

MORPHOLOGY AND DISTRIBUTION OF THE MIOCENE DINOFLAGELLATE CYST *OPERCULODINIUM?* *BORGERHOLTENSE* LOUWYE 2001, EMEND.

ALI SOLIMAN
Karl-Franzens University, Graz
Institute of Earth Sciences (Geology and Palaeontology)
Heinrichstrasse 26, A-8010 Graz
Austria
e-mail: ali.soliman@uni-graz.at
and
Geology Department
Faculty of Science
Tanta University
Tanta 31527
Egypt

MARTIN J. HEAD
Department of Earth Sciences
Brock University
500 Glenridge Avenue
St. Catharines, Ontario L2S 3A1
Canada
e-mail: mjhead@brocku.ca

STEPHEN LOUWYE
Research Unit Palaeontology
Ghent University, Krijgslaan 281/S8
B-9000 Ghent
Belgium
e-mail: Stephen.Louwye@ugent.be

Abstract

The extinct, organic-walled, proximochorate dinoflagellate cyst *Operculodinium? borgerholtense* Louwye 2001 was first described from Miocene shallow-marine deposits of northern Belgium, and has since been documented from the Miocene of the eastern North Atlantic, North Sea, Austria, Hungary, and Egypt. Conventional and confocal light microscopy and scanning electron microscopy are used to reveal new details of the archeopyle, wall structure, and ornament. The archeopyle is shown to have well-defined rather than rounded angles, a distinction we consider significant in assigning this species only provisionally to the genus *Operculodinium? borgerholtense* was a euryhaline neritic species highly tolerant of environmental stress, a feature consistent with its morphological variability. Present records indicate a tropical–subtropical to temperate paleoclimatic distribution. It ranges from the upper Lower Miocene to upper Middle Miocene, and promises to be a useful stratigraphic marker particularly in neritic settings where adverse paleoenvironmental factors have excluded other species.

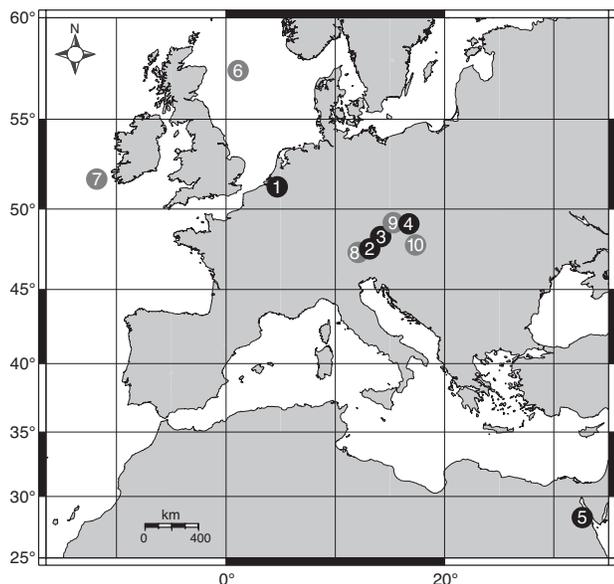
Key words: *Operculodinium? borgerholtense*; Miocene dinoflagellate cysts; morphology; taxonomy.

INTRODUCTION

Operculodinium? borgerholtense Louwye 2001 was formally described from the Lower to Middle Miocene Berchem Formation near Antwerp in northern Belgium (Louwye, 2001; Text-Figure 1). It was placed in the subfamily Cribroperidinioideae, but assigned questionably to the genus *Operculodinium* on account of the unusual development of low ridges demarcating the antapical plate (Text-Figure 2).

Operculodinium? borgerholtense is a distinctive cyst species, but its thin wall folds readily and this may explain why it has escaped the attention of palynologists until recently. Our study nonetheless shows this species to be a conspicuous and persistent component of neritic assem-

blages in the Miocene of the eastern North Atlantic, North Sea, Austria, Hungary and Egypt (Text-Figure 1), and future studies will undoubtedly expand this geographic range. The present study aims to refine our understanding of the morphology of this important species, and reassess its taxonomic position. We have done this by re-examining the holotype (Plate 1; Plate 2, figs. 11–20) and paratype (Plate 2, figs. 1–10) under the light microscope (LM) and the holotype under the confocal microscope (Plate 1), as well as by studying numerous specimens from Belgium, Austria, and Egypt under the scanning electron microscope (SEM; Plate 3). The species has been emended accordingly, but its provisional assignment to *Operculodinium* is maintained pending revision of this genus.

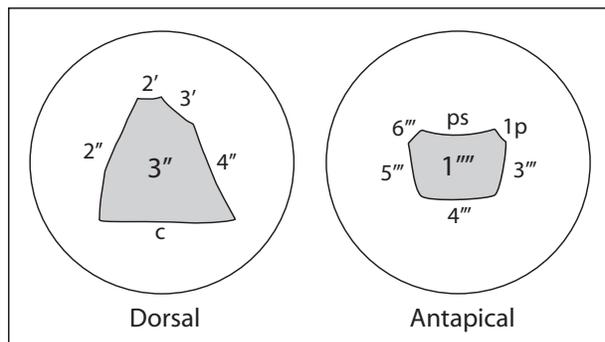


Text-Figure 1. Geographic distribution of recorded occurrences for *Operculodinium? borgerholtense*. Black circles indicate the location of samples examined by SEM in the present study: 1, Borgerhout Rivierenhof section near Antwerp, Belgium (the type locality); 2, Retznei surface section, Austria; 3, Waltersdorf-1 borehole, Austria; 4, Bad Deutsch Altenburg, Austria; and 5, Kareem-30 borehole, Egypt. Dark gray circles (or black where overlapping) indicate the location of additional occurrences recorded/verified by the present authors: 1, Zonderschot, Belgium; 5, East Shukheir-1, Shukheir-1, and Shukheir-11 boreholes, Egypt; 6, several commercial wells in the U.K. sector of the central North Sea; 7, IODP Hole 1318B, Porcupine Basin; 8, Wagner, Austria; 9, Baden-Sooss, Austria; and 10, Tengelic-2 borehole, Hungary.

Finally, we have also compiled published and unpublished records of *Operculodinium? borgerholtense* to elucidate its stratigraphic range and autecology.

THE GENUS *OPERCULODINIUM* WALL 1967

Operculodinium Wall 1967 emend. Matsuoka et al. 1997 is a large Cenozoic cyst-defined genus defined broadly to contain species characterised by a spherical to ovoidal central body bearing cones or short to long processes with circular bases, and a precingular archeopyle formed by loss of plate 3'' (Wall, 1967). The processes are diagnosed as having a nontabular to intratabular distribution (Matsuoka et al., 1997). The type species *Operculodinium centrocarpum* (Deflandre & Cookson 1955) Wall 1967 emend. Matsuoka et al. 1997, described from the Miocene of Australia, has a central body with a



Text-Figure 2. Schematic representation of the tabulation on *Operculodinium? borgerholtense* showing the asymmetrical 1P archeopyle with well-developed angles, and subrectangular appearance of the sexiform antapical plate. Based largely on the paratype (Plate 2, figs. 1–10).

distinctive fibroreticulate outer wall layer, and processes that are minutely expanded distally. It also has an archeopyle with rounded rather than well-defined angles, i.e. presumably not congruent with the thecal plate boundaries (Evitt, 1985, fig. 6.1 E, F). This feature was overlooked in the re-diagnosis of this species, and indeed of the genus itself, but would be a useful feature to consider in any re-assessment of the genus. Because many species currently assigned to the genus *Operculodinium* lack some or all of the distinctive features of the type, a review of *Operculodinium*, while beyond the scope of the present work, is long overdue.

Wall (1967) and Matsuoka et al. (1997) assigned the genus *Operculodinium* to the family Gonyaulacaceae. Wall and Dale (1966) had previously attributed modern cysts of the theca-defined species *Protoceratium reticulatum* (Claparède & Lachmann 1859) Bütschli 1885 to *Operculodinium centrocarpum* (as *Baltisphaeridium centrocarpum* [Deflandre & Cookson 1955] Gerlach 1961). While this attribution was in error because the cysts of *Protoceratium reticulatum* are smaller and more delicate than *Operculodinium centrocarpum* (Head and Wrenn, 1992; Head, 1996a), the two cyst types are otherwise very similar. Fensome et al. (1993) included *Protoceratium*, and by extension *Operculodinium*, questionably in the subfamily Cribroperidinioideae Fensome et al. 1993. The Cribroperidinioideae includes many other species whose archeopyles have rounded angles.

Our new observations of *Operculodinium? borgerholtense* show the archeopyle to have angles that are well defined, and not rounded as originally stated. We consider archeopyle angularity relevant to the systematic position of *Operculodinium? borgerholtense*.

MATERIALS AND METHODS

The following samples were analysed using the SEM (Text-Figure 1): nine samples from the Middle Miocene of the Kareem-30 Borehole (28°20'N; 33°5'E), Gulf of Suez, Egypt (Soliman et al., 2004; Soliman, 2006); one sample from the Middle Miocene Weissenegg Formation at Retznei, Styrian Basin, Austria (Erhart and Piller, 2004); one sample from the Middle Miocene of the Waltersdorf-1 Borehole (WA-RAG4, K3/927-936/Ki 5/058-068), Styrian Basin, Austria (Soliman and Piller, 2004); seven core samples from the Middle Miocene Leitha Formation at Bad Deutsch Altenburg (Hainburg) in the eastern part of the Vienna Basin, Austria (Gross, 2002; Soliman and Piller, 2007b); and two samples (XIBR15 and XIBR16) from the uppermost Lower? to Middle Miocene Borgerhout Rivierenhof section near Antwerp, Belgium (Louwye, 2001), which is the type locality for the species. Samples prepared for SEM analysis were processed using standard methods including HCl, HF, mild oxidation with HNO₃ (except for the Retznei sample), and sieving at 10 or 20 µm. Specimens were observed using a DSM 982 GEMINI SEM at 10–15 kV at the Institute for Earth Sciences (Geology and Palaeontology), Karl-Franzens University, Graz; where the residues and SEM stubs are now housed.

Specimens from the above localities were also examined using the LM, and specimens from the Middle Miocene Tengelic-2 borehole in Hungary and the Middle Miocene Baden-Sooss locality in Austria (Jiménez-Moreno et al., 2006; Rögl et al., 2008) were re-examined under LM.

Both the holotype and paratype of *O.?* *borgerholtense* were also re-examined under the LM. In addition, the holotype was examined under a EZC1-Nikon confocal microscope, with images rendered using VGStudioMax, at the Laboratory of General Biochemistry and Physical Pharmacy, Ghent University.

The Kofoid system of labelling applied to the standard gonyaulacalean pattern was used throughout.

SYSTEMATIC PALEONTOLOGY

- 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 GONYAULACALES Taylor 1980
- Suborder GONYAULACINEAE (Autonym)
- Family GONYAULACACEAE Lindemann 1928
- Subfamily UNCERTAIN

Genus *Operculodinium* Wall 1967
emend. Matsuoka et al. 1997 (?)

Type. The holotype of *Operculodinium centrocarpum* (Deflandre & Cookson 1955) Wall 1967 emend. Matsuoka et al. 1997.

Operculodinium? borgerholtense Louwye 2001 emend.
Text-Figures 1–4, Plates 1–3.

Operculodinium sp. 1. Louwye, 2000, tab. 1.

Operculodinium? borgerholtense Louwye, 2001, p. 126, figs. 4.1–4.12; Jiménez-Moreno et al., 2006, pl. 2, figs. 1–5, pl. 9, fig. 7; Soliman, 2006, p. 54–56, pl. 39, figs. 5–22, text-fig. 22; Soliman and Piller, 2007a, p. 411, pl. 1, figs. 6–12.

Original diagnosis. Spherical to ovoid proximochoerate cyst ornamented with low, granulate prismatic luxuriae and numerous, long virgae. The distribution of the granules and simple, solid virgae is non-tabular. The virgae are acuminate, capitate or bifurcated. A low septum located at the antapex arises directly from the pedium and forms an irregular polygon. The geometry of this septum conforms to the outline of an antapical plate in a gonyaulacoid sexiform hypocystal pattern. The archeopyle is formed by the release of the third precingular plate. The operculum is free. (Louwye, 2001; p. 126, 127.)

Emended diagnosis. Small, thin-walled proximochoerate cyst with spherical to subspherical central body bearing numerous solid erect processes and lower ornament. Processes nontabular, smooth or with granules, spinules, and short irregular branches. Lower ornament varies from low verrucae to round-topped coni, round-topped baculae, and clavae. Low bounding septum and more densely ornamented surface demarcate six-sided antapical plate of subrectangular shape. Archeopyle precingular (3") with well-defined angles, no accessory sutures. Operculum free.

Types. Holotype, specimen IRScN b3668, Sample BR15, Slide P1, England Finder reference H39/3; Plate 1, figs. 1–3; Plate 2, figs. 11–20. Also figured in Louwye (2001, fig. 4.1–4.5). Paratype (here designated), specimen IRScN b5054, Sample BR5a, Slide P1, England Finder reference N39/1; Plate 2, figs. 1–10. Also figured in Louwye (2001, fig. 4.8–4.10). Holotype is late Langhian–early Serravallian in age; paratype is latest Burdiglian? to early Langhian; ages based on dinoflagellate cyst biostratigraphy. Both types from the Antwerp Sands Member (uppermost Lower? to upper Middle Miocene) of the Berchem Formation, Belgium. Both types deposited at the Institut royal des Sciences naturelles de Belgique, in Brussels.

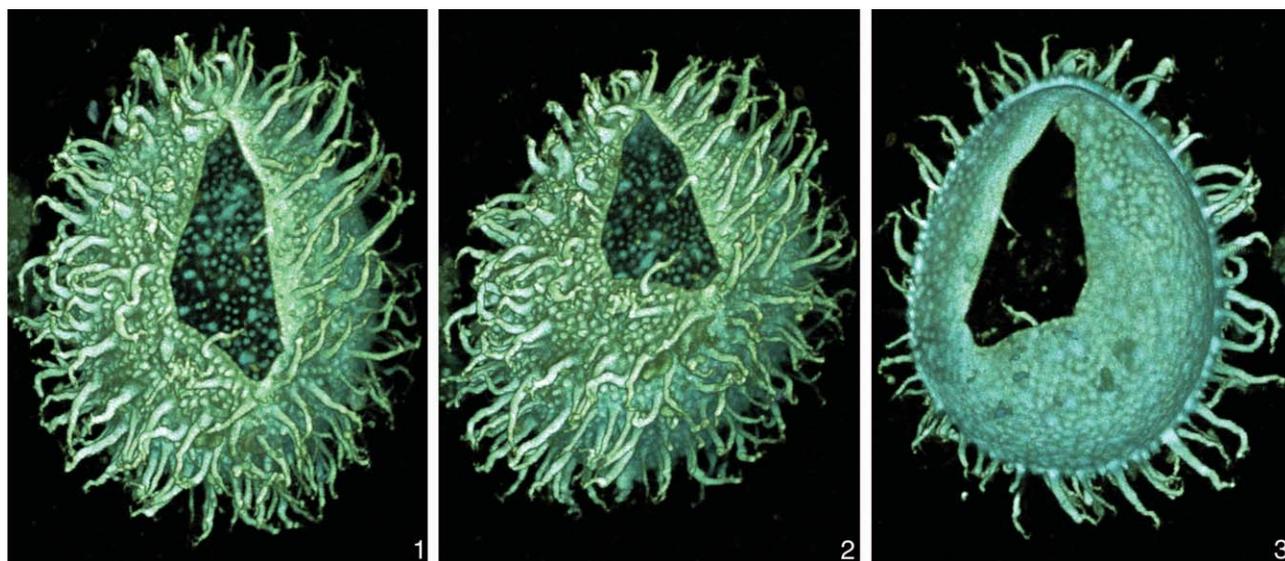


Plate 1

Confocal images of the holotype of *Operculodinium? borgerholtense* from the Antwerp Sands Member (uppermost Lower? to upper Middle Miocene) of the Berchem Formation, Belgium. Central body length = 38 μm .

- | | | | |
|---|---|---|--|
| 1 | Dorsal view of dorsal surface. | 3 | Optical section and internal view of dorsal surface. |
| 2 | Same as Fig. 1 but at a slightly different angle of view. | | |

Type locality. ‘Borgerhout Rivierenhof’ outcrop, Borgerhout, Antwerp Province, Belgium; for both holotype and paratype. A full description of the outcrop, lithology and position of the samples is given by De Meuter et al. (1976, p. 13, fig. 18).

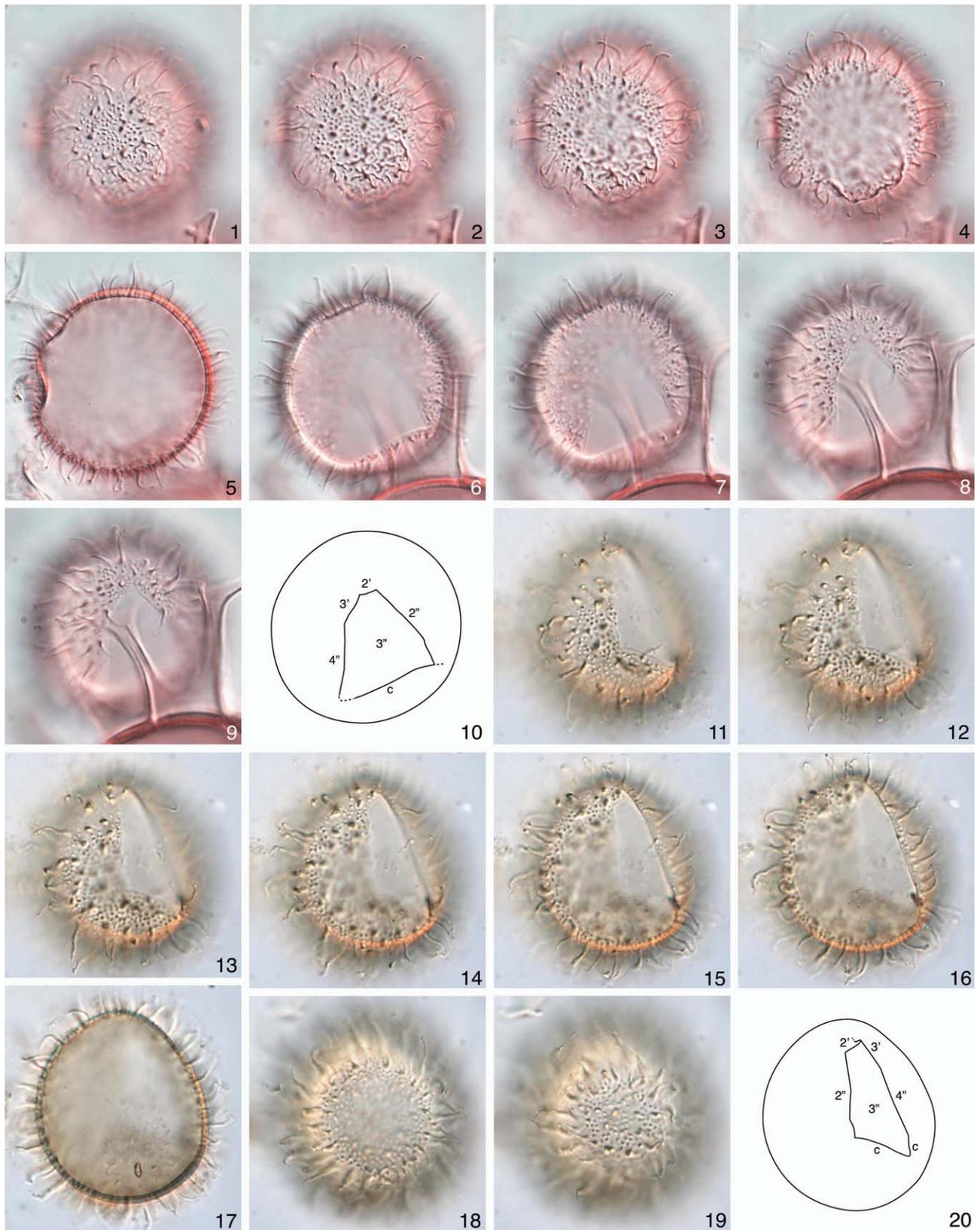
Emended description. Central body thin walled (ca. 0.2–0.3 μm), spherical to subspherical in shape, bearing

numerous solid processes and lower ornament. Processes and lower ornament nontabular and fairly evenly distributed over cyst, except in antapical area. Central body wall unstructured under LM but three appressed layers distinguishable under SEM: solid smooth thin inner and outer layers (ca. 0.03 μm) and much thicker densely granulate middle layer (Plate 3, fig. 11 and inset). Structure continu-

Plate 2

The paratype and holotype of *Operculodinium? borgerholtense* from the Antwerp Sands Member (uppermost Lower? to upper Middle Miocene) of the Berchem Formation, Belgium. All figures are interference contrast images, except for Figs. 10 and 20 which are tracings of the paratype and holotype respectively.

- | | | | |
|------|--|-------|--|
| 1–10 | Paratype (here designated), specimen IRScN b5054, Sample BR5a, Slide P1, England Finder ref. N39/1, in ventro-antapical view. Figs. 1–9 at successively lower foci. Figs. 1–4 show the antapical plate bounded by low ridges, Fig. 5 is an optical section through the central body, and Figs. 6–9 show the precingular archeopyle. Fig. 10 is a tracing and shows the precingular archeopyle on the lower surface of the cyst. Central body maximum diameter = 36 μm . | 11–20 | Holotype, specimen IRScNb3668, Sample BR15, Slide P1, England Finder ref. H39/3, in left latero-dorsal view. The ovoidal shape is due to distortion. Figs. 11–19 at successively lower foci. Figs. 13–16 show the precingular archeopyle which is distorted, Fig. 17 is an optical section through the central body, and Figs. 18–19 show the right latero-ventral surface. Fig. 20 is a tracing and shows the distorted precingular archeopyle on the upper surface of the cyst. Antapical plate not visible, presumably owing to spherical concealment of antapical region. Central body length = 38 μm . |
|------|--|-------|--|

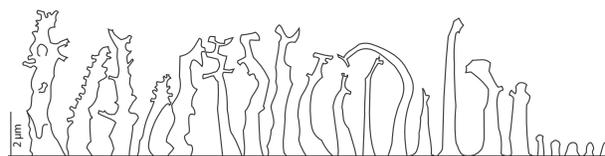


ous with lower ornament and presumably also with processes.

Processes erect, narrow, initially of approximately even thickness and straight, tapering and often sinuous distally. Processes may be smooth for entire length but more commonly have granules, spinules, and short irregular branches, particularly along their distal half (as in holotype, but see Text-Figure 3 for full morphological range). Separation between adjacent process bases typically ca. 1.9–3.5 μm .

Lower ornament ca. 0.3–0.7 μm in diameter and 0.6–1.0 μm high, conspicuous, varies from low verrucae to round-topped conical, round-topped narrow baculae, and occasionally clavae (Plate 3, fig. 7). Elements evenly distributed, typically separated from each other by one to two, or occasionally three times their diameter. Elements may be somewhat more sparsely distributed on specimens with smooth processes. Occasionally some, but never all, elements fused into low discontinuous ridges (Plate 3, figs. 4, 5, 9).

At antapex, low (less than 1.5 μm) almost continuous (Plate 2, figs. 1–4) to discontinuous (Plate 3, figs. 2, 3) septum demarcates six-sided antapical plate. Contact with posterior sulcal plate (which overlaps antapical plate) is long and concave; contacts with posterior intercalary and sixth postcingular plates are short; resulting in subrectangular shape of antapical plate (Text-Figure 2). Ornament on antapical plate more densely clustered and irregular than elsewhere, with many adjacent elements fused at base (Plate 3, figs. 2, 3, 13, 14), and central body surface may be finely pitted (diameter, 0.05–0.20 μm) as seen in Plate 3, figs. 3, 14.



Text-Figure 3. Schematic representation of variation in process morphology and lower ornamentation on *Operculodinium? borgerholtense*.

Archeopyle formed by release of third precingular plate; margin entire, well-defined angles, no accessory sutures (Text-Figure 2). Archeopyle margin may be slightly raised and thickened, as observed under SEM (Plate 3, fig. 1). Operculum free.

No other indications of tabulation.

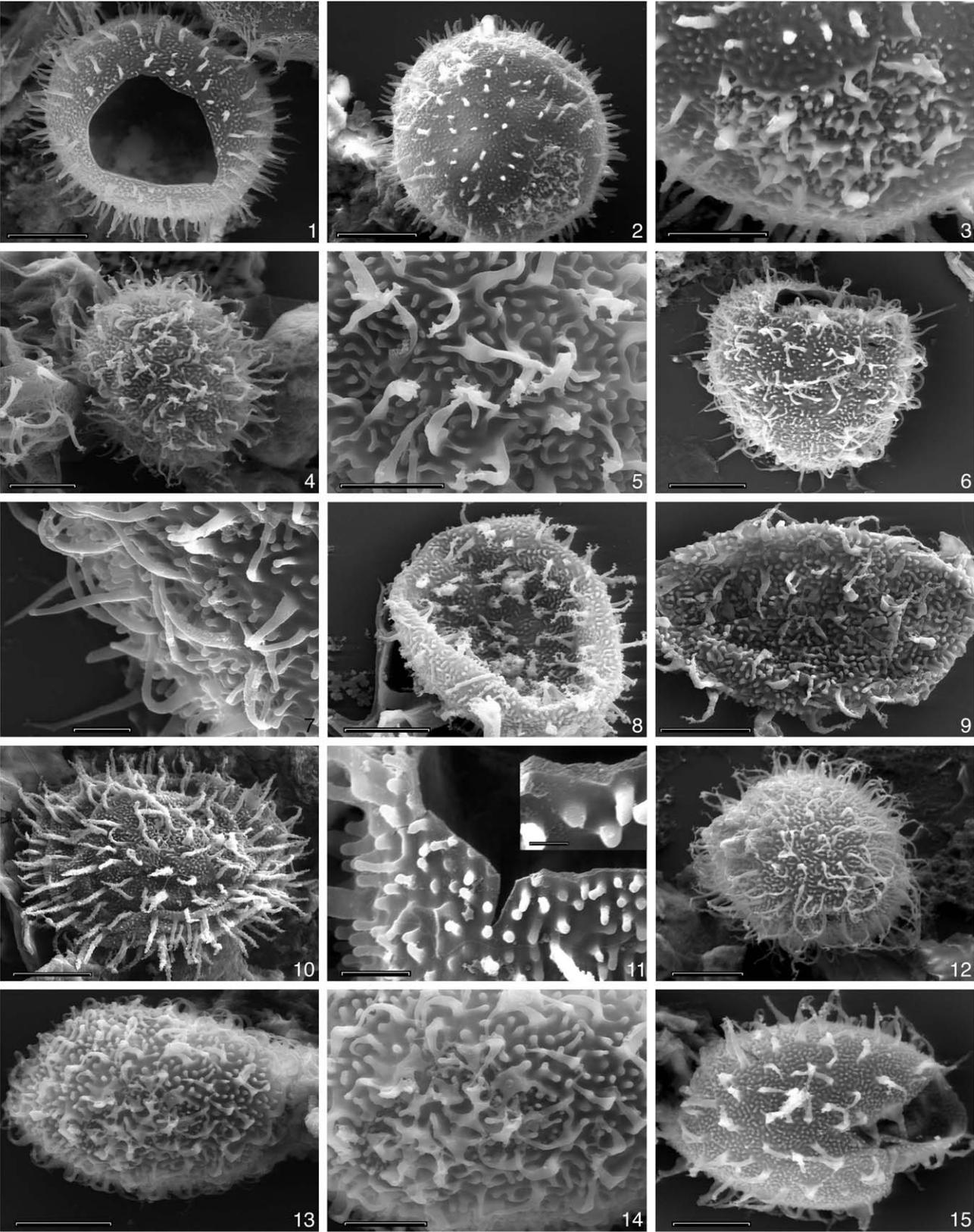
Dimensions. Holotype: central body length, 38 μm , central body equatorial diameter, 35 μm , length of processes, 6–7 μm . Paratype: central body maximum diameter, 36 μm , length of processes, 5–6 μm . Range based on all specimens measured in the present study: central body maximum diameter, 23(32.8)41 μm , length of processes, 2.5(5.6)8.5 μm ; 73 specimens measured (Text-Figure 4, Table 1). Average process width, 0.5(0.74)1.1 μm ; 12 specimens measured under SEM.

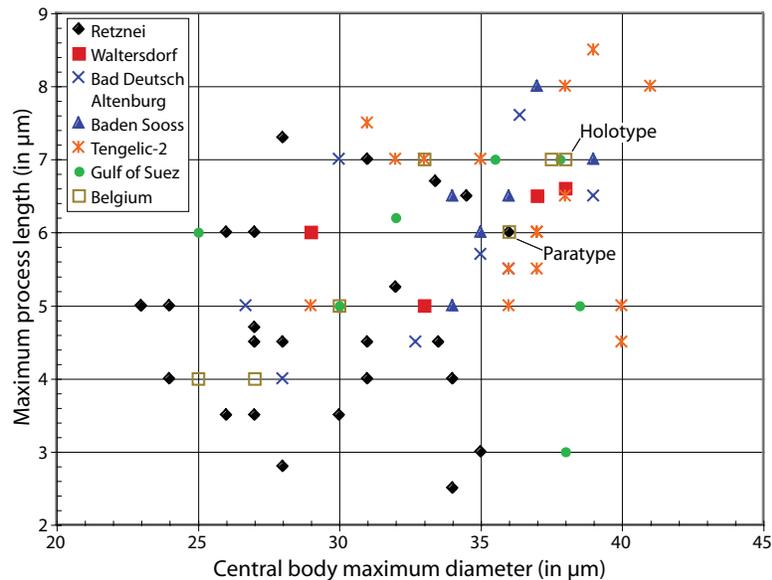
Comparison. *Operculodinium? eirikianum* Head et al. 1989 emend. Head 1997, described from the Upper Miocene of the Labrador Sea, has a microreticulate central body surface. The marine acritarch *Nannobarbophora walldalei* Head 1996b, described from the Pliocene of eastern England, has rootlike process bases and the vesicle

Plate 3

Scanning electron micrographs of *Operculodinium? borgerholtense*. The scale bar in Figs. 1, 2, 4, 6, 8–10, 12, 13, 15 = 10 μm ; in Figs. 3, 5, 14 = 5 μm ; in Figs. 7, 11 = 2 μm ; and the insert to Fig. 12 = 500 nm. Figs. 1–8, 11, 12 are from sample (R) at the base of the carbonate sequence of the Weissenegg Formation, Rosenberg Quarry, Retznei, Styrian Basin, Austria. Figs. 9, 10 are from the Waltersdorf-1 Borehole (sample no. WA-RAG4, K3/927-936/Ki 5/058-068), Styrian Basin, Austria. Figs. 13–15 are from the Borgerhout Rivierenhof section near Antwerp, Belgium (sample no. XIBR16), which is the type section for this species.

- | | | | |
|---|---|----|--|
| 1 | Dorsal view showing archeopyle. | 8 | Uncertain view of specimen whose processes have strongly granulate surface. |
| 2 | Oblique antapical view showing antapical plate. | 9 | Uncertain view. |
| 3 | Enlargement of specimen in Fig. 2, rotated about 45° clockwise with antapex pointing downwards, showing detail of antapical plate including change in surface ornament. | 10 | Uncertain view. |
| 4 | Uncertain view. | 11 | Uncertain view showing broken wall, and inset showing fine internal structure of wall. |
| 5 | Enlargement of specimen in Fig. 4 showing detail of wall ornament. | 12 | Uncertain view. |
| 6 | Uncertain view with archeopyle and partially displaced operculum visible at top of specimen. | 13 | Uncertain view but possibly showing antapical plate. |
| 7 | Enlargement of specimen in Fig. 6 showing processes with smooth surface. | 14 | Enlargement of specimen in Fig. 13 showing a change in surface ornament possibly reflecting the antapical plate. |
| | | 15 | Uncertain view, with gaping split in the wall probably representing an incipient archeopyle. |





Text-Figure 4. *Operculodinium?* *borgerholtense* showing central body maximum diameter vs. maximum processes length of all specimens measured in the present study. Specimens indicated as ‘Belgium’ in the key are from the Borgerhout Rivierenhof type section near Antwerp. See also Table 1.

surface has an irregularly scattered granulation unlike the more prominent and orderly distribution of lower ornament in *O.?* *borgerholtense*. *Nannobarbophora gedlii* Head 2003, described from the Lower Miocene of the Norwegian Sea, has hollow processes and a smooth to sparsely ornamented vesicle surface. *Operculodinium?* *eirikianum* has a range base in the uppermost Langhian (Louwye et al., 2007) and therefore overlaps stratigraphically with *O.?* *borgerholtense*. *Nannobarbophora gedlii* has a known range of upper Lower to Middle Miocene and also overlaps stratigraphi-

cally with *O.?* *borgerholtense*, whereas *Nannobarbophora walldalei* is not known from deposits older than Late Miocene (Head, 2003).

Previous records. In the eastern North Atlantic, Porcupine Basin, IODP Site 1318, recorded in low numbers from the upper Burdigalian (Chron C5Cn2r; 16.5 Ma) to mid-Serravallian (Chron C5Ar1n; 12.7 Ma) (Louwye et al., 2007).

In northern Belgium, recorded from the Antwerp Sands Member and its lateral equivalent, the Zonderschot Sands

TABLE 1. Measurements of *Operculodinium?* *borgerholtense* specimens examined in the present study, listed by locality, with minimum (average in parentheses) and maximum values indicated. The five specimens listed from the type section at Borgerhout Rivierenhof do not include the holotype and paratype as these are listed separately. See also Text-Figure 4.

Locality	Central body maximum diameter	Maximum process length	Number of specimens
Holotype	38	7	1
Paratype	36	6	1
Borgerhout Rivierenhof, Belgium	25(30.5)37.5	4(5.4)7	5
Retznei, Austria	23(29.3)36	2.5(4.8)7.3	25
Waltersdorf, Austria	29(34.2)38	5.0(6.0)6.6	4
Bad Deutsch Altenburg, Austria	26.7(33.0)39	4.0(5.7)7.6	8
Baden Sooss, Austria	34(35.8)39	5(6.5)8	6
Tengelic-2 borehole, Hungary	29(36.2)41	4.5(6.4)8.5	16
Gulf of Suez, Egypt	25(33.8)38.5	3(5.6)7	7
TOTAL	23(32.8)41	2.5(5.6)8.5	73

Member, of the Berchem Formation (Louwey, 2001, and as *Operculodinium* sp. 1 in Louwey, 2000). The Antwerp Sands Member is calibrated to planktonic foraminiferal zones N6 to N9 of Blow (1979) and calcareous nannofossil zone NN4 of Martini (1971) and is latest Burdigalian? to mid-Serravallian based on dinoflagellate cysts (Louwey et al., 2000; Louwey, 2001). The Zonderschot Sands Member has a suggested age of latest Burdigalian to Langhian based on dinoflagellate cysts (Louwey, 2000). In the U.K. sector of the Central North Sea, reported from several industry wells in an interval dated as Middle Miocene using dinoflagellate cysts (M.J.H., unpublished data).

In Austria, reported from the mid-Langhian (upper Lower Badenian regional Parathethys stage) of Baden-Sooss, while absent from the mid-Burdigalian (Middle Ottnangian regional Parathethys stage) (Jiménez-Moreno et al., 2006). Also reported from the lower Serravallian (Upper Badenian regional Parathethys stage) of Bad Deutsch Altenburg in the Vienna Basin (Gross, 2002; Soliman and Piller, 2007b). Other occurrences of Badenian age are from Retznei, Styrian Basin (Soliman and Piller, 2004), and the Waltersdorf-1 exploratory well, Styrian Basin (Soliman and Piller, 2004). A lowest occurrence was recorded just above the Karpatian/Badenian boundary at Wagna in the Styrian Basin (Soliman and Piller, 2004, 2007a), although an unconformity at this boundary means that the uppermost Karpatian and lowermost Badenian is missing (Latal and Piller, 2003; Spezzaferri et al., 2004). Generally, in the Central Paratethys, the Karpatian/Badenian boundary is equivalent to the Burdigalian/Langhian boundary based on the evolutionary lineage of *Globigerinoides*–*Praeorbulina* (Lourens et al., 2005; Piller et al., 2007, fig. 1, p. 158).

In Hungary, reported from the mid-Langhian (upper Lower Badenian regional Parathethys stage) through mid-Serravallian (Lower Sarmatian regional Parathethys stage) of the Tengelic-2 borehole (Jiménez-Moreno et al., 2006).

From the subsurface western margin of the Gulf of Suez, Egypt, reported rarely and sporadically from the East Shukheir-1, Shukheir-1, Shukheir-11, and Kareem-30 boreholes, where it is collectively restricted to the Rudeis and Kareem formations in deposits assigned to calcareous nannofossil zones NN4 and NN5 (mid Burdigalian–Langhian) and considered no older than late Burdigalian based on dinoflagellate cysts (Soliman, 2006; unpublished data).

In summary, *Operculodinium? borgerholtense* has a reported lowest occurrence within the upper Burdigalian (Chron C5Cn2r; 16.5 Ma) of the eastern North Atlantic, Porcupine Basin (Louwey et al., 2007), and uppermost Burdigalian or lowermost? Langhian of Belgium (Louwey, 2001), using the time scale of Lourens et al. (2005). Its highest well-constrained occurrence is within the mid-Serravallian (Chron C5Ar1n; 12.7 Ma) of the eastern North

Atlantic, Porcupine Basin (Louwey et al., 2007), and the mid-Serravallian of Hungary, although its disappearance at the latter locality seems to be controlled by local paleoenvironmental changes (Jiménez-Moreno et al., 2006).

Paleoecology. In Austria, the presence of *O.? borgerholtense* both in shallow-water deposits at Retznei and more open-marine deposits at Waltersdorf (Soliman and Piller, 2004; A.S., unpublished data) reflects a broad ecological distribution within the neritic realm. The relatively small size and short processes on the specimens from Retznei might be a response to shallow-water conditions. The ecological tolerance of *O.? borgerholtense* is emphasized by its occurrence in the Tengelic-2 borehole in Hungary where it is one of the few species to persist into the Lower Sarmatian (mid-Serravallian) Paratethyan stage, which is characterised by severely restricted marine conditions and aberrant water chemistry (Jiménez-Moreno et al., 2006). In the Gulf of Suez area, it is associated with such thermophilic species as *Tuberculodinium vancampoae*, *Melitasphaeridium choanophorum* and *Tectatodinium pellitum*, consistent with a tropical to subtropical climate, and hypersaline conditions as indicated by the dominance of *Polysphaeridium zoharyi*. It is therefore a euryhaline and adaptable species.

DISCUSSION AND CONCLUSIONS

Our new observations add detail to the original protologue for *O.? borgerholtense*, including that of the wall ultrastructure, which is shown under SEM to be differentiated into three layers (Plate 3, fig. 11), and morphological variability of the ornament (Text-Figure 3). The greater number of specimens examined also allows us to document the variability of this species more fully. Moreover, we have been able to correct some misconceptions. The cyst is spherical to spheroidal: the ovoidal shape as originally described results from folding of the holotype, as confirmed by confocal microscopy (Plate 1).

The archeopyle is usually distorted owing to the thin wall of the central body and its propensity to crumple due to pressure on the more rigid processes, and may not be seen at all. Its shape and geometry are reconstructed (Text-Figure 2) from several specimens, notably the paratype. This reconstruction shows the 2/3" margin shorter than the 3/3" margin, and the 3/4" margin shorter than the 3/2" margin, resulting in a strongly asymmetrical shape. The archeopyle on the holotype is deformed, with the adapical margin (at the junction of plates 2', 3', and 3" and cingular margin being strongly folded (Plate 1; Plate 2, fig. 20). Our observations unequivocally show that the archeopyle margin has well-defined angles (described as rounded in Louwey, 2001).

The antapical plate is well expressed in the paratype (Plate 2, figs. 1–4), the specimen illustrated in Louwye (2001, fig. 4.6–4.7), and in one or possibly two specimens illustrated by SEM (Plate 3, figs. 2, 3, 13, 14). Although not visible in the holotype, this is probably due to spherical concealment of the antapical region. The antapical plate is often not recognised on specimens unless they are well preserved and favorably oriented. This plate was described as having rounded angles in Louwye (2001), but they are well-defined on the paratype (Plate 2, figs. 1–4) and on the specimen illustrated on Plate 3, figs. 2, 3. The shape and geometry of this plate is consistent with a sexiform hypocystal tabulation that typifies the standard gonyaulacalean pattern, as noted by Louwye (2001).

Louwye (2001) assigned *O. borgerholtense* only questionably to the genus *Operculodinium* because of its clearly delineated antapical plate. Adding to this difference is the presence of an archeopyle with well-defined angles, a wall structure that is unlike the fibroreticulate outer wall layer of the type species *O. centrocarpum*, and a process morphology that is also unlike that of the type species. These differences do not support a close affinity with the cyst-defined genus *Operculodinium* or with the theca-defined genus *Protoceratium*. We consider *Operculodinium* to be an excessively large genus, in need of revision and contraction. Pending such revision, we maintain *O. borgerholtense* provisionally in this genus, although we reject an affinity with the subfamily Cribroperidinioideae.

Operculodinium? borgerholtense is a euryhaline neritic species tolerant of environmental stress, which is consistent with its morphological plasticity. Its present records indicate a temperate to tropical–subtropical paleoclimatic distribution. *Operculodinium? borgerholtense* appears to be confined to the Miocene, with a known range of upper Burdigalian (uppermost Lower Miocene) to mid-Serravallian (upper Middle Miocene). It promises to be a useful stratigraphic marker particularly in those neritic settings where adverse paleoenvironmental factors have excluded other species.

ACKNOWLEDGMENTS

A.S. thanks the Austrian Exchange Service (ÖAD) and the Commission for the Palaeontological and Stratigraphical Research of Austria (Austrian Academy of Science) for financial support, and M. Faris (Tanta University) and Salah El Beialy (El Mansoura University) respectively for providing samples from the Kareem-30 and East Shukheir-1 boreholes of the Gulf of Suez. Werner Piller (Karl-Franzens University, Graz) generously made available laboratory and SEM facilities, and provided the Waltersdorf-

1 samples. S. Müllegger (Karl-Franzens University, Graz) kindly provided the Retznei sample. We are most grateful to Dries Vercauteren (Ghent University) for use of the confocal microscope facility. M.J.H. acknowledges support from a Natural Sciences and Engineering Research Council of Canada discovery grant. It is a pleasure to thank D.K. Munsterman (Netherlands Institute of Applied Geoscience TNO) and S. Piasecki (Geological Survey of Denmark and Greenland) for their helpful reviews of the manuscript.

References Cited

- BLOW, W.H.
1979 *The Cainozoic Globigerinidae: A study of the morphology, taxonomy, evolutionary relationships and the stratigraphical distribution of some Globigerinidae*. Vol. 1–3. E.J. Brill, Leiden, 1413 p.
- BÜTSCHLI, O.
1885 Erster Band. Protozoa. In: *Dr. H.G. Bronn's Klassen und Ordnungen des Thier-Reiches, wissenschaftlich dargestellt in Wort und Bild*. C.F. Winter'sche Verlagshandlung, Leipzig and Heidelberg, p. 865–1088.
- CLAPARÈDE, É., and LACHMANN, J.
1859 Études sur les infusoires et les rhizopodes. *Institut national genevois, Mémoires*, 6 (Mémoire 1): 261–482. [Imprinted 1858.]
- DEFLANDRE, G., and COOKSON, I.C.
1955 Fossil microplankton from Australian Late Mesozoic and Tertiary sediments. (*Australian Journal of Marine and Freshwater Research*, 6(2): 242–313.
- De MEUTER, F., WOUTERS, K., and RINGELE, A.
1976 Lithostratigraphy from temporary outcrops in the Antwerpen City area. *Professional Paper of the Geological Survey of Belgium, 1976*, 3: 1–19.
- ERHART, C.W., and PILLER, W.E.
2004 Fazies und Geometrie des Leithakalk-Steinbruches Retznei/Rosenberg bei Ehrenhausen (Stmk.). *Berichte des Institutes für Erdwissenschaften der Karl-Franzens-Universität Graz*, 9: 116.
- EVITT, W.R.
1985 *Sporopollenin Dinoflagellate Cysts: Their Morphology and Interpretation*. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas, p. i–xv, 1–333.
- FENSOME, R.A., TAYLOR, F.J.R., NORRIS, G., SARJEANT, W.A.S., WHARTON, D.I., and WILLIAMS, G.L.
1993 A classification of living and fossil dinoflagellates. *Micropaleontology Special Publication No. 7*, 351 p.

- GERLACH, E.
1961 Mikrofossilien aus dem Oligozän und Miozän Nordwestdeutschlands, unter besonderer Berücksichtigung der Hystrichosphaeren und Dinoflagellaten. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 112(2): 143–228.
- GROSS, M.
2002 *Mittelmiozäne Ostracoden aus dem Wiener Becken (Badenium/Sarmatium, Österreich)*. Unpublished Ph.D. thesis, Institut für Geologie und Paläontologie, Karl-Franzens-Universität Graz, 343 p.
- HEAD, M.J.
1996a Modern dinoflagellate cysts and their biological affinities. In: Jansonius, J., and McGregor, D.C. (eds.), *Palynology: principles and applications*. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas, vol. 3, p. 1197–1248.
1996b Late Cenozoic dinoflagellates from the Royal Society borehole at Ludham, Norfolk, eastern England. *Journal of Paleontology*, 70: 543–570.
1997 Thermophilic dinoflagellate assemblages from the mid Pliocene of eastern England. *Journal of Paleontology*, 71: 165–193.
2003 Neogene occurrences of the marine acritarch genus *Nannobarbophora* Habib and Knapp, 1982 emend., and the new species *N. gedlii*. *Journal of Paleontology*, 77: 382–385.
- HEAD, M.J., and WRENN, J.H. (eds.)
1992 A forum on Neogene–Quaternary dinoflagellate cysts: The edited transcript of a round table discussion held at the Second Workshop on Neogene dinoflagellates. In: Head, M.J., and Wrenn, J.H. (eds.), *Neogene and Quaternary dinoflagellate cysts and acritarchs*. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas, p. 1–31.
- HEAD, M.J., NORRIS, G., and MUDIE, P.J.
1989 New species of dinocysts and a new species of acritarch from the upper Miocene and lowermost Pliocene, ODP Leg 105, Site 646, Labrador Sea. In: Srivastava, S.P., Arthur, M., Clement, B., et al., *Proceedings of the Ocean Drilling Program, Scientific Results, 105*. Ocean Drilling Program, College Station, Texas, p. 453–466.
- JIMÉNEZ-MORENO, G., HEAD, M.J., and HARZHAUSER, M.
2006 Early and Middle Miocene dinoflagellate cyst stratigraphy of the Central Paratethys, Central Europe. *Journal of Micropalaeontology*, 25: 113–139.
- LATAL, C., and PILLER, W.E.
2003 Stable isotope signatures at the Karpatian/Badenian boundary in the Styrian Basin. In: Brzobohaty, R., Cicha, I., Kovac, M., and Rögl, F. (eds.), *The Karpatian – a Lower Miocene stage of the Central Paratethys*. Masaryk University, Brno, p. 37–48.
- LINDEMANN, E.
1928 Abteilung Peridineae (Dinoflagellatae). In: Engler, A., and Prantl, K. (eds.), *Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere den Nutzpflanzen. Zweite stark vermehrte und verbesserte Auflage herausgegeben von A. Engler. 2 Band*. Wilhelm Engelmann, Leipzig, p. 3–104.
- LOURENS, L., HILGEN, F., SHACKLETON, N.J., LASKAR, J., and WILSON, D.
2005 The Neogene. In: Gradstein, F.M., Ogg, J.G., and Smith, A.G. (eds.), *A geological time scale 2004*. Cambridge University Press, Cambridge, U.K., p. 409–430. [Imprinted 2004.]
- LOUWYE, S.
2000 Dinoflagellate cysts and acritarchs from the Miocene Zonderschot Sands, northern Belgium: stratigraphic significance and correlation with contiguous areas. *Geologica Belgica*, 3: 55–65.
2001 New species of dinoflagellate cysts from the Berchem Formation, Miocene, northern Belgium (southern North Sea Basin). *Geobios*, 34: 121–130.
- LOUWYE, S., De CONINCK, J., and VERNIERS, J.
2000 Shallow marine Lower and Middle Miocene deposits at the southern margin of the North Sea Basin (northern Belgium): dinoflagellate cyst biostratigraphy and depositional history. *Geological Magazine*, 137: 381–394.
- LOUWYE, S., FOUBERT, A., MERTENS, K., VAN ROOIJ, D., AND THE IODP EXPEDITION 307 SCIENTIFIC PARTY
2007 Integrated stratigraphy and palaeoecology of the Lower and Middle Miocene of the Porcupine Basin. *Geological Magazine*, 145: 1–24.
- MARTINI, E.
1971 Standard Tertiary and Quaternary calcareous nannoplankton zonation. In: Farinacci, A. (ed.), *Proceedings of the Second Planktonic Conference, Roma 1970, Volume 2*. Edizione Tecnoscienza, Rome, p. 739–785.
- MATSUOKA, K., McMINN, A., and WRENN, J.H.
1997 Restudy of the holotype of *Operculodinium centrocarpum* (Deflandre & Cookson) Wall (Dinophyceae) from the Miocene of Australia, and the taxonomy of related species. *Palynology*, 21: 19–33.

- PASCHER, A.
1914 Über Flagellaten und Algen. *Berichte der Deutschen Botanischen Gesellschaft*, 36: 136–160.
- PILLER, W.E., HARZHAUSER, M., and MANDIC, O.
2007 Miocene Central paratethys stratigraphy – current status and future directions. *Stratigraphy*, 4(2/3): 151–168.
- RÖGL, F., CORIC, S., HARZHAUSER, M., JIMÉNEZ-MORENO, G., KROH, A., SCHULTZ, O., WESSELY, G., and ZORN, I.
2008 The Middle Miocene Badenian stratotype at Baden-Sooss (Lower Austria). *Geologica Carpathica*, 59(5): 367–374.
- SPEZZAFERRI, S., RÖGL, F., CORIC, S., and HOHENEGGER, J.
2004 Paleoenvironmental changes and agglutinated foraminifera across the Karpatian/Badenian (Early/Middle Miocene) boundary in the Styrian Basin (Austria, Central Paratethys). In: Buík, M., and Kaminski, M.A. (eds.), *Proceedings of the Sixth International Workshop on Agglutinated Foraminifera*. Grzybowski Foundation Special Publication, 8, p. 423–459.
- SOLIMAN, A.
2006 Lower and Middle Miocene dinoflagellate cysts, Gulf of Suez, Egypt. Unpublished Ph.D. dissertation, Karl-Franzens University, Graz, 327 p.
- SOLIMAN, A., and PILLER, W.E.
2004 Miocene dinoflagellate cysts of the Styrian Basin, Austria. *Berichte des Institutes für Erdwissenschaften der Karl-Franzens-Universität Graz*, 9: 379.
2007a Dinoflagellate cysts at the Karpatian/Badenian boundary of Wagna (Styrian Basin, Austria). *Jahrbuch der Geologischen Bundesanstalt*, 147: 405–417.
2007b Upper Badenian dinoflagellate cysts of Bad Deutsch Altenburg, Vienna Basin, Austria. *Joannea – Geologie und Paläontologie*, 9: 100.
- SOLIMAN, A., HEAD, M.J., and PILLER, W.E.
2004 Palynology and dinoflagellate cyst stratigraphy of the Gharandal Group (Miocene), Kareem-30 Borehole, Gulf of Suez, Egypt. 32nd International Geological Congress, Florence, Abstracts, p. 525.
- TAYLOR, F.J.R.
1980 On dinoflagellate evolution. *BioSystems*, 13: 65–108.
- WALL, D.
1967 Fossil microplankton in deep-sea cores from the Caribbean Sea. *Palaeontology*, 10: 95–123.
- WALL, D., and DALE, B.
1966 “Living fossils” in western Atlantic plankton. *Nature*, 211(5053): 1025–1026.