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MORPHOLOGICAL AND ANATOMICAL STUDIES OF THE COCONUT

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1. INTRODUCTION

The coconut palm is not only one of the most beautiful trees in existence, it is also the most important perennial producer of vegetable fat in the world; in Asia, the Far East and Oceania tens of millions of people are dependent on it. Yet our knowledge of this typical smallholders' crop is not in proportion to its importance and the increase in knowledge is slow.

Therefore, when some years ago an unusual discovery suggested the opportunity to make a contribution which could be of use to coconut research and lead to a better understanding of the flowers as well as the principal product of this palm, the coconut itself, this opportunity was not lost and has now resulted in the present publication.

This study was initiated in 1966 in Peru at the Agricultural University of 'La Molina' in Lima, where the present author was in charge of the national coconut research and development project. As part of a survey of the types of coconuts occurring in Peru, palms from many regions of the country were studied and their fruits analysed. During the analysis of a consignment of coconuts from the northern coastal region fruits were found with one carpel less than the normal number. As a review of the locally available literature indicated that this phenomenon was a very uncommon one, about which practically nothing was known and the Peruvian coconut palms had never been examined before, it was considered worthwhile to make a detailed study of this phenomenon.

The estate from which the coconuts were obtained was inspected and it happened that the occurrence of bicarpellate coconuts was not an isolated event; this made our find an even more unusual one as a repetition of the production of such special coconuts had never been mentioned in the literature available at the time.

Knowing that we had met with very exceptional material, the main lines of the study were established. Firstly the periodicity of the phenomenon as well as its pattern of occurrence had to be established to check its relationship to any specific tree or number of palms and to study possible seasonal tendencies. The morphological implications of carpel reduction were to be analysed and a study of the anatomy of such a coconut, especially the endocarp, was indicated. All these lines of approach were to lead to a theory explaining the reason(s) for the appearance of these abnormal fruits, in which environmental and genetic factors were to be taken into account.

Apart from bicarpellate fruits some other abnormalities were met: a few coconuts with more than one seedling sprouting from the same coconut and hermaphrodite and other abnormal flowers. Such flowers had been found elsewhere but in very limited numbers only. It was a remarkable coincidence to meet these uncommon abnormalities so frequently in such a limited number of palms. This led to the assumption that either there was something basically different in the growing conditions of the coconut palms, resulting in an abnormal environment, favouring the appearance of many kinds of abnormalities or there was some kind of link between the abnormal flowers and the bicarpellate coconuts. This was also to be related to the unusual periodicity in production prevailing in the area.

All this had to be studied with material detached from the palm, as the average height of our palms was over 15 m (50 ft), making it impossible to detect abnormalities and follow their development in situ. To this traditional handicap of coconut research was added the distance – 1300 km (800 miles) – from Lima, the shortage of professional climbers in the area, the scarcity of modern equipment for anatomical research and the limited documentation facilities. These latter problems have been overcome by concluding the work in the Department of Botany of the Agricultural University at Wageningen.

In the course of the study it became clear that not only very little was known about carpel reduction in the coconut but that even the normal fruit had been studied insufficiently. In order to compare normal and abnormal coconuts, the former had to be examined in more detail than had been done before.

As a result of this not only our knowledge of the bicarpellate coconut has increased but at the same time an answer has been found to a number of questions concerning the nature of the normal coconut, specifically with regard to the 'eyes' and the compressed locules. Similarly, an attempt at comparative analysis of the abnormal flowers made necessary a more thorough preliminary study of the normal flowers. Existing descriptions of normal inflorescences were found not to be in accordance with the morphological characteristics and therefore were a potential source of misinterpretation.

The answers concerning the morphology and anatomy of the normal fruits were found mainly thanks to the comparative study of normal and bicarpellate coconuts, showing once more that a study of teratological cases is not necessarily an exercise in science for its own sake, because such a study can provide a better insight into the normal structure and hence lead to an increase in knowledge, in this case of such an important plant as the coconut palm.

2. THE OCCURRENCE OF CHANGES IN CARPEL NUMBER IN PALMS, WITH SPECIAL REFERENCE TO THE COCONUT PALM

The Palmae are the only family in the order of the Palmales. The flowers are usually trimerous. The ovary is superior and usually tricarpellate and the number of more or less anatropous ovules is normally 3. There are sometimes more ovules but rarely 1 and usually only one developes. There is no doubt about the basically tricarpellate nature of the ovary, but from the remark on the development of the ovules it will be understood that this does not necessarily lead to a normal tricarpellate and three-seeded fruit.

The coconut palm belongs to the subfamily Cocoideae and this subfamily is characterized by the 3-celled ovary, the drupaceous fruit, and the woody or stony endocarp, provided with three germpores; the fruit is usually one-seeded.

The same basic pattern of fruits in Cocoideae provides the opportunity to compare the change in carpel number in one palm species with other palms of the sub-family and so to find similarities which may lead to a better understanding of the abnormalities encountered in the coconut palm.

DRUDE (1889, p. 20) states that in palms changes in the number of carpels are rare, that 1 or 2 can abort and that doubling of the basic number to 6 occurs in some genera. Also the occurrence of monstrosities with 2, 4 or 5 carpels is mentioned. It is interesting to note that the occurrence of only 2 carpels is listed twice in the text, once as a case of abortion and also as a monstrosity. With regard to carpel development in fruits of palms it is noted that when only one ovule develops into a seed, the non-fertile carpels also 'participate equally in the formation of the common fruit, of the stony shell as well as the mesocarp'. (id. p. 23)

In studying the literature on the process of development of the normal fruit of the coconut palm, the terminology used by some authors appears somewhat confused. In order to avoid misunderstanding it is considered advisable to review the terms used in the literature concerning this process to leave no doubt about the interpretation of the terms used by the present author.

During development from ovary to ripe fruit, the ovule which will grow into a seed develops more rapidly than the other two and thereby gradually reduces the space available to those. The ovary wall apparently develops normally. In the ripe fruit this development of the ovary wall is seen in the 3 ridges on the endocarp and the exocarp. Remnants of the two partly developed but compressed locules are found, pressed against the inner ovary wall. This process is commonly described as abortion of the carpels: BAILEY (1933), MENON and PANDALAI (1958), and EAMES (1961).

This last authors also describes these carpels as sterile, lacking a locule and 'solid' for part or all of their length (EAMES, p. 242). DANIEL SUNDERARAJ (1952) maintains that this is only an abortion of ovules and not of the carpels. This view is correct because the whole structure of flower suggests its tricarpellate character and the fruit shows that all carpels are present and accounted for. DAVIS (1948) and MENON and PANDALAI (1958) describe cases of development of more than one ovule into a normal seed, i.e. the non-abortion of one or both of the other two ovules, resulting in a two- or three-seeded fruit and they call this 'a condition of polycarpy' (MENON and PANDALAI, p. 313). This is possible only if one considers the normal coconut fruit as monocarpic with only one ovule in the cell, which is not the case.

The above mentioned authors are apparently of the opinion that polycarpy is 'the development of more than one carpel' (DAVIS, ANANDAN and MENON, 1953, p. 69) and they wrongly apply this to their special coconut. This definition of polycarpy is not the usual one.

The word 'polycarpic' is often used as a synonym for perennial, while 'polycarpous' is used either in the same sense as 'polycarpic' or for describing a gynoecium consisting of two or more distinct ovaries (JACKSON, 1953).

Finally 'polycarpellary' is employed to describe ovaries of many free or united carpels. None of these definitions are applicable in the above case and even if they were acceptable their use here is not recommended, as in a normal coconut the 3 carpels do develop.

Abortion of the carpels in the coconut palm can be defined as the process by which the carpels are formed and can be retraced at least to the flower primordium. During development one or more of the carpels do not participate in the further development of flower or fruit and remain rudimentary, resulting in a fruit with one or two rudimentary carpel(s).

Fusion of carpels is the process in which the normal number of carpels of approximately equal size is found up to a certain stage of development of the ovary or even the fruit. During further development a coalescence of two or more carpels takes place. Depending on the degree of fusion – partial or complete – the original number of carpels is recognizable morphologically even in the ripe fruit (partial) or not anymore (complete). In the latter case the fusion will usually be recognizable as such by anatomical analysis of the fruit.

Reduction of carpels is used to describe any appearance of fruits, composed of a number of carpels which is, morphologically, less than normal. The process by which this reduced number came about may have been either abortion, fusion or 'original reduction'. By 'original reduction' is meant a differentiation of the primordium tissue into a number of carpels, less than usual for that particular species.

To avoid misunderstanding 'reduction' will be used only for cases of 'original reduction' as defined above. 'Decrease in the number of carpels' will be applied to all instances in which morphologically the number of carpels is less than normal, regardless of the process by which this lower number was reached.

It goes without saying that the two main types of carpel number changes are a decrease in number on one hand and an increase in the number on the other.

First of all it is worth noting that, compared with other abnormalities in the coconut palm, changes in the number of carpels are rare. In their extensive treatises on the coconut palm authors like HUNGER (1920), SAMPSON (1923), COPELAND (1931), PATEL (1938), REYNE (1948) and CHILD (1964) give more or less ample attention to abnormalities of the flowers and fruits but they do not even mention changes in the number of the carpels.

2.1. INCREASE IN THE NUMBER OF CARPELS

Unusual increases in the number of carpels in palms have been found on various occasions. CORNER (1966) observes that occurrence of ovaries with 4, 5 and 6 carpels, reminiscent of the multilocular ovary of *Phytelephas* is not infrequent and cites as examples several species of *Attalea*, *Cocos*, and *Orbignya*.

DAVIS (1966) mentions the appearance of additional hornlike carpels in coconut palm, areca palm (*Areca catechu* L.) and palmyra palm (*Borassus flabellifer* L.). When these additional carpels, mostly three in number, fuse at an early stage of development with the original carpels of the ovary, this may result in a syncarpic fruit with 4, 5 or 6 carpels, depending on the degree of fusion. Also flowers with a number of underdeveloped carpels between 4 and 8, instead of a normal tricarpellate ovary, occur.

In one particular case the fruits of an areca palm showed an additional carpel. Davis also refers to a horn on a palmyra fruit which is presumably a carpel. Moreover, in the date palm (*Phoenix dactylifera* L.) a case of one specific fruit and flower with nine carpels is mentioned by him. The normal number in this palm is 3.

The best known example of an increase in carpel number in palms is the abnormal fruit type occurring in the African oil palm (*Elaeis guineensis* Jacq.) and known both as 'Poissonii' and 'diwakkawakka', where 6 additional carpels surround the main parts of the fruit as fleshy outgrowths (HARTLEY, 1967). The character is inherited and appears with a frequency of approximately 1:10.000. There is a similarity to some of the horns found in coconut, although 'horns' of diwakkawakka are usually as long as the fruit and the character is stable whereas in coconut the horns are usually small and the character is mainly unstable, except for the case described by PETCH (1924, p. 21), who adds to his description: 'Some palms never bear anything but fruits of this character'. However, 4- or 5- carpellate syncarpous ovaries do occur in the oil palm as rare abnormalities, very rarely resulting in 4- or 5-seeded fruits.

A palm, in which an increase in the number of carpels seems to be a frequent abnormality is *Sabal palmetto*, belonging to the Sabaleae (Coryphoideae). According to BOSCH (1947) such an increase in carpel number occurs in some 20% of all female flowers. It is not known whether the particular inflorescence analysed by Bosch was abnormal or that all inflorescences of this species show such a high proportion of abnormal flowers. The abnormal flowers were mainly concentrated in the lower part of the inflorescence.

Returning to specific examples of increases in the number of carpels in the coconut palm, we find that FORBES (1879, p. 193) mentions the occurrence of coconuts in the Cocos Keeling Islands 'with cells ranging from 4 to 8 to 10'. Even a case of a '14-celled coconut, in which the embryo in each cell germinated' (!), is recorded by him. He illustrates his description with a sketch of the tree developed from this coconut. It had 14 stems, united at the base (id., p. 194).

The case of the hornlike structure in coconut described by CHANDRASEKHARAN and DANIEL SUNDARARAJ (1950) implies the presence of additional carpels in coconut, from 'twin' or 'double ovaries'. The coconut is normal and tricarpellate and the horn also consists of three layers, including a solid endocarp. The number of carpels therefore is more than 3, although the authors neither describe the number of carpels of the hornlike structure nor that of the 'twin' ovaries.

MENON and PANDALAI (1958) apart from citing the cases of increase in carpel number described above, record an increase to 4 carpels as an abnormality and refer to observations by Davis of carpel numbers from 4 to 10 in young coconut fruits.

With respect to the cause and origin of the appearance of the additional carpels in flowers and fruits of palms the observations of BEIRNAERT (1935), BOSCH (1947), CHANDRASEKHARAN and DANIEL SUNDARARAJ (1950), and DAVIS (1966) are of interest.

BEIRNAERT (1935, p. 1096) observed various stages of modification of the androecium into carpels. This is the case with 'diwakkawakka' in the African oil palm, where the additional carpels have developed from the rudimentary lobes of the androecium. BOSCH (1947, p. 54–55) found that the increase in the number of carpels from 3 to 4 in *Sabal palmetto*, – an increase, which is accompanied by a reduction of the number of stamens from 6 to 5 – is caused by the replacement of a stamen by an additional carpel. Here it must be mentioned that in this palm the flower is normally hermaphrodite.

On the other hand CHANDRASEKHARAN and DANIEL SUNDARARAJ (1950) found that the additional carpels of the horned coconut described by them, are the result of the development of a second ovary, though no information is provided on the possible origin of that ovary.

DAVIS (1966, p. 318) locates the 3 additional free carpels in some coconut fruits between the 'papery ring' and the ovary, which means that this is not a case of a modification of the staminodal ring but, according to him, 'a duplication of gynoecium segments'. Also in some areca fruits he found that the extra carpel developed from 'below the ring of staminodes', again an example of carpel development not based on staminodal origin.

Summarizing, supernumary carpels are to be found in coconut and other palms as abnormalites. These originate from either a duplication of gynoecium segments, which may possibly include the aforementioned 'twin' ovary, or from a modification of the androecium. Increase in the number of carpels in palms is usually an abnormality and in most cases of a rare and unstable occurrence.

2.2 DECREASE IN THE NUMBER OF CARPELS

The other type of change in the number of carpels in palms is a decrease. While references to the increase of carpel number in palms can be considered as being few and sporadic, information on decrease in carpel number is even less. This is undoubtedly due in part to the fact that decreases in carpel number are less conspicuous than increases in these and their external results. One's attention is more easily drawn to the presence of an abnormal additional structure than by a fruit, which at first sight appears to be normal.

Furthermore, there are only three possible decreases in carpel number, from 3 to 2, 1 and 0, whereas the number of additional carpels is theoretically almost unlimited.

Last but not least, while we have seen that an increase in carpel number may have its origin either in a female development of androecium rudiments or in a duplication of gynoecium segments, in the case of a decrease of carpel number there is basically a partial or complete suppression or fusion of gynoecium segments only.

In the summary of cases which follows, we have distinguished between a decrease in number of carpels appearing as a normal characteristic in certain palms and the decreased number which occurs as a deviation from the normal process. It is interesting to mention in summarized form the decreases in carpel numbers which normally occur in some genera of palms so as to be able to draw comparisons with the teratological cases of reduced carpel number in others.

DRUDE (1877) has given a classification of palms, based mainly on the development of carpels and ovules. He records an early abortion of two carpels in *Geonoma*, where at receptivity of the female flowers only one carpel with basifixed style is seen. The other two carpels are present in the very young flower but do not develop except for their part of the common style and stigma. WESSELS BOER (1968) describes in detail this abortion of two carpels, just before anthesis of the female flower, in the gynoecium of three genera of the Geonoma tribe, i.e. *Geonoma*, *Taenianthera*, and *Kalbreyera*. This abortion is the normal procedure in these genera and is recorded throughout. Remants of these two aborted carpels are frequently present near the base of the fruit.

According to DRUDE (1877), abortion of carpels takes place in *Chamaedorea* at a latter stage than described above. At flowering a tricarpellate syncarpous ovary is present; one ovule becomes functional and the carpel developes. The other two carpels do not develop at all, wilt ('welken' – DRUDE) and are not found back on the ripe fruit.

In the Cocoideae the next step is the 'elimination' of two of the carpels which is initiated late and progresses so slowly that it is not completed.

The abnormal decrease in carpel number in palms has been recorded very infrequently. In the coconut palm such cases are relatively numerous.

WRIGHT (1869, p. 455) describes a case of a tree in the Seychelles producing very few nuts, 'all bicarpellate, but without a development of the hard shell and showing only two edges on the fruit'. This was the only case in some 180.000 palms. These bicarpellate fruits did not develop normally as there was 'a false development between the carpels, redividing the nut into two'.

COSTERUS and SMITH (1923b) describe two cases of apocarpous coconuts, one of which possibly had only two carpels, as only two of the cells are present. One of the figures, accompanying an earlier publication of the same authors (1923a, p. 26–27, fig. 23) possibly represents a monocarpic fruit but the description is confusing.

DAVIS and MENON (1953, p. 142) are the first to describe a bicarpellate female flower, appearing in the terminal(!) inflorescence of a midget coconut palm developed from a dwarf palm fruit. This bicarpellate flower consisted of an apocarpous ovary with two carpels appearing as two hemispherical bodies, surrounded by the perianth.

As no remarks are given on the number of bracts, bracteoles and perianth leaves of this particular flower we presume that this was normal.

It is quite possible that the *Cocos nucifera var. praecociflora* Becc., described by BECCARI (1916) is identical to the midget coconut palm and even maybe 'praecociflora' also had a reduced number of carpels of its female flowers, but as this 'variety' was only based on a drawing in the Museum at Kew it is unknown whether the flowers were normally developed or not.

COSTERUS and SMITH's (1916) specimen of a midget palm reached them with all its flowers shed. Other such midget palms, all with terminal and sometimes extra axillary spadices have been reported: RAO and SUBBIAH (1954), THOMAS and VERGHESE (1964); but no observations on the nature of the flowers are given. Flowers of the midget palm, described by GADD (1924) had an ovary with three carpels, fused at the base but free at the apex.

MENON and PANDALAI (1958, p. 313) describe bicarpellate and even monocarpic fruits. Of the bicarpellate coconut they provide the following details: 'the endocarp of the fruit has only two ridges and each carpel is indicated by a separate eye'.

A yet unpublished article by DAVIS (1970), apart from reviewing a number of his earlier findings and presenting many data on the variation of carpel number in fruits of many palm species, contains information on two particularly interesting cases of decrease in the number of carpels from 3 to 2 in coconut. Both concern coconut palms in Calcutta but apparently the palms are not related. In more than one inflorescence these two palms produced both normal and bicarpellate fruits. When the first palm was killed by a cyclone it had produced, during approximately 1½ year under observation more than 17% bicarpellate fruits. The second coconut palm, of recent discovery, already shows more than 36% of such abnormal coconuts, including young fruits. But this is, apart from our own findings, where records of decrease in carpel number in the coconut palm end.

On reduction in carpel number in other palms as teratological cases, the information is, as we mentioned before, very scant indeed.

BEIRNAERT (1935, p. 1102) has made very interesting remarks on the flowers in androgynous inflorescences, sometimes occurring in the African oil palm: all stages of transition between male flowers with rudimentary gynoecium and hermaphrodite flowers with normal stamens and carpels occur, including hermaphrodite flowers with one normal and two rudimentary carpels and also with two normal carpels and one rudimentary. He considers hermaphroditism in this case as an intermediate stage between the physiological male phase and the physiological female phase. No information is given on whether these hermaphrodite flowers with an ovary composed of one or two normal carpels finally resulted in fruits with only one or two normal carpels.

3. THE BICARPELLATE COCONUT PALMS, AS FOUND IN PERU

3.1 DESCRIPTION OF THE REGION, PLANTATION, PALMS STUDIED AND THEIR HISTORY

The coconut palms studied, which produce relatively high numbers of bicarpellate coconuts are located in Peru, in the Department of Piura. In this Department approximately 1,000 ha (2,600 acres) of coconut palms are planted, the largest area in Peru. It is situated between 4°-6°S and 79°-81°W, is bordered by the Republic of Ecuador and the Department of Tumbes on the north and the Pacific Ocean on the west. To the south and east respectively lie the Departments of Lambayeque and Cajamarca. (fig. 1).

According to Tosi (1960), following the Holdridge classification[1]), the most important ecological zones of the Piura Department, from the Pacific Ocean inland are: subtropical desert, tropical desert, tropical desert bush and tropical thorn forest. This last ecological zone, hot and semi-arid, is found in Peru only north of latitude 7° S. It is enclosed by tropical desert bush in the west and the subtropical thorn forest on the slopes of the Andes in the east. It occurs from approximately sea level up to 450 m.

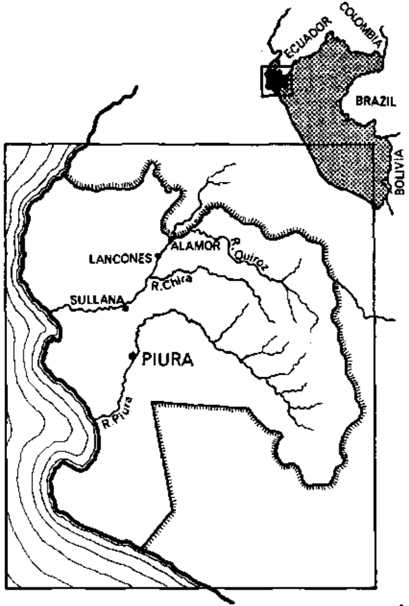

FIG. 1. The Department of Piura, Peru.

The average annual temperature is over 23° C, but because of the influence of the Ocean nearby, the temperature does not reach extreme values in any single month of the year. Rainfall does not exceed 100 mm per year and is limited to the summer months, January to April, with the largest amount in February and March. The data given in table 1 define this type of climate in more detail.

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[1]) HOLDRIDGE, L. (1947), Sci., 105: 367-368.

TABLE 1. Meteorological data; averages of the periods October 1960 – September 1963 inclusive and November 1966 – March 1969 inclusive*

Station: Chilaco
Altitude: 103 m above sea level
Latitude: 4° 43′ S
Longitude: 80° 31′ E

Month	Max. temp. in °C	Min. temp. in °C	2-hr.ly temp. in °C.	Rainfall in mm	Daily sunshine	Relative hum. in %
January	34.4	21.1	26.5	9.8	6h.29′	65.6
February	35.4	21.5	27.3	15.9	6h.39′	64.5
March	35.2	21.5	26.9	20.8	6h.25′	70.9
April	34.4	19.0	25.7	8.8	7h.16′	71.8
May	32.3	17.6	23.7	0.5	7h.27′	72.4
June	29.3	15.9	20.8	0.0	6h.52′	73.9
July	28.3	15.6	19.8	0.0	6h.40′	75.2
August	30.1	15.9	20.9	0.0	8h.04'	73.5
September	31.1	16.2	22.0	0.4	7h.50′	72.5
October	31.5	16.5	21.7	1.0	7h.22′	75.8
November	31.5	16.7	22.2	0.0	7h.12′	71.7
December	33.2	19.0	24.3	0.5	7h.40′	70.0
Total	386.7	216.4	281.8	57.7	85h.36′	857.8
Mean	32.2	18.0	23.5	4.8	7h.08′	71.5

* Due to malfunctioning and later non-functioning of the station no data are available for the period October 1963 – November 1966. As this station is the only one located in the vicinity of 'La Solana' its data are preferred to those of stations with more data but at a greater distance. For more details see chapter 6, paragraph 2 and appendix no. 1 and 2.

It is obvious that this climate is quite unusual for the latitude at which it is found. Both the annual and the daily variations of temperature are very large for a region so near to the Equator. The number of hours of sunshine is high, which is ideal for coconut growing.

The soils vary from sands to loamy sands, whereas in the river valleys a sandy loam is found. One of the subdivisions of the Department of Piura is the Province of Sullana, part of which is the district of Lancones. In this frontier district which is difficult to reach and sparsely inhabited the plantation 'La Solana'[1] is situated. The total area of 'La Solana' is some 5,000 ha (appr. 13,000 acres) of which only 160 ha (415 acres) are under cultivation. This is due to the fact that on one hand the terrain is sloping and the cost of bringing irrigation water to the higher parts is prohibitive. On the other hand the amount of irrigation water which the estate is allowed to draw from the rivers also limits the

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[1] Legally the plural 'plantations' should be used, as the estate 'La Solana' was split up after the death of the father of the present owners into 'Solana Alta' and 'Solana Baja', but for our purposes the estate is one unit.

area under cultivation. The highest point in the estate is 95 m above sea level, the lowest 65 m, near the river Chira.

'La Solana' exists as a thriving agricultural enterprise because of the river Alamor which forms the frontier between Ecuador and Peru, and the Chira, forming the northern and eastern boundaries of the estate (fig. 2).

Main activities are the culture of bananas, oranges, limes, mandarines, mangoes and coconuts. Rice cultivation and cattle farming are also practiced. Coconuts are classified as fruits, since up till recently in Peru the produce of coconut palms was sold exclusively as fresh husked nuts and no conversion to copra, desiccated coconut or other products was practiced.

The area of the plantation dedicated to coconut growing is small. The total number of coconut palms in production at the start of this study was nearly 300. These palms belong to the tall type of coconut palm, also called the 'group of allogamous varieties' (FREMOND et al., 1966), which implies that natural self pollination is probably very low. A few dwarf palms are in production on the estate.

Another detail of importance to our investigation is the fact that there are no other estates where coconuts are grown for a radius of 20 km, except for a small number of palms some 6 km from the most southern extreme of the estate, but these have been planted recently and are not yet in flower. Because no artificial pollination has ever been practiced, it can be stated with absolute certainty that all palms on the estate occurred without any foreign pollen.

Moreover it should be mentioned that the palms belong to three more or less distinct age groups (see table 2). The oldest group of palms, now about 95 years of age and still in production, has provided the seed for the second age group, while this in its turn has been the seed producer for the first part of group 3.

The origin of group 1 is unknown, but most probably these palms originated from seeds or seedlings of Ecuadorian origin. Local elders, of about the same

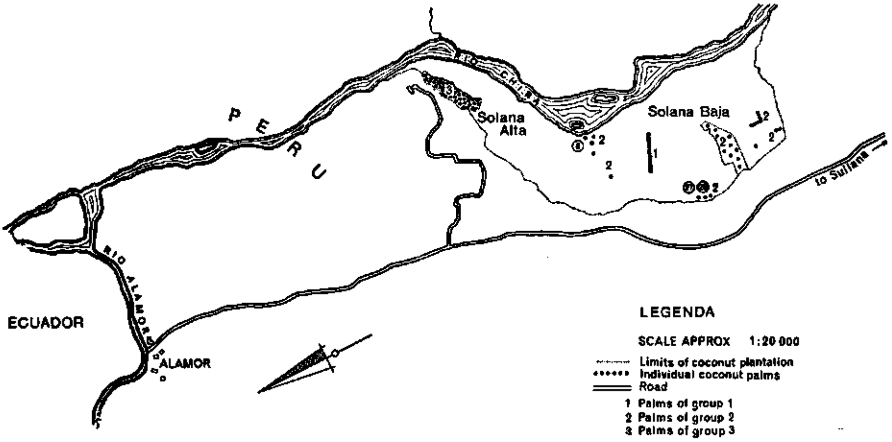


FIG. 2. The haciendas 'Solana Alta' and 'Solana Baja'.

TABLE 2. Coconut palms of 'La Solana', classified according to age

Age group	Number of palms	Years planted	Approximate age	Origin
1	16 (SB)[1]	1873–1875	94–96 years	unknown, probably s. Ecuador
2	6 (SA) + 51 (SB) = 57	1924–1926	43–45 years	group 1
3	222 (SA) + 1 (SB) = 223	from 1937 to 1954	15–32 years	group 2 and group 3 (see text)

[1] SB: 'Solana Baja'
SA: 'Solana Alta'

age as the first generation of coconut palms, say that it was known at that time, that the grandfather of the present owners returned with the seeds or plants from his trips to southern Ecuador, but this is hearsay evidence. No written data are available. The palms are among the oldest, if not the oldest, in Peru. The age of this group could be established within reasonable narrow limits by counting the number of leaf scars on the trunk of one of the palms which died. Group 1 originally consisted of 20 palms, but 4 have died, the last of these in 1966.

The palms are planted in a row and are located in a part of the estate which has been used for rice growing for at least the last 25 years (see map, fig. 2). This means that they are practically flooded for 6 months of the year, but do not receive any water other than the very sparse rainfall during the next 6 months. Due to their advanced age the upper part of the trunks are thin. Birds had nested in the trunks and some of the palms were already inclining dangerously. Under these circumstances harvesting was out of the question, because of the danger involved.

The 57 palms in the second age group are dispersed throughout the estate, but the majority is situated in rice fields in what is now 'Solana Baja'. There is also a grove of coconuts and mangoes which borders the rice fields. The reason for this dispersion is that originally the palms and mangoes were planted primarily to provide shade for the cattle and only later their productive capacity was taken into account. The height of the palms of this generation is now 20–25 m and they are of no further use as shade trees. The area in which 6 palms of this group in 'Solana Alta' are located is still pasture, maintained by flood irrigation.

The third and most numerous age group consists of 223 palms in production. Only one of the palms within this classification is situated in an isolated position in the 'Solana Baja' estate. The other 222 palms form a single plot in the hacienda 'Solana Alta' (see map, fig. 2). This consists of two parts which are not easily distinguishable. The north eastern side of the strip was planted some 30–32 years ago and comprises about 2/3 of the group, while the last 1/3 was planted 15–25 years ago. This was done gradually, extending the strip in south westerly direction. Seed from the second group of palms was used to plant the first part of this group and these palms are certainly third generation. The seed used for the younger part of this group has been taken from palms belonging to both the second and the first parts of the third group.

This third group in 'Solana Alta' was planted in a strip, which varies in width from 2–8 palms. The distance between the palms is approximately 8 m in a square. This group was planted for the purpose of coconut production. The soil here is sandy loam, detailed information on which is given in table 3. The palms have never received any kind of natural or artificial manuring and are irrigated with water from the Chira river. At a distance of some 100 m from age group 3 nine dwarf coconutpalms are in production. They were originally imported from Ecuador. During the period of observation these palms were also harvested and their coconuts analysed but no abnormalities were found. The production of these trees is excellent, with an average of about 175 coconuts/tree/year.

Except for signs of old age which have already been described briefly in the palms of age group 1, the external appearance of nearly all the palms studied is good. They have healthy crowns of 20–22 fully developed leaves and trunks undamaged, except for superficial marks caused by the iron hooks used as support by some climbers. They also have well-developed rootsystems with roots spreading to 6 m from the trunk and to an average depth of ± 1.50 m.

3.2. METHODS OF COLLECTION AND ANALYSIS OF MATERIAL

As explained in chapter 1, the original purpose of this study was to determine only the extent of the occurrence of bicarpellate fruits. Later on when studying its causes the relationship with other unusual phenomena was taken into account.

The basic information collected was therefore the production of coconuts per tree and their classification as normal or bicarpellate. The percentage of bicarpellate fruits per tree and whether these were produced in separate inflorescences or even trees was noted. This information was combined with data on the colour of the exocarp of the coconut and the age group to which the palm belonged.

Harvesting frequency in Piura is usually only once a year, but in a few estates it is twice. This is rather unusual as the coconut normally produces one leaf, one inflorescence and one bunch of ripe nuts per month, thereby theoretically permitting monthly harvest. Usually to save labour, in other coconut growing countries the number of pickings per year is 3 to 6. This low frequency of harvest will be discussed in more detail in chapter 6.

Harvesting at 'Solana Alta' was carried out twice annually, in April and July-August, but at 'Solana Baja' only once in October-November, after the rice harvest. As the owner of 'Solana Baja' did not permit harvesting as long as his rice was in the field, harvesting there was restricted. In 'Solana Alta' the number

TABLE 3. Characteristics of soil found in the area of age group 3.

depth	el. cond. mmhos/cm	sand %	loam %	clay %	type of texture	pH 1:1	N %	organic matter %	P_2O_5 Kg/Ha	K_2O Kg/Ha
5 cm	2.70	36	54	10	sandy loam	7.5	0.204	3.37	15	740
25 cm	0.80	20	60	20	sandy loam	7.4	0.080	1.58	26	544
50 cm	0.86	20	60	20	sandy loam	7.5	0.084	1.45	15	408
75 cm	0.75	34	56	10	sandy loam	6.8	0.092	1.65	20	544

depth	Total exchange cap. m.e./100 gr.	exchangeable cations				Boron ppm
		Na^+ m.e./100 gr.	K^+ m.e./100 gr.	Ca^{++} m.e./100 gr.	Mg^{++} m.e./100 gr.	
5 cm	25.20	0.26	3.40	13.20	1.40	9.60
25 cm	22.44	0.26	0.24	9.60	1.32	2.10
50 cm	20.48	0.35	0.24	15.20	1.12	1.80
75 cm	14.80	0.24	0.35	12.60	0.98	0.75

of harvests was increased to 3 times a year for this study: April, July–August and November–December; this was done from July 1966 to November 1968 inclusive, giving a total of nearly 3 years of record.

Palms producing bicarpellate coconuts were numbered and their production registered per bunch or infrutescence. This registration of bunch yields of numbered palms was maintained throughout the period of observation. All palms were harvested at each collection and their fruits examined for the presence of bicarpellate coconuts, but no production records were established for unnumbered palms.

Whether a fruit was normal or bicarpellate was usually easy to see. A normal fully developed ripe coconut of the type produced in 'La Solana' is somewhat globosely three-sided in shape and shows three ridges clearly, meeting at the apex of the fruit where they form three small knobs. In the bicarpellate fruit only two ridges and two knobs are found and the coconut is not globose and three-sided in shape, but more or less ellipsoid. After having seen a number of bicarpellate fruits it was easy to distinguish between these and normal ones by their external appearance. Random samples were taken and coconuts were husked to check the number of 'eyes', which nearly always corresponded to what had been determined on the basis of external characteristics. An exception was found in one particular case, to be described in the next chapter, in which details on the morphological differences between the two are given.

Ripe normal and bicarpellate coconuts were sampled to determine their physical characteristics and commercial value and to compare them to other types known in the world. These data include weight, volume, both of complete and husked fruits and weight of copra.

It is important to define exactly what is understood by 'ripe fruits' as harvesting takes place at various stages of ripeness and this naturally influences weight, volume etc. A coconut was considered ripe when the endosperm liquid could be heard to slosh when shaken. In addition the colour of the exocarp started to change as the husk dried out, producing brown to greyish-brown patches which covered approximately 1/4–1/3 of the surface. This is approximately 12 months after pollination.

To investigate the phenomenon of bicarpellate coconuts and its cause(s) it was necessary to study the flowers, especially the female ones; therefore inflorescences were collected and analysed. Unfortunately it proved to be impossible to study the inflorescence 'in situ' as climbing the tree was attempted without success. This handicap did not facilitate the study of flowers; complete absence of facilities of nearly every kind in the area, combined with the difficulty of bringing down an opened spathe in one piece led us to study the flowers mainly unopened spadices, which were relatively easy to transport over great distances.

Apart from flowers and fruits, root tips were also collected for chromosome countings. Both normal and bicarpellate coconuts were left to sprout in the greenhouse of the Agricultural University in Lima; roots were collected one month after the external symptoms of germination had first been observed.

3.3 DATA OF PICKINGS IN 1966–1968 INCLUSIVE: NUMBER OF COCONUTS, RELATIVE FREQUENCY OF BICARPELLATE COCONUTS, TYPE OF COCONUTS AND DISTRIBUTION OF BICARPELLATE COCONUT PRODUCING PALMS WITHIN THE PLANTATION

Although harvesting of the palms was difficult, it was carried out as systematically as possible under the circumstances.

3.3.1. *Number of coconuts, per harvest and per palm*

In table 4 production data are given of those palms which produced also bicarpellate coconuts, from both age groups 2 and 3.

The following additional information is necessary to complete the picture. In the case of such a low frequency of harvesting, it is normal for some ripe coconuts to fall off before harvesting. Others are picked between harvests for direct liquid consumption. The fallen coconuts are usually collected and counted at harvest, though some are stolen. As the coconuts collected between harvests were stored in one heap, they could not be traced to any specific palm. Their number was checked to obtain an idea of the percentage of unrecorded coconuts. From these data and taking into account direct consumption and theft, approximately two coconuts/tree/year should be added to the production records presented in table 4. This holds true for all other tables where production data are given.

Bicarpellate fruits were also found among coconuts collected between harvests, but naturally it was impossible to say from which palm they had come and therefore they were not taken into account. Their number varied from 0–3 per harvest.

In table 4 it is shown that the number of palms producing one or more bicarpellate coconuts amongst many normal ones does not increase very much during the period of observation.

TABLE 4. Results per harvest of bicarpellate coconut producing palms, July 1966–November 1968 inclusive, age groups 2 and 3

Date of harvest	Nr. palms harvested	Normal fruits	Bicarp. fruits	Total nr. fruits/ tree	Av. normal fruits/ tree	Av. bicarp. fruits tree	Av. all fruits/ tree
30. 7.66	15	310	34	344	20.7	2.3	22.9
4.11.66	16	29	2	31	1.8	0.1	1.9
15. 4.67	18	427	11	438	23.7	0.6	24.3
20. 7.67	18	856	2	858	47.6	0.1	47.7
20.12.67	18	229	0	229	12.7	0.0	12.7
18. 4.68	18	305	6	311	16.9	0.3	17.3
31. 7.68	18	623	7	630	34.6	0.4	35.0
21.11.68	18	38	0	38	2.1	0.0	2.1

In July 1966 15 palms were found which also produce bicarpellate coconuts; one other such palm was found at the next harvest and two more in April 1967. Since then at 5 subsequent harvests no further palms were found which showed this abnormality. Another remarkable tendency is the periodicity of bearing. Harvesting between July and April was considered to be impractical because of the lack of coconuts. This means that the main production was concentrated in a period of 4–5 months. This is shown in the yields of November 1966 and 1968. In 1967 a special effort was made to prove that harvesting was possible at the end of the year. It was postponed for one month until December and the harvest was reasonably encouraging, but this led to lower April results.

The total number of bicarpellate coconuts per harvest decreased sharply after the first year of observation. More than 75% of all bicarpellate coconuts were harvested during the first year, i.e. the first three harvests, while during the last five harvests bicarpellate coconuts became very rare and completely absent during the November-December harvest.

The production of individual palms known to produce bicarpellate coconuts is presented in table 5.

It was unfortunate that no records of harvest were kept after November 1968, particularly for the interpretation of the individual palm production; with only one more harvest we would have had three complete years. Now figures are easily misinterpreted as not all harvests are equally successful and the small November-December harvest is included three times, whereas the high April harvest is included only twice. SAMANIEGO (1969) mentions that in April 1969 'quite a few' bicarpellate coconuts were harvested; exact data are not available.

Nevertheless some interesting conclusions can be drawn from the data in table 5. First of all there is one striking fact: two palms, nos. 8 and 11, each produced more than twice the average of the others and can be considered good yielding coconut palms, with an average of more than 100 coconuts/tree/year. This is equivalent to more than 27 kgs/copra/tree/year for this particular type of coconut (see also the following paragraph). These two palms are not only outstanding with regard to their production of normal coconuts. They also outclass the other palms in production of bicarpellate coconuts, i.e. high production of normal coconuts goes together here with high production of bicarpellate coconuts.

A photograph of palm no. 11 is presented in fig. 3. In the field its immediate neighbours are palm nos. 10 and 12 and when one compares their levels of production of bicarpellate coconuts one may safely conclude that palm no. 11 is truly exceptional. The same can be said about palm no. 8 which alone among five other palms in a pasture repeatedly produced bicarpellate coconuts.

Palm no. 14 seems to produce more bicarpellate coconuts than palm no. 8 on a percentage basis, but this is only because the special coconut which is described in the following chapter, paragraph 4, is included in the percentage which otherwise would have been 2.72%.

Except for their high production of both normal and bicarpellate coconuts, palms nos. 8 and 11 do not have much in common. No. 8 produces fruits with

TABLE 5. Production of normal and bicarpellate coconuts per harvest of recorded palms

Palm nr.	Jul. '66		Nov. '66		Apr. '67		Jul. '67		Dec. '67		Apr. '68		Jul. '68		Nov. '68		Totals			aver. per harv.	% B/T	Exocarp colour
	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B	T			
1	25	1	0	0	27	0	53	0	14	0	20	0	29	0	0	0	168	1	169	21,1	0,59	RB*
2	23	2	6	0	12	0	42	0	11	0	0	0	31		0	0	125	3	128	16,0	2,34	R
5	16	2	1	0	23	0	23	0	12	0	35	0	34	0	4	0	148	2	150	18,8	1,33	R
8	15	6	2	0	43	2	90	0	21	0	67	2	60	0	0	0	298	10	308	38,5	3,25	R
10	22	1	5	0	20	0	30	0	8	0	15	0	23	0	0	0	123	1	124	15,5	0,81	R
11	17	9	0	0	27	1	96	1	29	0	36	3	73	1	14	0	292	15	307	38,4	4,89	G
12	21	1	0	0	21	0	57	0	12	0	29	0	28	1	0	0	168	2	170	21,0	1,19	GY
13	20	1	0	0	15	0	23	0	7	0	0	0	25	2	3	0	93	3	96	12,0	3,13	GB*
14	29	1	4	0	14	1+1	42	0	11	0	0	0	42	0	0	0	142	5[1]	147	18,4	3,40[1]	R
15	17	1	0	0	15	1	48	0	6	0	7	0	19	0	0	0	112	1	113	14,1	1,77	GY
16	19	3	0	0	19	0	43	0	6	0	2	0	28	0	0	0	117	3	120	15,0	2,50	G
17	22	2	4	0	24	1	48	0	12	0	0	0	46	0	0	0	156	3	159	19,9	1,89	R
18	29	1	6	0	23	2	64	0	22	0	14	0	48	0	6	0	212	3	215	26,9	1,40	R
19	30	2	0	0	20	0	22	1	4	0	19	0	13	0	0	0	108	3	111	13,9	2,70	R
20	–	–	1	2	43	0	31	0	8	0	0	0	28	0	0	0	111	2	113	16,1	1,77	G
21	5	1	0	0	34	0	53	0	20	0	36	0	38	0	11	0	197	1	198	24,8	0,51	R
27	–	–	–	–	18	0	52	0	9	0	4	1	29	0	0	0	112	1	113	18,8	0,88	G
28	–	–	–	–	29	2	39	0	17	0	21	0	29	0	0	0	135	2	137	22,8	1,46	G
norm.	310		29		427		856		229		305		629		38		2817		2879			
bic.		34		2		11		2		0		6		7		0		62				

Remarks table:
N = normal
B = bicarpellate
T = total (N + B)
G = green

Y = yellow -ivory
R = red-orange
B* = brown
1+1 = 1 bic. + 1 spec. (see text)
[1] including spec. coconut

FIG. 3. Palm no. 11, producer of many normal and bicarpellate coconuts. The trunk seen on the left belongs to palm no. 12.

an exocarp red-orange in colour, belongs to age group 2 and is located near the river Chira on well drained soil, at a distance of approximately 500 m (about 550 yards) from palm no. 11, which bears green fruits, belongs to the older palms of age group 3 and is situated at the side of an irrigation ditch.

The level of production of the other bicarpellate coconut producing palms is more than 50 coconuts/tree/year, corresponding to a copra production of over 13 kgs, some 10% above the average for the rest of the palm trees of 'La Solana', which is ± 45 coconuts. This shows that the fact that these palms produce also bicarpellate coconuts does not have a negative effect on the total yield and there might even be a positive correlation.

For the number of harvests at which each palm produced one or more bicarpellate coconuts, palm no. 11 leads with 5 out of 8, followed by palms nos. 8 and 14 with 3.

In summarizing the information of tables 4 and 5 we find a production of bicarpellate coconuts which is unique for the number of palms involved. It is also unique for the total number of bicarpellate coconuts produced and for the fact that some palms repeatedly produce abnormal fruits. Rarely the bicarpellate coconut is the only one in an infrutescence, but usually normal and bicarpellate coconuts are found together in one bunch.

On the other hand we notice a sharp progressive decrease in the number of abnormal fruits harvested during the period of observation. Over the same period the production of the normal fruits does not decrease. The decrease in the number of bicarpellate fruits is all the more apparent when we take into account that the original consignment of coconuts from the estate, which led to the initiation of this study, consisted of 100 red-orange coloured coconuts, 17 of which were bicarpellate. This means that in April 1966 at least 17 bicarpellate coconuts were harvested but almost certainly many more.

The fact that only certain palms are known to produce the abnormality and that some of these do so much more than others suggests an inherent difference in these palms; the fluctuation with time on the other hand favours a hypothesis of environmental influence. One does not necessarily exclude the other.

3.3.2. *Type of coconuts*

A presentation of production data of the coconut palm in number of fruits is incomplete without a description of the main characteristics of commercial interest of the fruits, because of the great variation in these. For this purpose a number of coconuts were collected at each harvest; this was done to exclude the influence of seasonal variation and this sample was analysed.

Because of the limited number of bicarpellate coconuts and therefore the limitation of sampling regarding these, two separate samples of normal coconuts were drawn. Sample 1 was taken from all normal coconuts at each harvest, the second from the normal coconuts of bicarpellate coconut producing palms only and from the same branch as the bicarpellate coconut, used for analysis. This second sample of normal coconuts can therefore be supposed to resemble somewhat the bicarpellate coconuts, while the first sample gives an idea of the type of coconuts in the estate as a whole.

TABLE 6. Principal characteristics of normal and bicarpellate coconuts (averages of 15 fruits each)

	normal coconuts		bicarpellate coconuts
	sample 1	sample 2	
volume	3620 cc	3880 cc	3820 cc
weight	1810 gr	1800 gr	1900 gr
weight husked coconut	1130 gr	1200 gr	1330 gr
weight of copra	260 gr	280 gr	285 gr
$\frac{\text{weight of copra}}{\text{weight husked coconuts}} \times 100$	23.0	23.3	21.4

The most important feature of table 6 is the weight of copra per coconut as this determines the number of coconuts needed to produce 1 ton of copra. Weight of copra was determined on a 6% moisture basis, the commercial standard. The number of coconuts necessary to produce one ton of copra (English long ton = 1,016 kg) varies from about 3,300 up to 8,000, according to types, climate etc.

In this case one can appreciate that 3,600–3,900 coconuts will produce 1 ton of copra, which means coconut size is excellent.

Comparing the samples and taking into account the very limited possibility for random choice of bicarpellate coconuts, we note that bicarpellate coconuts are in no way inferior to normal ones regarding their commercial characteristics.

Another way in which the coconuts can be distinguished is the colour of the husk. The occurrence of different colours in the palms studied is presented in table 7.

TABLE 7. Husk colour in palms of the 3 age groups in 'La Solana'

Husk colour	Group 1		Group 2		Group 3	
	no.	%	no.	%	no.	%
GREEN	2	12.5	13	22.8	70	31.4
Green-brown					5	2.2
Green-yellow			2	3.5	16	7.2
YELLOW-IVORY	5	31.3	20	35.1	53	23.8
Yellow-red	2	12.5			5	2.2
Red-brown					3	1.3
Red-green					2	0.9
Brown					12	5.4
RED-ORANGE	7	43.7	22	38.6	57	25.6
Total	16	100.0	57	100.0	223	100.0

The colour was defined jointly by two persons who examined the coconuts in all instances. In group 1 colour was checked by studying the coconuts in situ with the aid of binoculars.

Group 1 was excluded from the comparison of husk colour frequencies in bicarpellate and normal coconut producing palms as the bicarpellate coconuts found below the palms of that group could not be traced to any specific palm.

TABLE 8. Husk colour of normal and bicarpellate coconut bearing palms

Husk colour	Group 2			Group 3		
	Norm.	Bic.	Total	Norm.	Bic.	Total
GREEN	11	2	13	67	3	70
Green-brown				4	1	5
Green-yellow	2		2	14	2	16
YELLOW-IVORY	20		20	53		53
Yellow-red				5		5
Red-brown				2	1	3
Red-green				2		2
Brown				12		12
RED-ORANGE	21	1	22	49	8	57
Total	54	3	57	208	15	223

In table 8 the exocarp colour is given for age group 2 and 3, palms being classified as normal or bicarpellate coconut bearing.

It is interesting to note the high proportion of palms producing coconuts with a red-orange exocarp. The proportion is high in all three generations; also the number of bicarpellate coconut producing palms with red-orange coconuts is high. In group 3 more than 50% of the bicarpellate coconut producing palms show a red-orange husk colour.

3.3.3. *Distribution of bicarpellate coconut producing palms within the plantation*

Some of the palms recorded as producers of bicarpellate coconuts are found in the first age group (see fig. 2), but as explained before harvesting of these was not possible. The bicarpellate coconut producing palms for which production records are available belong mainly to age group 3, except nos. 8, 27 and 28, which belong to age group 2. Fig. 2 gives the exact location of palms nos. 8, 27 and 28. In fig. 4 the positions of all palms in age group 3 are indicated and the distribution of the bicarpellate coconut producing palms is shown.

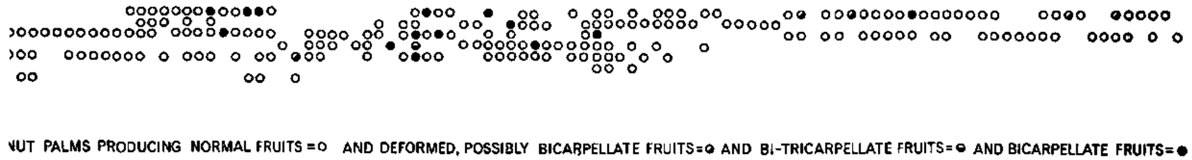


FIG. 4. Map indicating the location of palms in age group 3, showing distribution of producers of bicarpellate fruits.

3.4. COMPARISON OF FREQUENCY OF BICARPELLATE COCONUTS, AS FOUND IN PERU, WITH RESULTS OF A SURVEY ON THE APPEARANCE OF BICARPELLATE COCONUTS IN OTHER REGIONS OF THE WORLD

As stated in chapters 1 and 2, the appearance of bicarpellate coconuts is most uncommon. The almost complete lack of reference to this abnormality in the literature has been illustrated amply. However the abnormality is not so obvious as many others known to occur in the coconut palm and the few references are from the previous decade. It might be just possible that only in recent years the attention of coconut research workers had been drawn to this phenomenon and some unpublished information could be obtained.

To verify this and at the same time to try to obtain information on the frequency of occurrence of bicarpellate coconut production, a survey by questionnaire was carried out during 1968 and the beginning of 1969, the basis of reference being an introductory publication on this subject (SMIT, 1967). The survey covered 16 coconut research workers, with experience of or working in the major coconut growing regions of the world; 12 replies were received, a response of 75%.

The results of this survey are outlined in table 9.

Those workers, indicating that they have observed bicarpellate coconuts are

TABLE 9. Occurrence of bicarpellate coconuts around the world

Research workers surveyed: 16 replied: 12		Countries covered by repliers
Unfamiliar with the phenomenon	3	Ceylon, Philippines, Thailand
Familiar, but never observed bicarpellate coconuts	6	Ceylon, Dahomey, Indonesia, Ivory Coast, Malaysia, Papua and New Guinea, Philippines, Portuguese East Africa, Tonga, Trinidad and Tobago
Observed bicarpellate coconuts	3	India, Indonesia, Jamaica

DAVIS in India, ROMNEY in Jamaica and TAMMES in Indonesia. ROMNEY (1968) mentioned the discovery of only one bicarpellate coconut in 1964, in the District of Rosend, Province of St. Mary, Jamaica, in a coconut palm of the tall type and comments: 'very uncommon'. This information is all more interesting as the Research Department of the Coconut Industry Board of Jamaica has an agreement with many copra producers on the island that if any kind of abnormality is found, it is sent to the Research Department. This means that in Jamaica, where annually some 100 million coconuts are harvested, the bicarpellate coconut must be very uncommon indeed.

DAVIS (1968), who is considered as the most prominent specialist on abnormalities in coconut palms, had found up to 20 bicarpellate coconuts so far, all in India and all since 1955, both in Kerala and in Calcutta. All these coconuts came from tall type coconut palms. Bicarpellate female flowers were also seen by him (DAVIS and MENON, 1953). In the other countries visited by him in connection with his studies (Ceylon, Malaysia, and Indonesia), he did not meet with any bicarpellate coconuts or flowers.

TAMNES (1969) reported that in Indonesia (mainly Celebes) he has seen a few bicarpellate coconuts but there also this abnormality was very unusual. As most records on prewar work were lost during the Japanese occupation, no exact data could be produced but the number of bicarpellate coconuts observed by him over a period of 10 years does not exceed 3. These were all produced by tall type palms.

The survey has led to the following conclusions:

1. Bicarpellate coconuts are produced by coconut palms in various countries. A detailed survey would possibly find that this abnormality occurs in many more countries.
2. The frequency of the occurrence of bicarpellate coconuts is very low throughout the world. On the small amount of information available its frequency can be estimated as at most 1:100,000,000 and possibly even less frequent.
3. Bicarpellate coconuts have been found as yet in the tall type of palms only. This does not mean that they do not occur in dwarf type coconut palms but as there are about 100 times more tall than dwarf type palms, chances of finding a dwarf type bicarpellate coconut are extremely small.

4. Palms producing exclusively bicarpellate coconuts or even fruit branches with only bicarpellate fruits have not been observed, all coconuts having been found together with normal coconuts in the same branch.

When we compare the above information with the data of paragraph 3.3 the most striking fact is naturally the relatively high frequency of production of bicarpellate coconuts, the frequency in our grove being 1:500. This is 200,000 times more than the estimate for other regions of the world.

A second aspect of interest is that except by DAVIS (1970) in India no palms have been recorded as producing syncarpous bicarpellate coconuts on more than one occasion, i.e. in more than one fruiting branch while in 'La Solana' in some palms, especially the 'top producers' palms nos. 8 and 11, the process seems more or less continuous.

4. ANALYSIS AND DESCRIPTION OF THE BICARPELLATE COCONUT IN COMPARISON WITH THE NORMAL COCONUT

The descriptions of the normal fruit of the coconut palm have been summarized elsewhere (MENON and PANDALAI, 1958). In this chapter emphasis will be laid on the points in which the bicarpellate coconut differs from the normal one. Also variation among bicarpellate coconuts as well as a coconut, in appearance between normally tricarpellate and bicarpellate (fusion) will be described.

4.1. MORPHOLOGICAL DIFFERENCES

The external appearance of the bicarpellate coconut differs from the normal fruit in that the shape of the normal coconut produced by the palms of 'La Solana' is mainly globosely three-sided. The bicarpellate coconuts are never of this shape, but ellipsoid to spheroid. This is shown in fig. 5.

The exocarp of the bicarpellate coconut is clearly marked by two ridges near the 2 stigmatic lobes at the apical end of the fruit. These lobes include a perpendicular slit (the orifice of the pistil) and not a triradial one as in the normal coconut. The ridges become less pronounced around the centre of the coconut and again are recognizable at the basal end. The angle between the ridges is approximately 180°; the two segments into which they divide the exocarp are not equal. At the basal end the exocarp and the underlying mesocarp are frequently dented and even slit; these slits and dents are wider at the basal end but narrow towards the apex and their length is 2–4 cm. Similar marks also are found on normal coconuts but less frequently: 80% of the bicarpellate coconuts and only 10% of the normal ones show these marks.

It is known that the normal tricarpellate coconut is marked by 3 ridges on the exocarp, alternating with the ridges of the endocarp; the angles between segments are 90–120° for the smaller carpels and 160–180° for the section alternating with the main or functional carpel as retraced to the endocarp.

Apart from the dents and slits which sometimes penetrate the mesocarp, no difference between mesocarp of bicarpellate and normal coconuts has been found. Only the difference in shape between the two may result in lower mesocarp weight of the bicarpellate ones.

The endocarp of the bicarpellate coconut is marked by 2 'eyes' only, one 'soft' or 'functional' in the larger segment, the other 'hard' or 'non-functional'. The endocarp of the normal coconut shows 3 'eyes', 1 'functional' and 2 'non-functional'.

The number of sections into which the endocarp is divided by the ridges on it is reduced from 3 to 2. The ridges on the endocarp do not divide the fruit in two equal sections; the section containing the functional 'eye' is the bigger of the two, angles between ridges being again approximately 180°. The difference in size between the two sections can be seen in fig. 6.

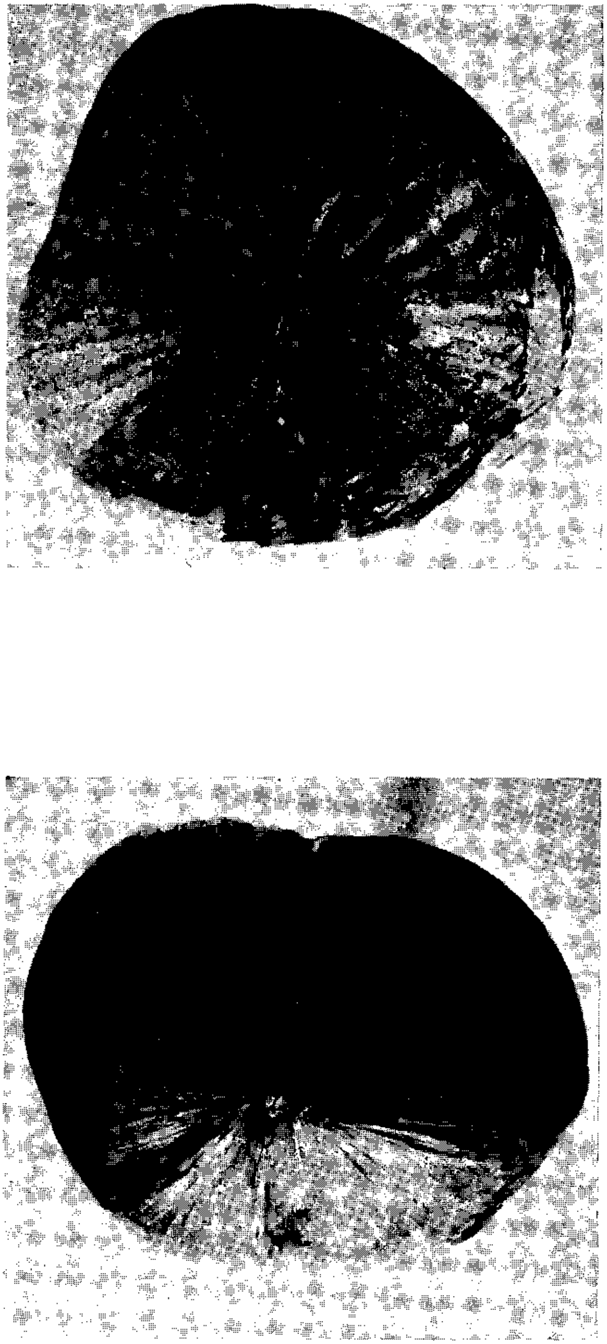


FIG. 5. The tricarpellate coconut (above) is easily distinguished from the bicarpellate one (below)

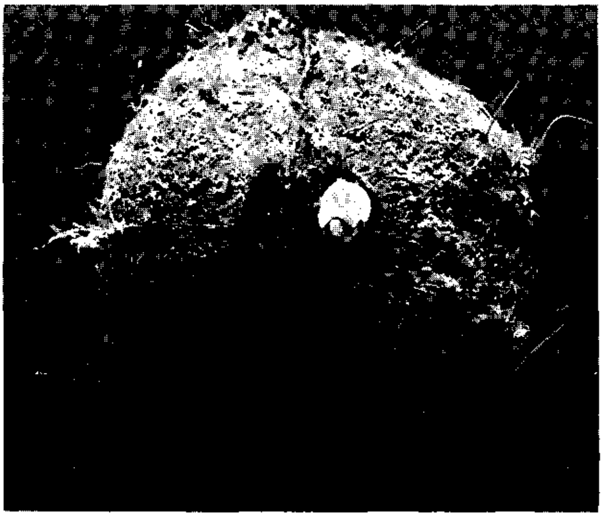


FIG. 6. A germinating bicarpellate coconut with the fibrous mesocarp removed. The section containing the embryo is the larger one.

Apart from the difference in number there is also a notable difference in the appearance of the 'non-functional eyes': the 'non-functional eye' of the bicarpellate coconut from the outside is more similar to a 'functional eye' than the 'non-functional eyes' of the tricarpellate coconut.

It is shown superficially to be composed of tissue different from that of the sclerified endocarp, while the 'non-functional eyes' of the normal fruit look like mere depressions in the putamen and at most an insignificant amount of tissue, softer than the stone cells of the endocarp is apparent.

Another expression of its bicarpellate nature is found in the cross-section of the coconut. While in normal coconuts remnants of the two compressed locules of the two underdeveloped carpels are found adhering to the inside of the putamen, each in its own carpel (fig. 7A), inside the bicarpellate endocarp wall only one such compressed locule is found (fig. 7B). This is an argument for considering that the bicarpellate nature of the coconut is the result of a development of the fruit out of a flower with a bicarpellate ovary.

Some 10% of the bicarpellate coconuts showed a depression in the endocarp wall, sometimes in the part corresponding to the larger carpel, sometimes involving both carpels and the ridge between them. In the latter case the ridge is not recognizable as such in the depressed part. The depression is triangular in shape with the base of the triangle parallel to the wider part of the husked coconut and 7–8 cm in length; the sides of the triangle towards the tip of the husked coconut are 5–6 cm in length. One such depression is shown in fig. 8. The mesocarp over this part did not undergo any change, nor is the presence of such a depression noticeable from the outside of the coconut; it is limited to the endocarp only. No tricarpellate coconuts have been found showing a similar abnormality.

Testa and endosperm have developed normally in the bicarpellate coconut and do not appear to be different from what is seen in tricarpellate coconuts.

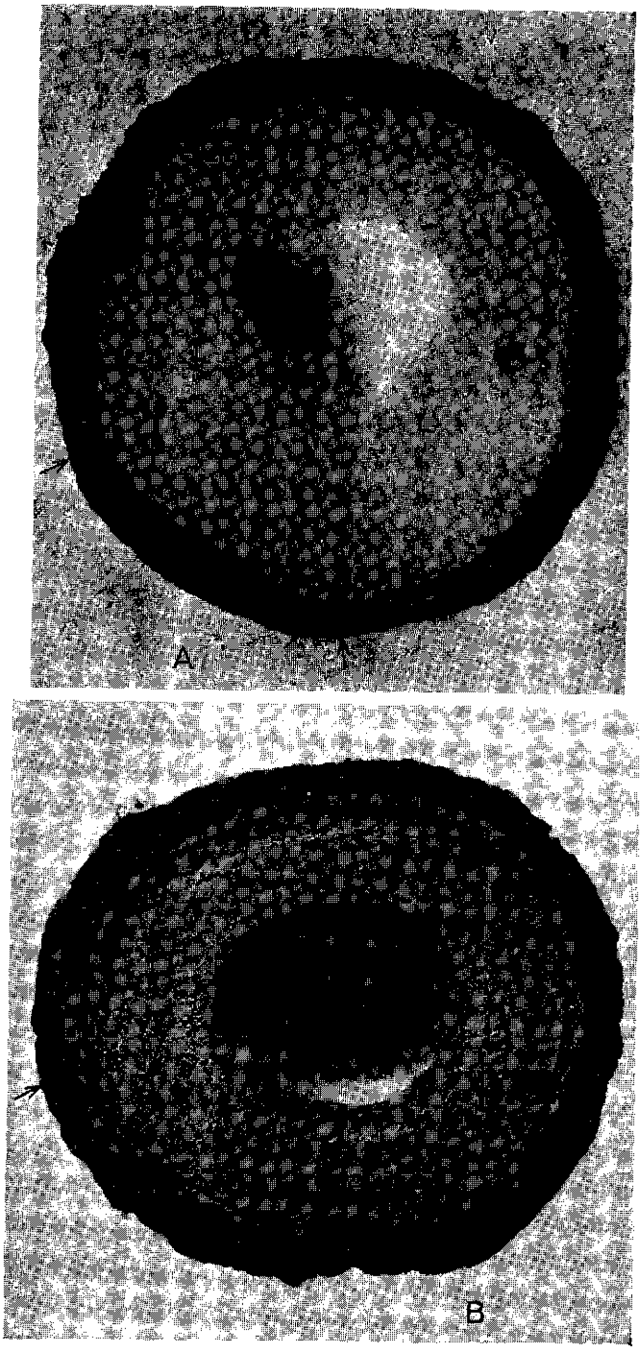


FIG. 7. Two compressed locules against the sclerified endocarp wall of a tricarpellate coconut (A). Only one such locule in the case of a bicarpellate coconut (B).

FIG. 8. Depression in the endocarp of a bicarpellate coconut.

4.2. THE ANATOMY OF THE 'EYES'

The 'eyes' are the most remarkable elements of the husked fruit; according to one of the theories (CHILD, 1964) on the etymology of the name 'cocos', the coconut is supposed to derive its name from the old vernacular Spanish or Portuguese word 'coco', which means a monkey's face. This is because of the similarity of a husked fruit which its three 'eyes', one larger, two smaller to such a face.

As in the bicarpellate fruit the reduction in the number of carpels also results in a reduction in the number of 'eyes' from 3 to 2, it was necessary to study the 'eyes' more closely and to compare the 'eyes' in normal coconuts with those in bicarpellate ones.

Remarkably little has been published on the development from female flower to ripe coconut. The only description of the 'eyes' of the coconut is incomplete (JULIANO, 1926); nevertheless it is cited as the latest on the subject by MENON and PANDALAI (1958) and therefore a more comprehensive theory on the origin and development of the 'eye' of the coconut had to be developed, as without this it would not be possible to describe and discuss possible differences between them in normal and abnormal coconuts.

The 'eyes' of the coconut are located in the sclerified endocarp at the basal end of the fruit near the point where the three ridges on the endocarp meet at the joints of the carpels. In both normal and bicarpellate fruits two types of 'eyes' are found: a 'soft', 'fertile' or 'functional eye', below which the embryo is located, embedded in the endosperm. Through this 'eye' the embryo will emerge at germination. This 'eye' forms part of the largest carpel of the 3 or 2 respectively. The other 'eye' (bic.) or 'eyes' (tric.) are named 'hard', 'non-fertile' and 'non-functional' to indicate that they do not provide a passage through the sclerified layer, from the endosperm to the mesocarp. Neither is there a reason for such a passage as there are no embryos capable of penetration. Nevertheless the 'eyes' are formed and in abnormal fruits where more than one locule is functional the corresponding 'eye' becomes functional too, so that is logical to assume that the 'eyes' are formed just after fertilization and before the development of the non-functional locule(s) is halted by the pressure of the faster developing functional locule.

The first extensive description and explication of the ontogeny of the 'eyes' in palm fruits was given by PFITZER (1885). He observed that in some Cocoideae three 'eyes' were found which are from the outside similar in appearance even when only one embryo develops. All three are formed regardless of whether the ovule will grow into a seed or not. Studies of subsequent stages of development of unripe fruits of *Cocos flexuosa* Mart. = *Syagrus flexuosa* (Mart.) Becc. led him to the following conclusions: 'the micropylar end of the anatropous ovule sinks soon after pollination into a groove of the inner ovary wall. Later the outer integument coalesces with the bottom of the groove, while the wall of the ovule lets loose easily from the slope of the groove. The epidermis of the inner ovary wall, consisting of high cells, stretches just under this joint in such a way that a layer of cells, thick in the centre and thin at the edges is formed, of brown colour, by which it is easily distinguished from the colourless tissue of the outer integument'. (PFITZER, 1885, p. 42). If we assume that a similar process occurs in *Cocos nucifera* L. and the joining of the micropylar end and integuments with the ovary wall takes place before the compression of two of the locules, many questions concerning the 'eyes' are answered.

The observations of JULIANO (1926, p. 194; pl. III, 12 and 13) on the morphology of the fertile 'eye' and his drawings of the 'micropylar tip' in the centre of the 'eye' coincide with Pfitzer's explanation. His thin plate of lignified cells forming the 'eye-lid', corresponds to the 'layer of cells, thick in the centre and thin at the edges, of brown colour', which Pfitzer described. The 'micropylar tip' appearing in Juliano's figure (pl. III, fig. 11) seems to consist of coloured cells of a small size; he does not describe this tissue. His observations on the sterile 'eyes' should be completed by stating that, due to the pressure of the developing locule the entire non-functional locule is compressed against the endocarp wall. The layers of parenchymatous tissue and the sclerified inner ovary wall epidermis remain unaffected also in the sterile 'eye' as pressure naturally will not move these very much. The two integuments however have come to lie sideways in the endocarp as a result of the pressure and therefore no passage is formed. This implies that Juliano's remark that other tissues play a role in the formation of the non-fertile 'eye', compared with those forming the fertile 'eye', is not correct.

Balley's (1937) remark that the 'eyes' of the coconut mark the positions of the micropyles also agrees with Pfitzer's theory. The view of **Corner** (1966) that in the coconut the 'eyes' are germ pores and not the micropyles is nearly correct; the 'eye' is not the micropyle but only marks its position, but only one of the 'eyes' will become a germ pore. However his theory that the three pores mark the points of entry of vascular supply is not tenable because of the complete absence of vertical vascular bundles in the 'eye'.

Our findings confirm the observations of Pfitzer to a certain extent and add certain essential information to his descriptions. They will be presented here as no complete account of the anatomy of the 'eyes' of the coconut has been published yet.

As the 'eyes' are surrounded by sclerified endocarp it proved to be extremely difficult to obtain good sections, particularly of the non-functional 'eyes' in which practically no soft tissue is present. The best results were obtained by embedding the 'eye', with a minimum of stone cells around, in paraplast and cutting with a Reichert rotary microtome at 12–15 μ thickness.

4.2.1. *The 'soft', 'fertile' or 'functional' 'eye'*

This 'eye' is a 'soft' spot in the sclerified endocarp; tangentially its shape varies from elliptical to nearly circular and triangular, somewhat flattened at the side of the carpel ridge, ranging in size from 18–24 mm for its larger, 9–13 mm for its smaller axis. As with the carpels, the functional 'eye' is always larger than the non-functional one.

In radial sections the 'eye' shows certain similarity in shape to a cross-section of a yoyo. From the endosperm, working outwards the following tissues are found.

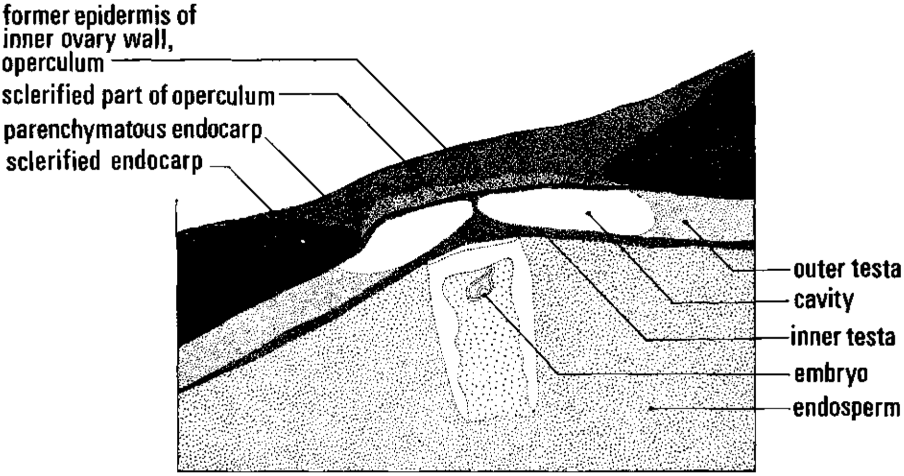


Fig. 9. Schematic representation of a radial section through the soft 'eye' of a coconut.

a. Endosperm enclosing the embryo

The descriptions of this tissue by Harz (1885) and Winton (1901) do not mention the special configuration of the layers of endosperm cells just below the 'eye', i.e. between the cavity which surrounds the embryo and the overlying part of the inner testa layer. The endosperm cells as such are not different but the walls are very thick towards both cavity and inner testa. In particular the walls forming the lining of the cavity have increased considerably in size from the normal 3–4 μ to 15–18 μ towards the inner testa the walls increase in thickness to approximately 10 μ.

b. Inner testa

A layer 0.15–0.2 mm wide which is red-brown coloured and 15–16 cells wide, except in the centre of the 'eye', where the layer widens to about 30 cells and becomes 0.5 mm wide. The cells are isodiametric to 2–3 times as long as wide, both in tangential and longitudinal sections. The diameter of the cells is 10–17 μ. Their walls are 1–1.5 μ thick and colourless, rarely with simple pits. The cell contents are coloured red to brown, fill the cell and are of no particular structure.

According to Pfitzer (1885), Winton (1901) and Juliano (1926) the inner testa has developed from the inner integument of the functional ovule. It seemingly does not participate in the formation of the 'eye' and Pfitzer and Juliano only mention that the outer integument meets the inner ovary wall. However, the fact that the inner testa layer widens considerably just in the centre of the 'eye' and approaches the inner ovary wall while the outer testa layer is replaced by large cavities around the centre of the 'eye', suggests that their theory does not cover this part.

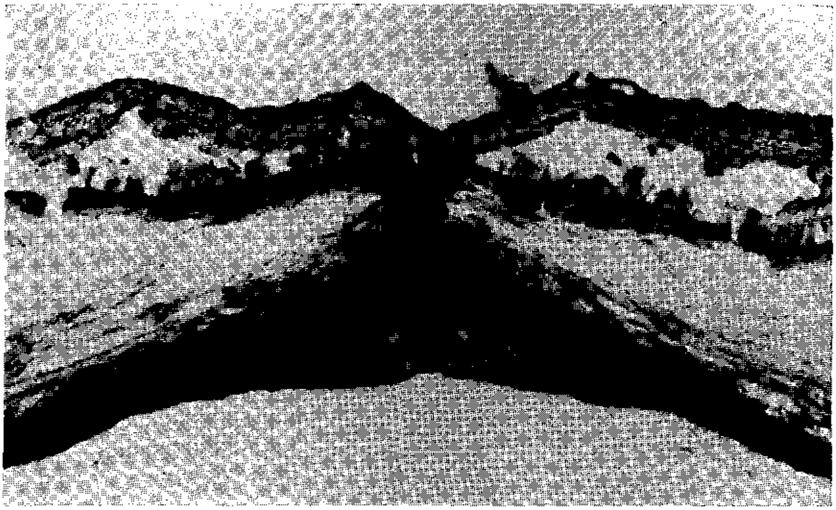


Fig. 10. Photograph of a radial section through the soft 'eye' of a coconut. This close-up shows the junction of the operculum and the inner testa.

Exactly radial slides show that the inner integument also joins the 'eye-lid'. This is shown in fig. 10. The junction occurs over a common surface of only some 10 × 24 cells and this probably explains why other authors have never described this. The present author would almost certainly have missed it also, had not the sections of the 'hard eye' of a bicarpellate fruit indicated that such a connection should also exist in the 'fertile eye'. To avoid misunderstanding it is stressed here that this joining of the inner integument and inner ovary wall is not a peculiarity of the bicarpellate fruits or of the tricarpellate fruits from the same location. The same process has been identified in the 'eye' of coconuts of African origin.

This means that earlier theories on the development of the fertile 'eye' should be amended to indicate that, when the anatropous ovule sinks with its micropylar end into the inner ovary wall, both the inner and outer integument meet and join with this wall.

The use of the word 'Grube' by Pfitzer suggests the presence of a groove in the wall of the carpel before the ovule commences its longitudinal growth. Sections of a number of developing fruits of the coconut have shown that there is no such groove till the ovule comes in touch with the inner ovary wall. Only then the wall-tissue is pressed aside and a depression appears.

When loosening the embryo and surrounding tissues from the 'eye-lid' the inner testa layer over the embryo remains firmly attached to the underlying endosperm. This results in an embryo crowned by a dark coloured tip, which is the point of attachment of the inner integument and the inner ovary wall.

DE POERCK (1950) describes a similar dark tip on top of the embryo from a fruit of the African oil palm and assumes that this tip represents the remnants of the synergids. Although a study of the 'eyes' in the endocarp of the oil palm fruit was not carried out, the remainder of the description by de Poerck as well as the earlier description of the 'eyes' by YAMPOLSKI (1922) bear many similarities to the findings in the 'eyes' of the coconut. Therefore the present author believes that the tip also represents the inner testa in the case of the oil palm.

SELVARATNAM (1952, p.714, fig. 1 and 2) in describing the embryo of the coconut calls this tip a 'dark circular patch of tissue on the surface of the embryo which tapers into the micropylar canal'. This description is nearly identical to DE POERCK's description (1950, p. 627) that 'the embryo carries on its top an appendix, which points into a small cavity of the operculum'.

c. Central cavity

The inner testa in the centre of the 'eye' protudes into a central cavity, which represents the space between the outer and inner integument at the moment of joining the inner ovary wall epidermis. The diameter of this cavity is approximately 1 cm with a maximum width of 0.9 mm near the rim of the 'eye'. This cavity, which neither Pfitzer nor Juliano mention, is important for the emerging embryo. Had the outer testa covered the inner testa also at the centre of the 'eye' and had that layer also been attached to the 'eye-lid' itself, this mass of closely adhering vascular bundles, firmly attached to that tissue would have presented a formidable barrier to the embryo. Because of the discontinuation of the outer testa in the centre of the 'eye', pressure from inside towards the 'operculum' will result in easy rupture of the inner testa layer.

d. Outer testa

Normally this layer is 0.7–0.8 mm wide; this layer also takes part in the formation of the 'eye', as the integuments sink into the inner ovary wall and become attached to it. In the region of the 'eye' the outer testa is much wider. It increases in width from 0.8 mm to a maximum of 1.7 mm towards the centre of the 'eye'. The cells forming the principal tissue of this layer are round to elongate, up to 4 times as long as wide, with diameters varying from 10–18 μ. There are some thin walled (1.5 μ) and many thick walled (3–4 μ) cells mostly without visible contents or colour. The walls are usually colourless.

Some larger sized cells are found which have thick (4 μ) brown walls, some with equally brown-coloured contents, granular or composed of disks; the latter being the case, the contents fill only part of the cell. Nearly all of the cells show numerous pits in their walls. The thick walled pitted cells turn gradually into pitted tracheids. These and the long spiral tracheids run parallel to the inner testa layer, i.e. horizontally in the outer testa layer. Except in the centre of the 'eye', the outer testa has joined with the 'eye-lid' (operculum).

e. Inner ovary wall epidermis (fig. 11a)

This layer appears at the rim of the 'eye' between the outer testa and the stone cells of the endocarp and is approximately 2–3 cells wide, increasing towards the centre of the 'eye' to 8–10 cells in width. Cells are isodiametric to 4 times as long as wide with a diameter of 12–15 μ. The walls are double and colourless, 2–3 μ thick. The contents are usually structureless or occasionally granular. The colour is usually brown to red-brown, rarely light-brown to yellow and similar to the cells of the inner testa layer. This tissue, together with the next layer, forms the 'operculum'.

f. Sclerified operculum tissue (fig. 11b)

Closely adhering to the previous layer is a layer of colourless stone cells produced by a sclerification of part of the inner ovary wall tissue at a very early stage, even before the expansion of the epidermis cells (PFITZER, 1885). At the rim of the 'eye' the sclerified cells cannot be distinguished from the stone cells of the endocarp but they are distinguishable at the centre of the 'eye'. In the centre of the 'eye' the tissue is up to 0.5 mm wide. The colourless stone cells are up to 0.1 mm long with thick walls (10–15 μ) and a small lumen with diameter from 4–8 μ. The pits in the walls are mostly ramified. The outer layers of this tissue contain cells with thick walls in between the stone cells. They have simple pits and a large lumen. Sometimes the walls are very thick with ramiform pits at the side of the other stone cell and a much thinner wall sometimes even without pits on the other side, as if sclerification had stopped in the middle of the cell. These cells are a transition from the stone cells to the adhering tissue above it.

FIG. 11. Photograph of a tangential section through the soft 'eye' of a coconut.
a. operculum, formerly the epidermis of the inner ovary wall
b. sclerified operculum tissue
c. parenchymatous endocarp

g. Parenchymatous endocarp (fig. 11c)

This part of the 'eye' is, according to Juliano: 'composed of spongy parenchymatous tissue, which morphologically belongs to the endocarp'. This is in accordance with the opinion of Pfitzer, who further supposes that this tissue has turned into cork during ripening of the fruit. However this could not be confirmed in our material as repeated attempts at staining this tissue with Sudan 3 failed.

From the sclerified operculum upwards two or three more or less distinct layers are found in this tissue. A first layer, some 0.5–0.7 mm wide, consists of cells varying from isodiametric to elongated with a diameter of 10–25 μ. The contents are granular in many cells and sometimes of thread-like appearance. The cell walls are light-brown coloured, layered, and 3–4 μ thick. This type of tissue is not always recognizable as such, since in dry husked coconuts it is much more reduced and is identical to the upper layer.

A second layer, about 0.2 mm wide, shows the same type of cells but the walls appear as if they have been under stress towards the rim of the 'eye'. The cells are elongated tangentially with a larger diameter of 30–50 μ. The contents are granular or clotted and compressed against the walls.

The third layer consists of cells of no recognizable shape because the walls have mostly ruptured. The walls of the cells of this layer are thin (1.5–2 μ) and colourless. The cells occasionally contain raphids, especially at the rim of the 'eye' and in the four outer layers; a few cells are found with brown coloured structureless contents. The outermost layer seems to consist mostly of compressed cell walls some of which are brown.

The parenchymatous 'eye-cover' is found in coconuts which are not completely ripe and dry. In dry ones only remnants of these layers are found. This is either because this tissue is destroyed during the husking or the drying of the fibrous mesocarp leads to dessication of the underlying parenchymatous tissue. The 'eye-lid' or 'operculum' which in a dry husked coconut is easily detached from the 'eye', is composed of the inner ovary wall epidermis and the adhering stone cell layer together. This was confirmed by leaving a number of husked coconuts to dry and detaching the 'eye-lid'. The layers which became loose were examined microscopically.

In concluding this description of the 'fertile eye' of the coconut, a short discussion of the terms 'papilla embryotega', 'tympanum' and 'operculum' is called for. The term 'papilla embryotega' is used by REINDERS (1964) to describe the thin, round lid in the hard endocarp of, among other fruits, the coconut, through which the embryo emerges.

The disadvantage of this term is that the 'eye-lid' has very little of a papilla. MARTIUS (1823) uses 'tympanum' for the 'eye-lid', which is more specific than papilla but not considered sufficiently descriptive.

To describe the 'eyes' of the fruit of the African oil palm several authors including YAMPOLSKI (1922) and DE POERCK (1950) use the term 'operculum'. This term is used botanically for a variety of lids and applying it to the lid of the 'eye' of the oil palm fruit or of the coconut is therefore acceptable.

The term 'pore' (Martius: porus) indicates the aperture or canal through the putamen but should not be used to describe the tissue which closes off this canal till germination.

4.2.2. *The 'hard', 'non-fertile' or 'non-functional eye'*

The function of the 'eye' is to provide a passage for the emerging embryo. As the ovule to which the 'hard eye' corresponds has become compressed against the endocarp wall, the passage, if any, will therefore not be found downwards through the endocarp to the outer testa of the seed. Its course will be sideways, within the stone layer towards its compressed locule.

Viewed from above, the hard 'eye' is triangular to nearly elliptical in shape with the larger axis at the side of the carpel ridge 11–13 mm and the smaller one 5–7 mm. On the side away from the carpel ridge the endocarp is 1–3 mm higher along the rim of the 'eye', forming an elevation.

Returning to Pfitzer's observation that the coalescence of the micropylar end of the ovule and inner ovary wall takes place soon after fertilization, this process should therefore have terminated before pressure of the functional locule sets in. Otherwise there would not be more than one 'eye'. The presence of the 'eyes' means also that near the 'eye' the integuments of the compressed ovule should be found, as these participated in its formation. It should also be possible to trace the operculum.

To confirm this by anatomical study of sections through the 'hard eye' of tricarpellate fruits proved to be very difficult because the preparation of good slides was almost impossible. In the 'hard eye' the lower proportion of soft to sclerified tissue (stone cells) renders it even more unfavourable for the preparation of sections.

It is possible to soften the masses of stone cells by boiling and submersion in solutions containing strong acids but such treatment either destroys the softer tissue or makes it unrecognizable.

Furthermore, to obtain radial sections of the 'hard eyes' of a tricarpellate fruit the direction of the corresponding compressed locule has to be established. This is found curving from the 'eye' towards the carpel ridge which forms the separation between the 'hard eyes' (fig. 12). Because of the curve it is difficult to obtain good radial sections.

FIG. 12. Schematic view of the 'eyes' and locules of normal (left) and bicarpellate coconuts (right). Dotted lines indicate the position of the compressed locules.

From several series of more or less successful sections the type of structures present in the 'hard eye' were established. Apart from endosperm and embryo all other tissues, i.e. also those taking part in the formation of the 'fertile eye', are present and recognizable. Both the outer and the inner integuments are seen to be attached to the operculum; the central cavity, the inner ovary wall epidermis, the sclerified operculum tissue and the parenchymatous 'eye' – tissue are clearly recognizable. This confirms the opinion that the formation of the 'eye' takes place at an early stage of development of the fruit.

When following the inner and the outer integuments through the endocarp in which they are partly embedded, their length is found to be 4–6 cm for the inner integuments and 5–7 cm for the outer integument, an enormous length for the integuments of a non-functional ovule. This means that in the initial stastages of development all three ovules grown in length rapidly. A similar longitudinal growth was recorded in non-functional ovules of the African oil palm by DE POERCK (1950).

As to the septa, separating the three ovules, the normal coconut, in which only one seed developes, is not a good source of information as the non-functional ovules as well as the septa are pressed away. In abnormal 2- or 3- seeded coconuts the septa are clearly recognizable and described as 'leathery': SMITH

(1915). In the case of the oil palm, when two or three seeds develop within a fruit the seeds remain completely separated from each other: JAGOE (1934).

The 'eyebrow', the pronounced ridge of the outer layers of the endocarp wall along part of the rim of the 'eye', is always located above the compressed locule and therefore it is assumed that it is formed by the outward pressure of the locule against the endocarp wall.

4.2.3. *The 'eyes' of bicarpellate coconuts*

No difference was encountered between the functional or 'soft eye' of the tricarpellate and bicarpellate fruits; neither was any such difference expected. As for the 'non-functional' or 'hard eyes' the differences are not structural but nevertheless sufficiently important to merit description.

As only one 'hard eye' and one compressed locule are present in the bicarpellate coconut, the position of the 'eye' and of the locule is different. The locule runs in the endocarp wall right through the centre of the carpel, i.e. at an approximately equal distance from the ridge on the endocarp wall. (fig. 12).

Tangentially the outer surface of the 'hard eye' is larger than that in a tricarpellate fruit. The larger axis is 16–19 mm and the smaller one 11–12 mm. The strongly reduced competition for space has meant that the structure of the compressed locule and the 'eye' are less disturbed and less compressed. It proved to be easier to obtain good radial sections through the 'eye' and the locule. This is shown in fig. 13a and b. The structures and relative positions of the tissues can be observed easily.

1. The connection between inner integument and inner ovary wall epidermis is apparent. This confirms the theory of the junction of these tissues described in the 'fertile eye'. The two cavities between the joints of inner integument and

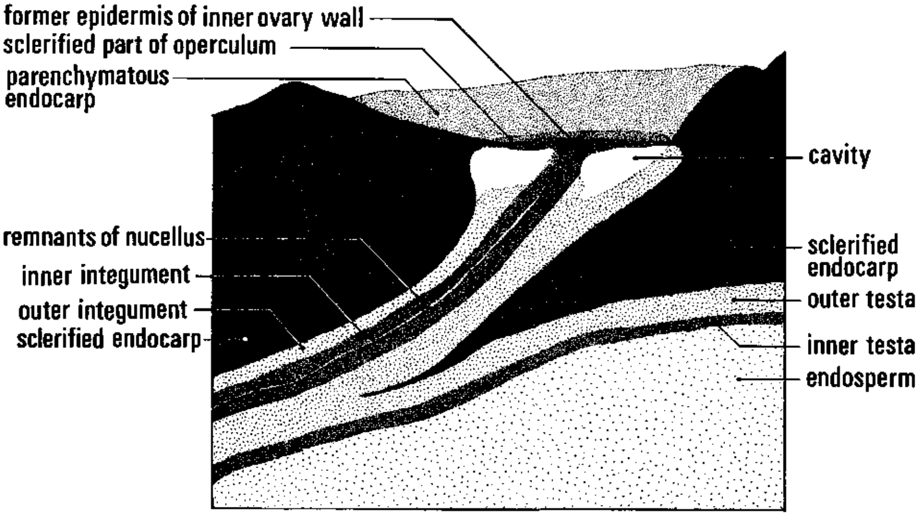


FIG. 13a. Schematic representation of a radial section through the hard 'eye' of a coconut.

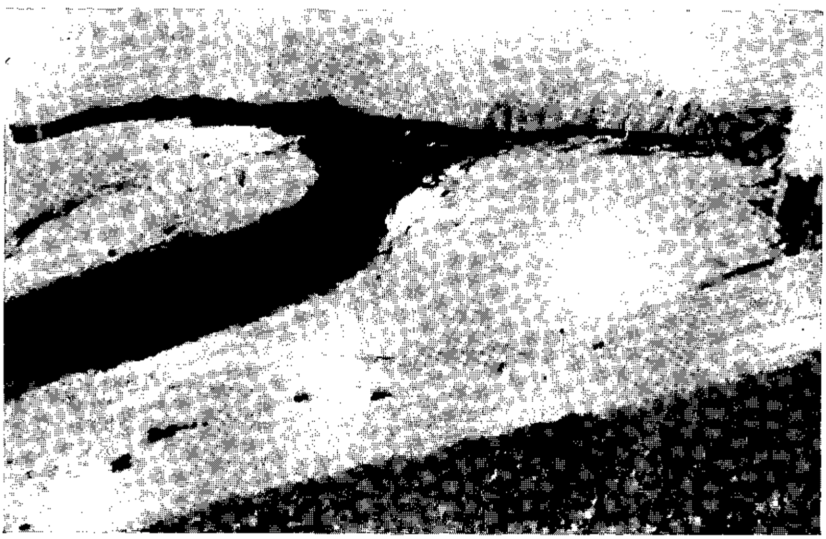


FIG. 13b. Photograph of a radial section through the hard 'eye' of a coconut. Also here the junction of the operculum and the inner integument is shown.

the connection of the outer integument with the operculum are also in accordance with the theory. The inner integuments are 0.25 mm wide, i.e. as wide as a normally developed inner testa layer.

2. In between the two layers of the inner integument the remnants of the nucellus are seen. In radial sections through the 'eye', following the course of the compressed locule, these remnants appear as a 2–3 celled layer. This layer is 10–13 µ wide and the cells are parenchymatous, 15–28 µ in length and 5–6 µ wide. The walls of the cells are double, 1–1.5 µ thick. This means that while the integuments have developed normally the nucellus, except for growth in length, has not been able to follow its normal course of development.

Based on the descriptions of the 'eyes in this paragraph, the development of the functional and the 'non-functional eye' can be summarized, as illustrated in fig. 14a–e. The ovule sinks with its micropylar end into the inner ovary wall (fig. 14a). Inner and outer integuments fasten on to the inner ovary wall epidermis (fig. 14b). Development of the functional 'eye': due to the growth of the functional ovule the integuments are gradually pressed against the endocarp wall. The integuments become testa, part of the inner ovary wall turns into the 2-layered operculum (fig. 14c–e). Development of the non-functional 'eyes': compression of the non-functional ovules occurs. The pressure of the developing seed pushes the entire locule towards the sclerified endocarp wall (fig. $14c^1$–e^1).

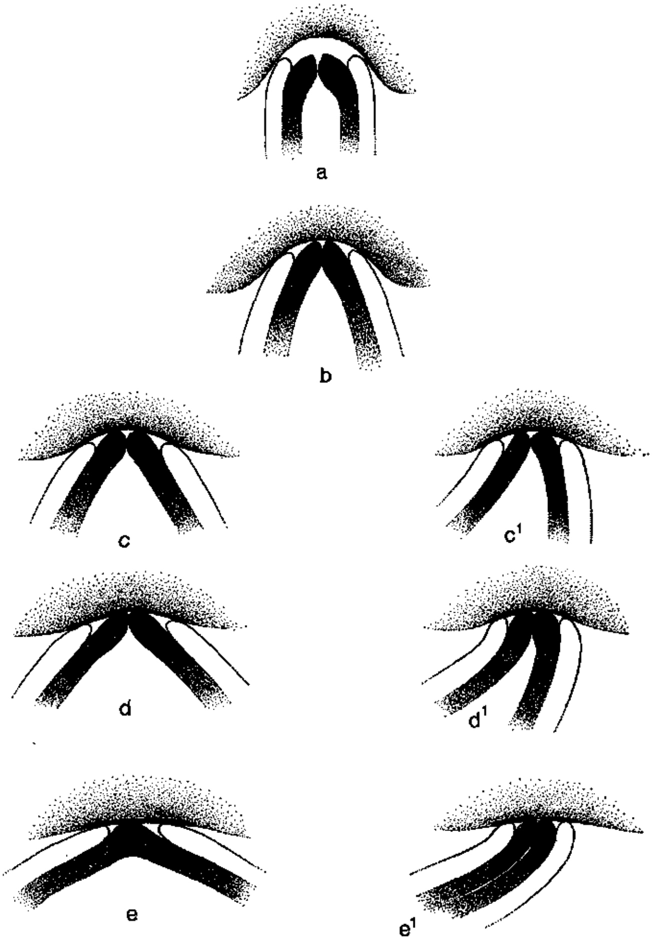


FIG. 14. Schematic representation of the joining of the inner and outer integuments with part of the inner overy wall (a-b) and of the development of the soft (functional) (c-e) and the hard (non-functional (c^1-e^1) 'eye'. See text.

4.3. THE CHROMOSOMES OF NORMAL AND BICARPELLATE COCONUTS

The chromosome number at meiosis, n = 16, was first published by SANTOS (1929). It was confirmed by SHARMA and SARKAR (1957). They also discovered 2 n = 32 in the somatic cells. Studies of chromosomes in unusual coconut palms have been initiated by NINAN and SATYABALAN (1963). They found that the meoisis chromosome number of spicata-type coconut palms was also n = 16, but that a number of irregularities occurred during the process.

As no facilities for the conservation or fixation of anthers could be obtained, only a study of the chromosomes in root tips of both normal and bicarpellate coconuts was carried out. Normal coconuts were chosen at random from nonregistered palms; the bicarpellate coconuts were all taken from palm no. 11.

A preliminary study revealed that also in our material, both from bicarpellate and normal germinating coconuts, 2 n = 32, i.e. there is neither a difference between the two types of coconuts nor a deviation from the normal chromosome number.

Deviations from the normal number had been recorded by Sharma and Sarkar in material from apparently normal palms. They observed n = 15, n = 17 and even 2 n = 18. A more detailed study of the chromosomes would only have been interesting if a repeatedly occurring deviation from the normal number had presented itself. As no such abnormality appeared this approach was not continued.

4.4. VARIATION WITHIN BICARPELLATE COCONUTS

The description of the bicarpellate coconut given in 4.1. represents the 'average' bicarpellate coconut and does not provide insight into the variation within this type.

Fig. 15 shows a number of bicarpellate coconuts which vary considerably in shape. The coconut immediately below the Spanish text in the photograph, is the most representative of the bicarpellate coconuts in 'La Solana'. It is clearly composed of two halves and there is a constriction of the mesocarp between the these, where the third carpel would have been, had it developed. On the other hand, the coconut just above the text is nearly cylindrical in shape, of larger volume and only the two ridges indicate its bicarpellate nature. The former type was more commonly found, but nevertheless it may be said that, apart from some of the specific characteristics described in paragraph 1, the variation in shape, weight, volume etc. is as great in bicarpellate coconuts as in the normal ones.

Two of the 20 bicarpellate coconuts that were husked show a peculiar depression of the endocarp wall, as was shown in fig. 8. Such cavities have not been recorded in any of the normal coconuts in the plantation, neither has any reference to similarly deformed coconuts been found in the literatutre on abnormalities in coconuts. A third coconut was found with a similar cavity; this particular coconut will be defined as 'fusing' tricarpellate. Such depressions are rare and although they have been observed exclusively in already abnormal coconuts it clearly is not a common feature of such a coconut. The inside of such a coconut is normal; the putamen, outer testa and inner testa as well as the endosperm are normally developed but have all moved inwards. The outer layers of the endocarp wall around the depression show areas with a tar-like appearance, interwoven with mesocarp fibre. Inside the depression the wound-tissue covers the stony endocarp and is of grey, granular appearance.

Because of lack of bicarpellate fruits in various stages of development, this abnormality is not easy to explain. Neither exocarp nor mesocarp showed a depression and a foreign body in the mesocarp which might have caused this shape was not found. Possibly damage had been caused by the pressure of a

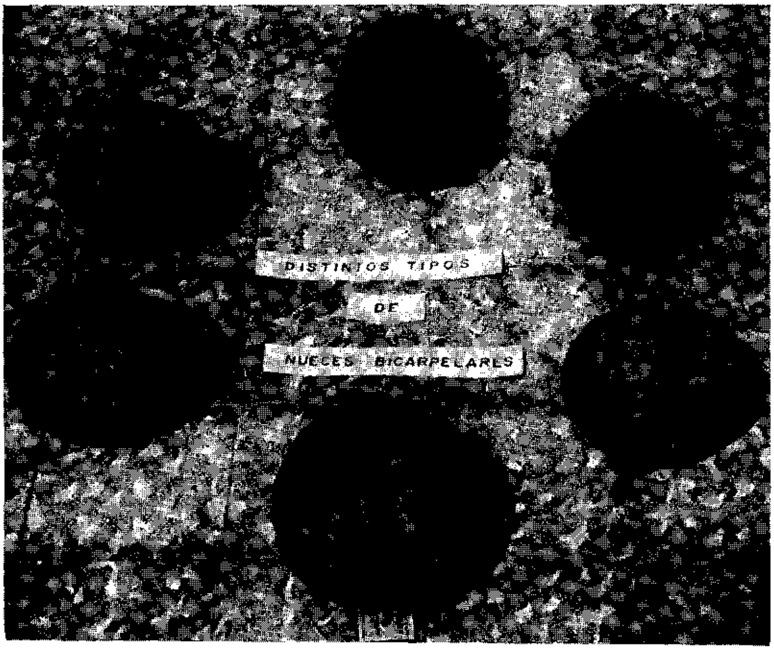


FIG. 15. Various types of bicarpellate coconuts.

globose shaped body on the lower part of the developing fruit, a pressure which also had not continued for a long time, otherwise the overlying tissues would not have had the opportunity to compensate for the damage and then would have shown a similar depression. The one coconut which showed the same cavity and was labeled 'fusing' tricarpellate had been harvested from palm no. 14 as a normal tricarpellate coconut, i.e. with three ridges on the exocarp. After husking the cavity was noted and the 'eyes' were examined more closely. Apart from the 'functional eye' two more 'non-functional eyes' were seen, but these were located side by side with only a very thin rudimentary ridge between the two; the 'eyes' being joined almost completely. This ridge becomes more pronounced towards the apical end of the husked coconut, where it forms an angle of 90° with the other ridge; the section with the functional 'eye' takes up half of the space available, like in a normal bicarpellate coconut. This coconut is depicted in fig. 16.

Sections through the 'non-functional eyes' and their corresponding locules show that inside the stony endocarp the compressed locules are partly joined; the inner integuments are still recognizable as separate entities but the outer integuments meet and join before both join the outer testa. This is therefore a case of three carpels, but the fact that the position of the 'eyes' and their locules indicate a tendency towards joining has resulted in the name given. The peculiar depression is present here also and therefore the assumption that in the bicarpellate coconut it could represent part or all of the third carpel is excluded.

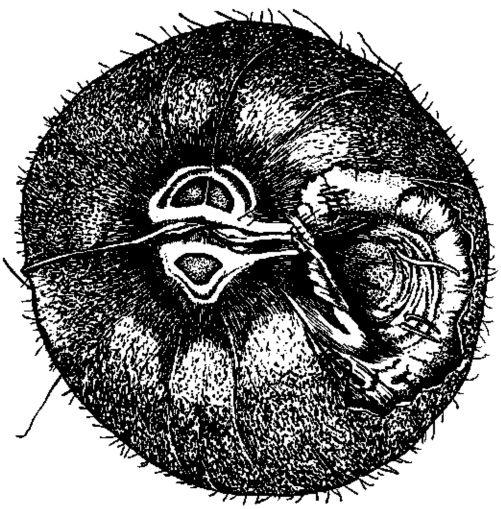


FIG. 16. Husked coconut showing almost complete fusion of the two nonfuctional eyes.

It does not however, exclude the possibility of an internal malformation caused for example by an abnormal arrangement of tissue in the ovule bearing region.

Similar cases of coconuts, in which two of the 'eyes' have partly joined are described by DAVIS (1970). He also found such fruits in palms producing also bicarpellate coconuts. In accordance with the terminology proposed in chapter 2, these coconuts are the result of a process of partial fusion. In case of a complete fusion the fruit would be similar in external appearance to a bicarpellate coconut. Anatomical evidence will then be necessary to conclude whether it is either a result of fusion or of original reduction.

4.5. TRICARPELLATE AND BICARPELLATE BARREN COCONUTS

Coconuts with the endocarp only partly developed or even undeveloped are referred to as barren. Such barren coconuts are found wherever coconuts are grown; sometimes such coconuts are the only ones in a specific infrutescence but they are also found together on the same bunch with perfectly normal fruits.

Occasionally the coconut palms of 'La Solana' also produced barren coconuts; their percentage of the total harvest was not high, somewhere between 0.5 and 1%. The variation within this type of coconuts was limited. Their main characteristics were: volume reduced to between 1/3–2/3 of that of a normal coconut, husk marked by numerous longitudinal slits starting at the basal end, the exocarp surface not smooth but ribbed.

The longitudinal slits sometimes penetrate deeply into the mesocarp; frequently the often partly developed endocarp is laid bare; the endosperm has sometimes developed partly but has mostly rotted away due to exposure to the outside air.

The exocarp ribs, the wrinkled appearance of the coconut together with the longitudinal slits made it nearly impossible to determine from the outside whether there were two or three ridges on the exocarp. Sometimes the shape suggested a possible barren or deformed bicarpellate coconut.

Such palms were observed and especially during the first phase of this study their production was recorded. These were classified as producing deformed, possibly bicarpellate coconuts. However, as in most of these coconuts of decompostion of the contents made a determination of the exact number of carpels – and especially 'eyes' – impossible, the production records for such palms were continued, but only if a 'normal' bicarpellate coconut was produced by such a tree later on were those palms reclassified as bicarpellate coconut producing.

Therefore the occurrence of barren bicarpellate coconuts is not excluded, although their determination was so difficult and uncertain that the information on these is not presented here, so as not to reduce the value of the data of the undisputably bicarpellate coconuts.

Generally speaking, the problem of barren coconuts deserves more attention from coconut research workers than it has received up till now. Although the number of palms involved was small and therefore no conclusion of a general nature can be drawn, the average yield of palms producing an occasional barren coconut was markedly below the average of the plantation. Such palms merit a specific study to determine the cause(s) of barrenness.

5. THE FLOWERS OF THE COCONUT PALM AND THE APPEARANCE OF BICARPELLATE COCONUTS

Since it is impossible to imagine that a normal syncarpous tricarpellate ovary could develop into a bicarpellate coconut, a study of the flowers was undertaken. In analysing a number of inflorescences a few abnormalities were observed which seemed of interest as such and also in connection with the occurrence of bicarpellate coconuts.

However, before describing these abnormal flowers a description and discussion of the normal flowers is required. This is necessary as the descriptions of the inflorescences of the coconut palm are incomplete in most or all monographs on this plant and thus are a possible source of confusion and misinterpretation. The flower pairs and groups in the inflorescences require particular attention.

The monographs on the coconut palm by HUNGER (1920), SAMPSON (1923), COPELAND (1931), PATEL (1938), REYNE (1948), MENON and PANDALAI (1958), CHILD (1964) and FREMOND et al. (1966) all have similar shortcomings. They describe the inflorescence and flower groups without sufficient attention to the bracts and bracteoles of the flowers and consequently do not show the relationship between the various forms and combinations in which the flowers appear.

Although a study of the normal flowers was at first considered of secondary importance in this study, the matter proved to be of sufficient interest as such while on the other hand a more detailed analysis and description of the normal flowers and their appearance together in partial inflorescences appeared to be necessary to be able to present a comparative analysis of the abnormal flowers.

5.1. THE INFLORESCENCE

The inflorescence is composed of a central axis, the rachis; in the axils of the bracts on the rachis the rachillae are borne, which in turn bear the flowers.

The sessile male flowers occur singly, in pairs, and according to some authors, even in groups of three in the axils of the bracts on the rachillae of the inflorescence. The male flower is also found together with the female. At the base of the rachilla in the axil of a bract a triad is usually found, consisting of a central female flower and two lateral male ones.

The single male flowers is usually described as 'bracteate' only, this bract being the one on the rachilla, while the female flower is described as 'bracteate and bracteolate'. In the case of the descriptions of the male flower by PATEL (1938) and MENON and PANDALAI (1958), this can be explained as they adopt the description given by JULIANO and QUISUMBING (1931). The latter authors have not considered the bracteole of the male flower.

In the material collected in Peru as well in herbarium specimens from Surinam, (Wessels Boer 477 [U], the single male flowers were found to be bracteate *and* bracteolate. The flowers of a dwarf coconut palm, originating from Indonesia and growing in a greenhouse of the Dept. of Tropical Crop Husbandry, Agricultural State University of Wageningen and flowers conserved in alcohol (Dept. of Systematic Botany [Wageningen], collected in the Ivory Coast) all show the same arrangement.

MARTIUS (1823) presented floral diagrams of the coconut palm and included a bract and a bracteole in his diagrammatic representation of the single male flower. HUNGER (1920) did not include the bracteole in the text of his description of the single male flower. However he does present a copy of Martius' diagram of that flower in his monograph. (HUNGER, 1920, p. 25–26, PL.IX). The present author also assigns a bract and a bracteole to the single male flower of the coconut palm. This judgement is based on the examination of material of various origin and supported by the opinions of Martius and Hunger. The diagram of such a flower is presented in fig. 17a.

No description of a pair of male flowers has been yet encountered. These pairs are interesting because the position of the bract and bracteoles gives the initial impression that one of the male flowers lacks the bracteole while the other seems to be subtended by 2 bracteoles. This is shown in fig. 17b. The explanation is that the reduced stalk of male flower no. 1 carries bracteole no. 1, in the axil of which appears male flower no. 2. On its similarly reduced pedicel bracteole no. 2 is borne.

The morphological interpretation of this arrangement will be dealt with together with that of the female flower.

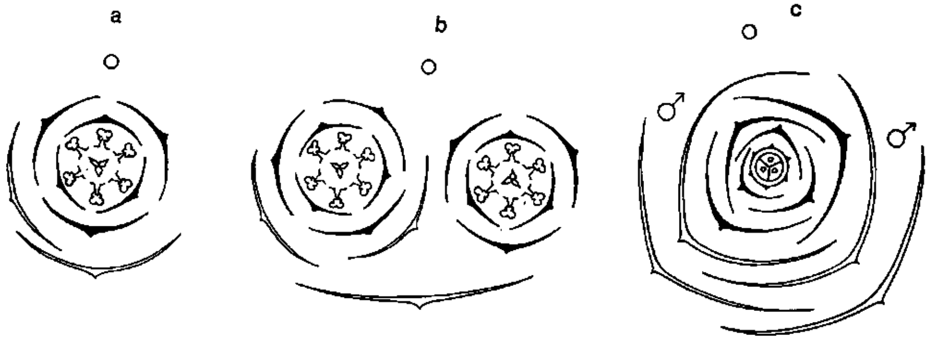


FIG. 17. Diagrams of the flowers of the coconut palm,
a. single male flower
b. pair of male flowers
c. triad of one female and two male flowers

Descriptions of the female flower have been given by JULIANO (1926) and PATEL (1938), however without paying sufficient attention to bracts and bracteoles. In addition, they did not take into account the relationship with the accompanying male flowers. The first named author considers that the female flower has two bracteoles. This opinion agrees with the studies of FURTADO (1924) and, to a certain extent, MÖBIUS (1908).

The last named author does not however use the term 'bracteole' and shows specific reservations as to the interpretation of his two 'Schuppenblätter'.

Though Patel states that the female flower is 'bracteate and bracteolate' he does not consider the accompanying male flowers either.

MARTIUS (1923) arrived at a total of 5 for the bracts and bracteoles of the triad of one female and two male flowers. According to him the triad represents a cincinnus. However he does not arrive at a logical explanation of the number and position of the bracts and bracteoles in his diagrams. EICHLER (1875) also suggests the possibility of the triads in palms representing cymes. WESSELS BOER (1968) describes a similar triad in *Geonoma* as a bostryx. TOMLINSON and MOORE (1968) interpret the flower cluster of *Nannorrhops ritchiana* (Griffith) Aitchison as a cincinnus. This has recently been confirmed by UHL (1969), whose conclusion is: 'Detailed studies confirm Tomlinson and Moore's tentative designation of this unit as a cincinnus and reveal basic constructional principles that apply to many, if not all, of the varied flowering units found in palms; e.g. the triad of a pistillate and two staminate flowers'.

All these opinions lead us to consider that the female flower together with its two male companions is also a partial inflorescence of cymous character in the coconut palm.

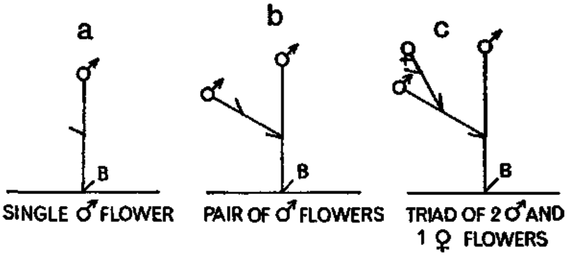
Returning to Martius' opinion on the number of bracts and bracteoles in the triad, it is of interest to note that HUNGER (1920), who copied the diagram of the single male flower from Martius' work, did not copy his diagrams of the female flower and accompanying male flowers. He presents a different version in which the number of bracts and bracteoles is reduced to 3. One may suppose that in this way Hunger expressed his doubts about the female flower diagrams presented by Martius. He may also have been influenced by Möbius' diagram of the female flower, to which his drawing bears a strong similarity (HUNGER, 1920, PL. IX and MÖBIUS, 1908, Taf. I). However, Möbius' discussion and his use of the term 'Schuppenblätter' indicate that he cannot arrive at a satisfactory explanation. Hunger uses the equally general and non-descriptive 'Schubben'.

Möbius considers it improbable that the flower of a plant belonging to the Monocotyledoneae has two bracteoles. Furthermore he expresses the opinion that the difference in size between the two implies that they are not equal in status or rank.

The present author's findings have resulted in a view, different from those expressed up till now with regard to the flowers of the coconut palm. In the material analysed the number of bracts and bracteoles is 4 in all triads consisting of one female flower and two male ones. This is shown in fig. 17 c. This gives a much more logical and comprehensive explanation than earlier descriptions. The relationship between flowers, bract and bracteoles in the three types of flower combinations in the coconut palm is shown in fig. 18.

One of the male flowers is the first or top flower of the triad. Its bracteole carries in its axil the stalk of the second male flower. This in turn has a bracteole, within the axil of which the female flower and its bracteole are borne. Not only does this explanation account for the position of the bract and bracteoles in the triad, but also the pair of male flowers as a condition, intermediate between the

FIG. 18. Position of bracts and bracteoles of the flowers, represented in diagrammatic form in fig. 17.
(N.B. The normally reduced stalks of the flowers have been enlarged to show clearly to which flowers the bracteoles correspond. B = bract.)



single male flower and the triad, supports this opinion. Further support for this interpretation is lent by the earlier cited interpretations of TOMLINSON and MOORE (1968) and UHL (1969) as well as by an earlier study by UHL (1966), in which her description of the triad in *Aristeyera spicata* Moore is also identical to the above, defining it as a 'monochasial branching unit'.

It is noteworthy that on a rachilla the triads are usually found at the base, the pairs of male flowers in the central part, while the single male flowers are found at the top. It is known that in a triad the male flowers flower before the female one.

The triad is to be considered a cincinnal cyme, i.e. a cincinnus. The pair of male flowers and the single male flower represent the reduced or undeveloped stage of this cyme. Depending on whether the second flower is located on the left or the right of the first floral axis the cincinnus can be considered as left-handed or right-handed. This means that the reflected images of figs. 17 and 18 are also applicable and do in fact occur.

The problem of Möbius' 'Schuppenblätter' is now solved. The smaller of the two is the bracteole of the second male flower, the larger one that of the female flower.

This interpretation of the interrelationship of the flowers of *Cocos nucifera* L. coincides in detail with Martius' analysis of what was then known as *Cocos oleracea* Mart. and has been reclassified since as *Syagrus oleracea* (Mart.) Becc. (cf. GLASSMAN, 1968). The flower analysis and the way Martius concluded that it was cincinnus is very similar to this author's analysis of the flowers of *Cocos nucifera* L. Long ago BECCARI (1887) arrived at the conclusion that what MARTIUS described as the flowers of *Cocus nucifera* L. and showed in his 'Historia naturalis Palmarum' in Vol. II, p. 124–125, Tab. 88 are not really the flowers of the coconut palm.

He supposes that the drawings were changed for others accidentally and that those representing *Cocos nucifera* L. are in reality those of a 'Cocos of the Arecastrum section' (*Cocos rozmanoffia* (Arecastrum)? CORNER, 1966). Whether this confusion of the drawings by MARTIUS may also be the reason that his floral diagrams, presented in Vol. I, Tab. Z. 16, fig. I, do not agree with the present author's could not be verified.

It was not possible to study the original material with which Martius worked.

The solution of the relationship between flowers in the inflorescence of the coconut palm is also applicable to its near relative within the Cocoideae, the

African oil palm, *Elaeis guineensis* Jacq. BEIRNAERT's diagram of the triad of flowers in the oil palm, though not completely correct (1935, p. 1094, pl. VII) bears many similarities to the one of the triad of the coconut palm. Analysis of a so-called 'female inflorescence', part of the collection of the Dept. of Tropical Crop Husbandry, Agricultural State University of Wageningen, confirmed this opinion. Here also the position of the two abortive male flowers and the central female flower as well as their bract and bracteoles show that the triad similarly represents a cincinnus. This is considered as additional support for this author's opinion on the flowers of the coconut palm.

This interpretation of the relationship between single flowers, pairs of male flowers and trials of two male flowers and one female should facilitate a further analysis of palm flower units and inflorescences. Special attention should be given to the position of each type of flower cluster in the inflorescence. RAWI (1945) presented a study on flower morphology of the Ceroxyloideae. He worked mostly with fragments of inflorescences, but nevertheless he has mentioned many species in which the triad-pair-single flower relationship appears. His observations on the presence of bracts and bracteoles are incomplete, but still his information together with the vast amount of data presented by Martius should make it psosible to initiate a renewed analysis of all inflorescences. Because of the small size of many of the bracts and bracteoles and also because the male flowers in the triad are frequently either rudimentary, abortive or have flowered long before the female one, a study of opened inflorescences is not sufficient. It is preferable to study also young inflorescences in various stages of development and before the opening of the spathe. This has not been common practice up till now and has resulted in incomplete descriptions.

A more comprehensive analysis with due attention paid to the contents of each bract on the rachilla will certainly lead to a better understanding of the 'spicata'-type coconut palm. This is a coconut palm with an unbranched inflorescence and a high number of female flowers. Similarly the 'androgena' coconut palm which has heavily branched inflorescences and exclusively male flowers can be analysed. The midget coconut palm can also be more easily classified when a complete analysis of its inflorescences, rachillae and flower clusters on the rachillae is presented.

5.2. THE NORMAL FLOWERS

To facilitate comparison with the abnormal flowers described in the following paragraphs a short description of the male and the female flower is included here.

The normal male flower is 11–14 mm long; sepals are small, triangular, of equal size and 3–4 mm long. Petals are oblong, acute and valvate and of equal size; they are 10–13 mm in length. Stamens 6; filaments free, cylindrical and erect; anthers 4-celled with longitudinal dehiscence. Pistil rudimentary, tricarpellate, separating into 3 erect teeth; the carpels are united at the base only.

Female flower globose, 24–27 mm long, 19–23 mm in diameter (measurements taken after the opening of the spathe). Sepals 3, round and concave; petals 3, alternating with and of similar shape as the sepals but smaller and thinner. A 6-toothed staminodal ring present. Ovary superior, globosy 3-sided, 10–12 mm long and 8–10 mm in diameter; style minute, stigma 3-sectioned nipple, sections triangular. The stigma is recognizable as such from about 4 days before receptivity. The 3-sectioned stigmatic surface encloses a central triradial canal which continues downwards to the ovule bearing region. Three nectary glands run from the ovule bearing region to the apex of the pistil; their orifices alternate with the 3 triangular surfaces of the stigma. Ovules 3, anatropous, with basal placentation; integuments 2.

5.3. HERMAPHRODITE FLOWERS

Hermaphrodite flowers are very unusual in the coconut palm and only very few such flowers have been reported up till now. Their occurrence only in the inflorescences of palms, which produced some bicarpellate coconuts, therefore suggested a possible relationship between the two abnormalities.

Either such a flower could perhaps develop into a bicarpellate fruit or the same factor causes the appearance of both abnormalities.

An inflorescence from palm no. 21 (see chapter 3) at the point of opening and measuring 125 cm in length was collected in April 1967 and analysed. The number of male flowers was 9,844, of female flowers 22. In the lower part of the inflorescence, just above a female flower on a rachilla a hermaphrodite flower was found. This flower differed from a normal female flower in the following characteristics:

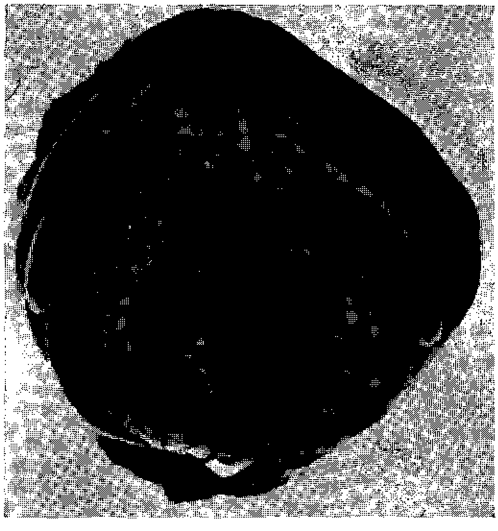
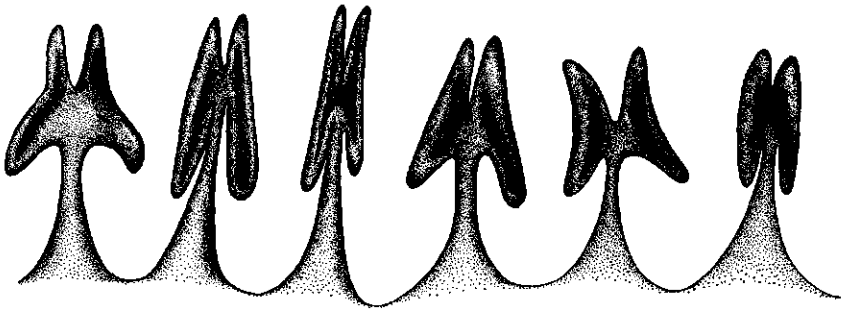


FIG. 19. Stamens surrounding the gynoecium of a hermaphrodite flower.



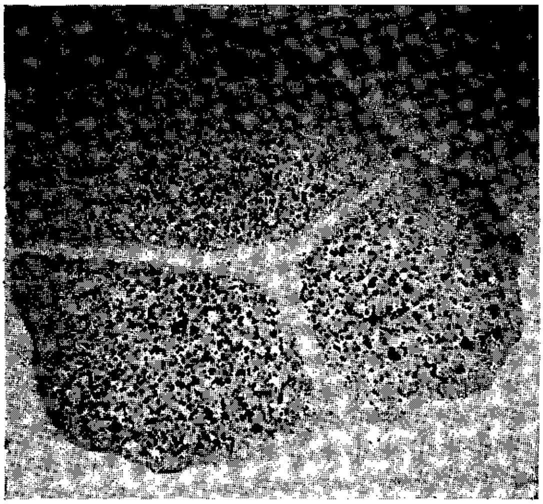
STAMENS OF HERMAPHRODITE FLOWER

FIG. 20. Staminal ring of the hermaphrodite flower in fig. 19.

1. Size: whereas normal female flowers from the same inflorescence were on average 26 mm in height and 22 mm in diameter, the height of the hermaphrodite flower was only 22 mm with a diameter of 16 mm.
2. The hermaphrodite flower had only one male companion and no mark was found to indicate that the second one had ever been there. This was also confirmed by the number of bracts and bracteoles of the pair being 3 rather than 4.
3. At the base of the ovary a ring with 6 fully developed stamens is located (fig. 19). This means that the staminodal ring, found in the normal female flower, has developed into a ring of stamens. In a male flower the stamens are not joined at the base of the filaments but are free. This ring of stamens is shown in fig. 20 to demonstrate the shape of the stamens. The filaments are 6–8 mm long, the anther lobes 3–4 mm.
4. Cross-sections from the top of the pistil to the base show that the 3 carpels are not equally developed. At the top, one of the carpels is wider than the other two combined and remains so to the base. One of the two small carpels increases in size towards the base, also in proportion to the third carpel. There is therefore one large, one middle-sized and one small carpel. This is shown in a cross-section, just above the ovule bearing region: (fig. 21). In cross-section the nectary glands, which in a normal pistil are situated in a line with each of the arms of the central triradial canal, are much longer in this particular pistil and so the separation into three parts is nearly complete. Only in the axile region the carpels are still attached to each other. This is also noticeable from the outside, where the ovary is more 3-sided than globose and the sides of the triangle are unequal, indicating the difference in size between the three sections. The whole pistil is 8 mm high, whereas the height of the pistil of a normal female flower from the same inflorescence is 10 mm.

Hermaphrodite flowers in the coconut palm have been described by RAO (1948) and DAVIS et al. (1954). Rao does not consider the possible occurrence of male accompanying flowers nor does he provide information on the number

FIG. 21. Cross-section through the ovary of the hermaphrodite flower in fig. 19.



of bracts and bracteoles. The staminal ring is present with 6 fully developed stamens. He described the shape of the anthers as 'sagittate'. This differs from what he found in a normal male flower, where the anthers are 'linear-shaped', whereas MENON and PANDALAI (1958) call these 'hammer-shaped'.

Davis et al. have classified the hermaphrodite flowers, found by them, into 3 types. Type 1 resembles the female flower, type 2 the male flower, whereas type 3 is intermediate between 1 and 2. According to their description the hermaphrodite flower mentioned above resembles mostly the type 3 flower, which differs mainly from the type 1 flower in the development of the stamens. In this type 3 flower all the 6 stamens are fully developed, whereas in the type 1 flower the variation in the number and shape of stamens is from normal to rudimentary. The diagram of the male flower in the same publication shows the bract, not the bracteole. Accompanying male flowers are not described (DAVIS et al., 1954, p. 137–138).

Any connection with the bicarpellate fruit, other than a suggestion that both abnormalities may have a common cause, cannot be established. The few hermaphrodite flowers found so far, which are known to have grown into fruits have developed into tricarpellate fruits (DAVIS et al., 1954). The only difference with normal fruits is that they are smaller. The fact that in the gynoecium described one of the carpels remains small does not support the assumption that the other two could have developed into a bicarpellate fruit.

While the hermaphrodite flower described above can be considered as one which resembles the female flower but shows a development of the staminodal ring into stamens, other abnormal flowers were found resembling the male flowers and in which the rudimentary pistil showed unusual development.

In November 1968 an 80 cm long, and not yet fully developed spadix, was collected from the bicarpellate coconut producing palm no. 11 and analysed. Female flowers were absent in the lower part; in the upper half one apparently normal female flower as well as 6 abnormal flowers, resembling male flowers, were found. Fig. 22 depicts this inflorescence.

The female flower as well as the 6 abnormal, male-like flowers are shown separately in fig. 23. The abnormal flowers are arranged according to size; in the row next to the female flower the three larger ones are found, to the right of these and adjoining the male flowers are the smaller ones. At the extreme right, a row of 3 male flowers from the same inflorescence has been included for comparison.

A normal triad was formed by the female flower and the 2 male flowers, with a total of one bract and 3 bracteoles. The female flower is 24 mm high, the maximum diameter is 28 mm and the petals and sepals are normal. The tricarpellate pistil is globose, 10 mm high and the maximum diameter of the ovary is 12 mm. Except for its position in the upper part of the inflorescence, there is nothing remarkable about it.

With only one exception, each abnormal, male-like flower has developed as one of a pair; the exception being a single flower. In the case of the pairs the abnormal flowers are lateral, normal male flowers being the top flowers. The

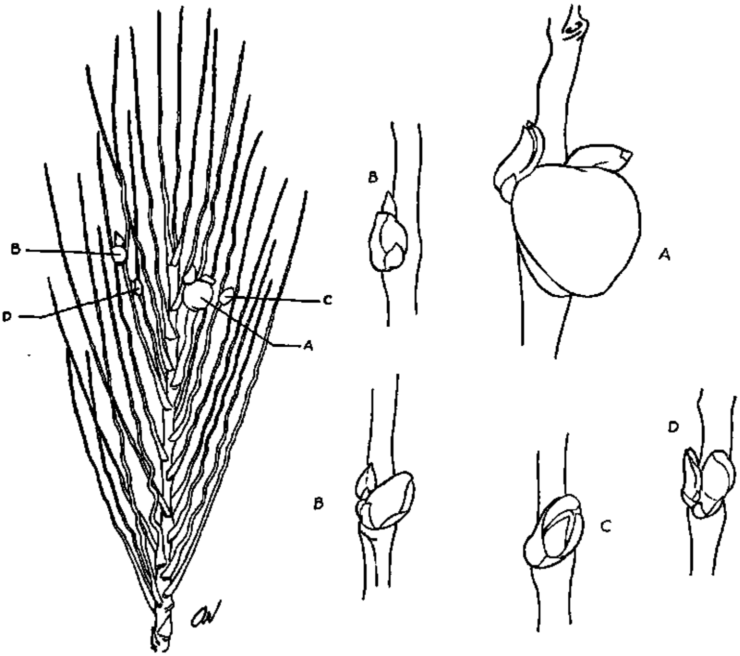


FIG. 22. Inflorescence of palm no. 21 with abnormal flowers. Normal male flowers not shown.

(N.B.: Flower pair B has been drawn twice to show the partly obscured normal male flower).

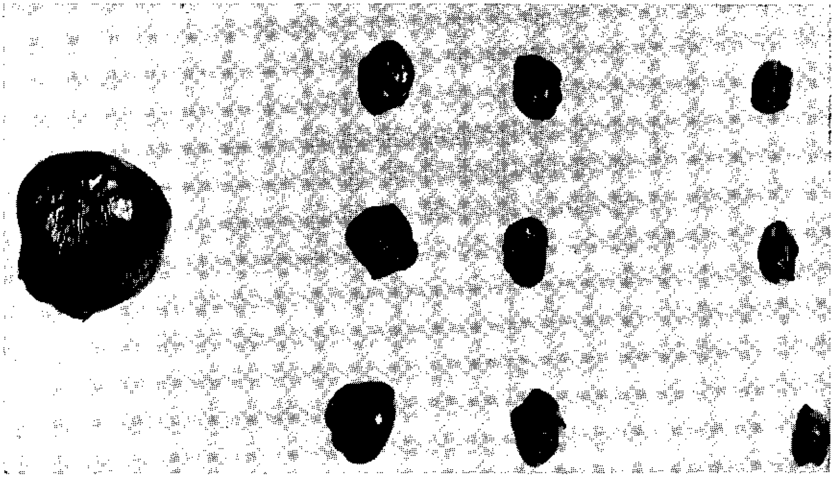


FIG. 23. The flowers of the inflorescence in fig. 22. left row: female flower right row: male flowers two centre rows: abnormal male flowers

sepals of the abnormal flowers are not, as in a normal male flower, of equal size.

One is small and triangular as in a normal flower, the second is slightly larger, whereas the third is similar in shape and size to that of a female flower. This sepal encloses half of the circumference of the flower and covers the petals up to near the apex; it is wide and fleshy at the base, but thin at the top. The petals, though slightly longer than those of a normal male flower of the same inflorescence are quite similar in shape to those of normal male flowers. Some of the stamens are united at the base of the filaments; the number of filaments that become united increases with the size of the flower, but in no case was an entire ring found. The stamens are similar in shape to those of the hermaphrodite flower described above; filaments are longer than in the normal flower; anthers are hastate or sagittate.

The rudimentary pistil in a normal male flower is tricarpellate, carpels being united at the base only; it is small, 4–5 mm in length. At the base it is thick as a match-stick, but tapers into a needle-thin point at the apex. In the pistils of the abnormal flowers one of the carpels has remained small as in a normal male flower. The other two have markedly increased both in length and volume. Data on this development and also on the measurements of the abnormal sepals are presented in table 10.

The development of the carpels is not equal in all flowers. Some are joined over a greater part of their length than others.

Fig. 24a shows the attachment of the carpels in the axile region in flower 1 (B). Three carpels are seen, two thick and one thin. Fig. 24b shows a cross-section of the ovary of flower 4. In this flower the carpels are of equal length but the photograph shows that they have not equally developed. One has remained thin as in normal male flower.

Table 10. Measurements of the abnormal flowers from an inflorescence of palm no. 11 (in mm).

Flower no.	Total length	Largest sepal length	Largest sepal width[1]	Length of large carpel	Length of small carpel	Remarks
1 (B)[2]	18	14	9	9	5	
2 (C)	16	11	10	10	6	
3 (D)	16	13	7	9	5	2nd. carpel 7 mm
4	14	12	8	10	10	carpels of equal length
5	13	11	7	6	5	2nd, carpel 6 mm.
6	12	6	5	6	4	
male 1[3]	12	5	3	5	4	carpels rudimentary
male 2	13	5	4	5	5	carpels rudimentary

[1] width at base

[2] letters correspond to those used in fig. 22

[3] male 1: at random from same inflorescence; male 2: fully developed flower from other inflorescence

In the basal region the carpels are attached to each other both in the centre and at the outside, but not in between. In cross-section the margins of the carpels, which have not joined, enclose slit-like cavities. These do not represent locules and ovules are absent. Only flower 2(C) has a more developed pistil with egg-shaped cavities. In one of these cavities, there is a protrusion of the wall with approximately axile attachment but the tissue is not sufficiently differentiated to conclude that it resembles an ovule. No such protuberances are found in the other two cavities.

It is therefore clear that these flowers could not have grown into fruits and no relationship between these flowers and the bicarpellate fruits exists. Even if flower 2 (C) had contained an ovule or if similar flowers had appeared which showed a stronger development of the rudimentary pistil in a female direction, it is not likely that the resultant fruit would have become bicarpellate and syncarpous, although there is no doubt that development of the normally rudimentary pistil in male flowers occurs occasionally in the coconut palm (Furtado, 1927; Patel, 1938). The first named author has seen bunches with both normal fruits in the lower part of the bunch and 'numerous banana-like fruits' in the upper part, such fruits 'being the result of the development of the usually abortive ovary in the male flowers'. Patel states that 'in rare instances these pistillodes have exhibited abnormal development into banana-like structures which persist in the axis'. Neither author specifies whether these fruits contained seed, or if the fruit was a result of an abnormal development without ovules. Nor is the number of carpels of the 'banana-like' fruit known. In any case these descriptions do not suggest that such flowers will develop into a bicarpellate fruit as found in 'La Solana'.

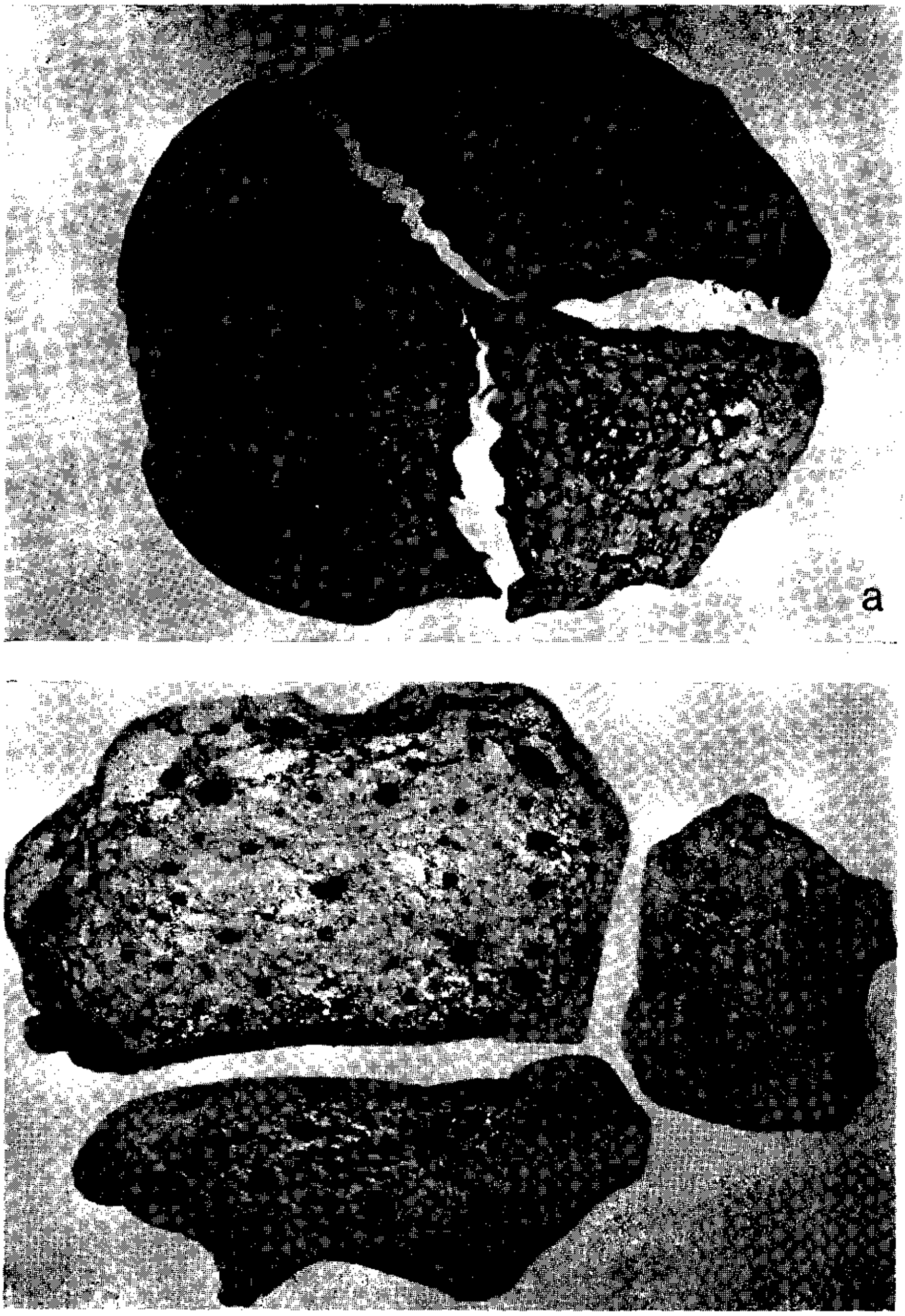


FIG. 24. Cross-sections through the partly developed carpels of abnormal flowers,
a. flower 1 (B)
b. flower 4

No reference to abnormal male-like flowers as described here has been encountered. Their description as well as that of the hermaphrodite flower have been included here as these flowers were found in the palms which produce bicarpellate coconuts. No direct relationship with the bicarpellate fruits could be established; it is remarkable that such abnormal flowers were found in the bicarpellate coconut producing palms only and that in both types of abnormalities one of the 3 carpels is smaller.

5.4. OTHER ABNORMAL FLOWERS

In addition to the flowers described in the preceding paragraph a number of other abnormalities of flowers were encountered. These are described here because of their appearance in the inflorescences of bicarpellate coconut producing palms. Some abnormalities are also important for the morphological interpretation of the flowers and flower clusters in the coconut palm.

5.4.1. *Pairs of female flowers*

In an inflorescence of palm no. 11, the spathe of which had recently opened, 21 normal female flowers as well as 2 pairs of female flowers were found. The length of this inflorescence, which was collected in December 1967, was 130 cm. These pairs of female flowers were located in the lower part of the inflores-

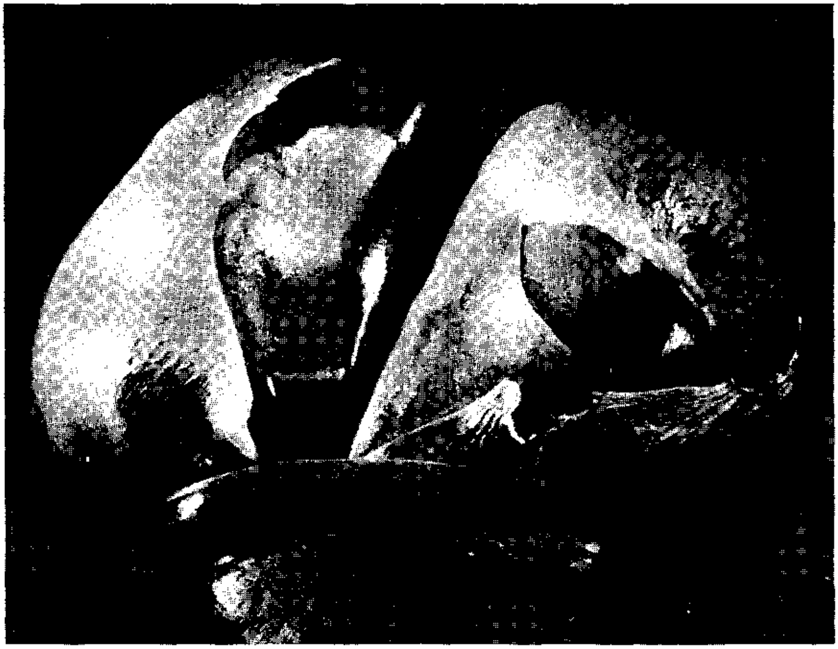


FIG. 25. Pair of female flowers. The position of the bracteoles indicates that the flower on the right is situated in the axil of the pedicel of the left one.

cence, each at the base of a rachilla; no other female flowers were present on the same rachilla. Such a pair of female flowers is shown in fig. 25. Each pair of female flowers was accompanied by 2 male flowers, one at either side of the pair.

The position of the bracteoles indicates that the second female flower is the continuation of the cincinnus into a fourth flower, which is located in the axil of the bracteole of the first female flower. This is shown in fig. 26. One of the flower clusters proved to be left-handed, the other right-handed and therefore both forms are shown.

When comparing fig. 26 with the different parts of fig. 18 we see that it represents a logical continuation of this series and could have been included as fig. 18 d.

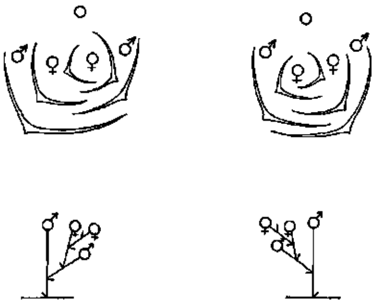


FIG. 26. Position of the bracts and bracteoles in flower clusters consisting of two male and two female flowers.

Such flowers clusters, commonly described as 'pairs of female flowers', have been encountered on the unbranched inflorescences of the 'spicata'-type coconut palms, which breed true for this character. (BECCARI, 1913; COSTERUS and SMITH, 1923a; FURTADO, 1927; PATEL, 1938). No references were found mentioning the occurrence of such pairs in normal, branched inflorescences. Costerus and Smith mention that in such pairs of female flowers the number of accompanying male flowers also doubled, the triad becoming a cluster of 6. The observations of Beccari and Furtado correspond more to our findings of 2 male flowers per cluster, one on either side. According to Patel the female flowers were quite normal except for their size, as the double flowers were smaller than normal.

Similar clusters of 4 flowers are also known to occur in the African oil palm. In describing such a cluster BEIRNAERT (1935) mentions that the pair of female flowers is accompanied by 2 male flowers, one at either side of the cluster.

The shape of the double flowers is unusual as they are not globose, but definitely flattened on the side where the other flower is located. The competition for space has also affected the shape of the ovaries. One of these is shown in cross-section in fig. 27. As for Patel's comment on the size of the flowers, the following table presents data on the measurements of the flowers, occurring in pairs and analysed by the present author. In the same table are included the corresponding measurements for a female flower chosen at random from the same inflorescence to facilitate comparison.

TABLE 11. Measurements of pairs of female flowers in mm.

	intact flower		flower with floral envelopes removed	
	length	diameter[1]	length	diameter[1]
Female flower pair no. 1:				
flower a	20	18–26	12	7–11
flower b	18	17–25	11	6–11
Female flower pair no. 2:				
flower a	22	19–29	13	6–12
flower b	21	15–24	12	4–10
Normale female flower	23	20–26	13	8–11

[1] Diameters are maximum and minimum diameters, measured at the greatest circumference of the flower.

Apparently the length of the female flower is not much affected by its appearance together with others in one cluster. Only the diameters of the flowers and ovaries are less, especially the minimum diameter; this is particularly the case in flowers 1b and 2b. These are the last developed flowers on each cluster; the minimum diameter of these flowers is much reduced.

Analysis of the ovary showed that the number of carpels is 3. One of these is much smaller than the other two; because of this the triradial canal is excentric at the top of the ovary. Somewhat lower in the ovary in cross-section (cf. fig. 27) it appears to be practically biradial as the third arm of the canal is nearly indistinguishable. As the photograph clearly shows, the cavity formed by this canal is abnormally wide; at the ovule bearing region of the ovary the cavity is again reduced to a small biradial slit. The 3 nectary glands are present, as are the 3 ovules. Given the tricarpellate nature of the ovary it cannot be expected to have grown into a bicarpellate fruit. It should also be mentioned that only the upper part of the ovary of flower 2b was so abnormal; in the other flowers the ovary

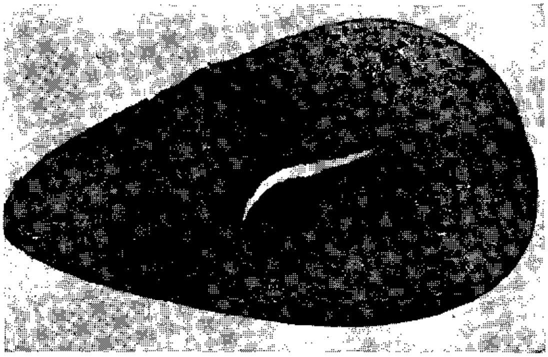


FIG. 27. Cross-section through the ovary of female flower 2b (see text).

is normal throughout. The fact that the ovary is abnormal in shape is probably due to a lack of space, because of the presence of another female flower immediately next to it.

5.4.2. *Female flower with a reduced number of perianth leaves*

A not yet completely developed inflorescence, still enclosed in its spathe, was collected from palm no. 11 in July 1968. Analysis showed 46 rachillae along the main axis with 11,596 male flowers and 15 female flowers. Counting from the base of the inflorescence the 10th rachilla, which was 61 cm in length, showed secondary branching at 45.5 cm from its implantation on the main axis, the branch being 8.5. cm in length. Similary the 17th rachilla with a total length of 57.5 cm bore a branch of 31 cm in length at 7 cm from its base. Both rachillae and their branches bore male flowers only, in pairs as well as single flowers. Such branching of the rachillae is abnormal and has been recorded as such with certain frequency (MENON and PANDALAI, 1958).

The female flowers were distributed as follows. On the lower 15 rachillae: 2 female flowers; on the middle 15 rachillae: 3 female flowers and on the upper 17 rachillae, including the flower carrying tip of the main axis: 10 female flowers. Contrary to what is normal most of the female flowers are therefore found in the upper part (third) of the inflorescence. The female flowers seemed to be normal except for one, which was not globosely three-sided but somewhat flattened. This particular flower was found on rachilla no. 46 and was uppermost female flower but one.

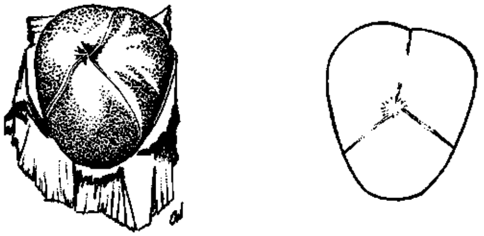
The number of sepals and petals of this flower had been reduced from 3 to 2. Also the gynoecium was abnormal in shape as is shown in fig. 28. The transverse section through the abnormally shaped ovary shows a distinct difference in the size of the 3 carpels. The 3 nectary glands are present but indicate by their position the irregular shape of the ovary. In the ovule bearing region 3 ovules are located, two of which are separated by a very thin wall only; they are parallel to each other.

Previously a reduction in perianth number from 3 to 2 had been noticed when examining ripe fruits to which the floral leaves were still attached. Such a reduction of floral leaves, detached from ripe fruits is shown in fig. 29. Only the bicarpellate fruits bore dry floral leaves in a reduced number.

On the other hand not all bicarpellate fruits carried a perianth consisting of a reduced number of floral leaves. No data could be obtained on the percentage of bicarpellate fruits with a perianth, reduced in number of floral leaves as many times during the process of harvesting the fruit had become loose its floral whorl.

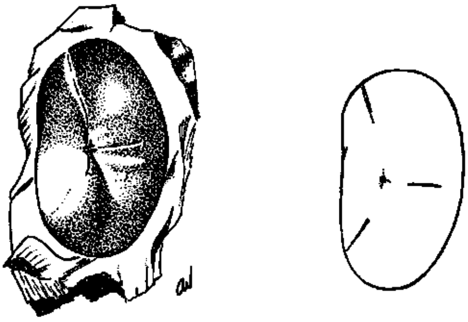
DAVIS (1970) found on many of his bicarpellate fruits that the number of perianth leaves was reduced from 3 to 2; also in the material examined by him some bicarpellate fruits had adhering floral envelopes in normal number.

On the basis of the reduction in the number of perianth leaves, the peculiar shape of its ovary and the special arrangement of the ovules one could assume that the abnormal flower would have developed into a fruit as described in par. 4.4., in which two of the 'eyes' have nearly joined.



GYNOECIUM OF NORMAL FLOWER

TRANSVERSE SECTION



GYNOECIUM OF FLOWER WITH ONLY TWO SEPALS AND PETALS

TRANSVERSE SECTION

FIG. 28. Gynoecium of a normal flower and of a flower with a reduced number of perianth leaves.

FIG. 29. Dry floral leaves detached from a bicarpellate fruit (left) and from a tricarpellate fruit (right).

5.4.3. *Pedicellate male flowers*

In the same inflorescence of palm no. 11 in which the pairs of female flowers were encountered (par. 5.4.1.) pedicellate male flowers were found. The position of the male flower in the axil of the bract on the rachilla is usually described as 'sessile', although it is not unusual to find sometimes one or two male flowers per inflorescence borne on a pedicel, short, 2–3 mm. Male flowers in triads are more fequently pedicellate, possibly because they would otherwise become so compressed that they could not open. The pedicellate male flowers which hitherto have not been described are morphological interesting, although their occurrence is not connected with the bicarpellate coconuts.

The pedicellate male flowers are found on the rachillae in the region of the paired male flowers. Amongst some normal sessile pairs numerous pairs were found in which one of the male flowers was pedicellate; length of the pedicels from 3 to 12 mm. Some of these are shown in fig. 30.

Analysis of the position of the bracteoles shows that it is always the terminal flower which is borne on a pedicel, the lateral male flower being sessile. This can be considered as additional proof for the opinion on the relative position of the two flowers as expressed in the first paragraph of this chapter, whereas such a pedicel can be expected to appear on a main axis rather than on a lateral branch. Here also right-handed and left-handed groups are encountered as in the normal pairs, triads and groups of 4. Fig. 31 shows the postion of bract and bracteoles of the pair as well as the location of the pedicel.

Other abnormalities of male flowers, e.g. male flowers at the tip of the rachillae with strongly increased number of perianth leaves, stamens and rudimen-

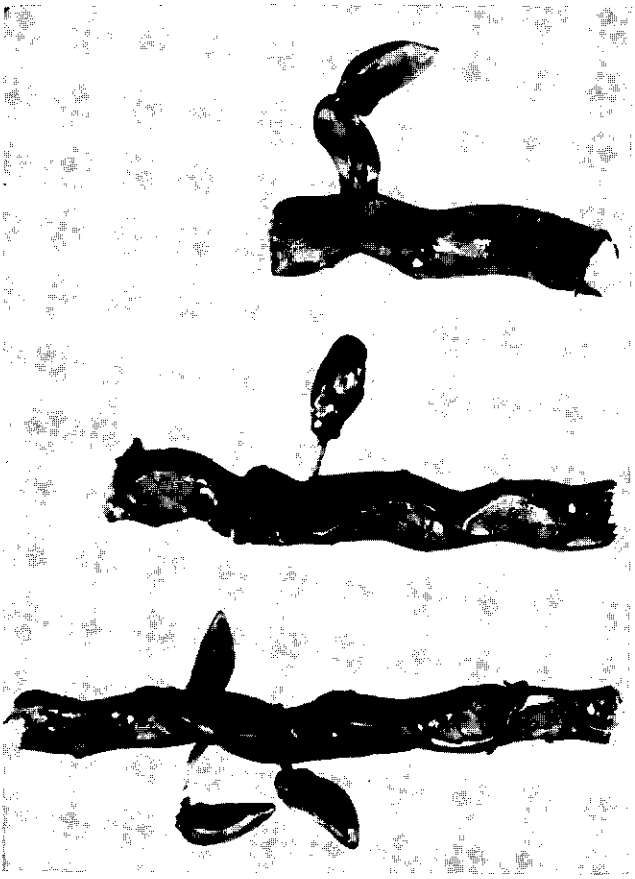


FIG. 30. Pedicellate male flowers. Top: pair of male flowers, terminal flower pedicellate. Centre and bottom: pedicellate flowers, second flower of each pair removed.

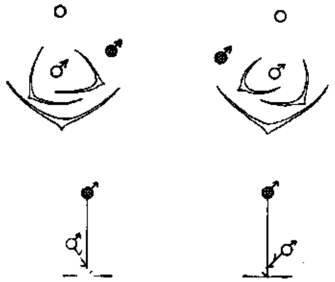


FIG. 31. Position of bracts and bracteoles in a pair of male flowers, one of which is pedicellate (dotted).

tary carpels, similar to those described by NINAN and RATNAM (1961), were encountered, again in an inflorescence from a bicarpellate coconut producing palm no. 8. These are neither of interest for the morphological interpretation nor related to the appearance of the bicarpellate coconuts.

In summarizing and reviewing the information on abnormalities of flowers encountered in 'La Solana', the number and types of abnormalities are large and varied. No references have been found which show so high numbers of abnormalities of all types in such a few coconut palms and in so short a period All these abnormalities were encountered in palms which also produce the abnormal fruits. Out of approx. 10 inflorescences taken from normal palms not one abnormality appeared, while in 5 out of 10 inflorescences, taken from palms producing also bicarpellate coconuts, abnormalities of flowers appeared. From the abnormalities described it is clear that there is no direct relationship with the bicarpellate coconuts. The nearest to a bicarpellate condition appears to be the flower with a reduced number of perianth leaves.

The fact that many unrelated abnormalities occur in these palms suggests that there is a common factor influencing the morphology of these flowers during their development. It may be coincidental that no bicarpellate flower was encountered amongst the abnormalities. On the other hand the sharp decrease in the number of bicarpellate fruits from 1966 onwards did not permit much chance of encountering such flowers. The 3 inflorescences taken from palm no. 11, top producer of bicarpellate fruits, in 1967 and 1968 did contain a.o. abnormal flowers described in this chapter but did not display a bicarpellate flower.

6. DISCUSSION OF THE POSSIBLE CAUSES OF DECREASE IN THE NUMBER OF CARPELS IN COCONUT

The cases of decrease in the number of carpels in coconut described and summarized in chapter 2 occur sporadically and concern one or two fruits only, or occur in isolated palms, so that there is no opportunity to look for an explanation of the phenomenon.

In this particular case the abnormality occurs repeatedly in a number of palms in one plantation. It is therefore considered of interest to review the available information in an attempt to isolate the cause(s) of the relative frequency of this abnormality and possibly of the others recorded.

Factors causing the occurrence of bicarpellate coconuts may be genetic, environmental or both. Some data are important in relation to the probable causes but do not favour either way of thinking.

An example of this is the fact bicarpellate coconuts are produced by three generations of coconut palms. This could be interpreted as meaning that the capacity to produce such an abnormality was inherited. However, our observations cover the production of bicarpellate coconuts in three generations at the same time and place, therefore environmental factors could also have affected the palms regardless of generation. Other data are more specifically in favour of one possible cause or another.

6.1. THE POSSIBILITY OF A GENETIC CAUSE

The main difficulty of studying the genetic basis of characters in the tall coconut palm is that between 10 and 12 years lapse before reliable information on the F_1 generation is available. Some bicarpellate coconuts were sown in 1968 under various environmental conditions but only around 1980 we will know what type of flowers and fruits those palms produce.

Consideration of the F_2 generation will be possible only near the end of this century. A second difficulty is that the tall coconut palm is a cross-pollinator since normally the male phase of flowering in an inflorescence has terminated before the female flowers are receptive. This results in a high degree of heterozygosity. This is why deductive reasoning is used to present arguments, which support the assumption that this abnormality is genetically determined.

Palm no. 8 has produced a high number of bicarpellate coconuts, while the other five palms in its immediate neighbourhood have not produced any abnormal coconuts. As no difference could be detected in the environmental conditions of these six palms, this can be considered as an argument for the assumption of a genetic background of the abnormality.

Furthermore, the high level of production of coconuts, both normal and abnormal, of palms nos. 8 and 11 is interesting also in connection with the abnormal flowers encountered. It shows that these palms are excellent bearers and could possibly be used as mother palms.

6.1.1. *Husk colour of bicarpellate and normal coconuts*

Husk and petiole colour of coconut and their inheritance have received little attention. The studies of REYNE (1948), which also refer to the work done by Tammes in the 1930's, have never been published in English and therefore have not received the attention they deserve. An attempt to study colour inheritance in coconut was initiated by WHITEHEAD (1966) but his preliminary data are inconclusive and their interpretation complicated by the combination with dwarf × tall crossings.

After having had the opportunity to study the manuscript and original colourings on which Reyne's conclusions are based, the present author agrees fully with his observations. Two colours are to be considered as basic, mixing them will result in any other colour in coconut. These colours are red-orange and green; ivory-yellow represents the absence of both. Mixing red-orange and green, for example. will in the right proportions produce brown. No conclusion on colour inheritance is yet available.

Data on husk colour of the coconuts, produced by the palms in 'La Solana', have been presented in chapter 3, tables 7 and 8. Attention is drawn to the complete absence of palms which produce bicarpellate coconuts with yellow-ivory husk colour, in spite of the high percentage of palms in the population producing coconuts with yellow-ivory husk colour.

Bicarpellate fruits with green-yellow husks were found but this could mean that the assumed bicarpellate fruit bearing tendency is connected with the husk colour of the green bearing parent. The chance is small with an occurrence of 53 palms, out of a total of 208, bearing yellow-ivory fruits that in an equally composed population of 15 palms not one would appear to bear yellow-ivory fruits. Applying the χ^2 -test for the 2 × 2 contingency table we find a probability near 0.05.

When introducing Yates' correction for continuity to avoid overestimation of significance because of small numbers the probability increases towards 0.15. It is possible though to include the data of the second age group and combine both. We then obtain probabilities of 0.03 without Yates' correction and 0.06 with the application of that correction.

These results and the distribution of husk colour in age groups 2 and 3 imply that palms which only bear normal coconuts and those which also bear bicarpellate fruits belong to different populations or rather are a reflection of the compostion of het oldest palms of 'La Solana' out of more populations, i.e. the possibility exists that the palms of age group 1 are samples from more than one population and those samples could have been taken on the basis of husk colour. This indicates that the bearing of bicarpellate coconuts has a genetic basis. To conclude this on the basis of the absence of yellow-ivory bicarpellate fruits only is taking a risk as age group 1 could not be analysed properly. Nevertheless their absence in age group 2 and 3 implies a strong argument for the assumption that bicarpellate bearing is genetically determined.

6.1.2. *Normal and abnormal fruits in the same infrutescence*

There are examples of cases in which a genetically determined abnormality appears together with normal fruits in the same plant and even infrutescence.

In Ceylon a bunch of coconuts was found on a tree producing green-coloured fruits. Two of the fruits were orange-coloured and two green-coloured (Anonymous, 1891). PETCH (1915) described a similar case of coconut palms 'bearing both yellow and green nuts on the same inflorescence'. These may have been cases of chimaerae or the result of somatic overcrossing. BOORSMA (1910) mentions the 'Kelapa linin'. This is known as the 'makapuno' coconut in the Philippines. Certain palms produce in addition to normal coconuts, coconuts with jelly-like endosperm. According to Boorsma about 2% of all fruits have an abnormal endosperm. He further adds that it seems that the production of such abnormal fruits is inherent to certain palms only. This has been confirmed by ZUÑIGA (1959), who found that controlled pollination of palms showing this abnormality could lead to an increase in the number of makapuno fruits per tree, in a proportion of 1 abnormal to 3 normal fruits. The makapuno-bearing tendency may become a genetic marker for use in coconut research, but it has a disadvantage that makapuno coconuts do not germinate; the factor is lethal.

To test the hypothesis that the bicarpellate bearing tendency is genetically determined, the sequel to this study should be a programme of selfings of palms nos. 8 and 11 as well as artificial pollination between these two. It would serve a multiple purpose; to study the bicarpellate bearing tendency, inheritance of colour and the yielding capacity of the progeny of two good mother palms. Such a programme however must continue for at least 15 years to be of any value...

6.2. THE POSSIBILITY OF AN ENVIRONMENTAL CAUSE

The fact that over a period of more than three years bicarpellate fruits were produced by some of the coconut palms of 'La Solana' is most probably genetically determined. This does not mean that environmental conditions cannot also play a role in the appearance of this abnormality. Environmental components could be necessary to reveal the genetically determined tendency. The frequency of bicarpellate coconut production, which was at a maximum during the period April–July 1966 and decreased sharply since then, suggests the influence of an unstable environmental factor such as the weather. In view of the non-randomized distribution of the palms in age group 3 which also produced bicarpellate fruits, factors such as soil composition and the possible influence of pests and diseases also merit discussion.

6.2.1. *Climatological and meteorological data of the region and their interpretation*

The climate of the region has been discussed in chapter 3. It is an unusual climate for coconut growing. The temperature is rather low during the winter months.

As temperatures were measured at 103 m above sealevel (table 1) and the coconut palms of 'La Solana' grow at an average of 70 m above sealevel, no major differences were expected.

The rainfall is another abnormal factor. It has been replaced almost entirely by irrigation and no data are available on the quantity of irrigation water supplied to the palms over the years. However, it should be mentioned that for the three age groups quite distinct irrigation regimes were followed.

The palms of group 1 receive much water during the period December to June because of the rice growing around them and practically none from July to December. Palm no. 8 and neighbouring palms of age group 2 receive water about once a month all the year around to maintain the pasture in which they are located. Age group 3 receives water all the year around about once every two weeks. It is improbable that these three different irrigation frequencies would all result in the appearance of bicarpellate fruits.

The low temperature during the winter months therefore remains as a possible influencing factor. The fact that more bicarpellate fruits have not been registered from other estates in the same region or other countries with such low temperatures e.g. the State of Florida (U.S.A.) or São Paolo (Brasil) may be caused by a different genetical composition of those populations, or by the fact that the coconut palms in those areas have not yet been examined in detail.

If the weather is to be correlated with the appearance of bicarpellate coconuts, it is necessary to consider the period during which the flower became abnormal. TAMMES (1940) studied the duration of each stage of development of the fruit. Approximately 12 months lapse from the opening of the spathe till the water in the coconut can be heard clearly to slosh and the husk has partially dried out.

As the bicarpellate fruit develops out of an ovary which is already abnormal, the process of development of the inflorescence and its flowers is also important. The only study of the subsequent stages of development is by PATEL (1938). According to him the primordia of the female flower are first differentiated about 12 months before the opening of the spathe while the ovary is first differentiated some 6 1/2 months before opening.The perianth leaves commence differentiation about 9 months before the opening of the spathe. Therefore the most probable period of malformation of the female flower lies between 6 and 12 months before the opening of the spathe. The harvesting of a bicarpellate fruit in April 1966 would then be the result of an abnormal occurrence in the weather in the period April 1964–September 1964.

Correlation between the theoretical critical periods and the data of the Chilaco meteorological station, which are summarized in table 1, is not possible because those data are non-existent for the period which is the most interesting, 1964 and 1965. Other data ara available from the Tablazo meteorological station, but the distance from the estate is much larger. 'La Solana' is approximately 50 kms in a straight line from Chilaco but over 80 kms from Tablazo.

This was the reason for using the data of Chilaco in table 1. For correlation

TABLE 12. Theoretical critical periods based on the moment of harvest of ripe bicarpellate coconuts.

Month of harvest	Number of bicarp. coconuts	Theoretical critical period
April '66	(at least) 17	April '64 – September '64
July '66	34	July '64 – December '64
November '66	2	November '64 – April '65
April '67	11	April '65 – September '65
July '67	2	July '65 – December '65
April '68	6	April '66 – September '66
July '68	7	July '66 – December '66

with the theoretical critical periods the data of Tablazo are used for want of better information. The data are presented in appendix 1.

From table 12 it appears that nearly all theoretical critical periods have the months June, July and August in common, with a maximum of abnormalities correlated with the period June–August 1964. These winter months are always the coldest of the year and in 1964 the averages of the minima, 14.3 °C and 14.7 °C are lower than the averages of the same months in other years. This might be more than a matter of mere coincidence, particularly because in other plants unusual low temperatures are known to lead to reductions in the number of carpels (ZELLER, 1955).

Though not providing details FREMOND et al. (1966, p. 60) make an interesting remark concerning the coconut palm: 'Frequent daily minima below 15° C modify the physiology and the morphology of the coconut palm'. Also: 'low temperatures cause abnormalities in the fructification of the coconut palm' (id., p. 63). Such low temperatures occurred in fact in the winter of 1964.[1]

The relationship between the 1967 harvest and the temperatures during June–August 1965 is not noticeable but the number of abnormalities is also much less; it is only about 25 % of the number produced during the preceding year.

The figures suggest a correlation with the low temperatures two years earlier. This will have to be followed over a number of years until another cold winter occurs in Piura. Then the analysis of flowers and fruits should be taken up again. The data of Tablazo up to 1969 show that during 1965 and 1966 low temperatures as in 1964 did not occur, but temperatures in 1967 again are low over a very long period. These low temperatures during the winter of 1967 can be correlated with the earlier mentioned observations of SAMANIEGO (1969) of the appearance of 'quite a few' bicarpellate coconuts in April 1969.

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[1] After conclusion of the manuscript of this study information was received from DAVIS (1969). His findings confirm the observations of Fremond et al., as the number of abnormal – i.e. bicarpellate – fruits encountered by him was much higher in the State of Assam (cold winter) than in other warmer states of India. The State of Assam is situated between 25° and 30° N; though coconut growing is restricted to the southern part of the State, this is still just outside the tropics.

The correlation between low winter temperatures and the appearance after a certain number of months of abnormal flowers and fruits is based on the aforementioned information on the time, needed for the subsequent stages of development of inflorescences, flowers and fruits. However, the data provided by PATEL (1938) and TAMMES (1940), are based on time studies under approximately normal conditions, i.e. without prolonged periods of rather low temperatures.

Empirical data on the effect of low temperatures are the only ones available; no experimental work on the effect of low temperatures on the coconut palm has yet been initiated. Mean temperatures, lower than normal over prolonged periods are known to slow down growth; the number of leaves produced is lower, leading to a decrease in the number of inflorescences. Normally also the number of female flowers is less. Low minimum temperatures do generally also lead to low mean temperatures, but not necessarily. They will also slow down growth and may even cause changes in the physiology of the plant. This in its turn may or may not result in morphological changes.

After a period of low temperatures is over, the number of leaves, inflorescences and flowers in the period immediately following is distinctly higher than normal. The process of growth is suddenly accelerated, frequently resulting in shorter periods between subsequent leaves, leading to a concentration of production. Such a concentration is found in Piura. The unusual periodicity in harvesting, mentioned in chapter 3, is due to this concentration of production.

On the other hand, the slow growth of inflorescences and flowers during winter months means that the period between two distinct stages of the ovary development, will be also longer. While for example the time between the first differentation of the perianth leaves and the differentation of the ovary is normally 2½ months, this may increase to 3 or even 3½ months under conditions of low temperatures. This means that the time, during which a certain stage of development can be affected i.e. damaged, is probably also longer.

The non-randomized distribution in age group 3 may be due to differences in the micro-climate, but lack of instruments and qualified personnel did not permit a study of the micro-climate. Another unusual occurrence in the weather is the heavy rainfall of March-May inclusive, 1965. At the Tablazo station a total of 287 mm was measured during these three months, i.e. more than 20 times the amount normally registered during that period. A rainfall gauge in the vicinity of 'La Solana' at, Lancones, (appendix 2) even registered three times that amount: 870 mm! This extremely heavy rainfall coincided with the period from the opening of the spathe to the initial development of those fruits, harvested during April–July 1966. It may have affected pollination, but the female flowers had developed already and as the abnormal fruit originates in an abnormal flower, no correlation can be suggested between the very heavy rainfall of 1965 and the high number of bicarpellate coconuts one year later.

6.2.2. *Pests and diseases as possible causes of carpel reduction*

It is extremely difficult to imagine that a pest or disease could cause the reduction of only one carpel of the ovary or of a fruit during its initial development. One would have to assume that the damage is produced in such a way that the two remaining carpels can develop into a healthy bicarpellate syncarpous fruit. It is possible that this could have happened once but it cannot explain the repeated production of healthy bicarpellate syncarpous fruits over the years.

Nevertheless, as it can be imagined that a somewhat more complicated process of indirect damage might influence the physiological processes, the possibility of such damage was studied. The distribution of the bicarpellate coconut bearing palms in age group 3 could be interpreted as being caused by an infectious disease. The pattern of decreasing production of bicarpellate fruits might then represent a reduction in intensity of the attack.

A number of inspections of the coconut palms showed that they were very healthy. Probably also because of the very isolated location of 'La Solana', none of the major diseases such as 'lethal yellowing' and 'red ring', which are known to affect also flowers and fruits, or pests of the coconut palm were detected. It should be added though that these inspections took place during 1967 and 1968, i.e. after the maximum bicarpellate coconut production, but no outbreaks of pests or diseases had occurred before. On the husks of some of the ripe fruits, both bicarpellate and tricarpellate, the scale insect *Aspidiotus* was encountered. This insect is known to occur on the coconut palm all over the world. It was found also on the leaves but the damage it caused was negligiable. It appeared in large numbers on the citrus trees planted nearby. It was never found in closed or open inflorescences. If this insect had connection with the occurrence of bicarpellate fruits then many more bicarpellate coconuts would have been reported from other parts of the world whereas other forms of damaage, normally related with this insect, would then have appeared in 'La Solana'. Neither can it explain the abnormal flowers. As it was found on coconuts of different locations and not limited to or concentrated on any specific palm or group of palms, its connection with the abnormalities can be discarded. Special attention was given to the occurrence of nematodes in the plantation. None were encountered in the palms themselves. Soil samples including parts of palm roots, taken around palms nos. 8 and 11 gave completely negative results. Random soil samples were taken in age group 3. Only one sample provided any information about the nematode population. This sample was taken near two palms, which were originally classified as producing also barren fruits, possibly bicarpellate. Both were low yielders. The nematodes found were: *Meloidogyne incognita, Xiphinema americanum* and *Pratylenchus* sp. None of these occurred at a density of more than 8 per 100 gr. of soil, which is a very low infestation.

These nematodes are not known to damage the coconut palm. As they could not be detected in the soil of the areas where high concentrations of bicarpellate coconut producing trees are observed no relation with the abnormalities could be established. No symptoms of bacterial or fungal diseases known to attack the coconut palm were detected during the period of observation. The study of the pests and diseases failed to establish any connection with the appearance of bicarpellate coconuts.

A possible explanation, which has not been offered yet but cannot be excluded, is that the reduced number of perianth leaves, frequently associated with bicarpellate coconuts and the occurrence of flowers and fruits with one carpel missing, is a 'normal' phenomenon. It could be that the flower of the coconut palm should be described as 'trimerous, sometimes bimerous'. Against this opinion, the other abnormalities appearing in the bicarpellate coconut producing palms must taken into account as these suggest a common cause and cannot be explained by this assumption. Furthermore, the theory that the appearance of bicarpellate flowers and fruits is normal is not supported by the extremely rare occurrence of the phenomenon.

7. SUMMARY

In the northern part of the Peruvian coastal region coconut palms were discovered which in addition to normal fruits produce larger numbers of bicarpellate fruits than have been previously recorded.

Deviations from the occurrence of 3 carpels in palm-fruits are discussed. In addition to the normal appearance of other carpel numbers in certain genera special attention is paid to unusual changes in their number and particularly to decreases. It is shown that the number of carpels is normally 3, but in some cases these do not develop equally and sometimes one or two remain rudimentary. In other cases they do not develop at all.

Comparison of the normal and bicarpellate coconuts shows a reduction of the third carpel in the latter, which has only one compressed locule, 2 'eyes' and 1 ridge. Anatomical analysis of the 'eyes' in normal and bicarpellate coconuts has resulted in the opinion that in all instances both the inner and outer integuments of each ovule coalesce with parth of the inner fruit wall.

A theory has been developed on the origin of the 'eyes'. A comparative study of the 'hard' and the 'soft eye' has resulted in a theory on their respective development and this theory explains why the 'soft' eye always corresponds to the functional carpel. When the non-functional ovules come under pressure from the strongly developing functional one, they gradually become compressed against the endocarp wall. The 'eyes' remain intact but become non-functional. This theory furthermore explains why in abnormal 2- or 3-seeded coconuts the corresponding 'eyes' are 'soft' or functional; because of their simultaneous development the 2 or 3 developing seeds establish a balance of pressure and consequently do not become compressed.

There is a marked similarity between the present author's findings in the coconut and studies on the development of the fruit in the Africain oil palm. Accordingly, the conclusion is drawn that the process of development of the 'eyes' in the fruits of both palms is very similar, if not identical.

Following the use of the word 'operculum' to describe similar tissues in the fruit of the African oil palm, this term is also adopted for the coconut palm to describe the 2 layers which together close off the 'eye'.

The number of chromosomes from root tips of germinating normal and bicarpellate coconuts was found to be 32.

The variation among bicarpellate fruits is described.

Also a coconut is discussed in which the 'hard eyes' and the corresponding locules have nearly joined.

The analysis of the morphology of the inflorescence has shown that the triad of a female flower and two accompanying male flowers is a partial inflorescence of cymous character, a cincinnus. Pairs of male flowers represent a reduced

stage of this cincinnus, as does the single male flower. The following abnormalities were observed: hermaphrodite flowers, abnormal male flowers and clusters of 2 male and 2 female flowers. The occurrence of this last abnormality has not yet been reported in normally branched inflorescences. A flower with a reduced number of perianth leaves was also found; its ovary was abnormal. Pairs of male flowers occurred in which the first flower was pedicellate, another abnormality which has not been described before. The analysis of these abnormalities confirms the theory on the morphology of inflorescences and flowers, which was initially only based on normal inflorescences and flowers.

The reduction in the number of carpels in the bicarpellate coconuts can be traced to the development of an abnormal syncarpous ovary. In the ripe bicarpellate fruits no remnants of the third carpel were found. Reduced numbers were registered, of floral envelopes, attached to both many of the bicarpellate fruits and to one female flower. Earlier studies on the morphogenesis of the flowers of the coconut palm, have served to determine the moment at which a flower, destined to become a bicarpellate fruit, is already abnormal. The moment at which the reduction of perianth leaves occurs is approx. 21 months prior to the harvesting of the bicarpellate fruits, while reduction in the number of carpels takes place about 18½ months before harvesting.

Statistical analysis of the available data shows that the *tendency to produce* bicarpellate coconuts is most probably genetically determined. The main argument for this theory is that no palms were observed which produced bicarpellate coconuts with yellow-ivory husk colour, although the percentage of coconut palms in the population studied, producing fruits with such husk colour was high. It is suggested that the oldest group of palms was composed of material of various origin. The remarkable yields of normal and bicarpellate fruits from two of the palms is also mentioned.

The influence of the environment, especially the weather has been studied. It is clear that the low winter temperatures favour the *appearance* of bicarpellate coconuts. Abnormally low temperatures result in high numbers of such fruits.

SAMENVATTING

In het noordelijk deel van het Peruaanse kustgebied zijn cocospalmen gevonden die naast normale vruchten ook bicarpellaire cocosnoten voortbrengen in hoeveelheden als nog niet eerder waren waargenomen.

Het voorkomen van afwijkingen van drie vruchtbladen bij palmen wordt besproken. Behalve aan het normaliter optreden van andere aantallen carpellen bij sommige genera is bijzondere aandacht geschonken aan abnormale veranderingen, speciaal gevallen van afname van het aantal vruchtbladen. Het blijkt dat het aantal carpellen meestal 3 is; deze ontwikkelen zich echter niet altijd gelijk en soms blijven 1 of 2 rudimentair. In andere gevallen komen zij geheel niet tot ontwikkeling.

Een vergelijking van normale met bicarpellaire coconsoten toont dat in de laatsten het derde vruchtblad afwezig is: slechts één samengedrukt hokje, 2 'ogen' en 1 vergroeiingsnaad. Anatomische studie van de 'ogen' in normale en bicarpellaire cocosnoten heeft tot de opvatting geleid dat in alle gevallen zowel het binnenste als het buitenste integument van elke zaadknop vergroeien met een deel van de binnenwand van de vrucht. Een theorie omtrent het ontstaan van de 'ogen' is ontwikkeld. Een vergelijkende studie van het 'harde' en het 'zachte' of 'kiemoog' heeft geresulteerd in verdere theorie betreffende hun respectievelijke ontwikkeling; hiermee kan verklaard worden waarom het 'zachte' oog altijd gevonden wordt in de functionele carpel. De niet-functionele zaadknoppen worden door de – sterk uitgroeiende – functionele zaadknop geleidelijk aan tegen de wand van het endocarp platgedrukt. De 'ogen' blijven intact maar hebben geen functie meer. Deze theorie verklaart tevens waarom in – abnormale – 2- of 3-zadige cocosnoten de respectievelijke 'ogen toch 'zacht' d.w.z. functioneel zijn: de 2 of 3 zich gelijktijdig ontwikkelende zaden vormen een wederzijds drukevenwicht en worden dientengevolge niet weggedrukt.

Er is een duidelijke overeenkomst in ontwikkeling van de vruchten der cocospalm en oliepalm. Op grond hiervan kan geconcludeerd worden dat de ontwikkeling van de 'ogen' in de vruchten van beide palmen veel gelijkenis vertoont en mogelijk zelfs identiek is.

Analoog aan het gebruik van het woord 'operculum' voor de lagen welke het 'oog' afsluiten in de oliepalmvrucht wordt deze term voor gebruik bij de ogen' van de cocospalm overgenomen.

Het aantal chromosomen in worteltoppen uit kiemende normale én bicarpellaire cocosnoten bedraagt 32.

Een beschrijving is gegeven van de variabiliteit binnen de bicarpellaire vruchten.

Voorts wordt een cocosnoot besproken waarbij de twee 'harde ogen' en de daarmee samenhangende hokjes bijna versmolten zijn.

De analyse van de morphologie van de bloeiwijze van de cocospalm heeft aangetoond dat de triade, bestaande uit een vrouwelijke bloem en twee begeleidende mannelijke bloemen, een cymeuze deel-bloeiwijze is en wel een cincinnus (schicht). Paren van mannelijke bloemen vertegenwoordigen een onontwikkelde vorm van deze schicht; zo ook de enkele mannelijke bloem.

De volgende afwijkende bloemen zijn waargenomen: hermaphrodiete bloemen, abnormale mannelijke bloemen en groepen van 2 mannelijke en 2 vrouwelijke bloemen. Deze laatste afwijking was nog niet eerder waargenomen in normaal vertakte bloeiwijzen.

Verder is een vrouwelijke bloem gevonden met een gereduceerd aantal perianth-bladen; ook het vruchtbeginsel was abnormaal. Paren van mannelijke bloemen werden waargenomen, waarbij de eerste bloem van het paar gesteeld was, eveneens een afwijking welke nog niet eerder beschreven was. De analyse van deze afwijkingen bevestigt de theorie met betrekking tot de morphologie van deel-bloeiwijzen en bloemen, welke eerst alleen op normale bloeiwijzen en bloemen gebaseerd was.

De reductie van het aantal carpellen in de cocosnoot is te herleiden tot de ontwikkeling van een abnormaal syncarp vruchtbeginsel. In rijpe bicarpellaire vruchten zijn geen overblijfselen van een derde vruchtblad gevonden. Een reductie van het aantal bloembladen is waargenomen zowel aan vele bicarpellaire vruchten als aan een vrouwelijke bloem. Vroeger onderzoek met betrekking tot de morphogenese van de bloemen der cocospalm heeft ertoe bijgedragen om het tijdstip vast te stellen waarop een bloem, welke later tot een bicarpellaire vrucht ontwikkelt, reeds abnormaal is. Dit tijdstip ligt ongeveer 21 maanden vóór de oogst der bicarpellaire vruchten, wanneer het ook de reductie van de perianth betreft en ± 18½ maand voor de reductie in het aantal carpellen.

Uit de statistische analyse van de beschikbare gegevens blijkt dat de *neiging tot het voortbrengen* van bicarpellaire cocosnoten hoogst waarschijnlijk genetisch bepaald is. Het voornaamste argument ten gunste van deze theorie is dat er geen palmen zijn waargenomen welke geel-ivoorkleurige cocosnoten, die tevens bicarpellair zijn, voortbrengen, hoewel het percentage cocospalmen, die vruchten met een dergelijke bolsterkleur produceren, hoog is. Dit doet veronstellen dat de oudste groep van palmen samengesteld is uit materiaal van verschillende herkomst. Verder verdienen de opvallende opbrengsten aan normale en bicarpellaire vruchten van twee der palmen vermelding.

Wat de mogelijke invloed van het milieu betreft is voornamelijk die van het weer nagegaan. De lage wintertemperaturen zijn van invloed op het *optreden* van bicarpellaire cocosnoten, waarbij abnormaal lage temperaturen grote hoeveelheden van dergelijke vruchten ten gevolge hebben.

RESUMEN

En la Costa norte peruana se han encontrado cocoteros los cuales aparte de producir frutos normales, producen frutos bicarpelares en cantidades no registradas hasta la fecha.

Se mencionan las desviaciones de la ocurrencia normal de frutos tricarpelares en palmeras. Además de la ocurrencia también normal de números diferentes de carpelos en algunos géneros, se ha dedicado atención especial a los cambios anormales en número, especialmente a reducciones en el número de carpelos. El ovario normalmente es tricarpelar pero muchas veces los carpelos no desarrollan uniformemente y a veces uno o dos quedan rudimentarios. En otros casos algunos de los carpelos no se desarrollan.

Se nota una reducción del tercer carpelo en los frutos bicarpelares al compararlos con los frutos normales. En los cocos bicarpelares encontramos un solo lóculo comprimido, dos 'ojos' y solamente una sutura. El estudio anatómico de los 'ojos' de frutos normales y anormales ha resultado en la opinión que en todos los casos tanto el integumento interno como el externo de los tres ovulos se juntan con una parte de la pared interna del fruto. Una teoria se ha desarrollado en cuanto al origin de los 'ojos'. Un análisis de 'ojos duros' y 'suaves' ha tenido como resultado una teoría referente al desarrollo de ellos, la cual explica porqué el 'ojo suave' siempre coresponde al carpelo funcional. Cuando los óvulos no funcionales son presionadas por el desarrollo del óvulo funcional gradualmente se van comprimiendo contra la pared del endocarpio. Aunque los tejidos de los 'ojos' quedan intactos los mismos serán no funcionales. Esta teoría explica porqué en frutos anormales con 2 ó 3 semillas los 'ojos' correspondientes siempre son 'suaves' o funcionales: debido al desarrollo simultáneo de los 2 ó 3 semillas la presión está balanceada y consecuentemente los 'ojos' no son comprimidos.

Hay notoria similitud entre lo que ha sido encontrado por el autor del presente trabajo en el fruto del cocotero y los estudios realizados sobre el desarrollo del fruto de la palma Africana de aceite, se llega a la conclusión que el proceso de desarrollo de los 'ojos' en los frutos de ambas palmeras es muy similar y posiblemente idéntico.

Continuando con el uso de la palabra 'operculum' para describir tejidos similares en el fruto de la palmera Africana de aceite, también este término ha sido adoptado para describir los 2 tejidos que encierran el 'ojo' del coco.

El número de cromosomas determinado en puntas de raices tanto de frutos normales como bicarpelares es 32.

Se describe la variación dentro de los frutos bicarpelares. Igualmente se ha descrito un coco en el cual los 'ojos duros' y los lóculos correspondientes se presentan casi juntos.

El análisis morfológico de la inflorescencia demuestra que la triada de la flor

feminina y las 2 flores masculinas que acompañan representa una inflorescencia parcial de típo cimoso: una cincina; los pares de flores masculinas representan una forma reducida, igualmente la flor masculina sola. Se han observado las siguientes anormalidades: flores hermafroditas, flores masculinas anormales y grupos de 2 flores masculinas y 2 flores femininas, siendo esta última anormalidad registrada por primera vez como ocuriendo en una inflorescencia normalmente ramificada. Se ha encontrado una flor feminina con número reducido de hojas del periantio y ovario anormal. Igualmente se describe pro primera vez pares de flores masculinas en las cuales la primera flor es pedicelada. El análisis de estas anormalidades confirma la opinión en cuanto a la morfología como se había observado antes unicamente en las flores normales.

La reducción en el número de carpelos en los cocos bicarpelares es el resultado del desarrollo de un ovario sincárpico y anormal. No se ha encontrado ningún del resto tercer carpelo en los frutos bicarpelares maduros. Se ha registrado un número reducido de hojas florales, agregados tanto a muchos de los frutos bicarpelares como a una flor feminina.

Estudios anteriores sobre la morfogenesis de las flores en la palmera cocotera han servido para determinar el momento en el cual una flor, que desarrollará en un fruto bicarpelar, ya es anormal. Esto sucede aproximadamente 21 meses antes de cosechar los frutos bicarpelares, para la reducción en el periantio, mientras que la reducción en el número de carpelos toma lugar más o menos a los 18 1/2 meses antes de la cosecha.

Análisis estadístico de los datos disponibles indica que la *tendencia a producir* cocos bicarpelares es determinada geneticamente. El argumento principal a favor de esta teoría es el hecho que no se han observado palmeras que produzcan cocos bicarpelares de color amarillo-marfil mientras que el porcentaje de cocoteros con frutos amarillo-marfil es alto. Esto último sugiere que el grupo mas antiguo de palmeras está compuesto por material de diferentes origines.

Las cosechas remarcables tanto de frutos normales como bicarpelares de dos de las palmeras tambien se mencionan.

La influencia del medio ambiente, especialmente del tiempo ha sido considerada.

Las temperaturas bajas en inviero favorecen la *aparición* de cocos bicarpelares. Temperatures anormalente bajas darán como resultado un alto porcentaje de tales frutos.

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APPENDIX 1. Meteorological data February 1962–December 1968 inclusive

Station: Tablazo Latitude: 4° 52′ S
Altitude: 122 m above sea level Longitude: 80° 33′ W

Year and month	Average of max. temp. in °C.	Average of min. temp. in °C.	Rainfall in mm.	Average of daily sunshine
February '62	32.8	21.7	8.3	5h.30′
March '62	33.5	19.3	6.6	5h.46′
April '62	31.4	19.7	9.5	7h.23′
May '62	30.2	17.0	0.5	6h.40′
June '62	27.4	15.6	0.0	5h.28′
July '62	27.0	15.2	0.0	6h.07′
August '62	26.2	15.7	0.0	6h.52′
September '62	28.6	17.6	0.0	8h.13′
October '62	30.0	16.4	0.0	8h.01′
November '62	29.8	16.9	1.2	8h.03′
December '62	31.5	17.9	1.4	9h.07′
January '63	32.2	19.1	15.5	8h.14′
February '63	32.7	20.6	7.5	5h.42′
March '63	32.0	21.4	2.8	6h.23′
April '63	—	19.2	0.0	8h.01′
May '63	30.1	18.8	0.0	8h.14′
June '63	26.6	16.4	0.0	6h.28′
July '63	—	16.1	0.0	6h.26′
August '63	29.0	16.1	0.0	7h.23′
September '63	29.4	16.5	0.0	6h.56′
October '63	30.4	16.3	0.0	7h.35′
November '63	30.4	16.4	0.2	7h.36′
December '63	31.9	19.2	7.2	7h.04′
January '64	33.2	20.9	1.8	5h.55′
February '64	34.1	21.6	2.9	5h.27′
March '64	34.7	21.9	4.0	6h.39′
April '64	33.6	20.0	9.4	7h.21′
May '64	31.2	17.2	0.0	8h.16′
June '64	29.6	16.1	0.0	7h.15′
July '64	27.7	14.3	0.0	6h.48′
August '64	29.0	14.7	0.6	7h.11′
September '64	30.1	14.7	0.0	8h.35′
October '64	30.5	15.5	2.8	7h.47′
November '64	31.1	16.8	1.5	8h.00′
December '64	31.9	16.5	0.0	8h.07′
January '65	33.3	20.3	0.7	5h.54′
February '65	35.3	24.5	3.7	6h.24′
March '65	33.5	22.1	166.4	6h.57′
April '65	32.8	21.4	109.1	6h.19′
May 65	33.0	20.3	11.4	6h.12′
June '65	31.8	19.3	0.0	6h.04′
July '65	29.1	18.3	0.0	4h.57′
August	30.7	17.6	0.0	6h.53′
September '65	30.5	16.7	0.0	6h.00′

APPENDIX 1 (*continued*)

Year and month	Average of max. temp. in °C.	Average of min. temp. in °C.	Rainfall in mm.	Average of daily sunshine
October	31.8	17.6	0.9	7h.20′
November '65	32.6	17.8	9.9	5h.43′
December '65	33.6	18.8	3.7	9h.29′
January '66	33.2	19.4	1.0	5h.50′
February '66	34.7	19.6	11.6	8h.55′
March '66	34.3	19.6	15.9	7h.44′
April '66	34.6	20.6	2.7	7h.52′
May '66	32.5	17.7	0.4	7h.17′
June '66	28.7	16.6	0.0	6h.56′
July '66	27.8	15.2	0.0	7h.25′
August '66	28.8	15.3	0.3	8h.32′
September '66	29.9	16.0	0.0	7h.34′
October '66	30.0	16.9	6.0	7h.14′
November	30.4	17.4	1.2	7h.19′
December '66	32.1	17.4	0.3	8h.49′
January '67	33.5	20.4	13.1	7h.04′
February '67	33.8	21.4	22.9	6h.11′
March '67	34.6	21.2	1.8	8h.10′
April '67	33.8	19.9	0.0	8h.32′
May '67	32.7	18.0	0.4	8h.12′
June '67	27.7	15.7	0.0	6h.29′
July '67	27.0	15.9 (3)[1]	2.3	6h.08′
August '67	27.2	14.5 (11)	0.0	7h.19′
September '67	29.4	14.6 (17)	0.0	8h.26′
October '67	30.7	15.6 (4)	5.2	8h.15′
November '67	29.6	15.5 (11)	0.0	7h.16′
December '67	31.3	17.5	0.0	8h.38′
January '68	33.4	20.4	0.0	6h.21′
February '68	24.3	20.4	0.0	7h.44′
March '68	34.6	20.4	0.1	7h.47′
April '68	33.5	17.8	0.0	9h.01′
May '68	30.3	15.4	0.1	7h.58′
June '68	27.9	14.8	0.0	6h.31′
July '68	28.9	15.4	0.0	7h.24′
August '68	29.7	16.3	0.0	7h.45′
September '68	30.6	16.7	0.0	8h.17′
October '68	29.9	16.9	6.4	6h.53′
November '68	30.8	16.6	0.0	7h.25′
December '68	32.5	18.1	0.0	8h.02′

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[1] Number of days per month with minimum temperature below 15 °C.

APPENDIX 2. Rainfall in mm. June 1963–December 1966 inclusive

Observation point: Lancones
Rain gauge: nr. 258
Altitude: 120 m above sea level

Latitude: 4° 34′ S
Longitude: 80° 29 ′W

Month	1963	1964	1965	1966
January	–	0.0	0.0	0.0
February	–	4.7	11.2	6.7
March	–	0.0	560.6	13.0
April	–	28.5	231.8	0.0
May	–	0.0	87.8	0.0
June	0.0	0.0	5.2	0.0
July	0.0	0.0	0.0	0.0
August	0.0	0.0	0.0	0.0
September	0.0	0.0	1.4	0.0
October	5.1	1.4	0.0	15.2
November	5.3	0.0	6.4	0.0
December	0.2	0.0	4.2	3.0
Total		34.6	908.6	37.9