DINOFLAGELLATE CYSTS FROM THE APTIAN TYPE SECTIONS AT GARGAS AND LA BÉDOULE, FRANCE

by ROGER J. DAVEY *and* JEAN-PIERRE VERDIER

ABSTRACT. Microplankton assemblages are described for the first time from the Aptian type localities at La Bédoule and Gargas, south-east France. A total of sixty-eight species and varieties of dinoflagellate cysts are recorded, a number of which are discussed in detail, and four new species are erected. These are *Aptea securigera*, *Cyclonephelium tabulatum*, *Meiourogonyaulax psoros*, and *Protoellipsodinium clavulum*. Microplankton distribution charts for the sections studied and a summary chart of selected age-significant forms are included. The following species are shown to be characteristic of, and confined to, the Aptian—*Aptea polymorpha*, *C. tabulatum*, *M. psoros* and *Trichodinium* sp. These species, together with longer-ranging forms, may be used to distinguish Aptian from Albian and Barremian strata. Finally, our stratigraphic results are compared with those described in studies of similarly-aged sediments.

SEDIMENTS of Aptian age have been rather neglected by earlier microplankton workers; they have been studied briefly only in Germany (Eisenack 1958; Alberti 1961), France (Millioud 1969), and Australia (Cookson and Eisenack 1958, 1960, 1962). The present paper, the first detailed study of Aptian dinoflagellate cysts, is intended to remedy this deficiency by presenting a taxonomic and stratigraphic analysis of microplankton recovered from Aptian stratotype material. This paper is a natural continuation from our previous contributions on Albian microplankton (Davey and Verdier 1971, 1973).

The sediments in the type localities of La Bédoule and Gargas, south-east France (text-fig. 1) consist predominantly of marls and clays, which usually yield rich palynologic assemblages dominated by dinoflagellate cysts, although spores, pollen grains, and woody material are generally common. The basal Bedoulian (Lower Aptian) consists only of post-Urgonian reefal limestones which proved to be almost barren of palynomorphs.

All slides containing holotypes are housed in the Laboratoire de Micropaléontologie de l'École Pratique des Hautes Études, 8, rue de Buffon, Paris 5ème, France.

STRATIGRAPHIC AND GEOGRAPHIC LOCATION OF SAMPLES

The Aptian stage (text-fig. 2) was introduced in 1840 by d'Orbigny, who subsequently, in 1842 and 1850, slightly refined his original definition. As envisaged by d'Orbigny, the Aptian was a stratigraphic unit that included only what is now considered to be the Upper Aptian (Gargasian substage). His choice of the Apt region (Vaucluse) as the type area for the Aptian stage was unfortunate in that it later lead to considerable controversy over delimitation of the stage. The main reason for this controversy was that in neighbouring areas, as several geologists pointed out (Matheron 1842; Reynes 1861; Hebert 1864, 1871, 1872), calcareous sediments containing a fauna with Aptian affinities were present between the massive 'Urgonian limestones' and the 'Aptian

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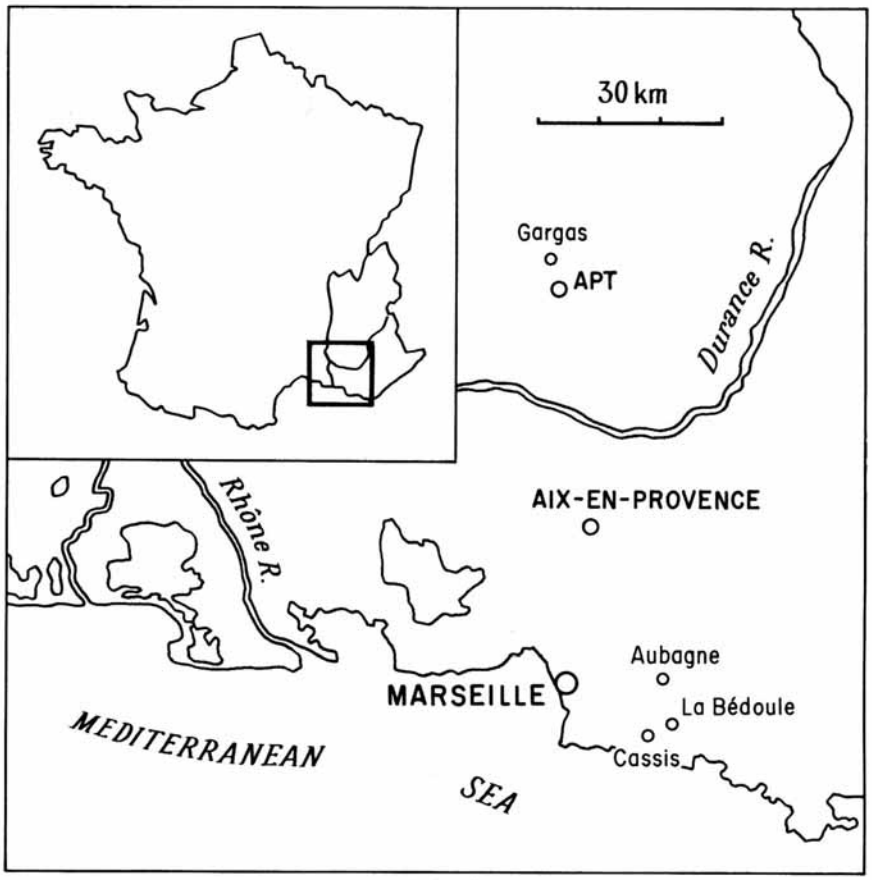


TEXT-FIG. 1. Locality map.

marls'. In the Apt region these latter two formations are practically in contact with only minor calcareous passage beds separating them; however, at La Bédoule (Bouches du Rhône) the passage beds are well developed. The above authors clearly recognized that the passage beds and the overlying marly sequence displayed sufficient faunal similarity to represent the same stratigraphic entity yet could be easily distinguished lithologically. Thus the concept of subdividing the Aptian stage originated. In 1887 Kilian introduced the term Gargasian for the 'Aptian marls', and in the following year Toucas (1888) defined the Bedoulian for the underlying passage beds. The positioning of the Gargasian–Bedoulian boundary resulted in considerable controversy but, suffice it to say, these terms have survived as substages and refer respectively to the Late and Early Aptian.

STAGE		SUB-STAGE	AMMONITE ZONES
APTIAN	LATE	CLANSAYESIAN	*Diadochoceras nodosocostatum*
		GARGASIAN	*Cheloniceras subnodosocostatum*
			Aconeceras nisus
	EARLY	BEDOULIAN	*Deshayesites deshayesi*

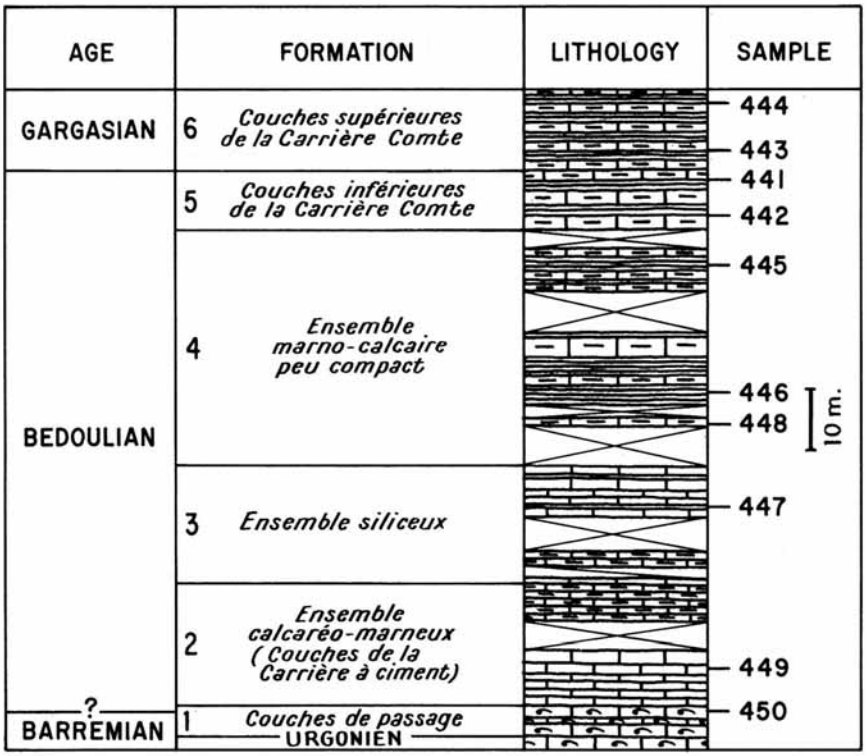
TEXT-FIG. 2. Stratigraphic subdivision of the Aptian.

La Bédoule Section

Sediments of latest Barremian to Early Gargasian age crop out in several active and abandoned quarries on both sides of the Aubagne–Cassis road near the village of La Bédoule. The Aptian succession (text-fig. 3) here is highly calcareous and consists of alternating beds of marls and argillaceous limestones. The latter become increasingly abundant towards the base of the Bedoulian and grade into the massive Urgonian Limestone of probable Barremian age. The Urgonian Limestone of the Vocontian Trough represents deposition in a relatively shallow water, quiet environment. The initiation of Aptian deposition corresponds to the beginning of a progressive deepening of the sedimentary basin, to an increasing influx of argillaceous material and to less well-oxygenated bottom conditions. A total of ten samples of Bedoulian and Early Gargasian age were collected from the marl and clay beds at this locality.

Gargas Section

In the Apt region, the Aptian crops out in a series of exposures between the towns of Apt and Gargas. The top of the Urgonian limestones (text-fig. 4), here of Bedoulian age, is exposed near the railway bridge about two kilometres north-west of Apt. As

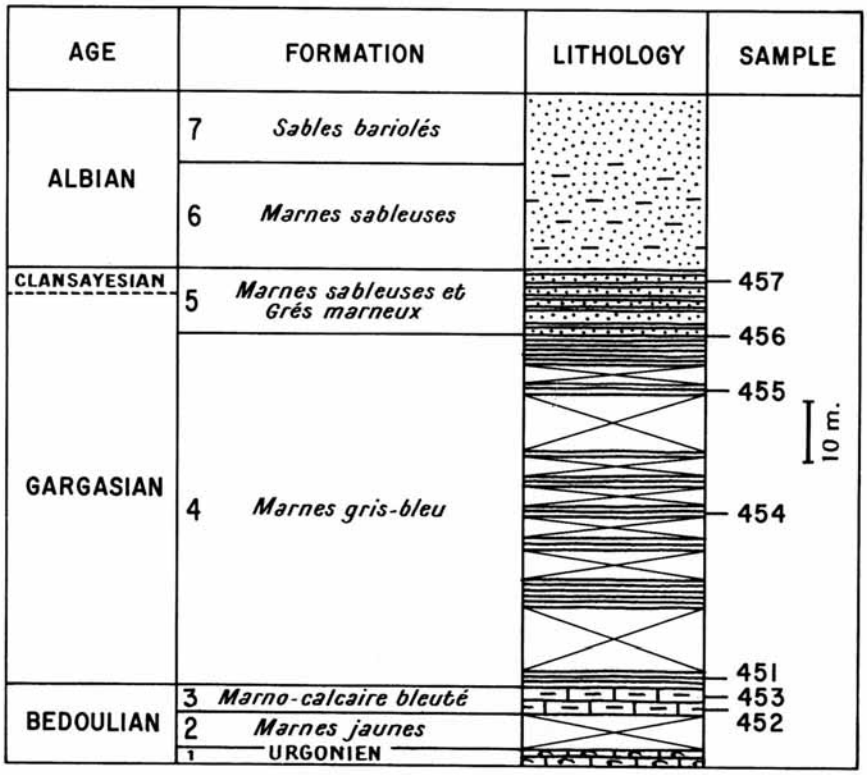


TEXT-FIG. 3. La Bédoule section showing the lithologic subdivisions and the position of samples (after Fabre-Taxy *et al.* 1965).

the hillside is ascended towards Gargas, progressively younger sediments are encountered, and the hill is capped by Albian marls and sands. A total of seven samples were collected and range in age from Bedoulian to Clansayesian.

SYSTEMATIC DESCRIPTIONS

This section is divided into two parts. The first part lists, in alphabetical order, the dinoflagellate cyst species which require no special remarks and have been previously described, with full stratigraphic annotations, by Davey and Verdier (1971, 1973). The second part deals with the cyst species recovered during the present study which were either not described in the above publications or require certain amplifying remarks. The species are arranged in alphabetical order within the Gonyaulacacean and Peridiniacean groups.



TEXT-FIG. 4. Gargas section showing the lithologic subdivisions and the position of samples (after Moullade 1965).

PART 1

Apteodinium granulatum Eisenack 1958.
Astrocysta cretacea (Pocock 1962) Davey 1970. (Pl. 93, fig. 4.)
'*Broomea*' *micropoda* Eisenack and Cookson 1960.
Callaiosphaeridium asymmetricum (Deflandre and Courteville 1939) Davey and Williams 1966.
Canningia colliveri Cookson and Eisenack 1960.
C. minor Cookson and Hughes 1964.
Cassiculosphaeridia reticulata Davey 1969.
Cauca parva (Alberti 1961) Davey and Verdier 1971.
Cleistosphaeridium armatum (Deflandre 1937) Davey 1969.
C. huguonioti (Valensi 1955) Davey 1969.
C. polypes clavulum Davey 1969.
C. polypes polypes (Cookson and Eisenack 1962) Davey 1969.
Cribroperidinium edwardsi (Cookson and Eisenack 1958) Davey 1969.
Cyclonephelium distinctum Deflandre and Cookson 1955.

Exochosphaeridium arnace Davey and Verdier 1973.
E. phragmites Davey, Downie, Sarjeant and Williams 1966.
Florentinia laciniata Davey and Verdier 1973.
F. mantelli (Davey and Williams 1966) Davey and Verdier 1973.
Fromea amphora Cookson and Eisenack 1958.
Gonyaulacysta cassidata (Eisenack and Cookson 1960) Sarjeant 1966.
G. helicoidea (Eisenack and Cookson 1960) Sarjeant 1969.
G. tenuiceras (Eisenack 1958) Sarjeant 1969.
Hystrichodinium pulchrum Deflandre 1935.
Hystrichosphaeridium arundum Eisenack and Cookson 1960.
H. recurvatum (White 1842) Davey and Williams 1966.
H. tubiferum (Ehrenberg 1838) Davey and Williams 1966.
Kalyptea sp. (as in Davey and Verdier 1971).
Microdinium crinitum Davey 1969.
Odontochitina operculata (O. Wetzel 1933) Deflandre 1946.
Oligosphaeridium complex (White 1842) Davey and Williams 1966.
Ovoidinium scabrosum (Cookson and Hughes 1964) Davey 1970.
Polysphaeridium laminaspinosum Davey and Williams 1966.
Protoellipsodinium spinocristatum Davey and Verdier 1971.
P. spinosum Davey and Verdier 1971.
Spiniferites cingulatus cingulatus (O. Wetzel 1933) Sarjeant 1970.
S. ramosus multibrevis (Davey and Williams 1966) Sarjeant 1970.
S. ramosus ramosus (Ehrenberg 1838) Sarjeant 1970.
S. ramosus reticulatus (Davey and Williams 1966) Sarjeant 1970.
Tanyosphaeridium variecalamum Davey and Williams 1966.
Trichodinium castanea (Deflandre 1935) Clarke and Verdier 1967.

PART 2

Class DINOPHYCEAE Pascher
Order PERIDINIALES Lindemann
GONYAULACACEAN Group
Genus ACHOMOSPHAERA Evitt 1963
Achomosphaera neptuni (Eisenack) Davey and Williams 1966

1958 *Baltisphaeridium neptuni* Eisenack, p. 51, pl. 26, figs. 7, 8.

Reported occurrence. Valanginian to Hauterivian, Germany (Gocht 1959). Hauterivian, Switzerland (Millioud 1967, 1969). Barremian, England (Davey 1974 in press). Upper Aptian, Germany (Eisenack 1958).

Achomosphaera cf. *neptuni* (Eisenack) Davey and Williams 1966

Plate 92, fig. 2

Description. This ovoidal cyst has a smooth to minutely granular, thin wall which bears many smooth to slightly fibrous processes. Each process has a wide flat base and tapers rapidly to become thin and parallel-sided. Towards the distal extremity they divide into two, rarely three, filamentous branches which occasionally can be seen to further bifurcate at their distal extremities. Some alignment of the processes is present and appears to mark the cingular margins; a short, stouter apical process is sometimes discernible. These two features allow cyst orientation which suggests that the archaeopyle is precingular in position. It is formed by the loss of a single plate and is roughly triangular in shape. The processes are apparently both gonal and sutural in position.

Dimensions.

	Figured specimen (μm)	Range (μm)
Central body diameter	44 × 51	41–51
Length of processes	7–15	7–15

Remarks. A. neptuni differs from *A.* cf. *neptuni* by being thicker walled with a coarser granulation and by having fewer and wider processes which often join proximally with neighbouring processes. The processes of *A. neptuni* appear to be only gonal and usually trifurcate distally to give thick spines.

Genus CHLAMYDOPHORELLA Cookson and Eisenack 1958
Chlamydophorella nyei Cookson and Eisenack 1958

1958 *Chlamydophorella nyei* Cookson and Eiseneck, p. 56, pl. 11, figs. 1–3.

Remarks. C. nyei is distinguished from *Gardodinium trabeculosum* (Gocht 1959) by being more or less rounded in outline (except for the apical prominence) and by not possessing a tabulation and process alignment.

Reported occurrence. Barremian, England (Davey 1974 in press, as *G.* cf. *trabeculosum*). Aptian to Lower Turonian, Australia (Cookson and Eisenack 1958, 1962*b*, 1971). Albian to Cenomanian, England (Cookson and Hughes 1964); Canada (Manum and Cookson 1964; Davey 1970; Cox 1971; Brideaux 1971*a*, *b*; Singh 1971).

Genus CORONIFERA Cookson and Eisenack 1958
Coronifera oceanica Cookson and Eisenack 1958

1958 *Coronifera oceanica* Cookson and Eisenack, p. 45, pl. 12, figs. 5, 6.

Remarks. C. oceanica occurs in most of the Aptian samples but is never abundant and, being thin-walled, is usually distorted. The range of morphological variation exhibited by this species is very great, and specimens approaching *C. albertii* Millioud 1969 are present. The variation can be summarized as follows: the cyst wall may be smooth, granular, or pseudo-reticulate; the processes may be simple or furcate, briefly or deeply, and distally may be acuminate, capitate, or knobbed; the apical process, when distinctive, is trifurcate and may be situated on an apical boss; the antapical process is cylindrical but varies considerably in size and denticulation of the distal margin. A precingular archaeopyle is always present.

Reported occurrence. Upper Hauterivian to Upper Albian, France (Millioud 1969; Davey and Verdier 1971, 1973). Middle Barremian to basal Coniacian, England (Cookson and Hughes 1964; Clarke and Verdier 1967; Davey 1969, 1974 in press). Albian, Cenomanian, Santonian/lowest Campanian, Australia (Cookson and Eisenack 1958, 1968, 1969).

Genus CRIBROPERIDINIUM Neale and Sarjeant emend. Davey 1969
Cribroperidinium sepimentum Neale and Sarjeant 1962

Plate 91, fig. 5

1962 *Cribroperidinium sepimentum* Neale and Sarjeant, p. 443, pl. 19, fig. 4.

Remarks. The present specimens from the Bedoulian closely resemble the type material. However, it is difficult to discern whether the cyst wall is densely microperforate or microgranulate.

Reported occurrence. Middle Hauterivian to Lower Barremian, England (Neale and Sarjeant 1962; Sarjeant 1966*b*; Davey 1974 in press).

Genus CYCLONEPHELIUM Deflandre and Cookson emend. Cookson and Eisenack 1962

Cyclonephelium tabulatum sp. nov.

Plate 92, figs. 1, 4; Plate 93, fig. 6

Derivation of name. Latin, *tabulatus*, plated or tabulate—with reference to the distinctive tabulation.

Diagnosis. The cyst is subcircular in outline and possesses a thin, smooth to lightly tuberculate wall. The processes are predominantly peritabular in position and clearly define the precingular and postcingular plates and the cingulum. The central part of the plates and the sulcal region are practically devoid of processes. The processes are short, stout, and capitate; they rarely branch distally or are joined proximally. The archaeopyle is apical and has a strongly zigzag margin and a sulcal notch; the operculum is typically detached.

Holotype. Slide FR 443/2, La Bédoule, south-east France; Upper Aptian (Gargasian).

Dimensions.

	Holotype (μm)	Range (μm)
Cyst height (without operculum)	57	52 (56) 60
Cyst width	72	59 (66) 72
Length of processes	4–8	2 (6) 9

Description. Since all the identified specimens possessed an apical archaeopyle and only rarely detached opercula were identified, it is difficult to precisely define the shape of the apical region. It is surmised, however, that it is of similar shape to that found in related species. That is, the cyst is rounded apically or has a reduced apical boss. The main part of the cyst is subcircular, or rarely slightly angular, in outline. The processes are neatly aligned just within the plate margins and hence clearly define the tabulation in the precingular and postcingular regions. In each case five or six plates appear to be present. The parallel lines of processes, either side of a plate boundary,

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EXPLANATION OF PLATE 91

Fig. 1. *Aptea polymorpha* Eisenack 1958. Complete specimen. Slide Gargas FR 456/1, ×450 ph.

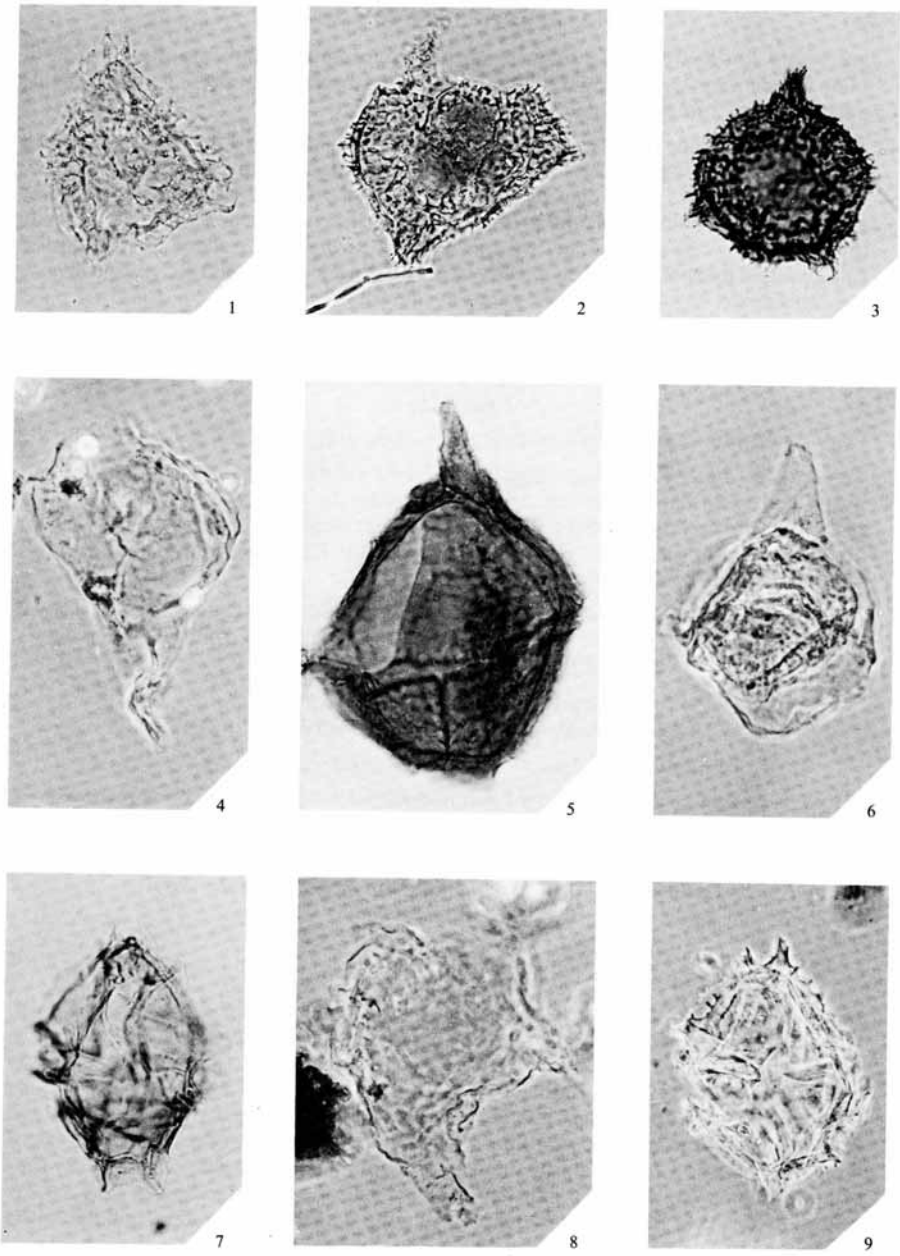
Figs. 2, 3. *Aptea securigera* sp. nov. 2, paratype illustrating apical archaeopyle, ×400 ph. 3, holotype, complete specimen, ×400.

Figs. 4, 8. *Muderongia* cf. *staurota* Sarjeant 1966. 4, specimen illustrating broad, centrally placed antapical horn. Slide La Bédoule FR 448/2, ×700 ph. 8, specimen illustrating reduced lateral horns. Slide La Bédoule FR 448/2, ×700 ph.

Fig. 5. *Cribroperidinium sepimentum* Neale and Sarjeant 1962. Archaeopyle to the north-west. Slide La Bédoule FR 446/1, ×600.

Fig. 6. *Dingodinium albertii* Sarjeant 1966. Apical operculum partially detached. Slide Gargas FR 454/1A, ×700 ph.

Figs. 7, 9. *Spiniferites* sp. 7, ventral view illustrating sulcus and displaced cingulum. Slide Gargas FR 451/2, ×650. 9, ventral view illustrating sutural spines and 'apical' horn. Slide Gargas FR 455/1A, ×650 ph.



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are 3 to 4 μm apart. Rare processes on the cingulum may indicate the position of plate boundaries; a distinct cingular tabulation, however, is not present. Two to three antapical and four apical plates appear to be present.

Remarks. The shape of the cyst and its processes are identical to that of *C. distinctum* Deflandre and Cookson 1955. *C. tabulatum* differs significantly from *C. distinctum*, and other members of *Cyclonephelium*, by the possession of peritabular processes and an encircling cingulum; the processes of *C. distinctum* are concentrated towards the circumferential region. The two species are clearly closely related, and although *C. tabulatum* does not conform exactly with the generic diagnosis of *Cyclonephelium* it is considered best placed in this genus at present.

Genus DINGODINIUM Cookson and Eisenack 1958

Dingodinium albertii Sarjeant 1966

Plate 91, fig. 6

1966*b* *Dingodinium albertii* Sarjeant, p. 210, pl. 21, fig. 3; pl. 23, fig. 1.

Remarks. D. albertii is distinguished from *D. cerviculum* Cookson and Eisenack 1958 by its considerably smaller size. At the moment the latter species appears to be restricted to Australia. The specimens described by Brideaux 1971*b* as *D. cerviculum* do, however, approach the type material in size but are here considered still to fall within the range of *D. albertii*.

Reported occurrence. Upper Hauterivian to Upper Barremian, France (Millioud 1969). Barremian, England (Sarjeant 1966*b*; Davey 1974 in press). Upper Barremian, Germany (Alberti 1961). Albian, Canada (as *D. cerviculum*; Brideaux 1971*b*; Singh 1971).

Genus GARDODINIUM Alberti 1961

Gardodinium trabeculosum (Gocht) Alberti 1961

1959 *Scriniodinium trabeculosum* Gocht, p. 62, pl. 4, fig. 5; pl. 8, fig. 2.

Reported occurrence. Lower Hauterivian to Lower Aptian, France (Millioud 1967). Lower Hauterivian to Upper Aptian, Germany (Gocht 1959; Alberti 1961). Middle Hauterivian to Upper Barremian, England (Sarjeant 1966*b*; Davey 1974 in press).

Genus GONYAULACYSTA Deflandre emend. Sarjeant 1969

Gonyaulacysta sp.

Plate 93, fig. 5

1958 Gen. et sp. indet. (ex. aff. *Wanaea*?) Eisenack, p. 398, pl. 25, fig. 2.

Description. Two well-preserved examples of this distinctive species were found and allow a relatively complete description to be given. The cysts are flattened and orientated such that the view is apical–antapical. Equatorially the cyst is subcircular (50–57 μm diameter) in outline and is surrounded by a distinctive flange 7–12 μm in height which is indented at the sulcus. This flange is formed by two expansions of the periphragm along the cingulum; these run parallel to the two cingular margins with the expansion on the apical side being less than the antapical one. Distally the expansions may be irregular and may bear conical or small bifid spines (1–2 μm in height). The apical region is broadly conical (20 μm at the base) and terminates with

a short, blunt process. The cyst surface is microgranulate and bears low, smooth ridges which appear to give a *Gonyaulacysta*-type tabulation. The archaeopyle is formed by the loss of one or two dorsal precingular plates.

Remarks. The present Gargasian specimens appear to be identical to Eisenack's form and are assigned to the genus *Gonyaulacysta*. Similar forms also have been described and figured as *Dinopterygium* sp. A by Brideaux (1971*b*, p. 97, pl. 28, figs. 89, 92) from the Albian of Canada. However, because of the unfavourable orientation of our specimens, they are impossible to describe completely and compare thoroughly with previously described species. The microgranulate ornamentation, the type of apical horn and sutural ridges, and the distinctive cingular periphragm expansions adequately differentiate this species from all known forms. *Wanea* Cookson and Eisenack 1958, from the Middle and Upper Jurassic, appears somewhat similar but differs significantly by the possession of an epitractal archaeopyle.

Reported occurrence. Upper Aptian, Germany (Eisenack 1958). Albian?, Canada (Brideaux 1971*b*).

Genus KLEITHRIASPHAERIDIUM Davey 1974

Kleithriasphaeridium simplicispinum (Davey and Williams) Davey 1974

1966*b* *Hystrichosphaeridium simplicispinum* Davey and Williams, p. 59, pl. 9, fig. 3.

Remarks. K. simplicispinum is extremely uncommon in the type Aptian and was only recorded a single time in each of four samples.

Reported occurrence. Valanginian to Hauterivian (Aptian?), Germany (Gocht 1959). Upper Hauterivian to Upper Barremian, England (Davey and Williams 1966*b*; Sarjeant 1966*b*; Davey 1974 in press).

Genus MEIOUROGONYAULAX Sarjeant 1966

Meiourogonyaulax cf. *bulloidea* (Cookson and Eisenack) Sarjeant 1969

Plate 92, fig. 5

1960*b* *Gonyaulax bulloidea* Cookson and Eisenack, p. 247, pl. 37, fig. 11.

Dimensions. (Single specimen.) Shell length 55 μm, shell width 60 μm, height of crests less than 2 μm.

Remarks. The single specimen of *M.* cf. *bulloidea* found during the present study differs from *M. bulloidea*, from the Portlandian of Australia, by the nature of its sutural crests. In *M. bulloidea* these are low, entire and granular; in *M.* cf. *bulloidea* they are smooth distally and composed of low, broad spines which widen and often join distally. Very similar specimens were described as *M. bulloidea* by Davey (1974 in press) from the Barremian of England.

Meiourogonyaulax stoveri Millioud 1969

Plate 93, figs. 2, 8

1969 *Meiourogonyaulax stoveri* Millioud, p. 429, pl. 3, figs. 1–3.

Dimensions. Length of shell (complete specimens) 64 (72) 83 μm, length of shell (with archaeopyle) 71–73 μm, width of shell 61 (73) 81 μm, maximum height of crests 7–12 μm.

Remarks. The present Aptian specimens resemble the type material in all respects. *M. stoveri* is characterized by its more or less circular outline, its thick (up to 3 μm),

perforate wall, and by its membranous crests which are often perforate and most strongly developed in the antapical region.

Reported occurrence. Lower Hauterivian, Switzerland; Upper Hauterivian, Barremian and Lower Aptian, France (Millioud 1969). Early and Middle Albian, France (Davey and Verdier 1971, questionable attribution).

Meiourogonyaulax psoros sp. nov.

Plate 92, figs. 8, 9

Derivation of name. Greek, *psoros*, scabby or mangy—with reference to the irregularly tubercled surface of the cyst wall.

Diagnosis. The cyst is subcircular to slightly angular in outline. The cyst wall is relatively thick and is characterized by a variable surface ornamentation consisting of isolated tubercles to low irregular vermicular ridges. The sutural ridges are low and are difficult to discern except at the margins of the cyst; they are formed by the coalescence of aligned tubercles and/or broad, flat-topped processes. The cingulum, which is narrow, is displaced by approximately one cingular width along the sulcus. The latter broadens on the hypotract and has a noticeable deep, centrally placed longitudinal groove. The apical archaeopyle is angular and the operculum sometimes remains attached.

Holotype. Slide FR 441/2, La Bédoule, south-east France; Lower Aptian (Bedoulian).

Paratype. Slide FR 444/2, La Bédoule, south-east France; Lower Aptian (Bedoulian).

Dimensions.

	Holotype (μm)	Paratype (μm)	Range (μm)
Cyst length (complete specimens)	69		59–69
Cyst length (specimens with archaeopyle)		51	51 (55) 60
Cyst width	66	64	52 (60) 68

Description. On one specimen a low (5 μm), conical, membranous apical horn is present. The remaining complete specimens only possess slight apical prominences which are indistinguishable from the other angularities of the cyst outline. The thick (up to 3 μm) cyst wall is densely warty and rugulate. The sutural ridges, which are often discontinuous, are of similar height (up to 5 μm) to this ornamentation and thus are difficult to locate. Only on the cyst margin is it possible to see that the ridges

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EXPLANATION OF PLATE 92

Figs. 1, 4. *Cyclonephelium tabulatum* sp. nov. Holotype. 1, dorsal view, × 600 ph. 4, ventral view, × 600 ph.

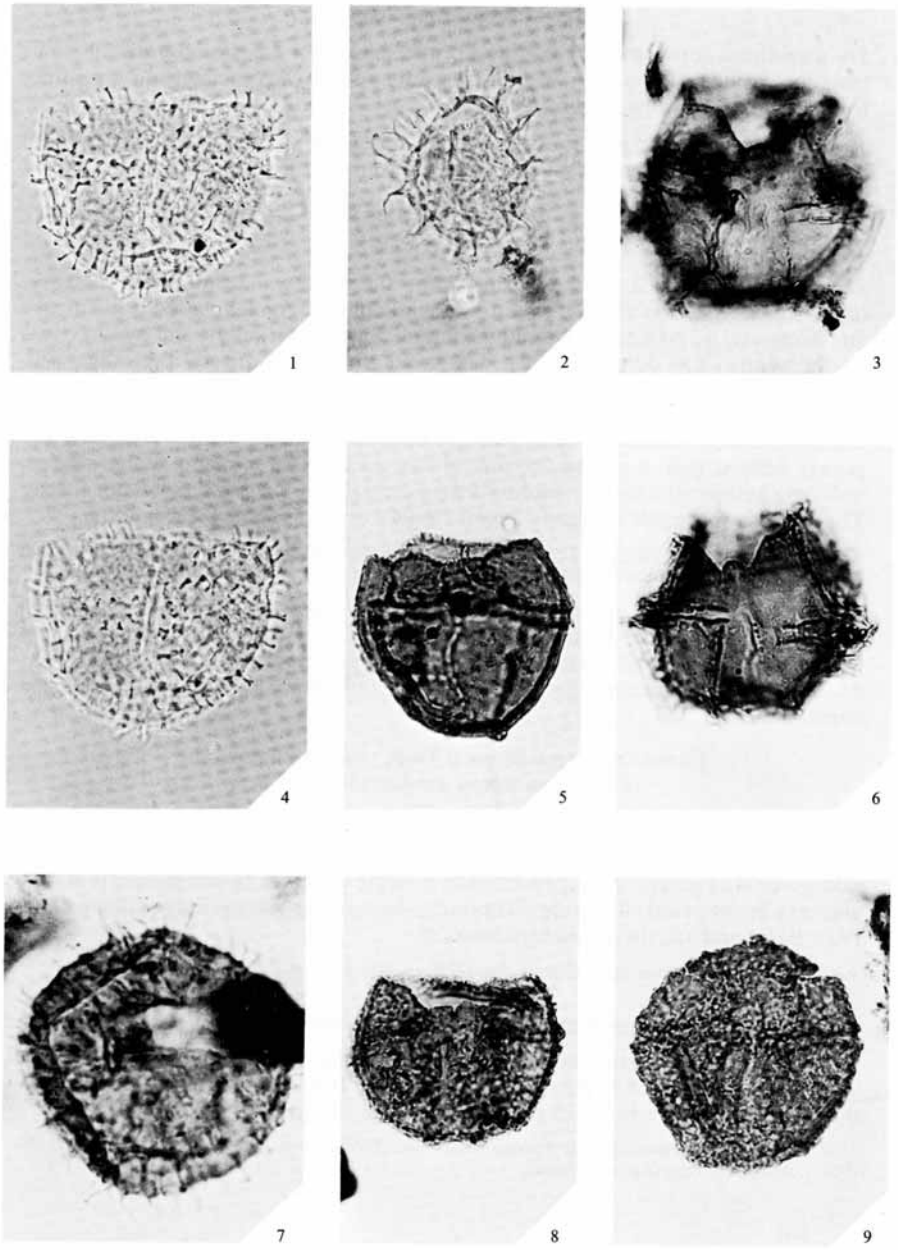
Fig. 2. *Achomosphaera* cf. *neptuni* (Eisenack 1958). Precingular archaeopyle is visible just beneath the apex. Slide La Bédoule FR 442/2, × 500 ph.

Figs. 3, 6. *Meiourogonyaulax* sp. Ventral views. Note the deeply incised sulcal notch, the insignificant crests on the ventral surface except for the cingulum and the high lateral crests. 3, slide La Bédoule FR 447/2, × 650. 6, slide La Bédoule FR 442/1, × 650.

Fig. 5. *Meiourogonyaulax* cf. *bulloidea* (Cookson and Eisenack 1960). Slide Gargas FR 454/1A, × 650.

Fig. 7. *Trichodinium* sp. Archaeopyle view; note long, fine spines. Slide La Bédoule FR 443/1, × 1000.

Figs. 8, 9. *Meiourogonyaulax psoros* sp. nov. 8, paratype, ventral view with apical archaeopyle developed, × 550. 9, holotype, complete specimen with operculum partially detached, × 550.



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are sometimes composed of long broad processes which anastomose distally. The cingulum is narrow (3–5 μm in width), does not appear to be tabulate, and sometimes forms ledges on the cyst circumference.

Remarks. M. psoros sp. nov. is easily distinguished from all other species of *Meiourogonyaulax* by its distinctive rugulate ornamentation and low sutural crests.

Meiourogonyaulax sp.

Plate 92, figs. 3, 6

Description. The cyst is subcircular in outline and has a wall of moderate thickness (approximately 1 μm) which is smooth to lightly pitted. The tabulation is distinctive and is marked by high crests around the lateral margins of the cyst and by low crests on the ventral and dorsal surfaces. The crests are smooth, rarely perforate, with a smooth distal margin and may develop pericoels on the lateral sides of the hypotract. The tabulation appears to be ?4′, 6″, ?6c, 5–6‴, 1p, 1⁗. The cingular plate crests are almost absent on the dorsal and ventral surfaces. Plate 1‴ is narrow and poorly defined and is practically part of the sulcus. The sulcus is wedge-shaped, widening antapically, with a deeply indented central groove; sulcal plates are absent. The apical archaeopyle is slightly angular with a deeply indented sulcal notch.

Figured specimens. Plate 92, fig. 3. Central body length 58 μm, width 55 μm, maximum height of crests 10 μm. Plate 92, fig. 6. Central body length 53 μm, width 51 μm, maximum height of crests 9 μm.

Remarks. The present specimens, only two were observed, strongly resemble *M. valensii* Sarjeant 1966*a*. *M. valensii* differs from *M.* sp. by the possession of a more evenly punctate wall and striate crests which are sometimes finely denticulate distally. *M. stoveri* differs in being larger, thicker walled, and having less uniformly developed lateral crests.

Genus OLIGOSPHAERIDIUM Davey and Williams 1966

Oligosphaeridium nannum Davey 1974

1974 *Oligosphaeridium nannum* Davey, pl. 4, figs. 9, 10 (in press).

Remarks. This species, which has only been reported from the Lower Barremian (Davey 1974 in press), was represented by a single specimen in one sample (FR 454) and may be reworked. Very rare (3) examples have been observed in the Albian of the Paris Basin and are also probably reworked.

Reported occurrence. Lower Barremian, England (Davey 1974 in press).

Genus PROLIXOSPHAERIDIUM Davey, Downie, Sarjeant and Williams 1966

Remarks. In the discussion below it is considered that *P. deirense* Davey *et al.* 1966 is a junior synonym of *P. parvispinum* (Deflandre 1937*c*) Davey *et al.* 1969. Hence, the latter species now becomes the type species of this genus.

Type species. Prolixosphaeridium parvispinum (Deflandre 1937*c*) Davey, Downie, Sarjeant and Williams 1969. Lower Cretaceous (Aptian), France.

Prolixosphaeridium parvispinum (Deflandre) Davey *et al.* 1969

1937*c* *Hystrichosphaeridium xanthiopyxides* var. *parvispinum* Deflandre, p. 29, pl. 16, fig. 5.
1958 *Hystrichosphaeridium parvispinum* Deflandre; Cookson and Eisenack, p. 45.
1960 *Baltisphaeridium parvispinum* (Deflandre) Klement, p. 59.
1966 *Prolixosphaeridium deirense* Davey *et al.*, p. 171, pl. 3, fig. 2; text-fig. 45.
1969 *Prolixosphaeridium parvispinum* (Deflandre) Davey *et al.*, p. 17.

Description. The present specimens of *P. parvispinum* are identical with *P. deirense* as described by Davey *et al.* 1966. It should be noted, however, that firstly, the two antapical processes of this latter form are not always distinctive; and secondly, that the basal portion of the larger processes may be perforate.

Remarks. P. parvispinum is undoubtedly identical to *P. deirense*. This relationship has been overlooked previously mainly because Deflandre's Aptian species was recorded in a publication dealing primarily with Late Cretaceous flints.

Reported occurrence. Uppermost Lower Barremian to Lower Aptian, France (Millioud 1969). Middle to Upper Barremian, England (Davey *et al.* 1966, Davey 1974 in press). Aptian, France (Deflandre 1937*c*). Albian, France (Davey and Verdier 1971, 1973).

Genus PROTOELLIPSODINIUM Davey and Verdier 1971

Protoellipsodinium clavulum sp. nov.

Plate 93, fig. 7

Derivation of name. Latin, *clavus*, nail—with reference to the shape of the processes.

Diagnosis. The cyst is elongate to ovoidal with a smooth wall. The cingulum usually lacks processes, and the hypotract is larger than epitract. The processes are fairly numerous and less than half the cyst width in length. They are typically hollow, with a restricted lumen, and distally are capitate or rarely bear two or three small spines. The archaeopyle is precingular, formed by the loss of a single plate.

Holotype. Slide FR 454/2, Gargas, south-east France; Upper Aptian (Gargasian).

Dimensions.

	Holotype (μm)	Range (μm)
Central body length	40	40 (42) 45
Central body width	23	23 (28) 32
Length of processes	4–11	4 (10) 13

Description. The cyst is thin-walled and often distorted, hence making orientation and archaeopyle identification difficult. The shape and structure of the processes are, however, very characteristic. Each process has a relatively broad base (2–3 μm wide), narrows rapidly above this, and for the more distal part of its length tapers only slightly and is more or less parallel sided (width approx. 1 μm). The processes expand at their distal extremities and are basically capitate; this expansion is usually slight (approx. 1 μm in width) but occasionally is wider and gives rise to two or three recurved spines (up to 2·5 μm long). The processes are rigid to slightly flexuous.

Remarks. The distal extremities of the processes distinguish *P. clavulum* sp. nov. from the two other species in this genus. The form of the processes is very similar to that

found in *Cleistosphaeridium huguonioti* (Valensi) var. *pertusum* Davey 1969 from the Upper Cenomanian of southern England and northern France. That species, however, is spherical to subspherical in shape and has an apical archaeopyle.

Genus SPINIFERITES Mantell emend. Sarjeant 1970

Spiniferites sp.

Plate 91, figs. 7, 9

Description. The specimens assigned to *Spiniferites* sp. are ovoidal in outline, smooth-walled, and have a distinct tabulation marked by membranous, sutural crests. The latter are highest at the plate corners where two or three crests meet and are especially noticeable in the apical region but do not appear to be best developed exactly at the apex. Between these gonal points the crests are lower (1–3 μm) and distally may vary from being slightly irregular to bearing strong, regularly or irregularly distributed, sutural spines up to 3 μm in height. In certain specimens, and in varying positions, the periphragm is detached from the endophragm, producing a bladder-like expansion reminiscent of Lejeune-Carpentier's (1937*c* and 1938*a*) specimens of *Spiniferites ramosus* (Ehrenberg 1838).

Dimensions. Length of central body 41–52 μm; width 31–45 μm; height of crestal spines up to 3 μm; height of gonal elevations up to 7 μm.

Remarks. Spiniferites sp. is not an easy species to classify; with only slight morphological variation, and such variations occur in the present specimens, this species can be assigned to any of three genera. The disappearance of sutural spines leads to a *Leptodinium* Klement or *Spiniferites cingulatus* (O. Wetzel 1933) assignation. The development of an apical expansion of the periphragm, or apical horn, leads to affinities with the *Gonyaulacysta cretacea/helicoidea* complex. The typical specimen of *Spiniferites* sp., however, does appear to represent a spiny form of *S. cingulatus.*

EXPLANATION OF PLATE 93

Fig. 1. *Pareodinia* cf. *aceras* (Manum and Cookson 1964) comb. nov. Specimen illustrating surface reticulation and attached opercular plates. Slide Gargas FR 455/2, × 1000 ph.

Figs. 2, 8. *Meiourogonyaulax stoveri* Millioud 1969. Slide Gargas FR 454/1. 2, dorsal view illustrating perforate antapical crest, × 800. 8, ventral view illustrating vacuolar wall, × 800 ph.

Fig. 3. *Deflandrea terrula* Davey 1974 (in press). Dorsal view illustrating tabulation and intratabular granulation. Slide La Bédoule FR 441/1, × 600 ph.

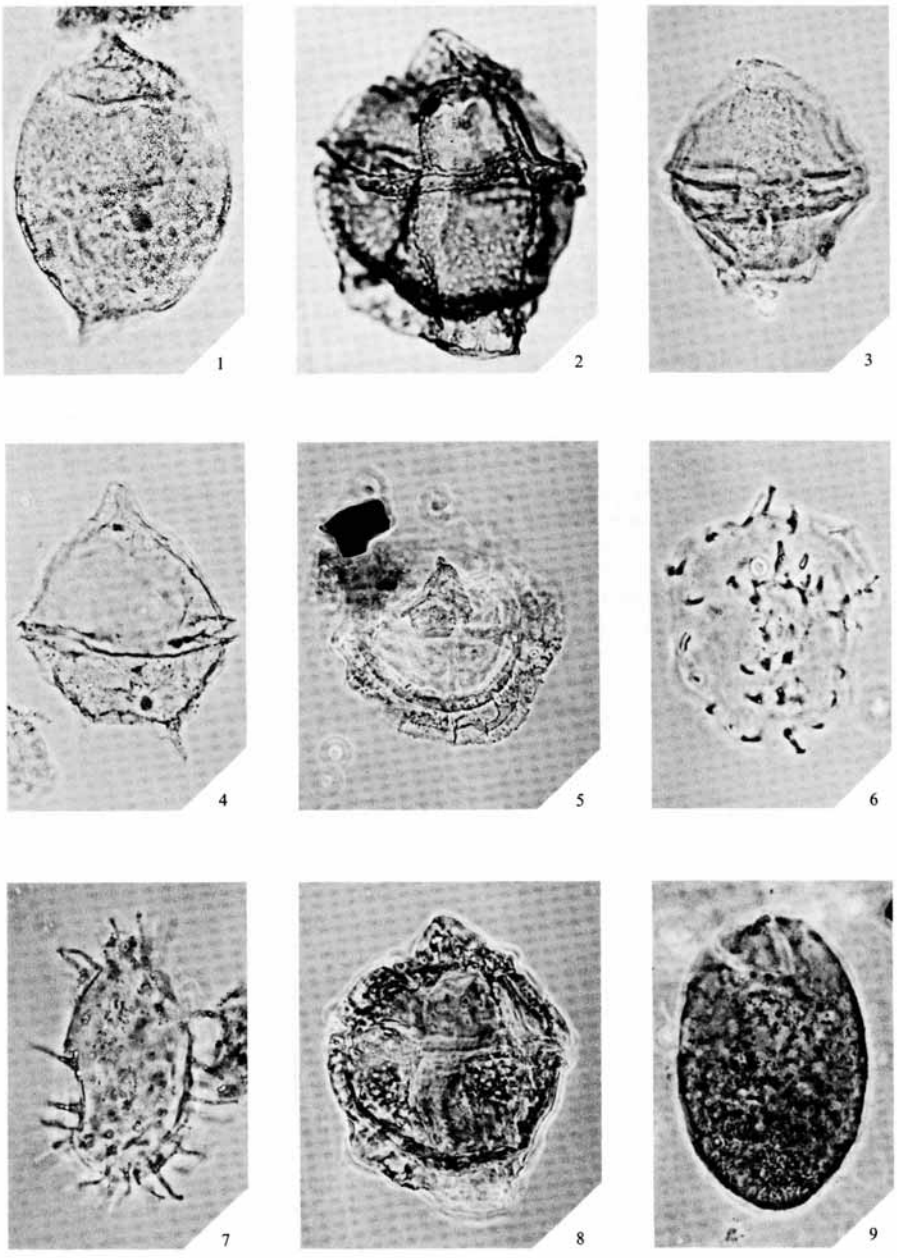
Fig. 4. *Astrocysta cretacea* (Pocock 1962). Specimen illustrating quasi-tabular ridges on the dorsal hypotractal surface. Slide Gargas FR 454/1A, × 800 ph.

Fig. 5. *Gonyaulacysta* sp. Apical view illustrating large precingular archaeopyle and two cingular flanges. Slide Gargas FR 455/1A, × 650 ph.

Fig. 6. *Cyclonephelium tabulatum* sp. nov. Apical operculum illustrating peritabular processes outlining four apical plates. Slide La Bédoule FR 443/2, × 1000 ph.

Fig. 7. *Protoellipsodinium clavulum* sp. nov. Holotype illustrating bald cingular region, × 900 ph.

Fig. 9. *Pareodinia* sp. Partially detached opercular plates are present just beneath the cyst apex. Slide Gargas FR 457/1B, × 800 ph.



DAVEY and VERDIER, Aptian dinoflagellate cysts

Genus SYSTEMATOPHORA Klement 1960
Systematophora schindewolfi (Alberti) Sarjeant 1966

1958 *Hystrichosphaeridium anthophorum* Cookson and Eisenack; Eisenack, p. 402, pl. 26, figs. 1, 2.
1961 *Hystrichosphaerina schindewolfi* Alberti, p. 38, pl. 10, figs. 1–3, 6, 7.
1961*c* *Hystrichosphaeridium* sp. 4 Evitt, p. 398, pl. 4, figs. 4, 5.
1966*b* *Systematophora schindewolfi* (Alberti) Sarjeant, p. 209, pl. 22, fig. 5.
1969 *Perisseiasphaeridium eisenackii* Davey and Williams, p. 6.
1974 *Perisseiasphaeridium eisenackii* Davey and Williams; Davey, pl. 6, fig. 5 (in press).

Remarks. Alberti's type specimen of *S. schindewolfi* comes from the Pirna borehole of Germany and was originally dated as Turonian; he also recorded specimens from the Upper Barremian of Salzgitter, Germany. Sarjeant (1966*b*) recognized this species in the Barremian of England and validly transferred it to *Systematophora*. Earlier, however, Evitt (1961*c*) had redescribed Eisenack's 1958 specimens of *Hystrichosphaeridium anthophorum*, and it is now obvious that the latter specimens belong to *S. schindewolfi*. Davey and Williams (1969), however, overlooked this relationship and erected a new species, *Perisseiasphaeridium eisenackii*, using Eisenack's specimens; this species is now considered to be a junior synonym of *S. schindewolfi*. An important stratigraphic point is that the dating of the Pirna borehole material has long been contested since seven of the reported fifteen species are of Aptian or older age; the oldest forms reported cannot be younger than Barremian. It thus appears probable that the type material of *S. schindewolfi* from the Pirna borehole is of Barremo–Aptian age rather than Turonian.

Reported occurrence. Middle to Upper Barremian, England (Sarjeant 1966*b*; Davey 1974 in press). Upper Barremian to Upper Aptian, Germany (Eisenack 1958; Alberti 1961).

Genus TRICHODINIUM Eisenack and Cookson emend. Clarke and Verdier 1967
Trichodinium sp.

Plate 92, fig. 7

Description. The rare specimens placed in *Trichodinium* sp. differ from *T. castanea* (Deflandre 1935*a*) in possessing finer and longer spines. An apical structure is not present. The cingulum and, more rarely, other sutural boundaries are marked by low thickenings of the shell wall.

Dimensions. Shell length 47–61 μm, width 44–59 μm, maximum length of spines 6–8 μm.

PERIDINIACEAN Group
Genus APTEA Eisenack 1958 emend.

Emended diagnosis. Dorso-ventrally flattened cysts with typically a rounded triangular outline and possessing an ornamentation of membranous crests and/or processes which is better developed in the circumferential region. The apices of the triangle are situated at the apex, antapex, and a little antapically to the right cingular margin of the cyst; they are typically marked by distinctively high ornamentation, and the cyst wall may or may not have prominent rounded protuberances in these positions. A detached inner body, elongate horns, and a flat or indented (two horns) antapical

region are never present. The crests and processes are intratabular and rarely show alignment parallel to plate boundaries. The archaeopyle is apical with a strongly zigzag margin and short breakages extending along the precingular plate boundaries. The sulcal notch is always offset from the mid-line of the cyst's ventral surface. Finally, the operculum often remains attached.

Type species. Aptea polymorpha Eisenack 1958, p. 394, pl. 22, figs. 5–12. Upper Aptian, Germany.

Remarks. The morphological structure of the genus *Aptea* is here described in detail so as to distinguish it from morphologically similar genera. Particular stress is placed on the typical and characteristic asymmetry of the cyst which, it is considered, distinguishes it from previously described and possibly related genera such as *Cyclonephelium* Deflandre and Cookson 1955, *Canningia* Cookson and Eisenack 1960*b*, and *Tenua* Eisenack 1958. These three genera have either a rounded or indented antapex and if protuberances or bulges are present in the cingular region then they are more or less symmetrically placed (text-fig. 5).

Aptea probably evolved directly from *Pseudoceratium* Gocht 1957 by the disappearance of the elongate horns, while still retaining the characteristic symmetry of this genus (text-fig. 5, VIII); for this reason *Aptea* is here considered to belong to the Pseudoceratioid branch of the Peridiniacean Group. This morphological change is apparently rapid and the first specimens assignable to *Aptea* appear in the topmost Barremian (Davey 1974 in press). However, this genus did not become a common constituent of the dinoflagellate cyst flora until Aptian time, only to disappear by the end of the Albian. *Doidyx* Sarjeant 1966*b* (see text-fig. 5, IX) is related to *Aptea* and is generically difficult to distinguish. However, *D. anaphrissa* Sarjeant 1966*b*, which has a Lower to Middle Barremian range (Davey 1974 in press), is the only member of this genus and is relatively easy to distinguish from similar species. For this reason it appears unnecessary to synonymize at present *Doidyx* with *Aptea*.

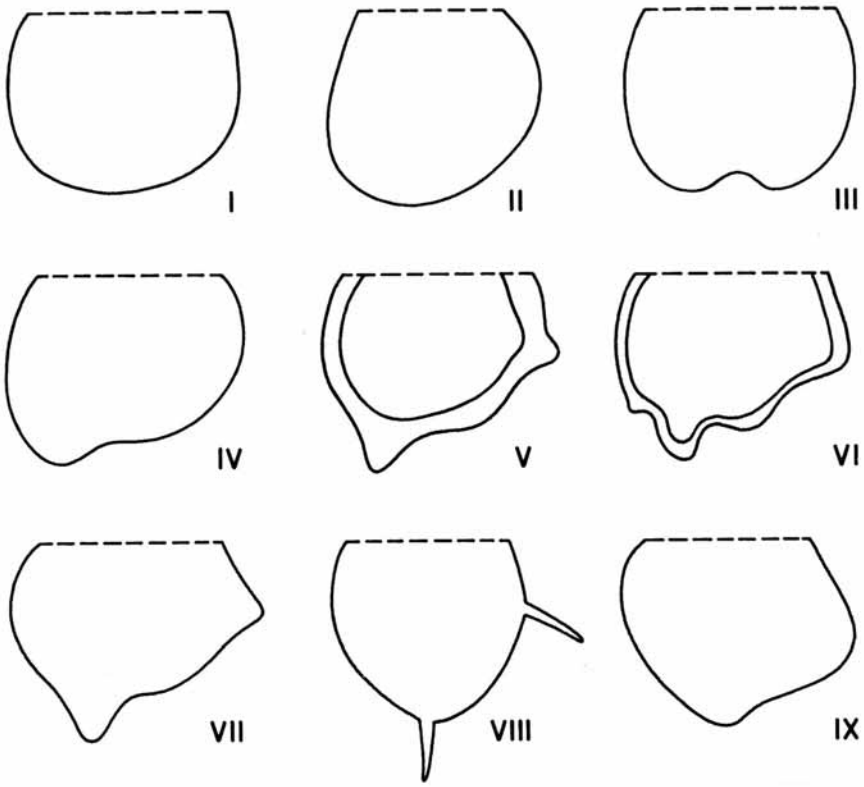
Aptea polymorpha Eisenack 1958

Plate 91, fig. 1; text-fig. 5 (V, VI)

1958 *Aptea polymorpha* Eisenack, p. 394, pl. 22, figs. 5–12.
1960 *A.* cf. *polymorpha* Eisenack; Eisenack and Cookson, p. 9, pl. 3, fig. 2 only.
1971 *A. polymorpha* Eisenack; Singh, p. 370, pl. 63, figs. 5–7; pl. 64, fig. 1.

Remarks. The present Tethyan specimens differ only in detail from the Boreal type material. The most noticeable differences are that our specimens are thinner-walled, have weaker and less continuous crests, and do not stain with safranin. These characteristics, we consider, are primarily preservational features and are not specifically significant. The Tethyan specimens, however, are generally more angular than the type material and sometimes possess relatively strong apical and antapical protuberances. *Aptea eisenacki* (Davey 1969) comb. nov. is more similar to the present examples of *A. polymorpha* than to the type material and may be distinguished only by the extremely low height of the crests.

Reported occurrence. Upper Aptian, Germany (Eisenack 1958). Albian?, Canada (Singh 1971).



TEXT-FIG. 5. Shape variation of certain related cysts (apex and ornamentation removed). I–IV, examples from the genera *Canningia*, *Cyclonephelium*, and *Tenua*. V and VI, *Aptea polymorpha* with ornamentation outline shown; V, from Eisenack's 1958 type material and VI, from the present French material. VII, *A. securigera*. VIII, *Pseudoceratium pelliferum*. IX, *Doidyx anaphrissa*.

Aptea securigera sp. nov.

Plate 91, figs. 2, 3; text-fig. 5 (VII)

Derivation of name. Latin, *securiger*, axe-bearing—with reference to the axe-shaped terminations of the processes.

Diagnosis. The cyst central body is dorso-ventrally flattened and rounded triangular in shape. The left side is strongly, but evenly, convex; the right epitractal and hypotractal sides are slightly convex to straight and meet at approximately right angles in the cingular region. The right hypotractal side often has a medial convexity. The apex and, to a lesser extent, the antapex are developed as protuberances of the central

body and are rounded distally. The cyst surface bears numerous short, flattened, solid processes which are concentrated in the circumferential region. A more or less circular area in the centre of the ventral and dorsal surfaces is devoid of, or possesses only rare, processes. The processes are of variable shape but are typically discrete, expanding both distally and proximally, and are flat-topped distally; their length is more than twice their medial width. The processes are longer and more variable at the cyst apices. Very rarely the cingulum and other tabulation is marked by narrow bands devoid of processes. The archaeopyle is apical and possesses a strongly zigzag margin. The operculum is usually detached.

Holotype. Slide FR 446/1, La Bédoule, south-east France; Lower Aptian (Bedoulian).

Paratype. Slide FR 446/2, La Bédoule, south-east France, Lower Aptian (Bedoulian).

Dimensions.

	Holotype (μm)	Paratype (μm)	Range (μm)
Central body length	73		73–90
Central body width	69	87	69 (75) 87
Central body length (operculum detached)		73	62 (67) 73
Height of processes	2–6	2–5	2 (3) 10

Description. The processes characteristically widen both distally and proximally. Very rarely, narrow processes may bifurcate or trifurcate, or neighbouring processes may be linked medially by a crest. Rarely the bases of two or three neighbouring processes may be linked by a low ridge or thickening of the cyst wall. These thickenings tend to parallel the cyst sides, as do the crests in *A. polymorpha*. Besides the longer processes at the cyst apices, slightly longer ones may also be present on the left side in the cingular region and on the convexity or bulge, if present, of the right hypotractal side. These longer processes were seen to be linked distally in one specimen.

Remarks. A. securigera sp. nov. is differentiated from *A. polymorpha* by the absence of well-developed crests and from *A. eisenacki* (Davey 1969) comb. nov. by the presence of numerous stout processes. *A. attadalica* (Cookson and Eisenack 1962*b*) comb. nov., from the Apto–?Albian of Australia, is most similar but possesses a wide distinctive cingulum and usually a ventral furrow.

Other species

The following two species now fall within the emended diagnosis of *Aptea* and are transferred to this genus.

Aptea attadalica (Cookson and Eisenack) Davey and Verdier comb. nov. = ?*Cyclonephelium attadalicum* Cookson and Eisenack 1962*b*, p. 495, pl. 5, figs. 12–15. Apto–?Albian, Australia.

Aptea eisenacki (Davey) Davey and Verdier comb. nov. = *Cyclonephelium eisenacki* Davey 1969, pp. 170, 171; pl. 8, figs. 3, 4; pl. 9, fig. 4; text-fig. 17A, B. Albian, Canada.

Genus DEFLANDREA Eisenack emend. Williams and Downie 1966

Deflandrea perlucida Alberti 1959

1959 *Deflandrea perlucida* Alberti, p. 102, pl. 9, figs. 16, 17.

Reported occurrence. Middle to Upper Barremian, England (Davey 1974 in press). Upper Barremian, Germany (Alberti 1961). Albian?, Australia (as *D. rotundata*, Eisenack and Cookson 1960).

Deflandrea terrula Davey 1974

Plate 93, fig. 3

1974 *Deflandrea terrula* Davey, pl. 8, figs. 4, 5 (in press).

Reported occurrence. Lower to Middle Barremian, England (Davey 1974 in press).

Genus MUDERONGIA Cookson and Eisenack 1958

Muderongia cf. *staurota* Sarjeant 1966

Plate 91, figs. 4, 8

Remarks. Three specimens attributable to *M.* cf. *staurota* were found, one in sample FR 445 and two in sample FR 448. In each case, preservation was poor and only the antapical region was present. It is characterized by a central body of subcircular outline, a single, proximally broad antapical horn, and two (or perhaps one) very reduced lateral horns. These forms are considerably smaller than the type material of *M. staurota* and closely resemble specimens described by Davey (1974 in press) from the late Middle and Upper Barremian of England.

Dimensions. Plate 91, fig. 8. Overall length 72 μm, length of antapical horn 27 μm, length of lateral horns 10 and 13 μm. Plate 91, fig. 4. Overall length 78 μm, length of antapical horn 33 μm, length of lateral horn 13 μm.

Stratigraphic comments. The presence of *M.* cf. *staurota* in the Lower Aptian extends the range of the genus *Muderongia* upwards. It is now late Upper Kimmeridgian (see Gitmez and Sarjeant 1972) to Lower Aptian.

Genus PAREODINIA Deflandre emend. Gocht 1970

Remarks. The present authors agree with Gocht (1970) that specimens attributable to *Pareodinia* may simply be poorly preserved specimens of *Kalyptea* Cookson and Eisenack 1960*b* which have lost their calyptra, the surrounding, veil-like covering. Hence, *Kalyptea* is considered to be a junior synonym of *Pareodinia*. The latter genus is characterized as being a single-walled ovoidal cyst possessing a two-plate intercalary archaeopyle near the apex. A calyptra and apical horn are often present.

Imbatodinium Vozzhennikova 1967 is distinguished from *Pareodinia* only with difficulty. It is characterized by an elongate body with a sulcus and cingulum, the latter being towards the antapex. The ornamentation may be coarse, and there may be an apical tentacle. At present the genus appears to be restricted to the latest Jurassic and earliest Cretaceous.

Caligodinium amiculum Drugg (1970), from the Danian of the U.S.A., is very similar to the specimens herein assigned to *P.* cf. *aceras*. *Caligodinium* Drugg (1970) is closely related to *Pareodinia* but may be distinguished by the type of archaeopyle present;

in the former the operculum consists of three parts—two dorsal intercalary plates and a larger plate composed of the three or four apical plates. If the latter large plate becomes detached only in damaged specimens, as appears likely, then *Caligodinium* would be a junior synonym of *Pareodinia*.

Pareodinia cf. *aceras* (Manum and Cookson 1964) comb. nov.

Plate 93, fig. 1

1964 *Kalyptea aceras* Manum and Cookson, p. 27, pl. 6, figs. 9–11.

Remarks. The rare Aptian specimens encountered are identical to the Canadian type material except that they are considerably smaller. A small apical horn may be present, and the archeopyle is formed by the displacement of two intercalary plates just beneath the apex.

Dimensions. Plate 93, fig. 1. Shell length, 48 μm, width 37 μm. Range: shell length 48–54 μm, width 37–40 μm, wall thickness approximately 1 μm, reticulation approximately 0·5 μm.

Reported occurrence. Early Upper Cretaceous?, Arctic Canada (Manum and Cookson 1964).

Pareodinia sp.

Plate 93, fig. 9

Description. The cyst is elongate-ovoidal, coarsely granular to finely reticulate, and possesses a two-plate intercalary archaeopyle just beneath the apex. A reduced calyptra is present. Polar structures and a cingulum are absent.

Dimensions. Plate 93, fig. 9. Shell length 62 μm, width 42 μm. Second specimen; length 58 μm, width 33 μm.

Remarks. Only two specimens of this distinctive species were recovered. Its lack of an apical horn distinguishes it from all associated species except *P. aceras*, from which it may be distinguished by its more elongate shape and less strongly reticulate wall.

Genus WALLODINIUM Loeblich and Loeblich 1968

Wallodinium luna (Cookson and Eisenack 1960) comb. nov.

1960 *Diplotesta luna* Cookson and Eisenack, p. 10, pl. 3, fig. 21.

Remarks. During the present study the procedure used by Davey (1974 in press) was followed. That is, due to continuous variation within this genus, all specimens can be assigned for practical purposes, to a single species. *W. luna* comb. nov. has priority. It is not our intention, at present, to synonymize these three species because their distinction in younger strata may be of importance.

Reported occurrence. W. luna, *W. krutzschi*, and *W. anglica* have a combined stratigraphic range of Lower Hauterivian to Cenomanian (see Davey 1974 in press).

Other species

Wallodinium anglica (Cookson and Hughes) Davey and Verdier, comb. nov. = *Diplotesta anglica* Cookson and Hughes 1964, p. 56, pl. 11, figs. 1–5. Albian to Cenomanian, England.

STRATIGRAPHIC DISCUSSION

The distribution of all the dinoflagellate cysts recovered from the two sections investigated is shown on text-figs. 6–7. The ranges of sixty-two species and varieties which are particularly meaningful stratigraphically are shown on the summarizing range chart (text-fig. 8). Occurrences of these taxa in older and younger strata, as reported earlier by the authors and as taken from selected European literature, are also tabulated on this chart. The stratigraphic distribution of certain species and comparisons with previously described Aptian assemblages are discussed below.

The Barremian–Aptian boundary

Barremian sediments in the Provence region were not sampled during this study because of their palynologically unfavourable lithology (Urgonian Limestone). The lowest part of the Bedoulian (Couches de passage) consisted of relatively clean limestones and proved to be practically barren. The older fossiliferous Bedoulian samples yielded two species, *Cribroperidinium sepimentum* and *Muderongia* cf. *staurota*, which had been reported previously only from the Barremian (Davey 1974 in press). These were extremely rare, and the latter form appears to be characteristically confined to the uppermost Barremian and lowermost Aptian. Of particular significance is the absence from the Lower Aptian of *Muderongia staurota* s.s. and *Pseudoceratium pelliferum*; these species apparently became extinct during the Late Barremian.

Bedoulian

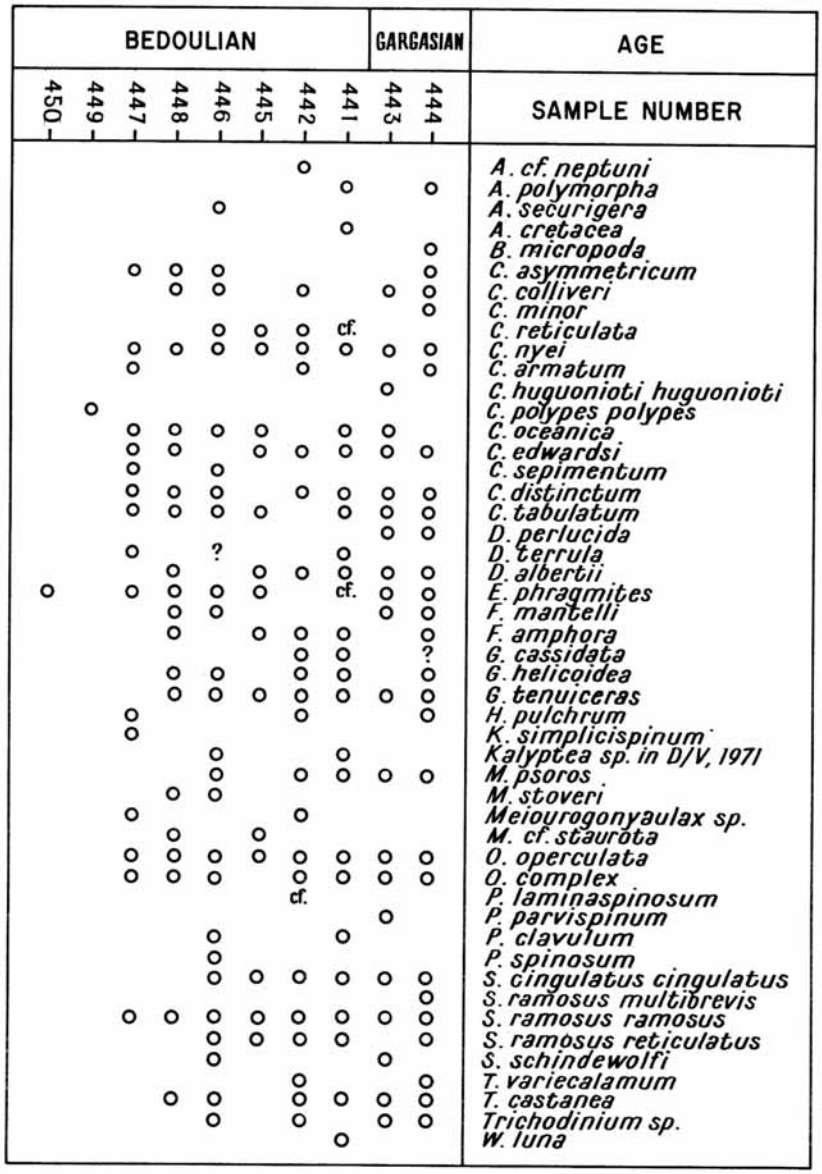
The following species first appear in the Bedoulian and are restricted to the Aptian—*Aptea polymorpha*, *Cyclonephelium tabulatum*, *Meiourogonyaulax psoros*, and *Trichodinium* sp. *Deflandrea terrula* and *Meiourogonyaulax* sp. became extinct in the Provence region during the Early Aptian, whereas other species, such as *Gonyaulacysta cassidata* and *Protoellipsodinium spinocristatum*, first occurred at that time and range into post-Aptian strata.

Gargasian

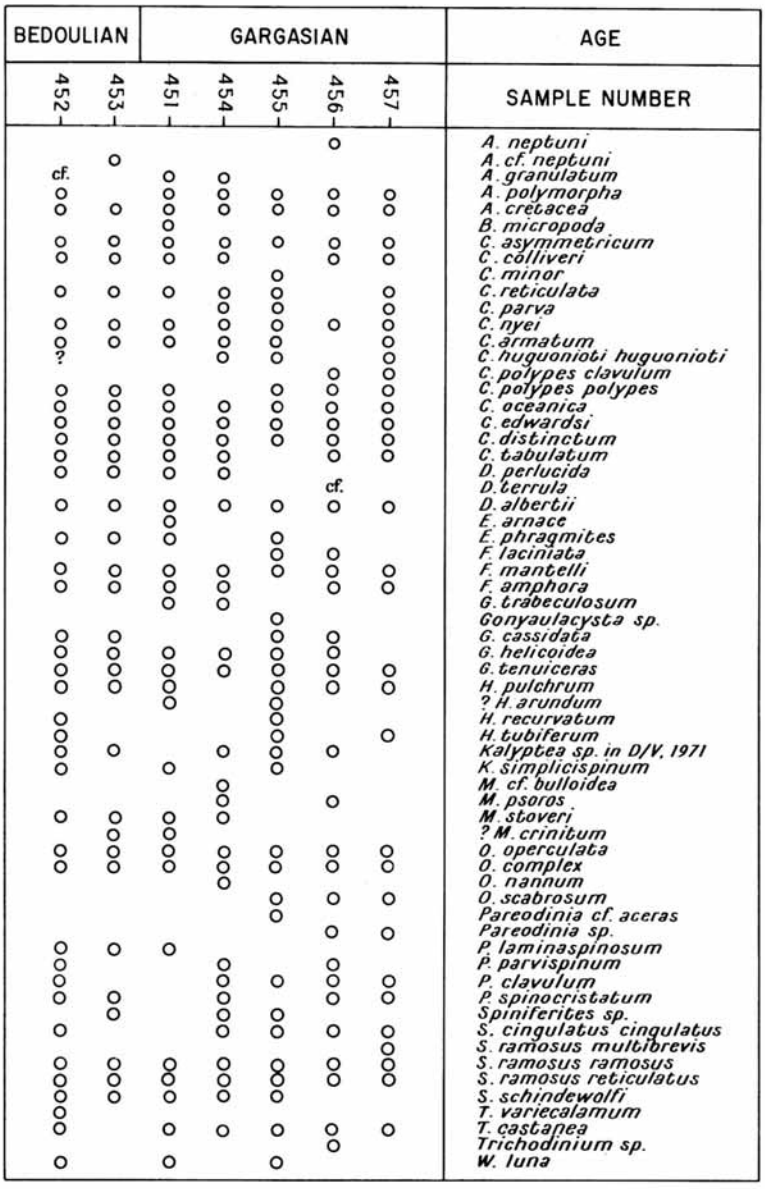
A few species first appear in the Upper Aptian and range into younger strata. Among these, the most restricted stratigraphically are *Astrocysta cretacea*, *Prolixosphaeridium parvispinum*, *Ovoidinium scabrosum*, and *Cleistosphaeridium polypes clavulum*. *Pareodinia* sp. and *Gonyaulacysta* sp. have limited ranges and seem, at present, to be restricted to the Gargasian. A number of species which first appear in pre-Aptian strata become extinct in the Gargasian and may be used, as may be the Aptian-restricted species, for differentiating Lower Aptian and Upper Aptian. These include *Achomosphaera neptuni*, *Dingodinium albertii*, *Gardodinium trabeculosum*, *Meiourogonyaulax stoveri* s.s., and *Systematophora schindewolfi*.

Comparison with previously described Aptian assemblages

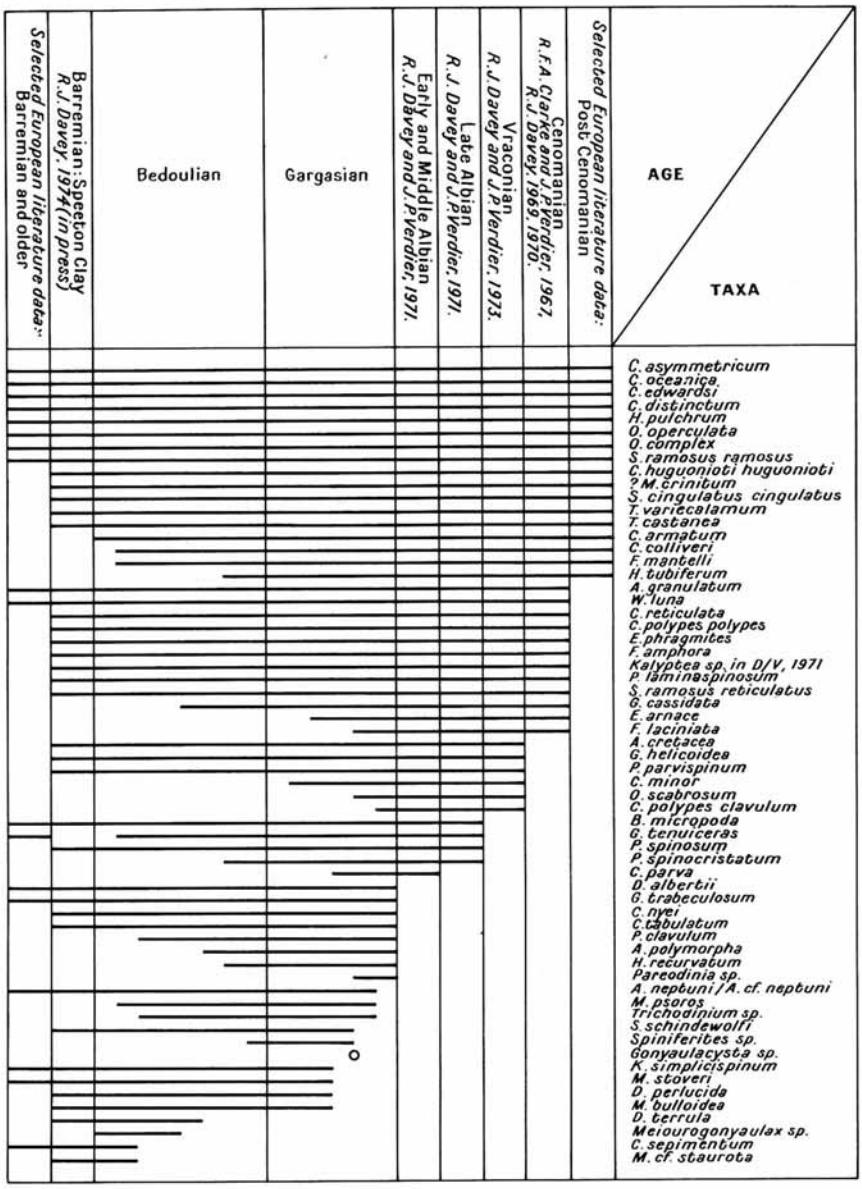
Europe. Eisenack 1958. Of the twenty-seven distinct species described by Eisenack from the Upper Aptian of Germany, eighteen have been found in the French stratotype sections. The restricted distributions of *Aptea polymorpha*, *Florentinia laciniata* (as *Hystrichosphaeridium ferox*), and *Gonyaulacysta* sp. (as Gen. and sp. indet.) in



TEXT-FIG. 6. Microplankton distribution in the samples analysed from the La Bédoule section.



TEXT-FIG. 7. Microplankton distribution in the samples analysed from the Gargas section.



TEXT-FIG. 8. Range chart of selected Aptian microplankton observed in this study and as reported in certain European Cretaceous publications.

our samples support the Late Aptian age for the German material and also confirm the stratigraphic value of these species.

Alberti 1961. Alberti describes three assemblages from the German Aptian; two are assigned to the Lower Aptian and one to the Upper Aptian. All three assemblages contain *Pseudoceratium pelliferum*, which has been reported otherwise only from pre-Aptian Early Cretaceous strata, and one assemblage contains *Muderongia simplex*, which occurs only in the pre-Barremian Early Cretaceous. Hence, it appears probable that these assemblages are of Barremian or older Early Cretaceous age.

Millioud 1969. The Angles section (south-eastern France) studied by Millioud included three samples of Early Aptian age. The assemblages he reported agree well with the microplankton distribution at La Bédoule, with the exceptions that *Gonyaulacysta aptiana* and *Phoberocysta neocomica* were not present in our samples. Their absence could be explained by the fact that the two oldest Aptian samples at La Bédoule (limestone facies) were practically barren and/or that these two species disappeared during earliest Aptian time.

Australia. Cookson and Eisenack 1958, 1960*b*, 1962*b*. Many Aptian assemblages from various formations and localities have been described by these authors. Although the assemblages do vary somewhat in species composition basically two associations are represented. The first one, from the Roma Formation (Santos Oodnadatta No. 2 borehole), and Osborne Formation (Rakich borehole), contains *Canningia colliveri*, *Gonyaulacysta cassidata*, *Spinidinium styloniferum*, *Carpodinium granulatum*, *Trichodinium castanea*, and *Gonyaulacysta tenuiceras*. Although in Europe, none of these species are restricted to the Aptian, the age of this association, according to the present study, could well be Aptian. The second association, reported from the Muderong Shale, Windalia Radiolarite, Birdrong Formation (Grierson Member), Roma series and several borehole samples from unspecified formations, contains *Dingodinium cerviculum*, *Muderongia mcwhaei*, and *M. tetracantha*. Unless these species of *Muderongia* have a younger range in Australia than in Europe, their presence would indicate a pre-Aptian age.

Canada. Singh 1971. Although reportedly no Aptian material was studied by Singh, some of the species he recovered strongly suggest an Aptian age for the lower part of the section. The upper part of the section does appear to be of the late Albian age, as assigned. However, the presence of *Gardodinium trabeculosum* (as *G. eisenacki*), *Dingodinium albertii* (as *D. cerviculum*), *Chlamydophorella nyei*, and certain of the illustrated specimens of *Aptea polymorpha* is certainly indicative of an Aptian age according to our recent studies. The association of some of these species with *Deflandrea limpida* (*D. gallia* Davey and Verdier 1973 is a junior synonym) and *Ovoidinium verrucosum* (as *Ascodinium verrucosum*), which indicate a Late Albian age, strongly suggests that there is reworked Aptian in the upper part of Singh's section.

Brideaux 1971*b*. The assemblages described by Brideaux from the Middle to Upper Albian of Canada strongly resemble those of Singh (1971) and also include *Chlamydophorella nyei* and *Dingodinium albertii* (as *D. cerviculum*), together with *Gonyaulacysta* sp. (as *Dinopterygium* sp. A). These species are strongly suggestive of an Aptian age, and their presence in Albian strata signifies erosion and redeposition of Aptian sediments during Albian time.

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