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A NEW INTERPRETATION OF THE COMPOUND STROBILAR STRUCTURES OF CORDAITES AND CONIFERS

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ABSTRACT

The compound strobili of cordaites and conifers (e.g. *Amentotaxiis)* is interpreted by the application, of the telome theory. Homologies of' organization among the strdbilar structures and. the pinnate phylloclade' of *Phylloeladus* are also suggested.

Buah runjung majemuk Cordaites dan tumbuhan berunjung (misalnya. *Amentotaxus)* ditafsirkan berdasarkan penerapan teori telom. Homologi organisasi antara susunan buah runjung dan filokladium bersirip daripada *Phylloeladus* ditunjukkan pula.

INTRODUCTION

In examining the structure of a pinnate phylloclade of *Phylloeladus* (figs. 18, 19), a curious conifer found in Malesia, New Zealand and Tasmania, the writer was perplexed by its extraordinary complexity (Keng 1974). The whole structure appears to be a product of several repeated processes of a stem within the axil of a leaf (figs. 18, 19). This is further complicated by the fact that its terminal bud can eventually give rise to a new crop of pinnate phylloclades. It is therefore suggested to abandon the classical leaf-stem concept which was formulated from the study of angiosperms, and to refer back to the most primitive land plants such as *Rhynia, Horneophyton* and allied plants which are com-, posed of • dichotomously forking branch systems, in which there is no clear distinction between stem and leaf. The ultimate terminal-portion of the dichotomizing axis, either fertile or sterile, was aptly termed a telome by Zimmermann. It is postulated that several processes are involved in further modifications of the dichotomizing branch systems, these include: planation (branching restricted to a plane), overtopping (unequal dichotomy), syngenesis (or webbing, lateral union between forked divisions) and reduction (Zimmermann 1930, 1952). Following this telome theory, the organization of the pinnate phyHoclade of *Phyllocladus* can be fully explained (Keng 1974).

In this paper it is attempted to apply the same theory to demonstrate that starting from the dichotomizing branch systems, through essentially the same procedure, the compound strobili of both the palaeozoic *Cordaites* and the living conifer, *Amentotaxus,* can be constructed. Should the homologies of organization be established among these structures, then it could probably assist us in stabilizing the nomenclature of the reproductive organs of these taxa, which at present, is in a state of confusion.

ON THE SPICATE COMPOUND STROBILI OF CORDAITES

The genus *Cordaitanthus* (or *Cordctianthus)* has been commonly applied to both ovulate and pollen bearing organs of *Cordaites* by the palaeobotanists. It was precisely a century ago, in 1877, when Grand' Eury first described cordaitean shoots with leaves and axillary compound strobili attached (fig. 1). Later it was found that the ovulate compound strobilus of the *Cordaites* has essentially the same organization as the staminate one although they were borne on separate branches (Florin 1951). A compound strobilus (fig. 2) may reach a length of 30 cm and it bears two rows of strobili each in the axil of an awl-shaped bract. Each strobilus* consists of a number of scale-like bracts spirally arranged on the axis (figs. 3, 4 & 5). Usually only the upper few scale-like bracts bear an ultimate unit of fertile shoot (either ovulate or staminate) each on their axils, while the others remain sterile**.

* The less rigid term *strobilus* is preferable to others such as: 'flower' (Florin 1951), 'fertile branch unit' (Wilde 1944), 'dwarf shoot' (Andrews 1961), 'bud' (Banks 1970), etc.

** The interpretation of the strobilar structure of *Cordaitanthus* presented here is in agreement with that of Renault (1879) and is rather different from that of Florin (1951). According to Florin, such strobilus is homologous to an angiospermous flower —— with sterile sporophylls below and fertile ones above. Because of this conviction, Florin (1951, p. 303) questioned Renault's interpretation of the staminate strobili of *Cordaitanthus penjoni* that these ultimate units of fertile shoots (called 'sporophylls' by Florin) were placed in the axils of bracts. Paradoxically, Florin (1951, p. 308) did not seem to challenge the earlier interpretation that in the ovulate strobili of *C. pseudofluitans,* the ultimate units of fertile shoots (called 'megasporophylls' by Florin) were being placed axillary to bracts. I am inclined to agree with Florin (1951, p. 307) in this particular aspect that *C. pseudofluitans* probably represented the most primitive type of the ovulate strobili of *Cordaitanthus.* I also tend to suggest that *C. penjoni* probably represents the most primitive type of staminate strobili. In both cases their ultimate units of fertile shoots were likely to be inserted in the axils of bracts. While in most of the other known species of *Cordaitanthus,* these bracteate structures were obsolete. It is probably significant to note the presence of the seemingly homologous bracteate structures in *Austrotaxus* and *Pseudotaxus,* but not in *Amentotaxus* and *Taxus* as going to be discussed below. A more or less similar view was expressed by Meeuse (1963,-p. 161).

The ovulate compound strobili of *Cordaites* (figs. 3 & 4) are especially of phylogenetic significance. From this Florin (1938-45, summarized in 1951) has constructed an evolutionary series, through the strobilar structures of such fossil plants as *Lebachia, Ernestiodendron* (fig. 6), *Pseudovoltrda* and *Voltzia,* to the ovulate strobili of the modern conifers (for details see Wilde, 1944, esp. her fig. 8). Essentially, it involves a reduction of an ovulate strobilus of *Cordaitanthus* into an ovuliferous scale of *Pinus,* and the entire spicate compound strobilus of the former into a seemingly simple ovulate strobilus of the latter. This interpretation thus satisfactorily solved the mystery of what Schleiden once called 'folium in axilla folii' (Coulter & Chamberlain 1917, p. 245), namely the insertion of an ovuliferous scale in the axil of a bract.

ON THE SPICATE STAMINATE STROBILUS OF AMENTOTAXUS

One of the most curious living conifers is *Amentotaxus* (Taxaceae) from Eastern Asia (Keng 1969). Its compound staminate strobili are produced within a large winter bud which is borne on the top of the" previous year's branchlets. They are short-stalked, usually four together, subtended by four rows of imbricate bud-scales (figs. 7 & 8).

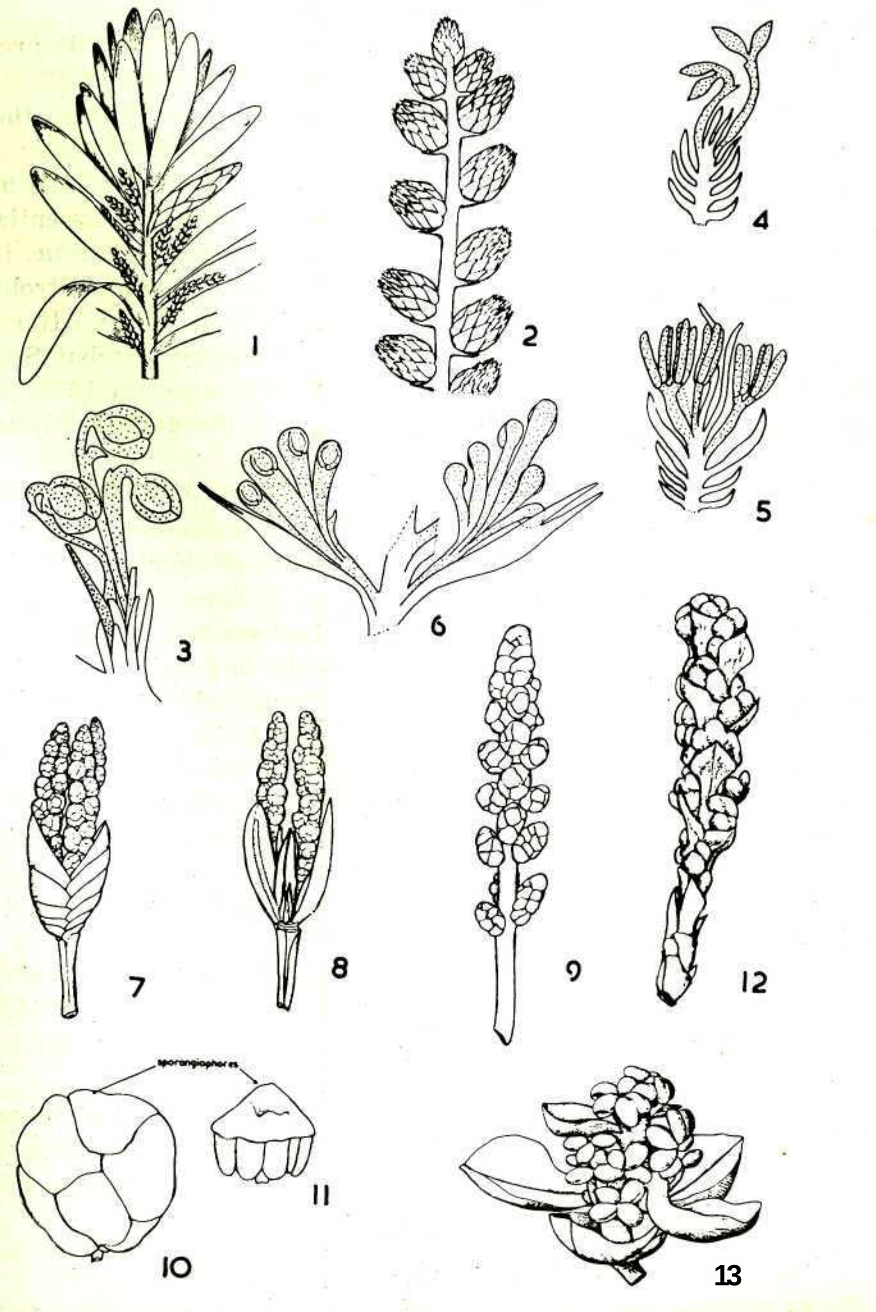
Each compound staminate strobilus is spike-like, when fully expanded it can reach a length of 2.5-3 cm long. It consists of 20-30 staminate strobili, growing along the main axis in four rows (fig. 9).

The globular or ovoid staminate strobilus is composed of 9-12 closely compacted peltate 'microsporangiophores' with four or five microsporangia hanging underneath in a semi-circle and with a short stalk near the centre (figs. 10 & 11). Although no trace of the bracts subtending the microsporangiophores was found at the base of the stalk in *Amentotaxus,* prominent bracts subtending the peltate microsporangiophores, however, were reported from *Austrotaxus* (Saxton 1934, Wilde 1975) (fig. 12) and *Pseudotaxus* (= *Nothotaxus,* Florin 1948, Wilde 1975) (fig. 13).

Because of the homology of the sporangiophores of these taxad genera, it was postulated that in ancestral form, each peltate sporangiophore of *Taxus* (Saxton 1934, p. 422) and *Amentotaxus* (Keng **1969, p.** 44) is likely subtended by a leafy bract.

DISCUSSION AND CONCLUSION

Florin (1951), in his excellent essay on evolution in *Cordaites* and conifers, included a special chapter to discuss on the application of the telome theory to explain the reproductive structures. But somehow, he



FIGS. 1-13. 1. Foliage branch of *Cordaites* bearing many spicate, compound strobili. — 2. Part of a compound strobilus of Fig. 1, showing a number of strobili arranged in two rows. — 3, Ovulate strobilus of *Cordaitanthus pseudofluitans.* — 4. Longitudinal

devoted most part of his treatise in elucidating the telome theory *per se*, rather than its application to explain the reproductive structures of *Cordaites* and conifers.

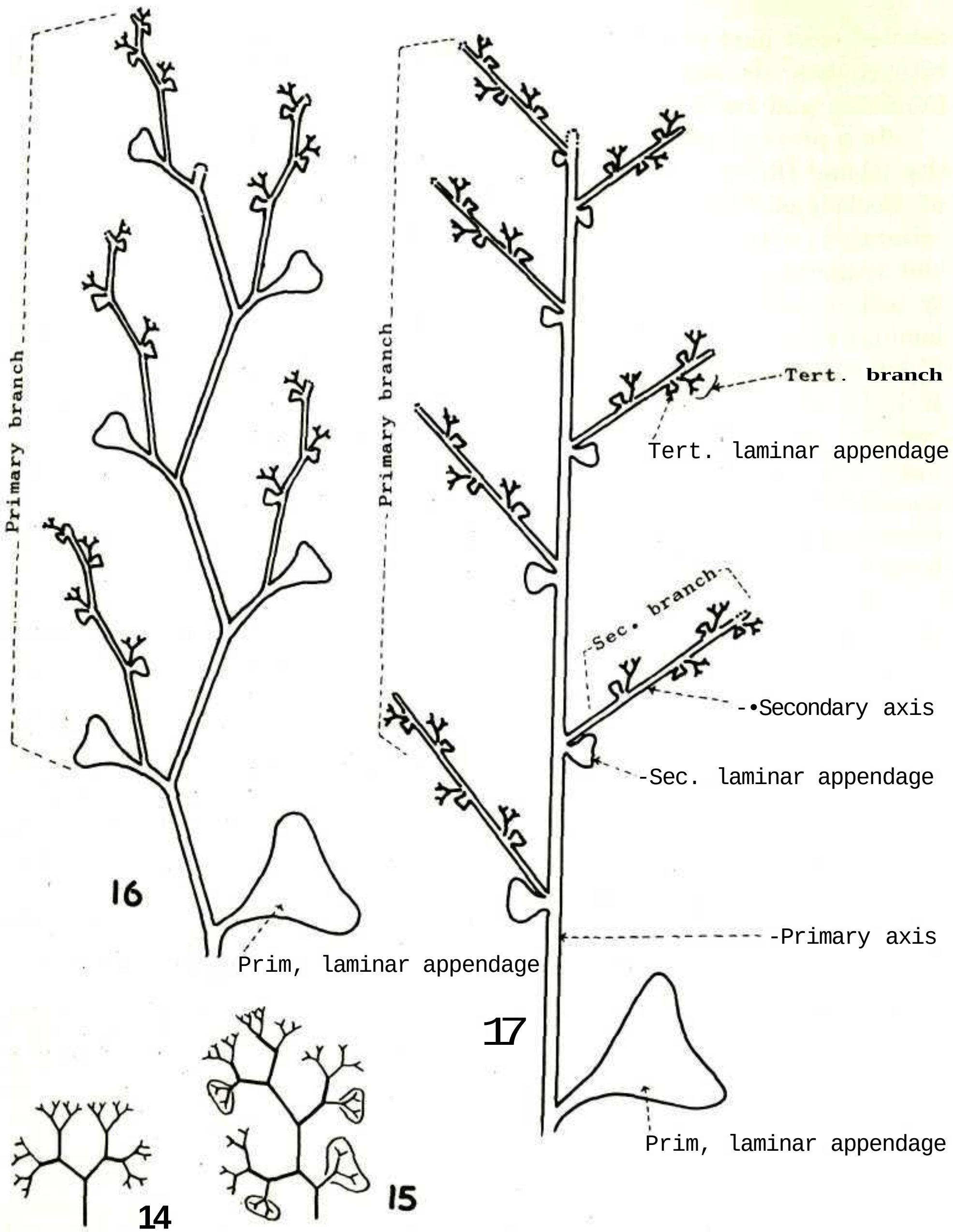
In a previous paper, as mentioned earlier, the present writer applied the telome theory to explain the complicated structure of the pinnate phylloclade of *Phyllocladus* (Keng 1974). The hypothesis can be briefly reiterated as follows (figs. 14-17). Through the processes of overtopping and syngenesis (or webbing), the lower half of the dichotomous branch system organizes into a leafy structure which is labelled as primary laminar appendage in fig. 17, the upper half retains its ability for further dichotomizing, and from which the primary branch is eventually formed. It is by the same procedure, that part of the remaining dichotomous systems, again through overtopping and syngenesis, organizes into a leafy structure, and part maintains its ability for further dichotomizing. Consequently, laminar appendages and branches (fertile, sterile or fertile/sterile) of secondary and tertiary (or even quaternary and so forth) degrees can be constructed in succession.

It is conceivable that the compound strobilar structures of *Cordaites* and conifers probably can also be constituted by the same procedure as hypothesized above. Adhering to this reasoning, the following plausible homologies can thus be established (figs. 18-28).

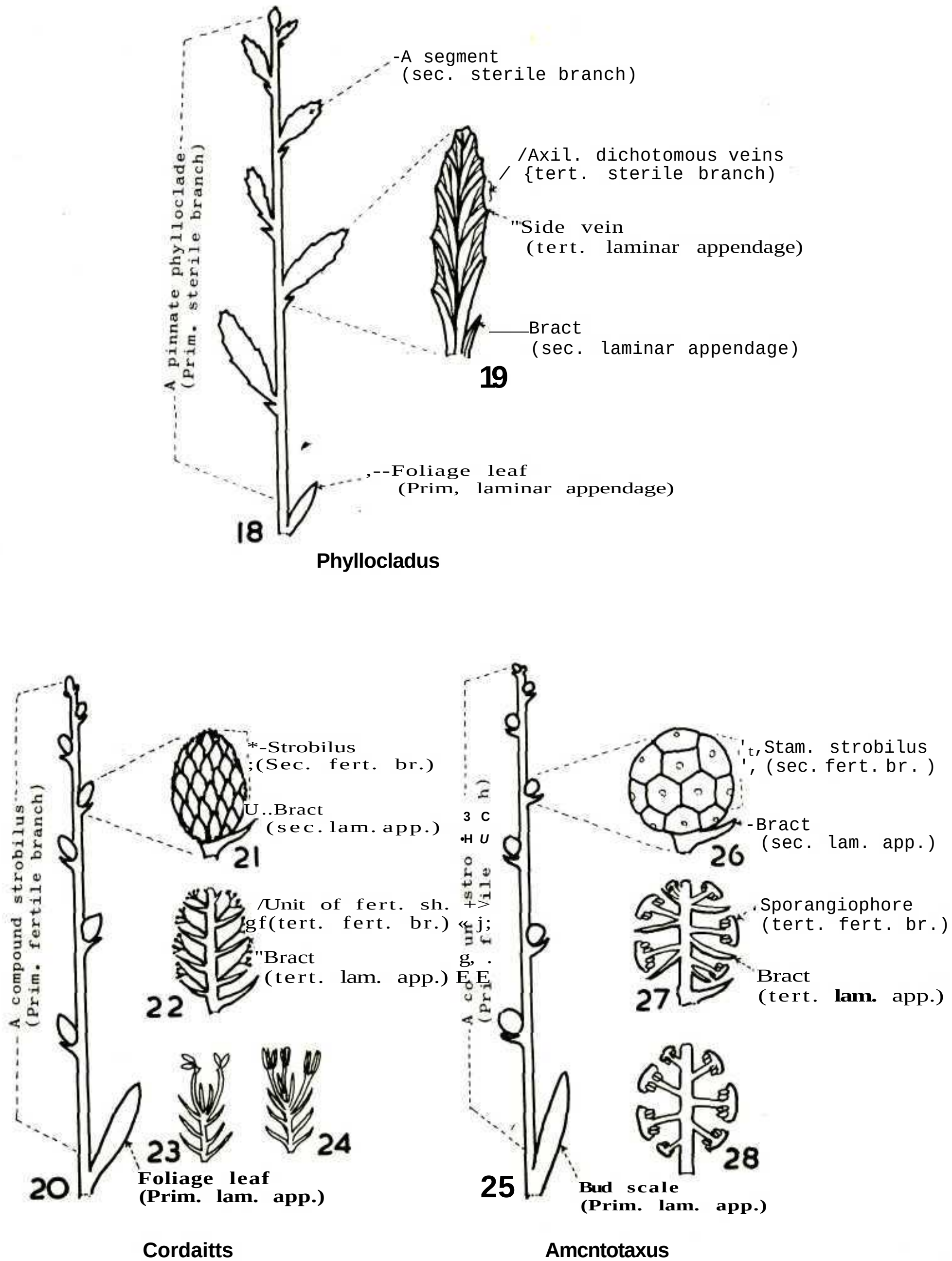
(1) It is suggested that the so-called foliage leaves of *Phyllocladus* and of *Cordaites*, and the bud-scales of *Amentotaxus* are probably homologous to the primary laminar appendages and that the pinnate phylloclade is probably homologous to the primary sterile branch, the compound strobili of *Cordaites* and *Amentotaxus*, and the primary fertile branches respectively (figs. 18, 20 & 25).

(2) It is also suggested that the segment of a pinnate phylloclade of *Phyllocladus*, the ovulate and staminate strobili of *Cordaitanthus*, and

section of a young ovulate strobilus of *C. pseudofluitans.* — 5. Longitudinal section of a staminate strobilus of *C. penjoni.* — 6. Two ovulate strobili (from the median of a compound strobilus) of *Walchistrobus (Ernestiodcndron)* sp. — 7. External view of an unfolded winter bud of *Amentotaxus formosana*, showing a cluster of four (one is not seen) compound staminate strobili. — 8. The same, with half of the bud scales and two of the compound staminate strobili removed. — 9. Compound staminate strobilus showing a member of ovoid to globular staminate strobili arranged on an axis. — 10. Staminate strobilus (taken from the median of fig. 9), enlarged. — 11. Sporangiophore. — 12. Staminate strobilus of *Austrotaxus spicata*, showing each sporangiophore subtended by a bract. — 13. Staminate strobilus of *Pseudotaxus (Nothotaxus) chienii*, showing each of the sporangiophore subtended by a prominent bract. (Fig. 1, originally by Grand'Eury, redrawn from Arnold 1947; Fig. 2, originally by Fry, from Banks 1970; Fig. 3, from Florin 1951; Figs. 4 & 5, from Wilde 1944; Fig. 6, from Florin 1951; Figs. 7-11, from Keng 1969, Fig. 12, from Saxton 1934; Fig. 13, from Florin 1948).



FIGS. 14-17. Diagrammatic representation of the hypothetical steps from an open dichotomous system (fig. 14), through overtopping and webbing (fig. 15), to the formation of laminar appendages and branches (figs. 16 & 17) (Based on Keng 1969).



FIGS. 18-28. Comparison of a pinnate phylloclade of *Phyllocladus* with (1) compound strobili (both ovulate and staminate) of *Cordaitanthus* and (2) compound staminate strobilus of *Amentotaxus*. (All highly diagrammatic).

the staminate strobilus of *Amentotaxus* (figs. 19, 21 & 26) are probably homologous to the secondary branches (of which the first one is sterile, and the others, fertile), and that these structures are subtended a bract which is homologous to a secondary laminar appendage.

(3) It is further suggested that the open dichotomous vein-systems in the axils of side veins in a segment of *Phylhcladus*, the ultimate units of fertile shoot of *Cordaitwnthus**, and the sporangiophores of *Amentotaxus* (figs. 19, 22, 23, 24, 27 & 28), are probably homologous to the tertiary branches, fertile and sterile, which again are subtended by the tertiary laminar appendages, known as bracts or the like.

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*It must be stressed here that in the case of an ovulate strobilus, the terminal structure on the ultimate'units of fertile shoots (figs. 3, 4 & 23) are ovules, *not* sporangia. A. succinct discussion on the telomic concept and the nature of the integument by Andrews (1961, pp. 372-375)'should be consulted.

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THREE NEW MALESIAN SPECIES OF GRAMINEAE

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ABSTRACT

Illustrated descriptions of three new Malesian species *(Racemobambos ceramica* S. Dransfield, *Nastus schmutzii* S. Dransfield and *Cymbopogon minutiflorus* S. Dransfield) are presented. *R. ceramica* is compared with *R. schultzei* (Pilger) Holttum, and *N. schmutzii* with *N. reholttumianus* S. Soenarko. *N. reholttumianus*, so far found only in the island of Sumba, is recorded also as occurring in Flores. *C. minutiflorus* is the first representative of the genus in Sulawesi.

ABSTRAK

Pertelaan bergambar tiga buah jenis baru suku rumput-rumputan dari Malesia disajikan. Jenis-jenis tersebut ialah *Racemobambos ceramica* S. Dransfield, *Nastus schmutzii* S. Dransfield dan *Cymbopogon minutiflorus* S. Dransfield. *R. ceramica* dibandingkan dengan *R. schultzei* (Pilger) Holttum, sedang *N. schmutzii* dengan *N. reholttumianus* S. Soenarko. *N. reholttumianus* yang dilaporkan terdapat di Sumba, ditemukan pula di Flores. *C. minutiflorus* merupakan jenis pertama daripada marga *Cymbopogon* di Sulawesi.

RACEMOBAMBOS Holttum

In the island of Seram, Rutten collected a bamboo characterized by its panicle with multiflorus spikelets and climbing culms. It belongs to *Racemobambos* and can be distinguished from the recognized species of the genus by its long, open and spreading panicle and hairy inflorescence axis. The species, here regarded as new, is very closely related to *R. schultzei* (Pilger) Holttum, which occurs in Japen Isl. (Holttum **1967).** It differs from *R. schultzei* in several respects, compared below

	schultzei	*ceramica*
spikelet	more or less sessile, with swollen base	pedicellate, pedicel 4.5 mm long, base not swollen
lemma	10 mm long	7 — 8.5 mm long
lodicules	minutely puberulous	glabrous
main axis and branches of inflorescence	glabrous	puberulous

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CONTENTS

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