Late Miocene (Tortonian) gonyaulacacean dinoflagellate cysts from the Pannonian Basin, Austria

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Abstract

During the Late Miocene (Tortonian or Pannonian regional stage), at around 11.6 Ma, a glacioeustatically-driven sea-level fall caused the final closure of the Paratethys Ocean and Lake Pannon was formed in central Europe. The lake was initially brackish, but slowly freshened and became slightly alkaline. These unusual changes in water chemistry produced the radiation of a characteristic assemblage of gonyaulacacean dinoflagellate cysts. This study examined 94 samples from the Pannonian of Hennersdorf Clay Pit, south of Vienna, Austria. From this material, *Achomosphaera breviata* sp. nov., *Seriliodinium*? *pannonense* sp. nov. and *Spiniferites hennersdorfensis* sp. nov. were apparently endemic to the Central Paratethys during the Late Miocene. *Spiniferites bentorii* (Rossignol, 1964) Wall and Dale, 1970 subsp. *oblongus* Sütőné-Szentai 1986 and *Spiniferites bentorii* (Rossignol, 1964) Wall and Dale, 1970 subsp. *pannonicus* Sütőné-Szentai 1986 are elevated to species status. The genus *Spiniferites* exhibited significant morphological variability especially in terms of general shape, apical boss development and process morphology. Supplementary descriptions and discussions of some other gonyaulacacean taxa which are present are provided.

Keywords: Austria; Central Paratethys; dinoflagellate cysts; Late Miocene (Tortonian/Pannonian); Pannonian Basin; taxonomy

1. Introduction

The Upper Miocene strata of the Pannonian Basin in Central Europe are characterised by highly endemic biotas (Magyar et al., 1999a; Müller et al., 1999; Gross et al., 2008). This provincialism arose due to the establishment of Lake Pannon from the rapidly diminishing Central Paratethys Ocean during the Late Miocene (Tortonian) part of the Pannonian Regional Stage (Piller et al., 2007; Harzhauser and Mandic, 2008; Gross et al., 2011). The Pannonian correlates to the Tortonian to Holocene interval in the formal geochronological classification (Hilgen et al., 2012, fig. 29.8). Lake Pannon covered an area of approximately 290,000 km^2, and was 860 km long and 550 km wide during its maximum extent between 10.5 and 10.0 Ma (Figure 1). It evolved due to the contraction and closure of the Central Paratethys Ocean around 11.6 Ma ago due to glacioeustatically-driven sea-level fall (Magyar et al., 1999a). Lake Pannon was initially brackish, but gradually freshened and the waters became slightly alkaline (Harzhauser et al., 2007). The development of the lake biota was controlled by this gradual freshening of the water body, together with area and depth changes (Rögl, 1998; Magyar et al., 1999a; Harzhauser et al., 2007). This scenario led to highly provincial faunas and floras, the latter which include an endemic gonyaulacacean dinoflagellate cyst flora and a decrease in diversity from 126 taxa in the Middle Miocene Badenian Regional Stage (Langhian to early Serravallian, Hilgen et al., 2012, fig. 29.8) to around 40 taxa in the Late Miocene (Soliman and Piller, 2009). These palaeoenvironmental changes led to significant morphological variability of dinoflagellate cyst genera such as *Impagidinium* and *Spiniferites*; for example most of the representatives of these genera are characterised by a prominent apical boss or horn. Similar morphologies have been documented in *Spiniferites* from the

Quaternary of offshore Mexico by Price and Pospelova (2014). The genus *Spiniferites* is known to exhibit characteristic morphological variations apparently forced by lowered salinities or freshwater conditions (Kouli et al., 2001).

This study is part of a project on the marine palynofloras of the Pannonian Stage at the type locality, the Hennersdorf Clay Pit south of Vienna (Figure 1). This quarry supplies clay to the nearby Wienerberger brickworks. The succession at the Hennersdorf Clay Pit is part of the Záhorie Member of the Bzenec Formation which can attain 340 m in thickness (Harzhauser and Mandic, 2004; Harzhauser et al., 2004). The Hennersdorf section comprises parts of the Mid-Pannonian (Tortonian) *Mytilopsis czjzeki* mollusc Zone, the *Lymnocardium schedelianum* mollusc Subzone and the *Spiniferites paradoxus* dinoflagellate cyst Zone, and is within magnetochron C5n (Magyar et al., 1999a; Hilgen et al., 2012, fig. 29.8). The entire succession is within the lower part of Pannonian Zone E (Figure 2; Harzhauser et al., 2008). A warm temperate palaeoclimate with a mean annual temperature (MAT) of around 17–18 °C was suggested by Jiménez-Moreno et al., (2008). This study builds on the work of Sütőné-Szentai (1986) and Harzhauser et al., (2008) in describing some endemic Late Miocene dinoflagellate cysts from the Vienna Basin.

2. Materials and methods

The Hennersdorf Core 1 (HC1) is 37 cm in length, and was drilled entirely within the Upper Miocene Záhorie Member of the Bzenec Formation close to the base of the Hennersdorf (Wienerberger) Clay Pit section (Figure 1). Seventy-four samples were collected at regular intervals (~0.5 cm) from HC1 for palynological analyss (Figure 2). This interval was selected because of its heterolithic nature; it comprises bioturbated clays and silts, and clays with several shell beds (Figure 2). Harzhauser et al., (2008) studied ostracods and palynomorphs from this core. In addition, 20 samples were collected from the ~14 m thick succession which outcrops in this quarry in order to provide a general overview of the dinoflagellate cyst assemblages (Figure 2). The samples were treated using a standard palynological preparation technique such as used by Soliman et al. (2012; 2013). The organic residues were screened using 125 µm and 15 µm sieves and at least one slide was scanned while the routine count stopped at 300 dinoflagellate cyst specimens for each sample. Scanning electron microscope (SEM) studies were made using a DSM 982 Gemini unit operating at a working voltage of 10 kv. All materials pertaining to this study, including the type material, are housed in the Institute of Earth Sciences, Graz University, Austria. Holotypes are deposited in the Joanneum Museum, Graz, Austria. The most significant dinoflagellate cysts are illustrated in Plates I to VI.

3. An overview of the dinoflagellate cyst assemblages

All the samples yielded well-preserved, relatively low diversity dinoflagellate cyst assemblages. These are documented in Tables 1 and 2 and Appendix 1; 31 formally-described species were recognised in addition to some informal taxa. The genera *Achomosphaera*, *Impagidinium, Protoperidinium* and *Spiniferites* are prominent throughout. Protoperidiniacean forms such as *Selenopemphix* and small round brown dinoflagellate cysts are consistently present, together with cf. *Algidasphaeridium* sp*., Polykrikos* spp., *Pyxidinopsis psilata* and *Komewuia*? spp. Additionally, *Habibacysta tectata, Lingulodinium* spp., *Melitasphaeridium choanophorum, Operculodinium* spp., *Polysphaeridium zoharyi* and *Tectatodinium pellitum* were recorded in low numbers. Some taxa are represented by single, poorly-preserved specimens, and these are interpreted as having been reworked from the Middle Miocene and older strata. These presumed reworked taxa are *Cleistosphaeridium placacanthum,* ?*Cordosphaeridium minimum, Dapsilidinium* spp., *Deflandrea* spp., *Distatodinium* spp., *Homotryblium* spp., *Hystrichokolpoma* spp. and *Reticulatosphaera* *actinocoronata*. Freshwater algae such as *Botryococcus* and *Pediastrum,* together with fungal spores, were also encountered in significant proportions throughout.

4. Systematic palaeontology

The classification of dinoflagellate cysts herein follows Fensome et al. (1993; 2008). Traditional Kofoidian shorthand for tabulation is used, and the morphological terminology follows Evitt (1985). Where dimensions are given, the three figures are the minimum, (mean) and maximum measurements.

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

Class DINOPHYCEAE Pascher, 1914

Order GONYAULACALES Taylor, 1980

Family GONYAULACACEAE Lindemann, 1928

Subfamily GONYAULACOIDEAE Fensome et al., 1993

Genus *Achomosphaera* Evitt, 1963

Type. *Achomosphaera ramulifera* (Deflandre, 1937) Evitt, 1963

Achomosphaera sp. cf. *Achomosphaera fenestra* Kirsch, 1991

Plate I, 1–3

Achomosphaera fenestra Kirsch, 1991, p. 54–55; pl. 2, figs. 4, 6–12; figs. 35a, b, 36a–j.

Description. An ovoidal to subspherical form of *Achomosphaera*. The wall is thin, and is smooth to microgranulate. A small apical boss may be present. The gonal processes are solid, membranaceous and distally-flared. They may be longitudinally striate and have clypeate distal terminations. No intergonal processes have been observed. The process shafts are unevenly distally fenestrate (Plate I, 2), and the fenestrae are oval to subcircular and are ~0.5 to 3 μm in diameter. The sulcal processes are normally thin and are distally capitate, bifurcate or trifurcate without fenestrae. The cingulum is indicated by two latitudinal rows of processes.

Dimensions. The maximum length of the cyst body, including the apical boss if present, is 44 (51) 56 μm; the maximum equatorial width is 32 (39) 41 μm; and the length of the processes is 5 (11) 18 μm. Fourteen specimens were measured.

Comparison. This form differs from *Achomosphaera fenestra sensu stricto* in the presence of fenestrae on the process shafts rather than at the distal ends only (Plate I, 2). Also, the apical and antapical processes are never connected by membranes, and the processes are solid and not hollow. It differs from *Achomosphaera andalousiensis* Jan du Chêne, 1977 by the absence of large fenestrae at the distal ends of the tubiform processes. It differs from *A. breviata* sp. nov. in having solid, membranaceous and distally-flared processes with fenestrae rather than relatively short processes which are hollow and multifurcate distally without fenestrae.

Distribution. This form was sporadically recorded in the material studied, and it is included in *Spiniferites*/*Achomosphaera* spp. in Tables 1 and 2.

Achomosphaera breviata sp. nov.

Plate III, 7, 8; Plate V, 13–16; Figure 3

Holotype. Sample HC1-16, slide A, England-Finder coordinate K39 (Plate V, 13, 14). Specimen number UMJ G and P 211335 of the Joanneum Museum, Graz University, Austria.

Paratype. Sample HC1-16, slide A, England-Finder coordinate O32 (Plate V, 15, 16).

Etymology. From the Latin *brevis,* meaning short, with reference to the short processes.

Type locality. Hennersdorf Clay Pit, Vienna Basin, Austria.

Lithostratigraphy of the type material. The Záhorie Member of the Bzenec Formation, Upper Miocene (Pannonian).

Diagnosis. A small ovoidal species of *Achomosphaera*. The wall is thin and smooth. The processes are exclusively gonal and relatively short, straight, wide proximally and multifurcate distally. Adjacent cingular processes are occasionally merged together. Usually there is a large box-like process in the sulcal area. No sutures are present. The archaeopyle is precingular (type P), and the operculum is free.

Description. A small species of *Achomosphaera* with an ovoidal cyst body. The wall is thin (~1.0 μm) with a smooth or shagreenate surface. The processes are gonal only and relatively short (up to ~25% of the cyst length), hollow, smooth and normally closed distally. Occasionally some processes are open distally (Plate III, 7). The width of the processes is variable although their length is fairly constant. They are bulbous proximally, where they are expanded to twice the width at the mid shaft; typically they are cylindrical in cross section. Fenestrations are rarely present at the process bases. Distally, the processes are expanded, branching and multifurcate; they may have serrate margins and have recurved tips. Closely adjacent processes in the cingular area may have merged bases (Figure 3). If they are not merged, the cingular processes are arranged in two parallel rows. The sulcus bears a single large box-like process (Plate III, 8). No intrasutural tabulation is developed. The archaeopyle is precingular, type P, formed by the loss of plate 3" and the operculum is free.

Comparison. *Achomosphaera breviata* sp. nov. is significantly smaller than most other species of this genus. It differs from *Achomosphaera ramulifera* (Deflandre, 1937) Evitt, 1963 in that the processes are exclusively gonal, hollow and multifurcate rather than trifurcate. It is also similar to *Achomosphaera andalousiensis* Jan du Chêne, 1977 but *Achomosphaera breviata* sp. nov. differs in that the distal ends of the processes lack large fenestrae, and the sulcus exhibits a large box-shape process (Plate III, 8). *Achomosphaera breviata* sp. nov. differs from *Achomosphaera argesensis* Demetresçu, 1989 by the lack of an apical boss and *A. argesensis* has 'a flat process developed on the apical area or on both apical and antapical areas' (Demetresçu, 1989) which is lacking in *Achomosphaera breviata* sp. nov. described here. It can be distinguished from *Achomosphaera bulla* Cookson and Eisenack, 1974 by its oval shape and hollow processes, and differs from *Achomosphaera fenestra* Kirsch, 1991 by lacking fenestrae in the processes shafts. *Achomosphaera improcera* Islam, 1983 is similar in size, but has gonal processes with trifurcate distal ends and intergonal processes with bifurcate ends.

Dimensions. The maximum overall length is 29 (37) 44 µm; the maximum overall width is 22 (87) 34 µm; and the maximum length of the processes is 3 (7) 10 µm. Thirty-four specimens were measured.

Distribution. This species was recorded sporadically in the current study.

Genus *Impagidinium* Stover and Evitt, 1978

Type. *Impagidinium dispertitum* (Cookson and Eisenack, 1965) Stover and Evitt, 1978.

Discussion. *Impagidinium* is indicative of outer neritic settings and oligotrophic environments (Dale, 1996). This genus covers a wide range of temperatures from cold water (e.g. *Impagidinium pallidum* Bujak, 1984) to warm water (e.g. *Impagidinium aculeatum* (Wall, 1967) Lentin and Williams, 1981) but usually has a low tolerance for lowered salinities (Edwards and Andrle, 1992; Rochon et al., 1999; Marret and Zonneveld, 2003; Zonneveld et al., 2013). The occurrences of *Impagidinium* in the brackish environments of Lake Pannon suggest that some species tolerated low salinities (Marret et al., 2004; Sorrel et al., 2006).

Impagidinium spongianum Sütőné-Szentai, 1985

Plate I, 4–6; Plate IV, 9–16

Form F_1 Balteş, 1971, pl. 4, fig. 1.

Form F_2 Balteş, 1971, pl. 4, fig. 3.

Impagidinium spongianum Sütőné-Szentai, 1982a, pl. 5, fig. 3 (*nomen nudum*).

Impagidinium spongianum Sütőné-Szentai, 1985, p. 519; pl. 81, fig. 5.

Impagidinium(?) sp. 1 Corradini and Biffi, 1988, pl. 3, figs. 7–11.

Impagidinium spongianum Sütőné-Szentai, 1985; Sütőné-Szentai, 1990, pl. 2, fig. 2.

Supplementary description. *Impagidinium spongianum* is ovoidal in shape. The epicyst has a rounded apex with a prominent apical boss ~3 to 5 µm in height (Plate I, 6). The wall is relatively thick (~1.5 µm) and spongy; in some specimens, scattered gemmae are present. Using light microscopy, the wall appears coarsely reticulate. The sutural crests are ~1.5 µm in height; they are undulate distally and are smooth to finely perforate proximally. The sutural crests delineate a standard S-type gonyaulacacean tabulation, however, the apical plate sutures may be faintly expressed (Plate I, 5). The sulcus is shallow, and some of the larger sulcal plates can be resolved in some specimens (Plate I, 4). The cingulum is offset by one cingulum width (Plate I, 4). The archaeopyle is precingular (type P) with a free operculum.

Dimensions. The maximum length of the cyst body, including the apical boss, is 42 (50) 60 µm and the maximum equatorial width is 34 (42) 51 µm. Nineteen specimens were measured.

Comparison. *Impagidinium spongianum* differs from other species of *Impagidinium* by its characteristic thick and spongy wall and the presence of an apical boss. *Leptodinium punctatum* differs from *I. spongianum* based on the illustrations and description of Balteş (1971, p. 3; pl. 4, figs. 2, 3; 6, 7) in having slender prominences and low sutural crests rather than a spongy wall and high sutural crests. *Impagidinium* (?) sp. 1 of Corradini and Biffi (1988; pl. 3, 7–11) and Forms 1 and 2 of Balteş (1971, pl. 4, 1, 3 respectively) resemble *Impagidinium spongianum* in surface ornamentation and in having high sutural crests. While the specimen illustrated in Balteş (1971, pl. 4, 2) is excluded because it has a smooth surface. However *Impagidinium* (?) sp. 1 of Corradini and Biffi (1988) appears to lack the apical boss which is not clear in Form 1 of Balteş (1971, pl. 4, 1) because of its antapical oblique orientation. *Impagidinium eugubinum* Biffi and Manum, 1988 has dome-shaped to nipple-like prominences. *Caspidinium rugosum* Marret et al., 2004 is also similar to *Impagidinium spongianum*, but differs due to its dextral torsion and the absence of an apical boss. The irregular height of septa and the low intratabular relief differentiate *I. caspienense* Marret et al. 2004 from *I. spongianum*.

Distribution. *Impagidinium spongianum* was recorded from most of the samples studied herein.

Previous records. *Impagidinium spongianum* has been recorded from the Pannonian of Hungary (Sütőné-Szentai, 1985; 1986; 1990; 1999; 2000; 2003). The only record outside the Pannonian Basin is from the Upper Miocene to Lower Pliocene of the Maccarone section, Marche, Italy (Popescu et al., 2007).

Impagidinium sp. 1

Plate I, 7

Comment. A form of *Impagidinium* which is characterised by an entirely smooth wall with occasional randomly distributed gemmae, and the denticulate distal terminations of the sutural crests. It is placed in open nomenclature because too few speciemens were recorded in the current study to warrant a full description.

Distribution. Three specimens were recorded (two of them outside the routine count) from the upper part of the core (Late Miocene; Pannonian).

Impagidinium sp. 2

Plate I, 8, 9

Comments: A form of *Impagidinium* which is characterised by its baculate wall and high, fibrous sutural crests. In particular, the surface ornamentation comprises numerous short baculae. It is placed in open nomenclature because too few speciemens were recorded in the current study for a full description.

Distribution. Two specimens were recorded outside the routine count from the upper part of the core (Late Miocene; Pannonian)

Genus *Seriliodinium* Eaton, 1996

Type. *Seriliodinium explicatum* Eaton, 1996

Synopsis. Trabeculate chorate cysts with a subcircular to oval overall outline, and a rounded cruciform to oval cyst body. The processes are gonal, distally trifurcate and largely confined to the peripheral areas. The midventral and middorsal areas are essentially process-free, imparting a marginate appearance. The processes are united distally by a network of single parasutural, rope-like trabeculae (Eaton, 1996, p. 152).

Seriliodinium? *pannonense* sp. nov.

Plate VI, 1–13

Holotype. Sample HC1-11, slide A, England-Finder coordinate S35/0 (Plate III, 4–6). Specimen number UMJ GandP 211336 of the Joanneum Museum, Graz University, Austria.

Paratype. Sample F1, slide A, England-Finder coordinate G28/0 (Plate III, 1–3).

Etymology. Named after Lake Pannon.

Type locality. Hennersdorf Clay Pit, Vienna Basin, Austria.

Lithostratigraphy of the type material. The Záhorie Member of the Bzenec Formation, Upper Miocene (Pannonian).

Diagnosis. Semitrabeculate chorate dinoflagellate cysts with an ovoidal to subcircular cyst body. The wall is thin with a scabrate to finely granulate surface. A prominent apical boss is generally present (Plate VI, 6). Processes are gonal, distally trifurcate and, at the cingulum, are distally multifurcate. Low sutural ridges/septa indicating a gonyaulacacean tabulation are variably developed; these are highest at the cingulum and may be entirely absent. Some processes may be linked distally by rope-like trabeculae. The archaeopyle is precingular (type P), and the operculum is free.

Description. *Seriliodinium*? *pannonense* sp. nov. is a medium-sized chorate cyst which is ovoidal or rarely subcircular in overall outline. The wall is thin (~l μm) with a scabrate to finely granulate surface. The sutural ridges are of variable height, but are normally highest equatorially. A prominent (2–6 μm) apical boss is generally developed. The gonal processes are solid, subcircular to triangular in cross-section, expanded distally and trifurcate. These trifurcations are either isolated or connected distally by rope-like trabeculae. Occasionally, the processes may have some proximal perforations (Plate VI, 13) and the processes are branched medially to distally. The cingular processes are distally multifurcate which a give a fenestrate appearance; they may be distally connected by trabeculae. Trabeculae, if present, are single and smooth. A standard gonyaulacean tabulation (4′, 6′′, 6c, 6′′′, lp, 1′′′′) is expressed by the sutural ridges and the distal trabeculae. The cingulum is indicated by two rows of parallel processes connected proximally by sutural ridges (Plate VI, 11). The archaeopyle is precingular (type P) with a free operculum.

Comments. *Seriliodinium*? *pannonense* sp. nov. is characterised by its spiniferate process architecture, the gonyaulacacean tabulation and a discontinuous distal rope-like trabeculum. It is questionably attributed to *Seriliodinium* because of the incomplete trabeculum.

Comparison. *Seriliodinium*? *pannonense* sp. nov. differs from *Seriliodinium explicatum* Eaton 1996 in having an apical boss, being ovoidal in outline rather than rounded cruciform and lacking complete trabeculae. Additionally, *Seriliodinium explicatum* has mid-ventral and mid-dorsal areas which are devoid of processes, which is not the case in *Seriliodinium*? *pannonense* sp. nov. *Seriliodinium*? *pannonense* sp. nov. resembles *Spiniferites validus* Sütőné-Szentai 1982 from the Late Pannonian of Hungary in the cyst outline and the presence of an apical boss. But the former differs in being significantly smaller than *Spiniferites validus*, and in having shorter and distally-connected processes. The shape and apical boss of *Seriliodinium*? *pannonense* sp. nov. means that it is similar to species of *Spiniferites* from the Eastern Paratethys (e.g. Sütőné-Szentai, 2000; 2002; 2003; 2004). However, the presences of the rope-like distal trabeculae distinguish it from all these taxa. *Seriliodinium*? *pannonense* sp. nov. differs from *Nematosphaeropsis* by lacking complete penitabular pairs of ribbon-like trabeculae and from taxa belonging to *Cannosphaeropsis* by incomplete trabeculae. *Spiniferites rhizophorus* Head in Head and Westphal, 1999 resembles *Seriliodinium*? *pannonense* sp. nov. in that some processes are supported by stilt-like columns, but differs in that the processes are not connected distally by discontinuous rope-like trabeculae and it lacks an apical boss.

Dimensions. The length of the cyst body, including the apical boss, of the holotype is 47 µm; the equatorial width is 32 µm and the maximum length of the processes is 16 µm. Overall, the length of the cyst body, including the apical boss, is 41 (55) 74 µm; the equatorial width is 31 (40) 50 µm and the maximum length of the processes is 10–24 µm.

Distribution. *Seriliodinium*? *pannonense* sp. nov. is present in the Middle Pannonian of the Hennersdorf Clay Pit, Vienna Basin, Austria.

Genus *Spiniferites* Mantell, 1850 emended Sarjeant, 1970

Type. *Spiniferites ramosus* (Ehrenberg, 1838) Mantell, 1854

Discussion. *Spiniferites* includes around 100 species (Fensome and Williams, 2004, p. 612–629; Fensome et al., 2008). Several species and subspecies of this genus have been described from the Late Miocene (Pannonian/Tortonian) of Central Paratethys by the eminent Hungarian palynologist Mária Sütőné-Szentai (e.g. Sütőné-Szentai, 1982b; 1986; 1990; 2000) and many of these taxa were encountered during this study. Light and scanning electron microscopy revealed new aspects of their morphologies. An ovoidal/subovoidal cyst body is a characteristic feature of this genus from Lake Pannon, and significant variations in the apical bosses and processes and sutural membranes were noted. Specimens of *Spiniferites* with apical bosses typify many of the cyst types of *Gonyaulax digitale* (Pouchet 1883) Kofoid 1911 (see Wall and Dale, 1968). Variations in the apical boss occur in *Spiniferites bentorii* and many subspecies have been described (e.g. Sütőné-Szentai, 1986). The significance of these observations is potentially important for palaeoecology. *Spiniferites* cysts with an apical boss potentially allow the recognition of different salinities. For example, small forms of *Spiniferites* with short and germinal processes with an apical boss are indicative of low salinities (Ellegaard, 2000).

Spiniferites hennersdorfensis sp. nov.

Plate II, 1–4; Plate IV, 1–8; Figure 4

Spiniferites paradoxus (Cookson and Eisenack, 1968) Sarjeant, 1970; Sütőné-Szentai, 1982b, pl. 7, 1.

Holotype. Sample HC1-16, slide A, England-Finder coordinate N33/4 (Plate IV, 1–4). Specimen number UMJ GandP 211337 of the Joanneum Museum, Graz University, Austria.

Paratype. Sample HC1-23, slide B, England-Finder coordinate R39/0 (Plate IV, 5–8).

Etymology. Named after the type locality.

Type locality. Hennersdorf Clay Pit, Vienna Basin, Austria.

Lithostratigraphy of the type material. The Záhorie Member of the Bzenec Formation, Upper Miocene (Pannonian).

Diagnosis. An ovoidal to subspherical murochorate spiniferate cyst with an apical boss (Pl. 4; Figure 4). Wall is relatively thick with a smooth, scabrate or granulate surface. Processes are gonal, short and connected proximally by high sutural crests. The crests are smooth with a hiate distal margin. The sutural crests are lower at the cingulum and around plate 6’’ (Plate II, 4). The archaeopyle is precingular (type P), operculum is free.

Description. A murochorate species of *Spiniferites* with an ovoidal to subspherical outline. A small (3–6 µm high) apical boss with a distinct trifid process is present (Plate II, 2). The wall is relatively thick (~1 µm) with a smooth, scabrate to granulate surface (Plate II, 1, 2). Processes are gonal and triangular in cross-section. The processes are connected by high sutural crests. The crest height can attain up to 20% of the cyst body width at the cingulum. The crests are distally hiate (Figure 4; Marheinecke, 1992, p. 17; Williams et al., 2000, p. 100, fig. 556) with denticulate or undulate margins. The crest surfaces are smooth or finely granulate, occasionally finely perforate or fenestrate (Plate II, 3). High sutural crests are lower at the boundaries of the cingular plates and between plates 5´´/6´´, 5´´´/6´´´ and 1´´/sulcus (Plate II, 4). Plate 6´´ is smaller than the other precingular plates (Plate II, 4). The tabulation is standard S-type gonyaulacacean. The archaeopyle is formed by the loss of precingular plate 3´´ with a free operculum.

Comparison. The sutural crests distinguish *Spiniferites hennersdorfensis* sp. nov. from other species of the genus; the high, distally hiate nature of these is unique. *Spiniferites falcipedius* Warny and Wrenn, 1997 and *Spiniferites rubinus* (Rossignol, 1964) Sarjeant, 1970 differ in lacking an apical boss. *Spiniferites membranaceus* (Rossignol, 1964) Sarjeant 1970 has very long trifurcations at the process tips, and a prominent sutural crest between the antapical processes only. *Spiniferites mirabilis* (Rossignol, 1964) Sarjeant,1970 differs from *Spiniferites hennersdorfensis* sp. nov. in having a high sutural flange which connects the antapical processes only, in having intergonal and gonal processes and the distally trifurcate processes with long tips. *Spiniferites hennersdorfensis* sp. nov. also differs from species of *Leptodinium* and *Pterodinium* in the absence of high sutural crests between the cingular plates and in the presence of an apical boss.

Dimensions. The maximum length of the cyst body of the holotype is 68 µm, the equatorial width is 42 µm, the maximum length of the processes is 13 µm and the apical boss is 6 µm long. Overall, the maximum length of the cyst body is 47 (58) 68 µm; the equatorial width is 41 (46) 52 µm, the maximum length of the processes is 9 (12) 14 µm and the apical boss is 3–6 µm long. Twelve specimens were measured.

Distribution. *Spiniferites hennersdorfensis* sp. nov. was recorded from most of the samples studied herein. This species was recorded from the Pannonian of Hungary as *Spiniferites paradoxus* by Sütőné-Szentai (1982b, pl. 7, 1).

Spiniferites oblongus (Sütőné-Szentai 1986) stat. nov.

Plate II, 7–8; Plate III, 9–12; Figures 5, 6

Basionym. *Spiniferites bentorii* subsp. *oblongus* Sütőné-Szentai, 1986, p. 36–37; pl. 2, 3; pl. 3, 1.

Spiniferites bentorii (Rossignol, 1964) Wall and Dale, 1970; Sütőné-Szentai, 1982b, pl. 1, 3.
Spiniferites bentorii subsp. *oblongus* Sütőné-Szentai, 1986; Sütőné-Szentai, 1999, pl. 3, 1; Sütőné-Szentai, 2003, pl. 1, 1; Sütőné-Szentai, 2004, pl. 1, 6; Fuchs and Sütőné-Szentai, 1991, pl. 5, 3.

Original diagnosis. “The form of the body is oval in shape with a well-developed apical horn. Archaeopyle 3”. The tabulation and the gonal processes are well-developed. There is a process on the apical horn in most specimens. The tabulation is the same as in *Spiniferites bentorii*. The processes are trifurcate, and the processes at the cingulum are the widest. The wall is 0.5 µm thick, finely granulate, sometimes smooth, and yellow in colour. The cyst body of the holotype is 72 μm long and 35 μm wide. It can be up to 98 μm long and 43 μm wide, and a process is developed on the apical horn" (translation from Hungarian to English by Sütőné-Szentai in 2008).

Diagnosis. Elongate ellipsoidal, spiniferate dinoflagellate cysts with an apical horn. Wall has a smooth to faintly granulate surface. Processes are gonal, germinal equatorially, distally aculeate, with or without distal fenestration. Processes at the cingulum are longer than those in the more polar areas. A standard gonyaulacean tabulation is expressed by sutural crests. Archaeopyle is precingular (type P) with a free operculum.

Description. An elongate to ellipsoidal, rarely ovoidal, spiniferate dinoflagellate cyst. The epicyst is longer than the hypocyst. A prominent (~10 μm long) capitate apical horn is present, terminating in an elongate, solid, distally truncate or weakly bifid process (Plate II, 8). The wall is ~1 μm thick with a faintly granulate or smooth surface. The processes are gonal, germinal at the cingulum (Reid, 1974), distally aculeate and may have distal fenestration. The cingular processes are longer than those in the precingular, postcingular and polar areas. The sutural crests are ~0.5 μm in height and reflect a standard S-type sexiform gonyaulacacean tabulation pattern (Figure 6). The archaeopyle is type P, formed by the loss of the middorsal precingular plate 3'' and with a free operculum.

Dimensions. The central body length, including the apical boss, is 49 (66) 90 μm; the equatorial width is 29 (34) 45 μm, the length of the equatorial processes are 6 (10) 13 μm; the length of the apical and antapical processes are 4 (6) 7 μm; and the length of the apical process is 6 (11) 21 μm. Twenty-one specimens were measured.

Comparison. *Spiniferites oblongus* (Sütőné-Szentai, 1986) stat. nov. differs from *Spiniferites bentorii* (Rossignol, 1964) Wall and Dale, 1970 by its elongate ellipsoidal outline, the well-developed capitate apical horn with a truncated or weakly bifid apical termination and in having distally aculeate processes. *Spiniferites oblongus* is distinct from *Spiniferites pannonicus* (Sütőné-Szentai, 1986) stat. nov. by its elongate cyst body and long apical horn (Figure 5). *Spiniferites oblongus* also resembles *Spiniferella cornuta* (Gerlach, 1961) emend. Stover and Hardenbol, 1994 in having a well-developed apical horn. But *S. cornuta* is characterised by an apical horn with spurs, intergonal processes and parasutural septa which are moderate in height and straight or concave between the processes. Moreover, precingular plate 6'' in *Spiniferella cornuta* is subquadrangular to pentangular and is in significant contact with plate 1' which it is not the case in *S. oblongus* (Sütőné-Szentai, 1986) stat. nov (Fig. 6).

Comments. *Spiniferites bentorii* subsp. *oblongus* Sütőné-Szentai, 1986 is considered to be sufficiently distinctive to be elevated to the rank of species. This is based on the elongate to ellipsoidal cyst body outline, the prominent apical boss and horn, and the distinctive processes. This form is biostratigraphically significant; Magyar et al. (1999a, fig. 1) erected a *Spiniferites bentorii* subsp. *oblongus* Zone within the Pannonian of Hungary.

Spiniferites bentorii has an ovoidal central body, a relatively thick, microgranular wall and a pronounced apical boss. The processes are gonal, occasionally intergonal and may be proximally fenestrate. They are conical to tapering, erect to curved, distally digitate and closed (e.g. Rossignol, 1964; Harland, 1977; Rochon et al., 1999). Due to the significant morphological variability of *Spiniferites bentorii*, Sütőné-Szentai (1983; 1986; 1990) and Fuchs and Sütőné-Szentai (1991) erected several subspecies. These are *Spiniferites bentorii* subsp. *"pseudooblongus"* Sütőné-Szentai, 1983, *Spiniferites bentorii* subsp. *budajenoensis* Sütő-Szentai, 1986, *Spiniferites bentorii* subsp. *oblongus* Sütőné-Szentai, 1986, *Spiniferites bentorii* subsp. *pannonicus* Sütőné-Szentai, 1986, *Spiniferites bentorii* subsp. "*matraensis*" Sütőné-Szentai, 1988, *Spiniferites bentorii* subsp. "*piriformis"* Sütőné-Szentai, 1988, *Spiniferites bentorii* subsp. "*coniunctus*" Sütőné-Szentai, 1990 and *Spiniferites bentorii* subsp. *granulatus* Fuchs and Sütőné-Szentai, 1991. The subspecies in quotation marks are not validly published (Fensome and Williams, 2004; Fensome et al., 2008).

Distribution. *Spiniferites oblongus* (Sütőné-Szentai, 1986) stat. nov. has been recorded from the Pannonian of Hungary by Sütőné-Szentai (1982b; 1986; 1999; 2000; 2003; 2004), and from the Vienna Basin by Fuchs and Sütőné-Szentai (1991).

Spiniferites pannonicus (Sütőné-Szentai, 1986) stat. nov.

Plate II, 9; Plate III, 13–16; Figure 5

Basionym. *Spiniferites bentorii* (Rossignol, 1964) Wall and Dale, 1970; Sütőné-Szentai, 1982b, pl. 1, 1–2, 4; Sütőné-Szentai, 1985, pl. 80, 3–5; Sütő-Szentia, 1999, pl. 2, 1–2; *Spiniferites bentorii* subsp. *pannonicus* Sütőné-Szentai, 1986; *Spiniferites bentorii* subsp. *pannonicus* Sütőné-Szentai, 1986, p. 35–36; pl. 2, 1, 2; *Spiniferites bentori* subsp. *coniunctus* Sütőné-Szentai, 1990, pl. 5, 1; fig. 78a; Fuchs and Sütőné-Szentai, 1991, pl. 1, 3, 6; pl. 4, 3; pl. 5, 4; Sütőné-Szentai, 2002, pl. 2, 5; pl. 3, 1, 3, 4; Sütőné-Szentai, 2003, pl. 1, 2, 3; Magyar et al., 2004, figs. 4a–c.

Original diagnosis. "Subspherical body with a well-developed apical horn. The cyst body at plates 2'' and 3'' is a little swollen. The processes are short, wide and weakly trifurcate. The processes show the same tabulation as *Spiniferites bentorii*. The tabulation is variably developed. The processes at the cingulum are longer. The wall is 1.5 μm thick, finely granulate and golden-yellow in colour. The archaeopyle is represented by plate 3'' and is irregularly pentagonal in shape. The tabulation is 4', 6'', 6c, 6''', 1p, 1''''. The holotype is 77 μm, long and 60 μm wide (translation from Hungarian to English by Sütőné-Szentai in 2008)".

Diagnosis. A spiniferate cyst with an ovoidal outline and a prominent apical boss which has a distal process. The wall is relatively thick with a smooth to scabrate surface. Processes are gonal, trilaminate peteinoid and distally aculeate. Archaeopyle is precingular, type P, with a free operculum. Gonyaulacacean tabulation expressed by faint sutural crests and the archaeopyle.

Description. Spiniferate cysts with an ovoidal or pear-shaped cyst body. The epicyst and hypocyst are equal or subequal in size. The wall is ~1 μm thick, and has a smooth to scabrate surface. A prominent apical boss, ~3–5 μm in height, is present and terminates in a simple, short, distally bifurcate process (Plate III, 13). The processes are gonal, solid, trilaminate peteinoid (Playford et al., 1995) and distally aculeate. Germinal processes are concentrated at the cingulum and sulcus. Intergonal processes are absent. A standard S-type sexiform gonyaulacacean tabulation pattern is expressed by faint sutural crests and the archaeopyle. The cingulum is narrow and offset, and the sulcus is shallow. A precingular archaeopyle is formed by the release of plate 3''; the operculum is free.

Dimensions. The central body length, including the apical boss, is 48 (59) 74 µm; the equatorial width is 34 (45) 58 µm; and the maximum processes length is 8 (13) 19 µm. Sixteen specimens were measured.

Comparison. Both *Spiniferites pannonicus* (Sütőné-Szentai, 1986) stat. nov. and *Spiniferites bentori* (Rossignol, 1964) Wall and Dale, 1970 have an apical boss. However, the former has a more pointed apex and bears only short, distally delicate, gonal processes, as opposed to the long gonal and intergonal furcate processes of *Spiniferites bentori*. *Spiniferites pannonicus* differs from *Spiniferites oblongus* (Sütőné-Szentai, 1986) stat. nov. in having a shorter apical boss, a more ovoidal cyst body and longer processes (Figure 5).

Comment. Consistent significant morphological differences between *Spiniferites pannonicus* (Sütőné-Szentai, 1986) stat. nov. and other forms of *Spiniferites* with apical bosses amply justify its elevation to species level.

Distribution. Middle Miocene (Badenian to ?Sarmatian regional stages) (the *Spiniferites bentorii oblongus* to *Pontiadinium pecsvaradensis* zones) of the Hod-1 borehole, Hungary (Szuromi-Korecz et al., 2004). Late Miocene (Pannonian) of the Zólád borehole, Hungary as *Spiniferites bentorii* (Sütőné-Szentai, 1982b).

Spiniferites septentrionalis Harland, 1977

Plate III, 1–4; Figure 7

Spiniferites septentrionalis Harland, 1977, p. 103–104; pl. 1, 12–18; fig. 4.

Discussion. The genera *Achomosphaera* and *Spiniferites* are identical except for the virtual absence of sutural features in the former. The tabulation of *Spiniferites* is indicated by prominent sutural ridges or septa (Stover and Evitt, 1978, p. 190, 283, 284). *Achomosphaera andalousiensis* Jan du Chêne 1977 was deemed to be a senior synonym of *Spiniferites septentrionalis* by Harland (1983, p. 326) and this topic has been further discussed by Mudie (1987, p. 802), Jan du Chêne and Londeix (1988, p. 241), Head and Wrenn (1992, p. 2), Strauss and Lund (1992, p. 169) and Head (1993, p. 26–27; 1996, p. 546). In the diagnosis of *Spiniferites septentrionalis,* Harland (1977, p. 103) stated that there was "generally no tabulation" except for that reflected by the type P archaeopyle. However, the holotype of *Spiniferites septentrionalis* (Harland, 1977, pl. 1, 12, 13, 17) exhibits faint sutural ridges, and Jan du Chêne in Head and Wrenn (1992, p. 2) proposed that the two species are therefore not conspecific. Based on the discussion above and the material herein (Plate III, 1–4) from the Upper Miocene of the Vienna Basin, *Spiniferites septentrionalis* can be distinguished from *Achomosphaera andalousiensis*.

Comparison. *Spiniferites speetonensis* Duxbury, 1980 has similar processes and septa to *Spiniferites septentrionalis* but differs in having intergonal processes.

Spiniferites tengelicensis Sütőné-Szentai, 1982

Plate II, 5–6

Spiniferites membranaceus Sütőné-Szentai, 1982a, pl. 7, 4.

Spiniferites tengelicensis Sütőné-Szentai, 1982a, p. 208–209, 217–218, pl. 1, 7, fig. 1; Sütőné-Szentai, 1990, pl. 5, 2; Sütőné-Szentai, 2000, pl. 6, 3–4.

Spiniferites sp. Sütőné-Szentai, 1999, pl. 1, 1–2.

Supplementary description. Spiniferate dinoflagellate cysts with an ovoidal or pear-shaped outline. An apical boss is present which terminates in a distally acuminate or truncate process. The wall is ~1.0–1.5 µm thick with a smooth or finely scabrate surface. The processes are gonal, variable in length, usually solid and with membranous trifurcate tips. The cingular processes are typically longer than the others. Processes are connected proximally by low sutural crests. The gonal processes in the sulcal and postcingular areas are connected by prominent sutural crests which are frequently distally smooth and are rarely perforate. The processes around the antapical plate are connected by a membrane or a flange (Plate II, 5). The distal ends of the processes and the membranous sutures are occasionally fenestrate. The laevorotatory cingulum is offset by approximately two cingulum widths. A standard S-type sexiform gonyaulacacean tabulation is indicated by faint sutural ridges. The archaeopyle is precingular, type P formed by the release of plate 3", with a free operculum.

Dimensions. The central body length, including the apical boss, is 52 (59) 75 µm; the equatorial width is 37 (43) 51 µm; the process length around the cingulum is 9 (12) 15 µm; the apical processes are 5 (12) 13 µm long; the antapical processes are 7 (8) 20 µm in length; and the process surmounting the apical boss is 6 (8)18 µm. Twenty-six specimens were measured. The holotype is 73 µm long and 67 µm wide (Sütőné-Szentai, 1982a, p. 209, 218).

Comparison. *Spiniferites tengelicensis* differs from *Spiniferites hennersdorfenses* sp. nov. in the absence of high sutural crests in the precingular and postcingular areas. It differs from *Spiniferites bentorii* (Rossignol, 1964) Wall and Dale, 1970 and *Spiniferites oblongus* in having a trumpet-shaped antapical flange and lacking a long apical horn. *Spiniferites scabratus* (Wall, 1967) Sarjeant, 1970 is also somewhat similar to *Spiniferites tengelicensis,* but lacks an apical boss. *Spiniferites tengelicensis* differs from *Spiniferites membranaceus* (Rossignol, 1964) Sarjeant, 1970 in the presence of an apical boss and robust processes, and the lack of intergonal processes and low membranous sutural crests. It differs from *Spiniferites frigidus* Harland and Reid in Harland et al., 1980 in the absence of the well-developed membranous parasutural crests.

Distribution. *Spiniferites tengelicensis* was recorded as *Spiniferites membranaceus* from the Pannonian of the Szólád Borehole, Hungary by Sütőné-Szentai (1982b, pl. 7, 4), and from the Lower Pannonian (*Spiniferites bentorii* dinoflagellate cyst Zone) of the Tengelic 2 Borehole, Hungary by Sütőné-Szentai (1982b).

Subfamily Uncertain Fensome et al., 1993

Genus *Komewuia* Cookson and Eisenack, 1960 emended Chen, 1982

Type. *Komewuia glabra* Cookson and Eisenack, 1960

Comment. *Komewuia* is characterised by single apical and antapical horns; the apical horn is usually slightly longer than the antapical counterpart (Chen, 1980, p. 30). The two morphotypes recorded herein, *Komewuia*? sp. A and *Komewuia*? sp. B are questionably assigned to the genus because the apical and antapical horns are poorly developed.

Komewuia? sp. A

Plate V, 5–7; Figure 8

Description. Subspherical to ovoidal proximate cysts with a faintly granulate surface. The wall is thin and the cysts exhibit several folds. This form has a pronounced apical horn and a smaller antapical protuberance. The archaeopyle is precingular, large with well-defined margins; the operculum is free. This is the only indication of tabulation; sutural crests are absent.

Dimensions. Overall length 53–60 µm; width 44–50 µm; apical horn 4–7 µm; antapical horn 2–3 µm. Two specimens were measured.

Comparison. *Komewuia*? sp. A differs from *Impagidinium*? *obesum* (Sütőné-Szentai, 1982) Lentin and Williams, 1989 and *Impagidinium*? *pecsvaradense* (Sütőné-Szentai, 1982) Lentin and

Williams, 1989 by the absence of tabulation. *Komewuia glabra* Cookson and Eisenack, 1960 has pronounced apical and antapical horns, a granulate to reticulate autophragm and is larger. The size range is 80–157 x 66–104 µm (Cookson and Eisenack, 1960, p. 257). *Komewuia stoveri* Chen, 1982 also has a relatively large apical horn and a reduced antapical horn; it is also large in size. This species is 100–155 µm long and 75–120 µm wide (Chen, 1982, p. 40). *Komewuia inequicornuta* (Baltes, 1971 ex Stover and Evitt, 1978) Chen, 1982 has more developed apical and antapical horns and more wide/broad at cingulum area.

Komewuia? sp. B

Plate V, 1–4; Figure 8

Description. A large spherical dinoflagellate cyst with an antapical horn; there is no apical horn. The wall is thin, susceptible to folding, with a smooth finely punctuate surface. The archaeopyle is precingular, with a free operculum; this is the only indication of tabulation.

Dimensions. The overall length is 70–74 µm, and the width is 49–65 µm. The antapical horn varies between 3 and 4 µm. Two specimens were measured.

Comparison. *Komewuia*? sp. B differs from *Komewuia*? sp. A by the absence of an apical horn, and being larger in size. It differs from other species of *Komewuia* due to the absence of an apical protuberance.

Genus *Pyxidinopsis* Habib, 1976

Type. *Pyxidinopsis challengerensis* Habib 1976, p. 382; pl. 1, 1a–b; pl. 3, 1–2.

Pyxidinopsis psilata (Wall and Dale in Wall et al., 1973) Head, 1994

Plate III, 5–6; Plate V, 8–12

Pyxidinopsis psilata (Wall and Dale in Wall et al., 1973) Head, 1994, p. 308.

Comments. The surface ornamentation of this species varies from finely scabrate to smooth or reticulate. Some specimens are slightly cruciform in shape, which may indicate a low salinity environment (Wall et al., 1973). All the specimens recorded have an apical boss about 3 µm high. The specimens are similar to the holotype in having a relatively large archaeopyle.

Dimensions. The maximum length of the central body is 56 (67) 79 µm, the maximum width is 43 (55) 67 µm and the apical boss is ~3 µm high. Ten specimens were measured.

Discussion. Wall and Dale in Wall et al., (1973) documented many variants of *Pyxidinopsis psilata* (as *Tectatodinium psilatum*) including cruciform, oval, rhombic and spherical morphotypes. In this study, only oval and spherical forms were encountered. Wall and Dale in Wall et al. (1973) noted that the ovoidal forms consistently exhibited an apical boss, and this is confirmed by this study. In the material from Austria, the ovoidal form is the dominant one and all the specimens exhibit an apical boss.

Previous records: *Pyxidinopsis psilata* was recorded from the Pannonian of the Szólád Borehole, Hungary as dinoflagellate indet. and as *Chytroeisphaeridia cariacoensis* Wall, 1967 by Sütőné-Szentai (1982b, pl. 5, 1–3 and fig. 5 respectively). It was also referred to as *Pontiadinium* sp. from the Lower Pannonian of the Vienna Basin by Fuchs and Sütőné-Szentai (1991, pl. 3, 4).

5. Conclusions

The Early and Middle Miocene dinoflagellate cysts of the fully marine Central Paratethys Seaway were relatively high in diversity. These, and other, biotas were disrupted by the final closure of

Paratethys in Central Europe due to glacioeustatic sea-level fall during the Late Miocene (~11.6 Ma), and this event instigated Lake Pannon. Initially this extensive lake was brackish, but it eventually became entirely freshwater. The water chemistry of Lake Pannon drove the development of an unusual, relatively low diversity association of Late Miocene gonyaulacacean and peridiniacean dinoflagellate cysts, which are described herein from the Hennersdorf Clay Pit, near Vienna, Austria. Some of these taxa are apparently endemic to the Central Paratethys area. *Impagidinium* and *Spiniferites* are the most prominent genera. Some specimens of *Spiniferites* exhibit significant morphological variability. For example the shape and size of the cyst body, the processes, and the apical boss are extremely variable. *Impagidinium* is an open marine genus (Dale, 1996), but has also been recorded from relatively nearshore settings (Marret et al., 2004; Sorrel et al., 2006). The occurrence of representatives of *Impagidinium* with specific morphological variations may help to trace fluctuations in the physicochemical conditions which affected Lake Pannon.

Acknowledgements

Sample preparation was supported by the Commission for Stratigraphical and Palaeontological Research of the Austrian Academy of Science, and by FWF-project P21414-B16. Ali Soliman would like to thank Professor Werner E. Piller of Graz University, Professor Mathis Harzhauser of the Natural History Museum of Vienna and Dr. Andrea Kern of the University of São Paulo, Brazil for their considerable help and microscope (LM and SEM) facilities. James B. Riding publishes with the approval of the Executive Director, British Geological Survey (NERC).

Appendix 1

An alphabetical list of dinoflagellate cysts identified below generic level in the Záhorie Member (Bzenec Formation) at Hennersdorf Clay Pit with full author citations. Taxa which are deemed to be endemic to the Pannonian Basin are asterisked. Species interpreted as being reworked from Middle Miocene and older strata are indicated with two asterisks. References to the dinoflagellate cyst author citations, apart from the new taxa described herein, can be found in Fensome and Williams (2004) and Fensome et al., (2008).

*Achomosphaera breviata sp. nov.

*Achomosphaera argesensis Demetresçu, 1989

Achomosphaera ramulifera (Deflandre, 1937) Evitt, 1963

Batiacasphaera sphaerica Stover, 1977

**Cleistosphaeridium placacanthum (Deflandre and Cookson, 1955) Eaton et al., 2001

**Cordosphaeridium minimum (Morgenroth, 1966) Benedek, 1972

Habibacysta tectata Head et al., 1989

*Impagidinium cf. Impagidinium eugubinum Biffi and Manum, 1988

*Impagidinium spongianum Sütőné-Szentai, 1985

* Komewuia? sp. A

*Komewuia? sp. B

Lingulodinium machaerophorum (Deflandre and Cookson, 1955) Wall, 1967

Melitasphaeridium choanophorum (Deflandre and Cookson, 1955) Harland and Hill, 1979

Operculodinium centrocarpum (Deflandre and Cookson, 1955) Wall, 1967

Polysphaeridium zoharyi (Rossignol, 1962) Bujak et al., 1980

Pyxidinopsis psilata (Wall and Dale in Wall et al., 1973) Head, 1994

**Reticulatosphaera actinocoronata (Benedek, 1972) Bujak and Matsuoka, 1986

Selenopemphix brevispinosa Head et al., 1989

Selenopemphix nephroides Benedek, 1972

**Seriliodinium*? *pannonense* sp. nov.

Spiniferites bentorii (Rossignol, 1964) Wall and Dale, 1970 (*sensu lato*)

**Spiniferites bentorii* subsp. *budajenoensis* Sütőné-Szentai, 1986

Spiniferites bentorii subsp. *truncatus* (Rossignol, 1964) Lentin and Williams, 1973

Spiniferites delicatus Reid, 1974

**Spiniferites hennersdorfensis* sp. nov.

Spiniferites lazus Reid, 1974

Spiniferites membranaceus (Rossignol, 1964) Sarjeant, 1970

Spiniferites nodosus (Wall, 1967) Sarjeant, 1970

**Spiniferites oblongus* (Sütőné-Szentai, 1986) stat. nov.

**Spiniferites pannonicus* (Sütőné-Szentai, 1986) stat. nov.

Spiniferites paradoxus (Cookson and Eisenack, 1968) Sarjeant, 1970 *sensu* Sütőné-Szentai, 1986

Spiniferites septentrionalis Harland, 1977

**Spiniferites tengelicensis* Sütőné-Szentai, 1982

Tectatodinium pellitum Wall, 1967

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Display material captions:

Figure 1. Maps of the area studied. 1 - the maximum extent of the palaeoshoreline of Lake Pannon according to Magyar et al. (1999b). 2 - the location of Hennersdorf Clay Pit (48° 6' 24" N; 16° 21' 12" E), modified from Harzhauser et al.(2008).

Figure 2. The Záhorie Member succession which is exposed in the Hennersdorf Clay Pit, south of Vienna, Austria (central column). The log has been modified from Harzhauser et al., (2008) and references therein. The letters (A-G) represent the zones of Papp (1951). The position of the Hennersdorf Core 1 (HC1) is shown by the grey ornament, and the 20 samples from the entire outcrop are indicated. The sample positions of the 74 horizons from HC1 are indicated in the right-hand column. Note that the even-numbered samples are intercalated between the odd-numbered samples. The succession is within the lower part of Pannonian Zone E.

Figure 3. The variability in distal process terminations and process size in *Achomosphaera breviata* sp. nov. The top row are gonal processes, and the bottom row represent the partially merged processes of the cingulum and sulcus.

Figure 4. Part of a distally hiate sutural crest of *Spiniferites hennersdorfensis* sp. nov.

Figure 5. The cyst body outline (ambitus) and processes of: a and b - *Spiniferites bentorii* (Rossignol, 1964) Sarjeant, 1970; c - *Spiniferites pannonicus* (Sütőné-Szentai, 1986) stat. nov.; and d - *Spiniferites oblongus* (Sütőné-Szentai, 1986) stat. nov.

Figure 6. The tabulation of *Spiniferites oblongus* (Sütőné-Szentai, 1986) stat. nov. in ventral view (A) and dorsal view (B).

Figure 7. Sketches illustrating the distal process terminations of *Spiniferites septentrionalis* Harland, 1977. Not to scale.

Figure 8. Sketches illustrating the outlines of *Komewuia* sp. A (A) and *Komewuia* sp. B (B).

Table 1. The distribution of dinoflagellate cysts in the Hennersdorf Clay Pit section, Vienna Basin, Austria.

Table 2. The distribution of dinoflagellate cysts in the Core 1, Hennersdorf Clay Pit, Vienna Basin, Austria.

Plate I. All photomicrographs are SEM images; the scale bar represents 20 µm except where indicated otherwise.

1–3. *Achomosphaera* sp. cf. *A. fenestra* Kirsch, 1991.

1. Sample HC1-38, right lateral view.

2. Sample HC1-57, ventral view, note the characteristic surface ornamentation and the fenestrations on the process shafts.

3. Sample HC1-55, note the process fenestrations at the distal ends; ventral view.

4–6. *Impagidinium spongianum* Sütőné-Szentai, 1985.

4. Sample HC1-12, ventral view.

5. Sample HC1-25, oblique apical view showing the apical plates.

6. Sample HC1-10, dorsal view.

7 *Impagidinium* sp. 1. Sample HC1-12; crumpled specimen probably in dorsal view, note the characteristic sutural denticulation.

8, 9. *Impagidinium* sp. 2. Sample HC1-12, lateral view with a close-up of the surface structure.

Plate II. All photomicrographs are SEM images; the scale bar represents 20 µm.

1–4. *Spiniferites hennersdorfensis* sp. nov.

1. Sample HC1-27, lateral view.

2. Sample HC1-30, dorsal view.

3. Sample HC1-55, lateral view showing the distal ends of the sutures.

4. Sample HC1-5, ventral view, illustrating the apical plates.

5–6. *Spiniferites tengelicensis* Sütőné-Szentai, 1982.

5. Sample HC1-30, dorsal view, note the relatively long apical process.

6. Sample HC1-30, dorsal view.

7, 8. *Spiniferites oblongus* (Sütőné-Szentai, 1986) stat. nov.

7. Sample HC1-27, dorsal view with attached operculum.

8. Sample HC1-55, dorsal view.

9. *Spiniferites pannonicus* Sütőné-Szentai, 1986 stat. nov. Sample HC1-20, ventral view, note the apical process.

Plate III. Images 1–8 are SEM photomicrographs, and images 9–16 were taken in bright field, England Finder reference = E/F ref. The scale bar represents 20 µm except where indicated otherwise.

1–4. *Spiniferites septentrionalis* Harland, 1977.

1. Sample HC1-20, right lateral view.

2. Sample HC1-38, lateral view.

3. Sample HC1-27, ventral view.

4. Sample HC1-27, deformed specimen showing the sutural septa.

5, 6. *Pyxidinopsis psilata* (Wall and Dale in Wall et al., 1973) Head, 1994.

5. Sample HC1-27, oblique lateral view of a specimen with vermiculate surface ornamentation.

6. Sample HC1-18, dorsal view of a specimen with vermiculate surface ornamentation.

7–8. *Achomosphaera breviata* sp. nov.

7. Sample HC1-10, oblique left lateral view.

8. Sample HC1-1, ventral view, note the merged sulcal processes.

9–12. *Spiniferites oblongus* (Sütőné-Szentai, 1986) stat. nov. Sample HC1-23, Slide B, E/F ref. P52/0; central body length including apical horn and apical process 84.0 µm, width at cingulum 37 µm, processes 5.5 µm. Right lateral view, successive foci.

13–19. *Spiniferites pannonicus* Sütőné-Szentai, 1986 stat. nov. Sample HC1-25, Slide B, ventral view, central body length including apical boss 60.5 µm, width at cingulum 44.5 µm, processes at cingulum 11.0 µm, successive foci.

Plate IV. All images in bright field, England Finder reference = E/F ref. The scale bar represents 20 µm.

1–4. *Spiniferites hennersdorfense* sp. nov. Holotype, sample HC1-16, slide A, E/F ref. N33/4, Specimen number UMJ GandP 211337 of the Joanneum Museum, Graz University, Austria.

1. Low focus, note the distally open sutures (arrowed).

2. Mid focus.

3. High focus, note the absence of the high sutures at the cingulum.

4. Lateral-dorsal view, note the apical boss (arrowed).

5–8. *Spiniferites hennersdorfense* sp. nov. Paratype, sample HC1-23, slide B, E/F ref. R39/0.

5. Dorsal view.

6. Cross section, showing the undulating distal margin of the sutures.

7. Dorsal view, showing the archaeopyle and the apical boss.

8. Dorsal view showing the sutures around the 3P’’ plate

9. *Impagidinium spongianum* Sütőné-Szentai, 1985. Sample HC1-18, Slide A, E/F ref. Y58/3, dorsal view. Note that plate 4’’’ is posterior to plate 3’’ and in contact with plate 1’’’’.

10–12. *Impagidinium spongianum* Sütőné-Szentai, 1985. Sample HC1-18, Slide A, E/F ref. Y59.

10. Ventral view, note the geometry of plate 6’’.

11. Mid focus

12. Left lateral-dorsal view.

13–16. *Impagidinium spongianum* Sütőné-Szentai, 1985. Sample HC1-14, Slide A, E/F ref. J33/0, different focal levels of a lateral-dorsal view respectively.

Plate V. All images in bright field, England Finder reference (E/F ref.). The scale bar represents 20 µm.

1–2. *Komewuia*? sp. A. Sample HC1-25, Slide B, E/F ref. N52.

1. Low focus of the dorsal surface.

2. High focus of the dorsal surface, note the antapical horn and the attached operculum.

3-4. *Komewuia*? sp. A. Sample HC1-18, Slide A, E/F ref. F402, specimen in left lateral view.

3. Low focus.

4. High focus.

5–7. *Komewuia*? sp. B. Sample HC1-32, Slide A, E/F ref. M48.

5. Low focus.

6. Mid focus, note the apical horn.

7. High focus.

8. *Pyxidinopsis psilata* (Wall and Dale in Wall et al., 1973) Head 1994. Sample HC1-18, Slide A, E/F ref. Y63, a specimen in right lateral view with a well pronounced apical boss and a large precingular archaeopyle.

9–12. *Pyxidinopsis psilata* (Wall and Dale in Wall et al., 1973) Head 1994. Sample HC1-26, Slide A, E/F ref. H394, different focal levels of a left lateral view of a specimen with a vermiculate surface.

13–14. *Achomosphaera breviata* sp. nov. Holotype; Sample HC1-16, Slide A, E/F ref. K39. Specimen number UMJ GandP 211335 of the Joanneum Museum, Graz University, Austria.

15–16. *Achomosphaera breviata* sp. nov. Paratype: Sample HC1-16, Slide A, E/F ref. O32.

Plate VI. All images in bright field, England Finder coordinate (E/F ref.). The scale bar represents 20 μm.

1-3. *Seriliodinium*? *pannonense* sp. nov. Paratype, Sample F1, Slide A, E/F ref. G28/0, central body length including apical boss 53.5 μm, width at cingulum 41.5 μm, processes 15.5 μm, successive focal levels.

4-6. *Seriliodinium*? *pannonense* sp. nov. Holotype: Sample HC1-11, slide A, E/F ref. S35/0, central body length including apical boss 47.0 μm, width at cingulum 32.0 μm, processes 13.5 μm successive focal levels. The arrow indicates the apical boss. Specimen number UMJ GandP 211336 of the Joanneum Museum, Graz University, Austria.

7–9. *Seriliodinium*? *pannonense* sp. nov. Sample HC1-50, Slide A, E/F ref. N32/1, central body length including apical boss 55.5 μm, width at cingulum 36.0 μm, processes at cingulum 20.5 μm successive focal levels showing the branching of processes and the distal trabeculae.

10. *Seriliodinium*? *pannonense* sp. nov. Sample HC1-38, uncertain orientation.

11. *Seriliodinium*? *pannonense* sp. nov. Sample HC1-38, right lateral view.

12. *Seriliodinium*? *pannonense* sp. nov. Sample HC1-55, close-up on process terminations.

13. *Seriliodinium*? *pannonense* sp. nov. Sample HC1-55, close-up on processes shafts and terminations.