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Combined LM, SEM and TEM studies of Late Cretaceous Pollen and Spores from Gmünd, Lower Austria

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Fine grained clastic sediments from the Late Cretaceous (Santonian) of Gmünd, Austria were investigated palynologically. Some important microfloral elements are presented in this paper, using a combination of LM, SEM and partly TEM photography. The Gmünd microflora consists of 30% moss and pteridophyte spores, 10% gymnosperm and 60% angiosperm pollen grains and represents a highly diverse spore and pollenflora (e. g., Schizaeaceae, *Clavatipollenites* types, *Aachenipollis aachenensis*) of the *Normapolles* pollen province. A completely new pollen form (hexaaperturate) has been described: *Gmuendipollis teppneri* gen. et spec. nov.

Z u s a m m e n f a s s u n g : ZETTER R., HESSE M. & K.H. HUBER (2002): Kombinierte licht- und elektronenmikroskopische Untersuchungen an Pollen und Sporen der Oberkreide aus Gmünd, Niederösterreich. – Stapfia **80**: 201-230.

Feinkörnige klastische Sedimente der Oberkreide (Santon) aus Gmünd, Niederösterreich, wurden palynologisch mit Hilfe des Licht-, des Raster- und des Transmissionselektronenmiokroskops untersucht. Die Mikroflora der Gmuendner Schichten setzt sich aus 30% Moos- und Farnsporen, aus 10% Gymnospermen- und 60% Angiospermenpollen zusammen. Das Ergebnis der Untersuchungen zeigt eine hohe Diversität der Mikroflora. Eine neue Pollenform wurde als *Gmuendipollis teppneri* gen. et spec. nov. beschrieben.

K e y w o r d s : Spores, Pollen, Gmünd, Lower Austria, Santonian, Late Cretaceous, LM, SEM, TEM.

Contents

Introduction

Terrestrial sediments of lacustrine to fluviatile origin (coaly and sandy clays) from Gmünd, Lower Austria, contain a rich and very well preserved Cretaceous microflora (moss and pteridophyte spores, gymnosperm and angiosperm pollen grains). Stratigraphically comparable microfloras from adjacent regions of the Czech Republic have been investigated by PACLTOVA (1961, 1981) on the bases of LM.

The aim of this study was to describe these exceptionally three-dimensional preserved spores and pollen grains more precisely, by using a combination of light and electron microscopy. In this paper we give an overview on representative moss and fern spores, gymnosperm and angiosperm pollen types. The emphasis of detailed examinations are focussed on a frequently found pollen tetrad, several types of *Clavatipollenites*, monosulcate pollen, some representatives of *Normapolles* and of tricolpate and tricolporoidate angiosperm pollen grains are described. The detailed studies of the dispersed microflora provide on one hand better information on the variation of particular taxa (e. g., *Normapolles*), and on the other hand results in a much higher diversity of particular pollen taxa (e. g., *Clavatipollenites* types). The usefulness of SEM to recognize this diversity was already stressed by, e. g., HUGHES et al. (1979), CHAPMAN (1987), PENNY (1988, 1991), HUGHES (1994), or FRIIS et al. (1999). The thorough investigation allows also a better comparison of dispersed pollen material with in situ pollen from Cretaceous mesofloras (flowers) which have been described in a great number in the last years (e. g., NIXON & CREPET 1993; CREPET & NIXON 1994, 1998a, 1998b; FRIIS et al. 1999). At least the SEM examination allows a much better identification of the microfloral elements, which can result in a better knowledge about their real stratigraphic range.

A more detailed investigation of the microflora of Gmünd together with the stratigraphical and geological background is in preparation.

Geology

Near the small Austrian town Gmünd (Lower Austria), which is situated directly at the Austrian-Czech border (northwestern Lower Austria), thick sediment series are deposited onto the crystalline rocks of the southeastern Bohemian Massif. These sediments are exposed mainly in the two South Bohemian basins: the České Budějovice basin (Českobudějovická pánev/Budweiser Becken), and the Trebon basin (Trebonská/Wittingauer Becken). Both are included into the "South Bohemian basin", occupying a total area of approximately 2.300 km^2.

Only the narrow southeastern marginal part crops out in the NW Waldviertel region. This small Austrian part of the Trebon basin is mainly limited to the community district of Gmünd. WALDMANN (1936, 1943, 1951) created the name "Gmünder Bucht" - a term already earlier used by ROSENKRANZ (1925) and by KASMANNHUBER (1931) -

meaning Gmünd bay, and called the sediments that continue to South Bohemia, the Gmünder Schichten (WALDMANN 1951), meaning Gmünd beds.

Although the Gmünd beds in Austria presumably cover an area of only about 50 km^2 at present, they can be stratigraphically correlated with the South Bohemian sediment series.

The stratigraphy of the South Bohemian basins is characterized by following main features (see MALECHA 1964, 1966; SLANSKÁ 1974, 1976; MALECHA & SUK 1985; CHÁBERA 1998): The up to 340 m thick Klikov Formation mainly overlies discordantly deeply weathered crystalline basement rocks. Only in the České Budějovice basin this formation overlies discordantly Permo-Carboniferous graben fillings (Budějovice Fm.; SKOČEK 1993). The Klikov Formation comprises fluvio-lacustrine freshwater sediments and is of Upper Cretaceous age.

After a period of non-deposition/erosion (± 30 Ma) a decumulation of freshwater sediments occurred at the end of the Palaeogene (Lipnice Fm.; 30 m thickness). Age constraints of the Lipnice Fm. are uncertain because of the lack of stratigraphically useful fossils, however it is lithologically comparable with the Oligocene sediments of NW Bohemia. The following 20 m thick (Helvetian ? resp. ? Ottnangian-Karpathian ?) Zliv Formation as well as the ca. 120 m thick (Tortonian ? resp. ? Badenian ?) Mydlovary Formation have brackish character. The Domanin Formation, as well as the almost 20 m thick Pliocene Ledenice Formation, consist of lacustrine sediments.

During the Quaternary river terraces, fluvial sediments, talus material, solifluidal sands, weathering residuals, peat bogs and other sediments have been deposited.

Lithostratigraphy of the Klikov Formation

The Klikov Formation is a terrigenous fresh-water-series of clastic sediments. It represents a more or less regularly reoccurring red bed association with alternating strata A-C. (A) Coarse- to fine-grained, occasionally (near the base) conglomeratic, rarely laminated light gray or light yellow sandstones, that often displays graded bedding. These sandstones are interpreted as alluvial fans or channel sediments. (B) Finer-grained red beds, i. e., brownish red, to dark red medium- to fine-grained muddy sandstones, sandy mudstones or sandy claystones, that are usually poorly sorted. Their red pigment - iron oxides or hydroxides - probably derives from red upland soils of the source area, deposited on a flood plain or subordinately in shallow lakes. (C) Gray beds, i. e., greenish gray or very dark gray coarse- to fine-grained sandstones, mudstones and claystones, that are partly laminated and better sorted than A or B, and are interpreted as swamp or lake deposits.

The sediments of the Klikov Formation continue from České Velenice to Gmünd (MALECHA 1964, 1966; SOUKUP 1968; THENIUS 1974; FUCHS 1977, 1980; MALECHA and SUK 1985; TOLLMANN 1985; CHÁBERA 1998). However, their exact limits within the Gmünd bay are not everywhere certain, as this terrain lacks exposures, and fieldwork at the Austrian-Czech border has not been possible.

In the eastern part of the Gmünd bay around the town Gmünd the Klikov Formation has few subsurface outcrops. During 1982, for only a short time, in the foundation pit of the Public Hospital of Gmünd beds of the Klikov Formation had been exposed.

Material and Methods

Pollen bearing sediments were collected from a horizon of the exposed Klikov formation in the foundation pit of the Public Hospital of Gmünd in 1982. The sediments were located at a depth of 5.65 to 6.50 m below the ground level (gray-black clays).

The gray-black clays that contain the microflora are terrestrial sediments of lacustrine to fluviatile origin. Lacking marine stratigraphical control, the dating of the microflora is problematic. Nevertheless, the microflora is suggested to be of Santonian age, because of characteristic microfloral elements and that co-occur in stratigraphically controlled palynofloras (e. g., PACLTOVA 1981, 1990).

After removing the surface sediment (to prevent possible contamination) the sample were ground by hand, in a mortar. The powder then was boiled in a copper pan with HF to remove the silicates. The remaining material was then transferred to a large polyethylene beaker, which was filled before with 3-4 l water. In the next 1-2 hours the sample was left to settle. After decanting the liquid, the residue was boiled in conc. HCl in a glass beaker for 5 minutes to prevent the formation of fluorite crystals. Once, this process was complete and the sample has settled to the bottom of the beaker, the supernatant HCl was decanted. The sample (with a rest of HCl) was then centrifuged in a test tube, again decanted, and afterwards washed in distilled water and centrifuged and washed 3-4 times before undergoing acetolysis (chlorination plus acetylation). After acetolysis, it was necessary to separate the organic fraction from the inorganic material by a heavy liquid separation using a solution of zinc bromide.

The organic residue was then mixed with glycerol to form a suspension. With a pipette a drop of this suspension was transferred to a glass slide and evenly distributed. Under LM, those grains which were of particular interest, were then moved - using a specially adapted dissecting needle with a human hair glued near its tip (ZETTER 1989) - to the margin of the glycerol, where they could be located and transferred to another glass slide with a fresh drop of glycerol for photography in a light microscope. Light microscope photography was done with a Nikon Optiphot-2 with reversed field of view. The same pollen grains were then transferred to an aluminum SEM stub onto which a drop of absolute ethanol has been applied with a pipette. As the alcohol evaporates very rapidly, it is necessary to keep on adding more ethanol until a number of pollen grains (not more than 10-15) have been transferred to the stub. The ethanol removes any traces of the glycerol from the surface of the pollen grains, so that these can be examined in great detail using SEM. Prior to examination with a JEOL 6400 at 10 kV the pollen grains were sputtered with gold using a BIORAD sputter coater for 4 minutes. The advantage of the method outlined above is that the same pollen grains can be examined under both LM and SEM.

For the quantitative analysis with SEM it was necessary to mix the organic residue with abs. Ethanol. With a pipette a drop of this suspension was transferred to a SEM-stub. It should be noticed that it is necessary to bring only a thin layer of organic material upon the SEM stub, otherwise it will be problematic to count the different elements of the microflora. From the samples 350 spores and pollen grains were counted.

For TEM studies the pollen material was treated as follows: after the removal of glycerol the samples were transferred to ethanol, then to acetone and infiltrated with Spurr's mixture. Ultrathin sections were stained either with uranyl acetate (UA: 1% methanolic solution, 45 min.) followed by lead citrate (Pb: 0.1% solution, 1 min.) or with a modified Thiéry-test (PA: periodic acid for 10 min., TCH: thiocarbohydracid for 15 min. and SP: silver proteinate for 10 min.) according to WEBER et al. (1998). The sections were examined with a ZEISS EM 900 at 50 kV.

Pollen terminology follows PUNT et al. (1994).

Fossil spore and pollen grains described in this work are stored in the Institute of Paleontology of Vienna.

Organic facies

The organic facies of the investigated samples is dominated by strongly gelified wood fragments (semi-opaque material), little cuticle and membranous material and accessory fusinite splinters. The organic components are heterogeneous in size (25-70 µm/3-7 µm) and display rounded and angular lath shaped fragments.

The dominance of strongly fractionated coalified wood fragments indicates either a lacustrine or a flood basin/flood plain environment.

Results

In this section selected spore and pollen types are described:

Division *Bryophyta*

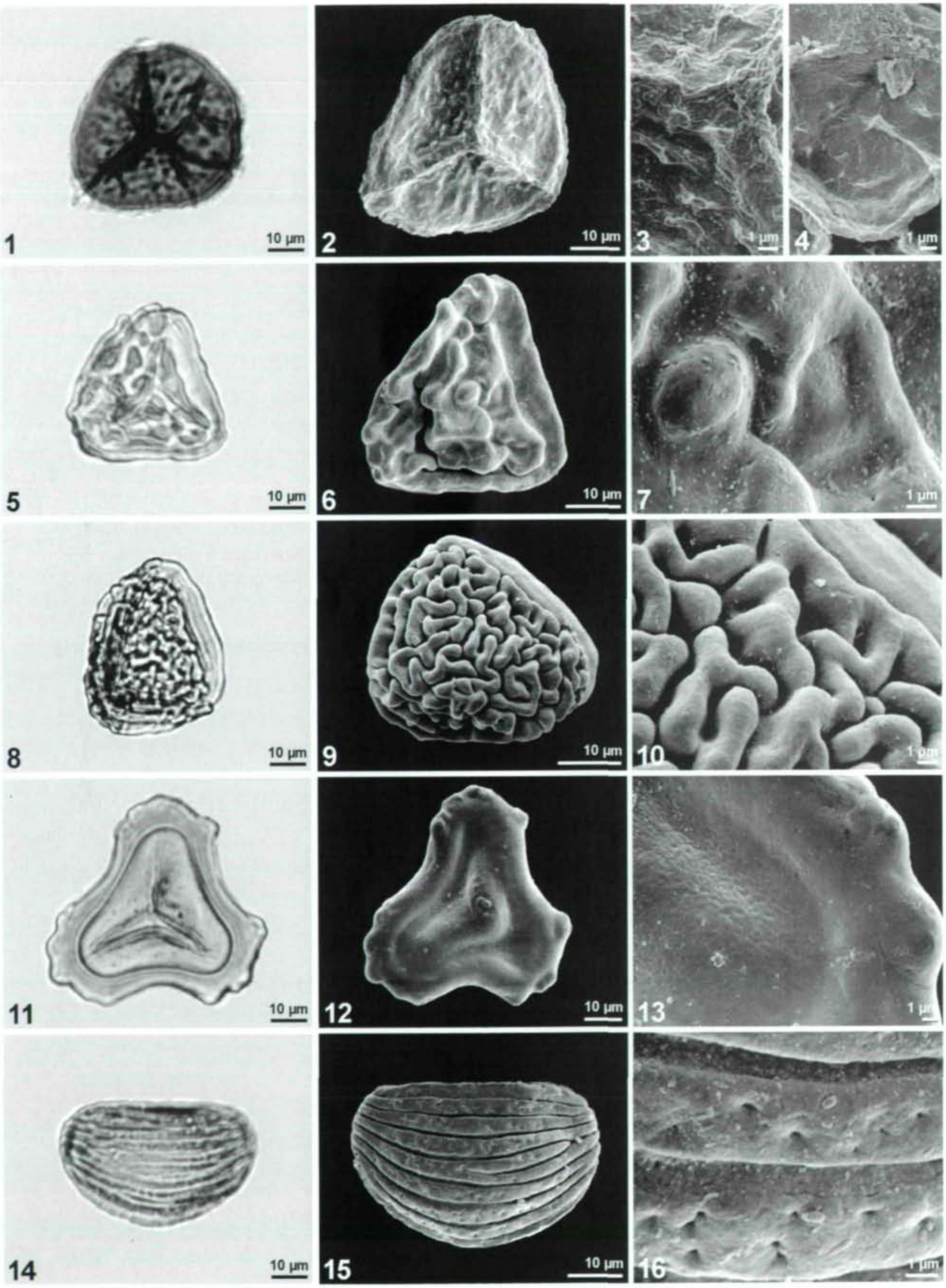
Zlivisporis PACLTOVA 1961

Zlivisporis blanensis PACLTOVA (Plate 1/1-4)

Tetrahedral-globose, flattened, in polar view triangular, with an equatorial narrow flange (c. 3 µm). Diameter 45-50 µm. Aperture trilete, the arms extending to the equatorial flange (Plate 1/2). Ornamentation: Proximal face (Plate 1/3) finely echinate, distal (Plate 1/4) with irregularly incomplete reticulum-like walls.

According to KRUTZSCH (1967) the liverworth family of Oxymitraceae produces very similar spores.

Plate 1 (opposite page): **1-4** *Zlivisporis blanensis*. **1** Whole spore, LM. **2** Whole spore, SEM. **3** Detail of the proximally located central area, SEM. **4** Detail of the distal area, SEM. **5-7** *Polypodiaceoisporites* sp. 1. **5** Whole spore, proximal view, LM. **6** Whole spore, distal view, SEM. **7** Detail of spore, distal view, SEM. **8-10** *Polypodiaceoisporites* sp. 2. **8** Whole spore, distal view, LM. **9** Whole spore, distal view, SEM. **10** Detail of spore, distal view, SEM. **11-13** *Trilobosporites* sp. **11** Whole spore, proximal view, LM. **12** Whole spore, distal view, SEM. **13** Detail of spore, distal view, SEM. **14-16** *Schizaeoisporites* sp. **14** Whole spore, distal view, LM. **15** Whole spore, distal view, SEM. **16** Detail of spore, SEM.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Division *Pteridophyta*

Polypodiaceoisporites R. POTONIE 1956

Polypodiaceoisporites sp. 1 (Plate 1/5-7)

Oblate, triangular with a prominent equatorial flange (c. 5 µm). Aperture trilete, arms two third to three fourths of the radius (Plate 1/5). Diameter 40-50 µm. Ornamentation: distal face coarsely rugulate, equatorial flange smooth (Plate 1/6-7), proximal face densely verrucate. Botanical affinity: *Pteridaceae*

Polypodiaceoisporites sp. 2 (Plate 1/8-10)

Oblate, triangular with a prominent equatorial flange (c. 4-5 µm). Aperture trilete, arms two third to three forth of the radius (Plate 1/8). Diameter 40-50 µm. Ornamentation: distal face densely rugulate, flange smooth (Plate 1/9-10).

Botanical affinity: *Pteridaceae*

Trilobosporites PANT 1954 ex POTONIÉ 1956

Trilobosporites sp. (Plate 1/11-13)

Oblate, in polar view concave triangular. With a prominent equatorial smooth flange (c. 6-7 µm), forming at the apices a corona (Plate 1/11-12). Aperture trilete, arms one to two third of the radius. Diameter 60-65 µm. Ornamentation smooth, with minute grooves (Plate 1/13).

PACLTOVA (1961) described a very similar spore as *Trilobozonosporites exoticus* from sediments of Pecak (Zliv-Gmünd series).

Schizaeoisporites R. POTONIÉ 1960

Schizaeoisporites sp. (Plate 1/14-17)

Ellipsoidal, in polar view elliptic, monolete. Diameter in long axis 45-50 µm. Ornamentation coarsely ribbed. Ridges perforated (Plate 1/15).

Botanical affinity: *Schizaeaceae* genus *Schizaea*/*Actinostachys*

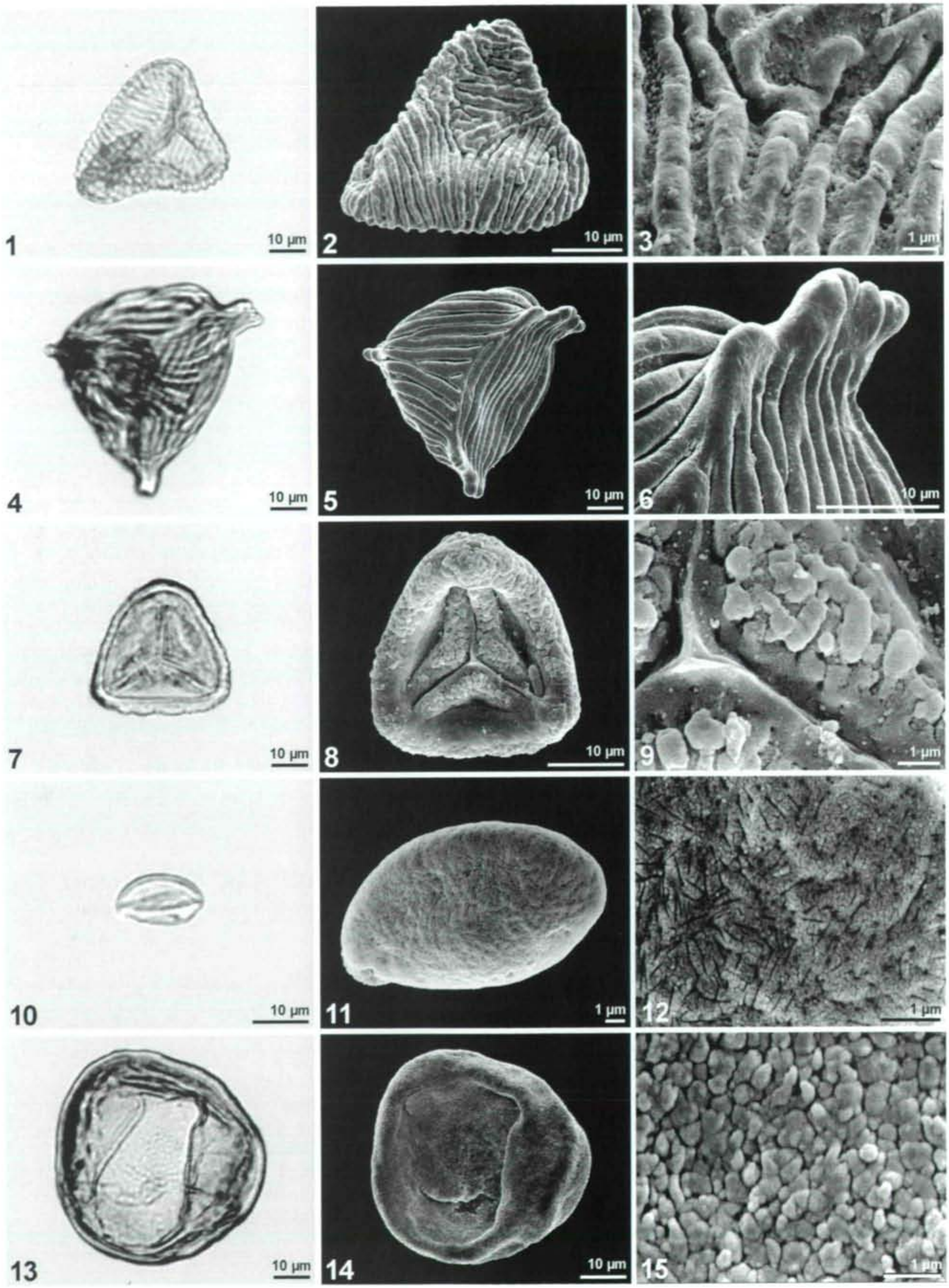
Cicatricosisporites R. POT. & GELL. 1933

Cicatricosisporites sp. (Plate 2/1-3)

Oblate, in polar view triangular, trilete, the arms two third to three fourths of the radius. Diameter 30-50 µm. Ornamentation: more or less coarse ridges with plicae in between, ridges knobbly (Plate 2/2-3).

Botanical affinity: *Schizaeaceae*

Plate 2 (opposite page): **1-3** *Cicatricosisporites* sp. **1** Whole spore, proximal view, LM. **2** Whole spore, distal view, SEM. **3** Detail of spore, SEM. **4-6** *Appendicisporites* sp. **4** Whole spore, distal view, LM. **5** Whole spore, distal view, SEM. **6** Detail of spore, SEM. **7-9** Trilete fern spore. **7** Whole spore, proximal view, LM. **8** Whole spore, proximal view, SEM. **9** Detail of spore, SEM. **10-12** *Cycadopites* sp. **10** Whole grain, distal view, LM. **11** Whole grain, proximal view, SEM. **12** Detail of grain, SEM. **13-15** *Araucariicidites* sp. **13** Whole grain, distal view, LM. **14** Whole grain, distal view, SEM. **15** Detail of grain, SEM.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Appendicisporites WEYLAND & KRIEGER 1953

Appendicisporites sp. (Plate 2/4-6)

Oblate, in polar view triangular, trilete, the arms two third to three fourths of the radius. Diameter 40-50 µm. Ornamentation: Coarse ridges, smooth, ridges at the equatorial ends with prominent prolonged angles, forming short appendices (Plate 2/5-6).

Botanical affinity: *Schizaeaceae*

Pteridaceae ? (Plate 2/7-9)

Oblate, in polar view triangular, the arms two third to three forth of the radius. Diameter 30-35 µm. Ornamentation: proximal around the tetrad mark (2 µm) smooth, perforated, contact areas densely rugulate (Plate 2/8-9). Distal area densely rugulate.

Division *Spermatophyta*

Gymnosperms

Cycadopites WODEHOUSE 1933

Cycadopites sp. (Plate 2/10-12)

Oblate. Diameter 12-15 µm long axis. Sulcate, perforate. Ornamentation perforate, with narrow short grooves (Plate 2/11-12).

Ornamentation: resembling *Encephalartos* and in this respect with a probable affinity to *Encephalartos*.

Araucariicidites COOKSON ex COUPER 1953

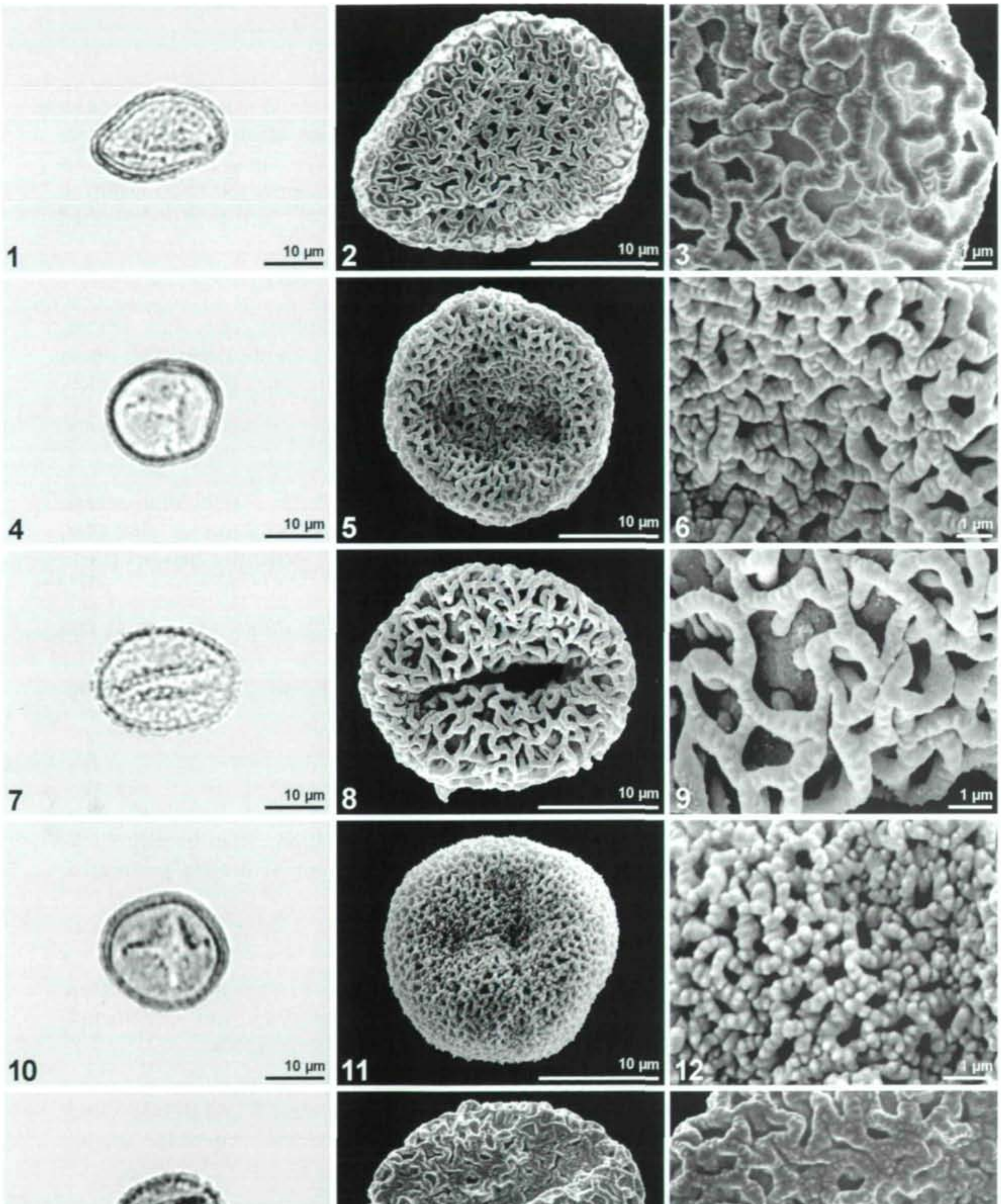
Araucariicidites sp. (Plate 2/13-15)

Originally spheroidal, more or less circular in polar view. Diameter 50-55 µm. Large, thinned distal area (Plate 2/13). Verrucate.

Angiosperms

Angiosperm pollen grains are significant for the Gmünd microflora. The microflora contains monoaperturate (monosulcate), tricolpate, tricolpor(oi)date and tricolporate pollen grains.

Plate 3 (opposite page): **1-3** *Clavatipollenites* sp. 1. **1** Whole grain, distal view, LM. **2** Whole grain, proximal view, SEM. **3** Detail of grain, SEM. **4-6** *Clavatipollenites* sp. 2. **4** Whole grain, distal view, LM. **5** Whole grain, proximal view, SEM. **6** Detail of grain, SEM. **7-9** *Clavatipollenites* sp. 3. **7** Whole grain, distal view, LM. **8** Whole grain, distal view, SEM. **9** Detail of grain, SEM. **10-12** *Clavatipollenites* sp. 4. **10** Whole grain, distal view, LM. **11** Whole grain, distal view, SEM. **12** Detail of grain, SEM. **13-15** *Clavatipollenites* sp. 5. **13** Whole grain, distal view, LM. **14** Whole grain, distal view, SEM. **15** Detail of grain, SEM.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Monoaperturates

Clavatipollenites COUPER 1958

At present the idea from COUPER (1960), MULLER (1981), WALKER & WALKER (1984), that *Clavatipollenites* types have a Chloranthaceous affinity is undisputed. Especially EM investigations from different *Clavatipollenites* types, e. g., CHAPMAN (1987), CHLONOVA & SUROVA (1988), FRIIS et al. (1999), show the relationship to *Chloranthaceae*. An assignment and delimitation of different described *Clavatipollenites* types can be done only with SEM.

Clavatipollenites sp. 1 (Plate 3/1-3)

Oblate, in polar view oval. Diameter long axis c. 15 µm. Sulcate, reticulate, heterobrochate. Broad, rounded muri with variable dimensions. Lumina polygonal, about 1.5-1.7 µm in diameter. Columellae high. Ornamentation: muri often segmented, protrusions in two rows (Plate 3/3).

Clavatipollenites sp. 2 (Plate 3/4-6)

Oblate, in polar view circular to oval. Diameter c. 23-25 µm. Trichotomosulcate, reticulate, heterobrochate. Rounded muri. Lumina about 1-1.2 µm in diameter, lumina towards sulcus more narrow. Ornamentation: muri generally banded (Plate 3/5-6).

Comments: In ornamentation intermediate between *Clavatipollenites* sp. 1 and *Clavatipollenites* sp. 3.

This *Clavatipollenites* type corresponds to pollen type J 4 in FRIIS et al. (1999, Figs. 105-107).

Clavatipollenites sp. 3 (Plate 3/7-9)

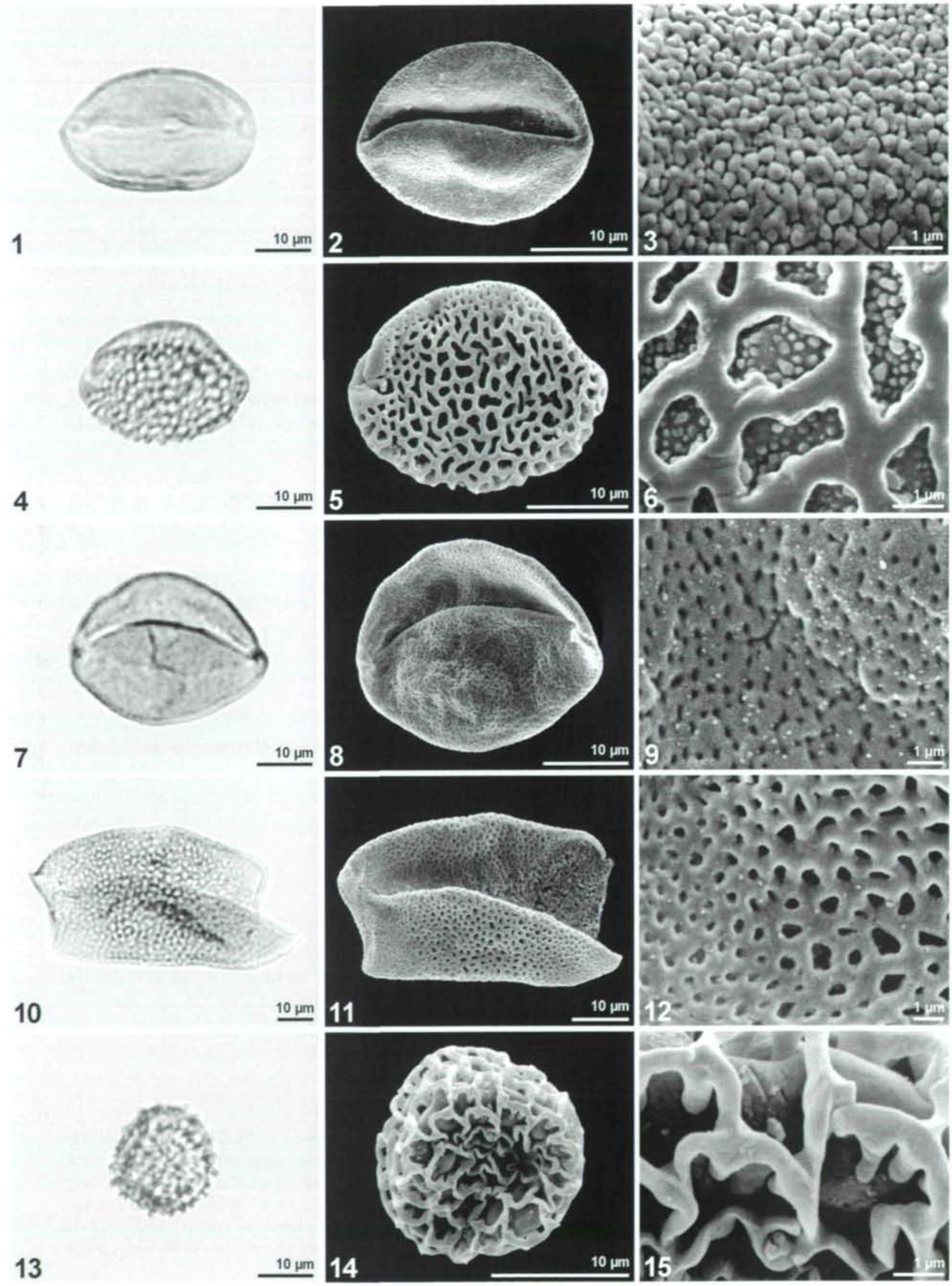
Oblate, in polar view oval. Diameter in long axis c. 25-28 µm. Sulcate, reticulate, heterobrochate. Rounded muri. Unicolumellar, columellae high, often basally thickened. Lumina polygonal, large, 2-3 µm in diameter, bottom of lumina perforated. Ornamentation: muri more or less segmented (Plate 3/9).

Clavatipollenites sp. 4 (Plate 3/10-12)

Oblate, in polar view more or less circular. Diameter 15-17 µm. Polytomosulcate (four arms), microreticulate to reticulate. Lumina polygonal, 0.5-1 µm. Ornamentation: Muri intensely sculptured (Plate 3/11) resembling strings of beads.

Comments: This *Clavatipollenites* type is comparable with *Clavatipollenites incisus* CHLONOVA, figured in CHLONOVA & SUROVA (1988, Plates 1/1-7 and 2/2-3). Other detail micrographs from their Plates 1, 8, 11, 12 maybe represent another *Clavatipollenites* type.

Plate 4 (opposite page): **1-3** *Monocolpopollenites* sp. 1. **1** Whole grain, distal view, LM. **2** Whole grain, distal view, SEM. **3** Detail of grain, SEM. **4-6** *Monocolpopollenites* sp. 2. **4** Whole grain, proximal view, LM. **5** Whole grain, proximal view, SEM. **6** Detail of grain, SEM. **7-9** *Monocolpopollenites* sp. 3. **7** Whole grain, distal view, LM. **8** Whole grain, distal view, SEM. **9** Detail of grain, SEM. **10-12** *Liliciacidites* sp. **10** Whole grain, equatorial view, LM. **11** Whole grain, equatorial view, SEM. **12** Detail of grain, SEM. **13-15** *Retimonocolpites* sp. **13** Whole grain, oblique view, LM. **14** Whole grain, oblique view, SEM. **15** Detail of grain, SEM.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Clavatipollenites sp. 5 (Plate 3/13-15)

Oblate, in polar view oval. Diameter long axis 20-22 µm. Sulcate, microreticulate. Lumina polygonal, 0.5-0.8 µm. Broad muri with rows of microspines (Plate 3/15).

Comments: the fine ornamentation resembles *Hedyosmum* (*Chloranthaceae*).

Clavatipollenites sp. 5 corresponds to pollen type J 9 (3) in FRIIS et al. (1999, Figs. 103-104).

The following monosulcate pollen types are clearly no *Clavatipollenites*, but at present we are unable to give a close relationship to an extant angiosperm family. Monosulcate pollen grains are found in basal angiosperms and also in the monocots.

On LM level many of those monosulcates were addressed as *Monocolpopollenites* types, because important details of ornamentation cannot be resolved. However, SEM studies with their higher resolving power clearly demonstrate that sometimes members of the *Monocolpopollenites* complex can be assigned to other form genera with, e. g., verrucate ornamentation, that are not recognized for the *Monocolpopollenites* forms sensu NICHOLS et al. (1973).

Monocolpopollenites PFLUG & THOMSON in THOMSON & PFLUG 1953

Monocolpopollenites sp. 1 (Plate 4/1-3)

Oblate, in polar view oval. Diameter long axis 25-28 µm. Sulcate, sulcus with rounded ends. In LM psilate, in SEM perforate, with short, rod-like, sometimes fused elements (Plate 4/3). Elements of the tectum 0.3-0.6 µm in length, tectum elements get more fused around the sulcus (Plate 4/2).

Monocolpopollenites sp. 2 (Plate 4/4-6)

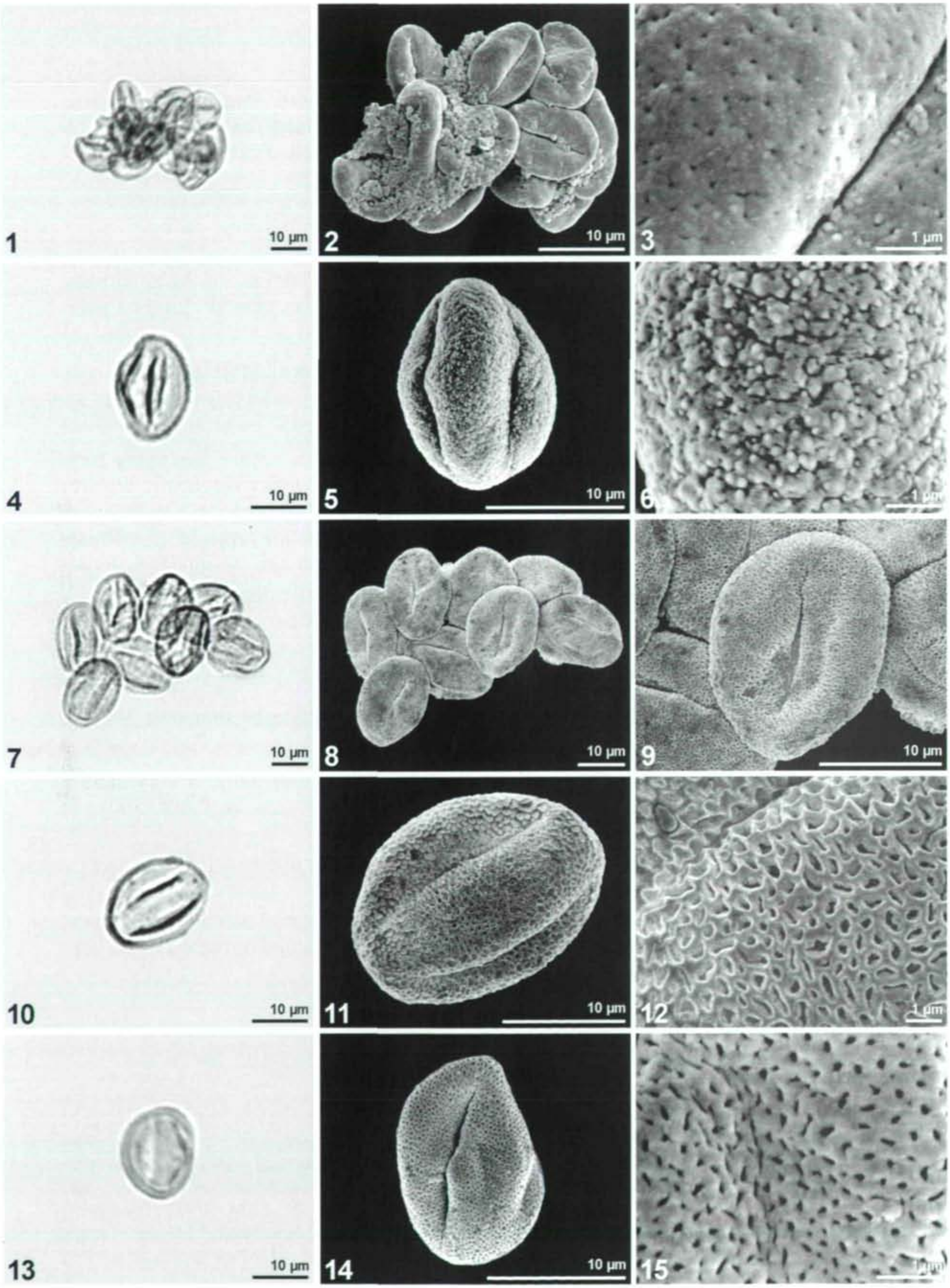
Oblate, in polar view rounded to oval, diameter long axis 25-30 µm. Sulcate, sulcus with rounded ends, reticulate. Lumina polygonal, 2-3 µm, lumina around the sulcus very narrow to completely missing (Plate 4/5). Ornamentation: muri smooth. Numerous small reduced baculae visible through lumina (Plate 4/6).

Comments: resembling Fig. 9.36 in HUGHES 1994.

Monocolpopollenites sp. 3 (Plate 4/7-9)

Oblate, in polar view oval, diameter long axis 30-32 µm. Sulcate, sulcus with pointed ends, perforate (Plate 4/8). Ornamentation: tiny granules scattered over the pollen surface (Plate 4/9).

Plate 5 (opposite page): **1-3** *Tricolpopollenites* sp. 1. **1** Group of monads, LM. **2** Group of monads, SEM. **3** Detail of a grain, SEM. **4-6** *Tricolpopollenites* sp. 2. **4** Whole grain, equatorial view, LM. **5** Whole grain, equatorial view, SEM. **6** Detail of grain, SEM. **7-12** *Tricolpopollenites* sp. 3. **7** Group of monads, LM. **8** Group of monads, SEM. **9** Single grain of monad group, SEM. **10** Whole grain, equatorial view, LM. **11** Whole grain, equatorial view, SEM. **12** Detail of grain, SEM. **13-15** *Tricolpopollenites* sp. 4. **13** Whole grain, equatorial view, LM. **14** Whole grain, equatorial view, SEM. **15** Detail of grain, SEM.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Liliacidites COUPER 1953

Liliciacidites sp. (Plate 4/10-12)

Oblate, rectangular in polar and in equatorial view, diameter long axis 50-55 µm, sulcate. The short sides of the rectangles and the zone around the sulcus are perforated, all other parts are microreticulate (Plate 4/10-12). Ornamentation smooth.

Retimonocolpites PIERCE 1961

Retimonocolpites sp. (Plate 4/13-15)

Oblate, in polar view circular, diameter 15-17 µm, sulcate, reticulate. Muri forming arcades, high columellae (up to 1.5-2 µm high), unicolumellar, smooth. Lumina polygonal, diameter 2-4 µm (Plate 4/14-15).

Comments: resembles Figs. 72-74, pollen type D 9 in FRIIS et al. (1999).

Tricolpates and Tricolporoidates

Within the so-called Tricolpates and Tricolporoidates of Cretaceous age many form species have been reported by using LM only. At LM level many diagnostic features are invisible, which can be seen with SEM at convenient magnification. On the other hand LM studies are necessary for the description of the aperture areas (e. g., colpate-colporate) or for the preliminary description of the exine structure. With SEM studies it would be easier to compare dispersed pollen with pollen from in-situ flowers.

Tricolpopollenites THOMPSON & PFLUG 1953

Tricolpopollenites sp. 1 (Plate 5/1-3)

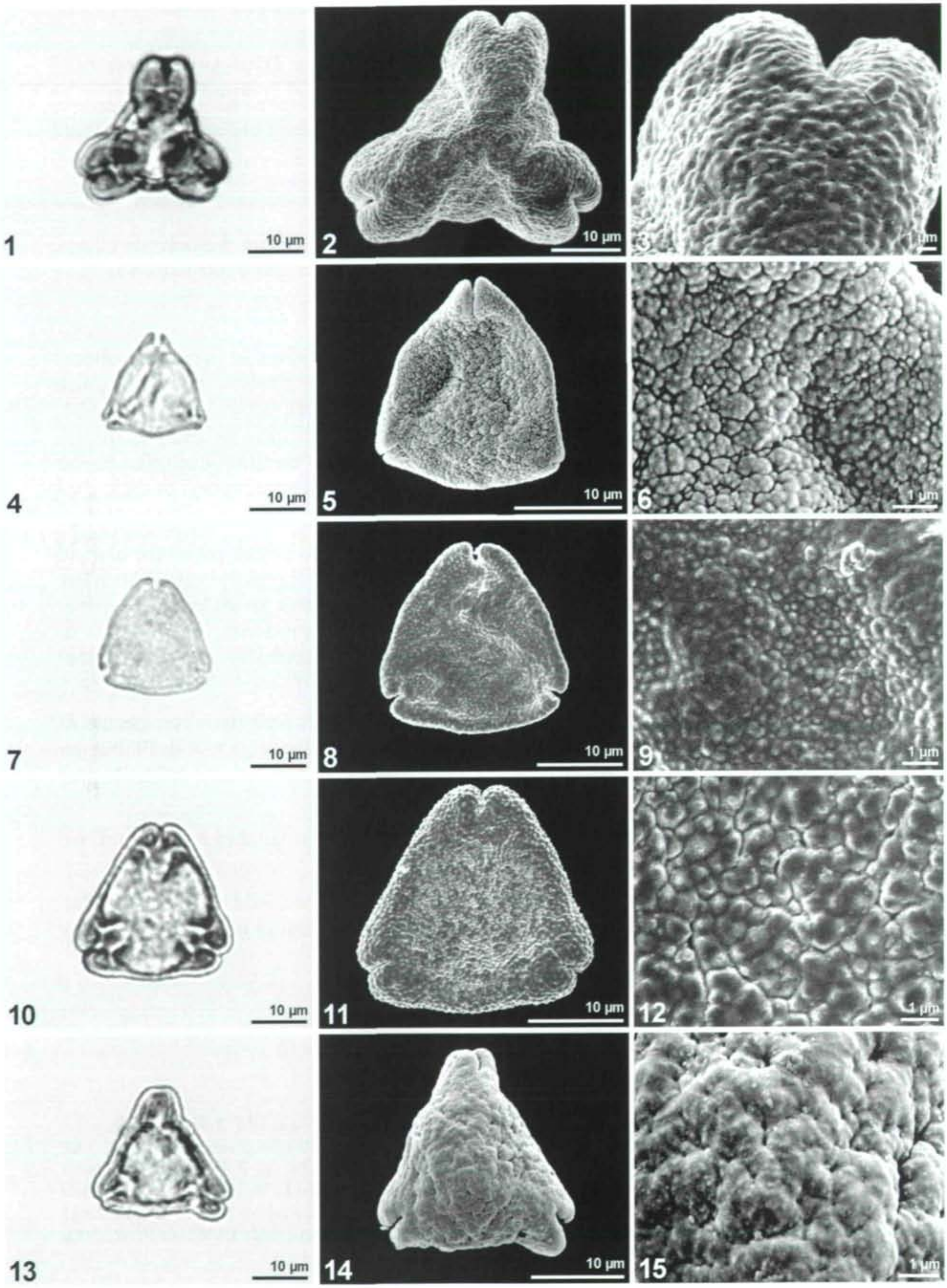
Prolate, in equatorial view oval, polar axis 10-12 µm, equatorial diameter 5-8 µm, tricolpate. Ornamentation perforate (Plate 5/3).

Comments: often found in clumps, FRIIS & PEDERSEN (1996) found a very similar pollen type in flowers of *Actinocalyx* sp., and SCHÖNENBERGER & FRIIS (2001) in *Paradinandra suecica*.

Tricolpopollenites sp. 2 (Plate 5/4-6)

Prolate, in equatorial view oval, polar axis 16-18 µm, equatorial diameter 10-12 µm, tricolpate to tricolporoidate (Plate 5/4-5). Ornamentation microverrucate, with conspicuous rod-like elements (Plate 5/6).

Plate 6 (opposite page): **1-3** *Oculopollis* sp. 1. **1** Whole grain, polar view, LM. **2** Whole grain, polar view, SEM. **3** Detail of aperture area, SEM. **4-6** *Plicapollis* sp. 1. **4** Whole grain, polar view, LM. **5** Whole grain, polar view, SEM. **6** Detail of grain, SEM. **7-9** *Neotriangulipollis* sp. **7** Whole grain, polar view, LM. **8** Whole grain, polar view, SEM. **9** Detail of grain, SEM. **10-12** *Trudopollis hemiperfectus*. **10** Whole grain, polar view, LM. **11** Whole grain, polar view, SEM. **12** Detail of grain, SEM. **13-15** *Extratriporopollenites* sp. **13** Whole grain, polar view, LM. **14** Whole grain, polar view, SEM. **15** Detail of grain, SEM.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Tricolpopollenites sp. 3 (Plate 5/7-12)

Prolate, polar axis 16-18 µm, equatorial diameter 10-12 µm. Tricolpate. Microreticulate, lumina 0.5-0.8 µm in diameter, heterobrochate (Plate 5/12). Muri smooth.

Comments: common pollen form, often in clumps, FRIIS & PEDERSEN (1996) found very similar pollen in *Platananthus scanicus*.

Tricolpopollenites sp. 4 (Plate 5/13-15)

Prolate, polar axis 15-17 µm, in equatorial view oval, equatorial diameter 9-11 µm, tricolpate to tricolporioidate. Microreticulate, lumina 0.2-0.3 µm (Plate 5/14-15).

N o r m a p o l l e s

Pollen grains of the *Normapolles* complex are frequent elements in many microfloras of Europe, eastern north America and Asia (*Normapolles* floristic province) since Cenomanian time (e. g., HERNGREEN & CHLONOVA 1981; ZAKLINSKAYA 1981, BATTEN & CHRISTOPHER 1981; BATTEN 1986). A great number of genera and species were described up to now mostly on LM level. Because of the low resolution power of LM important details which are necessary for a precise determination of taxa, cannot be seen.

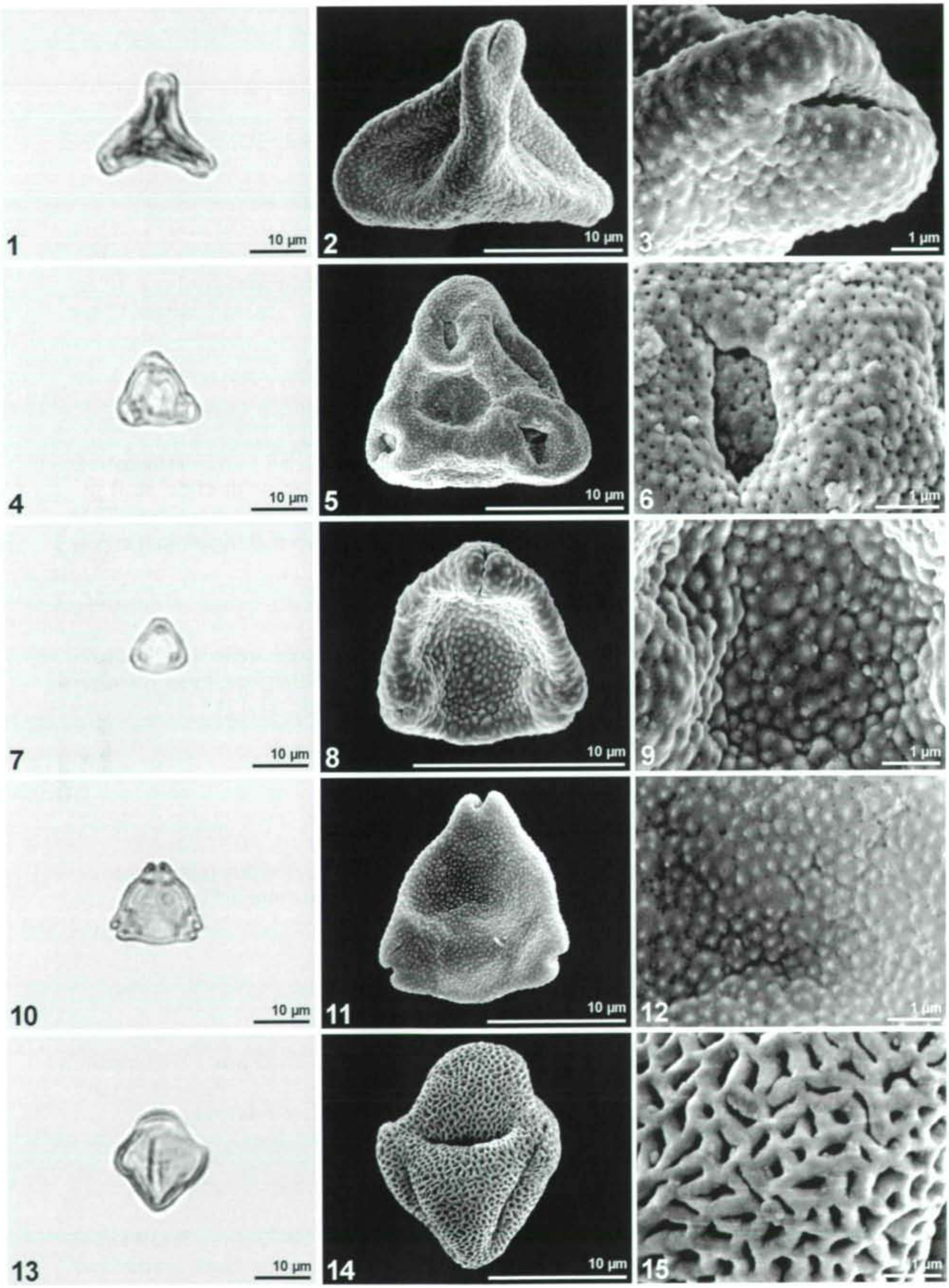
BATTEN (1996) brought it to the point: "Unfortunately, taxonomic problems abound within the group, partly because the characters of many of the morphotypes overlap, making it difficult to identify specimens confidently to generic level, let alone to species. This situation has not been helped by the fact that descriptions of the majority of *Normapolles* taxa failed to take into account the range of morphological variation that can be expected (BATTEN & MORRISON 1987; BATTEN 1989)".

We conclude that the *Normapolles* problem can only be solved by a conspectus of various localities by thorough investigations of mesofloras (e. g., FRIIS & PEDERSEN 1996; SIMS et al. 1999; SCHÖNENBERGER et al. 2001), and by additional SEM and TEM investigations of dispersed material.

Therefore we try to present some of the *Normapolles* taxa of Gmünd by LM and two SEM pictures in a reasonable, sufficient optical resolution.

We follow in naming the recent literature, to avoid confusion (the different naming, e. g., *Plicapollis* and *Pseudoplicapollis,* may describe - at least in our view - the same genus).

Plate 7 (opposite page): **1-3** *Complexiopollis* sp. **1** Whole grain, polar view, LM. **2** Whole grain, polar view, SEM. **3** Detail of grain, SEM. **4-6** *Interporopollenites* sp. **4** Whole grain, polar view, LM. **5** Whole grain, polar view, SEM. **6** Detail of grain, SEM. **7-9** *Oculopollis* sp. 2. **7** Whole grain, polar view, LM. **8** Whole grain, polar view, SEM. **9** Detail of grain, SEM. **10-12** *Plicapollis* sp. 2. **10** Whole grain, polar view, LM. **11** Whole grain, polar view, SEM. **12** Detail of grain, SEM. **13-15** *Gmuendipollis teppneri* nov. gen., nov. spec. **13** Whole grain, polar view, LM. **14** Whole grain, polar view, SEM. **15** Detail of grain, SEM.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Oculopollis PFLUG 1953b

Oculopollis sp. 1 (Plate 6/1-3)

Oblate, in polar view triangular, diameter 20-22 µm. Tricolporate (ectoapertures: short colpi), apertures extremely thickened, thickenings strongly elongate towards the polar regions (Plate 6/1-2). Perforate, microspines (Plate 6/3).

Oculopollis sp. 2 (Plate 7/7-9)

Oblate, convex triangular in polar view. Tricolporate (ectoapertures: short colpi). Equatorial diameter 10-12 µm. Ornamentation minutely echinate, perforate (Plate 7/8-9). Aperture thickened, with a small atrium between sexine and nexine (Plate 7/7).

Plicapollis PFLUG 1953

Plicapollis sp. 1 (Plate 6/4-6)

Oblate, in polar view triangular, equatorial diameter 15-17 µm. Tricolporate (ectoapertures: short colpi). Aperture areas slightly thickened, with clear, well defined atrium (Plate 6/4). Ornamentation: verrucate as seen in lower magnitude SEM micrographs, with isolated microspines as a suprasculpture seen at higher magnifications (Plate 6/6).

Plicapollis sp. 2 (Plate 7/10-12)

Oblate, convex triangular in polar view. Tricolporate. Aperture areas slightly thickened, prominent atrium between sexine and nexine (Plate 7/10). Equatorial diameter 17-19 µm. Ornamentation: clearly isolated microspines (Plate 7/11-12).

Comments: Deviates from *Plicapollis* 1 by the lack of verrucae.

Neotriangulipollis GOCZAN, GROOT & KRUTZSCH 1976

Neotriangulipollis sp. (Plate 6/7-9)

Oblate, in polar view triangular, diameter 15-17 µm. Tricolporate (ectoapertures: short colpi). Aperture areas unthickened. Ornamentation microspines (Plate 6/9).

Comments: Ornamentation resembles extant *Juglandaceae*.

Trudopollis PFLUG 1953

Trudopollis hemiperfectus PFLUG (Plate 6/10-12)

Oblate, in polar view triangular, equatorial diameter 22-25 µm. Tricolporate (ectoapertures: short colpi). Aperture areas thickened, atrium between sexine and nexine (Plate 6/10). Ornamentation verrucae, microspines (Plate 6/11-12).

Extratriporopollenites PFLUG 1952

Extratriporopollenites sp. (Plate 6/13-15)

Oblate, in polar view triangular, equatorial diameter 20-23 µm. Tricolporate (ectoapertures: short colpi) with prominent "annuli", atrium between sexine and nexine (Plate 6/13-14). Ornamentation perforate, sculptured verrucate, except of annuli, which are only slightly sculptured (Plate 6/14-15).

Complexiopollis (KRUTZSCH 1959) TSCHUDY 1973

Complexiopollis sp. (Plate 7/1-3)

Oblate, in polar view concave triangular. Equatorial diameter 15-20 µm. Tricolporate (Ectoapertures: short Colpi), atrium between sexine and nexine (Plate 7/1). Ornamentation: perforated, minutely echinate. Microspines clearly separated from each other (Plate 7/3). Three thinned regions of the intercolpi in the equatorial area (Plate 7/2).

Interporopollenites WEYLAND & KRIEGER 1953

Interporopollenites sp. (Plate 7/4-6)

Oblate, in polar view convex triangular. Hexaporate, with prominent apertures. Apertures not circular, but slightly elongate. Diameter 15-18 µm. Pores not exactly equatorially located, but shifted: the mouth of the apertures is parallel to the polar axis, and more or less rectangular to the equatorial plane. With three thinned regions in the equatorial area, and two in the polar regions (Plate 7/5). Ornamentation minutely echinate, extremely perforate, aperture membrane perforated (Plate 7/6).

Gmuendipollis gen. nov.

Etymology: The name *Gmuendipollis* refers to the locality Gmünd, Lower Austria.

Generic diagnosis: Oblate, in polar view rhomboidal. Aperture: hexacolpate, four of them in equatorial plane, the two others in the respective polar areas, and oriented perpendicular (Plate 7/13-14). Equatorial diameter 15-18 µm. Ornamentation semitectate microreticulate, heterobrochate. Brochi triangular to polygonal (Plate 7/15).

Gmuendipollis teppneri sp. nov. (Plate 7/13-15)

Etymology: The name *teppneri* refers to the renowned botanist Dr. Herwig Teppner.

Holotype: Plate 7/13-15.

Type locality: Gmünd/Lower Austria.

Type stratum: Gmünd beds.

Stratigraphic position: Upper Cretaceous, probably Middle to Upper Santonian.

Specific diagnosis: Oblate, in polar view rhomboidal. Aperture: hexacolpate, four of them in equatorial plane, the two others in the respective polar areas, and oriented perpendicular (Plate 7/13-14). Equatorial diameter 15-18 µm. Ornamentation semitectate microreticulate, heterobrochate. Brochi triangular to polygonal (Plate 7/15).

Comments: WARD (1986) described a pollen type *Tricolpites fragosus* (hexarugate form) with the same type of arrangement of colpi. However, this pollen type has a completely different ornamentation.

T e t r a d s

Aachenipollis aachenensis (KRUTZSCH 1970) ZETTER & HESSE emend.

Plate 8/1-15 (REMs) and Plate 2/1-4 (TEMs).

We agree with the description of *Aachenipollis aachenenis* by KRUTZSCH, but we emend his diagnosis, because we additionally have so many ultrastructurally supported characters.

The tetrahedral tetrads have a diameter of 25-35 µm and are clavate (Plate 8/3). The monads have a distal aperture and a diameter of c. 15-20 µm. TEM sections reveal a massive basal layer lacking any differentiation in electron density or separation into sublayers, but with remarkable variation in thickness: laterally up to c. 1.3 µm thick, proximally c. 0.5 µm, distally becoming very thin around the aperture area (Plate 9/1). Upon the undifferentiated basal layer clavae are found (Plate 8/4), while a tectum is completely missing (atectate). Near the aperture region the pollen wall thickness is reduced, and also proximally (Plate 9/1, 3), while in the equatorial area the exine thickness increases (Plate 9/1, 3). LM and SEM show a variable sulcus, ranging from slit-like to widely opened.

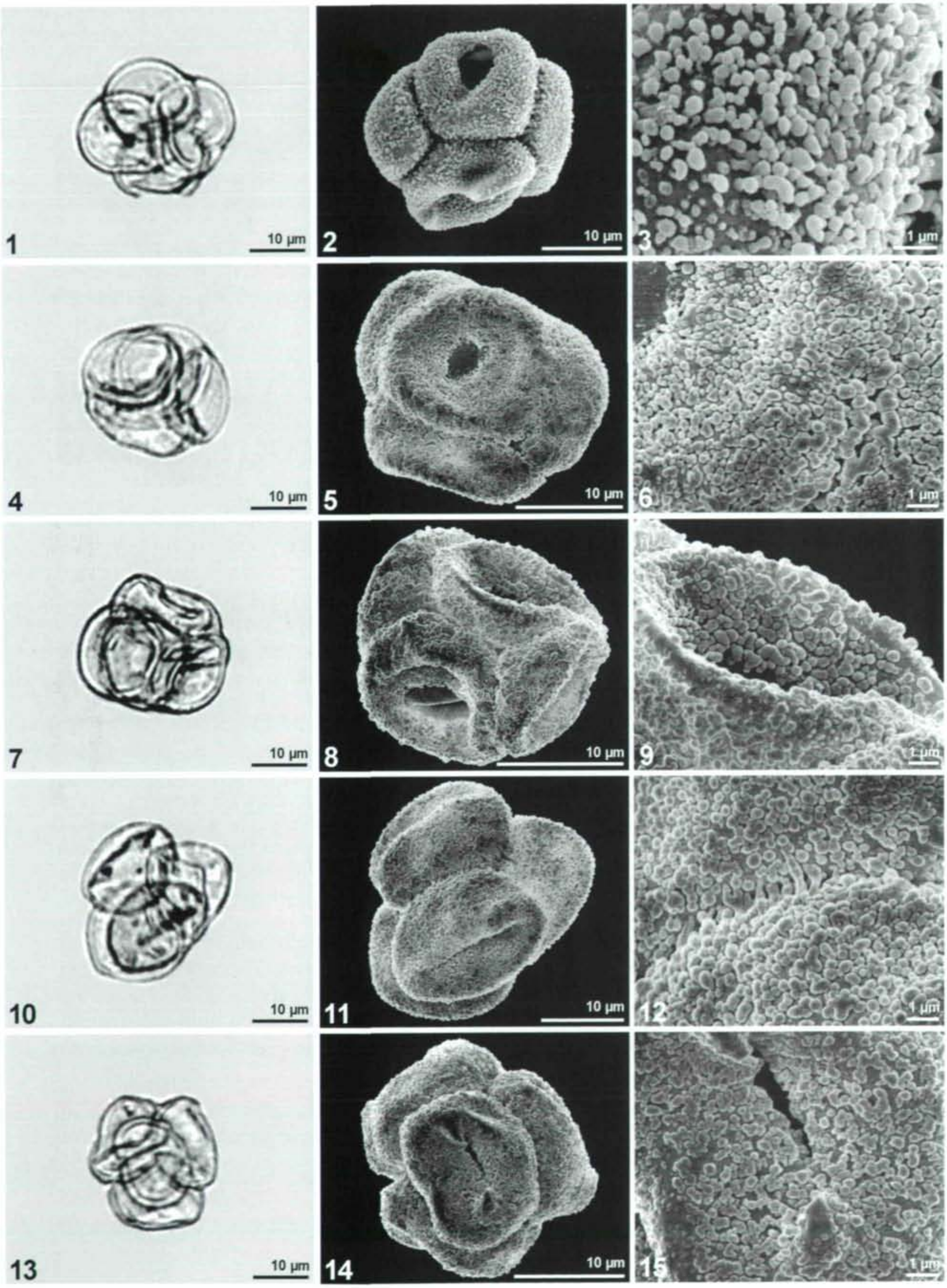
The ornamentation is characterized by a remarkable differentiation in dimension and shape of the capita of clavae (Plate 8/3, 6), and the variable distance in between clavae (Plate 8/3): towards the distal pole of an individual monad the clavae get shorter and more distant. The monads (within the tetrads) are often separated from each other by enlarged capita and simultaneously connected by tectal strings (Plate 8/12) like the monads of *Typha* tetrads. Sometimes isolated monads are found.

Comments: The botanical affinity is unknown. KRUTZSCH described this tetrad type in 1970 from Aachen, basal layers (?) Campan. KNOBLOCH (1997) noted that some megaspores, seeds and fruits of South Bohemian Klikov Formation are similar or identical with the taxa from Aachen.

Discussion

For the characterization of a fossil microflora, it is necessary to do both a qualitative (systematic examination) and a quantitative (point counting) analysis of the microfloral elements to receive crucial information about the distribution of floral elements in a particular facies (sedimentary and organic facies). High precision counting of microfloral elements can be obtained by using the SEM (for details see chapter material and methods).

Plate 8 (opposite page): 1-15 *Aachenipollis aachenii*. See text for explanation and details! 1, 4, 7, 10, and 13: whole tetrads, LM. 2, 5, 8, 11, and 14: whole tetrads, SEM. 3, 6, 9, 12, and 15: details, SEM.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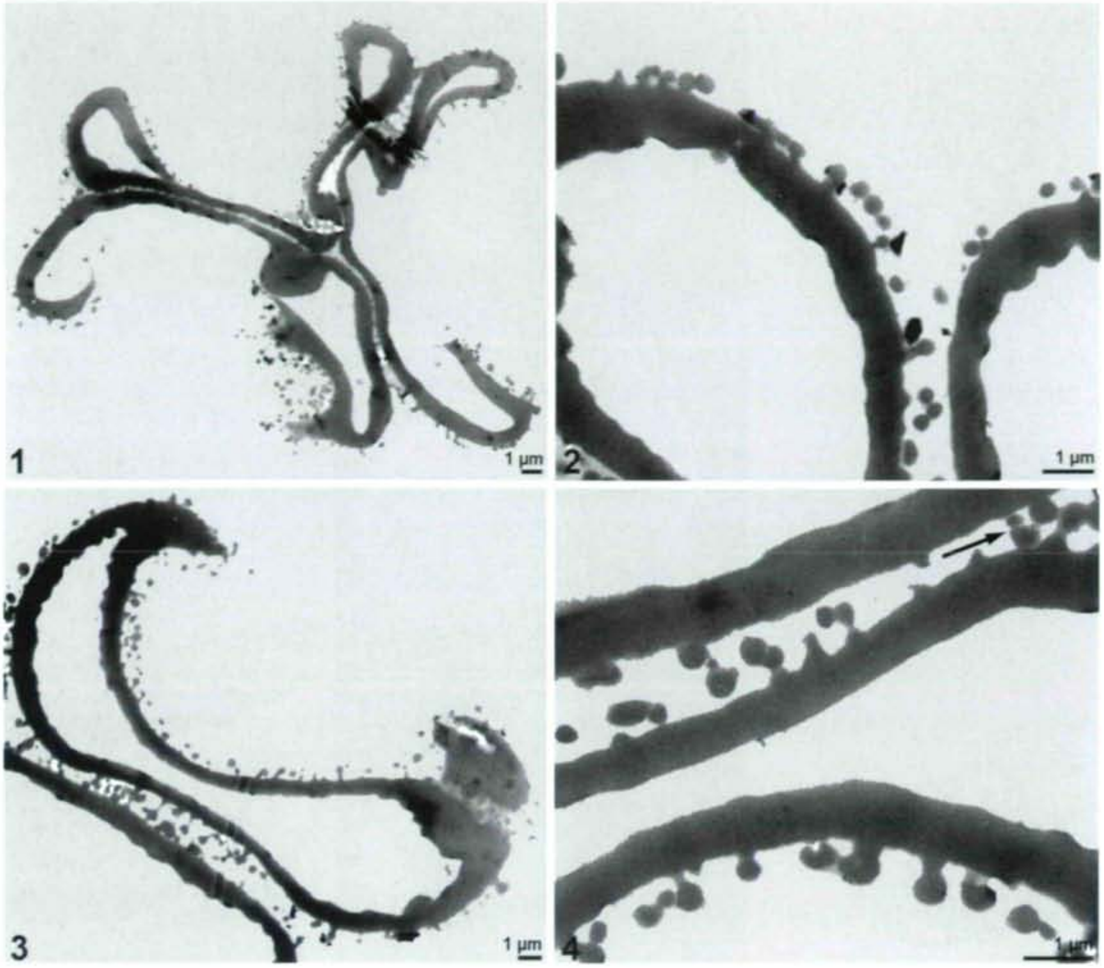

Plate 9: **1-4** *Aachenipollis aachenii*, TEM. **1** Cross section through whole tetrad. Stain: modified Thiéry test. **2** Detail of adjacent monads, proximal area. Stain: modified Thiéry test. **3** Cross section of a monad. Note large distal aperture area. Stain: Uranyl acetate and lead citrate. **4** Above: Details of two monads connected with strings (arrow), and part of a distal aperture area (below). Stain: modified Thiéry test.

The microflora of Gmünd includes spores of mosses and pteridophytes (30%), which show an astonishing high diversity (25 taxa). Beside different liverworth spores (3) and *Sphagnum* spores, *Gleicheniaceae*, *Pteridaceae*, different (5) *Schizaeaceae*, *Selaginellaceae* and *Lycopodiaceae* represent the Pteridophytes. Within the gymnosperms (10%) the formgenus *Auraucariacidites* dominates, saccate gymnosperm (*Pinus* sp.), *Taxodiaceae* and *Cycadaceae* pollen are rare.

Angiosperm pollen (60%) in a high diversity (65 taxa) dominate the microflora of Gmünd, similar to many other late Cretaceous microfloras of the *Normapolles* province (e. g., PACLTOVA 1981; WARD 1986).

Within the angiosperms, the sulcate types (sulcates) (five *Clavatipollenites* types and four monosulcate types) are represented by 15%. The sulcate types may belong to many basal Angiosperm groups or to the monocots. It can be expected that further investigations of mesofloras reveal details, that provide information for better assignments. Concerning the form genus *Liliacidites* (see Plate 4/10-12) the problematic assignment of dispersed pollen grains to special taxonomic groups can be shown. According to DOYLE (1973) and MULLER (1981) *Liliacidites* types are known to be valid as the earliest monocot pollen. This idea is now challenged by GANDOLFO et al. (2000).

Using the combination of LM and the SEM high resolution there is great potential to differentiate several *Clavatipollenites* types from dispersed material (see Plate 3/1-15). Similar results are mentioned by CHAPMAN (1987), CHLONOVA & SUROVA (1988) and FRIIS et al. (1999). *Clavatipollenites* types from Gmünd display many characteristics of *Chloranthaceae* pollen grains. Data from Early Cretaceous mesofloras of Portugal confirm the view that pollen of *Clavatipollenites* complex can be related to *Chloranthaceae* (FRIIS et al. 1999).

A further example for the importance of combined LM-SEM investigation on dispersed pollen material can be shown in the *Monocolpopollenites* group. Only little differences between *Monocolpopollenites* sp. 1 (Plate 4/1-3) and *Monocolpopollenites* sp. 3 (Plate 4/7-9) can be recognized under LM.

With SEM a completely different ornamentation of the two pollen surfaces can be shown. This might be well the case in many pollen types, even if the SEM examination does not allow an assignment to a particular plant taxon, at least this method allows a better differentiation of pollen types and therefore contributes greatly to the comprehension of taxa diversity versus taxa variation.

A peculiarity of the Gmünd microflora is the relatively frequent occurrence of a particular tetrad type (*Aachenipollis aachenensis*, representing 16% of angiosperm pollen grains).

This tetrahedral tetrad shows several uncommon features. The tectum is lacking and the clavae protrude from a compact, rather thick basal layer, that lacks any differentiation. At the proximal side the elongated clavae interconnect the monads and add mechanical stability to the tetrad. Distally the basal layer gets thin quickly near the aperture area, and it is suggested that such extremely thin parts may have been lost during fossilization. This fragile border of the distal exine may give rise to the sometimes large aperture. The presence of clavae is a rare feature, particularly in basal angiosperms (SAMPSON 2000a) and in monocots; even in eudicots it is not at all common.

A search for similar tetrad types ended without results: there are no recent similar types (for review, e. g., KNOX & MCCHONCHIE 1986; or SAMPSON 2000b), and to our knowledge there is no modern equivalent of our cretaceous tetrahedral tetrad type. In LM the tetrads of *Walkeripollis gabonensis* (DOYLE et al. 1990) and *Hedycaria angustifolia* (*Monimiaceae*) look similar to our tetrads (SHIMELD 2001). But in SEM and TEM sections they show no similarities. According to SAMPSON (1977) and JÉRÉMIE et al. (1984) the tetragonal (not tetrahedral!) *Hedycarya angustifolia, H. arborea* and *Kibariopsis caledonica* tetrads are characterized in TEM sections by a tectum and an infratectum (papillose elongations of the tectum sensu SAMPSON 1977). A basal layer is missing, and also the proximal tetrad connections are dissimilar to our tetrad type. The connections are much narrower and more rare, and therefore the tetrad may be less strong. This characters (seen only in TEM sections) demonstrate again clearly the importance of TEM application.

We conclude particularly from the aperture type that our tetrads derive from an extinct basal angiosperm or a monocot parent plant, but because of the general lack of pollen types with distally oriented apertures not from eudicots.

The *Normapolles* group dominates (37%) as in many other Late Cretaceous microfloras within the angiosperm pollen types. The *Normapolles* group is a morphologically diverse complex of Late Cretaceous and Paleogene angiosperm pollen, with relatively numerous taxa (SIMS et al. 1999). The reason for the often high percentages of *Normapolles* pollen (e. g., PACLTOVA 1961 and 1981 described samples with more than 60% *Normapolles* from South Bohemia, Czech Republic) can be explained that many of the *Normapolles* plants were wind pollinated (SIMS et al. 1999; SCHÖNENBERGER and FRIIS 2001), and consequently, because of higher pollen production in wind pollinated plants, a lot of *Normapolles* pollen was embedded in sediments. Additionally, it is assumed, that some of the *Normapolles* pollen producing plants comprised a significant part of the vegetation near deposition site (azonal).

Numerous genera within the *Normapolles* complex (about 80) have been described by various authors (see BATTEN & CHRISTOPHER 1981). But there are considerable problems with the delimitation of genera and species (e. g., SKARBY 1968; BATTEN 1989, 1996). Most of the genera have been described only on the base of LM investigations, where the enormous range in variation is impossible to recognize. Consequently it is difficult to decide, which characters of *Normapolles* pollen are diagnostically significant (e. g., SKARBY 1968; BATTEN 1989) and which not.

The Gmünd microflora contains about 20 different taxa of *Normapolles*. We have chosen 9 taxa to provide detailed information about micro-morphological structure (see chapter about systematics and Plate 6/1-15, Plate 7/1-12). All chosen taxa show affinities to extant Juglandales and Myricales with the exception of *Interporopollenites* sp. The particular characters of this taxon are thinnings of the exine: three in between the six subequatorial rounded or triangular to polygonal exoapertures, and one thinning at each pole. The pollen grain surface displays numerous perforations between the microspines. FRIIS & PEDERSEN (1996) described similar pollen grains from minute staminate, as well as, pistillate flowers born on elongated inflorescence axes.

The type *Plicapollis* sp. 1 (Plate 6/4-6) is comparable (rugulate to verrucate sculpture with microspines as suprasculpture) with the pollen of the so-called *Manningia* flowers. In contrast the type *Plicapollis* sp. 2, which looks under LM quite similar to *Plicapollis* sp. 1, displays under SEM a considerable different sculpturing (Plate 7/10-12).

The Tricolpates or Tricolporoidates of the Gmünd microflora are represented by about 15 taxa, despite the relative high diversity, only 4 taxa are described in this paper (Plate 5/1-15). Two taxa, *Tricolpopollenites* sp. 1 and *Tricolpopollenites* sp. 3 are known from flowers of a mesoflora from Southern Sweden (Santonian-Campanien). *Tricolpopollenites* sp. 1 is well comparable to pollen grains of the fossil flower *Actinocalyx bohrii* (FRIIS & PEDERSEN 1996) but also to those of *Paradinandra suecica* (SCHÖNENBERGER & FRIIS 2001, figs. 24-27).

Tricolporopollenites sp. 3 is identical with the pollen grains from *Platananthus scanicus* flowers (FRIIS & PEDERSEN 1996).

The new species *Gmuendipollis teppneri* is characterized by a conspicuous distribution and arrangement of the apertures: a pericolpate arrangement in the present form is quite rare, also in modern taxa. However, we are uncertain if the two colpi at the polar areas, that are arranged perpendicular to each other (Plate 7/13, 14), may be in fact pseudocolpi. A principal similar aperture arrangement was described by WARD (1986) in text-fig. 6 and (Plate 15/6-7) for a pollen type (*Tricolpites fragosus* - hexarugate pollen form), however, the ornamentation of this pollen differs strongly from our specimen.

The information obtained from the diverse microflora of Gmünd suggests a humid subtropical to warm-temperate climate.

Acknowledgements

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