A PALYNOLOGICAL STUDY IN GEONOMOID PALMS

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INTRODUCTION

In a previous palynological study in Cocoid palms the present authors (PUNT and WESSELS BOER, 1966) were able to demonstrate a rather strong but not absolute correlation between the pollen types and the staminate flower types within the genus *Attalea* in the broad sense. The existence of partly apparently primitive, partly very advanced flower types within the otherwise close related group of Geonomoid palms made it worthwhile to investigate the same feature in this group.

The Geonomoid palms are usually considered to comprise 7–9 genera of monoecious Arecoid palms which share a large number of characteristics (BURRET, 1930; MOORE, 1966). The group is very obviously a most natural one. The generic distinctions are mainly based on the flower morphology, notably on differences found in the androeceum and pistil.

Staminate palm flowers in general have most frequently 2 whorls of 3 stamens, rarely 1 whorl is lacking or, more frequently, a larger number of stamens or many stamens are present. Usually the anthers consist of 2 lengthwise connected thecae, sagittate at base, dorsifixed and erect in bud. Sometimes rather far derived forms occur. The complete series is observed within the Geonomoid palms. *Welfia* and *Aristeyera* have many stamens per male flower (about 20–40); *Calyptrogyne*, *Calyptronoma*, *Pholidostachys*, *Asterogyne*, *Geonoma*, and *Taenianthera* have 6 stamens; *Kalbreyera* has only 3 stamens. Also the shape of the stamens differs much in the different genera. *Welfia*, as well as *Calyptrogyne*, *Calyptronoma*, and *Pholidostachys* have the above described dorsifixed sagittate anthers erect in bud (Fig. 1). A more unusual type of stamens occurs in *Asterogyne*, *Kalbreyera*, and *Geonoma*. These genera have stamens with separate thecae born on a bifurcate connective and forming, also at anthesis, a sharp angle with the filament (Fig. 2). This stamen type can be derived from the normal type by a hypothetical reduction of the upper part of the thecae (Fig. 3). The bifid connective is again much more developed in *Aristeyera* and *Taenianthera*, bearing separate thecae at its terminal end. This connective with the thecae is inflexed in bud and becomes erect, in line with the filament, at anthesis (Fig. 4).

The pistil of palms in general consists usually of 3 free or more or less united carpels. Also in Geonomoid palms a 3-celled ovary with a terminal style having 3 recurved style branches is found in most genera (Fig. 5). *Geonoma* and *Taenianthera*, however, form an exception.

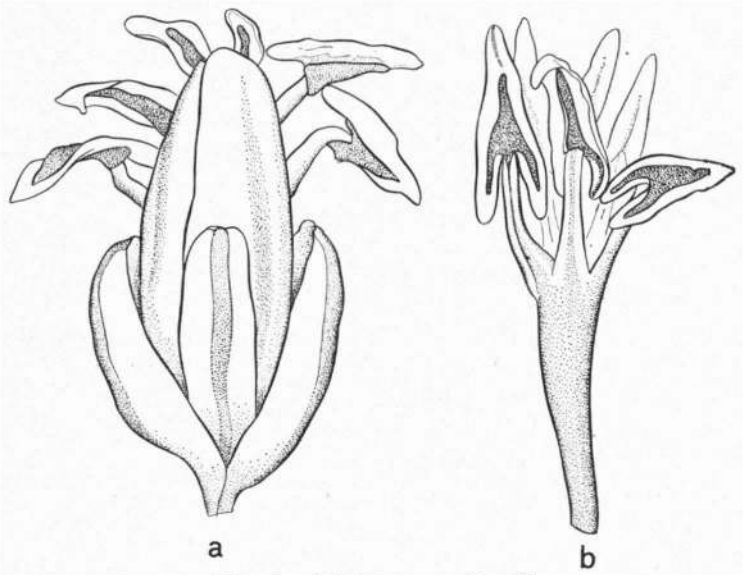


Fig. 1. *Calyptronoma occidentalis*
a. staminate flower; b. androeceum (Ekman H15685, Hispaniola).

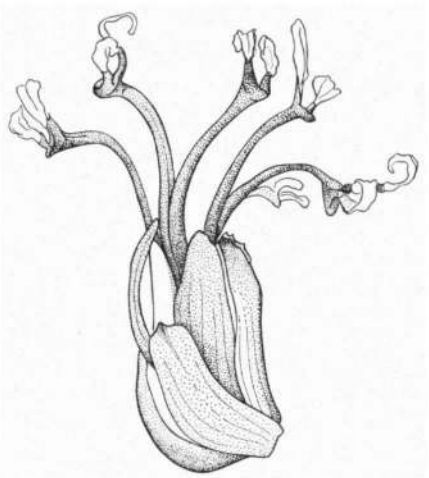


Fig. 2. *Geonoma baculifera*
Staminate flower (Killip 37437, Venezuela).

These genera have, by reduction of 2 locules, a 1-celled ovary with a basifixed style ending in 3 recurved style branches (Fig. 6). Also the degree of fusion of the staminodes in the pistillate flowers shows some variation. In most genera the staminodes are more or less connate at the base and free in the upper part (Fig. 5). In *Kalbreyera* and the majority of *Geonoma* species, the subgenus *Eugeonoma* of Burret, the

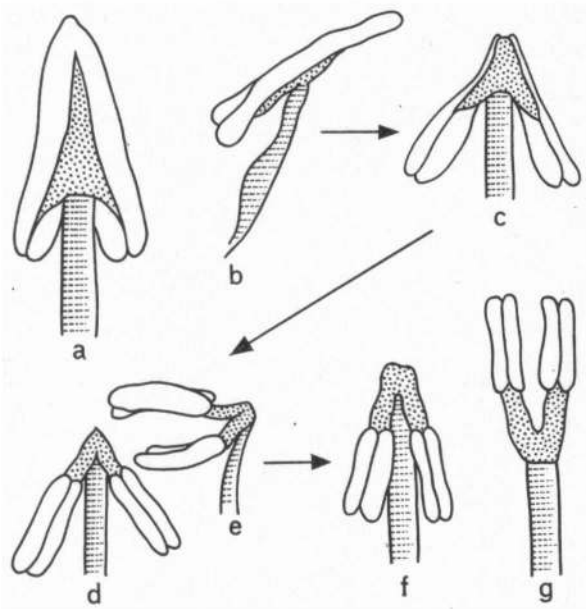


Fig. 3.
Scheme of the series of stamen types. a and b. Welfia type; c. theoretical intermediate; d. and e. Geonoma type; f. and g. Taenianthera type.

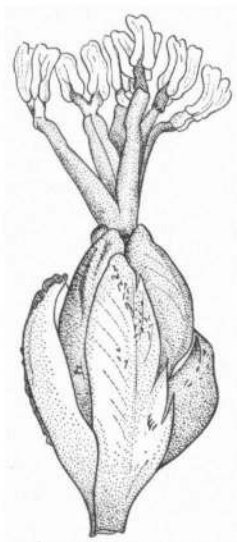


Fig. 4. *Geonoma* (= *Taenianthera*) *poiteauana*.
Staminate flower (Hulk 284, Suriname).

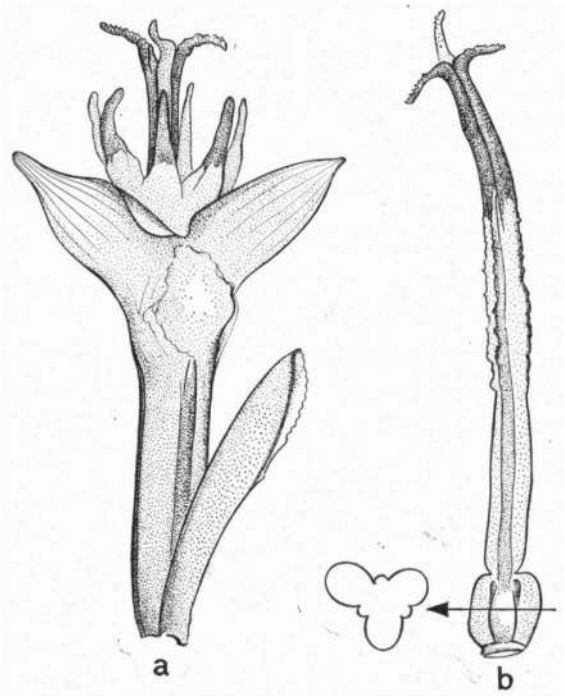


Fig. 5. *Asterogyne martiana*
a. pistillate flower; b. pistil (Englesing 350, Nicaragua).

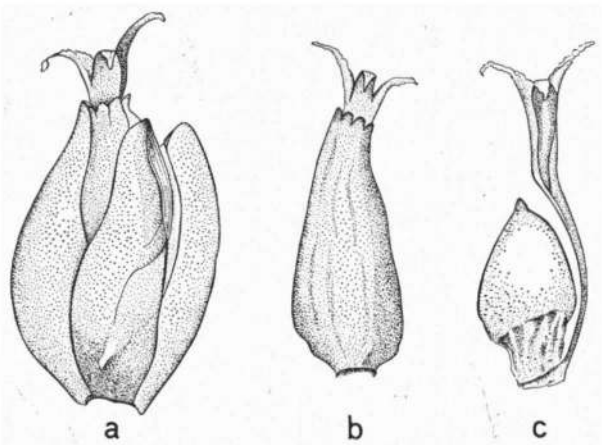
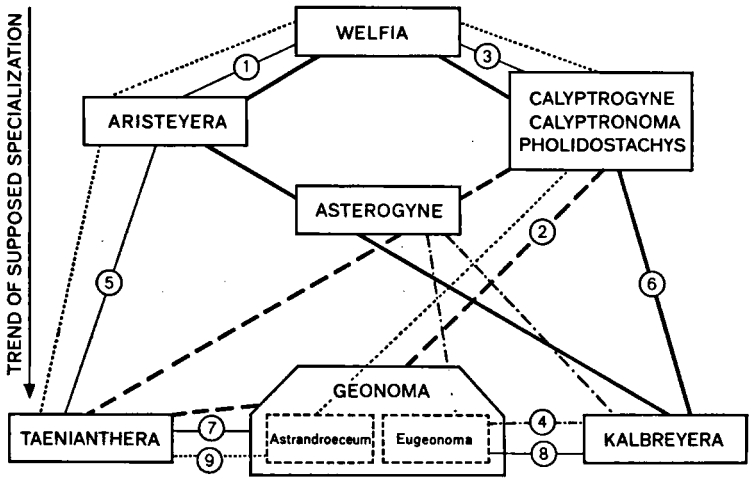


Fig. 6. *Geonoma simplicifrons*
a. pistillate flower; b. staminodial tube enclosing pistil; c. pistil (Killip and Lasser 37802, Venezuela).

staminodes are almost completely connate forming a truncate or slightly crenulate staminodial tube (Fig. 6).

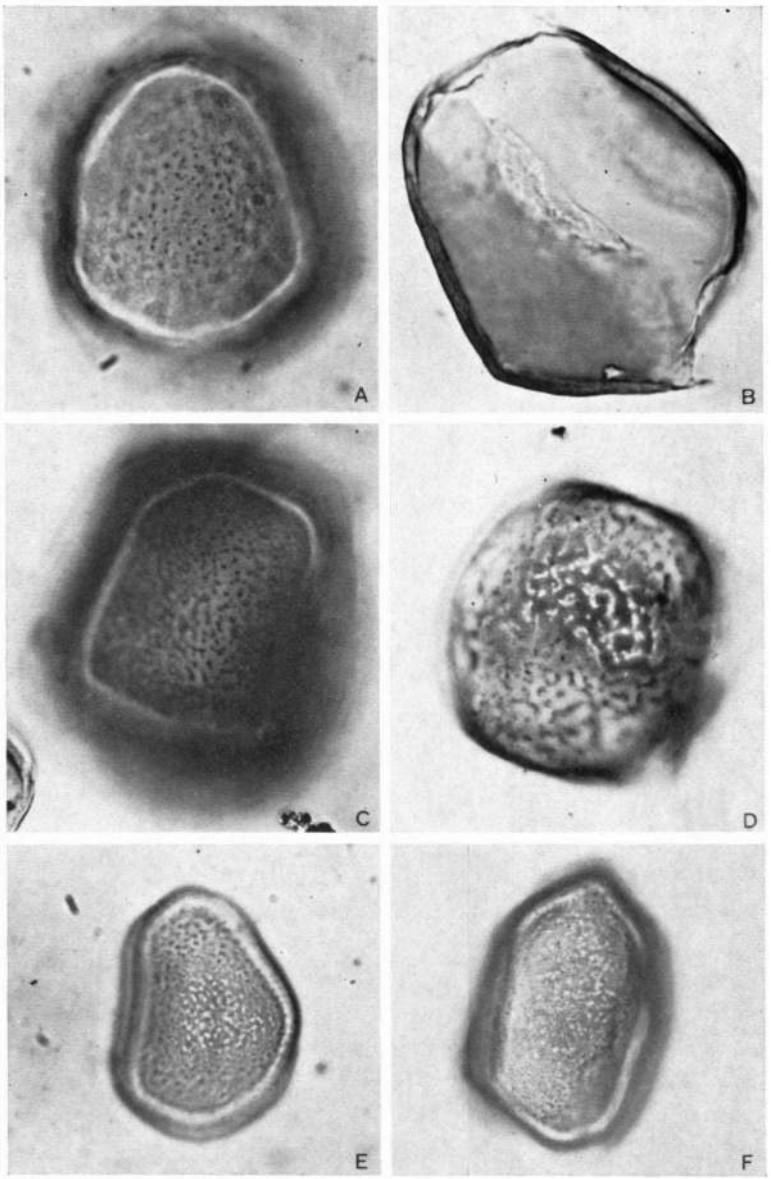
The occurrence of the different flower characteristics in the separate genera is visualized in the next scheme.



① numerous stamens
② 6 stamens
③ dorsifixed sagittate anthers with connected thecae
④ free thecae at anthesis sharply deflexed
⑤ free thecae at anthesis in line with the filament
⑥ 3-celled pistil
⑦ 1-celled pistil
⑧ staminodial tube crenate or truncate
⑨ staminodial tube digitate or lobate

The genus *Kalbreyera* was founded on a single Kalbreyer collection and never found again. As the type specimen got lost during war-time at Berlin the genus could not be investigated in the present study.

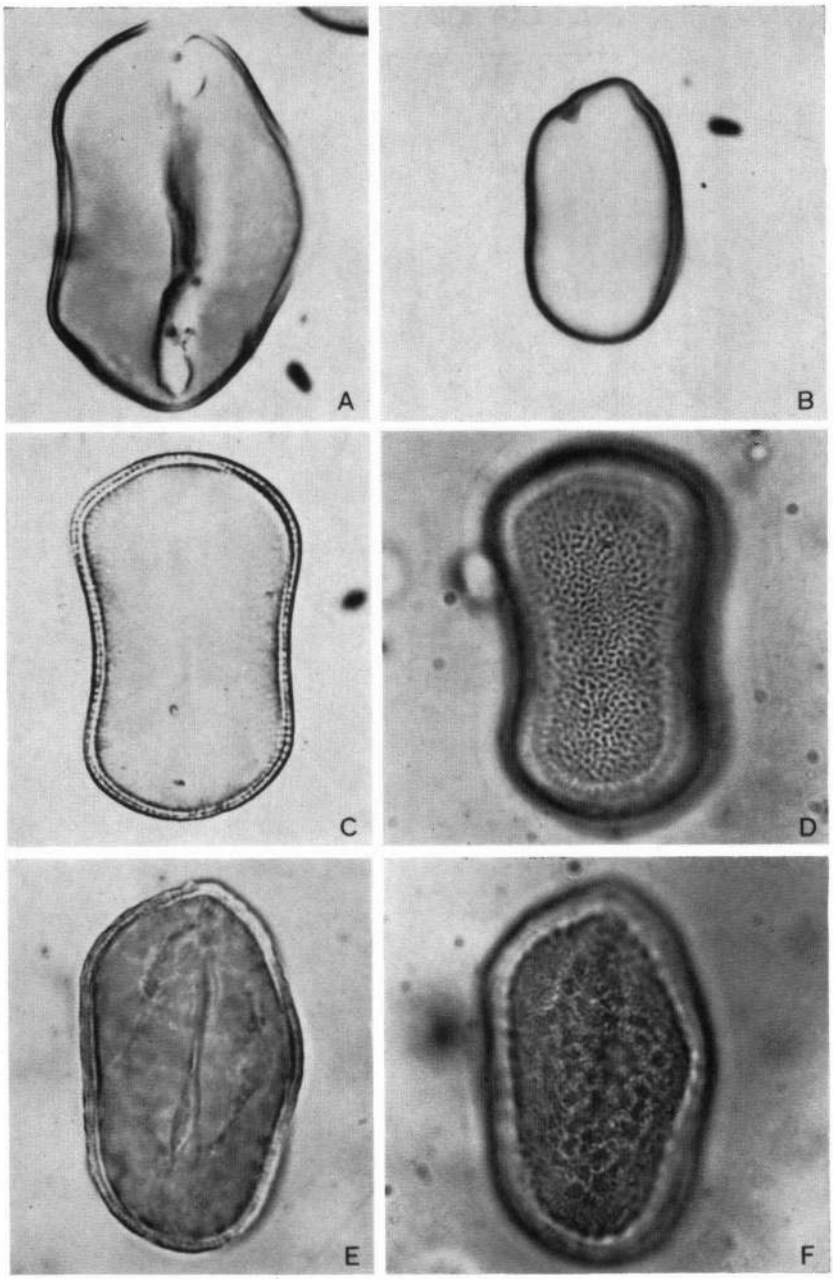
The herbarium material used for this study was mostly obtained from the Utrecht Botanical Museum and Herbarium, and from sheets, which the second author has on loan from several other herbaria. The treatment of the pollen grains was according to the method described by ERDTMAN in 1960. Descriptions have been made with the aid of a Leitz Ortholux microscope, apochr., obj. × 63, × 90 and an eyepiece × 10. Photographs were made with the same microscope and lenses. The same terminology was used as in the previous study of palm pollen grains (PUNT and WESSELS BOER, 1966).



A. and B. *Calyptrogyne donnell-smithii*; A. surface pattern at proximal pole, B. optical section. C. *Calyptronoma clementis*; surface pattern at proximal pole. D. *Calyptronoma occidentalis*; surface pattern at proximal pole. E. *Taenianthera tamandua*; surface pattern at proximal pole. F. *Geonoma poiteauana*; surface pattern at proximal pole.

PLATE I

Facing p. 270



A. *Welfia georgii*; optical section. B. *Geonoma schottiana*; optical section. C. and D. *Astrogyne martiana*; C. optical section, D. surface pattern at proximal pole. E. and F. *Pholidostachys pulchra*; E. optical section, F. surface pattern at proximal pole.

Plate II

Description of the material

In the Geonomoid palms the pollen grains do not have many distinctive characters. The grains are always monocolpate. In this respect they differ from the Cocoid palms, in which several species have a mixture of monocolpate and trichotomocolpate grains. The shape of the grains is usually slightly asymmetric, although there are some species having pollen grains which are nearly symmetric. Usually the longest axis of the grains, which follows the colpus, is distinctly larger than the diameter perpendicular on this axis. This diameter is largest when the pollen grains are observed from the distal or from the proximal view. In some pollen types (Calyptrogyne glauca type) the ratio between the two axes is nearly equal.

It is possible to group species into pollen types largely differentiated from one another on the basis of the exine characters. As was found in the Cocoid pollen grains the Geonomoid pollen grains show transitions from one type to another. The Geonoma type seems to be the basic type from which all other types can be derived. Several series of pollen variation can be constructed. One series can be made from small grains to large ones (e.g. *Geonoma schottiana* and allied forms → Welfia spec.). Another series is from thin exine without structure to thicker exine with distinct structure. This thickness is caused by the larger columellae and capita. Two types of structure can be distinguished:

1. Reticulate structure (Asterogyne type)
2. Vermiculate structure (Calyptronoma occidentalis type)

Geonoma type

Pollen grains monocolpate. Shape of the grains slightly irregular; the longest axis usually distinctly larger than the largest breadth. Sometimes the ratio between the axes is nearly equal. Grains usually between 30 and 40 μ. In *Welfia* the grains are larger.

Exine thin. Sexine (ektexine) thicker than nexine (endexine). Columellae usually indistinct. Most species have indistinct capita. Some species have capita which are more or less visible (*Geonoma stricta, G. piscicauda*).

To this type belong *Geonoma baculifera, G. deversa, G. interrupta, G. leptospadix, G. maxima, G. piscicauda, G. pohliana, G. schottiana, G. stricta, G. umbraculiformis, G. undata, Calyptronoma kalbreyeri, Calyptronoma synanthera, Welfia georgii,* and *W. regia.* ? *Geonoma poiteauana* and *Taenianthera tamandua.*

The Geonoma type is a type with rather indistinct characters. The pollen grains are rather small, the shape is slightly asymmetric with one usually noticeably longer axis and an exine without a distinct structure. In this basic type, however, some species are transitional in that they have certain characters typical of the types with a distinct ornamentation.

A. The *Welfia* species have pollen grains which are larger than those of the other species in the Geonoma type.
B. Some species have pollen with more distinct capita (e.g. *Geonoma*

deversa, G. piscicauda, Calyptronoma kalbreyeri). The pollen grains of *Geonoma stricta* have distinct capita and rather large columellae.

C. In *Geonoma umbraculiformis* the pollen grains have a rather thick exine (ca 2 μ) and the tectum is distinctly perforated. In this respect this species is transitional to *Geonoma poiteauana* and *Taenianthera tamandua* and also to the Calyptrogyne glauca type.

D. The pollen grains of *Geonoma poiteauana* and *Taenianthera tamandua* seem to be transitional to the Asterogyne type.

Asterogyne type

Pollen grains monocolpate. Shape only slightly asymmetric. Longest axis distinctly longer than the greatest breadth. Grains rather large; ca 45 μ. Exine rather thin. Sexine (ektexine) thicker than nexine (endexine). Grains finely, but distinctly reticulate. Columellae distinct. Lumina small; ca 1 μ, muri simplibaculate.

Asterogyne martiana, Taenianthera acaulis.
Geonoma poiteauana and *Taenianthera tamandua* are transitions to the Geonoma type.

The Asterogyne type can easily be recognised by its fine, but distinct reticulum. The muri (bacula) forming this reticulum are distinctly visible.

Geonoma poiteauana and *Taenianthera tamandua* have pollen grains which are very similar in most characters. However, the perforations in the *Taenianthera* species are larger than in the *Geonoma* species.

The pollen grains of these species are transitional between the Geonoma type and the Asterogyne type. The columellae are indistinct which character is in accordance with that in the Geonoma type. The distinct capita and large perforations in the tectum are characters which occur in the Asterogyne type. On the other hand the perforations are too small to call them a reticulum.

There is also a possibility that *Geonoma poiteauana* is a transition to the Calyptrogyne glauca type. The tectum perforatum is a character which occurs in this type too, but the shape of the grains is more in accordance with the Geonoma and Asterogyne types.

Calyptrogyne glauca type

Pollen grains monocolpate. Shape of the grains slightly asymmetric, more or less spheroidal. Longest axis slightly longer than the greatest breadth. Grains rather large; at least 40 μ. Exine thick. Sexine (ektexine) thicker than nexine (endexine). Tectum thick, slightly undulating. Perforations present in the tectum. These perforations inordinate arranged or sometimes in very short chains. Capita indistinct, columellae indistinct.

Calyptronoma clementis, Calyptronoma intermedia, Calyptrogyne donnell-smithii, Calyptrogyne glauca, Calyptrogyne trichostachys.

The type is characterised by the thick, slightly undulating tectum; by the inordinate arrangement of the perforations in the tectum and by its shape.

Calyptronoma occidentalis type

Pollen grains monocolpate. Longest axis larger than the greatest breadth. Grains rather large; at least 40 μ. Exine thick. Sexine (ektexine) thicker than nexine (endexine). Tectum thick, distinctly undulating. Perforations in the tectum arranged in chains. Ornamentation "vermiculate". Capita and columellae indistinct.

Calyptronoma occidentalis, Calyptrogyne brachystachys, Pholidostachys pulchra, Aristeyera spicata.

This type is characterised by its vermiculate ornamentation. Although *Pholidostachy spulchra* differs from the other three species in this type by the shape and largeness of the grains, the vermiculate ornamentation is so distinct, that it seems better to place the species in this type.

LIST OF INVESTIGATED SPECIES

Aristeyera spicata H. E. Moore — Tamayo 4177 (US)
Calyptronoma occidentalis type. Longest axis ca 50 μ. Exine ca 2,5 μ.

Asterogyne martiana (Wendl.) Wendl. [Plate II C, D]
Archer 1978 (US)
Schipp 392 (K)
Asterogyne type. Longest axis ca 45 μ. Exine ca 2 μ. Lumina of the reticulum ca 1 μ.

Calyptrogyne brachystachys Wendl. ex Burret — Standley et Valerio 44775 (US)
Calyptronoma occidentalis type. Longest axis ca 55 μ. Exine ca 2,5 μ. Perforations rather few in short chains, nearly inordinate.

Calyptrogyne donnell-smithii (Dammer) Burret [Plate I A, B]
H. Johnson 1135 (US)
Calyptrogyne glauca type. Longest axis ca 60 μ. Exine ca 2,5 u.

Calyptrogyne glauca (Oerst.) Wendl. — Pittier 4305 (US)
Calyptrogyne glauca type. Longest axis ca 55 μ. Exine ca 2 μ.

Calyptrogyne trichostachys Burret — Stork 117½ (US)
Calyptrogyne glauca type. Longest axis ca 60 μ. Exine ca 1,5 μ.

Calyptronoma clementis (León) A. D. Hawkes [Plate I C]
Wright 1466 (P)
Calyptrogyne glauca type. Longest axis ca 40 μ. Exine ca 2 μ.

Calyptronoma intermedia (Griseb. et Wendl.) Wendl. — Wright 3972 (P)
Calyptrogyne glauca type. Longest axis ca 40 μ. Exine ca 2 μ.

Calyptronoma kalbreyeri (Burret) Bailey — Killip et Smith 15314 (US)
Geonoma type. Longest axis ca 35 μ. Exine ca 1,5 μ. Capita distinct.

Calyptronoma occidentalis (Sw.) H. E. Moore [Plate I D]
Wessels Boer 1662 (U)
Calyptronoma occidentalis type. Longest axis ca 50 μ. Exine ca 3 μ.Perforations distinctly in chains.

Calyptronoma synanthera (Mart.) Bailey — Pavon s.n. (M)
Geonoma type. Longest axis ca 38 μ. Exine ca 1 μ.

Geonoma baculifera (Poiteau) Kunth — Wessels Boer 325 (U)
Geonoma type. Longest axis ca 35 μ. Exine ca 1 μ.

Geonoma deversa (Poiteau) Kunth — Wessels Boer 320 (U)
Geonoma type. Longest axis ca 30 μ. Exine 1–1,5 μ. Capita visible.

Geonoma interrupta (Ruiz et Pavon) Mart. — Wessels Boer 1635 (U)
Geonoma type. Longest axis ca 30 μ. Exine ca 1 μ.

Geonoma leptospadix Trail — Wessels Boer 912 (U)
Geonoma type. Pollen grains not quite mature.

Geonoma maxima (Poiteau) Kunth — Wessels Boer 1617 (U)
Geonoma type. Longest axis ca 30μ. Exine ca 1 μ

Geonoma piscicauda Dammer — Rombouts 880 a (U)

Geonoma type. Longest axis ca 45 μ. Exine ca 1,5 μ. Capita rather distinct.

Geonoma pohliana Mart. Reitz et Klein 2338 (HBR)

Geonoma type. Longest axis ca 35 μ. Exine 1–1,5 μ.

Geonoma poiteauana Kunth [Plate I F] Wessels Boer 1579 (U)

Asterogyne type. Longest axis ca 40 μ. Exine 1,5 μ. Rather thick tectum with distinct perforations, which are so large that it is a transition to a reticulum.

Geonoma schottiana Mart. [Plate II B] Reitz et Klein 9655 (HBR)
Foster 2503 (SPL)

Geonoma type. Longest axis ca 30 μ in Reitz et Klein specimen and 38 μ in the Foster specimen (ERDTMAN, 1952). Exine ca 1 μ.

Geonoma stricta (Poiteau) Kunth Wessels Boer 1558 (U)

Geonoma type. Longest axis ca 40 μ. Exine ca 1,5 μ. Capita and collumellae rather distinct.

Geonoma umbraculiformis Wessels Boer Versteeg 322 (U)

Geonoma type. Longest axis ca 40 μ. Exine thick; ca 2 μ. Capita distinct. Perforations in the tectum inordinate arranged. Transition to the pollen of *Geonoma poiteauana*.

Geonoma undata Klotzsch Linden s.n. (L)

Geonoma type. Longest axis ca 35 μ. Exine ca 1 μ.

Pholidostachys pulchra Wendl. ex Burret [Plate II E, F]
Standley et Valerio 48937 (US)

Calyptronoma occidentalis type. Longest axis ca 40 μ. Exine ca 1,5 μ.

Taenianthera acaulis (Mart.) Burret Ule 5594 (L)

Asterogyne type. Longest axis ca 45 μ. Exine 1,5–2 μ.

Taenianthera tamandua (Trail) Burret [Plate I E] Benoist 1708 (P)

Geonoma type or Asterogyne type. Longest axis ca 45 μ. Exine ca 1,5 μ. Perforations in tectum larger than in *Geonoma poiteauana*.

Transition between the Geonoma type and the Asterogyne type.

Welfia georgii Wendl. ex Burret [Plate II A] Wendland s.n. (K)

Geonoma type. Longest axis ca 45 μ. Exine ca 1,5 μ.

Welfia regia Wendl. Cuatrecasas 16932 (US)

Geonoma type. Longest axis ca 55 μ. Exine ca 1,5 μ.

DISCUSSION

As may be clear from the introduction, it is hardly possible to detect any correlation with the floral characteristics. In this case pollen morphology proves to be of little help in classification. The flowers as well as the pollen grains of *Welfia* seem to be less advanced. The apparently highly specialized flowers of *Geonoma* have pollen of the same type but smaller.

Most remarkable is the situation in the genera *Calyptrogyne*, *Calyptronoma*, and *Pholidostachys*. These genera, all with the same type of flowers, have been separated on the structure of inflorescence and fruit. Here the pollen morphology of the species belonging to these genera proved to be rather heterogeneous. The pollen diversity, however, is in disagreement with the other characteristics. The pollen of *Calyptronoma occidentalis* and the hardly distinguishable *C. clementis* and *C. intermedia* belong to different types. Furthermore the very closely related *C. kalbreyeri* and *C. synanthera* differ much in their pollen types which are placed in the Geonoma type and the Calyptronoma occidentalis type respectively.

The same holds true for Calyptrogyne: *C. brachystachys* has pollen of the Calyptronoma occidentalis type; pollen of the other investigated species is referred to a Calyptrogyne glauca type.

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