New aspects of the palynoflora of the lowermost Eocene (Krappfeld Area, Carinthia)

Reinhard ZETTER, Christa-Charlotte HOFMANN

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Abstract: Ongoing investigations of fine-grained samples from the Krappfeld area (Carinthia) have revealed at least seven new taxa and broadened our understanding of early Cenozoic terrestrial vegetation and vegetation dynamics. Palynomorph assemblages are species rich, particularly in Arecaceae, and display diverse taxa compositions. Light and scanning electron microscope examinations indicate many of the palynotaxa might be affiliated to genera/families that exist today under warm to tropical (paratropical) climates (Araceae, Arecaceae, Alangiaceae, Anacardiaceae, Bombacaceae, Burseraceae, Celastraceae, Chloranthaceae, Elaeocarpaceae, Gleicheniaceae, Icacinaceae, Mastixiaceae, Meliaceae, Moraceae, Nyctaginaceae, Olacaceae, Rhamnaceae, Rutaceae, Sapindaceae, Sapotaceae, Schizaeaceae, Sterculiaceae, Symplocaceae, Thymelaceae, Vitaceae etc.). Additionally, the mechanisms of pollination and diaspore dispersal are discussed in terms of vegetation dynamics. The species diversity and composition of the Krappfeld flora reflects the terrestrial response to the Eocene Thermal Maximum (ETM) recorded in marine sediments. The systematic work concentrates on the examination of the diverse and abundant Arecaceae (palms) and a newly discovered form of Araceae.

Zusammenfassung: Die weiterführenden palynologischen Untersuchungen der feinkörnigen Sedimente des Krappfeldes in Kärnten ergaben sieben neue Taxa und einen weiteren Einblick in die känozoische Vegetationsentwicklung. Die Palynomorphen-Vergesellschaftungen sind artenreich und besonders durch verschiedene Taxa aus den Arecaceae gekennzeichnet. Lichtmikroskopische und rasterelektronenmikroskopische Untersuchungen ergaben, daß zahlreiche der Taxa modernen Gattungen und Familien zugeordnet werden können, die heute in warmen bis tropischen Klima (paratropisch) gedeihen (Araceae, Arecaceae, Alangiaceae, Anacardiaceae, Bombacaceae, Burseraceae, Celastraceae, Chloranthaceae, Elaeocarpaceae, Gleicheniaceae, Icacinaceae, Mastixiaceae, Meliaceae, Moraceae, Nyctaginaceae, Olacaceae, Rhamnaceae, Rutaceae, Sapindaceae, Sapotaceae, Schizaeaceae, Sterculiaceae, Symplocaceae, Thymelaceae, Vitaceae u.v.m.). Es werden zusätzlich die Bestäubungsmechanismen und die Frucht und Samenverbreitung diskutiert, die einen Einblick in die damalige Vegetationsdynamik geben sollen. Der Artenreichtum und die Zusammensetzung der Krappfeldflora steht im engen Zusammenhang mit dem in marinen Sedimenten nachgewiesenen Eozänen Temperatur Maximum (ETM).

Keywords: Palynology, Arecaceae, Araceae, Paratropical, ETM, SEM

Institut für Paläontologie, Althanstrasse 14, A-1090 Wien, E-mail: reinhard.zetter@univie.ac.at, christa.hofmann@univie.at.ac

Contents

1. INTRODUCTION

The first palynological studies of the Paleogene sedimentary rocks of the Krappfeld area and isolated localities from the Karawanken mountains in Austria were done by Frutos (1968) and Zetter & Hesse (1995). A more detailed examination of samples from the Winkler Member in Pemberg quarry (Krappfeld) was carried out by Hofmann & Zetter (in press), this being the first of a series of papers dealing with the very diverse palynoflora. Hofmann & Zetter (in press) systematically described only a small part of the flora (20 taxa), because of the restricted number of photographic plates available.

In this paper, the results from the Winkler Member were re-examined and combined with data from the recently investigated contemporaneous Höhenwirt Member. The aim was to establish a more complete palynoflora and therefore to gain a better understanding of vegetation dynamics and development during the Paleogene. To make an approximation of the palaeovegetation and palaeoclimate, it is important to affiliate the taxa to modern families or genera, whenever possible. Dynamic processes, such as fruit and seed (diaspore) dispersal or pollination mechanisms of ancient vegetations can be only inferred if the affinities to modern taxa are well understood/connected. This work is, therefore, based only on the use of the light microscope, but also on scanning electron microscope investigations, which enables a much more precise identification. In this paper, the systematic descriptions and photographic plates concentrate on the monocotyledones (Arecaceae and Araceae) for no other reason than to get another part of the diverse palynoflora described and photographed; this emphasis, however, has nothing to do with the overall aim of the paper.

2. STUDY AREA

The more or less contemporaneous samples investigated were collected from the Winkler Member exposed in a quarry 200 m SW of Pemberg, a small village near Sittenberg

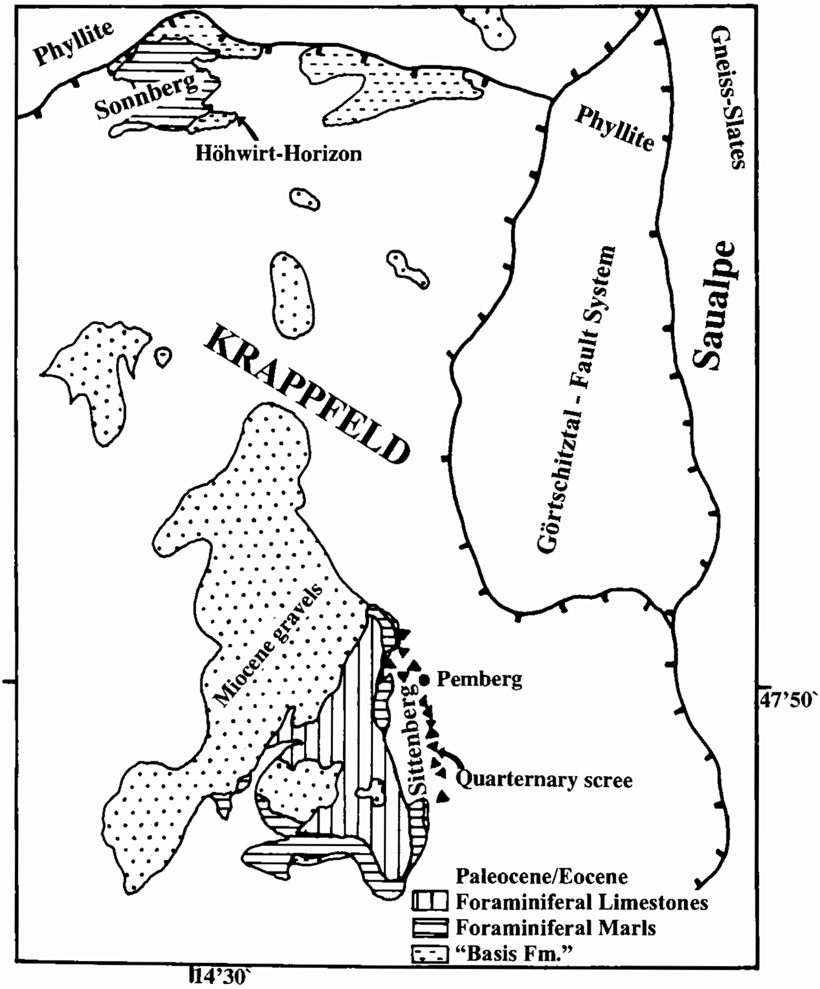

Fig. 1: Sketch of the Krappfeld area with sample localities (strongly modified after WILKENS, 1989).

hill, and also from the Höhenwirt Member at Sonnberg hill. Both localities are situated in the Krappfeld area, lying in northeastern Carinthia, 30 km NNE of Klagenfurt and the Klagenfurt basin (Fig. 1), which is characterized by Upper Cretaceous and 53 to 51 Ma old Paleogene rocks (NP zone 11/12). Samples were taken from the coal-bearing Basis Formation (including the Höhenwirt Member) of the Krappfeld sedimentary succession, which represents the interplay of shallow marine carbonates, marls and marine siliciclastic sediments with fluvial to deltaic deposits consisting of gravelly sandstones, mudstones and bituminous mudstones. The latter has two intercalated discontinuous small-scale coal seams of sub-bituminous A rank (Wilkens, 1985; 1989). The pollen bearing horizons are located between and around the two coal seams. The thickness and lateral continuity of the Basis Formation varies considerably from outcrop to outcrop, due to the palaeorelief (Wilkens, 1989).

The Palaeocene/Eocene sedimentary rocks of the Krappfeld, which form the most southern early Tertiary deposits of Austria (Wilkens, 1989), are confined to small-scale erosional relicts within the southern intra-Alpine Gosau basin (Faupl et al., 1987; Wagreich & Faupl, 1994; Oberhauser, 1995) and can be compared with the Paleogene of northern Italy, Croatia, Slovenia and Yugoslavia. Wilkens (1985, 1989) equates the Krappfeld Palaeogene with other Mediterranean Tethyan sedimentary deposits.

The palaeogeographic position of the Krappfeld area during Palaeocene/Eocene times is not certain, but it is assumed to have been situated at the northern margin of a southerly positioned landmass. During the Maastrichtian large-scale regression, marine sedimentation came to a stillstand and was finally capped by erosion, producing a hiatus. The following Eocene transgression lead to the development of barrier reefs fringing the southern landmass; these are now preserved as reefal limestones in the Northern Calcareous Alps (Oberhauser, 1995). The evolution of the disconformably overlying Paleogene succession was then controlled by short-term transgressive-regressive cycles, which led to the interlayered terrestrial and marine sediments typical of the Basis Formation. The carbonate rocks in this unit are well known for their macro-foraminifera (Wilkens, 1985, 1989) of Ypresian age, overlain by coralline algal limestones of Ypresian to Lutetian age (Rasser, 1994).

3. METHODS

Sample preparation followed the standard treatment, involving crushing the sample with mortar and pestle to a relatively coarse powder. In order to retain the palynomorphs smaller than 10 µm diameter, the rock powder was neither washed nor sieved. The powder was then treated with standard wet chemical processes, using HCl and HF, followed by acetolysis. The extract derived was mixed with few drops of glycerine and stored in small glass bottles. For examination, a drop of the extract was transferred to a glass slide, mixed with additional glycerine if necessary, and smeared into a narrow band. Light microscope (LM) investigation and palynomorph counting was carried out with a LM, in which the field of view is not optically reversed (Zetter, 1989) and without a coverslip. This allowed palynomorphs to be turned and moved around with a micromanipulator (a hair mounted on a preparation needle) to obtain the optimal positions for identification and photography, and further, with the help of the hair, palynomorphs were transferred to scanning electron microscope (SEM) stubs. Excess glycerine on the SEM stub was carefully washed away with absolute ethanol to prevent micro-morphological pollen wall features from being smeared over. The stubs were sputter coated with gold, followed by SEM analysis and photography. Clear and reliable distinction of the characteristics of pollen requires a combination of LM and SEM analyses, particularly when dealing with monocotyledons. Palynomorphs figured in the plates are represented by at least one LM image, an SEM overview image and a high magnification SEM image showing the tectum surface, with all the images taken from the same grain. The material is stored in the Institute of Palaeontology under the numbers Krapp2/87/1–35.

4. RESULTS

The palynomorph content of the Krappfeld area is shown in Table 1; whenever possible, this table also summarises the inferred pollination and diaspore dispersal mechanisms, temperature affinities, whether the plant was evergreen or deciduous and the presumed life form of the modern equivalents. Due to page limitations, the systematic descriptions and photographic plates consider only a part (monocotyledons, Arecaceae and Araceae) of the diverse Krappfeld microflora.

4.1. Organic facies

The organic facies of the Höhenwirt Member samples are characterized by more dinoflagellate cysts (3%), *Botryococcus* algal colonies (11%) and algal cysts of unknown origin (1%) than the organic facies of Sittenberg samples. Minor amounts of foraminifer linings (1%) occur in all samples and many palynomorphs (algal and higher plant origin) are filled with authigenic pyrite crystals; all the sediment samples have a pungent sulphurous smell. Bituminous material in the extracts result in bitumen smears when dispersing extracted material on the slide. The smears develop from heavily degraded organic matter, particularly heterogeneous amorphous organic matter (AOM, 10%), which is thought to be the relicts of *Botryococcus* colonies and other algal remains. This is corroborated by the occurrence of bituminous mudstones at the other Krappfeld locality at Sittenberg (Hofmann & Zetter, in press).

4.2. Palynomorphs

The quality of palynomorph preservation is generally excellent and the three dimensional shape is often preserved. However, corroded grains, reworked from older sedimentary rocks (presumed Cretaceous), such as Cretaceous *Normapolles* type pollen, with very rough and abraded surfaces, as well as pyritized palynomorphs, occur frequently. The surfaces of many Araceae pollen display regular roundish feeding traces, and the grains are often separated into halves along their zona-apertures; less than 30% are complete.

Abundant occurrences in the palynomorph assemblage are characterized by Arecaceae, such as *Nypa, Calamus* type, *Daemonorops,* a ?*Salacca affinis* type, two not fully determined Calamae, and several not yet fully determined genera. Also very common are the Araceae *Proxapertites operculatus* Van der Hammen 1956, *Myrica* in two different

family	genus	number of types	abunance	pollination mode	diaspore dispersal	megathermal	mesothermal	microthermal	no preference	evergreen/ deciduous	occurrence	life form
Ferns and Bryophhytes												
Sphagnaceae	*Sphagnum*		x	A/m					x		cosmo.	m
Polypodiaceae s.l.	indet.	4	xx	A/m					x		cosmo.	
Schizaeaceae	*Anemia*		x	A/m		x					neo/pantrop	
	Lygodium		x	A/m			x				pantrop.	cf
	Schizaea		x	A/m		x	x				pantrop.	
	indet.	2	x			x	x					
Pteridaceae s.l.	*Acrostichium*		x	A/m		x	x				pantrop	sf
	indet.	2	x						x			
Osmundaceae	*Osmunda*		x	A/m			x				pansubtrop.	sf
Gleicheniaceae	*Gleichenia* types	2	x	A/m		x					pantrop.	cf
indet.	forms	4	xx	A/m								
Gymnosperms												
Gnetaceae	*Ephedra*		x	A			x			ev	north. hem.	s
Pinaceae	*Cathaya*		x	A	wi/an		x			ev	China	t
	Pinus		x	A	wi/an		x	x		ev	north. hem.	t
Angiosperms:												
dicotyledones												
Alangiaceae	*Alangium*		x	E	an	x					paltrop.	s/t
Anacardiaceae	*?Campnosperma/*											
	Poupartia		x	E	an	x				ev	pantrop.	t
	Lannea		x	E	an	x				ev	paltrop.	t
	Spondias		x	E	an	x				ev	pantrop.	t
	indet.		xx			x	x					
Annonaceae	indet.		x	E	an	x	x			ev	pan/paltrop.	s/t
Apiaceae	indet.		x	E	wi/an		x	x			cosmo.	h
Aquifoliaceae	*Ilex*	2	xx	E	an	x	x			ev/de	subcosmo.	s
Araliaceae	indet.		x		an	x	x			ev	cosmo.	s/l
Avicenniaceae	*Avicennia*		x	E	wa/an	x	x			ev	pantrop.	t
Betulaceae	*Alnus*		x	A	wi		x	x		de	north. hem.	s/t
? Burseraceae+	*Brosipollis*		x			x						
Celastraceae	indet.		x		wi	x	x			ev/de	pansubtrop.	s/l
Chloranthaceae	*Hedyosmum*		x	A	wi	x	x				amphipac.	s
Cornaceae	*Cornus* type		x	E	an		x	x		de/ev	north. hem.	s
Elaeocarpaceae	*Elaeocarpus*		x	E	an/wa	x				ev	paltrop.	t/s
Ericaceae	indet.		x	A	an				x	ev	cosmo.	s
Eucommiaceae	*Eucommia*		x	A	wi?		x			de	China	t
Euphorbiaceae	indet.		x	E		x	x					
Fabaceae	*Cassia* type		x	E	an/wa	x	x				pantrop.	s/t
	indet.		x	E					x			
Fagaceae	*Lithocarpus*		xxx	A	an	x	x			ev	Indomalesia	s/t

Tab. 1 (for explanation see p. 480).

family	genus	number of types	abunance	pollination mode	diaspore dispersal	megathermal	mesothermal	microthermal	no preference	evergreen/ deciduous	occurrence	life form
	Quercus (evergreen)		x	A	an		x			ev	north. hem.	t/s
Fagaceae+	'trigonobalanoids'	3	x	A	an							
Hamamelidaceae	*Tetrathyrium* type		x	A	an?		x			ev	Hong Kong	s/t
Juglandaceae	*Engelhardia* types	3	xx	A	wi		x			de	E & SE Asia	t
	Platycarya types	2	xx	A	wi		x			de	China	t
Juglandaceae+	*Plicatopollis*	2	x	A	wi							
	Subtriporopollenites		x	A	an?							
	Interporopoll.											
	supplingensis		x	A	an?							
Icacinaceae	*Iodes* types	2	xx	E	an	x	x			ev	paltrop.	s/l
	indet.		x	E	an	x	x				paltrop.	s/l
Loranthaceae	indet.		x	A	an	x	x			ev	south. hem.?	e
Mastixiaceae	*Mastixia*		x	E	an	x	x			ev/de	paltrop.	s/t
Malvales s.l.	Bombacoid type		x	E*	an	x				de/ev	pantrop.	t
	?Kostermansia type		x	E*	an	x				de/ev?	paltrop	t
	Sterculioid types	2	x	E	an	x	x			de/ev	pantrop.	t
	?Leptonychia type		x	E	an	x				ev	paltrop	t
	Reveesia type		x	E	an		x			ev	China	t
	Tilioid types	2	x	E	wi	x	x			de/ev	subcosmo.	t
Meliaceae	*Aglaia* type		x	E	an/wa	x				ev/de	Indomalesia	t
Moraceae	indet.	2	x	E	an	x	x			ev/de	pansubtrop.	t
Myricaceae	*Myrica*	2	xxxx	A	an		x			ev	subcosmo.	s
Myrtaceae	indet.	2	x	A/E		x	x			ev	pansubtrop.	s/t
Nyctaginaceae	indet.		x	E		x					pantrop.	a
Nyssaceae	*?Nyssa* type		x	A	an		x			de	amphipac.	t
Olacaceae	*Anacolosa*		x	E	an	x				ev	paltrop.	s/l
	indet.		x			x						
Onagraceae	*Ludwigia*		x	E	wa		x				cosmo.	h
Platanaceae	*Platanus*		x	A	wi		x			de/ev	north. hem.	t
Rubiaceae	indet.		x						x		cosmo.	a
Rhamnacae	indet.		x	E	an?		x					t/s
Rutaceae	*Zanthoxylon*		x	E	an		x			de/ev	pansubtrop.	s/t
	indet.		x						x			a
Salicaceae	*Salix* type		x	A/E	wi			x		de	north. hem.	s/t
Sapindaceae	*Cupania* type		x	E	?	x				ev	S. Amer.	s/l
	Koelreutheria type		x	E	wi		x			de	Asia	t
Sapotaceae	*Palaquium* type		x	E*	an	x				ev	Asia	t
	indet.	3	xx	E*		x	x			ev		t
?Simaroubaceae+	Pentapollenites sp. 1		x			x						
Symplocaceae	*Symplocus*		x	E	an		x			ev	amphipac.	s/t
Thymelaceae	*Wikstroemia*		x	E	an		x			ev	SE Asia	s/t
Vitaceae	*Cissus/Parthenocissus*		x	E	an	x	x			ev/de	pantrop.	l

Tab. 1 (for explanation see p. 480).

family	genus	number of types	abunance	pollination mode	diaspore dispersal	megathermal	mesothermal	microthermal	no preference	evergreen/ deciduous	occurrence	life form
	Vitis		x	E	an	x	x			de	north. hem.	l
indet.												
	tricolporate reticulate form		x									
	small triang. tripor.big pores		x									
	Tricolporopoll. mansfeldensis		x									
	5-6 lobate form		x									
Angiosperms: monocotyledones												
Araceae-Monsterae	*Proxapertites operculatus*		xxx	E	an/wa?	x				ev		ch
	Daemonorops		x	E	an/wa	x				ev	paltrop.	pt/cp
	?Calamae	2	x	E		x				ev		pt/cp
	?Salacca affinis type		x	E	an	x				ev	paltrop.	
Arecaceae Nypoideae	*Nypa*		xx	E	an/wa	x				ev	paltrop.	sp
Arecac.Coryphoid/ Arecoid	*Arecipites*	6	xxx	E		x				ev		
Arecaceae-Arecoideae	*Monocolpopollenites*	2	xxx	E		x	x			ev		
?Commelinaceae	*indet.*		x	E		x	x				pansubtrop.	h
Restioniaceae	indet.		xxx				x				south. hem.	h
Sparganiaceae	*Sparganium*		x	A	wa				x		north. hem.	h
monocotyle indet.	indet.	3	xx						x			
Juglandac.-Myricac. aff.	*Normapolles* group	4	xxx									s/t?
indet	*Pentapollenites* sp. 2		xxx									
indet	*Plicapollis*		x									
indet.	*Stephanoporopollenites*		x									

Tab. 1: List and abundance (averaged: x = 0.5–1%, xx = 1–5%, xxx = 5–10%, xxxx = 10–20% of the total pollen sum) of all taxa occurring in the Krappfeld area, with deduced pollination mechanisms (A = anemophilous, E = entomophilous, E* = other animals) and diaspore dispersal (wi = wind, wa = water, an = animal), temperature affinities, life form (cf = climbing fern, sf = shrubby fern, m = moss, s = shrub, t = tree, l = liana, h = herb, ch = coarse herb, e = epiphyte, pt = palm tree, sp = shrubby palm, cp = climbing palm) and whether they are evergreen (ev) or deciduous (de) and the occurrence of their modern equivalents (cosmo. = cosmopolitical, subcosmo = cosmopolitical temperate to tropical, neo. = neotropial, pan = pantropical, pansubtrop. = pansubtropical, pal = palaeotropical, pansubtrop = pansubtropial, north. hem. = northern hemishere, south. hem. = southern hemisphere, amphipac = amphipacific, S Amer. = South America.

sizes (it is not clear if these represent different taxa or just variation), a range of Juglandaceae taxa, such as *Engelhardia* types, *Platycarya* types, a *Cyclocarya* type, *Plicatopollis* spp., and Fagaceae, such as *Lithocarpus*, and three extinct Fagaceae ('trigonobalanoids'), followed by *Ilex*, Sapotaceae and Anacardiaceae. The rich spore assemblage of ferns and fern allies is characterized by frequent occurrences of Schizaeaceae, such as *Anemia, Lygodium* and *Schizaea*, and of Polypodiaceae s.l. and *Acrostichium* (Table 1).

Taxa found which are new to the Krappfeld area are: *Avicennia* (Avicenniaceae) the black mangrove, one Annonaceae gen. indet., a few Arecaceae gen. indet. (? Calameae, Arecoideae), *Elaeocarpus* (Elaeocarpaceae), an evergreen *Quercus* (Fagaceae), and *Wikstroemia* (Thymelaceae).

4.3. Systematic description and remarks on the ecology

In all the Krappfeld samples, palms are one of the more dominant groups, with 14 taxa recognised to date. Several other forms look like typical palm pollen but are not easily affiliable, because a very high percentage of palm taxa and monocots, including Araceae, Commelinaceae, Liliaceae, Pontederiaceae, etc., produce relatively similar pollen morphologies (compare HARLEY, 1990; HARLEY & MORLEY, 1995). The not clearly affiliable pollen have been described under the formgenus *Monocolpopollenites* THOMPSON & PFLUG 1953 (2 types) and the collective term for fossil palm pollen Arecipites WODEHOUSE 1933 (6 types). The systematic treatment of Arecaceae follows UHL & DRANSFIELD (1987) and that of Araceae follows MAYO et al. (1997, 1998). However, it was difficult to compare the Krappfeld palm pollen types with the numerous fossil palm pollen types since these have only been illustrated by LM images in the literature. The descriptive pollen terminology follows PUNT et al. (1994). Botanical affinities of fossil pollen to modern taxa were based on LM and SEM analysis, but the description of wall thickness is based only on LM investigations, except for Pl. 3, Figs. 1–2. The affiliation to a modern genus has been given when the fossil pollen and modern comparative pollen were very similar (except for size; modern pollen are often, but not always, bigger) and was based on LM whole grain features and SEM micro-morphological details. If the affiliation to a taxon was not certain, the pollen type was accompanied with a question mark. The suffix 'type' behind a genus name means that the pollen type is very reminiscent of this genus. The term 'type' with a number does not necessarily mean that it represents a species.

Arecaceae

Nypoideae

Nypa sp. (Pl. 1, Figs. 1–12; Pl. 2, Figs. 1–10; Pl. 3, Figs. 1–5)

Spinizonocolpites MULLER

Description: Zonoaperturate, spheroidal to oblate pollen grain, 40–50 µm in diameter. The pollen are mostly separated into two halves and the margins are often enrolled (Pl. 1, Fig. 12; Pl. 2, Figs. 5 and 6). Exine thickness is ca. 1.5–2 µm; the sexine is thicker than the nexine under LM. Exine thickness can be well observed at broken walls under SEM and show that the tectum is 0.5–0.8 µm thick, the columellae are 0.8–1 µm thick, and the footlayer is 0.4 µm thick (Pl. 3, Figs. 1 and 2). The exine is tectate, perforate to microreticulate. The inner surface of the pollen wall is slightly rugulate (Pl. 3, Fig. 4). Supratectal spines are solid and in different shapes (pointed, blunt, knobbly) and sizes (2 to 10 µm long) (Pl. 1, Fig. 1–12; Pl. 2, Figs. 1–10; Pl. 3, Fig. 3).

Discussion: The fossil *Nypa* pollen is very similar to the modern *Nypa fruticans* pollen from the monotypic subfamily Nypoideae. *Nypa fruticans* prefers tidally influenced brackish waters and grows in small belts on clastic substrates along estuarine channels, rivers and lagoons, or produces extensive monotypic stands in the SE Asia and Pacific regions (TOMLINSON, 1994; UHL & DRANSFIELD, 1987). During the Palaeogene *Nypa* occurred pantropically (nearly all over the lower latitudes of the globe), growing in large, but often widely separated populations. *Spinizonocolpites echinatus* and *S. baculatus* are two forms described by MULLER (1968). Different spine shape (short and thick and long curved spines, or wart-like protrusions) was the reason for differentiation into the two taxa. That the fossil *Spinizonocolpites* might comprise more than one species was also suggested by HARLEY et al. (1991). They speculated that extant *Nypa fruticans* might be a relict species of an ancient more diverse genus, because the morphology of investigated recent *Nypa* pollen is notably more uniform than the morphology of dispersed *Spinizonocolpites*. Our examinations show many variations in both spine and other pollen micro-morphological details within a fossil *Nypa* pollen assemblage and single *Nypa* pollen grains (Pl. 1, Fig. 5; Pl. 2, Figs. 4 and 5). In our opinion, an assemblage of fossil *Nypa* pollen always represents a mixture of mature, immature and aberrant forms, thus displaying the whole pollen grain variations of the *Nypa*-population. A comparable degree in variability has been recognized in different fossil *Nypa* fruits from the London Clay by COLLINSON (1993), who analysed and compared them with the fruits of the extant monospecific *Nypa fruticans* and consequently, despite their variable appearance, lumped all fossil *Nypa* fruits into one taxon.

Calameae

Calamus type (Pl. 3, Figs. 6–15)

Dicolpopollis PFLANZL

Description: Disulcate pollen grain, ca. 20–25 µm in diameter. Wall thickness of 1.3–1.8 µm (meso-equatorial area); sexine thicker than nexine. Exine is semitectate, microreticulate to reticulate, heterobrochate; the apocolpium brochi are larger (reticulate) than the brochi in the equatorial area (microreticulate). The muri sometimes show perforations. Broad muri and areas were muri fuse are duplicolumellate; rudimentary columellar structures can be observed in the brochi. The sculpture is faintly striate.

Discussion: Disulcate pollen grains show the greatest affinities to the subtribe Calameae, particularly the genera *Calamus, Calospatha, Ceratolobus, Plectocomiopsis* and *Plectocomia* (HARLEY, pers. com.), most of them are climbing palms ('rattan palms'). The variability in shape and in the development of the reticulum of *Dicolpopollis* sp. could lead to the distinction of two taxa (Pl. 3, Figs. 6–15), but the sculpture on the muri (faint striations) let us assume that it might be a single, but variable taxon. *Calamus* as an example for the above-mentioned Calameae is an Old World tropical species rich genus (about 370 species), has a very wide ecological amplitude and is mainly restricted to seasonally controlled monsoon forests or primary rain forests, reaching from sea-level to mountainous areas (UHL & DRANSFIELD, 1987).

Calamae
Daemonorops BLUME (Pl. 4, Figs. 1–5)

? *Diporoconia iszkaszentgyoergyi* KEDVES

Description: Subequatorial diporate, ellipsoidal pollen grain, 38–45 μm in equatorial diameter. Exine is 1.4–1.6 μm thick; sexine is thicker than nexine, a thickening of the sexine can be observed in the aperture areas. Exine is tectate, perforate like an orange peel surface. Around the pores the tectum form an "annulus" which shows elongated perforations. The nexine extends beyond the tectum and form an inner rim.
Discussion: The fossil Krappfeld *Daemonorops* pollen is very similar in morphology (SEM) and size to those of extant *Daemonorops verticillaris* and *D. sparsifolia* depicted in FREDERIKSON et al. (1985, Pl. 2, Figs. 1–4), *D. sparsiflora* in UHL & DRANSFIELD (1987, Fig. I.8 C.), and *D. sparsiflora* in HARLEY (1999, Fig. 1. F). FREDERIKSON et al. (1985) argued that the *Diporoconia* pollen which they investigated cannot be affiliated to the modern *Daemonorops* because of morphological differences at the pores. Unfortunately, for the fossil type they provide only LM images and TEM sections and for the modern *Daemonorops* LM and SEM images in which these pore details cannot be seen. A SEM detail of a pore of *Daemonorops verticillaris* (Pl. 2, Fig. 6) shows that the footlayer extends beyond the tectum, to form a 'rim' or 'annulus' and displays sparse collumellae. This is exactly what is observed in the Krappfeld *Daemonorops* (Pl. 4, Figs. 2 and 3). The modern *Daemonorops verticillaris* is a short, stout undergrowth-palm in the lowland forests of Eastern Sumatra and the Malay Peninsula.

? Calameae
type 1 (Pl. 4, Figs. 6–11; Pl. 5, Figs. 1 and 2)

Description: Equatorial diporate, spheroidal to ellipsoidal pollen grain, 38–42 μm in equatorial diameter. Exine is 0.5–0.8 μm thick, tectate, perforate; sculpture is gemmate to spinose. Pore diameter 11–14μ; the sculpture elements around the pore margins are fused to form a more or less continuous rim.

Calameae
type 2 (Pl. 5, Figs. 9–12)

Description: Disulcate, ellipsoidal pollen grain, 28–32 μm in equatorial diameter. The exine is 1–1.8 μm thick, and thickest in the central distal and proximal areas. Exine is in the central distal and proximal areas rugulate fossulate and some fossulae are filled with microverrucae. The areas around the ends of the sulcus display smaller and denser rugulae.
Discussion: The micro-morphological details of the exine resemble those of *Daemonorops sarasinorum* depicted in HARLEY (1999, Fig. 1. N).

Calameae
? *Salacca affinis* type (Pl. 5, Figs. 3–8)

Punctilongisulcites microechinatus THIELE PFEIFFER

Description: Sulcate, ellipsoidal pollen grain, 32–35 μm in equatorial diameter. Exine is 2–2.5 μm thick; sexine is slightly thicker than the nexine. Exine is tectate, perforate and the perforation are approximately circular and vary in size. Regularly distributed spines of 1–1.5 µm length display variable tips (blunt to pointed; Pl. 5, Figs. 5, 7 and 8). Remnants of the sulcus membrane are represented by loosely packed ring-like elements (Pl. 5, Fig. 7).

Discussion: Under SEM this spiny palm pollen type reveals certain surface similarities with *Salacca affinis*, a calamoid rattan palm and the LM image resembles *Punctilongisulcites microechinatus* THIELE-PFEIFFER from the Mid-Eocene of Messel (THIELE-PFEIFFER, 1988). The density of perforations in the two depicted pollen grains (Pl. 5, Figs. 5 and 8) could either point to two different taxa or variation within one taxa, confirmation could be obtained by future TEM studies. The genus *Salacca* comprises 15 species centered in Indomalaysia. They are often spiny undergrowth palms of primary rain forests. Some species prefer swampy grounds where they produce dense thickets and others grow in more hilly areas (UHL & DRANSFIELD, 1987).

Arecipites WODEHOUSE
type 1 (Pl. 6, Figs. 10–12)

Description: Sulcate, ellipsoidal pollen grain, 20–24µ in equatorial diameter. The exine is 0.5–0.8 µm thick; the sexine is thicker than the nexine. The exine is microreticulate with rounded and elongated brochi; brochi are larger in the proximal area. The muri, which are irregularly incised and therefore display a knobbly outlook, are sculptured with faint grooves and granulae.

Discussion: see type 3.

Arecipites WODEHOUSE
type 2 (Pl. 6, Figs. 13–15)

Description: Sulcate, more or less symmetric ellipsoidal pollen grain, ca. 12–16 µm in equatorial diameter. The exine is ca. 1 µm thick; the sexine is thicker than the nexine. Exine is microreticulate, heterobrochate, with the largest brochi in the central distal and proximal areas. At the ends of the sulcus the microreticulum fuses to a foveolate tectum. The muri are strongly undulated and covered with granules.

Arecipites WODEHOUSE
type 3 (Pl. 7, Figs. 1–3)

Description: Sulcate ellipsoidal pollen grain, 15–20 µm in equatorial diameter. The exine is 1–1.3 µm thick, the sexine is thicker than the nexine. The exine is foveolate with mostly round fovae and covered with granules.

Discussion: LM images comparable to types 2 and 3 have been described by KRUTZSCH (1970) as *Cycadopites ? sp.* and *Cycadopites ? minutus*. Types 1, 2, and 3 could be accounted to the coryphoid formgenus *Sabalpollenites* (HARLEY, pers. com.). *Sabalpollenites* is a junior synonym for Arecipites WODEHOUSE 1933. Fossil diaspores and leaves of *Sabal* are known since the Eocene from Europe and the United States.

Arecipites WODEHOUSE
type 4 (Pl. 6, Figs. 1–3)

Description: Sulcate ellipsoidal pollen grain, 28–30 µm in diameter. Exine is ca. 1–1.3 µm thick; the sexine is much thicker than the nexine. The exine is reticulate, heterobrochate, simplicolumellate, toward the aperture the size of the brochi is slightly decreased. The muri are more or less straight and perpendicularly grooved.

Arecipites Wodehouse
type 5 (Pl. 6, Figs. 4–6)

Description: Sulcate ellipsoidal grain, 28–32 µm in equatorial diameter. The exine is about 0.8 µm thick, the sexine is obviously thicker than the nexine. The exine is reticulate, heterobrochate with partly elongated brochi that decrease in size from proximal to distal areas. The slightly undulating muri vary in thickness and are often incised.

Arecipites Wodehouse
type 6 (Pl. 6, Figs. 7–9)

Description: Sulcate (broad sulcus) ellipsoidal pollen grain, 22–25 µm in diameter. The exine is 0.5–0.8 µm thick; the sexine is thicker than nexine. The exine is reticulate ?duplicolumellate, heterobrochate with considerably larger brochi in the proximal area, brochi size decreases towards the sulcus. The muri are strongly undulating and produce irregularly shaped brochi.

Formgenus *Monocolpopollenites* Thompson & Pflug
type 1 (Pl. 7, Figs. 4–6)

Description: Sulcate (broad short sulcus with rounded ends) asymmetric ellipsoidal pollen grain, 30–34µ in equatorial diameter. The exine is 1–1.2 µm thick; the sexine is thicker than the nexine. The exine is in the proximal area rugulate foveolate and towards the distal area is more fused.
Discussion: This type is very reminiscent of pollen in subtribe Attaleinae (Arecoidae), which occurs today in South America (Harley, pers. com.).

Formgenus *Monocolpopollenites* Thompson & Pflug
type 2 (Pl. 7, Figs. 7–9)

Description: Sulcate (as long as the axis), slightly asymmetric ellipsoidal pollen grain, 37–40 µm in equatorial diameter. The exine is 1.2–1.5 µm thick; the sexine is thicker than the nexine. The exine is tectate perforate.
Remarks: The LM images of these pollen types are accounted to the formspecies *Monocolpopollenites tranquillus* Thompson & Pflug, which includes several pollen types. The formgenus *Monocolpopollenites* is thought to be a member of the Arecoideae, because this type was found in arecoid Eocene flowers at Messel (Schaarschmidt & Wilde, 1986). More recent investigations of Messel palm flowers (Harley, 1997) have led to the description of a new fossil pollen genus: *Palmaemargosulcites* Harley that includes two species, *P. fossperforatus* and. *P. insulatus*, based on exine characteristics described from SEM with affinities to the Coryphoideae and Arecoideae, respectively. Thiele-Pfeiffer (1988) illustrated dispersed palm pollen from Messel (Pl. 6, Figs. 13 and 14) that resembles the LM of the palm flower pollen *Palmaemargosulcites fossperforatus* Harley.

Araceae

Proxapertites operculatus Van der Hammen

(Pl. 7, Figs. 10–15)

Description: Zona-aperturate oblate, circular to elliptic pollen grain, 45–55 µm in diameter. Because of the aperture configuration, the fossil pollen grains often appear as two slightly different sized halves. The exine is tectate perforate. Further detailed descriptions are given in Zetter et al. (in press).

Discussion: This fossil representative of the Araceae is known under the formgenus *Proxapertites, P. operculatus* Van Der Hammen and was originally attributed to an extinct group of palms related to *Nypa*. However, comparison of SEM images with modern Araceae points towards the outer subfamily Zamioculcadeae, particularly the two endemic genera *Gonatopus* and *Zamioculcas*, both native to Mozambique, SE Africa. Three types of fossil Araceae leaf remains have been described from the Mid-Eocene Messel oil shale; these probably belong to the subfamilies Colocasioideae, Philodendroidae, and Monsteroideae (Wilde, 1989). Fossil Araceae seeds are well known from Oligocene to Pleistocene sediments in Europe and can be ascribed to the subfamilies Monsteroideae and Lasioideae (Gregor & Bogner, 1984). Surprisingly, diaspores with araceous morphology have rarely been recorded in Eocene sediments. When found, they are often considered to be of uncertain affinity. If they are assigned to Araceae they are often associated with Monstereae/Monsteroideae or Lasioideae (Madison & Tiffney, 1976).

The Araceae (Mayo, 1997, 1998) are a tropical to subtropical family, with some representatives in the more temperate regions. The lifeforms range from shrubby scramblers or climbers, small or coarse herbs, floating macrophytes to epiphytes.

5. DISCUSSION

The temperature affinities of the palynomorph assemblages are two-fold: a few typical 'arctotertiary' elements, such as *Salix* and *Alnus* are mixed with considerably more moisture and warmth loving (thermophile) elements, such as the representatives of the Arecaceae, Araceae, Bombacaceae-/Sterculiaceae-/Tiliaceae-complex, Burseraceae, Icacinaceae, Sapotaceae, Mastixiaceae, Schizaeaceae, Anacardiaceae, Alangiaceae, Celastraceae, Elaeocarpaceae, etc. These elements bear witness to an ancient vegetation which today is characteristic of the paratropical realm (Wolfe, 1979). This assemblage, which has been termed 'boreotropical flora' by Wolfe (1977), can be assigned to a paratropical (rain) forest vegetation type, similar to those which exist today in Southern China, Korea and Indo-Malaysia (Wolfe, 1979). However, if one acknowledges that the overall global climate during the Early Tertiary differed markedly from today, with the absence of polar ice caps favouring reduced atmospheric winds, and enhanced warm oceanic circulations leading to extremely warm and moist high latitudes (Sloan & Thomas, 1998; Rea, 1998), then there is no modern equivalent for this ancient vegetation.

5.1. Early Cenozoic radiation and migration of plants

The Early Cenozoic radiation and migration of flowering plants was characterized by the evolution of new taxa and genera adapted to high latitudes in both hemispheres, due to the rather uniform warm and humid climate during the Palaeocene/Eocene boundary interval (Wolfe, 1977). The uniform conditions over wide latitudes resulted in an unusual mixture comprising mainly thermophilic taxa with a few more or less boreal deciduous taxa. An east-west migration of taxa can be assumed via the island archipelagos that fringed the Tethyan coastline and were probably stepping-stones for the migration and speciation of boreo/palaeotropical taxa. In the higher northern latitudes, the Bering Strait (Wolfe, 1978) and North Atlantic land bridges (Thulean and De Geer routes; McKenna, 1983 cited in Tiffney, 1985a) led to the migration and exchange of more thermophilic taxa during warm spells in the Palaeogene (compare Tiffney, 1985a & b). Tiffney (1985b) suggested that the radiation of flowering plant taxa was promoted by the co-evolution of animal pollinators and animals responsible for seed dispersal and migration.

5.1.1. Pollination mechanisms

To understand at least a small part of the palaeoecology of the boreotropical Krappfeld flora, one must make comparisons with similar modern environments, such as rainforests or seasonal forest of the paratropics and tropics.

Wind pollination plays a very minor role in modern tropical floras, where most pollination is effected by bees, beetles, moths, birds, bats and small mammals (Jacobs, 1988, Mabberley, 1994; Whitmore, 1992). Most tropical plants that use wind pollination are found in the wind current prone canopy and emergent tree taxa (Mabberley, 1994).

Thus nearly all the Krappfeld pollen which appear to be from parent plants with tropical to sub-tropical climate affinities (ca. 80%), are assumed to be animal pollinated. The amphipacific wind-pollinated *Hedyosmum* (Chloranthaceae) is an exception, because its male flowers are arranged in strobus-like inflorescences, like those of the gymnosperms and is considered to be a 'living fossil' (Leroy, 1983). Palms are generally insect pollinated (cf. Henderson, 1986): Most of the species in the Calameae genera *Calospatha* and *Daemonorops* are assumed to be pollinated by beetles, whilst species of *Calamus* may have different pollinators, for example beetles, wasps or flies. *Ceratolobus* species may be pollinated by ants, lepidoptera and staphylinid adults and larvae. *Nypa* is assumed to be pollinated by drosophilid flies and *Salacca* by weevils. Many of the Araceae are assumed to be insect pollinated, particularly the tribe Zamioculcadeae with the spathe building a primitive trap for flies and beetles (Mayo et al., 1997).

The more mesothermal Fagaceae, Juglandaceae, *Eucommia, Myrica* and *Platanus* are wind pollinated. The taxa accounted to be mostly microthermal are *Alnus,* which is anemophilous, and *Salix,* which can be either entomophilous or anemophilous. The ferns and fern allies disperse their spores by a combination of wind and animal induced catapulting/hurling release; this type of spore dispersal mechanisms occurs throughout the pteridophytes (Tab. 1). Big, thick-walled, and thus heavy fern spores will fall down gravitationally and might 'germinate' near to the mother plant, whilst smaller and lighter ones could be picked up by wind currents and deposited in an unsuitable place. Although there is a higher percentage of wind-pollinated than animal-pollinated species both in air and sediment samples in temperate regions, this is not the case in subtropical and tropical forests, where the reverse is true. Some of the Fagaceae and Juglandaceae might represent canopy or emergent tree species, particularly the Juglandaceae *Engelhardia* and *Cyclocarya* type pollen, because they have wind dispersed seeds (see section 5.1.2.).

5.1.2. Diaspore dispersal

Seed and fruit (diaspores) dispersal mechanisms are discussed here since they might indicate the probability of latitudinal and longitudinal taxa migrations during the Caenozoic. Of particular interest are the more thermophilous elements and their occupation of the higher latitudes. Diaspores transported by animals have one or more of several features, such as nutritious nuts or fleshy, sugary, or oily fruits (e.g. Elaeocarpaceae, Lecythidiaceae, Moraceae, Meliaceae, Sapotaceae, Thymelaceae, Arecaceae).

In the moist tropical forest of Barra de Colorado (Central America), 85% of diaspores from large and medium-sized trees that ripen during the rainy season are animal dispersed and 12% are wind dispersed. In contrast, only 36% of the fruits maturing in the dry season are animal dispersed and 21% are wind dispersed. Approximately 99% of fruits from small undergrowth trees that ripen during the rainy season get dispersed by animals, but during the dry season, there is a significant decrease, to 35% animal dispersal. Smaller seeds of herbaceous plants may be dispersed by larger grazing mammals (MABBERLEY, 1994).

One can imagine that during the rainy season or in situations of persistent rain, the dispersal of winged or ballooned diaspores fails, because rain saturates their lightweight structure, making them too heavy to glide over long distances. For example, in seasonally controlled forests of modern West Africa and South America there is a characteristic increase in canopy species with wind dispersed diaspores (MABBERLEY, 1994), that mature during the dry season. Therefore, it might be concluded that the wetter and more uniformly warm the climate, such as during the Late Palaeocene and Eocene Thermal Maxima, the higher the percentage of animal dispersal mechanisms. Migrating frugivorous birds or larger mammals, and bats can transport diaspores against wind directions and over obstacles such as mountains and lakes. The seed dispersal and wide distribution of epiphytic Araceae, as well as epiphytic Cactaceae and Bromeliaceae have been observed to be effected by birds, who eat the flesh and clean their beaks by scraping the sticky seeds into bark crevices (MABBERLEY, 1994). Both frugivorous fish and water can transport diaspores in streams and ocean currents and may account for the dispersal of floating fruits and seeds (rheophytes in some *Elaeocarpus, Aglaia*, Araceae, Arecaceae, Leguminosae, Thymelaceae) over wide areas, such as island archipelagos or along the coastlines of major seaways. Frugivorous fish in particular, are responsible for dispersing diaspores upstream (MABBERLEY, 1994).

The Mid-Eocene Messel locality, with its well preserved fossil flora and fauna, reveals several clues of the interaction between plants and animals (SCHAAL & ZIEGLER, 1988). Although not fully comparable with the Krappfeld locality, because of its palaeogeographic position and younger age, a few processes have been inferred. Woodpecker-like birds with seeds in their stomachs have been preserved and several kinds of running birds occur; these may have been major diaspore transporters, similar to modern cassowaries. Mammalian examples from Messel are very ancestral frugivorous bovines (parocylaenids), an early horse with *Vitis* seeds in its stomach, and even-toed ungulates with seeds in the stomach. Most of the bat fauna was insectivorous, but some also had pollen lumps in their stomachs. Many of these species or their relatives migrated between Africa, Asia and North America during sea-level lowstand times, and in this way contributed greatly to the dispersal of plant taxa (SCHAAL & ZIEGLER, 1988). Unfortunately, no terrestrial fauna is known from the Krappfeld area, but we may imagine that this terrestrial coastal area flourished with animal life.

In the Krappfeld samples, pollen of plants with wind dispersed diaspores are generally uncommon and are restricted to the rarely preserved microthermal forms, such as *Alnus* and *Salix*, and a few mainly accessorial mesothermal elements, such as some of the Juglandaceae (*Engelhardia* and *Cyclocarya* type), Tiliaceae, *Eucommia*, and *Koelreutheria*. These were probably better adapted to the more seasonally controlled forests and could have released their diaspores during times of low precipitation. A few wind dispersed diaspores might also have been distributed by animals (birds and rodents); for example, the winged, but nutritious nutlets of the Pinaceae *Pinus* and *Cathaya*. The rest of the taxa were animal dispersed, or presumably animal (fish) and water dispersed (e.g. *Aglaia, Calamus* type, *Daemonorops, Nypa,* Araceae, and the Sparganiaceae) and therefore prone to migration processes.

5.2. Comparison with other localities

The Krappfeld area is a small erosional relict, with few sediment horizons suitable for sampling and consequently, the taxa yield is unlikely to be fully representative. The Palaeocene and Eocene marine sedimentary rocks indicate a coastal near shelf environment, with a small intercalated terrestrial sequence OBERHAUSER (1995). Hence the area can be interpreted as a remnant of an island archipelago that stretched along the northern margin of the propagating Alpine nappes.

Organic facies analysis indicates a coastal habitat, such as a lagoon or a bayou, in which freshwater conditions prevailed most of the time. These were occasionally overprinted by more brackish to slightly marine conditions during short intervals when saline waters were forced into the freshwater area by off-shore storms, carrying dinoflagellates and foraminifers. The remains of relatively few wood fragments (10%) and more semiopaque (coalified) matter (18%) also provide evidence of a lacustrine, rather than a swampy, depositional area.

The fossil pollen assemblage(s) include representatives of over 50 extant families, more than half of which are considered to be tropical to subtropical. Of the modern families represented, 22% are considered to be purely tropical (thermophilous), about 36% tropical to sub-tropical, 24% sub-tropical (mesothermal), 4% temperate to microthermal; ca. 14% of the taxa are considered to be cosmopolitan. From the over 120 taxa defined, 9 are extinct/old forms belonging to the Burseraceae, Fagaceae, Juglandaceae, and ?Simaroubaceae. The 5 Normapolles forms may have affinities to the Myricaceae or Juglandaceae or an intermediate form, and 6 forms have up to now no known affinities (compare Table 1).

Generally, in terms of taxa diversity, flora composition and temperature affinities of the taxa, the Lower Eocene of the London Clay (COLLINSON, 1983, 1996) and the Krappfeld area are very comparable, although the former is a macroflora and the latter a palynoflora. Both the London Clay and the Krappfeld floras, particularly the *Nypa*-

domination in 'mangrove type forests', reflect the ETM (Eocene Thermal Maximum), which lasted from at least the Early Ypresian to the Late Lutetian (COLLINSON, 2000). Although palynological work was undertaken in the London Clay by GRUAS CAVAGNETTO (1977), the LM photographic plates make it difficult to compare individual taxa (see below).

In contrast, the diaspore-flora of the Woolwich and Reading Beds (Palaeocene, Thanetian, CHANDLER, 1964; COLLINSON, 1996) are not at all comparable in biodiversity and taxa composition. From these beds, approximately 33 different taxa are known, only 15% of which show affinities to modern subtropical to tropical species; The majority preferred a temperate to warm climate. Even so, this less diverse, mainly mesothermal assemblage apparently existed at around the Late Palaeocene Thermal Maximum (LPTM), according to a carbon isotope excursion (BEERLING AND JOLLEY, 1998).

Palynological investigations of Ypresian fine-grained sediments in northern Belgium reveal a gradual warming, with a temperature- and humidity maximum in the LateYpresian ROCHE (1990). Most of the characteristic megathermal genera are also represented by pollen from the Krappfeld sites. Other notable Eocene palynofloras are preserved in the Paris Basin (GRUAS CAVAGNETTO, 1977, 1987) and the Belgian provinces of Epinois and Brabant (KRUTZSCH & VAN HOORNE, 1977). The latter two palynofloras comprise terrestrial lignitic sediments, interpreted as a very slightly brackish influenced continental sequence. These localities represent similar facies in a more or less broad regional continental depositional system. However, although comparison with these palynofloras are possible, only a handful of floral elements can be definitely recognized and compared, since the palynomorphs were investigated by LM. Most of the taxa are named as form genera or form species (KRUTZSCH & VAN HOORNE, 1977), or with modern botanical generic assignment only on the basis of light microscopy (GRUA CAVAGNETTO, 1977, 1987). Nevertheless, these assemblages also seem to be rich in taxa.

5.3. Variation, species diversity and climate oscillations

The floral assemblages recovered from periods of temperature maxima, such as the ETM, inevitably reflect only a part of the original species/taxa diversity. The morphological variability of the fossil pollen grains, diaspores and leaves will always be difficult to judge. The intra-specific variation observed in modern (tropical) taxa probably also occurred in the early Eocene.

Size and shape studies of recent tropical fruits within one species (or even within one individual) may show a surprising amount of variation. Speciation is an active process, and species limits are often controversial. For example, in the Amazonian tropical rain forests, one species of the tree genus *Aspidosperma* (Apocynaceae), which is distributed over thousands of square kilometres, displays small gradual changes in individuals, resulting in extreme variations across its range. These extremes are so different that, if the intermediate forms were unknown, they the would be described as different species. Similar perplexing examples of great variation have been described from the fruits of single species and even from individual trees (Lecythidaceae: fruits which 'ought' to have originated from two genera were sampled from one tree; Lecythidaceae fruits from Malaysian island species do not display such variability). JACOBS (1988) proposed that the phenomenon was caused by thorough climatic changes in the Amazonian area during the Quaternary, which forced speciation, although similar climate changes did not affect the Malaysian islands. Quaternary climate development and the history of tropical forests in the Amazonian area have been studied by HOOGHIEMSTRA (1997) and HOOGHIEMSTRA & VAN DER HAMMEN (1998) who considered that periods of reduced precipitation and cooling alternated with periods more controlled by fluvial autocycles and marine excursions. These climatic oscillations subsequently influenced the composition and diversity of species, probably stimulating further speciation. Apart from climatic causes, GENTRY (1989) suggested that speciation may result from significant changes in plant habitats or different edaphic niches; these are very abundant in the tropical fluvial realm and probably can undergo significant changes during tectonically active phases.

Short term climate oscillations at the Palaeocene-Eocene boundary have been recorded in north-western Wyoming, the North Sea, the North Atlantic and North Pacific areas (BEERLING & JOLLEY, 1998; CORFIELD & NORRIS, 1998; WING et al, 1998, 1999; WING, 2000) and give evidence for a nearly world-wide cooling phase during the Early Eocene, with a subsequent marked increase in temperature. This 'cool, warm, cool, warm climate' (WING, 2000) has been interpreted as an overall warming trend (ranging from the Lower Palaeocene to the ?Middle Eocene), with a superimposed cooling phase (CORFIELD & NORRIS, 1998).

If speciation processes were enhanced by similar climatic oscillations during the development of the "species rich" Eocene floras of the London Clay (COLLINSON, 1983) or the Krappfeld (HOFMANN & ZETTER, in press) the comparison with, and correlation of contemporaneous localities in terms of stratigraphically valuable taxa and species might be hampered by the difficulty in differentiating between variants of a species and different species. The general richness in taxa and composition of the floral assemblages are much better means for correlation.

6. CONCLUSIONS

The Krappfeld palynoflora, with over 120 taxa, is diverse and species rich.

The botanical affiliations of the taxa identified indicates that more than 80% of the pollen types represent parent species that flourished in a tropical to subtropical climate, comparable with a modern paratropical rain forest.

The pollination mechanism and seed dispersal of these thermophilous taxa have been deduced using the biology of the affiliated extant genera and are summarised in table 1.

The diversity and floral composition of the Krappfeld flora is characteristic of other floras of the Early Eocene, and are assumed to have evolved during the Eocene Thermal Maximum (ETM).

The fossil morpho-type *Proxapertites operculatus* VAN DER HAMMEN has been recognized as an Araceae of the outer subfamily Zamioculcadeae.

SEM analysis is a critical addition in comparative palynological studies. The possibility of establishing botanical affiliations between dispersed pollen and modern taxa is greatly enhanced.

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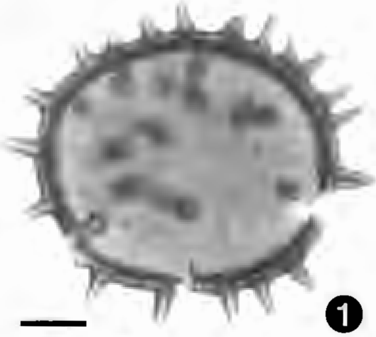
Plate 1

Light microscope (LM) images: bar = 10µ; SEM-overview: bar = 10µ; SEM Close-up: bar = 1µ

Figs. 1–12: *Nypa* sp. (*Spinizonocolpites* sp.)

Figs. 1–9: Variation; LM × 850

Figs. 10–12: Variation; SEM × 1000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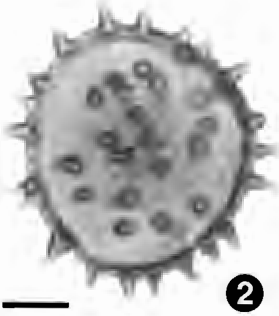
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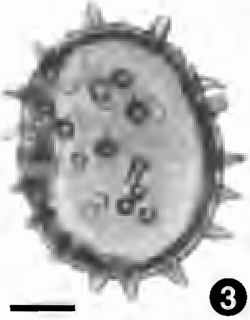
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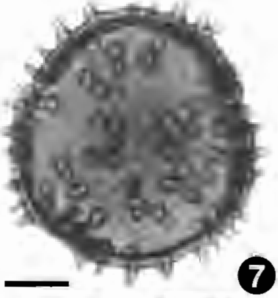
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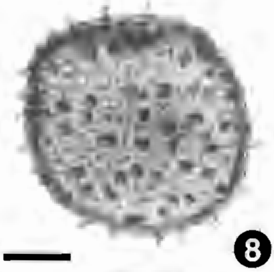
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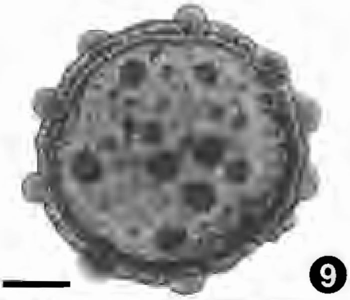
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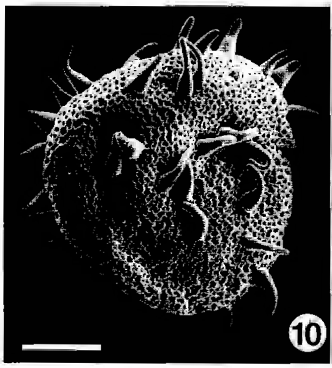
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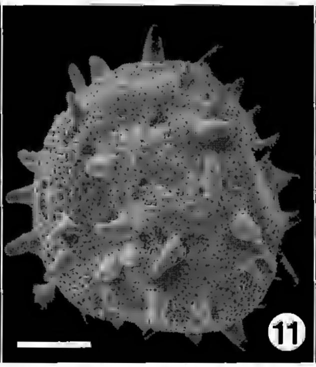
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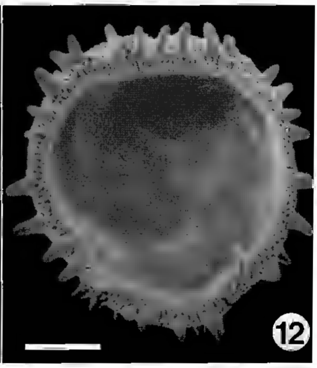
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Plate 2

Light microscope (LM) images: bar = 10µ; SEM-overview: bar = 10µ; SEM Close-up: bar = 1µ

Figs. 1–10: *Nypa* sp. (*Spinizonocolpites* sp.)
Figs. 1 and 2: Variation; SEM × 1000
Fig. 3: Close-up of the tectum; SEM × 6000
Fig. 4: Complete half grain with blunt and pointed spines; SEM × 1000
Fig. 5: Close-up of the aperture region; SEM × 2500
Fig. 6: Overview of the inner side with knobbly spines at the margin; SEM × 1100
Fig. 7: Close-up of a knobbly, not fully developed spine; SEM × 5500
Fig. 8: Close-up of not fully developed spines; SEM × 2800
Fig. 9: Group of spines in the aperture region; SEM × 6000
Fig. 10: Long curved spine; SEM × 5000

Plate 2

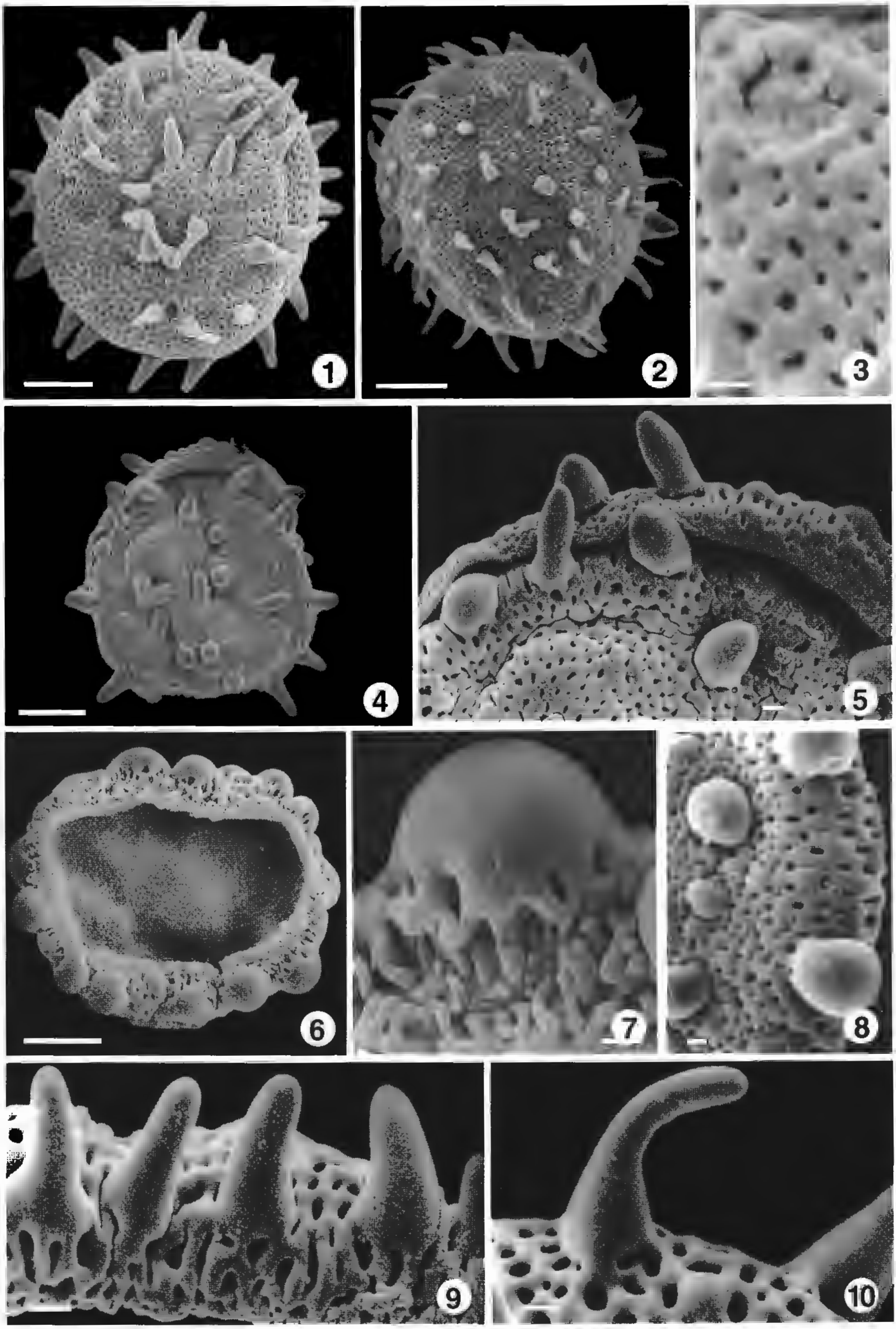

Plate 3

Light microscope (LM) images: bar = 10μ; SEM-overview: bar = 10μ; SEM Close-up: bar = 1μ

Figs. 1–5:	*Nypa* sp. (*Spinizonocolpites* sp.)
Fig. 1:	Artificial fracture of the exine showing columellae and footlayer; SEM × 14000
Fig. 2:	Artificial fracture showing exine stratification and spine; SEM × 12500
Fig. 3:	Isolated spine with underlying columellae and part of footlayer visible; SEM × 10000
Fig. 4:	Inner view close-up; SEM × 7500
Fig. 5:	Close-up of corroded tectum and spine; SEM × 6000
Figs. 6–15:	*Calamus* sp. (*Dicolpopollis* sp.)
Figs. 6, 7, 8 and 10:	Equatorial view; LM × 850
Figs. 9 and 11:	Polar view; LM × 850
Figs. 12 and 13:	Overview with variation of reticulum; SEM × 2100
Fig. 14:	Close-up of mesoequatorial area; SEM × 9500
Fig. 15:	Close-up of polar area; SEM × 8500

Plate 3

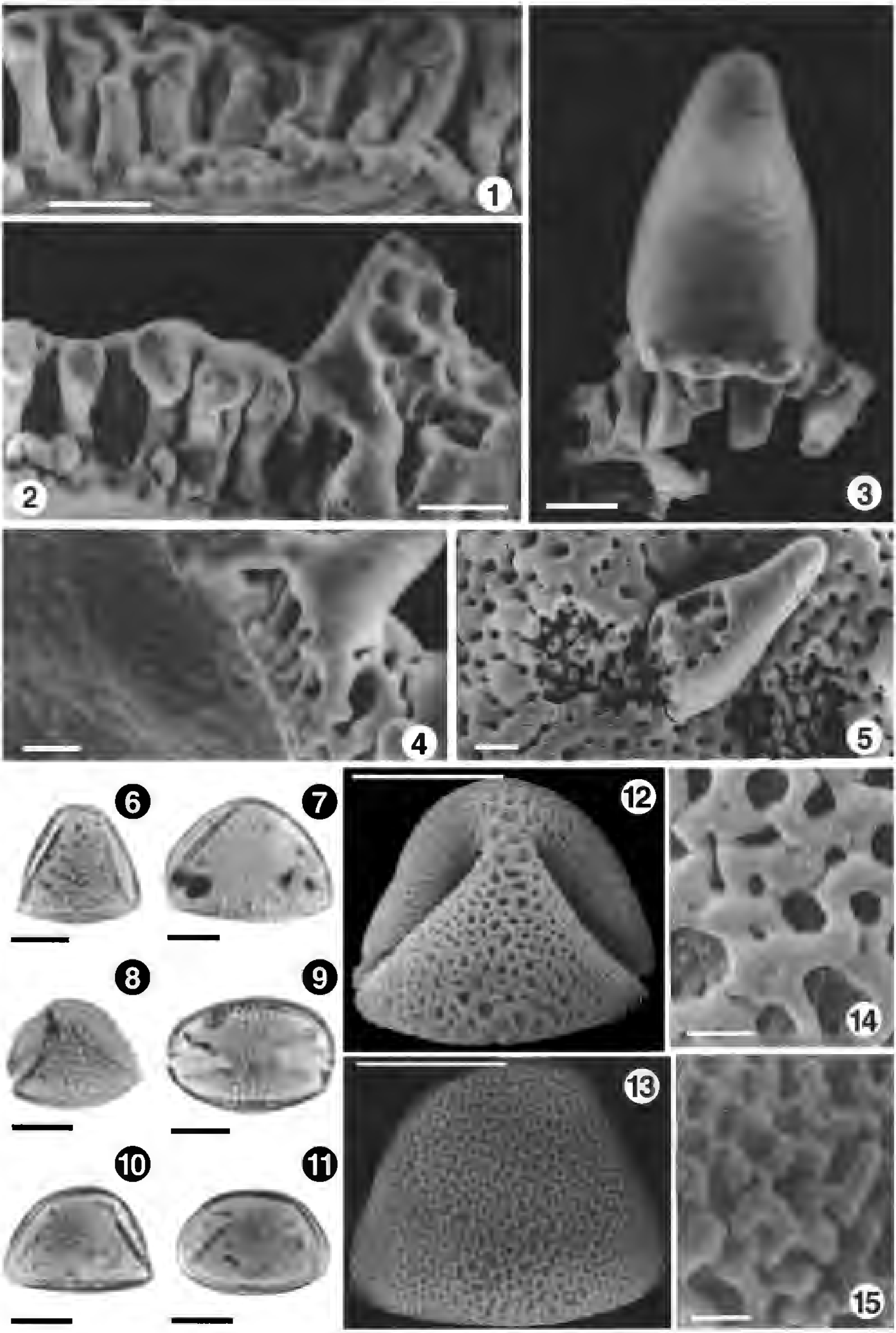

Plate 4

Light microscope (LM) images: bar = 10μ; SEM-overview: bar = 10μ; SEM Close-up: bar = 1μ

Figs. 1–5: *Daemonorops* sp. (?*Diporoconia iszkaszentgyoergyi*)
Fig. 1: Overview; LM × 850
Fig. 2: Overview; SEM × 850
Fig. 3: Close-up of the aperture region; SEM × 14000
Fig. 4: Overview; SEM × 1000
Fig. 5: Close-up of the tectum; SEM × 10000
Figs. 6–11: Variants of ? Calamae type 1
Fig. 6: Overview; LM × 850
Fig. 7: Overview; SEM × 1200
Fig. 8: Overview of the other face; SEM 1200
Fig. 9: Overview; SEM × 1000
Fig. 10: Overview of the other face; SEM × 900
Fig. 11: Close-up of the aperture; SEM × 5000


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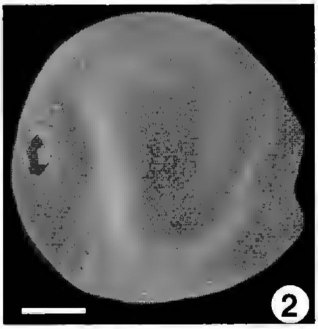
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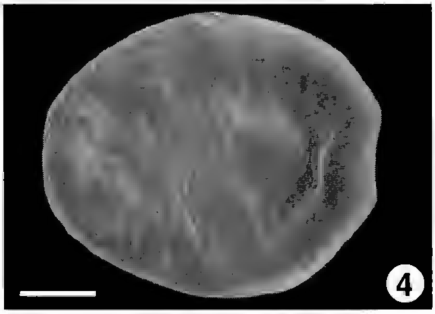
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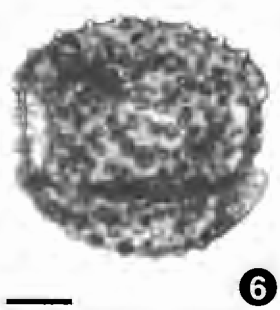
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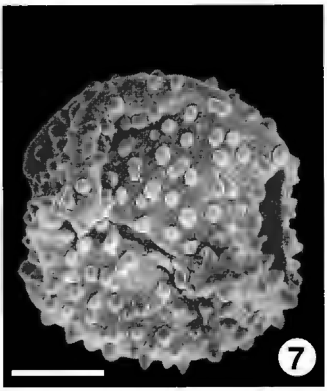
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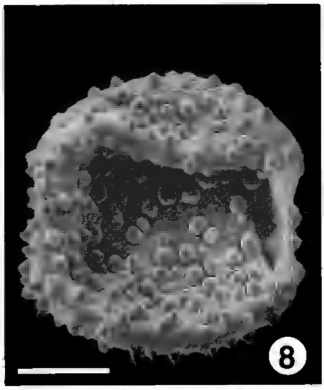
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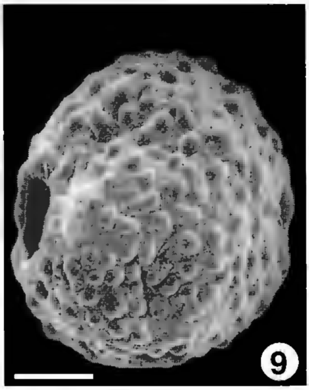
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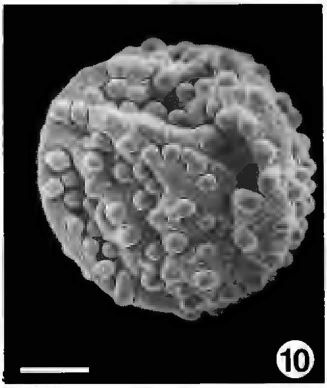
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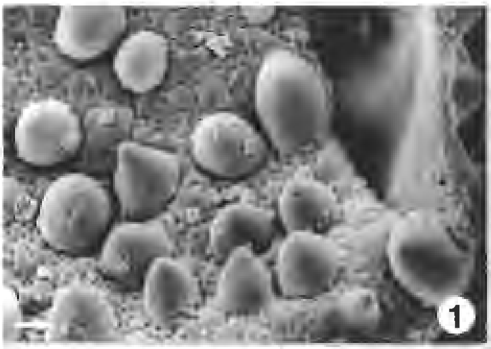
Plate 5

Light microscope (LM) images: bar = 10μ; SEM-overview: bar = 10μ; SEM Close-up: bar = 1μ

Figs. 1 and 2: ?Calamae type 1
Figs. 1 and 2: Close-up of the aperture region with variable spines; SEM × 4500
Figs. 3–8: ? *Salacca affinis* type (*Punctilongisulcites microechinatus*)
Fig. 3: Overview; LM × 850
Fig. 4: Distal face overview; SEM × 1500
Fig. 5: Close-up; SEM × 9000
Fig. 6: Overview, distal face; SEM × 1800
Fig. 7: Close-up of the aperture region, SEM × 8000
Fig. 8: Close-up of the tectum with variable supratectal spines; SEM × 6500
Figs. 9–12: Calamae type 2
Fig. 9: Overview; LM × 850
Fig. 10: Overview, distal face; SEM × 1300
Fig. 11: Overview, proximal face; SEM × 1300
Fig. 12: Close-up of the mesoequatorial area, SEM × 6000

Plate 5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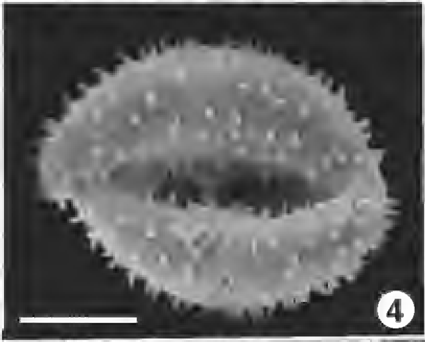
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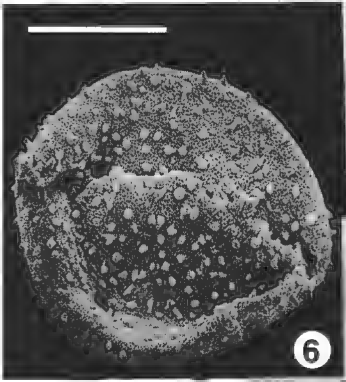
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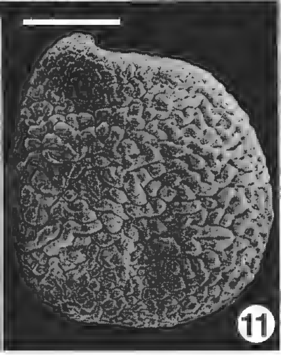
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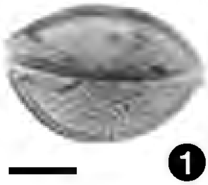
Plate 6

Light microscope (LM) images: bar = 10μ; SEM-overview: bar = 10μ; SEM Close-up: bar = 1μ

Fig. 1–3: *Arecipites* type 4
Fig. 1: Overview; LM × 850
Fig. 2: Overview, distal face; SEM × 1500
Fig. 3: Close-up of the tectum; SEM × 8000
Fig. 4–6: *Arecipites* type 5
Fig. 4: Overview; LM × 850
Fig. 5: Overview; SEM × 1700
Fig. 6: Close-up of the tectum; SEM × 8000
Fig. 7–9: *Arecipites* type 6
Fig. 7: Overview; LM × 850
Fig. 8: Overview; SEM × 2000
Fig. 9: Close-up of the tectum; SEM × 9000
Fig. 10–12: *Arecipites* type 1
Fig. 10: Overview; LM × 850
Fig. 11: Overview; SEM × 1900
Fig. 12: Close-up of the tectum; SEM × 8000
Fig. 13–15: *Arecipites* type 2
Fig. 13: Overview; LM × 850
Fig. 14: Overview; SEM × 2300
Fig. 15: Close-up of the tectum; SEM × 10000

Plate 6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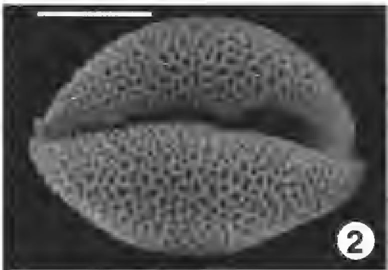
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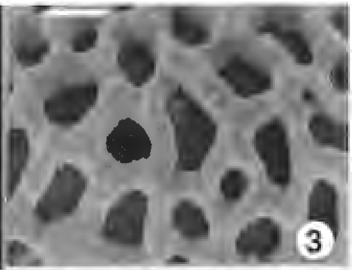
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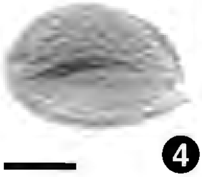
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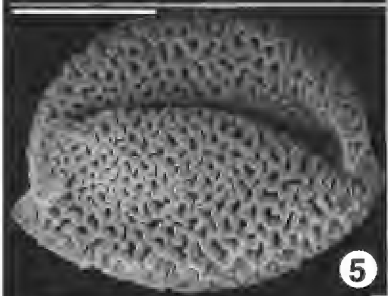
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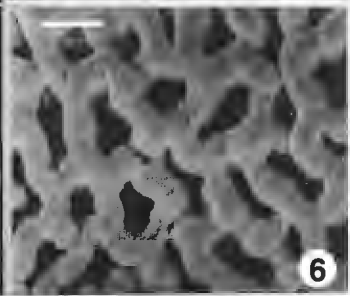
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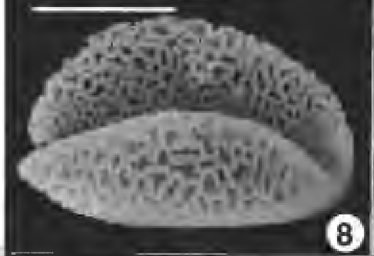
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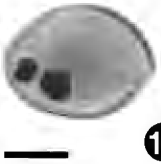
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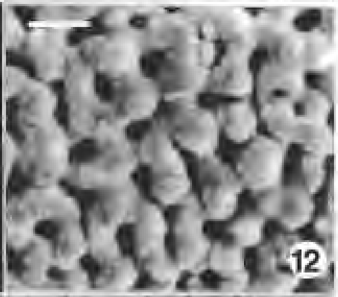
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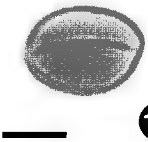
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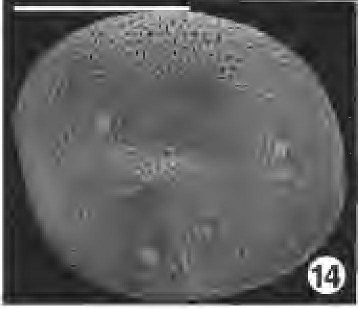
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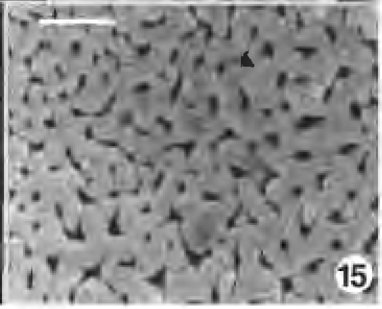
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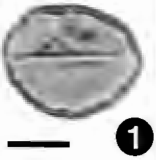
Plate 7

Light microscope (LM) images: bar = 10µ; SEM-overview: bar = 10µ; SEM Close-up: bar = 1µ

Fig. 1–3:	*Arecipites* type 3
Fig. 1:	Overview; LM × 850
Fig. 2:	Proximal Overview; SEM × 2000
Fig. 3:	Close-up of the proximal tectum; SEM × 9000
Fig. 4–6:	*Monocolpopollenites* type 1
Fig. 4:	Overview, LM × 850
Fig. 5:	Proximal overview; SEM × 1400
Fig. 6:	Close-up of the proximal tectum; SEM × 9000
Fig. 7–9:	*Monocolpopollenites* type 2
Fig. 7:	Overview; LM × 850
Fig. 8:	Overview, proximal face; SEM × 1350
Fig. 9:	Close-up of the tectum, proximal face; SEM × 9000
Figs. 10–15:	Araceae (*Proxapertites operculatus*)
Figs. 10 and 13:	Overview; LM × 850
Figs. 11 and 12:	Two different grains; SEM × 850
Fig. 14:	Close-up of the tectum; SEM × 8500
Fig. 15:	Close-up of the aperture region with connecting endexinous material; SEM × 10000

Plate 7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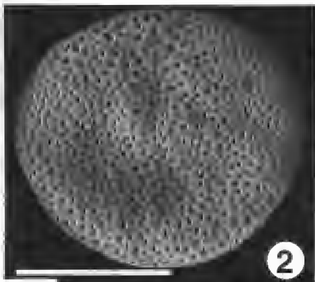
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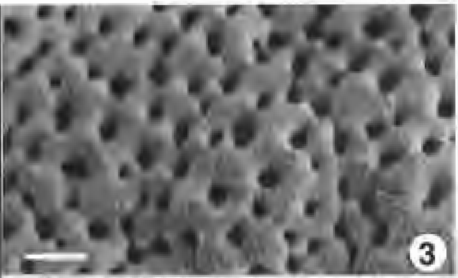
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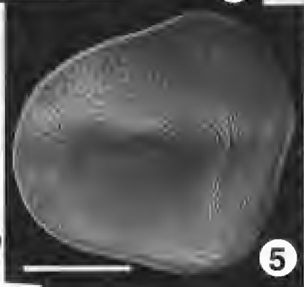
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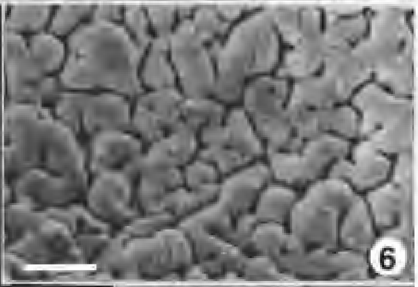
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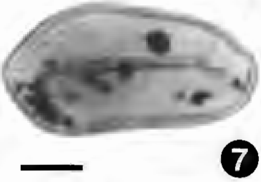
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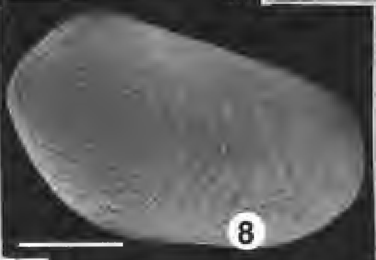
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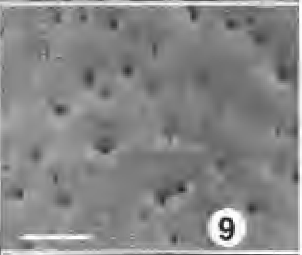
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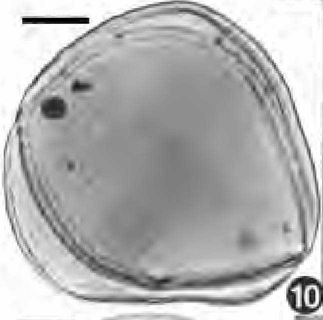
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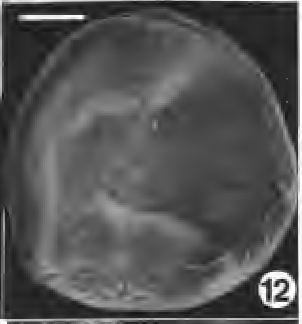
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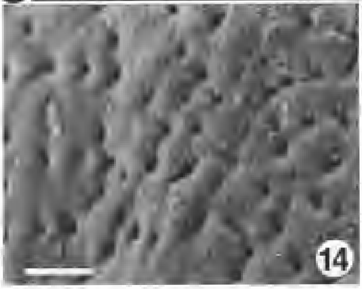
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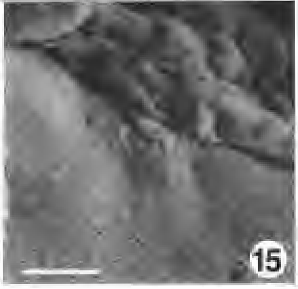
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