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VESTURED PITS OF COMBRETACEAE AND ALLIED FAMILIES

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SUMMARY

The structural variation of vestures in bordered pits, with special reference to Combretaceae, is described and classified. Two major types of vesturing are recognized: Type A, in which the vestures are attached to all parts of the roof of the pit chamber and branch into a mass of vestures of equal thickness; and type B, in which vestures with a trunk-like base are attached to the roof of the pit chamber near by the pit canal, and branch to various extents into thinner vestures. In type B three forms are recognized, based on the degree of branching of the vestures, and on the relative thickness of the trunks (cf. *fig. 1*). The diagnostic and systematic value of the major forms is restricted because of the occurrence of intermediates between them and because of infrageneric variation in *Terminalia*. However, the major types of vesturing follow the subfamily classification of the Combretaceae: type A in Strephonematoideae and type B in Combretoideae.

The variation in structure and distribution of warts and vestures is described and discussed. Morphological intermediates are suggestive of a homology of warts and vestures, contrary to conclusions based on limited ontogenetic research in the literature. The differences in wart development and vestures around the apertures in different vessel contact areas (inter-vessel, vessel-ray, and vessel-axial parenchyma) are also described and discussed.

1. INTRODUCTION

Vestured pits have been the subject of several publications (summarized by MEYLAN & BUTTERFIELD 1974; MILLER 1977; OHTANI & ISHIDA 1976) increasing in frequency since ultrastructural research was facilitated by the scanning electron microscope (SEM). They are now on record for a great number of families and are for instance characteristic for most of the families traditionally assigned to the Myrtales (cf. BAILEY 1933; METCALFE & CHALK 1950). Their absence from the Rhizophoraceae even provided an additional argument for reconsidering the taxonomic position of this family (VAN VLIET 1976). As part of an extensive wood anatomical study of the Myrtales, a comprehensive evaluation of the possible taxonomic position of this family (VAN VLIET 1976). As part of an extensive wood and in this paper the vestured pits of 67 species representing all genera of the Combretaceae (except *Meiostemon*) will be the main subject of discussion (for material studied see VAN VLIET, in prep.).

A study of vestured pits can be focussed on various aspects such as: 1. the ontogeny, 2. the development of a useful model for describing and classifying the various structures and subsequently 3. the evaluation of their taxonomic and diagnostic value, 4. their function, and 5. on the problem of how to differentiate

between vestures and warts using their morphology only. The first mentioned aspect is beyond the scope of this comparative study. Only few, partly conflicting data are available (BAIRD et al. 1974; CÔTÉ & DAY 1962; CRONSHAW 1965; SCHMIDT & MACHADO 1964; WARDROP & DAVIES 1962), all indicating strong relationships between vestures and warts. Most of these papers dealt with Gymnosperms, Schmid & Machado and Côté & Day studied a limited number of Angiosperms. According to observations by Schmid & Machado, vestures are formations of the living protoplast, deposited between the plasmalemma and the cell wall. Warts are remnants of the dying protoplast, located between the tonoplast and the plasmalemma. Côté & Day are of the opinion that vestures and warts are of similar nature and may prove to be of common origin. Vestures and warts both react in the same way to chemical treatment (SCURFIELD & SILVA 1970). For their definition only the localisation of the structures involved can be used.

Vestures are mostly branched structures present in, or distinctly associated with any part of a bordered pit (pit chamber, pit canal, pit apertures).

Warts are unbranched structures present on the vessel wall. However, where warts and vestures meet, the distinction is not always easy (sometimes impossible).

For the description of the structure of vestures, several terms have been used: coralloid, papillary, foliate, filamentous (e.g. BAILY 1933; MEYLAN & BUTTERFIELD 1974; SCURFIELD et al. 1974) or simply branched and unbranched (CÔTÉ & DAY 1962). In an earlier paper on Crypteroniaceae (VAN VLIET 1975) I have described the vesturing using their localisation in the bordered pit. OHTANI & ISHIDA (1976) recognized 15 different types, based on the structure of the individual vesture. They thus described vesturing by referring to the combination of types found in a particular pit. from a comparative study of the structural variation of vestures in Myrtalean families such as Combretaceae, Melastomataceae and Myrtaceae, and from data on other families in the literature, the combination of the overall structure of the vesturing and its localisation in the bordered pit prompted me to attempt an alternative classification of bordered, vestured pits. This classification, mainly exemplified by the variation found within the Combretaceae is the subject of this paper.

2. RESULTS AND DISCUSSION

2.1. Vesturing in the pit chamber

In Combretaceae two main types of vesturing can be recognized in the pit chamber.

A. The vestures are attached to all parts of the roof of the pit chamber, and branch into a compact mass of vestures of ± equal thickness, completely filling the pit chamber. Viewed from the pit floor into the pit chamber the result of this branching is a compact mass of bead-like endings of the terminal branches (*figs. 1a, 3–5*).

B. To the roof of the pit chamber, nearby the pit canal, a ring of trunk-like vestures is attached, pointing into the pit chamber and dichotomizing to various extents into thinner branches; on lower parts of the roof much thinner, partly

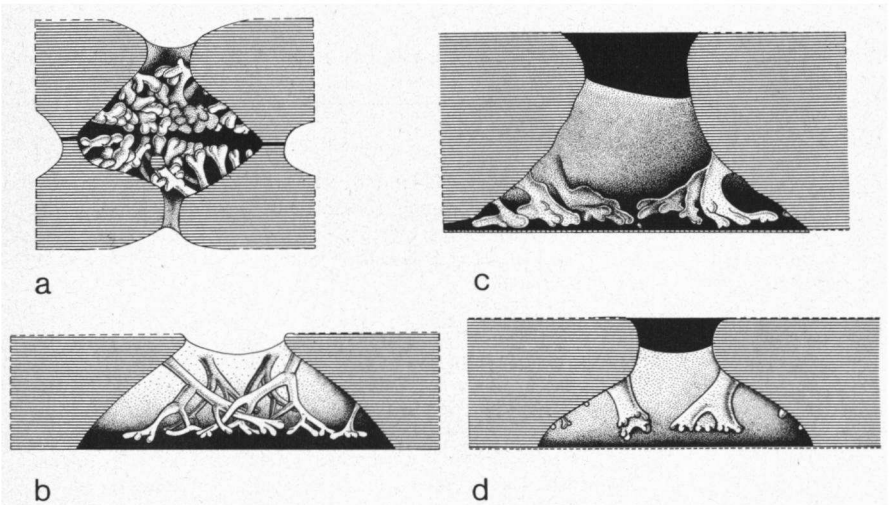


Fig. 1. Drawings of transverse sections of bordered pits, illustrating the different types of vesturing. a. Type A; b. Type B, form 1; c. Type B, form 2; d. Type B, form 3.

branched vestures may be infrequently present in various densities (*figs. 1b–d, 6–8, 12* and *13*). Viewed from the pit floor into the pit chamber the result of this branching is a compact to loose or very open mat of vestures of ± equal thickness (*figs. 9–11*).

On the lowest part of the pit chamber roof a small margin can mostly be observed that is devoid of vestures (*figs. 10* and *11*). This is possibly due to the lack of space in the narrow corner between pit roof and pit floor.

Type A vestures are present in Crypteroniaceae (VAN VLIET 1975), Sonneratiaceae p.p. (*Sonneratia*), Combretaceae p.p., and Melastomataceae. Vestures of type B are found in Myrtaceae, Lythraceae (ZWEYPFENNING & BAAS, in prep.), Punicaceae (BRIDGWATER & BAAS 1978), Melastomataceae (rare), and Sonneratiaceae (*Duabanga*).

When viewed into the pit chamber after removal of the pit floor, certain forms of type B can be very similar to the type A (compare *figs. 4* and *9*). Surface views from the vessel lumina can reveal much of the structure of vestures, but often the aperture is obscured by vestures (*figs. 16* and *17*), or the vessel wall is too thick (hence the pit canal too deep) to allow a good view with the scanning electron microscope. Sections through bordered pits (*figs. 3, 5, 12*) are then necessary for a good recognition of the vesture type.

The structure of the vestures is said to be fairly constant for a given pit type (MEYLAN & BUTTERFIELD 1974; VAN VLIET 1975), although a considerable variation was observed in *Robinia pseudoacacia* by ISHIDA & OHTANI (1970). A more restricted variation, especially in vessel-parenchyma and vessel-ray pits with type B vesturing, was also observed by me.

In pits with slightly or more strongly reduced borders on the vessel side, vestures

Table 1a. Distribution of the types and forms of vesturing in the pit chambers of the genera of the Combretaceae (see also *fig. 1*).

Type A.	Strephonema
Type B, form 2.	Bucida, Calycopteris, Combretum, Finetia, Laguncularia, Quisqualis, Ramatuella, Terminalia p.p., Terminaliopsis.
Type B, intermediate between form 2 & 3.	Calopyxis, Conocarpus, Guiera, Lumnitzera, Macropteranthus, Pteleopsis, Terminalia p.p.
Type B, form 3.	Anogeissus, Buchenavia, Terminalia p.p.

Table 1b. Distribution of the various forms of type B vesturing in the genus *Terminalia*.

Form 2.	T. acuminata, T. arbuscula, T. arjuna, T. bialata, T. brassii, T. catappa, T. chiriquensis, T. complanata, T. copelandii, T. dichotoma, T. edulis, T. impediens, T. ivorensis, T. kilimanscharia, T. laxiflora, T. lucida, T. manii, T. mollis, T. papuana, T. platyphylla, T. reitzii, T. samoensis, T. scutifera, T. sepicana, T. superba.
Intermediate between form 2 & 3.	T. amazonia, T. arostrata, T. brownii, T. chebula, T. glaucescens, T. grandiflora, T. macroptera, T. nitens.
Form 3.	T. burseriana, T. calamansanai, T. porphyrocarpa, T. volucris.

may be absent (see also SCURFIELD & SILVA 1970; MEYLAN & BUTTERFIELD 1974; VAN VLIET 1975) or have a reduced branching (*fig. 13*, top left), sometimes with thinner basal trunks (*fig. 13*, top right). Fully bordered pits with this type of reduced vesturing can sometimes be found in between "normally" vestured pits. Within a single pit the thickness of the basal trunks occasionally varies as well (*fig. 13*, arrows). In spite of this gradual variation, all vessel wall pits of a given wood still show the main type of vesturing, defined above as type B.

When comparing type B vesturing in Combretaceae and Melastomataceae it appeared that within this type, a more substantial variation in the degree of branching and in thickness of the vestures can be classified into three forms.

1. Most of the trunk-like bases of the vestures are only slightly thicker or more or less of the same thickness as the branches, but their arrangement in a ring is distinctly recognizable (*figs. 1b, 6, 7*); viewed from the pit floor a closed to open mat of coarse to fine branch-endings is visible. This form is not represented in Combretaceae and of infrequent occurrence in Melastomataceae.

2. Most of the trunks are thick and elaborately branch into thin vestures. From the pit floor a closed mat of fine branch-endings is visible (*figs. 1c, 8, 9*).

3. The trunk-like vestures are hardly branched, viewed from the pit floor the trunk-ends bear knobs in stead of distinct branches (*figs. 1d, 11*).

Intermediates between these forms are rather common (*fig. 12*). The first form may be interpreted as an intermediate towards type A.

2.2. Taxonomic and diagnostic value

The distribution of types and forms in Combretaceae is listed in *table 1a*. From this table the impression could be obtained that the various forms are of diagnostic value on the generic level. However, the fact that in *Terminalia* two forms of type B and their intermediates are present indicates that variation within the genus occurs as well. Of the latter genus 37 species (of one, *Terminalia catappa*, 5 samples) were studied and the infra-generic variation is recorded in *table 1b*. Such considerable variation was found in *Terminalia* only. In other genera of which more than one species (*Anogeissus*, 3; *Buchenavia*, 2; *Conocarpus*, 2; *Combretum*, 6; *Pteleopsis*, 2; *Ramatuella*, 12) or more than one sample (*Macropteranthus*, 2; *Strephonema*, 2) was studied, no such variation was found.

One possible interpretation of the diversity in *Terminalia* can be that it would make the use of the forms of type B vesturing of little diagnostic value at the generic level, leaving only the main types suitable for such a purpose. *Terminalia*, however, is very variable in many of its wood anatomical characters covering much of the wood anatomical variation in the whole family Combretaceae (VAN VLIET, in prep.) and the variation in type of vesturing is no exception. No correlation could be traced between vestured pit variation and variation in other wood anatomical characters. It was also impossible to match the different forms of vesturing in *Terminalia* with subgeneric classification since a subdivision of the genus based on a comprehensive revision is not available.

From the presence of several intermediates no important diagnostic or taxonomic significance of the different forms of vesturing in *Terminalia* can be anticipated.

A similar conclusion must be drawn when the distribution of the forms of type B vesturing over the genera is compared with the supra-generic classification of the subfamily Combretoideae by EXELL & STACE (1966).

In Lythraceae (ZWEYPFENNING & BAAS, in prep.) the variation in the type B vesturing is equally evident, but variation within a genus has not been encountered. The occurrence of type A and type B vesturing in Combretaceae follows its subdivision into two subfamilies: the Strephonematoideae (with type A) and the Combretoideae (with type B).

It is possible to arrange the structural types and forms of vesturing described above into a gradual series going from type A, via type B 1 to type B 3 (see *fig. 1*). The absence of a correlation with structural variation of other wood anatomical characters does not allow any phylogenetic interpretation of this series for Myrtales as a whole. The apparently independent occurrence of vestured pits in unrelated groups like Leguminosae, Myrtales or even in Gnetales p.p. (PARAMESWARAN & LIESE 1974) suggesting a polyphyletic origin of vestured pits, does not allow a comparison of structural variation in any of these groups with that found in Myrtales.

2.3. Vestures on pit apertures and warts

Vestures can also be found on the pit aperture, sometimes completely obscuring the latter and often spreading onto the vessel wall (*figs. 16, 17*, also present in

several genera of Melastomataceae and Myrtaceae; cf. BUTTERFIELD & MEYLAN 1974a; OHTANI & ISHIDA 1976; SCURFIELD et al. 1970; VAN VLIET 1975) and I frequently found that this type of vesturing was much more abundant over vessel-parenchyma than over vessel-ray pit contacts. The presence of vestures on inter-vessel pit apertures or vessel-fibre pit apertures is independent from the occurrence of similar structures over vessel-parenchyma and vessel-ray pits. Infrequently some pit apertures may be free of vesturing (compare *figs. 18* and *19*). Differences in type of vesturing, reported by SCURFIELD et al. (1970) are very probably due to different pit contacts. Up to this point the distinction between warts and vestures as defined in the introduction is still valid. However, in *Marumia* (Melastomataceae) the vestures of the apertures in part of the elements have completely (*fig. 21*) but in other elements only partly (*fig. 20*) colonized the vessel wall and they do not clearly fit the definition "associated with any part of a bordered pit". Similar situations were also observed by BAILEY (1933, see *fig. 2b*), SCHMID & MACHADO (1964) and OHTANI & ISHIDA (1976). The elaborately illustrated examples in the latter paper show a variation that is similar to what I observed in *Marumia*. In all these cases the structures present on the walls were distinctly branched and therefore they can still be easily recognized as vestures.

Warts are knob-like structures on the vessel wall, rarely they can also be found in the pit chamber (see also MEYLAN & BUTTERFIELD 1974). They can be present in various densities (compare *fig. 17–19*) and be absent from one vessel element yet frequent in the next, or present on parts of the wall of a single element only. Warts can sometimes be found on apertures of vessel pits, giving the impression of small unbranched vestures and these are often slightly larger and more abundant than those on the vessel walls (*figs. 8, 13*). Their presence may (*fig. 18*) or may not result in a more abundant covering of pit apertures. Sometimes it is not possible to differentiate between vestures on the pit apertures and warts on the vessel wall (*fig. 17*). This strong resemblence in structure and sometimes in distribution indicates a possible homology between vestures and warts, which is more convincingly substantiated by observations in another *Marumia* sample. Here delicate wall thickenings on part of the vessel wall bear slightly branched structures which, when abundant on the vessel wall, are also found on pit apertures; thus combining features of vestures and warts.

2.4. Vestures in fibres

Vestures which are present in distinctly bordered fibre pits are not or slightly branched (*fig. 22*, see also VAN VLIET 1975; MEYLAN & BUTTERFIELD 1974). They are also found on fibre pit apertures (MEYLAN & BUTTERFIELD 1974). In minutely bordered fibre pits (diameter up to 3 μm) vestures are as far as I know never present.

2.5. Vestures on perforation plates

Vestures on perforation plates have not often been recorded. They have until now been found in Rubiaceae, Onagraceae (KUČERA et al. 1977), and Myrtaceae (BAAS

1977; BUTTERFIELD & MEYLAN 1974b; VAN VLIET, in prep.) on both simple and multiple perforation plates. They were not observed by me in Combretaceae and Melastomataceae.

2.6. Light microscopical observations

The various types and forms I have recognized in the morphology of vestures are based on observations using a scanning electron microscope. For light microscopy thin sections ($\pm$ 7 μm) are needed, as shown by BAILEY (1933), from which paper the drawing of the vesturing in *Combretum* (*fig. 2a*; similar to my observations) is presented here. In thicker slides, commonly used by wood anatomists (20–30 μm thick) these structural variations cannot be recognized. Only the thick trunklike bases of type B (form 2 or 3) can sonetimes be observed as apparent,

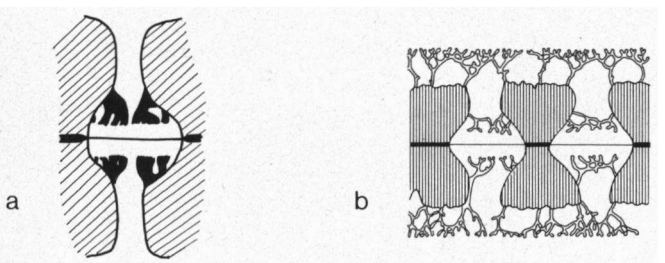


Fig. 2. Light microscopy drawings of vesturing, both from: BAILEY 1933.
a. Transverse section of a bordered pit, illustrating Type B vesturing of Combretum. b. Transverse section of a bordered pit, illustrating vesturing in the pit chamber (Type A) and on the vessel wall.

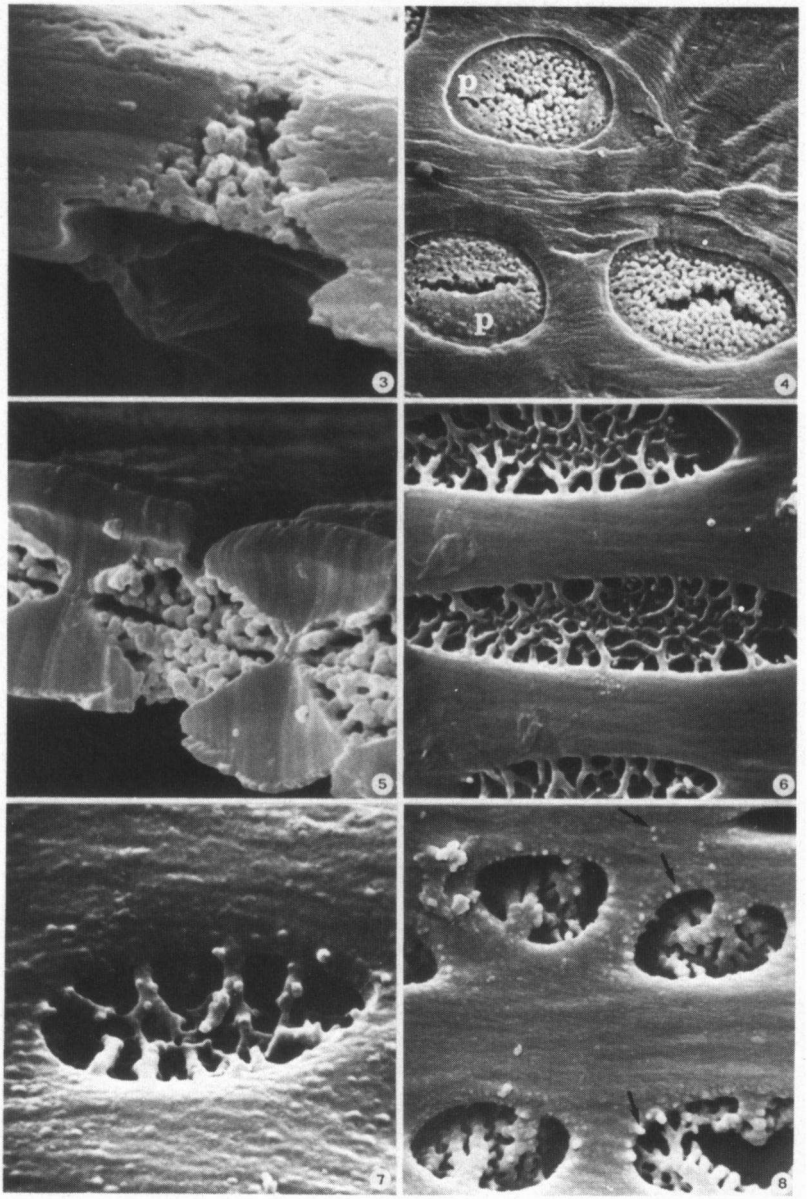
small outgrowths of the pit apertures, provided that these are wide and the staining deep enough. CARLQUIST's tentative conclusion (1977) based on light microscopic studies that the pit apertures in Penaeaceae are warted, is therefore probably incorrect, and it seems more likely that the Penaeaceae have type B vestures to their vessel wall pits, resulting in the light microscopic image referred to above.

2.7. Function

The function of vestures in bordered pits has recently been the subject of a paper by ZWEYPFENNING (1978). He suggested that they may play a role in decreasing the risk of pit membrane rupture, caused by pressure drops between vessel elements, arising from local air embolism.

3. CONCLUSION

In the introduction I have defined vestures as mostly branched structures distinctly associated with bordered pits, and warts as unbranched structures on the vessel walls. In many woods these definitions can be applied easily, although the unbranched vestures present in bordered fibre pits do not entirely fit these definitions. However, the exceptions mentioned in the previous part on "vestures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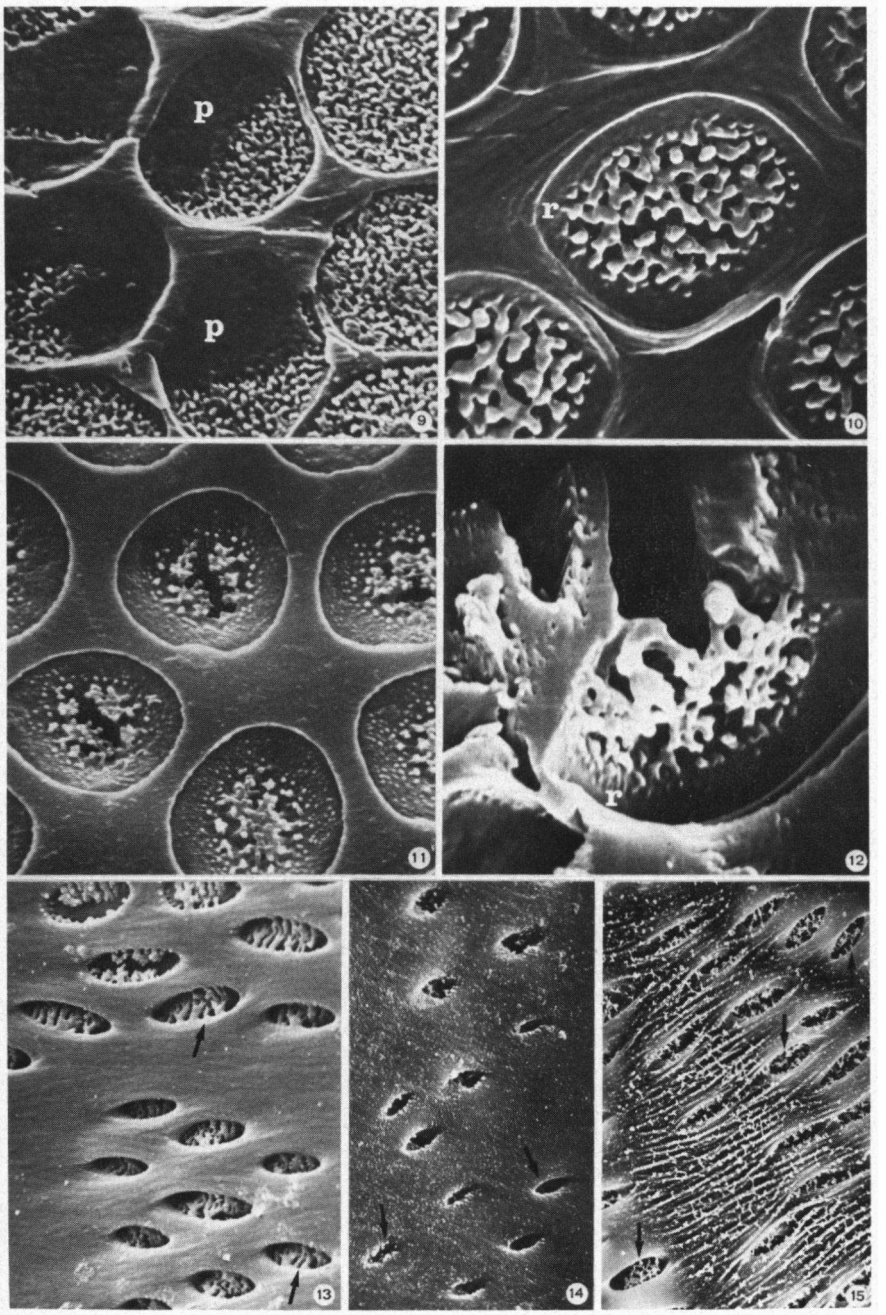
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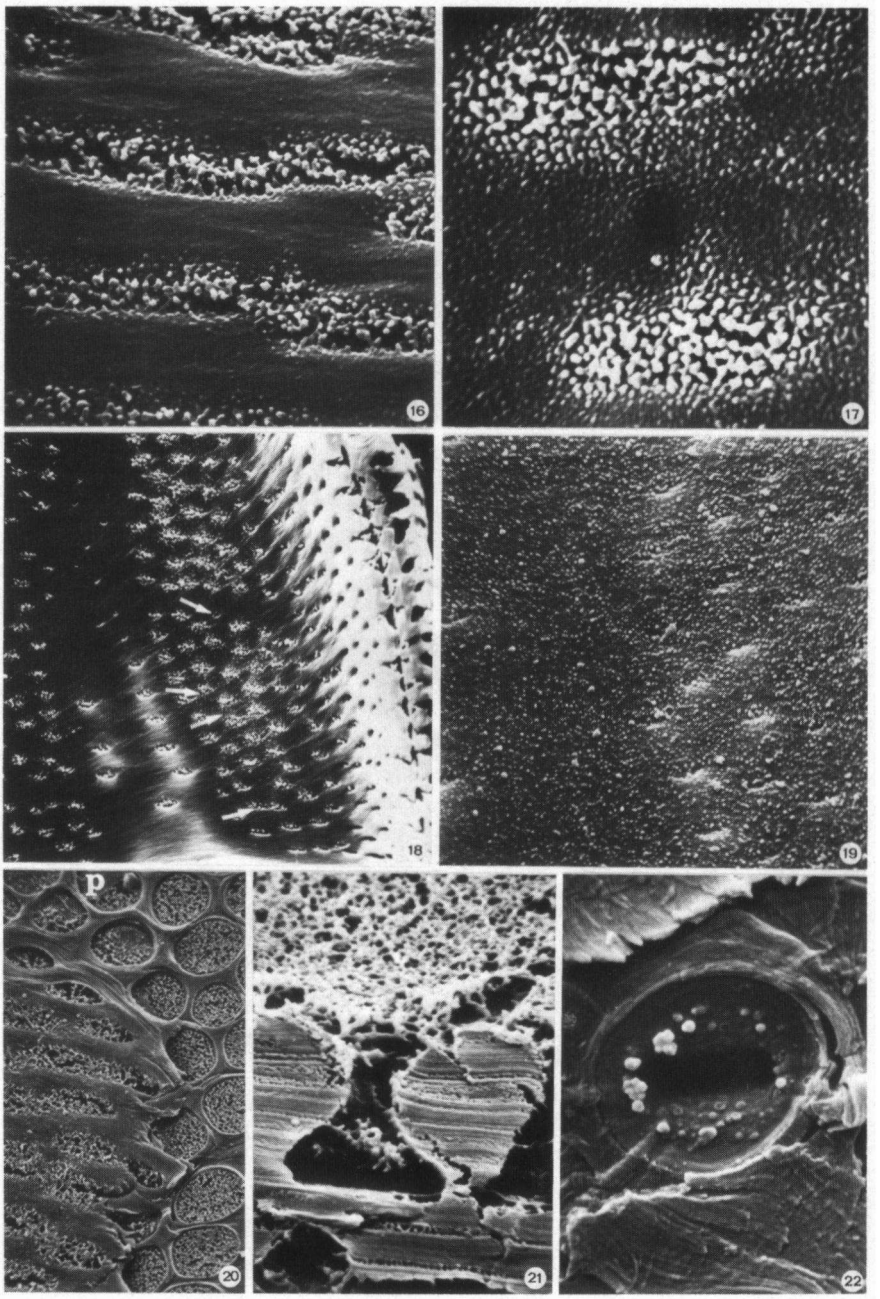
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Fig. 3 & 4. *Strephonema pseudocola* (Combret.)
Fig. 3. Section of vessel-parenchyma pit, vesturing of type A. × 7600.
Fig. 4. Vessel-ray pits; ray cell wall and part of the pit floor (p) removed. × 3400.
Fig. 5. *Medinilla crassinerva* (Melastom.). Section of intervessel pit showing type A vesturing. × 8000.
Fig. 6. *Dissotis arborescens* (Melastom.). Surface view of vessel-parenchyma pits; vesturing type B, form 1. × 4300.
Fig. 7. *Dichaetanthera rhodesiensis* (Melastom.). Surface view of inter-vessel pit; vesturing type B, form 1. × 8000.
Fig. 8. *Terminalia chiriquensis* (Combret.). Vessel-ray pits viewed from the vessel lumen side; vesturing type B, form 2, the pit floor is visible; note the occurrence of warts on vessel wall and on pit aperture (arrows). × 3900.
Fig. 9. *Combretum kraussii* (Combret.). Inter-vessel pits viewed into the pit chamber after removal of the pit floor (p), showing a compact mass of small branch-endings; vesturing type B, form 2. × 4000.
Fig. 10. *Lumnitzera littorea* (Combret.). Inter-vessel pits viewed from the pit floor, showing an open mat of vesturing (type B, form 2–3). Note the very small vestures (warts?) on the lowest part of the pit chamber roof, and the rim (r) which is free of vestures. × 7000.
Fig. 11, *Terminalia volucris* (Combret.). Inter-vessel pits viewed from the pit floor, vesturing type B, form 3. × 3300.
Fig. 12. *Pteleopsis hylodendron* (Combret.). Oblique section through vessel-parenchyma pit, pit floor removed; vesturing type B, form 2–3. × 7600.
Fig. 13. *Terminalia chiriquensis* (Combret.). Vessel-ray pits viewed from the vessel lumen, vesturing type B. Note the strongly reduced branching in pits with slightly reduced borders (top left), the reduction in thickness of some basal trunks (top right) and the incidental occurrence of one of two branches with thin basal trunks (arrows). × 1700.
Fig. 14. *Guiera senegalensis* (Combret.). vessel wall surface with frequent warts, which are irregularly present on pit apertures (arrows). × 1700.
Fig. 15. *Marumia* sp. (Melastom.). Vessel-parenchyma pits, vessel walls with delicate thickenings bearing unbranched and branched warts (or vestures?) which are of variable occurrence on pit apertures.

Fig. 16 & 17. *Lumnitzera littorea* (Combret.).
Fig. 16. Vessel-ray pits; vestures restricted to the coalescent pit apertures. × 5800.
Fig. 17. Vessel-parenchyma pits, vestures completely covering the aperture and continuous with the warty layer on the vessel wall. × 5900.
Fig, 18 & 19. *Quisqualis latialata* (Combret.).
Fig. 18. Vessel-parenchyma and vessel-fibre pits showing variation in abundance of vestures on pit apertures (arrows), partly in association with more abundant warts on vessel wall parts (arrows centre right). × 450.
Fig. 19. Vessel-parenchyma pits with distinct vesturing, although the vessel wall is heavily warted. × 850.
Fig. 20 & 21. *Marumia nemorosa* (Melastom.).
Fig. 20. Inter-vessel pits; vessel wall and pit floor (p) partly (top) or completely (right) removed. Vestures on pit apertures spreading onto the vessel wall, partly continuing with those of neighbouring pit apertures. Vesturing of type A. × 500.
Fig. 21. Vestures inserted on vessel wall and pit apertures, completely covering the former, vestures not present in the pit canal. Inter-vessel pits; vesturing type A. × 4000.
Fig. 22. *Strephonema pseudocola* (Combret.). Fibre pit, vestures not or weakly (left) branched. × 4200.

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and warts" suggest a close similarity between vestures and warts. This suggestion contradicts conclusions in the literature based on limited ontogenetic research (SCHMID & MACHADO 1964) and hence invites detailed ontogenetic and ultrastruc-

tural research on carefully selected genera (like *Marumia*).

The various types and forms of vesturing in the pit chamber, as found in Myrtales rarely follow any taxonomic classification. Only in Combretaceae the distribution of the main types was in agreement with a subfamily classification. The diagnostic and taxonomic value of the types and forms is also restricted because of the occurrence of frequent intermediates and because of infrageneric variation (in *Terminalia*), and must therefore, as holds true for so many other wood anatomical characters, be evaluated for each taxon seperately.

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