POLLEN MORPHOLOGY OF THE AMERICAN SPECIES OF THE SUBFAMILY COSTOIDEAE (ZINGIBERACEAE)

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SUMMARY

A pollen-morphological study has been carried out on the American Costoideae, a subfamily of the Zingiberaceae (*Costus* L., *Dimerocostus* O. KUNTZE, and *Monocostus* K. SCHUM.). Four pollen types and two subtypes could be established on the basis of size, exine and apertural characters. These types are: *Costus lima* type, *Costus warmingii* type, *Costus congestiflorus* type and *Dimerocostus* type. It is assumed that the pollen grains of the genus *Costus* are pollen morphologically more advanced than the grains of *Dimerocostus* and *Monocostus*.

INTRODUCTION

This paper has resulted from a cooperative study of a palynologist and a taxonomist on the American representatives of the subfamily Costoideae. It is, however, confined to the palynological studies whereas the gross morphology and the taxonomical conclusions will be published by P. J. M. Maas, taxonomist at the Botanical Museum and Herbarium at Utrecht.

Three genera of the *Costoideae* occur in America: *Costus* L., *Dimerocostus* O. KUNTZE, and *Monocostus* K. SCHUM. *Monocostus* is monotypic and this only species has been studied. *Dimerocostus* is a genus with two species and both species were available for study. The largest genus in the Costoideae, *Costus*, is pantropical with ca. 70 species. About 45 species out of this total number occur in the West Indies, Central America and tropical South America. About 25 species are found in Africa and only a few occur in Asia.

MATERIAL AND METHODS

The plant material was supplied by the taxonomist P. J. M. Maas, who also took care of the identifications and is responsible for the names and nomenclature given in the text. Some specimens were obtained from alcohol material,

but most of the slides were prepared from herbarium sheets. Polleniferous matei ial was obtained from the following herbaria:
C—Botanical Museum and Herbarium, Copenhagen.
F—Chicago Natural Museum, Chicago, Ill.
G—Conservatoire et Jardin Botanique, Genève.
GH—The Gray Herbarium of Harvard University, Cambridge, Mass.
L—Rijksherbarium, Leiden.
MO—The Missouri Botanical Garden, St. Louis, Mo.
NY—The New York Botanical Garden, New York, N.Y.
P—Laboratoire de Phanérogamie, Museum National d'Histoire Naturelle, Paris.
RB—Jardin Botanica, Rio de Janeiro.
S—Naturhistoriska Riksmuseum, Stockholm.
U—Botanisch Museum en Herbarium, Utrecht.
US—United States National Herbarium, Washington, D.C.
VEN—Instituto Botanico, Caracas.

The pollen grains were prepared using a slightly modified version of the acetolysis method of ERDTMAN (1961). The flowers were first boiled in water and afterwards treated with the acetolysis mixture. The embedding medium was glycerine jelly. The mounted grains were covered by a cover slip supported by two pieces of clay (PUNT, 1962) and sealed with paraffin. The clay is essential because it prevents deformation of the large pollen grains due to the weight of the cover slip.

Descriptions have been made with the aid of a Leitz Ortholux microscope, apochr. obj. $\times$ 40 and an eye piece $\times$ 10, periplan. The micro-photographs were taken with the use of the same microscope and lenses in combination with a Leitz Orthomat camera. The magnification of the photographs is given in the captions of Plates I and II.

It often proved to be impossible to find an adequate number of grains for statistical treatment of size measurements. On the other hand sizes differ so widely in this group, that it is of some value for classification. The sizes mentioned in Table I are usually based on five or six grains and are a rough approximation only. It is often claimed that sizes depend on the preparation method followed. For these reasons the values of the measurements should be considered as relative only.

It was possible to keep the terminology used in this paper simple, because the structure and ornamentation of the pollen grains are themselves simple.

DESCRIPTIONS

General part

The pollen grains of the Costoideae have a uniform shape and a simple exine structure. As a result the grains are easy to describe, using a few differentiating characters only.

The *shape* is distinctly ellipsoidal, but slightly asymmetrical. Since the pollen grains are large, they are easily deformed during mounting. Consequently, it was not always possible to determine the exact shape of the grains.

The *exine* apparently consists of one layer only. In mature pollen grains it is impossible to distinguish more than one layer. Even with a magnification of $\times$ 1000 (oil-immersion) two layers could not be recognized ("without apparent distinction between sexine and nexine", ERDTMAN, 1952). The exine is smooth and does not show any structure or ornamentation. The only variable character is the exine thickness. In practice this is a very important differentiating character. The exine is usually thin (1.5–3.5 μ), but in several species (*Dimerocostus* type, *Costus congestiflorus* type) the thickness can be considerably more (4–8 μ). The exine is usually slightly thicker in the porus area, but it is never thickened into a distinct annulus (annulus = distinct border around a porus).

The *size* of the pollen grains varies considerably within a species and within a single specimen. As a rule the pollen grains are large or very large (100–210 μ).

There are three different kinds of *apertures:*

(*1*) Colpi long, spirally shaped ("spiralaperturate", ERDTMAN, 1952); e.g., *Dimerocostus* type.

(*2*) Colpi rather short, straight or slightly curved. These colpi may have swollen apices. The extremes are sometimes enlarged into pori and the resulting aperture is dumb-bell shaped. In extreme cases the "dumb-bell" splits up in two separate pores (*Dimerocostus* type).

(*3*) Pori. The pores vary considerably in shape and size even within the same grain. The pores are usually rather large (ca. 20 μ), although in some cases the diameter is less (e.g., 10 μ in *Costus congestiflorus* type) or sometimes more (up to 35 μ). The pores are usually circular in outline, although elliptical apertures are also abundant. The apertures are only rarely elongated into a short colpus.

The *number of pores* is 5–16 per grain. However, most species have seven or eight pores while some have nine or ten (e.g., *Costus scaber*, *Costus arabicus*) and in rare cases more than ten apertures are met with (*Costus warmingii* ca. eleven; *Costus igneus* twelve or thirteen).

The pollen types can be separated by the following differential characters:

(*1*) *Exine* – (*a*) thin: usually 2–3 μ, and as a rule not more than 3.5 μ; (*b*) thick: more than 4 μ.

(*2*) *Size* – (*a*) pollen grains large: ca. 120 μ (100–160 μ); (*b*) pollen grains very large: ca. 180 μ (over 160 μ).

(*3*) *Number of pores* – (*a*) medium: ca. 8 (5–9); (*b*) large: ca. 11 or more (9–16).

TABLE I

SIZE, EXINE AND APERTURAL FEATURES OF THE COSTOIDEAE MATERIAL STUDIED

Taxon	Pollen size (μ)[1]	Exine (μ)[1]	Porus diameter (μ)[1]	Number of pores[1]	Colpus spiral shaped and short colpus
Costus lima type					
C. arabicus L.	118–140	ca. 2	18–22	9–11	—
Florschütz and Maas, 2574 (U)	130	—	ca. 20	ca. 10	
	118–132	ca. 2	24–34	7–10	—
Florschütz and Maas, 3158 (U)	127	—	ca. 25	ca. 8	
	130–150	1.5–2	18–38	6–7	—
Cult. Hort. Baarn (U)	138	ca. 2	ca. 25	7	
C. claviger R. Benoist	128–140	2.5–4	20–30	7–8	—
Florschütz and Maas, 2822 (U)	133	ca. 2.5	ca. 25	7	
C. comosus (Jacq.) Roscoe	114–142	2–3.5	18–28		
Aristeguieta, 1703 (VEN)	123	2–2.5	ca. 22	6	
C. chartaceus n.sp. (Maas, ms.)	104–113	—	22–30	6–8	—
Schultes, 3540 (GH)	109	ca. 3	ca. 25	ca. 8	
C. fusiformis n.sp. (Maas, ms.)	140–180	—	22–30	7–8	—
Kuhlmann, 1916 (RB)	156	ca. 2	ca. 25	8	
C. laevis Ruiz et Pavon	104–106	—	19–22	7–8	—
García-Barriga, 10953 (GH)	105	ca. 2	ca. 20	ca. 7	
	98–112	2–3	16–30	7–8	—
O. Haught, 1913 (GH)	103	ca. 2.5	ca. 20	ca. 8	
C. lima K. Schum.	114–125	2–3	14–21	7–8	—
Van Wedel, 1632 (GH)	119	ca. 2.5	ca. 18		
C. guanaiensis Rusby	?		?	6–7	—
Maas, 3400 (U)		ca. 3		ca. 7	

Asplund, 15412 (S)	130–162 148	2.5–3	17–22 ca. 20	9–11 ca. 10	—
Cardenas, 1851 (NY)	84–116 105	2–3 ca. 2.5	12–22 ca. 20	7–9 8	—
U. Williams, 6529 (F)	122–150 137	— ca. 2	11–37 ca. 25	6–8 ca. 7	—
W. L. Stern et al., 675 (GH)	122–136 130	2–3 ca. 2.5	20–26 ca. 22	9–10 10	—
C. malortieanus WENDL. Dodge et al., 5878 (MO)	110–118 114	1.5–2 ca. 1.5	10–22 ca. 18	7–8 ca. 8	—
Steiner, 1067 (Cult. Philipp.)	116–128 122	— ca. 2	— ca. 20	— ca. 8	—
C. montanus n.sp. (MAAS, ms.) Brenes, 22607 (NY)	100–116 110	3–3.5 ca. 3	18–24 ca. 20	6–8 ca. 8	—
C. pictus D. DON Ross, 12–58 (US)	92–116 106	3–4 ca. 3.5	10–12 ca. 10	7–8 ca. 8	—
C. pulverulentus PRESL Von Türckheim, 7686 (US)	104–127 111	2–3 ca. 2.5	16–24 ca. 20	8 —	—
Skutch, 2775 (GH)	104–138 128	— ca. 3	22–26 ca. 24	5–8 ca. 7–8	—
C. quasi-appendiculatus n.sp. WOODSON ex MAAS (MAAS, ms.) Krukoff, 10487 (U)	114–138 129	2–3 ca. 2.5	20–24 ca. 22	8 —	—
C. scaber RUIZ et PAVON Florschütz and Maas, 2474 (U)	96–116 107	— ca. 2	— ca. 22	8–12 ca. 9	—
C. scaber RUIZ et PAVON × *lasius* LOES. P. H. Allen, 4685 (U)	114–146 140	2–3.5 ca. 3–ca. 2	12–26 ca. 20–24	7–8 ca. 7	—
C. spicatus (JACQ.) SWARTZ Ernst, 1689 (US)	105–112 ca. 108	— ca. 2	— ca. 20	7–8 ca. 8	—
C. spiralis (JACQ.) ROSCOE Florschütz and Maas, 2790 (U)	114–128 121	2–3 ca. 3(2.5)	20–25 ca. 20	6–9 ca. 8	—

TABLE I *(continued)*

Taxon	*Pollen size (μ)*[1]	*Exine (μ)*[1]	*Porus diameter (μ)*[1]	*Number of pores*[1]	*Colpus spiral shaped and short colpus*
	106–112	3–4	20–30	6–7	—
Florschütz and Maas, 2788 (U)	108	ca. 3	ca. 25	6–7	
C. stenophyllus Standley et L. O. Williams	—	—	20–25	8	—
P. H. Allen, 6037 (US)	ca. 160	ca. 2	—	—	
C. villosissimus Jacq.	108–128	2–3	16–25	—	—
Cult. in C. (C)	121	ca. 2.5	ca. 22	7	
Costus congestiflorus type					
C. congestiflorus L. C. Rich. ex Gagnep.	110–134	4–7	—	6–9	—
Maas, 3166 (U)	121	ca. 5	ca. 10	ca. 8	
C. fragilis n.sp. (Maas, ms.)	138–160	—	12–22	—	—
Ducke, 14127 (RB)	148	ca. 5	ca. 20	6	
C. igneus N. E. Brown	130–150	—	14–20	11–14	—
Cult. in U (U)	142	ca. 8	ca. 18	12 or 13	
Costus warmingii type					
C. warmingii O. G. Pet.	180–210	—	18–24	11–16	—
Silva, 57750 (U)	195	ca. 2	ca. 20	ca. 11	
	158–170	—	00–25	10–12	—
Macedo, 1993 (MO)	162	ca. 2	ca. 20	ca. 11	
Dimerocostus subtype					
Dimerocostus strobilaceus O. Kuntze	114–124	4–5	—	sometimes 2	+
Ostenfeld, 75 (C)	117	ca. 4	—		

	162–190	3–4	—	sometimes 2	+
Pittier, 2307 (US)					
	144–200	3.5–4	—	rarely 2	+
Idrobo and Schultes, 844 (US)	178	ca. 4	—		
	162–194	—	—	2–several	+
Florschütz and Maas, 2533 (U)	178	ca. 4	—		
	154–176	3–4	—	sometimes 2	+
Wurdack, 2165 (US)	166	ca. 3.5	—		
	134–176	3.5–6	—	sometimes 2	+
Vargas, 14044 (US)	159	ca. 4	—		
D. argenteus nov. comb. (RUIZ et PAVON) MAAS[2]	144–184	4–5	—	—	+
Bang, 2058 (NY)	159	ca. 4	—	—	
Monocostus subtype					
M. uniflorus nov. comb. (POEP. ex O. G. PET.) MAAS[3]	118–154	—	—	sometimes 2	+
Klug, 4156 (US; GH)	140	ca. 1	—	—	

[1] In cases where two readings per specimen are given the first represents the total range and the second the average.
[2] Basionym: *Costus argenteus* RUIZ et PAVON, 1798, *Flora Peruv. Chil.*, 1: 3, t. 4.
[3] Basionym: *Costus uniflorus* POEP. ex O. G. PET., in Martius, 1890, *Flora Bras.*, 3(3): 58.

(*4*) *Diameter of pores* – (*a*) medium: usually ca. 15 μ (10–20 μ); (*b*) large: usually 20–25 μ (16–35 μ).

(*5*) *Colpi* – (*a*) spirally shaped; (*b*) straight or slightly curved.

Description of the pollen types

On the basis of these differential characters it is possible to establish four types and two subtypes:

Costus lima type: pantoporate; exine thin (*1a*); pollen grains large (*2a*); number of pores medium or large (*3*); diameter of pores usually large (*4b*).

Costus congestiflorus type: pantoporate; exine thick (*1b*); pollen grains large (*2a*); number of pores medium or large (*3*); diameter of pores medium (*4a*).

Costus warmingii type: pantoporate; exine thin (*1a*); pollen grains very large (*2b*); number of pores large (*3b*); diameter of pores large (*4b*).

Dimerocostus type: dicolpate or mixed colpate—porate. In dicolpate grains one spirally shaped colpus and a short colpus are present; in mixed grains one spirally shaped colpus and two pori are present. Pollen grains large (*2a*). This type comprises two subtypes, the *Dimerocostus* subtype: exine rather thick; and the *Monocostus* subtype: exine thin.

Costus lima type

Pollen grains pantoporate. Shape of the grains more or less ellipsoidal, slightly asymmetrical. Size of the grains large (ca. 120 μ, range 100–160 μ). Exine thin or rather thin, usually 2–3 μ (range 1.5–3.5 μ). The exine around the pori is slightly thicker. The exine wall is solid and smooth. No apparent distinction between sexine and nexine. Pores large, varying in size; usually 10–25 μ (rarely up to 38 μ in diameter). The outline of the pores is usually circular or slightly elliptical, the margins are rather sharply delimitated without a distinct annulus.

Costus congestiflorus type

Pollen grains pantoporate. Shape of the grains more or less ellipsoidal, slightly asymmetrical. Size of the pollen grains large (up to 160 μ). Exine thick (ca. 5 μ; up to 8 μ). The exine wall is solid and smooth. No apparent distinction between sexine and nexine. Pores rather small or large, diameter usually less than

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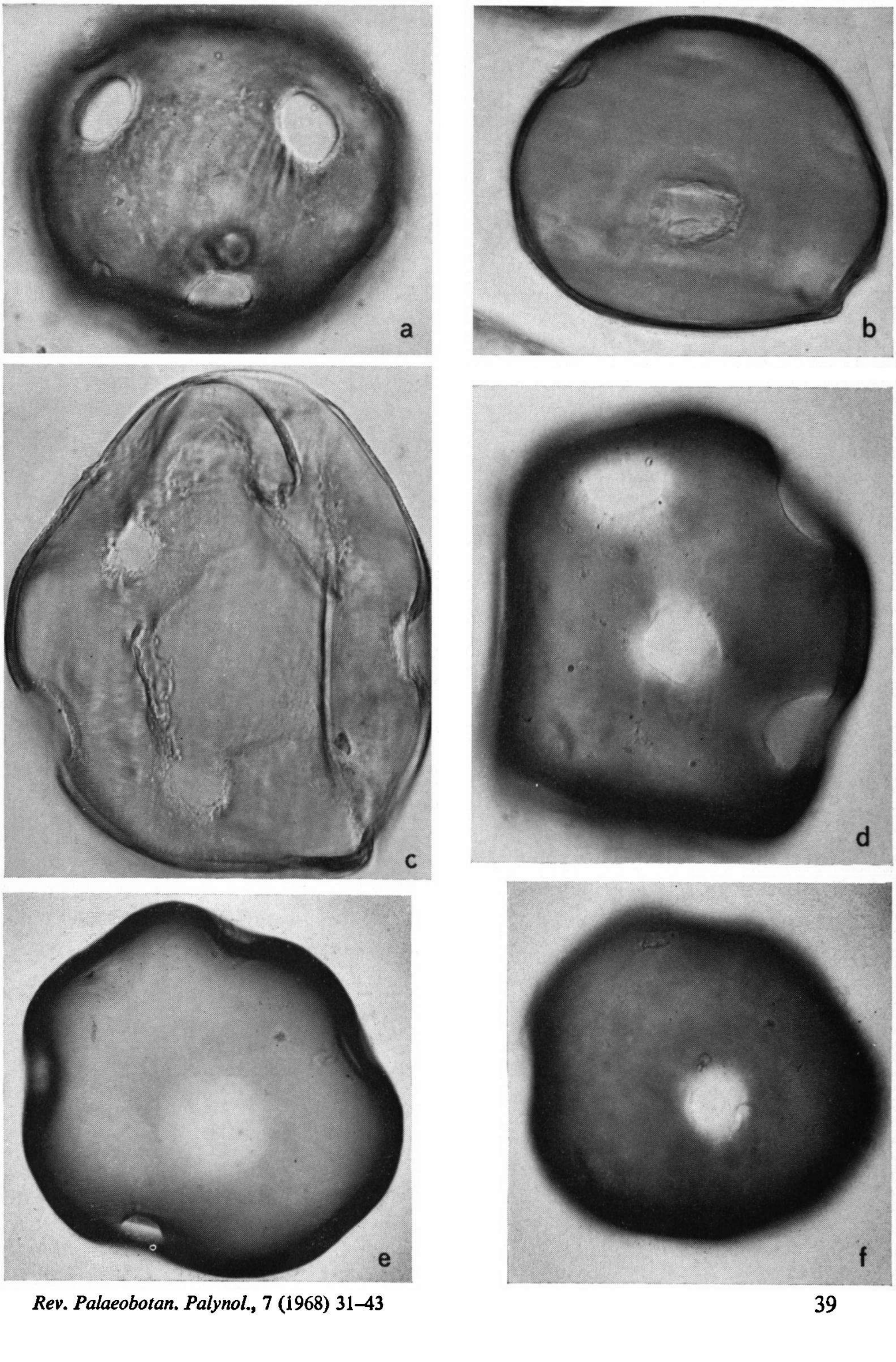
PLATE I

a. *Costus arabicus* L., × 640.
b. *Costus pictus* D. Don, × 640.
c. *Costus warmingii* O. G. Pet., × 640.
d. *Costus igneus* N. E. Brown, × 640.
e. *Costus congestiflorus* L. C. Rich. ex Gagnep.; optical section, × 640.
f. *Costus congestiflorus* L. C. Rich. ex Gagnep.; porus, × 640.

PLATE I



20 μ (range 10–22 μ). The outline of the pores is usually circular or slightly elliptical; the margins are rather sharply delimitated without a distinct annulus.

Costus warmingii type

Pollen grains pantoporate. Shape of the grains more or less spheroidal. Size of the pollen grains very large (up to 210 μ). Exine thin; exine wall solid and smooth. No apparent distinction between sexine and nexine. Number of pores large, usually 11 (range 10–16); the diameter of the pores large.

Dimerocostus type

Pollen grains dicolpate or mixed colpate and porate. The shape of the grains is more or less ellipsoidal, slightly asymmetrical. Size of the grains large or very large. Exine thin (*Monocostus* subtype) or thick (*Dimerocostus* subtype). The exine wall is solid and smooth. No apparent distinction between sexine and nexine. All grains have a long spirally shaped colpus ("spiralaperturate", ERDTMAN, 1952) and in addition to this aperture most of the grains also have a straight or only slightly curved colpus. The latter colpus is short and frequently swollen at the ends thus forming a dumb-bell shaped aperture. In several cases transitions from dumb-bell shaped apertures to pores may occur together in one slide.

In one preparation more than the normal two pores were present (up to six).

Dimerocostus subtype: exine thick (ca. 4 μ).

Monocostus subtype: exine extremely thin (ca. 1 μ).

DISCUSSION

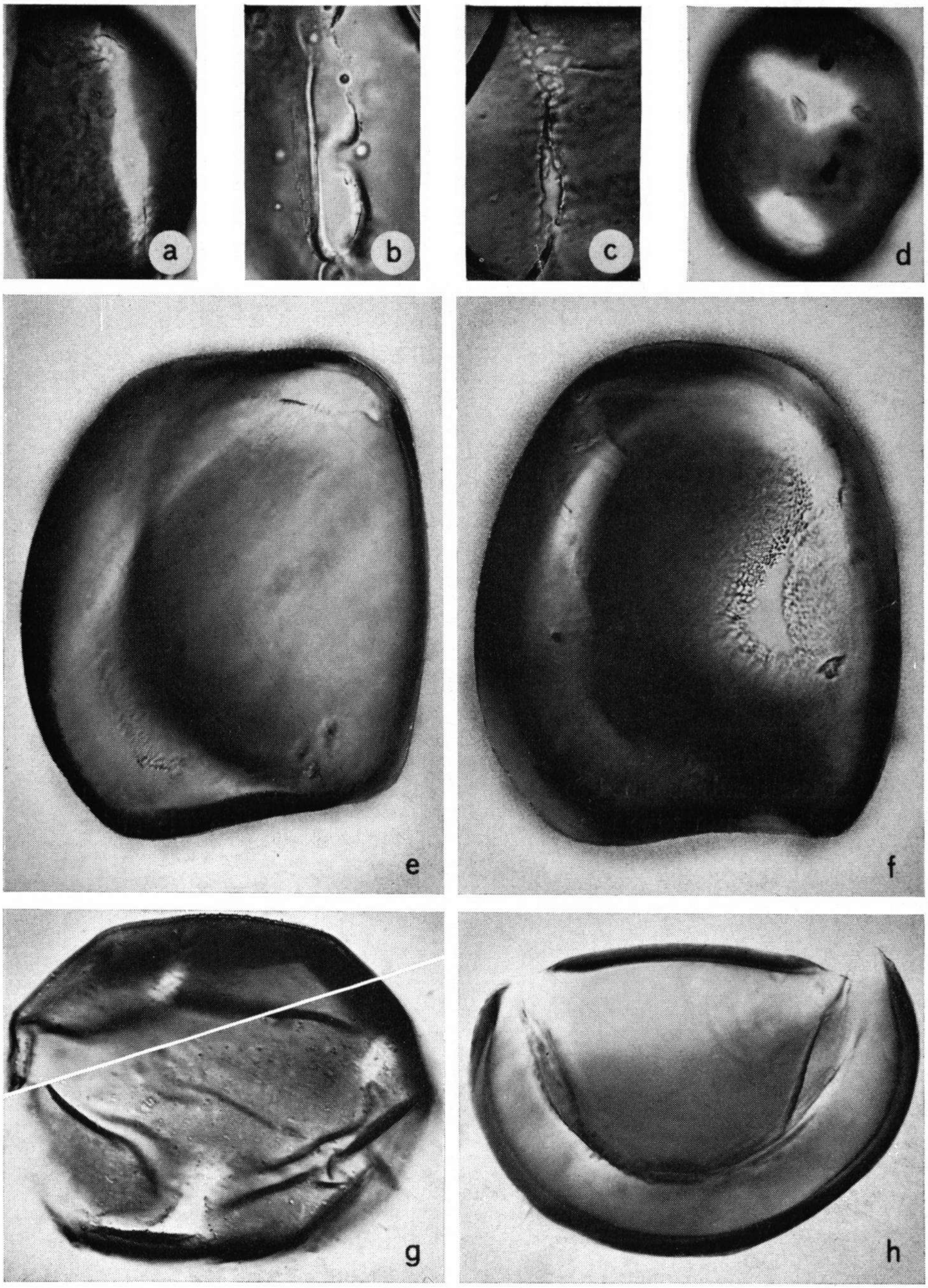
Relations with other families

All types resemble each other to a certain degree. The homogeneous exine is particularly striking since this feature is not met with frequently in angiosperm pollen. According to ERDTMAN (1952) indistinct stratification occurs in Musaceae, Marantaceae, Cannaceae and Araceae in the monocotyledons, and Asclepiadaceae

PLATE II

a. *Dimerocostus:* short colpus, × 400.
b. *Dimerocostus:* dumb-bell.
c. *Monocostus:* dumb-bell.
d. *Dimerocostus:* two pori, × 400.
e. *Dimerocostus argenteus* (RUIZ et PAVON) MAAS, × 640.
f. *Dimerocostus argenteus* (RUIZ et PAVON) MAAS, × 640.
g. *Monocostus uniflorus* (POEP. ex O. G. PET.) MAAS, × 640.
h. *Dimerocostus strobilaceus* O. KUNTZE, × 640.

PLATE II



in the dicotyledons. The constantly large size within the Costoideae is also worthy of note, although this character is found in other groups of angiosperms as well.

Evolutionary trends in Costoideae

As mentioned above, *Dimerocostus* and *Monocostus* are characterized by a long spirally shaped colpus combined with a short, straight or slightly curved colpus, which is frequently replaced by a dumb-bell shaped aperture or by two pori. It is remarkable that the short colpi and the two separate pori of *Dimerocostus* and *Monocostus* occur together in one flower. If we assume that the transition from colpi to pori is an evolutionary trend as indicated in other taxa of the angiosperms (e.g., in *Phyllanthus*, by PUNT, 1967; and in the Centrospermae, by VAN CAMPO, 1967) then *Dimerocostus* and *Monocostus* may be considered relatively primitive in comparison with the pantoporate types of *Costus*.

Costus shows the most advanced pollen grains of the subfamily in America. All *Costus* types are pantoporate with a total number of pores varying from five to sixteen. It is not certain which number of pores must be considered the most primitive (seven and eight are the most common numbers). It is even less certain that the origin of the pores is actually homologous with the colpi and pori in the *Dimerocostus* type. However, it is likely that more than eight pores might be considered a progressive trend and accordingly the *Costus warmingii* type is taken to be a derivative type from the *Costus lima* type.

Furthermore, it seems logical that the thick exine of the *Costus congestiflorus* type is an advanced character. Consequently, this type is considered less primitive than the *Costus lima* type.

These trends assumed for the Costoideae are highly speculative and it is not at all certain that the same trends observed in other taxa of the angiosperms can be applied to the Zingiberaceae.

Variations within the types

Dimerocostus type

Much variation was observed in the four collections of *Dimerocostus strobilaceus*. The collection Ostenfeld 75 shows much smaller pollen grains than the other ones. The slide shows perfect, well-developed, undeformed pollen grains. It is not clear why the size of the pollen grains is, in this case, so aberrant from other collections.

The collection Florschütz and Maas 2533 has pollen grains with several pori (up to six), while the other collections only rarely show two pori in place of the short colpus.

Costus types

In the genus *Costus* three different types have been described. All types are pantoporate and, therefore, it might seem logical to unite these types into one large type. However, the three types can be easily recognized and are based on more than one differential character. It, therefore, seems better to establish separate types instead of subtypes.

Most species belong to the *Costus lima* type. The variation in size, number of pores and diameter of pores is large. All species, however, have a thin exine and have a large size. According to their size some species have pollen grains, which are transitional with the *Costus warmingii* type *(Costus fusiformis, Costus stenophyllus)*. On the basis of the thickness of the exine other species are found to be intermediate between the *Costus lima* type and the *Costus congestiflorus* type; e.g., *Costus montanus, Costus pictus* and *Costus pulverulentus*.

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