

## Subdivision of the dinoflagellate cyst Family Suessiaceae and discussion of its evolution

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**ABSTRACT** – The recent description of *Umbriadinium mediterraneense* Bucefalo Palliani & Riding 1997 from the Early Jurassic of central Italy and Greece has provided new information on the phylogeny of the dinoflagellate cyst Family Suessiaceae. On the basis of the morphology of the five suessiacean genera, a subdivision of the family into two new subfamilies is proposed. These are the Late Triassic Suessioideae and the Early Jurassic Umbriadinoideae. The evolution of the Family Suessiaceae is related to the evolution of scleractinian corals, largely on the basis of the similarity of their evolutionary patterns and geographical palaeodistributions. *J. Micropalaeontol.* 19:(2) 133–137, December 2000.

### INTRODUCTION

The recent description of the suessiacean dinoflagellate cyst genus *Umbriadinium* by Bucefalo Palliani & Riding (1997) from the early Toarcian (Early Jurassic) of central Italy and Greece in the Tethyan Realm has contributed significantly to our understanding of the phylogeny of the Family Suessiaceae. On morphological grounds, the genera of the Suessiaceae fall into two groups that appear to have distinct stratigraphical ranges. The Norian–Rhaetian (Late Triassic) genera *Noricysta*, *Suessia* and *Wanneria* are placed within the Subfamily Sussioideae, which comprises proximate or proximochorate genera. The subfamily Umbriadinoideae is confined to the Hettangian–early Toarcian (Early Jurassic) and comprises the proximochorate/chorate genera *Beaumontella* and *Umbriadinium*.

### SYSTEMATIC PALAEOLOGY

Division **Dinoflagellata** (Bütschli, 1885) Fensome *et al.*, 1993

Subdivision **Dinokaryota** Fensome *et al.*, 1993

Class **Dinophyceae** Pascher 1914

Subclass **Gymnodiniophycidae** Fensome *et al.*, 1993

Order **Suessiales** Fensome *et al.*, 1993

Family **Suessiaceae** Fensome *et al.*, 1993

Subfamily **Suessioideae** (autonym)

Type genus *Suessia* Morbey, 1975 (Late Triassic, Rhaetian)

Other genera *Noricysta* Bujak & Fisher, 1976 (Late Triassic, Norian); *Wanneria* Below, 1987 (Late Triassic, Norian)

**Derivation of name.** From the genus *Suessia* Morbey, 1975.

**Diagnosis.** Acavate or cavate, proximate or proximochorate suessiacean dinoflagellate cysts which exhibit nonparatabular or parasutural ornamentation. Archaeopyle of combination type; operculum simple or compound.

**Stratigraphical range.** Representatives of the Subfamily Suessioideae nov. are confined to the Carnian to Rhaetian (Late Triassic interval).

**Remarks.** The Subfamily Suessioideae nov. includes *Noricysta*, the only cavate suessiacean genus. The genera of this subfamily are proximate (*Noricysta* and *Suessia*) and proximochorate (*Wanneria*). *Noricysta* exhibits nonparatabular ornamentation; the periphragm is typically granular, verrucate or sparsely spinose. Parasutural ornamentation, comprising low crests and spines, is present in *Suessia* and *Wanneria*. Below (1987, pl. 6) described and illustrated an outer pellicle in *Suessia* which has a

peridinacean paratabulation pattern. This pellicle was not mentioned in detail in the original description of *Suessia*, although Morbey (1975, p. 38), described the genus as ‘pseudocavate’ with a periphragm ‘closely appressed to or partially detached from (the) endophragm’. The pellicle has not been noted by any other authors. It seems likely that this pellicle is only present in well preserved material as both Morbey (1975) and Below (1987) figured many specimens of *Suessia swabiana* Morbey, 1975 which are apparently acavate. Furthermore, pellicles have not been observed in any other genera in the family Suessiaceae. All three genera have archaeopyles of combination type. The operculum is simple in *Wanneria* [operculum formula:  $(tn^4 + tn^3 + tn^2)_s$ ] and is compound in *Suessia* (operculum formula:  $tn^3 + tn^2 + tn^a$ ). The operculum formula style used here is that of Below (1987). The size of the three genera varies from small to intermediate (of Stover & Evitt, 1978, p. 5), with a maximum diameter of between 30  $\mu\text{m}$  and 55  $\mu\text{m}$ . A comparison of the two new subfamilies of the family Suessiaceae is presented in Fig. 1.

Subfamily **Umbriadinoideae** nov.

Type genus *Umbriadinium* Bucefalo Palliani & Riding 1997

(Early Jurassic, late Pliensbachian–early Toarcian)

Other genus *Beaumontella* Below, 1987 (Early Jurassic, Hettangian–Sinemurian).

**Derivation of name.** From the genus *Umbriadinium* Bucefalo Palliani & Riding 1997.

**Diagnosis.** Acavate, proximochorate and chorate suessiacean dinoflagellate cysts in which intraparatabular ornamentation is present. Archaeopyle type may be apical or combination; operculum compound.

**Stratigraphical range.** Members of the Subfamily Umbriadinoideae nov. are confined to the Hettangian–early Toarcian (Early Jurassic).

**Remarks.** The genera belonging to the Subfamily Umbriadinoideae nov. are proximochorate to chorate; proximate cysts are not represented. The ornamentation comprises processes arranged in intraparatabular positions. The archaeopyle is of combination type in *Umbriadinium* and apical in *Beaumontella* (Fig. 1). Both genera are characterized by compound opercula. The size is small (Stover & Evitt, 1978, p. 5); the maximum diameter varies between 15  $\mu\text{m}$  and 25  $\mu\text{m}$ . A comparison of the two new subfamilies in the family Suessiaceae is illustrated in Fig. 1






FAMILY SUESSIACEAE Fensome et al., 1993			
SUESSIOIDEAE SUBFAM. NOV.		UMBRIADINOIDEAE SUBFAM. NOV.	
Genus			
			
	Noricysta Bujak & Fisher 1976	Wanneria Below 1987	Beaumontella Below 1987
	Suessia Morbey 1975 emend Below 1987	Umbriadinium Bucefalo Palliani & Riding 1997	
Proximate to proximochorate	TYPE OF CYST	Proximochorate to chorate	
Acavate or cavate	CAVATION STYLE	Acavate	
Nontabular and parasutural	ORNAMENTATION	Intratabular	
Combination	ARCHAEOPYLE	Combination or apical	
Simple or compound	OPERCULUM	Compound	
Small to intermediate (sensu Stover & Evitt, 1978)	SIZE	Small (sensu Stover & Evitt, 1978)	
Seven or nine	APPARENT NUMBER OF PARAPLATES	Seven or eight	
UPPER TRIASSIC (Norian - Rhaetian)	STRATIGRAPHICAL DISTRIBUTION	EARLY TOARCIAN (Hettangian - lower Toarcian)	

Fig. 1. Schematic representation of the morphological features and stratigraphical distributions of the two subfamilies of the Family Suessiaceae.

### THE EVOLUTION OF THE FAMILY SUESSIACEAE

Significant morphological changes, which facilitate the subdivision of the dinoflagellate cyst Family Suessiaceae into two subfamilies, occurred at the Triassic–Jurassic transition. This boundary coincides with a mass extinction, that is clearly marked in the marine realm by a dramatic turnover of ammonites, the final disappearance of conodonts and substantial biotic changes to other fossil groups (Hallam, 1990, 1996). The dominant Triassic nannolith lineages became extinct, leaving only one coccolith species which survived into the Jurassic (Bown, 1992). Hallam (1990) linked this extinction event to a sea-level change in the form of a regressive–transgressive couplet associated with the inception of tensional

tectonic and volcanicity in the central part of Pangea. Dinoflagellate cysts underwent a significant extinction event at the Triassic–Jurassic boundary, *c.* 13 Ma after their first unequivocal occurrence.

### Morphological trends within the Suessiaceae

During the Late Triassic, the Order Suessiales was represented by the Subfamily Suessioideae (Family Suessiaceae); i.e. the genera *Noricysta*, *Suessia* and *Wanneria*. The highest species diversity is in *Noricysta* (*Noricysta fimbriata* Bujak & Fisher 1976; *Noricysta pannucea* Bujak & Fisher, 1976; and *Noricysta varivallata* Bujak & Fisher, 1976) (see Bujak & Fisher, 1976) and *Wanneria* (*Wanneria listeri* (Stover & Helby, 1987) Below, 1987;

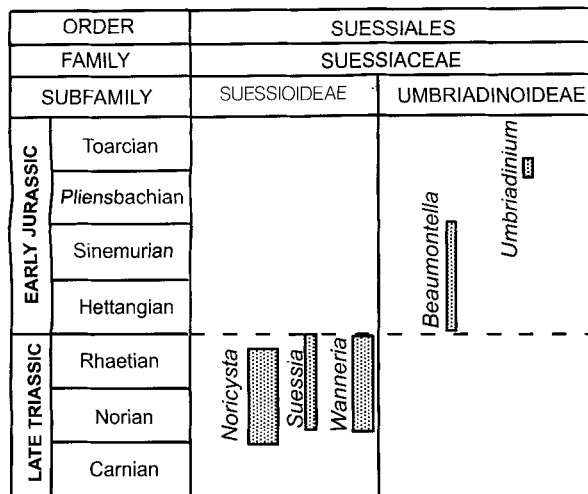


Fig. 2. Stratigraphical ranges of the genera belonging to the Subfamilies Suessioideae and Umbriadinoideae. The width of each column is directly proportional to the respective species diversity of each genus, for example *Umbriadinium* is monospecific.

and *Wanneria misolensis* Below, 1987) (see Below, 1987), whereas *Suessia* is a monospecific genus (*Suessia swabiana* Morbey, 1975; Fig. 2). The latest Triassic extinction did not profoundly affect the Suessiales dinoflagellate cyst lineage, which survived into the Early Jurassic (Fig. 2). However, they exhibit a number of changes which are manifested as dramatically decreased specific and generic diversity and significant morphological modifications. The Triassic Subfamily Suessioideae became extinct and was replaced by the Subfamily Umbriadinoideae during the earliest Jurassic (Fig. 2). This evolutionary pattern produced a transition from dominantly proximate dinoflagellate cysts with parasutural and nontabular ornamentation to proximochorate/chorate cysts with intrapartabular processes (Fig. 1). Within the Subfamily Suessioideae, *Noricysta* exhibits distinctive morphological features as it is cavate and has a simple operculum. Furthermore, the archaeopyle style differs between the two subfamilies. The Subfamily Suessioideae are characterized by combination exocystment apertures, whereas within the Subfamily Umbriadinoideae the genus *Beaumontella* has an apical archaeopyle. This evolution of archaeopyle style is consistent with the evolutionary trend from suessoid to pseudoceratioid dinoflagellate cysts described by Dörhöfer & Davies (1980). According to these authors, a significant feature of early dinoflagellate evolution was the stabilization of the archaeopyle in a definite position on the cyst. In Early Jurassic genera, the principal archaeopyle suture commences in an apical position (Below, 1987; Bucefalo Palliani & Riding, 1997). However, in Late Triassic taxa, this dehiscence apparently largely starts in a medio-dorsal position (Dörhöfer & Davies, 1980), probably in a similar way to *Rhaetogonyaulax* Sarjeant 1966 (see Harland *et al.*, 1975; Fisher & Van Helden, 1979). Therefore, changes in cyst configuration, operculum style and ornamentation are major morphological variations which occur within the Family Suessiaceae across the Triassic-Jurassic boundary. Other features, such as paratabulation and archaeopyle type, remained relatively conservative. For example, the

apparent number of major longitudinal paraplate series is 7 or 9 in the Suessioideae and 7 or 8 in the Umbriadinoideae (Fig. 1). This paratabulation style of 7–9 major longitudinal rows comprising many small paraplates is the principal characteristic feature of the Family Suessiaceae (Fig. 1).

**Symbiotic relationship with corals**

Several authors have suggested that the evolution of the family Suessiaceae was probably largely driven by the evolution of scleractinian corals, which first appeared in the geological record during the mid-Triassic (Newell, 1971; Fensome *et al.*, 1993). The similarities between the evolutionary patterns of the family Suessiaceae and the scleractinian corals supports their coevolution. The important role played by zooxanthellate scleractinian corals in modern reefs and the widespread occurrence of zooxanthellae symbioses among corals and other organisms suggested that this ecological phenomenon was pervasive within many ancient reef communities (Talent, 1988; Stanley, 1992). Living scleractinian corals were once thought to be symbiotic with a single species of the symbiodiniacean dinoflagellate *Symbiodinium microadriaticum* Freudenthal 1962. However, the recent discovery of different taxa occurring in different coral hosts (Rowan & Powers, 1991) suggests a more complex evolutionary history. Symbiodiniacean dinoflagellates are known almost exclusively as coccoid symbiotic cells within the tissue of host organisms (Fensome *et al.*, 1993). Production of motile biflagellate cells is rare and these are known exclusively from cultures. On the basis of studies of cultured motile cells of *Symbiodinium microadriaticum* (as *Zooxanthella microadriatica*), Loeblich III & Sherley (1979) observed a morphological resemblance between the Symbiodiniaceae and Suessiaceae. *Symbiodinium microadriaticum* showed, during the motile phase of the cell cycle, a thecal layer with the paratabulation formula: 1pr, 5', 5–6a, 9–10", c.20c, 8–9s, 7–8"', 3'''. The paracingular series consists of a double row of equatorial paraplates. The morphological similarity with the suessoid paratabulation pattern could suggest a significant similarity in life strategies. The appearance of the first scleractinian corals occurred during the Middle Triassic. They became established as major reef-builders during the Norian (Late Triassic) and dominated shallow-water reef communities during the latest Rhaetian (Late Triassic) to Early Cretaceous (Newell, 1971; Stanley, 1988; Stanley & Swart, 1995). Stanley (1988) suggested that scleractinian coral-zooxanthellae symbiosis began in the Norian–Rhaetian, based largely on the increased size of both colonial corals and reefs. This age is coincident with the first occurrence and maximum species richness of suessiacean dinoflagellate cysts in the geological record (Fig. 2).

**Coevolution**

The latest Triassic extinction event deeply affected the corals. During the Hettangian and Sinemurian (Early Jurassic), global reef development and carbonate sedimentation significantly decreased. However, during the Pliensbachian, a renewed phase of small-scale reef building began with increased volumes of coral framework in bioherms (Beauvais, 1984). The coral taxa known from these Early Jurassic reefs show less Norian affinities

at the familial and generic levels. A major generic turnover of corals occurred during the Toarcian (Stanley, 1988). According to Beauvais (1986), all Triassic genera had become extinct by this time. The Toarcian turnover phase coincided with a profound reorganization of reef ecosystems which continued into the Middle Jurassic; it comprised a major adaptive radiation unparalleled among reef corals (Stanley, 1988). This event signalled a renewed differentiation of corals between zooxanthellate and azooxanthellate types (Stanley, 1981; Krasimov, 1984).

The turnover in the Family Suessiaceae at the Triassic–Jurassic transition (Fig. 2) corresponded with a gradual taxonomic modification of corals. Both fossil groups lost their Triassic morphological characteristics at the family level and recorded a largely complete turnover. The major change of coral faunas at the generic level in the Toarcian seems to correspond with a profound change within suessiacean dinoflagellate cysts, responsible for their disappearance from the fossil record. A possible hypothesis is that, at this time, the suessiacean dinoflagellates lost the capacity to produce fossilizable resting cysts.

During the Carboniferous to Jurassic, the main global reef production shifted from the Southern Hemisphere to the Northern Hemisphere (Flügel, 1994; Flügel & Kiessling, 1996). Reef distribution was restricted to a latitudinal zone from 30°N to 30°S during the Middle Triassic and, during the Jurassic, bioherms seem to have been concentrated near 30°N, especially in Europe and at the eastern margin of North America (Flügel, 1994; Flügel & Kiessling, 1996). A similar trend is discernible in the distribution of suessiacean dinoflagellate cysts. They show a worldwide geographical distribution during the Late Triassic to the Triassic–Jurassic transition and have been reported from Arctic Canada, Australia, Austria and England (Morbey, 1975, 1978; Bujak & Fisher, 1976; Schuurman, 1979; Dörhöfer & Davies, 1980; Davies, 1983; Helby *et al.*, 1987; Riding & Thomas, 1992). During the Early Jurassic, however, suessiacean dinoflagellate cysts are confined to low-intermediate palaeolatitudes in the Northern Hemisphere (England, Denmark, Greece, Hungary, Italy and Portugal) (Riding & Thomas, 1992; Bucefalo Palliani, 1996; Poulsen, 1996; Bucefalo Palliani & Riding, 1997). Representatives of the Family Suessiaceae are not present in the Early Jurassic of the Southern Hemisphere (Helby *et al.*, 1987) or in high latitudes of the Northern Hemisphere, for example Arctic Canada, Greenland, the North Sea and Spitsbergen (Dörhöfer & Davies, 1980; Davies, 1983).

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