NEW ORGANIC-WALLED DINOFLAGELLATE CYSTS FROM RECENT SEDIMENTS OF CENTRAL ASIAN SEAS

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Abstract

Recent to sub-recent sediments from the Caspian Sea, the Kara-Bogaz-Gol Bay, the Enseli lake and the Aral Sea contain the new organic-walled dinoflagellate cysts *Caspidinium*, *Caspidinium rugosum* and *Impagidinium caspienense*. *Caspidinium rugosum* has S-type paratabulation, dextral torsion and low relief intratabular ornamentation. *Impagidinium caspienense* has low intratabular suturo-cavate relief, parasutural septa irregular in height and a high septum at the junction of paraplate 1'''' and the sulcus. The accompanying species consist of *Spiniferites cruciformis*, *Lingulodinium machaerophorum*, *Pyxidinopsis psilata*, cysts of *Pentapharsodinium dalei* and *Brigantedinium* spp. *Spiniferites cruciformis* varies from specimens with a cruciform body with a well-developed postero-lateral membranous flange to specimens with a pear-shaped body, reduced processes and no flange. Sea-surface data from these Central Asian seas suggests that the two new taxa *Caspidinium rugosum* and *Impagidinium caspienense* are probably related to low salinity conditions (12-13).

Keywords: Dinoflagellate cysts, taxonomy, Caspian Sea, Aral Sea, Late Holocene.

1. Introduction

Following the original work of Wall *et al*. (1973), several papers have focussed on Late Quaternary organic-walled dinoflagellate cysts from eastern Mediterranean regions (e.g. Atanassova, 1995; Bozilova *et al*., 1997; Mudie *et al*., 2001, 2002; Rochon *et al*., 2002). These studies document endemic species and morphological features, such as cysts of cruciform shape, which may have resulted from isolation and freshwater to brackish conditions prevailing in these regions. Recently, Rochon *et al*. (2002) described a new cruciform cyst, *Pterocysta cruciformis*, from glacial Late Pleistocene sediments from the southwestern Black Sea and the central Marmara Sea. Further east, the Late Quaternary palynomorphs from other Central Asian seas such as the Caspian and Aral Seas (Fig. 1A), however have received scant attention.

The Black, Caspian and Aral Seas constitute relics of the Paratethys basin and their isolation after the closing of the Tethys led to different environmental conditions in each basin. Dinoflagellate cyst assemblages, cyst morphology and endemism from each of these seas may provide information about the impact of various environmental parameters and a basis for palaeoenvironmental reconstructions (e.g. Mudie *et al*., 2001, 2002). Unlike the Black Sea, both the Caspian and the Aral Seas are presently experiencing dramatic environmental changes. Caspian Sea water levels (water surface at about 27 m below mean sea level in 1994) have recently fluctuated rapidly and suddenly, causing serious environmental and economic damage and adversely affecting oil and gas exploration, agriculture and fishing. These abrupt fluctuations in water level may be due in part to climate change (e.g. Froehlich *et al*., 1999) but other factors, ~~i.e.~~such as anthropogenic or tectonic causes, must have played a part (e.g. Shiklomanov *et al*., 1995). The Aral Sea area has been reduced by more than 50% since extensive irrigation systems developed during the 1960s, and water salinity has experienced a sharp increase, with salinity varying from 9 to over 30 over the last 40 years (Boomer *et al*., 2000).

As part of a French-Russian program to determine the causes of the Caspian water-level oscillations, a series of hydrological profiles, Kullenberg cores (including pilot and long cores) and box (Usnel) cores were collected in August 1994. A palynological study of several pilot cores was undertaken to determine vegetational and environmental changes. Palynomorphs recovered from down-core sediments document a relatively high diversity of pollen grains and spores, as well as prasinophycean phycoma and fresh-water algal remains. (Leroy *et al*., 2000). Organic-walled dinoflagellate cysts (=dinocysts) were also observed and counted. The dinocyst assemblages are remarkably similar to those described by Wall *et al*. (1973) from the Black Sea late Quaternary sediments, but there are also several new taxa. These include the species *Caspidinium rugosum* and *Impagidinium caspienense*, which occur in several top-samples of pilot-cores and subsurface sediment samples from different regions of the Caspian Sea. Analyses and description of dinocyst assemblages from subsurface samples from the Kara-Bogaz-Gol Bay (a large overflow basin east of the Caspian Sea), the Enseli lake (a coastal lake at the foot of the Elburz Mountains, south of the Caspian Sea) and the Aral Sea are also included in this study for comparison. There is a tentative interpretation of the ecological significance of the new taxa together and other dinocyst species.

2. Environmental and biological settings

2.1. The Caspian Sea

The Caspian Sea is the world’s largest sea in terms of both area and volume, stretching from 36ºN to 62ºN (Fig. 1B) and with a drainage basin covering about 3.1 million km^2. Water inputs comprise river discharges in particular the Volga (contributing up to 80-85 % of the total), Emba, Ural and Terek rivers (Rodionov, 1994). The relatively low salinity (12-13, Fig. 2C-D) of the Caspian Sea surface water and its substantial salinity gradient from north (freshwater) to south (brackish) (Kosarev and Yablonskaya, 1994) results in a variety of endemic zooplankton and phytoplankton species (Kasymov and Rogers, 1996).

The history of the Caspian Sea falls into a series of stages determined by orogenic and climatic events. During the Late Miocene, the fully marine Caspian and Black Seas were connected by a deep waterway and the Black Sea was linked to the Mediterranean Sea as part of Paratethys (Dercourt *et al*., 1985). In the Middle Pliocene, orogenic activity separated the southern part of the Caspian Sea from the Black Sea but later they were temporarily reconnected, where the Caspian Sea was part of a slightly salty

Pontic lake. The Caspian Sea was connected to the Aral Sea during the Pliocene and Pleistocene as the result of major transgressions linked to large-scale influx of melt water from high latitude ice caps (Dumont, 1998; Grosswald, 1980, 1993; Mamedov, 1997). For the last 300 ka, the Caspian Sea has existed as an isolated water body (Boomer *et al.*, 2000), ~~a~~with some short transgressive episods associated with interglacial periods and global sea-level changes (Svitoch *et al.*, 2000). The Amu Darya and the Sarykamysh rivers have occasionally flowed respectively from the Tien-Shan and from the Aral Sea to the Caspian Sea during the Holocene. Today, the Black and Caspian Seas are connected via the artificial Don-Volga canal, causing some faunal and floral exchanges.

The northern ice sheet during melting phases has changed the amount of fresh water reaching the Caspian Sea. Large ice-dammed freshwater lakes formed along the southern edge of the ice sheet, such as palaeolake Mansi and palaeolake Komi (Grosswald, 1993; Mangerud *et al.*, 2001). The history of these palaeolakes' drainage is not well known but their meltwater influx must have governed the change of the Caspian from a freshwater lake to a more saline water body. Indeed, the last change from freshwater to brackish conditions may have happened only 10,000 years ago (Mamedov, 1997; Mangerud *et al.*, 2001).

The Caspian basin area is subdivided into three sub-areas: the northern (80,000 km^2) (with average depth 5-6 m, maximum depth of 15-20 m); the middle (138,000 km^2) with a maximum depth of 788 m; and the southern (168,000 km^2) with an average depth of 190 m (Fig. 1B). The southern basin holds more than 65% of the Caspian water and reaches a maximum depth of 1025 m.

A north-south gradient of the water~~s~~ salinity (Fig~~s~~. 2C-2D) is observed with freshwater in the northern end of the basin to almost homogeneous 12.5-13.5 surface water salinity in the central and southern basins. In the southern basin, seasonal salinity changes are less than ~0.2-0.4. Mean annual salinity increases from the surface to the bottom waters only ~~of~~ by 0.1 to 0.3 (Zenkevitch, 1963; Kosarev and Yablonskaya, 1994).

Surface water temperature data record important seasonal variations. The shallow, less saline waters of the northern basin cause freezing of the surface water from December to March (Zenkevitch, 1963), whereas mean water temperature reaches ~24°C during July and August (Kosarev and Yablonskaya, 1994) (Fig~~s~~. 2A-B). In the southern basin, water temperatures near the coring sites vary from 9°C in winter to 26°C in summer (e.g. Zenkevitch, 1963). There is a sharp thermocline between 20 and 40 m~~.~~ depth during the summer (Fig. 2A), with seasonal temperature fluctuations of the deeper waters (water temperatures from 4.5 to 6ºC below 200 m ~~.~~) almost negligible.

Surface waters of the southern basin are near oxygen saturation in summer (94%) and slightly supersaturated in winter (104%) (Zenkevitch, 1963). The dissolved oxygen content ~~would~~ decreases with depth, ~50% saturation at 200 m and < 10% below 600 m but anaerobic conditions ~~would~~ are never ~~be~~ reached, even in the deepest~~r~~ waters. ~~Notable~~

Most nutrients enter the Caspian Sea in the northern basin via the Volga River. Today, the relatively low nutrient levels are depleted in the upper 100 m by phytoplankton activity, but they increase with depth. Concentration of nutrients in the northern ba~~s~~sin is presently lower than in the pre-regulation of the Volga River in the 1950s, except for the silicate group (Kosarev and Yablonskaya, 1994).

The Caspian Sea is characterised by a high level of endemism (e.g. Dumont, 1998) with modern assemblages derived from three sources: the Mediterranean Sea, the Arctic, and river input. The Caspian Sea biota ranges from freshwater to brackish to euryhaline and has a low diversity. In general, marine species comprise 72.1% of the zooplankton. Surveys of surface water of the Caspian Sea have recorded about 440 phytoplanktonic species, the northern basin containing the highest diversity (Kasymov and Rogers, 1996). Dinoflagellates represent about 14 % of the total phytoplankton composition with notably the cyst-producing species *Gonyaulax polyedra* (= *Lingulodinium polyedrum*), *Gonyaulax digitalis* and *Gonyaulax spinifera*.

2.2. The Enseli lake

The lake (at latitude 37º26’ to 37º32’ N, longitude 49º16’ to 49º25’ E) had a water level of –28 m at the time of the sampling in 1995 (Fig. 1B): it is characterised by a mixture of freshwater, from several rivers, and brackish waters from the Caspian Sea. Water temperature varies between 18 and 21ºC with salinity ranging from 0 near the coast to 6 in the middle of the lake.

2.3. Kara-Bogaz-Gol Bay

The Kara-Bogaz-Gol Bay (KBG) is a shallow bay (maximum depths not exceeding 10 m) connected to the eastern side of the Caspian Sea (Fig. 1B) by a narrow strait (110 to 300 m wide and eight to ten km long). Since the surface of the bay is below that of the Caspian Sea by 3-4 meters, there is a regular inflow of waters. An extreme very dry (less than 90 mm of rainfall) continental climate exhibits temperature fluctuations from 5°C in December to 29°C in July. The KBG is more than 160 ~~kilometers~~ km-long, 137 ~~kilometers~~ km-wide, and covers about 18,000 km^2~~square kilometers~~. Present-day water level is 28 ~~meters~~ m below sea level, but records show that over the last 100 years there have been considerable fluctuations (Lepeshevkov *et al*., 1981, Giralt *et al*., submitted). The Kara-Bogaz-Gol Bay is the largest sodium sulphate body of water in the world, and has a predominance of Cl$^-$, Na$^+$ and Mg^{++} with a high density (> 1.2 g/cm3). Consequently, the Bay's salinity is currently 10 to 20 times higher than that of the standard salinity of 12-13 of the Caspian Sea (Kosarev and Yablonskaya, 1994). Water temperature ranges from < 4°C in December to 25°C in July.

2.4. The Aral Sea

The Aral S~~s~~ea (Fig. 1A) is a relatively shallow water body (maximum water depth of 50 m), with water level at 36 m above sea level. This sea ~~water~~ has experienced dramatic changes in its hydrochemistry and surface area during the last four decades due to anthropogenic activities. Salinity drastically increased from 9 in the 1960~~'~~s to 30 in the 1990~~'~~s (Boomer *et al*., 2000) and surface temperature shows important seasonal contrast due to desiccation. The creation of irrigation channels in the 1960's for cotton and rice growing in Kazakhstan dramatically reduced the amount of river discharge into the Aral Sea. Therefore, it is difficult to characterise its environment before 1960.

3. Material and methods

3.1. Sediment material

For the purpose of this study, samples for the Caspian Sea were selected from the top of piston-cores, Kullenberg cores and a Usnel-type core (Table 1). In late summer 1995, T. Gulbabazade took a series of subsurface sediment samples (from 0 to 30 cm depth in Plexiglas tubes) in 1.5 m water in the centre of the Enseli (Anzali Mordab) lake (Kazanci *et al*., submitted). The sample just south of the outflow contains a numerous dinoflagellate cysts and therefore is included in this study. Other samples were from core AS17-section 5 collected in the Aral Sea (Steve Juggins, with a Livingstone piston corer) and sub-sampled at 6.5 cm depth for palynological investigation and the top centimetre of the Kara-Bogaz-Gol Bay core KBG 8-01 (Giralt *et al*., submitted). All sediment materials are in the text according to Table 1 (i.e. sample #).

The age estimation of the selected samples, in particular for the Caspian Sea sediments is uncertain, because the coring techniques do not permit sampling of the most recent sediment. In the Caspian Sea, comparison of the lithology between box cores, pilot cores and gravity cores indicates that the top of most of the gravity and pilot cores probably lacks the late Holocene. Only the box core may represent the last few centuries. For the KBG, Enseli and Aral samples, a recent age (a few centuries) is assumed but still remains to be confirmed.

3.2. Laboratory procedures

Initial processing of samples involved the addition of sodium pyrophosphate to deflocculate the sediment, before acid digestion. Most samples were treated with cold ~~attacks~~ hydrochloric acid (10%) and cold hydrofluoric acid (32%). The residual organic fraction was then screened through 120 µm and 10 µm mesh sieves and mounted on slides in glycerine gel coloured with safranin and sealed with paraffin. Surface sediments from the Enseli lake were similarly prepared but were also acetolysed. Results are given in Table 2. ~~+ Aral: ?~~ For scanning electron microscopy observations, specimens were handpicked, air-dried on a stub and gold-coated. Slides containing holotype and figured material are deposited at the Natural History Museum, London, UK. The archived half of each sediment core (with the exception of the Enseli sample which was not archived) is stored in the Museum d'Histoire Naturelle in Paris, France.

Sediment depth and core name are included in the plate captions for each figured specimen. Light microscopy (Leitz Laborlux K) photographs were taken by digital cameras in transmitted light. Coordinates of specimens are provided by an England Finder (EF).

4. Systematics

The classification of dinoflagellate cyst species follows that of Fensome *et al*. (1993) and Williams *et al*. (1998). Owing to the complexities of the paratabulation for gonyaulacacean taxa, the Kofoidian tabulation system described in Fensome *et al*. (1993) has been used for the description of the new cysts.

Division DINOFLAGELLATA (Bütschli, 1885) Fensome et al. 1993
Class DINOPHYCEAE Pascher 1914
Order GONYAULACALES Taylor 1980
Family GONYAULACACEAE Sarjeant et Downie 1966

Genus *CASPIDINIUM* Marret, gen. nov.

Type: *Caspidinium rugosum* Marret in Marret *et al*. sp. nov. Plate 1: 1-5.

Derivation of name: Named after the type locality, i.e. the Caspian Sea.

Type locality: Recent sediments from the Southern Caspian.

Diagnosis: Proximate cyst with ventral S-type gonyaulacacean paratabulation, dextral torsion and low, coarse intratabular ornamentation. Cyst ambitus subspherical, slightly cruciform, and reniform in apical view. Epicyst smaller than the hypocyst. Endophragm and periphragm appressed. Sulcal paratabulation is indistinguishable. Archeopyle is precingular (3'') with free operculum.

Remarks: The number (4) and arrangement of apical plates, together with a S-type paratabulation may indicate a gonyaulacoidean affiliation, although the dextral torsion suggests a possible affinity with the Cribroperidinoideae.

Comparison with other genera: *Caspidinium* differs from *Impagidinium* Stover and Evitt 1978 and *Corrudinium* Stover and Evitt 1978 in having dextral torsion. Although *Cribroperidinium* Neale and Sarjeant 1962 has dextral torsion, it has a L-type paratabulation. The slightly cruciform shape of the cyst suggests that *Caspidinium* may be characteristic of low salinity conditions, as indicated by the presence of other cruciform-shaped cysts, such as *Spiniferites cruciformis* or *Pyxidinopsis psilata* in similar environments.

Caspidinium rugosum Marret in Marret et al. sp. nov.

Plate 1: 1-9, Plate 5: 3; Figures 3A-C

Holotype: Recent sediments (0 cm) from US02-2 from Southern Caspian (51º29'E, 39º16'N at a water depth of 315 m). Plate 1: 1-5 (NHM registration number FD645(1)/EF: T49/2)

Repository: Slide: Natural History Museum of London (UK). Material: Museum d'Histoire Naturelle de Paris (France).

Type locality: Recent sediments from the Southern Caspian.

Derivation of name: from Latin, *rugosus* (wrinkled); with reference to the coarse ornamentation of the wall surface.

Diagnosis: Proximate gonyaulacacean cyst with S-type ventral paratabulation expressed by low and broad parasutural septa and dextral torsion. Subspherical to slightly cruciform cyst ambitus, and reniform shape in apical view. Epicyst smaller than the hypocyst. The endophragm and periphragm are appressed to form a relatively thick wall layer (1.5 µm). Low parasutural septa and a coarsely rugulate to papillate intratabular ornamentation. Precingular archeopyle (3'') of iso-camerate shape and free operculum.

Description: In equatorial view, the cyst has a subspherical to slightly cruciform shape with the epicyst being smaller and more conical than the hypocyst and more conical. In apical view, the cyst is reniform, with a concave ventral region. The epicyst has a rounded apex, with no apical horn or boss and the hypocyst has a flat antapex. In lateral view, the hypocyst is more expanded in the ventral region (Plate 1: 8-9). Ornamentation on the wall surface is highly variable, from coarsely papillate, verrucate to rugulate. Endophragm and periphragm are appressed and form a relatively thick wall layer (*ca* 1.5 µm). The S-type gonyaulacacean paratabulation (4', 6'', 6c, ?6''', 1p, 1'''') is expressed by low and pronounced parasutural septa formed by a thickening of the periphragm but differs in having dextral torsion (Plate 1: 5, 8; Fig. 3A). The plates marked by * (Fig. 3A-C) are considered as homologues of the standard gonyaulacacean paratabulation (Fensome *et al*., 1993). The coarse papillate to rugulate ornamentation in the ventral region obscures the sulcal and lateral paratabulation (Plate 1: 1-2). Paraplate 2' is smaller than paraplate 3', and the junction of paraplates 1'' and 2'' is a third along the boundary with paraplate 1' (Fig. 3C). The contact between paraplates 4' and 6'' is short. The archeopyle is precingular (3''), broad, iso-camerate shape and always free. Most specimens are transparent to yellow in light microscopic observation.

There is a high variability in the ornamentation of *Caspidinium rugosum* and some specimens are characterised by very coarse rugulation and low intratabular relief with indistinct parasutural septa. The only clear characteristic of the paratabulation is the precingular archeopyle (3'') and paraplate 4'''. These specimens were counted apart as it is possible that this morphological variation could relate to particular environmental conditions (see Table 2).

Dimensions: Holotype (Plate 1:1-5): body length = 48 µm; body width = 43 µm; thickness of the cyst wall = 1.5 µm. Average measurements on 8 specimens: body length = 45–(52)–60 µm; body width = 45–(52)–60 µm. Due to poorly orientation, and often broken specimens but few complete specimens, it was not possible to obtain extensive measurements.

Comments and comparisons: In the ventral region, the parasutural septa and surface relief merge, which obscures the sulcal and lateral paratabulation. Furthermore, specimens were often broken, or not well oriented for studying the sulcal area. *Caspidinium rugosum* differs from species of *Impagidinium* and *Corrudinium* species by its characteristic dextral torsion, and from *Cribroperidinium* species by the S-type paratabulation. The species differs from *Gonyaulax apiculata* (Evitt *et al*., 1985) in having 6 precingular paraplates so that the dextral torsion differs. In *Gonyaulax apiculata*, the 3c/4c suture is below paraplate 3'' whereas it is situated under paraplate 4'' in *Caspidinium rugosum*. Furthermore, in the apex region, *Caspidinium rugosum* has no apical boss and has a marked suture between paraplates 1' and 2'.

Genus *IMPAGIDINIUM* Stover and Evitt 1978

Type species: *Impagidinium dispertitum* (Cookson and Eisenak 1965) Stover and Evitt 1978

Impagidinium caspienense Marret in Marret et al. sp. nov.

Plate 3: 1-8; Plate 5: 1-2; Figures 3D-E.

Holotype: Recent sediments (0 cm) from US02-1 from Southern Caspian (51º29'E, 39º16'N at a water depth of 315 m). Plate 2: 1-4 (NHM registration number FD644(1)/EF: P43)

Repository: Slide: Natural History Museum of London (UK). Material: Museum d'Histoire Naturelle de Paris (France).

Type locality: Recent sediments from the Southern Caspian.

Derivation of name: Named *caspienense* from the French name of the Caspian Sea (*Mer Caspienne*).

Diagnosis: Proximate cyst with subspherical to ellipsoidal ambitus, endophragm and periphragm appressed and low intratabular linear relief. Gonyaulacacean paratabulation indicated by low parasutural septa and ventral S-type organisation. Paraplate 4' is in contact with paraplate 6''. Prominent septum is developed at the junction of paraplate 1'''' and the sulcus. Apical boss. Archeopyle is precingular (3''). Operculum is free.

Description: The cyst has a subspherical to ellipsoidal ambitus with both hypocyst and epicyst of equal size. The epicyst has a smoothly rounded apex with a pronounced apical boss (2 to 4 µm in height) (Plate 2: 3-4). Endophragm and periphragm are appressed except along the parasutural septa where a small cavation is observed, and form a relatively thin wall layer (1 µm). The surface of the wall has two different types of ornamentation: fine granulation and low intratabular suturo-cavate relief observed on all the paraplates. The parasutural septa are low (≤ 2 µm), of irregular height, with an undulating margin and are finely granulate. A 2 to 5 µm high septum occurs at the junction of paraplate 1'''' and the sulcus. The parasutural septa delineate a gonyaulacacean paratabulation (4', 6'', 6c, 6''', 1p, 1'''') with the ventral area showing S-type paratabulation. The sulcus is generally not divided into paraplates, although septa can start to develop between sulcal paraplates ps, rs and ls (Fig. 3E). The archeopyle is precingular (paraplate 3'') and the operculum is free. Paraplate 4''' lies posterior to paraplate 3''. Paraplates 4' and 1' are narrow and subparallel. The contact between paraplates 4’ and 6'' is very short, and paraplate 6'' is subtriangular and relatively narrow. All specimens observed are transparent in light microscopy.

Dimensions: Holotype: body length = 40 µm; body width = 31 µm; height of apical boss = 2 µm, thickness of the cyst wall = 1 µm, height of septa (except the antapical septum) = 2 µm. Average measurements on 15 specimens: body length = 35–(39)–50 µm; body width = 30–(35)–43 µm.

Comparisons: The irregular height of septa, the occurrence of a high septum at the junction of paraplate 1'''' and the sulcus, and the low intratabular relief separates *Impagidinium caspienense* from all other extant *Impagidinium* species. This species differs from *Impagidinium paradoxum* in its lack of sulcal paratabulation.

Genus *LINGULODINIUM* Wall 1967 emend. Dodge 1989

Lingulodinium machaerophorum (Deflandre and Cookson 1955) Wall 1967

Plate 3: 1-7

Comments: Specimens observed in the studied surface sediment samples are morphologically similar to those described in Wall *et al*. (1973). Process types, as documented by Wall *et al*. (1973) and Lewis and Hallett (1997), varied from small with acuminate tips to medium long processes with bulbous or roundly conical tips. Some specimens devoid of processes show a remarkable ornamentation, with a reticulate pattern instead of processes (Plate 3: 6-7) in the ventral region.

Genus *PYXIDINOPSIS* Habib 1976

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

Plate 2: 9; Plate 5: 6

Comments: The periphragm ornamentation varies from finely scabrate to strongly vermiculate in the Caspian Sea specimens; the ambitus is always cruciform.

Genus *SPINIFERITES* Mantell 1850 emend. Sarjeant 1970

Spiniferites cruciformis Wall and Dale in Wall et al. 1973

Plate 4: 1-11

Comments: The Caspian Sea specimens show great variability in the ambitus and processes as noted by Wall and Dale in Wall *et al*. (1973). Three morphotypes were observed based on the absence or presence of membranous flanges and the morphology of the cyst body (Fig. 4).

Morphotype A (Plate 4: 1-5, Plate 5: 4, Fig. 4B-C) has a cruciform ambitus and a conspicuous membranous flange in ventral view. Some specimens show a well developed left postero-lateral flange, others have a fenestrate flange, completely extended in the ventral region. These cysts differ from *Seriliodinium explicatum* Eaton (1996) in lacking the trabeculae that join the process tips. A pronounced apical boss is sometimes present.

Dimensions: Average size based on 25 specimens: body length = 48–(58)–68 µm; body width = 40–(49)–60 µm, process length = 10–(14)–20 µm. Plate 4: 1-5, Plate 5: 4.

Morphotype B (Plate 4: 6-9, Plate 5: 5, Fig. 4A) has stout processes, no membranous flange and mostly a cruciform ambitus similar to the holotype of Wall and Dale in Wall *et al*. (1973). Those cysts with a cruciform shape have a rounded apical apex. Some specimens with stout processes show a less cruciform-shape body and a low apical boss.

Dimensions: Average size based on 17 specimens: body length = 55–(68)–78 µm; body width = 48–(53)–60 µm, process length = 13–(18)–28 µm. Plate 4: 6-9, Plate 5: 5.

Morphotype C (Plate 4: 10-11, Fig. 4D-E) has a less pronounced cruciform ambitus than the holotype of Wall and Dale in Wall *et al*. (1973). Processes are usually straight, with no termination and folded on the endocyst. The apical boss is always present and very prominent. There is no membranous flange developed between processes.

Dimensions: Average size based on 20 specimens: body length = 60–(65)–70 µm; body width = 48–(52)–56 µm. Plate 4:10-11. Processes were not measured as they were folded on the endocyst.

Order PERIDINIALES Haeckel 1894

Family PERIDINIACEAE Ehrenberg 1831

Genus *PENTAPHARSODINIUM* Indelicato and Loeblich III 1986 emend. Montresor et al. 1993

Cysts of *Pentapharsodinium dalei* Indelicato and Loeblich III 1986

Plate 3: 8-9

Comments: Cysts of *P*. *dalei* observed in the studied samples are morphologically identical to the type material described by Dale (1977). Plate 3:8 illustrates the splitting of the wall.

Family PROTOPERIDINIACEAE Bujak et Davies 1998

Genus *BRIGANTEDINIUM* Reid 1977 ex Lentin et Williams 1993

Plate 2: 8

Comments: Since the archeopyle was not visible, the specimens could not be identified at the species level. Nevertheless, the observed specimens strongly resemble the "baggy cysts" of Traverse (1978) documented from Neogene sediments of the Black Sea and assigned to *Brigantedinium* species.

5. Ecological affinities of the Caspian Sea dinoflagellate cysts

The~~A~~ organic-walled dinoflagellate cyst taxa recovered from the recent sediments of the Caspian Sea are *Caspidinium rugosum*, *Impagidinium caspienense*, *Lingulodinium machaerophorum*, *Pyxidinopsis psilata*, *Spiniferites cruciformis*, *Pentapharsodinium dalei* and *Brigantedinium* spp. This low diversity ~~has been found~~is comparable to that of the Black Sea (e.g. Wall *et al*., 1973; Mudie *et al*., 2001, 2002). There is no published information on Holocene organic-walled dinoflagellate cysts from Caspian or the Aral Sea sediments and, as the most dominant taxon in this study is new, the interpretation of palaeoassemblages is hampered. We use the following two-fold approach to relate out cyst assemblages to present-day environmental conditions: 1) the occurrence ~~with~~ of taxa whose~~ich~~ global distribution and ecological affinities are relatively well known; and 2) ~~from~~ a ~~the~~ comparison of the Caspian dinocyst assemblages with records from the Black Sea. ~~A brief outline of the main~~The relative abundances of all taxa in the subsurface samples are illustrated in Figure 5.

Impagidinium caspienense is dominant in most of the assemblages from the Caspian Sea, followed by *Brigantedinium* spp. and cysts of *Pentapharsodinium dalei*. In the Aral Sea sample, *Lingulodinium machaerophorum* with long processes is the most abundant taxon, with *Impagidinium caspienense* being present. Only a few specimens *of Caspidinium rugosum* were observed from the Caspian Sea sediments and have not ~~not~~ been recorded from the Enseli lake, the Kara-Bogaz-Gol Bay and the Aral Sea.

Usually, cysts of the genus *Impagidinium* are found in open oceanic sediments, covering a wide range of temperatures but with little tolerance for salinities below 32 (e.g. Edwards and Andrle, 1992; Rochon *et al*., 1999; Marret and Zonneveld, 2003). The high numbers of *Impagidinium caspienense* in Caspian Sea sediments suggest that this species is more tolerant to lower salinity than other *Impagidinium* species.

The distribution of *Lingulodinium machaerophorum* in coastal to neritic surface sediments from polar to tropical areas shows its tolerance to a wide range of salinity, from 5 to 36. However, the species seems to be restricted to regions with summer temperatures above 10-12ºC (e.g. Marret, 1994; Dale, 1996; Rochon *et al*., 1999). The predominance of specimens with reduced processes in low saline conditions (*ca* 13), as in the Caspian Sea sediments, has been observed both in natural environments and in culture experiments (Dale, 1996; Lewis and Hallett, 1997). High abundances of *L. machaerophorum* cysts were found in sediments underlying upwelling cells off North West Africa (Targarona *et al*., 1999). Although turbulence is a limiting factor in the distribution of the thecate forms (*Lingulodinium polyedrum*), it is possible that this species requires high nutrient levels that can be supplied from a variety of sources (coastal upwelling, river runoff) (Lewis and Hallett, 1997).

Cysts of *Pentapharsodinium dalei* are relatively abundant in sub-polar to temperate oceanic regions of the North Atlantic (e.g. Rochon *et al*., 1999). Low percentages of this species have also been reported from recent sediments of the Black Sea (P. Mudie, pers. comm.). The global distribution suggests that *P. dalei* can tolerate large differences in salinity and nutrient (phosphate/nitrate) concentrations, as well as a seasonal sea-ice cover up to 12 months per year, and has an affinity for strong seasonal amplitude in sea-surface temperature. In the Southern Caspian, present-day surface salinity is around 12-13 in winter and summer and temperature ranges from 8 to 10 ºC in winter to 25-26ºC in summer, whereas the Middle Caspian has a slightly lower winter temperature (5 to 8ºC) (Fig. 2A-B) (Kosarev and Yablonskaya, 1994). The present-day global occurrence of *P*. *dalei* cysts (e.g. Rochon *et al*., 1999, de Vernal *et al*., 2001) possibly suggests that their presence in the Caspian Sea sediments may be related to seasonal temperature contrast in surface waters. The other heterotrophic taxon, *Brigantedinium* spp. has a higher relative abundance in samples from the Middle Caspian compared to those further south. Their presence, based on their known relationship with nutrient-rich conditions (e.g. Marret and Zonneveld, 2003), may be related to nutrient levels linked to river discharge, especially in the northern part of the Caspian Sea.

The dinocyst assemblages from subrecent sediments from the Caspian Sea can be further compared with those recorded by Wall *et al*. (1973) and by Mudie *et al*. (2001, 2002) from Late Pleistocene and Holocene cores of the abyssal plains of the Black Sea. However, *Impagidinium caspienense* and *Caspidinium rugosum* were not identified in the Black Sea sediments.

Spiniferites cruciformis was first described from late Quaternary sediments of the Black Sea (Wall *et al*., 1973). Subsequently it has been found in late Quaternary sequences from the Marmara Sea and the N.E. Aegean Sea (Aksu *et al*., 1995, Mudie *et al*., 2001), in Late Glacial sediments from Lake Kastoria, northern Greece (Kouli *et al*., 2001) and in Early Pliocene sediments from the Ptolemais Basin, northern Greece (Kloosterboer-van Hoeve *et al*., 2001). Since the thecate-cyst relationship is unknown, the only ecological data is based on the fossil records. Mudie *et al*. (2001) distinguished several morphotypes of *S. cruciformis* based on the shape of the body and the size and range of the parasutural septa, in an attempt to relate the different morphologies to specific salinity range. Kouli *et al*. (2001) noted morphological variability, similar to the initial observations of Wall *et al*. (1973). However, no clear relationship between the different morphotypes and salinity fluctuations has~~s~~ yet been established (Kouli *et al*., 2001; Mudie *et al*., 2001). According to Kouli *et al*. (2001), however, it can tolerate freshwater to brackish conditions. In our study, *S. cruciformis* occurs in almost all samples, except in CP18 and GS18 from the Middle Caspian, and within a range of salinity between ~ 12 to ~ 13 (Table 2). It occurs in low percentages (3%) in the sub-recent sample from the Aral Sea, where salinity prior to the 1960s was below 9 (Boomer *et al*., 2000).

The presence of *Spiniferites cruciformis* in sediments from the Caspian and Aral Seas indicates a more extended geographical distribution for the species than the "greater Black Sea region" described by Kouli *et al*. (2001). Kloosterboer-van Hoeve (2000) recorded *S. cruciformis* and *Gonyaulax apiculata* cysts, from Lower Pliocene lacustrine sediments of the Ptolemais Basin, northern Greece. Such results suggest that *S*. *cruciformis* may have been present throughout the Paratethys system. However, without more extensive stratigraphic records, it is difficult to pinpoint when and how this species has migrated and when it was isolated in various water bodies posterior to the Paratethysian period. Its occurrence in recent to sub-recent sediments from three seas (Black, Caspian and Aral Seas) suggests that *S. cruciformis* has adapted to new hydrological conditions.

Pyxidinopsis psilata, also first described from late Quaternary sediments of the Black Sea (Wall *et al*., 1973) occurs in recent brackish water sediments ~~of~~ of the Baltic Sea (salinity < 7) (Dale, 1996). A culture of living cysts produces a thecate form very similar to *Protoceratium reticulatum* (the cyst equivalent is *Operculodinium centrocarpum*) which led Kouli *et al*. (2001) to question the ecophenotypic character of this species. The low occurrence of *P. psilata* in recent to sub-recent samples of the Caspian Sea possibly indicates that the salinity conditions (12-13) at the present-day may not be favourable for its development.

Caspidinium rugosum has been recorded only from Caspian Sea samples. From this association with other dinocyst taxa, we can assume that it indicates brackish to low salinity (12-13) conditions.

7. Conclusions

The analysis of ~~observation~~ dinocyst assemblages from top-core sediments of the Caspian Sea documents the occurrence of two new gonyaulacacean taxa, *Caspidinium rugosum* and *Impagidinium caspienense. Caspidinium rugosum*, characterised by S-type paratabulation, dextral torsion and coarse low intratabular ornamentation, is present in low occurrences in all recent and sub-recent sediments except in the Kara-Bogaz-Gol Bay, the Enseli lake and the Aral Sea samples. *Impagidinium caspienense* dominates all assemblages with the exception of the Aral Sea sample where *L. machaerophorum* is the dominant species. The occurrence of these two new taxa *Impagidinium caspienense* and *Caspidinium rugosum* in the Caspian Sea confirms previous findings on phytoplankton endemism in that sea.

The morphological variability observed in *Spiniferites cruciformis*, based on the cyst body shape and the presence/or absence of a conspicuous membranous flange, could be interpreted as a result of environmental influences. However, the low number of samples does not allow further speculation on the nature of the environmental conditions controlling the cyst morphology. The presence of *Spiniferites cruciformis* in the Caspian Sea, the Kara-Bogaz-Gol Bay and the Aral Sea may be a legacy of the Paratethys Ocean.

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Table 1: List of core material with location and core types.

Nº on board	Nº MHN	Sample #	Longitude E	Latitude N	Depth (mbsl)	Core type	Location
SR9402 CP04	SR01 GS 9404CP	CP04	51º36'36"	38º43'34"	405	Pilot	south
SR9406 CP16	SR01 GS9414 CP	CP14	51º27'47"	39º16'18"	315	Pilot	south
SR9409 CP20	SR01 GS 9418CP	CP18	51º06'04"	41º32'53"	480	Pilot	central
SR9409 GS20	SR01 GS 9418	GS18	51º06'04"	41º32'53"	480	Kullenberg	central
SR9411 CP23	SR01 GS 9121CP	CP21	49º51'17"	42º50'31"	460	Pilot	north-central
SR9406 US14	SR01 US 9402	US02	51º29'	39º16	315	Box core	south
SR9402 GS05	SR01 GS9405	GS05	51º32'16"	38º45'39"	518	Kullenberg	south
n/a	n/a	Enseli				PVC tube	Enseli lake
n/a	n/a	KBG 8-01	53º00'	41º51'	80 cm	n/a	Kara-Bogaz-Gol Bay
n/a	n/a	AS17-5	60º41'55"	46º31'04"	12	n/a	Aral Sea

Table 2: List of counted dinoflagellate cysts. * indicates specimens of *C. rugosum* with very coarse ornamentation, § indicates specimens of *L. machaerophorum* with short processes.

Sample #	Sampling depth (cm)	*C. rugosum*	*C. rugosum**	*I. caspienense*	*L. machaerophorum*	*L. machaerophorum*§	*S. cruciformis Form A*	*S. cruciformis* Form B	*S. cruciformis* Form C	*P. psilata*	Cysts of *P. dalei*	*Brigantedinium* spp.	Total	Concentration (cysts/g)
CP04	0-2.5	7	2	127	15	21	67	3	13	5	13		273	3357
CP14	0-2.5	4	1	112	4	8	2	2	14	1	15	7	170	3220
CP18	1	3		110	8	1					7	22	151	11,180
GS18	2	3		163	10							72	248	n/a
CP21	5	6		90	2	4	3				6	24	135	5424
US02	0	5		87	7	15		14		1	47	27	203	4906
GS05	5.5-6	1	3	79		1	40	48	28	11	7	2	220	3415
Enseli	0-30			290	7	36	10				1	23	367	33,126
KBG 8-01	1-1			+	++	+	+							
AS17-5	6.5			40	151	51	8					8	258	3185

Figure captions

Figure 1: a) General location map of the Marmara, Black, Caspian and Aral Seas; b) The Caspian Sea, bathymetry (in meters) and location of the cores (squares) and subrecent material stations (stars).

Figure 2: Sea-surface conditions in the Caspian Sea with winter temperature (ºC) (A) and salinity (C), summer temperature (B) and salinity (D). In Fig. 2A, sea-ice limit is indicated (dotted line) and mixing in the water column is shown with, in zone 1, a mixing from bottom to surface waters, and in zone 2, a gradient of mixing with increased depth, from south to north (after Kosarev and Yablonskaya, 1994; Dumont, 1998).

Figure 3: Paratabulation of *Caspidinium rugosum* (A: dorsal view, B: ventral view, C: apical view) and *Impagidinium caspienense* (D: dorsal view, E: ventral view). Archeopyle (3'') is highlighted in grey. Scale bar represents 10 µm. The plates marked by * are considered as homologues of the standard gonyaulacacean paratabulation (Fensome *et al*., 1993).

Figure 4: Schematic representation of the variation of the cyst body shape of *Spiniferites cruciformis*. 4B-C: Morphotype A; 4A: Morphotype B; 4D-E: Morphotype C. Archeopyle (3'') is highlighted in grey. Scale bar represents 10 µm.

Figure 5: Dinoflagellate cyst assemblages in percentages in recent and subrecent samples. Total cyst concentration is illustrated at the right side of the diagram. * indicates specimens of *Caspidinium rugosum* with very coarse ornamentation.

Plate captions

Plate 1

Light micrographs x 400. England Finder coordinates in brackets. Scale bar = 10 µm.

1-5: *Caspidinium rugosum*, Holotype, slide US02-2, 0 cm (NHM registration number FD645(1)/T49/2), Southern Caspian. 1-3: high focus on ventral view, showing the sulcal region and the contact between paraplates 1'/4' and 6''; 4: optical view showing the thickness of the wall; 5: low focus on dorsal region showing paraplate 4''', archeopyle and the low coarse intratabular ornamentation.

6-7: *Caspidinium rugosum*, slide US02-1, 0 cm (NHM registration number FD644(2)/J52/3), Southern Caspian. High focus on dorsal view showing coarse, granular to verrucate ornamentation.

8-9: *Caspidinium rugosum*, slide US02-2, 0 cm (NHM registration number FD645(2)/S45/1), Southern Caspian. 8: high focus on lateral left view; 9: low focus on sulcal region and paraplate 1p. The paraplate 1''' could not been identified due to the low coarse intratabular ornamentation preventing the determination of the location of parasutures.

Plate 2

Light micrographs x 400. England Finder coordinates in brackets. Scale bar = 10 µm.

1-4: ~~*Impagidinium*~~ *Impagidinium caspienense*, Holotype, slide US02-1, 0 cm (NHM registration number FD644(1) /P43), Southern Caspian. 1: high focus on the ventral view; 2: optical view; 3-4: low focus on dorsal view, showing archeopyle.

5-7: *Impagidinium caspienense*, slide US02-2 (NHM registration number FD645(3)/R46/2), Southern Caspian. 5: high focus on sulcal region; 6: optical view showing the variability in septum height; 7: low focus on dorsal view showing archeopyle.

8: *Brigantedinium* sp., slide US02-1, 0 cm (NHM registration number FD644(3)/K55/4), Southern Caspian.

9: *Pyxidinopsis psilata*, slide GS05, 5-6 cm (NHM registration number FD646(1)/T41), Southern Caspian. High focus on dorsal view showing archeopyle and vermiculate ornamentation.

Plate 3

Light micrographs x 400 and x1000. England Finder coordinates in brackets. Scale bar = 10 µm.

1: *Lingulodinium machaerophorum*, slide US02-1, 0 cm (NHM registration number FD644(4)/S51/4), Southern Caspian. High focus on dorsal view showing archeopyle and short acuminate processes.

2-5: *Lingulodinium machaerophorum*, slide US02-1, 0 cm (NHM registration number FD644(5)/Q59/1), Southern Caspian. High focus on dorsal view showing archeopyle, short acuminate and bulbous processes.

6-7: *Lingulodinium machaerophorum*, slide US02-2, 0 cm (NHM registration number FD645(4)/J44/1), Southern Caspian. High focus on dorsal region showing broad reticulation.

8-9: Cysts of *Pentapharsodinium dalei*, slide US02-1, 0 cm (NHM registration number FD644(6)/M41), Southern Caspian. 7: high focus view on the split-like opening; 8: optical view.

Plate 4

1-5: *Spiniferites cruciformis* morphotype A, slide US02-2, 0 cm, Southern Caspian. Specimen (NHM registration number FD645(5)/F49/3) in 1: low focus on dorsal view showing archeopyle and in 2: high focus on ventral view, showing the membranous flange. Specimen (NHM registration number FD645(6)/F42/3) in 3: high focus on ventral view and in 4: low focus on dorsal view, showing the apical boss. Specimen (NHM registration number FD645(7)/C44/3) in 5: optical view showing membranous septa between processes and the flange.

6-9: *Spiniferites cruciformis* morphotype B, slide CP04, 0-2.5 cm, Southern Caspian. Specimen (NHM registration number FD647(1)/F52) in 6: high focus on dorsal view showing archeopyle and stout processes. Specimen (NHM registration number FD647(2)/G45/2) in 7: high focus on ventral region, in 8: optical view and in 9: low focus on dorsal region. Note the absence of apical boss compared to specimen in Fig. 6 and the more-pronounced cruciform shape of the cyst body.

10-11: *Spiniferites cruciformis* morphotype C, slide GS05, 5-6 cm (NHM registration number FD646(2)/X38/3), Southern Caspian. 10: high focus on ventral region; 11: optical view.

Plate 5

Scanning electron micrographs. Scale bar = 10 µm.

1-2: *Impagidinium caspienense*, slide CP14, 100 cm, Southern Caspian. 1: antapical view; 2: dorsal view showing archeopyle.

3: *Caspidinium rugosum*, slide CP14, 100 cm, Southern Caspian. Dorsal view, showing archeopyle and dextral torsion of paraplate 4'''.

4: *Spiniferites cruciformis* morphotype A, slide CP14, 30 cm, Southern Caspian. Ventral view with the membranous flange.

5: *Spiniferites cruciformis* morphotype B, slide CP14, 30 cm, Southern Caspian. Ventral view.

6: *Pyxidinopsis psilata*, slide CP14, 100 cm, Southern Caspian. Dorsal view.