A PALYNOLOGICAL STUDY IN COCOID PALMS

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INTRODUCTION

Because the palm family is almost entirely tropical with many species of a very great size, it has attracted only a few botanists to study them. As a consequence palms are poorly represented in herbaria and little understood in almost every respect. Notably their taxonomy is in a very poor condition since many taxa are described on inadequate material which allows only an arbitrary interpretation and, moreover, the family is grossly overnamed. Hence the second author (1965) proposed a large-scale lumping in his critical treatment of the Suriname palms. The present paper is intended to give some palynological evidence to support a few of these lumpings on the generic level.

Palynological evidence shall especially be rewarding in the genus Attalea in the broad sense inclusive of Maximiliana, Markleya, Orbignya, Parascheelea and Scheelea. These genera have been separated on the morphology of the staminate flowers only; no correlation with other characters could be worked out in a satisfactory way. Apart from the very distinct staminate flower types representing Attalea, Maximiliana, Orbignya, and Scheelea, in recent times also a few intermediate flower types have been found, again evaluated as separate genera: Markleya and Parascheelea. The main argument for accepting these single character genera is a feeling that the evolution of the staminate flowers in the palms has been very extraordinary. If this feeling is correct, it may be expected that the differences in the staminate flower morphology run parallel with the differences in the pollen morphology. To check this was one of the purposes of the investigation the results of which are presented in this paper.

Also the pollen morphology of the genus *Elaeis* in the broad sense was studied. The three species belonging to this genus have been separated into three monotypic genera based on very poor morphological evidence and these, consequently, were not accepted by the second author (1965).

Finally, a superficial exploration was done in the group of prickly Cocoid palms, referred to a separate group of Bactroid palms by TOMLINSON (1961).

As both groups resemble each other so much in several respects it is interesting to learn if this anatomical separation is in agreement with the pollen morphology.

Herbarium material has been used from the Botanical Museum and Herbarium, Utrecht (U), collection Wessels Boer. The investigation was also based on a large duplicate set of slides from the slide collection of the Shell Research N.V., which N.V. was so kind to supply these slides. Material from which this set was prepared was largely obtained from the herbaria at Berlin (B) and Genève (G).

Descriptions have been made with the aid of a Leitz Ortholux microscope, apochr. obj. \times 63, \times 90 and an eye piece \times 10. Photographs were made with the same microscope and lenses in combination with a Leitz Orthomatcamera. The magnification of the drawings and photographs are given in the text.

POLLEN MORPHOLOGY

Up till now only few publications on the pollen grains of palms have been published. The largest number of descriptions is found in ERDTMAN's book "Pollen Morphology and Plant Taxonomy" (1952). He described among others the pollen of Attalea princeps, Cocos nucifera, and Maximiliana venatorum. Elaeis guineensis was examined by ZEVEN (1964), and NAIR and SHARMA (1963) studied the variability of the pollen grains in different varieties of Cocos nucifera.

The following groups of characters are important in describing pollen grains: 1. the apertures, 2. the shape, and 3. the exine.

1. The apertures

Two different kinds of apertures have been observed in palm pollen: a) pollen grains with 1 colpus, the monocolpate grains, and b) pollen grains with a threeslit colpus, the trichotomocolpate grains. These apertures are situated at the distal part of the grain (ERDTMAN, 1952).

Most species have grains that show monocolpate grains only, e.g. Attalea cohune, Attalea tessmannii, and Scheelea dryanderae. Several species are a mixture of both kinds of apertures. However, in each of these species monocolpate grains prevail, e.g. Attalea insignis and Attalea sagotii. In Attalea maripa¹) trichotomocolpate grains occur frequently and Attalea oleifera has trichotomocolpate grains only.

The two kinds of apertures are not likely to be of much taxonomical value.

Altogether there seems to be a trend, that trichotomocolpate grains occur less frequently in the Orbignya type (*Attalea sagotii* only) than in the Scheelea type (most species of this type).

2. The shape

The shape of the grain depends upon the kind of aperture. Trichotomocolpate pollen grains are regular triangular. Monocolpate grains are oblong or oval and usually asymmetric. The longest axis of the grain coincides with the length of the colpus. The largest breadth is usually found not in the middle, but shifted towards one end of the

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¹) The name Maximiliana regia is illegitimate as it is a later homonym of the Bixaceous Maximilianea regia. The combination Attalea regia (Martius) W. Boer (1965) is antedated by Attalea maripa (Correa de Serra) Martius, based on Palma maripa Correa de Serra, Ann. Mus. Hist. Paris 8: 75.1806. Aublet's use of "Palma maripa" cannot be considered to be more than a listing of a vernacular name.

pollen grain. Some species in the Scheelea type, in fact those with a very thick exine, have a more rectangular shape. In equatorial view (transverse position, ERDTMAN, 1952) the pollen grains are kidney shaped.

3. The exine

The exine is very important and provides the most constant characters. In palm pollen three layers can be distinguished with a light microscope: a) the capita-layer, b) the columellae-layer, and c) the endexine.

a) capita-layer. The capita are fused to a tectum which is still perforated (tectum perforatum). The fused capita may form different structures. In the Scheelea type patches sometimes are formed. In the Orbignya type the fusing of the capita results in vermiculate streaks, but in the Maximiliana type the fusing does not give rise to any special pattern. Sometimes the capita are fused laterally only, thus forming a reticulum. This structure is seen in Attalea tessmannii.

b) columellae-layer. Columellae support the tectum. These elements can be low or high and distinct or indistinct.

c) endexine. Except for its thickness this layer is not differentiated any further.

In the description of the wall of pollen grains we refer to the proximal side of the grain. The thickness of the exine is less at the distal side where the aperture is situated and here the structure is usually fainter or is even missing.

POLLEN TYPES IN ATTALEA s.l.

Maximiliana type

Monocolpate, sometimes trichotomocolpate.

Exine rather thick, from 1,5 to 3μ . Tectum perforated, undulating. Perforations numerous, irregularly arranged.

Capita indistinct, fused. Structure indistinct; sometimes indistinct patches visible.

Columellae distinct but low. Endexine thin.

(Fig. 1)

Scheelea type

Monocolpate, sometimes trichotomocolpate Exine thick, from 2 to 6μ .

Capita indistinct, fused, sometimes forming distinct patches, but usually indistinct pattern. Tectum perforated. Perforations few, in some species scattered, in other species in strings.

Columellae distinct, low. Endexine usually thick.

(Plate I C, D)



Fig. 1. Attalea maripa (Correa de Serra) Martius. Proximal pole; a. columellae layer; b. tectum with perforations.

Orbignya type

Monocolpate, rarely trichotomocolpate. Exine thin or rather thick, from 1 to $2,5 \mu$. Capita distinct, fused, forming vermiculate streaks. Tectum perforated, undulating. Perforations numerous, often in chains. Columella distinct or indistinct, low. Endexine thin. (Fig. 2)



Fig. 2. Attalea cohune Martius

Description of the species

Attalea attaleoides (Barb. Rodr.) W. Boer Wessels Boer 1430 (U)

Monocolpate, longest axis ca 65 μ . Exine thick, ca 4 μ . Capita indistinct, fused. Tectum undulating, perforations in tectum rather crowded, sometimes in short chains. Columellae low, distinct. Endexine thick. Scheelea type.

Attalea cohune Martius

Sentle 3234 (B) Glaziou 16468 (B)

Monocolpate, longest axis ca 60 μ . Exine ca 2 μ . Capita distinct, fused in vermiculate streaks. Tectum undulating, perforations in tectum many. Columellae low, distinct. Endexine thin. Orbignya type.

Scheelea dryanderae Burret

Dryander XII (type) (B)

Monocolpate, longest axis ca 60μ . Exine thick, 2,5–3,5 μ . Capita indistinct, fused, forming distinct patches. Tectum undulating, perforations in tectum rather few, in chains. Columellae distinct, rather high. Endexine rather thin. Scheelea type.

Attalea dahlgreniana (Bondar) W. Boer Plate II B, C Wessels Boer 805 (U)

Monocolpate, longest axis ca 50 μ . Exine thin, 1,5-2 μ . Capita indistinct, not fused in a distinct pattern. Tectum undulating, perforations in tectum crowded. Columellae low, indistinct. Endexine thin. *Maximiliana type*.

Attalea insignis (Martius) Drude Plate I C, D Krukoff 5622 (G) Johnstone 1577a (B), 1573 (B)

Monocolpate, sometimes trichotomocolpate, longest axis ca 65 μ . Exine thick, 4-6 μ . Shape slightly rectangular. Capita fused, forming distinct patches. Tectum undulating, perforations in tectum few, sometimes in chains. Columellae low, distinct. Endexine thick. Scheelea type.

Scheelea leandroana Barb. Rodr. x S. huebneri Burret Johnstone 1845 (B).

Monocolpate, longest axis ca 65 μ . Exine thick, 2–3 μ . Shape slightly rectangular. Capita indistinct, fused, forming patches. Tectum undulating, perforations in tectum few. Columellae low, distinct. Endexine thick. Scheelea type.

Parascheelea luetzelburgii (Burret) Dugand Luetzelburg 21969 (type) (B)

Monocolpate, longest axis ca 65 μ . Exine thick, 4-5 μ . Capita indistinct, fused. Tectum undulating, perforations in tectum few and scattered. Tectum much thicker than endexine. Columellae low, distinct. Endexine thin. Scheelea type.

Attalea macropetala (Burret) W. Boer

Wessels Boer 1330 (U)

Monocolpate, longest axis ca 40 μ . Exine ca 2 μ . Capita fused into a tectum, indistinct. Perforations indistinct, many, not forming a distinct pattern. Columellae low, indistinct. Tectum only slightly undulating. Endexine thin. Maximiliana type.

Attalea maripa (Correa de Serra) Martius Plate I A, B

Martius s.n. (G) Wessels Boer 288 (U)

B. L. Meyer s.n. (?)

Monocolpate, sometimes trichotomocolpate, longest axis ca 55 μ . Exine rather thick, ca 2,5 μ . Capita distinct, fused in an indistinct pattern of patches. Tectum undulating, perforations in tectum many. Columellae low, distinct. Endexine thin. Maximiliana type.

Attalea oleifera Barb. Rodr.

Trichotomocolpate, longest axis ca 55 μ . Exine thin, 1,5–2 μ . Capita indistinct, indistinct pattern. Tectum undulating, perforations in tectum many. Columellae low, indistinct. Endexine thin. *Maximiliana type*.

Scheelea osmantha Barb. Rodr.

Johnstone 1854 (B)

Glaziou 15556 (B)

Monocolpate, rarely trichotomocolpate, longest axis ca 70 μ . Exine thick, 2-3 μ .

Capita indistinct, fused. Tectum undulating, perforations in tectum few, scattered. Columellae low, distinct. Endexine thick. Scheelea type.

Attalea parviflora Barb. Rodr.

Monocolpate, longest axis ca 55 μ . Exine rather thin, ca 2 μ . Capita indistinct, fused, thus forming an indistinct pattern. Tectum undulating, perforations in tectum rather many, irregularly arranged. Columellae low, distinct. Endexine thin. Transition to Maximiliana type. Scheelea type.

Scheelea preussii Burret

Monocolpate, rarely trichotomocolpate, longest axis ca 60μ . Exine thick, $3-3,5 \mu$. Capita indistinct, fused, forming distinct patches. Tectum undulating, perforations in tectum few, scattered. Columellae rather indistinct, low. Endexine thick. Scheelea type.

Orbignya cf. sabulosa Barb. Rodr.

Monocolpate, longest axis ca 45 μ . Exine thin, 1-1,5 μ . Capita distinct, fused in vermiculate streaks. Tectum undulating, perforations in tectum many. Columellae low, rather indistinct. Endexine thin. Orbignya type.

Attalea sagotii (Trail ex Im Thurn) W. Boer Wessels Boer 708 (U)

Monocolpate, sometimes trichotomocolpate, longest axis ca 50 μ . Exine rather thin, 1-1,5 μ . Capita distinct, fused in distinct vermiculate streaks. Tectum undulating, perforations in tectum many. Columellae low, rather indistinct. Endexine thin. Orbignya type.

Attalea spectabilis Martius Plate II A Wessels Boer 1365 (U)

Monocolpate, longest axis ca 50 μ . Exine thin, ca 1,5 μ . Capita distinct, pattern indistinct. Tectum smooth, only slightly undulating, perforations in tectum many, indistinct. Columellae low, indistinct. Endexine thin. Orbignya type.

Attalea speciosa Martius Plate II D, E

Cult. Hort. Bot. Georgetown (K)

Monocolpate, longest axis ca. 60 μ . Exine ca 2 μ . Capita rather indistinct, fused into slightly visible vermiculate streaks. Tectum undulating, perforations in tectum many. Columellae low and distinct. Endexine thin. Orbignya type.

Scheelea stenorhyncha Burret

Monocolpate, sometimes trichotomocolpate, longest axis ca 65 μ . Exine thick, ca 5 μ . Capita indistinct, fused into a thick tectum, perforations in tectum few and scattered. Tectum much thicker than columellae and endexine, only slightly undulating. Columellae low, indistinct. Endexine thin. Scheelea type.

Orbignya urbaniana Dammer

Monocolpate, longest axis ca 55 μ . Exine thin, ca 1,5 μ . Capita distinct. Tectum smooth, only slightly undulating, perforations in tectum many, indistinct. Colu-mellae low, indistinct. Endexine thin. Orbignya type.

Attalea tessmannii Burret

Monocolpate, longest axis ca 70 μ . Exine rather thick, ca 2,5 μ . Capita distinct, laterally fused into a fine reticulum. Lumina narrower than 1μ , transition to a tectum perforatum. Columellae long and distinct. Endexine thin. Maximiliana type?

COMMENT

Maximiliana type

Grains monocolpate, sometimes trichotomocolpate. The exine is

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Tessmann 5256 (type) (G)

Tessmann 5167 (type) (G)

Glaziou 22265 (K)

Huebner 74 (B)

Hassler 7165 (type) (G)

without collector s.n. (B)

varying in thickness, but does not exceed 3 μ . The capita are fused, thus forming a tectum which does not show a distinct pattern. Many perforations are visible. These perforations are not arranged in a special pattern. The columellae are usually low and indistinct.

To this type belong Attalea maripa, Attalea dahlgreniana, Attalea macropetala, and Atttalea oleifera.

Attalea oleifera resembles the Maximiliana type in structure but the grains are always trichotomocolpate. As the difference between monocolpate and trichotomocolpate grains does not seem to be of taxonomical value, this species is placed in the Maximiliana type.

Attalea tessmannii also resembles the Maximiliana type, but in this species the laterally fused capita form a distinct reticulum and, moreover, the columellae are exceptionally high. The columellaelayer is higher than the capita-layer or the endexine.

Scheelea type

The grains are usually monocolpate but sometimes trichotomocolpate grains are mixed with monocolpate grains. The most striking character is the thick exine. The capita are fused into a thick, massive tectum in which the number of perforations is smaller than in the other types. The perforations are sometimes arranged in chains. The chains are winding giving the surface of the grains a patchy appearance (Attalea insignis, Scheelea dryanderae). Other species have few perforations too, but these are scattered over the surface and do not form a special pattern. The columellae are usually distinct and low. The endexine often is thick.

To this type belong those species which most taxonomists distinguish as a separate genus Scheelea: Attalea attaleoides, Attalea insignis, Attalea parviflora, Scheelea dryanderae, Scheelea leandroana x S. huebneri, Scheelea osmantha, Scheelea preussii, and Scheelea stenorhyncha. Orbignya luetzelburgii (Parascheelea luetzelburgii) belongs also to this type.

In this type there is a transition from the typical Scheelea type into the Maximiliana type.

Scheelea type ----Maximiliana type A. insignis $- \rightarrow S$. dryanderae $- \rightarrow A$. attaleoides $- \rightarrow A$. parviflora S. leandroana x S. huebneri S. osmantha S. preussii

- S. stenorhyncha

Orbignya type

Grains monocolpate, rarely trichotomocolpate. The exine is usually thin and its thickness never exceeds $2,5 \mu$. The capita are fused and form a tectum, but in contrast to the two other types they remain clearly visible. The perforations in the tectum are numerous and arranged in short vermiculate chains thus forming irregularly curved lines. The columellae are low and often indistinct. The endexine is always thin.

To this type belong those species which most taxonomists distinguish as a separate genus Orbignya: Attalea cohune, Orbignya cf. sabulosa, Attalea sagotii, Attalea speciosa, Attalea spectabilis and Orbignya urbaniana. In this type too it is possible to make a series of species showing transitions from the typical Orbignya type to the Maximiliana type.

Orbignya type \longrightarrow Maximiliana type A. cohune $- \rightarrow 0$. cf. sabulosa $- \rightarrow A$. sagotii $- \rightarrow A$. speciosa A. spectabilis O. urbaniana

TAXONOMIC NOTES

It can be seen from the foregoing that as well as there are different staminate flower types, there are also distinguishable pollen types. There is a tendency towards a correlation between staminate flower types and pollen types and, consequently, the pollen types have been referred to a Maximiliana, a Scheelea, and an Orbignya type. Unfortunately only two species of the genus *Attalea* in the narrow sense could be examined. These two species show marked differences and no generalization as to an Attalea type is reached.

According to BURRET (1929) Attalea s. str. is the most primitive genus from which Orbignya and Scheelea have been evolved. Maximiliana is supposed to be very close to Scheelea. Subsequently intermediates between Orbignya and Scheelea (Parascheelea), and Orbignya and Maximiliana (Markleya) have been described.

The intermediate staminate flowers of *Parascheelea luetzelburgii*, described by Burret in the genus *Orbignya*, contain pollen grains which match the Scheelea type exactly. The staminate flowers of *Attalea* (*Markleya*) dahlgreniana have pollen grains of the Maximiliana type. *Attalea* (*Maximiliana*) attaleoides has pollen grains belonging to the Scheelea type so that in this case the staminate flower type also concurs with the pollen type. The species was placed in *Maximiliana* on account of the fruit having superficial endocarp pores with a cover and without fibers. The same fruit characters were observed in *Attalea* (*Markleya*) dahlgreniana and *Attalea spectabilis*, both species with staminate flowers of the Markleya type. The examined *Attalea oleifera* also has the Maximiliana pollen type but not the Maximiliana fruit type. Obviously the Maximiliana pollen type is not restricted to the Maximiliana flower type nor correlated with the Maximiliana fruit type.

The torded and twisted anthers of the Markleya and the Parascheelea flower type remind one of the irregularly twisted and inrolled anthers of the Orbignya flower type. Nevertheless, these twisted anthers produce pollen grains of the Maximiliana, Scheelea, and Orbignya type respectively. Apparently the torded anthers do not provide a very reliable character.

On the other hand the pollen grains also show some intergradations between the distinguished types. *Attalea (Orbignya) speciosa* with staminate flowers of the Orbignya type has pollen grains intermediate

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A. and B. Attalea maripa (Correa de Serra) Martius, Wessels Boer 288.
A. Monocolpate grains, B. trichotomocolpate grain, Krukoff 5622.
C. and D. Attalea insignis (Martius) Drude.
C. optical section, D. surface pattern.

PLATE I

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A. Attalea spectabilis Martius, Wessels Boer 1365.
B. and C. Attalea dahlgreniana (Bondar) W. Boer, Wessels Boer 805.
B. tectum perforatum, C. optical section.
D. and E. Attalea speciosa Martius; Cult. Hort. Bot. Georgetown.
D. surface pattern, E. optical section.

PLATE II

between the Maximiliana and Orbignya type. Attalea (Scheelea) parviflora with staminate flowers of the Scheelea type has pollen grains intermediate between the Maximiliana and Scheelea type.

Resuming we can state for the genus *Attalea* in the broad sense: 1. the pollen morphology does not allow to split up the genus into

- smaller groups notwithstanding the fact that different pollen types can be distinguished;
- 2. there is a rather strong but not absolute correlation between the pollen types and the staminate flower types.

As was done after the study of morphological characters alone, here again it must be concluded that the relationships among the species of the genus *Attalea* in the broad sense are so close in several respects that no satisfactory separation on the generic level can be worked out. The mutual relations are diagramatized in the scheme below.



BURRET (1929) also proposed an infrageneric division: in Scheelea based on a character of the endocarp, and in Orbignya on the position of the staminate flowers on the rachillas. Both divisions proved to have no correlation with the differences found in the pollen grains. Attalea (Scheelea) parviflora, Attalea (Scheelea) insignis, and Scheelea leandroana are all placed in the section Synalphocaryum, but the first matches the Maximiliana pollen type quite well, whereas the second differs strongly from that, and the third takes an intermediate position. Also the examined species of the section Dialphocaryum, Scheelea osmantha, Scheelea preussii, and Scheelea stenorhyncha, represent such intermediates; Scheelea dryanderae, supposed to be closely related to Scheelea stenorhyncha, again differs more strongly from the Maximiliana type.

The species examined in Orbignya also show a series in the Orbignya pollen type towards the Maximiliana pollen type in which the extremes were placed in the section Distichanthus, the intermediates in the section Pleiostichanthus.

POLLEN GRAINS OF ELAEIS

Elaeis guineensis Jacq. Wessels Boer 1341 (U) Trichotomocolpate, longest axis ca 40 μ . Exine thin, ca 1,5 μ . Tectum perforated, undulating. Perforations indistinct. Structure indistinct. Capita indistinct. Columellae low, indistinct. Endexine thin. Capita thinner than columellae and endexine together.

Elaeis oleifera (H.B.K.) Cortés (Corozo oleifera) Wessels Boer 155 (U) Monocolpate, slightly asymmetric, longest axis ca 40 μ . Exine rather thick, 1,5-2 μ . Tectum perforated, undulating. Perforations many, indistinct. Structure indistinct. Capita fused, indistinct. Columellae low, indistinct. Endexine thin. Capita thicker than columellae and endexine together.

Elaeis odorata Trail (Barcella odorata) Froés 28315 (P) Monocolpate, asymmetric, largest axis ca 50 μ . Exine thin, ca 1,5 μ . Tectum perforated, undulating. Perforations many, indistinct, sometimes in chains. Capita distinct. Columellae low, indistinct. Endexine thin. Faint structure present. Capita about as thick as columellae and endexine together. (Fig. 3)



Fig. 3. Elaeis odorata Trail.

The pollen grains of the three *Elaeis* species do not show any distinct character which might separate them from each other or from other palm taxa. The exine is thin and is not clearly structured. The capita are irregularly fused to a tectum with many perforations.

The only difference is the shape. *Elaeis guineensis* is trichotomocolpate and the other two species are monocolpate. This difference is of minor importancy in the palm family only.

NAIR and SHARMA (1963) found monocolpate and trichotomocolpate grains in *Cocos nucifera* both in one specimen. ERDTMAN (1952) described this phenomenon in the species *Euterpe oleracea* and *Jessenia bataua*. In the genus *Attalea*, too, this dimorphism occurs. The three species do not differ much in size. *Elaeis guineensis* and *Elaeis oleifera* are almost of the same size, only *Elaeis odorata* is slightly smaller.

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The exine is not very characteristic and therefore it is probable that palms in other groups of this family will show the same exine structure. *Elaeis odorata* only has an indistinct pattern. The surface is a little bit spotted.

TOMLINSON (1961) claimed a rather isolated position for *Elaeis* within the Cocoid palms. However, the uncharacteristic pollen grains do not provide much evidence for this and no separation either from the Cocoid palms nor from three distinct monotypical genera is supported by pollen morphology.

AN ADDITIONAL NOTE ON BACTROID PALMS

TOMLINSON (1961) separated the Bactroid palms from the Cocoid palms. The Bactroid palms have pollen grains which have only few characters in common with the three types from the genus Attalea. Examined species:

Wessels Boer 314 (U)
Wessels Boer 308 (U)
Wessels Boer 327 (U)
Wessels Boer 1591 (Ú)
Wessels Boer 520 (Ù)
Wessels Boer 468 (U)
Wessels Boer 174 (U)

The pollen grains of Acrocomia lasiospatha Martius (Wessels Boer 1338) have some resemblance with the Scheelea type. The thick exine and the few perforations in the tectum agree with what is found in the Scheelea type. All grains, however, are trichotomocolpate, whereas those in all species in the Scheelea type are predominantly monocolpate.

These preliminary data seem to agree with Tomlinson's opinion that the Bactroid palms should be separated from the Cocoid palms.

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