On the Nature of Leaf-opposed Inflorescences in *Aidia cochinchinensis* (Rubiaceae)

WONG KHOON MENG[1] & LIM AH LAN[2]
[1]*Forest Research Institute, Kepong, Malaysia*
[2]*University of Malaya, Kuala Lumpur, Malaysia*

Abstract

Leaf-opposed inflorescences in *Aidia cochinchinensis*, previously ascribed a terminal origin, is here shown to be axillary instead. Hence, the branch system in this species is not sympodial as believed, but a true monopodium along which inflorescences develop from the axils of reduced leaves at alternate nodes, exemplifying a specialised control of floral development.

Introduction

Aidia cochinchinensis Lour., a small tree-species distributed from the north-eastern part of the Indian subcontinent to Malesia, exhibits a specialised morphology in its branches. The flowering cymes develop only at alternate nodes along each branch, on its upper side. Along the branches, alternate leaf-pairs have laterally disposed leaves and the intervening (flowering) nodes have a fully developed leaf from the lower side of the branch, the leaf on the upper side being reduced to a tiny scale which subtends the inflorescence. As such, each inflorescence appears leaf-opposed.

Previous Hypothesis for the Origin of Leaf-opposed Inflorescences

Fagerlind (1943) had characterised *A. cochinchinensis* Lour. (therein as *Randia cochinchinensis* (Lour.) Merr.) as having inflorescences terminating the lateral shoots from which subsequent branch extension is formed by an axillary shoot from the most distal leaf-pair, so that a series of such shoots forms a sympodial branch system (Fig. 1A). It was explained that this inflorescence would subsequently be displaced to the upper side of the branch sympodium by the developing shoot from the final node preceding the inflorescence. The displaced inflorescence thus appears lateral and leaf-opposed because the leaf on the upper side of this final node fails to develop normally. Subsequently, Tirvengadum (1978) has also adopted this explanation for the leaf-opposed inflorescences in this species.

Hallé (1967) has recorded a similar mechanism of branch development in *Schumanniophyton problematicum* (Chev.) Aubr. and *Massularia acuminata* (Benth.) Bullock ex Hoyle; in the former he noted a series of three buds in the leaf axil on the lower side of the branch at the final node preceding the inflorescence. The most distal of these buds then develops to continue sympodial extension of the branch, and Hallé designated the period between two successive flowering nodes as equivalent to one year (Fig. 1B). In other words, the branch system is a sympodium of hapaxanthic modules (Hallé *et al.* 1978).

Evidence for an Axillary Origin of the Inflorescences in *Aidia*

In *A. cochinchinensis*, the origin of the inflorescence is in fact axillary. Several morphological observations lend evidence to this conclusion:-

(a) The branch system is remarkably straight, and during its growth may extend by several internodes and nodes which remain vegetative. In the vegetative state, the current season's branch-extension would be equivalent to a series of successive internodes, and to accept that this is in fact a series of two-internode segments forming a sympodium requires that a whole series of buds terminal to the sympodial segments remain dormant for some time.

(b) Often, an axillary shoot develops on the lower side of the node of leaf reduction, simultaneous with (or even earlier than) the development of the bud from the upper side of the node (which becomes the inflorescence).

An axillary origin of the inflorescence is confirmed by a longitudinal section through the apex of a branch shoot terminated by a node of leaf reduction (Fig. 2). Here, it can be seen that the primordia of the leaf axillary buds (the one subtended by the reduced leaf being destined to form an inflorescence) are already present at an early stage of development, and are distinct from the central terminal bud which develops to continue shoot extension.

At a later stage of development, the central terminal bud extends its growth to form the next node of two normally developed leaves (Fig. 3), while the axillary buds are still dormant. There are no serial buds in leaf axils, as confirmed by sections through nodes of vertical axes and the branches; each leaf axil produces one axillary bud.

On older parts of the branches which have not yet produced inflorescences, longitudinal sections through the potentially flowering (one-leaf) nodes indicate that while there is already a clear and straight continuation of the main vascular cylinder across into the next internode, the inflorescence bud can still remain in a dormant state, not supplied by any clear vascular connection.

The Flowering Habit in *Aidia cochinchinensis*

The branch system in *A. cochinchinensis* is thus a monopodium along which there is leaf reduction at alternate nodes. The dormant bud from the axil of the (reduced) scale leaf, on the upper side of the branch, is destined to develop into an inflorescence. Two modes of flowering behaviour may be seen: either several successive potentially flowering nodes can initially remain vegetative and subsequently flower together, or such nodes can develop inflorescences progressively as branch extension continues. These two modes of behaviour may occur on the same plant, their prevalence seems to depend on the number of internodes added through branch extension during each growing season.

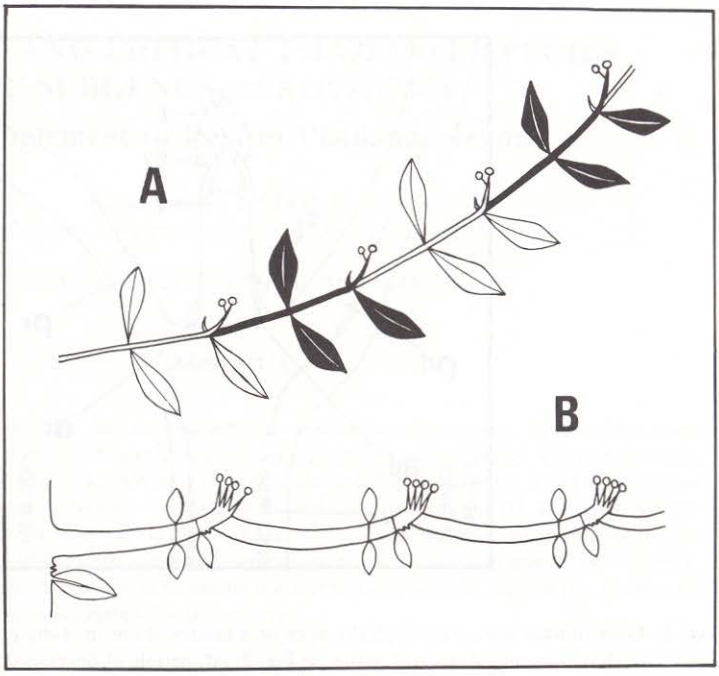

Fig. 1. *A*. Sympodial branch development explained for *Randia* sect. *Gynopachys*, from Fagerlind (1943); he included *R. cochinchinensis* (a synonym of *Aidia cochinchinensis*) in that section. *B*. Sympodial branch development explained for *Schumanniophyton problematicum*, from Hallé (1967); note serial buds in the leaf axils.

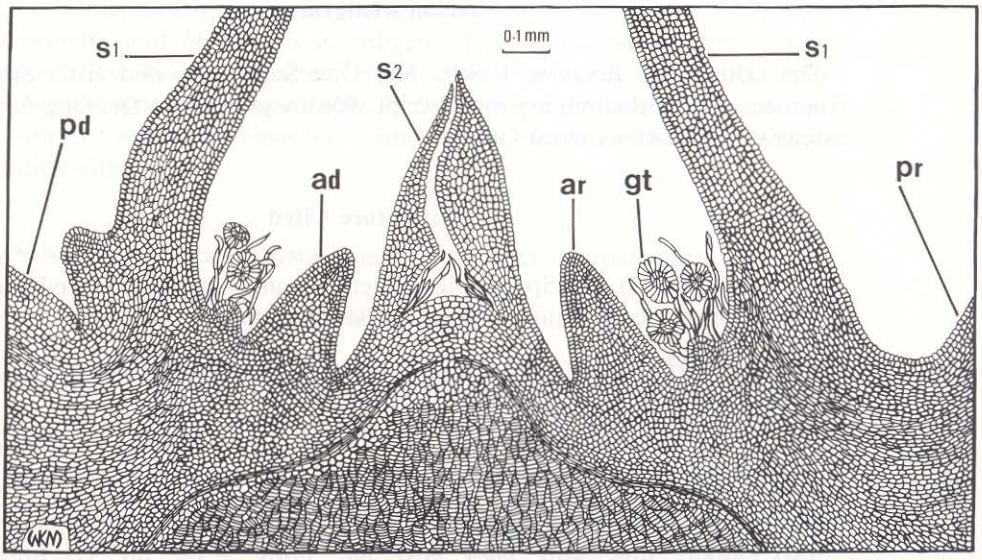

Fig. 2. Longitudinal section through the apex of a branch shoot in *Aidia cochinchinensis*. To the left of the section is the lower side of the branch, where the petiole of the developed leaf (*pd*) is found; to the right is the petiole of the reduced leaf (*pr*), and the stipules corresponding to these leaves are designated by *S1; ad:* axillary bud of developed leaf; *ar:* axillary bud of reduced leaf, which is equivalent to the inflorescence bud; *S2:* stipules corresponding to the next pair of leaves (at right angles to the plane of the section) and which protect the central terminal bud; *gt:* glandular trichomes or colleters found at the inner basal parts of the stipules.

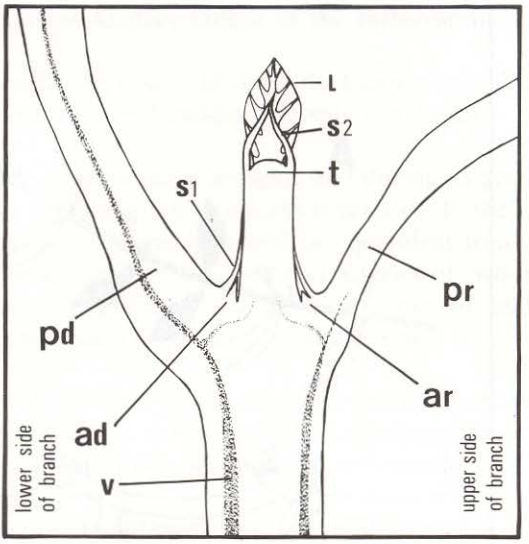

Fig. 3. Longitudinal section through the apex of a branch shoot in *Aidia cochinchinensis*, at the stage of development subsequent to that in Fig. 2. *pd:* petiole of developed leaf; *pr:* petiole of reduced leaf; *S1:* stipules corresponding to *pd* and *pr; ad:* axillary bud of developed leaf; *ar:* axillary bud of reduced leaf (which develops to form the inflorescence); *L:* one leaf from the most distal pair of differentiated leaves; *S2:* stipules corresponding to the most distal pair of differentiated leaves; *t:* terminal bud; *v:* vascular tissue.

Acknowledgements

Drs. Diane M. Bridson, F.S.P. Ng, Ong Siew Ling and B.C. Stone kindly commented on a preliminary manuscript. We are grateful to Dr. Ong for providing extensive translations from German.

Literature Cited

Fagerlind, F. (1943). Die Sprossfolge in der Gattung *Randia* und ihre Bedeutung für die Revision der Gattung. *Arkiv för Botanik* 30A (7): 1–57.

Hallé, F. (1967). Etude biologique et morphologique de la tribu des Gardeniées (Rubiacées). *Mem. ORSTOM*, no. 22.

Hallé, F., R.A.A. Oldeman & P.B. Tomlinson. (1978). *Tropical Trees and Forests: an architectural analysis.* Springer-Verlag, New York; xvii + 441 pp.

Tirvengadum, D.D. (1978). A Synopsis of the Rubiaceae — Gardenieae of Ceylon (Sri Lanka). *Bull. Mus. natn. Hist. nat. Paris,* 3^{e} sér. no. 521 Botanique 35: 3–33.