

A boreal early cradle of Angiosperms? Angiosperm-like pollen from the Middle Triassic of the Barents Sea (Norway)

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ABSTRACT – The origin of flowering plants is still a matter of dispute. Several lines of evidence suggest that their origin may go back to the Triassic. This paper reports on pollen grains with angiosperm-like morphologies from marine Middle Triassic sediments of the Boreal Realm (Norwegian Arctic, Barents Sea area). The morphology of these pollen grains is comparable to forms recorded from the Early Cretaceous, which are generally attributed to angiosperms. The new finds of angiosperm-like pollen are the earliest in the fossil record so far and show an astonishing high diversity. In contrast to other early records, they come from high palaeolatitudes with an inferred warm-temperate climate. The new finds suggest the presence of the first angiosperms during the Middle Triassic (242–227 Ma) or, alternatively, provide evidence for an as-yet unknown group of gymnosperms, possibly an extinct sister group of the flowering plants. *J. Micropalaeontol.* 23(2): 97–104, November 2004.

INTRODUCTION

Pollen grains of angiosperm-like morphology have been found in Middle Triassic deposits from exploration wells and shallow cores from the boreal Norwegian Arctic (Fig. 1). The pollen occur regularly, although are very rare in a limited stratigraphic interval, in deposits of Anisian–Ladinian age. These pollen types were first reported within a biostratigraphic context as *Retisulcites* sp. 1 and sp. 2 (Hochuli *et al.*, 1989) and, more recently, as *Retisulcites* sp. A (Vigran *et al.*, 1998). A morphological study shows their similarities to angiosperm pollen and reveals an unexpected diversity. The discovery of these angiosperm-like pollen grains of Triassic age provides important fossil evidence

for the yet-unsolved scientific puzzle of the origin of flowering plants.

MATERIAL STUDIED AND GEOLOGICAL BACKGROUND

The illustrated pollen grains have been found in siltstones from shallow cores. Between 1984 and 1986, in the context of a seafloor mapping project on the Barents Sea shelf, IKU (SINTEF Petroleum Research, Norway) drilled numerous shallow cores (max. depth 140 m) on the flank of the dome structure known as Svalis Dome (Figs 1, 2). In this area Late Palaeozoic and Triassic rocks subcrop under a cover of approximately 100 m of Pleistocene sediments. The studied cores, IKU 7323/07-U-05 and U-10, cover the Middle Triassic. A geological map and cross-section (Fig. 2) and the seismic section (Fig. 3) illustrate the geological situation at the Svalis Dome and give the precise location of the studied cores. A detailed lithological description of the Triassic rocks from the Svalis Dome, including the lithological logs of the cores studied herein can be found in Mørk & Elvebakk (1999). Ample information related to the IKU Stratigraphic Drilling Projects is available on the Internet under the following URL: <http://www.sintef.nolstatic/pelprodukt/shadriprod/>. This website includes *inter alia* a photographic archive of the cores, a full reference list and information on how and where to access the cores and related material.

The precise dating of the studied cores is based on extensive biostratigraphical studies of the associated ammonoids, bivalves and palynomorphs and is seismically tied to the regional geological framework. These two cores are attributed to the Snadd Formation and cover the interval of Palyzone Svalis 8, which is directly correlated with the *Tsvetkovites varius* ammonoid zone of Early Ladinian age (Vigran *et al.*, 1998). A Ladinian age is also confirmed by the presence of the marker pollen *Echinotsporites iliacooides* associated with rich and diverse fossil spore-pollen assemblages (Vigran *et al.*, 1998 and pers. obs.). In addition to the records from the IKU cores described herein, some of the angiosperm-like pollen grains have been observed

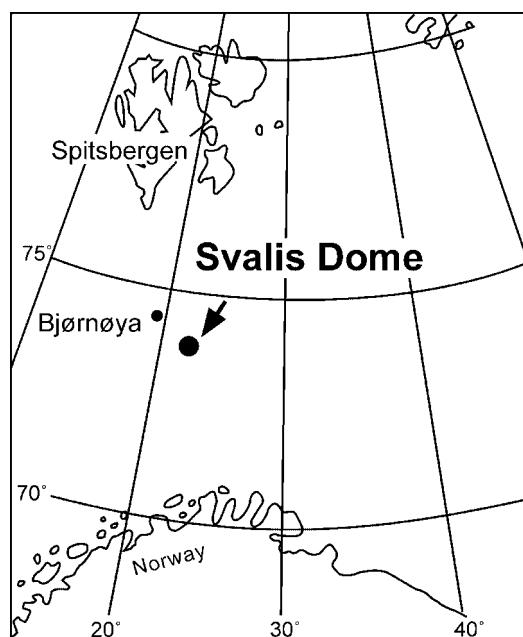


Fig. 1. Location map of the Svalis Dome on the Barents Sea shelf, Norway (from Vigran *et al.*, 1998).

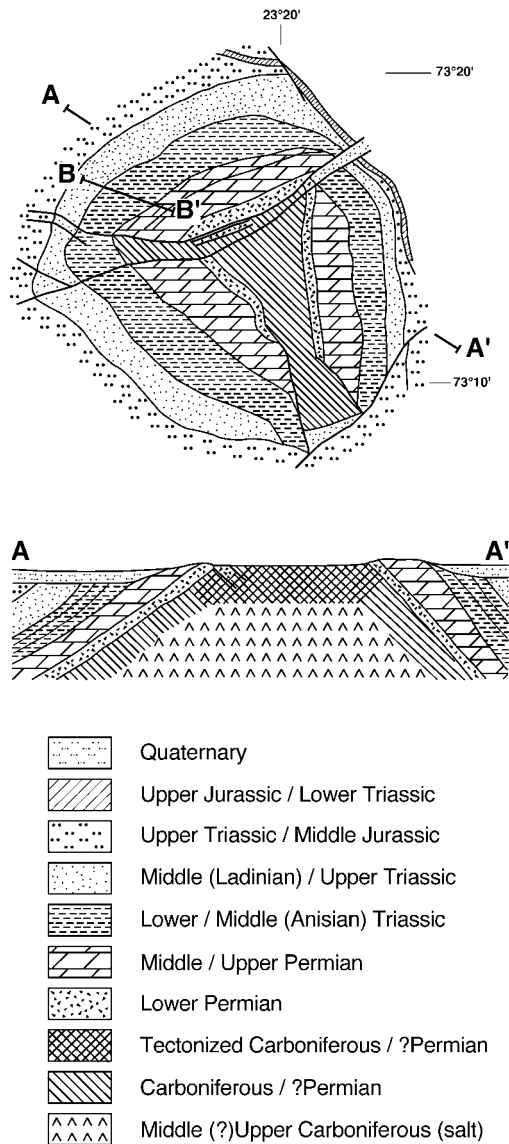


Fig. 2. Geological map and schematic cross section (A–A') of the Svalis Dome. The studied cores were drilled on the northwestern flank of the dome along one seismic line (B–B', see Fig. 3). Position of the cores: core 7323/07-U-05: 73°16'56.7"N, 23°01'09.2"E; core 7323/07-U-10: 73°16'51.5"N, 23°01'25.8"E. Modified after Vigran *et al.* (1998) and Mørk & Elvebakk (1999).

regularly in routine studies of hydrocarbon exploration wells in the Barents Sea area between the Late Anisian and the upper part of the Ladinian (Palynozones H to K in Hochuli *et al.*, 1989 and new pers. obs.). Contamination by younger fossil material or extant pollen grains can be ruled out for the studied cores because of the geological situation in the Svalis Dome area and the regular occurrence of these pollen grains also in exploration wells. Additionally, their distinct morphology differs from hitherto known pollen grains and those of extant plants.

MATERIAL AND METHODS

The described angiosperm-like pollen grains are quite rare, with about 20 specimens in glycerine jelly strew mounts available for

a morphological analysis using high-resolution differential interference contrast transmitted light microscopy (DIC-TL). With the aim of gaining more information on their morphology, the same grains were additionally imaged using confocal laser scanning microscopy (CLSM).

CLSM is a novel analytical and imaging technique in the application to palynological studies and has recently been described in detail for fossil, organic-walled dinoflagellate cysts (Feist-Burkhardt & Pross, 1999). For the present study, images were taken from grains mounted in glycerine jelly standard palynological slides, with a Leica TCS NT confocal microscope using 40× (UV 40×1.25NA oil PL APO 1.25; Pl. 1, figs 1, 2), and 100× (UV 100×1.4NA oil PL APO 1.4; Pl. 1, fig. 3, Pl. 2, figs 1–5) oil immersion objectives, respectively. Fluorescence images were obtained with an Argon–Krypton laser source and default TRITC-wide filter settings at an excitation wavelength of 568 nm and detection of emitted fluorescence light at wavelengths of 580 nm and longer. Optical sections were captured with an image resolution of 2048 by 2048 pixels and a distance between sections of generally less than 400 nm. The resulting image stack was then further processed using the Leica 3-D rendering software. Most of the illustrated extended focus images are prepared using 'solid' mode, which places special emphasis on the surface structures of the object and allows an optimal view of the object from the front (corresponding to a high focus TL image) and from the rear (corresponding to a low focus TL image). The slides with the figured specimens will be housed in The Museum of Natural History and Archaeology (Vitenskapsmuseet) at The Norwegian University of Science and Technology (NTNU) in Trondheim, Norway.

In order to distinguish unequivocally whether these pollen grains have either gymnosperm or angiosperm affinities, it is necessary to study the ultrastructure in SEM and, especially, TEM, to analyse the fine structure and layering of the exines. Ultrastructural study of these pollen grains is in progress, including procurement of new raw material from Barents Sea cores for new processing and preparation of individual specimens for SEM and TEM analysis.

MORPHOLOGICAL DESCRIPTION AND COMPARISON

The morphological analysis shows the similarities of these pollen grains to extant and fossil angiosperm pollen. Several distinct pollen types have been identified, each based on one or a few specimens only. Eight of these types are illustrated in Plates 1 and 2. Each pollen type is intentionally very narrowly defined and left in open nomenclature until more specimens can be analysed and further information on the morphological variability and diversity of this group becomes available. The morphological features of the illustrated pollen types are summarized in Table 1. The pollen grains are characterized by a distinct reticulate sexine and an extremely thin nexine, which seems to be missing in some types. Most of the illustrated grains are small and monosulcate; a few are ruptured, possibly triaperturate, syncolpate, or operculate.

Type A (Pl. 1, fig. 1) and type B (Pl. 1, fig. 2) are characterized by a relatively dense, heterobrochate reticulum. The ruptured, possibly triaperturate or operculate status of type A and the syncolpate arrangement of type B do not concur with the concept of primitive angiosperm pollen which are expected to be

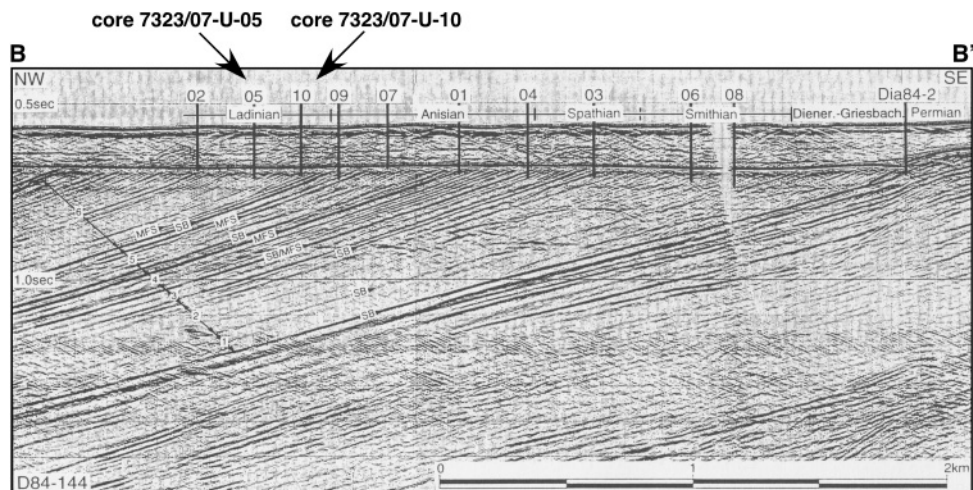


Fig. 3. Seismic section (B-B') with core localities. For position of the seismic line see Figure 2 (from Vigran *et al.*, 1998; Mørk & Elvebakk, 1999).

monosulcate (Traverse, 1988; Crane *et al.*, 1995). For these two pollen types no comparable forms are known to the authors, either from the fossil record, or from extant plants. Types C, D, E, F and possibly G and N (Pl. 1, fig. 3; Pl. 2) represent mono- or zonosulcate grains with various types of exine architecture. They show superficial similarity to the angiosperm pollen grains (e.g. *Pennipollis*, *Brenneripollis* and *Liliacidites*) of magnoliid or monocot affinity from the Early Cretaceous. All the observed forms lack the angiosperm pollen character of a well-developed footlayer and endexine below the sulcus. The inner layer generally seems to be very fragile and it is clearly recognizable only in Type B, C and N. The reticulate, acolumellate sexine of type G (Pl. 2, fig. 4) superficially resembles the pollen of the *Afropollis* group; however, type G is missing the segmented muri, the most distinct feature of this group. There is no evidence for the presence of a central body as observed in some of the group's Cretaceous species (Doyle *et al.*, 1982; Friis *et al.*, 1999) and, furthermore, the widened intersections of the muri characterizing Type G have never been observed in the *Afropollis* group. The morphology of the sexine of Type G is also comparable to *Polycolpopollis*, which has been described together with the Crinopolles group as angiosperm-like pollen types from the Late Triassic (Cornet, 1989). However, grains of *Polycolpopollis* and the Crinopolles group, in contrast to the current material, are characterized by well-developed, thick nexines and are much larger.

Comparison with 'anthophytes'

Pollen architecture of the gymnosperm groups Bennettitales, Gnetales and Pentoxylales (anthophytes) has been discussed more extensively in relation to primitive angiosperms (Crane, 1985; Kurmann & Zavada, 1994). These groups have been regarded as advanced and were considered, at least until recent molecular phylogeny studies, as the seed plants most closely related to angiosperms. The pollen grains of these groups, however, are characterized by a relatively thick inner layer (*pro parte* endexine) and a smooth massive tectum (Osborn & Taylor, 1994); none of them have reticulate exines and more than one distal aperture, such as found in the pollen described herein.

DISCUSSION

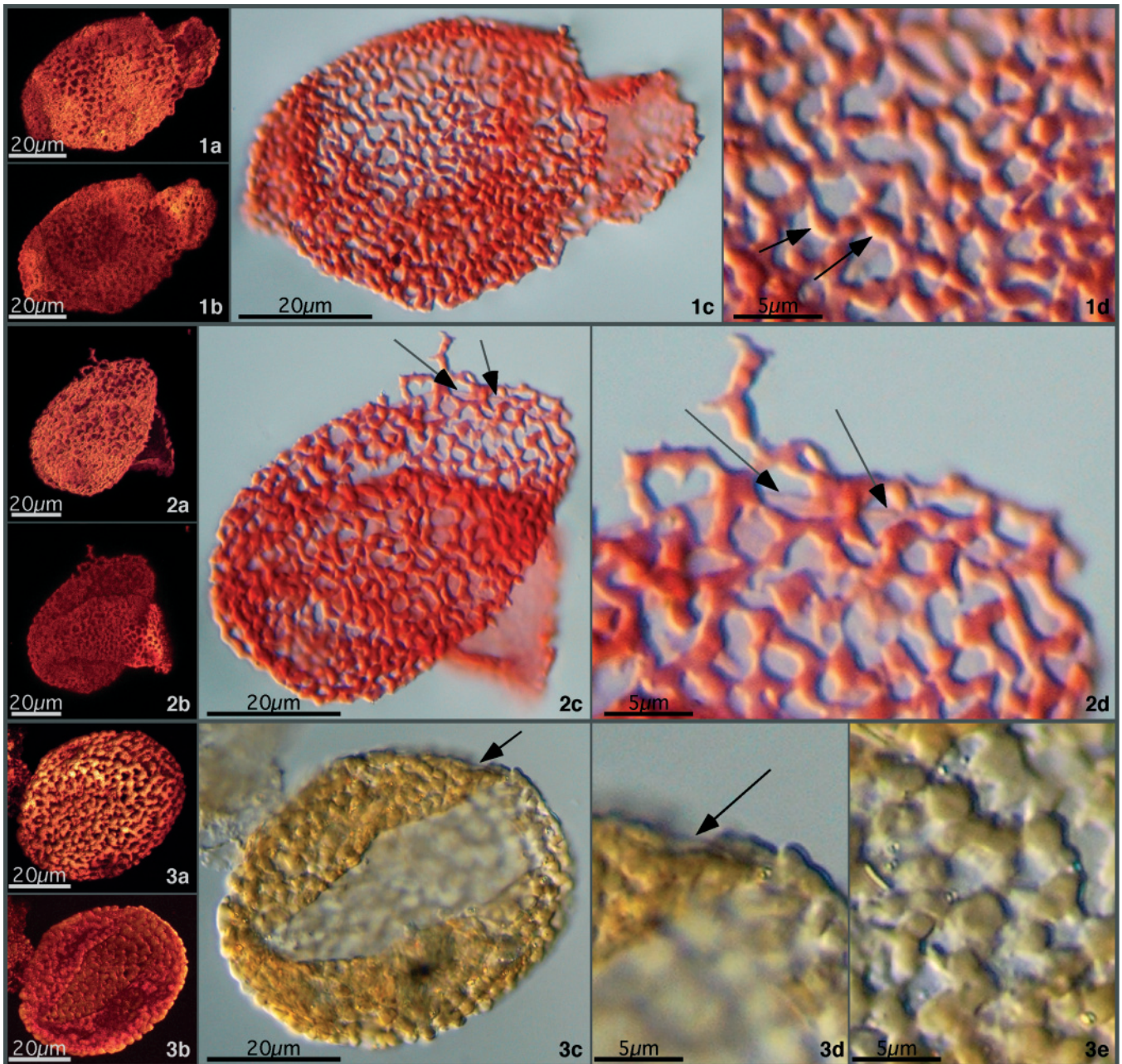
Dispersed grains of angiosperm-like pollen from the Early Mesozoic are equivocal evidence for an early origin of flowering plants. Botanical attribution of such grains remains questionable unless information on the parent plants with *in situ* pollen sacks containing pollen becomes available. Considering their morphology, the described pollen would be regarded as angiospermous origin in Late Mesozoic palynomorph assemblages. However, in sediments of the 'pre-angiosperm' period (Triassic/Jurassic), they appear as enigmatic elements.

Previous reports of pre-Cretaceous angiosperm-like pollen

There have been a few reports on pre-Cretaceous angiosperm-like pollen. The most important are pollen grains with a basic architecture similar to that of extant angiosperms, which have been reported from the Late Triassic Richmond rift basin, USA (Pocock & Vasanthy, 1988; Cornet, 1989). They have been described as the Crinopolles group (Cornet, 1989). The claim of the presence of angiosperms in the Late Triassic has provoked a lively discussion on the evolutionary significance of pollen morphology (Pocock & Vasanthy, 1988; Traverse, 1988; Cornet, 1989). Since it was first described, the Crinopolles group has been variously interpreted as related to angiosperms or gymnosperms, depending on the authors' interpretations (Pocock & Vasanthy, 1988; Doyle & Hotton, 1991; Crane *et al.*, 1995). Whatever the outcome, its morphology is very distinct and has no correspondence amongst extant angiosperms. *Polycolpopollis* (Cornet, 1989) described from the same site shows some similarity to the *Afropollis* group and to some angiosperm pollen known from the Early Cretaceous. In contrast to the latter groups, and to the material described herein, *Polycolpopollis* has well-developed nexines.

Origin and diversification of angiosperms

The sudden appearance of flowering plants and their very rapid radiation during the Early Cretaceous still appears an extraordinary feature in the evolution of plants and the connected ecosystems (Crane & Lidgard, 1989; Crane *et al.*, 1995). Their origin and time of first appearance are still controversial,



Explanation of Plate 1. Images are taken using high-resolution differential interference contrast transmitted light (DIC-TL), and fluorescence confocal laser scanning microscopy (CLSM), respectively. All specimens derive from core samples from the Snadd Formation, Svalis Dome area, Barents Sea shelf, Norway, Middle Triassic, Early Ladinian. **fig. 1.** Pollen type A. Large ?triaperturate or ?operculate pollen grain with double-layered exine, thin attached nexine, and irregular reticulate sexine: 1a, front view; 1b, rear view of the same grain in CLSM; 1c, DIC-TL image; 1d, detail of (c) showing irregular reticulum with beaded muri. Core 7323/07-U-10, depth 98.6 m, England Finder (EF) coordinates: J38-4, slide 3. **fig. 2.** Pollen type B. Large syncolpate or ?operculate pollen grain with double-layered exine, thin nexine partly detached, and reticulate sexine: 2a, front view; 2b, rear view of the same grain in CLSM; 2c, 2d, DIC-TL images showing heterobrochate reticulum with beaded muri. Arrows indicate the partly detached nexine. Core 7323/07-U-10, depth 98.6 m, EF coordinates: O38, slide 3. **fig. 3.** Pollen type C. Large monosulcate pollen grain with double-layered exine, thin attached nexine and sexine with corrugate-verrucate sculpture. Sculpture elements connected to an irregular reticulum: 3a, proximal face; 3b, distal face of the same grain in CLSM; 3c–3e, DIC-TL images – 3d, sculpture in optical section with nexine, 3e, sculpture elements forming reticulum. Similar type to *Retisulcites* sp. 1 of Hochuli *et al.* (1989). Core 7323/07-U-05, depth 121.01 m, EF coordinates: R58-2/4.

considering the conflicting evidence of both molecular biology (Sanderson & Doyle, 2001; Wikström *et al.*, 2001) as well as the fossil record. There is evidence from dispersed pollen and from

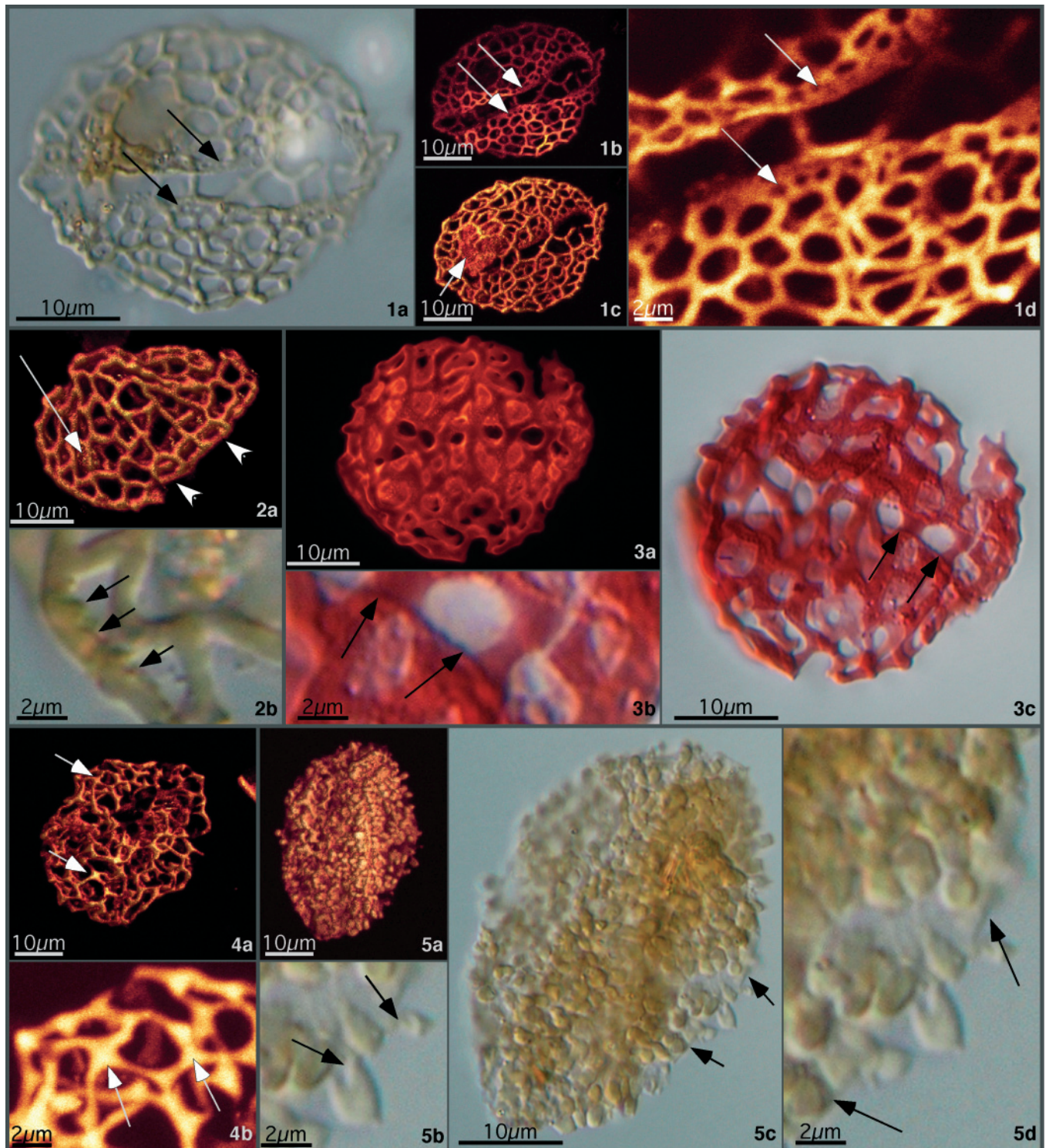
charcoalified (charred) reproductive structures (Friis *et al.*, 2000) for the rapidly increasing diversity of the angiosperms during the later part of the Early Cretaceous (Aptian–Albian). The fossil

Angiosperm-like pollen from Norway

evidence for angiosperms from pre-Aptian Early Cretaceous sediments is still sparse and, in many cases, controversial, or lacks appropriate stratigraphic control (Dilcher, 2001).

Recent phylogenetic studies are based on combined morphological and molecular data, or on molecular data alone (Crane *et al.*, 1995; Qiu *et al.*, 1999; Soltis *et al.*, 1999). They indicate

that the timing of angiosperm divergence, namely the splitting of the angiosperm stem lineage from its sister groups, had taken place before the Late Triassic (anthophyte theory). More recent molecular studies, which consider that the Gnetales are more closely related to conifers and that gymnosperms are a monophyletic group, indicate it took place in the Late Palaeozoic (Qiu



et al., 1999; Soltis *et al.*, 1999; Kenrick, 1999). These data concur with the distribution of the biomarker oleanane, which is a geochemical marker showing broad correlation with the distribution of angiosperms in the Cretaceous and Tertiary (Moldovan & Jacobson, 2000). This biomarker first occurs in Carboniferous rocks and seems to allude to the early roots of the group. The discovery of angiosperm-like pollen grains in the Middle Triassic fits well in this time framework. They provide the earliest morphological evidence, probably allowing a minimum age attribution for the origin of the total group.

The timing of angiosperm diversification, meaning the splitting of the crown group into extant clades, is equivocal and, using fossil evidence, open to the interpretation of what is unequivocal proof of crown group angiosperms. Some authors (Pocock & Vasanthi, 1988; Cornet, 1989) claim leaf structures and pollen as sufficient fossil evidence for the presence of angiosperms in the Late Triassic. Others (Doyle, 1978; Hughes, 1994; Brenner, 1996) rely on the continuous pollen records in the lower part of the Early Cretaceous (Valanginian or Hauterivian), whereas a third group (Crane *et al.*, 1995; Sun *et al.*, 1998, 2002; Friis *et al.*, 2000, 2001) accepts only reproductive structures (carpels and stamens with pollen sacs) of undoubted angiosperm morphology as proof for their existence.

The oldest undoubted fossil remains belonging to the earliest crown group clades are floral structures and associated monosulcate, reticulate pollen from Nymphaeales (water lilies) discovered in the mesoflora from continental sediments in Portugal (Crane *et al.*, 1995; Friis *et al.*, 2000, 2001). This record provides an Aptian, possibly Barremian, minimum age for the diversification of the angiosperm crown group.

The oldest claimed angiosperm, *Archaeofructus*, from the Late Jurassic (Sun *et al.*, 1998) came from continental sediments, which were at the time poorly dated. According to new data, especially from isotope studies, the famous fossil site of Liaoning, China, which yielded *Archaeofructus* macrofossils and pollen together with feathered reptiles and insects, has a maximum age of Barremian (Swisher III *et al.*, 1999; Zhou *et al.*, 2003). Because of the absence of certain floral features, *Archaeofructus* is no longer considered to belong to the angiosperm crown group, but to represent a probable stem group flowering plant.

Molecular clock studies using the newest phylogenetic trees considerably push back in time the origin of crown group angiosperms, namely to the Early to Middle Jurassic (179–

158 Ma) (Wikström *et al.*, 2001). These authors consider their time estimates as very conservative. Hence, the speculation seems to be that the crown group diversification of angiosperms might have happened even earlier, possibly as early as the Middle Triassic, and that the pollen grains described herein with angiosperm-like morphology might have been produced by the earliest crown group flowering plants.

Palaeogeographical distribution

In Middle Triassic times, the Boreal area of the Barents Sea, where the new angiosperm-like pollen was found, lay in middle to high latitudes at about 50–60°N in a zone of warm-temperate climate. This record in high palaeolatitudes contrasts with the other early angiosperm or angiosperm-like pollen records all of which derive from tropical or arid climate zones in low palaeolatitudes (Crane & Lidgard, 1989; Brenner, 1996). Cretaceous angiosperm diversification is well documented and shows a palaeolatitudinal gradient with angiosperms first becoming prominent in low palaeolatitudinal areas and spreading out subsequently, in parallel with an increase in diversity, to higher palaeolatitudes (Crane & Lidgard, 1989). Also the disputed angiosperm-like *Crinopolles* and *Polycolpopollis* from the Late Triassic derive from a low palaeolatitude site with an inferred arid or tropical climate.

CONCLUSIONS

The pollen grains described herein have shed new light on the evolution of pollen morphology. Most of the observed pollen morphologies seem to be new, or represent the oldest record of known morphological features. Unlike the boat-shaped, monosulcate pollen grains of primitive angiosperms, with a granular and tectate structure and lacking supratectal spinules (Doyle & Hotton, 1991), the finds here show reticulate or gemmate structures and resemble the pollen of palaeoherbs. Other features like the lack of aperture sculpture and the very thin or missing endexine are confirmed as basal.

The onset of the Middle Triassic is known as a time of great diversification of the gymnosperms. This renewal of the terrestrial floras occurred after the crisis at the Permian/Triassic boundary and the very slow recovery of the plant communities during the Early Triassic (Niklas *et al.*, 1983; Looy *et al.*, 1999). The amplitude of the radiation of gymnosperms in the Middle Triassic (around 242 Ma) is comparable to the angiosperm

Explanation of Plate 2. Images are taken using high-resolution differential interference contrast transmitted light (DIC-TL) and fluorescence confocal laser scanning microscopy (CLSM), respectively. All specimens derive from core samples from the Snadd Formation, Svalis Dome area, Barents Sea shelf, Norway, Middle Triassic, Early Ladinian. **fig. 1.** Pollen type D. Small monosulcate pollen grain with ?single-layered exine and possible remains of detached nexine (see arrow in fig. 1c). Fine reticulum with few verrucae on the surface, lumina reducing in size towards sulcus: 1a, DIC-TL image; 1b, distal face; 1c, proximal face of the same grain in CLSM; 1d, detail of sulcus in CLSM. Arrows show very small lumina at the sulcal margin. Core 7323/07-U-05, depth 132.07 m, England Finder (EF) coordinates: O61-1/3. **fig. 2.** Pollen type E. Small monosulcate pollen grain with ?single-layered exine and possible remains of detached nexine (see arrow in fig. 2a). Sexine consisting of heterobrochate reticulum: 2a, equatorial face in CLSM. Arrowheads point to sulcus. Arrow indicates remains of detached nexine near sulcus; 2b, detail on reticulum with irregular inner surface in DIC-TL. Arrows indicate small protuberances possibly representing columellae. Core 7323/07-U-05, depth 132.07 m, EF coordinates: L64-2. **fig. 3.** Pollen type F. Small monosulcate pollen grain with originally double-layered exine and remains of nexine near sulcus. Sexine consisting of a heterobrochate reticulum: 3a, proximal face in CLSM; 3b, 3c, DIC-TL images. Arrows indicate the sulcus margin. Core 7323/07-U-10, depth 98.6 m, EF coordinates: J26-4, slide 3. **fig. 4.** Pollen type G. Small ?monosulcate pollen grain with single-layered exine forming a heterobrochate reticulum with thickened intersections: 4a, 4b, CLSM images. Arrows indicate thickened intersections. Similar type to *Retisulcites* sp. 2 of Hochuli *et al.* (1989). Core 7323/07-U-05, depth 132.07 m, EF coordinates: O60-4. **fig. 5.** Pollen type N. Small mono-, possibly bisulcate pollen grain, with semitectate exine with gemmate-reticulate sculpture. Partly developed irregular reticulum formed by connection of sculpture elements: 5a, CLSM image; 5b–5d, DIC-TL images – 5b, 5d, details of thin nexine (arrows in fig. 5d) with gemmate, reticulate ornament; gemmae supported by one to several minute elements (arrows in fig. 5b). Core 7323/07-U-05, depth 121.01 m, EF coordinates: N58-2.

Pollen type	Shape/ preservation/ symmetry/ size	Aperture/sulcus	Exine layers	Sculpture	Reticulum: Type/surface	Reticulum: Lumina	Reticulum: Muri/Muri width	Columellae	Occurrence
Type A (Pl. 1, fig. 1)	oval, compressed, bilateral 70 × 42 µm	?triaperturate, ?operculate	double, nexine thin, attached	reticulate, slightly heterobrochate	irregular, surface verrucate	irregular, 1.5–3 µm	beaded, 1–1.5 µm	+ ?	single grain
Type B (Pl. 1, fig. 2)	oval, asymmetric, 62 × 39 µm	?syncolpate, ?operculate	double, nexine thin, attached	reticulate, heterobrochate	irregular, surface verrucate	polygonal -rounded, 1.5–4.5 µm	beaded, 0.7–1.5 µm	+	single grain
Type C (Pl. 1, fig. 3)	broad oval, bilateral, 45 × 54 µm	broad, monosulcate	double, nexine thin, attached	corrugate, reticulate	verrucae–corrugae connected to reticulum	irregular, 1.5–4 µm	irregular, beaded	+	single grain in cores, few records in exploration wells, <i>Retisulcites</i> sp. 1 of Hochuli <i>et al.</i> (1989)
Type D (Pl. 2, fig. 1)	round–oval, bilateral, 35 × 27 µm	monosulcate	?single layered, possibly with remains of nexine	reticulate, heterobrochate	surface with few verrucae	rounded polygonal, 0.5–5 µm, reduced size near sulcus	regular, 0.3–0.7 µm	?irregular inner surface of sexine	few in cores, several records in exploration wells
Type E (Pl. 2, fig. 2)	round–oval, bilateral, 23–24 × 31–33 µm	monosulcate	?single layered	reticulate, heterobrochate	surface verrucate	polygonal, 1.0–6.0 µm	regular, 0.8–1.3 µm	irregular inner surface of sexine	two records in cores
Type F (Pl. 2, fig. 3)	round–oval, bilateral 29–31 × 32–32 µm	monosulcate	double, remains of nexine near sulcus	reticulate, heterobrochate	smooth, few thickenings at intersections	rounded polygonal, 2–5.5 µm, reduced size near sulcus	0.9–1.5 µm	not observed	two records in cores, few occurrences in exploration wells
Type G (Pl. 2, fig. 4)	round, compressed radial? 30–32 × 39–47 µm	?monosulcate	single	reticulate, heterobrochate	surface with few verrucae, mostly thickened intersections	rounded polygonal and additional small lumina 1.5–6 µm	irregular, 0.3–1.5 µm, beaded	not observed	few in cores, regular occurrences in exploration wells, <i>Retisulcites</i> sp. 2 of Hochuli <i>et al.</i> (1989)
Type N (Pl. 2, fig. 5)	round–oval, bilateral?, 28 × 42 µm	Mono- possibly bisulcate	semitectate, thin layer with gemmate–reticulate sculpture	gemmate–reticulate, some gemmae pointed	partly developed reticulum	irregular, small lumina	beaded	+	single grain

Table 1. Architectural features of selected angiosperm-like pollen from the Middle Triassic of the Barents Sea.

radiation during the Aptian and Early Albian. It is possible that the first angiosperms, or their gymnospermous ancestors, evolved during this period of great floral renewal. So far, the unequivocal fossil evidence for the presence of crown group angiosperms are Nymphaeales reproductive structures with *in situ* pollen from Portugal (Friis *et al.*, 2000, 2001) of possibly Barremian or Aptian age. All the older records are either controversial (*Archaeofructus*), or are based on dispersed pollen grains or on isolated leaves (Cornet, 1986; Dilcher, 2001; Sun & Dilcher, 2002). These new finds from the Barents Sea suggest the existence of angiosperms in the Middle Triassic, or alternatively, since none of the known gymnosperm groups produces comparable pollen grains, the presence of an as-yet unknown group of gymnosperms.

ACKNOWLEDGEMENTS

The authors would like to thank Paul Kenrick (NHM) for valuable discussions and comments to this paper and IKU (Trondheim) for providing the sample material and the permission to publish. Thanks to Jorunn Os Vigran (Trondheim) and F. John Gregory (St. Albans) for the constructive reviews of this paper, and the anonymous reviewers of an earlier version of this manuscript for their comments and suggestions. CLSM studies have been carried out at the facilities of the Biology Department of Darmstadt University of Technology, Germany.

Manuscript received 2 February 2004

Manuscript accepted 7 June 2004

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