

ON FERTILITY, PLEIOMERY AND MEIOMERY IN THE FRUITS OF SOME CANARIUM SPECIES

by

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Some five or six years ago the second author described cases of meiomery and pleiomery in male flowers of *Canarium decumanum* GAERTN. (1, p. 41—53). A number of 3665 flowers were investigated; 98.8 % of these were trimerous, 0.9 % pleiomerous (tetramerous) and 0.3 % meiomerous (dimerous). These figures, however, are not fully trustworthy, as the smaller dimerous flowers were, as a matter of fact, easier overlooked than the bigger tri- and tetramerous ones which had a better chance to be picked from the ground. Secondly, the flowers were collected from under two or three trees standing together in the Botanic Gardens at Buitenzorg and no care was taken at the time to be sure that flowers of different trees were kept apart, as the purpose was to investigate the nature of these phenomena rather than their procentual occurrence. From these studies it was concluded that pleiomery and meiomery are to be considered as what EICHLER called an "originäre Variabilität", a variability inherent to the species.

Yet this variability may have a certain phylogenetic significance; both the amplitude and the frequency are reflecting the degree of fixation of the equilibrium ("normal") stage and prevalence of one side of the variation over the other may indicate whether or not the "average" has, phylogenetically speaking, already passed the fixed stage.

These considerations came to the mind of the second author when he received from the first-named one a collection of kernels (putamina), among which some meio- and pleiomerous ones, of two *Canarium* species, cultivated in Java, viz. (cf. the map on p. 104):

C. commune L., a native of Kangean, Celebes, Flores and the Moluccas (cf. 3, p. 509 ss.), and

C. Mehenbethene GAERTN. (= *C. moluccanum* BL. = *C. amboinense* HOCHR.), hailing from the Moluccas, New Guinea, the Bismarck Archipelago and the Solomon Islands (cf. 3, p. 515 ss.).

C. commune L. is abundantly cultivated everywhere as an alley-tree, *C. Mehenbethene* is only occasionally planted for decorative purposes. It is apparently closely related to *C. commune* but by no means so closely that it cannot be easily distinguished from it by a number of features. In many separate characteristics as well as in general appearance, *C. Mehenbethene* is larger, heavier, coarser than *C. commune* and it might therefore be suspected as a polyploid form of the more slender and delicate *C. commune*. We have no exact data concerning eventual hybridization of the two species.

As a matter of course we were much interested in the cases of meio- and pleiomery, discovered among the fruits¹⁾, which are normally trimerous, like all other whorls in the whole tribe of the Canarieae (cf. 2, p. 134—137). On pondering on the significance of these phenomena in the light of the evolution of features (cf. 2, p. 178—197; also 4) and of migration we came to the following points towards our problem:

1. in the Burseraceae-Canarieae the basic number of whorl parts is 3;
2. like in many other plant orders a general tendency is stated which may be called "contractive reduction" (cf. 2, p. 105) which in the Canarieae affects all flower whorls. As is a well-known fact, the gynaeceum is usually more advanced in reduction than the other whorls;
3. in addition, some whorls (corolla, androeceum, gynoeceum) show occasional meiomery as well as pleiomery;
4. if meiomery can be considered as a "prophecy" of a future phase, pleiomery may be considered as an atavistic phenomenon²⁾;
5. in connection with this variability in the number of whorl parts,

¹⁾ BUMPHIUS (Herb. Amb. II, 1741, 166) mentions also 4-celled fruits in *C. decumanum*, GUILLAUMIN (Ann. Sc. nat., 9e Sér., X, 1909) mentions meiomeric fruits in the same species.

²⁾ It is very doubtful whether this supposition is allowable in all cases; secondary "dédoublément" on the basic number is frequently found, even "ad absurdum" (cf. 4, p. 102). Therefore pleiomery is to be treated with great scepticism as far as phylogenetic conclusions are concerned.

it may be stated that the general tendency (cf. 2, p. 178—197) to reduce the number of carpels comprises the following phases of regression (in *Canarium*):

phase limits	phases									
1 —————										
	a	{ three carpels, each with two collateral fertile ovules; fruits with three times two seeds;								
2 —————										
3 ———										
	b	{ one of the seeds of each carpel may turn sterile in favour of the other ¹⁾ ; three phases, fruit ultimately 3-seeded;								
4 ———										
5 —————										
	c	{ one of the carpels may turn sterile; fruit two-seeded (3-celled);								
6 —————										
	d	{ two of the carpels turn sterile; fruit one-seeded (3-celled);								
7 —————										
8 ———	e	{ one of the carpels may turn abortive; fruit two-celled; two phases: two- or one-seeded;								
9 ———										
	f	{ two of the carpels may turn abortive; fruit one-celled;								
10 —————										
phase limits	1	2	3	4	5	6	7	8	9	10
phases	a		b		c	d	e		f	

Each systematic unit has its own frequency curve concerning this feature, the range being the greater as greater units are considered. Thus the genus *Canarium* as a whole ranges from 4 to 9 (with a top at about 6), but some species may have their top more towards 4, say at about 5 or 6, others more towards 9, say at 7 or 8. The latter are thus to be considered as more advanced relative to the feature in question.

¹⁾ The actual bearing is possibly to be understood in this way that either of the two ovules in each cell are equal in the competition to fertilization but that this is almost entirely stopped as soon as one of the ovules is fertilized. It would be worth while to investigate whether a definite ovule of each pair shows a certain predilection for being suppressed.

BUERT (Kew Bull. 1935, No. 5, p. 302) mentions for *Canarium solomonense*: "ovarii loculi u n i ovulati". If this is true, it would be very remarkable indeed!

Phase-limit 4 seems to occur but is extremely rare. VAN HEURN writes that he has met with a few cases, in which two seeds were found in the same cell (apparently in *C. commune*), but unfortunately no material has been preserved. One case will be mentioned underneath (*C. commune*, dimerous fruits) (*fig. 23*). Phase-limit 5 is found in some species, especially in Western ones (cf. 4, p. 136). Phase-limit 9 is represented by the meiomorous one-seeded fruits. It must be added that the above regression represents by no means the only possibility. It is, for instance, also possible that one of the carpels turns sterile before the second ovule of one of the other carpels, etc.

6. Phase advancement of a feature may go hand in hand with migration of the systematic unit in which the feature is located. The actual distribution of two or more consecutive phases of the same feature in closely related species may therefore be considered as a reflection of the migration of these species. For both the more primitive and the more advanced phases of a feature may have migrated, but in general, the more advanced one may be presumed to have migrated the longer way, as migration, again in general, implies a better chance to externally induced evolution than a static geographical localisation (environment).

In the light of the above considerations it seemed important to investigate besides the pleio- and the meiomery, also the fertility of "normal" trimerous fruits (cf. 2, p. 134—137) as well as the geographical distribution of the phases. We will therefore now give the results and see what might be concluded from them.

C. Mehenbethene.

177 fruits of one single tree.

One of these was tetramerous and 3-seeded (*fig. 1*).

The other 176 were trimerous and belonged to the following types:

	Phase-limit
I. 3-seeded: none	5
II. 2-seeded: 24	6
<i>a.</i> all cells equal (<i>fig. 2</i>): 1	
<i>b.</i> 2 cells large, 1 small (<i>fig. 3</i>): 23	
III. 1-seeded: 152, viz.	7
<i>a.</i> all cells equal (<i>fig. 4</i>): 2	
<i>b.</i> 2 cells large, 1 small (<i>fig. 5</i>): 25	
<i>c.</i> 1 cell large, 2 small (<i>fig. 6</i>): 125	

As a matter of course this result has to be interpreted with a certain scepticism, since VAN HEURN stipulates as his impression (based upon his observations in *C. commune*) that the ratio of pleiometry and meiometry and therefore probably also of fertility is individually different. The above proportionality may therefore be considered to a certain degree as valid for that definite tree only; as applicable to the species it has to be more or less mistrusted.

The principal types are, of course, IIb and IIIc. The undertypes *a* and *b* of II and *a*, *b* and *c* of III have not necessarily a phylogenetic significance; as a matter of course, as soon as two seeds are developing, the third cell is most probably repressed and will only rarely attain an equal size (it may be that the third ovule has developed for a short time) and the same is true in the case of one-seeded fruits. For the rest, there were no sharp limits between the types. Transition forms were particularly abundant between IIa—IIb, IIa—IIIb and IIb—IIIb.

C. commune.

1126 fruits from some trees.

Of these 26 were tetramerous (2.3 %) and 5 were dimerous (0.45 %).

These figures agree both in a relative and in an absolute sense pretty well with those found for the pleiometry and meiometry of the male flowers of *C. decumanum*, where they were 0.9 and 0.3 % respectively.

Tetramerous fruits.

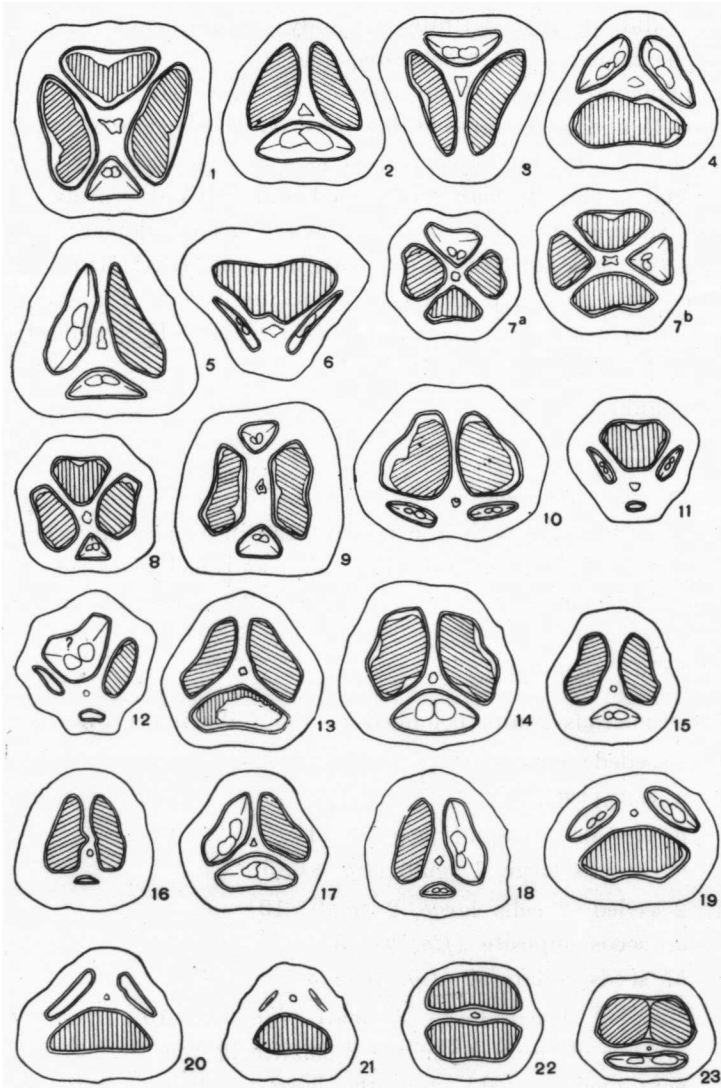
The 26 tetramerous fruits belonged to the following types:

- I. 4-seeded: none
- II. 3-seeded: 6
 - a. 4 cells \pm equal (*fig. 7*): 1
 - b. 3 cells large, 1 small (*fig. 8*): 5
- III. 2-seeded, 2 cells large, 2 small: 10
 - a. seeds opposite (*fig. 9*): 5
 - b. seeds collateral (*fig. 10*): 5
- IV. 1-seeded, 1 cell large, 3 small (*fig. 11*): 10
 - (in one of these one of the 3 small cells was slightly larger and contained a seed, while the largest cell was indicated to be empty, *fig. 12*).

Transition forms between all types occurred, especially between IIa and b—IIIa and between IIIb—IV.

Trimerous fruits.

We did not deem it necessary to investigate all the seeds available, as a smaller number would certainly give approximately the same results.



Explanation in the text.

**Figs 1—6. *C. Mehenbethene* GAERTN.; figs 7—23. *C. commune* L. — Natural size.
Embryos are hatched.**

We therefore chose an arbitrary number of fruits, viz. 406. These belonged to the following types:

	Phase-limit
I. 3-seeded; cells equal (<i>fig. 13</i>): 5 (one of the seeds always more or less deficient)	5
II. 2-seeded: 99	6
<i>a.</i> all cells equal (<i>fig. 14</i>): 19	
<i>b.</i> 2 cells large, 1 small (<i>figs. 15, 16</i>): 80	
III. 1-seeded: 302	
<i>a.</i> all cells equal (<i>fig. 17</i>): 14	
<i>b.</i> 2 cells large, 1 small (<i>fig. 18</i>): 26	
<i>c.</i> 1 cell large, 2 small (<i>figs 19, 20, 21</i>): 262	

Among this rich material many transition forms were found, especially between I—II*a* and *b*, I—III*a*—III*c* and I—III*b*.

Dimerous fruits.

The 5 dimerous fruits belonged to 2 types:

- I. 2-celled, 2-seeded (*fig. 22*): 1
- II. 2-celled, 1-seeded, 1 cell large, 1 small (*fig. 23*): 4

In the case of *fig. 23* the largest cell contained, according to VAN HEURN, two seeds (no material preserved).

Even these 5 specimens showed a transition from two-seeded with equal cells to one-seeded with a very small sterile cell.

Let us now compare the figures obtained in *C. Mehenbethene* with those from *C. commune*. I do not know whether the single case of tetramery in *C. Mehenbethene* is entirely due to the smaller number of fruits available. At any rate we can only compare the trimerous fruits.

		reduced		reduced
	<i>C. Mehenb.</i>	to 100	<i>C. comm.</i>	to 100
I. fruit 3-seeded	—	—	5	1.2
II. fruit 2- „	24	13.6	99	24.4
III. fruit 1- „	152	86.4	302	74.4
	176	100	406	100

Now the average position of either species in the range of phases of the reduction of the number of carpels, as shown on p. 99, can

perhaps be best estimated by attributing consecutive values to consecutive phases, e. g.:

fruit 3-seeded: a^3

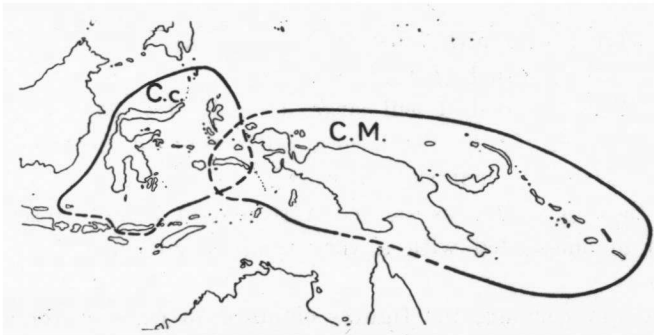
„ 2- „ : a^2

„ 1- „ : a

Canarium Mehenbethene then obtains the formula: $13.6 a^3 + 86.4 a$ or, if $a = 10$ the "phase index" of *C. Mehenbethene* = $1360 + 864 = 2224$.

Canarium commune gets: $1.2 a^3 + 24.4 a^2 + 74.4 a$ or, if $a = 10$ the "phase index" of *C. commune* = $1200 + 2440 + 744 = 4384$.

This means that — if the figures for the single tree of *C. Mehenbethene* could be taken for the whole species — this species is more advanced on the way of ovary reduction than *C. commune*. And as the area of *C. Mehenbethene* is more to the East than that of *C. commune* (the areas are partly overlapping; cf. the map), the general migration track of this "line of evolution" has apparently been eastward.



Areas of *C. commune* and *C. Mehenbethene*.

One of us has, some time ago, suggested similar conclusions relative to the Sapotaceae (4) and we are inclined to accept the same for *Canarium*. This view is supported by the fact that several eastern *Canarium* species have mostly 1-seeded fruits (*C. quadrangulare*, *C. acutifolium*, *C. vitiense*, *C. maofoa*, *C. oleosum*, *C. asperum*, *C. maluense*, *C. Balansae*, etc.), while typically western species are often 2-, or 3-seeded (*C. decumanum*, *C. Endertii*, *C. hirsutum*, *C. tomentosum*, *C. littorale*, *C. patentinervium*, etc.). It would be worth while to investigate this accurately. It is also supported by the inclination to meiomery, increasing towards the east (as in the Sapotaceae quoted; cf. also *Canarium decumanum*, *C. Balansae*, etc. described in 2, p. 134—137), which culminates in the constantly (?) dimerous gynoeceium of *Canariellum* (New Caledo-

nia). In this connection I may draw again the attention to BURTT's assertion that the cells of *C. solomonense* should be uniovulate.

It must be added that, although, in general, *C. Mehenbethene* appears to be more advanced concerning the reduction of the ovary, *C. commune* shows a greater range in the phases, which is probably only partly due to the greater number of fruits investigated. In *C. Mehenbethene* 3-seeded fruits and such fruits as shown in figs. 16 and 21 are wanting. Also the pleiomery seems to be more frequent. We are inclined to interpret this condition also as a more primitive one.

Summary.

In continuation of a previous publication by LAM, in which meiomery and pleiomery in male flowers of *Canarium decumanum* were described, the same phenomenon is now discussed concerning the fruits of *C. Mehenbethene* (176 of one single tree) and *C. commune* (1126 fruits mixed from more than one tree). An investigation of the material gave the following results:

1. *C. commune* and *C. Mehenbethene* are closely related; the latter may prove to be a polyploid of the former. Their areas are partly overlapping, but *C. commune* has its centre in the Moluccas, *C. Mehenbethene* in New Guinea and W. Polynesia.
2. A tendency to reduce the number of ovules and carpels in the ovary is assumed. By means of a statistical method ("phase index") the position of either species in the phases of this regression is indicated.
3. From this, it is concluded that *C. Mehenbethene* represents a more advanced phase than *C. commune* and that therefore an eastward migration must be accepted. This agrees with other facts stated earlier, both in the Burseraceae and in other plant families of western origin.
4. In *Canarium commune* pleiomery is found in 2.3 % of the fruits, meiomery in 0.45 %, which agrees fairly well with the figures found earlier for the corolla and the androeceum of the male flowers of *C. decumanum* (0.9 % and 0.3 % respectively).
5. The desirability is expressed to investigate the following points:
 - a. the ontogeny and the fertilization of ovaries and ovules in *Canarium*.
 - b. cytological relations between related trees in the tropics, especially as far as they may supply indications towards migration tracks (cf. the work of HAGERUP on *Vaccinium* [Hereditas 18, 1933]).

- c. the "phase index" of a number of related *Canarium* species.
- d. the exact distribution of some of the phases mentioned along those migration tracks which are both geologically and biogeographically supported (e.g. Sunda centre—Philippines, Philippines—Moluccas—New Guinea, New Guinea—Moluccas—Central Celebes, Malay Peninsula—Sumatra—Java, etc.).

Literature.

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