THE XANTHIDIA - THE SOLVING OF A PALAEONTOLOGICAL PROBLEM

by

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Summary

A brief biography of the German microscopist, Christian Gottfried Ehrenberg, is given. Microfossils he discovered in flint are shown to comprise two groups: dinoflagellates and spiny bodies, originally termed "xanthidia". The history of the development of ideas on the affinity of these "xanthidia" is outlined; renamed "hystrichospheres" in 1933, they have since been shown to comprise in part, cysts of dinoflagellates, in part, algae attributable to the Chlorophyceae. A residue remains whose affinity is undetermined; these are now termed "acritarchs". The geological distribution and classification of the dinoflagellate cysts and acritarchs are discussed and their value in stratigraphy is assessed.

Introduction

In the early part of the nineteenth century, there was little in the way of relevant University training available to young men with a penchant for natural history. Certainly, lecture courses in botany, zoology and geology were being given, but these were incidental, delivered to students whose prime concern might be law, religion, rarely mining, most often medicine. Thus it happened that many of the greatest nineteenth-century naturalists read for degrees in medicine; only afterwards did they obtain for themselves specific biological training, frequently by the arduous method of self-education whilst functioning as naturalists on some expedition of exploration. Charles Darwin followed this pattern, studying medicine at Edinburgh (though he never took a degree) and then participating in the historic voyage of the "Beagle"; Thomas Huxley studied at Charing Cross Hospital before accompanying the almost equally famous voyage of the "Rattlesnake"; Alexander von Humboldt undertook anatomical and botanical investigations during his studies at Gottingen, though supposedly working on political economy, and thereafter embarked upon extensive exploratory travels in South America; and the botanist Joseph Hooker studied medicine at Glasgow, went as naturalist with the ships "Erebus" and "Terror" to the Antarctic, and thereafter travelled extensively in the Himalayas. Each of these naturalists first attained fame by the description of collections made on their voyages; all of them went on to wider problems and greater discoveries.

One of the less familiar figures of nineteenth-century science who began his career in this fashion was Christian Gottfried Ehrenberg. Ehrenberg was born on the 17th of April, 1795, at Delitzsch in Saxony. He first attended Leipzig University, being originally destined for a theological career; but a growing interest in natural history caused him to switch to medical studies, completed at Berlin, where he duly graduated in 1818. In the course of his studies he had struck up a strong friendship with another student of similar interests, W. F. Hemprich, and they decided to embark upon some great journey together. Madagascar was their first thought; but, when they were invited to join an archaeological expedition to Egypt under the Prussian General von Minutoli, they eagerly accepted.

The expedition started from Alexandria in April 1820, but was bedevilled from the outset by difficulties with Bedouin guides; when the oasis of Ammon had been left behind, political complications added to their troubles and precluded a planned advance into Tripoli. At this point, von Minutoli lost patience and decided to turn back. The two friends found themselves returned to an Alexandria stricken by fever, to which several of their colleagues succumbed.

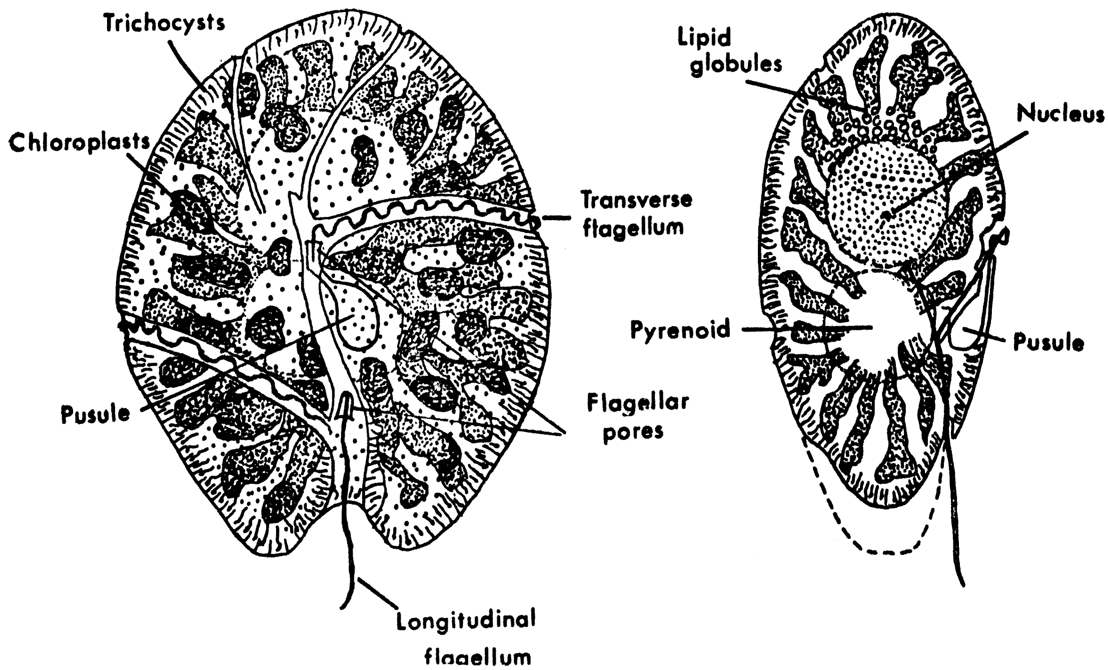
Ehrenberg and Hemprich decided to go off independently and embarked upon a collecting trip down the Nile Valley. At Sakkara, Ehrenberg went down with typhus, being saved by Hemprich's faithful nursing: despite this, they went on south, getting as far as the Nubian province of Dongola before returning north to send specimens home from Alexandria. This journey was followed by a visit to the Sinai Peninsula: they then went to Syria (crossing the desert to Baalbek); to the Lebanon; to Tripoli, where Hemprich came near to death from snake-bite; and back again to Egypt to send further material homeward. This was followed by a voyage down the Red Sea, which included visits to the newly discovered Dahlak and Farasan Islands, and a journey in Arabia that took them from the port of Djedda to Mecca. Their intention was to go on to the highlands of Abyssinia, but unfortunately, on disembarkation at Massawa (Eritrea), Hemprich succumbed to fever and died in Ehrenberg's arms. Ehrenberg himself was very ill: he gave up further travels and made a painful way back, by ship to Kosseir, across the desert by camel to Gizeh on the Nile and thence to Cairo. Eventually, in 1826, after prolonged quarantine in Trieste, he was allowed to go home to Germany, after an absence of almost six years.

The quantity of material collected had been immense; 46,000 botanical and 34,000 zoological specimens, plus specimens of some 300 rock types and numerous sketches and rough geological maps. The next few years were spent in beginning their study; in particular, Ehrenberg concentrated on examination of his specimens under the microscope. A welcome interruption to this work came in 1828, when he was chosen as one of two companions to accompany Alexander von Humboldt on a journey into Asiatic Russia. This was made at the invitation of the Czar and had, as its aim, the investigation of mineral deposits in the Urals and Altai. The journey took a year, including travel outwards via St. Petersburg (Leningrad) and Moscow, and return via Astrakhan.

Back again in Germany, Ehrenberg had no heart to return to the boring task of cataloguing his collections. Instead he devoted himself to the study of micro-organisms, first of all in present-day waters and sediments. This produced in 1830 a new classification, whose importance was considered so great that Cuvier described it as "one of those works which define epochs in science." Progressively his attention came to be transferred to the microfossils preserved in various types of sedimentary rocks: this research was begun in 1836. On the 20th July, 1837, in a paper read to the Berlin Academy, he astonished the geological world by demonstrating that large masses of rock, whole strata, might be made up entirely of the remains of microscopic animals and plants.

Dinoflagellates

Among the flood of new forms he described were some encountered in thin, translucent flakes of Cretaceous flint from Saxony. These fell into two groups. One group Ehrenberg immediately recognised, for he had many times seen their living representatives. They were dinoflagellates, members



Text-fig. 1. A typical modern unarmoured dinoflagellate from the present day Mediterranean shores. Gyrodinium pavillardi Biecheler, 1934, in ventral (left) and lateral views. (Redrawn after B. Biecheler).

of a group of unicellular organisms which are an important constituent of present-day plankton.

Plankton is usually conceived of as drifting helplessly in the surface waters of the seas; but, in fact, phytoplankton is present down to the lowest depths to which light can reach, and zooplankton goes down still deeper, feeding on dead organic material raining down from above. The microscopic plants of the phytoplankton frequently show a considerable diurnal migration with the aim of maintaining constant light conditions, sinking during the daytime and rising towards the surface at night: indeed, in bright sunlight, the top few feet of the sea is virtually devoid of plankton. (Individual species may migrate vertically up to a few hundred feet daily.) A minority of dinoflagellates are inhabitants of moist shoreline sands and some are parasitic; but the great majority are planktonic, some inhabiting lakes and estuaries, most the open sea. It is difficult to know whether to call them phytoplankton or zooplankton, for they straddle the boundary between the animal and plant kingdoms. Some species are true plants, containing chloroplasts and feeding by photosynthesis; other species behave like animals, feeding on other unicellular organisms; yet others start off life as plants, but then lose their chloroplasts and start gobbling up their fellows. Most systematists now prefer to allocate them to the plant kingdom and thus to the phytoplankton.

They are characterised by the possession of two flagellae. One of these is band-shaped and undulates in a transverse groove situated near the middle of the shell: this groove may be planar, but more frequently forms a left-handed spiral. The second is thread-like: it arises in a longitudinally-directed groove and trails out behind the cell. (Text-fig. 1.) The flagellae serve to maintain the cell in position in the water and to drive it along. Dinoflagellates under the microscope are seen to move in a corkscrew fashion at unexpectedly high speed; they are considered to be capable of a diurnal migration of several hundred feet. The cell may be naked or may bear a thick shell composed of an organic compound; this shell, called the theca, is divided by raised ridges into a pattern of fields. The fields, termed plates, show a very constant arrangement; this is termed the tabulation and is expressed as a formula (see Text-fig. 2).

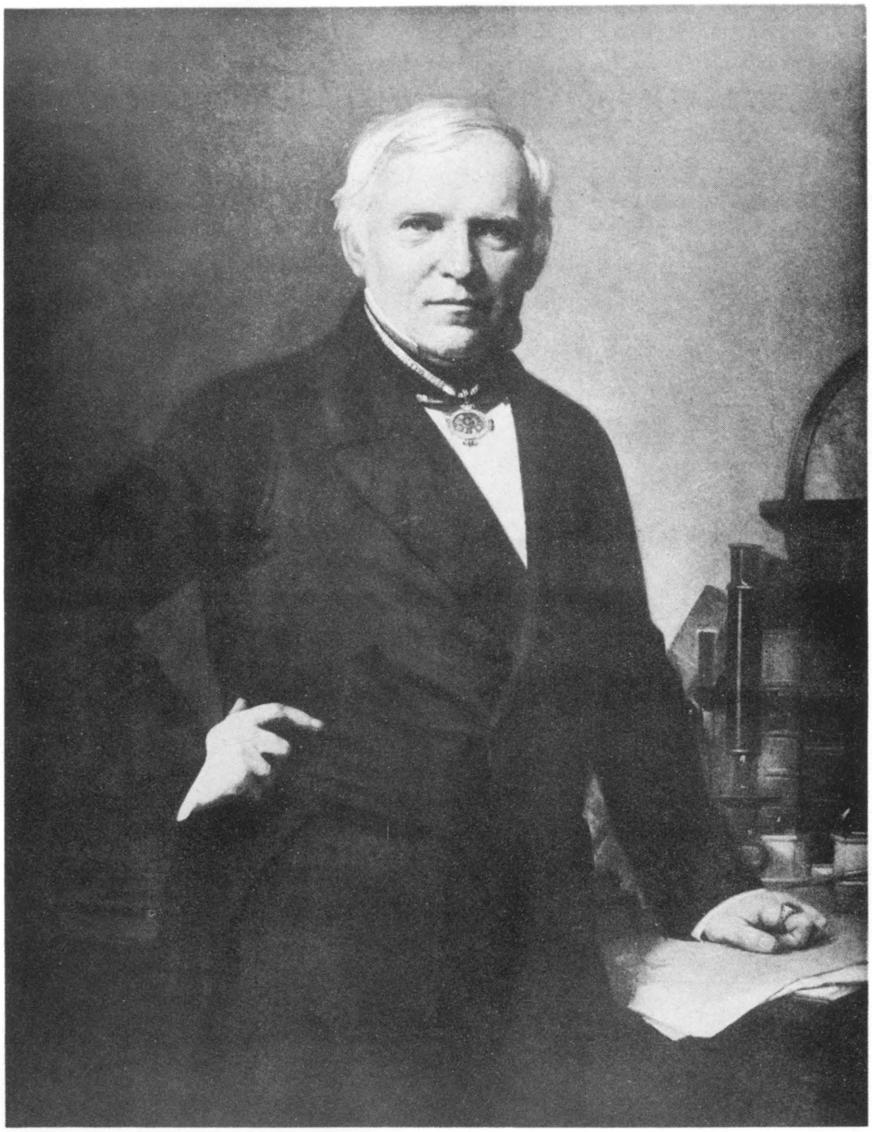
Dinoflagellates range down to a depth of at least 150 metres in the open ocean. Their vertical distribution is controlled by temperature and degree of light penetration and thus varies with latitude; they are found to achieve greatest concentration at levels between 10 and 50 fathoms. Some dinoflagellates, among them species of Ceratium and Peridinium, are confined to shallow depths, whereas others, such as the genera Heterodinium (found only at depths greater than 80 metres) and Triposolenia, and certain species of Ceratium, are only found in deep water.

Ehrenberg knew the dinoflagellates well: he had outlined a classification for them and had described many new species. These flint fossils showed the characteristic longitudinal and transverse furrows and a clear tabulation - dinoflagellates, certainly.

The Xanthidia

The affinity of the second group of fossils was much less obvious: they were of similar size to the dinoflagellates, but covered by a formidable armour of branching spines. Ehrenberg considered that both groups of fossils, to be preserved at all, must either consist of silica or have been replaced by it. He decided that the spiny bodies were the silicified remains of Desmids, conjugating algae living in fresh waters, and he placed them in one of his own genera, Xanthidium, under the new names X. furcatum and X. ramosum. Although Ehrenberg was quite wrong, the spiny spheres nonetheless came to be called "Xanthidia" for almost a century.

Before his paper was read in July 1837, some of Ehrenberg's slides, together with manuscript notes regarding their contents, had been forwarded to the Academy of Sciences in Paris. These were described to its members by C.R. Turpin on the 2nd January, 1837. Turpin disagreed with Ehrenberg's conclusions; he considered instead that the spiny objects were the hard-shelled reproductive bodies (statoblasts) formed in winter by Cristatella, a freshwater member of the Bryozoa (a group of colonial



Christian Gottfried Ehrenberg 1795–1876 (Photo – Paulsen, Lübeck)

invertebrates). Turpin's results were published later in 1837; Ehrenberg's did not appear till 1838, losing him the honour of first publication.

Ehrenberg travelled to England in the summer of 1838: he spoke at the Newcastle meeting of the British Association and attended a September meeting of the Geological Society of London, and also he sallied forth on collecting trips to various Chalk localities; these included Gravesend and Brighton, where his activities were abruptly terminated by a fall from a mail-coach. His descriptions of the microfossils in flint stirred the interest of a group of English amateur microscopists, most of whom were members of the Clapham Microscopical Society. The Rev. J.B. Reade, Henry Deane, Samuel J. Wilkinson and Henry Hopley White all published notes describing Chalk "xanthidia" (among which were a number of forms with tubular processes): James Scott Bowerbank recorded them also from the Upper Greensand. But it was the Society's most eminent member, Gideon Algernon Mantell (discoverer of the first dinosaur), who subjected them to the most searching analysis. He noted that the spines were often bent or contorted, sometimes crushed or torn; they could not be made of a brittle substance such as silica. (Similar observations were afterwards made independently by another microscopist, W.C. Williamson; quoted in Ralfs, 1848, pp. 12-13). He proceeded to subject them to heat and found that they charred and blackened; so they must be composed of an organic substance. Their very appearance was at variance with the true Xanthidium, which always shows a marked median constriction. He published his observations in 1845; but not until 1850 did he get round to renaming them, calling them Spiniferites and suggesting that they might be "gemmules of polyparia (corals) or the spores of marine plants". This name first appeared tucked away in a footnote in his "Pictorial Atlas of Fossil Remains": and when, later, he formally reattributed Ehrenberg's species to his new genus and added another of his own (S. reginaldi), he did it in the second edition of his textbook "Medals of Creation". It is scarcely surprising, therefore, that his admirable work came to be overlooked for more than a century.

[By strange coincidence, the holotype of Spiniferites reginaldi, lost for over a century, came to light among some slides being examined by Mr. E.P. Herlihy and myself on the very afternoon before this lecture.]

Ehrenberg himself did little further work on this group. Jurassic forms from Poland were mentioned in a paper published in 1843; and the elaborate plates of his massive "Mikrogeologie", published in 1854, contain a scatter of figures of dinoflagellates and "xanthidia". He did no more travelling; in his later years he was handicapped by an injury producing immobility and by semi-blindness, but he continued his researches, with the help of a daughter, right up to his death on 27th June, 1876.

After 1854, research on these microfossils dwindled away: it was some 70 years before further fossil dinoflagellates were recorded, and the "xanthidia" received only intermittent attention in the intervening period. J.W. Griffith and A. Henfrey noted shrewdly, in the second edition of their "Micrographic Dictionary", that:-

"It is a curious circumstance that (the Xanthidia) should be found in flint, which is supposed to be of marine origin, considering that the Desmidiaceae are none of them marine" (1856, p. 692)
but they were unaware of Mantell's work. E.W. Wetherell, whose mention of the spiny spheres from the London Clay (1892) constitutes the first Tertiary record, knew of it, but he compromised by calling his forms by both names. This was the last textual use of the name Spiniferites until my own rediscovery of Mantell's work in 1963; after such long disuse, it could not be resuscitated without causing confusion and so has had to be abandoned. (For full account see Sarjeant, 1964 a, b). The much less desirable name Xanthidium, in contrast, continued in intermittent use as late as 1937 (e.g. Gripp, 1925; Hiebenthal, 1930; Schuh, 1932; Staesche, 1937).

The geological range of the "xanthidia" was greatly extended when M.C. White (1862) described them from Palaeozoic rocks of New York (then thought to be Devonian, now known to be Upper

Silurian). Another American, J.A. Merrill (1895), recording spiny bodies from the Lower Cretaceous of Texas, repeated Ehrenberg's error by considering that they were siliceous; but he decided they were the spicules (components of the internal skeleton) of sponges! (For fuller discussion see Sarjeant, 1966a).

The first European Palaeozoic assemblages may have been described from Germany by A. Rothpletz (1880) and placed into a new genus, Sphaerosomatites. Subsequently Rothpletz's forms were stated to be "radiolaria" by Rodic (1931). This name also never came into general use, largely because it was never made clear whether his fossils were of siliceous or organic composition. His type material was destroyed in the wartime bombing of Munich.

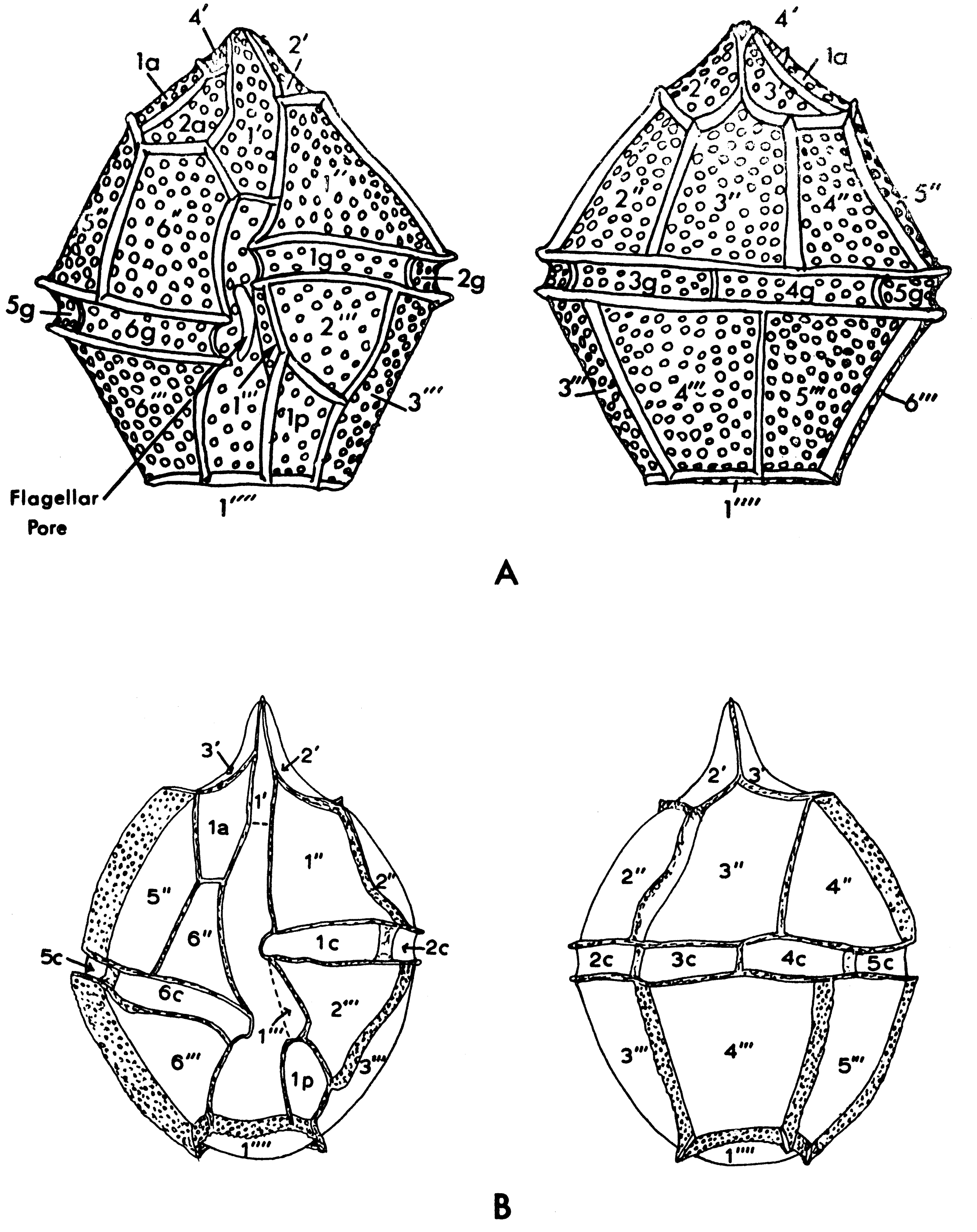
The late nineteenth century was the period of the great pioneer oceangraphic expeditions, the results of which were published progressively in massive series of fat volumes. A German expedition, studying the Humboldt Current off the western coast of South America, obtained a huge collection of microscopic organisms; among them were bodies very similar to the "xanthidia", which Lohmann, who described them, classed either as "problematica" or as planktonic eggs. Lohmann decided that the "xanthidia" also were planktonic eggs; he called them "ova hispida" (1904, p. 25). He was supported by Th. Fuchs (1905), who decided they were most probably eggs of Copepods, a group of minute planktonic crustacea: and this theory was originally adhered to by Walter Wetzel (1922), who listed both dinoflagellates and "ova hispida" from the German Cretaceous, and Alfred Eisenack (1931, 1932), in a description of Silurian forms.

Another German, P.F. Reinsch, published an alternative view, also in 1905. He decided that they were cysts of the type secreted round themselves by dinoflagellates under adverse conditions: and he christened them "palinospheres", another name that somehow got lost. This was not the last of the theories; in 1926 P. Kraft put forward the idea that the Palaeozoic forms were eggs of graptolites, and as late as 1939 Richard Kräusel suggested that they might be in part plant spores!

Hystrichospheres

The first major treatment this century appeared in 1933; this was a study of Upper Cretaceous assemblages from the Baltic region by Otto Wetzel. Like his immediate predecessors, he scouted the idea that the spiny spheres were Desmids, nor was he sure that they were planktonic eggs; instead, he erected a new genus, Hystrichosphaera, to accommodate them and stated its systematic reference to be uncertain. (Ehrenberg's species furcatum and ramosum were made joint types for the genus). In addition, he described a number of fossil dinoflagellates. His work was followed by a massive study of French Upper Cretaceous forms by Georges Deflandre (1936-7); Deflandre noted that the citation of two types for the single genus Hystrichosphaera was technically incorrect: most unfortunately he chose H. furcata as type. (It has since been demonstrated that these are variants of the same species; but that, whereas the slide containing the original H. ramosa survives in the collections of the Humboldt University, Berlin, the original H. furcata has been lost). Deflandre's figures showed much more of the detailed structure than had hitherto been recognised. In particular, a girdle band and a pattern of lines, suggestive of a dinoflagellate's tabulation, were present: but spines arising from the girdle ruled out the possibility of this being the position for a flagellum (Text-fig. 5). The forms without this patterning were separated off as a second genus, Hystrichosphaeridium: and later this name came to be used only for species with tubular processes (see Text-fig. 4c).

From this period onward, research on these groups grew in volume, especially when it was discovered that they could be extracted from sediments by acid treatment, obviating the necessity of peering into the thicknesses of flint chips. Deflandre extended his studies to the Jurassic and then to the Silurian and Carboniferous; a number of workers, most notably Maria Lejeune-Carpentier of Belgium, published descriptions of Cretaceous assemblages; and Alfred Eisenack described Jurassic dinoflagellates. In addition, Eisenack continued his studies on the Palaeozoic, discovering simple spherical forms and rod-like



Text-fig. 2. The tabulation of a modern armoured dinoflagellate compared with that of a fossil proximate cyst. Interpretation as follows: 1' – 3 or 4', apical plates; 1a – 2a, anterior intercalary plates; 1'' – 6 '', precingular plates; 1g – 6g or 1c to 6c, girdle or cingular plates; 1''' – 6''', postcingular plates; 1p, posterior intercalary plate; 1'''', antapical plate.
A. Gonyaulax polyedra Stein, 1883: a dinoflagellate living in present-day warm temperate seas. B. Gonyaulacysta whitei Sarjeant, 1966: a dinoflagellate cyst from the English Chalk.

forms, quite without spines; and later, an array of ancient types of very diverse morphology were added to the group (Text-fig. 10). The genus Hystrichosphaera became type for an order of uncertain systematic reference, the Order Hystrichosphaeridea; and its constituent genera came to be known as "hystrichospheres".

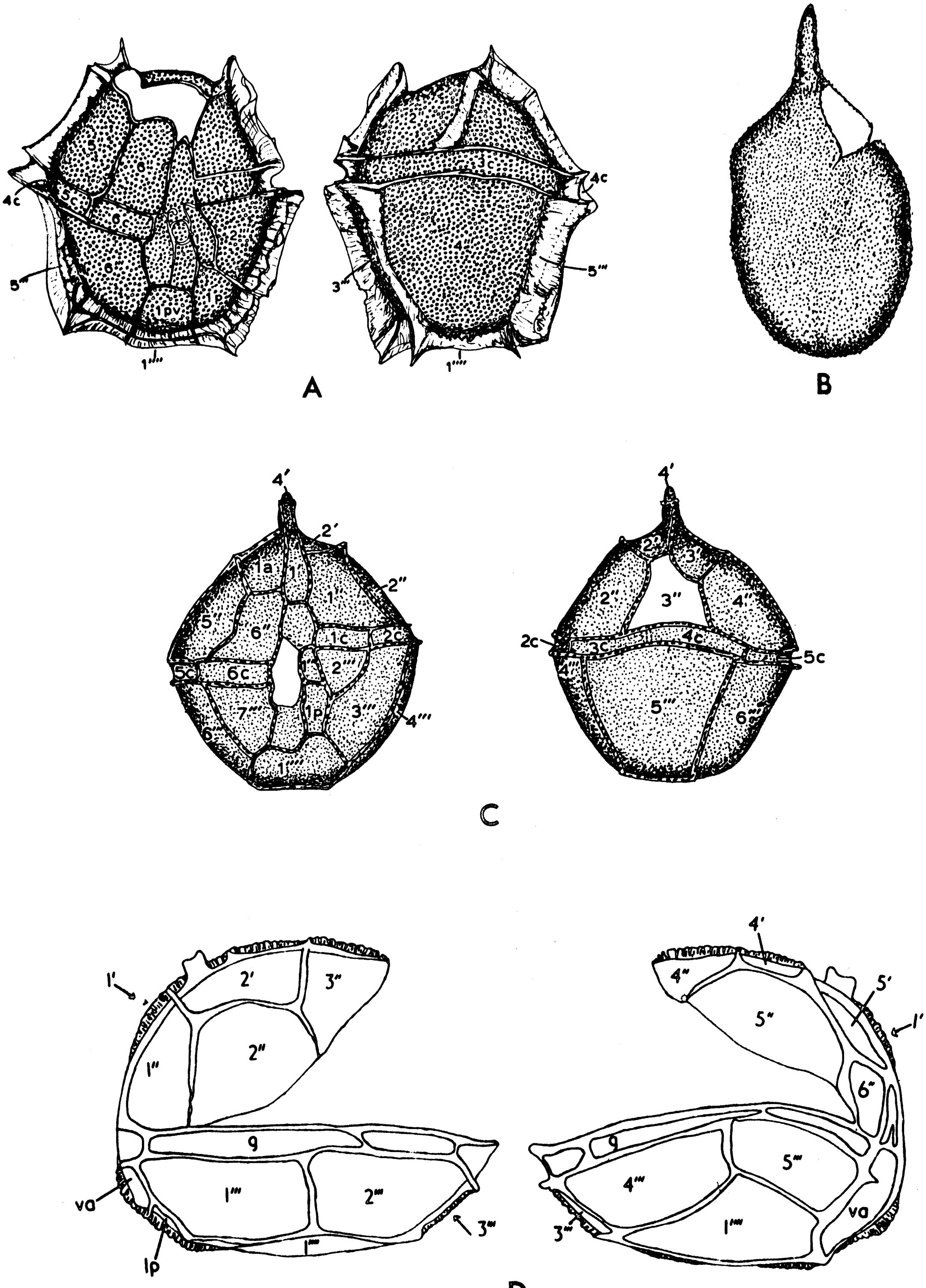
In 1947 Deflandre gathered together all the records of these "hystrichospheres" and analysed them in detail, to sort out some order from the welter of theories regarding their affinity. He found that they were known only from marine sediments, and that their wide distribution indicated a planktonic origin. Although arriving at no firm conclusions regarding their relationships, he expressed the view that the supposed "Order" was, in fact, a polyphyletic assemblage, containing a number of morphologically similar but unrelated components. I echoed Deflandre's conclusions in my own early reviews of the group (Sarjeant, 1960, 1961), suggesting that it certainly included cysts and abandoned egg-cases, and possibly also spores.

The breakthrough was made by an American, William R. Evitt, on the basis of a prolonged study of many hundreds of specimens of fossil dinoflagellates and "hystrichospheres". Evitt noticed a number of features, several of which had been observed before but from which the correct conclusions had not hitherto been drawn. First of all, he found that an opening of some kind was present in the majority of fossil dinoflagellate shells; this was formed either by rupture along the line of transverse furrow, or, more often, by the loss of a single plate or a group of plates from the epitheca. This suggested to him that the fossil dinoflagellates were not motile forms after all, but cysts: and that the opening, which he termed an "archaeopyle", was the means of escape after encystment. Some forms, whose shells showed little indication of tabulation other than a transverse furrow, nonetheless had openings with an angular margin, reflecting a tabulation that was not otherwise indicated (Text-fig. 3).

He next considered the "hystrichospheres" and noted a number of significant points. First and most important, they too frequently showed openings; sometimes these were exactly circular or in the form of irregular tears, but in the majority of Mesozoic and Tertiary species, the opening was markedly angular. Some oval-shelled forms had a tetrahedral opening in lateral position, paralleling an archaeopyle formed by loss of a precingular plate; others had a terminal opening of polygonal form, suggesting loss of the apical plates; there was even a slight embayment corresponding to the position of the longitudinal furrow.

Furthermore, the distribution of processes on the spiny forms attracted his attention. The processes of a single species had been thought to be quite variable in number, arrangement and relative proportions, but Evitt's studies showed the reverse to be the case. Not only the number, but also the arrangement, were in fact very constant: and though the relative dimensions might vary on a single specimen, he found that equivalent processes on different specimens were closely comparable; for example, the terminal process on the pole opposite an apical archaeopyle was often notably large and broad. He also found that, if one allowed for distortion, the length of processes was such that their tips would touch, but not cross, a postulated surrounding sphere or ovoid. By careful study of the process distribution, he found that their arrangement in many species corresponded to the pattern of a dinoflagellate tabulation, down to such details as large processes corresponding to large plates and vice versa.

He therefore concluded that these too were the cysts of dinoflagellates and that the cysts formed, not outside, but inside the cell wall of the living dinoflagellate. In some forms, the cyst developed very close to the original cell wall: the cyst would then resemble the motile form in shape and often in its close reflection of the original tabulation. Such forms were therefore immediately recognisable as dinoflagellates: they are now termed proximate cysts. In others the cyst formed well inside the original cell, linked to the wall only by the processes (Text-fig. 4). The tabulation was then reflected only by process distribution. Such forms included many of the so-called "hystrichospheres": we now term them chorate cysts. (Evitt, 1961, 1962 a, b, 1963). The genus Hystrichosphaera itself was very definitely a cyst, having an archaeopyle and processes positioned on plate boundaries: processes in the transverse furrow were no handicap to a cyst! (Text-fig. 5).



Text-fig. 3. Types of archaeopyles in proximate dinoflagellate cysts. A. Apical – formed by loss of the group of apical plates. Meiourogonyaulax valensii Sarjeant, 1966, seen in ventral (left) and dorsal views: Middle Jurassic, France. B. Intercalary – formed by loss of a single intercalary plate. Pareodinia ceratophora Deflandre 1947b, seen in oblique lateral view: Upper Jurassic, England. C. Precingular – formed by loss of the third precingular plate. Gonyaulacysta palla Sarjeant, 1966, seen in ventral (left) and dorsal views: Lower Cretaceous, England. D. Epitractal – formed by schism immediately anterior to the cingulum. Dichadogonyaulax schizoblata (Norris, 1965) Sarjeant, 1966, seen in left and right lateral views: Upper Jurassic, England. (Figure 3D by G. Norris).

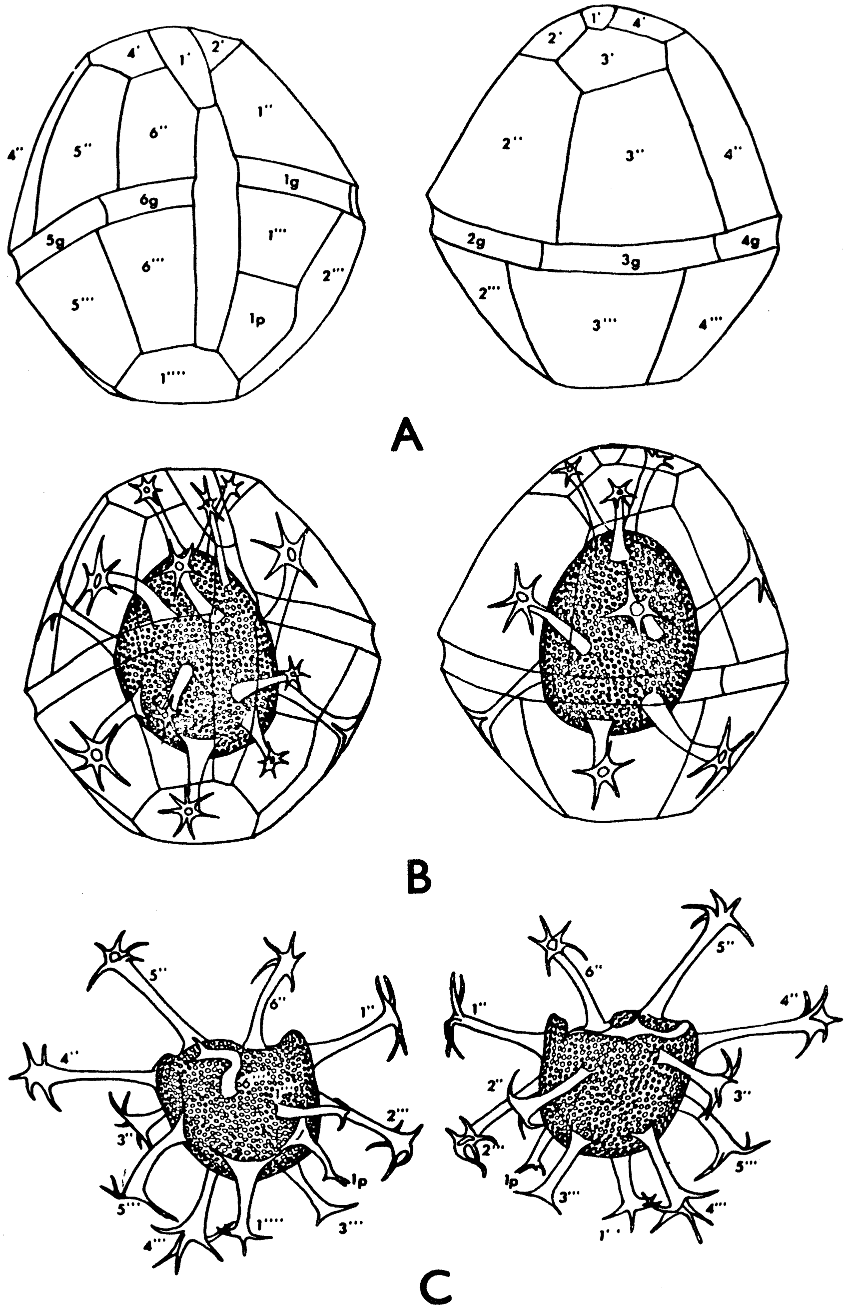
Perhaps all, certainly the majority of, dinoflagellate cysts have a wall consisting of two layers, any processes normally arising from the outermost layer: in the proximate and chorate cysts, these layers are in general contact. In the third group of cysts, the cavate cysts, the outer layer resembles a proximate cyst in outline, but the inner layer is partially or completely separate from it, forming an inner body of quite different shape. Both layers are perforated by the archaeopyle (Text-fig. 6). Some of these cysts surround themselves with a protective cloak of organic debris (Text-fig. 7).

After Evitt had reassigned all forms showing indications of dinoflagellate affinity, a residue of forms remained which afforded no such evidences. They included simple spheres and rods, spiny balls, box-shaped forms and a variety of other shapes. Sometimes these showed a circular or irregular opening (a pylome) which told nothing about their affinity save that they were eggs or cysts (Text-fig. 10d): in other cases no opening was present. A number of the spherical forms were later found to have thick walls penetrated by an arrangement of perforations that suggested an affinity to another group of algae, the Chlorophyceae (Wall, 1962); but the affinities of the majority have not yet proved capable of certain determination. Such forms were placed in a new group, the Acritarcha, by Evitt (1963): the word means simply "uncertain origin".

At this time, although cyst formation was known to occur in dinoflagellates (cf. for example Braarud, 1945), the process had attracted only incidental attention from marine biologists. There were a few records of chorate cysts (hystrichospheres) from modern sediments. The earliest was by W. B. Carpenter (1875) "embedded in sponge tissue" in deep-water Atlantic sediments. More recently, Erdtman (1950) found Hystrichosphaera in a Swedish fjord; Thalmann (1955) noted chlorate cysts in the Mediterranean; Wilson and Hoffmeister informed the Geological Society of America, in 1954, of their occurrence in Atlantic Ocean clays from Greenland to Puerto Rico; Muller (1959) turned them up near the Orinoco delta; and McKee, Chronic and Leopold (1959) found them in a Pacific atoll. Remains of dinoflagellates and acritarchs had also been recorded from Australian freshwater peats (Churchill and Sarjeant, 1963). But it could not be said that cyst formation, as visualised by Evitt, had ever been seen to happen.

His views, therefore, did not gain universal acceptance. In particular, Alfred Eisenack continued to battle for the "Einheitlichkeit der Hystrichosphären", the view that the hystrichospheres (n which he included Evitt's acritarchs) were a natural, coherent group of unicellular algae, with shells of constant basic form and chemical composition (1963). Analysis of the wall substance is in fact extremely difficult, since it is certainly composed of complex organic molecules: Eisenack concluded from stain tests that it is composed of a macromolecular substance of lipoid character, perhaps a polyterpene or a condensate of unsaturated fatty acid, comparable to cutin or sporopollenin. (Chemical techniques are not at present adequate to establish whether all of these organisms under study are composed of a single substance or merely a group of related substances.) Eisenack scouted the majority of modern records, either as mistaken or as dealing with reworked material, since many of them were from Continental margins - but he admitted difficulty in accounting for the Pacific atoll record. He felt that his hystrichospheres were a group of plankton that once had been abundant but were now extinct.

However, the extension of study of marine bottom sediments has brought a steadily increasing number of records of dinoflagellate cysts of all kinds (though acritarch records remain few). They have been recorded from widespread stations in the Atlantic (Stanley, 1965; Wall, 1966 a, b; Williams and Sarjeant, 1967); from the eastern Mediterranean (Rossignol, 1961); and from the Western Pacific (Evitt and Davidson, 1964). This in itself was a serious blow to Eisenack's ideas; but much more serious were observations by Rossignol (1963), by Evitt and Davidson (1964), by Wall (1966) and by Wall and Dale (1966) of living dinoflagellates within which cysts were forming: both proximate cysts, e.g. in Peridinium leonis, and chorate cysts, notably in Gonyaulax digitale whose cyst is morphologically a Hystrichosphaera. Final vindication for Evitt's ideas came at a recent conference in Utrecht, when David Wall showed a sequence of photographs of a dinoflagellate, first seen as a body within a Hystrichosphaera - type cyst, then emerging through the archaeopyle as an undifferentiated ovoid body,



Text-fig. 4. The development of a chorate cyst. A. Reconstruction of the original tabulation of the motile dinoflagellate, which accords with that of <u>Gonyaulax.</u> (The apical tabulation is entirely hypothetical). B. The cyst forming within the dinoflagellate, attached to the outer wall by its processes. C. The abandoned cyst, with an apical archaeopyle, after crushing and distortion during the consolidation of the enclosing sediment. <u>Oligosphaeridium vasiformum</u> (Neale and Sarjeant, 1962) Davey and Williams, 1966: Lower Cretaceous, England.

and finally developing a pattern of plates (to be published in Wall, 1967). So, although the acritarchs remain to be sorted out, the problem of the affinity of Ehrenberg's so-called "xanthidia" is solved.

Classification

The classification of dinoflagellate cysts presents certain problems. The cyst is often quite dissimilar from the motile dinoflagellate; their interconnection can only be proved by watching the process of cyst development or abandonment in cultures and it can only be presumed when there is a close geographic association between cyst and motile dinoflagellate. The palaeontologist can use neither of these methods; instead he must either infer the morphology of the motile dinoflagellate, in so far as he can, from the morphology of the cyst, or he must use his knowledge of modern cysts to deduce the probable morphology of the motile stage. Often he is dealing with a cyst for which there is no modern counterpart.

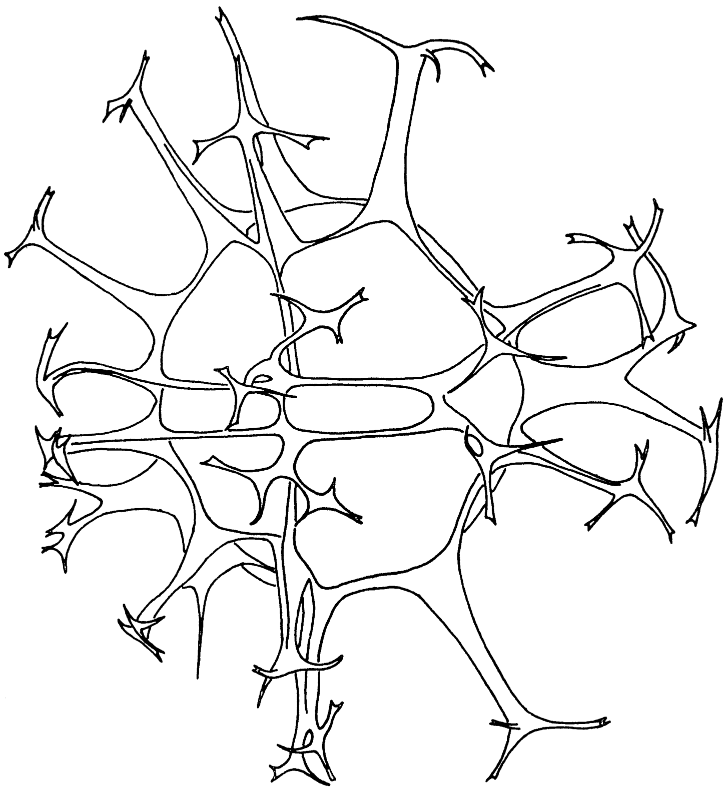
Thus he faces four possibilities. First, he might try to fit his cysts into a classification of modern dinoflagellates. This soon produces difficulties, for species of the same modern genus may produce a number of quite different types of cysts. For example, different species of the motile genus Gonyaulax produce cysts of proximate type, attributable to the cyst-genus Leptodinium, and of chorate type, attributable to the form-genera Hystrichosphaera, Nematosphaeropsis, and Exochosphaeridium: and in addition, a whole array of fossil proximate and chorate genera have a reflected tabulation of the Gonyaulax pattern. Does he therefore throw overboard all these useful names for distinct morphological cyst types, and call all just Gonyaulax? Secondly, he might base his classification entirely on cyst morphology: but Wall (1966 b) admits that ".....a few cases are at present known where identical cysts are produced by parental dinoflagellates with different tabulations", so that such a classification might lump together dissimilar motile types. Thirdly, he might use a hybrid classification, sometimes basing his groupings on cysts, at other times on motile morphology. This procedure may, in the long run, prove the most desirable, but our knowledge is not yet adequate to permit us to confidently set up such a classification. For the moment, the fourth alternative, to have separate classifications for cysts and for motile forms, seems an ideal interim procedure (see Sarjeant and Downie, 1966).

The acritarchs have to be classed entirely on their morphology, since this is the only criterion available. It is probable that such a classification brings together similar but unrelated forms: but this need cause no concern since, after all, once relationships are known, the species are "acritarchs" no longer! (See Downie, Evitt and Sarjeant, 1963).

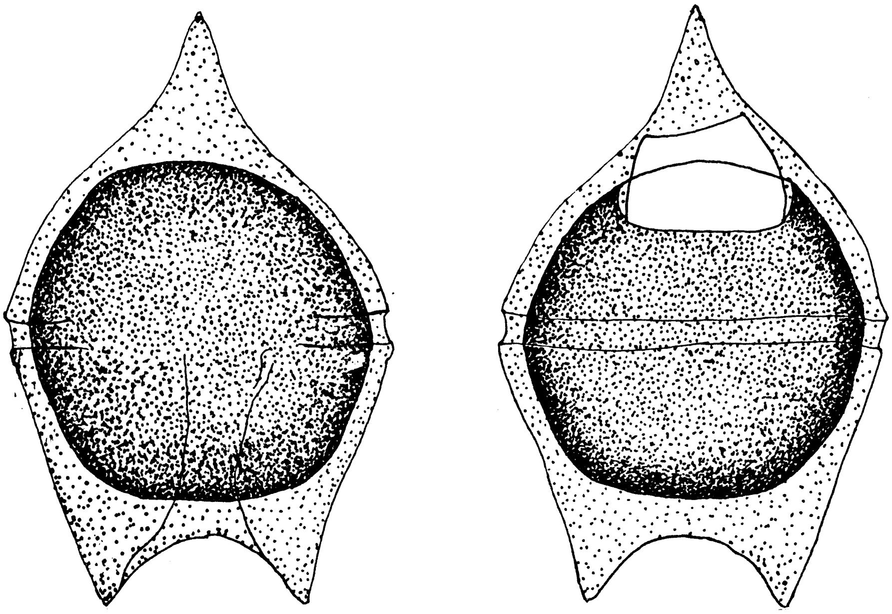
Stratigraphical Distribution

A number of problems remain. First of all, the problem of geological distribution. Dinoflagellate cysts do not appear early in the geological column: the first undoubted record is from the Silurian, from which a single tabulate dinoflagellate with a clear archaeopyle has been recorded (Calandra, 1964). After this there is a considerable hiatus. There are a few records from the Permian and Triassic (Tasch, 1963; Jansonius, 1962: Sarjeant, 1963) and then, in the Jurassic, dinoflagellate cysts became abundant, remaining so through to the present day. Except possibly for certain calcareous or siliceous forms, there are now no undoubted instances of the preservation of fossil motile dinoflagellates. It is always the cysts that survive.

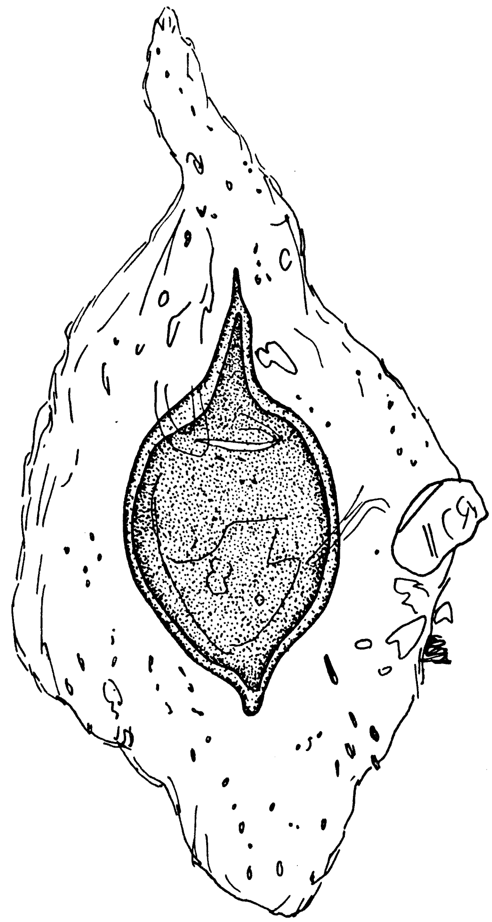
The acritarchs appear very much earlier: indeed, they are among the oldest recorded microfossils, being present in the Canadian Gunflint Chert, a Pre-Cambrian sediment dated at some 2,000,000,000 years (Barghoorn and Tyler, 1965 a, b). In the later Pre-Cambrian, they are sufficiently abundant and varied to have been used in the stratigraphic correlation of Russian and Scottish sediments (Naumova and Pavlovsky, 1961; Sutton, 1962). They attain greatest abundance and diversity in the Lower Palaeozoic: in the Upper Palaeozoic and Lower Mesozoic, they remain abundant but show less variety in morphology. A restricted number of types are present from the Upper Mesozoic to the present,



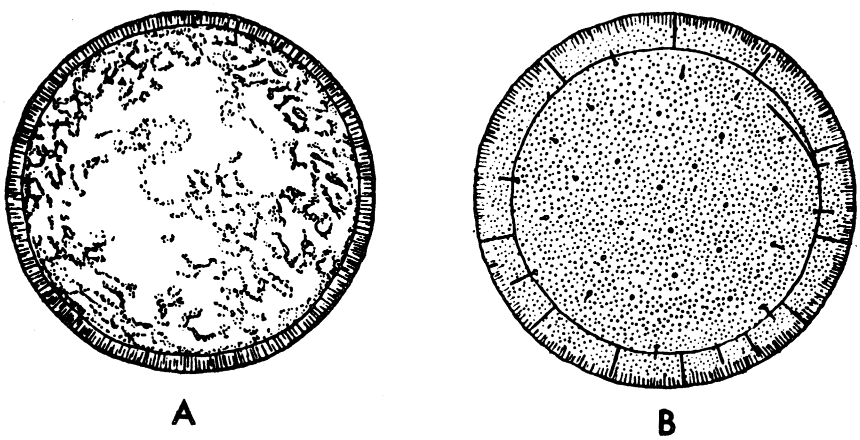
Text-fig. 5. The original "fossil Xanthidium" and basic type of hystichospheres: the type specimen of Hystrichosphaera ramosa (Ehrenberg, 1838) O. Wetzel, 1933, found in a Cretaceous flint from Delitzsch, Saxony (Figure by R. J. Davey, 1966).



Text-fig. 6. A typical cavate dinoflagellate cyst, with an intercalary archaeopyle. Deflandrea phosphoritica Eisenack, 1938; Lower Tertiary, Spitzbergen. (Redrawn after S. Manum).



Text-fig. 7. A cavate dinoflagellate cyst surrounded by a cloak of adherent organic debris. Netrelytron trinetron Sarjeant, 1966. Lower Cretaceous, Yorkshire.



Text-fig. 8. Comparison between living and fossil spherical green algae. A. Pachysphaera pelagica Ostenfeld, from modern Arctic seas. B. Tasmanites newtoni Wall, 1965, from the English Lower Jurassic. (From figures by D. Wall, 1962).

and they are known from Quaternary non-marine sediments as well as from marine sediments (Australia - Churchill and Sarjeant, 1963: England - Sarjeant, unpublished data).

The relatively late appearance of dinoflagellate cysts is difficult to account for: the very primitive character of the group would cause one to expect them to be among the first organisms to appear. There seem two possible explanations; either the early dinoflagellates simply did not form cysts, or the cysts are not recognisable as such, showing no features definitely indicative of dinoflagellate affinity. It is noteworthy that the decline of the acritarchs coincides with the increase of dinoflagellate cysts: and it may well be that many acritarchs are unrecognised dinoflagellate cysts.

Use in Environmental Studies

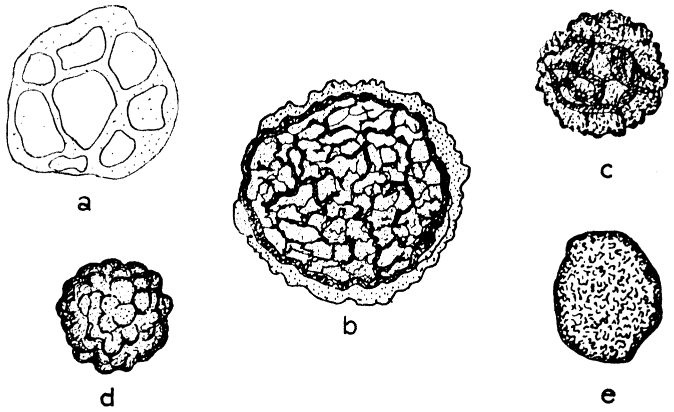
Dinoflagellate cysts and acritarchs turn up in sedimentary rocks of all types. They are most often abundant in clays and shales and they occur in variable abundance in limestones, sandstones and conglomerates; they have also been recorded from salt and phosphate deposits and even from crude petroleum. This wide distribution in a variety of sedimentary associations enhances their value as stratigraphic indices, but reduces their value as environmental indices. However, dinoflagellates do show distinct depth zonation, as already discussed; and it may in time prove possible to distinguish shallow-water cyst assemblages from deep-water ones. For example, Scull, Felix, et al., 1966, found an association between cysts and depth conditions in the Vicksburg Formation, Oligocene, U.S.A. Acritarchs have also been found to show distinct environmental relationships, though here the controlling factors are less readily determined. The degree of tranquillity or turbidity of the seawater may be an important factor: Staplin (1961) suggested this to account for the distribution pattern round Devonian reefs in Western Canada, and Wall (1965) suggested a similar explanation for the pattern he observed in the English Lias. In both cases, the richest and most varied assemblages were found in sediments deposited in deep, tranquil waters well off shore.

The most important application of these microfossils in environmental studies, however, promises to be in determining the distribution of ancient water-bodies. Unicellular micro-organisms are very immediately affected by their environment, for they are effectively at one with it. They become wholly adapted to the conditions prevailing in the water-body they are inhabiting; they cannot survive a sudden transition to different conditions. Thus, in the English Channel, at the point where the North Sea waters come into contact with the Gulf Stream waters from the Atlantic, there is a very precise boundary between the two plankton populations, with an enormous plankton mortality at the interface. This can be detected from the air on a sunny day, by the change in colour of the water.

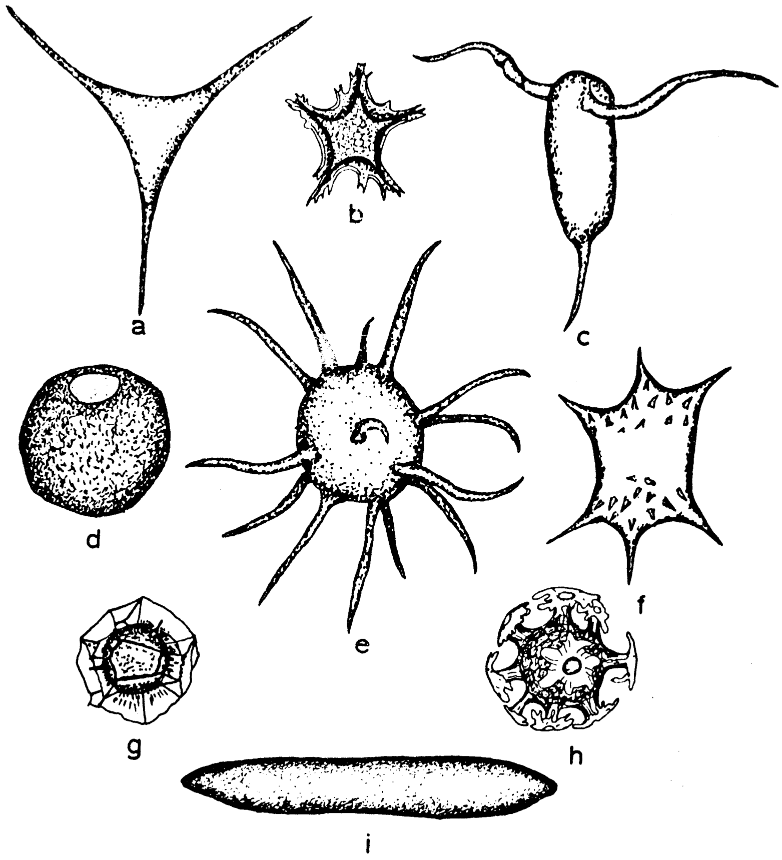
The oceans of the World are thus divisible into provinces, each of which has its characteristic plankton assemblage. Recently, D.B. Williams (unpublished thesis, 1965) has shown, by examination of the bottom sediments, that each province also has its concomitant assemblage of dinoflagellate cysts. Thus it may prove possible, in the future, to map the distribution of plankton provinces in ancient seas, and so to determine the patterns of water circulation of the globe in the past.

Economic Applications

After all this lengthy discussion, it may well be asked whether these studies have any practical application, other than the satisfying of academic curiosity. The answer is, very definitely, yes. These groups of fossil plankton are capable of ready use as a means for the correlation and relative dating of rocks. They have the asset of being present in large numbers, even in relatively small samples; numbers as great as 100,000 in a single gram of shale have been recorded (acritarchs in the Shineton Shales, Lower Ordovician: see Downie, 1958, p. 332). This makes them especially useful in studies based on borehole cores and thus in the determination of subsurface geology. They are, moreover, frequently present in rocks in which foraminifera and ostracoda, the other microfossil groups principally used as stratigraphical indices, are absent; and unlike those groups, they survive the decalcification of the rock.



Text-fig. 9. Pre-Cambrian acritarchs. a. Prototrematosphaeridium holtedahli, Timofeyev 1962. Pre-Cambrian, Norway. b. Archaeofavosina simplex Naumova, 1960. Pre-Cambrian, U.S.S.R. c. Protoarchaeosacculina atava Naumova, 1960. Pre-Cambrian, U.S.S.R. d. Microconcentrica orbiculata. Pre-Cambrian, U.S.S.R. e. Mycteroligotriletum marmoratum Timofeyev, 1960. Pre-Cambrian, U.S.S.R.



Text-fig. 10. Palaeozoic acritarchs. a. Veryhachium trispinosum (Eisenack, 1938) Deunff, 1954. Ordovician, Baltic region. b. Polyedryxium bathyaster Deunff, 1961. Devonian, Canada. c. Domasia elongata Downie, 1960. Silurian, England. d. Leiosphaeridia oelandica Eisenack, 1962. Lower Ordovician, Baltic region. e. Baltisphaeridium longispinosum (Eisenack, 1931) Eisenack, 1959. Ordovician-Silurian, Baltic region. f. Acanthodiacrodium sexcuspidatum Timofeyev, 1959. Upper Cambrian, U.S.S.R. g. Cymatiosphaera cornifera Deunff, 1955. Devonian, Canada. h. ?Hystrichosphaeridium huecospinosum Cramer, 1963, Devonian, Spain. i. Leiofusa navis Eisenack, 1938. Ordovician, Baltic region.

The acritarchs are the only microfossils which afford a hope of use in stratigraphic subdivision of the Pre-Cambrian and they are much the most useful group in the Cambrian. In the Ordovician, Silurian, and Devonian, they are second only to Chitinozoa in importance; but thereafter they decline in variety and are not of great stratigraphic significance. Dinoflagellate cysts become important in the Middle Jurassic and are probably the most useful of all microfossil groups for subdivision of the Upper Jurassic; they remain important thereafter right through to the present day. Both groups are becoming increasingly utilised by the petroleum industry, as a means of recognition of significant horizons and in the elucidation of structures; and so there is no question that such studies are of considerable commercial significance. It is increasingly considered that phytoplankton are the ultimate source of petroleum. One may indeed speculate that, in the future, petroleum may be produced commercially by the controlled breeding of dinoflagellates in enclosed seas -- perhaps the Red Sea itself, which Ehrenberg once explored.

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