

Dinoflagellate cysts from the Cretaceous–Paleogene boundary at Ouled Haddou, southeastern Rif, Morocco: biostratigraphy, paleoenvironments and paleobiogeography

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A palynological investigation of a section dated by foraminifera, at Ouled Haddou, south-eastern Rifian Corridor, northern Morocco, revealed a rich and well-preserved dinoflagellate cyst assemblage that allowed a palynological separation of Maastrichtian from Danian deposits. The gradual change of the dinoflagellate cyst assemblages and the biostratigraphic resolution attained, suggest that the studied Maastrichtian–Danian section is continuous. The recognition of the latest Maastrichtian and earliest Danian is based on global dinoflagellate cyst events, including the first occurrence of the latest Maastrichtian species *Disphaerogena carposphaeropsis*, *Glaphyrocysta perforata*, and *Manumiella seelandica*, the latest Maastrichtian acme of *Manumiella seelandica*, and the first occurrence of the earliest Danian markers *Carpatella cornuta*, *Damassadinium californicum*, *Eisenackia circumtabulata*, *Membranilarnacia tenella* and *Senoniasphaera inornata*. The Cretaceous–Paleogene boundary is placed above the latest Maastrichtian events, mainly immediately above the acme of *M. seelandica* and below the earliest Danian events, particularly below the first occurrences of *C. cornuta* and *D. californicum*. The biostratigraphic interpretations are based on a comparison with calibrated dinoflagellate cyst ranges from several reference sections, mainly in the Northern Hemisphere middle latitudes. The Cretaceous–Paleogene boundary is not marked by a mass extinction of dinoflagellate cyst species, but shows important changes in the relative abundances of different species or groups of morphologically related species. These changes are paleoenvironmentally controlled. The peridinioid assemblage suggests deposition in a subtropical to warm temperate province. One dinoflagellate cyst species, *Phelodinium elongatum*, is formally described.

Keywords: Cretaceous–Paleogene boundary; dinoflagellate cysts; stratigraphy; Ouled Haddou section; southeastern Rif; northern Morocco

1. Introduction

Since the discovery of the Chicxulub impact crater (Hildebrand et al. 1991) in southern Mexico, the impact hypothesis (Alvarez et al. 1980; Smit and Hertogen 1980) has become widely accepted as an explanation for the anomalously high concentration of iridium at the Cretaceous–Paleogene (K–Pg) boundary, and the global mass extinctions of the dinosaurs and many other groups at the end of the Cretaceous. However, other causes such as intense volcanism, multiple impacts, sea level fluctuations and climate changes (Keller and Stinnesbeck 1996; Hallam and Wignall 1999) have been proposed. The relationships between these phenomena, the iridium-rich deposits at the boundary, and drastic changes in the biosphere have been for decades the subject of intense, global research. The enrichment in iridium and other extra-terrestrial impact evidence were found at the base of the K–Pg boundary clay in several sites including

Caravaca (Spain) and El Kef (Tunisia), where the K–Pg Boundary Stratotype and Global Stratotype Section and Point (GSSP) were formally defined (International Union of Geological Sciences (IUGS) 1991; Molina et al. 2006).

Many studies on dinoflagellate cysts from around the world have focused on the K–Pg boundary. In contrast to calcareous planktonic foraminifera and nannoplankton, organic-walled phytoplankton, including dinoflagellate cysts, did not undergo a mass extinction across the K–Pg boundary (Benson 1976; Hansen 1977; De Coninck and Smit 1982; Hultberg 1986; Firth 1987; Brinkhuis and Zachriasse 1988; Moshkovitz and Habib 1993; Habib et al. 1996). Former dinoflagellate cyst studies from Morocco were based on material from the Gantour and Oulad Abdoun mining districts of the Phosphate Plateau (Doubinger 1979; Rauscher and Doubinger 1982; Rauscher 1985; Soncini and Rauscher 1988; Soncini

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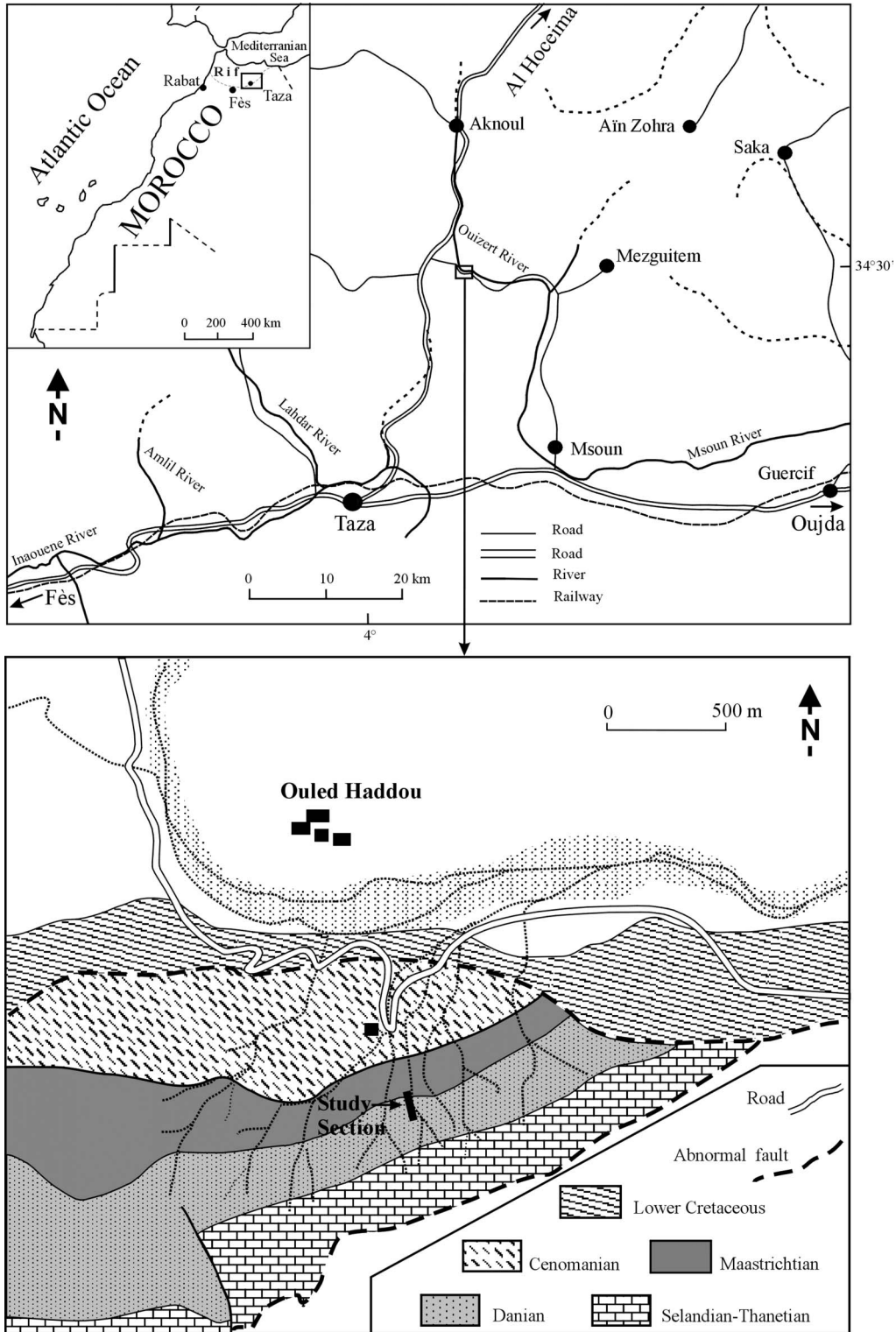


Figure 1. Location map and geological setting of the Ouled Haddou section (northern Morocco).

1990; Rauscher et al. 1990) and the Bou Anguer Syncline of the Middle Atlas Mountains (Herbig and Fechner 1994). The recorded dinoflagellate cyst

assemblages were diverse and well-preserved, but none of the sections studied encompassed a continuous transition across the K–Pg boundary. Our study is

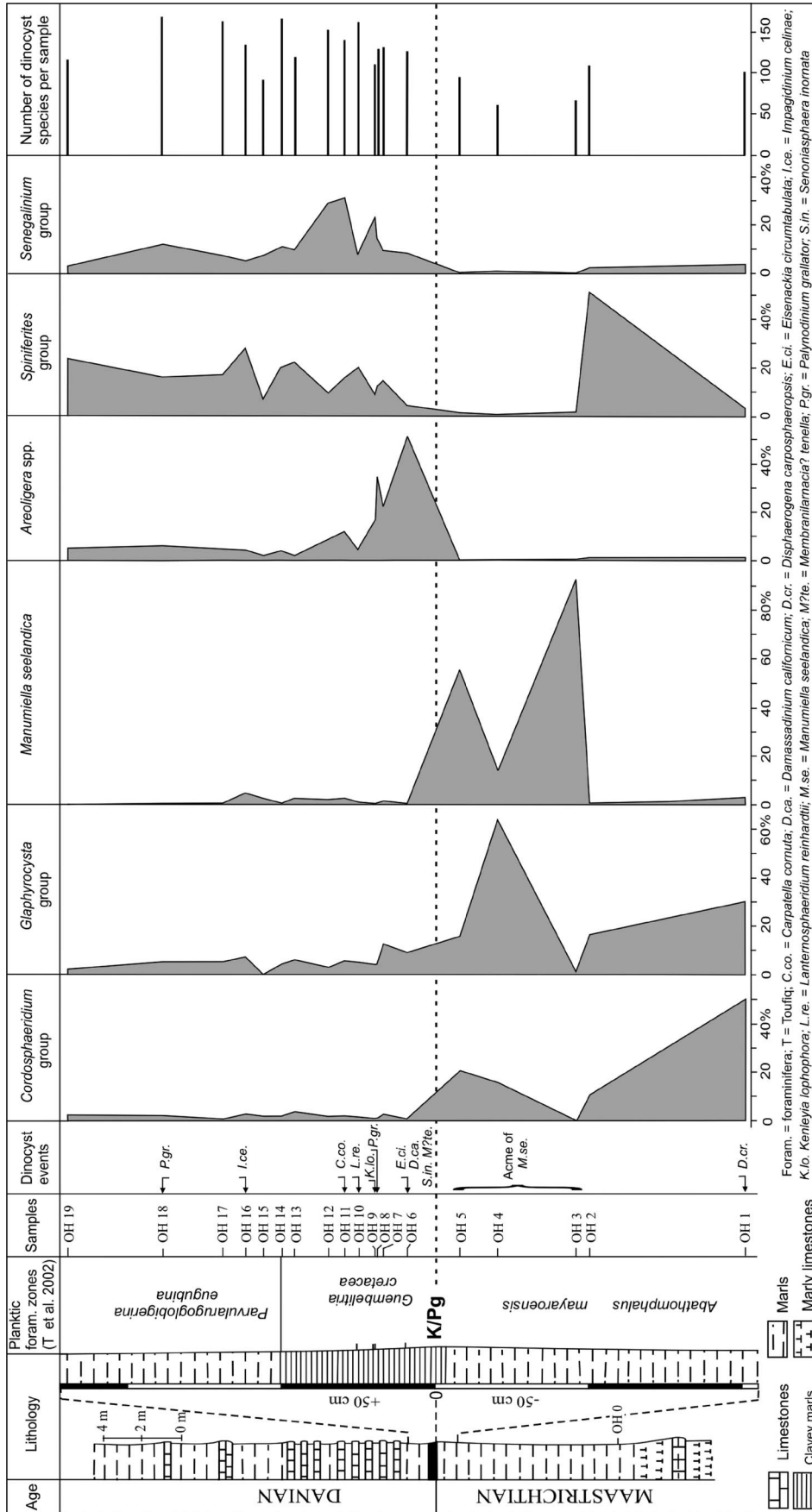
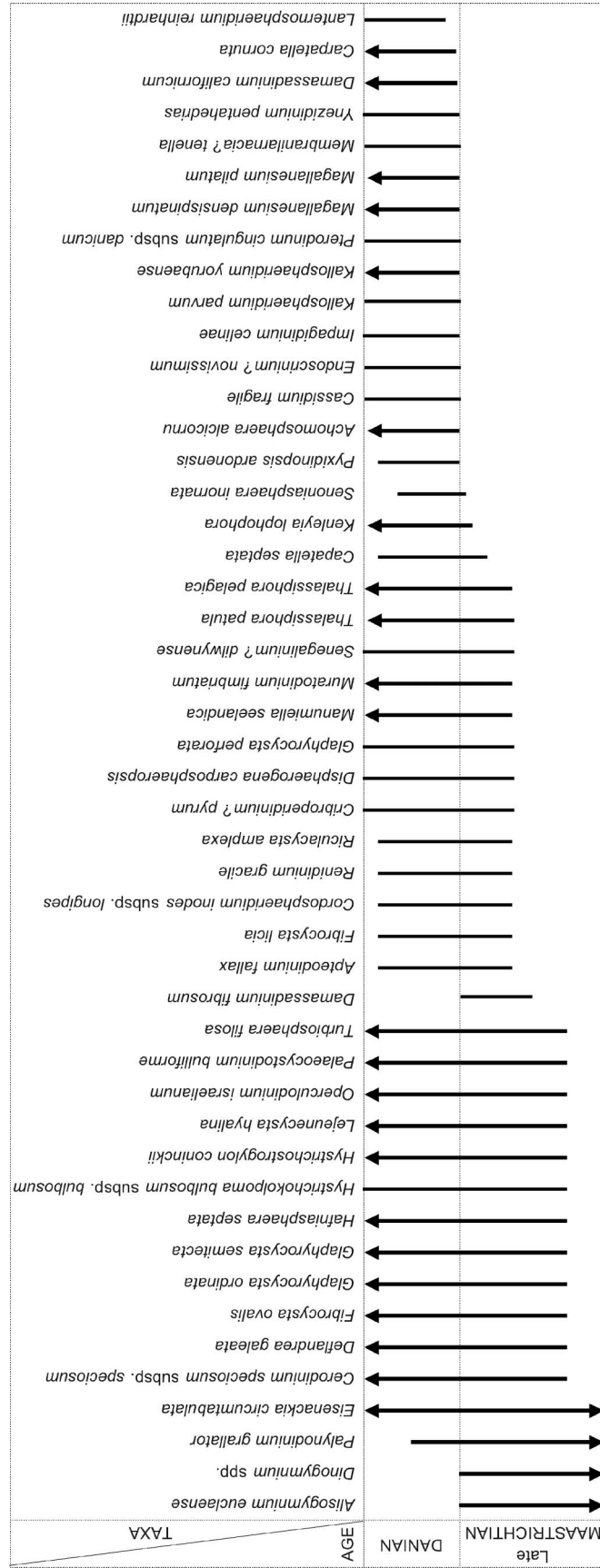


Figure 2. Relative abundances of selected species and groups of morphologically related species and dinoflagellate diversity patterns, compared against lithology, planktic foraminiferal zonation, dinoflagellate cyst events and sample positions across the Cretaceous/Paleogene boundary at the Ouled Haddou section (northern Morocco). Glaphyrocysta group = *Glaphyrocysta* spp. + *Ritaculacysta* spp., *Spiniferites* group = *Achomosphaera* spp. + *Spiniferites* spp., *Senegalinium* group = *Andalusitella dubia* + the small *Cerodinium mediterraneum* + *Geiselodinium psilatatum* + *Lejeunecysta* spp. + *Phelodinium* spp. + *Senegalinium* spp.

Table 2. Stratigraphic ranges of selected dinoflagellate cysts, taken from references cited in Section 4.



based on samples from a section at Ouled Haddou, which is a Moroccan section with a relatively complete record of the K–Pg transition (Toufiq et al. 2002; Toufiq and Boutakiout 2005; Toufiq 2006).

This paper presents selected results of a multi-disciplinary research program carried out on this section. A high-resolution dinoflagellate cyst analysis was carried out, the results are compared to dinoflagellate cyst studies from other K–Pg sections, including El Kef and Aïn Settara (Tunisia), Stevns Klint (Denmark), Caravaca (Spain) and Escarpado Canyon (California), Braggs (Alabama) and Bass River (New Jersey) in the USA. Preliminary dinoflagellate cyst analyses by Slimani et al. (2004, 2007, 2008) support the biostratigraphic interpretation of the boundary in the section.

2. Material and methods

2.1. The Ouled Haddou outcrop

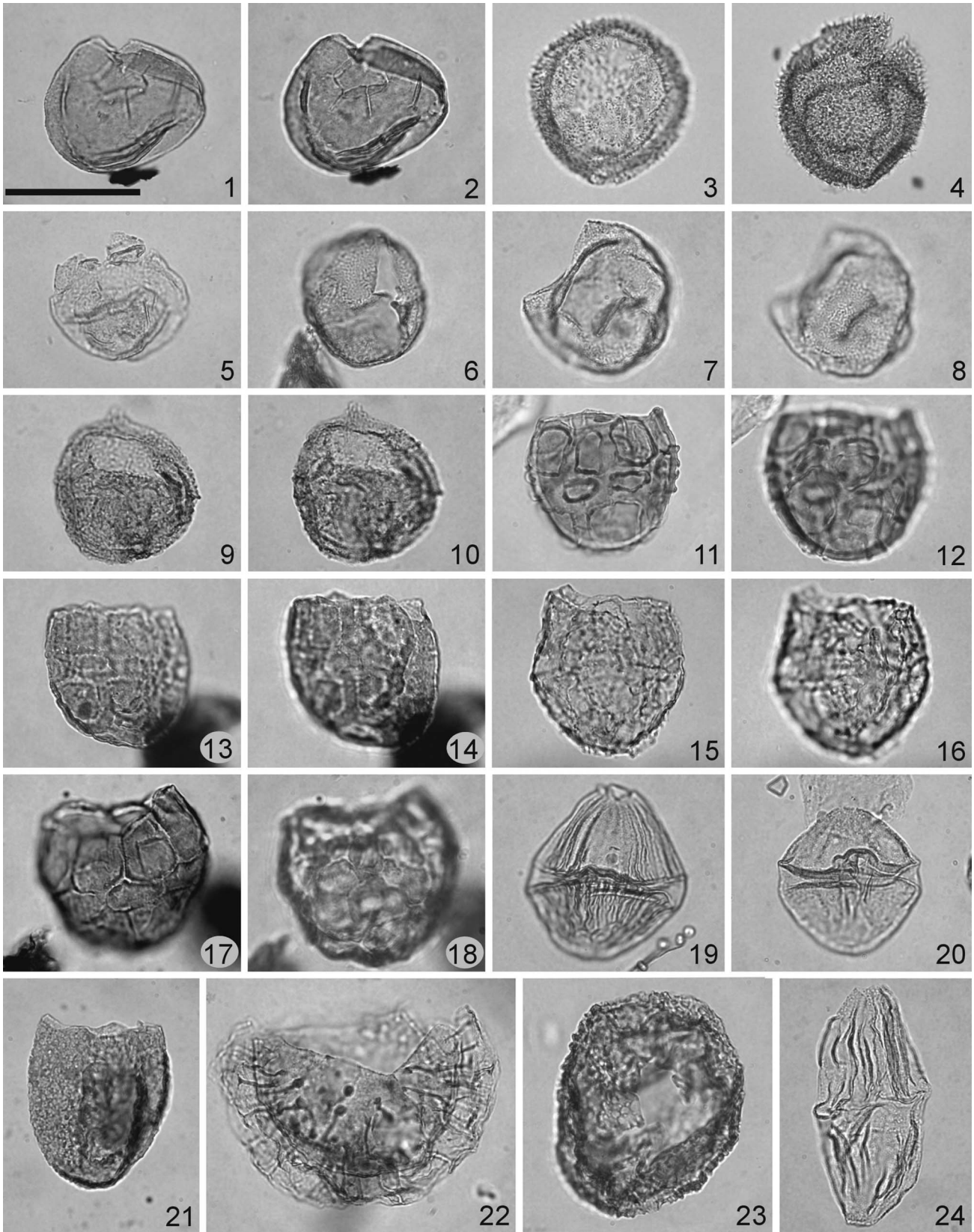
The Ouled Haddou section is located 48 km north of Taza, in the eastern external Rif of northern Morocco, in the southwestern Mediterranean region (Figure 1). The section is exposed along the road from Aknoul to Mezguitem, on the northern flank of Jbel bou Izerzene, which was considered as a part of the Bouhaddoud thrust-sheet (Leblanc 1979). Maastrichtian and Paleocene deposits are visible in the Msoun River, and occur in sub-vertical beds with an east–west strike. The Maastrichtian deposits consist of marls with marly limestone intercalations. The Maastrichtian–Danian boundary beds consist of clayey marls (0.5 m), and are

overlain by stiff marls (up to 2 m), followed by marls with limestone intercalations, both of Danian age (Figure 2).

2.2. Materials and methods

In order to obtain a correlation between the stratigraphic occurrences of dinoflagellate cysts and the planktonic foraminiferal record, this study is based on the same sampled levels as those studied by Toufiq et al. (2002). Nineteen samples were processed following standard palynological preparation techniques. Processing involved an initial treatment of 50 g of sediment per sample with cold HCl (20%), followed by a digestion in HF (40% at 70°C), to dissolve carbonates and silicates, respectively. Samples were rinsed with distilled water until neutral between the acid treatments. Silicofluorides were removed by repeated hot baths (60°C) with 20% HCl. Heavy liquid separation was performed with ZnCl₂, without oxidizing the residue. The residues were sieved on a nylon screen with a mesh of 20 µm, stained with methyl green and mounted in glycerine jelly on microscope slides. Two slides per sample were scanned and 400 specimens of organic-walled palynomorphs, mostly dinoflagellate cysts, were systematically counted at x 400 magnification. The rest of the slides were then scanned for rare species and exceptionally well-preserved specimens. Pollen, spores, and foraminiferal test linings are present but rare, and were not counted. Photomicrographs (Plates 1–10) were taken with a digital Olympus C-400 Zoom camera mounted on an Olympus BX51 microscope. All slides and

Plate 1. Scale bar in figure 1 represents 40 µm for all specimens. The photomicrographs were all taken using plain transmitted light. Figures 1, 2. *Kallosphaeridium yorubaense* Jan du Chêne & Adediran 1985. Sample OH 18, slide 1, EF Q45/1. Specimen in antapical view, apical surface; slightly differing levels of focus showing the apical archeopyle and adnate operculum *in situ*. Figures 3, 4. *Pilosidinium capillatum* (Davey 1975) Courtinat in Fauconnier & Masure 2004. 3 – sample OH 5, slide 1, EF M43. Specimen in antapical view, low focus on the apical archeopyle and processes. 4 – sample OH 0, slide 1, EF U42/1; note the displaced operculum and processes. Figure 5. *Kallosphaeridium parvum* Jan du Chêne 1988. Sample OH 11, slide 1, EF R33. Note the apical archeopyle and adnate operculum. Figures 6–8. *Pyxidinospis ardonensis* Jan du Chêne 1988. 6 – sample OH 15, slide 1, EF W45. Specimen in ventral view, low focus on the archeopyle and wall structure. 7, 8 – sample OH 12, slide 1, EF U31. 7 – focus on the archeopyle, 8 – focus on the wall structure. Figures 9, 10. *Apteodinium fallax* (Morgenroth 1968) Stover & Evitt 1978. Sample OH 9, slide 1, EF H31. Specimen in dorsal view, 9 – high focus on the archeopyle and wall structure, 10 – low focus on the sulcal area. Figures 11, 12. *Eisenackia circumtabulata* Drugg 1967. Sample OH 18, slide 1, EF X50. Specimen in dorsal view, 11 – high focus, 12 – low focus. Figures 13, 14. *Eisenackia crassitabulata* Deflandre & Cookson 1955. Sample OH 9, slide 2, EF K50. Specimen in right lateral view, 13 – low focus, 14 – high focus. Figures 15, 16. *Eisenackia reticulata* (Damassa 1979) Quattrocchio & Sarjeant 2003. Sample OH 12, slide 1, EF H45/4. Specimen in right ventrolateral view, 15 – low focus, 16 – high focus. Figures 17, 18. *Eisenackia msoumensis* Slimani et al. 2008. Sample OH 12, slide 1, EF V39/1. Specimen in dorsal view, 17 – high focus, 18 – low focus. Figure 19. *Dinogymnium cretaceum* (Deflandre 1936) Evitt et al. 1967. Sample OH 3, slide 2, EF K39/1. Specimen in dorsal view, high focus. Figure 20. *Alisogymnium euclaense* (Cookson & Eisenack 1970) Lentin & Vozzhennikova 1990. Sample OH 2, slide 1, EF Q47. Specimen in ventral view, high focus. Figure 21. *Batiacasphaera rifensis* Slimani et al. 2008. Sample OH 14, slide 1, EF O34/4. Specimen in ventral view, high focus on the archeopyle and wall structure. Figure 22. *Membranilarnacia? tenella* Morgenroth 1968. Sample OH 18, slide 1, EF L33/4. High focus. Note the apical archeopyle, processes and ectophragm. Figure 23. *Cassiculosphaeridia? intermedia* Slimani 1994. Sample OH 17, slide 1, EF Y31/2. Specimen in apical view, high focus on the apical archeopyle. Figure 24. *Dinogymnium nelsonense* (Cookson 1956) Evitt et al. 1967. Sample OH 14, slide 1, EF K54/1.



figured specimens are housed in the botanical collection of the National Herbarium (RAB), Scientific Institute, Mohammed V-Agdal University, Rabat, Morocco. England Finder (EF) specimen coordinates are given in the plate captions.

3. Stratigraphic framework

The Paleogene of the eastern external Rif is exposed in several thrust-sheets and rests on marly deposits of Campanian to Maastrichtian age. The lithostratigraphic and planktonic foraminiferal subdivisions of the pelagic deposits of the Ouled Haddou section by Toufiq et al. (2002) were based on 13 m of uppermost Maastrichtian and Danian sediments (Figure 2). The lowermost interval consists of marls assigned to the *Abathomphalus mayaroensis* Zone (uppermost Maastrichtian). These are overlain by clayey marls of the *Guembeltria cretacea* Zone, followed by stiff marls of the *Parvularugoglobigerina eugubina* Zone and marls with limestone intercalations of the *Parasubbotina pseudobulloides* and *Subbotina triloculinoides* zones (lower Danian). Although this section represents a complete K–Pg transition according to the planktonic foraminiferal analysis, the thin layer with the iridium anomaly has not been detected (Toufiq et al. 2002).

4. Dinoflagellate cyst biostratigraphy

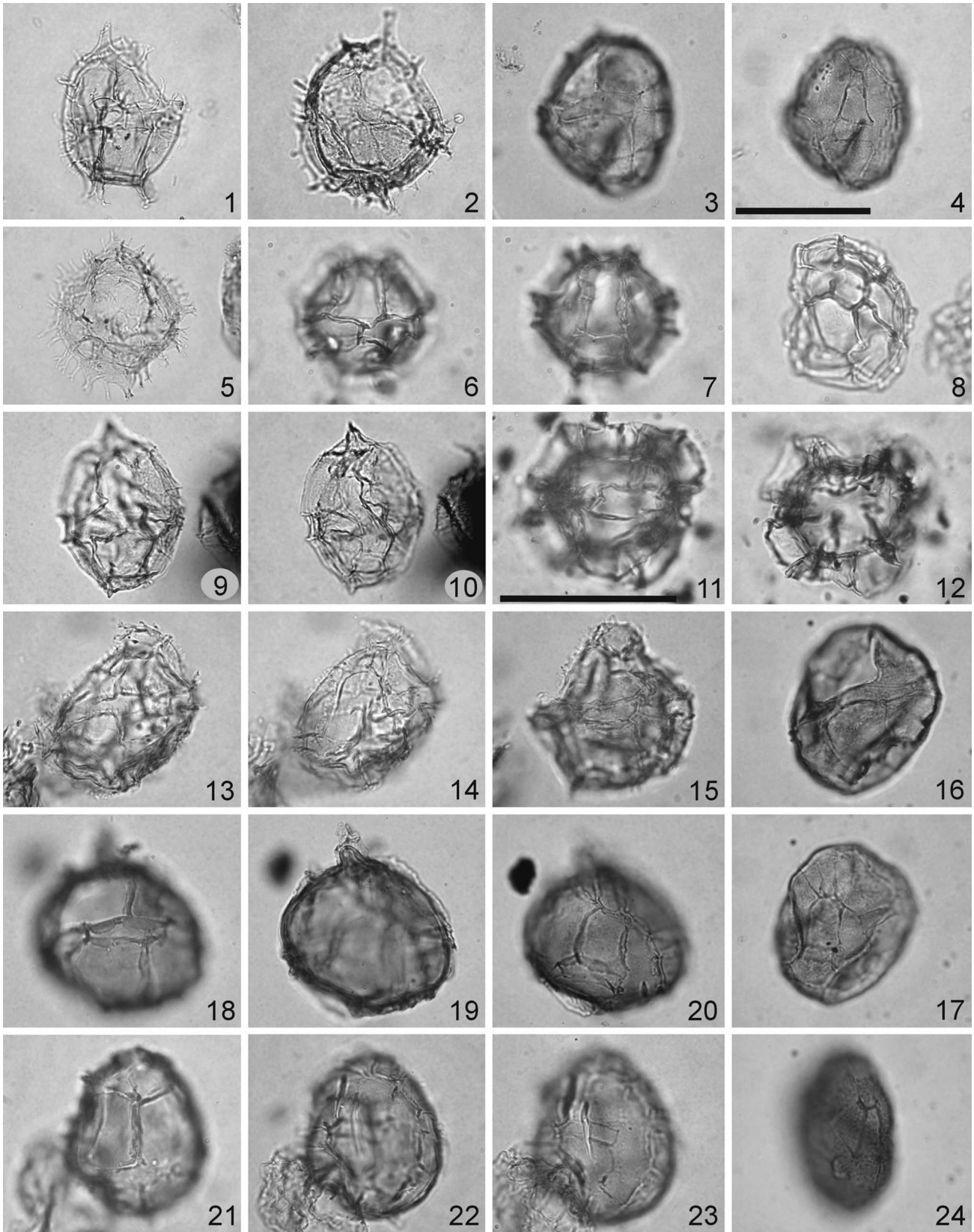
The palynomorph assemblages from the K–Pg section at Ouled Haddou consist of dinoflagellate cysts,

spores, pollen, foraminiferal linings, acritarchs, and chlorophyte algae (*Palambages* spp.). However, more than 90% of the palynomorphs are dinoflagellate cysts. All taxa identified during this study are listed in the supplementary table online, where their stratigraphic distribution is shown. The nomenclature of the dinoflagellate cysts follows Dinoflaj 2 (Fensome et al. 2008), Guerstein et al. (2005), Slimani et al. (2008) and Willumsen (2004). The dinoflagellate cyst assemblages are diverse and well preserved.

A total of 290 species and subspecies of dinoflagellate cysts, 1 acritarch species and 2 *Palambages* species have been recognized. Among these, 49 taxa are restricted to the Danian and most of the taxa (80%) recorded in the Maastrichtian occur after the K–Pg boundary, and persist into the Danian. These findings again indicate that no severe extinction occurred among the dinoflagellates and acritarchs, in contrast to the mass extinction recorded in the calcareous planktonic foraminifera assemblages (Toufiq et al. 2002).

Many globally recorded dinoflagellate cysts with a well-known first and/or last occurrence are present, and allowed a high-resolution biostratigraphic analysis of the Ouled Haddou section. Furthermore, the gradual change of the assemblages through time suggests stratigraphic completeness of the K–Pg section. Age determinations are based on comparison with dinoflagellate cyst assemblages described in many Maastrichtian to Danian biostratigraphically calibrated sections in the Northern Hemisphere middle latitudes and elsewhere. These include the Mediterranean sections from Tunisia such

Plate 2. Scale bars represent 40 μm ; scale bar in figure 11 applies to specimens 11 and 12; scale bar in figure 4 applies to all the other specimens. The photomicrographs were all taken using plain transmitted light. Figure 1. *Spiniferella cornuta* subsp. *laevimura* (Davey & Williams 1966) Williams et al. 1998. Sample OH 18, slide 2, EF D32/1. Specimen in left lateral view, high focus. Note the apical horn and laevigate wall. Figure 2. *Spiniferella* sp. cf. *Spiniferites* sp. A of Kirsch 1991. Sample OH 12, slide 2, EF E46. Specimen in dorsal view, high focus. Note the apical horn and microgranulate wall. Figures 3, 4. *Impagidinium* sp. cf. *I. patulum* (Wall 1967) Stover & Evitt 1978. Sample OH 12, slide 2, EF G49. Specimen in left ventrolateral view, 3 – low focus on the precingular archeopyle, 4 – high focus. Figure 5. *Spiniferites twistringiensis* (Maier 1959) Fensome et al. 1990. Sample OH 0, slide 1, EF T48/3. Specimen in dorsal view, high focus. Figures 6–8. *Impagidinium* sp. 1 of Thomsen & Heilmann-Clausen 1985. 6–7 – sample OH 5, slide 2, EF P32/4. Specimen in dorsal view, 6 – high focus showing the precingular archeopyle, 7 – low focus on the sulcal area, 8 – sample OH 5, slide 1, EF W30/3. Specimen in right latero-apical view, high focus showing the discontinuous septa separating the apical plates. Figures 9, 10. *Pterodinium cingulatum* subsp. *danicum* Jan du Chêne 1988. Sample OH 12, slide 1, EF J34/1. Specimen in ventral view, 9 – low focus, note the precingular archeopyle, 10 – high focus on the sulcus and the apical protrusion. Figures 11, 12. *Pterodinium cretaceum* Slimani et al. 2008. Sample OH 2, slide 2, EF R45/3. Specimen in ventral view, 11 – low focus on the archeopyle, 12 – high focus on the ventral surface. Figures 13–15. *Impagidinium celineae* Jan du Chêne 1988. 13, 14 – sample OH 16, slide 1, EF Y46. Specimen in right lateral view, 13 – low focus, 14 – high focus showing the denticulate sutural crests, 15 – sample OH 19, slide 1, EF F34/1. Specimen in right lateral view, low focus. Figures 16, 17. *Ynezidinium tazaensis* Slimani et al. 2008. Sample OH 12, slide 1, EF V39/1. Specimen in ventral view, 16 – low focus on the wall structure and archeopyle, 17 – ventral face showing the apical (1', 4') and the precingular (1'', 5'', 6'') plate arrangement. Figures 18–20. *Ynezidinium malloyi* Lucas-Clark & Helenes 2000. Sample OH 15, slide 2, EF W42. Specimen in ventral view, 18 – low focus on the precingular archeopyle, 19 – optical section showing the apical protrusion, 20 – high focus showing the apical (1', 4') and the precingular (1'', 5'', 6'') plate arrangement. Figure 21–23. *Ynezidinium pentahedrias* (Damassa 1979) Lucas-Clark & Helenes 2000. Sample OH 15, slide 1, EF U34. Specimen in ventral view, 21 – low focus on the precingular archeopyle and operculum *in situ*, 22 – high focus on the apical (1', 4') plates which contact the two anterior sides of the pentagonal precingular (6'') plate, 23 – high focus on the sulcal area. Figure 24. *Impagidinium maghribensis* Slimani et al. 2008. Sample OH 12, slide 2, EF U40/1. Specimen in right ventral view, right ventral surface.



as El Kef (Brinkhuis and Leereveld 1988; Brinkhuis and Zachariasse 1988; Brinkhuis et al. 1998) and Ain Settara (Dupuis et al. 2001), from Caravaca, Spain (De Coninck and Smit 1982; Brinkhuis et al. 1998), Morocco (Doubinger 1979; Rauscher and Doubinger 1982; Rauscher 1985; Soncini and Rauscher 1988; Soncini 1990) and from the Middle East (Eshet et al. 1992). They also include northern European sections from Denmark (Stevns Klint) and Sweden (Limhamn) (Hansen 1977, 1979a, 1979b; Kjellström and Hansen 1981; Hultberg 1985, 1986; Hultberg and Malmgren 1986, 1987; Brinkhuis et al. 1998), The Netherlands (Geulhemmerberg) (Brinkhuis and Schiøler 1996), the Maastricht area (Schumacker-Lambry 1977), Belgium (Turnhout) (Slimani 1995, 2000, 2001) and Germany (Kuhn and Kirsch 1992). Other relevant K–Pg sections are from California (Drugg 1967), Maryland (Benson 1976), New Jersey (Olsson et al. 1997; Habib and Saeedi 2007), Georgia (Firth 1987) and Alabama (Moshkovitz and Habib 1993; Habib et al. 1996) in the USA, and from Mexico (Helenes 1984; Helenes and Téllez-Duarte 2002) and India (Jain et al. 1975).

K–Pg dinoflagellate cyst assemblages from low latitudes of the Northern Hemisphere are also used for comparison. They include assemblages from Colombia and Venezuela (Yepes 2001), Côte d'Ivoire-Ghana Transform Margin (Masure et al. 1998; Oboh-Ikuenobe et al. 1998) and Nigeria (Willumsen et al. 2004b). From the Southern Hemisphere we included: Australia (Helby et al. 1987; Brinkhuis et al. 2003; Williams et al. 2004), New Zealand (Wilson 1987; Willumsen 2000, 2002, 2004, 2006; Willumsen et al. 2004a), Brasilia (Sarkis et al. 2002), and the Antarctic Peninsula (Askin 1988).

Other dinoflagellate cyst studies not specifically on the K–Pg boundary were also used: Argentina (Quattrochio and Sarjeant 2003), Belgium and the Netherlands (Wilson 1974; Schiøler et al. 1997),

Denmark (Schiøler and Wilson 1993), Germany (Morgenroth 1968; Kirsch 1991; Marheinecke 1992), Italy (Corradini 1973; Roncaglia and Corradini 1997a, 1997b), Nigeria (Oloto 1989), Senegal (Jan du Chêne 1988), and USA (Drugg 1970; Koch and Olsson 1977; Damassa 1979; Srivastava 1995).

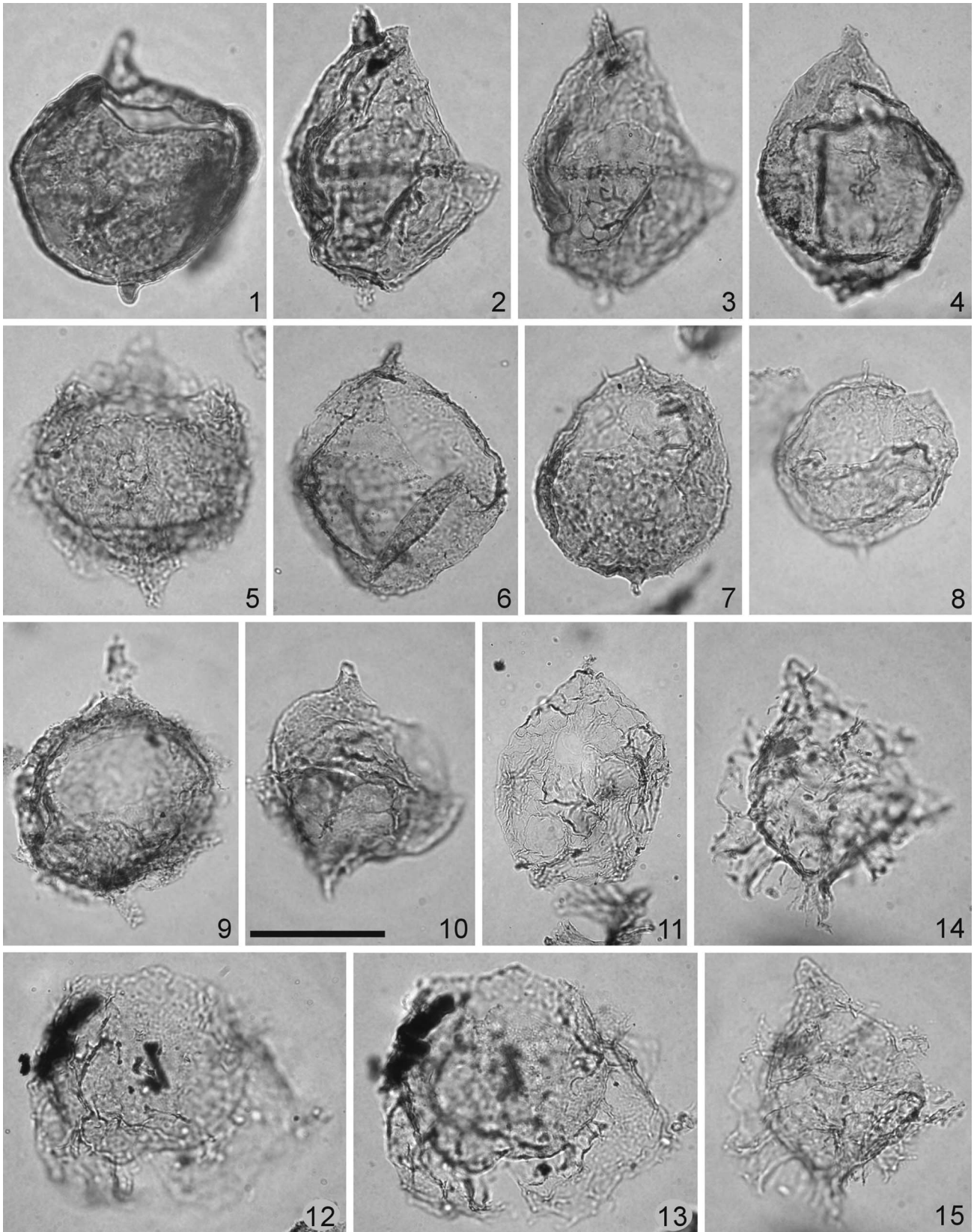
The most important biostratigraphic dinoflagellate cyst events used in this study are described below in ascending stratigraphic order. Table S1 (see supplementary material online http://www.informaworld.com/mpp/uploads/tpal_463502_table_1.xls) gives an overview of the recorded palynomorphs and Table 1 gives the distribution of the stratigraphically important taxa. Table 2 gives the stratigraphic ranges used here for selected taxa, based on most of references cited above and on Powell (1992) and Williams et al. (1993).

4.1. Latest Maastrichtian

Six samples (OH 0 to OH 5) contain species whose stratigraphic ranges include the upper Maastrichtian (Table 2), such as *Apteodinium fallax*, *Damassadinium fibrosum?*, *Disphaerogena carposphaeropsis*, *Fibrocysta bipolaris*, *Fibrocysta licia*, *Glaphyrocysta perforata*, *Manumiella seelandica*, *Operculodinium israelianum*, *Renidinium gracile*, *Riculacysta amplexa*, *Senegalinium? dilwynense* and co-occur with *Dinogymnium* spp. and *Alisogymnium euclaense*.

The first occurrences (FO) of *Disphaerogena carposphaeropsis*, *Glaphyrocysta perforata*, and *Manumiella seelandica* were usually used to identify upper Maastrichtian strata in many areas. However, it is important to show that these species have been named differently, particularly in Mediterranean areas, with which correlations could be easier here. *Disphaerogena carposphaeropsis* has been identified as *Cyclapophysis monmouthensis* (Brinkhuis and Leereveld 1988; Brinkhuis and Zachariasse 1988; Soncini and Rauscher

Plate 3. Scale bar in figure 10 represents 40 μm for all specimens. The photomicrographs were all taken using plain transmitted light. Figure 1. *Carpatella cornuta* Grigorovich 1969. Sample OH 16, slide 1, EF L53/4. Specimen in dorsal view, high focus on the wall structure, precingular archeopyle and apical and antapical horns. Figures 2, 3. *Carpatella septata* Willumsen 2004. Sample OH 1, sample 1, EF E27/1. Specimen in left lateral view, 2 – focus on the apical and antapical horns, 3 – high focus on the reticulum and septa. Figure 4. *Carpatella?* sp. cf. *Cribroperidinium* sp. A of Brinkhuis & Schiøler 1996. Sample OH 1, slide 1, EF O55/4. Specimen in left dorsolateral view, low focus on the archeopyle and wall structure. Figure 5. *Kenleyia lophophora* Cookson & Eisenack 1965. Sample OH 14, slide 1, EF G47. Specimen in dorsal view, high focus on the wall structure, archeopyle, cingulum and antapical horn. Figure 6. *Cribroperidinium cooksoniae* Norvick 1976. Sample OH 19, slide 2, EF V33/3. Specimen in left dorsolateral view, high focus. Figures 7, 8. *Kenleyia?* sp. A. 7 – sample OH 14, slide 1, EF F35/1. Specimen in dorsal view, high focus on the precingular archeopyle, reticulate wall and apical and antapical horns. 8 – sample OH 14, slide 1, EF X38/4. Specimen in left dorsolateral view, high focus showing the precingular archeopyle with a displaced operculum. Figure 9. *Kenleyia leptocerata* Cookson & Eisenack 1965. Sample OH 17, slide 1, EF E46. Specimen in dorsal view, high focus showing the precingular archeopyle, and apical and antapical horns. Figure 10. *Kenleyia pachycerata* Cookson & Eisenack 1965. Sample OH 12, slide 1, EF U49/1. Specimen in left lateral view, high focus. Figure 11. *Phelodinium elongatum* sp.nov. Sample OH 2, slide 1, EF O44/2. Figures 12, 13. *Riculacysta* sp. of Soncini & Rauscher 1988. Sample OH 17, slide 2, EF F58/2. Specimen in dorsal view, 12 – high focus showing the wall structure and acuminate processes on the ectophragm, 13 – low focus on the apical archeopyle. Figures 14, 15. *Lanternosphaeridium reinhardtii?* Habib in Moshkovitz & Habib 1993. OH 12, slide 1, EF E48. Specimen in left lateral view, 14 – high focus, 15 – low focus.



1988; Soncini 1990; Eshet et al. 1992; Dupuis et al. 2001) or *Cyclapophysis lemniscata* (De Coninck and Smit 1982). *Glaphyrocysta perforata* has been considered as *Senoniasphaera inornata* (Rauscher 1985, plate 1, fig. 7; Eshet et al. 1992) and *M. seelandica* as *Manumiella druggii* (Soncini and Rauscher 1988), *Isabelidinium cretaceum* (Doubinger 1979), *Isabelidinium tingitanense* (Rauscher and Doubinger 1982; Rauscher 1985) or *M. druggii* (Brinkhuis and Zachariasse 1988; Brinkhuis and Leereveld 1988). *Manumiella seelandica* has also been recorded recently in the uppermost Maastrichtian and Danian at Ellès (Tunisia) (H. Slimani, personal observation).

In the Ouled Haddou section, *G. perforata* and *M. seelandica* first occur in the lowest sample OH 0, while *D. carposphaeropsis* has a higher FO in sample OH 1. The global acme of *M. seelandica* immediately below the Maastrichtian–Danian boundary has been observed in many locations (Oboh-Ikuenobe et al. 1998; Yebes 2001; Habib and Saeedi 2007). In the Mediterranean region, the highest abundance of this species was recorded in the uppermost Maastrichtian deposits of the El Kef sections (Habib and Saeedi 2007; p. 88) and the Moroccan Phosphate Plateau (Rauscher and Doubinger 1982; Rauscher 1985; Soncini 1990). Rauscher and Doubinger (1982) considered this acme as an excellent reference for correlations of uppermost Maastrichtian deposits and observed a great morphological variation in the cysts of *M. seelandica* (see also Soncini 1990 and Habib and Saeedi 2007). At Ouled Haddou, *M. seelandica* has a highest abundance in samples OH 0 (30.5%), OH 3 (92%) and OH 5 (57.5%) just below the K–Pg boundary, and also shows large morphological variation. In contrast, the frequency of this species does not exceed 2% above the K–Pg boundary (samples OH 6 to OH 19).

The co-occurrences of *D. carposphaeropsis*, *G. perforata*, and *M. seelandica* (samples OH 0 to OH 5) with species of *Dinogymnium* spp., with regular

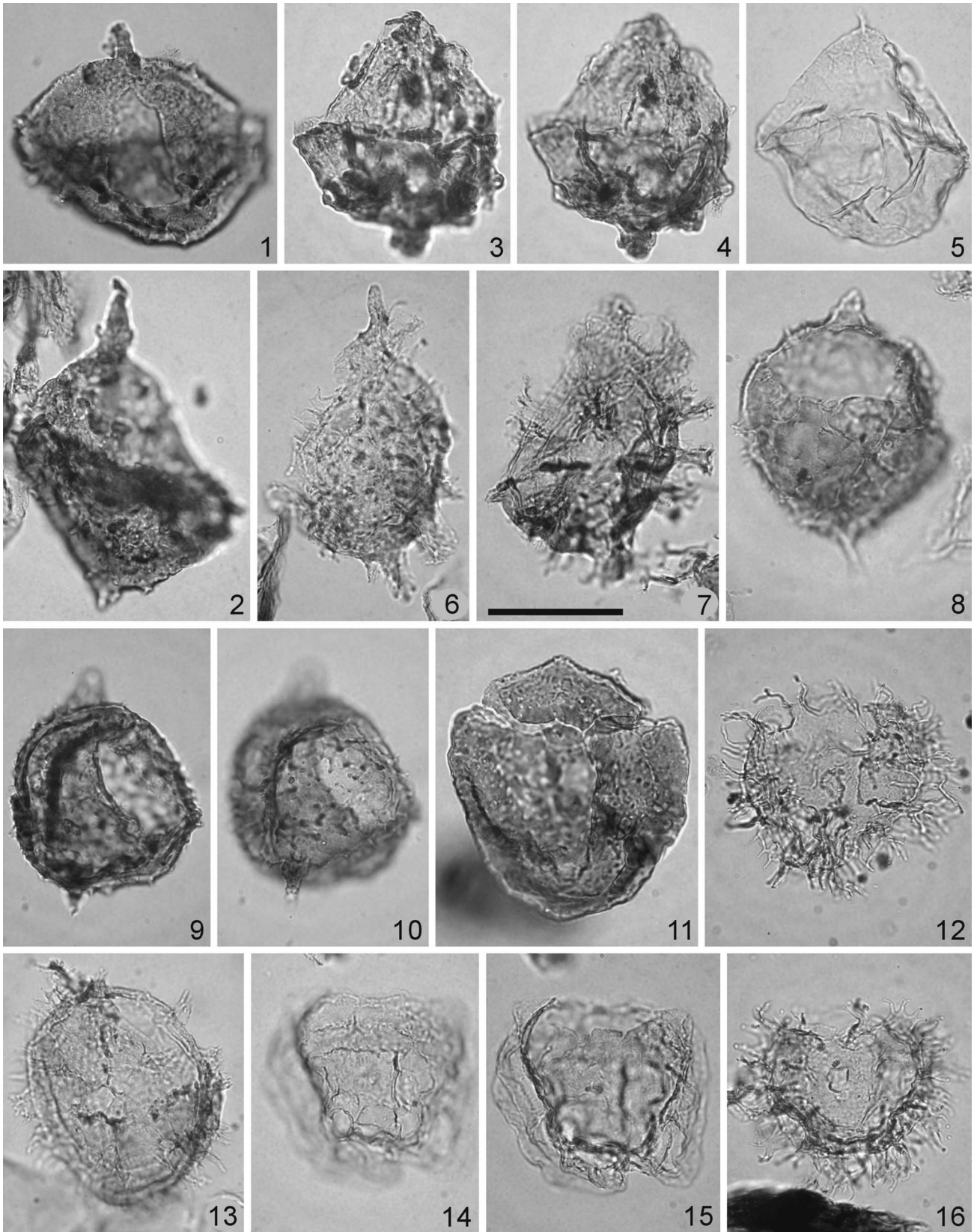
presence and common abundance, suggest a latest Maastrichtian age for this interval, and based on the very high abundance of *M. seelandica*, a terminal Maastrichtian age for the interval from OH3 to OH 5.

The lowest occurrences of the other stratigraphically significant species have been documented in the uppermost Maastrichtian of northwestern Europe, eastern USA and the Mediterranean region: e.g. *D. fibrosum*, *A. fallax*, *F. licia*, *O. israelianum*, *R. gracile*, *R. amplexa*, and *S? dilwynense*. *F. bipolaris*, known as a Paleogene species, has been recorded also in upper Maastrichtian strata by Moskhovitz and Habib (1993) and Soncini (1990). In the Ouled Haddou section, *F. bipolaris* and *S? dilwynense* first occur in sample OH 1, and *O. israelianum* and *A. fallax* first occur, respectively, in samples OH 2 and OH 5, while the four other species occur from sample OH 0 upwards. This also points to a range not older than latest Maastrichtian for samples OH 0 to OH 5.

This interval contains some species which have been described from Maastrichtian strata, such as: *Carpatella septata* (Willumsen 2000, 2002 as *Carpatella* sp. 1; Willumsen 2004), *Homotryblium* sp. (Brinkhuis and Zachariasse 1988), *Lejeunecysta izerzenensis* (Slimani et al. 2008) and *Riculacysta* sp. of Soncini and Rauscher (1988). Apart from *L. izerzenensis*, which first occurs here in sample OH 2, the other species first occur in sample OH 0. *Riculacysta* sp., renamed later as “forme *Cyclonephelium expansum*” by Soncini (1990) occurs lower (uppermost Maastrichtian) in this section than in the Moroccan Phosphate Plateau (at the K–Pg boundary?).

The first occurrences of *Cerodinium speciosum* subsp. *speciosum*, *Deflandrea galeta*, *Fibrocysta ovalis*, *Hystriochokolpoma bulbosum* subsp. *bulbosum*, *Hystriochostrogylon coninckii*, *Hafniasphaera septata* and *Turbiosphaera filosa* have been recorded in the upper Maastrichtian in many areas in the Northern Hemisphere, and have been calibrated against the belemnite

Plate 4. Scale bar in figure 7 represents 40 μm for all specimens. The photomicrographs were all taken using plain transmitted light. Figures 1, 2. *Fibrocysta* sp. A of Brinkhuis & Schiöler 1996. 1 – sample OH 17, slide 1, EF E43/3. Specimen in dorsal view, high focus on the precingular archeopyle. 2 – sample OH 14, slide 2, EF G36/3. Specimen in left lateral view, high focus on the precingular archeopyle, wall structure and processes. Figures 3, 4. *Damassadinium fibrosum?* (Hultberg 1985) Fensome et al. 1993. Sample OH 5, slide 1, EF X43/3. Specimen in right lateral view, 3 – low focus, 4 – high focus. Figure 5. *Cribopteridinium? pyrum* (Drugg 1967) Stover & Evitt 1978. Sample OH 12, slide 1, EF C39/4. Specimen in dorsal view, high focus on the cingulum. Figure 6. *Fibrocysta bipolaris* (Cookson & Eisenack 1965) Stover & Evitt 1978. Sample OH 14, slide 1, EF U57/4. Specimen in right lateral view, low focus. Figure 7. *Damassadinium californicum* (Drugg 1967) Fensome et al. 1993. Sample OH 9, slide 1, EF G60/1. Specimen in right lateral view, high focus. Figures 8–10. *Fibrocysta licia* (Jain et al. 1975) Stover & Evitt 1978. 8 – sample OH 12, slide 1, EF S54/2. Specimen in dorsal view, high focus on the precingular archeopyle. 9, 10 – sample OH 2, slide 1, EF X30/4. Specimen in left dorsolateral view, 9 – low focus, 10 – high focus. Figure 11. *Cassidium fragile* (Harris 1965) Drugg 1967. Sample OH 12, slide 1, EF E33/4. Focus on the wall structure, archeopyle and operculum. Figure 12. *Areoligera senonensis* Lejeune-Carpentier 1938. Sample OH 10, slide 2, EF W38. Specimen in dorsal view, high focus. Figure 13. *Damassadinium spinosum* Slimani et al. 2008. Sample OH 12, slide 1, EF T42/3. Specimen in left dorsal lateral view, high focus on processes. Figures 14, 15. *Renidinium gracile* Hultberg & Malmgren 1985. Sample OH 14, slide 1, EF R37. Specimen in dorsal view, 14 – high focus, 15 – low focus. Figure 16. *Glaphyrocysta ordinata* (Williams & Downie 1966) Stover & Evitt 1978. Sample OH 17, slide 1, EF H30. Focus on processes.



Belemnitella junior Zone (Wilson 1974; Schumacker-Lambry 1977; Herengreen et al. 1986; Marheinecke 1992; Schiøler and Wilson 1993; Slimani 1995, 2000, 2001; Schiøler et al. 1997) and planktonic foraminifer *Globotruncana gansseri* Zone (Aurisano 1989; Kirsch 1991). The presence of these species in samples OH 0 to OH 5 of this section indicates an age not older than late Maastrichtian.

Other species with a well-documented FO in the late Maastrichtian in the Northern Hemisphere occur for the first time in this interval (in ascending order): *Glaphyrocysta semitecta* (sample OH 0), *Lejeunecysta hyalina* (sample OH 1), and *Glaphyrocysta ordinata* (sample OH 3). These taxa appear in uppermost Maastrichtian deposits in the Mediterranean region as *G. ordinata* (Soncini 1990) and *Glaphyrocysta semitecta* and *L. hyalina* (Brinkhuis and Leereveld 1988; Brinkhuis and Zacharisse 1988).

The last occurrences of *Dinogymnium* spp. and *Alisogymnium euclaense* in the uppermost Maastrichtian deposits are usually considered important for identifying the K–Pg boundary, mainly in the Northern Hemisphere middle latitudes (Williams et al. 2004). However, their irregular and sporadic occurrences together with other upper Cretaceous taxa (latest occurrences in the Campanian) such as: *Palaeohystrichopora infusorioides*, *Surculosphaeridium? longifurcatum*, and *Odontochitina* spp. within the lowermost Danian in the studied section can be explained by reworking. Although, they could also represent the final demise of taxa during earliest Tertiary times (cf. Habib 1994; Brinkhuis and Schiøler 1996). The last occurrence of *Pterodinium cretaceum* (Slimani et al. 2008) is not younger than latest Maastrichtian in our section (sample OH 5) and also elsewhere (Schiøler and Wilson 1993; Slimani 1995, 2000, 2001; Roncaglia and Corradini 1997a, 1997b; Torricelli and Amore 2003 as *Pterodinium* sp. B).

The uppermost Maastrichtian age of the six samples OH 0 to OH 5 from the Ouled

Haddou section is in agreement with the planktonic foraminiferal data (the latest Maastrichtian *Abathomphalus mayaroensis* Zone) of Toufiq et al. (2002).

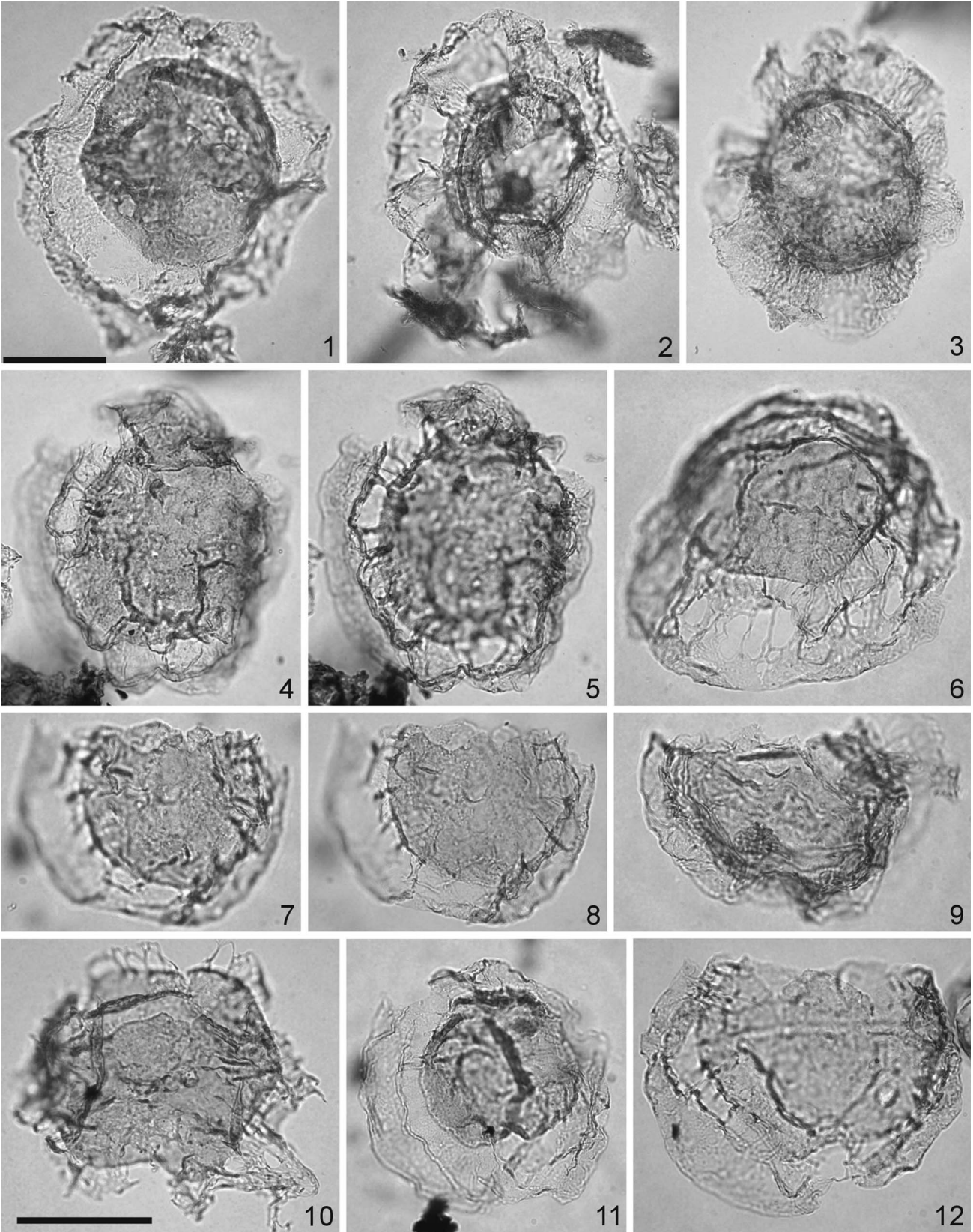
4.2. Latest Maastrichtian event disconformities

The following dinoflagellate cysts have been reported to occur in the lowest Paleocene, but are recorded here within the uppermost Maastrichtian of the Ouled Haddou section: *Cordosphaeridium inodes* subsp. *longipes*, *Cribroperidinium* sp. A, *Fibrocysta* sp. A of Brinkhuis and Schiøler (1996), *Kallosphaeridium yorubaense*, *Kenleyia leptocerata*, *Kenleyia pachycerata*, *Lingulodinium bergmannii* and *Pyxidiniopsis ardonensis*.

Fibrocysta sp. A of Brinkhuis and Schiøler (1996) occurs regularly from sample OH 0 upwards in the studied section. The other Paleocene taxa cited above have sporadic and irregular occurrences below the K–Pg boundary: OH 1 (*C. inodes* subsp. *longipes*, *Cribroperidinium* sp. A, *K. pachycerata*, *L. bergmannii*), OH 4 (*P. ardonensis*) and OH 5 (*K. yorubaensis*, *K. leptocerata*).

Some uppermost Maastrichtian to Paleocene taxa occur for the first time within the earliest Danian at Ouled Haddou. Their FO is reported from uppermost Maastrichtian deposits in the Northern Hemisphere middle latitudes: *Cribroperidinium? pyrum* and *Thalassiphora patula*. *Palynodinium grallator* and *Thalassiphora pelagica* were widely used as index species for the uppermost Maastrichtian in higher northern latitudes, where the *Palynodinium grallator* Zone and the *Thalassiphora pelagica* Subzone are commonly used (Hansen 1977, 1979a; Schiøler and Wilson 1993; Habib et al. 1996; Schiøler et al. 1997). *Thalassiphora pelagica* and *T. patula* have also been recorded in the uppermost Maastrichtian of the equatorial realm. In the Mediterranean realm, *T. pelagica* also appears for the first time in the

Plate 5. Scale bars represent 40 μm ; scale bar in figure 1 applies to specimens 1 and 2; scale bar in figure 10 applies to all the other specimens. The photomicrographs were all taken using plain transmitted light. Figure 1. *Thalassiphora pelagica* (Eisenack 1954) Eisenack & Gocht 1960. Sample OH 14, slide 1, EF Z56/1. Specimen in ventral view, low focus on the precingular archeopyle. Figure 2. *Thalassiphora patula* (Williams & Downie 1966) Stover & Evitt 1978. Sample OH 18 slide 1, EF V35/2. Specimen in ventral view, low focus on the precingular archeopyle. Figure 3. *Turbiosphaera galatea* Eaton 1976. Sample OH 0, slide 1, EF D52. Specimen in ventral view, low focus on the precingular archeopyle. Figures 4, 5. *Glaphyrocysta castelcasiensis* (Corradini 1973) Michoux & Soncini in Fauconnier & Masure 2004. Sample OH 4, slide 1, EF O39. Specimen in dorsal view, 4 – dorsal surface, 5 – median focus showing the ectophragm, displaced operculum and processes. Figure 6. *Glaphyrocysta semitecta* (Bujak in Bujak et al. 1980) Lentin & Williams 1981. OH 0, slide 1, EF Q36/3. Specimen in ventral view, dorsal surface. Figures 7, 8. *Riculacysta amplexa* Kirsch 1991. Sample OH 5, slide 1, EF 54/4. Specimen in dorsal view, 7 – high focus, 8 – low focus showing the apical archeopyle and short processes connecting ventrally the central body with the ectophragm. Figure 9. *Senoniasphaera inornata* (Drugg 1970) Stover & Evitt 1978. Sample OH 7, slide 1, EF O45. Specimen in dorsal view, high focus. Figure 10. *Riculacysta* sp. cf. *Riculacysta* sp. A of Kirsch 1991. Sample OH 0, slide 1, EF S36/2. Specimen in ventral view, high-median focus. Note the perforate ectophragm bearing short processes. Figure 11. *Glaphyrocysta expansa* (Corradini 1973) Roncaglia & Corradini 1997. Sample OH 4, slide 2, EF X52/2. Note the apical archeopyle and operculum *in situ*. Figure 12. *Glaphyrocysta perforata* Hultberg and Malmgren 1985. OH 0, slide 1, EF U41/3. Specimen in dorsal view, ventral surface.



uppermost Maastrichtian of the Moroccan Phosphate Plateau, in Italy and in Turkey.

Palynodinium grallator has a last occurrence at the top of the Maastrichtian in northern higher latitudes, but only occurs for the first time close to the K–Pg boundary at El Kef (Brinkhuis et al. 1998). This younger FO is interpreted by Brinkhuis et al. (1998) as the result of a southward migration caused by a cooling event in the earliest Danian. However, the lowest occurrence of this species has also been recorded in the late Campanian in France (Masure 1985), and Belgium (Slimani 2001) and in the latest Maastrichtian in Caravaca (Brinkhuis et al. 1998), the Moroccan Phosphate Plateau (Rauscher and Doubinger 1982) and Nigeria (Oloto 1989).

Thalassiphora bononiensis and *Muratodinium fimbriatum* are two other taxa with lowest occurrences within uppermost Maastrichtian strata, but they first occur also above the K–Pg boundary in the Ouled Haddou section. The FOs of the taxa cited above have been calibrated previously against the upper part of the Upper Maastrichtian planktonic foraminifera zones *Abathomphalus mayaroensis* (De Coninck and Smit 1982; Brinkhuis and Zachariasse 1988; Olsson et al. 1997), the belemnite zone *Belemnella casimirovensis* (Schjølter and Wilson 1993; Schjølter et al. 1997) and the calcareous nannofossil zone *Micula prinsii* (Moshkovitz and Habib 1993; Habib et al. 1996; Eshet et al. 1992). However, the last occurrence of *P. grallator* is calibrated with the lower Danian foraminifera zones PØ (45 cm above the boundary at Caravaca) and P1a1 (25 cm above the K–Pg boundary at El Kef) by Brinkhuis et al. (1998) and P1a by Habib et al. (1996) and the calcareous nannofossil zone NP2 by Moshkovitz and Habib (1993).

In the Ouled Haddou section, the FOs of the following species are recorded in the early Danian: *C. pyrum*, *T. patula* and *T. pelagica* first occur in sample OH 6, while *P. grallator* first occurs in sample OH 8

and *M. fimbriatum* and *T. bononiensis* in sample OH 10. Their absence in uppermost Maastrichtian deposits might be caused by their extreme scarcity, taphonomic processes, unfavorable environmental and climatic conditions or oceanic paleocurrents. The FO of *P. grallator* at 20 cm above the K–Pg boundary, and thus above the FO of the earliest Danian species might be attributed to its scarcity and also to unfavorable environmental conditions.

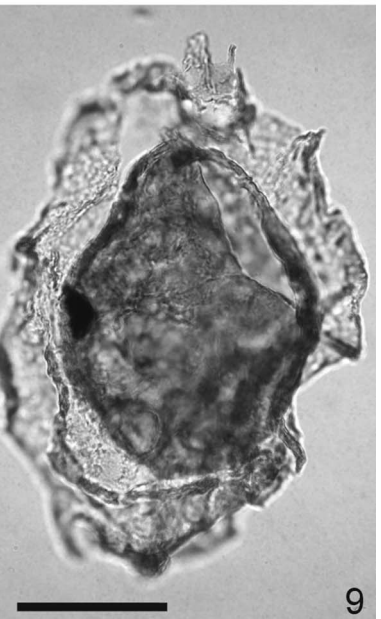
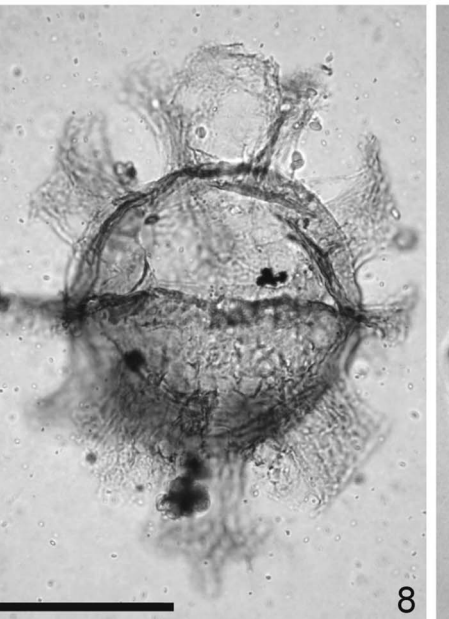
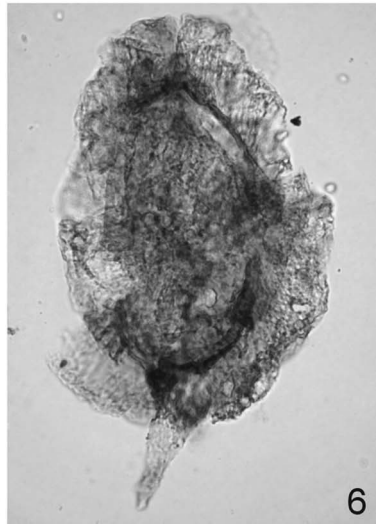
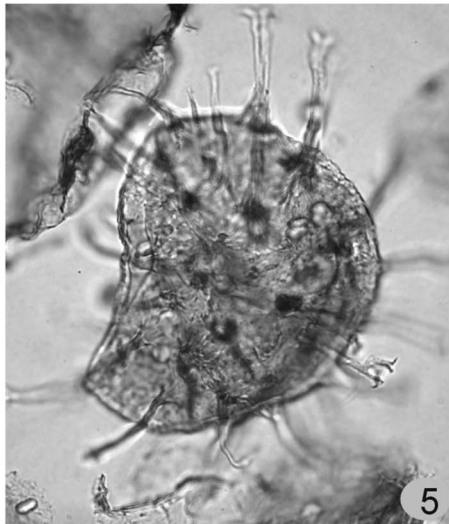
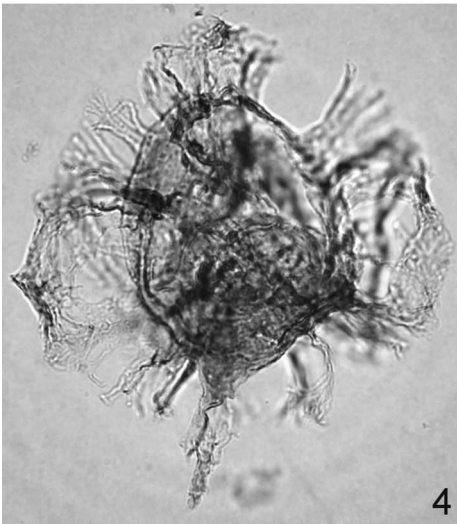
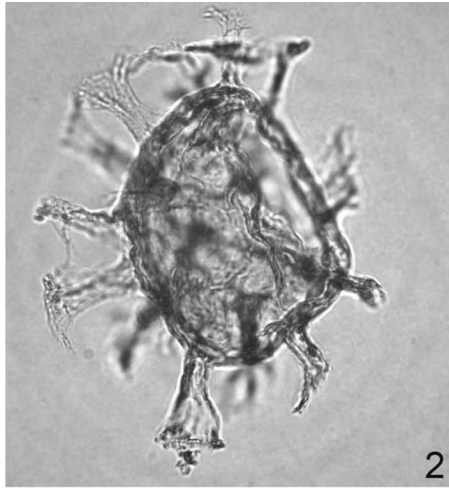
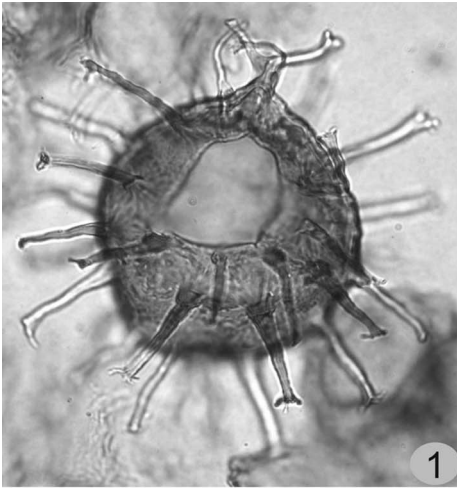
The last occurrence (LO) of this species in sample OH 18, 90 cm above the K–Pg boundary, and within the *Parvularugoglobigerina eugubina* foraminifer Zone is slightly younger than in El Kef and Caravaca (Brinkhuis et al. 1998), but older in comparison to the Alabama sections (Moshkovitz and Habib 1993; Habib et al. 1996). *Micrhystridium fragile* occurs sporadically in the uppermost Maastrichtian, but becomes abundant above the K–Pg boundary (Firth 1987; Moshkovitz and Habib 1993, Habib et al. 1996).

4.3. Cretaceous–Paleogene boundary and Early Danian

The dinoflagellate cysts *Carpatella cornuta* and *Damassadinium californicum* are global Danian index fossils, and *Eisenackia circumtabulata*, *Kenleyia lophophora*, *Lanternosphaeridium reinhardtii*, *Membranularnacia? tenella*, and *Senoniasphaera inornata* may also be valuable for the identification of the K–Pg boundary in the Northern Hemisphere middle latitudes, mainly the Mediterranean region. Their FOs are consecutive in ascending stratigraphic order within the lowermost Danian in biostratigraphically calibrated sections such as the Danish and Tunisian K–Pg stratotypes, and elsewhere in the Northern Hemisphere.

According to Williams et al. (2004), *E. circumtabulata* appears for the first time at the K–Pg boundary (65 Ma) in the mid latitudes and equatorial realm from

Plate 6. Scale bars represent 40 μm ; scale bar in figure 9 applies to the specimen 9; scale bar in figure 8 applies to all the other specimens. The photomicrographs were all taken using plain transmitted light. Figure 1. *Fibrocysta axialis* (Eisenack 1965) Stover & Evitt 1978. Sample OH 14, slide 2, EF H35/1. Specimen in dorsal view, high focus on the wall structure, precingular archeopyle and processes. Figure 2. *Cordosphaeridium inodes* (Klumpp 1953) Eisenack 1963 subsp. *longipes* Hansen 1977. Sample OH 4, slide 1, EF Y49/3. Specimen in left lateral view, low focus on the precingular archeopyle, wall structure and antapical process. Figure 3. *Cerodinium diebelii* (Alberti 1959) Lentin & Williams 1987 subsp. *diebelii*. Sample OH 18, slide 2, EF S41/4. Specimen in dorsal view, high focus. Figure 4. *Disphaerogena carposphaeropsis* Wetzel 1933. Sample OH 9, slide 2, EF G43. Specimen in ventral view, low focus showing the precingular archeopyle. Figure 5. *Fibrocysta ovalis* (Hansen 1977) Lentin & Williams 1981. Sample OH 17, slide 2, EF Q44/4. Focus on the wall structure, precingular archeopyle and processes. Figure 6. *Lanternosphaeridium lanosum* Morgenroth 1966. Sample OH 0, slide 2, EF Z44/2. Specimen in left lateral view, low focus. Note the precingular archeopyle. Figure 7. *Cordosphaeridium exilimurum* Davey & Williams 1966. Sample OH 1, slide 1, EF F27. Specimen in ventral view, low focus on the precingular archeopyle and processes. Figure 8. *Cordosphaeridium inodes* (Klumpp 1953) Eisenack 1963 subsp. *inodes*. Sample OH 0, slide 2, EF J48. Specimen in dorsal view, high focus showing the wall structure, precingular archeopyle, and fused apical processes. Figure 9. *Muratodinium fimbriatum* (Cookson & Eisenack 1967) Drugg 1970. Sample OH 14, slide 1, EF V34. Specimen in ventral view, low focus. Note the precingular archeopyle.



the northern Hemisphere, and earlier in the latest Maastrichtian (67 Ma) in the mid-latitudes of the Southern Hemisphere, however, this species has been also recorded in the early Maastrichtian (Marheinecke 1992) and the Campanian (Slimani 1995). Moreover, its FO marks exactly the basal Danian at El Kef, where this species defines the lowermost dinoflagellate cyst subzone (Brinkhuis and Zachariasse 1988). This species has also been reported in Danian strata from Aïn Settara (Dupuis et al. 2001), Caravaca (De Coninck and Smit 1982), Alabama (Moshkovitz and Habib 1993; Habib et al. 1996), California (Drugg 1967) and Baja California (Mexico) (Helenes 1984).

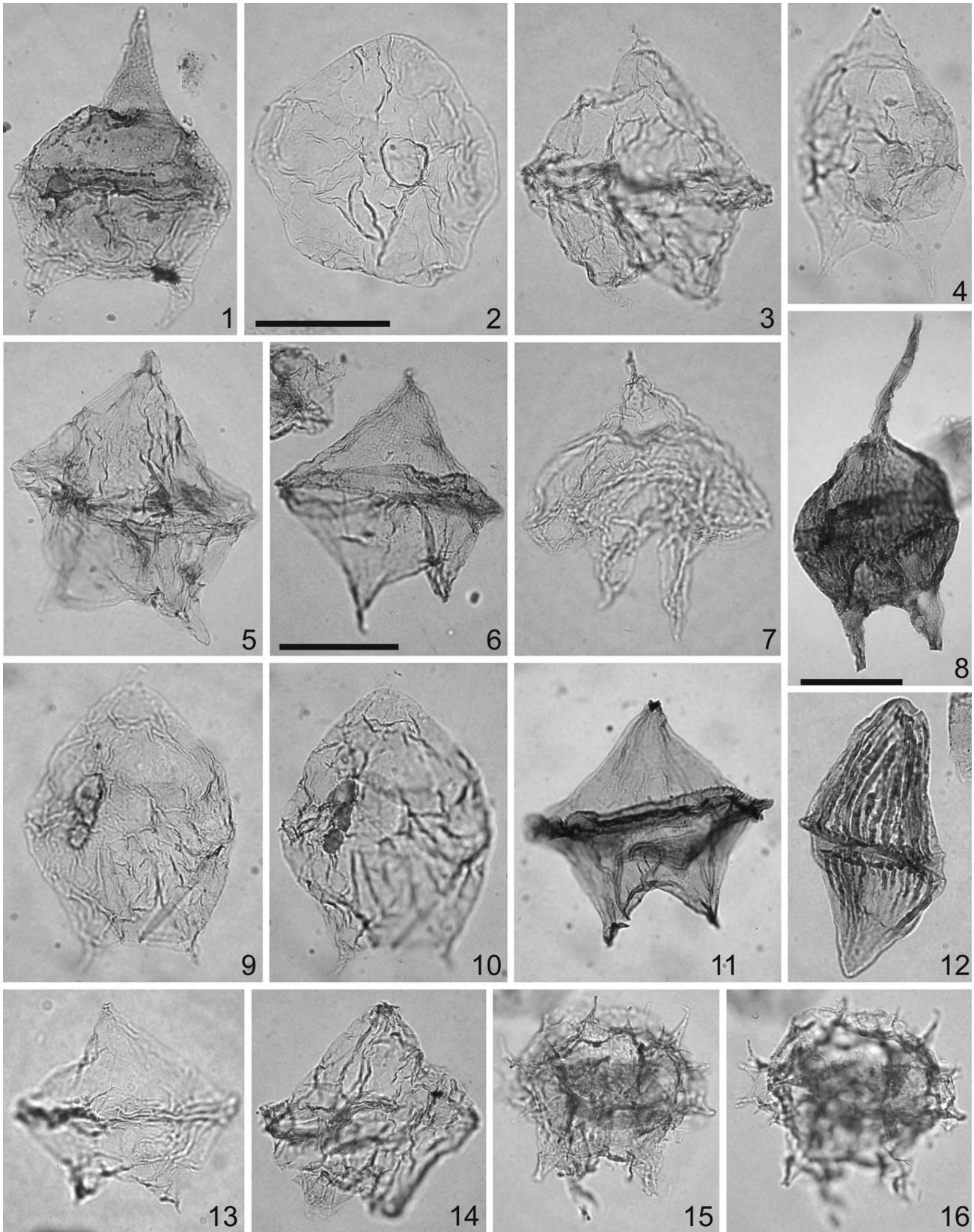
The FO of *S. inornata* is only slightly younger at 64.95 Ma in the Northern Hemisphere middle latitudes and the equatorial realm (Williams et al. 2004), and its stratigraphic range is restricted to the early and middle Danian (64.95–62.6 Ma). Its FO was recorded in the uppermost Maastrichtian deposits by Hansen (1977, 1979a, 1979b), and was later placed at the K–Pg boundary by Hultberg (1986) based on Hansen's material (1979a) who confused it with his latest Maastrichtian species *Glaphyrocysta perforata*. However, it was reported later that *S. inornata* occurs for the first time 2 to 3 cm above the K–Pg boundary in the Stevns Klint (Hansen et al. 1986) and El Kef (Habib and Saeedi 2007) sections. The FO of this species may then occur in basal Danian deposits in widely separated areas such as New Zealand and Denmark, where it defines respectively the lowermost dinoflagellate cyst interval zone (Willumsen et al. 2004a) and subzone (Hansen 1977). The FO of *S. inornata* lies above (Habib et al. 1996; Williams et al. 2004) or below the FO of *E. circumtabulata* (De Coninck and Smit 1982; Moshkovitz and Habib 1993; Brinkhuis and Schiøler 1996).

The FO of *D. californicum* occurs globally in the lowermost Danian at 64.75 Ma (Williams et al. 2004), often above the first occurrence of *S. inornata*. The FO of *C. cornuta* is often reported above (Hultberg 1985; Brinkhuis and Zachariasse 1988; Habib et al. 1996; Sarkis et al. 2002), but rarely simultaneously with the FO of *D. californicum* (Hansen 1977; Brinkhuis et al. 1998; Williams et al. 2004). *Carpatella cornuta* has a FO in the basal Danian of New Zealand and Denmark, where it defines respectively the second Danian dinoflagellate cyst interval zone (Willumsen et al. 2004a) and first zonule of the lowest Danian *Senoniasphaera inornata* Zone (Hansen 1977). According to Willumsen et al. (2004a), the ranges of *S. inornata* and *C. cornuta* in New Zealand are comparable to the ranges in the Northern Hemisphere.

The FOs of *M? tenella* lies at the K–Pg boundary (Hansen 1977), or higher within the lowermost Danian in the Mediterranean region and southeastern USA, slightly below (Habib et al. 1996) or above (Brinkhuis and Zachariasse 1988) the FO of *C. cornuta*, whereas, the FO of *L. reinhardtii* lies usually above the K–Pg boundary, within the lowermost Danian (Moshkovitz and Habib 1993; Brinkhuis and Schiøler 1996). *Kenleyia lophophora* has been recorded above the K–Pg boundary (within the lowermost Danian) and also in the latest Maastrichtian (Oloto 1989) or just below the K–Pg boundary (Obok-Ikuenobe et al. 1998; Dupuis et al., 2001). At Ouled Haddou, *M? tenella*, *K. lophophora* and *L. reinhardtii?* first occur respectively in samples OH 6, OH 9 and OH 10.

The progressive younger first documented occurrences of *C. cornuta*, *D. californicum* and *K. lophophora* from lower to higher northern latitudes may be interpreted here as a northward migration of these species, due to the inception of warmer conditions

Plate 7. Scale bars represent 40 μm ; scale bar in figure 6 applies to the specimen 6; scale bar in figure 8 applies to the specimen 8, 11 and 12; Scale bar in figure 2 applies to all the other specimens. The photomicrographs were all taken using plain transmitted light. Figure 1. *Deflandrea galeata* (Lejeune-Carpentier 1942) Lentin & Williams 1973. Sample OH 17, slide 1, EF D25/2. Specimen in dorsal view, high focus. Note the intercalary archeopyle and operculum *in situ*. Figure 2. *Lejeunecysta globosa* Biffi & Grignani 1983. Sample OH 12, slide 1, EF F43. Specimen in dorsal view, high focus. Note the intercalary archeopyle. Figure 3. *Phelodinium gaditanum* (Riegel 1974) Lentin and Williams 1981. Sample OH 11, slide 1, EF Q42/4. Specimen in dorsal view, low focus. Figure 4. *Cerodinium mediterraneum* Slimani et al. 2008. Sample OH 12, slide 1, EF U33. Specimen in dorsal view, low focus. Figure 5. *Phelodinium magnificum* (Stanley 1965) Stover and Evitt 1978. Sample OH 2, slide 1, EF H 45. Specimen in dorsal view, high focus. Figure 6. *Lejeunecysta decorinassa* Srivastava 1995. Sample OH 12, slide 2, EF X47. Specimen in dorsal view, high focus. Note the granulose wrinkles on the wall. Figure 7. *Lejeunecysta communis* Biffi & Grignani 1983. Sample OH 14, slide 1, EF C30/3. Specimen in ventral view, low focus. Figure 8. *Cerodinium striatum* (Drugg 1967) Lentin & Williams 1987. Sample OH 14, slide 1, EF W35. Specimen in dorsal view, high focus. Note the intercalary archeopyle and striated wall. Figures 9, 10. *Phelodinium elongatum* sp. nov. Paratype. Sample OH 10, slide 1, EF O46/2. Specimen in ventral view, 9 – low focus showing the intercalary archeopyle, 10 – focus on the apical horn. Figure 11. *Lejeunecysta izerzenensis* Slimani et al. 2008. Sample OH 1, slide 1, EF L27. Specimen in dorsal view, high focus on the circular denticulate septa. Figure 12. *Dinogymnium acuminatum* Evitt et al. 1967. Sample OH 1, slide 1, EF V34/4. Figure 13. *Lejeunecysta hyalina* (Gerlach 1961) Artzner & Dörhöfer 1978. Sample OH 1, slide 1, EF G29/3. Specimen in ventral view, low focus. Figure 14. *Phelodinium africanum* Biffi & Grignani 1983. Sample OH 11, slide 1, EF P46/2. Specimen in ventral view, low focus. Note the large pericoel on the right antapical horn. Figures 15, 16. *Palynodinium grallator* Gocht 1970. Sample OH 18, slide 1, EF N34/4. Specimen in dorsal view, 15 – high focus, 16 – low focus.



(Brinkhuis and Schiøler 1996) after the cooling event across the K–Pg boundary.

In the Ouled Haddou section, *E. circumtabulata*, *D. californicum*, *M. tenella*, and *S. inornata* have simultaneous FOs in sample OH 6, which thus indicates the basal Danian and the base of the PØ Zone. *K. lophophora* (sample OH 9), *L. reinhardtii* (sample OH 10) and *C. cornuta* (sample OH 11) appear in the same stratigraphical order as at El Kef (Brinkhuis and Leereveld 1988; Brinkhuis and Zachariasse 1988). The FOs are older within the upper part of the planktonic foraminifer *Guembelitra cretacea* Zone, rather than in the lower part of the *Parvularugoglobigerina eugubina* Zone. The simultaneous FOs recorded here with the FO of *D. californicum* might be explained by the wide spacing (20 cm) between samples OH 5 and OH 6. The occurrence of *S. inornata* in samples OH 6 to OH 19, in association with the other Danian markers such as *C. cornuta*, *D. californicum*, and *M? tenella*, allows us to assign an early to middle Danian age to this 1.25 m thick interval. However, the last occurrence of *P. grallator* in sample OH 18 indicates an age not younger than early Danian (P1a Zone of Smit 1982) for this interval. This age is the same as that determined by the planktonic foraminifers for this interval (Toufiq et al. 2002).

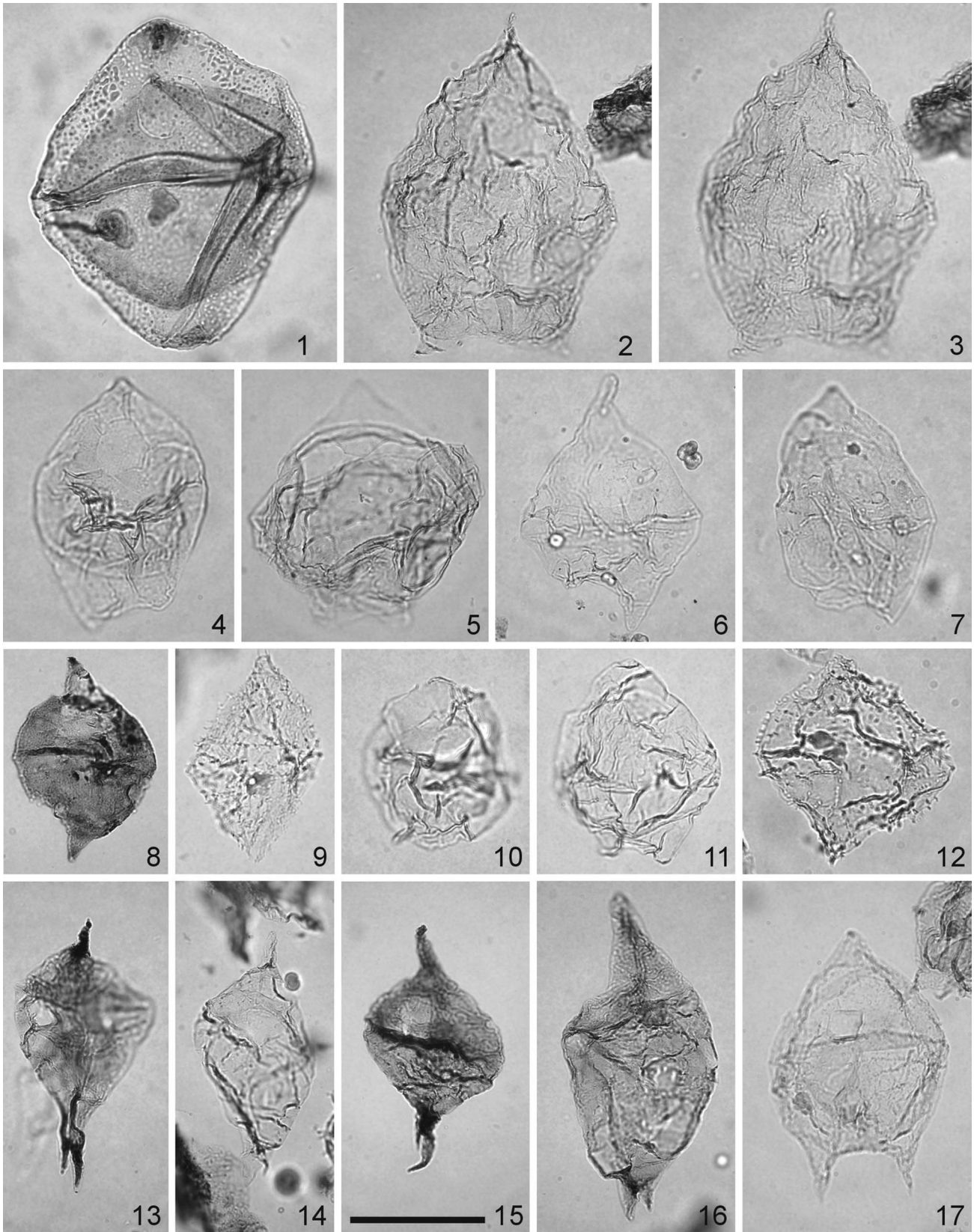
The K–Pg boundary is placed here between the samples OH 5 and OH 6, above the FOs of the latest Maastrichtian index species (*D. carposphaeropsis*, *G. perforata*, *M. seelandica*), immediately above the latest Maastrichtian acme of *M. seelandica*, and below the FO of the earliest Danian markers. The FOs of *C. cornuta*, *K. lophophora*, *D. californicum*, and probably *L. reinhardtii* are recorded here earlier than their FO reported in Alabama by Habib et al. (1996). This diachronism might also be interpreted as the result of a

northward migration of these species in response to early Danian warming. The slightly earlier FO of *C. cornuta* observed here in comparison with its FO at El Kef (Brinkhuis and Zachariasse 1988) has not been taken into consideration, since Brinkhuis et al. (1998) recorded *C. cornuta* in an earlier stratigraphic level (upper part of the PØ Zone) at the same locality.

Other species have their first documented occurrences in the Danian: i.e. *Cassidium fragile*, *Impagidinium patulum*, here as *Impagidinium* sp. cf. *I. patulum*, *Endoscrinium? novissimum*, and *Ynezidinium pentahedrias*. In the Ouled Haddou section, these species have FOs at the same level (sample OH 6) as *S. inornata* and *D. californicum*. However, Brinkhuis and Zachariasse (1988) and Hultberg (1985) recorded, respectively, *Y.* (as *Impagidinium*) *pentahedrias* and *E? novissimum* in the latest Maastrichtian.

The following species with a well known FO in the Danian are recorded at Ouled Haddou: *Achomosphera alcicornu*, *Impagidinium celinae*, *Pterodinium cingulatum* subsp. *danicum*, *Kallosphaeridium parvum*, and *Magallanesium pilatum*. The first appearance of *Magallanesium densispinatum* in the Danian is global (Drugg 1967; Askin 1988; Brinkhuis and Zachariasse 1988; Jan du Chêne 1988; Eshet et al. 1992; Moshkhovitz and Habib 1993; Slimani 2001; Guasti et al. 2005). The FOs of the above mentioned species lie above the FOs of *D. californicum* and *S. inornata*. They are presented successively in ascending stratigraphic order, in samples OH 7 (*A. alcicornu*) and OH 8 (*P. cingulatum* subsp. *danicum*) below the FO of *K. lophophora*, in sample OH 10 (*M. pilatum*, *M. densispinatum*) between the FO of *K. lophophora* and the FO of *C. cornuta*, in sample OH 11 (*K. parvum*) at the same level of the FO of *C. cornuta* and in sample OH 16 (*I. celinae*). The FO of *I. celinae* recorded above

Plate 8. Scale bar in figure 15 represents 40 μm for all specimens. The photomicrographs were all taken using plain transmitted light. Figure 1. *Manumiella seelandica* (Lange 1969) Bujak & Davies 1983. Sample OH 3, slide 1, EF L45/1. Specimen in dorsal view, high focus. Note the intercalary archeopyle and operculum *in situ*. Figures 2, 3. *Phelodinium elongatum* sp. nov. Holotype. Sample OH 6, slide 2, EF L57/2. Specimen in dorsal view, 2 – high focus on the intercalary archeopyle and wall structure, 3 – low focus. Figure 4. *Isabelidinium bakeri* (Deflandre & Cookson 1955) Lentin & Williams 1977. Sample OH 12, slide 1, EF F34/3. Specimen in dorsal view, high focus on the intercalary archeopyle. Figure 5. *Trithyrodinium fragile* Davey 1969. Sample OH 12, slide 1, EF J45/1. Specimen in dorsal view, high focus. Note the anterior intercalary type 3I archeopyle. Figure 6. *Pierceites pentagonus* (May 1980) Habib & Drugg 1987. Sample OH 17, slide 2, EF L35/2. Specimen in ventral view, low focus. Note the anterior intercalary type 3I archeopyle and operculum *in situ*. Figure 7. *Chatangiella spectabilis* (Alberti 1959) Lentin & Williams 1976. Sample OH 3, slide 1, EF F24/4. Specimen in dorsal view, high focus. Figure 8. *Andalusiella rhomboides* (Boltenhagen 1977) Lentin & Williams 1980. Sample OH 17, slide 1, EF T54. Specimen in dorsal view, high focus. Figure 9. *Magallanesium densispinatum* (Stanley 1965) Quattrocchio & Sarjeant 2003. Sample OH 14, slide 1, EF D31/4. Specimen in ventral view, low focus. Figures 10, 11. *Endoscrinium novissimum* (Morgenroth 1968) Riding & Fensome 2002. 10 – sample OH 6, slide 2, EF G30/4. 11 – sample OH 8, slide 1, EF E49/2. Figure 12. *Magallanesium pilatum* (Stanley 1965) Quattrocchio & Sarjeant 2003. Sample OH 14, slide 1, EF M52/4. Specimen in dorsal view, low focus. Figure 13. *Andalusiella acicornuta* Srivastava 1995. Sample OH 11, slide 1, EF B28. Figure 14. *Andalusiella mauthei* Riegel 1974 subsp. *aegyptiaca* (Schrank 1988) Masure et al. 1996. Sample OH 0, slide 2, EF J45. specimen cornucavate. Figure 15. *Andalusiella mauthei* Riegel 1974 subsp. *mauthei*. Sample OH 13, slide 1, EF N47/3. Specimen in ventral view, low focus. Note the intercalary archeopyle. Figure 16. *Andalusiella polymorpha* (Malloy 1972) Lentin & Williams 1977. Sample OH 18, slide 1, EF T56/4. Figure 17. *Deflandrea severnensis* Benson 1976. Sample OH 18, slide 2, EF B42. Specimen in dorsal view, high focus. Note the periphragm ornamented by short spines.



the FOs of *D. californicum* and *K. lophophora* by Masure et al. (1998) is possibly a significant bioevent in the early Danian. The stratigraphic level of the FO of *A. alcicornu* is here earlier compared to the Danish sections where this species first occurs in the basal part of the *Xenicodinium lubricum* dinoflagellate cyst Zonule (Hansen 1977). Also, the FO of *M. densispinatum* is earlier in comparison with Alabama and El Kef sections where this FO is calibrated against the calcareous nannofossil NP1 Zone (Moshkhovitz and Habib 1993; Guasti et al. 2005) and the foraminifer P1c (Brinkhuis and Zachariasse 1998), P1b (Guasti et al. 2005) and P1 (Jan du Chêne 1988) zones.

5. Paleoenvironment

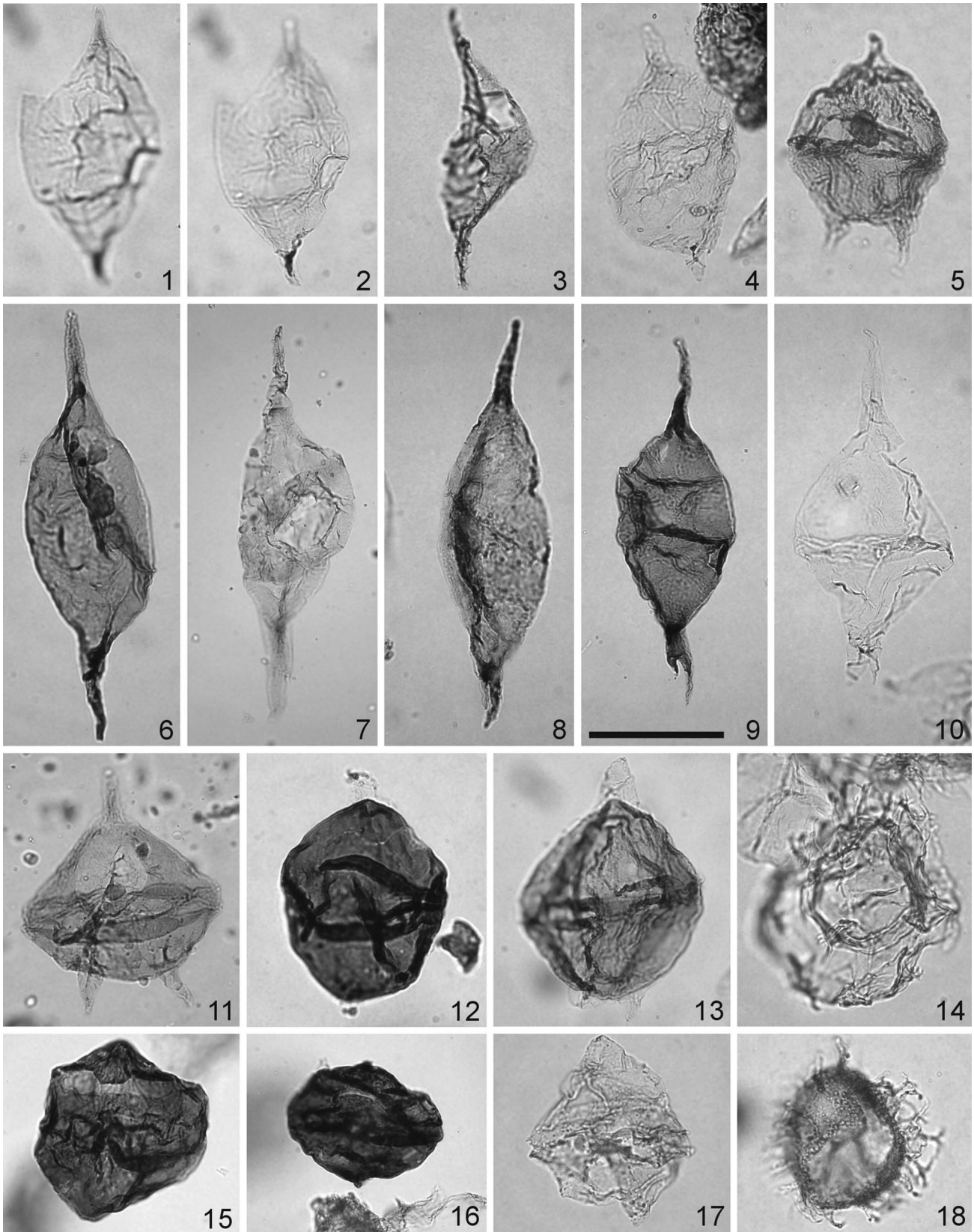
The K–Pg boundary interval at Ouled Haddou shows important changes in the relative abundances of morphologically related dinoflagellate cysts (Figure 2), probably reflecting changes in the paleoenvironment. The uppermost Maastrichtian deposits are dominated by *Cordosphaeridium* spp., *Manumiella seelandica*, and the *Glaphyrocysta* and *Spiniferites* groups (up to 80% of the assemblage), while the early Danian is dominated by *Areoligera* spp., *Senegalinium* spp. and *Spiniferites* spp. (40%–70% of the assemblage). The following genera show quantitative changes: *Areoligera* spp., *Cordosphaeridium* spp., *Manumiella seelandica* and the *Glaphyrocysta*, *Spiniferites*, and *Senegalinium* groups.

The *Cordosphaeridium* group (mainly *Cordosphaeridium exilimurum* and *Cordosphaeridium inodes* subsp.

inodes) and the *Glaphyrocysta* group (mostly *Glaphyrocysta castelcasiensis*, *Glaphyrocysta expansa*, *Glaphyrocysta perforata* and *Riculacysta amplexa*) dominate the assemblage in sample OH 1. Their relative frequency decreases gradually, while the *Spiniferites* group increases (mainly *Spiniferite ramosus* subsp. *ramosus* and *Spiniferites twistringiensis*). The species of the *Glaphyrocysta* group were considered as indicators of a nearshore shallow marine environment (Brinkhuis and Zachariasse 1988; Eshet et al. 1992) and the *Spiniferites* group as indicative of an open marine environment (Schrank 1984; Brinkhuis and Zachariasse 1988; Eshet et al. 1992; Brinkhuis and Schiøler 1996, Brinkhuis et al. 1998). The relative abundance changes of *Spiniferites* and *Glaphyrocysta* groups suggest nearshore (sample OH 1) to open marine (sample OH 2) environments.

Manumiella seelandica dominates the assemblage in samples OH 3 (90%) and OH 5 (60%), whereas the *Glaphyrocysta* group dominate in sample OH 4 (70%). *Manumiella seelandica* shows here an inverse relationship with the *Glaphyrocysta* group. The high relative abundance of *M. seelandica* may indicate low salinity or even brackish conditions (Hultberg 1986; Firth 1987), or shallower and cooler conditions (Strong et al. 1977; Wilson 1978; Firth 1987). Habib and Saeedi (2007) suggested that *M. seelandica* might have been restricted to inner neritic environments during regressive phases, but thrived in these environments when the climate cooled. Therefore, the high relative abundance of *M. seelandica* suggests that the upper Maastrichtian strata at Ouled Haddou were deposited in a nearshore marine environment during a regressive

Plate 9. Scale bar in figure 9 represents 40 μm for all specimens. The photomicrographs were all taken using plain transmitted light. Figures 1, 2. *Andalusiella* sp. A. Sample OH 14, slide 1, EF Q46/4. Specimen in dorsal view, differing levels of focus showing the intercalary archeopyle, and apical and antapical horns. Figure 3. *Palaeocystodinium* sp. B of Oboh-Ikuenobe et al. 1998. Sample OH 14, slide 1, EF V52/3. Specimen in dorsal view, high focus. Figure 4. *Palaeocystodinium bulliforme* Ioannides 1986. Sample OH 2, slide 1, EF O54/4. Figure 5. *Cerodinium pannuceum* (Stanley 1965) Lentin & Williams 1987. Sample OH 7, slide 1, EF P52. Note the striated and granulated wall. Figure 6. *Palaeocystodinium golzowense* Alberti 1961. Sample OH 17, slide 1, EF D43/2. Figure 7. *Palaeocystodinium australinum* (Cookson 1965) Lentin & Williams 1976. Sample OH 1, slide 2, EF J32. Specimen in dorsal view, low focus. Note the lateral spur on the antapical horn. Figure 8. *Andalusiella mauthei* Riegel 1974 subsp. *punctata* (Jain & Millepied 1973) Masure et al. 1996. Sample OH 9, slide 2, EF H34/3. Note the two antapical horns with forking close to the central body. Figure 9. *Andalusiella gabonensis* (Stover & Evitt 1978) Wrenn & Hart 1988. Sample OH 18, slide 1, EF S31/2. Specimen in right dorsolateral view, low focus. Note the intercalary archeopyle and operculum *in situ*. Figure 10. *Andalusiella spicata* (May 1980) Lentin & Williams 1981. Sample OH 14, slide 1, EF N56/2. Specimen in left lateral view, high focus. Note the intercalary archeopyle and two antapical horns. Figure 11. *Cerodinium navarrianum* (Srivastava 1995) Williams et al. 1998. Sample OH 1, slide 2, EF N56/1. Specimen in ventral view, high focus. Figure 12. *Trithyrodinium evittii* Drugg 1967. Sample OH 18, slide 1, EF K55/4. Specimen in dorsal view, high focus. Note the intercalary type 3I archeopyle and operculum *in situ*. Figure 13. ?*Senegalinium* sp. D. of Jain & Millepied 1973. Sample OH 3, slide 1, EF D35. Specimen in ventral view, high focus. Figure 14. *Hystrichostrogylon coninckii* Heilmann-Clausen in Thomsen & Heilmann-Clausen 1985. Sample OH 10, slide 1, EF U33/2. Specimen in dorsal view, low focus. Figure 15. *Trithyrodinium striatum* Benson 1976. Sample OH 11, slide 1, EF G49/1. Specimen in dorsal view, high focus. Note the intercalary type 3I archeopyle and striated wall. Figure 16. *Andalusiella dubia* (Jain & Millepied 1973) Lentin & Williams 1980. Sample OH 19, slide 1, EF J50/4. Specimen in ventral view, low focus. Note the intercalary archeopyle and operculum *in situ*. Figure 17. *Chatangiella* aff. *verrucosa* (Manum 1963) Lentin & Williams 1976. Sample OH 14, slide 1, EF V40. Specimen in dorsal view, high focus. Figure 18. *Hafniasphaera septata* (Cookson & Eisenack 1967) Hansen 1977. OH 12, slide 1, EF B32, focus on the wall structure, archeopyle and processes.



phase in cool climatic conditions. This is supported by the scarcity of the *Senegalinium* group, which is indicative of open marine and transgressive conditions (see below). The high abundance of the *Glaphyrocysta* group in sample OH 4 might indicate temporary warmer climatic conditions. This interval is also marked by a decrease in dinoflagellate cyst diversity (samples OH 3 and OH 4).

Just above the K–Pg boundary (sample OH 6), species of *Areoligera* display a sudden relative abundance increase, whereas *M. seelandica* and species of *Glaphyrocysta* show an abrupt decrease. However, species of the *Spiniferites* and *Senegalinium* groups are common. Firth (1993) considered *Areoligera* spp. as indicative of open marine environments representing maximum transgressive events. The assemblage from OH 6 mirrors an open marine environment at the beginning of a marine transgression.

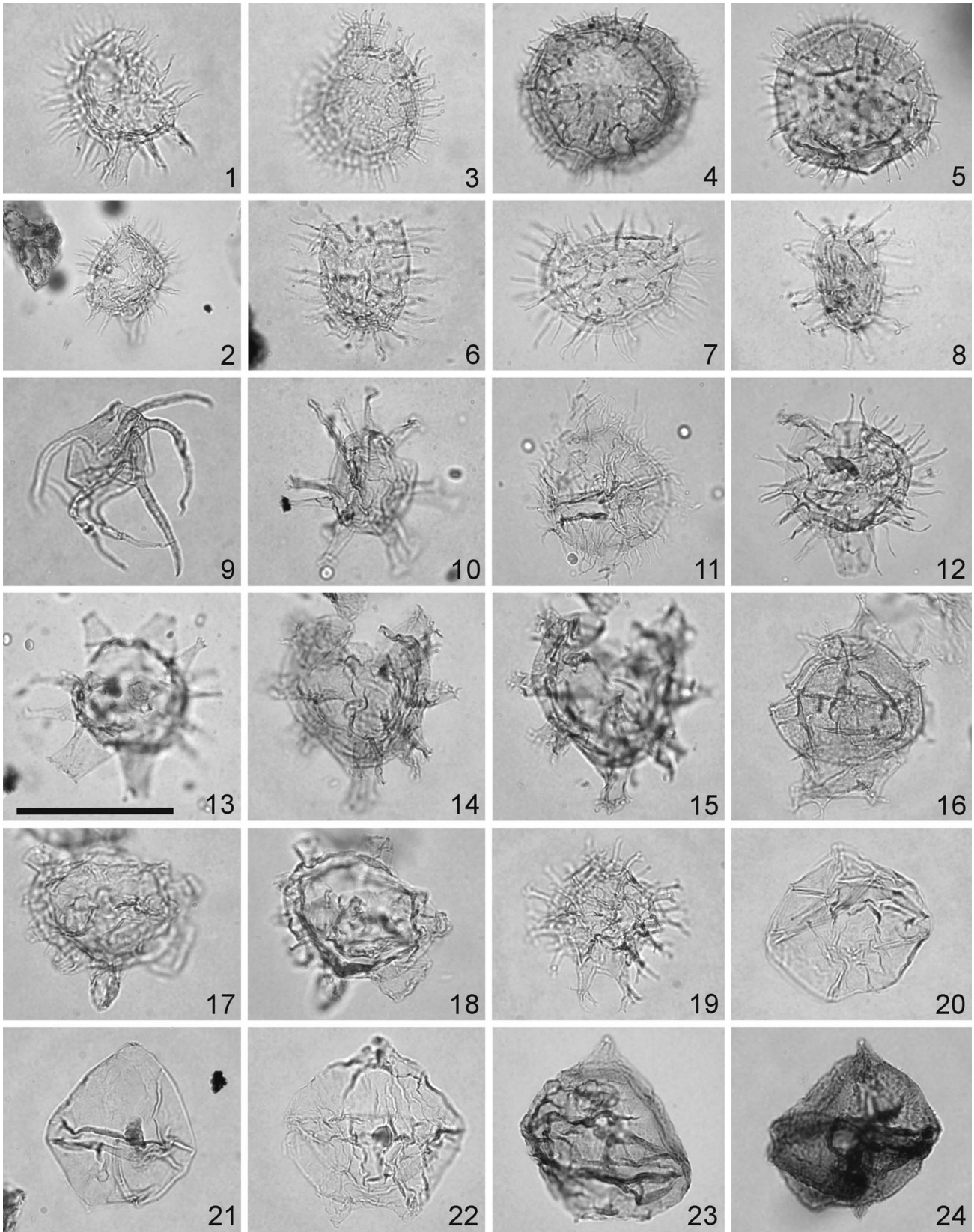
Higher in the section, the relative abundance of *Areoligera* spp. declines gradually and the species became rare from sample OH 10 upwards, while the *Spiniferites* and the *Senegalinium* groups display an increase in their relative abundances. A higher abundance (around 30%) of the *Senegalinium* group is recorded in samples OH 11 and OH 12. High abundance of the *Senegalinium* group is associated with elevated nutrient and productivity levels (Brinkhuis

and Zachariasse 1988; Eshet et al. 1992; Firth 1993; Nøhr Hansen and Dam 1997). The increase of the relative abundance of the *Senegalium* group (mainly *Senegalinium bicavatum*, *Senegalinium laevigatum*, *Senegalinium obscurum*), and the *Spiniferites* group is striking, in comparison to the low relative abundance of the other groups, and is indicative of more open marine conditions with higher productivity. This supports the assumption that the sediments above OH 6 were deposited under a transgressive regime. The planktonic foraminifera also indicate high productivity, related to an increase of the calcium carbonate content in this interval (Toufiq et al. 2002; Toufiq and Boutakiout 2005). This interval coincides with an increase in dinoflagellate cyst species abundance, which is also suggestive of more open marine conditions (Habib and Miller 1989; Habib et al. 1992). The relative frequency of *Carpatella cornuta*, *Senoniasphaera inornata*, and the acritarch *Micrhystridium fragile* increases also here under a transgressive regime in this interval, as noted by Moshkovitz and Habib (1993).

6. Paleobiogeography

The dinoflagellate cyst assemblages of the Maastrichtian–Danian transition at Ouled Haddou reflect pronounced provincialism. According to Lentin and

Plate 10. Scale bar in figure 13 represents 40 μm for all specimens. The photomicrographs were all taken using plain transmitted light. Figures 1, 2. *Coronifera* sp. cf. *Coronifera? tubulosa* Cookson & Eisenack 1974. 1 – sample OH 11, slide 1, EF Y52. Specimen in left lateral view, focus on the archeopyle, antapical horn and processes. 2 – sample OH 10, slide 2, EF F46/4. Specimen in right lateral view showing the precingular archeopyle and operculum *in situ*. Figure 3. *Impletosphaeridium clavulum* (Davey 1969) Islam 1993. Sample OH 0, slide 1, EF J36/4. Note the processes, apical archeopyle and displaced operculum. Figure 4. *Operculodinium israelianum* (Rossignol 1962) Wall 1967. Sample OH 9, slide 1, EF N44/4. Specimen in dorsal view, high focus. Note the precingular archeopyle and acuminate processes. Figure 5. *Operculodinium centrocarpum* (Deflandre & Cookson 1955) Wall 1967 subsp. *centrocarpum*. Sample OH 18, slide 1, EF F49/3. Specimen in right dorsolateral view, high focus. Note the precingular archeopyle and capitate processes. Figure 6. *Tanyosphaeridium regulare* Davey & Williams 1966. Sample OH 2, slide 1, EF K56. Note the distal extremities of processes. Figure 7. *Lingulodinium bergmannii* (Archangelsky 1969) Quattrocchio & Sarjeant 2003. Sample OH 18, slide 1, EF X47/4. Focus on the archeopyle and processes. Figure 8. *Tanyosphaeridium xanthiopyxides* (Wetzel 1933) Stover & Evitt 1978. Sample OH 18, slide 1, EF O49. Focus on processes. Figure 9. *Micrhystridium fragile* Deflandre 1947. Sample OH 9, slide 1, EF D45/2. Figure 10. *Oligosphaeridium* sp. cf. *Homotryblium* sp. of Brinkhuis & Zachariasse 1988. Sample OH 0, slide 2, EF D39. Note the operculum and buccinate processes. Figure 11. *Palaeohystrichophora infusorioides* Deflandre 1935. Sample OH 0, slide 2, EF C29/2. Figure 12. *Diphyes colligerum* (Deflandre & Cookson 1955) Cookson 1965. Sample OH 10, slide 2, EF Z45/1. Focus on processes. Figure 13. *Hystrichokolpoma bulbosum* (Ehrenberg 1838) Morgenroth 1968 subsp. *bulbosum*. Sample OH 0, slide 2, EF G54. Note the apical archeopyle and processes. Figures 14, 15. *Hystrichokolpoma* sp. cf. *Hystrichokolpoma rigaudiae* Deflandre & Cookson 1955. Sample OH 6, slide 1, EF Q58. Differing levels of focus showing processes. Note the apical archeopyle. Figure 16. *Hystrichosphaeropsis ovum* Deflandre 1935. Sample OH 14, slide 1, EF N29/4. Specimen in right lateral view, high focus. Figures 17, 18. *Hystrichokolpoma* sp. cf. *Hystrichokolpoma truncatum* Biffi & Manum 1988. Sample OH 14, slide 1, EF Q52/1, 17 – focus on the antapical process, 18 – focus on the apical archeopyle. Figure 19. *Spiniferites* sp. cf. *Spiniferites hyperacanthus* of Jan du Chêne 1988. Sample OH 0, slide 1, EF S26. Note the two longer antapical processes. Figure 20. *Senegalinium laevigatum* (Malloy 1972) Bujak & Davies 1983. Sample OH 9, slide 2, EF H46/2. Figure 21. *Senegalinium obscurum* (Drugg 1967) Stover & Evitt 1978. Sample OH 18, slide 2, EF Q45. Specimen in dorsal view, high focus showing the intercalary archeopyle, operculum *in situ* and very short apical and antapical horns. Figure 22. *Senegalinium bicavatum* Jain & Millepied 1973. Sample OH 14, slide 1, EF T56/2. Specimen in dorsal view, median focus showing the antapical horns. Figure 23. *Senegalinium microgranulatum* (Stanley 1965) Stover & Evitt 1978. Sample OH 8, slide 1, EF G42. Note the microgranulate endophragm. Figure 24. *Senegalinium microspinum* (Boltenhagen 1977) Lentin & Williams 1980. Sample OH 18, slide 1, EF W52/4. Specimen in ventral view, low focus showing the intercalary archeopyle, operculum *in situ* and wall ornamented with microspines.



Williams (1980), latitudinal distribution of Campanian peridinioid dinoflagellate cysts allows the definition of three provinces: a tropical to subtropical province, a temperate province and a boreal province. These provinces are discussed below based on studies published after the Lentin and Williams (1980) paper. The tropical to subtropical – or Tethyan – province is characterized by *Andalusiella*, *Cerodinium*, *Lejeunecysta*, and *Senegalinium* (the Malloy suite of Lentin and Williams, 1980). These assemblages are recognized in Campanian to Danian deposits in the Mediterranean region (Rauscher and Doubinger 1982; Schrank 1987; Brinkhuis and Zachariasse 1988; Soncini 1990), Senegal (Jan du Chêne 1988), equatorial areas (Oloto 1989; Oboh-Ikuenobe et al. 1998; Masure et al. 1998; Yepes 2001; Willumsen et al. 2004b), southeastern USA (Firth 1987, 1993; Moshkovitz and Habib 1993; Srivastava 1995), Caribbean region (Helenes and Somoza 1999) and Mexico (Helenes and Téllez-Duarte 2002). The temperate province is characterized by species of *Alterbidinium*, *Chatangiella* (smaller forms), *Isabelidinium*, *Spinidinium*, and *Trithyrodinium* (the Williams suite of Lentin and Williams 1980). In the Northern Hemisphere, this province is recognized in central and northern Europe (Kirsch 1991; Marheinecke 1992; Powell 1992; Schiøler and Wilson 1993; Schiøler et al. 1997; Slimani 2001) and northeastern USA (May 1980; Firth 1987, 1993; Habib and Miller 1989). The boreal province is characterized by species of *Chatangiella* (larger forms) and *Laciniadinium* (the McIntyre suite of Lentin and Williams 1980), and is recognized in higher latitudes in Greenland (Nøhr Hansen 1996; Nøhr Hansen and Dam 1997), Arctic Canada (Ioannides 1986) and Russia (Lebedeva 2006).

The latest Maastrichtian and early Danian dinoflagellate cyst assemblages at Ouled Haddou consist mainly of dark brown species such as *Andalusiella* (10 species), *Cerodinium* (12 species), *Lejeunecysta* (5 species) and *Senegalinium* (7 species) of the Malloy suite, and species of *Alterbidinium* (2 species), *Chatangiella* (2 small species), *Isabelidinium* (3 species), *Spinidinium* (5 species, including *Magallanesium densispinatum* and *Magallanesium pilatum*, attributed formerly to *Spinidinium*) and *Trithyrodinium* (3 species) of the Williams suite (Table S1). Species of the McIntyre suite are absent. Apart from the relatively few species of *Alterbidinium*, *Chatangiella*, and *Isabelidinium* of the Williams suite, which are rare to sporadic, all the taxa of the Malloy and Williams suites are abundant, especially in the lower Danian deposits. Moreover, previous studies demonstrate that the other taxa of the Williams suite (*M. densispinatum*, *M. pilatum*, and *T. evittii*) are not restricted to the temperate province, but occur also in the Tethyan province. *Trithyrodinium evittii*, recognized before as a warm-water species (Smit and Brinkhuis 1996) appears in the Late Cretaceous Tethyan province,

while its FO is located just above the K–Pg boundary in the higher latitudes of both Northern and Southern Hemispheres. This is interpreted as bipolar migration of this species in response to the global warming during the early Danian (Smit and Brinkhuis 1996; Nøhr Hansen and Dam 1997; Brinkhuis et al. 1998; Willumsen 2006). Furthermore, *Trithyrodinium* spp. was considered as a common member of the Williams suite by Lentin and Williams (1980), and has later been included in a transitional Malloy–Williams suite (Rauscher and Doubinger, 1982; probably Soncini, 1990), and also in the Malloy suite (Yepes, 2001). *Magallanesium densispinatum* has been also reported in the Tethyan realm (Morocco, Tunisia, Senegal and Equatorial Africa) as well as *M. pilatum* (Morocco). *Trithyrodinium evittii* in this section is well presented in the latest Maastrichtian and early Danian but shows changes in its abundance, while *M. densispinatum* and *M. pilatum* occur in the early Danian with significant abundance.

It is obvious that the overall peridinioid assemblage is largely dominated by taxa previously reported from the tropical to subtropical Malloy suite, whereas taxa of the Williams suite constitute a minority. Therefore, the latest Maastrichtian to early Danian dinoflagellate cyst assemblages from the Ouled Haddou section suggest deposition in a subtropical to warm temperate province, and are most similar to Tethyan assemblages from Tunisia, southern Spain, the Moroccan Phosphate Plateau, and the southeastern USA (Alabama, Georgia, Texas). Comparisons with other dinoflagellate cyst assemblages suggest that the Maastrichtian assemblage is most similar to other Tethyan assemblages from India, Egypt, Senegal, Nigeria, Ghana, Côte d'Ivoire, Brazil, Venezuela, Colombia, Mexico, and the western USA (California), than with assemblages from the rest of Europe and northeastern USA. The assemblage differs markedly from the boreal assemblages. However, the Danian assemblage compares well with the Tethyan, north European and north American assemblages. Moreover, the Danian assemblage shares similarities with many other assemblages from both Northern and Southern Hemispheres. This similarity in widely-separated areas may be caused by a higher oceanic circulation and decrease in provincialism during the Danian.

7. Conclusions

The palynological analysis of the K–Pg transition at Ouled Haddou revealed a succession of chronostratigraphically significant dinoflagellate cyst events. Significant latest Maastrichtian dinoflagellate cyst events are the FOs of *Carpatella septata*, *Glaphyrocysta perforata*, and *Manumiella seelandica*, followed by the FO of *Disphaerogena carposphaeropsis*, and the acme

of *M. seelandica* just below the K–Pg boundary. The early Danian events are the first occurrences of *Eisenackia circumtabulata*, *Damassadinium californicum*, *Senoniasphaera inornata*, and *Membranilarnacia? tenella* (OH 6), *Palynodinium grallator* (OH 8), *Kenleyia lophophora* (OH 9), *Lanternosphaeridium reinhardtii* (OH 10), *Carpatella cornuta* (OH 11), *Impagidinium celinae* (OH 16), and the last occurrence of *P. grallator* in sample (OH 18).

The K–Pg boundary is placed above the latest Maastrichtian events – essentially directly above the acme of *M. seelandica* – and below the earliest Danian events. These dinoflagellate cyst age determinations corroborate the planktonic foraminifer biostratigraphic results in the same section by Toufiq et al. (2002). The gradual succession of the dinoflagellate cyst events suggests a rather complete record of the Cretaceous–Paleogene transition at Ouled Haddou.

Accepting the hypothesis of a southward migration of *P. grallator* caused by a cooling event in the earliest Danian and a northward migration of *K. lophophora*, *L. reinhardtii*, and *C. cornuta* in response to the early Danian warming, the recorded dinoflagellate cyst events correlate well with the records from the Northern Hemisphere middle latitudes (mainly Mediterranean region, northwest Europe, and USA) and the equatorial realm. However, the absence of *Cribooperidinium? pyrum*, *Micrhystridium fragile*, *Muratodinium fimbriatum*, *Thalassiphora bononiensis*, *Thalassiphora patula*, and *Thalassiphora pelagica* in the Maastrichtian strata at Ouled Haddou might be caused by extreme scarcity, unfavorable environmental and climatic conditions, or paleocirculation changes.

The K–Pg boundary at Ouled Haddou is not marked by a mass extinction of dinoflagellate cyst species, but shows important changes in the relative abundances of species or groups of morphologically related species.

The overall peridinioid assemblage is dominated by species of the tropical to subtropical suite whereas species of the temperate suite are sporadic and those of the boreal suite are absent. Therefore, deposition in a subtropical to warm temperate province for the studied interval of the Ouled Haddou section is suggested.

8. Systematic paleontology

One new species is described. The morphological terminology follows Stover and Evitt (1978) and Williams et al. (2000). Suprageneric classification follows that of Fensome et al. (1993). The holotype and paratype of the new species are housed in the botanical collection of the National Herbarium (RAB), Scientific Institute, Mohammed V-Agdal University, Rabat, Morocco. England Finder (EF)

coordinates of the holotype and paratype of the new species are given in the text and in the plate captions.

Division DINOFLAGELLATA (Bütschli, 1885)
Fensome et al. 1993

Subdivision DINOKARYOTA Fensome et al. 1993

Class DINOPHYCEAE Pascher 1914

Subclass PERIDINIPHYCIDAE Fensome et al. 1993

Order PERIDINIALES Haeckel 1894

Suborder PERIDINIINEAE (Autonym)

Family: CONGRUENTIDIACEAE Schiller 1935

Subfamily: CONGRUENTIDIOIDEAE (autonym)

Genus *Phelodinium* Stover & Evitt 1978

Phelodinium elongatum sp. nov.

Plate 3, fig. 11; Plate 7, figs. 9, 10; Plate 8, figs. 2, 3

Diagnosis. Elongate, rounded pentagonal, thin-walled *Phelodinium* with delicate and wrinkled periphragm and short conical apical and antapical horns. When visible the cingulum is indicated by transverse irregular fine folds or ridges. Antapical depression shallow or absent. Intercalary archeopyle, expressed by loss of the intercalary 2a plate.

Description. Peridinioid, cornucavate, proximate, dorso-ventrally compressed cyst with a rounded pentagonal outline and a longer than wide central body. The antapical depression is shallow or absent. The apical horn is conical with a truncate to blunt end. The antapical horns are slender, of equal length and have slightly pointed ends. The cyst wall consists of a thin (about 0.5 μm) and smooth endophragm and a very thin (less than 0.5 μm), smooth, hyaline, delicate and finely wrinkled periphram. The endophragm is closely appressed to the periphragm except at the horns and occasionally along the hypocystal flanks. The cingulum is rarely visible and indicated by irregular fine folds or ridges. The sulcus is rarely expressed by a slight longitudinal depression and/or folds. When present, the intercalary archeopyle is of type 2a. The operculum is free.

Derivation of name. From Greek *elongatus* meaning elongate, with reference to the elongate shape of this species.

Holotype. Plate 8, figs. 2, 3, sample OH 6, slide 2, England Finder coordinates L57/2. Specimen dimensions: Total length 105 μm ; central body length 89 μm ; breadth 70 μm .

Paratype. Plate 7, figs. 9, 10, sample OH 10, slide 1, England Finder coordinates O46/2. Specimen dimensions: Total length 93 μm ; central body length 80 μm ; breadth 63 μm .

Type locality. Ouled Haddou section, north of Taza, northern Morocco.

Type stratum. Lower Danian, clayey marls, at 10 cm above the K–Pg boundary.

Dimensions of measured specimens. Total length 60(80)105 μm . Central body length 58(77)82 μm . Breadth 45(61)80 μm . (14 specimens measured).

Discussion. *Phelodinium elongatum* sp. nov. is characterized by its elongate and rounded pentagonal shape with or without antapical shallow depression and by its delicate and finely folded periphram with slightly expressed cingulum. It resembles *Lejeunecysta globosa* Biffi & Grignani 1983 in its overall shape but differs in being elongate and cornucavate. *Phelodinium gaditanum* (Riegel 1974) Riegel & Sarjeant 1982 differs from the new species in being wider than long with clearly expressed cingulum.

Stratigraphic occurrence. Samples OH 2–18, planktonic foraminiferal *Abathomphalus mayaroensis* Zone (Upper Maastrichtian) and *Guembelitra cretacea* and *Parvularugoglobigerina eugubina* zones (Lower Danian), Ouled Haddou section.

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Appendix 1.

Dinoflagellate cysts from the Ouled Haddou section (northern Morocco) used in the text and illustrated in the plates, listed alphabetically by genera. The generic allocation of taxa follows dinoflag 2 (Fensome et al. 2008), Willumsen (2004) and Slimani et al. (2008). Illustrated taxa are followed by plate and figure references in parenthesis.

- Achomospaera alicornu* (Eisenack 1954) Davey & Williams 1966
- Alisogymnium euclaense* (Cookson & Eisenack 1970) Lentin & Vozzhennikova 1990 (Plate 1, Fig. 20)
- Andalusiella acicornuta* Srivastava 1995 (Plate 8, Fig. 13)
- Andalusiella dubia* (Jain & Millepied 1973) Lentin & Williams 1980 (Plate 9, Fig. 16)
- Andalusiella gabonensis* (Stover & Evitt 1978) Wrenn & Hart 1988 (Plate 9, Fig. 9)
- Andalusiella mauthei* Riegel 1974 subsp. *aegyptiaca* (Schrank 1988) Masare et al. 1996 (Plate 8, Fig. 14)
- Andalusiella mauthei* Riegel 1974 subsp. *mauthei* (Plate 8, Fig. 15)
- Andalusiella mauthei* Riegel 1974 subsp. *punctata* (Jain & Millepied 1973) Masare et al. 1996 (Plate 9, Fig. 8)
- Andalusiella polymorpha* (Malloy 1972) Lentin & Williams 1977 (Plate 8, Fig. 16)
- Andalusiella rhomboides* (Boltenhagen 1977) Lentin & Williams 1980 (Plate 8, Fig. 8)
- Andalusiella spicata* (May 1980) Lentin & Williams 1981 (Plate 9, Fig. 10)
- Andalusiella* sp. A (Plate 9, Figs. 1–2)
- Apteodinium fallax* (Morgenroth 1968) Stover & Evitt 1978 (Plate 1, Figs. 9–10)
- Areoligera senonensis* Lejeune-Carpentier 1938 (Plate 4, Fig. 12)
- Batiacasphaera rifensis* Slimani 2008 (Plate 1, Fig. 21)
- Carpatella cornuta* Grigorovich 1969 (Plate 3, Fig. 1)
- Capatella septata* Willumsen 2004 (Plate 3, Figs. 2–3)
- Carpatella?* sp. cf. *Cribroperidinium* sp. A of Brinkhuis & Schiøler 1996 (Plate 3, Fig. 4)
- Cassiculosphaeridia? intermedia* Slimani 1994 (Plate 1, Fig. 23)

- Cassidium fragile* (Harris 1965) Drugg 1967 (Plate 4, Fig. 11)
Cerodinium diebelii (Alberti 1959) Lentin & Williams 1987 subsp. *diebelii* (Plate 6, Fig. 3)
Cerodinium mediterraneum Slimani 2008 (Plate 7, Fig. 4)
Cerodinium navarricum (Srivastava 1995) Williams et al. 1998 (Plate 9, Fig. 11)
Cerodinium pannuceum (Stanley 1965) Lentin & Williams 1987 (Plate 9, Fig. 5)
Cerodinium speciosum subsp. *speciosum* Alberti 1959
Cerodinium striatum (Drugg 1967) Lentin & Williams 1987 (Plate 7, Fig. 8)
Chatangiella spectabilis (Alberti 1959) Lentin & Williams 1976 (Plate 8, Fig. 7)
Chatangiella aff. *verrucosa* (Manum 1963) Lentin & Williams 1976 (Plate 9, Fig. 17)
Cordosphaeridium exilimurum Davey & Williams 1966 (Plate 6, Fig. 7)
Cordosphaeridium inodes (Klumpp 1953) Eisenack 1963 subsp. *inodes* (Plate 6, Fig. 8)
Cordosphaeridium inodes subsp. *longipes* Hansen 1977 (Plate 6, Fig. 2)
Coronifera sp. cf. *Coronifera?* *tubulosa* Cookson & Eisenack 1974 (Plate 10, Fig. 1–2)
Cribroperidinium cooksoniae Norvick 1976 (Plate 3, Fig. 6)
Cribroperidinium? *pyrum* (Drugg 1967) Stover & Evitt 1978 (Plate 4, Fig. 5)
Damassadinium californicum (Drugg 1967) Fensome et al. 1993 (Plate 4, Fig. 7)
? *Damassadinium fibrosum* (Hultberg 1985) Fensome et al. 1993 (Plate 4, Figs. 3–4)
Damassadinium spinosum Slimani 2008 (Plate 4, Fig. 13)
Deflandrea galeata (Lejeune-Carpentier 1942) Lentin & Williams 1973 (Plate 7, Fig. 1)
Deflandrea severnensis Benson 1976 (Plate 8, Fig. 17)
Dinogymnium acuminatum Evitt et al. 1967 (Plate 7, Fig. 12)
Dinogymnium cretaceum (Deflandre 1936) Evitt et al. 1967 (Plate 1, Fig. 19)
Dinogymnium nelsonense (Cookson 1956) Evitt et al. 1967 (Plate 1, Fig. 24)
Diphyes colligerum (Deflandre & Cookson 1955) Cookson 1965 (Plate 10, Fig. 12)
Disphaerogena carposphaeropsis Wetzel 1933 (Plate 6, Fig. 4)
Eisenackia circumtabulata Drugg 1967 (Plate 1, Figs. 11–12)
Eisenackia crassitabulata Deflandre & Cookson 1955 (Plate 1, Figs. 13–14)
Eisenackia msounensis Slimani 2008 (Plate 1, Figs. 17–18)
Eisenackia reticulata (Damassa 1979) Quattrocchio & Sarjeant 2003 (Plate 1, Figs. 15–16)
Endoscrinium? *novissimum* (Morgenroth 1968) Riding & Fensome 2002 (Plate 8, Figs. 10–11)
Fibrocysta axialis (Eisenack 1965) Stover & Evitt 1978 (Plate 6, Fig. 1)
Fibrocysta bipolaris (Cookson & Eisenack 1965) Stover & Evitt 1978 (Plate 4, Fig. 6)
Fibrocysta licia (Jain et al. 1975) Stover & Evitt 1978 (Plate 4, Figs. 8–10)
Fibrocysta ovalis (Hansen 1977) Lentin & Williams 1981 (Plate 6, Fig. 5)
Fibrocysta sp. A of Brinkhuis & Schiøler 1996 (Plate 4, Figs. 1–2)
Geiselodinium psilatatum Jain & Milleped 1973
Glaphyrocysta castelcasiensis (Corradini 1973) Michoux & Soncini in Fauconnier & Masure 2004 (Plate 5, Figs. 4–5)
Glaphyrocysta expansa (Corradini 1973) Roncaglia and Corradini 1997 (Plate 5, Fig. 11)
Glaphyrocysta ordinata (Williams & Downie 1966) Stover & Evitt 1978 (Plate 4, Fig. 16)
Glaphyrocysta perforata Hultberg & Malmgren 1985 (Plate 5, Fig. 12)
Glaphyrocysta semitecta (Bujak in Bujak et al. 1980) Lentin & Williams 1981 (Plate 5, Fig. 6)
Hafniasphaera septata (Cookson & Eisenack 1967) Hansen 1977 (Plate 9, Fig. 18)
Hystrichokolpoma bulbosum subsp. *bulbosum* (Ehrenberg 1838) Morgenroth 1968 (Plate 10, Fig. 13)
Hystrichokolpoma sp. cf. *Hystrichokolpoma rigaudiae* Deflandre & Cookson 1955 (Plate 10, Figs. 14–15)
Hystrichokolpoma sp. cf. *Hystrichokolpoma truncatum* Biffi & Manum 1988 (Plate 10, Figs. 17–18)
Hystrichosphaeropsis ovum Deflandre 1935 (Plate 10, Fig. 16)
Hystrichostrogylon coninckii Heilmann-Clausen in Thomsen & Heilmann-Clausen, 1985 (Plate 9, Fig. 14)
Impagidinium celinae Jan du Chêne 1988 (Plate 2, Figs. 13–15)
Impagidinium maghribensis Slimani 2008 (Plate 2, Fig. 24)
Impagidinium sp. cf. *I. patulum* (Wall 1967) Stover & Evitt 1978 (Plate 2, Figs. 3–4)
Impagidinium sp. 1 of Thomsen & Heilmann-Clausen 1985 (Plate 2, Figs. 6–8)
Impletosphaeridium clavulum (Davey 1969) Islam 1993 (Plate 10, Fig. 3)
Isabelidinium bakeri (Deflandre & Cookson 1955) Lentin & Williams 1977 (Plate 8, Fig. 4)
Kallosphaeridium parvum Jan du Chêne, 1988 (Plate 1, Fig. 5)
Kallosphaeridium yorubaense Jan du Chêne & Adediran 1985 (Plate 1, Figs. 1–2)
Kenleyia leptocerata Cookson & Eisenack 1965 (Plate 3, Fig. 9)
Kenleyia lophophora Cookson & Eisenack 1965 (Plate 3, Fig. 5)
Kenleyia pachycerata Cookson & Eisenack 1965 (Plate 3, Fig. 10)
Kenleyia? sp. A (Plate 3, Fig. 7–8)
Lanternosphaeridium lanosum Morgenroth 1966 (Plate 6, Fig. 6)
Lanternosphaeridium reinhardtii? Habib in Moshkovitz & Habib 1993 (Plate 3, Figs. 14–15)
Lejeunecysta communis Biffi & Grignani 1983 (Plate 7, Fig. 7)
Lejeunecysta decorinassa Srivastava 1995 (Plate 7, Fig. 6)
Lejeunecysta globosa Biffi & Grignani 1983 (Plate 7, Fig. 2)
Lejeunecysta hyalina (Gerlach 1961) Artzner & Dörhöfer 1978 (Plate 7, Fig. 13)
Lejeunecysta izerzenensis Slimani 2008 (Plate 7, Fig. 11)
Lingulodinium bergmannii (Archangelsky 1969) Quattrocchio & Sarjeant 2003 (Plate 10, Fig. 7)
Magallanesium densispinatum (Stanley 1965) Quattrocchio & Sarjeant 2003 (Plate 8, Fig. 9)
Magallanesium pilatum (Stanley 1965) Quattrocchio & Sarjeant 2003 (Plate 8, Fig. 12)
Manumiella seelandica (Lange 1969) Bujak & Davies 1983 (Plate 8, Fig. 1)
Membranilarnacia? *tenella* Morgenroth 1968 (Plate 1, Fig. 22)
Micrhystridium fragile Deflandre 1948 (Plate 10, Fig. 9)
Muratodinium fimbriatum (Cookson & Eisenack 1967) Drugg 1970 (Plate 6, Fig. 9)
Oligosphaeridium sp. cf. *Homotryblium* sp. of Brinkhuis & Zachariasse 1988 (Plate 10, Fig. 10)
Operculodinium centrocarpum (Deflandre & Cookson 1955) Wall 1967 subsp. *centrocarpum* (Plate 10, Fig. 5)
Operculodinium israelianum (Rossignol 1962) Wall 1967 (Plate 10, Fig. 4)

- Palaeocystodinium australinum* (Cookson 1965) Lentin & Williams 1976 (Plate 9, Fig. 7)
- Palaeocystodinium bulliforme* Ioannides 1986 (Plate 9, Fig. 4)
- Palaeocystodinium golzowense* Alberti 1961 (Plate 9, Fig. 6)
- Palaeocystodinium* sp. B of Oboh-Ikuenobe et al. 1998 (Plate 9, Fig. 3)
- Palaeohystrichophora infusorioides* Deflandre 1935 (Plate 10, Fig. 11)
- Palynodinium grallator* Gocht 1970 (Plate 7, Figs. 15–16)
- Phelodinium africanum* Biffi & Grignani 1983 (Plate 7, Fig. 14)
- Phelodinium elongatum* sp. nov. (Plate 3, Fig. 11; Plate 7, Figs. 9–10; Plate 8, Figs. 2–3)
- Phelodinium gaditanum* (Riegel 1974) Lentin and Williams 1981 (Plate 7, Fig. 3)
- Phelodinium magnificum* (Stanley 1965) Stover and Evitt 1978 (Plate 7, Fig. 5)
- Pierceites pentagonus* (May 1980) Habib & Drugg 1987 (Plate 8, Fig. 6)
- Pilosodinium capillatum* (Davey 1975) Courtinat in Fauconnier & Masure 2004 (Plate 1, Figs. 3–4)
- Pterodinium cingulatum* subsp. *danicum* Jan du Chêne 1988 (Plate 2, Figs. 9–10)
- Pterodinium cretaceum* Slimani 2008 (Plate 2, Figs. 11–12)
- Pyxidinospis ardonensis* Jan du Chêne 1988 (Plate 1, Figs. 6–8)
- Renidinium gracile* Hultberg & Malmgren 1985 (Plate 4, Figs. 14–15)
- Riculacysta amplexa* Kirsch 1991 (Plate 5, Figs. 7–8)
- Riculacysta* sp. of Soncini & Rauscher 1988 (Plate 3, Figs. 12–13)
- Riculacysta* sp. cf. *Riculacysta* sp. A of Kirsch 1991 (Plate 5, Fig. 10)
- Senegalinium bicavatum* Jain & Milleped 1973 (Plate 10, Fig. 22)
- Senegalinium?* *dihwynense* (Cookson & Eisenack 1965) Stover & Evitt 1978
- Senegalinium laevigatum* (Malloy 1972) Bujak & Davies 1983 (Plate 10, Fig. 20)
- Senegalinium microgranulatum* (Stanley 1965) Stover & Evitt 1978 (Plate 10, Fig. 23)
- Senegalinium microspinosum* (Boltenhagen 1977) Lentin & Williams 1980 (Plate 10, Fig. 24)
- Senegalinium obscurum* (Drugg 1967) Stover & Evitt 1978 (Plate 10, Fig. 21)
- ?*Senegalinium* sp. D. of Jain & Millieped 1973 (Plate 9, Fig. 13)
- Senoniasphaera inornata* (Drugg 1970) Stover & Evitt 1978 (Plate 5, Fig. 9)
- Spiniferella cornuta* subsp. *laevimura* (Davey & Williams 1966) Williams et al. 1998 (Plate 2, Fig. 1)
- Spiniferella* sp. cf. *Spiniferites* sp. A of Kirsch 1991 (Plate 2, Fig. 2)
- Spiniferites* sp. cf. *Spiniferites hyperacanthus* of Jan du Chêne 1988 (Plate 10, Fig. 19)
- Spiniferites twistringiensis* (Maier 1959) Fensome et al. 1990 (Plate 2, Fig. 5)
- Tanyosphaeridium regulare* Davey & Williams 1966 (Plate 10, Fig. 6)
- Tanyosphaeridium xanthiopyxides* (Wetzel 1933) Stover & Evitt 1978 (Plate 10, Fig. 8)
- Thalassiphora bononiensis* Corradini 1973
- Thalassiphora patula* (Williams & Downie 1966) Stover & Evitt 1978 (Plate 5, Fig. 2)
- Thalassiphora pelagica* (Eisenack 1954) Eisenack & Gocht 1960 (Plate 5, Fig. 1)
- Trithyrodinium evittii* Drugg 1967 (Plate 9, Fig. 12)
- Trithyrodinium fragile* Davey 1969 (Plate 8, Fig. 5)
- Trithyrodinium striatum* Benson 1976 (Plate 9, Fig. 15)
- Turbiosphaera filosa* (Wilson 1967) Archangelsky 1969
- Turbiosphaera galatea* Eaton 1976 (Plate 5, Fig. 3)
- Ynezidinium pentahedrias* (Damassa 1979) Lucas-Clark & Helenes 2000 (Plate 2, Figs. 21–23)
- Ynezidinium tazaensis* Slimani 2008 (Plate 2, Figs. 16–17)
- Ynezidinium malloyi* Lucas-Clark & Helenes 2000 (Plate 2, Figs. 18–20)