A REVISION OF THE TRIASSIC TO LOWEST JURASSIC DINOFLAGELLATE *RHAETOGONYAULAX*

by R. HARLAND, S. J. MORBEY *and* W. A. S. SARJEANT

ABSTRACT. A re-evaluation of the dinoflagellate cyst genus *Rhaetogonyaulax* shows it to have a complex tabulation of 4′–?6′, 5a–?6a, 1av, 7″, 7c, 7‴, 1p, 1pv, 3s, 3⁗. The archaeopyle is shown to be developed by loss of the epitract anterior to the precingular plate areas. In consequence of recognition of the high degree of intraspecific variability, all specimens examined are attributed to the single species *R. rhaetica*; the former species *R. chaloneri* is recognized as an extreme in the morphological range and reduced to varietal status.

ONE of the authors (S. J. M.), in his research on the Rhaetic Formation (Morbey and Neves 1974, p. 161) of a borehole at Bunny Hill, Nottinghamshire, and the Rhaetian Stage of the Kendelbachgraben, Austria, encountered dinoflagellate cysts attributable to the genus *Rhaetogonyaulax* Sarjeant, 1966. Since the holotypes of the two species of this genus (including the type species) were lodged with H.M. Geological Survey, now the Institute of Geological Sciences, a request was made to I.G.S. for permission to study the type material, which was located, remounted, and re-examined. In addition, it was decided to supplement the types by processing topotype material from a sub-sample of the original rock specimen. Normal palynological processing techniques were used and a total of thirty-eight single grain mounts were made, together with several strew mounts. The type material and topotype material, together with other specimens from other localities under investigation by S. J. M., are used here in a reconsideration of the genus.

The two described species of *Rhaetogonyaulax* have a particular significance in dinoflagellate studies, since they are among the oldest undoubted dinoflagellate cysts known. They have in consequence figured in many discussions of dinoflagellate evolution (see Wall and Dale (1968, p. 288), Sarjeant in Erdtman (1969, p. 179), Evitt in Tschudy and Scott (1969, p. 462), and Evitt (1970, p. 31)).

HISTORICAL BACKGROUND

In 1963 W. A. S. S. described two new species of dinoflagellates that had been discovered, initially by Professor W. G. Chaloner, during a palynological study of H.M. Geological Survey Stowell Park Borehole. The specimens were encountered at a depth of 2059 ft 2 in (627·63 m) in Rhaetic (Upper Triassic) strata. Their tabulation, which is poorly developed, was interpreted as being of a relatively simple character, according with that of the living motile genus *Gonyaulax*; in consequence, though they were from the outset recognized to be cysts, they were named *G. rhaetica* and *G. chaloneri*. The holotypes were deposited by W. A. S. S. in the collections of H.M. Geological Survey. Archaeopyle formation was said to have taken place 'by breakage immediately anterior to, and not along, the transverse furrow' (Sarjeant 1963, p. 353).

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Sarjeant, in Davey *et al.* (1966), reviewing cysts with a *Gonyaulax*-type tabulation, erected the new genus *Rhaetogonyaulax* to accommodate the species *R. rhaetica* and *R. chaloneri*, arguing that, although they possessed a gonyaulacacean tabulation, they were spindle-shaped and had an epitractal archaeopyle. This is in marked contrast to *Gonyaulacysta* (Deflandre) Sarjeant, the genus to which most fossil species formerly attributed to *Gonyaulax* had by then been referred; this latter genus had been diagnosed as being spheroidal, ovoidal, or polyhedral with a single-plate precingular archaeopyle. Unfortunately, the transference of the two species to the genus *Rhaetogonyaulax* did not conform to Article 33 of the International Code of Botanical Nomenclature (Lanjouw *et al.* 1966), since their basionyms were not clearly indicated; Loeblich and Loeblich (1968) rectified the position for *Gonyaulax rhaetica* and subsequently Sarjeant, in Davey *et al.* (1969), did likewise for *G. chaloneri*.

The original studies of these cysts were made with a monocular petrological microscope, with a maximum attainable magnification of $\times 800$ and relatively low intensity of illumination. The new studies here reported have taken full advantage of the improvements in microscope technology since 1963. The work was done using a Vickers microscope, Gillet and Sibert and Leitz photomicroscopes equipped for phase-contrast work, and a Zeiss photomicroscope equipped for both phase-contrast and Nomarski-interference contrast work. In addition, specimens were mounted for scanning-electron photomicrography.

The morphology of this genus is one of especial complexity. It was early recognized that the original interpretation of the tabulation was greatly oversimplified and that archaeopyle formation was by schism between plates, not across plates as had originally been believed. Moreover, difficulty was encountered in assigning specimens to the two species originally proposed by Sarjeant. The results of our restudy of the genus are presented below.

GENERIC RECONSIDERATION

Introduction

It has become increasingly apparent in dinoflagellate taxonomy that one of the principal criteria in any systematic scheme is the form and method of archaeopyle formation (Wall and Dale 1969, p. 287). Evitt (1967) has suggested, for instance, that

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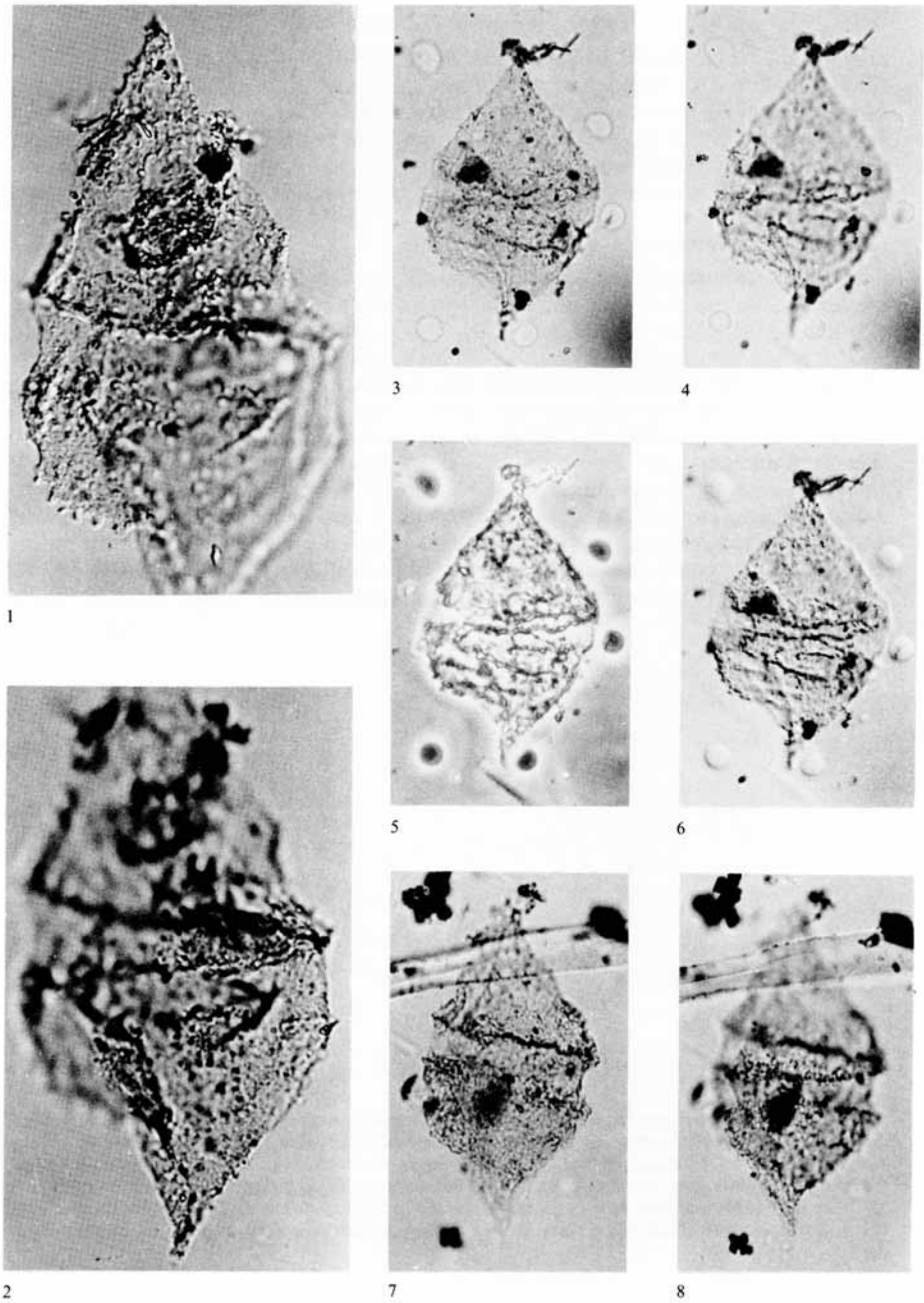
EXPLANATION OF PLATE 100

All figures at a magnification of $\times 750$ and in plain light unless otherwise stated.

Figs. 1–6. *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich emend. 1, dorsal view of specimen MPK 805. On the epitract plates 4″, 5″, and 4a are most readily seen; on the hypotract, plate 5‴. Cingular plate 4c is also well shown; all other reflected plates are not in clear focus. Nomarski interference contrast $\times$ *c.* 1200. 2, ventral view of MPK 805. Only the hypotract is in focus showing plates 6‴, 7‴, 2⁗, and 3⁗, together with 7c and the median sulcal plate. Nomarski interference contrast $\times$ *c.* 1200. 3–6, holotype, specimen 1, PF 1983. 3, dorsal view. 4, ventral view. 5, dorsal view showing the antapical horn, the initial separation of one of the intercalary plates (?5a). Phase contrast. 6, ventral view showing some of the intercalary plates and the suture between those and the apical plates. Nomarski interference contrast.

Figs. 7–8. Holotype of *Rhaetogonyaulax rhaetica* (Sarjeant) var. *chaloneri* stat. nov, specimen 2, PF 1983. 7, oblique dorsal view showing the reticulate ornamentation and sutures between precingular and intercalary plates. 8, oblique ventral view showing antapical horn and some precingular plates.

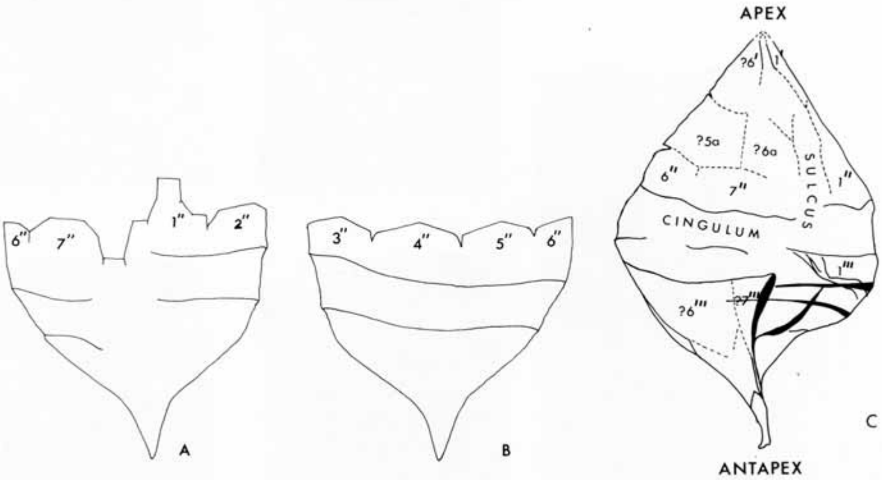


HARLAND *et al.*, *Rhaetogonyaulax*

archaeopyle type or form should be used in circumscribing taxa at the generic level, though it should be noted that Wall, Dale and Harada (1973) have demonstrated some variation in archaeopyle form in *Lingulodinium*, a Cainozoic genus. Wall and Dale (1968, table 2) included *Rhaetogonyaulax* with genera possessing an apical archaeopyle, whereas Evitt (1967) regarded the genus as having an $\overline{\mathrm{AP}}$ combination archaeopyle, i.e. one in which all plates of the apical and precingular series were lost.

Archaeopyle formation and reflected tabulation

Detailed examination of cysts with archaeopyles shows that the margins left, after the operculum has been shed, are regular in form and show a consistent 'scalloping' (Pl. 101, figs. 5, 6 and Pl. 102, figs. 2, 3). This does not accord with the cross-plate schism originally visualized by Sarjeant (1963), which is in any case without parallels in other genera; instead, it indicates that separation has taken place along the boundary between two reflected-plate series. There is a distinct sulcal notch which enables ready orientation of such specimens, and seven precingular plates, of very meagre dimension, are shown to be present between cingulum and archaeopyle margin. Some specimens appear to show only six precingular plates together with a doubtful area around the sulcus (Pl. 101, figs. 5, 6). We believe that the stereoscan photomicrographs demonstrate the presence of seven precingular plates, the sulcal area lying immediately to the right of reflected plate 1″ (see especially Pl. 102, fig. 3). A particular feature of this plate series is the prominent 1″ plate. Text-fig. 1A, B



TEXT-FIG. 1. A, B, a semidiagrammatic sketch of *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich emend. showing complete archaeopyle development, particularly the prominent 1″ reflected plate and the scalloped suture on the dorsal surface. A—ventral surface, B—dorsal surface. C, an interpretative semi-diagrammatic drawing of the ventral surface of the holotype of *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich emend. showing the tabulation where discernible. The dorsal surface of the specimen is not shown, as no clear tabulation could be seen on that surface. (For abbreviations, see legend to text-fig. 2.)

gives a diagrammatic representation of a fully ruptured cyst of *Rhaetogonyaulax* showing the precingular plate series.

In certain of the specimens studied (e.g. Pl. 103, figs. 1–3), some plates anterior to the precingular series are still attached to the abandoned cyst. This might result from chance damage only; but we consider it much more probable that this is evidence that the archaeopyle is developed by successive loss of opercular pieces, not by the complete apical third of the cyst being simultaneously thrown off. The recovery of complete apices with four definite (possibly six) apical plates still present, quite separate from the anterior intercalary plates (Pl. 103, fig. 4, and Pl. 104, fig. 9), supports this concept.

The plates posterior to the apical series and anterior to the precingular series, five or six in number, appear to form a complete ring surrounding the epitract. However, we do not consider them truly analogous to the anterior circle plates of *Egmontodinium* (see Gitmez and Sarjeant 1972), since their position is rather on the flanks of the cyst than on its anterior surface. One of the authors (Morbey 1975) has proposed the term 'postapical plates' for a similarly positioned plate series in another genus. For the moment, however, we have preferred to follow Wiggins (1973) by designating these plates as 'intercalary plates'.

We believe that the archaeopyle begins to develop by initial splitting along the margins of some of the reflected intercalary plates (Pl. 103, fig. 13; Pl. 104, figs. 1–3). One or more intercalary plate-areas separate from each other and from the cyst, leaving the cyst otherwise intact. Further splitting results in the progressive loss of the remaining intercalary plate-areas, the apex as a unit, the anterior ventral and anterior sulcal plates; the order of these events has not yet been definitely determined, but it seems likely that the apex and sulcal plates are the last to detach. The holotype of *R. rhaetica* shows initial separation of one of the intercalary plates (Pl. 100, fig. 5; text-fig. 1C), and other specimens have been observed in which the only discernible rupture is between the apical and intercalary plates. Although several detached apices have been found (see above), none show any surviving attachment to the anterior ventral and anterior sulcal plates; the latter, if they separate (as seems probable), would be so small as to be difficult to identify as such.

The reflected tabulation of *Rhaetogonyaulax* is extremely difficult to observe on complete specimens, including the holotypes, whose orientation is consequently often indeterminate. Indeed, the original photographs of the holotypes of *R. rhaetica* and *R. chaloneri* are inverted, as are the specimens illustrated by Orbell (1973) and Fisher (1972*b*). Some suture lines are occasionally evident, and in some cases the plate boundaries are defined by partially or incompletely developed rows of 'ornament'. Plate areas are most readily to be observed after complete or partial rupture, especially on the epitract. The hypotractal tabulation is especially difficult to decipher clearly, as evidenced in the stereoscan photomicrographs. The interpretation here presented was arrived at only after some weeks of study by one of us in particular (W. A. S. S.), of specimens by Nomarski-interference contrast, in which it proved possible laboriously to trace the plate boundaries (Pl. 100, figs. 1, 2; Pl. 101, figs. 1, 2). Even after this study, some doubt concerning the tabulation exists. In particular, a rupture line has been observed on some specimens, perhaps separating off a polygonal platelet at the apical end of plate 1″ (see text-fig. 1A). It is also possible that additional posterior intercalary plates may be developed (see text-fig. 2D). Some degree of variation in plate shape is also apparent, as seen especially in the most prominent and easily recognizable plate, 1″ (see text-figs. 1 and 2; Pl. 101, figs. 6, 12; Pl. 102, fig. 2; and Pl. 103, figs. 7, 9).

The tabulation inferred is of great complexity, according neither with the gonyaulacacean lineages nor the peridiniacean lineages of Wall and Dale (1968). There is, however, close accord with the tabulation of the Upper Triassic dinoflagellate *Shublikodinium* Wiggins, 1973, which likewise has 4–6 apical plates lost together with a complete series of 'intercalary' plates in archaeopyle formation, and has a hypotract with three antapical plates. The two genera, though differing in symmetry and in other tabulation details, are quite evidently closely related and may represent an ancestral stock from which the two named lineages diverged. In fact, any residual differences in tabulation are probably a result of two subjective interpretations. The long-ranging genus *Pareodinia* Deflandre, whose tabulation has not yet been fully determined but is known to be complex, may be a persistent representative of this ancestral stock.

Variability

It is apparent that there is a great deal of variability in many aspects of the morphology of *Rhaetogonyaulax*. The cysts are typically spindle-shaped but vary in outline from slender and elongate to broad and squat (see Pls. 103 and 104); specimens have been seen which appear to show the presence of an incipient second antapical horn (see Pl. 104, figs. 2, 5). Although this may be of some significance, the authors wish to reserve further comment at this time. In addition, specimens have been observed, typically from the Swabian Facies and the Limestone ± *Lithodendron* (Group VI), Kendelbachgraben, Austria, which show only rudimentary antapical horn development (Pl. 103, figs. 1, 2).

The nature of the cyst 'ornamentation' is such that specimens may carry variously

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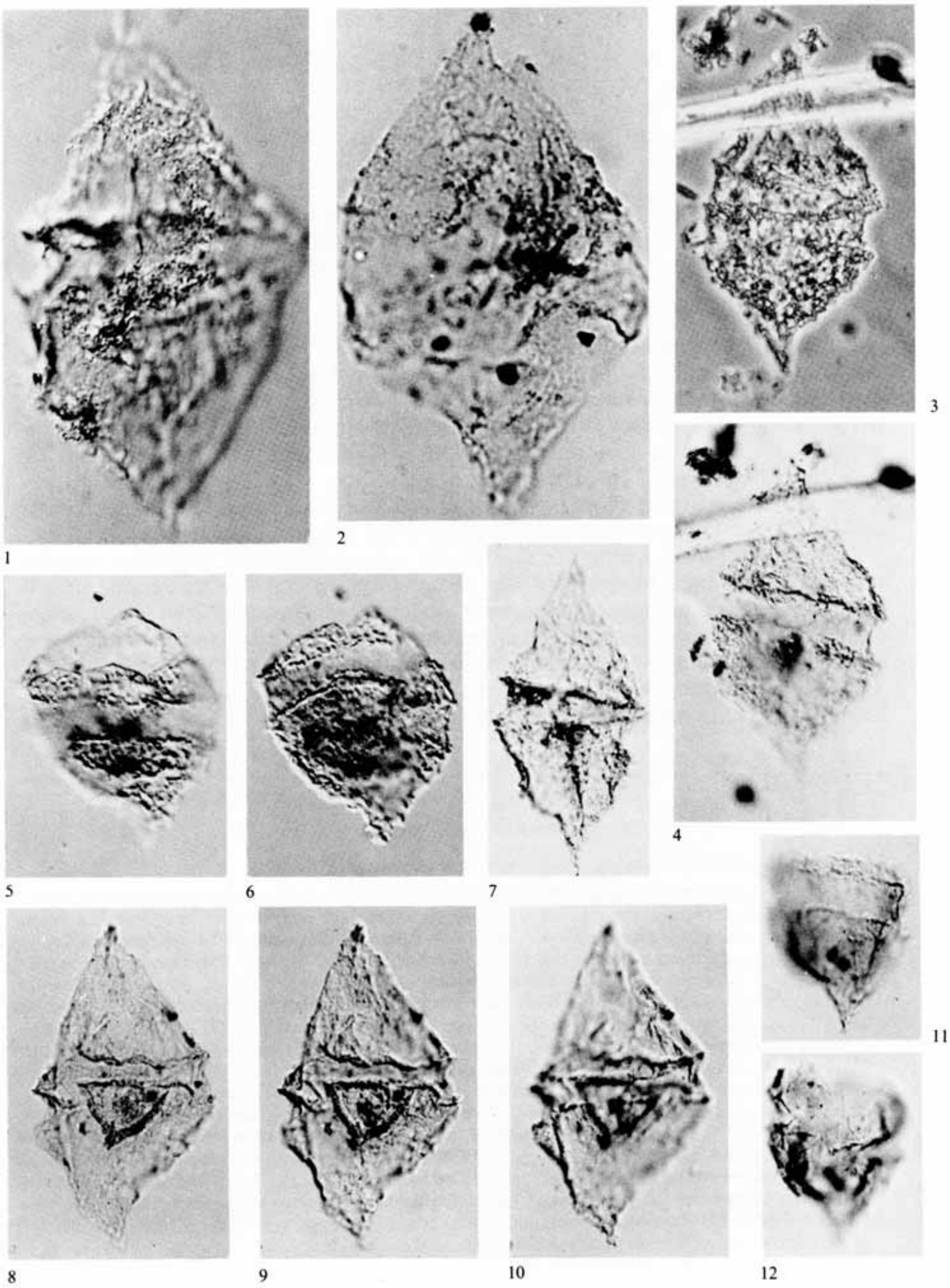
EXPLANATION OF PLATE 101

All figures at a magnification of × 750 and by Nomarski interference contrast unless otherwise stated.

Figs. 1–2, 5–12. *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich emend. 1, dorsal view of MPK 806 showing a prominent cingulum, plates 2″, 3″, and 4″ on the epitract and plates 2‴ and 3‴ and the edge of plates 1‴ and 1p and the antapical plates 2⁗ and 3⁗; compare with text-fig. 3A. × *c.* 1200. 2, ventral view of MPK 807, showing plates ?5a, ?6a, 1av, 1a, and 2a on the epitract and plates 1‴, 1p, and 1pv on the hypotract, compare with text-fig. 3C. Plain light × *c.* 1200. 5, specimen MPK 804, in dorsal view showing the 'scalloping' and precingular plates 4″, 5″, and 6″. 6, specimen MPK 804, in ventral view showing the sulcus and prominent 1″. 7, specimen MPK 803, ventral view showing some intercalary and postcingular plates together with a broad sulcus and plate bounding granular ornamentation on hypotractal plate 2‴. 8, specimen MPK 802, oblique ventral view showing apical and intercalary plates. Plain light. 9, specimen MPK 802, oblique ventral view. 10, specimen MPK 802, oblique dorsal view showing the antapical horn. 11, specimen MPK 809, dorsal view showing broad cingulum. Plain light. 12, specimen MPK 809, ventral view showing prominent 1″, as and 7″ plates. Compare with fig. 6 for variation in plate shapes. Plain light.

Figs. 3–4. *Rhaetogonyaulax rhaetica* (Sarjeant) var. *chaloneri* stat. nov. 3, holotype in oblique ventral view showing the ornamentation. Phase contrast. 4, holotype in oblique dorsal view showing lack of ornamentation on the cingulum.



HARLAND *et al.*, *Rhaetogonyaulax*

developed elements, i.e. spinelets, granules, and/or bacules. The elements of the 'ornamentation' (i.e. granules-spinelets) possess tapered or expanded stems and truncate, furcate, or rounded terminations; a reticulation and a microgranulation may also be developed. Any one specimen may carry several types of such abbreviate 'processes', in addition to being rough- or smooth-walled. (The holotype of *R. chaloneri* (Pl. 100, figs. 7, 8, and Pl. 101, figs. 3, 4) carries both a reticulation and granules and spinelets.) Occasionally, forms may occur which are more or less completely smooth-walled and virtually devoid of 'ornament' (Pl. 103, fig. 12). The 'ornamentation' is so disposed that the cingulum may, for instance, be devoid of 'ornament' (Pl. 102, fig. 2) or may not differ in ornamentation from that on the epitract or hypotract (Pl. 102, fig. 1). The 'ornamentation' occurs in the form of random or orientated intratabular or plate-bounding processes on the epitract and hypotract, being distinctly plate-bounding between the cingulum and precingular and postcingular plates, and between the sulcus and adjacent hypotractal plates. The continuation of the sulcus on the epitract is defined either by plate-bounding processes or by an apparent difference in texture between the wall structure of the sulcus and the adjacent plate areas (Pl. 103, fig. 2).

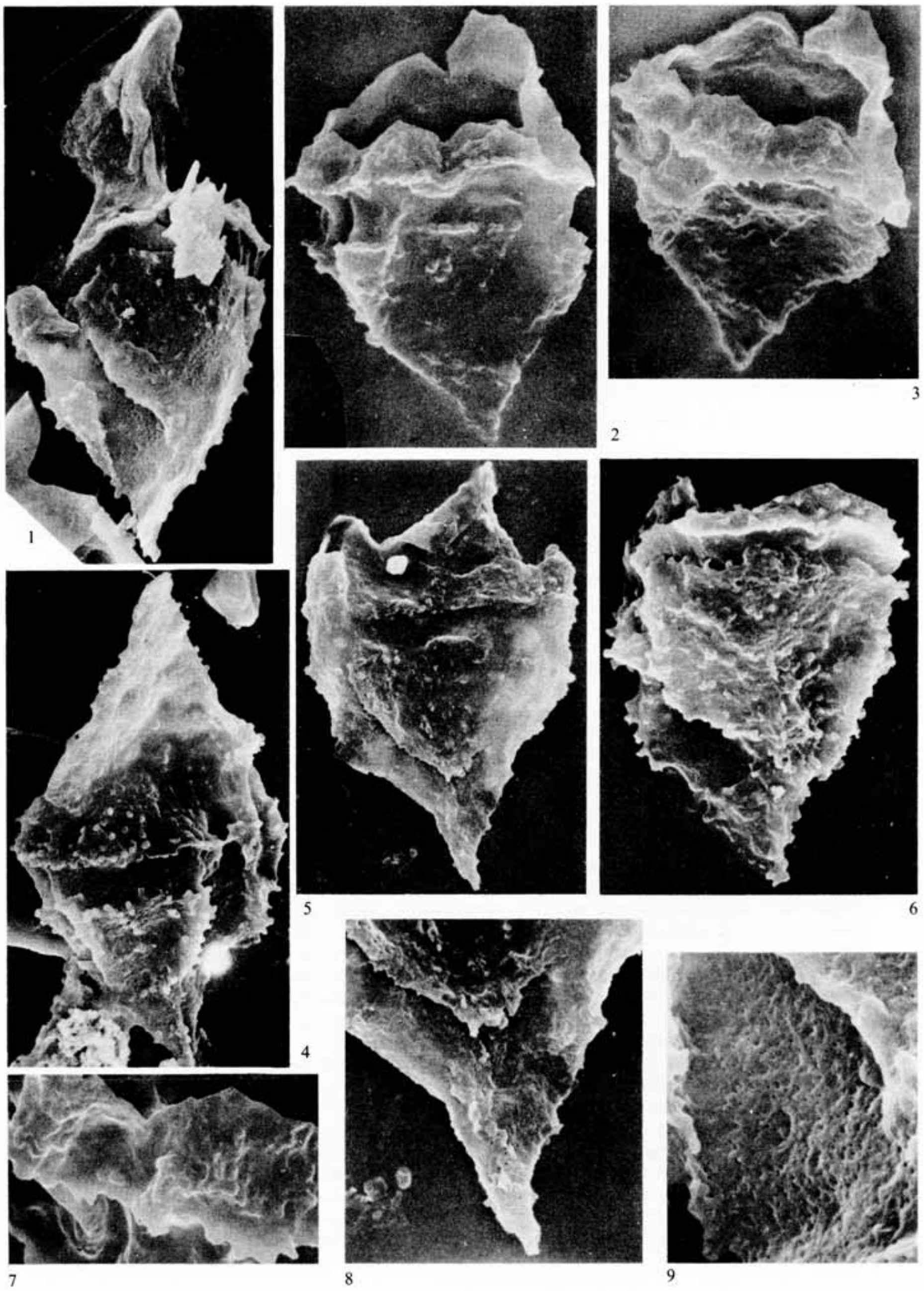
Variation in reflected plate morphology has also been noted and is commented upon in the section on archaeopyle formation and reflected tabulation.

A biometrical study was undertaken on the topotype material. Sixty-five complete specimens were used to construct the scatter diagram and the histograms seen in text-figs. 3–5. The parameters used were the length (distance between the apex and antapex), width, and the maximum cingulum width of the cysts and it was hoped to learn something of the variation within the topotype population of *Rhaetogonyaulax*. The resulting scatter diagram of cyst length/cyst width *v*. cyst length/width of cingulum (text-fig. 3) produced a distribution of points indicating a relationship between

EXPLANATION OF PLATE 102

All figures at a magnification of $\times c$. 1500 unless otherwise stated.

Figs. 1–9. *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich emend. Scanning electron photomicrographs of specimens showing archaeopyle formation and the variability of the cyst surface 'ornamentation'. 1, a reticulate form in oblique ventral view that carries granules and bacules; the ornamentation is also present on the cingulum and sulcus. Plates ps, pv, 1p, 1‴, and 2‴ are possibly discernible. MPK 820. 2, a form in lateral view showing complete archaeopyle formation, the seven precingular reflected plate areas, and the over-all smooth cyst surface with some intratabular 'ornamentation' elements and a cluster of intratabular elements in the centre of a postcingular plate area. MPK 815. 3, a specimen in lateral view showing complete archaeopyle formation and a slightly rougher 'ornament' than fig. 2. MPK 813. 4, as form in oblique ventral view showing a rough cyst surface with plate-bounding and intratabular granules and bacules. Compare with text-fig. 2B. MPK 819. 5, a specimen in dorsal view showing complete archaeopyle formation, rough 'ornamentation' and two antapical plates 1⁗ and 2⁗, also 1pv, ps, and the inbulge of ms, a single intercalary plate, at least three precingular plates, three postcingular plates, and two antapical plates. MPK 814. 6, form with well-developed granules and bacules in oblique ventral view, plates ps, pv may also be seen. MPK 824. 7, detail of MPK 813 showing the shape of the precingular plates 4″ and 5″ and a cingular plate boundary and their ornament, $\times c$. 3000. 8, detail of MPK 814 showing the plates and ornament of the antapex, $\times c$. 3000. 9, detail of MPK 820 to show the nature of the reticulate ornamentation in the sulcus, $\times c$. 4500.



HARLAND *et al.*, *Rhaetogonyaulax*

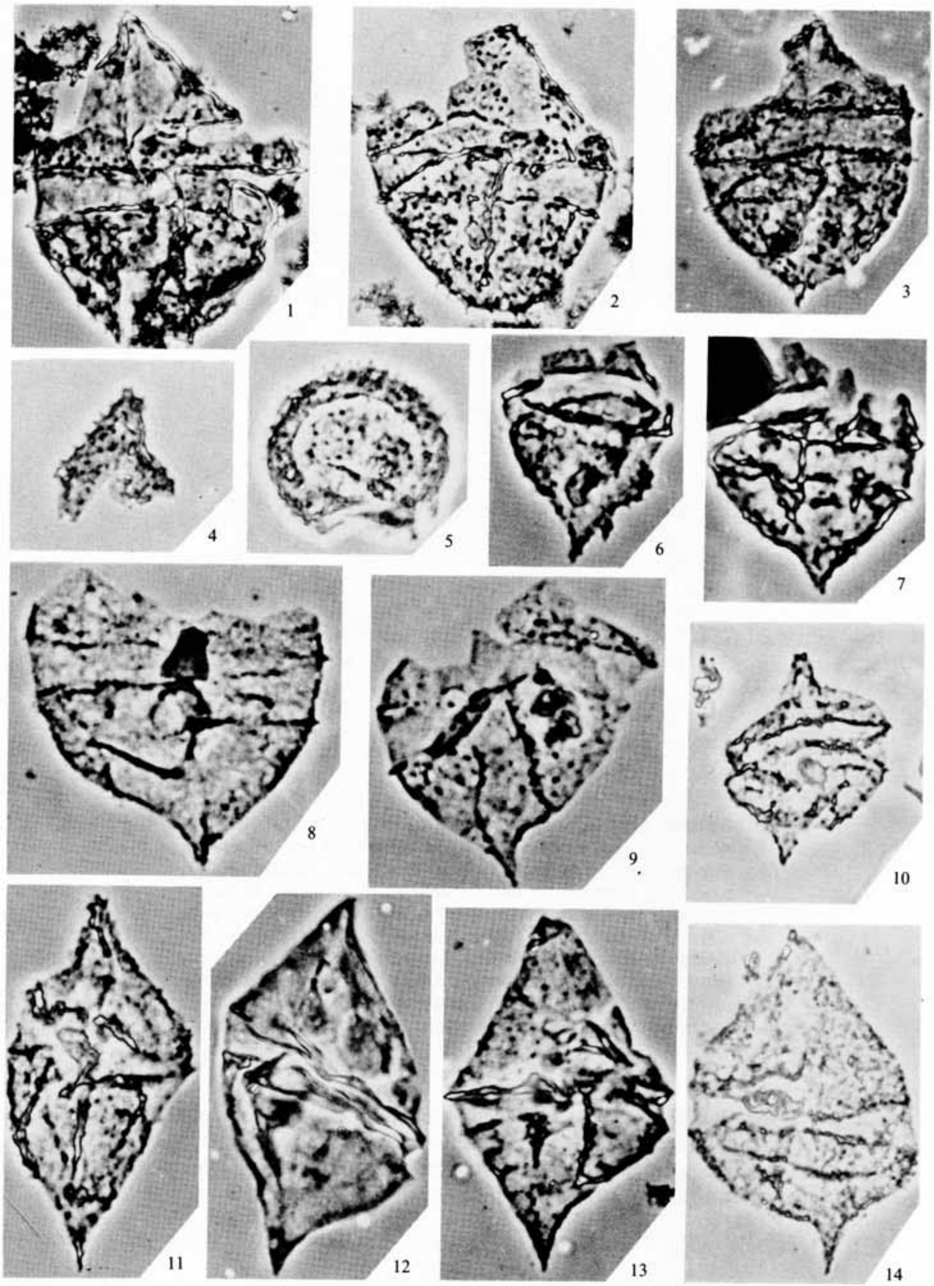
the parameters, that the more slender the cyst the wider the cingulum width in relation to the length. The data gives a correlation coefficient of 0·3706. It would appear that only one population is involved here, with respect to the parameters measured, as there is no suggestion of clumping or separation into two or more groups, and the histograms of the frequency of cyst length/cyst width (text-fig. 4) and of cyst length/cingulum width (text-fig. 5), are unimodal and are skewed to the right. The biometrical study does not and cannot, however, in itself prove or disprove the existence of one, two, or many species; but it is additional evidence for treating the topotype specimens as belonging to a single population.

In the light of the present study, the authors feel that an emendation, not only of the genus *Rhaetogonyaulax* but also of the species *R. rhaetica*, is necessary. Sarjeant's (1963) division into two species, *rhaetica* and *chaloneri*, based largely upon ornamentation, is no longer felt to be justified. In particular, we believe that *Rhaetogonyaulax*

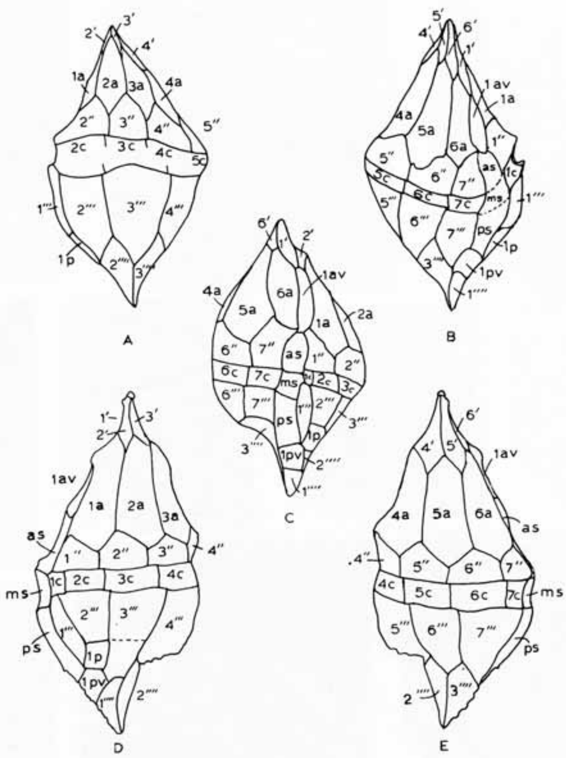
EXPLANATION OF PLATE 103

All figures are phase contrast photomicrographs and at a magnification of $\times 750$ unless otherwise stated. Slide co-ordinates given here and subsequently refer to microscope No. 158226 housed in the Department of Geology, University of Sheffield.

Figs. 1–14. *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich emend. 1–9, cysts in various stages of rupture, archaeopyle formation, and preservation. 1, specimen slide ref. 23//1q/1/458/1254; Limestone $\pm$ *Lithodendron* (Group VI), Kendelbachgraben, Austria; Rhaetian (*sensu lato*). Antapical horn rudimentary in development and partial archaeopyle formation. 2, specimen slide ref. 23//1q/1/347/1214; as above, following incomplete rupture, a single intercalary, seven precingular reflected plates clearly visible. Antapical horn rudimentary in development. Ornamentation well developed. Processes clearly intratabular on anterior intercalary and precingular reflected plates. 3, specimen slide ref. 5//2j/2/300/1254; Swabian Facies (Lower), Kendelbachgraben, Austria; Rhaetian (*s. l.*). Antapical horn showing greater development and also showing precingular plates, one intercalary, and some apical plates. Specimens not possessing clear antapical horns are morphologically very similar to some specimens of *Shublikodinium* and possibly bridge the gap between the two genera. 4, specimen slide ref. 26d/246/1305; Westbury Member, Rhaetic Formation, Bunny Hill Borehole, Notts., England; Rhaetian. Detached apical horn comprising at least four reflected apical plates. 5, specimen slide ref. 52c/420/1254; Cotham Member, Rhaetic Formation, Bunny Hill Borehole, Notts., England; Hettangian Stage, apical compression of completely ruptured cyst. 6, specimen slide ref. 44//$\times$13/beta/400/1276; $\times 875$. Equatorial compression of completely ruptured cyst. Archaeopyle clearly evident. Precingular reflected plates splitting apart. 7, specimen slide ref. 44//$\times$13/beta/363/1291; $\times 875$. 6 and 7, in Salzburg Facies, Kendelbachgraben, Austria; cyst illustrating archaeopyle formation. 8, specimen slide ref. 14//1z/5/252/1284; $\times 875$; cyst illustrating archaeopyle formation and also the boundary between 2'''' and 3''''. 9, specimen slide ref. 14//1z/4/332/1285; $\times 875$. 8 and 9, in Swabian Facies, Kendelbachgraben, Austria; cysts illustrating archaeopyle formation. 10–14, cysts illustrating various outline shapes and degrees of development of body ornamentation. 10, specimen slide ref. 52c/420/1254; Cotham Member, Rhaetic Formation, Bunny Hill Borehole, Notts., England; Hettangian Stage; randomly ornamented with processes. Orientation indeterminate. Cyst complete. 11, specimen slide ref. 29//1j/2/586/1276; Carpathian Facies, Kendelbachgraben, Austria; Rhaetian (*s. l.*); $\times 875$; sulcus well developed, ornamentation randomly developed. Sulcus tending to be broader in hypotract. 12, specimen slide ref. 16//1x/1/375/1294; Swabian Facies (Upper), Kendelbachgraben, Austria; Rhaetian (*s. l.*); $\times 875$; cyst unornamented, wall smooth. Orientation indeterminate. 13, specimen slide ref. 16//1x/3/269/1289; $\times 875$; Swabian Facies (Upper), Kendelbachgraben, Austria. Orientation indeterminate. 14, specimen slide ref. 33b/418/1219; Westbury Member, Rhaetic Formation, Bunny Hill Borehole, Notts., England; Rhaetian. Cyst inequifusiform in outline, wall reticulation superimposed by 'ornament'.

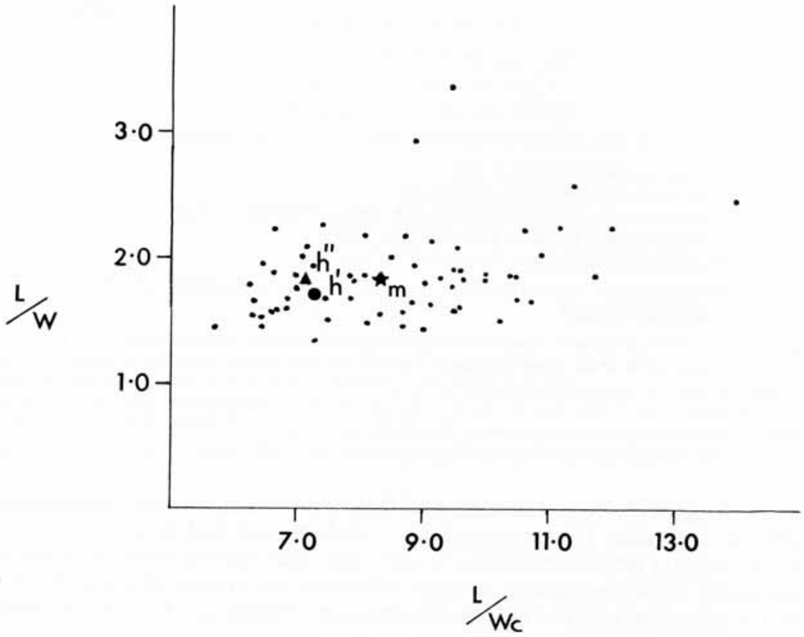


HARLAND *et al.*, *Rhaetogonyaulax*

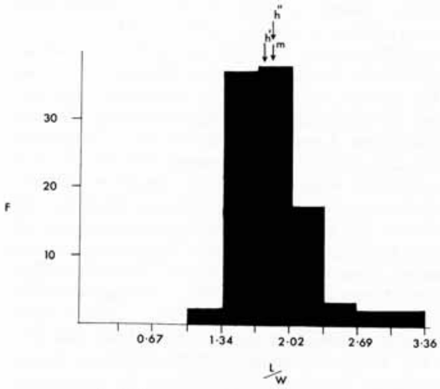


TEXT-FIG. 2. An interpretative reconstruction of the tabulation of *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich emend. A–B, specimen MPK 806. A, in left lateral view, slightly oblique; B, in right lateral view, slightly oblique. C, specimen MPK 807 in ventral view. D–E, specimen MPK 805. D, in left lateral view; E, in right lateral view. Abbreviations: 1′–6′, apical plates; lav, anterior ventral plate; 1a–6a, anterior intercalary plates; as, anterior sulcal plate; ms, median sulcal plate; 1″–7″, precingular plates; 1c–7c, cingular plates; 1‴–7‴, postcingular plates; 1pv, posterior ventral plate; 1p, posterior intercalary plate; 1⁗–4⁗, antapical plates.

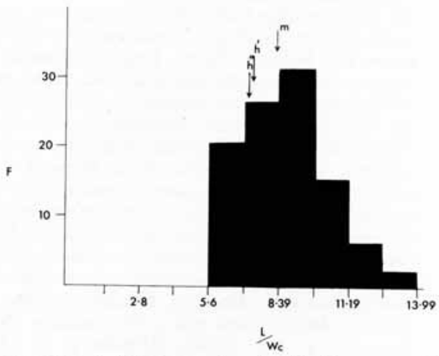
is a genus that has a demonstrably large variation of surface ornamentation, such that there is no justification in treating a reticulate form as a separate species. The fact that the topotype material, based upon certain measurable parameters, acts as a unified population, is additional evidence for our view.



TEXT-FIG. 3. Scatter diagram of the topotype material based upon sixty-five complete specimens. h'—holotype of *Rhaetogonyaulax rhaetica*; h''—holotype of *R. chaloneri*; m—mean. The diagram has a correlation coefficient of 0·3706.



TEXT-FIG. 4. Histogram showing the frequency of the L/W parameter in the topotype material h', h'', and m as in text-fig. 3. F calculated as percentages of the total. Standard deviation of L/W is 0·36.



TEXT-FIG. 5. Histogram showing the frequency of the L/Wc parameter in the topotype material h', h'', and m as in text-fig. 3. F calculated as percentages of the total. Standard deviation of L/Wc is 1·72.

SYSTEMATIC PALAEONTOLOGY

Division PYRRHOPHYTA Pascher
Class DINOPHYCEAE Pascher
Order PERIDINIALES Lindemann
Genus *Rhaetogonyaulax* Sarjeant, 1966, emend.

1966 *Rhaetogonyaulax* Sarjeant, p. 152.
1967 [*Rhaetogonyaulax* Sarjeant]; Evitt, p. 46.
1968 *Rhaetogonyaulax* Sarjeant; Loeblich Jun. and Loeblich III, p. 212.
1968 *Rhaetogonyaulax* Sarjeant; Wall and Dale, table 2.
1973 *Rhaetogonyaulax* Sarjeant; Lentin and Williams, p. 119.

Type species. *Rhaetogonyaulax rhaetica* (Sarjeant 1963) Loeblich Jun. and Loeblich III, 1968 O.D. emend. Upper Triassic (Rhaetic), England.

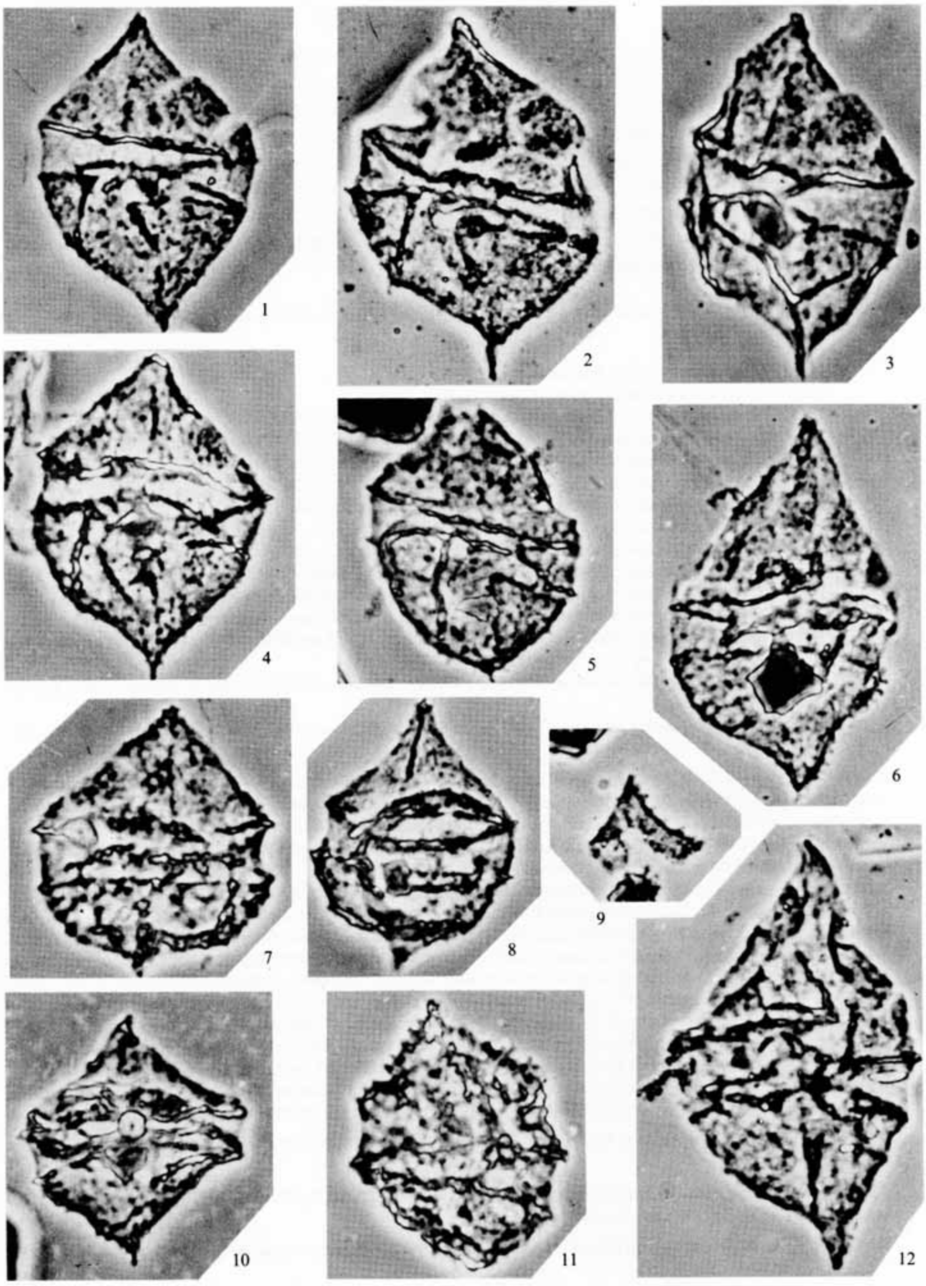
Emended diagnosis. Cyst proximate, elongate-biconical to spindle-shaped, with rudimentary or pronounced apical and antapical horns. Wall apparently single-layered, smooth, rough; punctate, granulate, or reticulate. Cingulum helicoid, laevorotatory, moderately indented; cingulum and sulcus generally defined by ridges. Tabulation 4′–?6′, 5–?6a, 1av, 7″, 7c, 7‴, 1p, 1pv, 3s, 3⁗; boundaries of plate-areas marked by raised lines, lines of short processes, or rupture. Processes, where developed, may be sutural or intratabular, simple or furcate. Archaeopyle development by progressive loss of all plates anterior to the precingular series.

Remarks. Wiggins (1973, p. 4) commented that 'it is remarkable that *Shublikodinium* superficially resembles *Rhaetogonyaulax* . . . in both cyst and archaeopyle outline, when their sutural tabulation series is so different'. Our restudy emphasizes the close comparability of the two genera; residual differences are in over-all shape, *Shublikodinium* being ovoidal with two antapical horns, one of which may be reduced, whereas

EXPLANATION OF PLATE 104

All figures are phase contrast photomicrographs and at a magnification of ×875.

Figs. 1–12. *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich emend. 1–5, cyst specimens illustrating partial rupture of some anterior intercalary plates, variation in over-all outline with development of antapical horn, and broad sulcus on hypotract. 1, specimen slide ref. 44//×13/beta/400/1276; Swabian Facies, Kendelbachgraben, Austria; Rhaetian (*s. l.*). Cyst equifusiform in outline, broad sulcus on hypotract. 2, specimen slide ref. 33a/274/1248; Westbury Member, Rhaetic Formation, Bunny Hill Borehole, Notts., England; Rhaetian. On epitract, apical, anterior intercalary, and precingular reflected plates clearly defined, broad sulcus on hypotract, rudimentary secondary (?) horn developing (? process) in addition to prominent antapical horn. 3, specimen slide ref. 44//×13/gamma/397/1310, Salzburg Facies, Kendelbachgraben, Austria; Rhaetian (*s. l.*). 4, specimen slide ref. 54//×4/5/589/1290; Pre-*planorbis* Beds, Kendelbachgraben, Austria; Rhaetian (*s. l.*). 5, specimen slide ref. 5//2j/beta/380/1295; Swabian Facies (Lower), Kendelbachgraben, Austria; Rhaetian. Rudimentary antapical horn (? process), coarsely ornamented. 6–8, 10–12, cyst specimens showing variation in over-all outline, preservation, and development of ornamentation. 6, specimen slide ref. 55//×3/gamma/612/1200; Pre-*planorbis* Beds, Kendelbachgraben, Austria; Rhaetian. 7, specimen slide ref. 45//×12/beta/305/1283; Salzburg Facies, Kendelbachgraben, Austria; Rhaetian. 8, specimen slide ref. 44//×13/beta/400/1276; Salzburg Facies, Kendelbachgraben, Austria; Rhaetian (*s. l.*). 9, specimen slide ref. 56//×3/1/691/1230; Pre-*planorbis* Beds, Rhaetian. Kendelbachgraben, Austria; apical horn comprising at least four prominent reflected apical plates. 10, specimen slide ref. 44//×13/gamma/588/1303, Salzburg Facies, Kendelbachgraben, Austria; Rhaetian (*s. l.*). 11, specimen slide ref. 29//1j/2/586/1276; Carpathian Facies, Kendelbachgraben, Austria; Rhaetian. Coarse body ornament. Antapical horn developed (preservation ?). 12, specimen slide ref. 41d/352/1228; Cotham Member, Bunny Hill Borehole, Notts., England, Rhaetic Formation; Hettangian. Oblique ventral view, with plates 1‴, 2‴ visible also 1p and much of 7‴, 1⁗, and 3⁗.



HARLAND *et al.*, *Rhaetogonyaulax*

Rhaetogonyaulax is basically spindle-shaped, rarely ovoidal, and rarely exhibiting two antapical horns. *Rhaetogonyaulax* is also much more sharply attenuated than *Shublikodinium*. The two genera also differ in tabulation details, especially on the hypotract, as *Rhaetogonyaulax* possesses postcingular, posterior intercalary, sulcal and antapical plates as opposed to the postcingular and antapical plates of *Shublikodinium*. Since the plate designated 1′ by Wiggins (1973, text-fig. 2) does not in fact form a part of the apex, we have preferred to refer to it as an anterior ventral plate (1av) in reference to its position. The plate which Wiggins (1973) referred to as the 'apical closing plate' is here designated 1′.

Rhaetogonyaulax rhaetica (Sarjeant 1963) Loeblich and Loeblich 1968 emend.

Plates 100–104; text-figs. 1–2

v* 1963 *Gonyaulax rhaetica* Sarjeant, p. 353, figs. 1, 2 left.
1963 *Gonyaulax chaloneri* Sarjeant, p. 354, figs. 2 right, 3.
1964 *Gonyaulax rhaetica* Sarjeant; Downie and Sarjeant, p. 115.
1966 *Gonyaulax chaloneri* Sarjeant; Downie and Sarjeant, p. 114.
1966 *Rhaetogonyaulax rhaetica* Sarjeant *nom. nud.*; Sarjeant, p. 153.
1966 *Rhaetogonyaulax chaloneri* Sarjeant *nom. nud.*; Sarjeant, p. 153.
1968 *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich, p. 212.
1969 *Rhaetogonyaulax chaloneri* (Sarjeant); Sarjeant, p. 15.
1972*b* *Rhaetogonyaulax* sp.; Fisher, p. 105, pl. 2, fig. 15.
1973 *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich; Orbell, pl. 2, fig. 1.
1973 *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich; Lentin and Williams, p. 120.
1973 *Rhaetogonyaulax chaloneri* (Sarjeant) Sarjeant; Lentin and Williams, p. 119.
1974 *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich; Morbey and Neves, p. 168, pl. III, figs. 3, 4.
1975 *Rhaetogonyaulax rhaetica* (Sarjeant) Davey, Downie, Sarjeant and Williams; Felix, pl. II, fig. 2.
1975 *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich and Loeblich; Morbey, pl. 14, fig. 17, pl. 15, figs. 1–4.

Emended diagnosis. Cyst proximate, typically spindle-shaped, unornamented or ornamented. Antapical horn may be rudimentary or well developed. Wall apparently single-layered, thin, smooth, rough, punctate, reticulate or granulate. Processes small, variable in development and distribution; random or orientated, intratabular or plate-bounding, simple and furcate. Cingulum helicoid laevorotatory, unornamented or ornamented, forming a moderately indented furrow; displacement may be as much as twice the cingulum width. Seven cingular plates are developed. Sulcus ornamented or unornamented, generally expanded on the hypotract. Cingulum and hypotractal sulcus clearly defined by plate-bounding processes or ridges; the epitractal sulcus defined by plate-bounding processes or by textural differences between the epitractal plate wall and the sulcal wall. Plate sutures most readily evident where partial or complete detachment of opercular plates has occurred; hypotractal tabulation especially difficult to define. Reflected tabulation 4′–?6′, 1av, 5a–?6a, 7″, 7c, 7‴, 1p, 1pv, 3a, 3⁗; an additional plate-area may be present in the anterior extension of plate 1a as here delineated. Archaeopyle formed initially by detachment of one or more intercalary plates, thereafter by loss of the remaining intercalary plates, the apex as a unit, and the anterior ventral and anterior sulcal plates; cysts with archaeopyles thus show a 'scalloped' edge formed by the anterior margins of the precingular plates and a deep sulcal notch resulting from the loss of the anterior sulcal plate. The median sulcal plate is often deeply indented and probably corresponds to the position of origin of the two flagella.

Typification. Holotype specimen 1, slide PF 1983 (not specimen 98, slide PS 1983, as quoted by Sarjeant (1963)).

Type locality. Rock specimen Bj 6011, Stowell Park Borehole (N.G.R. SP 0835 1173), Northleach, Gloucestershire. Depth 2059 ft 2 in, i.e. 627·63 m.

Repository. The holotype and all figured specimens from the topotype material are held in the Palynological

Collections of the Institute of Geological Sciences, Leeds, England, and are registered in the PF and MPK collections. Comparative material from the Bunny Hill Borehole, Nottinghamshire, and the Kendelbachgraben, Austria, is held in the collections of the Department of Geology, University of Sheffield.

Dimensions. Holotype: cyst length 63·75 μm, width 37·5 μm, cingulum width 8·75 μm.

Topotype material: length 47·5 (64·72) 77·5 μm, width 17·5 (35·72) 48·75 μm; cingulum width 5·0 (7·73) 11·25 μm, based upon sixty-five complete specimens.

Bunny Hill Borehole and Kendelbachgraben material: cyst length 50·0 (69·0) 92·0 μm; width 34·0 (43·0) 54·0 μm; cingulum width 7·0–13·0 μm, based upon thirty-one complete specimens. (The data given are the minimum, mean, and maximum measurements.)

Rhaetogonyaulax rhaetica (Sarjeant) var. *chaloneri*, stat. nov.

Plate 100, figs. 7, 8; Plate 101, figs. 3, 4

v*1963 *Gonyaulax chaloneri* Sarjeant, p. 354, figs. 2 right, 3.
1964 *Gonyaulax chaloneri* Sarjeant; Downie and Sarjeant, p. 114.
1966 *Rhaetogonyaulax chaloneri* (Sarjeant), *nom. nud.*; Sarjeant, p. 153.
1969 *Rhaetogonyaulax chaloneri* (Sarjeant); Sarjeant, p. 15.
1973 *Rhaetogonyaulax chaloneri* (Sarjeant); Lentin and Williams, p. 119.

Typification. Holotype specimen 2, slide PF 1983.

Remarks. *Rhaetogonyaulax chaloneri* is here redesignated as a variety of *R. rhaetica* as no justification can be found in maintaining this form as a distinct species in an obviously variable morphological group.

Geological and geographical range of Rhaetogonyaulax rhaetica

Cotham Beds [Rhaetic], Stowell Park Borehole, Gloucestershire, England (Sarjeant 1963); Cotham Beds [Rhaetic] and Pre-*planorbis* Beds [Lias], Barnstone Railway Cutting, Nottinghamshire, England (Fisher 1972*a*); lower 'Cotham Beds' [lower Rhaetian and basal upper Rhaetian], Bristol Channel region, England (Fisher 1972*b*); Grey Marls, Westbury Beds, Cotham Beds, White Lias, lowermost Watchet Beds [Rhaetic], Lavernock Point, Glamorgan, Wales. Westbury Beds, Cotham Beds [Rhaetic], Owthorpe, Nottinghamshire, England. Westbury Beds, Cotham Beds [Rhaetic], Upton Borehole, Oxfordshire, England (Orbell 1973); Tea-green Marl Member, Parva Formation and Westbury Member, Cotham Member, Rhaetic Formation [Rhaetian *sensu lato* and Hettangian], Bunny Hill Borehole, Nottinghamshire, England. Swabian Facies, Limestone ± *Lithodendron* (Group VI), Carpathian Facies, Kössen Facies, Salzburg Facies, Pre-*planorbis* Beds [Rhaetian *sensu lato* and Hettangian], Kendelbachgraben, Austria (Morbey and Neves 1974); Highest Grey Marls [Keuper Marl], Westbury Beds, lower Cotham Beds [Rhaetic], Watchet, Somerset, England (Warrington 1974); Westbury Beds, Cotham Beds [Rhaetic], Larne Borehole, Antrim, Northern Ireland (Warrington and Harland *in press*). Westbury Beds, Cotham Beds [Rhaetic], Steeple Aston and other boreholes near Chipping Norton, Oxfordshire, England. Westbury Beds, Cotham Beds [Rhaetic], borehole near Chipping Sodbury, Gloucestershire, England (G. Warrington, pers. comm.). Flatsalen Formation [?Rhaetian], Hopen, Svalbard, Norway (D. Smith, pers. comm.) and recorded as cf. B *R. rhaetica* (Smith, Harland and Hughes 1975).

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