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THE EXTANT THERMOPHILIC DINOFLAGELLATE *TECTATODINIUM PELLITUM* (AL. *TECTATODINIUM RUGULATUM*) FROM THE DANIAN OF DENMARK

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ABSTRACT—*Tectatodinium rugulatum* (Hansen, 1977) McMinn, 1988, from the lower Danian of Denmark, is considered conspecific with, and a junior synonym of, the extant thermophilic species *Tectatodinium pellitum* Wall, 1967. However, the Danian material, based on holotype and topotype specimens, appears to show a degree of morphologic variability not seen in younger material. The accepted stratigraphic range base of *Tectatodinium pellitum* is now extended to the lower Danian, where this species appears to be a useful biostratigraphic marker in the Danish North Sea basin.

INTRODUCTION

TECTATODINIUM PELLITUM Wall, 1967 emend. Head, 1994 is a warm-temperate to subtropical species of dinoflagellate cyst whose distribution today is restricted to latitudes below 45°N in the North Atlantic, where it seldom comprises more than 10 percent of assemblages (Wall et al., 1977; Edwards and Andrle, 1992). The name *T. pellitum* is based on a fossil cyst from Holocene sediments. Living cysts of this species have been incubated to produce the motile stage known as *Gonyaulax spinifera* (Wall and Dale, 1967, 1968).

Tectatodinium pellitum was first described from modern sediments off Lebanon in the Mediterranean Sea (Wall, 1967). It has since been recognized persistently in the Neogene record, and these occurrences are broadly consistent with the known thermophilic affinities of this cyst (Head, 1994). The stratigraphic occurrence of *T. pellitum* was discussed extensively by Head (1994), who accepted a range base of lower Eocene based on records from northern Germany and on direct observation of specimens from the subsurface of the Labrador Sea. Head noted, additionally, that *Tectatodinium rugulatum* (Hansen, 1977) McMinn, 1988, described from the Danian of Denmark, might be conspecific with *Tectatodinium pellitum.* If upheld, this synonymy would extend downwards the range of *T. pellitum* (Head, 1994). *Tectatodinium rugulatum* has been reported mostly from the Danian of onshore Denmark, where it characterizes the *Tectatodinium rugulatum* Zonule of Hansen (1977, 1979a, 1979b).

Our work assesses the synonymy of *Tectatodinium pellitum* and *T. rugulatum.* Re-examination of the holotype of *Tectatodinium rugulatum* (Fig. 1) shows that it lies within the morphologic range of *T. pellitum.* These two names are therefore placed in synonymy, with *Tectatodinium pellitum* having priority.

Those *Spiniferites* and *Achomosphaera* specimens co-occurring with the holotype of *T. rugulatum* were examined with respect to their endoblast morphology for any evidence of a phylogenetic or developmental relationship with *T. pellitum.* Careful inspection showed no strong similarities with *T. pellitum.*

Tectatodinium pellitum is thus now shown extending back to the early Danian, giving this modern cyst an accepted antiquity of about 64 Ma. *Tectatodinium pellitum* is one of several extant dinoflagellate species, including *Lingulodinium machaerophorum* (Paleocene) and *Polysphaeridium zoharyi* (early Eocene), that have a long stratigraphic record. These species are thermophilic and neritic, and their longevity can be attributed to an ability to "track" warmer waters as they retreat into lower latitudes during late Cenozoic glacial intervals (see Dale and Dale, 1997). Because *Tectatodinium pellitum* has a warm-temperate to subtropical distribution today (Harland, 1983), its presence may prove useful as an indicator of warm intervals as far back as the Danian.

MATERIAL

The holotype of *Tectatodinium rugulatum* is strew mounted in glycerine jelly. Both the microscope slide and holotype are in good condition, and the holotype can be moved and rotated by pressing gently on the coverslip once the glycerine jelly has warmed on the microscope stage. The holotype is from the TUBA 13 borehole, Copenhagen, and is of early Danian age (Hansen, 1977). It is curated in the type collection of the Geological Museum of the University of Copenhagen under the number MGUH 13 963.

The slide containing the holotype was searched carefully for additional specimens since no paratypes had been designated by Hansen. The holotype and other specimens from the same slide are described in the Systematic Paleontology section that follows.

SYSTEMATIC PALEONTOLOGY

Division DINOFLAGELLATA (Bütschli, 1885) Fensome et al., 1993
Class DINOPHYCEAE Pascher, 1914
Subclass PERIDINIPHYCIDAE Fensome et al., 1993
Order GONYAULACALES Taylor, 1980
Family GONYAULACACEAE Lindemann, 1928
Subfamily GONYAULACOIDEAE (autonym)
Genus TECTATODINIUM Wall, 1967 emend. Head, 1994
TECTATODINIUM PELLITUM Wall, 1967 emend. Head, 1994
Figures 1.1–1.3, 2

Tectatodinium pellitum WALL 1967, p. 113, pl. 16, fig. 12; emend. HEAD, 1994, p. 308–314, pl. 1–4, pl. 11, figs. 1–9, text-figs. 3, 5 (see for full synonymy).
Xenicodinium rugulatum HANSEN 1977, p. 12–13, fig. 20H-J; HULTBERG, 1986, pl. 1, fig. 6.
Tectatodinium rugulatum (Hansen, 1977) MCMINN, 1988, p. 152; SCHIØLER AND WILSON, 1993, pl. 4, fig. 12.
? *Tectatodinium rugulatum* (Hansen, 1977) MCMINN, 1988, fig. 8A, B.

Dimensions of Danian specimens.—Holotype of *T. rugulatum*: length, 54 μm; equatorial diameter, 40 μm; wall thickness, ca. 4.0–5.0 μm. Range: maximum diameter, 41(45.4)54 μm, average wall thickness, ca. 2.1(3.7)5.7 μm. Sixteen specimens were measured. See also Figure 2.

Description of Danian specimens.—The holotype of *T. rugulatum* is egg shaped (length, 54 μm; equatorial diameter, 40

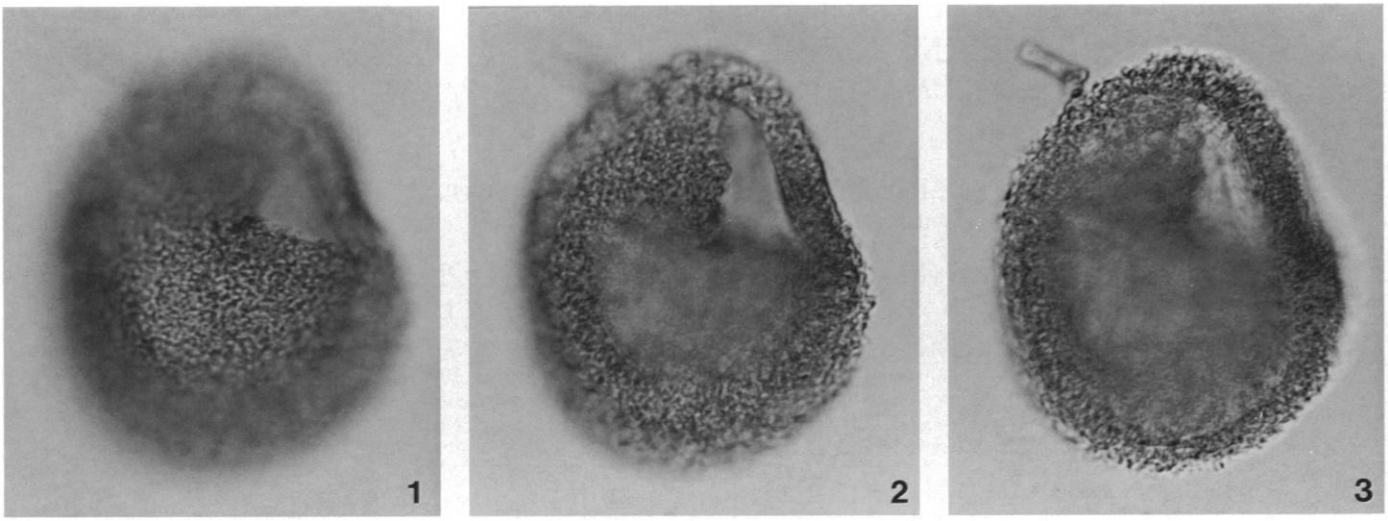

FIGURE 1—The holotype of *Tectatodinium rugulatum* (MGUH 13 963) from the lower Danian of Denmark, now considered to be a junior synonym of *Tectatodinium pellitum*. Photomicrographs are in bright field and show a left dorsal view of *1*, upper surface, *2* slightly lower focus showing irregular archeopyle margin and extremely thin, solid pedium, and *3* mid focus revealing a spongy-fibrous, distally-open luxuria. Length of specimen, 54 μm.

μm), with a solid pedium indicated by a thin dark line that is less than 0.3 μm thick. The pedium is overlain by a thick, spongy-fibrous luxuria that is distally open with numerous fibrils extending as much as 1.5 μm from the surface (Fig. 1). The basal ca. 0.5 μm of the luxuria has a vesicular sublayer. The wall thickness varies between ca. 4.0 and 5.0 μm. The archeopyle is precingular Type 1P (presumed 3") with distinctly irregular margins and well defined angles. There are no other indications of tabulation.

Twenty-one other specimens of *Tectatodinium pellitum* occur on the slide containing the holotype of *T. rugulatum* (see Fig. 2). These specimens generally resemble the holotype of *T. rugulatum*, and have a thin (less than 0.3 μm) solid pedium and a thick spongy luxuria. Some specimens have fibrils extending from the luxuria surface, but others do not. In some specimens, the sublayer at the base of the luxuria appears granular in surface view, with "granules" being of variable size up to ca. 1.0 μm in diameter. In one specimen, traces of the cingular margins occur on the dorsal surface within this sublayer. The precise structure of this sublayer is uncertain because it is obscured by a considerable thickness of overlying spongy luxuria. However, the "granules" might be an optical effect formed by vesicles, a vesicular sublayer being seen in other specimens.

Discussion.—Our observations generally match the careful description given by Hansen (1977, p. 12) but we consider the pedium to be thinner than previously stated (ca. 0.5 μm in Hansen, 1977). We also observe the uneven nature of the archeopyle margins, and the presence on the holotype and some other specimens of a vesicular sublayer forming the basal ca. 0.5 μm of luxuria. These features are all found on *T. pellitum*.

No apical protuberances were observed on the Danian specimens but detection was sometimes hindered by poor preservation or unfavorable orientation. An apical protuberance is not diagnostic of this species although it occurs on some well preserved modern and fossil specimens, including the holotype (Head, 1994).

Specimens therefore fall generally within the morphologic range now accepted for *T. pellitum* although most have thicker walls than is known for modern *T. pellitum* (Fig. 2). There also seems to be a degree of structural variation in the basal luxuria that is not seen in younger specimens of *T. pellitum*. SEM analysis of broken specimens will be necessary to document properly this apparent structural variation.

Stratigraphic range.—Holocene through lower Danian (Head, 1994; present study). The present record from the lower Danian of Denmark extends the stratigraphic range of *T. pellitum* below

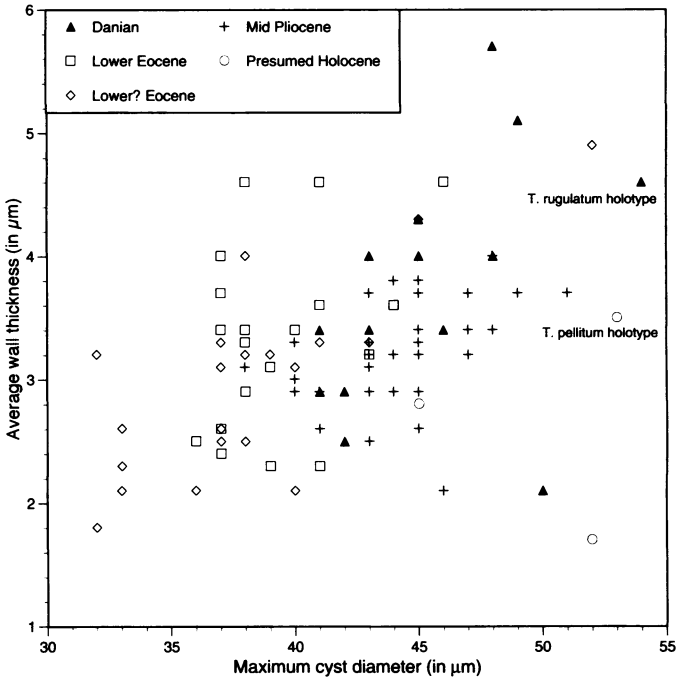

FIGURE 2—Average wall thickness (excluding fibrils projecting from surface) vs maximum cyst diameter for specimens of *Tectatodinium pellitum* from the Danian of Denmark (holotype and topotypes of *T. rugulatum*; this study), compared with specimens from the lower Eocene and lower or middle Eocene of the Labrador Sea, mid Pliocene of eastern England, and presumed Holocene of the Gulf of Mexico, Mediterranean Sea, and Gulf of Mexico (from Head, 1994, text-fig. 5).

its previously accepted range base of lower Eocene. Hence we now accept as *T. pellitum,* Danian records from onshore Denmark and southern Sweden (as *Xenicodinium rugulatum* in Hansen, 1977; Kjellström and Hansen, 1981; Hultberg, 1986) and from the Danish North Sea (as *T. rugulatum* in Schiøler and Wilson, 1993). We question the identification of a specimen from the Danian of Australia (as *T. rugulatum* in McMinn, 1988, fig. 8A, B) because a spongy luxuria is not clear from the illustration, and we cannot evaluate a record from the Maastrichtian of the Netherlands by Herngreen et al. (1986) since no illustration was provided. Specimens from the Danian of Senegal (as *Xenicodinium* cf. *rugulatum* in Jan du Chêne, R., 1988) appear from the illustrations to have a more finely textured wall than is typical for *T. pellitum,* and we agree that they are not definitively assignable to this species. We have examined two specimens of *T.* cf. *pellitum* from the Maastrichtian of The Netherlands as figured by Schiøler et al. (1997, pl. 3, figs. 9–11). Both have similar archeopyles to *T. pellitum.* One specimen (Schiøler et al., 1997, pl. 3, figs. 9–10), at 27 μm in diameter, is smaller than *T. pellitum* and has a denser wall structure. It is not *T. pellitum.* The other (Schiøler et al., 1997, pl. 3, fig. 11), at 34 μm in diameter, resembles *T. pellitum* in size and has a similar internal wall structure, including a thin pedium and thicker (2.5 μm) spongy luxuria. However, a thin (less than 0.5 μm) condensed outermost sublayer is apparently present on this specimen, in contrast to the distally open luxuria of *T. pellitum.* We agree that it should not be assigned definitively to *T. pellitum,* and thus there remain no confirmed records of *T. pellitum* below the Danian.

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