that this latter one looks only superficially like the thecal forms of *Pyrocystis*. The Loeblichs and I differ however in the taxonomic importance given to the apparent disconnection between Po and 1' observed by

Gaarder. Additionally, they preferred the generic designation of *Gessnerium* for *concavum* and the group of species that I assigned to *Alexandrium*.

Concerning the generic assignment, I think that more weight should be given to the thecate form. Therefore, even the forms found as pairs inside the spheres and cysts should be located in *Alexandrium*. Consequently, the name *Pyrocystis* is only being maintained for practical reasons to designate vesicular stages of dinoflagellates that may correspond to very different genera. Even as early as 1921, Kofoid and Swezy (1921, p. 62) held this point of view and said that earlier notes (probably the Michener observations mentioned above) show that the "*Pyrocystis* stage" is an integral part of the life cycle of genera as different as *Gymnodinium* and *Gonyaulax*. In my opinion, these *Pyrocystis* stages seem more typical of pelagic species than of neritic species.

Alexandrium sp. I

Plate XVII, fig. 30-34

The cell is small-sized, rather flattened anterior-posteriorly. This species forms chains. Epitheca has barely marked shoulders and a slight apical protuberance. Posteriorly, the hypothecal flanks abruptly curve inward to join with the somewhat asymmetric antapical concavity. The descending (1) cingulum is deep and has strong lists. The sulcus is rather excavated and widens posteriorly with barely conspicuous lists.

The Po is oval, relatively small. It has a well-emphasized comma. The connecting pore, which merges with the larger alveole, is rather large and dorsally located. 1' is rather narrow. The anterior tip is sharply pointed and is connected by a very short filament to the Po. The anterior right margin is concave to straight and has a ventral pore. 6" is relatively long and medium wide.

1"' is long. 1"" is narrow and has a short posterior internal margin and an exceptionally long posterior external margin. 2"" is almost as long (in dorsoventral direction) as wide and is a transitional type.

S.a. is longer than wide. S.p. is almost elliptical and has an anterior margin that is interrupted by a deep V-shaped depression. The connecting pore is circular and centrally located.

All the general plates and the S.p. are noticeably reticulated.

Dimensions: L 42-44, Trd 38.5. The cell is clearly wider than it is long, but width was not measured.

Only a short chain of this interesting species was found in the Gulf of Mexico in a sample collected at 24°18'N, 88°26'W on February 28, 1965. This very brief description is based on notes taken then. It is probably an undescribed species, but the limited data prohibit its description as a new species. The only other known species that is completely reticulated is *A. insuetum*, which is very different in its shape, size, 1', and other tabular details and is not a chain-former. The region where it was found should be explored to obtain material for a reliable study and a formal description.

Alexandrium sp. II

Plate XI, fig. 13-23

The cell is generally rather wider than long, sometimes isodiametric. The epitheca has either no shoulders or barely emphasized ones. Usually shoulders are only on the right side; individuals with both shoulders clearly outlined are rare. The hypotheca has a somewhat flexuous left flank. The posterior concavity is shallow and may incline slightly. The descending (1) cingulum has thick lists.

The Po is medium-wide. Both lateral margins are subdivided into two parts, although sometimes the left margin is somewhat irregularly convex. The right margin has a dorsal half that is straight and outwardly oblique and a ventral half that is concave and slopes in the opposite direction. The ventral end is truncated. The callus is thick. One to three (usually two) medium-sized secondary pores are found along the right side. Sometimes small marginal pores are located on the left side.

1’ is directly connected to the Po. Its anterior right margin is concave with an angle in the middle or a little below the middle. The posterior end is briefly truncated. There is no ventral pore. 3’ is rather variable in relative height and in asymmetry. 6" has a reinforced and curved posterior internal margin that has a strongly reinforced and projected posterior corner.

The internal margin of 1"’ is strongly reinforced, concave, and oblique. It supports a narrow list. The external border is twice as long. 5"’ is rather narrow, practically triangular. Its internal margin is not reinforced, is somewhat concave in the middle, and supports a rather wide sulcal list.

1"" has a convex or S-shaped internal margin (concave anteriorly and convex posteriorly) that supports a well-developed list. Because the list is positioned almost perpendicularly, its fullness is only appreciated when the plate is in an oblique position. The posterior external margin is oblique and short. 2"" is transversely elongated (type B).

The sulcus is rather wide. S.a. is almost as long as it is wide. The posterior sinus is rather deep. The unciform apophysis is regularly convex. In the anterior-right corner of the plate, an oblique fold is usually present. S.p. has the usual *tamarense* shape. A small- to medium-sized connecting pore, which varies from not quite circular to clearly longitudinally elongated, is located near the right margin.

The S.s.a. has a reinforced anterior margin that is sometimes so oblique that it appears to be continuous with the internal margin. The length of the posterior triangular portion is a little bit more than a third of the plate’s total length and the posterior external border is short. The S.s.p. has the usual shape and is somewhat narrowed posteriorly. The ratio of length to width varies, but usually the plate is clearly longer than it is wide. The S.d.a is somewhat longer than wide. The S.d.p. also varies in the length/width ratio and in the convexity of the external margin. The anterior and posterior margins are oblique, more pronounced on the posterior.

The median sulcal plates are relatively large; the anterior one is wide, the posterior one is narrow. The accessory plates are small, especially the posterior.

The nucleus is transversely elongated, sausage-shaped, and rather thin.

Dimensions: L 31-43, usually less than 38. A 32.5-46.5, generally greater than L. Trd 26.5-39.5, slight dorsoventral flattening, 2 to 4 µm less than A in the medium-sized specimens.

Discussion: Considering the general characteristics, shape, tabulation, and absence of a ventral pore, this material from Mexico is similar to *A. catenella* and *A. fundyense*. In the studied sample, the majority of the specimens formed chains with 2 to 6 individuals, but I do not know if it should be considered a chain-forming species because some non-chain-forming species occasionally have linked individuals that form small chains of up to four, rarely six, cells. The truly catenate species form chains with more than eight cells. Possibly, this material contained long chains that fragmented during handling and shipment; however, Dr. Leon Alvarez says that he does not recall seeing chains.

The chain-forming species closest to the present material is *A. catenella*, which usually is more flattened (although it can become less flattened, especially in cultures). *Alexandrium catenella* usually has a 1’ with a straight or scantly curved anterior right margin, and the plate is wider in most specimens. The Po has a dorsal margin that is wider and straighter. Its foramen looks more like a comma and it has a distinctive connecting pore to the right of the comma’s head. However, in *A.* sp. II, the main pore is smaller and is located to the right of the callus, which is a more ventral position. The margins of 2’, 3’, and 4’ in *A. catenella* are reinforced and elevated. They often have denticulations that have not been observed in the Mexican specimens. The sulcal lists are less developed than those in *A.* sp. II. 5"’ is wider. 1"" of *A. catenella* is narrower and has a shorter posterior margin. 2"" is narrower in the dorsoventral direction and has a somewhat different shape. The S.p. is wider and more rhombic with a larger connecting pore that almost always is triangular or elongated quadrangular. The posterior lateral sulcal plates are almost always wider. The S.d.a has an anterior internal margin that is more curved and less oblique. Almost always, *A. catenella* has segmented transversal crests on at least some of the hypothecal plates, especially 4"’.

I think that the most distinguishingly different features are in the S.p. and the antapical plates.

Between *A.* sp. II and *A. fundyense*, the differences are perhaps minor because their general shape and S.p. are similar. The Po is also similar between the two species and sometimes *A. fundyense* has a connecting pore near the callus. Also in *A. fundyense*, 1’ is wider and has a straight or almost straight right margin. The S.a. is longer and has a portion that often penetrates into the epitheca. The S.s.a. is longer. The anterior external margin of S.s.p is rather more inclined. Sulcal lists are smaller. 1"" is wider and its posterior external margin is rather longer. Finally, the S.p. of *A. fundyense* is more curved in side view.

As a whole, the differences exist, but they are very small and do not justify species distinction based on morphology alone. However, the two described species are found in habitats that differ from *A.* sp. II. *Alexandrium catenella* and *A. fundyense* are cold water species. Anderson (personal communication) reported that *A. fundyense* extends south along the North American Atlantic coast only to 40°30’N. However, *A.* sp. II comes from warm waters off Mexico.

In summary, I do not know if these individuals from Mexico correspond to a warm water subspecies or if they represent a taxon differentiable at specific level. At the moment, it is too difficult to decide based upon the thecal characters. Perhaps, cultures and biochemical studies could determine this.

This sample was from Pacific waters off Mexico (Chamela in the state of Jalisco).

Alexandrium sp. III

Plate XVIII, fig. 12-24

This taxon is presently somewhat enigmatic. It is similar to *A. catenella* because it has similar tabulation, lacks a ventral pore, and has a fully asymmetrical 3' as well as a similarly shaped 2"" and a rather wide S.p. Nonetheless, it also has some important differences: 1) the general shape is different, 2) the Po is narrower and does not have a connecting pore (sometimes small pores can be seen along the right margin), and 3) the S.p. either lacks a connecting pore or has a not quite circular one that is very different from the one in *A. catenella*. Because of these characteristics, it is closer to *A.* sp. II from Mexico. Both have well-developed sulcal lists. However, the shape of *A.* sp. III clearly differs from the shape of the other three species that lack a ventral pore: *A. catenella*, *A.* sp. II, and *A. fundyense*. All *A.* sp. III specimens studied are clearly longer than they are wide. This does not happen in *A. catenella* or *A.* sp. II and rarely occurs in *A. fundyense*. The shape is more reminiscent of *A. acatenella*, but the two are easily differentiated by tabular details.

The epitheca is conical, with or without shoulders.

To elucidate its status, it should be studied from samples collected at different times.

It was found in a plankton sample that was collected Jan. 8, 1988 from southeastern Australia (Port Phillip Bay).

Dimensions: L 35-42, A 31-37.5, Trd 26-33.

Subgenus *Gessnerium* Halim nov. comb.

Halim (1967) created this name for a Gonyaulacidae species that he thought was new. It is similar to the subgenus *Alexandrium*, except that 1' is not connected to the Po; the two plates are not linked in any way. The anterior right margin of the 1' in *Alexandrium* has been transformed into an anterior margin in *Gessnerium*. The epithecal patterns of the two subgenera differ, but the remaining cell characters are essentially the same, although the sulcal plates in some *Gessnerium* species differ from the typical *Alexandrium*.

Subgenus *Gessnerium* = genus *Gessnerium* Halim (1967: 729)
Species type *Gessnerium monilatum* (Howell) Loeblich (1970[2]) = *Gonyaulax monilata* (1953: 153, fig. 1-5) = *Gessnerium mochimaensis* Halim (1967: 729, Pl. IV (49) and Pl. VIII (101-108) (*mochimaensis* is a mistake for *mochimaense*).
Presently, nine species are assigned to this subgenus: *Alexandrium* (*G.*) *monilatum*, *A.* (*G.*) *balechii*, *A* (*G.*) *foedum*, *A.* (*G.*) *pseudogoniaulax*, *A.* (*G.*) *taylori*, *A.* (*G.*) *margalefi*, *A.* (*G.*) *insuetum*, *A.* (*G.*) *hiranoi*, and *A.* (*G.*) *satoanum*.

Alexandrium monilatum (Howell)

Plate XV, fig. 1-16

Gonyaulax monilata Howell (1953: 153, fig. 1-5)

Gessnerium mochimaensis Halim (1967: 729, Pl. IV (fig. 49) and Pl. VIII (fig. 101-108))

Gessnerium monilata (Howell) Loeblich (1970: 903)

Pyrodinium monilatum (Howell) Taylor (1976:110)

Cell size is medium to large. It is very anteriorly-posteriorly flattened, like a rather irregular loaf; sometimes epithecal shoulders may be noted. This species forms rather long chains. The apical pore region is somewhat projected and rather large. The cingulum is very deep, without lists, and descending (1-1.3). The sulcus abruptly curves dorsally in the portion containing the S.p. plate. There are no emphasized sulcal lists.

The Po is large and oval. Its dorsal margin is somewhat irregular and rather flattened. The left margin is regularly convex, and the right one is concave. The ventral end is sharply pointed. The foramen or comma is relatively small, is shaped almost the same as the plate, and barely extends dorsally beyond the midpoint of the plate. The callus is barely emphasized, but it extends almost to the comma's dorsal end in what seems to be the right margin of the reinforced or folded canopy. A large, almost circular connecting pore is located a little to the right of the comma's dorsal end. Small granules and pores are located on the plate's periphery.

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[2] This combination does not meet the requirement in the Code of Botanical Nomenclature, but in my opinion, it does meet those of the Zoological Nomenclature.

The very characteristic 1’ is short and completely disconnected from the Po. It is pentagonal and wider than long. The right anterior margin that borders 4’ is longer than the left anterior one. In cultured material from the U.S.A. (Galveston in Texas), this plate is much narrower (Pl. XV, fig. 5[right]) than in the planktonic material from a different U.S.A. location (Florida). Rarely, 1’ appears to have a ventral pore close to its anterior apex, but this could be the result of alterations in the general pores that are rather conspicuously located near the anterior margins. One of these could have enlarged or several could have combined. According to K. A. Steidinger (personal communication), a well-defined ventral pore occurs in Florida specimens.

2’ and 3’ have the usual shape for the genus. However, 3’ is larger, particularly in width, than in other species. Furthermore, in most thecae, 3’ has between one to four crests that extend from the margin that borders with the Po. They spread divergently towards the posterior margin but do not reach it.

6" is medium wide. Its sulcal margin is neither very concave nor strongly projecting posteriorly, as in several other species.

The external margins of 1"’ and 5"’ are not much longer than their internal margins.

1"" is short and wide. Its anterior and posterior margins are long and parallel. The two external margins are short and not quite equal. The internal margin is reinforced and convex and sometimes has a small roll or protuberance in the middle. 2"" (type B) is wide, short, and boomerang-shaped. Its dorsal margin, which touches the 3"’, is rather longer than the left side.

The ten sulcal plates are quite characteristic, especially the S.p., which is very different from those of the other species. The S.a. is rather narrow and has a posterior sinus that is regular and very deep. When the plate is not flattened, the anterior part is quite bent ventrally making the sinus seem to go almost to the anterior margin. When the plate is flattened, the anterior margin usually has a right part that is somewhat more elevated than the rest.

The S.s.a. is wide with reinforced anterior and right margins. The S.s.p. is characterized by having, along the internal margin, a prolonged reinforcement that is directed towards the anterior-right corner. This plate is rather short and wide.

The S.d.a. is triangular and approximately as wide as long. Its anterior-internal margin is oblique, lacks marked inflections, and has a reinforcement that is not very thick and is rather regular. The anterior internal corner is abruptly truncated. In this case, it is a true truncation -- abrupt, straight, and still somewhat concave.

The S.d.p. is a rather weak plate that tapers posteriorly. Its anterior margin has two parts: the right one is almost horizontal and the oblique left portion borders the S.ac.p. The internal margin is concave and the external is convex. Small pores can usually be observed near the plate margins. Pores are sometimes also seen in the S.s.p.

The S.p. is the most distinct plate in this species. It is large, wide, and rhomboid. Its anterior corner is replaced by a short, V-shaped cavity. The edges of the cavity form two folds that converge on a large, central, circular pore. From this pore, a narrow, small channel extends towards the anterior right margin. The channel is straight or flexuous and has elevated margins. Also from this pore, small crests or folds are directed towards the other margins. These folds vary in number.

The two median sulcal plates are rather large and elongated. In most of the other species, the S.m.a. has a strongly oblique axis to the right, but in this species, it is longitudinal and aligned with the S.m.p. axis.

The two accessory sulcal plates have a somewhat exceptional size for this genus. The S.ac.p. is pentagonal and almost as wide as long (in almost all the other species, it is very small and, particularly, very narrow). Its anterior margin is reinforced. The size of S.ac.a. is similar only to a few other congenera, such as *A. pseudogoniaulax* and *A. margalefi*. Its shape is a little reminiscent of an inverted and horizontal L.

The general plates have numerous small pores.

The protoplasm is dark and contains chloroplasts that radiate from the center. The nucleus is equatorial with the characteristic banana-shape. It is very large and rather anterior-posteriorly flattened, which causes it to appear thicker in apical or antapical view than in ventral view. Its chromosomes are relatively homogeneous, but thick and dense. When the nucleus is observed from either end or in transverse section, it has a honeycomb appearance.

The longest chains that I observed had 22 to 24 individuals (more frequently 16). However, Howell, who studied fresh and more complete material, counted up to 40 individuals in some chains.

The sexual reproduction of this species was studied by Walker and Steidinger (1979).

Dimensions: L 28-42, A 39-67, Trd 33.5-60. The thickness is from 1 to 7 µm less than the width. Halim talks about a width of 57-70 and Howell found larger variations: L 24-51.5.

This species is unmistakable. The characters that most easily distinguish this species are the general shape and the S.p. Undoubtedly, the species that Halim called *Gessnerium mochimaense* is the same that Howell described so well.

This species is found in the Atlantic littoral of the U.S.A. (Florida), in the Gulf of Mexico, off Venezuela (Caribbean), and off Ecuador (the Guayas River estuary).

Studied material: plankton from the U.S.A. (Pensacola Bay in Florida), culture from the U.S.A. (Galveston, Texas), and pictures of specimens from Ecuador.

Alexandrium balechii (Steidinger) nov. comb.

Plate XIV, fig. 1-23

Gonyaulax balechii Steidinger (1971: 183, fig. 1 (A-D))

The cell is medium-sized. The epitheca is long and conical with sides that are generally concave near the cingulum. The apex is variable from largely convex to more or less flattened. The hypotheca is almost always a little shorter. Its shape can vary from rounded or rather irregular to trapezoid with a somewhat convex and quite asymmetric posterior outline. The hypotheca is often rounder than the epitheca and, therefore, is wider near the cingulum.

The cingulum is fully excavated, descending (approximately 1), with thick margins. The sulcus, however, is moderately excavated. The cruciform region is very peculiar because the S.a. plate is angled up to the right and its acute anterior right edge projects into the epitheca.

The Po is oval with the dorsal side more or less flattened. The left side is gently convex, while the right side is obscurely divided into two almost straight segments. The ventral tip is almost always pointed. The comma or foramen is large and has a slightly marked callus. It is surrounded by a peripheral thickening that is perforated by numerous small marginal pores. Frequently, this thickening is interrupted at the right side by a cut or notch that is located where the two segments of the right margin join.

The 1' is short, completely disconnected from the Po, and has a very irregular pentagonal shape. It has two straight lateral margins of which the left one is quite larger than the right one. Of the two anterior margins, the left is very short, sometimes almost a vertex, and it articulates with the ventral edge of 2'. The posterior margin is reinforced and sinuous and is formed by two parts. The left part is almost horizontal and the right one is markedly oblique. The thickening caused by the reinforcement is considerable where the two segments join each other. There is no ventral pore.

The 2' is mostly on the dorsal side and ends ventrally in a point or in a very short and oblique margin. The 3' has the usual wide hexagonal shape with variable asymmetry. The 4' is quite long and ends ventrally in a point. The 6' is small and triangular and does not share a common margin with 1'. Its anterior vertex may not even touch 1'.

The hypotheca has a short, robust 1"" that is more or less subdivided into two parts and has a strong thickening on the right margin. The posterior left margin is short. The anterior corner is clearly truncated. A sulcal list is not detectable. The 2"" is clearly elongated in the dorsoventral direction (type A). Its margin with the S.p. is straight or slightly convex and not concave as in almost all other species.

The S.a. is wide, short, and oblique and has an anterior margin that is concave in the center. The large posterior margin has a sinus. The left branch of the plate is short and wider than the right branch, which is the unciform apophysis.

The S.p. is relatively narrow, long, almost arrowhead-shaped, and pointed at the posterior. The reinforced anterior margin has an angle that is sometimes almost symmetric but, at other times, the left half is horizontal and the right is markedly oblique. Of the two left margins, the anterior one is vertical, shorter, straight, and articulated with 1""; whereas, the posterior one is very oblique, straight, or rather concave. The right margin can be divided into an anterior main part and a more or less short posterior part. This description corresponds to most of the Italian specimens, but, in many of the North American (U.S.A. [Florida]) specimens, this plate is much shorter.

The S.d.p. is a typically shaped plate that is more or less an elongated rectangle with wide borders. The anterior left corner is briefly truncated to house the S.ac.p. plate. The S.d.p. has numerous pores, especially in its right half where they tend to form longitudinal lines. The S.d.a. has the usual triangular shape and, in this case, has equal lateral sides. Its reinforced, anterior-internal margin is abruptly folded at both ends.

The S.s.p. has a long and almost completely straight margin that in other species is called the anterior-left. Both the S.s.p. and the S.s.a. have an unusual but very characteristic shape. Additionally, the S.s.p. usually has lines of pores. The S.s.a. is clearly differentiated from its counterpart in congeneric species because it is superficially positioned and because it is wide, almost triangular, and short. Its truncated posterior left corner connects with 1"". The right part of the anterior margin curves anteriorly, coinciding with a similar curvature on the posterior margin of C_1. The posterior margin of the S.s.a. is slightly sinuous.

The two accessory plates are adequately visible. The S.ac.a. is triangular, narrow, and relatively large with a concave anterior margin. It is found lying upon the anterior-internal margin of the S.d.a. The S.ac.p. is much smaller and quadrangular, but it is somewhat easily detected due to its robustness. The median plates, however, are very difficult to see, not because of their size but because of their thinness. They are almost membranous and, therefore, easily damaged or lost. The S.m.p. is narrower and fits in the concavity of the short anterior-internal border of the S.s.p. The S.m.a. almost closes the posterior sinus of the S.a.

The cingulum, delimited by thick margins, is descending (<1) although the S.a. increases the apparent displacement of its extremes. A peculiarity of the cingulum is the constriction of its left end by the upward twist of the posterior, but not the anterior, margin of the C_1. Noticeable pores are close to the margins.

The general plates have a peculiar sculpture, exceptionally marked for this genus. The epitheca has pores that are densely, but irregularly, distributed and are variably sized. Occasionally, some small and irregular crests or slight reticulation can be seen. The hypotheca has, besides the pores, very irregular crests or ridges that, on some occasions, form a very strong and heterogeneous reticulation when the ridges connect with each other. Rarely, the S.p. can show developing crests.

Dimensions: L 25-42, A 24-39.5, Trd is 4.5-7.5 less than A. The species is quite variable in size and the L/A relation also varies. Steidinger (1971) found specimens up to 49 μm in both length and width.

This species was well-described in its original description.

Its structure is very different than the structure of its other congenera. It is useful to note that the S.a., S.p., S.s.a., S.s.p, and 6" plates along with the sculpture are very characteristic.

This species produced discolored water and bioluminescence in the two localities where it was found: the U.S.A. (Tampa Bay in Florida) and Italy (Gulf of Salerno in the Tyrrhenian Sea). According to Steidinger (1971), it is not toxic.

Alexandrium foedum

Plate XIV, fig. 24-32

Alexandrium foedum Balech 1990: 392, figs. 19-27

In ventral view, the cell is medium-sized and irregularly hexagonal with concave sides on the epitheca and hypotheca adjacent to the cingulum. The epitheca is almost trapezoid with a quite irregular and flattened anterior end. The hypotheca is flattened posteriorly and may be slightly depressed near the sulcus. In ventral view, it slopes upward to the right. In lateral view, the longitudinal axis is inclined.

The cingulum is very excavated and slightly descending (0.5-0.7). It has thick margins that support narrow membranes.

The Po is oval to triangular with marginal pores. The callus is barely developed.

The anterior edge of 1’ is far from the Po. 1’ is irregularly pentagonal with two major lateral sides. The right one is approximately half as long as the left one. To compensate, the right anterior side is very oblique and much longer than the left anterior side, which is very reduced in some specimens. There is no ventral pore. 2’ is ventrally projected in a very narrow part whose extreme is connected with the left anterior margin of the 1’.

The sulcal plates have very peculiar characteristics, especially the S.a., which is almost as long as it is wide. In its relatively long anterior margin, there is a very typical small notch that is unique in the genus. The S.s.a. is large. The S.s.p. is short and has an oblique anterior left margin that is much longer than the posterior left margin. The posterior margin is strongly oblique. The accessory plates are fully developed, especially the anterior one. The S.p. is long. Its length is at least double its width. Posteriorly, it is very obliquely directed toward the right and has a strong V-shaped anterior opening.

The rough surface appearance of this species is emphasized by the very noticeable, numerous, and irregularly placed pores on both the epitheca and the hypotheca. Pores are found in the cingular plates and in some of the sulcal plates.

Dimensions: L 37-49, A 40-53. A dorsoventral flattening is detectable.

The most related species is *A. balechii*, which is relatively longer and has a different sculpture. Its 6" is triangular and very reduced and all its sulcal plates are different from those of *A. foedum*.

This species is found in Italy (Gulf of Salerno).

Alexandrium pseudogoniaulax (Biecheler) Horiguchi, ex Yuki & Fukuyo

Plate XVI, fig. 1-18

Goniodoma pseudogoniaulax Biecheler (1952: 55, fig. XX-XXII)

Alexandrium pseudogonyaulax (Biecheler) Horiguchi (1983)

Alexandrium pseudogonyaulax (Biecheler) Horiguchi, Yuki *et* Fukuyo (1992: 398)

The cell is medium- to large-sized and irregularly pentagonal- shaped. The short, convex, wide, and dome-shaped epitheca is rather irregular and approximately equivalent to one-third of a sphere. The hypotheca is somewhat longer with a slight antapical concavity that is wide and slopes up to right. The descending cingulum (0.75-1) has practically no lists and is barely excavated.

The 1’ appears as the first precingular and is completely disconnected from the Po. It is wider anteriorly. The anterior margin is sloped to the right and is interrupted by a big notch or "ventral pore" that is wider than long. The left margin is divided into a short anterior segment that is one quarter to one half of the total length and oblique to the left. The posterior segment is sinuous and oblique inward. The posterior margin is reinforced and short. The anterior two-thirds of the right margin is straight, while the posterior third is oblique, concave, and reinforced to form the left side of an asymmetrical notch. The anterior part of the S.a is located in the notch. The right margin of this notch is formed by the 6".

The remaining apical plates are typical of *Alexandrium*. It should be noted that the right margin of 3’ is about half the length of the left margin. The Po is oval and rather regular. In some specimens, its right margin tends to be straight, but in others, it is almost as convex as the left one. The dorsal side is regularly curved, sometimes it may be pointed or flat. The ventral end is always pointed. In some specimens, the foramen is a fishhook-shaped groove with a short right hook. In others, the foramen is a poorly defined, narrow comma with a barely evident callus. In the plate periphery around the comma or hook, numerous, irregular pores are present.

In the hypotheca, 1"" is large and wider than long with a slightly reinforced sulcal edge. 2"" is large, pentagonal, and almost completely located in the left side of the hypotheca. The sulcus has several distinct peculiarities. It lacks lateral lists. It penetrates somewhat into the epitheca in an asymmetrical way, oblique towards the right. The S.p. is very large, very lateral, and directed obliquely to the right. The S.s.a. is very large with strongly reinforced anterior and right margins; it clearly has hypothecal characteristics.

The S.a. has a quite long, irregular precingular portion that is not delimited posteriorly by a crossbar or dividing bar. The body of the plate expands left below the anterior cingular margin. The left branch, with a somewhat oblique posterior margin, is rather wider than the unciform apophysis. The S.p. is very irregular. It has an asymmetric ventral notch and a somewhat irregular oblique branch that makes the left ventral side different from the right ventral side.

The S.s.p. is a short trapezoid that is wider posteriorly (more than twofold) than anteriorly. The posterior-left corner is truncated. The anterior-right corner is prolonged in a thin apophysis that is sharp-pointed and quite long (0.5 of the plate body’s height). The S.s.a. is an asymmetrical pentagon that is longer than wide. The reinforced anterior margin has a horizontal left portion and an oblique right portion that supports the S.m.a. The internal margin is straight, rather long, and also reinforced. The two oblique posterior margins are not reinforced. The right posterior margin is shorter and articulated with the left side of the S.s.p. The left posterior margin articulates with 1"". The left margin, which is longest, is almost straight and somewhat oblique.

The S.d.p. is very large and elongated (2.5-3 times longer than wide). The external margin is convex and sometimes rather sinuous. The posterior margin is oblique posteriorly. The left margin is clearly divided into two portions. The anterior portion, where the well-developed S.ac.p. is located, is a little shorter and slightly more concave than the posterior portion. The S.d.a has a very oblique anterior margin. The posterior-right corner is noticeably truncated at its articulation with 5"'.

The median sulcal plates are large. The S.m.p. is long and narrow with an oblique anterior margin, which has a reinforced anterior-right edge that is sometimes extended a short distance down. The right margin of this plate shows a peculiar membranous portion that is approximately 0.5 of the margin height. This list is usually visible on the ventral side of the plate. It could never be separated, therefore, I consider it an integral part of the S.m.p. The S.m.a. is approximately as wide as long and has an oblique and somewhat sinuous right margin. This plate fills the posterior sinus of the S.a.

The S.ac.a. is located upon the anterior margin of the S.d.a. to which it is similar because of its shape. It is exceptionally large. The S.ac.p. is elongated, pointed posteriorly, and larger than in any other species.

The theca has very thin, hyaline walls. With the light microscope, they look smooth and lack pores.

The chloroplasts radiate from the center to the periphery. The nucleus is very large, transversely elongated, and curved. In some cases, it appears somewhat twisted with easily seen chromosomes.

Dimensions: L 41-51, maximum A 58-69.5, Trd usually 4-6 less than maximum width. The cell is moderately flattened dorsoventrally.

Discussion: The generic assignment of this species has been questioned since its discovery. Biecheler specified that the epitheca corresponds to *Goniodoma* but that the hypotheca is more like *Gonyaulax* with the exception of the S.p. (Biecheler's "X"), which is more lateral and does not seem to extend the sulcus. Very accurately, she brought attention to the similarities with her *Gonyaulax dimorpha* and the homology of the "first precingular" with 1' from the latter.

Indisputably, this species is connected to both *Goniodoma* and *Alexandrium*. The arrangement and general morphology of the epithecal plates correspond to *Goniodoma* with two important exceptions: 1) the 1' plate, which appears as a precingular, is connected with two apical plates and 2) the Po is directed posteriorly (toward the 1' plate) instead of laterally.

The sulcus differs between genera. In *Goniodoma*, the S.a. is always rough and wide and has a very deep posterior sinus. The S.d.a. is also very different in its shape. In the three well-analyzed species of *Goniodoma* (see Balech 1979a), the S.s.p. has the typical shape that is characteristic of that genus. Based on what we currently know, *Goniodoma* lacks accessory plates, and the two median sulcal plates are located far apart, whereas in *Alexandrium*, they are in contact.

Given the characteristics described above, I unhesitatingly place this species in the genus *Alexandrium*, subgenus *Gessnerium*. This species also demonstrates that the S.s.a. or Kofoid's 1"' is a transitional plate because in *A. pseudogoniaulax*, the S.s.a. has the characteristics of a truly postcingular plate.

As Biecheler noted in this species, the protoplasm separates very easily from the theca, rounds up, and excretes a mucilaginous substance. In samples from Norway (Fiekkefjord) that were collected in July and August 1984, the individuals that I examined were in the mucilaginous state and were abundant. In one sample, they were dominant and many of the normal individuals became stuck in these mucilaginous masses.

Sousa e Silva sent me several samples of cultured material cataloged as this species. Unluckily, almost all of the thecal plates separated before arrival. From the sample that she personally delivered to me in Canada, I was able to rescue a few almost whole thecae. These thecae cultured in Portugal had quite different shapes from the Norwegian material. They were almost always longer than wide, and the epitheca was not short. Their approximate dimensions were L 41-54, A 41-49. However, two specimens (L 44, A 47.5, and L 41, A 44.5) had a very typical shape, especially the smallest specimen. The general plates, especially 1', and the S.p. were essentially equal to those just described, but the thecal distortions, which are characteristic of cultures, prevented a deeper analysis. Based on the above observations and on the results of recent studies, the taxonomic designation of the cultured material from Portugal is uncertain. Other *Alexandrium* (*Gessnerium*) were described recently that, while very similar to *A. pseudogoniaulax*, are clearly different from it. Japanese researchers, after first misidentifying these species as *A. pseudogoniaulax*, created two new species: *A. hiranoi* and *A. satoanum*. Perhaps, the Portuguese strain belongs to *A. hiranoi*. The characteristics of another European taxon found in France by Nezan (personal communication) also appear to agree better with those of *A. hiranoi*. Both European taxa appear to be more similar to *A. hiranoi* than to *A. pseudogoniaulax*; however, detailed tabular study is required before identifications may be ascertained.

The combination *Alexandrium pseudogoniaulax* was first proposed in Horiguchi's doctoral thesis and thereafter accepted by Kita and Fukuyo (1988). However, this proposal did not fulfill the requirements of the codes of nomenclature concerning the distribution of a paper, and therefore, the combination was not legally established. This was confirmed by a letter that I received from Horiguchi in which he said, "I do not regard my Ph.D. thesis as an official publication." The final step to transfer the species to *Alexandrium* legally has been taken by Yuki and Fukuyo (1992).

The correct spelling of the epithet is still, in my opinion, uncertain. According to Article 32 of the Code of Zoological Nomenclature, the original spelling of a name is retained unless it contradicts provisions of Articles 26-31 (which does not occur in this case) or it is the result of an "inadvertent error." "Inadvertent" is the key word. Evidently, *pseudogoniaulax* is not a *lapsus calami*, a copyist's or printer's error. Instead, following the example of Schiller in his 1937 monograph of the dinoflagellates, Biecheler accepted the spelling of *Gonyaulax* as *Goniaulax* even though the latter is wrong. Still, did Biecheler make an "inadvertent error"? Furthermore, this issue is further complicated if we consider that, from an etymological perspective, both spellings are acceptable.

It is a coastal and interior brackish water species that is found in southern France, Norwegian fjords, Portugal, and Japan.

Alexandrium taylori Balech

Plate XV, fig. 17-35

Alexandrium taylori Balech (1994)

Cells are medium-sized and rather pyriform. The epitheca is usually a little shorter than the hypotheca, somewhat flattened ventrally and sometimes slightly depressed at the apex. The sides are slightly concave above the cingulum. The hypotheca is more or less trapezoidal. In some specimens, it is rather long. The antapical region is flattened or slightly concave and sloped upward to the right slightly.

The cingulum is well excavated. It does not have lists but it does have reinforced margins. It is descending (1) and has a curtain fin that extends between the anterior and posterior margins of the cingulum. The sulcus is narrow and not very excavated.

The Po is rather large, oval or triangular, and more or less straight on the dorsal side. It has a well-delineated comma that almost reaches the dorsal margin. The callus is usually thin. The marginal pores are small and hardly noticeable.

The 1' is short and pentagonal, although the posterior margin is subdivided into a straight horizontal left portion and a curved right portion that houses the anterior part of the S.a. The greatest width occurs between the posterior ends of the two straight anterior margins. They are oblique and uneven because the left margin is very short. This plate does not have a ventral pore. Rarely, a small notch can be seen near the anterior vertex.

However, the ventral pore exists and is rather large. It is almost exclusively excavated in plate 4' and is located in the confluence point of the 1', 2' and 4' plates. The 4' is rather wide, but its posterior margin towards 6" is short. Occasionally, it has not one, but two ventral pores. The 2' and 3' are typical of the genus. The 3' is almost symmetrical in the majority of the specimens. The 1' usually contributes to the formation of the ventral pore, but not as much as 4' does.

The 6" plate is quite a bit longer than wide. Its posterior left margin, which borders with the S.a., is reinforced and is almost straight or smoothly curved.

The 1''' has a narrow membranous prolongation of its right margin. A strong vertical crest is found close to this margin. The 5''' also has a narrow sulcal list that is supported by its left margin.

The antapical plates are relatively large. The 1'''' is transversely extended with a long margin bordering the 2''''. The 2'''' is pentagonal and slightly asymmetrical.

In the sulcus, the S.a. has a right portion that penetrates into the epitheca. The left portion of the anterior margin is wider. The posterior sinus is deep. The S.p. is long, relatively narrow, and very oblique to the right. It has a V-shaped anterior notch that markedly slopes to the right. This plate has two left margins: the shorter anterior one that articulates with 1'''', and the posterior one that articulates with 2''''. Most S.p. plates have an oblique groove that extends from the right margin to the center at least. This groove is usually oblique, is sometimes curved, and, on some occasions, continues toward the left margin. Frequently, it ends in a pore; sometimes, it is essentially formed by a succession of differently sized pores.

The two posterior lateral plates are very distinctive. The S.d.p. is long and narrow, especially posteriorly. The S.s.p. is shorter with a reinforced right margin that is longer than the rest. The reinforcement is projected anteriorly like a small spine. The short anterior margin supports a relatively large S.m.p. Likewise, the S.m.a. is large. It is oblique, is more extended transversely, and closes the posterior sinus of the S.a.

The S.s.a., which in this species looks more postcingular than sulcal, is large and pentagonal. It is almost uniform in width and has fully reinforced internal margins. Its anterior-right corner is truncated and supports the S.m.a. The S.d.a. does not have special characteristics, but its oblique anterior-internal margin supports an S.ac.a. of exceptional size. The much smaller S.ac.p. is located near the posterior-left corner of the S.d.a.

The whole theca has thin walls. Therefore, the numerous pores in the plates become difficult to resolve with bright field microscopy.

The protoplasm is very dark and full of food reserve bodies that make it difficult to perceive the nucleus that is located at cingulum-level and is very transversely elongated and curved.

Dimensions: L 31-44, A 32-46, Trd 27-37.5. Most of the specimens are somewhat wider than long, but others are isodiametric or almost as long as they are wide. The relationship between the epithecal and the hypothecal height is also variable. Some specimens have a hypotheca that is conspicuously longer than the epitheca, but in other specimens, the two are almost the same.

Discussion: Undoubtedly, this species is very closely related to *A. pseudogoniaulax* Biecheler, with which it was confused before both were studied in detail.

One of the characteristics that place *A. taylori* in *Alexandrium* rather than in *Goniodoma* is its thin theca that does not have strong areolation or conspicuous lists. Another is the fact that 1' touches 2', whereas in *Goniodoma*, the 1", which is the equivalent of 1' in *Alexandrium*, is disconnected from the left apical plate.

Alexandrium taylori differs from *A. pseudogoniaulax* in both shape and size. *Alexandrium pseudogoniaulax* is larger, and its epitheca is more flattened. Furthermore, *A. pseudogoniaulax* has a 1' that has a much narrower posterior margin and an anterior margin that is interrupted by the large notch of the ventral pore. It also has a more oval Po. On the Po, the comma ends far from the dorsal margin, and marginal pores are very visible. The two antapical plates are very different, and all the sulcal plates differ rather clearly. I especially emphasize that *A. pseudogoniaulax* has the strong anterior-left hook of the S.p. plate, a large S.ac.p., a very distinctively shaped S.m.p., an S.m.a. that is not transversely elongated, and the clearly different S.d.p. and S.a., which is longer and narrower.

The material I studied is from a planktonic sample from France (Arcachon) collected on August 14, 1985. It was abundant and clearly dominated the sample.

The specific name honors the prominent specialist, F.J.R. Taylor, who has produced highly significant studies.

Alexandrium margalefi Balech

Plate XVI, fig. 19-32

Alexandrium margalefi Balech (1994)

Cell is medium-sized with a subspherical to irregularly pentagonal shape. In some specimens, the wide, conical epitheca has a rounded apex while in others, the apex is slightly pointed. The epitheca does not have distinct shoulders.

The hypotheca is convex and either almost hemispherical or somewhat antapically flattened. The antapex can be sloped slightly upward toward the right. In some small specimens and in somewhat oblique view, a deep antapical notch can be seen.

The cingulum is fully excavated, lacks lists, and is barely descending (approximately 0.5). The sulcus is wide and barely excavated.

The Po is oval, large, and rather regular, although, in some thecae, the ventral half of the right margin can be almost straight or rather concave. The comma is large and leaves a relatively narrow flange on the left side where quite regular marginal pores can usually be seen. The well-developed callus penetrates into the cavity as a rather long, oblique, and blunt spur.

The 1' is completely disconnected from the Po. It is short and shaped as in *Goniodoma*, but its anterior margin does not have the marked obliquity observed in *A. insuetum* and in the species of *Goniodoma*. It is almost always curved. A ventral pore is present in the anterior-left corner of the plate (an unusual position) and is delimited by both the 1' and the 4'.

The 2' is large and has the usual shape, except in the relative length of its right ventral margin, which is articulated with 4'. The 3' is hexagonal and wide, as it usually is in congeneric species. It is asymmetric and comparatively wider than in most other species. The 4' is approximately as wide as long and has six sides. As expected, it is modified by the displacement of 1'.

The 6" is rather narrow. Due to the slight descent of the cingulum, the posterior left margin of 6" is rather short. Also, it is abruptly curved, encompassing the most projecting part of the S.a.'s anterior margin.

In the hypotheca, the 1"" is large and relatively wide. Its slightly reinforced right margin is subdivided into three rather noticeable segments. The anterior and middle segments are short and linked to the left lateral sulcal plates. The posterior segment, which is as long as the other two, borders the anterior half of the S.p. The list is narrow. The 2"" is a little wider than long. It has two ventral margins, not quite equal, that border the S.p. and 1"", and two lateral margins, slightly different in length, that border the 2"' and 4"' plates. The dorsal border is longer than the other plate margins and is either straight or somewhat sinuous.

The S.a. is wider than long. The posterior sinus is deep and the left branch is rather wide. A more or less accentuated but narrow prominence that penetrates into the epitheca is found on the anterior margin. The S.p. is longer than wide and has an extremely oblique anterior margin delimited by two rather inconspicuous projections. In some specimens, a notch occurs in the right margin.

The S.s.a. is short, very wide, and fully visible in whole thecae. The anterior margin is relatively wide. The right posterior margin that borders the S.s.p. is longer than the left posterior margin that touches 1"". The right margin is somewhat reinforced and clearly subdivided into two portions, each portion bordering a median sulcal plate. The S.s.p. is wide and exceptionally short. It is usually approximately as wide as it is long but is sometimes wider than long. The left margin is more convex than usual and, on some occasions, has a blunt projection above the midpoint.

The S.d.p. is clearly longer than the S.s.p.; usually the S.d.p. is twice as long as the S.s.p. The anterior and posterior margins are very oblique. The posterior margin has a very short horizontal part. The somewhat concave or straight left margin has a short anterior oblique segment, where the small S.ac.p. is located. The right margin is gently convex. The S.d.a. is triangular, rather regular, and somewhat longer than wide.

Both median sulcal plates are rather large. The S.m.p. is long and narrow, whereas, the S.m.a. is oblique and elongated in the transversal direction.

The S.ac.a. is relatively large, thin, triangular, and located in the normal position, i.e., at almost half height of the S.d.a's anterior-left margin.

The general plates show, besides very delicate pores, superficial irregularities that tend to form a diffuse reticulation.

Dimensions: Most of the thecae are isodiametric, but some are longer than they are wide or *vice versa*. L 27.5-39, A 27.5-35, Trd 5 to 7 less than A. The theca has a very small dorsoventral flattening.

Discussion: *A. margalefi* is very clearly differentiated from all the species that have the 1' plate positioned away from the Po. *Alexandrium balechii* has a very different shape and is clearly differentiated by the 1' shape, by the lack of a ventral pore, by the very small 6" that is almost disconnected from the 1', by the antapical plates, and by its very peculiar sulcal structure. *Alexandrium monilatum* has a totally different shape, a clearly different Po, a 1' that is wide with two very sloped anterior margins, no ventral pore, and an unmistakable S.p. The accessory sulcal plates are well-developed and the other sulcal plates are very distinct. *Alexandrium insuetum*, unmistakable because of its strong reticulation, is ovoid in shape and has a well-marked epithecal vertex, an apically located nucleus, a Po that is also reticulated, and a 1' with a sloping anterior margin on which a ventral pore is located at about the midpoint. Its antapical plates and, especially, its sulcal plates are clearly different. The shape of both *A. pseudogoniaulax* and *A. taylori*, especially their hypothecae, is different from the shape of *A. margalefi*. Also, their 1' plates have two oblique and straight anterior margins, instead of only one that is curved and horizontal. The location of the ventral pore is different in all three species. Their antapical plates and sulcal plates are also very different, especially the S.a. and the S.p.

The above comparisons clearly separate this organism as a new species. It is dedicated to the prominent hydrobiologist and ecologist Dr. Ramon Margalef, in respect for his studies of plankton, including dinoflagellates, and for his international leadership in aquatic ecology.

This species was obtained from Spain (the Ria de Vigo in Galicia).

Alexandrium insuetum Balech

Plate XVII, fig. 1-23

Alexandrium insuetum Balech (1985b: 37, fig. 1a-b)

The cell is small and rather regularly oval. The theca is reticulate. The epitheca is conic-convex, is more sharp-pointed anteriorly than is usual for the genus, and lacks shoulders. The hypotheca is rounded, has a very slight posterior asymmetry, and is approximately the same length as the epitheca. The cingulum is well-excavated, descends (1), lacks lists, but has fairly thick flanges. Sulcus is medium-wide, and its left margin has a clear anterior protrusion at the location of the S.s.a.

The precingular plates are long. The Po is irregularly oval to almost triangular and has a straight dorsal margin. Its right margin is almost straight and is sometimes subdivided into two straight segments; the left margin is strongly convex. The comma or foramen is centrally located and is delimited by strong peripheral alveoli. The barely visible and short callus corresponds to the internal wall of an alveolus that is almost ventral, is on the right side, and is somewhat larger than the other alveoli.

1' is a *Goniodoma*-type plate and is completely disconnected from the Po. Its left margin is longer than the other sides and is convex. The short anterior part of the left margin articulates with 2', is more or less straight, and is more inclined than the longer posterior part. The anterior margin is oblique and is interrupted by a ventral pore. The right margin is almost straight as is the posterior margin, which is the smallest of the four.

2' is rather dorsoventrally elongated and its margin towards 3" is relatively long. 3' has the usual hexagonal shape, but it is rather long and almost symmetric. 4' is rather wide. Its left margin borders with two plates in addition to its border with the Po. The anterior part of the left margin connects with 2', is a little longer than the posterior portion, and is vertical or scantly oblique to the left. The posterior part touches the anterior margin of 1' and is very oblique outward.

The 6" is somewhat longer than wide. Its posterior internal margin is almost straight and is moderately reinforced.

The 1"" plate has a very regular shape, is longer than wide, and has five almost straight sides. The two internal margins, of which the anterior is longer, form a very open angle and support a very narrow sulcal list. The two external margins form a more closed angle. The anterior external margin, which borders 1"', is more oblique than the posterior external margin, and, in some specimens, is almost twice as long. The posterior margin is straight and horizontal. 2"" is somewhat wider than long and has an almost central location. It has two anterior margins; the left one touches the 1"" and is straight and rather shorter than the right one, which is smoothly concave and touches the S.p.

The sulcus is slightly excavated. The S.a. is longer than wide and its relatively long, anterior margin is straight. The posterior sinus is fully visible but is not very long. The S.p. is wider than long and has a regularly concave anterior (ventral) margin. The posterior margin has moderate convexity.

The S.s.a. is irregularly rhomboid and not very wide. However, because it does not lie within the sulcal cavity, it is readily visible in the anterior portion of the left sulcal margin. It has two distinct external margins of which the anterior is approximately twice as long as the posterior. The internal anterior margin is somewhat sinuously convex. Grooves begin at some of the plate margins but do not continue to the opposite margins. The S.s.p. is pentagonal, rather narrow, and wider anteriorly than posteriorly.

The S.d.p. is rather regularly shaped and has slightly sloped anterior and posterior margins. The lateral margins are almost parallel (the plate is sometimes a little wider in the posterior). The anterior part of the internal margin has a small, shallow, but well-marked notch that houses a small S.ac.p. The S.d.a. is approximately as long as it is wide. The median sulcal plates are relatively large. The S.ac.a. is very small and narrow.

All the general plates have a well-defined reticulation, which includes some perforated nodules. Usually the nodules are more regular and more abundant near the cingular margins. Sculpture in the cingulum is composed of irregular longitudinal crests that may end in perforated nodules. Striae occur on the S.p. plate and some other sulcal plates. These striae, generally short, almost never connect to enclose spaces.

The protoplasm is dark. Refracting bodies occur in the posterior two-thirds of the cell. In the anterior third, there is a helmet-shaped clear space, almost totally occupied by the banana-shaped nucleus, which has very thick chromosomes.

Dimensions: L 26.5-28.5, A 24-26.5, Trd 19.5-22. The DV measures around 2 µm less than the Trd. The dimensions are remarkably constant; the length of almost all the specimens is from 28 to 28.5.

It is a very characteristic species due to 1) an epitheca that is oval and almost acuminate, which is not found in other species, 2) its reticulation, 3) the aspect of the Po, 4) the *Goniodoma*-type 1', and 5) the anterior location of the nucleus, which is not typical of the genus. However, its sulcal structure places it securely in the genus *Alexandrium*.

Because of all these peculiarities, it was named using the Latin adjective *insuetum* that means "unusual, extraordinary".

It was obtained from Korea (Jinhae Bay) in a sample that was collected on September 21, 1982. Yuki and Yoshimatsu (1990) found it in Japan (Seto Inland Sea).

Alexandrium hiranoi Kita and Fukuyo

Plate XVIII, fig. 25-27

Alexandrium hiranoi Kita and Fukuyo (1988: 2, fig. 1 a-f and Pl. I a-k)

Cells are usually isodiametric or a bit longer than wide. The epitheca is convex-conical. The antapex has a moderate flattening that slants a little obliquely toward the anterior from left to right. It has a shallow sulcus. The cingulum is gently concave. The Po is narrowly oval, its lateral sides are almost parallel in most of their length, and its dorsal margin is straight and oblique. It has a strong callus and numerous marginal pores. 1' is pentagonal and narrow. Its right anterior margin is very slanted and has a ventral pore in the middle. 2"" is pentagonal and transversely elongated (type B). The S.a. is rather wide. The S.s.a. is long and narrow. The S.d.p. is long, narrow, and much longer than the S.s.p. The S.p. is long and slants very much to the right from the ventral end to the opposite border.

Dimensions: L 18-75 (average 40), Trd 18-75 (average 37).

It is found in rockpools of Japan (in the Prefecture of Kanagawa on Jogashima Island and in Arasaki).

It is a good species. It is most similar to *A. pseudogoniaulax*, but the two are easily distinguished because *A. hiranoi* has an almost isodiametric form with a rather long epitheca, a differently shaped 1', and apparently all differently shaped sulcal plates. Kita and Fukuyo (1988) make *A. pseudogoniaulax sec* Sousa e Silva (1965) a synonym of this species.

Alexandrium satoanum Yuki & Fukuyo

Figure I

Alexandrium satoanum Yuki et Fukuyo (1992: 395-399, figs. 1-12)

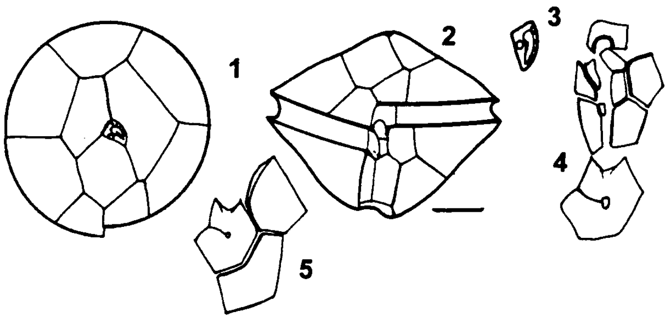

Figure I: 1-5. *A. satoanum*: 1) apical view; 2) ventral view; 3) Po; 4) sulcal plates; 5) the two antapical plates, 1"", and 2"", and S.p. The bar, indicating 10µm, refers to 2). (Adapted from Yuki and Fukuyo)

This species is medium-sized, broadly pentagonal in ventral view, and wider than long. The epitheca is shaped like a broad, short cone that has slightly convex lateral sides. The cingulum is median, deep, and descending (1); it has very narrow lists. The hypotheca is trapezoidal in ventral view and has almost straight sides. The antapical concavity is very noticeable and ascends somewhat to the right. The deep sulcus is bordered by narrow left and right lists.

The Po plate is rather narrow and triangular. Its dorsal and right margins are straight; its left one is regularly and strongly convex. The comma is rather small. A rounded connecting pore is located to the right of the comma's head. Several marginal pores occur along the plate's left margin.

The 1' is asymmetrically pentagonal. Its two anterior borders are quite different: the left one (connected with 2') is very short, and the right one is long and very slanted. This species does not have a ventral pore. The 3' has the usual almost symmetric hexagonal shape. In the hypotheca, the 2"" is type B.

In the sulcus, the S.a. is rather short and wide. Both left lateral plates (S.s.a. and S.s.p.) are wide; both right plates are narrow. The median and accessory plates are well-developed. The S.p. is the *tamarensis*-type and has a round or elliptical connecting pore located in the center.

Dimensions: L 30-38, A 40-50. The cell shows a slight dorso-ventral compression.

Discussion: Initially, this species might be misidentified as *A. pseudogoniaulax* because both species have a rather similar outline. However, their tabulations differ greatly. The shape of all the apical plates differs between the two, especially 1', which in *A. pseudogoniaulax* has a conspicuous ventral pore. Striking differences also occur between their antapical and sulcal plates.

Because of the anterior-posterior flattening, *A. satoanum* vaguely resembles *A. monilatum*, although the latter is differently shaped, forms chains, and has a large Po and a large dorsally located connecting pore. Between the two species, the apical plates and the sulcal plates differ, especially the S.p., which is quite typical in *A. monilatum*. The other species of the subgenus *Gessnerium* (*hiranoi*, *taylori*, *margalefi*, *balechii*, *foedum*, and *insuetum*) differ because they have a different shape, a ventral pore, and an evident difference in the sulcal plates, especially in the S.p.

This is a good species, well-described. Toxicity has not been reported.

This species has only been found, so far, in Japan (Matoya Bay) where it frequently occurs in rather warm waters (18-23°C).

SPECIES *INQUIRENDAE*

I include here several species, assigned either to "*Gonyaulax*" or to some other genus such as *Goniodoma*, that are probably *Alexandrium*. However, because the validity and independence of these species have not been demonstrated, these taxa are invalid or doubtful at the moment. I did not study them personally.

The species in the specialized literature that are in this category are the following:

Gonyaulax lebourae Balech (1979a: 102) = *Goniaulax orientalis* Lindemann *sec* Lebour (1925: 92, Pl. XIII 3a-d), *non* Lindemann

Gonyaulax dimorpha Biecheler (1952: 50-55, fig. 26-29)

Goniaulax conjuncta Wood (1954: 258, fig. 161)

Pyrodinium phoneus Woloszynska and Conrad (1939: 1-5, fig. 1-12)

Alexandrium depressum (Gaarder) Balech and Tangen (1985: 342) =*Gonyaulax depressa* (Gaarder) Balech (1979a: 105) =*Goniodoma depressum* Gaarder (1954: 28, fig. 33)

Gonyaulax catenella sec Postek and Cox (1976)

Gonyaulax lebourae Balech

Plate XVIII, fig. 1-2

Goniaulax orientalis Lindemann *sec* Lebour (1925: 93, Pl. XIII 3a-d, *non Gonyaulax orientalis* Lindemann (1924: 222, fig. 24-27), *nec Goniodoma orientale* (Lindemann) Balech (1979a)

Gonyaulax lebourae Balech (1979a: 102)

Lebour (1925) presented this organism, probably an *Alexandrium*, as the Lindemann species *ut supra*. This seems peculiar because Lebour's and Lindemann's species have different tabulation. Indeed, I demonstrated that this latter species of Lindemann's did not belong in *Gonyaulax* but belonged instead in *Goniodoma* (although the status of this generic name is uncertain) (Balech, 1979a). It is also odd that this former organism of Lebour's has not been found by any other specialist, even though Lebour reported it in two samples from each of three places that were distant from one another (the Bosporus, the English Channel, and the coast of England [Plymouth]). We also do not know if her dinoflagellate with a strongly alveolated theca from the Bosporus is the same species as her dinoflagellate with a smooth theca from Plymouth. In fact, her drawings only include material from the English location. According to the drawings, this questionable taxon is very similar to *A. tamarense*. It is unusual that Lebour did not make any comparison between this material reported as *G. orientalis* and her new species *A. tamarense*. Possibly, Lebour's epithecal plate interpretation for the former was the cause of this omission; the apical tabulation shown in her fig. 3c is almost surely an error because a probable 3' plate is missing. This odd tabulation could have resulted from an oversight of the author or from an anomalous theca with the 3' and 4' plates fused. Given these oddities, one might suspect that Lebour's *G. orientalis* is the same organism as the new species that she figured on Plate XIV. However, it seems unlikely that the researcher who described the new species would not recognize such a similarity if it existed. Indeed, even if the apical plate formulas were determined to be the same, the two organisms are sufficiently different to argue against synonymy: the contact between 2' and 3' is much briefer in *orientalis* than it is in *tamarense*, and the hypothecal plates are appreciably different. In summary, information about the organism that I called *Gonyaulax lebourae* is insufficient.

Pyrodinium phoneus Woloszynska and Conrad

Plate XVIII, fig. 10-11

Pyrodinium phoneus Woloszynska and Conrad (1939: 3-5, fig. 1-12)

Gonyaulax phoneus (Woloszynska and Conrad) Taylor (1975)

Woloszynska and Conrad (1939) described a new species of dinoflagellate that was globose, had a very delicate theca, was toxic, and produced brown-pink discolorations in the sea channel that links Bruges with Zeebrugge in Belgium. The same species has reportedly caused discolorations in the water of the Lilloo fortifications at the right border of Escaut, north of Anvers in Belgium. This location is mesohaline (about 2 - 14 ppt salinity). This species is similar to those of the group *ostenfeldii* in *Alexandrium*; it is not a synonym of "*G. excavata*" as supposed by Steidinger (1973) and Taylor (1975). The discoverer of this taxon did not perceive (or did not annotate) a ventral pore. Nonetheless, this species undoubtedly belongs to the group *ostenfeldii* because of its shape, the aspect of 1', and the type-A 2"". Possibly, it is the Paulsen species, *A. ostenfeldii.*

Gonyaulax dimorpha Biecheler

Plate XVIII, fig. 7-9

Goniaulax dimorpha Biecheler (1952: 50-55, fig. 26-29) (as spelled by Biecheler)

Undoubtedly, this species would belong in the group *ostenfeldii* of *Alexandrium*. It is also the best-studied of these doubtful species because its description is of the same high quality as all the works of this excellent investigator who died prematurely and before her thesis was published. However, in the half century since her death, this group has been intensely studied, some very similar species have been described, and much more importance is now given to sulcal structures. Consequently, it is now very difficult to determine whether this species is independent from or synonymous with the other two well-known species of this group, *A. ostenfeldii* and *A. peruvianum*. Furthermore, there is another uncertainty because, according to Biecheler, it has two different shapes: one that is not quite globose, as in the described species, and another that is narrow and clearly elongated. I think that the conspecificity of these two forms is still to be demonstrated. If both shapes were the same taxon, the elongated form would probably correspond to zygotes or to some kind of thecal distortion. The common form would be the not quite globose, more or less isodiametric shape that has a width of 30-35 µm.

For several years, I tried to obtain material from the salt lagoons in southern France without success. The original type location does not exist anymore, but stations with similar characteristics to the type region should be explored.

If Biecheler's drawings were completely accurate, the S.a. projects into the epitheca, and the S.p. has a rather different shape from that in the other species of the group. Unfortunately, if adequate material from the south of France is not obtained, the real situation cannot be elucidated.

Alexandrium depressum Gaarder

Plate XVIII, fig. 3-5

Goniodoma depressum Gaarder (1954: 28-29, fig. 33a-h)

Gonyaulax depressum (Gaarder) Balech (1979a: 105)

Alexandrium depressum (Gaarder) Balech and Tangen (1985: 342)

Based on tabulation, this species is unquestionably an *Alexandrium*, probably from the *ostenfeldii* group with which it shares the narrow 1'. This plate has a very curved or bent anterior right margin and the transverse groove that divides it was already observed by Biecheler in *Goniaulax dimorpha*. Because the epithecal tabulation is typical of *Alexandrium* (or, at the time when the species was described, typical of "*Gonyaulax* from the tamarensis group"), it is strange that Gaarder located the species in *Goniodoma*, especially since she recognized its resemblance to "*Gonyaulax tamarensis globosa*" (now *A. ostenfeldii*). However, the shape of *G. depressum* raises doubts about Gaarder's species being synonymous with *A. ostenfeldii*: her drawings show a more or less biconic theca that is wider than long (her L/A ratio is 0.79). If her drawings b-f are correct, 2' is very different from the one in *A. ostenfeldii* and the S.s.a. might be larger. Therefore, Tangen and Balech (1985) formally transferred it to the genus *Alexandrium* keeping the species name, even though the species should be reexamined in order to complete its validation. The "diameter" (we did not know if this dimension referred to the longitudinal or transversal axis) equals the length of *G. dimorpha*.

Goniaulax conjuncta Wood

Plate XVIII, fig. 6

Goniaulax conjuncta Wood (1954: 258, fig. 161)

This species appears to be an *Alexandrium*. However, almost nothing is known about it. It has a regular shape and is a little longer than wide. Its cingulum is descending (1). It forms chains.

Even when published, its description was totally inadequate because the epithecal and hypothecal tabulations were incompletely represented, dimensions were not provided, and comparisons with other taxa were inadequate. Indeed, Wood only refers to *Gonyaulax catenata* and *G. series*. However, *G. catenata* is so different from *Alexandrium* and *Gonyaulax* that it was transferred to another genus (Balech, 1977), and *G. series* is a questionable species that may actually be based on an anomalous chain. On the other hand, he does not mention "*G. catenella*", which, at the time of his description, was the only chain-forming species that was tabularly similar to his *conjuncta*. Upon close examination, his drawing appears to be incorrect: 1' is not like the 1' of any of the known *Alexandrium* species and an antapical plate is missing from the right side of the hypotheca. This omission contradicts the formula given in the text; such discrepancies between drawings and description occurred frequently with this author.

If *G. conjuncta* does belong to the genus *Alexandrium*, as seems probable, it could be any of the chain-forming species of the *fraterculus* group. However, because adequate comparisons are lacking and the description contains seriously inaccurate statements, *G. conjuncta* should probably be a null name.

Gonyaulax catenella sec Postek and Cox

Gonyaulax catenella Whedon and Kofoid *sec* Postek and Cox (1976); *non Gonyaulax catenella* Whedon and Kofoid (1936)

In 1974, Postek asked me to confirm the identification of a *Gonyaulax* that they were studying; he sent copies of photographs that are Figures 10 and 11 in their published paper. I responded that, although I was not positive, I did not believe that the organism was Whedon and Kofoid's *G. catenella*. Apparently, my opposite opinion did not satisfy the authors because the paper was published using *G. catenella* without mentioning the consultation or my opinion. Today, after acquiring more experience of the genus, I have no doubt that their organism was misidentified. The taxon they studied is not *A. catenella* because *A. catenella* has a different general shape, is concatenated, and lacks a ventral pore. Postek and Cox's Figure 11 is a praiseworthy effort to determine and reconstruct the thecal elements but is only partially successful. The Po is inverted; consequently, the dorsal end appears as ventral. The 1' is also inverted and would have to be rotated 180° to be correctly positioned. 4' is not only inverted but is also inside out. For some reason, neither 3' nor 6' are recognizable, perhaps due to strong deformation. 6''' (5''' according to my notation) is badly oriented. The S.p. is evidently fragmented and perhaps folded.

In spite of these objections, the paper is meritorious. Its Figure 9 is the best photograph of the lateral, median, and accessory sulcal plates that has been published so far, although the authors did not recognize the independence of the accessory plates. This photograph seems to support Fukuyo's assertion that a very small eleventh sulcal plate exists, but its independence as a separable plate must still be proved. I must point out that, in certain positions of the S.d.a., a membranous fold may be observed on the anterior-internal margin. This membrane might appear to be a tiny plate, but it never separates as an independent plate.

In the photograph that I received of an entire specimen, the theca is very regularly globose, which differs from the other known species. I think that this form is an artifact caused by the fixation procedures for electron microscopy because the form shown in the light micrograph of their Figure 2 resembles that of *A. tamarense*.

GEOGRAPHIC DISTRIBUTION AND TOXICITY

The primary purpose of this paper is to provide a foundation for the morphological and taxonomic studies of the genus *Alexandrium*, which has been recognized officially but imperfectly since 1960. However, I am adding this section to complement the primary information.

In 1937, a small team of North American investigators (Sommer et al., 1937) discovered that a species belonging to the "group of *Gonyaulax*" caused the very dangerous Paralyzing Shellfish Poisoning (PSP) in bivalve molluscs. This major discovery greatly intensified the study of this genus. Later studies brought to light two important facts: 1) that other species within the same group produced toxins of the same kind and 2) that, in fact, it was not only one toxin but a complex of toxins in which the fundamental component is a tetrahydropurine. At the time of this writing, 13 of these toxic compounds had been characterized. All of them produced the same symptoms in warm-blooded animals, but the toxic activity and intensity of each one differed considerably. The ingestion of small amounts of PSP can produce severe symptoms and even death in man. Consequently, since 1937, medical and economic reasons have prompted many scientists to intensify their own studies and to encourage others in the study of these organisms. Investigators of this genus include not only planktologists and protistologists, but also chemists, physiologists, medical doctors, hygienists, and others.

This increased interest is also reflected in how the *Alexandrium* species complex has been enriched over time. Until 1925, only one species was known (*A. ostenfeldii*), and it was not even placed into *Gonyaulax*, which has been the most commonly used genus for this group of dinoflagellates. Until the late 1940's, the number of known species was four. In the next decade, two more were described. In the 1960's, three more were added. The genus *Alexandrium* was also created but was practically forgotten until 1985. Through 1976, the number of species published for *Alexandrium* and "*Gonyaulax* group *tamarensis*" was nine. Since then, the number has increased threefold and will probably increase rapidly for some time to come.

Furthermore, the geographic area known for several of these taxa has expanded considerably. Until the 1980's, only three species reportedly had a wide distribution: *A. catenella*, *A. tamarense*, and *A. concavum* (this latter species is not abundant and reports may represent several species). However, we know now that the genotype is found not only in Egypt but also in several places in Europe, Asia Minor, the U.S.A., and Australia. As a whole, the genus is distributed worldwide, except in the Antarctic. *Alexandrium* species have been reported in waters of the Mediterranean, the Gulf of Mexico, and the Caribbean and has been observed along the coasts of western Europe, Iceland, the Faeroes Islands, Newfoundland, southeastern Canada, almost all of the eastern U.S.A., eastern South America from Santos (Brazil) to the southern tip of the continent, South Africa, western South America from southern Chile to Ecuador, western North America, Korea, Taiwan, Japan, Thailand, Australia, New Zealand, and the Philippines.

Two questions have arisen lately: 1) can a species have both toxic and non-toxic representatives and 2) are some species expanding into new areas? The answer to the latter is uncertain because an apparent expansion could be the result of improved monitoring programs and increased awareness of the genus which facilitates identification.

I use my experience as an example. Despite my extensive studies of dinoflagellates, I did not document the genus in South American waters until 1964, nor did I read of it in published literature for this region. The first species that I observed in the South American Atlantic littoral was *A. fraterculus*, which was obtained for the first time from the Brazilian Current in 1954. I considered it a new species, but I did not publish a description (because of insufficient study) until 10 years later, after I obtained good material in 1962 (Balech, 1964). Much later, the first human intoxications in Argentina caused by PSP were reported in 1980 when *A. tamarense* was confirmed. Two inevitable questions arise: 1) has the genus been present but previously undetected in the Argentinian Sea and 2) were these really the first intoxications caused by PSP in my country? The answer to both is the same: we do not know.

With regard to the last question above, previous intoxications may have occurred. Certain societal circumstances contribute to this uncertainty. For example, in Argentina (Patagonia), where the presence and abundance of *Alexandrium* were well documented, the population is very scattered along most of the coast, communications are difficult, and medical assistance for many inhabitants is sporadic and delayed. Considering the tremendous speed at which the toxin may act, medical assistance may be ineffective for many people. By the time that the doctor comes from his far-away residence, the patient has either died or recovered already. Furthermore, the doctor probably knows nothing about this kind of intoxication because it was unknown in this country until 1980. He will probably make a generalized diagnosis such as food poisoning or respiratory or cardiac problems.

Further indication that toxic events may have occurred before in South America comes through verbal lore in which discolored water has, indeed, been reported in South American waters. Because we know that *Alexandrium* blooms may sometimes cause discolored water, such events in South America could possibly be due to *Alexandrium*. Additionally, while the water was discolored, some people did not eat mollusks, which indicates the existence of some oral tradition about the danger of consuming bivalves during these times. Unfortunately, we have no written documentation about these possible blooms in South America nor do we have any information about the causative organism.

Another consideration that is insufficiently studied is the possibility of acquired immunity to the toxin(s). Patagonian inhabitants habitually consume mollusks, and studies from 1980-81 demonstrated that many people who consumed bivalves from areas with high toxin levels suffered moderate or no consequences. In contrast, the two fishermen who died in 1980 from PSP were not from the area and came from the Buenos Aires province.

Another circumstance, which suggests prior intoxications, occurred before this first official report of PSP intoxication in Argentina. I had some rather vague references to intoxications occurring after fresh mussels and clams were consumed. So, in 1973, I published a warning and asked for collaboration. Interestingly, some of these intoxications were more similar to those caused by Diarrheic Shellfish Poisoning (DSP), which results from a toxin that is different from PSP and is produced by dinoflagellates of another order.

At least one reference to bivalve intoxications in South America is available from the early 1890's. In a speech to the Society of the History of the Medicine of Buenos Aires, Zarranz (1983) revealed that, in 1891, the physician P. Segers studied intoxications of the Yaganes natives of Tierra del Fuego (southern tip of South America). These intoxications were caused by ingesting bivalve mollusks and could have been PSP. These events were reported by the newspaper La Prensa on July 23 and August 1, 1891. Because we cannot be sure that PSP was the cause (although it probably was), we certainly are unsure about the identity of the causative organism, although the most likely species would be *A. catenella.*

Given all of the above information, the 1980 intoxications may not have been the first for Argentina. If not, then PSP-producing organisms were present before 1980. If previous intoxication events have, indeed, occurred along the southern coast of Argentina, such events would be indirect proof that *Alexandrium* was present in Argentinian waters before 1980. However, information from the south cannot be applied to the northern part of the country because the Tierra del Fuego region is biogeographically dissimilar from northern Patagonia and is even more dissimilar from the Buenos Aires areas, which is in a different biogeographical province.

A circumstance that makes the prior presence of *Alexandrium* in Argentinian waters seem unlikely is its absence in the long history of record-keeping associated with phytoplankton in these waters. Neither *Alexandrium* nor any of its previous taxonomic designations have been reported in either the scarce foreign studies of dinoflagellates in this area or the Argentinian planktonic surveys that were conducted during a 40-year period prior to 1980. This seems to support the idea that these dinoflagellates are recent invaders in our marine waters with the exception of the species *A. fraterculus* that was obtained off Buenos Aires almost 20 years before these intoxications. However, the possible toxicity of this species was, and still is, uncertain. On one hand, recent North American studies determined that bivalves from Uruguay contained varying levels of PSP; these bivalves were collected at times when the only suspect species was *A. fraterculus*. On the other hand, Japanese researchers obtained negative results when they analyzed a Japanese clone of *A. fraterculus*. Apparently, this is another instance, similar to that for *A. tamarense*, in which the dinoflagellate species is toxic at one site but non-toxic at another.

Given the circumstances discussed above, we might say that 30+ years ago, *Alexandrium* did not occur in Argentina, except possibly in the southern portion. However, we need to be extremely cautious about such a statement. It could be valid for countries with well-designed, longterm plankton surveys, but it is dubious for my country in which the total number of samples collected in a five-year-period, for example, was very small and very few of these samples were examined by dinoflagellate specialists. Sometimes, sampling was limited to a small region, such as one gulf. The most extensive surveys were usually conducted too far offshore (remember that *Alexandrium* is composed mostly of coastal species, with the exceptions of *A. concavum* and *A. tropicale*) and at times when the motile stage does not usually appear in the plankton.

Before 1960, plankton samples were collected by inadequate means; net mesh size was 62 μm, which is too big to retain even a small proportion of *Alexandrium* species if they were present. Consequently, their absence in our reports is rather insignificant and more probably reflects the inadequacy of our methods. Between 1960 and 1980, studies of coastal dinoflagellates were very few, particularly at the coastal midpoint of Patagonia, where the subsequent intoxications occurred and the highest level of toxicity was detected.

If *Alexandrium* were present before 1980 in sparse populations, toxic events would not have occurred because the concentrations were too low to make the bivalves toxic enough to cause illness. Also, in order for a bloom to be noticed because of its toxicity in mollusks, it must occur at a place where mollusks exist and are exploited for consumption.

In summary, concerning the presence of *Alexandrium* along most of the Argentinian littoral before 1962 when *A. fraterculus* was found, several hypotheses are possible and one is as defensible as the other. Three are the most plausible: 1) it is a recent invader of our seas, 2) it existed here but only in sparse populations that were difficult to detect because plankton samples were inadequate and because not enough toxin was produced to call attention to the organism (this second hypothesis assumes that for some unknown reason, the dinoflagellates abruptly increased their population and also increased their toxicity per cell), and 3) lack of documentation was entirely due to the insufficiency of Argentinian biological and medical studies.

All considered, the last hypothesis is probably correct. However, the worldwide increase in detection of *Alexandrium* species is rather noteworthy, especially because they are appearing in places where plankton studies are rather intensive and long-standing. Indeed, in some cases, bloom concentrations have been high enough to cause discolorations. In Argentina, the third hypothesis is justified for the period before 1960, but it seems unlikely that I did not detect any *Alexandrium* later, especially during the frequent sampling in the Mar del Plata. The presence of *A. fraterculus* there in summer 1962 was an infrequent occurrence attributed to rather exceptional oceanographic conditions (Balech, 1962). Normally, the distribution of this species is rather more northward and more oceanic. Subsequent observations of this species were rare. The other two species that have now been documented for the coastal region between Buenos Aires and the Patagonia region were not found before 1980. However, since 1980, in places such as the Gulf of San Jorge, *A. tamarense* can be the dominant dinoflagellate (Akselman, personal communication). Carreto et al. (1985) proved that after 1980 the concentration of this species along the northern coast of Patagonia was large at certain times, and they give details of what seems to be a real expansion of its area.

In southern California, the distribution of *A. catenella* seems to be expanding because the species (normally found more northward) is being reported more frequently and more toward the south (B. C. Abbott, personal communication). Along the eastern U.S.A., species expansion may also be happening. During a careful investigation, Anderson et al. (1982) noticed that cysts were found in places that had no history of reported PSP. The authors proposed two hypotheses: 1) the massive red tide of 1972 extended the range of *A. tamarense* to these areas and 2) isolated and sparse populations existed previously but went unnoticed because they either did not produce noticeable amounts of PSP or did not produce toxins.

If these observations indicate real expansion of areas, the enigma of the causes remains to be resolved. Because *Alexandrium* forms resistant cysts, colonization of new areas may result from cyst transport by man (transport of the motile form seems more improbable). In addition to the transport of cysts along with live mollusk loads, we should consider other ways of dissemination, such as by adhering to ship hulls, by aquatic birds, and, especially, in ballast waters (Hallegraeff et al., 1988a).

Let us consider the hypothesis about variable toxin production that Anderson et al. (1982) proposed. Based on numerous analyses often conducted by Japanese and North American investigators, we know that a species' toxicity varies greatly and depends upon several factors, such as the physiological state of the cells (more noticeable in cultured material), the salinity (White, 1978), the site where the analyzed individuals grew, and the clone or lineage (proving that some individuals of a species may be more toxic than others [Alam et al., 1979]). The extreme case is *A. tamarense* that is not toxic in the Tamar River estuary and very toxic in some other places. A series of samples that were taken along the east coast of the U.S.A. showed that the toxicity of *A. tamarense* decreases from north to south (Maranda et al., 1985).

MacLean (1979) studied the toxicity of the monospecific genus *Pyrodinium*, which is closely related to *Alexandrium*, and reported that toxicity varied notably depending on the physical location in which the population developed. Toxicity decreased in open waters, increased in relatively coastal waters, and reached maximum values in embayments. The variety *compressum* of *Pyrodinium bahamense* is commonly cited as a toxin producer in the Indian and western Pacific oceans. However, this "variety", which should be considered a subspecies if the taxonomic distinction were valid, is based more on the production of toxins than on morphological details, i.e., the species in tropical American waters is non-toxic. However, the recent severe and massive intoxications produced in Guatemala by this species seems to invalidate the premise that the American "variety" is non-toxic.

The aforementioned gradual variation in toxicity of *A. tamarense* along the Atlantic North American coast also seems to argue against the existence of cryptotaxons. It appears then that exogenous factors intervene. In precise and well-documented contributions, the eminent Portuguese investigator Sousa e Silva (1979, 1981) said that toxin production in dinoflagellates is induced by intracellular bacteria.

Certain studies that reject the possibility of bacterial participation in toxin production appear to lack the necessary requirements to dispute this thesis correctly. Contrarily, a well-qualified and well-equipped team of Japanese investigators (Noguchi et al., 1987) found that certain bacteria produced tetrodotoxin, a poison found in some fish and various invertebrates. These bacteria were from the genus *Vibrio*, and the species *V. alginoliticus* is particularly notable. Another team (Yasumoto et al., 1987) proved that bacteria of the genera *Alteromonas* and *Pseudomonas* also produced the same toxin. This toxin differs structurally from PSP, but the tetrodotoxin molecule is only slightly larger and has a similar action upon the neurobasal membrane.

One might argue that a situation that applies to tetrodotoxin does not necessarily apply also to PSP. However, Kodama (1988) discovered a bacteria, *Moraxella* sp., that grows inside *A. tamarense* and is capable of producing PSP independently. In fact, after *A. tamarense* has bloomed and disappeared from the water column, the bacteria maintains and even increases the toxicity of the region.

However, the above studies do not negate the accepted theory that dinoflagellates produce PSP toxins. Two well-known factors strongly support that theory: 1) PSP intoxications have always been coincident with blooms of certain *Alexandrium* species and 2) toxicity curves in the vector mollusks usually correspond with population development of these dinoflagellates. Nevertheless, the bacterial studies mentioned above also seem to support the importance of bacterial action. It could be inferred from this that toxin production in some dinoflagellate species is induced by the action of certain bacteria. Kodama's (1988) discovery now adds a disturbing element. We ask then: when certain bacteria are previously conditioned in some unknown way, can they continue to produce, independently, the toxins that we associate with dinoflagellates?

We do not know with certainty how many dinoflagellate species commonly produce PSP. However, these are considered to be producers: *A. tamarense*, *A. fundyense*, *A. acatenella*, *A. catenella*, *A. tamiyavanichi*, *A. minutum*, *A. angustitatulatum*, and *A. ostenfeldii*. Probably, *A. cohorticula*, *A. fraterculus*, and *A. lusitanicum* are also. I think that all species within the genus

should be considered as potentially dangerous, at least the ones from the subgenus *Alexandrium*. Nevertheless, the first eight that I mentioned would be the usual toxin producers and the rest would only produce toxins in rather special conditions (for instance, abundance of certain bacteria in the environment). For the subgenus *Gessnerium*, PSP production in noticeable amounts has not been sufficiently demonstrated, although some species do produce icthyotoxins and hemolysins.

Because of the potential danger that I suspect, much attention should be given whenever this genus is detected. Practical repercussions may certainly follow.

The numerous questions that are raised in this final chapter demand thorough investigation.

Because the genus *Alexandrium* is being described in this paper for proper recognition and acceptance, I believe a table summarizing the genus' distribution as known through 1988 would be useful. In the second column, a location followed by a question mark indicates that the species identification is probably correct but not certain. The species *inquirendae* are not included. In the right column, I note when analyses confirmed the presence of PSP (+) or when they had a negative result (-). The "?" indicates that no data are available and "+,-" means that in some places these toxins were found and in other places not.

Subgenus *Alexandrium*

Species	Distribution	PSP
A. acatenella	Pacific coast of northern U.S.A. and Canada, Argentinian coast from north of the Patagonia littoral to south of the Buenos Aires littoral, northern Japan, northern Chile?, Asiatic Russia (Kamchatka)	+
A. affine	Japan (Sea of Okhotosk, Mutsu Bay, interior Sea of Seto), Korea (Jinhae Bay), Gulf of Thailand, Philippines (Bay of Manila)?, Iberian Peninsula	-
A. andersoni	Atlantic coast of the U.S.A. (Cape Cod)	-
A. catenella	Pacific coast of North America (mostly from Alaska to northern California, rare in southern California), central and southern Chile (Channel of Beagle in Tierra del Fuego), west coast of South Africa, Japan (east coast from approximately 40°N to the southern extreme, southwest coast), southern Australia	+
A. cohorticula	Gulf of Mexico, Gulf of California?	?
A. compressum	Pacific coast of Japan, southern California	?
A. concavum	Center of the North Atlantic (between 45° and 48°N, west of the Gulf of Vizcaya), South Atlantic off Santos in Brazil; always far from the coast. Other locations doubtful	?
A. fraterculus	Southern Brazil, Uruguay, Argentina (from the northern littoral of Buenos Aires south to 39°S), Brazil Current, Ecuador, Japan (especially in the south), Korea (Bay of Jinhae), Gulf of Thailand, Phillipines (Bay of Manila)	+,-
A. fundyense	Canada (Bay of Fundy and Gulf of St. Lawrence), North Atlantic coast from Canada extending south to 41°N along the littoral of the U.S.A.	+
A. *kutnerae*	South Atlantic from approximately 24°S to 38°S along the coasts of southern Brazil, Uruguay, and northern Argentina	?
A. leei	Korea (Bay of Jinhae), Japan (Bay of Kagoshima), Gulf of Thailand, Philippines (Bay of Manila)	-
A. lusitanicum	Iberian Peninsula (Portugal [Lagoon of Obidos] and Spain [Galicia])	?
A. minutum	Egypt (Alexandria Harbor), Italy (Bay of Naples in the Tyrrhenian Sea), Turkey (Bay of Izmir in the Aegean), Greece, Spain (Galicia and Barcelona), Portugal (Lagoon of Obidos), France (coast of Bretagne), southern England, U.S.A. (state of New York), southern Australia	+
A. ostenfeldii	coast of western Europe from Norway to Spain, Faeroes Islands, Iceland, U.S.A. (state of Washington), Egypt (Alexandria Harbor), northern Japan?	+
A. peruvianum	Peru (Callao), U.S.A. (Mineola in the state of New York)	
A. tamarense	southern and eastern England, Scotland, coast of western Europe from Norway to Portugal, Faeroes Islands, Atlantic coast of the U.S.A. from Maine to 40°N, Argentina (from the littoral of Buenos Aires to the Gulf of San Jorge in the littoral of Patagonia), Uruguay?, Japan, Korea, Gulf of Thailand, Japan (east and west coasts from 44°N to the southern extreme), southwest coast of Canada, Venezuela (Gulf of Cariaco), southern Taiwan (*fide* Su et al., 1989)	+,-
A. tamiyavanichi	Gulf of Thailand, Philippines (Bay of Manila), Andaman Sea (southwest of Thailand)	+
A. tropicale	west equatorial Atlantic (occasionally to the Rio de la Plata between Argentina and Uruguay), U.S.A. (state of Florida)?	?
A. angustitabulatum	New Zealand	+

Subgenus *Gessnerium*

Species	Distribution	PSP
A. balechii	U.S.A. (the Gulf of Mexico and Tampa Bay in the state of Florida), Italy (Gulf of Salerno in the Tyrrhenian Sea), Greece	-
A. foedum	Italy (Gulf of Salerno in the Tyrrhenian Sea)	?
A. hiranoi	Japan (Jogashima Island and Arasaki, Kanagawa)	-
A. insuetum	Korea (Bay of Jinhae), Japan	?
A. margalefi	Spain (Ria de Vigo in Galicia), Australia (Bass strait of southern Tasmania)	-
A. monilatum	U.S.A (east coast of the state of Florida and the coast of the Gulf of Mexico from south Florida to Galveston [the state of Texas]), Venezuela (Caribbean Sea), and Ecuador (estuary of Guayas)	-
A. pseudogoniaulax	southern France (in brackish lagoons), Portugal (Lagoon of Obidos), Norway, Pacific coast of Japan (Island of Jogashima)	?
A. satoanum	central Japan (Matoya Bay)	?
A. taylori	France (Bay of Arcachon)	?

This paper was already finished when I received valuable reports from Dr. Y. Okolodkov (Botanical Institute, Soviet Academy of Sciences, Leningrad) about the presence of *Alexandrium* in the former Soviet Union. *Alexandrium tamarense* has been found in the Sea of Okhotsk (Kiselev, 1959) and in the Barents Sea (Rouchijajnen, 1961). *Alexandrium ostenfeldii* has been found in the Bering Sea (Kiselev, 1937, 1947), in the Kara Sea (Zabelina, 1946; Koltzova and Il'Jash, 1982), and in the Chukchi Sea (Kiselev, 1937; Okolodkov, 1987). Konovalova (1989) cites the following for the eastern coast of the Kamchatka peninsula: *A. excavatum*, *A. tamarense*, and *A. acatenella* were obtained during toxic red tides in August 1984 and June 1987. In 1991, she reported *A. ostenfeldii* in the same places (Kenovalova, 1991). I thank Dr. Konovalova for sending me some samples, which confirmed the presence of *Alexandrium catenella*, *A. ostenfeldii*, and *A. tamarense* in waters around the Kamchatka Peninsula.

GENUS RELATIONSHIPS

I will be brief in this chapter because some information has already been noted, especially in the chapter entitled "Subdivision of the Genus".

All of the characteristics of the genus *Alexandrium* locate it readily in the family Gonyaulacidae. In this family, it is obviously related to three genera: *Gonyaulax*, *Goniodoma*, and *Pyrodinium*.

Alexandrium is well differentiated from *Gonyaulax* by epithecal structure. *Gonyaulax* has two intercalary plates (one dorsal and one ventral); *Alexandrium* has no intercalary plates, has one more apical plate, and, consequently, has a total of one less epithecal plate. The Po plates are very different. Other differences are not as absolute. For example, the majority of *Gonyaulax* species have 1) strong sculptures, spines, and horns, 2) fully developed cingular membranes, and 3) a cingular displacement that is notably wider and, often, strongly overlapping. This contrasts with *Alexandrium* in which these features are either lacking or much less developed. However, similarities also exist. The fact that the cingular, sulcal, and hypothecal tabulations are not generically distinguishable made me doubt for a long time which was the better choice: whether to consider the smaller group as a different genus or as a subgenus within the same genus. I leaned towards this last solution when I wrote my monograph on the dinoflagellates of the southwest Atlantic (Balech, 1988), mostly because unnecessary emphasis of the epithecal characters might have split the genus *Gonyaulax* inappropriately. Finally, after thorough research on *Alexandrium*, I adopted the generic separation that I think is well-founded (Balech, 1985b). Cyst development provides further support for separating the two genera; they each produce a different kind of cyst.

The problem of whether to split the genus *Gonyaulax* further is still unresolved and requires a longterm, sustained study of abundant material in order to attempt a well-founded resolution.

The other related genera, *Goniodoma* and *Pyrodinium*, are not as easily distinguished from *Alexandrium*. They are dissimilar because they both have strong thecae, noticeable sculpturing, and excellently developed cingular and sulcal membranes, whereas almost all *Alexandrium* species essentially lack these features. However, *Alexandrium* has a few exceptional species that have rather noticeable sculpture. Two of them, *A. insuetum* and *A.* sp. I, are covered by a reticulation. So far, neither *Goniodoma* nor *Pyrodinium* have any reticulated species. *Alexandrium balechii* and *A. foedum* have obvious pores, but their pore structure is not similar to that of the other two genera.

Generally, these other two genera are separated from the subgenus *Alexandrium* because both have a Po that is disconnected from 1'. However, this is not a fundamental characteristic if we accept, as I did, *Gessnerium* as a subgenus of *Alexandrium*. Indeed, tabular formula does not separate *Gessnerium* from either *Pyrodinium* or *Goniodoma*. Also, some individuals of *Pyrodinium* (Balech, 1985a) have both plates connected. Another interesting similarity is that *Pyrodinium* and *Alexandrium* seem to be the only armored dinoflagellate genera that produce PSP. Their sulcal organization and S.a. are also similar.

However, there are several other differences (Balech, 1985a). For instance, *Pyrodinium* has strong thecal walls and large pores that are surrounded by a conspicuous thickening. The pores in some plates are regularly distributed (e.g., in 2') and may be somewhat variable in number

(e.g., in 1'). Other characteristics of *Pyrodinium* that clearly separate it from *Alexandrium* are as follows: 1) very strong cingular and sulcal lists (especially in the two ventral postcingulars, of which 5"' has a very special structure that is unique among dinoflagellates [see Balech, 1985a: 20-21]), 2) development of spines, 3) the apical horn, and 4) sutures that are usually noticeably raised. The shapes of the posterior lateral sulcal plates in *Pyrodinium* are not the same as those in *Alexandrium*. Also, *Alexandrium* does not form the hystrichosphaerid-type cysts that are known for *Pyrodinium*.

In summary, I find no reason to doubt the independence of *Pyrodinium* and *Alexandrium*, although they are more easily separated by the differences in their general morphological characters than in their tabular characters. It is, perhaps, somewhat paradoxical that the true specialist is more likely to doubt the independence of both genera than is the general observer of dinoflagellates.

I left the comparison with *Goniodoma* last because the relationship between *Goniodoma* and *Alexandrium* is more difficult to clarify. Although *Goniodoma* is easily distinguished from the subgenus *Alexandrium*, it is much more difficult to separate from the subgenus *Gessnerium*. Generally, *Goniodoma* is different because of its strong theca, well-developed and sculptured cingular membranes, raised sutures, and very emphasized pores. However, its epithecal tabulation is barely different from some *Gessnerium* and their tabular formulae are identical if the modified Kofoidian tabulation is applied to *Goniodoma* as I have done with the subgenus *Gessnerium*. When the modified designations are used, the 1' plates are alike in *Goniodoma* and *A. insuetum*. However, as previously noted, the Po in *Goniodoma* has a totally transverse orientation, while in both subgenera of *Alexandrium*, it is oblique and has a predominantly sagittal direction. Furthermore, the foramen of the Po in *Alexandrium* is not similar to the foramen of *Goniodoma*. As a result of the Po plate's orientation, the suture between 2' and 4' is transversal in *Goniodoma* and more or less sagittal in *Gessnerium*. Also, in this subgenus, 2' and 1' are usually in contact (very briefly in *A. balechii* and *A. foedum*), which causes a fifth margin in this last plate. In *Goniodoma*, both plates are clearly far away from one another. Finally, 1' in *Gessnerium* is usually pentagonal; whereas in *Goniodoma*, it (usually called 1") is quadrangular. In spite of their morphological resemblance, the homology of the 1' of *Gessnerium* and the traditional 1" of *Goniodoma* is perhaps more apparent than real.

As previously noted, however, structure within *Gessnerium* varies greatly. For example, in one of its species, *A. margalefi*, the 1' and 2' are disconnected as in *Goniodoma*. As a result, 1' has only four margins (unique within the genus). In compensation, the Po has a comma and a well-formed callus, and the one suture between Po and 1' is clearly longitudinal.

Considering the rest of the theca, certain characteristics of the subgenus *Gessnerium* are again more similar to those of *Goniodoma* than they are to those in the subgenus *Alexandrium*. For instance, the S.s.a. in the latter is rather small and inconspicuously sunk into the sulcus, whereas, in both *Gessnerium* and *Goniodoma*, it is larger and more superficial.

Another example is the relationship of 2"" with S.p. In *Goniodoma*, the 2"" plate is somewhat lateral of the S.p. In *Alexandrium* (*Alexandrium*), the 2"" is almost completely dorsal (also, the 1"" is clearly elongated and generally rather narrow). However, in some species of *Gessnerium*, the S.p. is more oblique to the right and 2"" becomes more lateral than dorsal (e.g., *A. foedum* and, especially, *A. pseudogoniaulax*).

As a whole, however, the differences between *Goniodoma* and *Gessnerium* are well maintained. All the sulcal plates in *Goniodoma*, in particular the two posterior lateral plates (especially the S.s.p.), are very different from the corresponding plates in the genus *Alexandrium*. In the latter, these plates, especially the S.s.p., look more like those in *Pyrodinium* and some in *Gonyaulax*.

I do not believe that we have enough data to provide well-founded arguments about the derivation of these genera. However, given current micropaleontological data, we at least know that these genera seem to have been differentiated for a long time. Present day *Alexandrium* cysts are Acritarcha type, without paratabulation and, therefore, without any characteristics that would distinguish them as dinoflagellates.

Most micropaleontologists believe that thecae do not fossilize and that all dinoflagellate fossils with noticeable tabulation (or paratabulation) are cysts. I do not share this opinion, and I still believe that, in many cases, these fossils correspond to motile forms (i.e., they are thecae and not cysts). Some researchers argue that the chemical differences between these fossils and modern thecae support the former opinion, but I think this reasoning is inconsistent. While many microfossils may very well correspond to "cysts", I have in the past and still do think that some of these microfossils are fossilized thecae.

Regardless, dinoflagellates representing two well-differentiated phylogenetic lines of Gonyaulacidae were present in the Cretaceous. Apparently, the earliest one corresponded to *Gonyaulax sensu stricto* and the later one to *Goniodoma - Alexandrium*. The close affinity of the fossil genus *Cribroperidinium* with *Alexandrium* is very evident.

Just as the fossil genus *Gonyaulacysta* corresponds well with the modern genus *Gonyaulax*, *Cribroperidinium* is very similar to *Alexandrium*. This similarity includes the very evident general tabulation as well as the less evident, but still observed, sulcal tabulation. Therefore, the observed characteristics are insufficient to separate the latter two from each other. If we were to acknowledge them as inseparable, then *Alexandrium* should be called *Cribroperidinium*. However, I think, as do most authors of dinoflagellate systematics, that fossil taxa should be kept separate from modern taxa. Too many questions persist and the basis of the two systems is very different.

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PLATES

Plate I

Fig. 1-50, *Alexandrium minutum.*

Fig. 1-10, *material from Egypt (Alexandria Harbor)*: 1-4) ventral view; 5) apical view; 6) three Po and 1' with distinct types of connections; 7) antapical view; 8) sulcals and 1""; 9) 5"' and 1"'; 10) three 2"".

Fig. 11-29, *material from Spain (Galicia)*: 11-15) ventral view; 16) apical view; 17) Po, 1', 4', and 6"; 18) Po, 1', 4', and S.a.; 19) Po plates; 20) two 1', left one includes 6"; 21) antapical view; 22) 5"' and 1"'; 23) sulcals; 24) sulcals and antapicals; 25) left lateral sulcals; 26) sulcals (without the S.a.); 27) four S.a.; 28) three S.d.p.; 29) four 1"".

Fig. 30-35, *specimens from the U.S.A. (New York state)*: 30-32) ventral view; 33) Po, 1', and 6"; 34) S.p. and two antapicals; 35) sulcals.

Fig. 36-39, *material from France (Bretagne)*: 36 and 37) ventral view; 38) two 1' without pores (the pore indents the 4'); 39) sulcals (without the median plates) and 1"".

Fig. 40-43, *material from southern Australia*: 40) ventral view; 41) Po, 1', 4', 6", and S.a.; 42) three 1', right one includes the Po; 43) sulcals (without the S.ac.p.) and 1"".

Fig. 44-47, *material from Italy (Naples)*: 44-45) ventral view; 46) Po, 1', 2', and 6"; 47) sulcals (without the accessories) and 1"".

Fig. 48-50, *material from Portugal*: 48) ventral view; 49) Po, 1', 6", and S.a. (2 sets); 50) sulcals (without the S.a. or accessories).

The bar underneath Figure 9 applies to all the whole thecae.

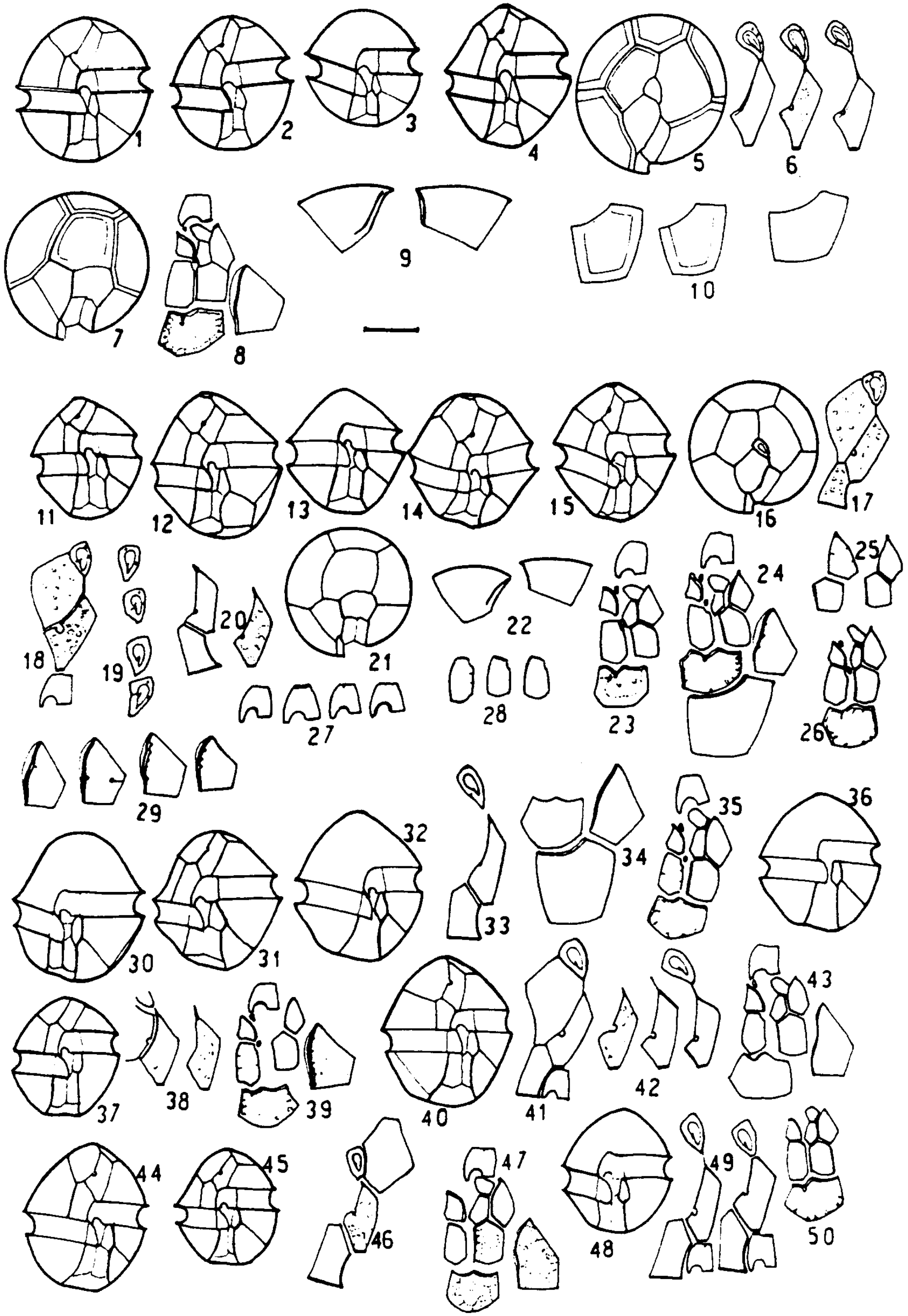


Plate II

Fig. 1-15, *A. lusitanicum*: 1-3) ventral view; 4) apical view; 5) antapical view; 6) two Po plates; 7) Po, 1’, 4’, and 6"; 8) Po, 1’, and 2’; 9) 1’ and 6"; 10) sulcals and 2""; 11) five S.a.; 12) sulcals (without the median sulcals and the S.ac.p.) and 1""; 13) S.d.p. and S.s.p.; 14) left lateral sulcals and medians; 15) median sulcals.

Fig. 16-30, *A. angustitabulatum*: 16-18) ventral view; 19) apical view; 20) two hypothecas in antapical view; 21) Po, 2’, and 4’; 22) Po, 1’, 4’, 5", and 6"; 23) five 1’; 24) S.d.a., S.d.p., S.s.p., S.m.p., and S.ac.p.; 25) sulcals and 1""; 26) the principal sulcals; 27) sulcals (without the S.a., S.p., or S.ac.a.); 28) incomplete sulcals and other ventrals; 29) 1"’ and 1""; 30) 6".

Fig. 31-41, *A. andersoni*: 31-34) ventral view; 35) apical view; 36) three Po and 1’; 37) ventral plates; 38) 1"" and 2""; 39) two 1""; 40) 6" and S.a. (2 sets); 41) sulcals (without the accessories).

The bar next to Figure 1 is valid for Figures 1-3; the one above Figure 33 applies to all other whole thecae.

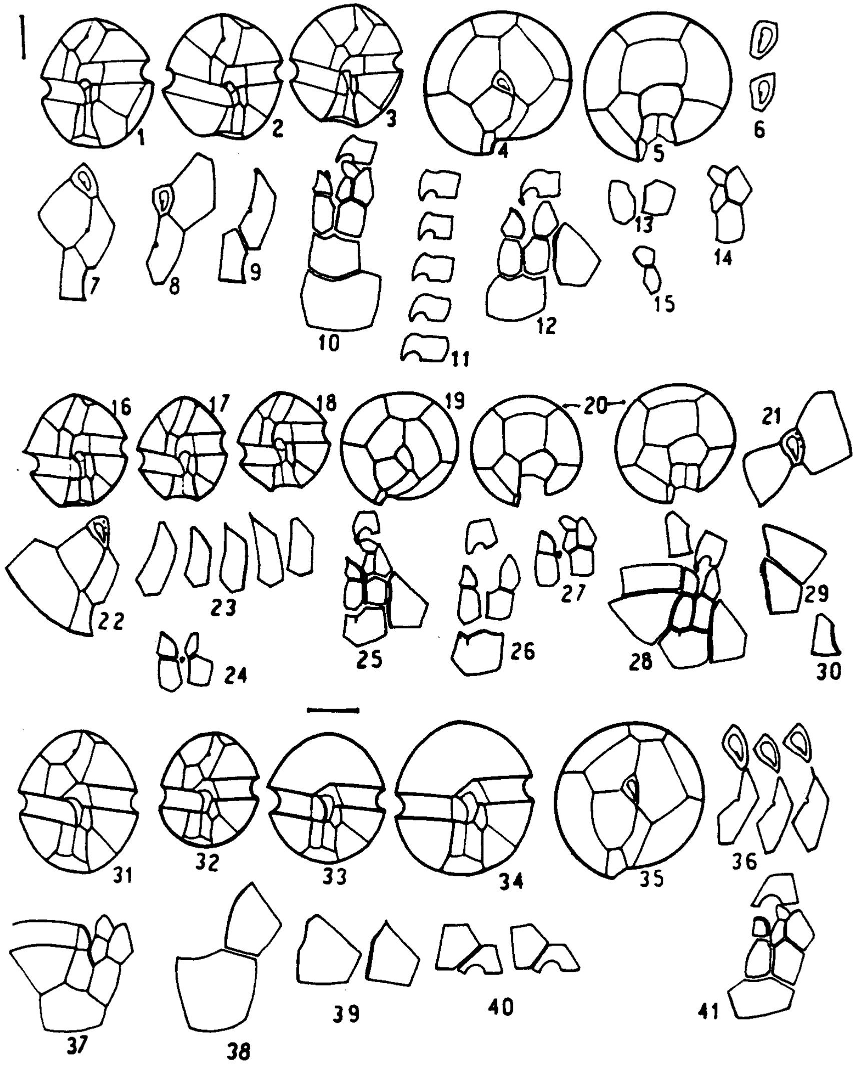


Plate III

Fig. 1-24, *A. ostenfeldii.*

Fig. 1-15, *material from Norway*: 1-3) ventral view; 4) two Po and 1’; 5) apical view; 6) antapical view; 7) sulcals; 8) three Po and 1’; 9) S.a., S.s.a., S.s.p., and S.m.p.; 10) S.s.p. and S.m.p.; 11) S.s.p.; 12) the two right sulcals with one accessory (6 sets); 13) two 1""; 14) 5"’ and S.d.p.; 15) three S.p.

Fig. 16-24, *material from Spain (Galicia)*: 16) apical view; 17) three S.a.; 18 and 19) ventral view; 20) antapical view; 21) four 1’, three with the Po; 22) S.p.; 23) right lateral sulcals (some with accessories); 24) sulcals and 1"".

The bar between Figures 1 and 2 is valid for all the whole specimens.

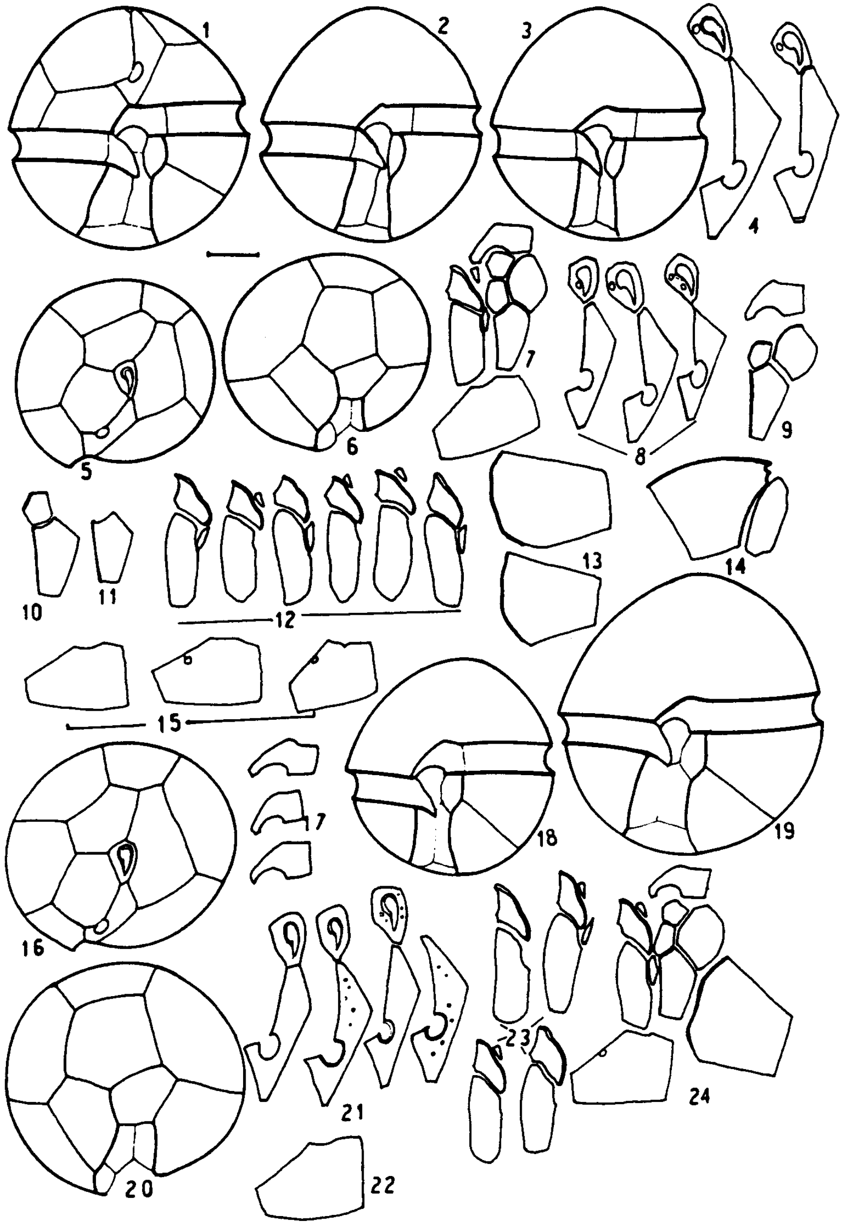


Plate IV

Fig. 1-19, *A peruvianum*

Fig. 1-12, *material from Peru*: 1-3) ventral view; 4) apical view; 5) antapical view; 6) Po, 1’, and 6’; 7) three Po; 8) sulcals and 1""; 9) two 1’ plates of somewhat unusual form; 10) two 1’; 11) four S.a.; 12) three S.p.

Fig. 13-19, *material from the U.S.A. (New York state)*: 13 and 15) specimens in ventral view; 14) 1’; 16) sulcals; 17) Po, 1’, 2’, 4’, and 6"; 18) 1""; 19) two S.a.

Fig. 20-28, *A. leei*: 20, 21, and 24) ventral view; 22) three Po; 23) 6"; 25) apical view; 26) antapical view; 27) three 1’; 28) right lateral view.

The bar between Figures 1 and 2 applies to Figures 1-5, 13, and 15.

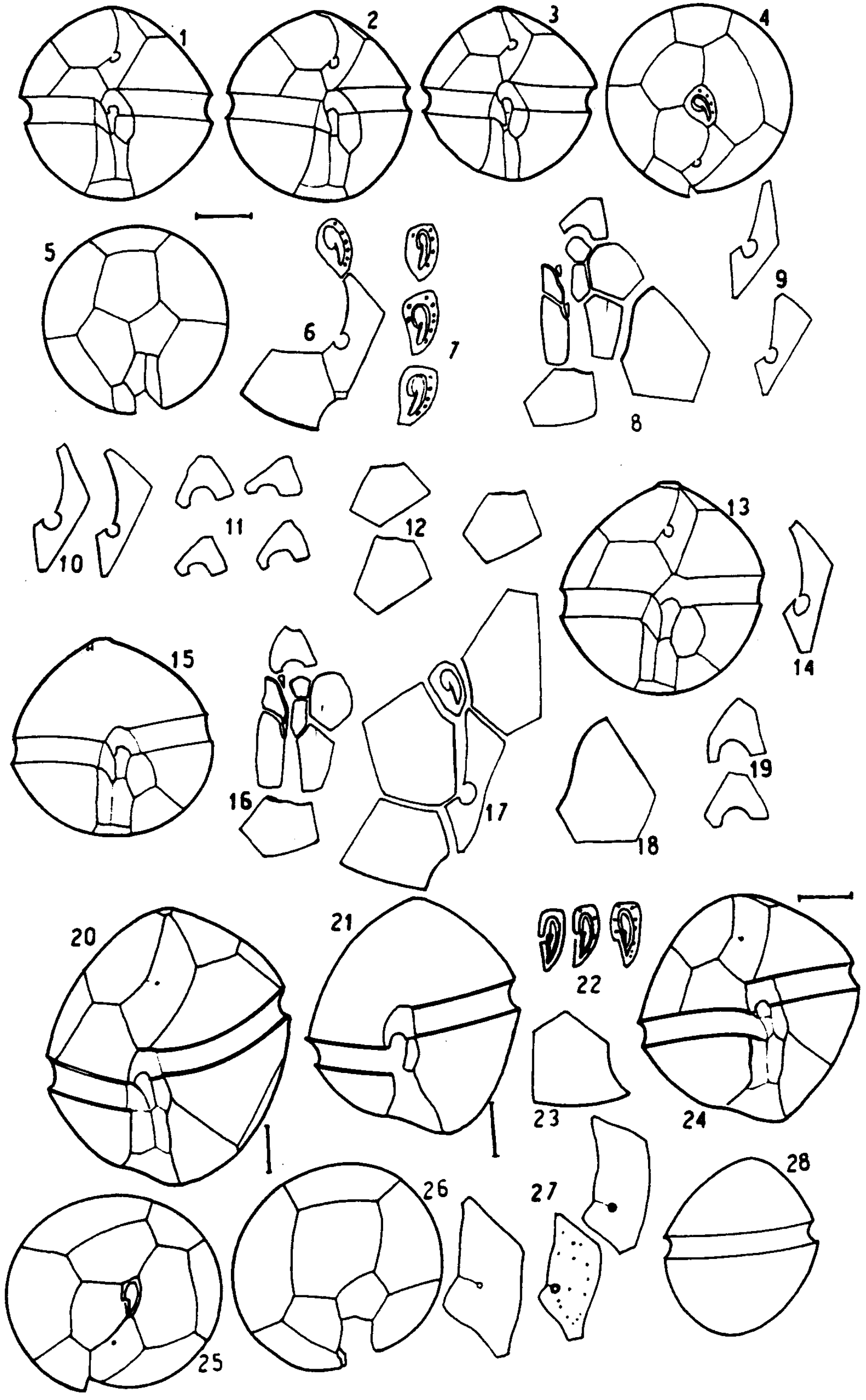


Plate V

Fig. 1-13, *A. leei*: 1) 1"", 2"", and S.p.; 2) 1"' and 1""; 3) 1""; 4) two 5"'; 5) the two left lateral sulcals and the two medians; 6) S.s.a. and the two median sulcals; 7) two S.d.a. with S.ac.a.; 8) S.d.p., S.ac.p., and S.s.p.; 9) three S.s.a.; 10) two S.d.p. with S.ac.p.; 11) S.p.; 12) sulcals; 13) three S.a., one with an S.ac.a.

Fig. 14-26, *A. kutnerae*: 14, 15, and 17) ventral view; 16) Po and 1' (2 sets); 18) apical view; 19) antapical view; 20) sulcals (without an S.ac.p.); 21) 5"' and 1""; 22) 1', 6", and S.a.; 23) two Po; 24) 5"' and 1""; 25) sulcals; 26) sulcals (without the S.a. or the S.ac.p.).

Figures 14, 16, 20, and 21 represent specimens from Brazil; the rest are from Argentina.

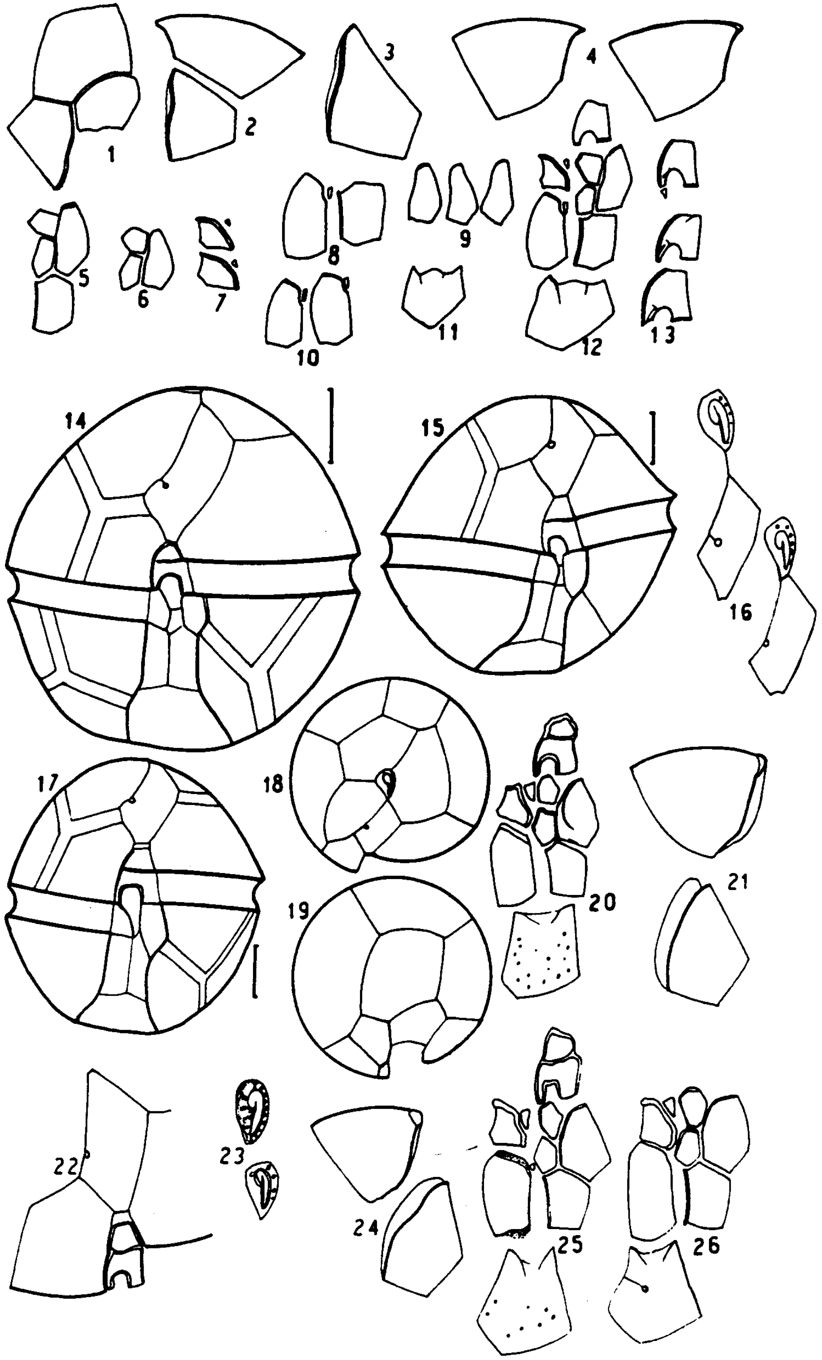


Plate VI

Fig. 1-40, *A. tamarense.*

Fig. 1-11, *material from England (the Tamar River)*: 1-4) ventral view; 5 and 8) Po and 1’; 6, 7, and 11) antapical views demonstrating the variation in 2""; 9) sulcals and 1""; 10) three S.a.

Fig. 12-22, *material from southwest England (Cornwall)*: 12-16) ventral view; 17) two Po and 1’; 18) Po, 1’, 2’, and 3’; 19) sulcals; 20) S.p., 1"", and 2""; 21) example of a ventral pore shared between 1’ and 4’; 22) Po, 1’, and 4’ with the ventral pore only in 4’.

Fig. 23-28, *material from Spain (Pontevedra in Galicia)*: 23-25) ventral view; 26) Po and 1’; 27) sulcals; 28) S.p., 1"", and 2"".

Fig. 29-40, *material from Argentina*: 29-33, 38, and 39) ventral view; 34) Po and 1’; 35 and 36) antapical view; 37) five S.a.; 40) sulcals.

The bar between Figures 1 and 2 applies to Figures 1-4. The one between Figures 12 and 13 applies to Figures 12-16. The one between Figures 30 and 31 is valid for the rest of the whole thecae.

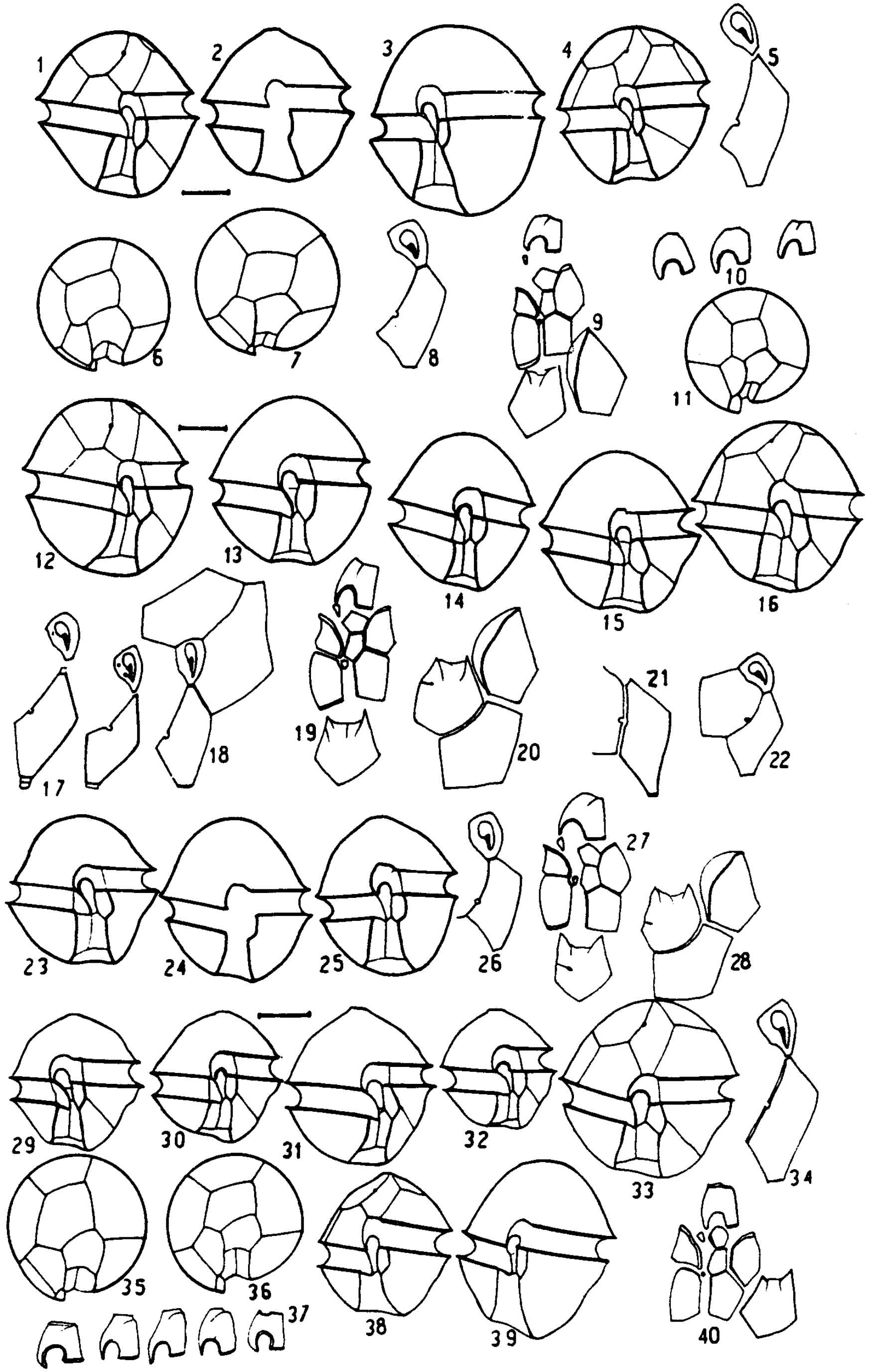


Plate VII

Fig. 1-9, *A. tamarense*

Fig. 1-4, *material from Korea*: 1-2) ventral view; 3) sulcals (without accessories); 4) Po and 1'.

Fig. 5-9, *material from the U.S.A. (state of Massachusetts)*: 5-7) ventral view; 8) Po, 1', and S.a. (2 sets); 9) sulcals.

Fig. 10-22, *A.* species cf. *tamarense*, *material from Thailand:* 10-14) thecae in ventral view; 15) Po, apicals, and 6"; 16) four Po; 17) 1"'; 18) three S.a.; 19) four 1'; 20) S.p. and 2""; 21) two S.s.a.; 22) sulcals and Po, 1', and 1"".

Fig. 23-32, *A. fundyense*: 23-31) ventral view; 32) two Po and 1'.

The bar beneath Figures 6 and 7 applies to all of the whole specimens.

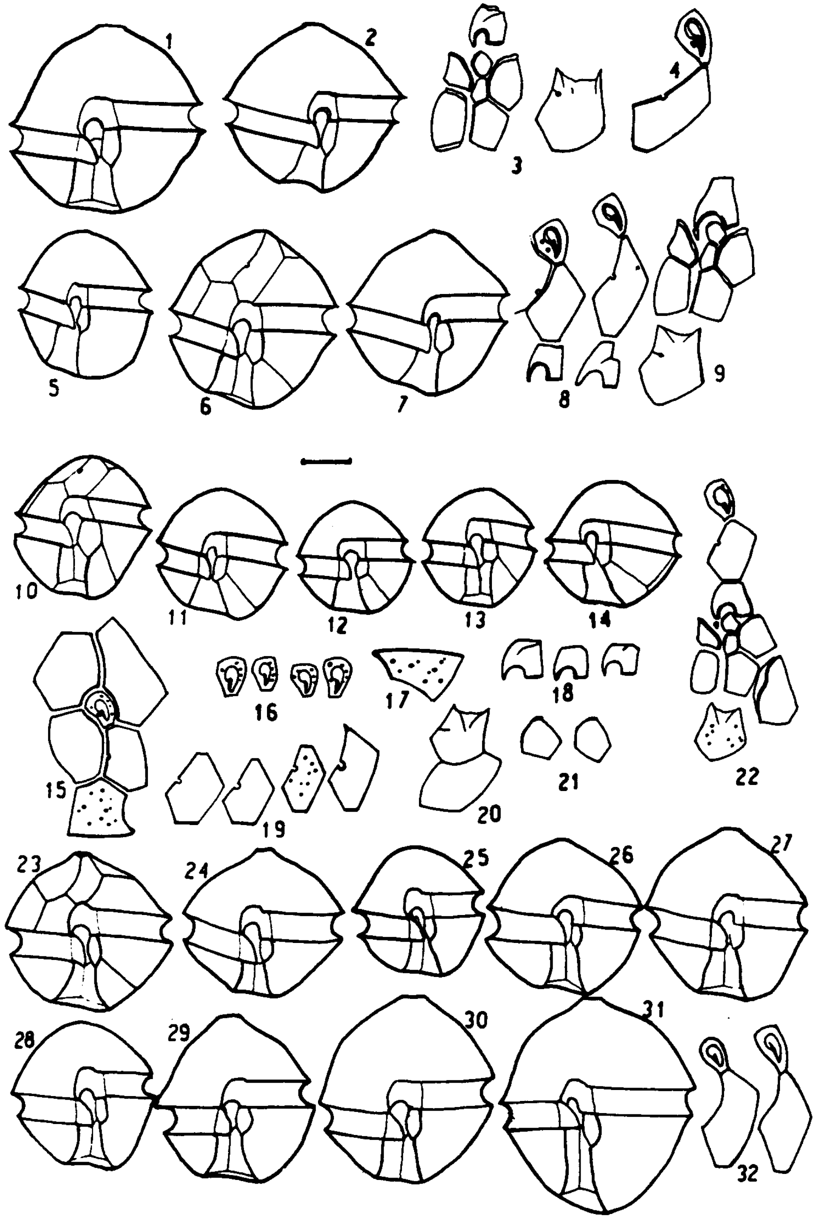


Plate VIII

Fig. 1-19, *A. fundyense*: 1) an abnormal individual in ventral view; 2) apical view; 3) antapical view; 4) four Po and 1'; 5) sulcals; 6) eight S.a.; 7) S.d.p., S.s.p., S.s.a, and median sulcals; 8) five S.s.a; 9) S.d.p.; 10) three 1''''; 11) three S.p.; 12) Po, 1', and S.a.; 13) Po and 1'; 14) two S.a.; 15 and 17) S.d.p.; 16) two S.p.; 18) S.s.a.; 19) two S.s.p.

Fig. 20-31, *A. acatenella.*

Fig. 20-30, *material from Japan:* 20-22) ventral view; 23) apical view; 24) antapical view; 25) sculptural detail of theca; 26) 5''', 1''', and 1''''; 27) two Po and 1'; 28) lateral posterior sulcals and the two medians; 29) four S.a.; 30) sulcals (without S.ac.p.).

Fig. 31, *material from Argentina:* 31) ventral view.

The bar between Figures 21 and 22 applies to Figures 20-22 and 31.

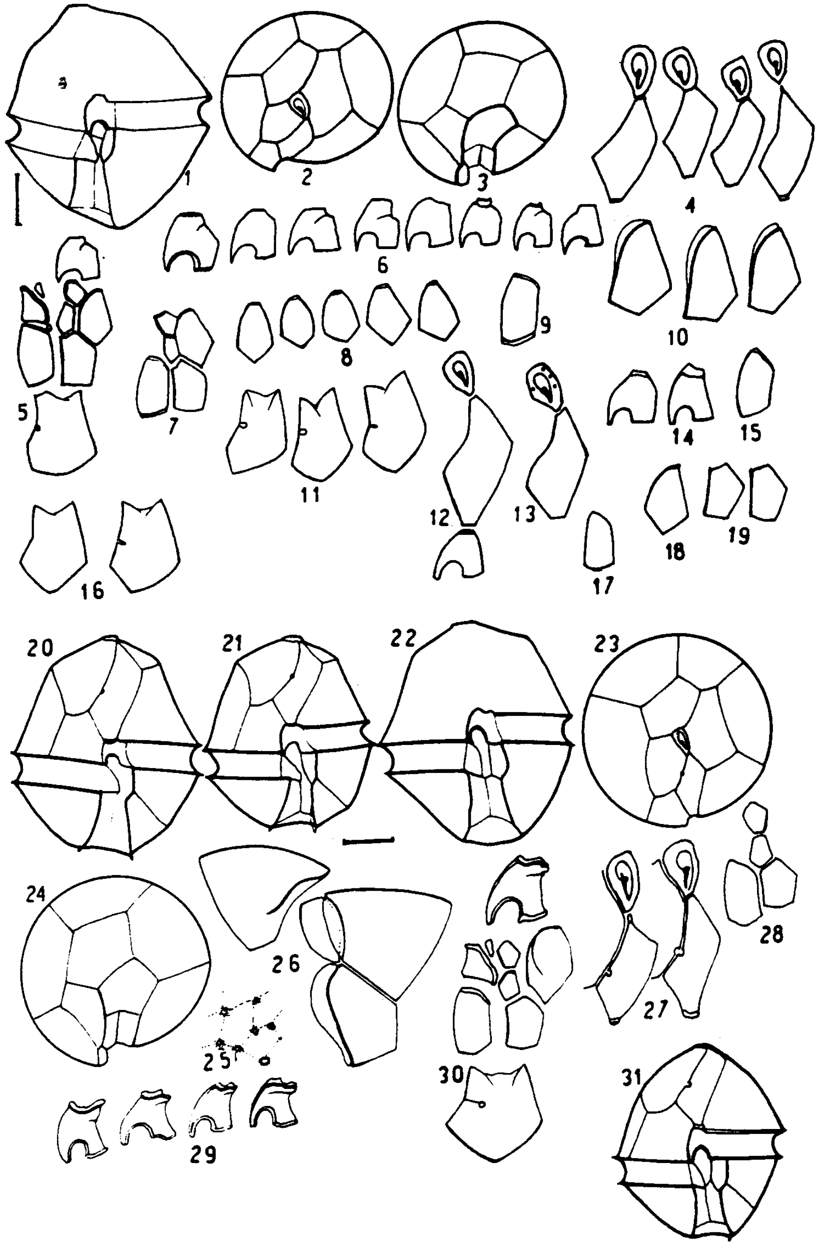
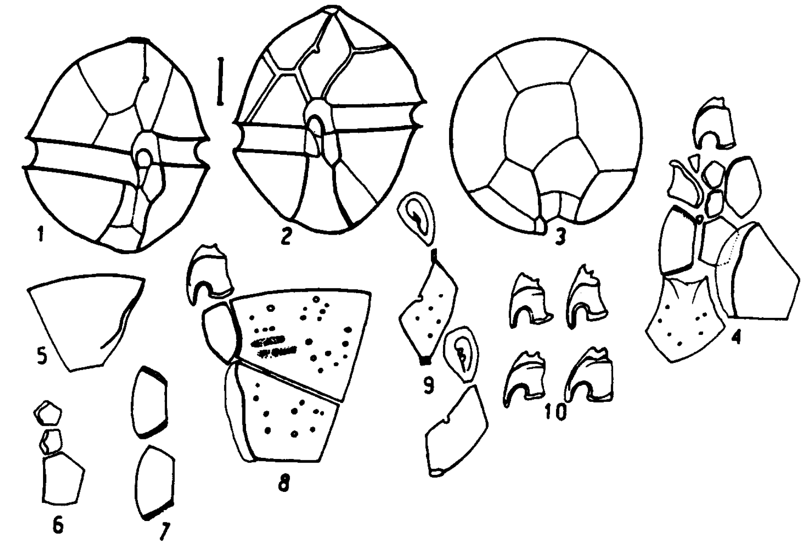


Plate IX

Fig. 1-10, *A. acatenella*, material from Argentina: 1-2) ventral view; 3) antapical view; 4) sulcals and 1""; 5) 5"'; 6) S.s.p. and median sulcals; 7) two S.d.p.; 8) S.a., S.s.a., 1"', and 1""; 9) two Po and 1'; 10) four S.a.

Fig. 11-27, *A. tropicale*: 11, 12, 17, 18, and 25) ventral view; 13) apical view; 14) antapical view; 15) Po, 1', and 2'; 16) two 1' plates; 19) Po, 1', 1", and 6"; 20) Po; 21) sulcals and 1""; 22) five S.a. and one S.m.a.; 23) 2""; 24) Po and 3'; 26) Po, 1', 4', and 6"; 27) sulcals (incomplete).

The bar between Figures 1 and 2 applies to both figures. The bar between Figures 11 and 12 applies to all the whole thecae of *A. tropicale*.



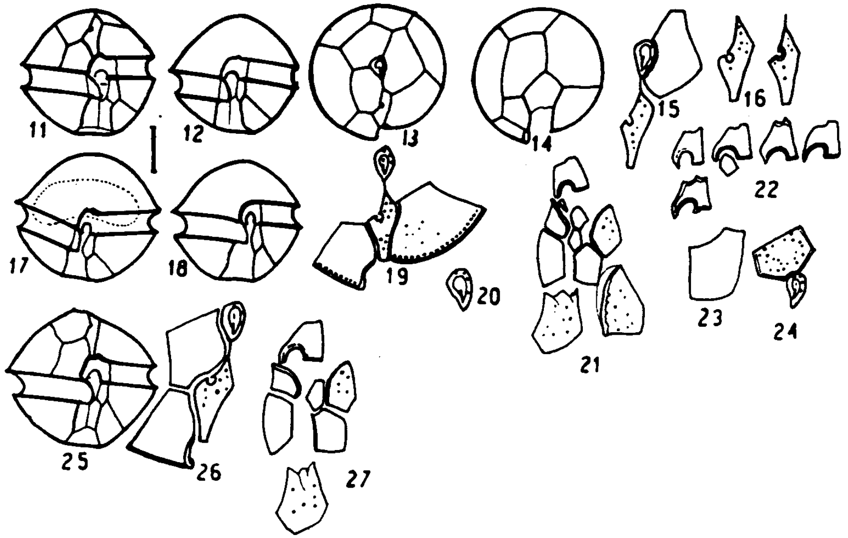


Plate X

Fig. 1-31, *A. catenella.*

Fig. 1-20, ***material from a natural population from the U.S.A. (Washington state)***: 1) two individuals in a chain; 2) an isolated individual; 3) apical view; 4) antapical view (1"' not observed because of shape and inclination of hypotheca); 5) Po and the apicals; 6) nine Po; 7) two 2'; 8) two 1'; 9) Po, 1', 4', and 6"; 10) 1', 4', and 6"; 11) two 3'; 12) 1"' and 1""; 13) sulcals; 14) two S.p.; 15) two 5"'; 16) four 1"" (the one on the right giving a view of the internal margin); 17) four S.a.; 18 and 19) left sulcals (3 sets); 20) four S.d.p.

Fig. 21-29, ***material (cultured) from the U.S.A. (southern California)***: 21 and 27) three S.p.; 22) sulcals (without the S.d.a., S.m.a., or the accessories); 23 and 29) abnormal specimens in ventral view; 24) 5"'(top) and 1"' (bottom); 25) Po, 1', and S.a.; 26) the lateral sulcals; 28) 5"' and 1"".

Fig. 30-31, ***material from southern Australia***: 30) Po and apicals; 31) sulcals and 2"".

The bar between Figures 1 and 2 applies to both figures. The bar between Figures 23 and 29 applies to those two figures.

Plate XI

Fig. 1-12, *A. catenella*, material from southern Chile (Punta Arenas): 1) ventral view; 2) Po and apicals; 3) apical view; 4) Po and anterior margins of the apicals, demonstrating denticular development; 5) sulcals; 6) four S.a.; 7) three S.s.a.; 8) small individual; 9) Po and apicals; 10) S.p., 1"", and 2""; 11) sulcals (without accessories); 12) 5"'.

Fig. 13-23, ***Alexandrium*** sp. II, material from Mexico: 13-14) ventral view; 15) apical view; 16) antapical view; 17) two Po and 1' (2 sets); 18) two Po; 19) two 5'; 20) 2""; 21 and 22) sulcals (Fig. 22, without S.a.); 23) two 1"".

Fig. 24-33, *A. cohorticula*: 24) ventral view; 25) apical view; 26) antapical view; 27) Po, 1', 4', 6", and S.a.; 28) Po; 29) 6"; 30) 1"' and 1""; 31) sulcals (without the S.p.); 32) S.p.; 33) S.d.p., S.ac.p., and S.s.p.

The bar beside Figure 1 also applies to Figure 8. The bar beside Figure 13 also applies to Figure 14.

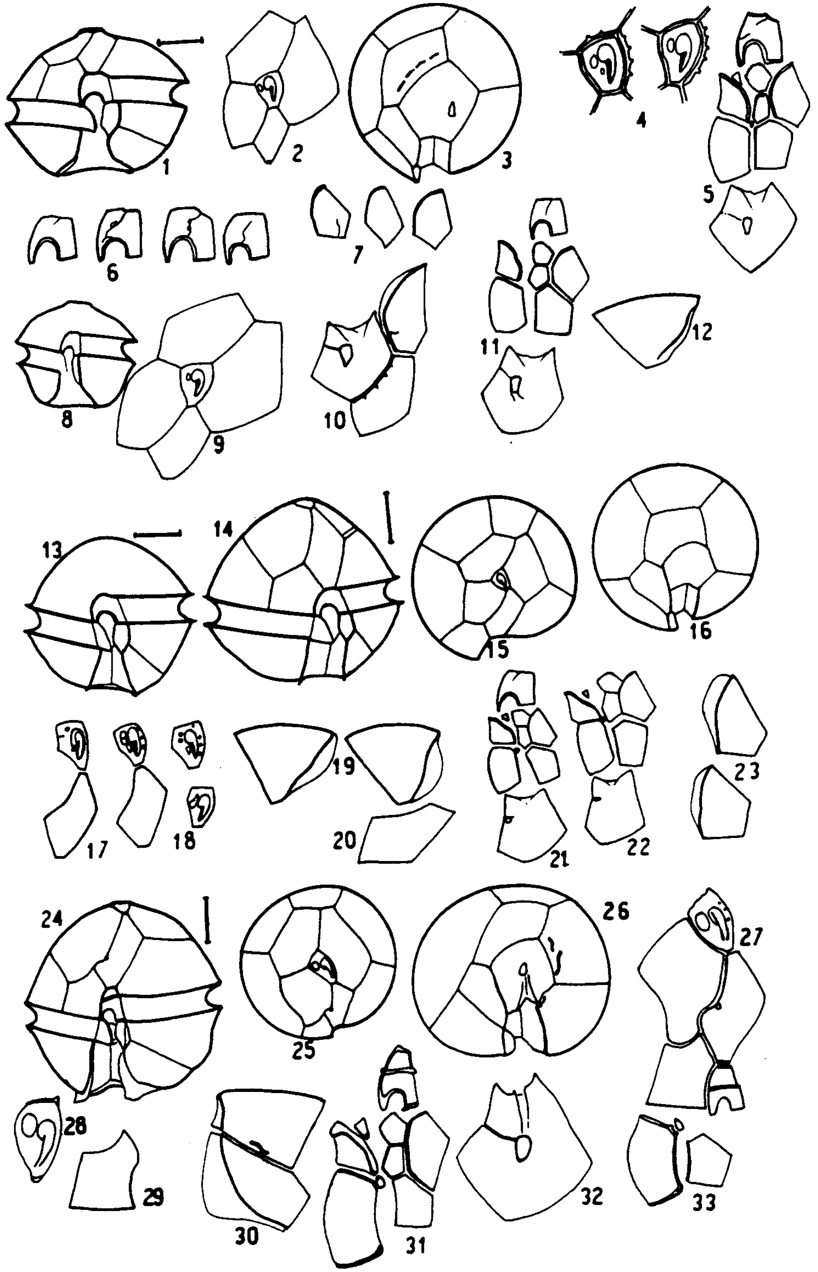


Plate XII

Fig. 1-9, *A. compressum*: 1) ventral view; 2) apical view; 3) antapical view; 4) Po, 1', 3', 4', 4", 5", and 6"; 5) Po; 6) detail of sculpture; 7) 1"' and 1""; 8) S.a., S.d.a., S.d.p, and S.ac.a.; 9) two united individuals.

Fig. 10-26, *A. fraterculus*.

Fig. 10-22, ***material from the southwestern Atlantic***: 10) two individuals in a chain; 11 and 12) isolated specimens in ventral view; 13) apical view; 14) five Po; 15) antapical view; 16) S.p. and 2""; 17) an S.p. in a partial lateral view; 18) three 1'; 19) two 1""; 20) two 5"'; 21) sulcals (without the S.p.); 22) 1', 6", and sulcals.

Fig. 23-26, ***material from Korea***: 23) ventral view; 24) sulcals and 1""; 25) Po and 1'; 26) two Po.

The bar between Figures 11 and 12 is valid for Figures 10-13 and 23.

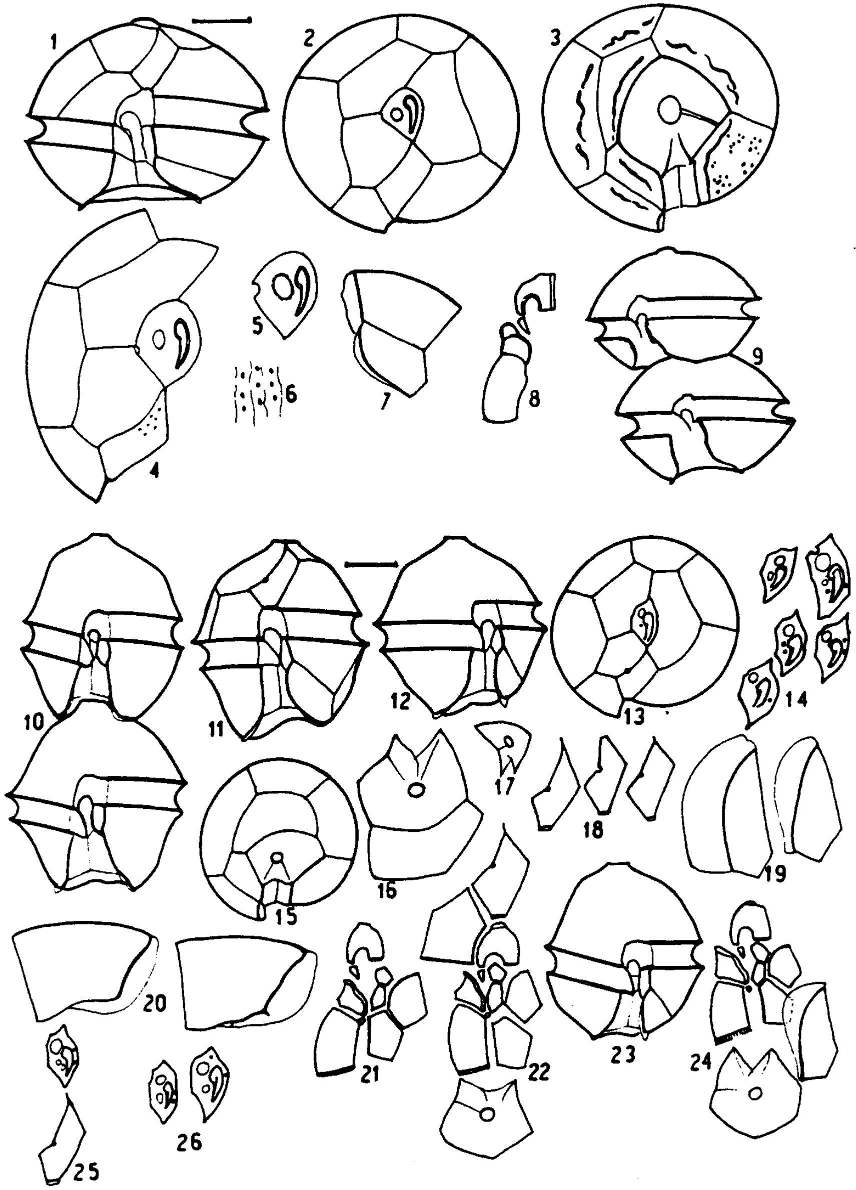


Plate XIII

Fig. 1-19, *A. tamiyavanichi*: 1) two individuals in a chain; 2) dorsal view; 3) apical view; 4) four 1’; 5) 1’ and 1"; 6) Po, 1’, 4’, and 6"; 7) antapical view; 8) ten Po; 9) two 3"’; 10) 5"’ (top) and 1"’ (bottom); 11) sulcals and 1""; 12) three S.d.a. with the S.ac.a.; 13) variations of the S.a.; 14) variations of the S.s.a.; 15) S.d.p., S.s.p., S.ac.p., and S.m.p.; 16) the median sulcals; 17) two S.p.; 18) variations of the S.d.p.; 19) 2"".

Fig 20-36, *A. affine*: 20) two individuals of a chain; 21) isolated individual; 22) right lateral view; 23) apical view; 24) antapical view; 25) Po and 1’; 26) Po, 1’, and 2’; 27) Po in left profile; 28) Po, 1’, 2’, 3’, and 6"; 29-31) sulcals (Fig. 31, incomplete); 32) two S.d.a. and S.ac.p.; 33) two 1""; 34) three 1’; 35) variations of the Po; 36) 1"’ and 1"".

The bar between Figures 1 and 2 applies to both figures.

The bar between Figures 20 and 21 applies to Figures 20-24.

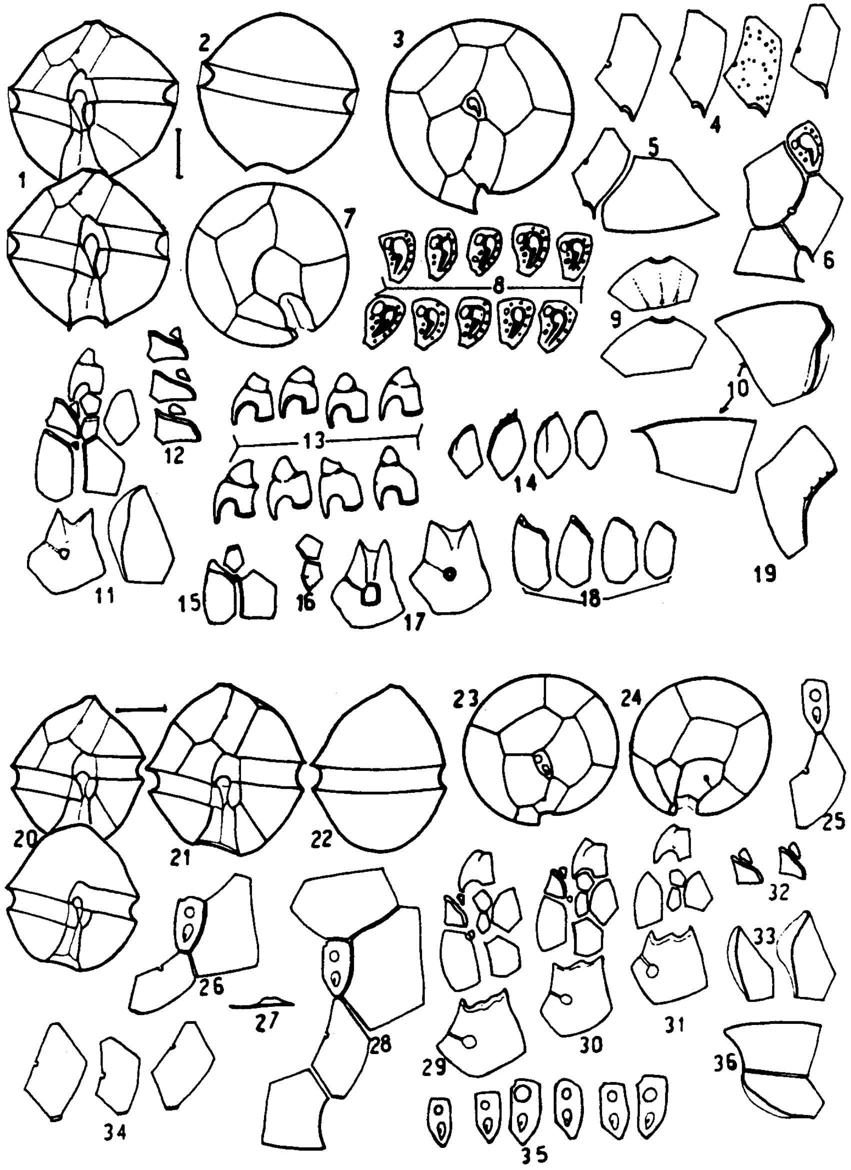


Plate XIV

Fig. 1-23, *A. balechii*: 1-5) ventral view; 6) S.a., S.d.a., S.s.a, S.s.p, and median sulcals; 7) apical view; 8) antapical view; 9) two Po and 2'; 10) variations of the Po; 11) sulcals, C_1, 1"", and 2""; 12) 2""; 13) sulcals (incomplete), C_1, and 1""; 14) two S.p.; 15) two 1'; 16) Po, apicals, and 6"; 17) four variations of the S.p.; 18) right lateral sulcals and accessories; 19) sulcals and 6"; 20) Po, 2', 3', 4', and 5"; 21) variations of the 1'; 22 and 23) 1"' and 1"".

Fig. 24-32, *A. foedum*: 24) ventral view; 25) apical view; 26) antapical view; 27) Po, apicals, and 6"; 28) two Po; 29) sulcals; 30) S.p. and 2""; 31) 5"', 1"', and 1""; 32) two S.a.

The bar between Figures 1 and 2 applies to Figures 1-5.

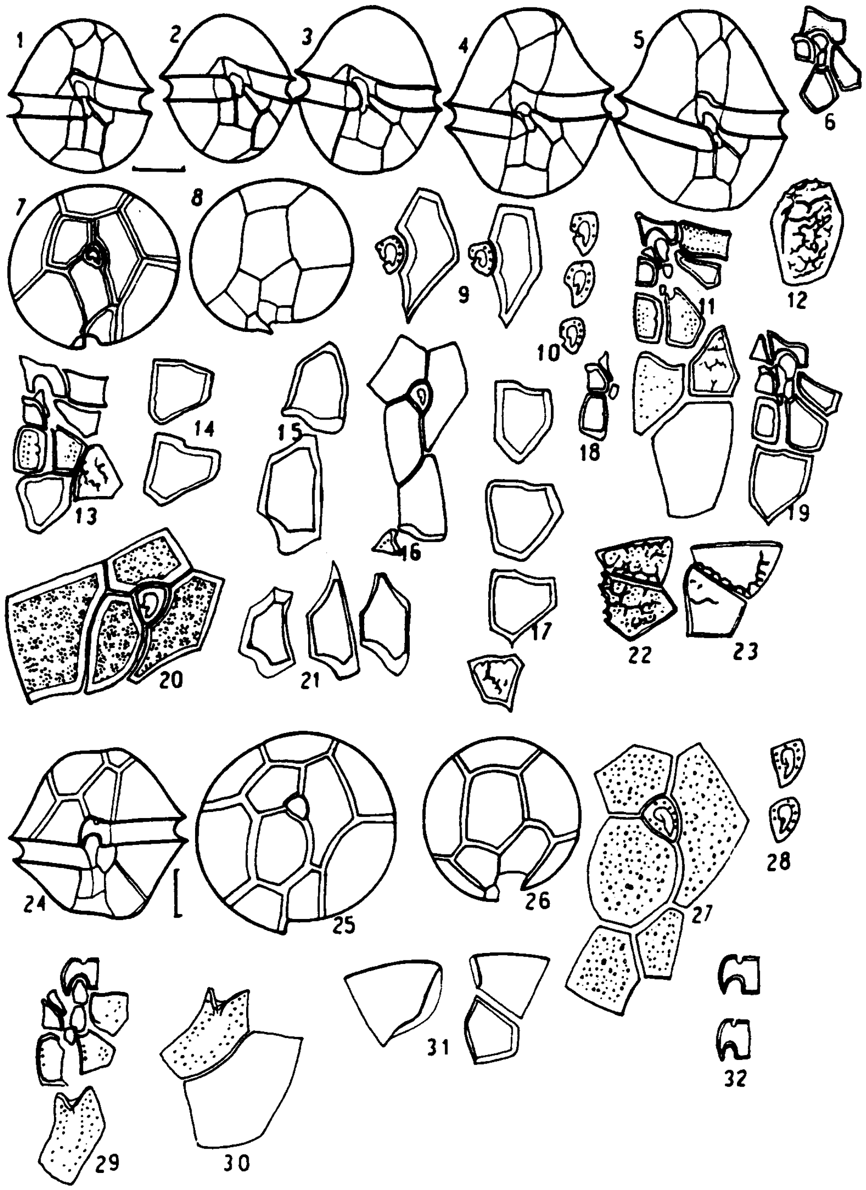


Plate XV

Fig. 1-16, *A. monilatum*: 1) two cells of a chain; 2) apical view; 3) antapical view; 4 and 5) 1’ and 6" (5 sets); 6) variations of the Po; 7) sulcals; 8) four S.a.; 9) S.a. and the two median sulcals; 10) three S.d.p. and an S.ac.p.; 11) the left lateral sulcals and the two medians; 12) S.s.p.; 13) S.d.a and accessories; 14) two S.s.a; 15) 5"’; 16) 1"’ and 1"".

Fig. 17-35, *A. taylori*: 17-20) ventral view; 21) three Po; 22) apical view; 23) antapical view; 24) the ventral hypothecal region; 25) sulcals; 26) S.d.p. with S.ac.p. (4 sets); 27) variations of the S.p.; 28) the two median and the two left lateral sulcals; 29) S.s.a. and S.s.p; 30) 5"’ and 1"’; 31) two 3’; 32) two 6"; 33) S.s.p; 34) 4’ with duplicate ventral pores; 35) detail of the junction forming the ventral pore.

The bar beneath Figure 17 applies to Figures 17-20.

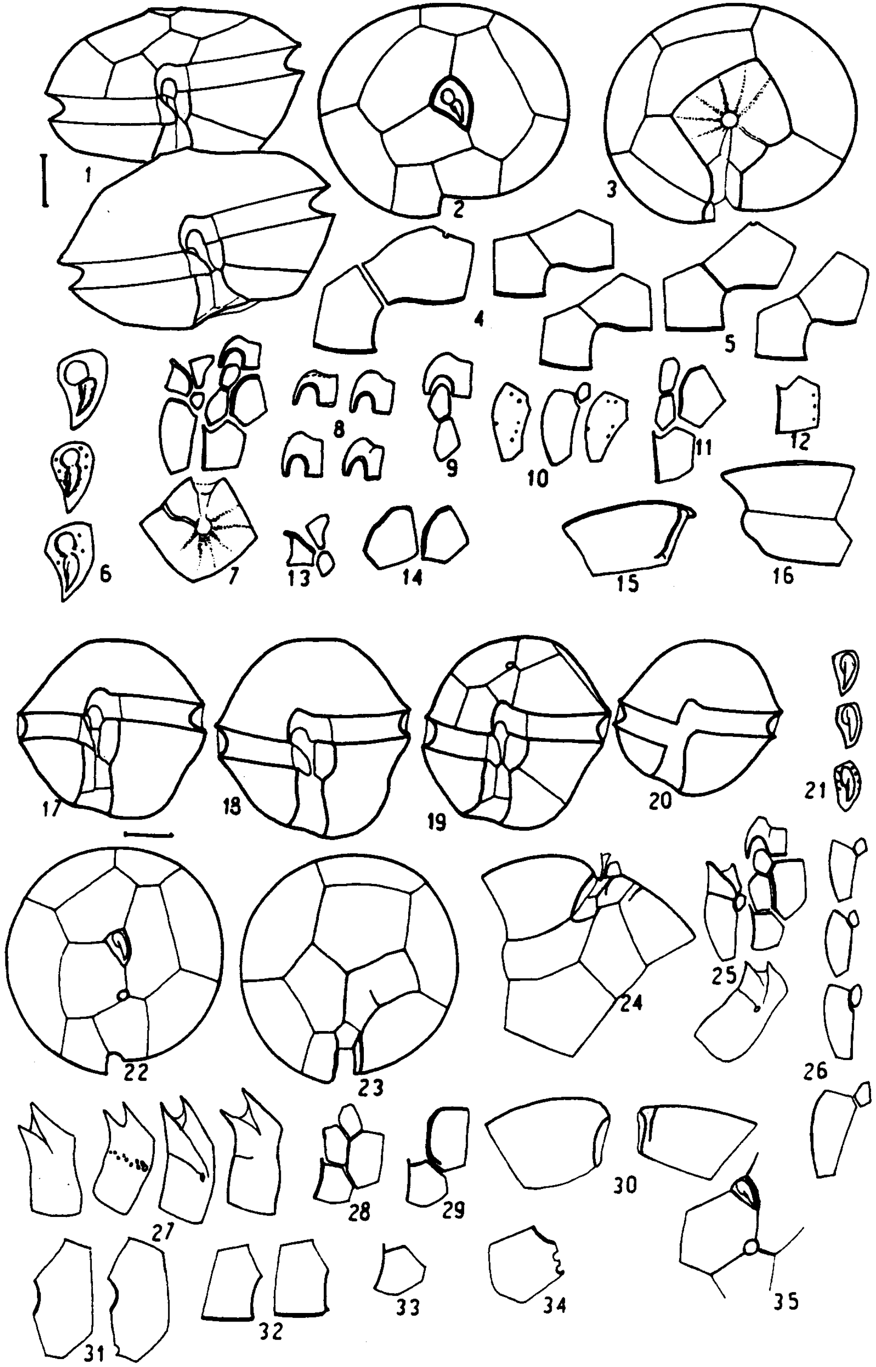


Plate XVI

Fig. 1-18, *A. pseudogoniaulax*: 1) ventral view; 2) apical view; 3) the apical region and S.a.; 4) antapical view; 5) variations of the Po; 6) two 1' plates; 7) 5"' and 1"'; 8) S.s.a., 1"', and 1""; 9) S.d.p.; 10) sulcals without the S.p.; 11) S.m.a.; 12) S.m.a. and S.s.a.; 13) S.p.; 14) two S.a.; 15) variations of the S.m.p.; 16) S.d.a.; 17) two S.ac.p.; 18) two S.s.p.

Fig. 19-32, *A. margalefi*: 19 and 20) ventral view; 21) apical view; 22) antapical view; 23) 6"; 24) Po and 3'; 25) variations of the Po; 26) the junction forming the ventral pore and 6"; 27) 6"; 28) two S.a.; 29) the right lateral sulcals, the first pair with an accessory plate; 30) variations of the median and left lateral sulcals; 31) two S.p.; 32) sulcals and antapicals.

The bar between Figures 19 and 20 applies to both figures.

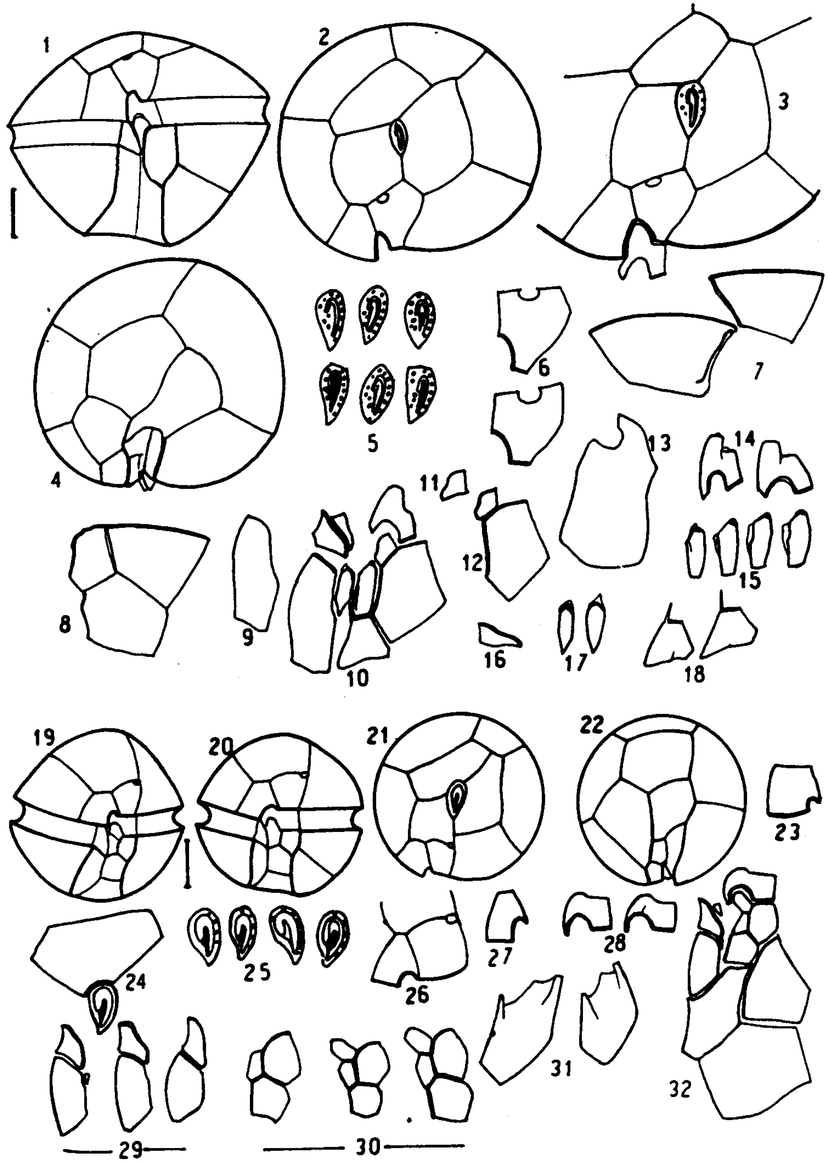


Plate XVII

Fig. 1-23, *A. insuetum*: 1-3) ventral view; 4) left lateral view; 5) Po; 6) epithecal tabulation (plates partially separated in the ventral region); 7) antapical view; 8) ventral portion of the epitheca; 9) S.a. and C_1; 10) Po; 11) Po and 2'; 12) variations of the 1'; 13 and 17) 6", S.a., S.ac.a., and S.d.a.; 14) sulcals without the S.p.; 15) S.p. and antapicals; 16) 4', and 6"; 18) 3' and 2'; 19) S.a. and S.d.p.; 20) 1', sulcals, 5"', and 1""; 21) 1"" and left lateral sulcals; 22) 2"" and 1""; 23) 5"'.

Fig. 24-29, *A. concavum*: 24) ventral view; 25) antapical view; 26) Po and 1'; 27) 1""; 28) two S.p.; 29) sulcals (without the S.p.).

Fig. 30-34, *Alexandrium* sp. I, material from the Gulf of Mexico: 30) anterior individual of a chain; 31) 1' and 6"; 32) Po; 33) S.a.; 34) 1"", 2"", and S.p.

The bar beneath Figures 1 and 2 applies to Figures 1-4.

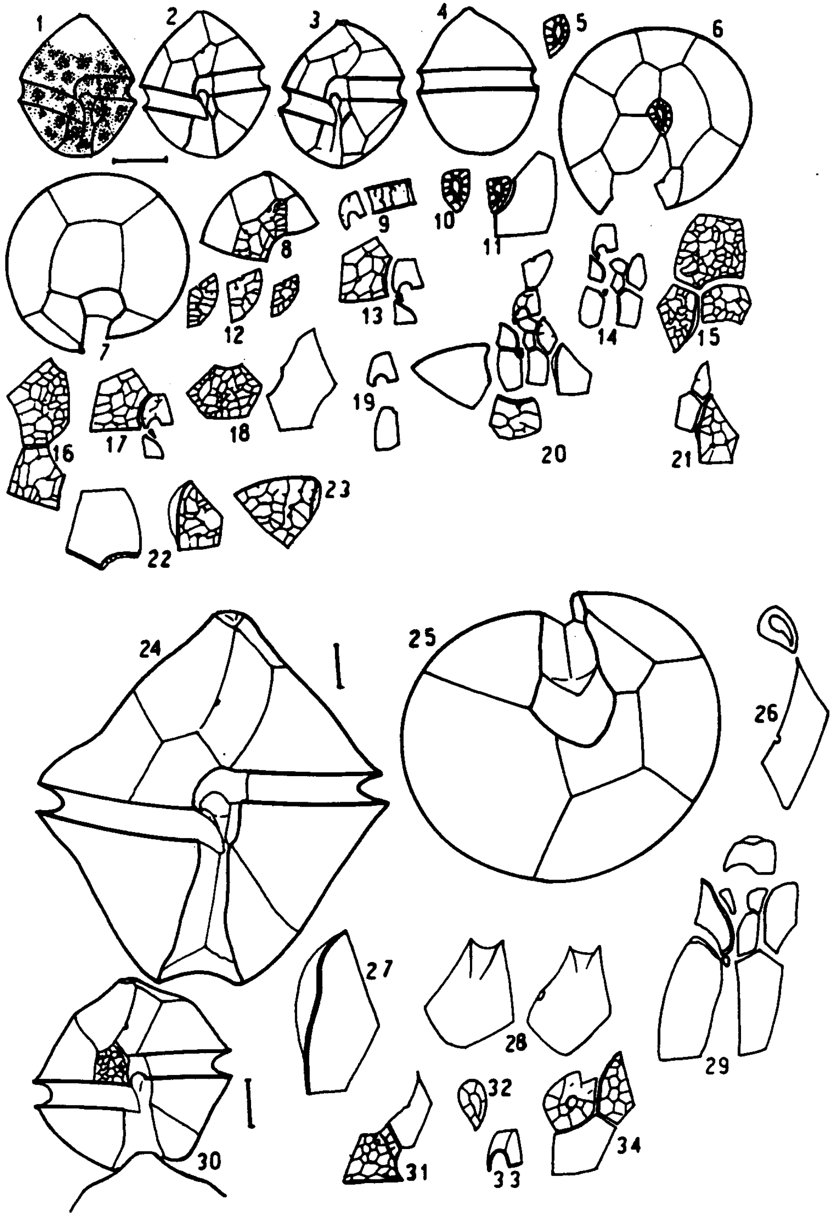


Plate XVIII

Fig. 1-2, *Gonyaulax lebourae*: 1) ventral view; 2) apical view (both views adapted from Lebour).

Fig. 3-5, *A. depressum*: 1) ventral view; 2) apical view; 3) antapical view (all views reproduced from Gaarder).

Fig. 6, *Goniaulax conjuncta* (adapted from Wood).

Fig. 7-9, *Gonyaulax dimorpha*: 1) wide individual in ventral view; 2) narrow individual in ventral view; 3) antapical view (all views adapted from Biecheler).

Fig. 10-11, *Pyrodinium phoneus*: 1) ventral view; 2) apical view (both views adapted from Woloszynska and Conrad).

Fig. 12-24, *Alexandrium* sp. III: 12 and 13) ventral view, 14) dorsal view; 15) apical view; 16) antapical view; 17) Po, 1', 6", and S.a.; 18) Po, 1', and 3'; 19) 5"' (left) and 1"" (right); 20) six Po; 21) sulcals; 22) 1"'; 23) three S.s.a.; 24) S.p. without a pore.

Fig. 25-27, *A. hiranoi*: 25) ventral view; 26) Po; 27) antapical view.

The bar applies to Figures 12-14.