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STOMATAL TYPES IN ICACINACEAE. ADDITIONAL OBSERVATIONS ON GENERA OUTSIDE MALESIA

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SUMMARY

The stomatal types of most Icacinaceous genera (28) outside Malesia are reported for a limited number of species. In addition to the stomatal types recognized in Malesian Icacinaceae in an earlier paper, complex cyclocytic stomata are recorded in some genera, notably *Leretia*, for the first time. A fairly comprehensive survey of the genus *Citronella* indicates some trends of differentiation between the Asiatic and Pacific species and the American and Australian species. The results are further discussed with reference to previous hypotheses on level of specialization and stomatal types.

1. INTRODUCTION

In a recent paper the epidermal characters in 109 species of Malesian Icacinaceae and in the genus *Pennantia* from Australia and New Zealand were described in detail (VAN STAVEREN & BAAS 1973). A great diversity in stomatal types was encountered within this part of the family, including paracytic, anomocytic, cyclocytic, anisocytic, helicocytic, and several intermediate types. In comparing the distribution of stomatal types over the different genera with the specialization levels in wood and nodal anatomy (BAILEY & HOWARD 1941) and in pollen morphology (LOBREAU-CALLEN 1973), it was moreover found that the paracytic and anomocytic types are restricted to genera with a low specialization level, that the anisocytic type is restricted to genera with an intermediate specialization level, and that the cyclocytic type is mainly found in the most specialized genera. These results were considered to be indicative of the paracytic and anomocytic stomata being primitive for the family and the other types being more derived.

In this paper the stomatal type for 28 genera from outside Malesia and for most of the American and Pacific species of *Citronella* (also occurring in Malesia) is reported. Although the number of specimens and species studied was very limited, these additional results afford a comparison with the data on Malesian genera and are a test case for our suggestions about stomatal specialization.

2. MATERIALS AND METHODS

Techniques employed are the same as described elsewhere (VAN STAVEREN & BAAS 1973). In addition to cuticular macerations it was frequently necessary to use free-hand sections, because the cuticular anticlinal flanges were not always sufficiently distinct for determining the stomatal types. Herbarium material used is mainly from the Rijksherbarium, unless indicated as obtained from Kew (K) or Utrecht (U) in *table 1*.

3. RESULTS

The results are presented in *table 1*. The specialization level according to Bailey & Howard and Lobreau-Callen is indicated in roman figures. Group I represents the most primitive condition; group III is the most specialized. Apart from the stomatal type some notes are given on submersion of subsidiary cells below the guard cells and the occurrence of aberrant types. In addition to the types encountered in Malesian taxa (van Staveren & Baas), complex cyclocytic stomata are reported for the first time for Icacinaceae. They are most conspicuous in the monotypic genus *Leretia*, where the guard cells are surrounded by a large number of subsidiary cells. For an explanation and possible derivation of complex cyclocytic stomata see JANSEN & BAAS (1973). New for the family is also the occurrence of paracytic and cyclocytic types within one genus (*Citronella*).

Table 1. Stomatal types in Icacinaceae outside Malesia.

Material studied	Specia-lization level	Stomatal type(s)	Notes
Alsodeiopsis poggei Engl. Zaire, Donis 2742	III	cyclocytic and anisocytic	very rarely also paracytic
A. rowlandii Engl. Zaire, Louis 10595	III	cyclocytic and anisocytic	many arrested stages of stomatal development present
Anisomallon clusiifolium Baill. New Caledonia, Schlechter 15479	I	anomocytic	
Calatola venezuelensis Pittier Venezuela, Steyermark 94755	I	cyclocytic	subsidiary cells not or hardly submersed
Cassinopsis ilicifolium (Hochst.) O.K. S. Africa, Lam & Meeuse 5084	I	cyclocytic	subsidiary cells partly submersed
C. madagascariensis Baill. Madagascar, d'Alleizette s.n.	I	cyclocytic	subsidiary cells not or hardly submersed
Chlamydocarya klaineana Pierre Gabon, Courtet s.n.	III	cyclocytic	subsidiary cells partly submersed
C. thomsoniana Baill. Zaire, Louis 12791	III	cyclocytic	subsidiary cells partly submersed

Material studied	Specia-lization level	Stomatal type(s)	Notes
Citronella, section *(Eu) Citronella*			
C. apogon (Griseb.) Howard Bolivia, Steinbach 8245	I	cyclocytic	subsidiary cells partly submersed
C. costaricensis (Don. Sm.) Howard Venezuela, Bernardi 89	I	cyclocytic	subsidiary cells strongly submersed. Rarely paracytic
C. engleriana (Loes.) Howard Brazil, Brade 16546	I	cyclocytic	subsidiary cells partly submersed
C. gongona (Mart.) Howard Brazil, Hatschbach 357	I	cyclocytic	subsidiary cells partly submersed
C. incarum (Macbr.) Howard Ecuador, Steyermark 54166	I	cyclocytic	subsidiary cells partly submersed
C. megaphylla (Miers) Howard Brazil, Occhioni 3456	I	paracytic to cyclocytic	lateral subsidiary cells with 0 to several division walls perpendicular to the pore
C. mucronata (R. & P.) Don Chile, Junge 1040 and Looser s.n.	I	cyclocytic	subsidiary cells partly submersed. Occasionally tending to complex cyclocytic in Junge 1040
C. paniculata (Mart.) Howard Paraguay, Hassler 11872	I	cyclocytic	subsidiary cells partly submersed
C. toledoi Hashimoto Brazil, Hatschbach & Maguire 16359	I	cyclocytic	subsidiary cells partly submersed. Rarely paracytic
Citronella, section *Eucharissia*			
C. moorei (F. v. M.) Howard Australia, Dunn s.n.	I	anomo- to cyclocytic; a minority paracytic	neighbouring/subsidiary cells not or hardly submersed
C. sarmentosa (Baill.) Howard New Caledonia, Schlechter 15480	I	paracytic	subsidiary cells occasionally subdivided perpendicular to the pore. Rarely cyclocytic
C. smythii (F. v. M.) Howard Australia, Dallachy s.n.	I	anomo- to cyclocytic; a minority paracytic	subsidiary cells not or hardly submersed
C. philippinenesis (Merr.) Howard Philippines, B. S. 33267	I	paracytic	subsidiary cells rarely subdivided (this species was not included by van Staveren & Baas)
C. vitiensis Howard Fiji Isl., MacKee 2843	I	paracytic	subsidiary cells rarely subdivided perpendicular to the pore
Dendrobangia boliviana Rusby Bolivia, Bang 1694	I	cyclocytic; a minority anomocytic	subsidiary cells not submersed, occasionally complex with secondary division walls

Material studied	Specia-lization level	Stomatal type(s)	Notes
Desmostachys brevipes (Engl.) Sleum. Cameroons, Zenker 3086	III	cyclocytic	subsidiary cells partly submersed
D. planchonianus Miers Madagascar, d'Alleizette s.n.	III	cyclocytic and paracytic rarely anisocytic	subsidiary cells partly submersed
D. preussii Engl. Cameroons, Zenker 1393	III	mainly anisocytic, sometimes cyclocytic	subsidiary cells not or hardly submersed
Discophora guianensis Miers Brazil, Herb. Rio de Jan. 116150	II	anisocytic	
Emmotum acuminatum (Benth.) Miers British Guiana, Schomburgk 970	I	cyclocytic to complex cyclocytic	subsidiary cells not or hardly submersed
Grisollea thomassettii Hemsl. Seychelles, Jeffrey 807	II	anisocytic to cyclocytic	subsidiary cells not or hardly submersed
Hosiea sinensis Hemsl. China, Wilson 960 (K)	III	cyclocytic	subsidiary cells partly submersed
Humirianthera duckei Hub. Brazil, Ducke 20623	III	cyclocytic	subsidiary cells partly submersed
Icacina mannii Oliv. Zaire, Robijns 1397	III	cyclocytic	subsidiary cells strongly submersed
Irvingbaileya australis (White) Howard Australia, Brass 20004	II	anisocytic	
Lasianthera africana P. B. Zaire, Toussaint 313	II	anisocytic	
Lavigeria macrocarpa (Oliv.) Pierre Cameroons, Zenker 3537	III	cyclocytic	subsidiary cells partly submersed
Leptaulus daphnoides Benth. Zaire, Jans 1060	II	mainly anisocytic, sometimes cyclocytic	subsidiary cells not or hardly submersed
Leretia cordata Vell. Brazil, Jard. Bot. Rio de Jan. 2389	III	complex cyclocytic	subsidiary cells with many division walls
Mappia mexicana Rob. & Greenm. Mexico, Pringle 6645	III	anomocytic to cyclocytic	neighbouring/subsidiary cells not submersed
M. racemosa Jacq. Jamaica, Eggers 3789	III	anomocytic to cyclocytic or complex cyclocytic	neighbouring/subsidiary cells not or hardly submersed

Material studied	Specia-lization level	Stomatal type(s)	Notes
Metteniusa nucifera (Pittier) Sleum. Venezuela, Steyermark 95924	I	anomocytic to cyclocytic	neighbouring/subsidiary cells not submersed
Oecopetalum mexicanum Greenm. & Thomps. Mexico, Matuda 2437 (K)	I	cyclocytic	subsidiary cells partly submersed
Ottoschulzia cubensis (Wright) Urban Cuba, Ekman 7425 (K)	I	cyclocytic to complex cyclocytic	subsidiary cells not or hardly submersed
Pleurisanthes parviflora (Ducke) Howard Brazil, Krukoff 6954 (U)	III	cyclocytic	subsidiary cells partly submersed
Polycephalium poggei Engl. Zaire, Louis 6682	III	anomocytic to cyclocytic	neighbouring/subsidiary cells not submersed
Poraqueiba guianensis Aublet French Guiana, Oldeman B 675	I	anomocytic to cyclocytic	neighbouring/subsidiary cells not submersed
P. paraensis Ducke Brazil, Burchell 9590	I	anomocytic to cyclocytic	neighbouring/subsidiary cells not submersed
Raphiostylis beninensis (Hook f.) Planch. Zaire, Louis 9524	III	cyclocytic to complex cyclocytic	subsidiary cells not or hardly submersed
R. ferruginea Engl. Cameroons, Zenker 2978	III	cyclocytic to complex cyclocytic	subsidiary cells not or hardly submersed
Stachyanthus zenkeri Engl. Cameroons, Zenker 1093	III	cyclocytic	subsidiary cells partly submersed

4. DISCUSSIONS

4.1. Taxonomic aspects

The stomatal type alone does not provide sufficient arguments for taxonomic discussions on or above the genus level in a family like the Icacinaceae, in which the diversity is so great and in which intermediate types occur in a considerable number of genera. Within the genus *Citronella* there is, however, an interesting diversity, partly correlated with the subdivision into two sections proposed by HOWARD (1942). Howard recognized section *Eucitronella* consisting of New World species and section *Eucharissia* consisting of Old World species. SLEUMER (1971) challenged this subdivision because the distinguishing characters are "rather vague or do not hold" (l.c., p. 4). Of section *Eucitronella* I studied all species except *C. melliodora* and *C. ilicifolia*. In most species the stomata are cyclocytic, with the exception of *C. megaphylla* in which a majority is paracytic with frequent subdivisions perpendicular to the pore in the subsidiary cells, often resulting in a cyclocytic appearance. Of section *Eucharissia* all species have now been studied (see also van Staveren & Baas), and in 7 of the 9 species the stomata are paracytic with occasional to fairly frequent subdivisions parallel to the pore (however, much less frequent than in *C. megaphylla*), and only in the two species from Australia, *C. moorei* and *C. smythii*, the stomata are mainly anomo- to cyclocytic with only few paracytic ones. So, the stomatal type does not absolutely support Howard's subdivision of the genus, but certainly indicates a trend of infrageneric differentiation into three groups of species: American, Australian, and Malesian and Pacific species.

4.2. The stomatal type and level of specialization

All data available on stomatal type and level of specialization in nodal anatomy, wood anatomy and pollen morphology for Icacinaceae are presented diagramatically in *fig. 1.* With the inclusion of extra-Malesian taxa the pattern has become less clear (compare van Staveren & Baas l.c. fig. 27), but the same basic conclusions remain valid: paracytic and anomocytic stomata are restricted to a few genera with low level of specialization; anisocytic stomata are wholly restricted to genera with an intermediate specialization level, and cyclocytic stomata, though of frequent occurrence in genera of all specialization levels, are most frequent in genera with specialization level III. Another interesting phenomenon is the greater homogeneity of levels II and III for stomatal types, and the greater heterogeneity of specialization level I. Genera with specialization level I may have paracytic, anomocytic, cyclocytic or 3 intermediate types. Stomata in genera with specialization level II are cyclocytic, anisocytic, or intermediate, and those in genera of level III are cyclocytic, cyclocytic to paracytic, cyclocytic to anisocytic, or cyclocytic to anomocytic. This could be interpreted by assuming that a similar primitive level of specialization in wood anatomy or pollen morphology is no proof for mutual affinity, but only means that a group of miscellaneous genera has retained this low level of specialization. Similar conclusions must frequently be drawn on the level of families or orders in Dicotyledons as a whole, because primitive wood structure occurs in a great number of unrelated groups. The heterogeneity of the Malesian Icacinaceae of level I is also supported by the diverse types of indumentum (v. Staveren & Baas).

4.3. Scope for further studies

In Malesian Icacinaceae the whole complex of cuticular characters provides a useful tool for the identification of sterile material down to the genus and can be profitably employed in discussions on relationships within the family. Additional studies of Icacinaceae outside Malesia on the same scale still remain necessery and will certainly prove a rewarding extension of this preliminary survey and HEINTZELMANN & HOWARD's (1948) work on hair types and crystals. The leaf epidermides of the genera *Casimirella* and *Natsiatopsis* still remain to

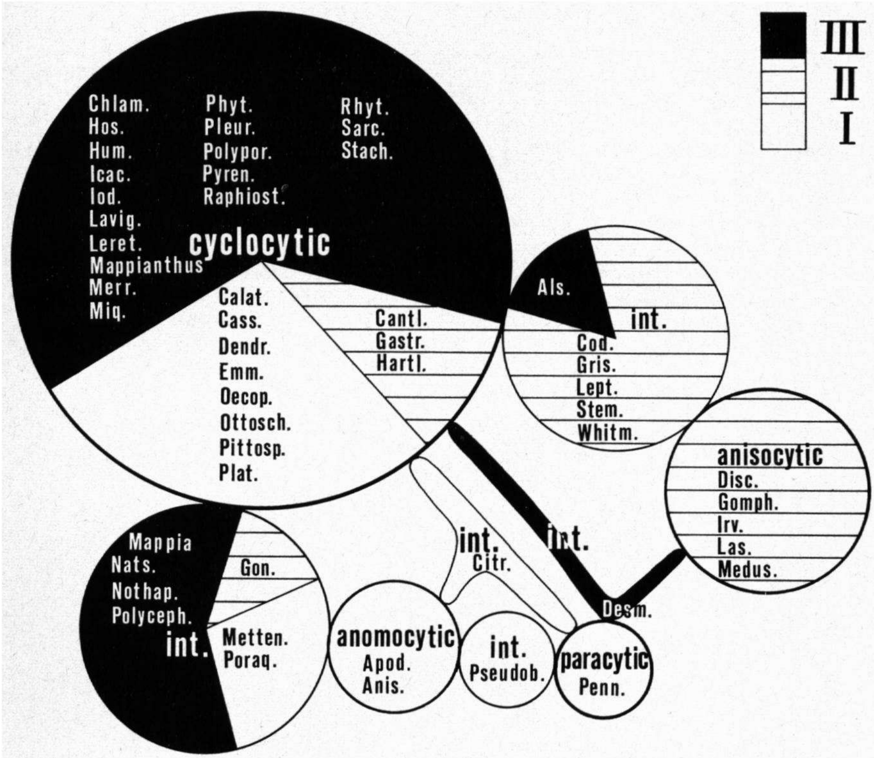

Fig. 1. Stomatal types and level of specialization in wood, node, and pollen in 53 genera of Icacinaceae. The circle with cyclocytic stomata also includes genera with complex cyclocytic stomata; the circle with anisocytic stomata includes taxa with helicocytic stomata. 'Intermediate' (int.) genera may have truly intermediate stomatal types or have species with different stomatal types (e.g. *Citronella, Desmostachys* and *Pseudobotrys*). Names of genera abbreviated.

be studied for their stomatal type as well as other features. Ontogenetic studies are indispensable for a better understanding of the range of variation found in stomatal types and would probably enable us to use stomatal characters more confidently in taxonomic and phylogenetic discussions.

I would like to encourage any taxonomist or anatomist to embark on such studies in Icacinaceae, because they will not be the subject of further research in the Rijksherbarium, with its emphasis on Malesian plants and mature herbarium material.

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