





3 2044 105 179 626

**Library**  
**Arnold Arboretum**



of

**Harvard University**











THE GARDENS' BULLETIN  
SINGAPORE

---

VOL. XXIX

31ST AUGUST, 1977

---

# Tropical Botany

ESSAYS PRESENTED TO E. J. H. CORNER  
FOR HIS SEVENTIETH BIRTHDAY, 1976

*Published by Authority*

—  
Printed by the Singapore National Printers (Pte) Ltd  
—

1977

To be purchased at the Botanic Gardens, Singapore

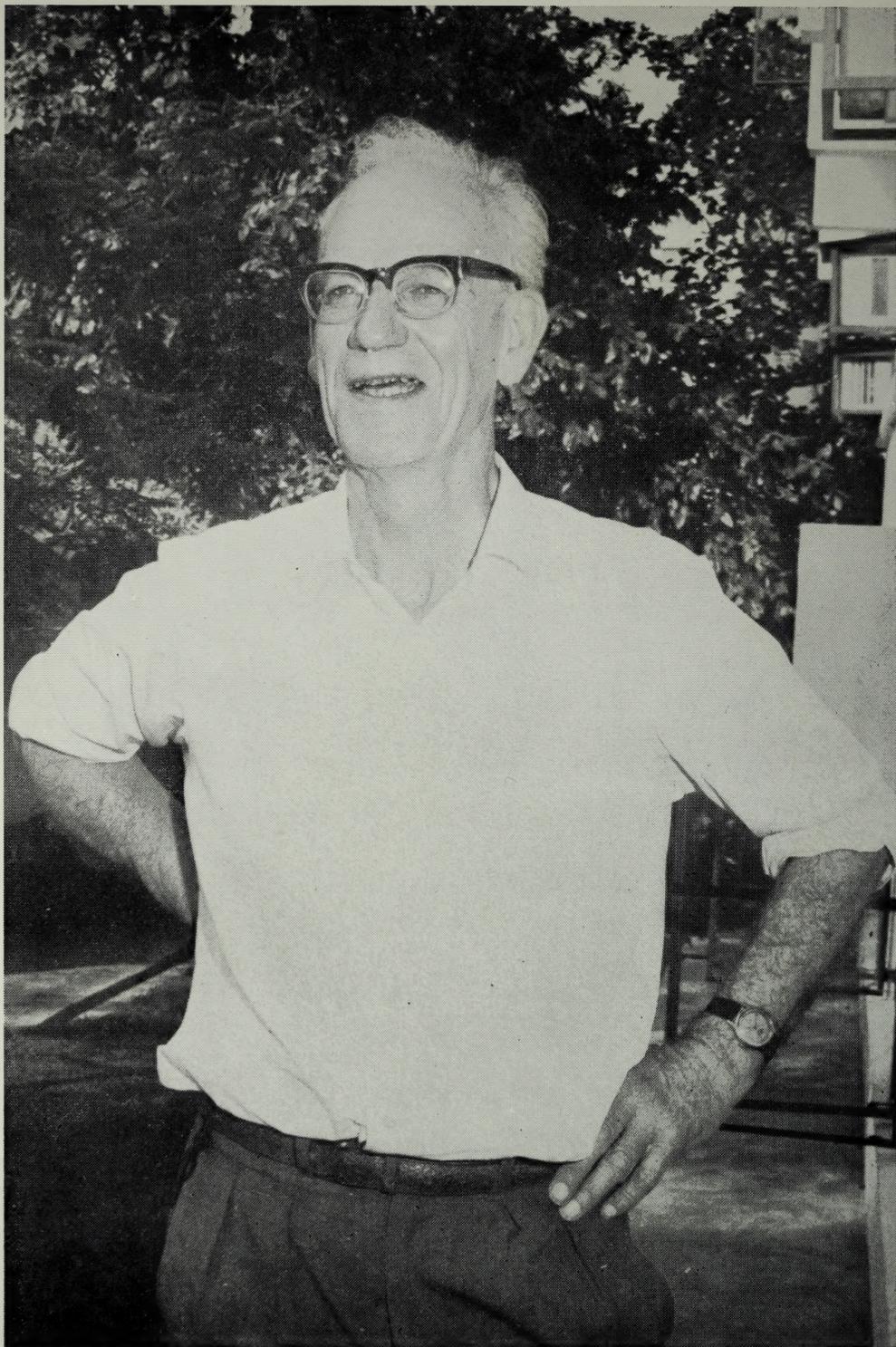
Price: S\$20.00

M

1.3

136 /  
19





Edred John Henry Corner, 1972.

*photograph by Ismail bin Ahmad*

THE GARDENS' BULLETIN  
SINGAPORE

---

TROPICAL BOTANY

Essays presented to  
**E. J. H. Corner**  
for his seventieth birthday, 1976

Compiled and edited by

D. J. MABBERLEY and CHANG KIAW LAN

*Published by Authority*

*Issued by the Commissioner, Parks and Recreation Department*

—  
Printed by the Singapore National Printers (Pte) Ltd  
—

1977

To be purchased at the Botanic Gardens, Singapore

*Price: S\$30.00*

# CONTENTS

	PAGE
H. M. BURKILL: Introduction - - - - -	1-2
D. J. MABBERLEY: E. J. H. Corner's Botany - - - - -	3-11
William T. STEARN: The Earliest European Acquaintance With Tropical Vegetation - - - - -	13-18
P. S. ASHTON: Ecology and the Durian Theory - - - - -	19-23
E. SOEPADMO & B. K. EOW: The Reproductive Biology of <i>Durio zibethinus</i> Murr. - - - - -	25-33
Frances M. JARRETT: The Syncarp of <i>Artocarpus</i> — a unique biological phenomenon - - - - -	35-39
D. J. MABBERLEY: The Origin of the Afroalpine Pachycaul Flora and its Implications - - - - -	41-55
Frank WHITE: The Underground Forests of Africa: A preliminary review - - - - -	57-71
B. L. BURTT: Notes on Rain-Forest Herbs - - - - -	73-80
E. F. BRUNIG & H. KLINGE: Comparison of the Phytomass Structure of Equatorial "Rain-Forest" in Central Amazonas, Brazil, and in Sarawak, Borneo - - - - -	81-101
C. G. G. J. VAN STEENIS: Autonomous Evolution in Plants: differences in plant and animal evolution - - - - -	103-126
Andrey A. FEDOROV: On Speciation in the Humid Tropics: some new data - - - - -	127-136
Benjamin C. STONE: The Morphology and Systematics of <i>Pandanus</i> Today (Pandanaceae) - - - - -	137-142
Hsuan KENG: <i>Ternstroemia corneri</i> (Theaceae) - - - - -	143-144
R. E. HOLTUM: Thelypteridaceae Allied to <i>Phegopteris</i> in Malaya - - - - -	145-150
A. DAVID & M. JAQUENOD: Tremellales with Tubular Hymenophores Found in Singapore - - - - -	151-153
Jacqueline PERREAU & ROGER HEIM: Sur Un Nouveau Bolet Tropical à Spores Ornées - - - - -	155-160
A. FAHN & D. M. JOEL: Development of Primary Secretory Ducts in the Stem of <i>Mangifera indica</i> L. (Anacardiaceae) - - - - -	161-164
Kenneth R. SPORNE: Girdling Vascular Bundles in Dicotyledon Flowers - - - - -	165-173
F. HALLE & D. J. MABBERLEY: Corner's Architectural Model - - - - -	175-181
Robert F. THORNE: Where and When Might the Tropical Angiospermous Flora Have Originated? - - - - -	183-189
J. GALIL, M. STEIN & A. HOROVITZ: On the Origin of the Sycomore Fig ( <i>Ficus sycomorus</i> L.) in the Middle East - - - - -	191-205
J. T. WIEBES: A Short History of Fig Wasp Research - - - - -	207-232
V. H. HEYWOOD: The Taxonomist's Dilemma - - - - -	233-237
D. G. FRODIN: On the Style of Floras: some general considerations - - - - -	239-250
Edwin A. MENNINGER: This World We Live in Will Be Only as Beautiful as You and I Make It - - - - -	251-253
Index - - - - -	255-266
Errata - - - - -	266

THE  
GARDENS' BULLETIN  
SINGAPORE

Vol. XXIX

31st August, 1977

**Introduction**

H. M. BURKILL

*Royal Botanic Gardens, Kew*  
(Botanic Gardens, Singapore, 1954-1969)

Corner's septuagenary fell on 12 January, 1976. It was the intention of a number of his research students and friends to develop an idea mooted by David Frodin into a little book to mark the occasion. However,

'The best-laid schemes o' mice an' men  
Gang aft a-gley,  
And lea'e us nought but grief an' pain  
For promised joy.'

(Robert Burns: *To a mouse*, 1785.)

Very considerable difficulties have arisen over the preparation and publication, so that only now, by the courtesy of the Editor of the Gardens' Bulletin, Singapore, does it appear — in retrospect, but, nevertheless, in a token of our esteem.

It was but inevitable that with such innate stimulating enthusiasm for botany, Corner should find the opportunity during his service in Singapore to give free rein to it. The 'Durian Theory' of evolution is here discussed, as along with the tropical rain-forest which Corner demonstrated in his later years as Professor of Tropical Botany at Cambridge ought to form the central pillar of any basis for teaching botany. Universities in tropical regions in centres of floral evolution with the plant materials on their door-step should be mindful of establishing leading research schools instead of letting the world rely on botanists tutored on temperate botany. Long before announcing his Durian Theory but with perhaps the seeds of the idea quietly growing in his mind, Corner began teaching, amongst his other duties in the Botanic Gardens, students in the Raffles College and in the King Edward VII College of Medicine in Singapore. These are now integral parts of the University of Singapore, and many of the older collegiates recall his lectures with interest and pleasure.

In 1937 while on expedition in N.E. Malaya he brought a young *berok* monkey (*Macaca nemestrina*). This is the species that is trained to pick ripe coconuts, and Corner saw the possibility of training one to pick plant specimens from high forest trees at a height of perhaps 50-60 m from the ground. The *berok* had its debut on a trip to Fraser's Hill and proved to be so successful that two more were acquired, and later a fourth. Words of a command had to be taught to guide the monkey to what was wanted visible to the operator lying on the ground scanning the tree-canopy through binoculars. Infinite patience was necessary, and both he and his assistant, Ngadiman bin Haji Ismail, often suffered painful monkey-bites. Closer to Singapore, the Mawai-Sungei Sedili swamp-forest, accessible on single-day forays, was an area of much interest to Corner, and the monkeys were often used there. To 'those-in-the-know', this area is called Corner's Corner, and it was here that he contracted a disease akin to black-water fever that very nearly killed him, an end frustrated by skilled and devoted nursing in the Singapore General Hospital. At that time the only access to Kuala Sedili was by river from Mawai. Now the time-conscious and hurry-mad swoosh down to the river-mouth by highway and agricultural settlement has pushed back very large tracts of the drier forest, and has chased out the elephants, tigers and wild-life that I have been fortunate enough to see there. But the actual swamp-forest, by virtue of its wetness, still has a life-expectancy (who knows?) for many years till

'development' demands further rapine. So it is good to learn that Corner has written an account of the Southern Malayan swamp forests that he knows so well and that his account is soon to appear as a supplement to the *Gardens' Bulletin, Singapore*.

Under a growing consciousness for conservation of biological resources, nature reserves were created in Singapore in 1937 and were put under the Gardens control. Ngadiman was Head Ranger and the team of monkeys were daily exercised there when they were not out on expedition. Thus Corner had constant interest in the reserves, especially the Bukit Timah Reserve where the use of the monkeys added to our knowledge of the tree flora. The mangrove reserve at Pandan was patrolled by an honorary warden, the late Towkay Chua Ho Ann, who was allowed to take a limited amount of timber for charcoal burning as *quid pro quo* for replanting and his wardenship. During the Japanese occupation Chua had a big charcoal contract with the Japanese Navy and consequently was 'in the money.' Both Holtum and Corner were retained by the Japanese in an advisory capacity in the Gardens, and Chua was able to pass not inconsiderable sums of money over to Corner which he used for the benefit of Gardens staff on the black market. During the latter part of this time, he and Holtum lived in a single room in the Botanic Gardens Director's house which was my study while I lived there. Corner, it seems, liked to 'live dangerously.' Contact with outside persons was not allowed and the receipt of money, had it been discovered, would have had the most serious consequences. Furthermore, Japanese Military Officers lived upstairs and their radio had its attractions and risks.

When Singapore surrendered to General Yamashita in 1942, the arrival of Professor Hidezo Tanakadate rescued the Botanic Gardens from military occupation. Sir Shenton Thomas, as former Governor of the Straits Settlements, had written a letter requesting the Japanese authorities to respect libraries, scientific collections, and places of historic interest. This letter Corner gave to Tanakadate who, with his own high influence and a long friendship with the General from student days, combined the Botanic Gardens and Raffles Museum into a unit of conservation. Presidency of this unit was accepted by Marquis Tokugawa, Supreme Consulting Adviser to the Nippon Military Administration, and this organisation received the personal approval of Count Terauchi, Supreme Commander of S.E. Asia. On the return of Tanakadate to Tokyo, Professor Kwan Koriba took charge of the Botanic Gardens. He was assisted by K. Watanabe who, in Singapore and Penang, assembled a remarkable collection of drawings of economic plants. In 1945 the drawings were deposited for safety in the Singapore herbarium. In 1960 Watanabe asked if they might be returned to him for publication, but they could not be found. Then blew an ill wind. In 1963 the old herbarium was in danger of collapse; its contents were hurriedly removed, and the drawings came to light. There followed an encyclopaedic work of reference prepared jointly by Corner and Watanabe: *Illustrated Guide to Tropical Plants* (1969).

Of the early days, Dr. Furtado, of the Gardens Staff, recalls a matter of interest and importance that is worth recording. Corner foresaw looting and persuaded the authorities to have officially signed notices of prohibited entry to the Raffles Library, the Raffles College and the building of the offices of the law firm Donaldson and Burkinshaw in which lay the largest private collection of lawbooks. Corner personally drove Tanakadate in the Gardens lorry to fix up these decrees. Equipment and the books of these buildings were thus saved from looting and damage. Count Terauchi also directed the valuable books from the Government House Library to be stored in the Tanglin Barracks. Corner was also able to salvage parts of the library of the Colonial Secretariat in Empress Place which had been thrown out of the building. At the end of the war when the Allied Forces entered Singapore Corner was again instrumental in obtaining similar protection from the British Military Administration, and though the Garden became a tented campsite no unauthorised entry was made into the buildings.

During these difficult years both Corner and Holtum, free from administrative duties, were able to devote much time to research. Corner worked on the larger fungi; and the development of flowers and fruits of various families of trees. The monograph on *Clavaria*, as indeed also, the *Durian* Theory began to take shape at this time, and in the post war years we have seen with admiration a succession of major works that must have had their origins in adversity. But this period had made a mark: he was invalidated out of service in 1947, though happily he was soon to regain good health, and we have been delighted to see him return again and again to Singapore, and as leader of the Royal Society's expeditions of 1961 and 1964 to Kinabalu in Sabah and of 1965 to the Solomon Islands.

This note started as a brief introduction to the articles that follow. Write something about Corner's Singapore days, said the Editors of this Festschrift. There is much, but let this suffice.

*Salam masera! Lanjutkan usia!*

(All hail! Long Life!)

Thus we hope it will be with him and with his charming wife, Helga.

## E. J. H. Corner's Botany

by

D. J. MABBERLEY

*Botany School, Oxford*

The spirit of our little book is one of progress; although nodding to the past, we are looking ahead. Here then, is not the place to list the events of Professor Corner's life, his appointments, wanderings and honours: it has been done before\*. What has not been written is that courses of Tropical Botany at Cambridge begun by Professor Corner and now, alas, discontinued, were an inspiration to generations of undergraduates and research students. Further, those beginning in less favourable surroundings and hearing Professor Corner as a visiting lecturer, have been led to see through the blinkers of that botany which is orientated to the plants of the temperate zone and peddled by the pusillanimous. These are the blinkers which have dragged the study of the whole plant down to the popular image of "pressing flowers", and driven many to the narrow reaches of the esoteric in pursuit of academic respectability. Of those fortunate to have been able to shake off such tyranny, and of the few who were able to do so at the Botany School in Cambridge under Professor Corner's supervision, I am privileged to say that I was one, though the last.

How did it begin? A new schoolmaster fresh from Cambridge went to Rugby: in the sixth form was John Corner. The schoolmaster had read the writings of A. H. Church, a remarkable philosopher of botany, then working in the Botany School at Oxford. Corner read Church's unassuming, unillustrated and rather slim *Oxford Botanical Memoir* entitled *Thalassiophyta*. Despite the tightly argued and rather heavy prose, much of which was not understandable to a schoolboy, the blinkers fell away. Much of the botany taught at Cambridge, whither he went from Rugby, was, in consequence, dull and uninteresting. He cut lectures. He read. In 1928 he presented a paper (still preserved at the Botany School) on *Thalassiophyta* to the Botany Club. A friend introduced him to Church, and, whilst still a research student in mycology at Cambridge, he travelled to Oxford to see Church and became his disciple. Church's works and teaching, unfashionable at the time, reflected an astounding vision and an unparalleled grasp of the fundamental problems of botany. He, who had never ventured beyond Plymouth, could discourse on the floras of the world. When Corner set out for the forests of Malaya, Church advised him, "Note everything! Draw everything! Photograph everything!", advice passed through Corner to his pupils, and now to Church's "great-grand-pupils".

This is not the only legacy as we hope this volume shows. It reflects Professor Corner's interests as shown by comparison with his list of publications. Some of the papers are controversial: Professor Corner's writings have never avoided controversy. Obvious are the Durian Theory, the new classification of *Clavaria*, as well as papers on conservation and the teaching of botany which have encouraged and excited discussion.

\* *Flora Malesiana* I, 1: 117-118 (1950) & I, 8: XXVI (1974); *Biol. J. Linn. Soc.* 2: 322-324 (1970); *Who's Who*: 680 (1975); *Flora Malesiana Bull.* (29): 2536-2538 (1976).

The Indomalayan flora and "funguses", figs and breadfruit, durians and pachycauls; from trees, their form and evolution, to trees and man, to trees in horticulture and trees in conservation — a few of his subjects. And so here is offered Stearn's paper on the impact of tropical rain forest on those introduced to it for the first time; Ashton on the ecology of the Durian Theory; Soepadmo and Eow on the reproductive biology of *Durio* itself; Jarrett on the construction of the syncarp of *Artocarpus*; Mabberley on the afroalpine pachycaul flora; White on the origins of African geoxylic suffrutices, the final bars of the leptocaul opera; remarks on the evolution of rainforest herbs by Burt. Brunig & Klinge compare the structure of forests in Borneo and South America. Van Steenis takes up the question of differing modes of evolution in animals and plants, while Fedorov deals with the 'Vavilovian' evolution he sees in Dipterocarpaceae. Stone sets down the infrageneric classification of *Pandanus*, pachycaul monocotyledons *par excellence*. Of the Malayan flora so well known to Professor Corner, Hsuan Keng describes a new species of Theaceae and Holttum monographs a group of thelypterid ferns, whilst David and Jaquenoud describe new Tremellales from Singapore. Perreau & Heim continue the mycological papers with a new *Boletus* whilst developmental anatomy is represented by Fahn & Joel's paper on the secretory ducts of the mango, and Sporne presents an essay on the enigmatic girdling bundles of dicotyledonous flowers. The construction studies pioneered by Professor Corner are represented by the paper of Hallé and Mabberley on primitive tree-forms while the origin of primitive flowering plants is tackled from a different angle by Thorne. Professor Corner's monographic work on Asian and Australian *Ficus* is here complemented by a study of the origin of the sycomore in the Middle East by Galil and co-workers, and by Wiebes's history of fig wasp research. The importance and limits of taxonomy are stressed by Heywood and the problems and objectives of Flora-writing by Frodin, whilst Menninger ends the volume with a consideration of the aesthetic importance of trees in tropical and subtropical horticulture.

Although Professor Corner has retired, the flow of work is unabated. The monumental *Seeds of Dicotyledons* which appeared in 1976, is the fruit of over thirty years' painstaking investigation and interpretation, whilst even now in Shelford surrounded by his books, notes and collections in a veritable *thesaurus botanicus*, enlarged to contain his fungus herbarium and other specimens, he is writing up the flora of the Sedili River in eastern Johore!

### List of Publications

(excluding reviews, letters and reports of discussion)

(To 1 January 1977)\*

- CORNER, E. J. H. (1927). A cytological investigation of a sport in a plant of the garden stock. *Proc. Linn. Soc. Lond.* **139**: 75–77.
- (1929). A Humariaceous fungus parasitic on a liverwort. *Ann. Bot.* **43**: 491–505.
- (1929). Studies in the morphology of Discomycetes I. The marginal growth of apothecia. *Trans. Br. mycol. Soc.* **14**: 263–275.
- (1929). Studies in the morphology of Discomycetes II. The structure and development of the ascocarp. *Trans. Br. mycol. Soc.* **14**: 275–291.
- (1930). Studies in the morphology of the Discomycetes III. The Clavuleae. *Trans. Br. mycol. Soc.* **15**: 107–120.

\* The compiler is indebted to Mrs. Heap of the Botany School Library, Cambridge for assistance, particularly in tracing some of the rarer items.

- (1930). Studies in the morphology of the Discomycetes IV. The evolution of the ascocarp. *Trans. Br. mycol. Soc.* **15**: 121–134.
- (1931). Studies in the morphology of the Discomycetes V. The evolution of the ascocarp (continued). *Trans. Br. mycol. Soc.* **15**: 332–350.
- (1931). The identity of the fungus causing wet rot of rubber trees in Malaya. *J. Rubb. Res. Inst. Malaya* **3**: 120–123.
- (1932). The fruit body of *Polystictus xanthopus* Fr. *Ann. Bot.* **46**: 72–111.
- (1932). A *Fomes* with two systems of hyphae. *Trans. Br. mycol. Soc.* **17**: 51–81.
- (1932). The identity of the brown-root fungus. *Gdns' Bull. Straits Settl.* **5**: 317–352.
- (1933). A revision of the Malayan species of *Ficus*: *Covellia* and *Neomorphe*. *J. Malay. Brch R. Asiat. Soc.* **11**: 1–65.
- (1934). An evolutionary study in Agarics: *Collybia apalosarca* and the veils. *Trans. Br. mycol. Soc.* **19**: 39–88.
- (1935). The fungi of Wicken Fen, Cambridgeshire. *Trans. Br. mycol. Soc.* **19**: 280–287.
- (1935). Observations on resistance to powdery mildews. *New Phytol.* **34**: 180–200.
- (1935). A *Nectria* parasitic on a liverwort: with further notes on *Neotiella crozalsiana*. *Gdns' Bull. Straits Settl.* **8**: 135–144.
- (1935). *Cassia* in Malaya. *Malay. Agri-hort. Ass. Mag.* **5**: 37.
- (1935). The seasonal fruiting of agarics in Malaya. *Gdns' Bull. Straits Settl.* **9**: 79–88.
- (1936). *Hygrophorus* with dimorphous basidiospores. *Trans. Br. mycol. Soc.* **20**: 157–184.
- (1938). *Annual Report of the Director of Gardens for the year 1937*. Singapore: Govt. Printing Office.
- (1938). The systematic value of the colour of withering leaves. *Chronica bot.* **4**: 119–121.
- (1939). Notes on the systematy and distribution of Malayan phanerogams. Part I. *Gdns' Bull. Straits Settl.* **10**: 1–55.
- (1939). Notes on the systematy and distribution of Malayan phanerogams. Part II. *Gdns' Bull. Straits Settl.* **10**: 56–81.
- (1939). A revision of *Ficus*, subgenus *Synoecia*. *Gdns' Bull. Straits Settl.* **10**: 82–161.
- (1939). Notes on the systematy and distribution of Malayan phanerogams. Part III. *Gdns' Bull. Straits Settl.* **10**: 239–329.
- (1940). Botanical monkeys. *Malay Agri-hort. Ass. Mag.* **10**: 147–149.
- (1940). *Wayside Trees of Malaya*. Vol. I: 770 pp; vol. II: 228 pl. Singapore: Government Printing Office [2nd Ed. 1952].

- (1940). Note: larger fungi in the tropics. *Trans. Br. mycol. Soc.* **24**: 357.
- (1941). The flora of Singapore. *Malay. Agri-hort. Ass. Mag.* **11**: 59–62.
- (1941). Further notes on the Moreton Bay Chestnut, (*Castanospermum australe*). *Malay. Agri-hort. Ass. Mag.* **11**: 151–154.
- (1941). A naturalist's companion. *Malay. Nat. J.* **2**: 11–14.
- (1941). Notes on the systematy and distribution of Malayan phanerogams IV — *Ixora*. *Gdns' Bull. Straits Settl.* **11**: 177–235.
- (1946). Suggestions for botanical progress. *New Phytol.* **45**: 185–192.
- (1946). Tropical biology — an international problem. *Biol. & Human Affairs.* **12**: 53–57.
- (1946). Centrifugal stamens. *J. Arnold Arbor.* **27**: 423–437.
- (1946). The pig-tailed monkey as a plant-collector. *Zoo Life* **1**: 89–92.
- (1946). Need for the development of tropical ecological stations. *Nature* **157**: 377.
- (1947). Variation in the size and shape of spores, basidia and cystidia in Basidiomycetes. *New Phytol.* **46**: 195–228.
- (1948). *Asterodon*, a clue to the morphology of fungus fruit-bodies: with notes on *Asterostroma* and *Asterostromella*. *Trans. Br. mycol. Soc.* **31**: 234–245.
- (1948). Studies in the basidium 1. The ampoule effect, with a note on nomenclature. *New Phytol.* **47**: 22–49.
- (1949). The Annonaceous seed and its four integuments. *New Phytol.* **48**: 332–364.
- (1949). The Durian Theory or the origin of the modern tree. *Ann. Bot. (N.S.)* **13**: 367–414; translated (1964) as “La théorie du Durian ou l'origine de l'arbre modern. Adaptation française par N. & F. Hallé” *Adansonia (N.S.)* **4**: 156–184.
- (1950). *A Monograph of Clavaria and allied Genera*. *Ann. Bot. Mem.* **1**: 740 pp. + 16 pl.
- (1950). Descriptions of two luminous tropical agarics (*Dictyopanus* and *Mycena*). *Mycologia* **42**: 423–431.
- (1950). Report on fungus-brackets from Star Carr, Seamer. Pp. 123–124 in F. G. D. Clark, Preliminary report on excavations at Star Carr, Seamer, Yorkshire (Second season 1950). *Proc. prehist. Soc.* **1950** (9): 109–129.
- (1951). Prof. H. Tanakadate. *Nature* **167**: 586.
- (1951). The Leguminous seed. *Phytomorphology* **1**: 117–150.
- (1951). Lectotypes in mycology: a taxonomic proposal. *Nature* **168**: 1031.
- (1952). Durians and dogma. *Indones. J. nat. Sci.* **5–6**: 141–145.
- (1952). Generic names in Clavariaceae. *Trans. Br. mycol. Soc.* **35**: 285–298.

- (1952). Addenda Clavariaceae I. Two new Pteruloid genera and *Deflexula*. *Ann. Bot. (N.S.)* **16**: 269–291.
- (1952). Addenda Clavariaceae II, *Pterula* and *Pterulicium*. *Ann. Bot. (N.S.)* **16**: 531–569.
- (1953). Addenda Clavariaceae III. *Ann. Bot. (N.S.)* **17**: 347–369.
- (1953). The construction of polypores — I. Introduction: *Polyporus sulphureus*, *P. squamosus*, *P. betulinus* and *Polystictus microcylus*. *Phytomorphology* **3**: 152–167.
- (1953). The Durian Theory extended — I. *Phytomorphology* **3**: 465–476.
- (1953). Proposal No. 10, principles for stability of nomenclature (VIIIth Int. Bot. Congr. prop. 10). *Taxon* **2**: 101.
- & L. E. HAWKER (1953). Hypogeous fungi from Malaya. *Trans. Br. mycol. Soc.* **36**: 125–137.
- (1954). The classification of higher fungi. *Proc. Linn. Soc. Lond.* **165**: 4–6.
- (1954). The Durian Theory extended — II. The arillate fruit and the compound leaf. *Phytomorphology* **4**: 152–165.
- (1954). The Durian Theory extended — III. Pachycauly and megaspermy — Conclusion. *Phytomorphology* **4**: 263–274.
- (1954). Evolution of tropical rainforest. Pp. 34–46 in J. Huxley, A. C. Hardy & E. B. Ford (eds.), *Evolution as a Process*. London: Allen & Unwin.
- (1954). Further descriptions of luminous agarics. *Trans. Br. mycol. Soc.* **37**: 256–271.
- (1955). Botanical collecting with monkeys. *Proc. R. Instn Gt Br.* **36** (no. 162): 1–16.
- (1955). *Epilogia [sic] pro monographia sua*. *Taxon* **4**: 6–8.
- (1956). Taxonomy and tropical plants. *Proc. Linn. Soc. Lond.* **168**: 65–70.
- (1956). A new European *Clavaria*: *Clavulinopsis septentrionalis* sp. nov. *Friesia* **5**: 218–220
- K. S. THIND & G. P. S. ANAND (1956). The Clavariaceae of the Mussoorie Hills (India) II. *Trans. Br. mycol. Soc.* **39**: 475–484.
- (1957). *Craterellus* Pers., *Cantherellus* Fr. and *Pseudocraterellus* gen. nov. *Sydowia, beih.* 1, *Festschr. f. Franz Petrak*: 266–276.
- (1957). Some Clavarias from Argentina. *Darwiniana* **11**: 193–206.
- , K. S. THIND & SUKH DEV (1957). The Clavariaceae of the Mussoorie Hills (India) VII. *Trans. Br. mycol. Soc.* **40**: 472–476.
- (1958). The Clavariaceae of the Mussoorie Hills (India) IX. *Trans Br. mycol. Soc.* **41**: 203–206.
- (1958) Transference of function. *J. Linn. Soc. Bot.* **90**: 33–40; *J. Linn. Soc. Zool.* **44**: 33–40

- (1958). An introduction to the distribution of *Ficus Reinwardtia* 4: 15-45.
- CASH, E. K. & E. J. H. CORNER (1958). Malayan and Sumatran Discomycetes. *Trans. Br. mycol. Soc.* **41**: 273-282.
- CORNER, E. J. H. (1959). Vegetation of the humid tropics. *Nature* **183**: 795-796.
- (1959). The importance of tropical taxonomy to modern botany. *Gdns' Bull. Singapore* **17**: 209-214.
- (1960). Taxonomic notes on *Ficus* Linn., Asia and Australasia. I-IV. *Gdns' Bull. Singapore* **17**: 368-485.
- (1960). The Malayan flora. Pp. 21-24 in R. D. Purchon (ed.), *Proc. Centen. & Bicenten. Cong. Biol.*, 1958 (Singapore).
- (1960). Taxonomic notes on *Ficus* Linn., Asia and Australasia. V-VI. *Gdns' Bull. Singapore* **18**: 1-69.
- (1961). Impact of man on the vegetation of the humid tropics. *Nature* **189**: 24-25.
- (1961). Agnes Arber. *Phytomorphology* **11**: 197-198.
- (1961). A tropical botanist's introduction to Borneo. *Sarawak Mus. J.* **10**: 1-16.
- (1961). Taxonomic notes on *Ficus* Linn., Asia and Australasia. Addendum. *Gdns' Bull. Singapore* **18**: 83-97.
- (1961). Introduction. Pp 1-7 in J. Wyatt-Smith & P. R. Wycherley (eds), *Nature Conservation in Western Malaysia*. Kuala Lumpur: Malay. Nat. Soc.
- (1961). Evolution. Pp. 95-115 in A. M. McLeod & L. S. Cogley (eds), *Contemporary Botanical Thought*. Edinburgh: Oliver & Boyd.
- (1961). A note on *Wiesnerina* (Cyphellaceae). *Trans. Br. mycol. Soc.* **44**: 230-232.
- CORNER, E. J. H. & K. S. THIND (1961). Dimitic species of *Ramaria* (Clavariaceae). *Trans. Br. mycol. Soc.* **44**: 233-238.
- (1962). Botany and prehistory. Pp. 38-41 in [U.N.E.S.C.O.], *Symposium on the Impact of Man on the Humid Tropics Vegetation, Goroka 1960*.
- (1962). The Royal Society Expedition to North Borneo, 1961. *Emp. For. Rev.* **1962**: 224-233.
- (1962). The classification of Moraceae. *Gdns' Bull. Singapore* **19**: 187-252.
- (1962). Taxonomic notes on *Ficus* L., Asia and Australasia. Addendum II. *Gdns' Bull. Singapore* **19**: 385-415.
- & C. BAS (1962). The genus *Amanita* in Singapore and Malaya. *Persoonia* **2**: 241-304.
- (1963). The tropical botanist. *Advmt Sci, Lond.* **20**: 328-334.
- (1963). *Ficus* in the Pacific region. Pp. 233-249 in J. L. Gressitt (ed), *Pacific Basin Biogeography*. Honolulu: Bishop Mus. Press.

- (1963). A criticism of the gonophyll theory of the flower. *Phytomorphology* **13**: 290–292.
- (1963). A Dipterocarp clue to the biochemistry of Durianology. *Ann. Bot. (N.S.)* **27**: 339–341.
- (1963). Studies in the flora of Thailand 16. Moraceae. *Dansk Bot. Ark.* **23**: 19–32.
- (1936). Exploring North Borneo. *New Scient.* **366**: 488–490.
- (1963). Royal Society Expedition to North Borneo 1961: reports. *Proc. Linn. Soc. Lond.* **175**: 9–32 (General Report); 37–45 (Special Reports).
- (1964). *The Life of Plants*. Pp. 315 + 41 pl. London: Weidenfeld & Nicholson. [Also trans. Léo Dilé as *La Vie des Plantes* (1964), and trans. Lucia Maldacea as *La Vita delle Plante* (1972), both with additional pp. after p. 316 by P. Coursin.]
- (1964). A discussion of the results of the Royal Society Expedition to North Borneo, 1961. Organized by E. J. H. Corner. *Proc. R. Soc. Lond.* **B161**: 1–91 (Commentary on the general results: pp. 3–6; Conclusion: pp. 90–91).
- (1965). Check-list of *Ficus* in Asia and Australasia with keys to identification. *Gdns' Bull. Singapore* **21**: 1–186.
- (1965). Mount Kinabalu East. *Sabah Soc. J.* No. **4**: 170–187.
- (1966). *A Monograph of Cantharelloid Fungi*. *Ann. Bot. Mem.* **2**: 255 pp. + 5 pl.
- (1966). *The Natural History of Palms*. Pp. 393 + 24 pl. London: Weidenfeld & Nicholson.
- (1966). Debunking the New Morphology. *New Phytol.* **65**: 398–404.
- (1966). Species of *Ramaria* (Clavariaceae) without clamps. *Trans. Br. mycol. Soc.* **49**: 101–113.
- (1966). Kinabalu. *Straits Times Annual 1966*: 34–37.
- (1966). On *Clavaria inaequalis* Fr. *Nova Hedwigia* **12**: 61–63.
- (1966). The clavarioid complex of *Aphelaria* and *Tremellodendropsis*. *Trans. Br. mycol. Soc.* **49**: 205–211.
- (1966). *Paraphelaria*, a new genus of Auriculariaceae. *Persoonia* **4**: 345–350.
- (1967). *Ficus* in the Solomon Islands and its bearing on the post-Jurassic history of Melanesia. *Phil. Trans. R. Soc. Lond.* **B253**: 23–159.
- (1967). On thinking big. *Phytomorphology* **17**: 24–28.
- (1967). Notes on *Clavaria*. *Trans. Br. mycol. Soc.* **50**: 33–44.
- (1967). Clavarioid fungi of the Solomon Islands. *Proc. Linn. Soc. Lond.* **178**: 91–106
- (1967). Biological expeditions. *May & Baker Lab. Bull.* **7**: 90–92.
- (1967). Moraceae. [Bot. Rep. Danish Noona Dan Expedition]. *Dansk bot. Ark.* **25**: 64–67.

- (1968). A monograph of *Thelephora* (Basidiomycetes). *Beih. zur Nova Hedwigia* **27**: 110 pp + 4 pl.
- (1968). Mycology in the tropics— *apologia pro monographia sua secunda*. *New Phytol.* **67**: 219–228.
- (1968). Conservation — future prospects. *Biol. Conserv.* **1**: 21–26.
- (1969). Notes on Cantharelloid fungi. *Nova Hedwigia* **18**: 738–818.
- (1969). A discussion of the results of the Royal Society Expedition to the British Solomon Islands Protectorate, 1965. Organized by E. J. H. Corner. *Phil. Trans. R. Soc. Lond.* **B255**: 185–631 (Introduction: 187–188; *Ficus*: 567–570; The botany of Jaagi Is., Santa Isabel: 571–573; Mountain flora of Popomanusen, Guadalcanal: 575–577; Larger fungi of the Solomon Islands: 579; Summary of the discussion: 621–623).
- (1969). The complex of *Ficus deltoidea*; a recent invasion of the Sunda Shelf. *Phil. Trans. R. Soc.* **B256**: 281–317.
- (1969). *Ficus* sect. *Adenosperma*. *Phil. Trans. R. Soc.* **B256**: 318–355.
- (1969). The conservation of scenery and wild life. *Proc. Ceylon Asst. Advmt Sci.* **2**: 220–231.
- (1969). Ecology and natural history in the tropics. *Proc. Ceylon Asst. Advmt Sci.* **2**: 261–273.
- WATANABE, K. & E. J. H. CORNER (1969). *Illustrated Guide to Tropical Plants*. 1147 pp. Tokyo: Hirokawa.
- CORNER, E. J. H. (1970). *Ficus* subgen. *Ficus*. Two rare and primitive pachycaul species. *Phil. Trans. R. Soc.* **B259**: 353–381.
- (1970). *Ficus* subgen. *Pharimosycea* with reference to the species of New Caledonia. *Phil. Trans. R. Soc. Lond.* **B259**: 383–433.
- (1970). New species of *Streblus* and *Ficus* (Moraceae). *Blumea* **18**: 393–411.
- (1970). *Phylloporus* Quél. and *Paxillus* Fr. in Malaya and Borneo. *Nova Hedwigia* **20**: 793–822.
- (1970). Supplement to “A Monograph of *Clavaria* and allied genera”. *Beih. zur Nova Hedwigia* **33**: 299 pp. + 4 pl.
- (1970). 37. *Ficus* (Moraceae). *Ident. Lists Malaysian Spec.*: 537–648b. Foundation Flora Malesiana.
- (1971). Meruloid fungi in Malaysia. *Gdns' Bull. Singapore* **25**: 355–381.
- (1971). Mycological reports from New Guinea and the Solomon Islands. 4. Enumeration of the Clavariaceae. *Bull. natn Sci. Mus., Tokyo* **14**: 423–427.
- (1972). New taxa of *Ficus* (Moraceae). *Blumea* **20**: 427–432.
- (1972). Studies in the basidium — spore spacing and the *Boletus* spore. *Gdns' Bull. Singapore* **26**: 159–194.
- (1972). *Boletus in Malaysia*. 263 pp. + 23 p. Singapore: Govt. Printing Office.

- (1972). 43. *Ficus* (Moraceae) from India, Burma, Thailand, China, Korea, Japan, Ryu Kyu, Formosa and Hainan. *Ident. Lists Malaysian Spec.*: 735–784. Foundation Flora Malesiana.
- (1972). Urgent exploration needs: Pacific Floras. *Pac. Sci. Assoc. Inform. Bull.* **24**: 17–27.
- (1974). *Boletus* and *Phylloporus* in Malaysia: further notes and descriptions. *Gdns' Bull. Singapore* **27**: 1–16.
- (1975). New taxa of *Ficus* (Moraceae) 2. *Blumea* **22**: 299–309.
- (1975). Prototypic organisms XIII. Tropical trees. *Theoria to Theory* **9**: 33–43.
- (1975). The evolution of *Streblus* Lour. (Moraceae): with a new species of sect. *Bleekrodea*. *Phytomorphology* **25**: 1–12.
- (1975). *Ficus* in the New Hebrides. *Phil. Trans. R. Soc. Lond.* **B 272**: 343–367.
- (1976). The climbing species of *Ficus*: derivation and evolution. *Phil. Trans. R. Soc. Lond.* **B 273**: 379–386.
- (1976). *The Seeds of Dicotyledons*. Vol. I: 311 pp.; Vol. II: 552 pp. Cambridge: Cambridge University Press.
- (1976). Further notes on Cantharelloid fungi and *Telephora*. *Nova Hedwigia* **27**: 325–342.
- (1976). A new species of *Parartocarpus* Baillon (Moraceae). *Gdns' Bull, Singapore* **28**: 183–190.
- (in press). The freshwater swamp-forest of south Johore and Singapore. *Gdns' Bull. Singapore, Supp.* **1**.



## The Earliest European Acquaintance with Tropical Vegetation

by

WILLIAM T. STEARN

*British Museum (Natural History), London*

“Das Glanzstück der botanischen Mitteilungen über ost-indische Pflanzenwelt die unter Alexander erschienen, ist die Schilderung des riesigen Feigenbaums, des Banyan,” wrote Hugo Bretzl in his massive work on the botanical results of Alexander the Great’s invasion of northern India in 326-325 B.C., *Botanische Forschungen des Alexanderzuges* (1903). With this account of the banyan (*Ficus benghalensis* L.) preserved in Theophrastus’s *Enquiry into Plants* (*pēri phytōn histōria*), there began well over two thousand years ago the European investigation of the genus *Ficus* in tropical Asia to which Professor John Corner has made such illuminating contributions. Theophrastus (370–c.285 B.C.) himself never went to India; as a pupil first under Plato, then under Aristotle, whose library and garden he inherited, and later as an academic teacher, he spent almost all his life in Athens. His career spanned completely the life of Alexander (356–323 B.C.), whose army undoubtedly included well-educated highly intelligent observers and recorders, and the reports of these officers came into Theophrastus’s hands. Their firsthand accounts disappeared long ago but parts have survived, being embedded, like fragments of Roman masonry in medieval walls, within the writings of others, notably Theophrastus and Arrian, and among them is the description of the banyan, the Indian fig (*sukē hē indikē*), praised so highly by Bretzl. This occurs in Theophrastus’s *Enquiry* IV. iv. 4–5.

Since so much of Professor Corner’s life, research and writing has been devoted to the study of tropical plants, particularly those of Indo-Malaya, the celebration of his seventieth birthday provides a fitting occasion on which to bring to notice again these first records of the impact of tropical vegetation upon the receptive analytic Western mind.

Even for a present-day young botanist versed firsthand only in the north temperate flora, first acquaintance with the strange diverse vegetation of the tropics, with plants of a luxuriance and character unknown in Europe and North America, is a stimulating and mentally bewildering or overwhelming experience. A succession of narratives indicate that this has always been so.

Thus Henry Walter Bates arrived with Alfred Russel Wallace at Parâ, Brazil, on 28 May 1848, having left Liverpool on 26 April. They immediately walked across the town, then small and closely encompassed by native vegetation. “The impressions received during this first walk,” Bates wrote in his *The Naturalist on the River Amazons* (1863) after eleven years in the Amazon valley, “can never wholly fade from my mind ... so striking, in the view, was the mixture of natural riches and human poverty ... But amidst all, and compensating every defect, rose the overpowering beauty of the vegetation ... Strange forms of vegetation drew our attention at every step.” Tropical fruit trees, tall palms with smooth columnar stems, epiphytes perched amid boughs, slender woody lianes, luxuriant creeping plants overrunning alike tree-trunks, roofs and walls, sword-leaved bromeliads and many other plants remarkable in leaf, stem or manner of

growth together exemplified for them "the teeming profusion of Nature", to which, as night came on, the whirring of cicadas, the shrill stridulation of grasshoppers, each sounding its peculiar note, the hooting of tree frogs, the croaking of toads and frogs in pools together provided an audible expression almost deafening. This rich diversity had earlier affected Alexander von Humboldt and Aimé Bonpland as vividly. They arrived at Cumana, Venezuela, on 16 July 1799, having sailed from Spain on 4 June 1799. The effect of the tropical environment upon both the travellers led Alexander to write to his brother Wilhelm: "What trees! Coco-nut trees 50-60 feet high; *Poinciana pulcherrima*\* with a foot high bouquet of magnificent bright red flowers; pisang and a host of trees with enormous leaves and scented flowers, as big as the palm of a hand, of which we knew nothing ... We rush around like the demented; in the first three days we were unable to classify anything; we pick up one object to throw it away for the next. Bonpland keeps telling me he will go mad if the wonders do not cease."

Even earlier James Wallace (d. 1724), an Orkney man who had taken part in the ill-fated Scottish attempt of 1698-1700 to found a colony at Darien, Panama, wrote: "This place affords legions of monstrous plants enough to confound all the methods of Botany ever hitherto thought upon ... some of their leaves exceed three ells in length and are very broad, besides these Monsters, reduceable to no Tribe, there are here a great many of the European kindred but still something odd about them". The equally remarkable tropical vegetation of Amboina in the East Indies inspired Georg Everard Rumpf. (c. 1627-1702) to the vast task of preparing his *Herbarium Amboinense* (6 vols, 1741-1750) which describes vividly and accurately some 1200 species.

In southern India the governor of the Dutch possessions along the Malabar coast, Hendrik Adriaan von Rheede tot Draakenstein (1637-1692), was so impressed by the diversity of plants there, particularly by the epiphytes — "on one tree ten or twelve different sorts of leaves, flowers and fruits might be met with," as he said — that he set in hand the preparation of a detailed account, on which were engaged himself, an Italian missionary, about sixteen learned Brahmins, four artists and various native collectors. His *Hortus Indicus Malabaricus* (12 vols. folio, 1678-1703) was the first major work to bring a tropical flora to the notice of stay-at-home botanists in Europe. He introduced the banyan into cultivation at Amsterdam.

These works were by-products of European conquest and dominion, above all of the establishment of the Dutch empire in the East Indies during the 18th century A.D., an empire reached only after a long and hazardous voyage around Africa. The first European contact with tropical vegetation likewise resulted from European empire-building in Asia, but was made overland in the 4th century B.C. Having defeated Darius in 331, Alexander marched his army into Turkistan (Bactria) and then in 327 invaded north-western India by way of the Khyber Pass and entered the Punjab; the river Indus became the eastern boundary of his extended Asiatic empire. Short-lived though this was, it led to a flow of Greek ideas and art into northern India and a flow of information about the country back to Greece. Such information must have been very extensive, since the surviving fragments of it, preserved in the writings of Theophrastus, Plutarch, Strabo and Pliny, for example, embrace Indian customs and geography as well as plants. Bretzl has so exhaustively collected all which is available of a botanical nature that were his book better known and easy to acquire — it seems to be scarce, is accessible in few libraries and has never been translated — there would be little justification for calling attention to this here. It deserves, however, not to be forgotten.

\* *Caesalpinia pulcherrima* (L.) Swartz.

The banyan (*Ficus benghalensis* L.) is an evergreen tree widespread in India with entire leathery leaves and small red fruits, and rises to about 26 m. (85 feet) and by pushing down, from its horizontally spreading branches, supporting prop- or pillar-roots at intervals, spreads over so wide an area that, as Corner has said, it "develops the biggest crown of any plant in the world". One individual tree can thus make a small wood.

This habit of the banyan, sending down aerial roots from its branches away from the main stem, caught Greek attention. It raised moreover an interesting morphological question such as indeed could only be seen as a question when the study of plants had passed from being purely utilitarian, as was presumably that of unlettered herb-gatherers, the *rhizotomoi* (literally 'root-cutters'), to being scientific and philosophical as was that of Theophrastus and his associates, namely the distinction between root and shoot. Clearly Theophrastus rejected the common view that any underground organ of a plant is a root, in other words, that all underground parts are homologous, by emphasizing the differences between the tuber of arum, the bulbs of squill, garlic and onion and the roots they send out. "His whole treatment of the subject of the roots of plants reads as if he had gone stealthily to work," so E. L. Greene wrote in 1909, "to undermine an old and everywhere received opinion that roots are simply the underground parts of plants." He based his definition on natural function and not position. This means that roots like shoots can be aerial and the banyan, though he can never have seen it himself, had been so well described, possibly even sketched, by Greek observers in India that it provided a most remarkable example of them. "The character and function of the roots of the Indian fig are peculiar, for this plant sends out roots from the shoots until it has a hold upon the ground and roots again; and so there comes to be a continuous circle of roots around the tree, not connected with the main stem but at a distance from it" (Loeb Classical Library translation by A. Hort, 1: 41; 1916).

Theophrastus had indeed made a detailed study, very remarkable for his period, of the underground parts of plants, distinguishing between rhizomes, tubers, bulbs and roots and distinguishing within the last-named various types, a matter discussed by Greene (1909), Strömberg (1937) and Arber (1950).

Theophrastus's fuller account of the banyan occurs later in his work, in a section on trees and herbs special to Asia: "The Indian land has its so-called fig-tree which drops its roots from its branches every year, as has been said above, and it drops them not from the new branches, but from those of last year or even from older ones; these take hold of the earth and make, as it were a fence about the tree, so that it becomes like a tent, in which men sometimes even live. The roots are easily distinguished from the branches being whiter, hairy, crooked and leafless. The foliage above is also abundant and the whole tree round and exceedingly large. They say that it extends its shade for as much as two furlongs; and the thickness of the stem is in some instances more than sixty paces, while many specimens are as much as forty paces through. The leaf is quite as large as a shield, but the fruit is very small, only as large as a chick-pea, and it resembles a fig. And that is why the Greeks named this tree a 'fig-tree'. The fruit is curiously scanty, not only relatively to the size of the tree, but absolutely. The tree also grows near the river Akesines". The mixture here of plain fact and of exaggeration suggests strongly that it is a description made from memory, perhaps told to Theophrastus by a soldier returned from India. Thus the leaves of the banyan, though up to 20 cm. long and, 12 cm. broad, are much smaller than the smallest round shield (*peltē*, Latin *pelta*) of the Ancient Greeks. Nevertheless, in addition to the general description of habit, this account contains two very significant remarks. The tree's prop-roots, though aerial, woody and stem-like, are distinguished from stems by being leafless (*aphullōi* seems a more correct rendering than the *diphullōi* of most codices). Moreover the fruits are compared to those of the

fig (*sukē*, *Ficus carica* L.) on account of their structure, though not their size; hence the Greeks classified the banyan as a fig, *sukē hē indikē*; this indicates real taxonomic insight since the banyan, except for these, is so utterly different from the cultivated Mediterranean figs.

Theophrastus also mentions in Book IV. iv. 5 other Indian plants, e.g. a very large tree with a large sweet fruit, presumed to be the jack-fruit (*Artocarpus heterophyllus* Lam.), another with a crooked sweet fruit, presumed to be the mango, (*Mangifera indica* L.), one with a fruit like the cornelian cherry (*Cornus mas* L.), presumed to be the jujube (*Zizyphus jujuba* Mill.), and another with an oblong leaf, like the feathers of the ostrich, 2 cubits (3 feet) long, presumed to be the banana (*Musa*).

The clothes of the Greeks were made from linen, hemp and wool. In India they found people wearing clothes that were the product of a tree with a leaf like the mulberry but resembling the wild rose; this was cotton (*Gossypium*); the plants were grown in the plains in rows, so that seen from a distance they looked like vines.

The mangroves on the sea-coast provided another kind of tropical vegetation wholly strange to men from the Mediterranean region, which has no counterparts to these trees growing in tidal waters and partly submerged at high tide. In December 325 B.C. the Cretan admiral Nearchus with a fleet built for Alexander on the Hydaspes (now the Jhelum) river sailed into the Persian Gulf from Pattala (now Tatta east of Karachi), then at a mouth of the Indus though now inland, while Alexander marched his army into Gedrosia, the modern Makran region of Baluchistan and adjacent southern Iran, evidently along the coast over part of the way, for Arrian, quoting Aristobulus, records mangrove trees: "one, with a leaf like laurel, is found growing below high-water mark on the sea-shore; this tree is left high and dry by the ebb tide, and on the succeeding flood looks as if it were growing in the sea. Some of them, growing in hollows which do not dry at low tide, are never out of the water, but even so take no harm from the constant immersion of their roots. Some trees are as much as 45 feet in height and were in blossom when Alexander saw them; the flower is rather like the white violet [i.e. stock, *Matthiola incana* (L.) R. Br.] but much more fragrant" (Arrian, *Life of Alexander the Great*, transl. A. de Sélincourt, 214; 1958). This was either *Avicennia marina* (Forsk.) Vierh. or *Rhizophora mucronata* Lam.

An essentially similar account, derived evidently from Nearchus's voyage past the mangrove-fringed creeks on the northern coast of the Persian Gulf, occurs in Theophrastus's *Enquiry*, IV. vii: "There are plants in the sea which they call 'bay' [*daphnē*, *Laurus nobilis* L.] and olive [*ēlaia*, *Olea europaea* L.] In foliage the 'bay' is like the aria [*aria*, holm oak, *Quercus ilex* L.], the 'olive' like the real olive. The latter has a fruit like olives." To this Theophrastus added: "On the islands which get covered by the tide they say that great trees grow, as big as planes or the tallest poplars, and that it came to pass, that when the tide came up, while the other things were entirely buried, the branches of the biggest trees projected and they fastened the stern cables to them, and then, when the tide ebbed again, fastened them to the roots. And that the tree has a leaf like that of the bay, and a flower like gilli-flowers [*iōn*, *Matthiola incana*] in colour and smell, and a fruit the size of that of the olive, which is also very fragrant. And it does not shed its leaves, and that the flower and the fruit form together in autumn and are shed in spring." The roots to which the ships were fastened at low tide must have the prop-roots of *Rhizophora*, but evidently the Greeks were not there at the right time to observe the viviparous germination of the fruit; otherwise they would surely have noted the long club-shaped radicle produced while the fruit still clings to the bough.

Theophrastus also incorporated observations referring to *Avicennia marina* made on the northern coast of the Persian Gulf, probably in the Strait of Hormuz

near Bandar-Abbas, southern Iran: "In Persia in the Carmanian district where the tide is felt there are trees of fair size like the andrachne [*andrachlē*, *Arbutus andrachne* L.] in shape and leaves; and they bear much fruit like in colour to almonds on the outside but the inside is coiled up as though the kernels were all united". This obviously refers to the longitudinally folded cotyledons, one enclosing the other, in the seed of *Avicennia*. "These trees are all eaten away up to the middle by the sea and are held up by their roots".

Through an exploratory voyage by Androstheneas along the southern coast of the Persian Gulf the Greeks also became acquainted with the island of Tylos, a very ancient centre of trade and civilization, now known as Bahrain, and recorded some of the plants grown there, as noted by Theophrastus. These included cotton, date palms, an evergreen fig and vines. They also stated "that there is another tree with many leaves [i.e. leaflets] like the rose and that this closes at night but opens at sunrise and by noon is completely unfolded; and at evening again it closes by degrees and remains shut at night, and the natives say that it goes to sleep". This is the first record of the sleep-movement of the tamarind (*Tamarindus indica* L.), indeed of any plant.

Bamboos are so important in the rural economy of India and grow there to so much greater heights than those of the two similar plants known to the Greeks, the common reed (*Phragmites australis* (Cav.) Trin. ex Steud.) and the giant reed (*Arundo donax* L.), that it would be strange indeed if the Greeks had failed to mention them at all. Theophrastus's reference to them in his *Enquiry* IV. xi. 13 is, however, brief: "The Indian reed is very distinct and as it were of a wholly different kind; the 'male' is solid and the 'female' hollow ... a number of reeds of this kind grow from one base and they do not form a bush, the leaf is not long, but resembles the willow leaf, these reeds are of great size and good substance, so that they are used for javelins". The terms 'male' and 'female' are used here metaphorically as they were for other plants, excluding however the date-palm; the 'male' has been identified as *Dendrocalamus strictus* (Roxb.) Nees, the 'female' as *Bambusa arundinacea* (Retz.) Willd.

Since Theophrastus, Arrian and other Ancient Greek writers only incorporated such information about tropical plants and vegetation as was relevant to their own work, almost indeed incidentally, it is reasonable to believe that the sources whence this came must have contained much more which has long been lost. Theophrastus's task in his botanical writings — he also wrote on astronomy, education, ethics, logic, mathematics, odours, meteorology, religion and rhetoric — was to bring together an immense quantity of information, no small part based upon his own observations, which he presented in a classified form, using facts not simply for themselves but also to provide examples for general statements, giving particular attention to differences which delimited or expressed the essential nature of subjects. It was his intention not to list all the known individual kinds of plants but simply those characteristic of certain features or regions. His fourth book in the *Enquiry* deals with the plants special to particular districts and habitats; in the sections relating to Asia, since he had never been there himself, he accordingly extracted what seemed especially interesting or relevant from the writings and recollections of his contemporaries who had accompanied Alexander on his invasion of India. Indeed he said "there are also many more different from these found among the Hellenes, but they have no names. There is nothing surprising in the fact that these trees have so special a character; indeed, as some say, there is hardly a single tree or shrub or herbaceous plant, except a few, like those in Hellas".

The task of Arrian, who lived some four hundred years later, was to write a reliable biography of Alexander, again taking what seemed relevant from earlier sources. The loss of these sources is not surprising. Thus the immense libraries of Pergamon and Alexandria had virtually perished by the 5th Century A.D., their

decline hastened by fanatical Christians who regarded them as pernicious repositories of pagan literature. Because of this, the effect upon the Hellenic world of the new knowledge stemming from Alexander's Asiatic conquests can only be dimly surmised. In the field of botany it enlarged European vision by bringing to notice plant structures, such as the banyan with its prop-roots, and ways of life, such as that of the mangroves growing as trees within the sea, as well as individual plants, which had no counterparts in Europe. Various European plants perform nyctitropic movements of the leaflets but none so conspicuously as does the tamarind. This extension of biological concepts through contact with tropical vegetation is necessary to counteract the impoverishing narrowness of outlook and experience which afflicts botany taught from a few plants in the laboratory by teachers who have never felt the excitement of seeing the plant world in its most complex form, above all in tropical rain forest regions. As Professor Corner has said in the last chapter of his *The Life of Plants* (1964), "high rainfall, sunshine and temperature make the tropical forest the prime of plant life ... But the forests, which show how trees were made, are going. They are vanishing nowhere faster than from the alluvial plains where the vestiges of the last creative phase of plant life, that prepared the way for the modern world, may survive". Because Professor Corner, with a stimulating breadth of outlook fostered in the tropical environment of Malaya, has striven so much to make stay-at-home European botanists aware of the evolutionary significance of tropical plants and the urgent need to study them before destruction of their habitats deprives humanity of many of them forever, it has been appropriate to recall here the first chapter in the history of European botanical contact with their challenging diversity.

### Some Sources of Further Information

- ARBER, A. 1950. *The Natural Philosophy of Plant Form*. Cambridge University Press.
- ARRIAN, 1958. *The Life of Alexander the Great*. Transl. by A. de Sélincourt. London, Penguin Books.
- BRETZL, H. 1903. *Botanische Forschungen des Alexanderzuges*. Leipzig.
- GREENE, E. L. 1909. *Landmarks of Botanical History*. Part 1 (Prior to 1562 A.D.). Washington, D.C.
- SENN, G. 1934. *Die Pflanzenkunde des Theophrast von Eresos*. Basel.
- STEARNS, W. T. 1957. Botanical exploration to the time of Linnaeus. *Proc. Linn. Soc. Lond.* **169** (sess. 1956-57): 173-196.
- STRÖMBERG, R. 1937. *Theophrastea: Studien zur botanischen Begriffsbildung*. (*Göteborgs Kungl. Vet. Handl.* V. A. 6 no 4). Göteborg.
- THEOPHRASTUS. 1916. *Enquiry into Plants*. Transl. by A. Hort. 2 vols. (Loeb Classical Library). London & New York.

# Ecology and the Durian Theory

by

P. S. ASHTON

*Department of Botany, University of Aberdeen*

The Durian Theory (Corner 1949-1964) is on a base of comparative morphology, yet provides insight on the ecology and evolution of tropical forest. The hypothetical angiosperm archetype that is deduced from it no longer exists; from ecological theory though we may speculate why this is so, and may deduce the conditions in which these plants evolved. What ecological bonuses and limitations does each of the primitive characteristics impose?

*Large spiny loculicidally dehiscent capsule or follicles, with large black seeds more or less enveloped in a colourful fleshy aril and dangling on persistent funicles.* A large seed provides a large food store, essential in the perennial shade of evergreen forest. In a windless climate fruit dispersal of forest plants is most effectively accomplished by animals, yet the large slowly developing seed must be protected from them until ripe. The significance of colour and movement to attract animal vectors has been discussed at length by Corner. It is astonishing how disinterested even monkeys are with green fruits; we have observed that the embryo and flesh of wild rambutan (*Xerospermum intermedium* Radlk.) fruits matures before the pericarp changes from green to yellow, yet the voracious monkeys always failed to distinguish maturity before the colour change. Experience of modern trees may have led them to fear all green fruits as unpalatable or poisonous; primitive armour, once pierced, provides protection against no predator, but the evolution of specific poisons reduces attacks to a few specialists. When in Sarawak I had the opportunity to identify the food of orangutans set free in Bako National Park, I was struck by the dexterity with which they dismembered the horrid defenses of rotan and nibong cabbages, and wondered whether these primates might be recent immigrants, possibly to the extending Holocene forests; otherwise such plants as the hapaxanthic *Plectocomia*, a particular favourite, would have disappeared as, we can assume, already have many other spiny but palatable organisms of former days.

Moreover, these great spiny primitive fruits are expensive and can only be produced in small numbers at a time; they confine those plants that bear them to stable habitats where their populations are least likely to suffer large fluctuations, and in places where opportunities for establishment are greatest. Such is the case in the shade of the forest canopy, but where is the pioneer with such a fruit? The mature phase of the forest is hence the home of our large seeded tropical fruits, and many more live there still awaiting cultivation; destroy the forest and this bounty will be lost.

*Stout, pithy-stemmed, unbranching and monocarpic trees, with a terminal inflorescence.* Such a habit and reproductive strategy still occurs in some palms and other monocotyledons, but is rare among dicotyledons. The polygamodioecious tree-ivy *Harmsiopanax* of New Guinea is one example. It is a semigregarious treelet with huge pinnatisect leaves, of mid-mountain glades. As a nomad, however, it produces an abundance of flowers and small fruit as do such monocarpic palms. A large fruited monocarpic progenitor could only maintain cross-pollination, and hence the genetic variability for further continued evolution, by growing in

gregarious stands; each unbranching treelet would thus be analogous to the monocarpic stems of the rhizomatous branching sago-palm *Metroxylon*. A stout pithy stem is the perfect adaptation to the unbranched monocarpic habit; The tube as a supporting structure is cheap and provides adequate tensile strength for a vertical member in a windless environment; while, as every Melanau sago farmer knows, the pithy core, which in dicotyledons expands as the apex enlarges (eg. Mabberley, 1974b), is the bank where insoluble polysaccharides gradually accrete until, in a flamboyant vegetable sneeze, they are converted to soluble sugars and surge up the giant terminal inflorescence into the developing flowers and fruits. The biochemistry of durianology demands further attention!

*Large pinnate leaves borne spirally with short internodes.* Givnish has elegantly defined the adaptive significance of leaf size and shape: large entire leaves are structurally and photosynthetically efficient individually, but carry a high heat load and are therefore expensive on water resources. They more completely exclude light beneath than small leaves do and thus reduce the leaf area index. Pinnate leaves comprise small leafy organs borne on deciduous twigs; when arranged in dense spirals they will still cast the deep shade of large entire leaves yet bear a lesser heat load. Evergreen trees with large thin leaves, whether entire or variously divided and in dense spirals, are confined to well-watered habitats even in the humid tropics. Some, such as the pinnate-leaved *Chisocheton* and pinnatisect *Heliciopsis* are in the forest understorey and bear large, usually dehiscent fruits; here, as Givnish points out, the large thin leaf is advantageous on the 'gamblers ruin' principle, by spreading a given number of chloroplasts horizontally the chance of encountering sunflecks is increased. Others, such as the small fruited tree-ivies *Harmsioplanax* and *Arthrophyllum* skirt the forest fringe on river banks and in gaps. Here large rapidly transpiring leaves, which prevail among nomad trees of well-watered places, provide the most economic means of building a photosynthesizing mantle for rapid growth and at the same time cast deep shade, deterring competition. In a densely spirally pinnate-leaved slow-growing tree the latter advantage is still conferred, as anyone who has rested in the uncluttered shade of *Dracontomelum mangiferum* Bl. on a Bornean river bank will remember with gratitude.

If now we add a massive inflorescence of large actinomorphic magnoliaceous flowers, with weakly differentiated perianth and many centrifugal stamens, we further define our plant's ecology. Such flowers are a crude means of ensuring cross-pollination, unless self-incompatible. They are expensive to produce, and the greater part of the costly pollen will be wasted, unless the trees are gregarious which, as we have already suggested, they probably were, or the flowers conspicuous and the vectors specific and far-roaming. The simple thin-walled short-lived pollen grain so common among still existing primitive families has, like the fruit, confined them to habitats where the atmosphere is warm and humid at least during the flowering season.

The stage may now be set for the reenactment of angiosperm evolution: we can visualise hills clothed in tall *Araucaria* forest; ferns grow in the deep shade beneath, while Cycadophytes and Caytoniales occupy the open fringes, along rocky ridges and in swampy plains. The gap phase of the *Araucaria* forest would have lacked the fast growing opportunists of modern rain forests. Here, on moist stable fertile slopes, hence especially on basic volcanic soils, the protoangiosperm would have found its niche; from a massive seed a tall shoot rapidly overtopped its gymnosperm seedling competitors in the shafts of light penetrating the crowns of ageing giants, allowing the building of the light-excluding *schopf* of densely spiral large pinnate leaves. Only its own kind could survive beneath its shade, and thus small, temporarily isolated but eventually expanding and coalescing, gregarious stands would accumulate on these slopes. These short unbranched trees hence excluded gymnosperms from the most favourable sites by depriving them of suitable conditions for establishment. This remains the secret of angiosperm

success, and even now it is the gymnosperms which, if allowed to, can finally achieve the greater growth and stature, as the dwarfing of New Guinean angiosperm forest by the scattered araucarias still witnesses.

Here then are the perfect conditions for further evolution and diversification: small gregarious colonies with few flowers and free cross-pollination, temporarily isolated along the slopes and thus allowing rapid local diversification; yet each valley, and each mountain chain, more permanently isolated. The significance of animal dispersal now becomes apparent.

The evolution of the enclosed seed in an eventually dehiscent fruit is seen, then, not to be a response to increasing aridity, for which there is little evidence in the upper Jurassic-lower Cretaceous period of continental drift, but for the need to develop a protective covering for the enlarged endosperm until the seed is ready to germinate.

Why should not cycads have accomplished the same? On the upper slopes of Susungdalaga in Camarines Sur, Luzon, I have seen *Cycas circinalis* L. growing in forest shade on volcanic soils. Their leaflets were sparse and their crowns diffuse; perhaps their less evolved vascular system and physiology prevents them from rapidly building and subsequently maintaining the dense excluding crown of the primitive angiosperm?

Thus the first flowering plants, not gymnosperms, would have provided the environment in which their further evolution could occur. Only angiosperms could survive beneath their own shade and hence only angiosperms could eventually overtop them. The Durian Theory provides a morphological means by which this could be accomplished. This increase in diversity of tree habit would initially have been the main source of increased species diversity in the forest, which in itself necessitated greater subsequent fruit production to overcome declining opportunities for establishment as interspecific competition increased, and led to the extinction of the large-fruited monocarpic ancestors. The evolution within the rain forest of more flexibly arranged, smaller, leaves would also allow a further spread of angiosperm hegemony into the domain of gymnosperms. Yet the sparsely branching protoangiospermous habit and spiral divided leaves still retain their advantage in the forest shade and many modern leptocauls, including a Philippine *Knema* (Myristicaceae) and a New Guinea *Sloanea* (Elaeocarpaceae) with durian-like fruit, retain this habit as saplings, as Corner has noted in other forest trees.

The evolutionary sequence of early angiospermous forest is partly reenacted in modern seral succession on moist hillsides. The seeds of modern forest nomads are small, with little food-store, and germinate in response to light but, once germinated the saplings rapidly build a tortoise-shell of large overlapping leaves, expanded by the early formation of ascending pithy shoots; among them are microperm pachycauls such as *Senecio mannii* Hook. f. (illustrated by Mabblerley (1974a) ). This at first, if complete, can effectively deter competition but after a few years the stems and branches begin to open under their own weight, providing the setting for the next stage, which will involve the first true leptocauls. Among them though, and particularly on these well watered sites, the pagoda tree (Corner, 1940) comes to predominate, an ingenious compromise between pachycaul and leptocaul and probably ancient. This, by intermittent rapid extension of a stout pithy leader grows first into a tall unbranched sapling with spiral or whorled leaves; but then, after a period of dormancy, it sprouts a whorl or pseudowhorl of more or less horizontal branches around the apex, bearing dense ascending rosettes, typically of obovate leaves by *Terminalia* branching (Corner, 1940). Thus an aerial blanket of leaves, often large and presumably rapidly metabolizing is early formed which overtops and suppresses its many-stemmed predecessors and, by successive bold extensions, apical dominance is maintained until the final forest canopy is reached. Only then does apical dominance give way to allow the expansion of a dome-shaped sympodial crown, often associated with a decline in the size

and density of the leaves and twigs. The ascending spires of *Alstonia*, *Terminalia*, *Bombax*, *Endospermum*, *Tetrameles* and *Octomeles* proclaim such a stage in the forest cycle. Meanwhile other truly leptocaul species are establishing beneath to fill in the forest frame.

It can be seen then that, first, the complexity of mature phase forest structure must have been formed; this also by its nature provided obstacles to cross-pollination, and thus initiated the evolutionary sequence of floral specialization and diversification by which our modern families are distinguished.

Meanwhile also, microsperm pachycauls evolved into the gap phase of the forest and the alpine forest fringe, and the differing conditions for reproduction there led to the origin of such other taxa as *Senecio* and *Lobelia* (Mabberley, 1973, 1974c) and eventually herbaceous forms.

It is now apparent why the Myristicaceae, primitive in so many respects and with primitive arillate fruit, have nevertheless developed the leptocaul habit with small leaves and plagiotropic branching, and flowers which are small, much reduced and borne on dioecious trees. Here is a family that has evolved with the forest from earliest times: first the fruit, then further evolution of the habit, and subsequently the flower while the earlier evolved fruit and habit continue to retain their adaptive advantage in the shade of the storied modern forest. But the Myristicaceae, as Corner points out, are tied to the rainforest by their fruit; fell the forest and they do not return.

As the origin of the primitive angiospermous fruit must be interdependent with the early evolution of vertebrate vectors, birds and mammals, so the evolution of the structure of the angiospermous rain forest-not by coevolution this time but in response to previous vegetational change-provided the means for their rapid diversification. Animal diversity, once thus initiated, in turn enhanced the coevolution of flowers and their pollen vectors, of plant hosts and their predators, which still continues and defines the modern complexity, long after the possibilities of structure, habit and leaf design had been exhausted and retained or repeated by many families.

In geological time the disposition of land masses has changed, and the area occupied by different climates, but the *range* of climates and soils can rarely have changed. Life itself provides the changing scene. Evolution of species and phyla proceeds from what has already evolved before; similarly it is in those habitats where biotic change has been greatest that we should expect major paths of further evolution to originate, not in the deserts or the mountains but in the lowland forests especially those of the humid tropics.

Why, then, do we find monocarpic pachycauls prevailing in the paramo, and the massive primitive flower more often in the mountains than the lowlands? Evolution has proceeded outwards from the lowland forests where only the ancient fruit and pinnate leaves have sometimes survived the palimpsest of subsequent biotic change in the understory. But the paramo retains the moist open conditions of the primitive angiosperm forest while the pachycaul stem is preadapted to year-round frost (Mabberley 1973, 1974a) and the structural simplicity of the montane forest, though derived and leptocaul, allows the survival of clumsy pollination systems.

It is therefore naive to conjecture the centre of angiosperm origin from modern distributions. Besides, great changes in the distribution of climates have occurred since the Jurassic, necessitating massive migration if not always extinction; even in South-East Asia Muller has shown that temperate species prevailed, presumably on long-vanished mountains, during the Miocene.

Similarly, plants only fossilize under restricted conditions. The most primitive pollen types appear not to fossilize well and it is likely anyway that plant, and possibly also fruit, form diversified both within the rainforest and into other

environments largely *before* flower and pollen diversification. Recent fossil evidence is therefore likely to be misleading. Using the Durian Theory as a basis for prediction we should pursue a different approach and should consciously search out volcanic ash deposits rather than riverine, swamp or aquatic, from the western tropical margins of the great late Jurassic oceans. If they do not exist, or bear no fossils, the origin of the angiosperms will remain enigmatic.

## REFERENCES

- CORNER, E. J. H. 1940. *Wayside Trees of Malaya*. Vol. I: 770 pp; vol. II: 228 pl. Government Printing Office, Singapore.
- 1949. The Durian Theory or the origin of the modern tree. *Ann. Bot. (N.S.)* **13**: 367–414.
- 1953. The Durian Theory extended — I. *Phytomorphology* **3**: 465–476.
- 1954a. The Durian Theory extended — II. The arillate fruit and the compound leaf. *Phytomorphology* **4**: 152–165.
- 1954b. The Durian Theory extended — III. Pachycauly and megaspermy — Conclusion. *Phytomorphology* **4**: 263–274.
- 1964. *The Life of Plants*. Pp. 315 + 41 pl. Weidenfeld & Nicholson, London.
- GIVNISH, T. J. 1975. Ecological aspects of plant morphology. Unpublished MS of paper delivered at XII International Botanical Congress, Leningrad (Abstract in [A. Takhtajan], *Abstracts of the papers presented at the XII International Botanical Congress, July 3–10, 1975*, **I**: 214).
- MABBERLEY, D. J. 1973. Evolution in the Giant Groundsels. *Kew Bull.* **28**: 61–96.
- 1974a. Branching in pachycaul Senecios: the Durian Theory and the evolution of angiospermous trees and herbs. *New Phytol.* **73**: 967–975.
- 1974b. Pachycauly, vessel-elements, islands and the evolution of arborescence in 'herbaceous' families. *New Phytol.* **73**: 977–984.
- 1974c. The pachycaul Lobelias of Africa and St. Helena. *Kew Bull.* **29**: 535–584.
- MULLER, J. 1966. Montane pollen from the Tertiary of N. W. Borneo. *Blumea* **14**: 231–235.



# The Reproductive Biology of *Durio zibethinus* Murr.

by

E. SOEPADMO & B. K. EOW

Department of Botany, University of Malaya

Kuala Lumpur

## SUMMARY

*Durio zibethinus* Murr. or the common durian is a fruit-tree species widely cultivated in villages or orchards or a semi-wild plant found growing around aborigines' settlements in Peninsular Malaysia. The species is generally considered by botanists as a native tree in Borneo and Sumatra, though currently it is commonly planted throughout South East Asia, extending from the south-eastern parts of India to New Guinea.

In Peninsular Malaysia the flowering is seasonal and normally falls during the months of March-April and September-October, though accessory flowering may take place in between. Development of flowers takes about five to seven weeks and the flowering lasts for about three weeks. Floral parts develop acropetally and the epicalyx, calyx, corolla and stamens fall off soon after anthesis. Floral anthesis is initiated at about 16.00 hrs. and completed by about 20.00 hrs. Pollination is carried out by nectarivorous bats (*Eonycteris spelaea*) and by an unidentified noctuid moth, and takes place between 20.00 and 01.00 hrs. Pollen grains are more or less spherical, 80-150  $\mu$  in diameter, 3-4- or rarely 6-porate, with a smooth but sticky exine; kept under room temperature they remain viable for about 48 hrs. The flower is self-compatible, though the percentage of successful fertilisation and production of fruit reaching maturity increase if the flowers are crossed.

The anthers though initially tetrasporangiate become bisporangiate at maturity. Wall development conforms with the basic type. Before anthesis the epidermis is made up of more or less rectangular and isodiametric cells, but towards anthesis these cells become papillate and filled with tannin, and eventually shed off from the anther wall. The endothelial cells become fibrous and both the middle layers and the tapetal layer are crushed and disappear, leaving the endothecium the only wall enclosing the pollen grains. Cytokinesis of microspore mother cells is simultaneous and gives rise to tetrahedral tetrads. Anther dehiscence is through a longitudinal slit caused by the breakdown of the wall at the meeting point of the anther-lobes. Pollen grains are binucleate at the time of shedding.

The ovule is anatropous, bitegmic and crassinucellate. The micropyle is formed by both integuments. Embryo-sac development conforms with the *Polygonum*-type. Antipodal cells are ephemeral.

The seed is arillate and its mode of germination is epigeal and takes place within three days after sowing in garden soil. Seed viability can be prolonged up to 32 days (90% germination) if the seeds are surface-sterilised, kept in an air-tight container and placed under 20°C.

## INTRODUCTION

Previous works on *Durio* (Wyatt-Smith, 1953; Kostermans, 1958; Reksodi-hardjo, 1962 and Kochummen, 1972) indicate that there are at least 28 species in the genus, distributed throughout Burma, Thailand, Peninsular Malaysia, Singapore, Sumatra, Borneo and Palawan Island. Though considered by botanists as a tree native to Sumatra and Borneo, *Durio zibethinus* or the common durian is now widely cultivated as a fruit-tree in the South Asia region, covering the south-eastern parts of India, Ceylon, Burma, Thailand, Indo-china, Malaysia, Singapore, Indonesia, the Philippines and New Guinea.

Species of *Durio* are found growing naturally in lowland and hill primary forests (up to 1000 m altitude) usually not more than 3 to 4 trees per hectare. Apart from *Durio zibethinus* there are five other species which produce edible

fruits (Reksodihardjo, 1962). These are *D. dulcis* Becc. (found in Sabah and Indonesian Borneo), *D. grandiflorus* (Mast.) Kost. (Sabah, Sarawak and the Indonesian Borneo), *D. graveolens* Becc. (Peninsular Malaysia, throughout Borneo and Sumatra), *D. kutejensis* (Hassk.) Becc. (throughout Borneo), and *D. oxleyanus* Griff. (Peninsular Malaysia, throughout Borneo and Sumatra). All five are cultivated in Brunei and some to a limited extent elsewhere in Malaysian Borneo. The other species of the genus, though not producing edible fruits, possess several desirable features for breeding and bud-grafting purposes. These features are: disease and pest resistance (most wild species), more regular flowering (*D. acutifolius* (Mast.) Kost. & *D. griffithii* (Mast.) Bakh.), flowers and fruits borne on the lower parts of the stem (*D. beccarianus* Kost. & Soeg., *pinangianus* (Becc.) Ridl. and *testudinarum* Becc.), or on the stem as well as on the lower branches (*D. malaccensis* Mast.). Though this does not necessarily mean that all species are easily hybridised, it does imply that, since the specific delimitation of the genus is mainly based on morphological attributes and since there are several species which are closely related to each other (e.g. *D. zibethinus*, *malaccensis* and *wyatt-smithii* Kost.), and, there seem to be many intermediate forms among natural populations of and between species, there is a possibility to improve the quality as well as the productivity of the existing edible-fruit producing species, at least by bud-grafting.

In spite of the fact that durian fruit is of high economic importance to local inhabitants (Lai, 1974), as far as we know there is no large scale plantation or estate in the region, nor is there a well documented and systematic breeding and selection programme. This lack of interest may partly be due to the fact that very little is known about the autecology, flowering biology, cytology and breeding system of the species. The only paper dealing with some aspects of reproductive biology of *Durio* species so far published is that by Valvayor, Coronel & Ramirez in 1965.

It is therefore the aim of the present study to gather more information about *D. zibethinus* and its related species so that their economic potential and contribution to "durianology" in general is not completely forgotten.

## MATERIALS & METHODS

Field work to determine the distribution and frequency and to observe the phenology, floral anthesis and pollination processes of *D. zibethinus* and its related species was carried out in the University of Malaya campus, Damansara village, Ulu Gombak, Mantin and Kuala Selangor (all in Selangor State), Kuala Pilah and Pasoh Forest Reserve (in Negri Sembilan), Krau Game Reserve, Taman Negara and Tioman Island (Pahang). For detailed studies on the floral anthesis and for pollination experiments, a tree growing in the compound of the Faculty of Agriculture, University of Malaya was used.

Flowers of different developmental stages were collected regularly during the flowering periods, fixed in 50% F.A.A. solution and then sectioned and stained according to normal schedules. Guano samples were collected weekly from Cavern C of the Batu Caves Limestone Hill from February 1974 to January 1975. Pollen content was extracted from these samples and acetolysed and then stained with safranin.

## OBSERVATIONS & RESULTS

*Phenology.* Depending on the clones, soil and climatic condition in which the durian tree is planted, it starts to bear flowers and fruits at the age of 5 to 12 years. In Peninsular Malaysia there seem to be two main flowering seasons, normally falling in the period of March-April and September-October. However, it should be noted that minor or accessory flowering may occur in between. The flowers are born in fascicles of 3-30 on the older branches. Flowers of the same

inflorescence usually mature more or less at the same time and open one after another within a few days. Since during the flowering each individual tree produces hundreds of flowers, and the maturation of the flowers of different inflorescences is not necessarily synchronised, the flowering period of a particular season usually lasts for about two or three weeks. It was also observed that normally the first flowering of a particular year is heavier than the second. What causes this remains to be investigated. The fruit set is usually very low since many of the ovaries will drop after anthesis, either because their ovules are not fertilised or have been disturbed or destroyed by the pollinators. Fruits take approximately three months to reach maturity.

*Floral morphology and development.* At its early stage of development, each individual flower-bud is a globose structure made up of a mass of homogeneous cells surrounded and enclosed by bracts and epicalyx. The sepaline, petaline, staminal and carpellary primordia develop acropetally at more or less the same rate. The anthers develop from the distal cells of the phalanges as globular protuberances. Each protuberance is composed of a homogeneous mass of meristematic cells surrounded by an epidermis. As the phalanges elongate and differentiate into distinct filaments the developing young anthers assume their 4-lobed appearance. Just before anthesis the buds attain a size of about 2 cm in diameter. Both the epicalyx and calyx are externally densely covered with brownish peltate fimbriate scales, and the petals are yellowish-white and sparsely hairy outside. The scales are multicellular and originate from the epidermal cells. The nectary is located at the inner basal part of the calyx-cup. At anthesis the flower reaches about 5-6 cm long and 2-3 cm in diameter and emits a strong odour reminiscent of sour milk but somewhat fragrant. The carpels develop and originate from a common primordium situated at the centre of the flower-bud. This primordium is made up of homogeneous and more or less isodiametric cells. These cells divide and differentiate into five carpels which fuse at their marginal and central parts to form a 5-loculate ovary with a central placental column. The style is formed by vertical growth of the five carpels and is topped by a capitate stigma. The stigmatic surface is uneven in outline with deep depressions or notches here and there (Plate 4a). By the time the megaspore mother cell is formed, the spine-primordia of the ovary wall start to develop. These primordia originate from the hypodermal layer and appear as conical protuberances each of which is topped by a multicellular, peltate and fimbriate scale similar to those of epicalyx and calyx. As the flower develops fully, cells in the tissues of the epicalyx, calyx and petals contain tannin and become mucilaginous.

*Development of anther-wall.* In each of the anther lobes and just below the epidermis, a row of hypodermal cells increase in size and contain more conspicuous nuclei and denser cytoplasm. These cells form the archesporial tissue. Each archesporial cell divides periclinally into a primary parietal cell and a primary sporogenous cell (Pl. 1a). The primary parietal cell further divides periclinally into two secondary parietal cells. The outer secondary parietal cell divides once again to give rise to an endothelial cell and outer middle-layer cell. The inner secondary parietal cell also divides further and produces the inner middle-layer cell and the tapetal cell. Thus the anther-wall formation conforms well with the basic type. By the time the sporogenous cell divides and produces numerous microspore mother cells, the anther wall is greatly stretched and the middle layers as well as the tapetum are crushed and their cells become flattened. Meanwhile through the disintegration of the septa separating the four original anther cavities, the anther becomes two-loculate. Towards the end of meiosis the epidermal cells become papillate and filled with tannin, and just before the anther dehisces they are shed off leaving the endothelial cells as the only surviving wall enclosing the pollen grains. At this stage the wall of the endothelial cells becomes fibrous and the wall thickening appears as radially oriented bar-like structures.

*Microsporogenesis.* By the time the anther wall attains its 4-cells thickness, the primary sporogenous cell divides into two daughter cells (Plate 1b). These cells divide both periclinally and anticlinally to form numerous microspore mother cells (Plate 1c & d). Meiotic division starts from those microspore mother cells situated at the centre of the anther cavity and progresses outwards (Plate 1e & f). Many of the peripheral microspore mother cells fail to complete the division and become abortive and assume a flat outline. The first division of the microspore mother cell is not immediately followed by wall formation (Plate 1e). The resulting four microspores are formed simultaneously and clustered in a tetrahedral arrangement (Plate 1f). At the time of shedding most of the pollen grains are binucleate. It may be noted that development as well as formation of microspores are not synchronised in all anthers of the same flower.

*Pollen morphology.* Mature pollen grains are more or less spherical, 3-4 rarely 6-porate, and measuring 80-150  $\mu$  in diameter (Plate 2a). The exine is very much thicker than the intine, smooth but covered with sticky substances, and thicker around the pores. At anthesis they are released singly or in clumps (Plate 2b).

*Pollen germination.* Pollen grains collected from the anthers at the beginning of floral anthesis do not show any sign of germination, but those collected from the fallen phalanges on the following morning start to germinate. Two hundred of these pollen grains were kept under room temperature, and after 40 hours from 23.5 to 80% of the pollen grains germinated. This seems to indicate that stigmatic exudate is not the sole prerequisite of germination and that kept under room temperature the pollen remain viable for at least 48 hours. Germination experiment using sucrose solution of various concentrations shows that after culturing the pollen for 12 hours, the optimal percentage of germination (c. 77%) takes place in 6% solution. In this experiment it was also observed that the higher the concentration of the sucrose, the longer the pollen-tube is.

*Development of ovule.* In each of the carpellary cavities two alternate rows of 5-7 ovular primordia appear from the central placental column as minute and somewhat conical protuberances (Plate 2c). Each primordium is at first composed of homogeneous, thin-walled and more or less isodiametric cells, but later one of the hypodermal cells becomes larger in size than the surrounding cells and contains dense cytoplasm and a more conspicuous nucleus (Plate 2c). This cell develops into the archesporial cell and divides periclinally into a primary parietal cell and sporogenous cell (Plate 2c). The primary parietal cell divides periclinally and anticlinally to form the 5-6 cells thick nucellus. Soon after the division of archesporial cells is completed, the integument primordia develop more or less simultaneously on both sides of the nucellus (Plate 2d). However, the outer integument grows faster and eventually overtops the inner one. The micropyle is formed by both the inner and outer integuments. At the formation of the megaspore mother cell the integuments are 2-3 cells thick, and later more cells are laid down. Several cells of the outer integument are eventually filled with tannin. It may be noted here that on two occasions binucleate ovules were observed. The two nucelli are enclosed by a common outer integument but each has its own inner integument.

*Megasporogenesis.* The sporogenous cell enlarges and functions as the megaspore mother cell (Plate 2d). This cell divides into two (not seen) and eventually into four daughter cells arranged in a linear tetrad (Plate 2e). Three of these daughter cells degenerate, leaving the cell at the chalazal end to develop further. This functional megaspore undergoes vacuolation and forms an elongated uninucleate embryo-sac. Subsequently it passes through two-, four- and eight-nucleate stages before cytokinesis commences (Plate 3a, b & c). One of the four micropylar daughter nuclei moves towards the centre of the embryo-sac, and the other three form the egg apparatus and two synergids. Similarly, one of the chalazal nuclei also moves to the centre of the embryo-sac while the other three form the ephemeral antipodals (Plate 3c & d). The two polar nuclei then fuse

with one another to form the secondary polar nucleus (Plates 4c & 5a). The development of the eight-nucleate embryo-sac, therefore, conforms well with the *Polygonum*-type.

**Pollination.** Opening of the flower usually takes place according to the following sequence: epicalyx splits into 2–3 ovate-concave lobes about 12–24 hours before anthesis; the calyx then splits open at its tip into 5–6 acute lobes about 8–10 hours before anthesis; for the next two hours or so the petals, styles and stamens which initially take an incurved position within the calyx become fully exerted and soon after dark the petal-lobes become recurved outwards exposing both stamens and styles; meanwhile some of the anthers may start to dehisce but the majority do not do so before c. 19.30 hrs; the stigmatic surface becomes receptive at about 20.00 hrs. The flower remains at this stage until about 01.00 hrs., and then the calyx, petals and stamens begin to drop off, leaving the lone ovary remains attached to the branch. Though initially many of these ovaries remain attached to the branch following pollination, within a few days most of them drop off and leave only 1–2 per inflorescence.

During the late afternoon, the flowers are visited by various insects as they open. Among these are honey bees, house-flies, lady-bird beetles, scarab beetles, and lacewings. Pollen grains were found on the legs and bodies of these insects but not in their guts. Since these insects visit the flowers before the latter reach full anthesis, they cannot be considered as pollinators. In the evening, namely between 20.00 and 01.00 hrs, the flowers are visited by three different species of bats. These are the nectarivorous bat (*Eonycteris spelaea*) and the frugivorous bats *Cynopterus brachyotis* and *Pteropus vampyrus*. Occasionally nocturnal moths also visit the flowers during this period. Among the bats, only *Eonycteris spelaea* could be considered as the genuine pollinator, since the other two directly feed on and chew up the flowers (Start, 1974). Our observation suggests that *Eonycteris spelaea* feeds on nectar as well as on pollen grains, and it does not chew the flower. The bats also visit the flowers regularly during the flowering season; they land on and clutch the flowers with the frontal parts of their body facing the open flowers. Analysis of guano samples also confirms that pollen grain of *Durio zibethinus* constitutes a significant part of the bat's diet during durian flowering season and that the highest number of grains in the samples coincides well with the flowering season of the trees. Other important pollen grains found constantly in the guano samples are those of *Parkia*, *Ceiba pentandra* (L.) Gaertn., *Bombax vuletonii* Hochr., *Oroxylon indicum* Vent., *Duabanga grandiflora* (Roxb. ex DC.) Walp., *Artocarpus* spp. (Plate 6a-d). This suggests that the bats feed on nectar or pollen, or both, of different species of plants which flower at different times of the year, and pollinate the flowers.

**Pollination experiments.** To test the compatibility of the flowers, a series of preliminary experiments were carried out during the flowering seasons in 1974. In each experiment a set of 20 flowers having a similar stage of development were selected and tagged. These flowers were then given the following treatments: (1) all anthers were removed at anthesis and the stigmas were exposed to natural pollinators, (2) the flowers were bagged before anthesis, (3) the stigmas were applied with Cutex nail varnish to prevent pollination, (4) the flowers were self-pollinated by hand and bagged, and (5) the anthers were removed and the stigmas were cross-pollinated by hand with pollen of other flowers of the same tree, and then bagged. At the beginning of these experiments the ovaries of all flowers used were between 0.35 and 0.4 cm in diameter and light-brown in colour. After 5 days all tagged flowers were re-examined and the following results were obtained: in treatment no. 1, 45% of the ovaries remained attached to the branch and showed further development, i.e. increase in diameter (0.5–0.6 cm) and change in colour to olive green; in experiment no. 2, only 15% of the ovaries showed further sign of development and the others either shrivelled or fell off; in the 3rd treatment

none of the ovaries underwent further development and shrivelled or dropped off; in the 4th, 50% of the ovaries exhibited further development and remained attached to the branch; and in the 5th 65% of the ovaries underwent further development and remained attached to the branch. At the end of the flowering season only 5% of the successfully pollinated ovaries developed into mature fruits.

The above experiments seem to suggest that (i) natural pollinators contribute at least 45% of the successful pollination, (ii) natural self-pollination can take place and contribute to 15% successful pollination, (iii) pollination is a prerequisite of fruit development, (iv) up to 50% of the flowers are self-compatible, and (v) cross-pollination between flowers of the same tree is the better means for successful fertilisation and eventual fruit development.

However, it should be emphasised here that since the number of flowers used in the experiments is small and the work was conducted on a single tree only, the above mentioned results should be considered as tentative. Future experiments using larger number of flowers and trees will either confirm or contradict the above results.

*Fertilisation.* The receptive stigma is heavily papillate and has a glistening and sticky surface. Pollen grains deposited on the stigmatic surface germinate within 3 or 4 hours. The germinating pollen grains are mostly monosiphonous, and the tubes make their way through the stigmatic papillae into the style. The pollen tubes grow downwards through the intercellular spaces of the vertically elongated protoplasmic cells of the transmitting tissue (Plate 4b). The successful tube enters the embryo-sac through the micropyle (Plate 4d). Although hundreds of slides were examined by us, the actual process of fertilisation has not been observed in detail. From the specimens available it seems that just before fertilisation the secondary polar nucleus moves nearer to the egg apparatus (Plates 4e & 5a).

*Endosperm.* The secondary polar nucleus which is situated near to the egg apparatus is then fertilised by one of the male gametes to form the primary endosperm cell (Plate 5a). This cell enlarges and undergoes free nuclear division. Most of the nuclei produced are distributed along the periphery of the embryo-sac and aggregated mainly at the chalazal end (Plate 5b). The endosperm remains in a free nuclear condition until a late stage of embryogeny and then becomes cellular.

*Development of embryo and seed.* In the present study the embryogeny has not been followed in detail. Sections of developing seed indicate that the endosperm does not persist and the cotyledons occupy the greater part of the seed cavity. The starchy food reserve is therefore stored in the cotyledons. Cells of the inner integument are crushed and disappear, and those of the outer integument become fibrous with the epidermal cells developing into rectangular and heavily lignified stone cells each with a very small lumen. The aril develops from the funicular end and eventually completely encloses the seed. This aril is very variable in thickness, colour, taste, smell and moisture content. It may be noted here that in a few clones, there is a high incidence of seed abortion, in which the seeds shrivel and measure less than 4 by 1.5 cm, while fully developed and viable seeds measure up to 7 by 4 cm.

*Seed germination.* The first sign of germination is indicated by cracking of the hilum at the micropylar end, and this takes place within 3 to 4 days after sowing the seeds in suitable medium. The radicle will emerge from this crack, elongate and grow downwards. After approximately 10 days numerous lateral roots appear at the proximal end of the radicle and the hypocotyl elongates and straightens up bringing the cotyledons still enclosed by the testa slightly above the soil surface. Subsequently the petioles or stalks of the cotyledons elongate allowing the plumule to emerge. The plumule elongates and from it the first and second leaves appear. These leaves are much smaller than the normal leaves and are deciduous. The cotyledons shrivel and drop off within 38 days following germination.

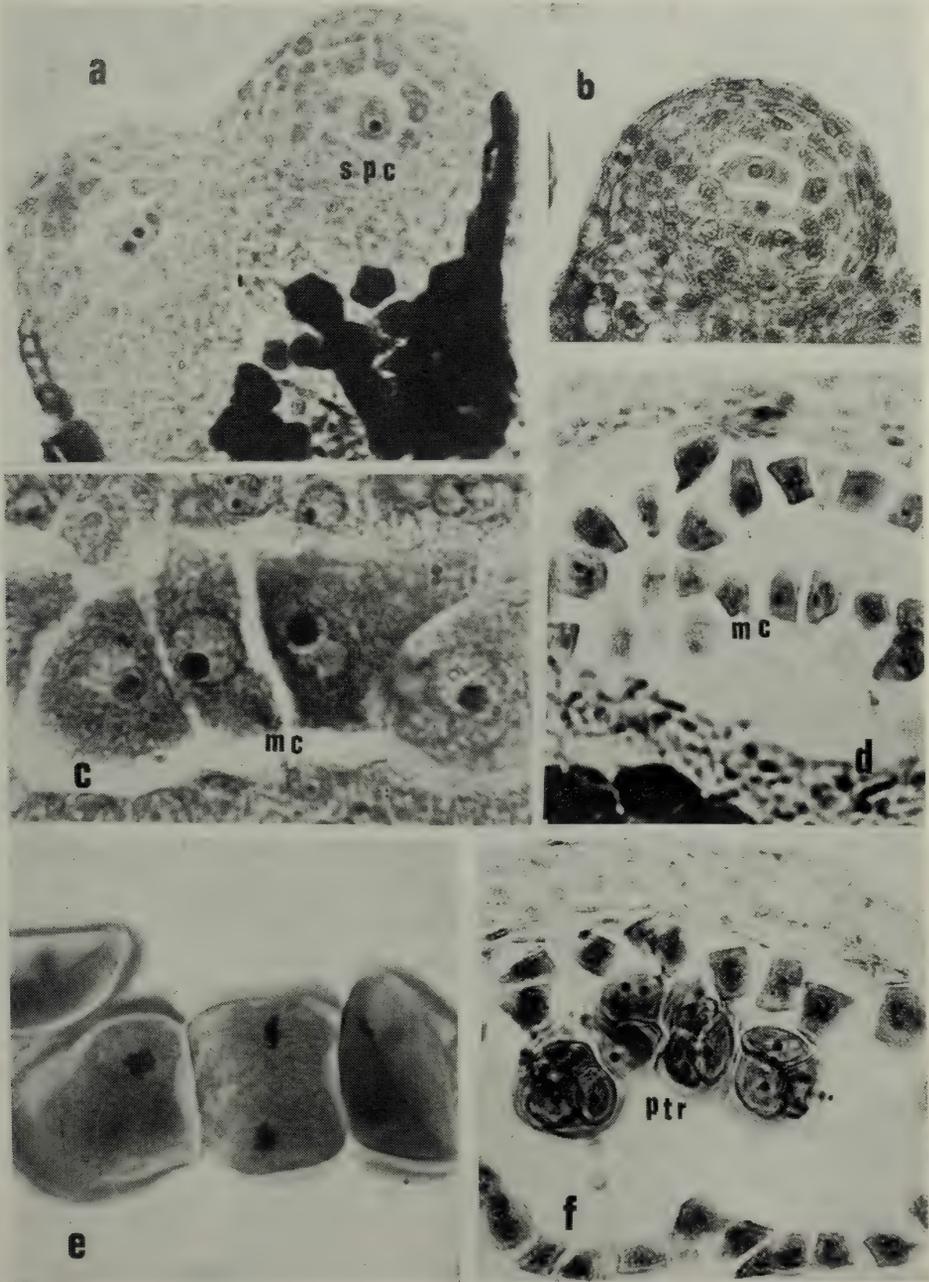


Plate 1: *a* & *b* developing anthers with sporogenous cell (*spc*); *c* & *d* dividing and developing microspore mother cells (*mc*); *e* division of microspore mother cells; *f* end of meiosis and formation of pollen tetrads (*ptr*).

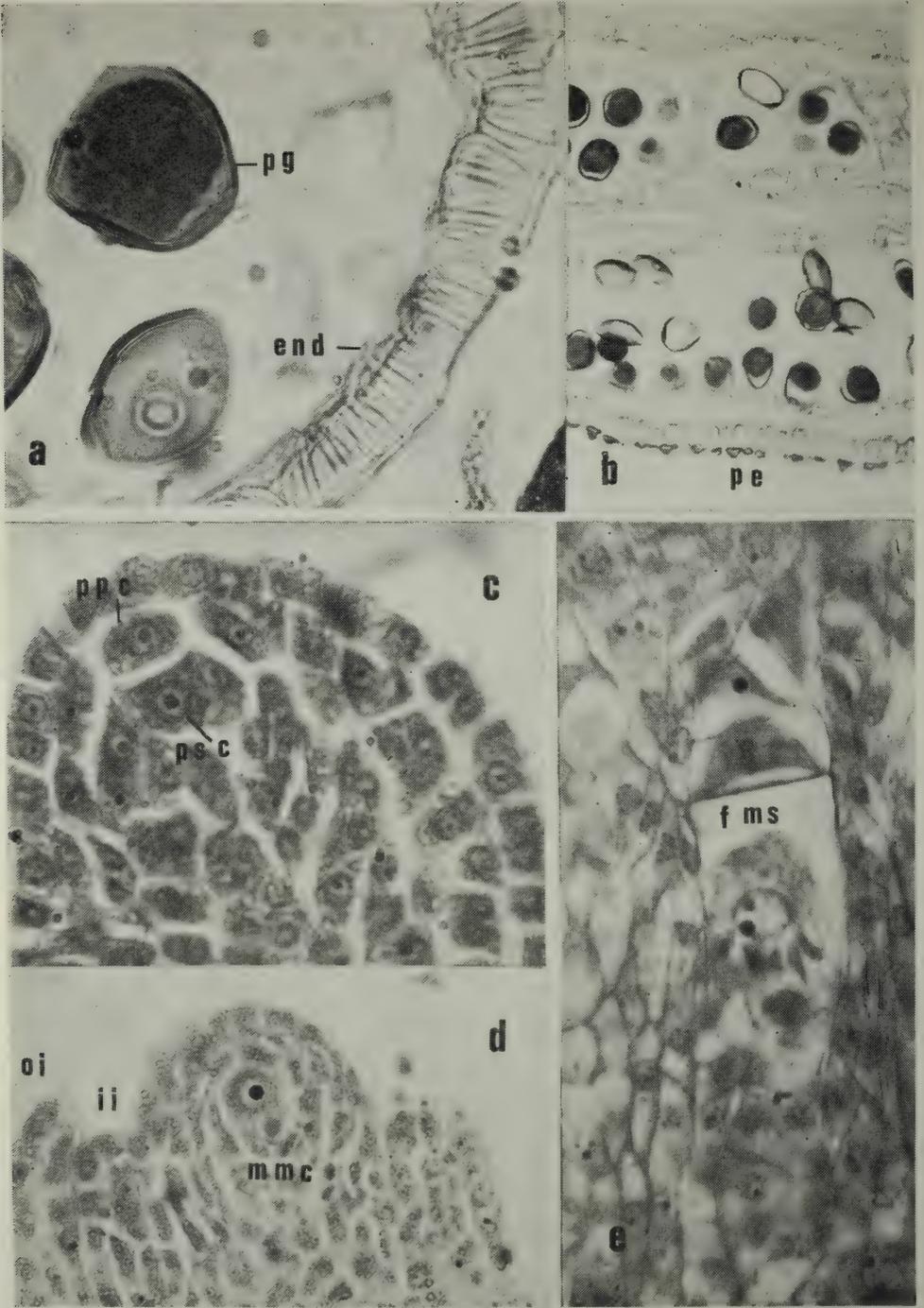


Plate 2: *a & b* cross-sections of anthers just before anthesis showing fibrous endothecium and mature pollen grains; *c* ovule primordium showing primary parietal cell (ppc) and primary sporogenous cell (psc); *d* ovule primordium showing developing megaspore mother cell (mmc) and integuments; *e* linear tetrad and functional megaspore (fms).



Plate 3: *a* 2-nucleate embryo-sac; *b* 4-nucleate embryo-sac; *c* & *d* 8-nucleate embryo-sac; pn = polar nuclei.

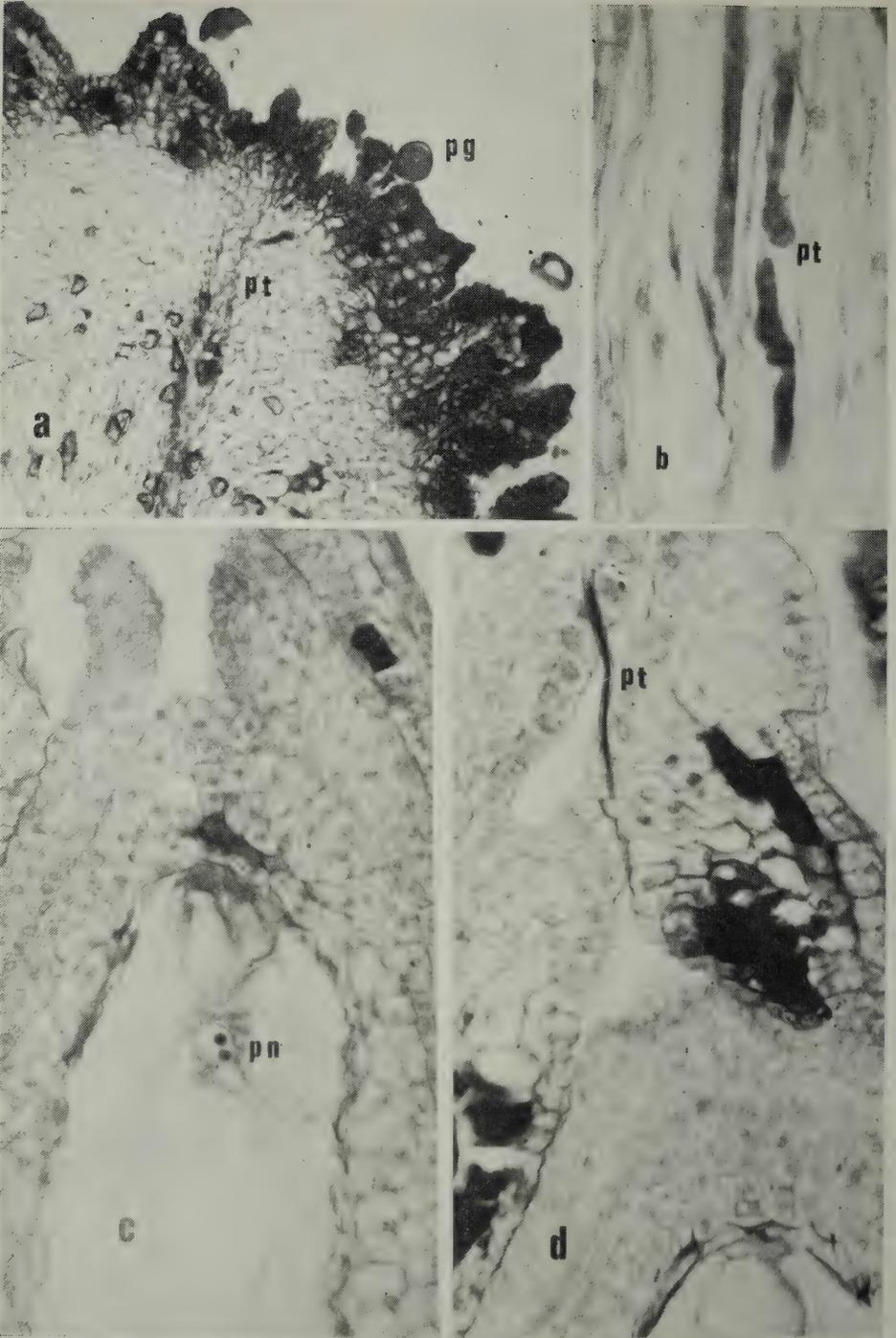


Plate 4: *a* longitudinal section of stigma (pg = pollen grain; pt = pollen tube); *b* pollen tube (pt) growing downwards through the stilar tissue; *c* migration of polar nuclei (pn) towards micropylar end of the embryo-sac; *d* pollen tube (pt) entering embryo-sac through micropyle.

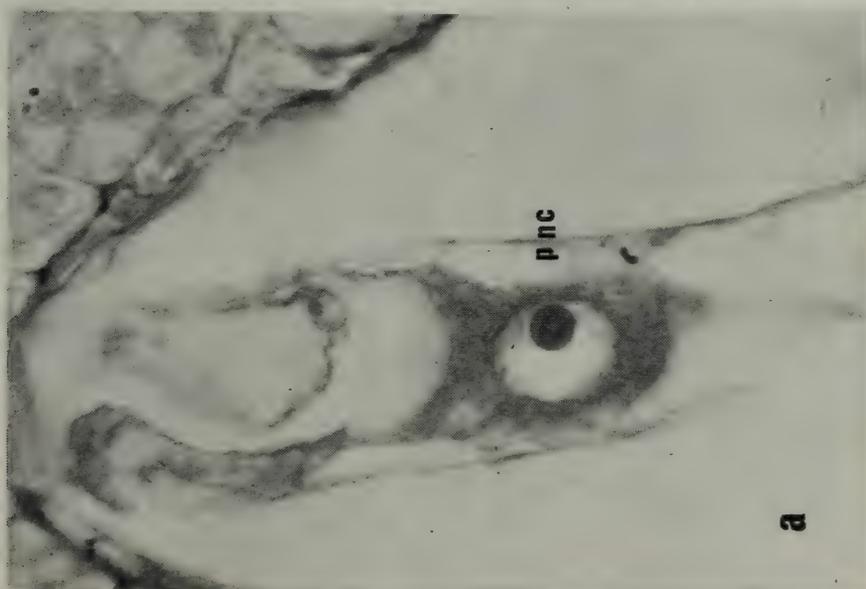


Plate 5: *a* formation of secondary polar nucleus (pnc) just before fertilisation; *b* nuclear endosperm (ne).

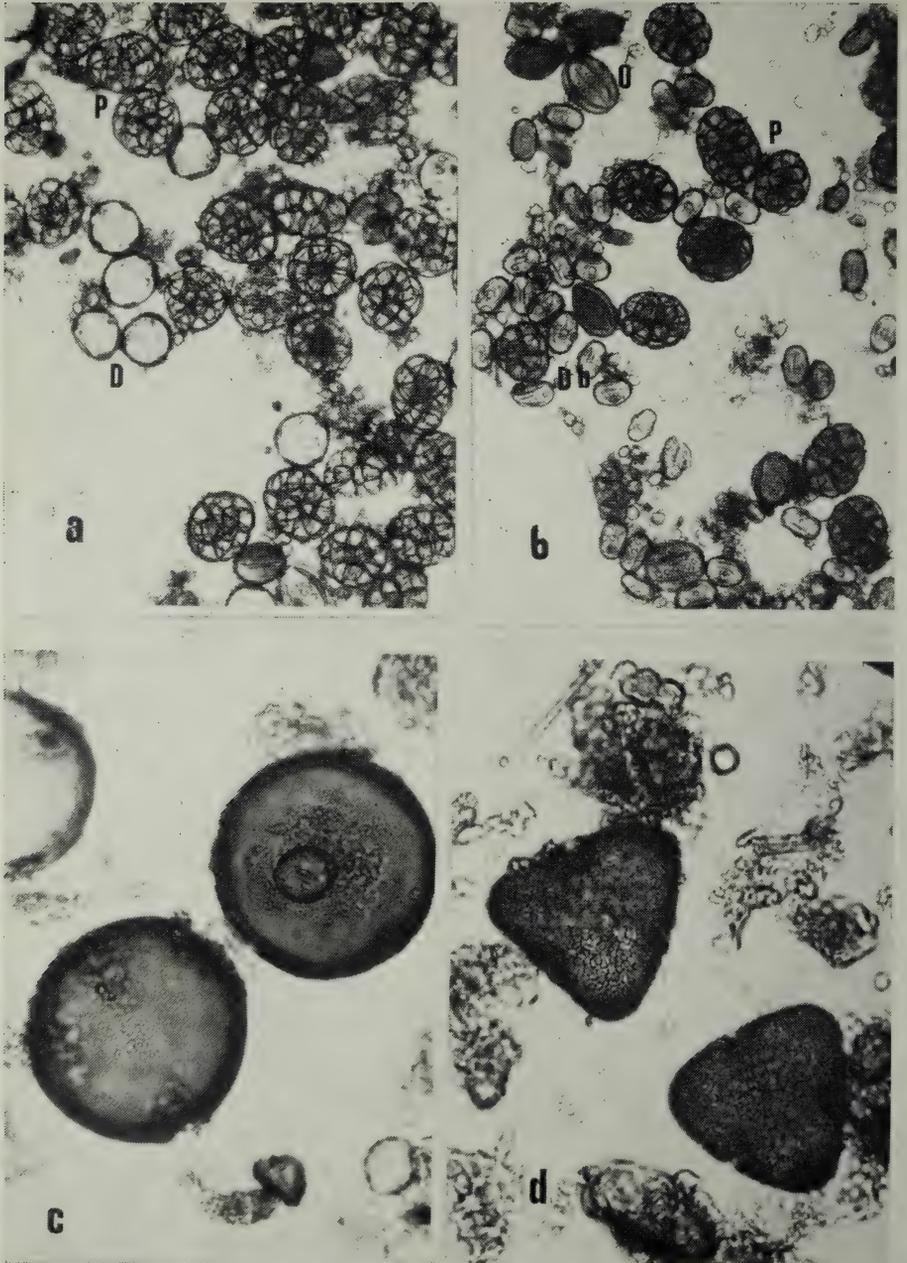


Plate 6: a & b pollen grains extracted from guano samples (D = *Durio*; P = *Parkia*; Db = *Duabanga grandiflora*; O = *Oroxylon indicum*); c pollen of *Durio zibethinus*; d pollen of *Bombax vuletonii*.

Experiments show that: (i) if the aril is removed from the seedcoat, up to 95% of the seeds tested germinate 3 days after sowing in various media (saw-dust, sands, and garden soil); (ii) if the aril is not removed, only 40% of the seeds begin to show signs of germination 6 days after sowing, and to reach 95% germination rate, 10 days after sowing is required; (iii) though initially there seems to be no significant difference in percentage of germination, for further growth of seedlings the garden soil is the best medium; (iv) the average moisture content of a fresh seed is c. 51% (wt). Kept under room temperature (36°C) the moisture content drops to c. 23% after 32 days of storage. If, however, the temperature is lowered to 20°C and the seeds are stored in an air-tight container, the moisture content can be kept at 43–45% level for the same length of storage time; (v) surface sterilised, kept in an air-tight container and stored under 20°C the seeds remain viable (up to 90% germination rate) for at least 32 days, but if the seeds are stored under 36°C they lose viability after only 6 days' storage.

### DISCUSSION

From the foregoing chapters it is evident that in order to understand the reproductive biology and the breeding system of *D. zibethinus* and its related species, and to appreciate their economic potential, more detailed studies remain to be carried out in the future. In particular, the questions — whether all existing varieties and clones are self-compatible or require cross-pollination to produce a good crop of fruits, and whether it is possible at all to hybridise at least the closely related species of the genus, etc. — remain to be clarified.

Our observation on a single tree suggests that, in this particular clone at least, there is a certain degree of self-compatibility if the flowers are cross-pollinated by hand. This seems to disagree with the results obtained by Valmajor and his co-workers (1965) in the Philippines, in which they observed that all trees under their investigation were completely self-incompatible, and that the trees set fruits only if they were reciprocally cross-pollinated. However, since in Peninsular Malaysia alone there are at least 44 clones (Ho, 1971), differing slightly from one another in their fruit-yield, intensity and frequency of flowering, floral and fruit morphology, and quality of the aril, it is reasonable to assume that different clones might have different patterns of breeding system and reproduction. This assumption is substantiated by the fact that among the clones observed there are trees which have the styles shorter than the stamens and exerted from the enclosing corolla more or less at the same time with the stamens; and, there are those trees which possess styles longer than the stamens and exerted from the enclosing corolla before the stamens, with the stigmas thus positioned way above the anthers. Judging from the way the bats alight on the flowers during feeding, it seems likely that in the first category of clones both self- and cross-pollination are possible, whereas in the second case only cross-pollination can take place. Furthermore, since in the latter case there is a time interval intervening between the dehiscence of anthers and the receptivity of the stigmas, under natural condition only cross-pollination between flowers of the same or of different trees is possible. In this case any pollinator alighting on the flowers before the stigmas become receptive will not affect pollination, but during feeding, pollen grains of dehiscing anthers may get attached to the mouth and frontal parts of the pollinator's body. In moving and alighting to another flower later in the evening the pollinator will brush pollen grains on the now receptive stigma.

In their paper, Valmajor and his co-workers stated further that reciprocal cross-pollination by hand of the self-incompatible trees resulted in 87.3 to 90% fruit set. This is obviously a very high rate of fruit set by any standard, since at least in Peninsular Malaysia, 20 to 25% fruit set is generally considered as a very good crop already. In addition to this, our experiment also shows that up to 65%

successful pollination can be obtained if the flowers are cross-pollinated by hand with pollen grains of other flowers of the same tree. These seem to suggest that if a means could be found to store and keep the pollen grains viable for a longer period than their natural viability, and a method could be devised to deposit pollen grains on the receptive stigmas efficiently, artificial pollination may turn out to be the best way to increase fruit production of a durian tree.

With regard to the possibility of hybridizing at least the closely related species of the genus, Reksodihardjo (1962) stated that a natural hybrid between *D. zibethinus* and *D. graveolens* has been discovered in the north-eastern parts of the Indonesian Borneo. More recently, Heaslett (1972) reported that in Johore State he found several trees of *D. malaccensis* with pink- or red-tinged flowers. Since normally this species has a white or creamy flower, and moreover in Peninsular Malaysia the only species with pink or red flowers are *D. lowianus* King and *D. pinangianus* (Kochummen, 1972), the trees observed in the forests of Johore by Heaslett may yet represent another natural hybrid between parents of closely related species. If the status and origin of these "natural hybrids" could be determined and confirmed, then there is a great possibility that through a breeding and selection programme much improved clones could be obtained.

Finally it is re-emphasised here that the detailed processes of fertilisation and embryogenesis, the significance of binucellate ovules and high incidence of seed abortion, and the factors affecting the development and quality of the edible aril also need further studies.

#### ACKNOWLEDGMENTS

We wish to express our sincere thanks to the Vice Chancellor of the University of Malaya and to the Director of the Malaysian Agricultural Research and Development Institute (MARDI) for the research grants which made the present work possible.

We are also very grateful to Dr. N. Prakash for his kind cooperation and help given during the execution of this work and to Dr. P. S. Ashton for his constructive criticisms on the manuscript. For their technical assistance we are very much obliged to Mrs. Babe Foo and Mr. Mahmud bin Sider.

Finally we would like to thank Prof. E. J. H. Corner for his continual interest and encouragement extended to us in pursuing works on tropical plants.

#### SELECTED BIBLIOGRAPHY

- ALLEN, B. M. 1967. *Malayan Fruits*. Donald Moore Press Ltd., Singapore. pp. 94-99.
- BURKILL, I. H. 1935. *A Dictionary of Economic Products of the Malay Peninsula*. Vol. 1, 871-875. Crown Agents for the Colonies, London.
- CORNER, E. J. H. 1949. The Durian Theory or the origin of the modern tree. *Ann. Bot.* **13**: 267-414.
- 1952. *Wayside Trees of Malaya*. 2nd ed., vol. **1**, 437-440. Government Printing Office, Singapore.
- 1953. The durian theory extended. *Phytomorphology* **3**: 465-476; *ibid.* 1954, **4**: 152-165; 263-274.
- 1964. *The Life of Plants*. Weidenfeld and Nicholson, London.
- DAVIS, G. L. 1966. *Systematic embryology of the Angiosperms*. John Wiley & Sons Inc., N. Y. pp. 59-60.

- FAEGRI, R. & L. van der PIJL 1966, *The Principles of Pollination Ecology*. Pergamon Press, London.
- HEASLETT, E. A. 1972. *Durio malaccensis* Planch. with pink-tinged flowers. *Malay. Nat. J.* **25**, 39.
- HO, C. C. 1971. Status of conservation of genetic resources of indigenous crops in Malaysia. *Pl. Introd. Rev.* **8**. C.S.I.R.O. Australia, 28-49.
- JONG, K., B. C. STONE & E. SOEPADMO 1973. Malaysian Tropical Forest: An underexploited genetic reservoir of edible-fruit tree species. *Proc. Symp. Biol. Res. & Nat. Dev.*, Mal. Nat. Soc., 113-121.
- KOCHUMMEN, K. M. 1972. Bombacaceae. In T. C. Whitmore (Ed.), *Tree Flora of Malaya*, **1**: 100-120. Longman Malaysia Sdn. Bhd., Kuala Lumpur.
- KOSTERMANS, A. J. G. H. 1958. The genus *Durio* Adans. *Reinwardtia* **3**: 357-460.
- LAI, ANDREW K. K. 1974. The economics of establishing a 500-acre fruit orchard in Peninsular Malaysia. *Malay. agric. J.*: **49**: 421-432.
- MEIJER, W. 1969. Fruit trees in Sabah (North Borneo). *Malay. Forester* **32**: 252-265.
- NG, F. S. P. 1973. Germination of fresh seeds of Malaysian trees. *Malay. Forester* **36**: 54-65.
- NG, F. S. P. & H. S. LOW, 1974. Flowering to fruiting periods of Malaysian Trees. *Malay. Forester* **37**: 127-132.
- OCHSE, J. J. & R. C. BAKHUIZEN v.d. BRINK Sr. 1931. *Fruits and fruit cultures in the Dutch East Indies*. pp. 27-30.
- REKSODIHARDJO, W. S. 1962. The species of *Durio* with edible fruits. *Econ. Bot.* **16**: 270-282.
- START, A. N. 1974. The feeding biology in relation to food source of nectarivorous bats (Chiroptera: Macrogloninae) in Malaysia. Unpublished Ph. D. Thesis, Department of Zoology, University of Aberdeen, Scotland.
- VALMAJOR, R. V., R. E. CORONEL & D. A. RAMIREZ, 1965. Studies on floral biology, fruit set and fruit development in Durian. *Philipp. Agric.* **47**: 355-366.
- WYATT-SMITH, J. 1954. Materials for a revision of Malayan *Durio* with notes on Bornean species. *Kew Bull.*: 513-532.



# The Syncarp of *Artocarpus* — a unique biological phenomenon

by

FRANCES M. JARRETT

*Royal Botanic Gardens, Kew*

The unique compound fruit or syncarp of *Artocarpus* is a fascinating object of study, both for its basic morphology and for its structural and functional diversity. The opportunity that was given to me as a student of Professor Corner to continue his studies on *Artocarpus* and carry out a revision of the genus (Jarrett 1959a, 1959b, 1960) is one that I shall always appreciate. In honouring him in this volume it may be of value to provide a general consideration of the syncarp, drawing together facts that became somewhat scattered in my monograph. The insights into both its internal structure and its biological significance originated with Professor Corner. The revisionary work extended knowledge of the syncarp structure to nearly all species of the genus and made it possible to place the variations observed in a more detailed taxonomic framework.

If one turns first to the morphology, it is found that in *Artocarpus* the compound inflorescence of the Moraceae is condensed into capitate, unisexual inflorescences in which each of the numerous perianths contains a single stamen or ovary. In the male inflorescence the perianths remain free (as they do in both sexes in the allied genus *Prainea*) but in the female head the perianths are more or less completely fused. Where the fusion is only partial it occurs in a highly specialized manner, which is not evident until the syncarp is dissected. It can then be seen that each perianth has a proximal free tubular region with a broad lumen enclosing the ovary. Distally, however, the perianths are early adnate to their neighbours, either fusing with them completely or leaving the perianth apex free. They thus form a continuous external wall to the syncarp which has considerable mechanical strength and is pierced only by the narrow lumen in each perianth through which the style is exerted. Passing from the axis to the outer surface, each perianth thus has either two or three zones, free—fused or free—fused—free. The latter condition was illustrated by Corner (1939) for *A. integer* (Thunb.) Merr. and *A. heterophyllus* Lam. The varying internal structure of the syncarp and some aspects of its external appearance are illustrated below.

In other species, however, the fusion between the perianths is complete or, alternatively, it may be said that the ovaries are enclosed in cavities in a receptacle in which axial and floral elements are not clearly distinguishable.

This then is the basic structure of the compound syncarp of *Artocarpus*, but such a highly specialized and apparently restrictive ground plan can, nevertheless, allow considerable morphological and biological diversity, especially in those species in which the perianths remain free proximally. Monographic study of *Artocarpus* showed that these variations could be linked with the taxonomic subdivision of the genus in which other characters, especially details of leaf anatomy, were taken into consideration, although it also became evident that some parallel evolution had occurred in the syncarp.

Thus a primary taxonomic subdivision into two subgenera, *Artocarpus* and *Pseudojaca*, which can readily be made on the basis of spirally arranged *versus* alternate and distichous leaves, and amplexicaul *versus* lateral stipules, can be

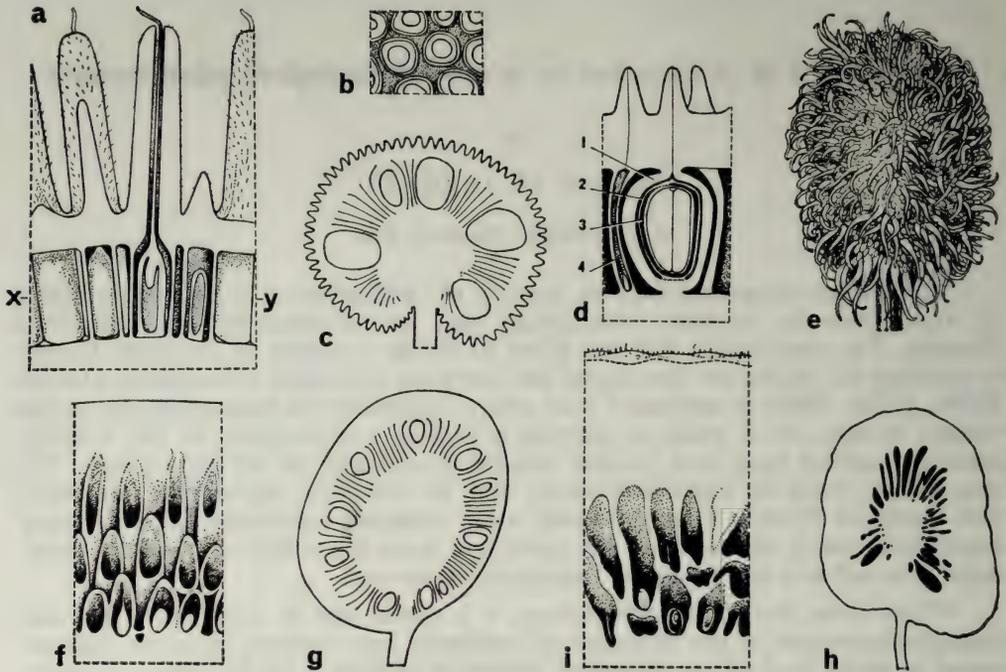


Fig. 1. The syncarp in *Artocarpus*. Subg. *Artocarpus*. *A. hispidus*. a, b, longitudinal section and tangential section in plane x-y at anthesis,  $\times 10$ ; c, longitudinal section at maturity,  $\times \frac{1}{2}$ ; d, part of the same (1, fruiting perianth; 2, ovary; 3, testa; 4, unexpanded perianth),  $\times 1$ . *A. elasticus*. e, submature head,  $\times \frac{1}{2}$ . Subg. *Pseudojaca*. *A. peltatus* Merr. f, oblique section at anthesis (perianths free proximally),  $\times 2\frac{1}{2}$ ; g, longitudinal section at maturity,  $\times \frac{1}{2}$ . *A. fulvicortex* Jarrett. h, oblique section at anthesis (perianths completely fused),  $\times 1$ ; i, part of the same,  $\times 3$ . a-d redrawn from Jarrett (1959a).

correlated quite closely with syncarp characters. In subg. *Artocarpus* the syncarp is usually ellipsoid or cylindric and the perianths are nearly always free both proximally and at the apex. Most species can in fact be identified by the perianth apices alone (cf. Jarrett, 1959b, f. 16). In subg. *Pseudojaca*, on the other hand, the syncarp is much more uniform in appearance. It is either subglobose or shallowly lobed with a smooth or papillate surface and although in most species the perianths are free proximally, there are several in which they are completely fused.

*Artocarpus* subg. *Artocarpus* was further subdivided (Jarrett, 1959b) into two sections based mainly on characters of the inflorescence, including those of the embryo, and into several series based primarily, though not solely, on the distinctive, microscopic, capitate hairs on the leaves. Considered biologically and morphologically, three different syncarp types can be recognised in the subgenus corresponding with one or more of these taxonomic subdivisions, while subg. *Pseudojaca* forms a fourth type to which three species from subg. *Artocarpus* (ser. *Rugosi*) should also be referred.

The biological evolution of the syncarp has apparently proceeded in two different directions. It is, of course, indehiscent and is broken down only by the frugiferous mammals and birds that feed upon it or by decay. Nevertheless it can be attractive either as a whole, if the entire syncarp is more or less fleshy, or for the individual fruiting perianths in species where the free proximal region of the perianth is hypertrophied.

The least specialized condition of the syncarp would seem to be found in a number of species in subg. *Artocarpus* sect. *Artocarpus* in which the distal regions of the perianths forming the external wall of the syncarp and the free perianth apices are fleshy but more or less firm while the free proximal regions are thin-walled or only slightly hypertrophied (but sweet and juicy at least in *A. elasticus* Blume and *A. sericicarpus* Jarrett). In contrast with this comparatively undifferentiated internal structure the external appearance of these syncarps is remarkably varied, depending on the shape and indumentum of the perianth apices. They range from scarcely projecting so that the surface appears areolate, each areola representing the tip of a perianth, to long drawn-out and flexuous, giving the figurative appearance of the head of a Medusa. Such elongation of the perianth apices is often associated with dimorphism. There is then usually a marked contrast between the short, perforate apices from which the styles emerge and the intermingled solid processes, which may bear distinctive hairs — long, appressed and silky in *A. sericicarpus* but short and patent in *A. elasticus* (Terap in Malaya) and recurved in *A. tamaran* Becc. and *A. multifidus* Jarrett. In *A. teysmannii* Miq., on the other hand, comparatively few of the perianth apices are elongate and intermediates occur. It is interesting to note that this dimorphism is found in one or more (but not all) of the species in each of the three series in Sect. *Artocarpus* (*Incisfolii*, *Angusticarpus* and *Rugosi*) which have this type of syncarp and that it apparently represents parallel evolution.

The fourth series in this section (*Cauliflori*) possesses the most remarkable syncarps in the genus. The enormous fruits of *A. heterophyllus* Lam. (Jack) and *A. integer* (Thunb.) Merr. (Chempedak), which are borne on the trunk and larger branches, may measure as much as one metre in length and half a metre across. The very numerous seeds are enclosed in the strongly hypertrophied proximal free region of the perianths and in the Chempedak (but not the Jack) these separate from the wall and the core at maturity, falling out when the baggy syncarp is cut open. The taste and smell is highly characteristic of each species and was described by Corner (1939) as “sickly sweet” in the Jack and much stronger (“of durian and mango”) in the cultivated Chempedak (but lacking in the wild var. *silvestris* Corner). The syncarp surface is covered by firm, but not indurated, conical perianth apices.

The smaller, globose or short-cylindric, armoured fruits of sect. *Duricarpus* representing the third type of syncarp in subg. *Artocarpus*, have seeds that are likewise surrounded by succulent, hypertrophied perianths. The free tips of the perianths are, however, woody and, while in some species such as *A. lanceifolius* Roxb. (Keledang) and the pinnate-leaved *A. anisophyllus* Miq. they are merely cylindrical, in others such as *A. rigidus* Bl. (Monkey Jack) and the related *A. hispidus* Jarrett, they form tapering spines.

The smooth or papillate, fleshy syncarps of subg. *Pseudojaca* (Tampang in Malay) present a strong contrast to those just described and, as already stated, there is relatively little variation in appearance and morphology. Only in *A. styracifolius* Pierre from southern China is the surface covered by flexuous processes and these appear to be formed from enlarged interfloral bracts. (Bracts are present among the flowers in most species of *Artocarpus* at least in juvenile inflorescences but their heads are usually minute and discoid or infundibuliform.) As regards internal structure, where the proximal portion of the perianths is free it is thin-walled, but in several species, including *A. fulvicortex* Jarrett among Malayan species (Orange-Barked Tampang in Corner, 1940), the perianths are completely fused. Finally a few species in subg. *Artocarpus* such as *A. kemando* Miq. have small fleshy fruits which should be classified biologically with this group.

The biological significance of the syncarp in *Artocarpus* was taken up by Corner in his discussion of the Durian Theory, in which the genus was frequently mentioned (1949, 1954a, 1954b). Vegetatively it shows both massive pachycaul

and slender leptocaul construction and, in particular, the association of the latter with cauliflory in *A. integer* and *A. heterophyllus*. The compound syncarp, moreover, shows striking parallels in some species with fruits of the Durian type. The surface may be armoured but here this is by perianth apices rather than by simple spines; the fruit may be strong smelling as, for example, in *A. elasticus*, *A. heterophyllus* and *A. integer*; and; finally, fleshy perianths can take on the function of an aril (Corner, 1962). However, other parallels may also be seen in the genus since the fleshy syncarp. of subg. *Pseudojaca* can be compared with a berry, although the flesh is formed from the perianths and axis rather than from the carpel wall. It may be added that in the allied genus *Prainea*, in which the perianths remain free in the female inflorescence, the few that form seeds and project from the surface each resemble a single-seeded berry in which, again, the flesh is formed by the perianth.

It might be assumed that these biological variations in the syncarp would be reflected in marked differences in the animals acting as distributors. However, while differences do exist they are not very clear-cut. Precise information is scanty and mainly derived from cultivated trees, which is not surprising since in the forest *Artocarpus* is usually widely scattered. However, it is clear from observations gathered together by Ridley (1930) and others made by Corner (1939, 1940) that it is the attractive flesh, variously dispersed in the syncarp, that brings about the distribution of the seeds. Arboreal mammals, especially monkeys and civet cats break open the larger fruits, nibbling the juicy perianths and scattering at least some of the seeds. Docters van Leeuwen (1935) also records several species including two of the most important cultivated species, Chempedak & Breadfruit, as being eaten by bats, a fact first mentioned by Rumphius. Ridley suggests that the cauliflorous fruits are eaten by wild pig, cattle and elephants. The smaller fleshy fruits may be eaten by birds or bats and could be carried off whole and thus more widely distributed. However the distribution patterns of the species, which were mapped in my monograph, suggest that water is a strong barrier to dispersal, as might be expected with such large seeds lacking in dormancy.

The uniqueness of the syncarp in *Artocarpus* lies in the partial fusion between tubular perianths which exists in most species. This character has made possible the differentiation for attractive or protective functions of the proximal and distal regions of the perianth and hence the remarkable biological parallels between this compound fruit and syncarps derived from a single flower. It is evident that field observations are still needed to enrich our biological knowledge of this diverse genus.

## REFERENCES

- CORNER, E. J. H. 1939. Notes on the systematy and distribution of Malayan phanerogams, II. The Jack and the Chempedak. *Gdns' Bull., Singapore* 10: 56-81.
- 1940. Wayside Trees of Malaya, Vol. 1. Govt. Printer, Singapore. 770 pp.
- 1949. The Durian Theory or the origin of the modern tree. *Ann. Bot. N.S.* 13: 367-414.
- 1954a. The Durian Theory extended — II. The arillate fruit and the compound leaf. *Phytomorphology* 4: 152-165.
- 1954b. The Durian Theory extended — III. Pachycauly and megaspermy — Conclusion. *Phytomorphology* 4: 263-274.
- 1962. The classification of Moraceae. *Gdns' Bull., Singapore* 19: 187-252.

- DOCTERS Van LEEUWEN, W. M. 1935. The dispersal of plants by fruit-eating bats. *Gdns' Bull., Singapore* **9**: 58-63.
- JARRETT, F. M. 1959a. Studies in Artocarpus and allied genera, I. General considerations. *J. Arnold Arbor.* **40**: 1-29.
- 1959b. Studies in Artocarpus and allied genera, III. A revision of Artocarpus subgenus Artocarpus. *J. Arnold Arbor.* **40**: 113-155, 298-368.
- 1960. Studies in Artocarpus and allied genera, IV. A revision of Artocarpus subgenus Pseudojaca. *J. Arnold Arbor.* **41**: 73-140.
- RIDLEY, H. N. 1930. *The Dispersal of Plants Throughout the World.* Reeve, London. 774 pp.



# The Origin of the Afroalpine Pachycaul Flora and its Implications

by

D. J. MABBERLEY  
Botany School, Oxford

## Summary

The morphological, anatomical and biogeographical implications of the apparently primitive nature of the forest pachycaul form in *Senecio* and *Lobelia* are discussed. The preadaptation of high altitude swamp pachycaul forms for temperate rhizomatous vegetation and the adaptations of hyperpachycaul forms to the conditions of the tropical alpine belt are stressed.

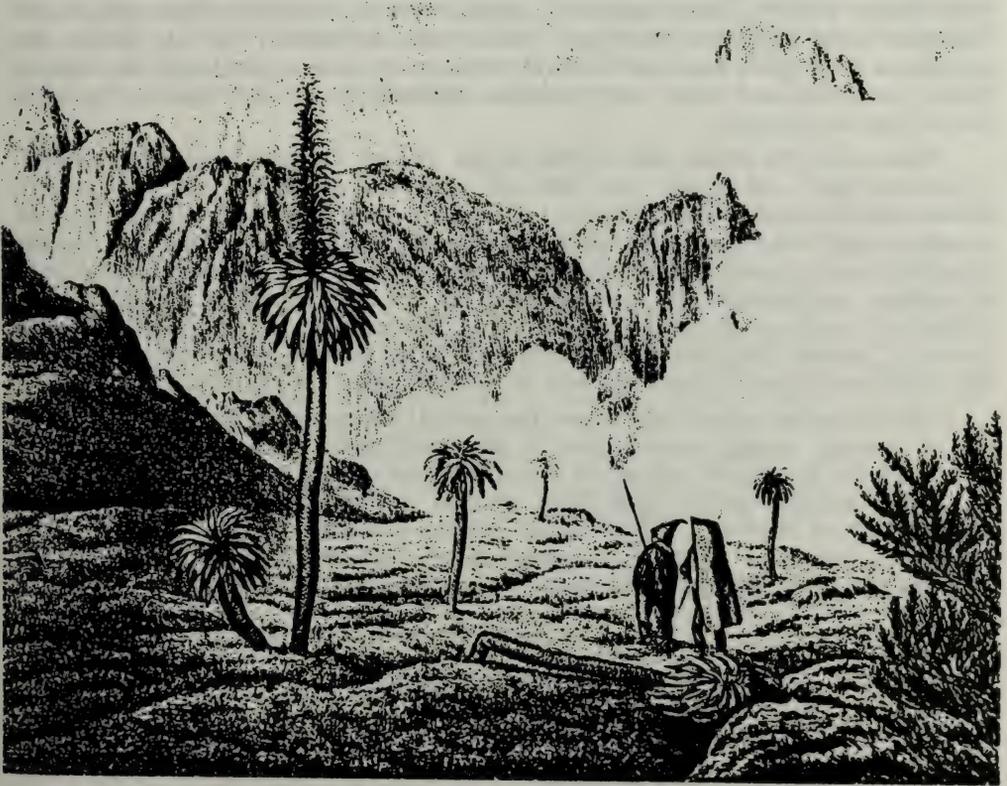


Fig. 1. *Lobelia rhynchopetalum* in the High Simien of Ethiopia during von Ruppell's expedition of 1833. (From von Ruppell, 1840: t. 6). Reproduced by kind permission of the University Librarian, Cambridge.

“Ausserdem charakterisiert diese Zone eine sehr fremdartige Pflanze, die einer Aloekrone gleicht, welche auf einem mannshohen hohlen Stengel aufsitzt. Ihr Landesname ist Gibarra, und ihr systematische Stelle die Familie der Lobeliaceen. Da sie nur an der Schneeegränze vorkommt, und doch in der Form einige Ähnlichkeit mit den der wärmsten Tropenvegetation eigenthümlichen Pflanzen hat, so gibt dieses der Landschaft einem höchst fremdartigen Charakter.”

Eduard von Ruppell (1836).

### Introduction

With the baobab and *Welwitschia*, the Giant Groundsels and Lobelias are perhaps the most famous botanical curiosities of Africa. The layman's familiarity with herbaceous senecios and lobelias, the unfamiliar habit of the 'giant' plants and their exotic tropical montane home have given the Giant Groundsels and Lobelias an exalted place in botanical travelogues, popular horticultural works and other writings and made them a tourist attraction attained by few members of the vegetable kingdom.

The adjective 'giant' in botanical works has connotations of teratology or polyploidy and is used here only in the nicknames 'Giant Groundsels' for *Senecio* L. subg. *Dendrosenecio* Hedb. and 'Giant Lobelias' for *Lobelia* L. sect. *Rhyncho-petalum* (Fres.) Benth. & Hook.f., the general term 'pachycaul' being used for those plants with massive primary construction, large buds and large leaves, of which fine examples are provided by the Giant Groundsels and Lobelias (Corner, 1949).

Pachycaul senecios have been known from Africa since the eighteenth century; those first brought back to Britain were not from the continent but from the isolated Atlantic island of St. Helena, 900 km east of the Mid-Atlantic Ridge (Mabberley, 1975b). Later, pachycaul species were discovered in West Africa and Ethiopia where the first pachycaul lobelia was collected (Fig. 1); finally the mountains of tropical East and Central Africa were rediscovered and the famous Giant Groundsels and more Giant Lobelias collected for the first time, in the latter half of the last century.

Meanwhile the alpine belts of the Andes yielded the pachycaul "Frailejones" (*Espeletia* spp.) and puyas, and although pachycaul plants are not restricted to islands and mountain-tops (Corner, 1949), their conspicuous appearance in such situations, and the superficial correlation between their presence and the 'insular situation' had aroused considerable discussion. The study of the floras and faunas of islands, continental and oceanic, and of insular situations, geological and altitudinal, has been of continuous interest to biologists, for much evidence for the theory of Natural Selection was derived from it by Darwin, whose observations in the Galapagos Islands paved the way to modern ideas on evolution:

"The principle which determines the general character of the fauna and flora of oceanic islands, namely that of the inhabitants, when not identically the same, yet are plainly related to the inhabitants of that region whence colonists could mostly readily have been derived — is of the widest application throughout nature . . . . For alpine species, excepting in so far as the same forms, chiefly of plants, have spread widely throughout the world during the glacial epoch, are related to those of the surrounding lowlands."

Charles Darwin, *Origin of Species* (1859: 342)

The fallacy in the blind comparison of 'altitudinal islands' and oceanic islands has been explored by White (1971). Nevertheless, certain families, e.g. Campanulaceae and Compositae are represented by pachycaul forms on islands both geographical and altitudinal. One genus in each of these families *viz.* *Lobelia* and *Senecio* is similarly distributed. Within their respective families, these genera are large, *Lobelia* with perhaps 350 species (Wimmer, 1956, 1968) and *Senecio*, as understood at present, is perhaps the largest of flowering plant genera with 2000-3000 species (Willis, 1973). Unlike other genera with arborescent forms in these predominantly herbaceous families, *Lobelia* and *Senecio* have herbaceous as well as woody forms (Good, 1974: 85) and almost the whole gamut of life-forms represented in their families is to be found in them. If the genera, or sections of them, are monophyletic, then it should be possible to discern evolutionary trends within them and hence investigate the relationship of the pachycaul habit to that

of the herbaceous habit. It is only in the mountains and on the islands of Africa that pachycaul species of both genera grow together. Thus it was felt that a study of these 'Giant Lobelias and Groundsels' would throw considerable light on the evolution of the woody pachycaul in florally advanced families. Currently seven pachycaul species of *Senecio* (Mabberley, 1973a; 1974a; 1975b) and seventeen pachycaul species of *Lobelia* (Mabberley, 1974c) are recognized. Revisions had been made piecemeal before those, but the origin of the pachycaul habit was undecided through the lack of either developmental studies or the comparison of pachycaul with herbaceous forms. In consequence, two opposing theories had been proposed. Fries & Fries (1922) suggested that the pachycauls were primitively forest plants of the Tropics, whereas Cotton (1944) argued that they had arisen from temperate plants which had reached the Tropics along mountain chains and elaborated pachycaul construction there. Recently these arguments have been voiced by Coe (1967) and Carlquist (1965: 199) respectively.

Besides in these speculations, the Giant Groundsels and Lobelias appeared in a more profound work, the Durian Theory of Corner (1949-54b; 1964), the pachycaul construction which they exhibit being a keystone of much of the theory, which argues the origin of leptocaul trees from pachycaul ancestors. Are they relics of those from which the leptocaul and herbaceous evolved and multiplied to populate the temperate zones, or are they rare elaborations of herbaceous groups selected for their longevity in 'insular situations'?

### Senecio

The first African pachycaul senecios to be discovered were *S. leucadendron* (Forst.f.) Hemsl. and *S. redivivus* Mabberley, the He- and She- Cabbage Trees respectively, first collected by Banks on St. Helena on Cook's *Endeavour* voyage in 1771 (Mabberley, 1975b). No pachycaul species from the mainland was collected until 1859, when Sir John Kirk collected scraps of a woody *Senecio* on Livingstone's Zambezi Expedition; his specimens were not received at Kew until 1867, by which time the tree had been discovered on Clarence Peak, Fernando Po in April 1860 by Gustav Mann, whose name it bears, *Senecio mannii* Hook.f. It is now known from Nigeria, Cameroun and from Zaïre to Ethiopia and Tanzania, Mozambique and Angola (Mabberley, 1973b). In June 1864, the Middle East botanist Wilhelm Georg Schimper collected a related species, *S. gigas* Vatke, on his third expedition in Ethiopia.

It was not until the Royal Society and the British Association put the 'Kilima-Njaro Expedition' of 1884 into the field with the energetic Harry Hamilton Johnston as its leader that the first Giant Groundsel was collected and named *S. johnstonii* Oliv.; later many collections from the other mountains were also given specific rank, but with *S. johnstonii* these are now considered to constitute three species in all (Mabberley, 1973a), the second being *S. keniodendron* R.E. & T.C.E. Fr., an hyperpachycaul tree of Mt. Kenya and *S. brassica* R.E. & T.C.E. Fr., a 'creeping tree' of Mt. Kenya and the Aberdare Mts. of Kenya. The African pachycaul senecios are thus: *Senecio leucadendron*, *S. redivivus*, *S. mannii*, *S. gigas*, *S. johnstonii* comprising eight geographical and altitudinal subspecies including subsp. *refractisquamatus* (De Wild.) Mabberley and subsp. *barbatipes* (Hedb.) Mabberley, *S. keniodendron* and *S. brassica*.

In Hoffmann's treatment of *Senecio* (1892), all the Giant Groundsels then known as well as the Cabbage Trees and *S. mannii* and *S. gigas* were included in the 'Arborei', an heterogeneous assemblage of species put together merely on their woody habit; some leptocaul shrubs of Madagascar were also included. Recent

study of the details of the flowers (Mabberley, 1974a) has shown that the allegiance of the Giant Groundsels is with the herbaceous sect. *Crociserides*, that of *S. gigas* and *S. mannii* with the lianoid and herbaceous '*Crassocephalum-Gynura*' complex, whilst *S. leucadendron* is quite isolated in the genus as is *S. redivivus*. It is more easily argued (Mabberley, 1974a) that the tropical pachycauls with the primitive '*Dendrosenecio-branching*' are relics of a pachycaul ancestry for the herbaceous group than that they are sporadic arborescent innovations from primarily herbaceous stocks. This is supported by the observation that pachycaul trees with this branching habit are to be found in other alliances in *Senecio* in New Zealand, Mexico, Cuba and the Canary Islands.

It was argued that in the *Dendrosenecio-Crociserides* assemblage, evolutionary trends within the Giant Groundsels provided a clue to the origin of the herbaceous forms by the stem's becoming a '*truncus superficialis*' as in *S. brassica* and thence a subterranean rhizome suited to perennation and the invasion of the temperate zones (c.f. 'herb-making' in *Hedysarum*, etc. analyzed by Gatsuk, Dervis-Sokolova, Ivanova & Shafranova (1974)). The massive alpine pachycauls, 'hyperpachycauls', are seen as dead ends as far as evolution of temperate vegetation is concerned, but adapted to the exacting climate of the afroalpine belt in elaborating characters such as leaf-movements etc. (see below). By contrast the creeping form adapted to the swampy habitat is seen as pre-adapted to a seasonal climate.

#### ALPINE PACHYCAULS

In the pachycaul alpine species are elaborated certain characteristics which are weakly developed in the forest forms. Marcescence is more marked; Hedberg (1964) has shown that the marcescent collars of leaves act as efficient insulators, the temperature around one tree dropping to  $-4^{\circ}\text{C}$ , whilst remaining  $+1.8^{\circ}\text{C}$  within the 'collar'. This warm microhabitat is exploited by animals, e.g. the frills of *S. keniodendron* provide a night shelter for the chironomid midges which breed in the buds of Giant Lobelias, and for many beetles and spiders (Coe, 1967) whilst the groove-toothed rat, *Otomys orestes orestes* Thomas burrows up into the marcescent leaves and leaf-bases (Coe, 1967). In another tree, Hedberg (1964) found that the pith remained at  $+3^{\circ}\text{C}$  whilst the temperature dropped to  $-5^{\circ}\text{C}$  outside. If the collars are removed, Hedberg suggests that the tree may die. In *S. johnstonii* subsp. *barbatipes*, an alpine plant of Mt Elgon, the rôle of the frills is taken by the highly developed bark, which is again exploited by animals. As *Dendrosenecios* are hygrophilous, they are often to be found in hollows which are frost pockets, where insulation is even more important than in the plants of the steep slopes. The movements of the leaves which protect the bud (Diels, 1934: 68) and the production of antifreeze slime are also exploited by the invertebrate fauna which overnight in the ameliorated micro-habitat thus provided, e.g. snails and insects which also receive shelter from desiccation by day (Coe, 1967).

The marked xeromorphy of alpine forms (Hare, 1941) is linked with the severe alpine climate; the thick leaves may be important in preventing water loss. The pubescence of the leaves of many forms may reflect incoming radiation (Hedberg, 1964), but several alpine forms, e.g. *S. keniodendron* have glabrous leaves. The shiny adaxial surface may be of importance in reflection of radiation. The *abaxial* surface of the leaves of *S. brassica* may protect the bud at night when closed over it by preventing outward radiation, as has been discovered by the scarlet-tufted malachite sunbird, *Nectarinia johnstonii johnstonii* Shelley, which gathers the hairs to line its nest (Coe, 1967). There is marked endemism in the insects paralleled by their host distribution patterns. Further, there is an increase in flightlessness with altitude, probably associated with the alpine habitat favouring 'cryptozoic' modes of life (Salt, 1954).

## Lobelia

The first pachycaul *Lobelia* from Africa was collected by the zoologist, Eduard von Rüppell, in the High Simien in Ethiopia in 1833 (Fig. 1). Now seventeen (one undescribed) such species are known and all are referable to sect. *Rhynchopetalum* (Fres.) Benth. & Hook.f. (Mabberley, 1974c), in subsect. *Haynaldianae* E. Wimmer, subsect. *Nicotianifoliae* Mabberley and subsect. *Rueppellianae* Mabberley. The *Haynaldianae* are a Brazilian group with three African outliers. The *Nicotianifoliae* are found from eastern Africa to S.E. Asia with closely related taxa in Hawaii (Mabberley, 1974c). They include *L. giberroa* Hemsl. of montane forest and clearings and *L. bambuseti* R.E. & T.C.E. Fr. of the upper forest belt. The alpine species are the creeping *L. deckenii* (Asch.) Hemsl. and *L. rhynchopetalum* Hemsl. of the *Rueppellianae* and, of the *Nicotianifoliae*, *L. wollastonii* Bak.f. and *L. telekii* Schweinf., which seem to be parallel alpine types as is *L. nubigena* Anth. of Bhutan in the *L. nicotianifolia* [Roth ex] R. & S. complex. All seem to be derived from forest ancestors (Mabberley 1974c, 1975a). In the Far East the *Nicotianifoliae* include the rhizomatous *L. sumatrana* Merr. of high mountains.

### ALPINE PACHYCAULS

The stems of the forest species of Giant Lobelia are usually bare of marcescent foliage; the stems of the alpine species are either prostrate, as in the paludal *L. deckenii*, acaulescent as in *L. telekii*, or erect, with a conspicuous frill of marcescent foliage like that of a *Dendrosenecio* as in *L. wollastonii*. The base of the leaf has a plug of corky tissue which holds the withered lamina to the stem. Erect flowering shoots of *L. deckenii* are also thus clothed as figured by Hedberg (1964). Diurnal leaf movements of the leaves also protect the buds which are bathed in antifreeze slime as in *Senecio*.

Coe (1967) reports that chironomid midges shelter in the closed rosettes of *Lobelia deckenii* subsp. *keniensis* and that the larvae are found in the slimy water therein. The water is said never to dry up, even in cultivation (McDouall, 1927) and does not freeze solid except at very low temperatures: the larvae are thus protected. Hedberg (1964) measured the temperature outside and inside the bud of *Lobelia telekii* and found it to drop to  $-3.5^{\circ}\text{C}$  outside, whilst falling no lower than  $+1.0^{\circ}\text{C}$  within.

Scott (1935) worked on the assemblages of Coleoptera restricted to the pachycaul lobelias. Some species, e.g. a silphid, spend their entire life cycle in a *Lobelia* plant as do certain bionid flies in *Lobelia* flowers (Coe, 1967). The distribution of the associated species of *Trechus* (Coleoptera) matches that of the lobelias (Scott, 1958). As with those of the *Dendrosenecios*, many of the insects are flightless and 'giant' within their own genera.

### Dendrosenecio, Rhynchopetalum, and Altitudinal Distribution

The study of the pachycaul *Lobelioideae* and *Senecioneae* of Africa has given support to Croizat's (1962: 257) forecast of 'similar' evolutionary patterns in the Giant Groundsels, Lobelias and the South American espletias. This study has supported the view of the origin of alpine forms from forest ones in parallel as supposed by Humbert (1935) for *Dendrosenecios* and Fries & Fries (1922) for *Lobelia*.

*Dendrosenecios* occur on the wet mountains of eastern Africa at altitudes over 2100 m, but only on those mountains higher than 3300 m. Although found on the Cheranganis (c. 3400m), they are not found on the nearby Mau Massif (3050m); the difference between these two appears to be critical. Similarly, the difference between the Aberdares (3940m) and the Cheranganis may be critical for *Lobelia telekii*, which is absent from the latter range.

*Dendrosenecio* and *Lobelia telekii* distributions may be explained by the hypothesis of Wood (1971), wherein former amelioration of climate would have forced the *Senecio* and *Lobelia* belts to higher altitudes; those mountains, which were high enough to harbour them then, still possess them, now that the vegetation belts are once more depressed. The adaptive radiation of the *Dendrosenecios* seems not to have proceeded as far as that in *Lobelia* in the East African mountains. It may be that the longer life-cycle of the *Dendrosenecios* has permitted slower change (c.f. Arber, 1928).

### Argument

Starting from the pachycaul members of both genera, interpretations of many morphological and ecological features are possible. Can as much be explained if herbs are taken as the primitive condition and the pachycaul as the advanced?

Starting from herbs in the *Crassocephalum-Gynura* and *Crociserides* alliances of *Senecio*, it is necessary to postulate a mechanism for increasing woodiness (that so far suggested (Carlquist (1962) ) seems to be untenable (Mabberley (1974b) ), and for postponing flowering. All the available evidence points to a forest ancestry for the creeping swamp pachycauls and the erect alpine 'hyperpachycauls' so that there would be no indication of how the presumed herbaceous ancestors attained the forest pachycaul condition. *S. brassica* would be a 'herb' for the second time in its evolution (c.f. Arber, 1928). It would have to be argued that the characteristic '*Dendrosenecio*-branching' ('Modèle de Leeuwenberg' of Hallé & Oldeman, 1970) had been attained in herbaceous, succulent, woody, lianoid and pachycaul groups independently; furthermore, in the wholly pachycaul groups, there would be no indication of their presumed herbaceous ancestors.

Similarly, it must be argued that several herbaceous lines of distinct appearance, e.g. in *Lobelia*, plants like *L. sumatrana* and *L. deckenii*, have colonized the Tropics and produced very similar pachycaul plants in America and Africa as well as India and Hawaii. It must also be assumed that the inflorescence has become more complicated, the fruit baccate, the seeds winged and the leaf-size increased, all in several lines. If this is so, then wind-pollination and dispersal must be antecedent to bird and insect pollination and dispersal, the short-lived temperate herb antecedent to the tropical pachycaul (c.f. Mabberley 1975a).

No sense can be made of phytogeography, associations with animals or the origin of a range of life form within plant genera. It is simpler, then, to follow the easier line of argument, and, in short, arrive at the same conclusion as Corner (1967b) working with the woody genus *Ficus*, for if the herb (*Senecio*, *Lobelia*) or leptocaul tree (*Ficus*) is primitive and the pachycaul advanced, then:

(i) The primitive species are the most common and widespread, contrary to much of biogeography which would have the primitive as relics;

(ii) the pachycauls are advanced but make least contribution to tropical forest (*Ficus*) or temperate floras (*Senecio*, *Lobelia*) which the flowering plants have been evolving;

(iii) the most leptocaul trees (*Ficus*) or herbs (*Senecio*, *Lobelia*) have the simplest inflorescences, supplying no evidence of their evolution.

As Corner continues, morphological series, [whether in *Ficus*, the *Crociserides*, '*Crassocephalum*' or *Rhynchopetalum*] can be read in either direction; the ecological factor is 'time's arrow'. In the case of *Ficus*, the arrow is aimed at tropical rainforest via leptocaul trees; in the *Crociserides* it is aimed at the conquest of the temperate zones via preadapted rhizomatous perennials, in '*Crassocephalum*' at filling the secondary habitats of the African Tropics with fast-growing plants and in *Rhynchopetalum* it is aimed at both.

### The hypothesis

The hypothesis is that *Lobelia* sect. *Rhynchoptalum* and *Senecio* sect. *Crociserides* are derived from pachycaul ancestors and that, in parallel, these groups have given rise to herbs which have reached the temperate zones, and to extreme 'hyperpachycaul' forms which have conquered the tropical mountains of Africa, living in wet situations above the treeline away from other arborescent competition. The hypothesis implies that there have been physiological and morphological adaptations for simplification and overwintering in the herbs and remarkable elaborations of characteristics of the forest plants in the hyperpachycauls adapted to the alpine environment.

The evolution of subg. *Dendrosenecio* and sect. *Rhynchoptalum* in Africa can be seen as the conquest of the highlands, either by becoming hyperpachycaul with marcescent foliage, reduction of hydathodes, enhanced pubescence, etc., or by becoming prostrate and lying down in wet places. The latter is the method which has permitted the colonization of the temperate zones in these groups. The marked increase in pachycauly with altitude may have an ecological explanation, for Daubenmire (1947: 186) has shown that massive organs may withstand short periods of extreme temperatures better than less massive ones. Hyperpachycauls are thus adapted to diurnal climate fluctuations, whereas rhizomatous plants with intermittent growth are adapted to a seasonal climate. It becomes clear then, why no *Lobelia* of North Africa and the Mediterranean is of the *Rhynchoptalum* alliance compared with the *Crociserides* with many Asian and European relatives, for, in Africa, the alpine species which reaches furthest north is the hyperpachycaul *L. rhynchoptalum* with a highly peculiar structure; herbaceous *Rhynchoptala* are the result of 'miniaturisation' (Hallé & Oldeman, 1970: 150) in the Far East.

On the other hand, sect. *Rhynchoptalum* has reached the Pacific as fast-growing pachycauls from both east and west, such that the presence of pachycauls on both sides of the Pacific is readily explicable (Mabberley, 1975a). Indeed, the immigration of the 'pachycaul starter' has permitted the development of herbaceous plants from Japan to Sumatra. By contrast the *Crociserides* seem to have spread very little as pachycauls but have romped and excelled in the temperate zones as coarse herbs.

Sect. *Rhynchoptalum* and '*Crassocephalum*' have elaborated fast-growing pachycauls, which have thus become 'nomads' (van Steenis, 1958) of the sub-montane forests of Africa, and India, incidentally predisposing them to cultivation as *shamba* [small-holding] hedges (*S. mannii*) (Mabberley, 1974a) and as pot plants (*L. nicotianifolia* [Roth ex] R. & S. (Anon., 1904) etc.) in Victorian greenhouses. By contrast, subg. *Dendrosenecio* with a longer life-cycle has ascended the mountains to make woodlands above the 'treeline'.

In general, then, there is factual support for the predictions of the Durian Theory, with the important proviso that the groups here studied are capable of hyperpachycauly under the selective pressure of the alpine environment.

### Implications

According to our hypothesis, then, such statements as "... highly probable that the development of the arborescent habit and delayed flowering among the tree *Senecios* and *Lobelias* of the East African Mountains, was a photoperiodic response ... fixed by Natural Selection", (Melville, 1953) and "The ancestors of the equatorial alpine rosette trees are temperate zone herbs, which arrived on the equatorial peaks by long distance dispersal just as did the ancestors of island rosette trees" (Carlquist, 1965: 200) seem to be unsubstantiated by the available evidence. On the contrary, it is more easily argued that the pachycaul state is the primitive, which leads to the following considerations.

## GROWTH HABIT

*Herbs*

The primitive growth-form in the *Senecioneae* appears to be *Dendrosenecio* branching, examples of which are found scattered throughout the tribe; it appears that it represents the 'pachycaul starter' condition for 'Senecio'. The aerial parts of the *Crociserides*, so difficult to describe in 'cauline' terms appear to be inflorescences and are more readily comparable with one another and other life-forms once this is recognized. Similarly, the creeping lobelias like *L. sumatrana* show that the aerial parts of many lobelias are also merely 'inflorescence'.

*Hyperpachycauly*

Enhanced pachycauly exemplified in the alpine hyperpachycauls is a feature of both genera. It appears to be associated with the basally growing leaves in these families. Thus, under the selective forces of the alpine environment, there are hyperpachycaul *Dendrosenecios* and lobelias in Africa, *Pachypodium* in the Malagasy Mts. (Koechlin, 1969), espeletias in the Andes (Smith & Koch, 1935), *Saussurea gossipiphora* D. Don and *Rheum nobile* Hook.f. & Thom. in the Himalaya (Anthony, 1936) and, under the selective forces of the horticulturalist, the hyperpachycaul vegetables such as lettuce and cabbage, large European and Asiatic varieties of which are figured by Herklots (1972: 190–224).

The pachycaul construction of massive buds permits the tolerance of the *Tageszeitenklima* (Troll, 1947) of the tropical alpine belts by 'arborescent' plants above the tree-line, e.g. besides *Senecio* and *Lobelia* in Africa, *Puya ramondii* Harms and *Lupinus weberbaueri* Ulbr. in the Peruvian Andes (Pontecorvo, 1972), *Lupinus alopecuroides* Desr. (Heilborn, 1925), puyas and espeletias in the Colombian Andes (Fosberg, 1944) as well as the Andine *Ceroxylon* (Corner, 1966: 289) and even *Cyathea* in the Papuan mountains (Wardle, 1971), but not their spread beyond the Tropics into a seasonal climate. Such diurnal fluctuations in deserts may favour pachycauly e.g. Cactaceae, succulent *Euphorbia* species, *Yucca* spp. etc., and fire may favour pachycaul forms with wide cortex and hence deeply seated or weakly developed cambium, e.g. *Xanthorrhoea* spp. in Australia, *Aloe capitata* Bak. var. *cipolinicola* H. Perr. in the 'prairies' of Madagascar and again *Cyathea* in New Zealand and New Guinea. In the dicotyledonous examples there is a reduction in branching, and in *Puya*, the inflorescence is unbranched in *P. ramondii*. Similar simplification of structure is to be found in *Echium* (Bramwell, 1972a). In that genus, and other 'temperate' genera, the pachycauls of the Canary Islands appear to represent relics of the pachycaul starters which initiated the herbaceous lines so common in Europe, e.g. *Echium* (Meusel, 1952; Bramwell, 1972a), *Sonchus* (Bramwell, 1972b), *Carlina* (Meusel, 1952). Similarly, species of *Erysimum*, *Crambe*, *Aeonium*, *Chrysanthemum*, *Campanula*, *Bupleurum*, *Dendriopoterium*, *Bencomia*, *Digitalis* and *Limonium* ('Statice') appear as pachycaul relics in the Atlantic Islands (Meusel, 1952).

## STEM ANATOMY

In general, the anatomy of the herbs in *Senecio* and *Lobelia* is a good deal simpler than that of their pachycaul relatives — fewer cell-layers, leaf-traces, ducts, less modification in the pith and cortex with aerenchyma etc. The seedlings of the pachycauls are more 'conventional'; the differences arise when the apex increases in size.

*Cortical and medullary bundles*

Associated with hyperpachycauly, there is the appearance of the phylloclad leaf-base and cortical bundles in *Lobelia*; some species have relic medullary bundles showing that the medullary bundle condition is the primitive one in

*Lobelia*, and the cortical bundle condition the advanced. Davis (1961) points out that in the Compositae, medullary bundles are particularly abundant in the *Cichorieae*, especially in those plants with the 'rosette-habit'.

In *Lobelia*, the medullary bundles serve the base of the primitive 'forest leaf'; the cortical bundles are often associated with the phyllodic leaf. In a similar way, cortical bundles are often associated with leaves of the 'monocotyledonous' type in the Dicotyledons, e.g. *Eryngium* spp. of the monocotyledonous habit (Metcalf & Chalk, 1950: 717), *Gentianaceae-Gentianoideae* (*ibid.*: 933) and groups with leaves which have few costae, e.g. *Melastomataceae* (*ibid.*: 637).

The appearance of cortical bundles seems to be a 'way out' in evolutionary lines where a larger leaf is being favoured and yet the number of traces to serve such a leaf has been lost; hence in *Lobelia*, the cortical bundles are found in the most massive pachycauls (*Rueppellianae*), whose massiveness has been selected for by the alpine and swamp environments. Such bundles also give support to those massive inflorescences formed by the reduction of branching of a forest form, and for which the capacity for supporting lignification has been lost.

It has recently been suggested (Zimmermann & Tomlinson, 1972) that the regular dicotyledonous ring of vascular bundles may be the equivalent of the outer of the monocotyledonous systems seen in some woody monocotyledons. If this is indeed the case, then *Lobelia* sect. *Rhynchopetalum* may demonstrate how the two systems as exemplified by *L. gibberoa* may give rise to the typical dicotyledonous system as seen in *L. bambuseti* by loss of the inner system and the origin of a 'monocotyledonous' system as shown by *L. rhynchopetalum* with the appearance of a 'new' cortical system associated with basally growing leaves (*c.f.* Burt, 1974).

### *Hyperpachycauly*

Selection has favoured the hyperpachycaul in the extreme alpine climate; the hyperpachycaul is marked by its massive apex and reduced branches compared with its forest relatives. Dominance of the apex over lateral meristems is found in the absence of suckers in *L. wollastonii*, the unbranched inflorescences of the alpine *L. rhynchopetalum*, *L. wollastonii*, etc. with the basipetal inflorescence gradient (Mabberley, 1975a) lost etc., the untoothed leaves of alpine *Nicotianifoliae* and the large capitula on weakly branched inflorescences of the alpine *Dendrosenecios*; in short, there is a common constraint determining the morphology of the hyperpachycaul 'syndrome' (*c.f.* Beketoff, 1858; Uittien, 1928; and the particular case of *Sonchus* (Bramwell, 1972b)). The balance of growth factors determining differentiation in the tissues must be tipped in favour of apical dominance. Such may be an increase in 'auxin' as has been suggested by Cotton (1944) and was discovered in *Aster* by Delisle (1937) who found that there was more auxin in the apices of the inflorescences of *A. novae-angliae* L. than in those of *A. multiflorus* Ait. which is much more branched, (*c.f.* also Smith, 1967).

## LEAF

### *Venation*

The venation of *Senecio* (Mabberley, 1973a) and *Lobelia* (Mabberley 1974c) leaves is mainly or entirely basipetally formed. In *Dendrosenecio*, the fraction of the leaf formed acropetally is very small; some herbaceous species have a larger part of the lamina thus formed and may be amphipetal.

In the East African *Lobelias*, my studies have shown a series demonstrating the loss of teeth and acropetally formed venation. This series is interpreted as the failing of the marginal meristem in the leaf with the consequent loss of teeth, and the increasing importance of the spreading growth of the 'midrib', giving the phyllodic leaf-base. The reduction of toothiness in both *Senecio* and *Lobelia* reduces the number of hydathodes per leaf. The action of hydathodes is not well understood;

despite their supposed efficiency in extruding water, the hydathodes of the toothed leaves of *L. assurgens* L., a pachycaul of Jamaica, investigated by Shreve (1914) could not prevent the 'injection' of the leaves by water during heavy rain.

The reduction of the acropetal venation would appear to be irreversible. Vassal (1970) has shown the appearance of the phyllodic leaf in *Acacia* to be polyphyletic and formed in various ways, but that there is a progressive loss of pinnae, with a 'mucro' left in some species, as in *Senecio* and *Lobelia*.

On the other hand, there appears to be a constraint on the number of primary costae derived from basipetal development of the lamina. In *Senecio*, the largest leaves have about 18–20 veins in *Dendrosenecio*; most herbaceous species have costal numbers lower than 18. However, some coarse herbaceous species of Uruguay, e.g. *S. bonariensis* Hook. & Arn., appear to have very large numbers of costae; on close examination, it can be seen that the intercostals have been 'pulled out' during development, thus increasing the apparent costal number, as in *S. keniodendron*, (Mabberley, 1973a).

### *Abscission*

Abscission is not a common characteristic in the Compositae (Bentham, 1873), and is almost restricted to those shrubby and arborescent plants of leptocaul construction with narrow leaf-bases, e.g. *Brachylaena*. These characters tend to be associated with the discrete midrib and looped costae, early-formed venation consummate with compact buds and the sudden expansion of intermittent growth, making them comparable with other tree leaves. The insulating marcescent frills and persistent leaf-bases of *Dendrosenecio* and *Lobelia wollastonii* are conspicuous in the afro-alpine flora. When young, however, all *Dendrosenecios* and *Lobelia* sect. *Rhynchopetalum* display this phenomenon, as do herbaceous species, e.g. *L. urens* L., where the rootstock is covered with persistent leaf-bases (Brightmore, 1968).

How widespread is the absence of abscission and the persistence of leaf-bases? Within *Senecio*, all herbs examined have persistent leaves and it appears very commonly in the herbaceous Compositae but is more familiar to flower arrangers than to monographers. The shrubby *S. hypargyraeus* DC. (Madagascar), the climbing *S. maranguensis* O. Hoffmann (Tanzania) and the leaf-succulent species are exceptions. Their small-based leaves are easily lost, even during drying in the press. In the shrubby Compositae, leaf-fall is often not clear-cut and the marcescent foliage makes a useful character for recognizing sterile Compositae in 'the bush'. The leptocaul *Brachylaena* loses leaves as others are formed (Humbert, 1962: 45) or may lose them altogether in the cold season (Lecomte, 1922). However, marcescence is a general feature of herbs and pachycauls of Compositae, e.g. the pachycaul *Espeletia* in the Andes and pachycaul *Conyza vernonioides* (A. Rich.) Wild of East Africa. Such persistent leaf-bases cover the 'stock' of many herbs, e.g. *Andryala* spp. and *Senecio asperulus* DC. (Hutchinson, 1946: 255), and make the climbing hooks of *Mikaniopsis* (Exell, 1956). Comparable contrast of leptocaul and pachycaul and herb is to be found in the Boraginaceae (*s.l.*) with pachycauls, e.g. *Echium* spp. of the Canary Islands, and herbs, e.g. *Myosotis*, with marked marcescence, compared with the leaf-dropping trees, *Cordia* and *Ehretia*, of the Tropics.

Much has been written of the 'abscission layer' with regard to marcescence, but Gawadi & Avery (1950) pointed out that abscission is not always associated with such a layer and that the layer is a protective feature of the cicatrice; indeed, it sometimes appears after abscission. Nevertheless, the range of forms of marcescence and abscission in monophyletic groups shows that abscission has been gained or lost many times in the angiosperms.

Many young tropical trees retain their leaves in the dry season (Schaffalitzky de Muckadell, 1959) rather like the beech (Knight, 1795) in winter or when kept horticulturally short as a hedge. It is one of a syndrome of 'juvenile' characters (Schaffalitzky de Muckadell, 1959) which appear to represent a primitive condition in wood anatomy etc. (Mabberley, 1974 a-b).

If it is postulated that the primitive pachycaul had marcescent leaves, it seems reasonable to argue that such marcescence may have been selected against with the increasing trunk size due to increasing wood formation through secondary thickening, but elaborated where such a mantle would act as an insulator, e.g. in hot conditions the Joshua Tree (*Yucca brevifolia* Engl.) of the deserts of S.W. United States (Menninger, 1967: 2) and in the cold, *Espeletia* in the Andes. The origin of the leptocaul tree in many lines according to the Durian Theory must have been accompanied by the origin of the small leaf with abscission which seems to have been achieved in various ways (Gawadi & Avery, 1950); especially efficient abscission mechanisms would have been selected for in seasonal conditions, such as 'savanna' and the temperate zones.

#### EUROPEAN FLORA

The ecological preference of lobelias for wet places (Woodhead, 1951a) is a direct result of a wet tropical ancestry through upland swamp habitats to the temperate zones; the predominance of aerenchyma and hydathodes in *Lobelia* is thus explicable as is the remarkable habit of the aquatic *L. dortmanna* L. The rare branching of *L. dortmanna* inflorescences (Woodhead, 1951b) is explicable as an ancestral trait, and the minute undeveloped flowers at the apex and smaller cell-size in the upper leaves (Tenopyr, 1918) are to be expected from the primitive 'die-away growth' (Corner, 1949) of the primitive tropical pachycaul ancestor.

#### Pachycaul Outlook

We need to know more of pachycaul plants (Corner, 1967a). In the Compositae, we want to know how some tribes have elaborated leptocaul trees as in *Dicoma* and *Brachylaena*; the latter genus has even reached the 'willow pattern stage' (Corner, 1964: 143), the ultimate in leptocauly, in *B. neriifolia* R.Br. (Hutchinson, 1964: 228). Such pachycaul-leptocaul trends are not open to simple computer analysis, for they are in parallel within related phylads. Are the principles governing pachycauly in Compositae and Campanulaceae of general application?

In Compositae, we need to know more of hyperpachycauly and the reappearance of the big leaf when the acropetal venation has been lost, as in the lettuce in cultivation, and why the basipetal venation of Compositae never seems to exceed about eighteen major costal pairs. We need to know more of the pachycaul *Dendrocacalia* of the Bonin Islands (Tuyama, 1936) and of the Siberian *Petasites* the petioles of which are higher than a man (Gilbert-Carter, 1947: 143). We need to know more but we are almost too late: introductions of continental plants to the islands of Hawaii and St. Helena, and the introduction of animals to those islands and to Kerguelen have had disastrous effects on the passive native pachycauls. In the mountains, the puyas are being grubbed up by shepherds, for lambs can get entangled in *Puya* spines (Pontecorvo, 1972) and in Africa, the *Dendrosenecios* of Kilimanjaro are becoming rare through excessive cutting (Hedberg, 1969). Having fled the rising forests of leptocauly to reach the refuge of islands and mountain, the pachycauls are now cornered by Man the Explorer and Exploiter. We scarcely have time to begin to follow the leads to an understanding of plant evolution provided by the Durian Theory.

## References

- ANON. 1904. *Lobelia nicotianaefolia*. *Gdner's Chron.* III, 35: 194, 195.
- ANTHONY, J. 1936. A remarkable alpine *Lobelia* from Bhutan. *Notes R. bot. Gdn Edinb.* 19: 175–176.
- ARBER, A. 1928. The tree habit in Angiosperms: its origin and meaning. *New Phytol.* 27: 69–84.
- BEKETOFF, A. 1858. Ueber die morphologischen Verhältnisse der Blatt-theile zu einander und zum Stengel. *Linnaea* 29: 417–462.
- BENTHAM, G. 1873. Notes on the classification, history and geographical distribution of the Compositae. *J. Linn. Soc. (Bot.)* 13: 335–577.
- BRAMWELL, D. 1972a. A revision of the genus *Echium* in Macaronesia. *Lagascalia* 2: 37–115.
- 1972b. Endemism in the flora of the Canary Is. In D. H. VALENTINE (Ed.), *Taxonomy, Phytogeography and Evolution*: 141–159. Academic Press, London.
- BRIGHTMORE, D. 1968. Biological Flora of the British Isles. *Lobelia urens* L. *J. Ecol.* 56: 612–620.
- BURTT, B. L. 1974. Patterns of structural change in the flowering plants. *Trans. bot. Soc. Edinb.* 42: 133–142.
- CARLQUIST, S. 1962. A theory of paedomorphosis in dicotyledonous woods. *Phytomorphology.* 12: 30–45.
- 1965. *Island Life*. Natural History Press, New York.
- COE, M. J. 1967. The ecology of the alpine zone of Mount Kenya. *Monog. Biol.* 17: 1–136.
- CORNER, E. J. H. 1949. The Durian Theory or the origin of the modern tree. *Ann. Bot.* 13: 367–414.
- 1953. The Durian Theory extended — I. *Phytomorphology* 3: 465–476.
- 1954a. The Durian Theory extended — II. The arillate fruit and the compound leaf. *Phytomorphology* 4: 152–165.
- 1954b. The Durian Theory extended — III. Pachycauly and megaspermy — Conclusion. *Phytomorphology* 4: 263–274.
- 1964. *The Life of Plants*. Weidenfeld & Nicholson, London.
- 1966. *The Natural History of Palms*. Weidenfeld & Nicholson, London.
- 1967a. On thinking big. *Phytomorphology* 17: 24–28.
- 1967b. *Ficus* in the Solomon Islands and its bearing on the post-Jurassic history of Melanesia. *Phil. Trans. R. Soc. B.* 253: 23–159.
- COTTON, A. D. 1944. The megaphytic habit in the tree *Senecios* and other genera. *Proc. Linn. Soc. Lond.* 156: 158–168.
- CROIZAT, L. 1962. *Space, Time and Form. The Biological Synthesis*. Caracas.
- DARWIN, C. 1859. *On the Origin of Species*. Murray, London.

- DAUBENMIRE, R. F. 1947. *Plants and Environment. A textbook of Plant Autecology.* Wiley, New York.
- DAVIS, E. L. 1961. Medullary bundles in the genus *Dahlia* and their possible origin. *Amer. J. Bot.* **48**: 108–113.
- DIELS, L. 1934. Die paramos der äquatorialen Hoch-Anden. *Sber. preuss. Akad. Wiss.* **1934**: 57–68.
- EXELL, A. W. 1956. Supplement to the Catalogue of the Vascular Plants of S. Tomé (with Principe and Annobon). British Museum, London.
- FOSBERG, F. R. 1944. El Páramo de Sumapaz, Colombia., *J. N. Y. bot. Gdn* **45**: 226–234.
- FRIES, R. E. & T. C. E. FRIES. 1922. Die Riesen-Lobelien Afrikas. *Svensk bot. Tidskr.* **16**: 383–416.
- GATSUK, L. E., T. G. DERSVIS-SOKOLOVA, I. V. IVANOVA & L. M. SHAFRANOVA. 1974. Puti perckhoda at Kustarnikovykh form k travianistym v nekotorykh taksonakh pokrytosemennykh. *Trudy mosk. Obshch. ispyt. Prir.* **561**: 16–36.
- GAWADI, A. G. & G. S. AVERY. 1950. Leaf abscission and the so-called “abscission layer”. *Amer. J. Bot.* **37**: 172–180.
- GILBERT-CARTER, H. 1947. *A Guide to the University Botanic Garden.* Cambridge Univ. Botanic Garden.
- GOOD, R. d’O. 1974. *The Geography of the Flowering Plants.* 4th Ed. Longmans, London.
- HALLÉ, F. & R. A. A. OLDEMAN. 1970. *Essai sur l’Architecture et la Dynamique de Croissance des Arbres Tropicaux.* Masson, Paris.
- HEDBERG, O. 1964. Features of afro-alpine plant ecology. *Acta phytogeogr. suec.* **49**: 1–144.
- 1969. Evolution and speciation in a tropical high mountain flora. *Biol. J. Linn. Soc.* **1**: 135–148.
- HEILBORN, O. 1925. Contributions to the ecology of the Ecuadorian páramos with special reference to cushion plants and osmotic pressure. *Svensk bot. Tidskr.* **19**: 153–170.
- HERKLOTS, G. A. C. 1972. *Vegetables in South-East Asia.* Allen & Unwin, London.
- HOFFMANN, O. 1892. Compositae. In A. ENGLER & K. PRANTL, *Die Natürlichen Pflanzenfamilien IV*, **5**: 187–391, Engelmann, Leipzig.
- HUMBERT, H. 1935. Sur un *Senecio* arborescent nouveau des hautes montagnes du Congo belge et sur les liens phylogénétiques des espèces alliées. *Bull. Soc. bot. Fr.* **81**: 830–848.
- 1962. Flore de Madagascar et des Comores. 189<sup>e</sup> famille Composées, Tome II. Mus. Nat. Hist. Nat., Paris.
- HUTCHINSON, J. 1946. *A Botanist in Southern Africa.* Gawthorn, London.
- JOHNSTON, H. H. 1886. *The Kilima-Njaro Expedition.*, Kegan Paul, London.
- KNIGHT, T. A. 1795. Observations on the grafting of trees. *Phil. Trans. R. Soc.* **85**: 290–295.

- KOECHLIN, J. 1969. Contribution à l'étude morphologique du genre *Pachypodium*. *Adansonia* N. S. **9**: 403-420.
- LECOMTE, H. 1922. Les Bois de la Forêt de l'Analmazaotra. Paris.
- MABBERLEY, D. J. 1973a. Evolution in the Giant Groundsels. *Kew Bull.* **28**: 61-96.
- 1973b. 'Mutomboro' and 'Shukuku Gomen': *Senecio manni* and *Senecio gigas*. In: The pachycaul species of *Senecio* and *Lobelia* in Africa: 15-28. Ph.D. thesis, Univ. of Cambridge.
- 1974a. Branching in pachycaul Senecios: the Durian Theory and the evolution of angiospermous trees and herbs. *New Phytol.* **73**: 967-975.
- 1974b. Pachycauly, vessel-elements, islands and the evolution of arborescence in 'herbaceous' families. *New Phytol.* **73**: 977-984.
- 1974c. The pachycaul Lobelias of Africa and St. Helena. *Kew Bull.* **29**: 535-584.
- 1975a. The Giant Lobelias; pachycauly, biogeography, ornithophily and continental drift. *New Phytol.* **74**: 365-374.
- 1975b. The pachycaul *Senecio* species of St. Helena, 'Cacalia materna' and 'Cacalia paterna'. *Kew Bull.* **30**: 413-420.
- McDOUALL, K. 1927. The gardens at Logan. *J. R. hort. Soc.* **52**: 1-14.
- MELVILLE, R. 1953. Growth and plant systematics. *Proc. Linn. Soc. Lond.* **165**: 173-181.
- MENNINGER, E. A. 1967. *Fantastic Trees*. Viking, New York.
- METCALFE, C. R. & L. CHALK. 1950. *Anatomy of the Dicotyledons*. 2 vols. Oxford University Press.
- MEUSEL, H. 1952. Über Wuchsformen, Verbreitung und Phylogenie einiger mediterran-mitteuropäischer Angiospermen-Gattungen. *Flora (Jena)* **139**: 333-393.
- PONTECORVO, G. 1972. Alpine plants of the Callejón de Huálas. In R. C. ELLIOTT (Ed.), 4th International Rock Garden Plant Conference 1971: 51-97. Alpine Garden Soc., London.
- Von RÜPPELL, E. 1836. Bemerkungen über Abyssinien, im Bezug auf der Physiognomie der Landschaft (Forsetzung). *Zeitsch. Phönix Frankfurt-am-Main* **120**: 479-480.
- 1840. *Reise in Abyssinia, Abbildung*. Frankfurt.
- SALT, G. 1954. A contribution to the ecology of upper Kilimanjaro. *J. Ecol.* **42**: 375-423.
- SCHAFFALITZKY De MUCKADELL, M. 1959. Investigations on aging of apical meristems in woody plants and its importance in silviculture. *Forst. ForsVaes. Danm.* **25**: 310-455.
- SCOTT, H. 1935. Coleoptera associated with the giant Lobelias and arborescent Senecios of Eastern Africa. *J. Linn. Soc. (Zool.)* **39**: 235-284.
- 1940. General and zoogeographical considerations regarding the Coleoptera associated with giant Lobelias and Senecios in Eastern Africa. *Int. Congr. Ent.* **6, 2**: 443-446.

- 1958. Biogeographical research in High Simien (Northern Ethiopia) 1952-3. *Proc. Linn. Soc. Lond.* **170**: 1-91.
- SHREVE, F. 1914. The direct effects of rainfall on hygrophilous vegetation. *J. Ecol.* **2**: 82-98.
- SMITH, A. C. & M. F. KOCH. 1935. The genus *Espeletia*: a study in phylogenetic taxonomy. *Brittonia* **1**: 479-530.
- SMITH, D. L. 1967. The experimental control of inflorescence development in *Carex*. *Ann. Bot.* **31**: 19-30.
- STEBBINS, G. L. 1951. Natural selection and the differentiation of Angiosperm families. *Evolution* **5**: 299-324.
- Van STEENIS, C. G. G. J. 1958. Rejuvenation as a factor for judging the status of vegetation types: the Biological Nomad Theory. *Proc. Kandy Symp. U.N.E.S.C.O.* : 212-218.
- TENOPYR, L. A. 1918. On the constancy of cell-shape in leaves of varying shape. *Bull. Torrey bot. Club* **45**: 51-76.
- TROLL, C. 1947. Der asymmetrische Aufbau der Vegetationszonen und Vegetationsstufen auf der Nord und Südhalbkugel. *Ber. geobot. ForschInst. Rübél* **1947**: 46-83.
- TUYAMA, T. 1936. *Plantae Boninenses novae vel criticae V.* *Bot. Mag. (Tokyo)* **50**: 129-134.
- UETTIEN, H. 1928. Ueber den Zusammenhang zwischen Blattnervatur und Sprossverzweigung. *Recl. Trav. bot. néerl.* **25**: 390-483.
- VASSAL, J. 1970. Contribution à l'étude de la morphologie des plantules d' *Acacia*. Acacias insulaires des océans indien et pacifique: Australie, Formose, Iles Maurice et Hawaii. (*Trav. Lab. For. Toul.* I, **9**: art. VIII) *Bull. Soc. Hist. nat. Toulouse* **106**: 191-276.
- WARDLE, P. 1971. An explanation for alpine timberlines. *N.Z. J. Bot.* **9**: 371-402.
- WHITE, F. 1971. The taxonomic and ecological basis of chorology. *Mitt. bot. StSamml., Münch.* **10**: 91-112.
- WILLIS, J. C. 1973. *A Dictionary of the Flowering Plants and Ferns*. 8th ed. Revised by H. K. AIRY SHAW. Cambridge University Press.
- WIMMER, F. E. 1956. Campanulaceae-Lobelioideae. I teil. In A. ENGLER & L. DIELS, *Das Pflanzenreich, Regni Vegetabilis Conspectus IV*, **276a**: 1-260. (reprint of 1943 ed.). Akad. Verlag, Berlin.
- 1968. Supplementum. *Idem*, **276c**: 815-916.
- WOOD, D. 1971. The adaptive significance of wide altitudinal range for montane species. *Trans. bot. Soc. Edinb.* **41**: 119-124.
- WOODHEAD, N. 1951a. Biological Flora of the British Isles. *Lobelia* L. *J. Ecol.* **39**: 456-457.
- 1951b. *Idem*, *Lobelia dortmanna* L. *J. Ecol.* **39**: 458-464.
- ZIMMERMANN, M. H. & P. B. TOMLINSON. 1972. The vascular system of Monocotyledonous stems. *Bot. Gaz.* **133**: 141-155.



# The Underground Forests of Africa:

## a preliminary review

by

FRANK WHITE

*Departments of Botany & Forestry, University of Oxford*

“Evolution in *Ficus* is from the thick to the thin” — E. J. H. Corner *in litt.* 27. ii. 74.

‘Evolution in Barotseland is from the thin to the thin’. Abridged summary of this paper.

### Summary

The growth-form of the geoxylic suffrutex, which has massive, woody, underground axes but only annual or short-lived shoots above ground is described. The species considered are all related to large forest or woodland trees or lianes and occur in genera with no herbaceous members. They are confined to tropical and subtropical savanna regions. Their distribution and ecology are considered. Geoxylic suffrutices are most diversified in Africa, where they have independently evolved in 31 families. Very few occur in the Sudanian Region and they are rare there. Most are endemic to the climatically similar Zambezi Region where they are centred on the Kalahari Sands which cover much of the upper Zambezi basin and its periphery. Arguments are developed which suggest that the growth form of the geoxylic suffrutex has evolved, not primarily in response to fire, nor to frost, as has been previously supposed, but as a response to the unfavourable edaphic conditions provided by extremely oligotrophic, seasonally waterlogged sandy soils in a region of extremely low relief.

### Introduction

Corner’s fruitful hypothesis, that the proto-Angiosperm was of pachycaul construction with an unbranched or sparsely branched stem, monopodial growth, massive apical meristem, wide pith and cortex, sparse secondary xylem, very short internodes and large compound leaves, illuminates the early adaptive radiation of the vegetative architecture of the Angiosperms and has inspired a number of important detailed studies (e.g. Hallé & Oldeman, 1970; Mabberley, 1974 a, b).

The further diversification of the leptocaul descendants of pachycaul plants, however, has received much less consideration. The purpose of this short account is to draw attention to a group of *geoxylic suffrutices*, which, despite their short stature and quasi-herbaceous habit are closely related to large forest or woodland trees or lianes, and, despite their exiguous subaerial parts, usually have massive woody subterranean structures. Most of them are trees which, for some reason, now live underground. It is interesting to enquire how this has come about.

Geoxylic suffrutices with this kind of phylogenetic relationship to large woody plants are almost confined to those parts of the tropics with a markedly seasonal distribution of rainfall, and where the prevalent vegetation is ‘savanna’ in which woody plants and grasses occur together in various proportions. The term savanna is used here in the general sense of Chapman & White (1970: 82) and not as a precise classificatory unit. Today savanna vegetation is everywhere subjected to extensive man-made fires and consists largely of pyrophytic species. It has probably always been subjected to natural fires which were formerly less frequent and more localized. Some authors, e.g. Exell & Stace (1972), believe that the suffruticose

habit in savanna regions has evolved largely as a response to fire. Fire has certainly played a part in the evolution of the geoxylic suffruticose habit, but its relative importance and significance seem to have been misunderstood.

The distribution of geoxylic suffrutices within the savanna regions of the world is very uneven. Their greatest concentration is in south-central Africa on the Kalahari Sands which cover most of the Upper Zambezi basin and its periphery. Since other elements in the Zambezi flora also show a similar distribution, White (1965) recognized a Barotse centre of endemism, which takes its name from the ancient Kingdom of Barotseland, situated near its heart.

Within the Barotse centre the most characteristic habitat of these suffrutices is a sparse open grassland which burns much less fiercely than most savanna vegetation. They are scarce or absent from the more fiercely burning types. This fact, and their localized distribution within the fire-prone savanna regions, suggests that their origin should be sought not exclusively in relation to fire but that other factors should be considered.

A few suffrutices, which occur on Kalahari Sand, also extend their range into the Highveld grassland of the Transvaal, and a few others are endemic there. This is a part of Africa where frost is severe, a fact which led Burt Davy, writing at a time (1922) when the flora of Barotseland was completely unknown, to suggest that the suffruticose habit had been moulded in response to frost.

For the majority of suffruticose species occurring in the Zambezi Region speciation appears to be complete. Either their geographical ranges overlap with those of closely related large woody species, with which they presumably share a common ancestor, or they are taxonomically isolated and have no very close relatives. For a significant minority, however, speciation is incomplete. Within a single species some populations are suffruticose, whilst others are trees, shrubs or lianes. By studying these species, together with non-suffruticose species in the same general area, which have proceeded part-way towards the suffruticose habit, or show, perhaps sporadically, some of the attributes suffrutices must acquire, it is possible to reconstruct the probable ancestry of this particular growth form.

Evidence is presented in this paper which suggests that, in Africa, the geoxylic suffrutex originated primarily as a response to extremely unfavourable edaphic conditions, but that for some species, at least occasionally, fire is necessary for vigorous growth. The suffrutex is better adapted to frost than the tropical trees and lianes which gave rise to it, but it is unlikely that frost played any significant part in the evolution of the habit.

Literature on geoxylic suffrutices is sparse and scattered. Only Burt Davy (1922) has attempted a general review.

### **Growth Forms**

There are many kinds of suffrutex and the term is often loosely or erroneously applied. The stems of a suffrutex are woody at the base and persist for several years, giving rise to less persistent shoots, which die back after a relatively short time, sometimes each year, sometimes after a longer interval. The suffrutices dealt with here are unusual, in that, at least under present-day conditions, their stems are burnt back almost to ground-level nearly every year. Suffrutices are clearly adapted to this condition. Shortly after burning and well before the onset of the rainy season they send out new shoots, which often produce flowers precociously at the base of the shoot before it is fully developed. The associated grasses and other herbs, which when fully grown may completely conceal the suffrutices, do not begin their vegetative development until after the rains break, by which time the suffrutices have finished flowering.

The suffrutices dealt with here are very sensitive to fire. Even if their shoots are only lightly singed, they die back to the base. A severe fire might kill all the subaerial parts, in which case renewal is from subterranean stems and the plant behaves as a geophyte. Normally, however, the basal parts of the subaerial stems remain and the plant behaves as a chamaephyte.

Different species of suffrutex, and sometimes different populations within species, behave differently when they are protected from fire. In some species there is a considerable die-back every year almost to the base. In other species there is a limited amount of upward growth which may continue for a few years. In obligate suffrutices, however, upward growth is severely restricted and ultimately the subaerial parts become moribund. Few flowers are produced and there is progressive die-back towards the base. In *Parinari capensis* all herbarium specimens from the northern Transvaal are less than 15 cm. tall. Burt Davy transplanted *P. capensis* "to more favourable conditions of temperature and soil moisture" but it "did not show any change of habit after several years". North of the Limpopo, when individuals escape fire, they are capable of attaining a height of 40 cm. but no more. At the extreme south-eastern limits of its range in southern Moçambique and northern Natal it can grow up to a height of 2 m.

All the suffrutices dealt with here have massive woody underground parts and the term 'geoxylic', used by Du Rietz (1921) in a somewhat different context, is appropriate. In the majority, several axes radiate just beneath the surface of the soil from the main vertical subterranean axis, which, except in young plants, is relatively poorly developed. Sometimes they extend for a distance of several metres. In some species these axes can reach a diameter of 10 cm. or more. They are usually very hard and consist mostly of secondary xylem, the total amount of which is probably no less than that of a medium-sized woodland tree growing in the same general region. These radiating axes are usually referred to as 'rhizomes'. Their true nature, however, requires careful investigation since the arboreal relatives of some suffrutices are said to sucker freely from their extensive superficial roots. The suffruticose *Parinari capensis*, for instance, looks very similar to a suckering clump of the tree species *P. curatellifolia* Planch. ex Benth. though their proportions are different.

Some species, e.g. *Erythrina baumii* Harms, have specialised water-storing tissue (Duvigneaud, 1954), but this does not seem to be a general feature.

Some species are not rhizomatous or only slightly so and the underground part consists of a large vertical axis which may be greatly expanded at ground level where many annual shoots arise. Rawitscher & Rachid (1946) describe these for *Cochlospermum insigne* St. Hil. and a palm, of the genus *Acanthococos*. They call them 'xylopodia' and say they are stems. This type seems to be rare in Africa.

This account is confined to suffrutices which not only are closely related to large trees or lianes and have presumably evolved from large trees or lianes, but occur in genera which except for their suffruticose members consist exclusively of large woody plants. Suffrutices of similar habit, though usually with smaller underground parts, which belong to otherwise shrubby groups are excluded from consideration. Similarly the suffruticose species of genera which include true herbs and trees, e.g. *Cassia* and *Phyllanthus* are omitted.

Fig. 1 illustrates *Euclea crispa* a typical "rhizomatous" geoxylic suffrutex. In this polytypic species some subspecies, like the one illustrated are obligate suffrutices, whereas others are always trees. The latter sometimes occur as single-stemmed individuals, but sometimes form thickets of trees which arise from suckers from the superficial 'roots'.



Fig. 1. *Euclea crispa* (Thunb.)  
Gürke. A typical rhizomatous,  
geoxylic suffrutex. Note the charred  
remains of last-year's stems.

## Distribution and Ecology

### General distribution

Geoxylic suffrutices are a conspicuous feature of the *campos cerrados* of the Planalto of Central Brazil, and are recorded in the classical literature (Schimper, 1898: 376; Warming, 1892). No general review has been published but information can be gleaned from a scattered literature — *Andira inermis* Mart. and *Anacardium pumilum* St. Hil. (Rawitscher *et al*, 1963) *Jacaranda decurrens* Cham., *Cochlospermum insigne* St. Hil. and *Acanthococos* sp. (Rawitscher & Rachid, 1946), *Byrsonima verbascifolia* Rich. ex Juss. (Aubréville, 1961), *Chrysophyllum soboliferum* Rizzini (Mangenot, 1969), *Licania dealbata* Hook. f. and *Parinari obtusifolia* Hook. f. (Prance, 1972), and *Caryocar brasiliense* Cambess. subsp. *intermedium* (Wittmack) Prance & Freitas da Silva (Prance & Freitas da Silva, 1973).

It appears that geoxylic suffrutices are fewer in species in South America than in tropical Africa, and that taxonomically isolated, obligate suffrutices are proportionally less well represented.

In Asia it appears that there are very few geoxylic suffrutices. From Australia they seem to be absent, though many multiple-stemmed, tall-shrubby species of *Eucalyptus* have large woody underground parts (*mallee*).

It is in tropical Africa that this growth form is found in its greatest diversity. Here there are no less than 109 species belonging to 56 genera occurring in 31 families. These are listed systematically in an appendix.

### Distribution in Africa

In Africa geoxylic suffrutices are almost confined to the two great savanna regions — the Zambezan and Sudanian. Only a few species occur in the transitional region to the south of the Zambezan Region, the prevalent vegetation of which is grassland and wooded grassland. There are also a few others in the southern part of the Indian Ocean coastal belt, the Tongaland-Pondoland Region, which is a mosaic of savanna-like and forest formations (Fig. 2). Since very few species are confined to the Tongaland-Pondoland Region it is not considered further.

The Sudanian Region occurs as a wide band north of the equator between the rainforests of the Guineo-Congolian Region and arid and semi-arid regions to the north. The Zambezan Region occupies a comparable position south of the equator. In area these two regions are comparable. Their vegetation which consists mainly of woodland, wooded grassland and various types of edaphic and secondary grassland, is broadly similar, as is their climate. The mean annual rainfall varies from 500 to 1500 mm. and the dry season lasts from 5 — 7 months. The Zambezan Region, however, is somewhat more diverse in its physiography and climate. In both regions dry season fires are an annual occurrence over extensive areas. Neither region can be said to be more fire-prone than the other.

The representation of geoxylic suffrutices in the two great savanna regions is very uneven. Only 7 species belonging to 2 genera in 2 families are known from the Sudanian Region, whereas 102 species in 55 genera in 30 families occur in the Zambezan Region. Of the 7 Sudanian suffrutex species, 6 belong to the genus *Combretum* and 5 of them are closely related. 4 species are of very restricted distribution and are confined to upland areas such as Fouta Djallon and the Jos Plateau. Another species, *C. sericeum* G. Don f., is of uncertain taxonomic status and is connected by intermediates to a climbing species, *C. paniculatum* Vent.

The Sudanian and Zambezan Regions are so different in their suffruticose floras that an explanation must be sought, either in their unequal opportunities for the evolution of suffruticose species or in those for the survival of a suffruticose flora which was formerly common to both.

It is well known that the flora of the Sudanian Region is, in general, much poorer than that of the Zambezan Region. In two analyses of the larger woody plants occurring in the two regions, White (1962, 1965) has shown that the flora of the Zambezan Region is probably between two and four times as rich as that of the Sudanian Region. He suggests (1962) that this may, at least in part, be due to differential extinction during the Pleistocene. A region as physiographically diverse as the Zambezan offers better opportunities for migration and survival than does a region of low general relief such as the Sudanian. There is much phytogeographical evidence to support this idea. Several species which are widespread in the Zambezan Region, e.g. *Ochna schweinfurthiana* F. Hoffm., *Protea*

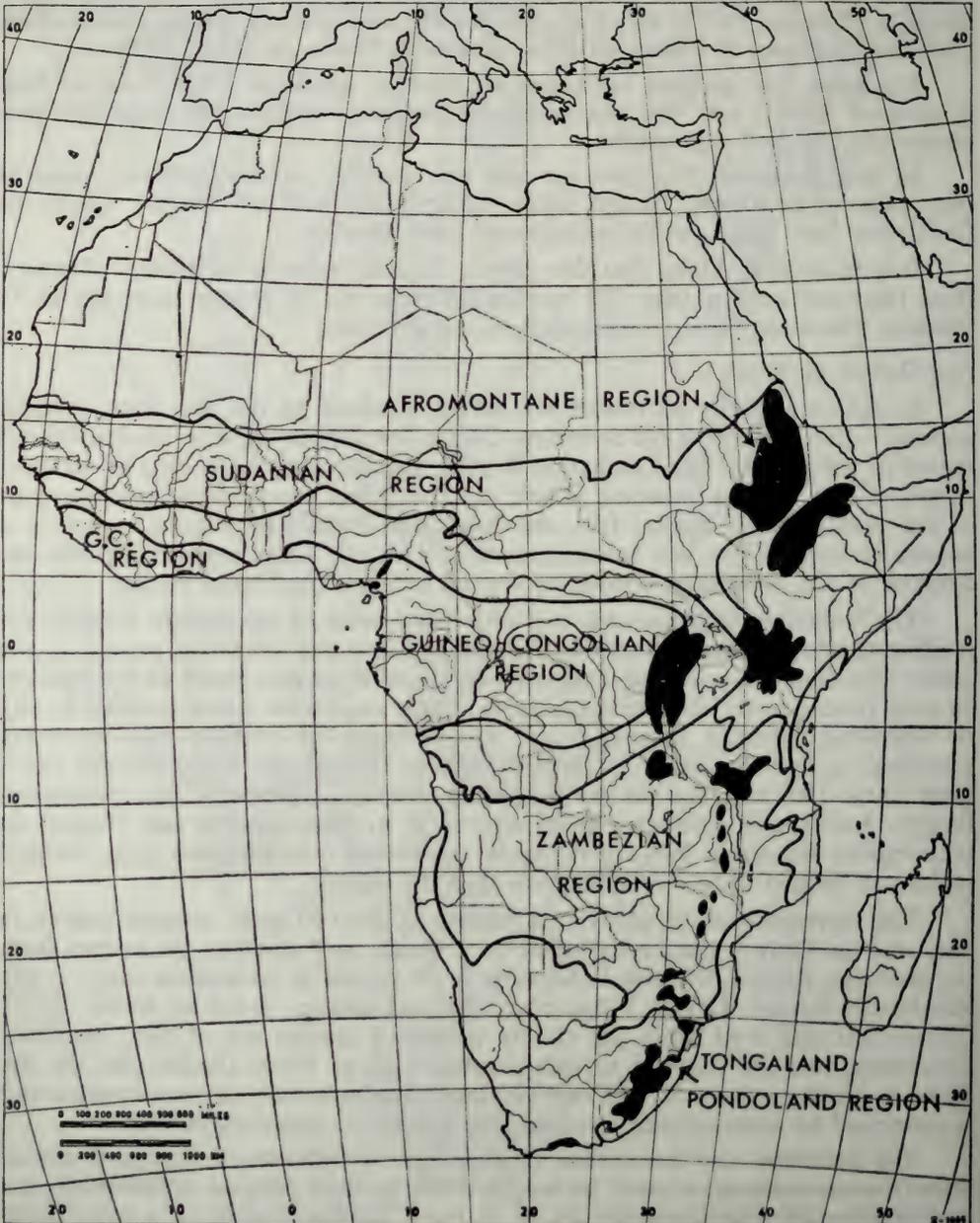


Fig. 2. Map of Africa showing chorological regions referred to in the text.

*madiensis* Oliv., *Terminalia mollis* Laws., are very sporadic in the Sudanian Region. Their distributions suggest that in the Sudanian Region they have only just avoided extinction due to climatic change. If they have only just managed to persist, is it not likely that some of their former associates have perished? Similar considerations might apply to the suffrutices, but here the discrepancy between the two regions is so much greater — the Zambezan suffruticose flora is 15 times as rich as the Sudanian and, at the generic level, 22 times as diversified — that the explanation must surely be sought in differential opportunity for speciation. This leads us to a consideration of the ecology of geoxylic suffrutices.

### *Ecology in Africa*

The most characteristic habitat of the geoxylic suffrutex in the Zambezan Region is seasonally anaerobic grassland, mostly on sandy, extremely oligotrophic soils, which are waterlogged and badly aerated for part of the year and dry out at least in their upper layers during the dry season. Such conditions are inimical to the growth of trees. Even the growth of the grasses, which share dominance with Cyperaceae, is sparse and wiry.

The best-known occurrences of this habitat are at the edges of *dambos*, the seasonally waterlogged grassy depressions which are such a characteristic feature of the unrejuvenated plateau surface representing the African cycle of erosion (King, 1951) which occupies a large part of the Zambezan Region.

By far the most extensive occurrences, however, are on the Kalahari Sands which occupy the Upper Zambezi basin and its periphery, and extend northwards as a narrow belt far into the Guineo-Congolian Region (fig. 3.). The relief of this region is so gentle that waterlogged soils occur very extensively in the Zambezi basin on the virtually flat interfluves between the lower reaches of the tributary rivers of the Zambezi, and, locally, on watersheds of higher elevation which in general are better drained.

This type of anaerobic grassland with suffrutices is the most widespread vegetation type in the upper Zambezi basin (White, in press). Apart from the *dambos* mentioned above, it does not occur anywhere else in Africa, except very locally. There are small areas associated with impeded drainage in places near the coast in the Tongaland-Pondoland Region, which is contiguous with the Zambezan Region, and a few suffrutices occur there.

In the Sudanian Region anaerobic grasslands on sandy oligotrophic soils comparable to those of Zambezia are fragmentary in the extreme, because the land surface has reached a different stage in the cycle of erosion. Apart from a few small patches scattered along the coast they are confined to small areas, each only a few acres in extent, on the flat tops of mesa-like hills where the drainage is impeded by the occurrence of hardpan near the surface (J. B. Hall, *in litt.*). Under these circumstances it is difficult to see how a suffruticose flora could have evolved.

Geoxylic suffrutices are normally absent from secondary grassland following the destruction of forest or woodland. They are only plentiful on soils which are so impoverished that they can only support sparse secondary grassland which in composition and luxuriance is similar to edaphic suffruticose grassland. This occurs chiefly in montane areas and on Kalahari Sand.

Chapman & White (1970) present evidence which indicates that during the last 1000 years extensive areas of montane forest in Malawi have been destroyed by fire and replaced by grassland which owing to soil erosion has become progressively shorter and less luxuriant. The ultimate stage is a sparse grassland in which suffrutices such as species of *Protea* and *Parinari capensis* are often conspicuous. According to Fanshawe (1969: 45) sparse grassland with abundant suffrutices, which has spread from the waterlogged interfluves and depressions, may represent the last stage of degradation of Kalahari forest and woodland following clearing and persistent burning.

Kalahari Sand formerly covered a much larger area than it does today as is shown by the many residual patches which still survive.

The great majority of geoxyllic suffrutices occurring in the Zambezi Region are either confined to the main occurrence of Kalahari Sand centred on Barotse-land, e.g. *Trichilia quadrivalvis* C. Dc. (fig. 3), or have their centre of distribution there, or occur within the range of the former distribution of Kalahari Sands.

The most abundant species on Kalahari Sand is *Parinari capensis*, which is also the most widespread Zambezi geoxyllic suffrutex (fig. 3). It occurs beyond the former limits of Kalahari Sand on other types of sandy soil, not only the sandy

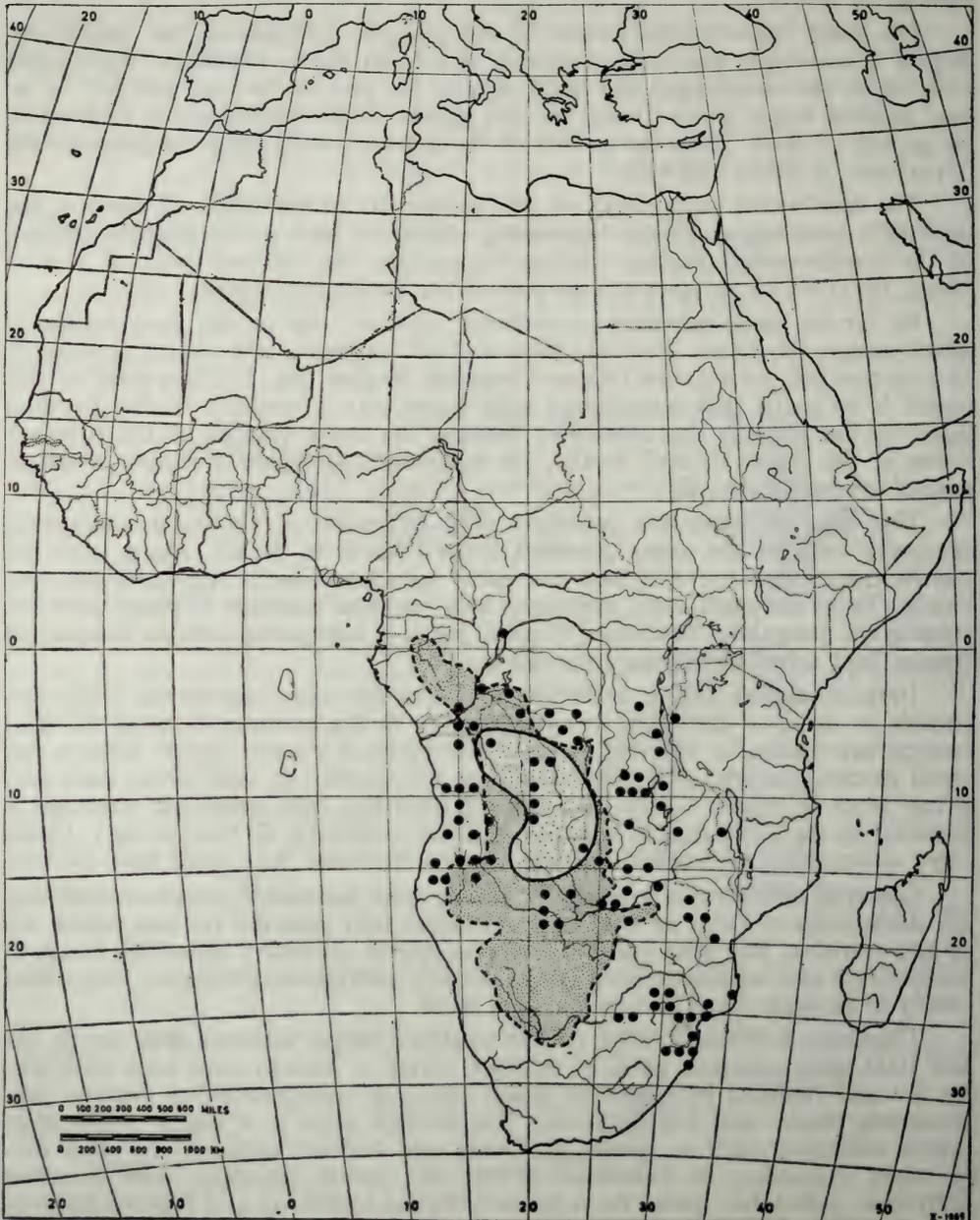


Fig. 3. Map of Africa showing distribution of (a) Kalahari Sand (broken line); (b) *Trichilia quadrivalvis* C. DC. (continuous line); (c) *Parinari capensis* Harv. (solid circles).

edges of *dambos* but also on shallow sandy soils surrounding granite *inselbergs* in the Transvaal and on maritime sands of the Tongaland coastal plain. Most Zambe-zian geoxylic suffrutices have distributions intermediate between those of *Trichilia quadrivalvis* and *Parinari capensis*.

### Evolution

#### *The significance of fire*

In the absence of fire, some, perhaps most, suffrutices are capable of a limited amount of upward growth, but eventually the shoots become moribund and die back. Fire destroys this slowly dying, not very floriferous, material, and stimulates the production of numerous precociously-flowering shoots. This response to fire is clearly adaptive. Flowering takes place some weeks or months before the associated grasses, which eventually conceal the suffrutices, begin their growth. Their flowers are visible and accessible to pollinating insects and much of the season's growth is completed before competition for light becomes a serious factor.

It is difficult, however, to see how the suffruticose habit *arose* in response to fire. Chorological and ecological evidence are both against it.

We have seen that in Africa geoxylic suffrutices have a very uneven distribution. The great majority are concentrated in part of the Zambe-zian Region. The Sudanian Region, with various qualifications mentioned elsewhere, is comparable in size, climate and flora to the Zambe-zian. The incidence of fire is the same in both, or, if anything, greater in the Sudanian, and yet the latter is almost bereft of suffrutices.

Because of the climatic vicissitudes of the Pleistocene, the Sudanian Region has suffered more extinction than the Zambe-zian, but the disparity between the two suffruticose floras, compared with that of some other growth forms, is so great, that differential extinction from a former common suffruticose flora provides an unlikely explanation.

Within the Zambe-zian Region geoxylic suffrutices show a very uneven distribution in relation to the intensity of burning. Their most characteristic habitat is edaphic grassland. This is a fire-sensitive community and is frequently burnt. But it does not burn fiercely, in contrast to most types of secondary grassland occurring in the same general area. Suffrutices are conspicuously absent from the latter. It has been demonstrated experimentally (Trapnell, 1959, White, unpublished) that when Zambe-zian woodland is subjected to annual fires at the end of the dry season, when the burn is more intense, the trees are progressively eliminated, and the grass becomes more luxuriant. Suffrutices are not normally found under these conditions. Whether fire or competition with the coarse grasses is the primary cause is uncertain. The trees may be eliminated as trees, but they are not always killed outright. The underground parts survive, and, each year, after the fire, produce an annual crop of *non-flowering* coppice shoots. Even after 40 years of yearly late burning, the rootstocks survive and, were the fires to cease, could give rise to trees again. Burning as prolonged and intense as this far exceeds the destructive effects of natural fires, or fires started in connection with land clearance and farming. Lawton (1972) has shown that under the latter conditions many tree species, even some which are relatively fire-sensitive, can become established from seed in secondary grassland which is subjected to fierce, though not necessarily annual, fires. The inescapable fact is that the woodland trees of the Zambe-zian Region are well-adapted to withstand fire — even to withstand a fire-regime far fiercer than anything they have experienced in their whole evolutionary history. They have no need to evade a menace which does not exist. In some cases the tree which is adapted to fierce fires and the related suffrutex which evades them are so similar in everything other than pattern of growth and habit that identification is difficult

when the habit is unknown. Examples of such pairs of sibling species are *Parinari curatellifolia* Planch. ex Benth. (tree) and *P. capensis*, and *Diospyros batocana* Hiern (tree) and *D. chamaethamnus* Dinter ex Mildbr. It is perhaps significant that *Parinari curatellifolia* is as common in the Sudanian Region as it is in the Zambezan, but has not given rise to a suffrutex there.

#### *The significance of frost*

Burt Davy's early account (1922) was concerned with the Highveld in the Transvaal. Here the prevalent vegetation is grassland "bare of trees except in the shelter of rocky kopjes and even there only a few scattered individuals are met with". A few suffrutices, which also occur on Kalahari Sand, e.g. *Dichapetalum cymosum*, *Elephantorrhiza elephantina* and *Parinari capensis* extend into the Highveld grassland. A few other suffrutices, e.g. *Elephantorrhiza obliqua*, *Erythrina zeyheri* and *Eugenia pusilla*, are more or less confined to it. The winters on the Highveld are cold with considerable extremes. Frosts are a regular feature. Killing frosts fall as early as March and as late as October. Burt Davy suggests that in the Transvaal the suffruticose habit has evolved in response to frost. This could very well be so for the endemic species, but probably less than 10% of the suffrutex flora of South Central Africa occur mainly in frosty regions and many species occur in or are confined to frost free regions. Other chorological and ecological evidence points in another direction.

#### *Edaphic control*

We have seen that in Africa the great majority of geoxylic suffrutices occur on the mantle of Kalahari Sand centred on Barotseland, or within the region of its former extent. They are mostly found on sandy soils on very gently sloping or almost flat surfaces. The sands, some of which have been redistributed by water, are extremely poor in nutrients. Because of the low relief and seasonal climate, the sandy soils are seasonally waterlogged and seasonally dry. The fluctuating water-table causes the formation of impervious horizons near the surface. This accentuates the seasonal differences in soil-water content and restricts the rooting environment and hence the nutrient supply of woody plants. In general, seasonally waterlogged soils in the same general region favour the growth of grasses *vis à vis* woody plants, but the Kalahari Sands are sometimes so deficient in nutrients that, even in the absence of competition from woody plants, the grass growth is sparse.

The trees of the Zambezan Region cannot withstand seasonal waterlogging followed by seasonal drying out of the soil. Under such conditions on the Kalahari Sand, and at the sandy edges of *dambos* on the Central African plateau, trees are replaced by suffrutices. Where flooding is prolonged, woody plants are completely excluded.

Except when the suffrutices are flowering, the communities they occur in have the appearance of grassland and are usually described as such. The phytomass of the suffrutices however greatly exceeds that of the grasses.

The correlation between the edaphic conditions just described and the distribution of geoxylic suffrutices is so great, and the correlation between the incidence of fire and the incidence of frost and the occurrence of suffrutices so weak, that we must postulate a causal connection for the former. We must also look for confirmatory evidence.

Although edaphic grassland with suffrutices is the most extensive vegetation type in the upper Zambezi basin, dry forest (now largely destroyed) occurs on the deeper well-drained sands, and is separated from the edaphic grassland by an ecotone of woodland and wooded grassland.

Within the upper Zambezi basin there is a complex mosaic of different edaphic conditions largely dependent on effective depth of soil and its water-relations. It is under circumstances such as these, especially where soil fertility is at a critical low level, that one would expect to find intermediate stages in the evolution of the suffruticose habit. The best example is provided by *Baikiaea plurijuga* Harms.

*Baikiaea* is a small genus of trees which is confined to the Guineo-Congolian Region, except for *B. plurijuga* which dominates dry semi-deciduous forest on deep well-drained Kalahari Sand in the lower half of the upper Zambezi basin. The northernmost occurrences of *B. plurijuga* are separated from the Guineo-Congolian Region by an interval of 600 km. *B. plurijuga* is normally a tree 20 m. or more in height. There are no suffruticose species of *Baikiaea*, but *B. plurijuga* has recently (Fanshawe & Savory, 1964) been found to occur on sites which appear to be intermediate between typical forest sites and typical suffruticose grassland. Here *Baikiaea* forms dwarf forests less than 2 m. tall. "If the root is excavated a candelabra effect is exposed". Just below the soil surface the original tap root gives off a number of comparatively short twisted branches from the ends of which tufted shoots arise. The latter apparently persist for no more than 4 years. This life-form of *Baikiaea* is very similar to that of a rhizomatous geoxylic suffrutex. Fanshawe and Savory suggest that the curious growth-form of *Baikiaea* might be due to a peculiarity of nutrient status but is more likely to be due to impeded drainage. A more detailed study of the edaphic conditions would be most instructive.

A change in growth-form as drastic as that between a forest tree and a geoxylic suffrutex could not be caused by the tree invading a new and very different habitat under a stable environment, followed by its descendants gradually adapting to the different conditions by mutation and selection. The original invader would be eliminated by selection from the start. Such a change is much more likely to happen if the environment of a population undergoes a gradual change to which the population gradually adapts. In a region of such low relief and imperfect drainage as Barotseland, relatively little change, either climatic or physiographic, would be necessary to bring this about. Indeed, in another publication, Fanshawe (1969b) discusses evidence which suggests that in one part of Barotseland the water-table is at present rising and causing the deaths of trees over a large area.

It is currently fashionable to interpret most patterns of plant distribution in Africa and some patterns of taxonomic relationship, especially where closely related species are involved, in terms of climatic events of the Pleistocene, very often in terms of the most recent phases, involving a period of no more than 20,000 years. Much, doubtless, can be interpreted in this way, but much cannot. It is likely that edaphic conditions favourable for the evolution of suffrutices were greatly extended in Barotseland during the pluvial periods of the Pleistocene, but this does not mean that the suffrutices originated then. Quite small physiographic events such as minor warping of the earth's crust or the capture of major tributary rivers could produce, over quite extensive areas, the kind of edaphic change required for transformation in growth form. This could have happened repeatedly over a very long period of geological time. The genus *Parinari*, which has figured so prominently in this discussion, is well represented in tropical America, Africa and Asia, and occurs in Madagascar. In its leaves, flowers and fruits it is remarkably uniform, and has diversified little since the breakup of Gondwanaland. Is it necessary to postulate that its speciation occurred in the Pleistocene? Is it not more likely that the tumultuous events of that period have merely sharpened the edges of taxa which began their differentiation a very long time before?

## APPENDIX

Systematic List of Obligate and Facultative Geoxylic Suffrutices occurring in Africa.

S — occurring in Sudanian Region. T-P — occurring in Tongaland-Pondoland Region.  
Z — occurring in Zambezi Region.

## ANACARDIACEAE

- Z. *Heeria nitida* Engl. & v. Brehm. and c. 8 other species  
Z. *Lannea edulis* (Sond.) Engl.  
Z. *L. gossweileri* Exell & Mendonça  
Z. *L. katangensis* Van der Veken  
Z. *L. virgata* R & A. Fernandes  
Z. *Rhus kirkii* Oliv. and c. 4 other species

## ANNONACEAE

- Z. *Annona stenophylla* Engl. & Diels

## APOCYNACEAE

- Z. *Chamaeclitandra henriquesiana* (K. Schum. ex Warb.) Pichon  
Z. *Landolphia gossweileri* (Stapf) Pichon — facultative; liane  
Z. *Rauvolfia nana* E. A. Bruce  
Z. *Strophanthus angusii* F. White

## ARALIACEAE

- Z. *Cussonia corbisieri* De Wild.

## CELASTRACEAE

- Z. *Salacia bussei* Loes. — facultative; shrub  
Z. *S. luebbertii* Loes.  
T-P, *S. kraussii* — (Harv.) Harv. — facultative; shrub

## CHRYSOBALANACEAE

- Z. *Magnistipula sapinii* De Wild.  
Z. *Parinari capensis* Harv.

## COCHLOSPERMACEAE

- S. *Cochlospermum tinctorium* A. Rich.

## COMBRETACEAE

- Z. *Combretum argyrotrichum* Welw. ex Laws.  
S. *C. brassiciforme* Exell  
S. *C. harmsianum* Diels  
S. *C. lineare* Keay  
Z. *C. platypetalum* Welw. ex Laws.  
S. *C. relictum* Hutch & Dalz.  
S. *C. sericeum* G. Don f.  
Z. *C. viscosum* Exell

## DICHAPETALACEAE

- Z. *Dichapetalum bullockii* Hauman  
Z. *D. cymosum* (Hook.) Engl.  
Z. *D. rhodesicum* Sprague & Hutch.

## DILLENACEAE

- Z. *Tetracera masuiana* De Wild. & Th. Dur.

## EBENACEAE

- Z. *Diospyros chamaethamnus* Dinter ex Mildbr.  
Z. T-P. *D. galpinii* Hiern  
Z. T-P. *D. lycioides* Desf. — facultative; shrub, small tree  
Z. *D. virgata* (Gürke) Brenan  
Z. *Euclea crispa* (Thunb.) Gürke — facultative; shrub, small tree

## FLACOURTIACEAE

- Z. *Caloncoba suffruticosa* (Milne-Redh.) Exell & Sleumer

## GUTTIFERAE

- Z. *Garcinia buchneri* Engl.  
Z. *Psorospermum mechowii* Engl.

## IXONANTHACEAE

- Z. *Ochthocosmus candidus* (Engl. & Gilg) Hall. f.

## LECYTHIDACEAE

- Z. *Napoleona gossweileri* Baker f.

## LEGUMINOSAE: CAESALPINIOIDEAE

- Z. *Brachystegia russelliae* Johnston  
Z. *Cryptosepalum exfoliatum* De Wild. — facultative, small tree  
Z. *C. maraviense* Oliv.

## LEGUMINOSAE: MIMOSOIDEAE

- Z. T-P *Elephantorrhiza elephantina* (Burch.) Skeels  
Z. *E. obliqua* Burt Davy  
T-P *E. woodii* Phillips  
Z. *Entada dolichorrhachis* Brenan  
Z. *E. nana* Harms

## LEGUMINOSAE: PAPILIONOIDEAE

- Z. *Erythrina baumii* Harms  
Z. *E. zeyheri* Harv.

## LINACEAE

- Z. *Hugonia gossweileri* Bak. f. & Exell ex De Wild.

## LOGANIACEAE

- Z. *Strychnos gossweileri* Exell — facultative; liane

## MALPIGHIACEAE

- Z. *Sphedamnocarpus angolensis* (A. Juss.) Planch. ex Oliv.

## MELIACEAE

- Z. *Ekebergia pumila* I. M. Johnston  
Z. *Trichilia quadrivalvis* C. DC.

## MORACEAE

- Z. *Ficus pygmaea* Welw. ex Hiern  
 Z. *F. verruculosa* Warb. — facultative;  
 small tree

## MYRTACEAE

- Z. *Eugenia angolensis* Engl.  
 T-P *E. capensis* (Eckl. & Zeyh.) Sond.  
 — facultative; tree  
 Z. *E. pusilla* N. E. Br.  
 Z. *Syzygium guineense* (Willd.) DC.  
 subsp. *huillense* (Hiern) F. White

## OCHNACEAE

- Z. *Brackenridgea arenaria* (De Wild. &  
 Dur.) N. Robson — facultative;  
 shrub.  
 Z. *Ochna conjusa* Burttt Davy & Green-  
 way  
 Z. *O. katangensis* De Wild.  
 Z. *O. leptoclada* Oliv.  
 Z. *O. macrocalyx* Oliv. — facultative;  
 shrub  
 Z. *O. manikensis* De Wild.  
 Z. *Ochna mossambicensis* Klotzsch —  
 facultative; shrub  
 Z. *O. pygmaea* Hiern  
 Z. *O. richardsiae* N. Robson

## PASSIFLORACEAE

- Z. *Paropsia brazzeana* Baill. — faculta-  
 tive; shrub

## PROTEACEAE

- Z. *Protea angolensis* Welw.  
 Z. *P. heckmanniana* Engl.  
 Z. *P. paludosa* Welw.  
 Z. *P. trichophylla* Engl. & Gilg

## RHAMNACEAE

- Z. *Ziziphus zeyherana* Sond.

## RHIZOPHORACEAE

- Z. *Anisophyllea quangensis* Engl. ex  
 Henriques

## RUBIACEAE

- Z. *Ancylanthus rubiginosus* Desf.  
 Z. *Gardenia subacaulis* Stapf & Hutch.  
 Z. *Leptactina benguelensis* (Welw. ex  
 Benth. & Hook. f.) R. Good  
 Z. *Morinda angolensis* (R. Good) F.  
 White  
 Z. *Pachystigma pygmaeum* (Schlecht.)  
 Robyns  
 Z. *Pavetta pygmaea* Brem.  
 Z. *Psychotria* spp.  
 Z. *\*Pygmaeothamnus conerescens*  
 Bullock  
 Z. *P. zeyheri* (Sond.) Robyns  
 Z. *Tapiphyllum* spp.  
 Z. *Tricalysia cacondensis* Hiern  
 Z. *T. suffruticosa* Hutch.

## SAPINDACEAE

- Z. *Deinbollia fanshawei* Exell

## TILIACEAE

- Z. *Grewia decemovulata* Merxm. —  
 facultative; shrub  
 Z. *G. falcistipula* K. Schum. — faculta-  
 tive; shrub  
 Z. *G. herbacea* Welw. ex Hiern

## VERBENACEAE

- Z. *Clerodendrum buchneri* Gürke  
 Z. *C. lanceolatum* Gürke  
 Z. *C. milne-redheadii* Moldenke  
 Z. *C. pusillum* Gürke  
 Z. *C. triplinerve* Rolfe

\* This genus only has suffruticose members. It is however very closely related to the arborescent *Canthium*.

## References

- AUBRÉVILLE, A. 1961. *Étude écologique des principales formations végétales du Brésil*. Centre Techn. For. Trop. Nogent-sur-Marne.
- BURTT DAVY, J. 1922. The suffrutescent habit as an adaptation to environment. *J. Ecol.* **10**: 211–219.
- CHAPMAN, J. D. & F. WHITE. 1970. *The evergreen forests of Malawi*. Comm. For. Inst. Oxford.
- DU RIETZ, G. E. 1931. Life-forms of terrestrial flowering plants, I. *Act. a phytogeogr. suec.* **3**: (1).
- DUVIGNEAUD, P. 1954. Une Erythrine à xylopode des steppes du Kwango. *Lejeunia* **15**: 91–94.
- EXELL, A. W. & C. A. STACE. 1972. Patterns of distribution in the Combretaceae. In VALENTINE, D. H. (ed.) *Taxonomy, phytogeography and evolution*. Academic Press, London & New York.
- FANSHAWE, D. B. 1969a. The vegetation of Zambia. *For. Res. Bull.* **7**. Kitwe, Zambia.
- 1969b. The vegetation of Kalabo District. *For. Res. Pamphl.* **22**. Kitwe, Zambia.
- & B. M. SAVORY. 1964. *Baikiaea plurijuga* dwarf-shell forests. *Kirkia* **4**: 185–190.
- HALLÉ, F. & R. A. A. OLDEMAN. 1970. Essai sur l'architecture et la dynamique de croissance des arbres tropicaux. *Coll. Monogr. Bot.* **6**. Paris.
- KING, L. C. 1951. *South African scenery*, ed. 2. Oliver & Boyd, Edinburgh.
- LAWTON, R. M. 1972. *An ecological study of miombo and chipya woodland with particular reference to Zambia*. Thesis, Oxford University.
- MABBERLEY, D. J. 1974a. Branching in pachycaul Senecios: the Durian Theory and the evolution of Angiospermous trees and herbs. *New Phytol.* **73**: 967–975.
- 1974b. Pachycauly, vessel-elements, islands and the evolution of arborescence in 'herbaceous' families. *New Phytol.* **73**: 977–984.
- MANGENOT, G. 1969. Réflexions sur les types biologiques des plantes vasculaires. *Candollea* **24**: 279–294.
- PRANCE, G. T. 1972. *Fl. Neotropica Monogr.* **9**, Chrysobalanaceae. Hafner, New York.
- & M. FREITAS da SILVA. 1973. *Fl. Neotropica Monogr.* **12**, Caryocaraceae. Hafner, New York.
- RAWITSCHER, F. K., M. G. FERRI & M. RACHID. 1943. Profundidade dos solos e vegetação em campos cerrados do Brasil Meridional. *Anais. Acad. bras. Cienc.* **15**: (4).
- & M. RACHID. 1946. Troncos subterrâncos de plantas Brasileiras. *Anais. Acad. bras. Cienc.* **18**: 261–280.
- SCHIMPER, A. F. W. 1898. *Pflanzen-Geographie auf physiologischer Grundlage*. Fischer, Jena.

- TRAPNELL, C. G. 1959. Ecological results of woodland burning experiments in Northern Rhodesia. *J. Ecol.* **47**: 129-168.
- WARMING, E. 1892. *Lagoa Santa*.
- WHITE, F. 1962. Geographic variation and speciation in Africa with particular reference to *Diospyros*. *Syst. Assn Publ.* **4**: 71-103.
- 1965. The savanna woodlands of the Zambebian and Sudanian Domains: an ecological and phytogeographical comparison. *Webbia* **19**: 651-681.
- (ed.) (in press). *Vegetation map of Africa*. UNESCO, Paris.



## Notes on Rain-Forest Herbs

by

B. L. BURTT

*Royal Botanic Garden, Edinburgh*

Concise summaries of views on the herbaceous plants of rain-forest have been given by Richards (1952, pp. 96–102) and by Walter (1971, pp. 118–122). The present notes are an attempt to expand the subject a little further, by recording some observations on the growth patterns of dicotyledonous herbs and emphasising the contrasts both with monocotyledons and with temperate forest dicotyledons. At present the relation between structural features of the leaves and physiological function is, in general, rather uncertain, and this is not the field for a taxonomist to enter. Nevertheless I have ventured a few remarks, if only as a reminder of the questions a field-botanist wants to ask. These notes are inevitably limited by my personal experience, which wholly excludes the New World and is derived largely from collecting trips in Sarawak.

The importance of the massive tropical palms (Palmae) and screw-pines (Pandanaeae) in attaining a balanced appreciation of monocotyledons as a group is now widely recognized. But even at the level of rain-forest herbs a comparison between monocotyledons and dicotyledons illuminates some fundamental differences more brightly than a similar study in temperate forests. When these are brought into the picture, it is immediately apparent that, under the impact of a strongly seasonal climate, the contrast between monocotyledon and dicotyledon has been lessened.

First let us look at growth-habits, particularly at the underground parts. In temperate forests rhizomes or stolons with scale-leaves are frequent, both amongst dicotyledons and monocotyledons: for instance, *Mercurialis* (Euphorbiaceae — see Mukherji, 1936) or *Paris* (Liliaceae — see Kirchner, Loew & Schröter, 1934) in Europe; *Podophyllum* (Berberidaceae — see Holm, 1899) or *Medeola* (Liliaceae — see Bell, 1974) in North America. Examples could easily be multiplied.

Of the herbs of tropical rain-forest Richards (1952, p. 98) says “... plants with underground rhizomes are frequent, but the rhizomes are adapted for multiplication and migration rather than perennation”. He is echoed, despite a slightly different concept of perennation, by Walter (1971, p. 118): “the herbs are often equipped with underground perennating organs such as rhizomes and tubers. But these serve less as storage organs for reserve food than as a means of vegetative reproduction”. These statements need some qualification. They might seem to imply, no doubt unintentionally, that the rhizomes of temperate forest herbs do not serve for spread or vegetative reproduction; of course, they clearly do so. Secondly, in my experience, rhizomes may be common on tropical monocotyledons but they are certainly very rare amongst the dicotyledons. In considering rain-forest herbs the two groups *must* be distinguished.

It may be as well to restrict the words “storage” and “perennation” to use when a seasonal dormancy is accompanied by complete die-back of aerial shoots. Then the situation found in most non-seasonal rain-forest herbs with underground rhizomes may be described as the accumulation of food-reserves. The importance of this must not be underestimated in the monocotyledons. The rhizomes of many

Zingiberaceae eventually throw up massive new leaf-fronds anything from 1.5 to 9 metres in height. This can scarcely be achieved without the backing of some accumulated reserves, even though there is continuity through the rhizome or stolon to older actively photosynthetic fronds. Very often the tip of the rhizome becomes decidedly swollen when it turns up to form the new leaf-frond.

Some Zingiberaceae grow in tight clumps, and these, of course, have short slow-growing rhizomes; others form dense or diffuse patches, and in these the rhizome is extended as a far-ranging stolon. Apart from question of size, the patterns are those of rhizomatous herbs in temperate forests.

Dicotyledonous herbs also form patches in the rain-forest, but this is achieved without the aid of scale-clad underground rhizomes or stolons. A characteristic pattern of growth can be observed in *Cyrtandra radiceflora* C.B.Cl. (Gesneriaceae). This species forms stands with erect leafy shoots keeping a more or less even height of about 0.75 metre. These shoots are evergreen and their duration is unknown. Flowering is axillary and basal, at or near ground level. The terminal bud remains vegetative and produces a succession of leaves. What prevents the shoots from growing higher and higher?

It seems that the average height is maintained because, as upwards growth proceeds, the lower part of the stem becomes more and more decumbent. If a handful of shoots are pulled up it will be found that they are linked by pieces of prostrate, sometimes buried, stem. Buds on the prostrate stems give rise to new shoots that help to thicken the patch, and the process of becoming prostrate helps to expand it. At all times the main growing points of the shoots are aerial and are directed upwards. There is no horizontal (diageotropic) growing point like that of a rhizome or stolon.

The pattern just described for *Cyrtandra radiceflora* is found in a number of species of this genus (which is very large and very varied in growth-patterns), and in other genera where some species have axillary inflorescences: *Argostemma* (Rubiaceae), *Elatostema* (Urticaceae), *Linariantha* (Acanthaceae), *Gomphostemma* (Labiatae) come to mind. Other rain-forest herbs (e.g. some Acanthaceae) have terminal inflorescences; these plants retain their herbaceous stature by dying down to near the base after fruiting and form new shoots from basal buds: scars of old shoots are often visible, though I have never noticed a dead shoot in situ. Observations on the death-patterns of tropical herbs are badly needed: there are indications that the fruiting shoot may die slowly, so that its leaves are still photosynthetic long after the seeds are shed. This could be a necessary feature, in the absence of underground storage organs, to support the growth of a new shoot: but that is speculation until careful studies can be made. This pattern of growth is shown in some forest species of *Pseuderanthemum* (Acanthaceae); other members of the genus do not die back but produce shoot-buds from the axils of leaves just below the dead infructescence — and become shrubs. Another genus of Acanthaceae which has terminal inflorescences and dies down is *Cosmianthemum*; it is unusual in having somewhat fleshy roots; otherwise the roots of these forest herbs are thin and wiry.

By no means all the dicotyledons with axillary flowers become decumbent at the base. A very frequent habit is a stiff erect unbranched stem with the leaves tending to be in the upper part, sometimes in a distinct cluster near the top — rather the habit of a miniature palm tree. Once again we have no knowledge of the duration of such plants. This habit is found in a number of genera, for instance *Didymocarpus*, *Didissandra* and *Cyrtandra* (Gesneriaceae), *Sonerila* (Melastomaceae) and *Neckia* (Ochnaceae).

A simple modification is found when species grow horizontally from vertical cliff faces; then the terminal tuft of leaves is eccentric, the leaves on the lower side being longer; in *Cyrtandra mirabilis* C.B.Cl. the longest leaves may be as much as

70 cm, and as they are thin and delicate this would be an impossible size on an erect stem. In this habitat, too, is found an elaboration of the simple pattern; the stem is branched, each branch having its characteristic tuft of leaves: in a form of *Didymocarpus gracilipes* C.B.Cl. there may be as many as 20 leaf-tufts. Again it is difficult to envisage this pattern being successful as an erect stem. Cliff-plants with these fans of pendulous leaves are found in both Asiatic and American Gesneriaceae (cf. *Resia* H. E. Moore, 1962), and also in such genera as *Steenisia* (Rubiaceae).

Another variant is the plant with an erect fan of leaves sometimes found on steep slopes and banks in the forest. Here the stem is short, or the lower part becomes prostrate keeping the leaf tuft near ground level. Such a fan of leaves, each about 30 cm long, is beautifully shown in *Cyrtandra penduliflora* Kraenzl. and is associated there with marked anisophylly—one leaf of each pair is reduced to a small stipule-like structure — and the development of prop roots, perhaps 20–30 cm long and 2 mm diam. quite rigid and branching only when they have reached the soil. These are of obvious value in supporting the plant in steep habitats.

It might seem that the simple erect stem and the decumbent, branched, patch-forming type stand widely apart. However, *Didymocarpus malayanus* Hook. f. is a plant of the Malay Peninsula which occurs in two forms: one has an erect unbranched stem, but the leaves show rather less apical aggregation than characteristic of that pattern, while the other is a prostrate mat-forming type, the shoots never being more than about 6 inches above the surface of the ground. Although the inflorescences of the erect plant carry many more flowers, there appears to be no essential difference between the two: if eventually separable as distinct species, they are at least very closely allied.

One noteworthy type of growth that I have not personally encountered in Sarawak (and I think it is not recorded there) is the much branched monocarpic herb represented by several species of *Strobilanthes* (Acanthaceae). These plants are well known for their gregarious habit and their periodic simultaneous flowering. Records for Sumatra and Java are summarized by van Steenis (1942); they include *S. kunthianus* Benth. from open grassy places and *S. cernuus* Bl. and others which are "hygrophytes of rather dark mountain forests". The habit is best known in species of *Strobilanthes* found in the seasonal forests of India, and also occurs in other genera of Acanthaceae (*Isoglossa*, *Mimulopsis*) in the evergreen but distinctly seasonal forests of eastern and south-eastern Africa.

In these seasonal forests underground storage organs become much more frequent in dicotyledons: climbers with annual stems and tubers become prominent (*Gerrardanthus*, *Cissus fragilis* Harv., *Tacazzea* in Natal) and genera which lack storage organs in rain-forest, or in the always-damp habitats in these seasonal forests, develop them: for instance *Begonia*. In south-east Africa *Impatiens duthieae* L. Bolus is found in always-damp situations in the forest and has no storage organs, *I. flanaganae* Hemsl., more exposed to seasonal change at the forest margin, has tubers; in northern Malaya *Impatiens mirabilis* Hook. f., a plant of the somewhat seasonal forests on the limestone, has a thickened storage trunk resembling an *Adenium*.

Two genera of monocotyledons that range from the seasonal monsoon forests of south-east Asia down into the rain-forest are particularly interesting. These are *Arisaema* (Araceae) and *Hedychium* (Zingiberaceae). By far the greater number of the species of *Arisaema* live under markedly seasonal conditions: they have an underground corm which produces leaves and inflorescence annually and has a distinct period of rest. This pattern is found also in *Arisaema fimbriatum* Mast. of the Langkawi Islands, N. Malaya, where the forest is largely evergreen, but with a proportion of deciduous species and a distinctly dry and cool winter. Species are found further south on the mainland (*A. anomalum* Hemsl.) and in Borneo

and Java (*A. umbrinum* Ridl., *A. filiforme* Bl. etc.), which have a thick fleshy rhizome, rather than a corm, and these plants have leaves present all the year round. *Hedychium* is rhizomatous throughout its range, but in the northern seasonal area all the leaf fronds die down in winter and the plant is dormant; in the Bornean *H. cylindricum* Ridl. there are leaf fronds present throughout the year.

Another aroid, *Amorphophallus*, seems to be somewhat anomalous in its behaviour. It has a large corm and Walter (1971, p. 118) reports that in Africa, where it grows in seasonal areas, it flowers before it leaves. In Sarawak, where it is by no means uncommon, a corm will produce a flower in one year, a leaf in another: adjacent corms are in growth simultaneously so that flowers and leaves may be found together. However there is probably no strict alternation of flowering and leafing years: it seems likely that flowering only takes place at intervals of several years; one can see 50 plants in leaf for every one with an inflorescence. In any case *Amorphophallus* is, I think, unique among the rain-forest herbs in having a well-marked annual dormancy.

To return to the comparison of monocotyledons and dicotyledons, we find that rhizomes and stolons with scale leaves are virtually restricted, in the rain-forest, to the monocotyledons. The dicotyledons lack subterranean, or superficial, shoots with scale leaves and diageotropic growing points. As these features are well known amongst the dicotyledons of temperate forests, it is reasonable to suppose that they have been developed there in response to a markedly seasonal climate. In the monocotyledons they seem to be part of the normal developmental pattern of the plants: their well developed scales represent only the sheaths of the mature leaf and remind us that in the monocotyledons the sheath is a much more important part of the leaf than it is in the dicotyledons, where it is well-developed only sporadically in quite diverse families (Umbelliferae, Polygonaceae etc.). The important role of the rhizome in monocotyledons is perhaps another aspect of growth linked to their fundamentally hypogeal pattern of germination (cf. Burt, 1972).

Many of the dicotyledonous herbs of the forest floor have small seeds; such are all the Gesneriaceae, *Begonia*, some Rubiaceae and a few Acanthaceae (e.g. *Staurogyne*). Such seeds are probably dispersed by rainwash or by carriage on the feet of animals, and these two methods probably provide the best chance of dispersal under rain-forest conditions. Small seeds may also be favoured by the fact that they do not offer a desirable food-store to seed-predators. Salisbury's comparative study of seed size in relation to open and woodland habitats in temperate Europe showed that amongst closely related species those of shady habitats had larger seeds. Such a comparison is scarcely possible in Sarawak where the primary vegetation of virtually the whole country is forest.

The advantages of small seeds in rain-forest, suggested above, may be enough to outweigh the limitations imposed by the seedling having to start life with a very small capital of food reserves. These limitations would, however, exert a selection pressure in favour of any seedling strategy that evaded or ameliorated them. I have suggested elsewhere (Burt, 1970) that this is just what is achieved by the continued post-germination growth of one cotyledon in Gesneriaceae. The enlarged photosynthetic surface enables the seedling to build up energy for the organization of the plumular bud, which is delayed by comparison with its rapid appearance in most plants. The fungal association formed by the roots of the microspermous orchids is, of course, another way in which this difficulty is overcome, and the same argument may be applied to a widespread dicotyledonous saprophyte of the Malesian rain-forest, *Cotylanthera* (Gentianeae). In another microspermous family of monocotyledons, Burmanniaceae, both (fully?) autotrophic (*Burmannia longifolia* Becc.) and heterotrophic species (*B. sphagnoides* Becc., etc.) are found in the forest, but here the heterotrophic association is with blue-green algae, not with fungi.

*Begonia* is a microspermous genus of herbs in tropical forests all over the world. It does not seem to have any means of offsetting this disadvantage of small seeds: yet although *Begonia* plants are common, and seed-setting apparently prolific, seedlings are in my experience (which I admit is inadequate) curiously rare — especially as collected seed germinates freely in the greenhouse. This, of course, is not a situation affecting *Begonia* alone. Seedlings of herbaceous plants are so uncommon in the rain-forest that very little can be said about them. However the situation is similar, but perhaps a little less pronounced, in temperate forests, so this is not a rain-forest peculiarity. Nonetheless their rarity in the very open vegetation of the forest floor is noteworthy and needs investigation.

To this seedling rarity there are a few exceptions. Seedlings of two genera of Gesneriaceae are not infrequent, sometimes very prolific, in rocky forests on limestone. These genera are *Monophyllaea* and *Epithema*. We do not know the exact duration of the normal life cycle of these plants but it is certain that in both genera it is relatively short. In other words seedlings occur plentifully when they are necessary for the maintenance of the species. We are reminded that the biennial *Digitalis purpurea* L. produces seedlings freely in European woodlands, while young plants of *Primula vulgaris* Huds. need to be carefully sought. Similarly in subtropical evergreen kloof forests near Durban, Natal, the short-lived monocarpic *Streptocarpus molweniensis* Hilliard (Gesneriaceae) produces myriads of seedlings. Thus reproduction by seed seems to present similar problems for investigation in forest herbs under a wide range of climatic conditions.

If there is one lesson to be learnt from the history of botany, it is surely that attempts to give physiological explanations of leaf-structure without adequate physiological experiment are extremely hazardous. And physiological experiments in tropical rain-forest have so far been quite inadequate both in precision and in the range of subject used. All I can do here is to abstract some current thought from the physiological literature and try to relate it to the features I have seen in rain-forest herbs. If it spurs someone to write an authoritative account I shall be more than satisfied.

Even the physical measurements of the environment are very difficult in rain-forest (cf. Schulz, 1960); however it seems probable that the following conditions often obtain near the forest-floor. There is a low or very low saturation deficit; the carbon dioxide concentration is somewhat above normal (though not as high as was at one time suggested); average light intensities are low; and the incidence and intensity of sun-flecks, leading to sudden rises in leaf-temperatures, are a factor of great physiological significance (Evans, Whitmore & Wong, 1962). In this latter connexion Evans (1972, p. 34) has emphasized the extreme complexity of leaf temperatures, the extent of changes and their effects.

As to the plants' behaviour under these conditions, the early hypothesis of Stahl (1896) has now been abandoned: it was that a high transpiration rate was necessary to permit adequate salt absorption from weak soil solutions, and he interpreted various structural peculiarities as aiding this high transpiration rate. It is now known, from greenhouse studies, that an increase in the CO<sub>2</sub> concentration not only enhances assimilation, but lowers the transpiration rate (Hughes 1966; Meidner & Mansfield 1968, p. 76). Plants on the forest floor actually have very low transpiration rates (McLean 1919, Walter 1971); so this feature harmonizes with the higher CO<sub>2</sub> concentrations found there.

Rain-forest herbs have typical shade-leaf histology in that they are thin and the palisade often consists of only a single layer of shallow cells. However a more specifically rain-forest feature is the frequent occurrence of a well-developed water-storing hypodermis, or in its absence the epidermis itself is large-celled and aqueous (for notes on *Cyrtandra* see Bokhari & Burt, 1970). It has been shown (McLean, 1919) that development of conducting tissue in rain-forest herbs is relatively weak.

One is tempted to link water storage to the sudden effects of sun-flecks on the one hand and poorly developed xylem on the other: but no experimental work in this field is known to me. Nor, as far as I am aware, has the working of stomata on raised "turrets" (common in Gesneriaceae, and see the illustration of *Ruellia* in Strasburger, 1965) been studied experimentally. Until we know how they affect transpiration when they are open, and how often they are open, speculation can only be wild.

Leaf-surface is of considerable interest amongst rain-forest herbs. Not infrequently the upper surface is thrown up into numerous small peaks with corresponding hollows below; this is the condition usually described as "mammillate". It occurs, at least, in some species of *Cyrtandra* and *Didymocarpus* (Gesneriaceae), and *Begonia* (Begoniaceae), and in Tropical America species of *Pilea* (Urticaceae) show the same feature. The palisade tissue is continuous over these peaks and thus its quantity is increased within a given leaf area. Although the direct incident light on that area remains the same, it may be that this type of surface permits the plant to make better use of the lateral component of the lighting. It would be interesting to compare the assimilation of smooth and mammillate leaves when direct illumination is excluded.

Another well-known feature of certain plants growing in deep forest shade is their blue-green iridescence. Lee & Lowry (1975) have recently returned to a study of this phenomenon and now suggest that the iridescence is produced by a structural layer in the wall of the epidermis which increases the reflection of light rays in that part of the spectrum that is of least value in photosynthesis, but enhances the penetration of the most useful wavelengths. *Selaginella* is probably the commonest plant showing this iridescence, but it is also found in flowering plants such as *Begonia* and is very well-marked in *Mapania* (Cyperaceae).

Leaf colour in forest herbs is a subject that has attracted much speculation; but I have not found much detailed information in the literature on its occurrence. The phenomena generally discussed are red coloration in general and red-green or silver-green mottling; adaptive advantages have been sought for these conditions. It is therefore worthwhile to put on record that any advantage that they do confer on the plant has often been inadequate for them to become constant within the species concerned. For instance, closely adjacent or mixed populations of *Sonerila tenuifolia* Bl. (Melastomataceae) may be found with green or purple leaves, either colour being with or without whitish blotches; some *Begonia* species occur in colonies showing a mixture of blotched and unblotched leaves; *Sonerila borneensis* Cogn. may have leaves of plants growing within a short distance of one another silver-streaked or plain green, and the same applies in *Monophyllaea glauca* C.B.Cl. var., in which silvering, when present, is more conspicuous in the seedling phase. Similarly in *Cyrtandra splendens* C.B.Cl. plain green leaves, leaves mottled in darker and lighter green, leaves flushed or wholly coloured red on the underside or leaves red on both surfaces seem to occur indiscriminately. It is also well known that some 'forms' of the species popular for greenhouse cultivation have leaves more spectacularly coloured than others (e.g. cultivars of *Episcia reptans* Mart. — Gesneriaceae — and *Bertolonia* — Melastomataceae). Little emphasis has been placed on the implication of intraspecific variation when considering the possible adaptive significance of these colour patterns. This is not to deny that they may be adaptive, and in some species (e.g. in *Dossinia marmorata* Bl., or in the light and dark green mottling of many species of *Paphiopedilum*, both Orchidaceae) they do seem to be constant. But the examples of inconstancy within a species are too frequent to be ignored.

One thing is clear in this physiological uncertainty: that the forest-floor environment in evergreen tropical forest is far from optimal. Richards (1952, p. 98) has emphasized this, and points to the relatively low number of families represented in the herbaceous flora. It will have been noted how often the genera *Begonia*, *Cyrtandra*, *Didymocarpus*, *Argostemma*, *Sonerila* have recurred as examples; this is partly due to my limited experience but it does also demonstrate that these large genera have shown parallel evolutionary diversification to cover several successful growth-forms. There is scope for an interesting study in assessing how many groups of genera have representatives in, or are wholly confined to, the herbaceous flora of the rain-forests and the extent of their diversification there.

### References

- BELL, A. 1974. Rhizome organization in relation to vegetative spread in *Medeola virginiana*. *J. Arnold Arbor.* **55**: 458–468.
- BOKHARI, M.H. & B. L. BURTT. 1970. Studies in the Gesneriaceae of the Old World XXXII: Foliar sclereids in *Cyrtandra*. *Notes R. bot. Gdn Edinb.* **30**: 11–21.
- BURTT, B. L. 1970. Studies in the Gesneriaceae of the Old World, XXXI: Some aspects of functional evolution. *Notes R. bot. Gdn* **30**: 1–10.
- 1972. Plumular protection and some related aspects of seedling behaviour. *Trans. bot. Soc. Edinb.* **41**: 393–400.
- EVANS, G. C. 1972. *The quantitative analysis of plant growth*. Blackwell, Oxford.
- EVANS, G. C., T. C., WHITMORE & Y. K. WONG. 1962. The distribution of light reaching the ground vegetation in a tropical rain-forest. *J. Ecol.* **48**: 193–204.
- HOLM, T. 1899. *Podophyllum peltatum*: a morphological study. *Bot. Gaz.* **27**: 419–434.
- HUGHES, A. P. 1966. The importance of light compared with other factors affecting plant growth. In Bainbridge, R., Evans, G. C. & Rackham, O. *Light as an ecological factor*, pp. 121–146. Blackwell, Oxford.
- KIRCHNER, O. von, E. LOEW & C. SCHRÖTER. 1934. *Lebensgeschichte der Blütenpflanzen Mitteleuropas* **1** (3): 645.
- LEE, D. W. & J. B. LOWRY. 1975. Physical basis and ecological significance of iridescence in blue plants. *Nature (Lond.)* **254**: 50–51.
- McLEAN, R. C. 1919. Studies in the ecology of tropical rain-forest. *J. Ecol.* **7**: 5–54, 121–172.
- MEIDNER, H. & T. A. MANSFIELD. 1968. *Physiology of stomata*. McGraw Hill, London.
- MOORE, H. J. 1962. *Resia* — a new genus of Gesneriaceae. *Bot. Mus. Leaflet. Harv. Univ.* **20**: 85.
- MUKERJI, S. K. 1936. Contribution to the autecology of *Mercurialis perennis* L. *J. Ecol.* **24**: 36–81.
- RICHARDS, P. W. 1952. *The Tropical Rain Forest*. University Press, Cambridge.
- SCHULZ, J. P. 1960. Ecological studies on rain forest in northern Suriname. *Meded. bot. Lab. Herb. Rijks-Univ. Utrecht* No. 163.

- STAHL, E. 1896. Über bunte Laubblätter, ein Beitrag zur Pflanzenbiologie. *Annls Jard. bot. Buitenzorg* 13: 137-216.
- STEENIS, C. G. G. J. van. 1942. Gregarious flowering of *Strobilanthes* (Acanthaceae) in Malaysia. *Ann. R. bot. Gdn Calcutta*, 150th Anniv. vol. 5: 1-5, 7.
- STRASBURGER, E. 1965. *Textbook of Botany*. New English ed, from 28th German ed. Trans. P. R. Bell & D. E. Coombe, Longmans, London.
- WALTER, H. 1971. *Ecology of Tropical and Subtropical Vegetation*. Trans. D. Mueller-Dombois. Oliver & Boyd, Edinburgh.

# Comparison of the Phytomass Structure of Equatorial "Rain-Forest" in Central Amazonas, Brazil, and in Sarawak, Borneo

by

E. F. BRUNIG

*Chair of World Forestry, University of Hamburg*

H. KLINGE

*Max Planck Institute of Limnology, Department of Tropical Ecology, Ploen/Holstein*

## Introduction

The ombrophilous predominantly evergreen lowland forests parts of Sarawak and Amazonia grow on very similar geologic formations, on similar soils and in a similar climate. The one author enumerated very intensively the phytomass structure on a 0.2 ha rectangular plot, 64 km from Manaus on the Itacoatiara road (Klinge and Rodrigues, 1971, 1973; Fittkau and Klinge, 1973; Klinge, 1972, 1973a; Klinge *et al.*, 1973). The other author enumerated similarly, except without weighing phytomass, 55 rectangular 0.2 ha plots on a wide range of sites in Sarawak and Brunei, two 20 ha full enumerations on podzol soils on Tertiary and Quarternary parent materials respectively and a 0.04 ha plots random sampling of 60 plots on a Holocene terrace (Brunig, 1968, 1970, 1974). The purpose of the Amazonian project was the analysis of phytomass structure, of the Bornean study the analysis of diversity within and between stands and of the diversity/site interrelationship (Ashton and Brunig, 1975; Brunig, 1973a, b). General information on forest types, flora, and ecological conditions in the Amazonian area is given by Duke and Black (1953), and by Hueck (1966), in the Bornean area by Ashton (1964), Richards (1974) and Brunig (1975).

In this paper the term 'Central Amazonia' and 'Central Amazonian rain forest' are used according to Fittkau (1969) who defines 'Central Amazonia' as a geochemical-ecological unit which is clearly distinguished from other parts of Amazonia.

## The Sample Stands

The Amazonian plot is typical for mixed "terra firme" forest on well drained loamy soils (Anon., 1969). Bleached sands and podzols occur in the neighbourhood at some distance but not in the plot area (Klinge, 1965, 1968, 1973b). Close to the plot were short steep slopes and alluvial valley bottom which carry different types of forest (Takeuchi, 1961).

Plots were selected from the Bornean material to represent a wide range of site conditions and of stand structure, and also to indicate the size of within-stand variation of essential phytomass features against which the Amazonian plot could be assessed. The selected plots are briefly characterized in tab. 1. The plots selected from the 20 ha sampling area in Sabal Forest Reserve have not yet been fully analysed as they are intended for comparison with data from the San Carlos "MAB" project area, Amazonas, Venezuela, which is being enumerated in 1975-1976.

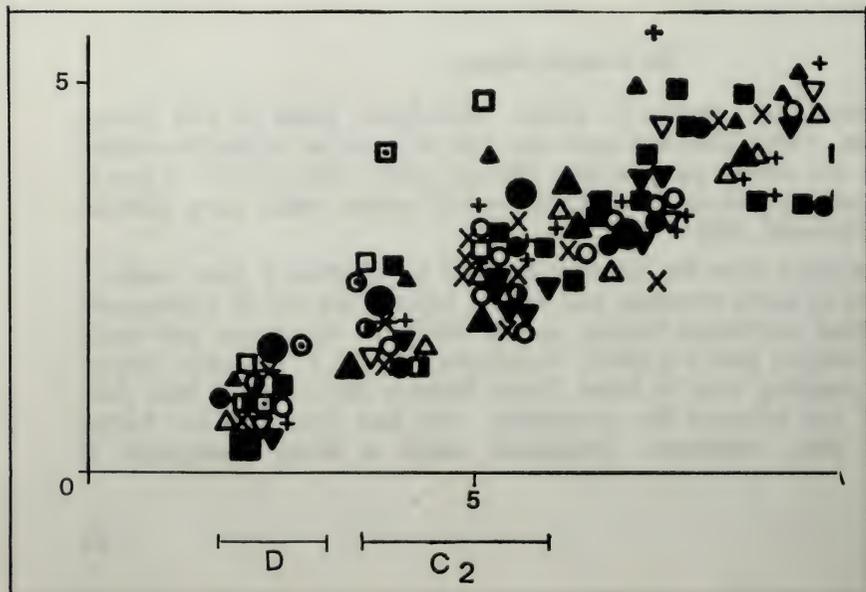
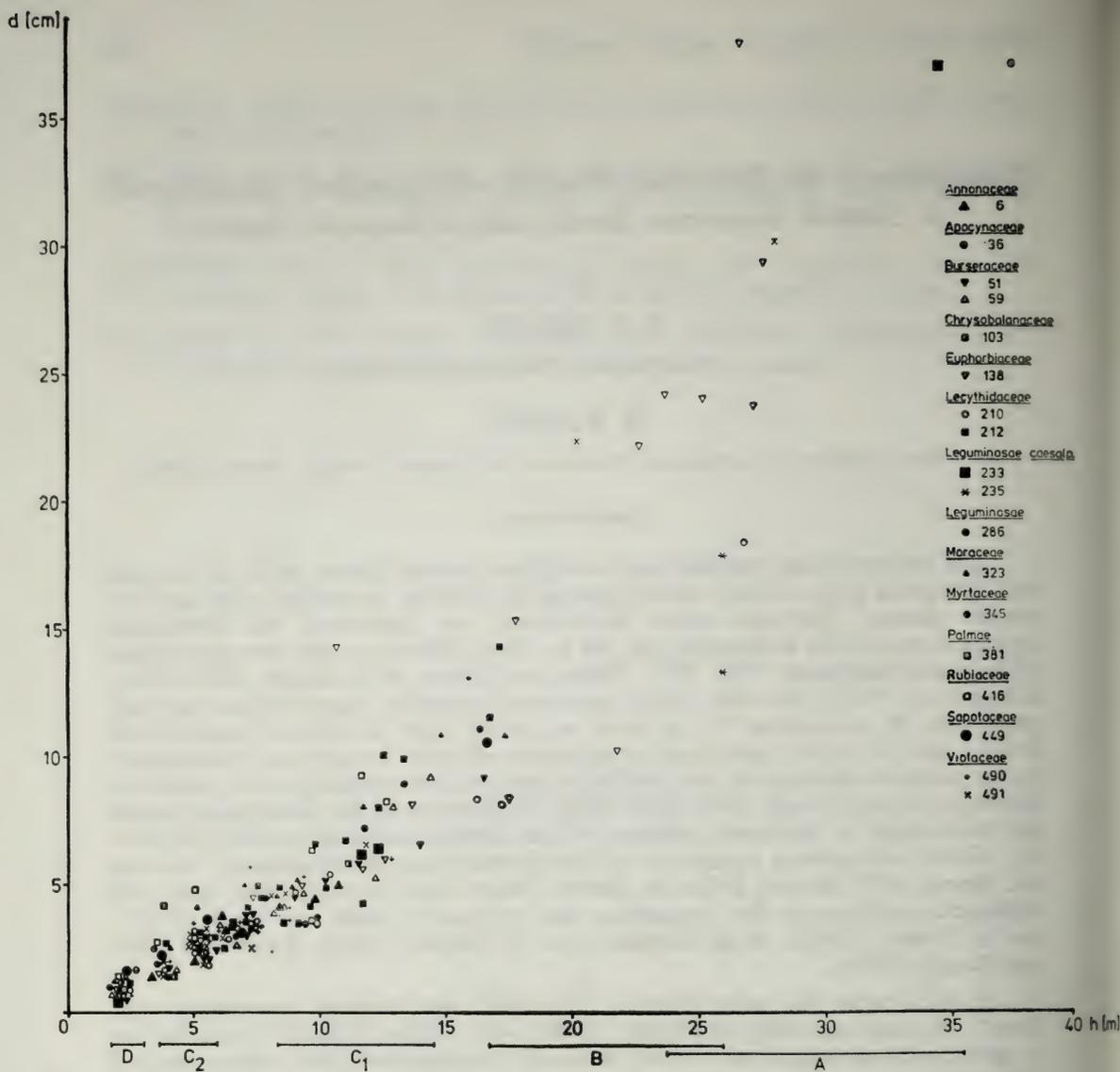


Fig. 1. Diameter — height correlation for representatives of plant families which according to their number of species and/or individuals are the most important ones in the Central Amazonian rain forest (acc. to Klinge & Rodrigues). Top = whole stance, bottom = enlarged for undergrowth.

Table 1. Sarawak sample plots selected for comparison with the Manaus sample plot

Geology	Landform	Soil	Plot No.	Forest type
Tertiary sandstone	High plateau	Medium Humus Podzol	51	Submontane Kerangas
		Shallow Humus Podzol	52	Submontane Kerangas
	Grey-White Podzolic clay	53	Submontane Kerangas	
	Peat bog	40	Submontane Kerapah.	
	Coastal plateau	Medium H.P.-Red-Yellow Podzolic loam	16	Mixed Dipterocarp forest
Pleistocene gravel	Coastal terrace, edge	Deep Humus Podzol	43	Coastal Kerangas
	Coastal terrace, top	Medium Mumus Podzol	44	Coastal Kerangas
Tertiary conglomerate	Gentle slope base	Medium Humus Podzol to Red-Yellow Podzolic (heterogeneous)	Sabal 1-25 26-50	Kerangas/MDF transition Kerangas/MDF transition
		Shallow to medium Humus Podzol (uniform)	251-275 276-300	Kerangas Kerangas
		m.h.p. — red latosol (moderately heterogeneous)	451-475 476-500	Kerangas/MDF transition Kerangas/MDF transition

## Forest Structure

### *Stratification and stand height*

Our data indicate overlapping ranges of height in the various strata (tab. 2) and consequently indistinct storey formation of diameter/height relationships. The question whether tropical rain forest is stratified or not is controversial and views are conflicting (Rollet, 1973; Whitmore, 1975). While geometric stratification is often indistinct and obscure in mature stands on well-drained normal sites and soils, addition of floristic variation and plant geometry often produces more distinct layering in terms of overall diversity variation pattern. Distinct layering with discernible gaps between two or more layers is common on sites with extremes of environmental conditions or in some phases of development (Brunig, 1970, 1975; Ashton and Brunig, 1975). For Amazonian rain forest Klinge and Rodrigues (1968), Aubréville (1961) and Soares (1957) describe the existence of storeys in general terms but the information is not supported by quantitative analysis. Maximum heights of 35 and 40 m are reported by Klinge and Rodrigues, Rodrigues, and by Takeuchi, and of 25 to 30 m by Aubréville, and Soares.

The following general description of the stratification of the forest is mainly based on our own data, amended by data of the other authors:

A-layer: a few very large trees overtowering the following

B-layer: a non-continually, vertically ill-defined upper tree layer

C<sub>1</sub>-layer: lower tree layer composed of mainly young or suppressed individuals of species which are dominant in the upper tree layer. Occasionally, there are palm-trees.

Almost all trees of the A-, B- and C<sub>1</sub>- layers show stem-rot increasing in severity from smaller to thicker stems.

C<sub>2</sub>- and D-layers: a rather continual, vertically illdefined upper shrub layer with many saplings and with especially many acaulous palms.

E-layer: dominated by acaulous palms and composed predominantly of saplings and seedlings; real herbs being scarce.

All layers are heavily interlaced by lianes, many of which have thick stems. Vascular epiphytes are rare; there are some hemi-epiphytes, saprophytes, and parasites. Old palm fronds and old leaves of many tree species are heavily covered with algae and bryophytes. Crowns of the upper layer are up to 40 m wide; in the lower layers crowns have narrower conical forms.

In comparison, Bornean forests on similar sites are taller, the A and B strata are more complex, and generally exhibit much diversity of structural characteristics in relation to site and phasic development.

### *Number of trees*

The total number of trees, lianes, palms and herbs per unit area varies very widely in tropical moist forests as a result of differences in site, in stage of phasic development and spatial distribution pattern. In the Manaus plot the density per ha of all trees and palms above 20 cm height is 94,000 individuals (tab. 3). This agrees very well with the 73,000 trees and 6,000 palms recorded by Aubréville. Both figures do not include lianes, vascular epiphytes etc. Much lower figures for tree and palm density or total density were found by Takeuchi. Lechtaler's figure 745 stems (dbh 8 and more cm) agrees well that of Takeuchi.

In the Bornean plots (nos. 43 to 53) the total number of trees > 2 cm d varies between 8028 and 12,133 per ha which indicates the scale of variation in number of trees which is of about the same order as the variation of basal area (35.3 to 50.9 m<sup>2</sup>/ha in the selected plots, sample mean of all 55 plots 36.5 m<sup>2</sup>/ha with a range of 27.0 to 88.0 m<sup>2</sup>/ha).

Table 2. Stratification of the Central Amazonian rain forest on level terra firme acc. to Klinge &amp; Rodrigues (plot size 0.2 ha)

Stratum	Upper crown height (m)		Lower crown height (m)		Individuals per ha
	Mean	Range	Mean	Range	
A	35.40	38.10 — 32.10	23.70	29.00 — 20.00	50
B	25.90	30.50 — 20.40	16.70	24.60 — 8.70	315
C <sub>1</sub>	14.50	21.90 — 10.05	8.40	8.70 — 2.70	775
C <sub>2</sub>	5.90	11.00 — 2.70	3.60	7.80 — 0.70	2,920
D	3.00	4.50 — 1.55	1.70	2.90 — 0.20	6,070
E	1.00	1.50 — 0.20	0.10	0.20 — 0.05	83,650
					93,780

*Bole diameters*

Height/breast-height diameter (h/d) ratios vary with species, site and age. Emergent trees frequently have ratios between 25 and 50, trees in the B-layer about 50 and trees in the lower canopy between 60 and above 100. Ratios vary strongly even within one species in a stand and even more between species often obscuring any existing tendency to layer formation.

Fig. 1 shows the relationship between total height and d for 14 plant families which according to numbers of species and/or individuals are the most important in the Manaus plot. The wide scatter in the taller strata is typical and agrees with observations in the Sarawak plots (Brunig, 1975, fig. 11d).

Table 3. Plant density per height class and ha in the terra firme rain forest of Central Amazonian acc. to Aubréville (plot size 500 m<sup>2</sup> (1) and 175 m<sup>2</sup> (2), respectively)

Height class (m)	1		2	
	Trees	Palms	Trees	Palms
> 15	340	60	514	0
7 — 15	300	20	629	57
1 — 7	2,940	1,560	3,714	1,143
1 — > 15	3,580	1,640	4,857	1,200
≤ 1	?	?	68,229	5,029
Total	—	—	73,086	6,229
Lianas > 1 m l	880		1,254	
Herbs ≤ 1 m l	?		7,467	
Herbs < 1 m h	?		6,327	
Total	—	—	94,363	

The ecological significance of stand curves (tree frequency distributions over *d*) in tropical forests has been recently reviewed by Rollet (1973). The shape of the stand curves is subject to many environmental influences and to intrinsic properties of the stand; variation between stands and sites, and within stands with time, is correspondingly large (Ashton and Brunig, 1975; Brunig, 1975). The Manaus plot shows a strongly truncated distribution, the largest diameter being only 55 cm, compared with a site related range of 50 to 100 cm in the 5 Bornean plots.

### Phytomass

The phytomass data from the Manaus plot are the only available precise figures for the Amazonian lowland forest. The data are summarized in tab. 4. The

Table 4. Fresh phytomass of the Central Amazonian rain forest acc. Klinge & Rodrigues (size of study plot 0.2 ha)

Fraction		Phytomass (t/ha)
Trees and palms, — above ground	A	190.2
	B	399.5
	C <sub>1</sub>	77.2
	C <sub>2</sub>	15.7
	D	4.7
	E	1.5
— below ground		255
Lianas, epiphytes, etc.		89
Total		1,033

corresponding volume of tree boles in m<sup>3</sup>/ha is 385 > 15 cm *d* and 304 > 25 cm *d*. These volumes and the corresponding fresh phytomass lie within the range of data reported by authors (tab. 5) and by the data of the FAO inventories south of the Amazon River. Compared with other tropical moist forests, the amount of stem volume and, consequently, of stem wood volume is rather low in the Central Amazonian rain forest. However, the terra firme forest of the Manaus area is not the most luxurious forest in Amazonia (Rodrigues, 1967). The total tree

Table 5. Fresh phytomass of the Central Amazonian rain forest stands calculated under the assumption of a phytomass content equal to that in the Manaus plot.

Authors	Fresh phytomass (t/ha)	Remarks
Soares	360	Average of 2 surveys of 9 and 36 ha respectively
Rodrigues	413	Average of 27 ha
Aubréville	510	Average of 2 surveys of 500 and 175 m <sup>2</sup> respectively
Lechthaler	1,000	1 survey of 1 ha
Klinge-Rodrigues	1,000	1 survey of 0.2 ha
Takeuchi	1,350	0.16 ha section of 3 surveys comprising 0.185 ha
Mean	770	

volumes above ground estimated as  $V = G \cdot 0.5 h$  (where  $G$  = basal area per diameter class,  $h$  = height of the diameter class) in the 55 sample plots in Borneo range between 195 and 1760  $m^3/ha$ . Determining factors are again site, developmental phase and the presence or absence of gregarious species which successfully reduce competitors on certain, often extreme and difficult sites. The mean value is 778  $m^3/ha$  (mean basal area 36.5  $m^2/ha$  of trees above 2 cm d). The fresh weight of phytomass is of the same order in t/ha as the volume estimator in  $m^3/ha$ , and varies in the same range. The tree volumes naturally vary not only in relation to natural factors, but also to the size and shape of the plots. Variation increases as the size of the sample plots decreases, and deviations are less for transects than for squares.

Maximum and minimum figures for total above-ground phytomass of living trees and palms in layers A-D were calculated for sub-plot sections which vary in size and shape (fig. 2). These figures indicate that sampling the phytomass distribution of an area by transects apparently gives a better representation than by blocks. It can also be seen that the curves for maximum and minimum phytomass figures are not symmetrical.

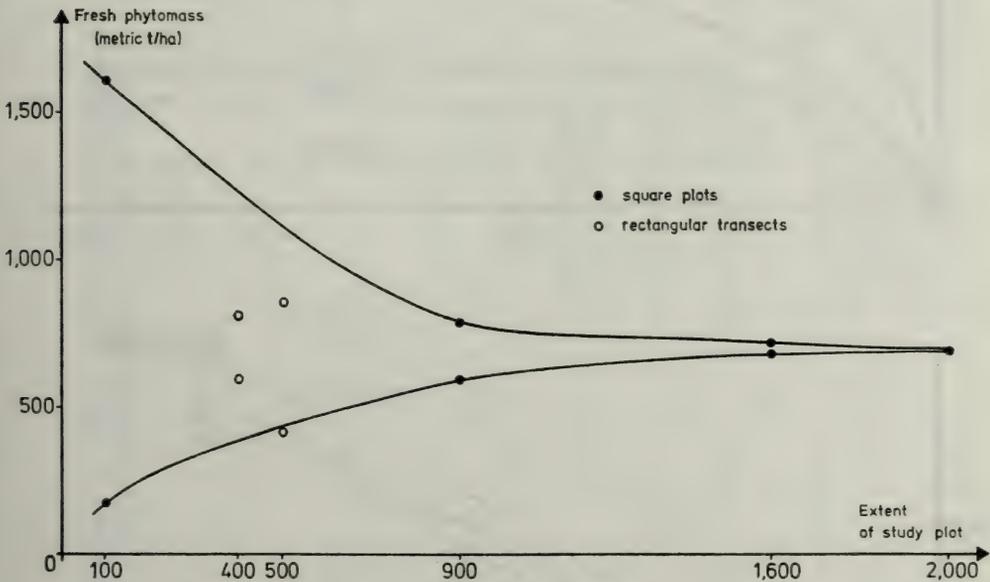


Fig. 2. Maximum (upper curve) and minimum figures (lower curve) for fresh phytomass of layers A—D, calculated for square blocks and rectangular transects of different extent within the 0.2 ha plot of Klinge & Rodrigues, in the Central Amazonian rain forest.

Assuming the above-ground living phytomass in layers A-D to be 68.7 % of the total living above-ground phytomass, the total living above-ground phytomass reported by Aubréville (0.05 ha plot) as 350 t/ha is less than the figure of 415 t/ha which we obtain in a corresponding transect. Takeuchi's 0.16 ha transect would include 927 t/ha which is more than the 710 t/ha we get in the Manaus plot for a square block of equal area. The figures of Lechthaler and Klinge & Rodrigues are identical despite the fact that Lechthaler's plot is 5 times larger than Klinge & Rodrigues' plot. Very low figures are obtained for the data of Rodrigues (27 transects of 1 ha each), and of Soares (9 and 36 transects, respectively, of 1 ha each): 284 t/ha for Rodrigues' plot, and 247 t/ha for Soares study.

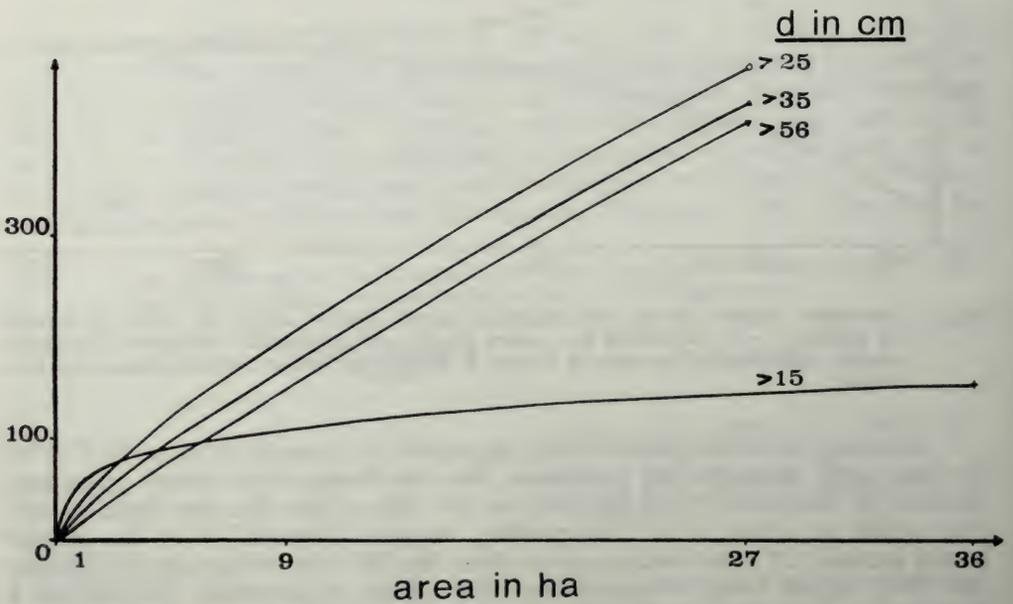
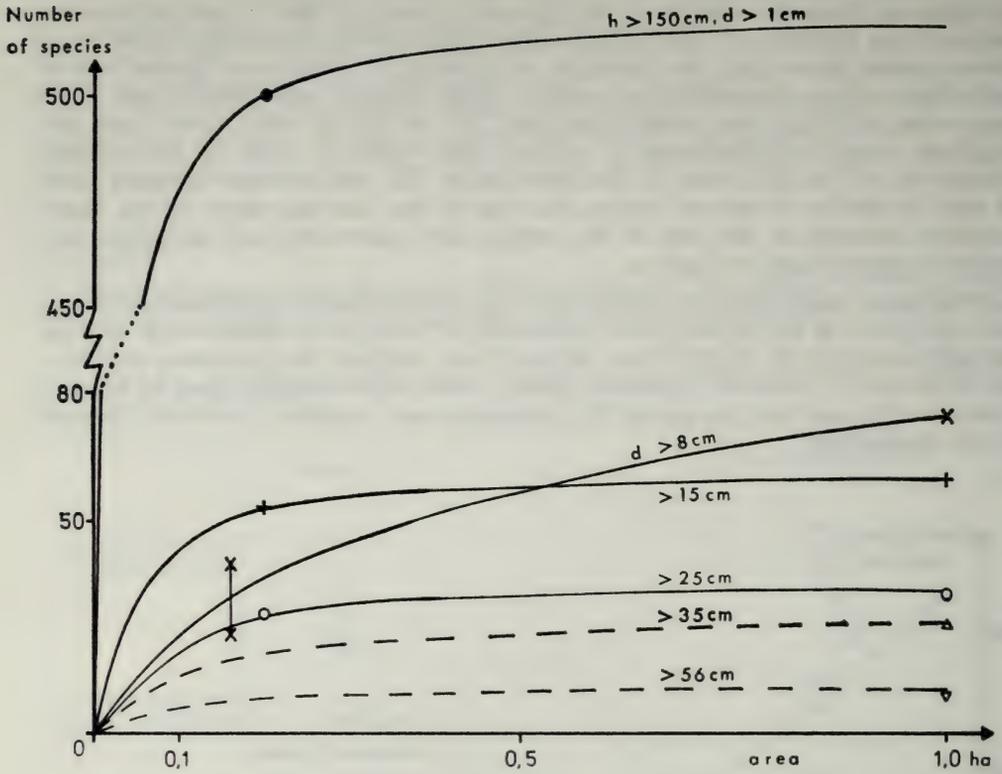


Fig. 3. Species number as a function of diameter class, size and shape of study plots in the Central Amazonian rain forest.  
 Upper part: plots up to 1 ha in size.  
 Lower part: plots up to 36 ha in size.

Table 6. Maximum (1) and minimum (2) figures for number of plant species in layer D and additional plant species numbers in each layer in blocks and transects of different size in the Central Amazonian rain forest acc. to Klinge & Rodrigues.

Blocks	40 x 40 m		30 x 30 m		10 x 10 m	
	1	2	1	2	1	2
A	4	5	2	3	1	0
B	23	22	18	13	3	1
C <sub>1</sub>	21	20	18	15	4	6
C <sub>2</sub>	94	77	60	69	9	17
D	270	294	180	210	24	69
	$\frac{A+B}{C+D} = 0.07$	$\frac{A+B}{C+D} = 0.069$	$\frac{A+B}{C+D} = 0.072$	$\frac{A+B}{C+D} = 0.054$	$\frac{A+B}{C+D} = 0.11$	$\frac{A+B}{C+D} = 0.01$
Total	412 = 88.4 %	418 = 89.7 %	278 = 59.7 %	310 = 66.5 %	41 = 8.8 %	93 = 20 %
Transects	10 x 40 m, E-W		10 x 50 m, N-S		40 x 50 m plot	
	1	2	1	2	1	2
A	0	1	1	0	4	
B	12	5	7	10	27	
C <sub>1</sub>	11	16	13	16	21	
C <sub>2</sub>	41	35	69	30	84	
D	126	104	171	136	330	
	$\frac{A+B}{C+D} = 0.067$	$\frac{A+B}{C+D} = 0.039$	$\frac{A+B}{C+D} = 0.032$	$\frac{A+B}{C+D} = 0.055$	$\frac{A+B}{C+D} = 0.07$	
Total	190 = 40.8 %	161 = 36.7 %	261 = 56.0 %	192 = 41.2 %	466 = 100 %	

These low figures are possibly caused by site heterogeneity. The 5,000 m long transects of both authors in addition to latosol also included groundwater-influenced valley soils, bleached white sands and podzols, and flanks of valleys.

### *Floristic structure*

Sample plots contain architectural and floristic variation of small-scale (tree groups in the order of 0.1 ha) and medium-scale (stands of 1 to several ha) (Brunig, 1975; Ashton and Brunig, 1975). Accordingly, in addition to the wide variation in architectural features (basal area, height, layering, diameter, frequency), there is considerable floristic variation (species complement and species dominance pattern, species for a number of reasons often occurring vicariously) between plots which is governed by chance the more the smaller the plot size. As a result, family, generic and species dominance figures for small plots are only meaningful if they are supported by data from larger-scale sampling of the wider surrounds on the same site types (Brunig, 1973). However, some features of floristic structure are somewhat more general and more consistent even in small plots, such as species-area and species-dominance curves.

In the Manaus plot the 5 leading plant families Moraceae, Lauraceae, Leguminosae, Lecythydaceae and Sapotaceae on an average represent 50 to 60 % of all species, and 50 — 70 % of all individuals. Leguminosae and Lecythydaceae strongly exceed Lauraceae, Moraceae and Sapotaceae. The other authors for the reasons given above report different proportions and family dominances, e.g. in Takeuchi's survey the Guttiferae are conspicuous, the Olacaceae in Lechthaler's plot and Olacaceae and Euphorbiaceae in Rodrigues' survey.

Generally in Central Amazonia, second in number of species and/or individuals are the Apocynaceae, Annonaceae, Rosaceae (Chrysobalanaceae), Burseraceae, Euphorbiaceae, Myrtaceae, Olacaceae, Celastraceae, Humiriaceae, and Myristicaceae. These 10 plant families on an average represent 20 — 40 % of the number of species and 20 — 50 % of the individuals.

The group of rare plant families is the Guttiferae, Caryocaraceae, and Bombacaceae, and 40 plant families are very rare.

Palms as a family are generally well represented. The acaulous species belong to the lower strata of the forest and are included only when the survey includes small sizes. A few palm species are cauliferous and intrude the middle forest layers; their heights may measure up to about 15 m.

The Central Amazonian rain forest is composed of about 55 families and about 500 more common tree species (fig. 3). Rare species or families increase these figures for more extensive areas. Despite this high number of species and plant families, the Central Amazonian rain forest is poorer in species and less diverse than the Bornean Mixed Dipterocarp forest in Sarawak (Brunig, 1973a).

Including small palms and woody species of low habit, herbs of the ground vegetation, and epiphytes, the total number of plant families in the Central Amazonian rain forest is supposed to be about 70, and its number of species about 700. There is no information on the number of cryptogam and vascular cryptogam species and families. The latter group is not well represented, but the cryptogams are very numerous, especially in the phyllosphere.

We used data of the other authors for the construction of various species-area curves. The curves for the girth classes of 25, 35, and 56 cm rise steeply and smoothly (lower part of fig. 3). The curve for the next lower girth class (15 and more cm) is in its lower part above the curve of the 25 cm dbh class and its inclination is stronger. The curves for area below 1 ha are reproduced at larger scale in the upper part of fig. 3 which also includes the curve for dbh of 8 cm

or 10 cm. It also includes  $> 1$  cm d or  $> 150$  cm h, which increase extremely rapidly to 0.2 ha and then flattens. It eventually would cross the curves for girth classes 25, 36 and 56 cm at plot sizes of 30 — 35 ha and species numbers of about 500. This agrees with the contention of Brunig (1968 and 1973a) that small plots cover the total species population satisfactorily, if very low diameter limits below or of 1 cm are adopted. Larger minimum sampling sizes require very much larger plot sizes if the less common and rare species should be adequately sampled. A diameter limit of 25 cm requires plot sizes of 30 and more ha. Intermediate diameter limits between 10 or 15 cm require about 15 to 20 ha, provided the forest and site are reasonably uniform.

In the same sections of our 40 x 50 m plot, previously used for maximum and minimum phytomass calculations, maximum and minimum numbers of species were counted (tab. 6 and fig. 4). Differences between maximum and minimum species numbers are much smaller than the differences between maximum and minimum phytomass. The number of species is somewhat larger in transects than in blocks of similar size.

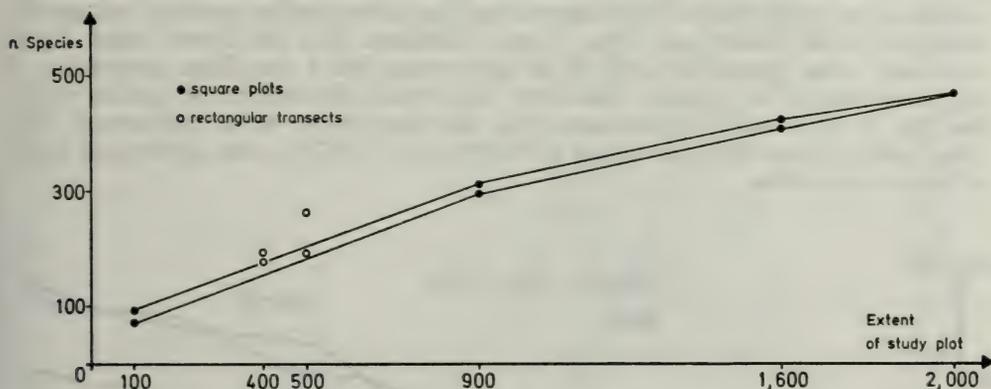


Fig. 4. Species number as a function of plot size in the Central Amazonian rain forest according to Klinge & Rodrigues.

Upper curve: maximum figures for species number.

Lower curve: minimum figures for species number.

The shape of species-areas curve is strongly influenced by site heterogeneity. In the Sabal sampling area, Sarawak, the increase of species number with transect length (20 x 500 m) is first steeper but then flatter in more xeric, oligotrophic and relatively homogeneous parts with tendency to single-species dominance (transect pairs 251–275 and 276–300 in fig. 5). It is first flatter but continues to rise steeper on more heterogeneous medium sites (1–25, 26/50), but again similar to the first pair on transitions to red latosols where again one species attains strong dominance (*Dryobalanops beccarii* Dyer). This is discussed in detail in an earlier paper (Brunig, 1973a).

#### Floristic and phytomass structure

The floristic and phytomass structure of a stand can simultaneously be expressed by the species-dominance curve. The curve for this purpose represents the contribution of each species to the stand basal area. The species are plotted in order of their contribution in percent of the stand total. The starting point of each curve is chosen arbitrarily so that crossing of the curves is avoided. One advantage of the species-dominance curve for purposes of comparison is that its significance is independent of the chances of species presence which is useful for small plots in floristically heterogeneous, diverse stands. The species-dominance

curves of a number of plots in different forest types in Sarawak (incl. sample plot 43) is shown in fig. 6. The stands are arranged in order of improving site and soil conditions from the left (SP 40, *Dacrydium pectinatum* Delaubenf. bearing Kerangas on peat bog) to the right (SP 16, *Dryobalanops beccarii* bearing Mixed Dipterocarp forest). The dominance of the leading species is strong to the left (*Shorea albida* Sym. in SP 27 and *Agathis dammara* (Lamb.) L. C. Rich. in SP 43) and weak to the right. Increasing flatness indicates that the mutual exclusion principle weakens and random distribution of ecological niches prevails. The species-dominance curve of the Manaus plot shows by comparison the least degree of species dominance and the flattest trend of the curve. This means that distribution is largely governed by chance and more so than in the Bornean plots. This result cannot, however, be generalized because the Bornean plots, including SP 16, are on less favourable soils than the terra firme plot at Manaus.

Figures for both phytomass and species numbers in sections of different size and shape of the original 40 x 50 m plot were calculated separately for each layer as percentages of the figures for the total plot (fig. 7 — blocks; fig. 8 — transects). The minimum figures for phytomass and the corresponding numbers of species are shown in the upper part of both figures and the corresponding maxima and species numbers in the lower part. Figs 7 and 8 indicate that the lower forest layers represent a low proportion only of the phytomass, but a very large proportion of the total number of species. Therefore, the overall distribution of species within the plot is much more homogenous than the distribution of the phytomass. This observation agrees with the finding of Webb *et al.* (1972) in the subtropical forest of eastern Australia.

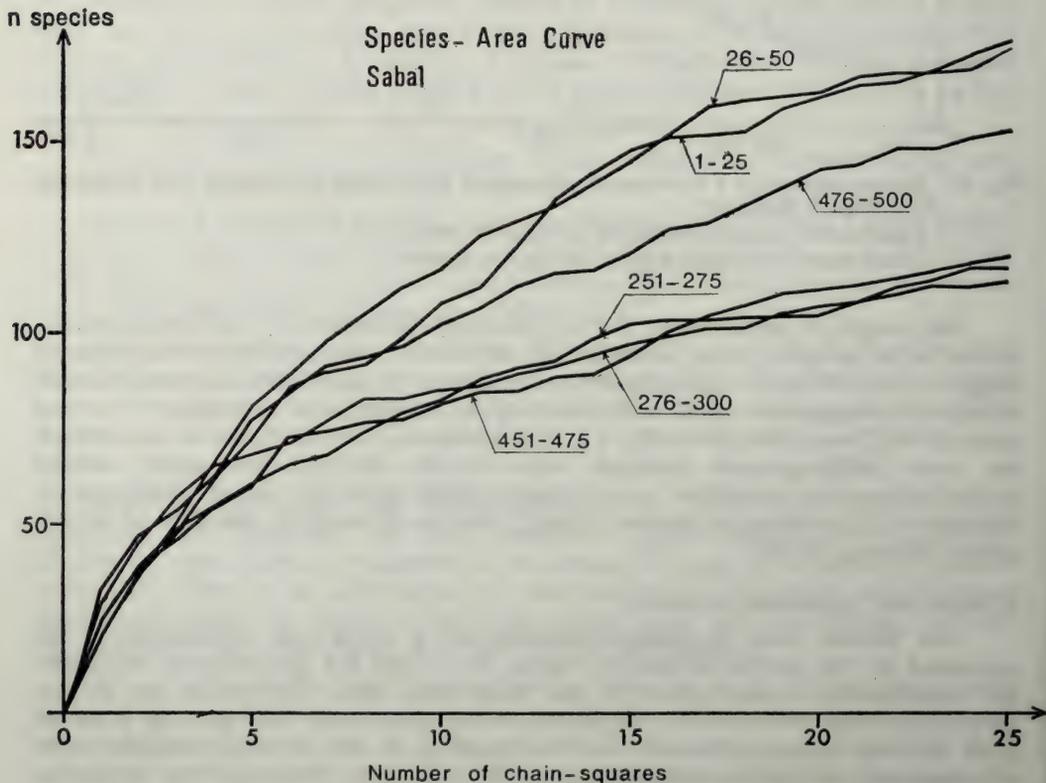
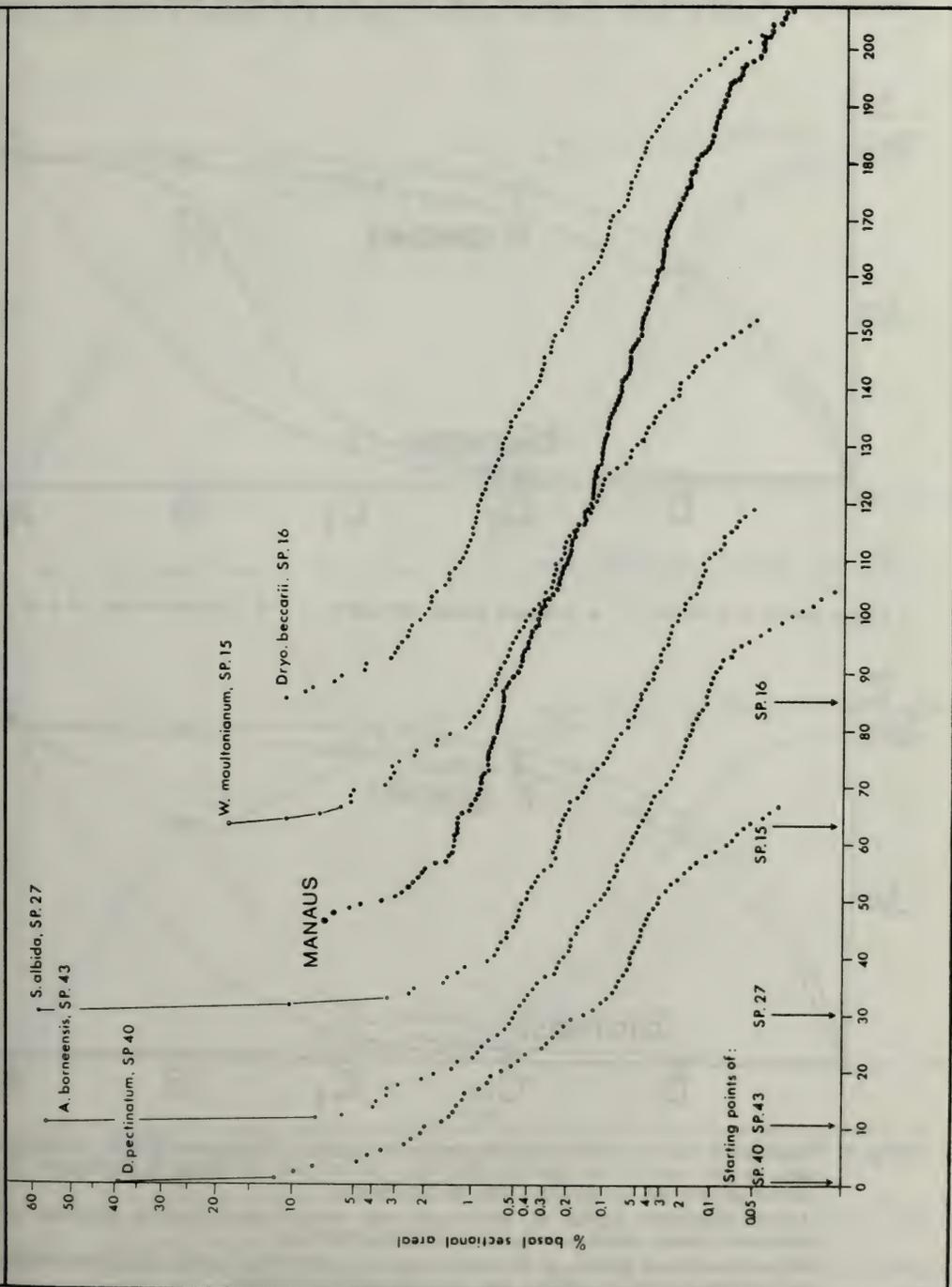


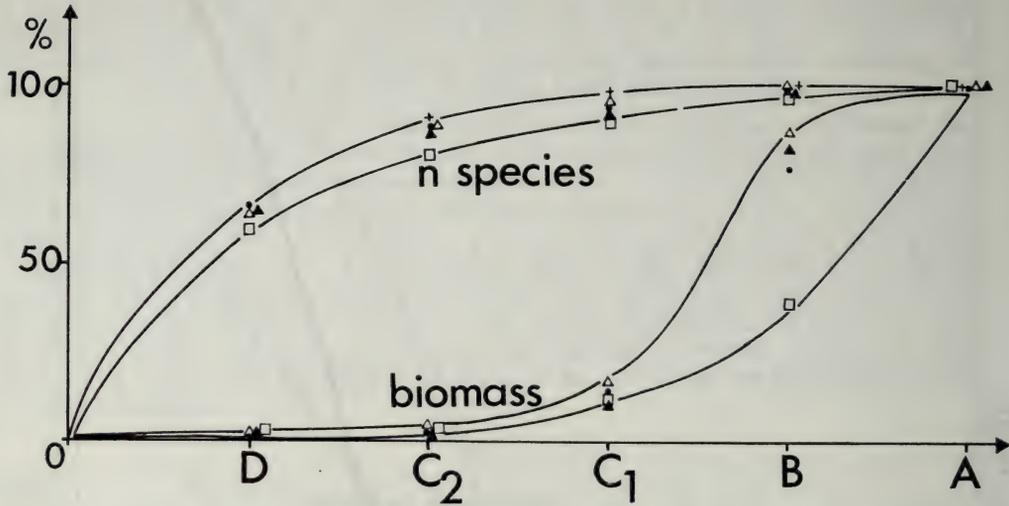
Fig. 5. Species-area lines for pairs of transects, each 20 × 500 m, in the Sabal sampling area, Sarawak. For plot description see tab. 1.

Fig. 6. Species-dominance curves for Sarawak sample plots, 0.2 ha each, on peat bog/Humus Podzol (left) to more mesic and fertile transition to red-yellow podsol soil (right, SP. 16) in Sarawak, and for the 0.2 ha Manaus plot on latosolic "terra firme", Amazonas, D. = *Dacrydium*, A. = *Agathis*, S. = *Shorea*, W. = *Whiteodendron*, Dryo. = *Dryobalanops*

DOMINANCE - DIVERSITY CURVES IN 5 SAMPLE PLOTS



The inverse importance by phytomass and by number of species of the various size classes or stand strata is general for tropical moist forests. Fig. 9 shows the same relationship for SP 43 as an example of a stand in which a single species attains extreme dominance, and fig. 10 for SP 53 with a more balanced floristic structure. The two samples again demonstrate the wide variation of structural parameters which exists in tropical moist forests. This is supported by the summaries of the cumulative species/size class and cumulative biomass/size class



• square blocks, 40 x 40 m

▲ square blocks, 30 x 30 m

□ + square blocks, 10 x 10 m

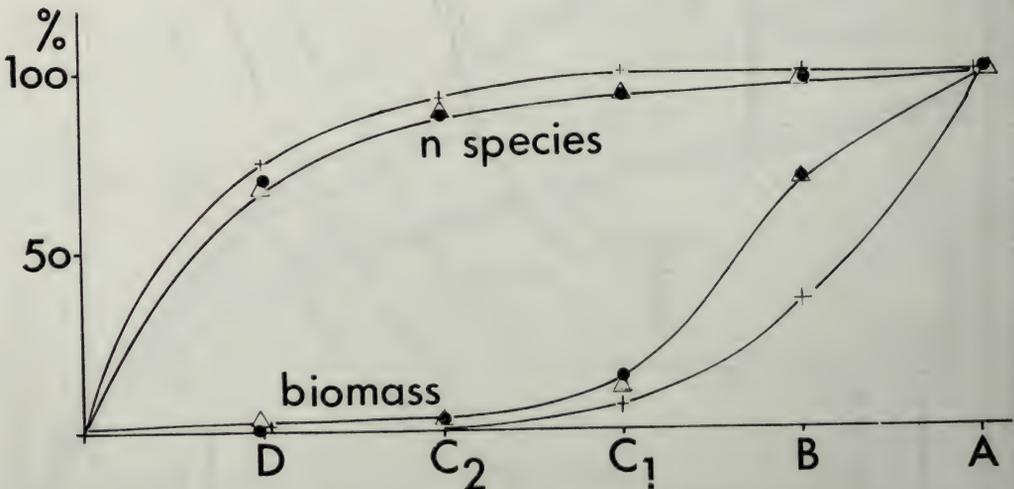


Fig. 7. Increase of species number and phytomass of layers A-D in square blocks of different size, as per cent of the totals in the 40 x 50 m plot of Klinge & Rodrigues. The curves delimit the variability range of the figures.

Above: minimum figures of phytomass and corresponding species numbers, and minimum species number and corresponding phytomass.

Below: maximum figures of phytomass and corresponding figures of species number, and maximum species number and corresponding phytomass.

curves for the 5 selected Bornean sample stands (fig. 11 and 12). These examples show clearly that efficient biomass sampling can be done with a relatively large minimum diameter limit which may be as high as 20 cm in stands such as in SP 43 or 10 cm in SP 53. But efficient sampling of species composition would require much lower minimum diameter limits close to zero. It was for this reason, that such low limits were chosen in the sampling of the 55 plots in Borneo which in fact covered an estimated 90.3 % of the species which are present in the association group of Kerangas and Kerapah forests (Brunig, 1973a, 1975).

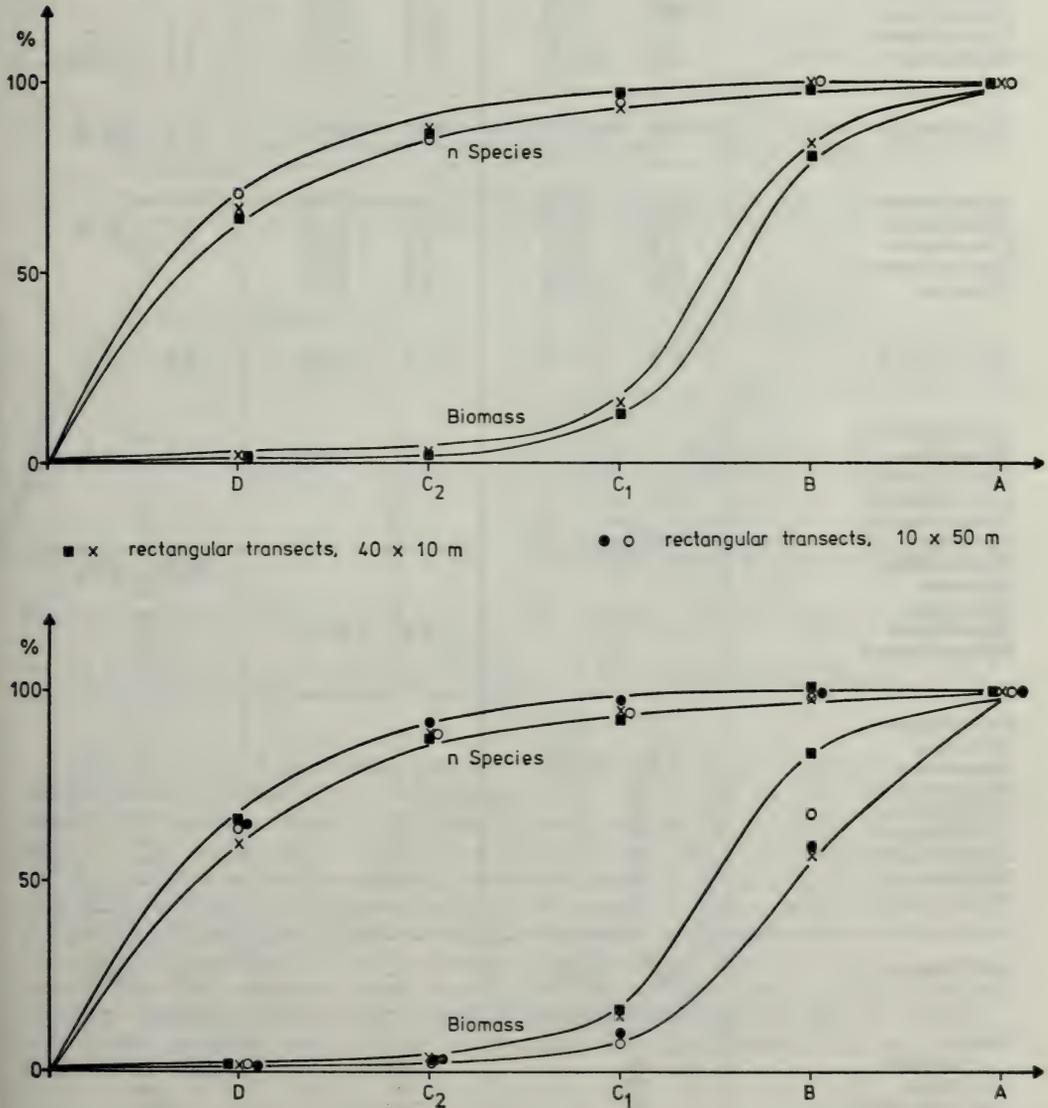


Fig. 8. Increase of species number and phytomass of layers A-D in rectangular transects of different size and direction, as percent of the totals in the 40 × 50 m plot of Klinge & Rodrigues.

The curves delimit the variability range of the figures.

*Above:* minimum figures of phytomass and corresponding species number, and minimum species number and corresponding phytomass figures.

*Below:* maximum phytomass figures and corresponding species number, and maximum species number and corresponding phytomass figures.

Table 7. Percentages of plant families on total numbers of species and individuals in the Central Amazonian rain forest acc. to Klinge & Rodrigues (dbh 15 and more cm), Lechthaler (dbh 16 and more cm), and Soares (dbh 15 and more cm)

Plant families	Klinge & Rodrigues		Lechthaler		Soares(2) (3)	
	0.2 ha		1 ha		9 ha	
Moraceae	1.8	(1.4)	3.6	(6.5)	0.7	(1.7)
Lauraceae	1.8	(1.4)	5.4	(6.0)	—	—
Leguminosae	20.0	(17.1)	21.4	(18.1)	—	—
Lecythidaceae	9.1	(7.1)	16.1	(27.4)	1.4	(11.2)
Sapotaceae	21.8	(17.1)	14.3	(11.6)	2.1	(9.4)
<b>1st Subtotal</b>	<b>54.6</b>	<b>(44.3)</b>	<b>60.7</b>	<b>(69.7)</b>	<b>4.3</b>	<b>(22.3)</b>
Apocynaceae	3.6	(4.3)	5.4	(1.9)	—	—
Annonaceae	1.8	(1.4)	3.6	(1.9)	0.7	(1.9)
Celastraceae	1.8	(1.4)	1.8	(1.9)	—	—
Euphorbiaceae	10.9	(21.4)	1.8	(0.9)	—	—
Olacaceae	3.6	(2.8)	3.6	(4.7)	—	—
<b>2nd Subtotal</b>	<b>21.8</b>	<b>(31.4)</b>	<b>16.1</b>	<b>(11.2)</b>	<b>0.7</b>	<b>(1.9)</b>
Anacardiaceae	—	—	×	—	—	—
Burseraceae	—	—	3.6	(8.4)	0.7	(7.7)
Combretaceae	—	—	×	—	—	—
Cucurbitaceae	—	—	×	—	—	—
Flacourtiaceae	—	—	×	—	—	—
Guttiferae	—	—	×	—	—	—
Myristicaceae	—	—	×	—	0.7	(2.4)
Rosaceae	—	—	×	—	—	—
Rubiaceae	—	—	×	—	—	—
Sapindaceae	—	—	1.8	(2.3)	—	—
Simaroubaceae	—	—	×	—	—	—
Vochysiaceae	7.3	(5.7)	—	—	—	—
Violaceae	3.6	(4.3)	—	—	—	—
Humiriaceae	3.6	(2.9)	—	—	—	—
Icacinaceae	×	—	—	—	—	—
Myristicaceae	×	—	—	—	—	—
Caryocaraceae	×	—	—	—	—	—
Nyctaginaceae	×	—	—	—	—	—
Myrtaceae	×	—	—	—	—	—
Bombacaceae	—	—	—	—	0.7	(2.3)
<b>3rd Subtotal</b>	<b>23.6</b>	<b>(24.3)</b>	<b>—</b>	<b>—</b>	<b>2.9</b>	<b>(9.9)</b>
<b>Total</b>						
n families	18		21		11	
n species	55		56		140	
n individuals	70		215		2250	
Palmae						
species	1		2		?	
individuals	1		3			

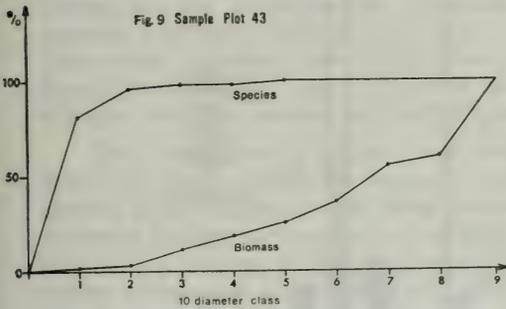


Fig. 9. Cumulative relative species number and phytomass (biomass) with increasing diameter class in an *Agathis dammara* bearing Kerangas forest on Deep Humus Podzol, SP. 43, Sarawak.

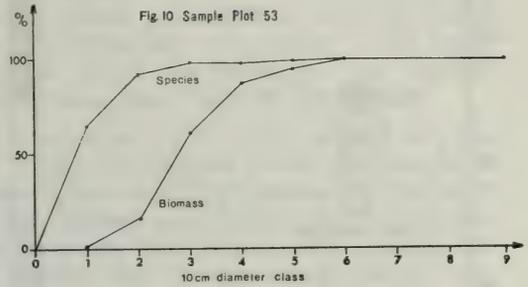


Fig. 10. Cumulative relative species number and phytomass (biomass) with increasing diameter class in a mixed Kerangas forest on Grey-White Podzolic clay soil, SP. 53, Sarawak.

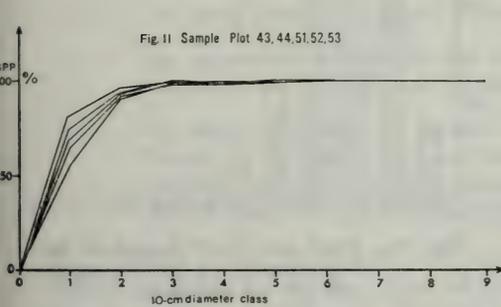


Fig. 11. Cumulative relative species number with increasing diameter class in 5 selected sample plots, 0.2 ha each, in Sarawak.

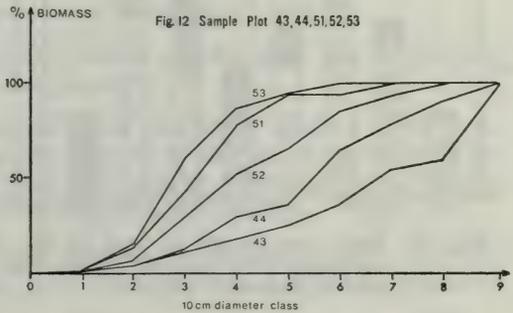


Fig. 12. Cumulative relative phytomass (biomass) with increasing diameter class in 5 selected sample plots, 0.2 ha each, in Sarawak.

The variation of phytomass between 5 square 20 x 20 m subplots in the two sample plots SP 43 and SP 53 is illustrated in fig. 13 and fig. 14. The figures show clearly the common feature: variation is much smaller in the lower size classes than in the larger size classes, but variation in the single-dominant stand (SP 43) is again less in the dominant emergent layer (71-80 cm d). It is interesting that the latter feature disappears again in the course of phasic development along a time-related ecological gradient which culminates in sample plot 44 (fig. 15). The strong dominance of *Agathis dammara* has weakened. The top canopy is more mixed, the stand structure more diverse and the stocking more variable between subplots. Obviously, such features have important significance not only for biomass and species sampling, but also for the structure and functioning of the ecosystem as a whole (Brunig, 1970, 1973b).

### Conclusion

Available information on the Central Amazonian and Bornean rain forest permits the conclusion that relatively small plot sizes, such as the 40 x 50 m and 20 x 100 m plots we used, have advantages for sampling both species composition and its phytomass. The small size is time and labour saving and cost-benefit efficient. Very large plots are proportionally costly and time consuming, and require an inordinate amount of facilities and organization because of the enormous

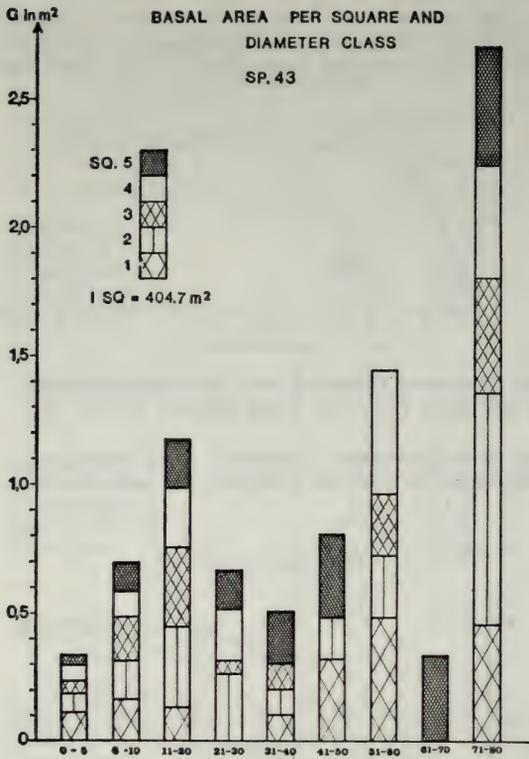


Fig. 13. Basal area in m<sup>2</sup> in each of the 5 subplots (1 sq. ch.) of sample plot SP. 43, Sarawak.

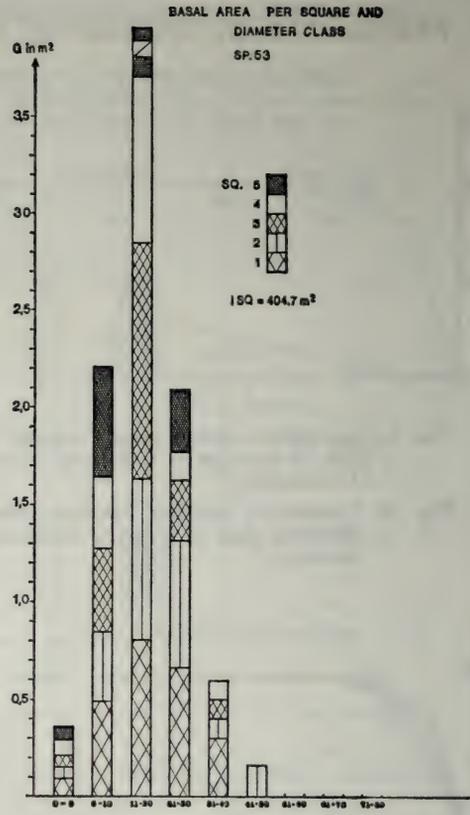


Fig. 14. Basal area in m<sup>2</sup> in each of the 5 subplots (1 sq. ch.) of sample plot SP. 53, Sarawak.

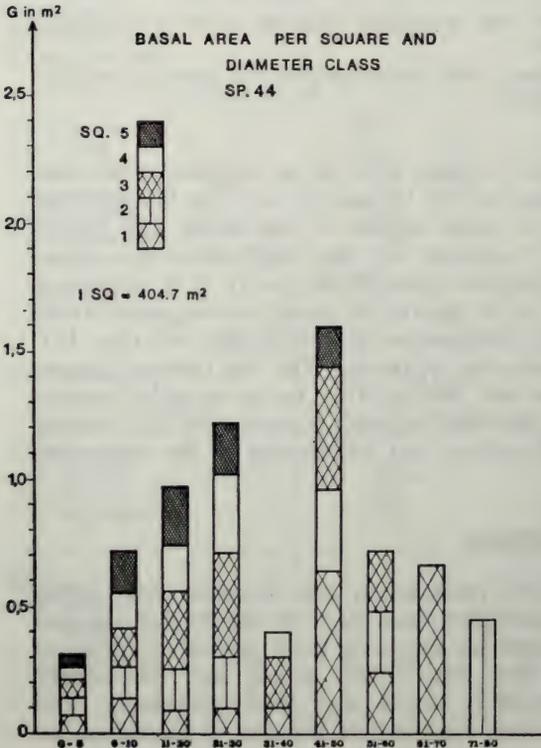


Fig. 15. Basal area in m<sup>2</sup> in each of the 5 sub-plots (1 sq. ch.) of sample plot SP. 44, Sarawak. The plot follows in a succession-related catena on SP. 43. The X-axis denotes diameter at breast height in cm. d in cm.

number of individuals and the greater number of species especially if site and forests are not homogeneous. However, if emphasis is on the rare or very rare species, plot sizes must be very large and diameter limits low. If only the forest phytomass is studied, small plots are adequate, especially with respect to the lower layers of the stand, and minimum diameter limits can be larger. The smaller material can be conveniently subsampled without much loss of precision.

Our conclusion is in agreement with Lang *et al.* (1971) who studied tropical forest at Barro Colorado, Panamá, and found that almost a 100 % sample is needed if the objective is to sample the rare species with high precision. The more common species are however adequately documented even if the sample comprises only a tiny portion of the total area. The examples from Borneo also confirm our earlier contention and Ashton's (1964a) opinion that between-stand diversity and site diversity limit the useful size of vegetation sampling plots to around 0.2 to 0.5 ha if within-plot homogeneity is desired. Expansion of plots beyond this size introduces excessive heterogeneity by including different site and stand conditions. The variation of biomass parameters is of such magnitude and its pattern so complex that sampling of stand biomass and other structural stand features in natural virgin tropical rainforest must be done:

- by using small area plots if biomass is to be measured directly
- by rigorously stratifying the sampling design according to site conditions, phasic development and species composition
- by supplementing the biomass sampling in intensively studied plots by a survey of the wider plot surround with respect to the variations of biomass-related parameters such as basal area, stand height, tree shape, tree density, tree frequencies per diameter class and species composition.

Unless these conditions are met, the results of studying small biomass sampling plots, as of other types of yield observation plots, will produce meaningless, because uncoordinated, information.

### Acknowledgments

Thanks are due to W. A. Rodrigues, Botany Department, Instituto Nacional de Pesquisas da Amazonia, Manaus, Amazonas, Brazil, who made some of his staff available for the fieldwork from June to November 1970, and who also helped in many other ways.

The Amazonian data have been obtained through cooperation between the INPA, Manaus, and the Department of Tropical Ecology, M.P.I., Ploen. The Bornean data have been processed with financial assistance from the German Research Foundation. (DFG).

### Literature

- ANON. 1969. Os solos da área Manaus — Itacoariara. IPEAN, Série Estudos e Ensaios 1, Manaus, 116 pp.
- ASHTON, P. S. 1964a. A quantitative phytosociological technique applied to tropical mixed rainforest. *Malay. Forester* 27 (3): 304–317.
- 1964b. Ecological studies in the Mixed Dipterocarp Forest of Brunei State. *Oxford Forestry Memoir* 25, Oxford.
- and BRUNIG, E. F. 1975. The variation of tropical moist forests in relation to environmental factors as key to ecologically oriented land-use planning. *Mitt. Bundforsch.-Inst. Forst-u. Holzw.* 109: 59–86.

- AUBRÉVILLE, A. 1961. Etude écologique des principales formations végétales du Brésil et contribution à la connaissance des forêts de l'Amazonie brésilienne. Centre Technique Forestier Tropical, Nogent-sur-Marne, 268 pp.
- BRUNIG, E. F. 1968a. Some observations on the status of heath forests in Sarawak and Brunei. Proceedings, Symp. on Recent Advances in Tropical Ecology, Varanasi, 1967. Int. Soc. Trop. Ecol., Varanasi: 451-457.
- 1968b. Der Heidewald von Sarawak und Brunei. *Mitt. Bund. Forsch.-Anst. Forst- u. Holzw.* Nr. 68, Bd. I u. II, 431 pp.
- 1970. Stand structure, physiognomy and environmental factors in some lowland forests in Sarawak. *Trop. Ecol.* **11** (1) 26-43.
- 1973a. Species richness and stand diversity in relation to site and succession of forests in Sarawak and Brunei (Borneo). *Amazoniana* **4** (3): 293-320.
- 1973b. Biomass diversity and biomass sampling in tropical rain forest. In: IUFRO Biomass studies, Univ. Maine, Orono.
- 1975. Ecological studies in the Kerangas forests of Sarawak and Brunei. Borneo Lit. Bureau, Govt. Printer, Kuching (in press).
- DUCKE, A., and BLACK, G. A. 1953. Phytogeographical notes on the Brazilian Amazon. *Anais Acad. Bras. Ciênc.* **25**: 1-46.
- FITTKAU, E. J. 1969. The fauna of South America. In: E. J. Fittkau, J. Illies, H. Klinge, G. H. Schwabe, and H. Sioli (Editors): Biogeography and Ecology in South America, Junk, The Hague. Vol. II: 624-658.
- FITTKAU, E. J., and KLINGE, H. 1973. On biomass and tropic structure of the Central Amazonian rain forest ecosystem. *Biotropica* **5** (2): 2-14.
- HUECK, K. 1966. Die Wälder Südamerikas. Fischer, Jena, 422 pp.
- KLINGE, H. 1965. Podzol soils in the Amazon basin. *J. Soil Sci.* **16** (1): 95-103.
- 1968. Report on tropical podzols. 1st draft. F.A.O. Rome, 88 pp.
- 1972. Biomasa y materia orgánica del suelo en el ecosistema de la pluviselva centro-amazónica. *Acta cient. Venez.* **24**: 174-181.
- 1973a. Struktur und Artenreichtum dez zentralamazonischen Regenwaldes. *Amazoniana* **4** (3): 283-292.
- 1973b. Root mass estimation in lowland tropical rain forests of Central Amazonia, Brasil. I., *Trop. Ecol.* **14**: 29-38; II. *Anais Acad. bras. cienc.* (1975, in press).
- KLINGE, H., and FITTKAU, E. J. 1972. Filterfunktionen im Ökosystem des zentralamazonischen Regenwaldes. *Mitt. deutsch. bodenk. Ges., Göttingen.* **16**: 130-135.
- KLINGE, H., and RODRIGUES, W. A. 1968. Litter production in an area of Amazonian terra firme forest. Part I. Litter-fall, organic carbon and total nitrogen contents of litter. *Amazoniana* **1** (4): 287-302.
- 1971. Matéria orgânica e nutrientes na mata de terra firme perto de Manaus. *Acta amazon., Manaus* **1** (1): 69-72.
- 1973. Biomass estimation in a Central Amazonian rain forest. IUFRO Biomass studies, Univ. Maine, Orono.

- KLINGE, H., RODRIGUES, W. A. BRUNIG, E. F., and FITTKAU, E. J. 1973. Biomass and structure in a Central Amazonian rain forest. In: *Ecological Studies, II. Tropical Ecological Systems*. Springer, New York & Berlin.
- LANG, G. E., KNIGHT, D. H., and ANDERSON, D. A. 1971. Sampling the density of tree species with quadrats in a species-rich tropical forest. *Forest Sci.* **17**: 395-400.
- LECHTHALER, R. 1956. Inventário das árvores de um hectare de terra firme da zona Reserva Florestal Ducke, Município de Manaus. *Inst. Bras. Bibliografia e Documentação, Rio de Jan. Botânica, Publ. 3*, 7 pp.
- RICHARDS, P. W. 1974. *The tropical rain forest*. 5th Ed. Cambridge Univ. Press.
- RODRIGUES, W. A. 1967. Inventário florestal piloto ao longo da estrada Manaus — Itacoatiara, Estado do Amazonas: Dados preliminares. Atas Simpósio sobre a Biota Amazônica, Belém 1966, **7**: 257-267.
- ROLLET, B. 1973. L'architecture des forêts denses humides sempervirentes de plaine. Centre Techn. For. Trop., Nogent sur Marne. 298 pp.
- SOARES, R. O. 1957. Inventario florestal Reserva Florestal Ducke. Relatório. Mimeogr., 26 pp.
- TAKEUCHI, M. 1961. The structure of the Amazonian vegetation. II. Tropical rain forest. *J. Fac. Sci. Tokyo Univ. Sect. 3, Bot.*, **8** (1/3): 1-26.
- WEBB, L. J., TRACEY, J. G. and WILLIAMS, W. T. 1972. Regeneration and pattern in the subtropical rain forest. *J. Ecol.* **60** (3): 675-695.
- WHITMORE, T. C. 1975. *Tropical rain forests of the Far East*. Clarendon Press, Oxford, 282 pp.



# Autonomous Evolution in Plants

## Differences in plant and animal evolution

by

C. G. G. J. VAN STEENIS

*Rijksherbarium Leiden*

### CONTENTS

	<i>Page</i>
Summary - - - - -	103
1. Introduction - - - - -	104
2. Survival level and <i>patio ludens</i> - - - - -	107
Anatomical features and structural fitness of Gymnosperms - - - - -	109
3. Pre-adaptations in plants - - - - -	111
4. Early differentiation - - - - -	112
5. Saltatory evolution in plants - - - - -	113
6. Gliding evolution in animals - - - - -	117
7. Co-evolution of animals and plants - - - - -	119
Evolution of orchids - - - - -	121
Evolution of figs - - - - -	122
8. Reticulate phylogeny - - - - -	123
9. Embryology and ontogeny - - - - -	124
References - - - - -	125

### Summary

It is argued that after 'decisions' were made in the early stages about the basic matrix of plant life later evolution followed in an autonomous way, not as a consequence of the competition/selection principle.

Evolution of plants is characterized by their passive tolerance and lack of active aggression. Their main struggle is to evolve against the environment; mutual competition is no agency for their evolution. Animal evolution has, besides this same struggle, a second impetus by competition.

Under this dual pressure animal evolution is proceeding more rapidly and form-making is more abundant, and has led to more complicated specialized structural and behavioural development than in plants because of sexual selection, which is absent in plants.

Competition and survival of plants is more passive and mainly directed against the inanimate environment. This tolerance led to a slower and conservative evolution.

The survival level, which tops all requirements necessary for survival for a certain place and time, lies much lower in plants than in animals and allows for plants a greater free space (*'patio ludens'*) for structural development of non-adaptive characters, which fall beyond competition, selection, and adaptation. This free space in animal development is generally considered to be very narrow.

So-called 'pre-adaptations' in plants have not come into existence because of competition pressure, and is a misleading term in evolutionary sense.

In early differentiation structural decisions for later phyla may well have been made by chance, or these characters may have had in those early stages a lower 'genetical weight' than they got during later establishment.

In plants, the usual way of evolving evolutionary development is through sudden (saltatory) change which is amongst others proved by preponderance of allopolyloid and aneuploid chromosome numbers.

This saltatory evolution proceeded through a small number of specimens.

Saltatory development may also have occurred through sudden change of a few genes which physiologically upset pathways to morphogenesis, partly through neoteny, and gave rise to systematical teratologies, and thus to creation of isolated taxa.

Racial segregation may have led to new species but in plants only in exceptional cases (in long isolation): the term micro-evolution used for this development should be abandoned for plants.

It seems not possible as yet to translate structural changes in genetical terms and define the constancy in genetical weight of genome structure, though there must be a considerable genetical difference between characters common to phyla and those common to families, genera and species. It is peculiar that by a sudden saltation of a 'physiological gene' a very constant structure may be upset, for example by a peloric form in an orchid.

In animals on the other hand 'gliding evolution' by gradual accumulation seems to be the usual way of development. This is attributed to competition and sexual selection, and it goes by populations, through *convivia*, *commiscua* and *comparia*.

Mutations irrelevant to divergent survival may be possible but they will play a minor role, as *patio ludens* is for animals a very narrow measure. Saltations, if they occur, must be quite exceptional.

Co-evolution of plants and animals is usually a one-sided affair, in which changes in plant structure occur first, and adaptation by animals follows. Except for negligible exceptions plant evolution goes independent of animal evolution in an autonomous way; novelties arising in plants are exploited by animals for their evolution and specialization.

This does not exclude that in a restricted number of cases plants got into a situation where animal action became a vital factor for their survival, as in orchids and figs. In these cases animal populations have forced their way of gliding evolution on that of plants, but even in these cases changes of plant structure do not arise perforce of competition among the plants themselves. their changes remain autonomous, it is the animals which adapt themselves.

It is argued that, whereas in the gliding, divergent evolution of animals there will be hardly any chance of reticulate phylogeny, though their will be of course reticulate affinity.

In plants, however, it has been shown that reticulate phylogeny has played an important role in their evolution.

Finally attention is given to the basic difference between animals and plants in their embryological and ontogenetical development which must have had essential implications for their evolution.

## 1. Introduction

It is, I believe, generally accepted that evolution in plants and animals is caused by similar impulses and that its mechanism(s) has been the same for both. It should be remarked that this holistic principle is philosophically an extremely attractive axiom. It should, however, also be remarked that the development of evolutionary theory has largely been in the hands of zoologists and zoo-palaeontologists. They had of course no reason to check whether the axiom is fully valid for plants or whether there are differences, either in degree or in quality.

From the side of botanists there have been, as far as I can remember, remarkable few queries about the validity of the holistic axiom. And those I know of concern only the proportional speed of evolution.

J. D. Hooker (1859: xii, footnote) pointed to the marked contrast of the showy, vivid differentiation of the fauna as compared with the conservative, rather monotonous development of the plant kingdom, writing: "the much narrower delimitation in area of animals than plants, and greater restriction of Faunas than Floras, should lead us to anticipate that plant types are, geologically speaking, more ancient and permanent than the higher animal types are, and so I believe them to be, and I would extend the doctrine even to plants of highly complex structure". The idea that changes in the development of the Angiosperms have been extremely slow was also stressed by Hamshaw Thomas (1961: 3).

It appears in fact, that certain types of life, especially among the bacteria and algae, have persisted over immense periods, some two, or at least one and a half billion years, before showing further evolutionary development.

It is true that this observation relates only to the quantitative aspect, the speed of evolutionary progress, but it leads nevertheless to consider the qualitative aspect, even if this would mean a re-appraisal of the holistic principle.

Therefore we have to consider the mechanism(s) of evolution gradually developed through the ideas of Buffon *c.s.*, Lamarck, Hutton, Malthus, Lyell, and finally synthesized by Darwin & Wallace, by whom the gradually grown idea of adaptation was more closely defined as adaptation caused by selection on the basis of competition, more popularly explained as survival of the fittest.

Competition, resulting in selection, must of course have been a powerful agent through the history of life. It is supposed to have been already present on the abiotic level. Probably already at this stage was it effective, with the understanding that 'decisions' were made resulting in a restricted number of initial organic compounds (see Quispel, 1968). The same principle of competition is held responsible for the evolution at the akaryotic and later karyotic stages at the biotic level. It is clear that competition results in restriction of the pre-existing variability, either by adapting the mechanism of segregation or by preferential elimination of less adapted individuals.

In these early stages, again, 'decisions' were made about basic features of structure which became the matrix of later evolution. One may well imagine that, if 'decisions' had materialized in different ways, other matrix structures would have originated. Thus, the impact of these early competitions must have contained a very important factor of chance. Chance is in this context of course to be understood as causal, but it includes the possibility that matrix structures of genomes could have been different. The early 'decisions' made, must thus have had a decisive, hence restrictive influence on later evolutionary lines for further development. Once a stable basic matrix pattern of genome design was established, the fate of further evolution based on this design was curbed, the stakes of its potential boundary being set out, comparable to 'evolution' of basic designs in industrial tool and machine development.

This implies that only part of the potentially possible organic structures really have got into actual existence as viable living organisms. We cannot fathom what other basic designs could have had viability, and so, questioning what percentage of the total potentiality of living matter was ever realized, becomes an impossible and useless exercise.

The main basic design for plant evolution must have been the unicellular algae and bacteria\*, probably soon followed by fungi. They must have been capable of conquering the earth, as they still do. They coupled plasticity against environmental factors with diversification, resulting in the occupation of all niches, as they still do. This diversification consisted of the origin of species adapted to the environmental niches of an unimaginable variety: freshwater, seawater to brine, arctic to tropical conditions, rock faces and snow, even extremely high water temperatures. It seems doubtful whether this can be explained or that it needs to be explained by the competition/selection axiom; the world was bare and niches unoccupied, it was free for all.

Our unique planet once occupied by bacteria and algae, we are confronted with the question why there was any ecological or adaptational need or necessity for evolution to more complicated organisms according to the competition/selection axiom as the mechanism of evolution.

---

\* I have always been surprised that virus is usually advanced as more primitive living matter, due to a more simple design. Since virus is inert matter, only capable of multiplication as a parasite in the protoplasm of more complicated real organisms, they cannot have preceded, or be ancestral to, the latter.

It is likely that the unicells were followed by thread-like, branched and foliar algae, which also needed space. They may have locally shaded out, but not replaced all the unicells. They were received as affiliated newcomers, to belong to one happy family. Under favourable environmental conditions there is no end to the extension of the family, as is e.g. shown by the tropical rainforest, the flora of the Cape or of New Caledonia or Western Australia which are not only very rich, but where also each family and each genus is represented by many species thriving peacefully together.

Here we glimpse a first difference, the passive tolerance of plants as compared with animals. Plants are tolerant living beings, they do not eat their close allies, they do not hunt and kill in order to survive, they do not need all sorts of devices towards upmanship in order to live. This passive tolerance, lack of active aggression, suffering in silence, subdued happy-go-lucky mode of living, just waiting what will happen, this inertia as compared with animals, is characteristic of plants. To no mean degree this is due to the sedentary bond with the terrestrial substratum.

Animals show generally motility, they show aggression, they are out to exterminate rivals, show competition and intolerance, and are for a great deal not sedentary and bound to the substratum, but move around. It should be mentioned that among the most highly evolved animals, viz. birds and mammals, there are striking examples of tolerance within the species, mutual aid, and even birth control by various sophisticated devices. Still, these are exceptions, and especially tolerance towards the members of other species is very rare.

These two opposite tendencies, passivity and activity, must, I believe, have the important corollary, that animals are under greater pressure to develop steadily more complicated means and ways, including structures in order to keep up with competition and have to use all possible advantages, which by mutation occur, in order to survive. Their structure becomes in this way adapted to competition, leaving hardly room for organs or other features which are useless or irrelevant to survival. Their organization is thus changing rather rapidly; organs once useful have been superseded by others and though they often do not disappear entirely, they soon are hidden away and can only by careful comparative anatomy be traced as insignificant vestiges.

Thus I believe that, while the competition/selection axiom is valid for animal life, plants behave more conservatively, as they do not suffer from similar pressure. They develop more slowly and give free way to inventiveness in forms and structures which are irrelevant to competition/selection, creating features which sometimes are called adaptively-neutral.

It should be noted of course, that rudimentation in flowering plants, due to saprophytism, parasitism, or secondary aquatic life, is comparable to rudimentation in animals. Nevertheless, it seems to be less stringent in general, and it seems to proceed much more slowly.

Competition and survival in plants is passive; it is mainly caused by or directed against the inanimate environment, heat and cold, drought and water, seasonal desiccation, exceptional soil types, and presence of toxic minerals, etc. A few exceptional cases of allelopathic behaviour mean only that certain plants may not tolerate others in their immediate vicinity, but there is plenty of room for them elsewhere. Besides, allelopathy does not concern competition between allied species, but rather implies an influence of exudates of non-related species. Parasitic plants may destroy or harm their hosts, but they usually come to a balance agreeable to the survival of both host and parasite, sometimes even to a parasitical symbiosis (*Rafflesia*, *Balanophora*, etc.). In their strife for light plants may shade out others, but there are always open places where the shade-giving plants cannot thrive and have to give way to the smaller ones.

There is no case known to me that a so-called better adapted plant completely outrooted another allied species. It has been shown that seedlings of one species may have an advantage over those of another in experiments, but I doubt whether these experimental conditions can be applied to germination in nature, and if it were so, in nature it will always turn out to be a mere question of proportional abundance, not of extinction through competition. This can hardly be otherwise, as each plant species has its own ecology, including resulting abundance: no two species have exactly the same ecology. To be precise, and to quote a simple example: very few closely allied species of plants will be able to survive in a peat bog of high acidity, or in soils loaded with heavy metal ions, but we never observe that one species eliminates all others.

In conclusion, it appears that intra- and inter-specific competition as well as natural selection (in the sense of elimination of weak individuals by stronger ones) among plants is insignificant. The occurrence and abundance of plants is almost entirely defined by environmental factors.

Against animals in search for food, the plants behave passively. Many may contain poisonous substances, or elaborate structural devices which seem to be effective in keeping off some of the potential predators, but even in these cases it is the animals which adapt themselves; as a matter of fact the most toxic plants have animals which feed on them. Thus, it is essentially a question of equilibrium, based on mutual adaptation.

Animals on the other hand have the problem of surviving two kinds of struggle for life. The first struggle is the same as that of plants, against the inanimate environment, but the second is against each other. Instead of the basic autotrophy of plants there is a food chain in animals, often very complicated, in which besides plants other animals take part. This dual struggle means a high degree of competition among animals, and thus a much higher pressure towards upmanship. This must inevitably lead to more rapid change and development, that is, evolution.

A third point is that the number of niches for animals is much greater than for plants, and far more finely knit, enabling them to develop through the pressure of competition/selection an immensely greater display of form-development and specializations.

A fourth, though minor, point is that animals can occupy certain environments unfit for plants, such as the depths of the oceans, the atmosphere, caves, etc.

Concluding, this concise discussion may serve to explain the observation Hooker made, that the variety in the animal kingdom is far greater than that in the plant kingdom.

What is more important, it throws also doubt on the holistic view of evolution in animate nature, in particular on the intensity of competition in the struggle for survival.

## 2. Survival level and *Patio Ludens*

The views exposed in the introduction lead to certain consequences which I have alluded to in my essay on plant speciation in Malesia (1969), *viz.* that there is a difference in the situation of the survival level in plants as compared with animals. I have illustrated this in a generalized schematic figure (Fig. 1).

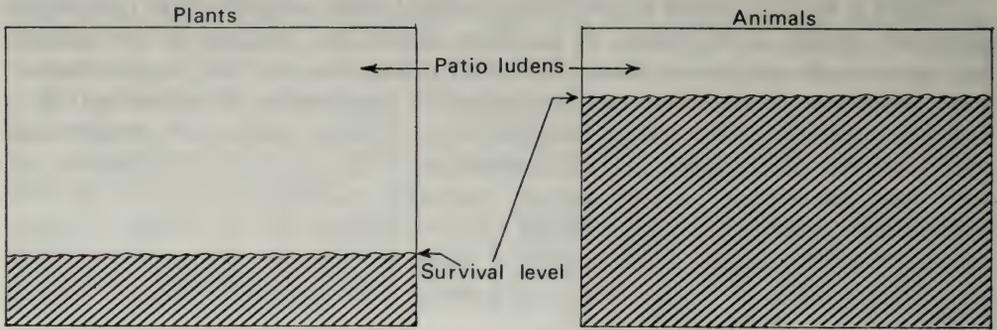


Fig. 1. For explanation see the text.

The rectangles represent the total potential space for structural development, in conjunction with the degree of the minimum requirements necessary for survival, indicated by the hatched space. The demarcation is marked by a line, which I call the 'survival level'; beneath it one has to think of all structures and functions compulsory for survival.

Above the survival level there is '*patio ludens*', represented by the blank space which can be occupied — but will not always be necessarily fully occupied — by structures which are irrelevant to survival, hence fall beyond competition, selection, and adaptation.

Through the more intense competition and more complicated life of animals, I believe that *patio ludens* is for animal life only a narrow zone as structural development is under high pressure of competition/selection, and development is more acutely directed towards trying to employ and adapt any new feature which it can use for its survival. The survival level in animals lies thus considerably higher. It should be admitted though, that adaptive-neutral features have occurred in animals as well, at very primitive levels, e.g. when the divergence started in arthropods into the insect and arachnid phyla, but also at the level of speciation, as exemplified e.g. by protuberances (often allometric in behaviour) in protozoans, arthropods, vertebrates, etc. See p. 112. Also I would not exclude the possibility of a lower survival level in primitive groups of animals.

In plants the survival level must generally lie much lower and primary structure equipment is more primitive. There is no such competition in perfection of adaptive structures as among animals. Consequently there is ample allowance for the possibility of structural features (form development) which are irrelevant to competition and adaptation.

These irrelevant or adaptatively neutral characters in plants concern both gross morphological characters and internal characters. It is for a woody plant not a matter of competition whether it develops into a tree or liana or a scrambler; or whether a liana twines to the right or to the left. Phyllotaxis seems also a quite irrelevant character, all types are equally well fit to let a plant live and survive. Presence or absence of stipules can equally not be attributed to have special function for survival. To prevent any misunderstanding: functional adaptations are very important, but they are not in any way restricted by neutral basic features like e.g. phyllotaxis.

Merousness of flowers also seems a matter of chance choice. Thus it would be a far-fetched idea to postulate that 5- or 4-merous flowers have a competitive value, the one better than the other, or 3-merous ones over 2-merous flowers (cf. also Bateson, 1894: 67). Monocotyledons are characterized by 3-merous flowers, but 2-merous ones do equally well (*Stemona*, *Paris*, etc.).

In the flower the number and position of anthers, obdiplostemony, etc. is an often systematically very constant structure, but it seems futile to ascribe competition value to such structures. In a very uniform genus, such as *Tristania*, the number ranges from 5 to very many (and then in phalanges); in Borneo many species grow together and none of them is crowding out the others.

As to gynoecium, its position: superior or inferior, its merousness, the position of ovules, erect or pendent, axial or parietal, seems not to have any bearing on competition. It just happens that in families like Theaceae one or a few have by exception an inferior ovary (*Anneslea*) and in Rubiaceae some have a superior ovary (*Gaertnera*). Or this may vary even within one genus (*Mastixiodendron*). A similar situation prevails with the seed. It could not be argued with good reason that the presence of two cotyledons would be of any competitive value above the presence of one cotyledon, or for that matter of more than two. The same holds for the place where reserve food is stored, in the cotyledons or in albumen, or in both, or whether seeds are large or small. They all come up equally well ecologically. As a matter of fact any systematic structure (systematic character) may be constant in one group and vary in another; properly none of them have absolute value.

In this context it is noteworthy what A. C. Smith remarked, when he spoke of the phylogenetic systematy of the Monimiaceae (1973: 55): "The basic complex with which we are here concerned, within the Ranales, is characterized by having comparatively primitive xylem, ethereal oil cells, monocolpate pollen or pollen derived from that type, and unilacunar nodes. Incidentally, these are not glaringly apparent characters, but they are some of the basic characters that taxonomists concerned with Angiosperm evolution must use if they seek to understand (phylogenetic) relationships".

In all these structures plants do not compete, their only concern is to stand certain primary minimum conditions under the survival level.

Concluding, it must be well understood as a major point that it is precisely these 'technical characters' which serve for the schemes of the evolutionary system of the Angiosperms, that is, that they reflect phylogenetic affinity and are employed for the reconstruction of their ancestral relations and derivation. Though these structures have no adaptive value, the way of evolution is traced by them. And this shows their importance.

#### **Anatomical features and structural fitness of Gymnosperms**

Even for anatomical features the evidence that complicated, specialized structures would have originated as a result of competition/selection to enhance their functional value, is dubious, if we try to measure their success.

One might imagine that vessels for transport of water, assimilates and minerals would mean a great advantage over tracheids. This rough assumption is, however, not borne out by the facts, as among both groups are the highest trees known to exist, and the oldest in life-span are even among those without vessels. Furthermore, it is not so that among the vesselless trees growth need to be hampered by absence of vessels and thus growth would be slower. Saplings of certain conifers may show a very rapid upgrowth indeed, comparing favourably with that in eucalypts. Conversely it is not so that saplings or trees with vessels always show a rapid upgrowth; some grow extremely slowly. This whole matter is dependent on several factors, sometimes individually on soil and climate conditions, and structure and capacity of root system, but mainly on the ecological capacity of the different tree species of each group, irrelevant of presence or absence of vessels.

A conclusion is sometimes made about the better adaptation by presence of vessels with reference to the palaeontological experience that Gymnosperms have very gradually been partly replaced by Angiosperms, in the sense that terrestrial space now occupied by Angiosperms was in pre-Cretaceous time the domain of Gymnosperms. This is certainly true, but it is doubtful whether this generality can be explained by improved 'adaptive values'. On the one hand it should be remarked that anatomically and functionally the Jurassic *Ginkgo* was obviously a success, but similar things can be said of *Araucaria*, *Metasequoia*, *Cycadaceae*, and others. On the other hand trees equipped with Angiosperm-type wood from the Cretaceous had also to make place for newcomers. In addition it should be remarked that anatomists tell us that various anatomical features seem to be without function. Finally, the 'decline' of Gymnosperms is, I feel, slightly exaggerated; they are still responsible for a high percentage of all organic matter produced on our globe. This idea of 'decline' may, possibly in part be due to the proportionally low form-development which is indeed negligible if compared with the enormous diversity in structural development of Angiosperms.

But this is altogether another matter than inadequacy or deficiency of structural and functional fitness. This matter belongs to the question one can also put for structural development of many phyla and groups: why some are ancient but remained small and others grew to great diversified groups. Even in the Mesozoic the Gymnosperms as to number of genera and species were probably always fewer in number than the Angiosperms are today. The only guess one can make in this obscure field of speculation is that the basic genome pattern of groups remaining small was 'rigid' and did not allow for abundant form-development, and that the genome pattern of so-called more successful groups or phyla was more suitable or 'versatile' and had the promise of more potentialities. Similarly as in chemistry certain atoms (for example C, Si, etc.) have more potentialities as the basis of compounds than others: or in terms of plants, certain species appear to be fit to be 'developed' into a large number of edible or ornamental variations, while others simply resist this and do not possess genome potentialities fit to be exploited by domestication.

In chemistry potentialities of chemical evolution — in the sense of capacity of producing compounds — can be foretold. This should then also be possible for the chemical compound named genome-structure. But this is so complicated that it will never be possible to compute why the pattern in the Linaceous genus *Ctenolophon*, which existed already in the Upper Cretaceous, persisted all the time in the tropical forests (now extinct in the neotropics) but produced at most three species, while the obviously much later evolved Compositae, Acanthaceae, etc. showed an astounding diversification though they are structurally very homogeneous from the taxonomic point of view.

I may mention a few other examples of old genera which are known from the Upper Cretaceous or Palaeocene which have never evolved into large groups, e.g. *Pachysandra*, *Nypa*, *Knightia*, and *Ginkgo*; contrasting these with *Ilex*, *Quercus*, *Nothofagus*, *Alnus*, *Symplocos*, etc., we cannot account for the latter's successful development, taxonomically and geographically.

I do not believe that it will ever be possible to compute the causality of structural development or account for the potentialities of the genome matrices and show that it could not have been otherwise and could be foreseen, or at least expected.

I have stressed (1969) that a congenial, equable climate, such as the tropical rain forest, which has persisted ecologically unhampered for aeons, has the lowest competition pressure, hence the lowest survival level in all habitats for plants, hence for them the widest *patio ludens*. Consequently the tropical rain forest offered the longest and largest opportunity towards form creation on the globe, for all kinds of structural developments which came up to survival conditions. It became the cradle of the development of Angiosperms as well as many other groups of the plant kingdom. This is also the reason why the tropical flora contains so many isolated genera and, besides, the frame-work of all larger families, which swarmed out later to other parts of the globe.

### 3. Pre-adaptations in plants

This term has sometimes been loosely applied in an evolutionary sense, to explain for example the structure of seeds and fruits on the sandy beach.

These fruits and/or seeds, which are all provided with some buoyancy device, are either hard-shelled, or have their seed surrounded by a stone and/or fibrous tissue and thus protected against the surf and grinding on sand, rock, coral and pebbles. But it must be kept in view that the representatives of the beach and the tropical beach-forest are just single or very few beach-specialized species of large inland genera which all display the same fruit-seed structure in inland vegetation, whether it be the hard-shelled Leguminosae (*Caesalpinia*, *Canavalia*, *Desmodium*, *Erythrina*, *Pongamia*, *Sophora*) or species of for instance the genera *Barringtonia*, *Calophyllum*, *Casuarina*, *Clerodendrum*, *Colubrina*, *Cordia*, *Cycas*, *Cyperus*, *Dodonaea*, *Euphorbia*, *Fimbristylis*, *Guettarda*, *Hernandia*, *Hibiscus*, *Ipomoea*, *Ischaemum*, *Morinda*, *Pandanus*, *Scaevola*, *Spilanthes*, *Terminalia*, *Tournefortia*, *Wedelia*, etc.

To bring their morphological capacities in conjunction with adaptation, as so-called 'pre-adaptation', seems to me a serious misleading of evolutionary thought, as it suggests the childish idea of pre-sighting on the part of the plants that it might be useful to develop such structures, just in case it might be helpful to cope with the exigency of sharing the future life of a beach-comber. These structures were already there in the genera and have nothing to do with the axiom of competition/selection pressure. Invading the beach just meant for these genera invading new terrain, in part unoccupied. The effort often was not even considerable, as they remained for their root system largely freshwater plants, and for several genera the hot beach conditions did not differ much from their main development in dry inland savannahs.

I could for many other specialized habitats give a similar picture, in the way that so-called pre-adaptations were already represented in existing structures outside these specialized habitats. A development of large hypocotyls with food-reserve in the seed, is for example represented in many tropical inland trees; it developed strongly in the littoral Rhizophoraceae, but certainly not as a result of competition/selection pressure. In passing: this feature is also not necessary at all, as the tiny seed of *Sonneratia* mangrove trees does not show anything of the kind.

A similar picture is displayed in almost all ecological specializations, be it rheophytes, therophytes, etc.

It should be added that, whereas the survival level scheme holds for one species or group at one time and in one place, the corollary is that *patio ludens* characters may, in later stages, or during migration of a taxon to other places with

different environments be 'pushed down' under the survival level as they become essential for survival in these stages or places where their latent existence is activated. Such characters may be physio-ecological as well as morphological.

In conclusion: (1) structures originate and may suit more than one ecological class or niche, necessarily leading to the peopling of specialized habitats with an array of unrelated, 'generic waifs' coming up to the minimum requirements of the habitat.

(2) 'Pre-adaptation' is often used in a misleading way, as a fancy term invented through pre-occupied thought. It should be defined more clearly, as in most instances in plants it has nothing to do with adaptation. It should preferably be replaced by the neutral term: 'pre-disposed structure'.

#### 4. Early differentiation

The survival level scheme set out in fig. 1 is, of course, meant for one time of each plant or animal in one place: it is dynamic, because in the course of time the significance of characters will, or at least may change. Structural characters as they appear today to belong to a rigid scheme may, in the far past, in primitive ancestors not have had the organizational significance they have now. Such characters may have been then irrelevant not only in plants but also in animals, because the more primitive the organisms are the lower is their survival level and the larger their *patio ludens* must have been.

I have in this context questioned zoologists in asking why in the great phylum of Arthropoda the Insecta are based on an organization scheme with 6 feet, while the Arachnoidea are based on a scheme with 8 feet, and whether they assume that such a basic structure has been the result of competition and natural selection; their answer was in the negative. Similar questions can be asked about the fact that Vertebrates all have 4 extremities, Cephalopods have either 8 or 10 arms, that the basic scheme of Echinodermata is 5-merous (in an exceptional small group 'running wild' towards an 11-merous structure) and why this would have advantage over a 3-, 4-, or 6-merous structural scheme which would equally have been feasible. In corals, on the other hand, there are again two large classes, the Octocorallia and Hexacorallia; why are there no Pentacorallia? With the exception perhaps of the quadrupedal organization which may be the most 'economical' solution from the structural point of view as well as for neuro-locomotor organization, these numbers like many others in animals (e.g. 5 fingers in tetrapods, 21 scleral elements in sauropsids) and like merousness in flowers, appear to be quite accidental and devoid of adaptive or selective significance. These structural schemes must have been fixed at initial stages, but the agency which caused the 'decision' seems very obscure. Still this decision was extremely important, being decisive for later phylogenetic organization.

It seems a far-fetched idea that this decision had anything to do with competition/selection; to me it appears a matter of casual structural development for which the potential was already embedded in the basic genome matrix. Once triggered development could not proceed otherwise.

In the initial primitive stage these basic structures may well have been *patio ludens* characters of the group concerned, irrelevant of competition/selection pressure, similar as must have been the case with many phylogenetic characters of plants, as has been advanced earlier in the preceding chapter.

This leads then to consider the genetical status of the merousness, and to the question: were these characters which have now class or phylum value at the early initial stage of much lower genetical value and apt to variation, maybe even at species level? How could it then be understood in the genetical sense that, what initially was possibly defined by a few genes could later develop into a strictly fixed bond characteristic of a whole phylum, and obviously so essentially integrated in its genome structure that it was not liable to be influenced by later mutations? In fact, except for rudimentation, secondary changes of such accidentally fixed primitive numbers are very rare indeed.

### 5. Saltatory evolution in plants

It is axiomatic that structural development is always proceeding stepwise, never completely gradual. In this point there can be no difference in inanimate or animate chemical compounds: both energy and matter are discontinuous, 'molecular': quanta, atoms, genes, and so their changes must be discontinuous.

The changes brought about by evolution in organisms can of course be small or large; if the steps are very small, the process looks to us gradual and one can speak of 'gliding evolution'; a mutation concerns at least one gene change. But if the changes are larger steps, one speaks of saltatory changes and development.

As in animals evolution in plants starts with divergence, and divergence must start from diversity, often called variability, of a genetical nature.

The first major step to evolution is speciation, that is, changes on the species level. This holds for all levels, as the first representative of the suprageneric taxa must also belong to a species. The origin of species is thus the most important phenomenon in evolution. But what is the criterion for a species, especially its delimitation? In two previous essays (1949, 1957) I have extensively treated the causes of variability and species delimitation respectively. I have come to the conclusion that there are essentially two ways of speciation, viz. through racial segregation and through saltation.

With racial segregation a species population segregates in the course of the slow process of dispersion into spatially (ecologically or geographically) isolated (replacing = vicarious genetically differentiated ecotypes, races and subspecies, in response to the ecological environments in the new lands (see van Steenis, 1949: xlv—1, and 1957: clxxxiii—xcxvi).

Such riaciation may finally result into a compound string or array of 'beads' representing *convivia* in Danser's sense.

Such races differ from one another in their gene combinations, but these differences usually concern only a restricted number of genes and in the intervening border zone where two adjoining races meet there is a transition zone where fertile hybridization takes place and intermediary specimens occur. On the borders marginal differentiation takes place by pioneer advances (genetic drift).

The general experience in plants is that riaciated species populations form together one *commiscuum* (*syngameon* of Lotsy) in Danser's sense (1929). Such a *commiscuum* is really a net of interfertility, as all races are miscible with the adjoining ones. Even if widely spaced races may become isolated through circumstances, fertility usually remains intact. There are many cases to support this. For instance the Pleistocene glacial period has broken up many populations, but through this cause now widely disjunct 'species' of, for example, *Platanus* and *Campsis*, in East Asia and America are still miscible; properly they should be treated as races of one species population and classified taxonomically as subspecies.

The possibility that the furthest remote races have accumulated so many hereditary differences that they prove incompatible if brought artificially into contact cannot be excluded. They may still be crossable but not miscible any more, that is, in hybridization will not go beyond the sterile  $F_1$  hybrid.

I would not go so far as to exclude the possibility that accumulating differences in gene composition may, after a long period of isolation, in a restricted number of cases lead to new species. This possibility is still more likely if partial populations survive in isolation on islands.

But the general impression is that in plants speciation through racial segregation must be a rare phenomenon and that this so-called 'micro-evolution', however interesting it may be for an understanding of the variability within a species is, in plants, of little significance in phylogenetic evolution. Racial segregation is a restricting agency, pruning variability; it is in phylogenetical sense not a creative agency. Goldschmidt (1933) defined this in saying concisely: "Geographische Variation ist weder eine Vorstufe noch ein Modell des Artbildungsvorganges".

Saltatory evolution appears, on the other hand, to be the common way in which form-making in plants takes place, and this can easily be observed from the still growing, important body of facts about chromosome numbers. Scanning these it is obvious that a very large number of species are polyploids, either autopolyploids or allopolyploids. Still more interesting is the fact that this increasing information shows within families the frequent occurrence of dysploid, aneuploid and allopolyploid numbers which are not seldom characteristic of genera of higher taxa. Genera can have allopolyploid genomes, as occurs e.g. in *Gossypium*.

Cultivated cotton is generally tetraploid (52 chromosomes), and is supposed to be an allotetraploid of *Gossypium arboreum* L. x *G. thurberi* Tod. (or some other Asian and American diploid species) (Brown, 1951). Note that the cultivated types are natural allotetraploids and that they behave as diploids. The product *arboreum* x *thurberi* is not quite similar.

Stebbins (1971: 179-201) emphasized the important creative role of polyploidy in Angiosperm phylogeny and concluded (*l.c.*: 198) that "extensive polyploidy must have taken place during the early evolution of woody Angiosperms. The most probable hypothesis, therefore, is that the polyploidy which gave rise to the basic numbers of woody plants took place at various times during the Cretaceous and the earliest part of the Tertiary Period, while the diversification of species on the basis of secondary basic numbers is largely a product of the Tertiary and Quaternary periods". He cited many examples of tropical taxa in this context and estimated that between one-fourth to one-third of the flowering plants are polyploid with reference to their nearest relatives.

In some families taxonomic affinities can thus be supported cytogeographically and attempts can be made towards a reasonable reconstruction. See for instance the most interesting papers on Australian Proteaceae by Johnson & Briggs (1963), on *Pomoideae* by Challice (1974), on the Casuarinaceae by Barlow (1959), the Loranthaceae by Barlow & Wiens (1971), the Oleaceae by Briggs (1970), and the Malvaceae by Bates (1968).

There are at least two processes by which chromosome changes are brought about, *viz.* hybridization (proved in many cases) and obviously irregularities in meiosis (translocation or 'centric fusion and fission', aneuploidy, duplication); there may be others.

The main point is, that major genomic rearrangements of the type quoted above, occur in a single generation, indubitable proof that saltatory form-making has been the major feature in plant evolution. See fig. 2.

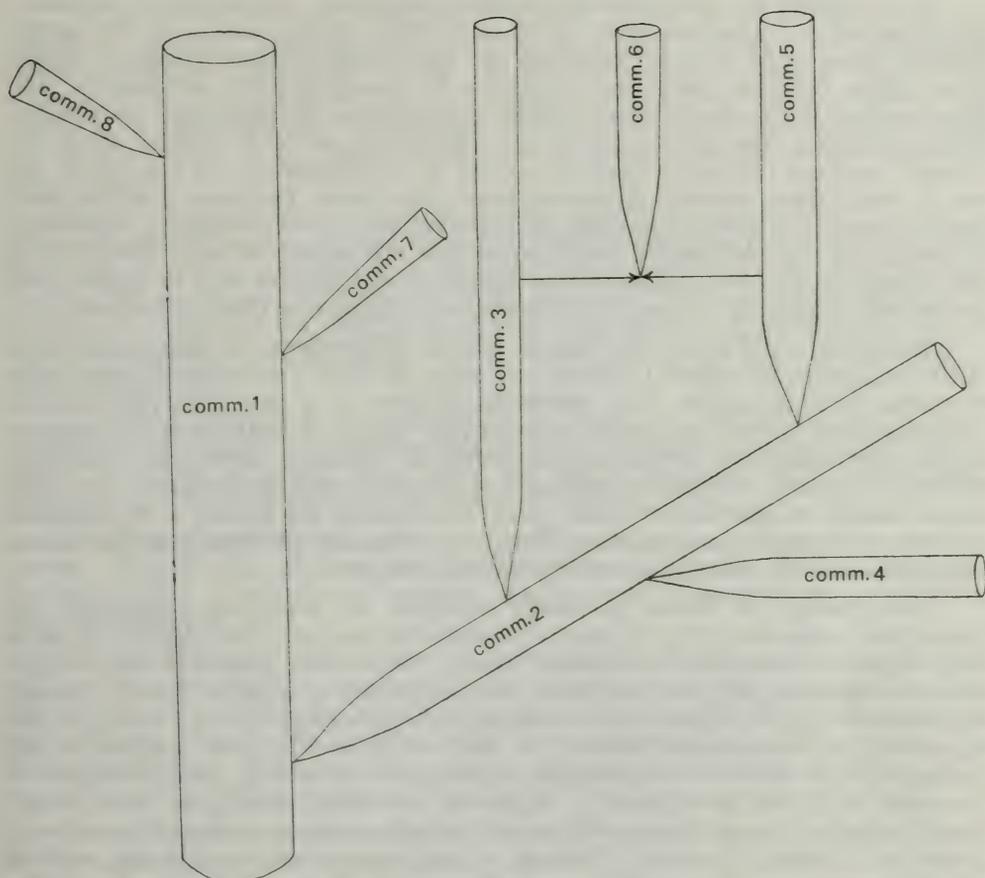


Fig. 2. Scheme of saltatory evolution in plants by individuals.

*Commiscuum 1* has produced the daughter *commiscua 2, 7, and 8*. *Commiscuum 2* has produced the daughter *commiscua 3, 4, and 5*.

*Commiscua 1, 7, and 8* show mutual affinity and so do *commiscua 2, 3, 4*.

*Commiscuum 6* is an allopolyploid between *commiscua 3 and 5*; it shows affinity with several other *commiscua* but is also an example of reticulate phylogeny.

Even though they may not become established at once, they certainly re-occur with a given probability and sooner or later will result in a population of individuals with novel characteristics. Thus, the idea seems justified that evolution in plants is largely of a saltatory type. For instance, polyploidy undoubtedly has been instrumental in many cases, in producing new forms. Some botanists claim that autopolyploids are side-products of evolution, being variations on a given level only, whereas evolutionary progress occurs on the diploid level. There is on the other hand no doubt that amphidiploid combinations are significant in evolution. More importantly, saltatory genomic changes in the diploid range are well-documented, especially in the genus *Clarkia* (Lewis, 1953).

In any case it appears that such evolutionary changes have nothing to do with competition pressure or selection of the fittests.

Naturally, the fit survives, the new plant arisen must come up to survival level and be able to germinate, grow, and propagate, but that is all there is to it, harmless extras are allowed.

It is admitted that not all families show an important array of ploidy variation, e.g. Pinaceae or Lauraceae seem to be exceptions. In the Lauraceae the family number seems to be  $x = 12$ , including the vegetatively aberrant parasitic, herbaceous genus *Cassytha*, according to Okada & Tanaka (1975). Incidentally, this number seems to be common in primitive Angiosperms. In such cases the number of chromosomes does not tell much, and information would be needed about the internal structure (chemical composition) of the chromosomes and also about the way in which these 'internal' differences have come about. The same should be said about genera in which the number of chromosomes is very constant; sometimes differences in size and shape already reveal this in a superficial way. The study of the genome architecture in plants is of course a most difficult field to explore and we are only beginning to enter it, for instance by measuring DNA hybridization.

Finally I would here also remark on the phenomena of teratological and neotenus forms, for which I refer to my essay of 1969. Teratological forms arise as sports all of a sudden. With teratological forms it is clear that physiological chain-reactions in plants have undergone change. Classes of terata so much resemble taxonomical characters (proliferation, antholysis, enations, cohesions, fasciation, laciniation, adesmy, reduction, petaloidy, scyphogeny, and ceratomania) that they cannot simply be ignored or waved away. Some terata are known to be inherited and due to a single gene mutation. Bringing terata and phylogeny in line means that they should be hereditary (see e.g. Stubbe, 1966).

The concept of terata is mostly accepted as something 'abnormal' or 'monstrous', and should be disposed of as meaning inferior. This appears to me a very superficial, emotional evaluation. Many evolutionary processes are brought about by reduction, suppression, fusion, etc.: a panicle of separate flowers changes into a head or fig, or is reduced to a raceme, or even a single flower; meristems are suppressed and contraction follows; or they are joined to other meristems and fusion follows (ovaries of *Morinda*; epiphyllous flowering; concaulescence in *Solanum*, etc.); leaf production is suppressed on twigs which grow into thorns; lateral branches do not develop inflorescences and are metamorphosed into curved hooks for climbing (*Uncaria*). There is no end to these metamorphoses, each of which represents an 'abnormality' or 'malformation' if compared with that of the immediate ancestor which did not possess the new structure. Thus the 'concept' of terata has a very definite structural meaning in biology, viz. a sudden change of structure which differs from the taxon from which it evolved.

Comparing trees of the *Naucleaeae* with the miserable *Uncaria*, a climbing plant, of which part of the flower-bearing side-branches are flowerless and deformed into curved hooks, the latter is an abnormality; but surely *Uncaria* has found its niche, proved its vitality and developed into quite a large genus. Considered unemotionally from a broad outlook, systematical teratologies are really hereditary teratologies.

Many of these changes are morphological reductions or suppressions, and that stamps them to belong to neotenus behaviour, that is: reaching maturity before all parts have developed as in the immediate ancestral form. Precocious flowering may turn a woody plant into a herb; precociously flowering herbs may be reduced to flower production on the cotyledons of the seedling (*Monophyllaea*).

For plant evolution I ascribe (1949, 1969) great importance to neoteny which I regard as one of the two crucial processes in their evolution. Takhtajan (1954) spoke of 'phylogenetic teratology' and correctly generalized and applied it to all contractions and reductions, as a vital element in form-making.

Systematical teratologies originated in all probability suddenly as saltations, in one or more steps and survived if they were viable in the sense that their ecological and reproductive capacity reached survival value, with their morphological caprices tolerated.

In contrast with the chromosome 'mutations' caused by hybridization or other mutative changes I have the conviction that important changes in morphogenesis might often have been caused by not too integral genetical changes. I derive this from the fact that fasciation (as in *Celosia cristata* L.) or pelorial flowers (as occur in Scrophulariaceae, Orchidaceae, etc.), which give a fundamental change to structure, seem to be based on presence or absence of one or very few vital genes only.

I once discussed with a famous botanist how he thought that a pitcher of *Nepenthes* might have originated. To my surprise he said that this might have been gradually built up, may be by a thousand gene mutations. Obviously he was ignorant of scyphogenous structures in the cultivated 'crotons', fancy varieties of *Codiaeum variegatum* (L.) Bl., in which the rough skeleton of a *Nepenthes* pitcher can be observed, the blade, tendril (naked midrib) and at the end a pitcher with an appendage (the lid).

If such a structure can be formed in a 'sport' of one known species, little imagination is necessary to assume the origin of a pitcher, through scyphogenous action, in a few saltatory steps. Once the initial step was made, autonomous perfection can be imagined in a few more orthogenetic steps.

Blocking of certain vital genes by mutation may cause development to follow another physiological pathway in the chain-processes leading to morphogenesis and production or reduction of proteins, hormones or other substances controlling form-development.

I have talked about this matter with geneticists, both on the matter of stability of structure and obviously responsible genome patterns on one hand, and sudden changes in a few vital genes on the other hand, but it seems that these seemingly contradictory phenomena cannot easily be translated in genetical terms of molecular biology. They find this a most complicated matter about which even generalized ideas of morphogenesis in genetical terms can not yet be given.

However unfortunate this may be, I hope the meaning of the arguments given above is clear. They lead to the following conclusions:

(i) In both major causes of evolution of plants, that is either changes in the gross chromosomal patterns (allopolyploidy, dysploidy, aneuploidy) or the physiological function changes of morphogenesis by neoteny, the changes are sudden, saltatory.

(ii) The saltatory steps are at least at species level, but higher categories, for instance genus level, may also be involved.

(iii) The conclusions given above imply that evolution of plant structure is essentially not caused by competition but is an autonomous process in which chance plays a distinct rôle.

(iv) For form-making the gradual accumulation of gene changes resulting into raiation may not be excluded as a cause of segregation of species but should be considered as of minor importance, while also their competition is not the overwhelming agency as frequently supposed.

In fig. 2 I have drawn a scheme reflecting the above considerations.

## 6. Gliding evolution in animals

As explained in the introduction the mechanism of evolution in animals must be much more complicated than in plants, as in addition to autonomous development in *patio ludens* at early stages it must include competition. As in most plants raiation in species populations easily occurs, sympatric and allopatric, the main difference with plants being that such raiation is largely a matter of competition partially for food and shelter, but with the additional agency of sexual selection,

which is absent in plants. Through these combined factors and competition racial segregation will in animals usually develop more rapidly than in plants. By this sexual selection partial populations drift apart and become in the practical sense incompatible, and thus a start is given to divergent development. In several cases it has been shown experimentally by artificial insemination that recognized good species of insects, which in nature keep strictly apart, are factually compatible. But through their isolation by sexual selection and then occupation of a specialized ecological niche they will finally drift apart, by populations, to such degree that they become incompatible genetically. Thus they start as *convivia* but gradually become *commiscua* and finally *comparia*, to stand on their own for future development. Mutations irrelevant to survival will be possible, but these will play a much smaller rôle than in plants as *patio ludens* in animals allows for much less free form development than in plants by predominant competition and sexual selection pressure: any new feature arising is 'tested' on its usefulness for competition. See fig. 3. The reader may recall that a prominent zoologist and geneticist, R. Goldschmidt, has put forward the idea that in the macro-evolution of animals, saltatory re-arrangements of the genome, and 'teratological' mutations "the hopeful monster") have been important. But there seems to be little evidence to support this concept.

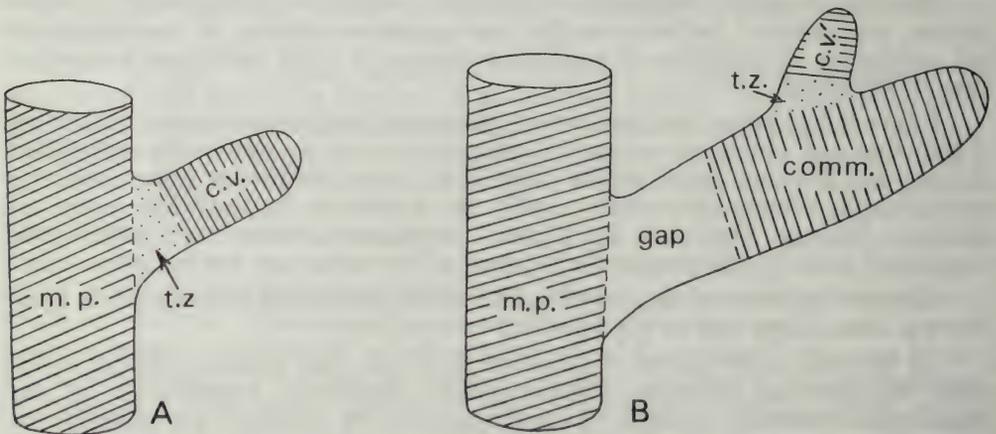


Fig. 3. Scheme of two initial stages of divergence in the gliding evolution of animals by populations.

A. A mother population (*m.p.*) starts to form a *convivium* (*c.v.*); it is still loosely connected and compatible with the mother population by a transition zone (*t.z.*) of rare miscibility.

B. In a further stage the *convivium* of fig. A has developed into a new independent *commiscuum* (*comm.*) which has become incompatible (indicated by a 'gap') with the mother population (*m.p.*). This new *commiscuum* is undergoing in its turn a similar differentiation and has formed a new *convivium* (*c.v.*) comparable to the scheme in fig. A.

The main conclusions on the differences of animal evolution as compared with plants appear to be fourfold:

(i) Evolution in animals will be gradual, through accumulation of competition/selection characters by 'gliding evolution', through separation of divergent populations, riation with practical incompability into *convivia* which gradually develop into truly incompatible *commiscua*, and finally into *comparia*.

(ii) Evolution of animals goes in general by populations and not by individual specimens as usual in plants.

(iii) There is little opportunity for *patio ludens* characters to develop, as all are tested on usefulness for competition and survival, and are subject to sexual selection which is unknown in plants.

(iv) Saltatory steps are not excluded, but they must be extremely rare in proportion to their frequent occurrence in plants.

In fig. 3 a scheme has been drawn reflecting these considerations.

### 7. Co-evolution of animals and plants

As I have emphasized in the first chapter plants were the first organisms of all organic evolution by their capacity of assimilation, capturing and storing energy. Animal life developed later, and never became independent. Food chains always have to go back on plant life.

Animals could in a broad sense be considered to lead a parasitic life; they browse and feed on plants which make their life possible.

Except for negligible exceptions plants play the passive rôle, and the organic matter they produce is at the disposal of animals which are specialized for taking advantage of anything they can find, even the most indigestible organic products. From this follows that plant evolution goes independent of animal evolution and that novelties arising in plants are secondarily exploited by animals. Notable exception: a large part of Angiosperm evolution has been aligned to pollination 'symbiosis' with animals.

Apart from the plant bodies themselves, used as food, animals are attracted to them by colours, scents, and obvious shelter. Evolutionists seem generally to assume that glands, floral and extra-floral, give competitive advantage to plants through the prowling animals. They have theorized that in such a way the competition/selection principle was forced on the plants, inducing plants to excrete more nectar or other substances, and thus induce numerical advantage over those which produced less, or less abundant, attraction to animals.

This is a very crucial problem indeed, and it seems difficult to prove or to disprove whether the assumption of this advantage is true or not, and that it worked under natural conditions.

For one thing, experiments lack of course the factor time. Even if it were proved that there was advantage to plants by animals this would mean that this assumed advantage would result into greater numbers of the plants (higher population density) which had the advantage. It is hard to believe, however, that this would mean extinction of those which offered less benefit. The latter would have a lower population density, but we can observe that precisely such a phenomenon is ubiquitous in the plant kingdom. In each genus certain species are rarer than others, but it would be a far-fetched idea that all the rare or rarer ones are nearer to, or nearing extinction. This is largely a matter of ecology, available niches, etc., not an immediate result of competition pressure: each species has its own ecology, including frequency of occurrence.

For another thing experiments never reflect the situation in nature. Imagine an experiment in which seeds of two allied species were sown together with the result that the seedlings of the one crowded out the other. Would it be conclusive to speak of higher competitive value and selection? It would certainly not be conclusive, except for the experimental conditions, the soil used, etc., and not for the varied conditions nature offers to the two, where such situations as in the experiment will hardly ever occur, and then only extremely locally, if ever. The very existence of the two species disproves already the assumption: in nature both occupy obviously their own particular ecology, otherwise one of the two would not exist.

Excretion in plants is mostly a physiological necessity. Dripping from hydathodes occurs when evaporation is insufficient: organic and mineral substances excreted in this way may serve animals. A similar reasoning could be held for excretions by glands.

Shelter is 'offered' by plants to animals, in many ways.

On the under-surface of leaves a fairly large number of woody plants develop domatia in the axils of the main nerves. The physiological function of these domatia is not known, according to Jacobs (1966), who published a classic paper on them. They do not excrete and are not glands; they appear often only when seedlings have reached a certain age. Their distribution in the plant kingdom is large but restricted; they have never been found in plants of arid countries. They were not infrequently termed '*acarodomatia*', derived from the observation that small arthropods seek shelter in these small cavities. It is proved that they originate irrespective of animal irritation and appear to be a whim of plant structure. The fact that animals exploit them as shelter means nothing special: animals will of course exploit anything they find favourable for their comfort and survival, animate or inanimate, just as primitive man would employ anything which he found useful or of advantage. Our urgent strife of locating useful things is of course not different from the same urge in animals. In fact we and the animals are completely possessed by this strife. But from a strictly detached point of view there is every reason to accept that domatia are an irrelevant structure in plants which is secondarily exploited by animals. That is, if we really want to detach ourselves from the inherent prejudice that all characters of animate nature must have some useful meaning.

I am of course by no means the first who ventilates criticism and in this context I want to refer to Bateson (1894: 12) who "undertook the study of adaptation as a test to the theory of natural selection and the hypothesis that there is a tendency for useful structures to be retained and for useless parts to be lost. We have no right to consider the utility of a structure demonstrated, in the sense that we may use this demonstration as evidence of the causes which have led to its existence. In absence of correct and final estimates of utility, we must never use the utility as a point of departure in considering the manner of its origin. It thus happens that we can only get an indefinite knowledge of adaptation, which is not an advance beyond the original knowledge that organisms are more or less adapted to their circumstances. No amount of evidence of the same kind will carry us beyond this point".

If we cannot perform this mental effort towards objectivity we will have to account for the presence of hairs, stipules, phyllotaxis, etc. etc. as well as for their absence in terms of utility. "No doubt", Bateson (1894: 79) says, "that ingenious persons would find ecological explanations of all these characters, for on this class of speculation the only limitations are those of the ingenuity of the author".

Various kinds of shelter are employed by ants in tropical plants. In these myrmecophilous plants the devices may be very simple, stem-appressed leaves of root-climbing plants (*Hoya*, *Dischidia*), reflexed appressed lowest pinnae of palm fronds (*Calamus* sp.), palm-sheaths (*Korthalsia*), appressed stipules, saccate domatia (several neotropical Melastomataceae, *Callicarpa saccata* van Steenis), but also pithy stems (*Cecropia*, *Endospermum* spp., *Clerodendrum fistulosum* Becc.) and pithy branches in a large number of Malesian trees of various families, the tendrils of one species of *Nepenthes*, and stipular thorns of *Acacia*, in which the pith is removed to shelter ant colonies. The most spectacular shelter is offered by the root tubers of the epiphytic rubiaceaceous genera *Myrmecodia*, *Hydnophytum* and some allied genera. These tubers have large labyrinth-like cavities inhabited by ant colonies where they tend fungal gardens as food.

There is a host of literature on this subject, a survey of which would fill a book in itself. The essential question turns round the adaptation theory of Beccari (1884-1886) and Schimper (1888) who advanced that such structures in plants arose by the mutual action of plants and animals to the advantage of both. And they tried to collect data to show the advantage of ants for plants. The latter evidence appears, however, very dubious indeed.

One crucial point has been cleared by Treub (1883) who showed that the cavities in the *Myrmecodia* tubers originate already in seedlings without any action of ants and excellent upgrowth follows without them. Whether these cavities have any ecological meaning to the plant is uncertain; they may physiologically serve for aeration or evaporation for regulation of temperature, but this has not been proved.

It is doubtful even, whether they are essential to the ants. We note in this context, that certain European ants build their nests around the base of plants, preferably Rosaceae and Umbelliferae, but they survive equally well without them.

It stands to reason, however, that in an objective view there is no necessity to assume co-evolution, if we advance that these structures would also have been developed by plants without any ants in existence. Why should not leaves be appressed to stems in root-climbers, stipules leave cavities, leaves have domatia, pinnae be reflexed, stems and thorns have pith, all representing structural developments *sui generis*?

Conversely, it is clear that if ants evolved and would find these structures, they would employ them and take full advantage. Some species might even become entirely dependent.

Plant structure evolves first and it is the animals which will adapt themselves and often will evolve to greater specialization. This principle applies to chemical differentiation as well.

It has sometimes been advanced that the supposed profit the plants would have from the ants would consist of protection against other predators, but this is proved to be a fallacy. For *Myrmecodia* the profit for the plant was supposed to consist in accumulating minerals etc. for growth, but there are many large woody epiphytes without ants showing that in this aspect epiphytes can well manage this themselves. Then it was advanced that for several other myrmecophytes the ants are attracted by their seeds with their oil-containing elaiosome, which seeds are deposited in their nests. This is true and may locally add to their frequency, but none of these ant plants is confined to ant nests and their seeds can germinate on any suitable bark.

It must be concluded that the co-evolution of ants and plants is only a one-sided evolution, namely for the ants.

I fully agree with von Ihering (1907: 710) who said that *Cecropia* needs its ants as much as a dog its fleas.

#### Evolution of orchids

The spectacular development of Orchidaceae is of course a classic of co-evolution. Leaving apart a fairly considerable number of orchids which are self-fertilizers or are cleistogamous, the majority is compulsory cross-fertilized by insects and this has led to most ingenious devices of the orchid labellum.

Systematically the queer fact is that in orchids so many generic hybrids are found, and that still more can be made by artificial insemination. The definite impression is that the whole of the family is genetically only one comparium with many commiscua, and that the species are usually convivia. They maintain their distinction by the grace of compulsory cross-pollination and the use of selected insect species to achieve that goal. Orchid evolution thus reflects insect evolution.

As soon as in the variability range of an orchid a deviation, differing only in a few genes presumably, occurs, it may be favoured with an insect form from the variability range of the latter's population and the two will consequently form a couple of consorts. This is the first step towards more specialized couples of orchid/insect.

Here again, however, the deviating plant structure comes first; if there is no suitable insect partner, it will probably succumb; if there is a more or less suitable partner attracted by colour, shape, scent, etc., within the range of variability of the insect population, the couple is formed and the new plant is saved and lives on by the grace of the pollinating insect. The latter is of course in no way dependent on the orchid for its survival.

It cannot be the reverse, as there can be no stimulant or inductive influence emanating from an insect causing a plant towards a gene combination which it wants to have. Plant structure comes first, animal adaptation may follow.

Though we conclude that thus evolution in orchids will have been effected in a gliding way, imitating that of animals, saltations may occur by hybridization. It is namely known that insects may, incidentally, make errors in pollination by which even intergeneric fertile hybrids may occur. Their offspring will in subsequent generations produce a host of new forms which may again start couples with other insects and consequently lead to further form-development.

This sudden occurrence of hybrids may be termed 'saltatory', but for the essential difference that the saltation is of a much lower status than that discussed for other plants, as all the offspring remains within the orchid comparium in a net of interfertility.

A further curious observation can be made in orchids, *viz.* that by a single other 'saltation' the orchid flower does not develop in the proverbial bisymmetrical way, but as a normal regular monocotyledonous flower. Such 'peloric' forms, of which I have formerly listed some from the tropics (1949: xli-xlii), are only recognizable vegetatively by comparison, otherwise they are unidentifiable, even by first-grade specialists.

Whereas pelorias are generally caused only by one or a very few gene changes, this tallies with the considerations above that obviously the most remarkable build-up of the orchid labellum may be a beautiful façade, but that it is genetically and hence, taxonomically, not such a stable component.

It shows also that few genes may, in cases, bring about a sudden radical change in morphogenesis.

#### Evolution of figs

The evolution of figs is a culmination point of co-evolution, as here the pollinating wasps have still more specialized relations with the plant in that also their life is bound to the figs in a most intimate way, a compulsory symbiosis. This is certainly not so with orchid insects, not even in the highly specialized cases of pseudo-copulation. Much of what I have said about the relations between orchids and insects will hold here too.

New forms of *Ficus* will arise and succeed if from the variability of the insect populations a more or less suitable mate is available. If it is available, adaptation of a new insect population will follow. Much of this evolution seems not to have been competitive. Evolution seems to have resulted from the "extremely gradual alteration of the *Ficus*-protoplasm" (Corner, 1961: 113). In this aspect it is noteworthy that all species of *Ficus* seem to have the same chromosome number,  $x = 13$ .

If this assumption is true it would theoretically follow that artificial insemination of closely allied species of figs would in all probability lead to fertile hybrids. I am not aware that such crucial, certainly difficult experiments have ever been carried out.

A conclusion on this chapter on co-evolution runs as follows:

(i) In a large number of situations attributed to co-evolution, evolution is primarily of the animals. Plant structures are utilized by animals for their benefit

and they specialize. The plant structures arose *sui generis* and not in so-called 'response' to animal agency.

(ii) Even in the vital association of insects and flowers in orchids and insects and figs in *Ficus* plants change (evolve) independently in an autonomous way and insects adapt themselves.

(iii) Speciation in orchids and figs imitates (follows) the gliding evolution as is usual in animals. Small changes accumulate in populations which diverge and gradually develop into races, subspecies and species respectively which in nature gain (ecological) isolation through the coupling with the particular insects. Insects are thus secondarily stimulated towards further evolution themselves.

(iv) Saltatory evolution in both groups, more especially in orchids, may occur incidentally through hybridization.

### 8. Reticulate phylogeny

I have termed this chapter reticulate phylogeny instead of reticulate affinity, because it concerns real ancestry which is meant here.

In general plant evolution through speciation will run divergent as in the branching mode of a tree, similarly as in animal evolution. Fig. 2.

There are, however, many instances known of allopolyploid species hybrids which are truly new species; they certainly in part share the characters of the two parent species but exhibit also new characters of their own.

By definition genetical contacts are prohibited between comparia. In plants a *comparium* is not rarely equivalent with a subgenus or genus, and as a rule species of different genera are incompatible and merging or exchange of genetical material is excluded.

However, exceptions occur, and there are several cases known where clearly through previous hybridization different generic genomes were blended through allopolyploidy. In the Cruciferae an allopolyploid generic hybrid was made between *Brassica* and *Raphanus*. Many genera are supposed to have originated in this way, e.g. *A Armoracia*, and certain allopolyploid species known in Gramineae from parents belonging to different genera, such as *Aegilops* and *Triticum*, *Agropyron* and *Elymus*, etc. As early as 1881 Focke mentioned generic hybrids from the families Amaryllidaceae, Cactaceae, Campanulaceae, Compositae, Ericaceae, Gesneriaceae, Rubiaceae, and Scrophulariaceae; others have been found since. This opens the possibility for allopolyploidy.

I would certainly not suggest that all cases of reticulate affinity, a phenomenon which occurs frequently in plants, should be deemed to be the result of reticulate phylogeny.

On the other hand I suppose that in very many cases allopolyploid genera and species have as yet not been recognized as such and my estimate is that there is a fair number of them.

Allopolyploid blending means that two divergent 'twigs' of the ancestral trees are joined which caused a local 'netting' of its 'canopy'. There is good reason to suppose that this 'intertwining' has also acted in the past during the ancestral development of the plant kingdom. See fig. 2.

I emphasize that these allopolyploids may be extremely important in plant evolution, as from them other types, aneuploid, dysploid, or polyploid, may have originated.

Compared with plants such reticulate phylogeny may be tacitly assumed to be in the great minority in animal evolution. This is quite obvious, because sexual selection will prohibit to no mean degree genetical contacts at the level of species

and genus. It makes it especially unlikely, or very rare, because in animals sexual behaviour, attraction and structure of the sexual organs play such an important rôle in the divergence of populations. Many 'experimental' specific and few generic hybrids are known, especially among insects, birds and mammals. But they are sterile as a rule, and even hybrids on a racial or sub-species level in the animal kingdom are very often sterile, a situation which is exceptional among plants.

### 9. Embryology and ontogeny

The fact that embryological and subsequent ontogenetic development in animals is so different from that in plants must have had evolutionary implications.

In animals the development of the embryo leads via metamorphoses, eventually alternated by larval generations, to the mature stage, but from the start it concerns the whole individual and its complete organization. This changes and grows and differentiates by a long series of internal structural transformations; it is a closed system. It is thus quite conceivable that for animals the subsequent stages in ontogeny can to a certain degree reflect the sequence of phylogenetic stages, as defined in Haeckel's principle or law of biogenetics. It can also be assumed that genetical changes may occur at all stages of this 'centripetal' development.

This is essentially different in plants where development is centrifugal and structure is proportionally so simple. Though the individual in *statu nascendi* is as the embryo contained in the seed coat, the internal development concerns only the development of the archegonium to a mature seed. There is no question of further internal transformation; it is an open system. Reserve food is stored either in albumen or cotyledons or both, but there is no reason to assume that either of the two is a reflection of ancestry in shape or otherwise. It should be admitted that a few ancestral characters e.g. primary vascularization, may be preserved as vestiges, as in plants all parts are end-products preserved thanks to the presence of cell-walls.

Also the first leaves above the cotyledons cannot be seen as reflecting ancestral shape. The ancestral, primitive shape of the leaf in Angiosperms is, as Corner (1954) has argued, in all probability the compound leaf, as still retained in many tree families as a primitive character, token of possible derivation from compound-leaved seed ferns. It is not impossible that also the seed ferns had seedlings with simple leaves and that the whole complex of vegetative upgrowth of seed fern ancestors is *grosso modo* retained in certain woody families of Angiosperms.

Under this point of view the simple leaf is among Angiosperms a derived stage. Such reduction should be considered as a manifestation of neoteny (see p. 116) by which principle is meant that the new form is simplified as compared with its ancestor at attaining the fertile stage. Neoteny causes ontogeny to be condensed; it is probably as frequent in plants as it is in animals.

The matter considered in this essay has lingered in my thoughts for many decades, in fact since I was a student and studied Carl von Naegeli's 'Mechanisch-physiologische Theorie der Abstammungslehre'. I realize very well that it will be provocative to those thinking in neo-Darwinistic terms.

For these reason I felt it not unnecessary to feed some ideas to the biological world in honour of Professor Corner as a token of my admiration for his immense achievement in botany from his studies in the tropics and his admirable attempts to pour new wine in old vessels of biological theory.

I feel much indebted to my friend and colleague, Prof. Dr. H. Gloor, Geneva, for improvement of the text.

## References

- BARLOW, B. A. 1959. Chromosome numbers in the Casuarinaceae. *Aust. J. Bot.* **7**: 230–250, 1 pl.
- BARLOW, B. A. & D. WIENS. 1971. The cyto geography of the Loranthaceous mistletoes. *Taxon* **20**: 291–312, 14 fig.
- BATES, D. M. 1968. Generic relationships in the Malvaceae, tribe Malveae. *Gentes Herb.* **10**: 117–135, 1 tab.
- BATESON, W. 1894. Materials for the study of variation treated with special regard to discontinuity in the origin of species. 598 pp. Macmillan, London.
- BECCARI, O. 1884–1886. Piante ospitatrici, ossia piante formicarie della Malesia et della Papuasie descritte ed illustrate da O. Beccari. *Malesia* **2**: 1–284, 54 tab. Genova.
- BRIGGS, B. 1970. Some chromosome numbers in the Oleaceae. *Contr. N.S.W. natn. Herb.* **4**: 126–129, 5 fig., 1 tab.
- BROWN, M. S. 1951. The spontaneous occurrence of amphiploidy in species hybrids of *Gossypium*. *Evolution* **5**: 25–41.
- CHALLICE, J. S. 1974. Rosaceae chemotaxonomy and the origins of the Pomoideae. *Bot. J. Linn. Soc.* **69**: 239–259.
- CORNER, E. J. H. 1954. The Durian Theory extended. II. The arillate fruit and the compound leaf. *Phytomorphology* **4**: 152–165.
- 1961. Evolution. In: A. M. McLeod & L. S. Copley (eds), *Contemporary Botanical Thought*: 95–114, Oliver & Boyd, Edinburgh.
- DANSER, B. H. 1929. Ueber die Begriffe Komparium, Kommiscuum and Konvium und ueber die Entstehungsweise der Konviven. *Genetica* **11**: 399–450.
- FOCKE, W. O. 1881. Die Pflanzenmischlinge. 569 pp., Berlin.
- GOLDSCHMIDT, R. 1933. Some aspects of evolution. *Science, n.s.* **78**: 539–547.
- HOOKE, J. D. 1859. On the flora of Australia, its origin, affinities and distribution. *Bot. Antarct. Exp.* pt III, Fl. Tasman. vol. **1**: i–cxxxviii.
- IHERING, H. von. 1907. Die Cecropien und ihre Schutzameisen. *Bot. Jb.* **39**: 666–714, t. 6–9.
- JACOBS, M. 1966. On domatia — The viewpoints and some facts. *Proc. Kon. Ned. Ak. Wet. C* **69**: 275–316.
- JOHNSON, L. A. S. & B. G. BRIGGS. 1963. Evolution in Proteaceae. *Aust. J. Bot.* **11**: 21–61.
- LEWIS, H. 1953. The mechanism of evolution in the genus *Clarkia*. *Evolution* **7**: 1–20.
- OKADA, H. & R. TANAKA. 1975. Karyological studies in some species of Lauraceae. *Taxon* **24**: 271–280, 10 fig.
- QUISPEL, A. 1968. Pre-biological evolution. *Acta biotheor.* **18**: 291–315.
- SCHIMPER, A. F. W. 1888. Die Wechselbeziehungen zwischen Pflanzen und Ameisen im tropischen Amerika. *Bot. Mitt. Trop.* **1**: 95 pp.

- SMITH, A. C. 1973. Angiosperm evolution and the relationship of the floras of Africa and America. In: B. J. Meggers, c.s. (eds), Tropical forest ecosystems in Africa and South America. Smiths. Inst. Press, Washington, DC.: 49-65.
- STEBBINS, G. L. 1971. Chromosomal evolution in higher plants. 216 pp. Arnold, London.
- STEENIS, C. G. G. J. van. 1949. General considerations. *Fl. Malesiana* 1, 4: xiii-lxix.
- 1957. Specific and infraspecific delimitation. *Fl. Malesiana* 1, 4: clxvii-ccxxxiv.
- 1969. Plant speciation in Malesia with special reference to the theory of non-adaptative, saltatory evolution. *Biol. J. Linn. Soc.* 1: 97-133.
- STUBBE, H. 1966. Genetik und Zytologie von *Antirrhinum* L. sect. *Antirrhinum*.
- TAKHTAJAN, A. L. 1954. Essays on the evolutionary morphology of plants. Amer. Inst. Biol. Sc. Washington, D.C. (English transl., 1959): 139 pp.
- THOMAS, H. HAMSHAW. 1961. The evolution of Angiosperms. *Proc. Linn. Soc.* 172: 1-6.
- TREUB, M. 1883. Sur le *Myrmecodia echinata*. *Ann. Jard. bot. Buitenzorg* 3: 129-159, pl. 20-24.

## On Speciation in the Humid Tropics: some new data

by

ANDREY A. FEDOROV

*Komarov Botanical Institute, Leningrad*

During the author's travels to Sri Lanka (Ceylon) and to Indonesia and, particularly, in the course of his examination of herbaria and botanical iconography pertaining to Dipterocarpaceae (see Foxworthy, 1927, 1932; Van Slooten, 1932, 1940, 1941, 1942, 1952; Symington, 1943; Ashton, 1962, 1964, 1967, 1969) he has already established many facts elucidating speciation in the humid tropics on the basis of the Law of Homologous Series in Hereditary Variation discovered as early as the beginning of this century by N. I. Vavilov (1920, 1922), elaborated by him somewhat later (1930, 1935) and subsequently by his numerous collaborators and pupils.

As is well known, Vavilov established this law mainly in the course of his studies on cultivated plants, his attention being attracted by their infraspecific diversity. But Vavilov had no opportunity to observe this phenomenon in a sufficiently large number of species of wild plants, nor those belonging to perfectly homologous genera.

Vavilov was sure that no homologous series of hereditary variation had been discovered in our wild holarctic genera and species merely because, in this respect, they had been extremely poorly studied.

In the Holarctic it is difficult to find homologous variation not only at the specific level, but at the infraspecific level as well. Many wild species occurring there appear to be surprisingly homogeneous. The cause of the apparent homogeneity is associated with their heterozygosity as has been pointed out by Vavilov himself (Vavilov, 1936, pp. 78-79) with cross-pollination, with the latent state of their recessive characters. However, the latent diversity of characters can be made apparent by means of compulsory self-pollination, or inbreeding. This fact is well known by all the geneticists and plant breeders.

Besides the actual homogeneity there is a delusive homogeneity. A conviction is very widespread among taxonomists about the perfect homogeneity of many widespread species over vast areas. The reason is that many botanists work mainly with herbarium material. The uniformity of herbarium specimens, sometimes accumulated in large numbers can be explained by the fact that many collectors involuntarily discarded specimens inconvenient on account of their dimensions or some other characteristics and thus made collections of standard specimens suitable for drying and mounting on standard sheets of herbarium paper.

As I know, tropical herbaria differ in this respect from holarctic ones. It is difficult to sort out series of standard samples in the tropics, even though the desire to do it be very keen, since many species, particularly large trees are so sparsely scattered in a tropical forest, that sometimes herbaria contain only their type or isotype specimens. This precludes the possibility of revealing infraspecific systems of hereditary forms in these plants by means of sheer observation even if they actually exist in nature.

There are at least a few genera of plants indigenous to the northern part of the Holarctic in which homologous series are observed not *within* species but

among the species of the given genus. Such are the genera *Verbascum* and *Celsia* (Scrophulariaceae) and *Astragalus* and *Oxytropis* (Leguminosae). It is true that here the taxonomic delimitation of these genera is not perfectly reliable, however.

The state of affairs in the humid tropics is very interesting. I venture to assert that, within the family Dipterocarpaceae, almost all the representatives of which are confined to tropical rain forests of Southern and South-Eastern Asia, the law of homologous series is conspicuous in all the genera and numerous species belonging to this family, including the monotypic genus *Upuna*, the single species of which, *U. borneensis*, also exhibits homology, at least in the leaf structure, as do the species of the other genera of this family.

It should be pointed out that Vavilov anticipated all this on the basis of his theoretical considerations with respect to plant taxa of almost any rank, having emphasized the universal significance of the law he had formulated, but practically he had no opportunity himself to encounter such interesting material for investigation as the Dipterocarpaceae.

The genetic affinity of the genera of Dipterocarpaceae is so close, that almost all the characters pertaining to the shape and structure of leaves, fruits and other organs and parts are subjected to homologous variation except the main generic characters felicitously designated by Vavilov as "generic radicals".

It is only the existence of such radicals, sometimes not quite distinct and also transgressive (e.g. genera *Shorea*, *Hopea*, *Doona*) that made it possible to classify the Dipterocarpaceae family, comprising a total of up to 580 species, into 15 genera.

Owing to the indistinctness of certain generic radicals (or, more precisely, unsuccessfully distinguished genera) taxonomists classifying Dipterocarpaceae were compelled to reduce to synonyms certain taxa described earlier at the rank of genus. Thus disappeared such generic names as *Pachynocarpus*, *Richetia* and some others.

When I am writing about the family Dipterocarpaceae, I have in mind only its Asiatic subfamily *Dipterocarpoideae* comprising the greatest number of genera and species, leaving aside for the time being the African subfamily *Monotoideae* (48 species of the genus *Monotes* and 4 species of the genus *Marquesia*), since I have not the necessary material at my disposal. The law of homologous series is manifest within the Dipterocarpaceae with the utmost distinctness and cogency in the first place in consequence of the numbers of species in many of its genera (see Ashton, 1964; Willis, 1966).

<i>Shorea</i> ... ..	180	<i>Doona</i> ... ..	11
<i>Hopea</i> (including <i>Balanocarpus</i> ) ...	90	<i>Parashorea</i> ... ..	11
<i>Dipterocarpus</i> ... ..	76	<i>Dryobalanops</i> ... ..	9
<i>Vatica</i> ... ..	76	<i>Cotylelobium</i> ... ..	5
<i>Vateria</i> (incl. <i>Stemonoporus</i> ) ...	21	<i>Pentacme</i> ... ..	3
<i>Anisoptera</i> ... ..	13	<i>Monoporandra</i> ... ..	2
<i>Upuna</i> ... ..	1		

If all these genera of Dipterocarpaceae were arranged in a table following the sample of similar tables presented in Vavilov's works, it would at once become obvious that with respect to all the characters (studied up to the present time) species within each genus form homologous series.

The table does not show the combinations of characters of particular species, but only lists individual characters and their occurrence in the genera. Furthermore, they are only the most conspicuous ones, revealed either from herbarium material or from drawings published in the botanical literature. Many characters,

such as the leaf pubescence, the details of venation etc., are still to be studied. It is important to point out, that the characters of many species presented in the table were observed in isotype specimens a fairly great abundance of which is available in the Herbarium (LE) of the Komarov Botanical Institute of the Academy of Sciences of the USSR in Leningrad. The numbers of isotype specimens found there are 30, 15, 22, 13, 12, 5, 8, 3, 2, 3 and 2 for the genera *Shorea*, *Hopea*, *Dipterocarpus*, *Vatica*, *Vateria* (= *Stemonoporus*), *Anisoptera*, *Doona*, *Parashorea*, *Dryobalanops*, *Cotylelobium* and *Monoporandra* respectively. This is some guarantee against errors in the identification of numerous other specimens deposited in the Herbarium as 'ordinary' specimens and examined in the course of my investigations.

The table, the principle of composition of which is described here does not, of course, deal with the infraspecific homologous variation as yet unstudied at all in the representatives of the Dipterocarpaceae. My purpose was to demonstrate homologous series of species within genera, which in their turn are also homologous to the same extent. Thus, I do not merely repeat what has been done by Vavilov, but, as far as possible, endeavour to develop his theory.

Homologous characters are given in Latin terminology. The best illustrations of these characters might have been the drawings or photos, but, unfortunately they would have been too numerous and there would not be enough place for all of them in the table.

Unfortunately the names of the examined species not indicated are omitted but I hope I shall be able to add them in the very near future in a separate paper.

Similar to infraspecific systems of the forms of cultivated plants studied by N. I. Vavilov, the homologous characters in species belonging to the genera of Dipterocarpaceae exhibit in many cases independence of other characters, but in approximately 50% of species a rather distinct correlation is observed; for instance, between the characters of leaves on the one hand and, on the other the characters of fruits, with respect to their general similarity of appearance in the first place, and to their equal relative and absolute dimensions as well.

Being perfectly aware of the significance of the law he formulated, Vavilov quoted the remarkable, indeed prophetic, words of de Candolle (A. de Candolle, 1888, *La Phytographie*, p. 80) who wrote, that a day will come, when science will interpret the elements of a species as the elements of a genus, as the elements of a family, and all these groups will be coordinated according to a definite uniform system. Vavilov was perfectly justified in his conclusion: "This day has come" (Vavilov, 1936, p. 79).

The tropical family of arborescent plants, Dipterocarpaceae, is a good illustration for the ideas of Alphonse de Candolle and Nikolay Ivanovich Vavilov. All the taxonomic ranks of this family follow the law of homologous series that is common for all plants and, in fact, for all organisms. The genera of the Dipterocarpaceae are so closely allied to one another, that they can be regarded as initial species, as it were, evolved up to the generic level.

Thus, it is not only the infraspecific systems of hereditary forms of cereals, legumes, Cucurbitaceae and other cultivated plants, but also the species of gigantic tropical trees belonging to the Dipterocarpaceae that form homologous series. As it is illustrated by the example of this family, the Law of Homologous series in Hereditary Variation is directly associated not only with the initiation of new forms within a species as in the case of cultivated plants, where the action of the natural selection is superseded by artificial selection and where many forms and varieties of plants therefore have good chances for survival but also with speciation.

The obvious fact of the abundance of species characteristic of the genera of Dipterocarpoideae, particularly, of such genera as *Shorea*, *Hopea*, *Dipterocarpus*

and *Vatica* almost confined to the tropical rain forests of Southern and South-Eastern Asia should be explained.

Earlier I assumed (Fedorov, 1966) and this provoked some criticisms in the botanical literature (see Van Steenis, 1969, pp. 108-109; Ashton, 1969) that in a tropical rain forest the abundance and diversity of species within many genera and families of trees is explained by the fact that their natural selection does not eliminate indifferent characters; these characters remain in the populations, their frequency being governed by genetic drift. Of these forms possessing such characters, those having the rank of species survive. As it becomes clear at present, the possibility of initiation of such characters is afforded by the law of homologous series: being indifferent, they are homologous to the corresponding characters that are useful in certain closely allied forms. Despite the abovementioned criticisms of my views, I am still convinced, that if the speciation in the humid tropics was accomplished only by means of natural selection, without participation of genetic drift, there too, similarly to the northern zone of the Holarctic, each genus of wild plants would be represented by fragmentary group of species that would not form any perceptible homologous series.

One of the good examples of parallel (according to my concept, homologous) series, probably also formed by genotypic factors, within subgenera and other infrageneric taxa of the tropical genus *Ficus* having an extremely wide range (comprising about 900 species) is pointed out by E. J. H. Corner (1959, pp. 106-108), who designated this phenomenon, after Darwin, parallel evolution. Here the characters pertaining to the form of inflorescences and their position on a shoot are subjected to parallel (homologous) variation, as well as ramiflory and cauliflory and also geocarpy. The forms of growth or life forms in the subgenera of the genus *Ficus* also exhibit parallel (homologous) variation manifested in all the types from pachycaul trees to leptocaul trees. Epiphytic species of *Ficus* occur in at least three series. Creeping forms occur in five series in various combinations with epiphytic. Still more diverse are the homologous forms pertaining to the structure and venation of leaves, as well as to their size, both relative and absolute. Corner (*l.c.*) emphasizes that there can be no doubt in the convergent origin of all these forms, since parallel (homologous) species of different genera differ distinctly from one another in the structure of flowers, by the characters of which the main taxonomic subdivisions of the genus *Ficus* are delimited.

Corner makes an important reservation, that for instance, the case of a parallel (homologous) appearance of species of the genus *Ficus* with narrow leaves resembling the leaves of willow occur in the groups of the genus *Ficus* indigenous to different phytogeographical regions (Corner, 1961, p. 108; Corner, 1967, p. 33).

The same phenomenon in different families of tropical plants had already been mentioned by C. G. G. J. van Steenis (1948-1954, pp. LVII-LVIII).

As yet the mechanism of the origin of homologous series in different genera and families of plants in the humid tropics is not quite clear. The assumption that it is to a great extent based on mutagenesis leading to genotypic changes is quite justified, although, undoubtedly, many specific examples can also be phenotypic. Since allied species possess homologous characters, it is most probable that the genes responsible for these characters are also homologous or even identical at least within the same family. It was Vavilov himself (Vavilov *l.c.*) who referred to the facts of induction of artificial mutations in species of *Drosophila* that followed the law of homologous series.

Recombinations resulting from hybridization, serving, like mutations, as it were as raw material for natural selection, hardly played any significant role in speciation with respect to tropical trees, since hybrids occur rarely here (see Van

Steenis, 1969, p. 111). Chromosome numbers, for example, in different genera of the family Dipterocarpaceae, the object of my interest, in many cases prove to be the same. In most species of the genus *Dipterocarpus* studied (as yet not many) the prevailing chromosome number is  $2n = 20$  (see Fedorov, ed. 1969, p. 262; Moore, ed. 1973, p. 274).

Corner (1954, pp. 33-34) was the first to assume that selfpollination prevails in the trees of tropical rain forests. Later I advanced a similar hypothesis (Fedorov, 1966) although I overlooked Corner's priority. Quite recently, as the result of the investigations of Bawa (1974), as well as of Bawa and Opler (1975) various types of pollination became known for both the tropical and temperate regions. By the way, it was revealed, that many trees apparently having bisexual flowers are actually dioecious in many cases, since either gynoeceum or androeceum prove to be underdeveloped, or their development proves to be asynchronous. Other details of the "reproductive biology" as it is designated by these authors and Ashton have been elucidated. Ashton quite recently published (Ashton, 1975, p. 109) an abstract of a paper on the existence, in tropical rain forest trees, of both panmixis and apomixis. It should be pointed out, that all the details of these phenomena in Tropics are as yet insufficiently studied by far, but only one fact, but a most the important one, should be apparently recognized to be beyond doubt: interspecific hybridization is a very rare event in tropical rain forests.

Nature itself has established many almost insuperable obstacles to spontaneous hybridization between species of tropical trees which would lead to heterozygosity. This fact was mentioned in my earlier paper (Fedorov, 1966). The difficulty of such hybridization is, in the first place, the consequence of non-coincidence of the time of flowering, particularly, in the equatorial zone where there are no seasons of the year. This non-coincidence is observed even among individuals belonging to the same species, let alone those belonging to different species; another obstacle is the prolonged and irregular period of sterility, sometimes lasting for several years, then the low population density of many species, up to almost perfect dissociation of separate individuals of these species, i.e. their spatial isolation, and also biotic isolation and, in general, the diversity of biological niches.

The survival of a large number of species belonging to the genera of Dipterocarpaceae and their resistance to the pressure of natural selection can be explained by the early development of isolation from one another of the most diverse types. This problem was successfully studied by P. W. Richards (1969, pp. 149-153) and by F. R. Fosberg, who delivered a paper on this topic at one of the symposia of the XIth International Botanical Congress held in Seattle (Fosberg, 1969, p. 62).

Th. G. Dobzhansky (1950, pp. 219-221), in his study especially devoted to the problem of evolution in the tropics, correctly emphasizes, that in the temperate and in the cold zones such elementary factors as the sufficient or insufficient quantity of food and the degree of resistance to low winter temperatures played the most important rôle in the process of natural selection. In the humid tropics the interrelations with the environment are more complicated; its requirements are more refined, while the response of organisms is more diverse and complicated; the rôle of the biotic environment is significantly more important, than in temperate and cold regions.

Polyploidy, apparently, also played a certain role in the speciation in tropical trees. At least polyploids have been found in some species belonging to the families Leguminosae, Simaroubaceae, Meliaceae, Anacardiaceae, Sapindaceae, Bombacaceae, Sterculiaceae and to some other families, represented in the flora of tropical semideciduous forests of Costa Rica (Bawa, 1973, pp. 422-434). However, polyploid series are very rare in these cases.

The counts of chromosome numbers in species belonging to the genera of Dipterocarpaceae were commenced only quite recently. Chromosome numbers have been determined for only thirty species (see Fedorov, ed. 1969, p. 262; Moore, ed. 1973, p. 274). If it is remembered that this family comprises 580 species, it would be clear, that any conclusions concerning the rôle of polyploidy in the evolution of this family would be as yet premature. Nevertheless, the prevailing chromosome number being  $2n = 20$  (genus *Dipterocarpus*), cases have already been recorded of diverse numbers in certain species of the genus *Shorea*, where the chromosome number is  $2n = 14$  or  $28$ . There are cases when  $2n = 12$  (*Pentacme*), while in the genus *Dipterocarpus* rarely occur species with  $2n = 30$ . The main "x" numbers in different genera of the family are probably close to 5-7-11.

It is possible to interpret from a new point of view the phenomenon of convergence, which is very conspicuous and widespread in the trees of a tropical rain forest. This convergence pertains to the shape of leaves, inflorescences and other parts of plants belonging to different genera and families, particularly in the tropical Lauraceae, Annonaceae, Sapotaceae, Fagaceae and many others. This convergence is adaptive, but probably it is based on the law of homologous series in hereditary variation as dealt with in this paper.

Homologous characters		Genera Dipterocarpacearum											
		1	2	3	4	5	6	7	8	9	10	11	12
		<i>Shorea</i>	<i>Hopea</i>	<i>Dipterocarpus</i>	<i>Vatica</i>	<i>Vateria</i>	<i>Anisoptera</i>	<i>Doona</i>	<i>Parashorea</i>	<i>Dryobalanops</i>	<i>Cotylelobium</i>	<i>Pentacme</i>	<i>Monoporandra</i>
1	Folia late-elliptica vix acuminata, obtusa vel retusa ca 20 cm. longa et 15 cm. lata	+	+	+	+	+			+				
2	Praeced. similia, ca 10-15 cm. longa et 5-7 cm. lata	+	+	+	+	+	+	+		+	+		
3	Praeced. similia, ca 5-10 cm. longa et 3-5 cm. lata	+	+	+	+	+	+						
4	Folia oblongo-elliptica vix acuminata, ca 25-35 cm. longa et 10-15 cm. lata	+	+	+	+	+		+					
5	Praeced. similia, ca 10-15 cm. longa et 3-7 cm. lata	+	+	+	+		+	+		+	+		

Homologous characters		Genera Dipterocarpacearum											
		1	2	3	4	5	6	7	8	9	10	11	12
		Shorea	Hopea	Dipterocarpus	Vatica	Vateria	Anisoptera	Doona	Parashorea	Dryobalanops	Cotylelobium	Pentacme	Monoporandra
6	Folia late-ovata acuminata, ca 10-15 cm. longa et 6-8 cm. lata	+	+	+									
7	Praeced. similia, ca 5-10 cm. longa et 3-7 cm. lata	+	+	+	+			+	+				
8	Folia obovata vix acuminata, 10-20 cm. longa et 5-6 cm. lata	+		+	+	+							
9	Praeced. similia, ca 3 cm. longa et 2 cm. lata	+		+	+								
10	Folia obovata obtusa, ca 4.5 cm. longa et 3 cm. lata	+		+	+	+							
11	Folia rotunda obtusa, ca 15 cm. longa et lata			+									
12	Folia rotunda vix acuminata, ca 15 cm. longa et lata	+		+									
13	Folia fere rotunda vix acuminata, ca 3 cm. longa et 2.8 cm. lata		+										
14	Folia late lanceolata acuminata, ca 20 cm. longa et 5 cm. lata	+	+		+	+							
15	Praeced. similia, ca 7 cm. longa et 4 cm. lata	+	+		+			+		+			
16	Folia elliptica apice caudata, ca 7 cm. longa et 3 cm. lata	+	+		+	+		+		+			+

Homologous characters		Genera Dipterocarpacearum											
		1	2	3	4	5	6	7	8	9	10	11	12
		Shorea	Hopea	Dipterocarpus	Vatica	Vateria	Anisoptera	Doona	Parashorea	Dryobalanops	Cotylelobium	Pentacme	Monoporandra
17	Praeced. similia, ca 6 cm. longa et 2-3 cm. lata		+		+	+		+					
18	Folia late ovata apice caudata, ca 6 cm. longa et 2.5-3 cm. lata		+		+	+		+		+			
19	Folia oblanceolata obtusa, ca 10-15 cm. longa et 4.5 cm. lata				+		+						
20	Praeced. similia, ca 3-5 cm. longa et 1-3 cm. lata	+											
21	Folia basi subcordata	+				+						+	
22	Folia basi truncata	+	+	+	+	+	+			+			
23	Folia basi rotundata	+		+								+	
24	Folia basi cuneata	+	+	+									
25	Lamina foliorum omnino glabra	+	+	+	+	+	+	+	+	+	+		
26	Lamina foliorum plusminusve pilosa, tomentosa vel hirsuta	+		+	+			+					
27	Fructus magni, ca 10-15 cm. longi	+		+			+		+	+			
28	Fructus mediocres, ca 5-7 cm. longi	+	+	+	+		+	+	+	+	+		
29	Fructus parvi, ca 2-3 cm. longi	+	+	+	+			+	+	+	+		
30	Calycis lobi post anthesin accrescentes	+	+	+	+	+	+	+	+	+	+	+	+
31	Calycis lobi abbreviati, fructus globosi	+	+	+	+	+			+	+			

## References

- ASHTON P. S. 1962. Some New Dipterocarpaceae from Borneo. *Gdns' Bull., Singapore* **19**: 253-319.
- 1964. Manual of the Dipterocarp trees of Brunei State. Univ. Press, Oxford.
- 1967. Taxonomic notes on Bornean Dipterocarpaceae, 3. *Gdns' Bull., Singapore* **22**: 259-352.
- 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biol. J. Linn. Soc.* **1**: 155-196.
- 1975. The reproductive biology of some rain forest trees and their evolution. Abstract of the paper presented at the XII Internat. Botan. Congress, Leningrad.
- BAWA K. S. 1973. Chromosome numbers of tree species of a lowland tropical community. *J. Arnold Arbor.* **54**: 422-434.
- 1974. Breeding Systems of the species of a lowland tropical community. *Evolution* **28**: 85-92.
- P. A. OPLER. 1975. Dioecism in tropical forest trees. *Evolution* **29**: 167-179.
- CORNER E. J. H. 1954. The evolution of tropical forest. In: J. Huxley, A. C. Hardy, and E. B. Ford (eds.). *Evolution as a process*. Allen & Unwin, London.
- 1961. Evolution. In: A. M. McLeod and L. S. Copley, *Contemporary botanical thought*. Oliver & Boyd, Edinburgh.
- 1967. Ficus in the Solomon Islands and its bearing on the post-Jurassic history of Melanesia. *Phil. Trans. R. Soc. Lond. B.* **253**: 23-159.
- DOBZHANSKY, Th. 1950. Evolution in the Tropics. *Am. Scient.* **38**: 209-221.
- FEDOROV, An. A. 1966. The Structure of the tropical rain forest and speciation in the humid tropics. *J. Ecol.* **54**: 1-11.
- 1969. (Ed.). Chromosome numbers of flowering plants. Leningrad.
- FOSBERG, F. R. 1969. The problem of isolation in the lowland tropical rain forest. Abstracts of the papers presented at the XI Intern. Botan. Congress, Seattle.
- FOXWORTHY, F. W. 1927. Commercial Timber Trees of the Malay Peninsula. *Malayan Forest Records* **3**.
- 1932. Dipterocarpaceae of the Malay Peninsula. *Malayan Forest Records* **10**.
- MOORE, R. J. 1973. (Ed.). Index to plant chromosome numbers 1967-1971. I.B.P.T., Utrecht.
- RICHARDS, P. W. 1969. Speciation in the tropical rain forest and the concept of the niche. *Biol. J. Linn. Soc.* **1**: 149-153.
- SLOOTEN, D. F. Van 1932. The Dipterocarpaceae of the Dutch East Indies, 6. The genus *Dryobalanops*. *Bull. Jard. bot. Buitenzorg Ser. 3*, **12**: 1-45.

- 1940-1949. Sertulum Dipterocarpacearum Malayensium I, II, III, IV. *Bull. Jard. bot. Buitenzorg*, Ser. 3, **16**: 430-454 (1940); *Ibid.* **17**: 96-138 (1941); *Ibid.*, **17**: 220-225 (1942); *Ibid.* **18**: 229-269 (1949).
- (1952). Sertulum Dipterocarpacearum Malayensium 5. *Reinwardtia*, **2**: 1-68.
- STEENIS, C. G. G. J. Van 1948-1954. *Flora Malesiana*, Ser. 1, **4**.
- 1969. Plant speciation in Malesia, with special reference to the theory of non-adaptive saltatory evolution. *Biol. J. Linn. Soc.* **1**: 97-133.
- SYMINGTON, C. F. 1943. Foresters' manual of Dipterocarps. *Malayan Forest Records* **16**.
- VAVILOV, N. I. 1920-1935. The law of homologous series in variation (in Russian). Saratov (1920). *Idem* in *J. Genet.* **12** (1) (1922). *Idem* in Theoretical basis of plant selection, **1** (1) (in Russian). Revised and enlarged edition by the author (1935).
- 1930. Linnean species as a system (in Russian). *Trudy po prikladoni botanike, genetike i seleksii* **26** (3).
- WILLIS J. C. 1966. A Dictionary of the Flowering Plants and Ferns, 7th edition. Revised by H. K. Airy Shaw. Univ. Press, Cambridge.

# The Morphology and Systematics of *Pandanus* Today (Pandanaceae)\*

by

BENJAMIN C. STONE

Department of Botany, University of Malaya, Kuala Lumpur,  
Malaysia

## Summary

More than 500 species of *Pandanus* are now known, and 70% of these have been described since 1900, nearly half since 1939, and new ones are being discovered. Many obstacles have prevented the completion of a monograph (dioecism, large structures, remote locales) but perhaps the most serious has been ignorance of morphology and morphogenesis. Studies of these are thus of critical importance. Micromorphological-anatomical data and cytotaxonomic data have recently become available, permitting data integration not previously possible. This has resulted in a new detailed infrageneric classification which can contribute to understanding of the phylogeny. This classification recognizes 8 subgenera, 62 sections, and 22 subsections covering 468 species and numerous synonyms. Chromosome numbers are  $2n = 60$  (1 species of *Pandanus*, *P. spiralis* R. Br., has  $2n = c. 120$ ). Remarkable stomate variability is tied almost exclusively to systematic relationship.

## I. Introduction

The Pandanaceae is a family now generally conceded to be the sole member of the Order Pandanales (Monocotyledonae). The Typhaceae and Sparganiaceae (formerly included) are not closely related to Pandanaceae and form a distinct Order Typhales.

Although known to botanists for some three centuries, the Pandanaceae accounted for in Warburg's Monograph (1900) were 180 species of *Pandanus*, about fifty spp. of *Freycinetia*, and one of *Sararanga*. No further genera have been discovered but the number of known species has grown and there are about 700 binomials currently. The foremost students of the family since 1900 have been Martelli, Merrill, Pichi-Sermolli, and St. John. More vigorous exploration in the Palaetropics has vastly increased the available study material; much fieldwork has significantly augmented the herbarium study.

But many problems remain which impede full understanding of the family, in particular the largest genus *Pandanus*. With over 500 species, *Pandanus* posed severe difficulties in establishing interspecific relationships and an infrageneric classification.

## II. Traditional taxonomic characters and unresolved problems

The salient features of previous taxonomic work on *Pandanus* was the virtually complete dependency on the characters of the ripe fruits. Nearly all described species and infrageneric taxa were based on fruit-characters. Since all the plants are dioecious, this resulted in almost sure ignorance of the males. Staminate specimens could seldom be identified. The problem was brought about by the

---

\* Based on a paper read at the International Botanical Congress at Leningrad, 1975 (Abstract in [A. Takhtajan (Ed.),] *Abstracts of the papers presented at the XII International Botanical Congress July 3-10, 1975* (I):100).

rarity of good staminate material in herbaria (in turn the result of the ephemeral nature of the male flowers in nature), and the difficulty of correlating staminate and pistillate specimens both in the field and in the herbarium. Sterile material was impossible to identify.

Clearly, a taxonomic system which relied entirely on fruit characters, in a genus of strictly dioecious plants, was inadequate both for practical identification and for studies of phylogeny. For the purposes of most botanists, identification of *Pandanus* was either uncertain or impossible.

In view of this situation it was obviously desirable to seek taxonomic characters which were shared by both staminate and pistillate plants, i.e. vegetative characters, including those revealed by micromorphology and anatomy. During the past two decades our efforts have been turned to solutions to the problems described. The main features of the work, carried out by various persons at several institutions, are described below.

### III. New Investigations and their Results

A. Gross Morphology. — In general three main aspects have been developed: (1) Fuller quantification of characters, particularly of vegetative structures. Example: the mainly qualitative descriptions of leaves have been replaced by analyses giving data such as tooth (prickle) size and spacing, vein number, variation in leaf length and width, etc. (2) The discovery and correlation of staminate with the pistillate-plants of the same species, and full descriptions and taxonomic use of staminate characters. Example: field work yielding field knowledge of population structure, phenology, breeding behaviour, and ecological distribution, has often led to correct correlation of sexes. Pollen characters have been studied only to a limited extent but may throw some light on species relationships, as has been demonstrated in a few cases (e.g. *Pandanus sigmoideus* St. John). (3) Habit and morphogenetic field characters supplementing the existing herbarium knowledge, made possible by augmented collection techniques, photography, field analysis of individuals in various growth stages, etc.

B. Morphogenesis and architecture (habit). — Work in this field has revealed the changes which occur in ontogeny from seedling to adult and has necessitated the recognition of 'juvenile' states which may differ radically from adult states, even in the same species. Progressive changes in anatomical features are correlated with the external changes in size and form, and indicate that anatomical characters must be derived from adult structures for reliable use in taxonomy and classification. Habit classification has become possible through the analysis of growth phases and it is now clear that adult form can be a major taxonomic character. This is especially clear in the case of *Pandanus* Sect. *Acanthostyla*, of Madagascar, a group of species which share the 'coniferoid' habit. Further studies of habit have been carried out by Guillaumet (1973), based on the more general work of Hallé and Oldemann (1970; 1975). The 'lateral' inflorescences of Sect. *Cauliflora* and Sect. *Tridens* are similar examples of habit specialization which offer taxonomic utility.

C. Anatomy. — Anatomical studies of *Pandanus* date back at least as far as Solla (1887) but their significance in relation to taxonomy was not appreciated. With resumption of such studies by Tomlinson (1965), Kam (1969), Gineis (1969), and now especially by K. L. Huynh (1974), the correlation between anatomical features and other characters became clear. It is now evident that, in general, anatomical characters form a fairly reliable basis for the discrimination of species-groups, and furthermore, it has become clear that these species-groups usually correspond to sections. Occasionally, single species stand out on anatomical grounds, and there are some cases in which anatomy seems not to offer clear support to sectional discrimination, but in a great majority of cases the anatomical data has had a beneficial and significant effect on infrageneric taxonomy. The

anatomical characters used have been chiefly from the leaves, and as demonstrated by Kam, only fully adult organs could be compared. Within these limits the appearance of particular anatomical features seems sufficiently constant and in rare cases may be diagnostic.

The tissues which furnish the characters are especially the epidermis, the stomatal complex, the hypodermis, the crystal cells, the chlorenchymatous layers, the fibrous strands and the vascular bundles. In particular, the range of variation in the epidermal tissues (including the stomata) proves to be of very great value. In order to rationalize the variation found, Tomlinson founded a classification of stomatal types, based on progressive complexity. This system was used by Kam and others and shown to correlate well with sectional taxa. More recently (1974) the classification has been refined by Huynh, who defines seven stomatal types and in turn finds a remarkably good correspondence with the infrageneric classification being developed by Stone. In fact, the anatomical data became the test by which the infrageneric taxa could be evaluated; where serious disharmony in anatomical features was revealed within a section, it was usually found to indicate an artificial classification which could be remedied by remodeling the Section e.g. by dividing it, or by reassigning some of its supposed component species to other sections. The anatomical data thus often revealed a 'hidden' flaw in previous taxonomic systems.

Examples of the variety of stomatal-complex structures revealed that all retain the basic tetracytic pattern but vary in relation to the production of elaborations, which are commonly in the form of papilliform protuberances arising from the cells of the stomatal complex and of the epidermis proper. The simplest arrangement is an essentially flat epidermis, the stomate flush with the surface, the epidermal cells merely forming a tessellate pattern. On adaxial surfaces of leaves the epidermis may be zoned or not; zonation involves differing cell shape and presence or absence of stomata in alternating bands corresponding to veins and inter-vein spaces. Such zonation produces a further character that may be used in addition to the stomatal type. Increasingly complex stomatal types develop as various cells produce papillae, and the entire epidermal surface or all the relevant zonal bands, may thus become papilliferous. The papillae themselves may be limited to one per cell, or may occur in sets on a cell: they may be of various simple forms or in more elaborate forms such as forked or dendritic. Papillae may form a stockade around the stomate, or around a group of stomata. The stomata may become considerably sunken below the general level of the epidermis.

The hypodermis may be of one or more cellular layers and may include crystal cells in various patterns and in various orientations. The crystals may be rhomboidal or occur as raphides; the former usually are more common in leaves, and may exist in two distinct forms, and in various sizes. The patterns of distribution of the crystal cells may be of some taxonomic value.

The chlorenchyma may be continuous or interrupted, and this distinction sometimes has a taxonomic significance.

The association of fibrous strands with particular tissues may also be constant enough for taxonomic use.

A considerable number of other anatomical features occur, some of which may on occasion have a taxonomic use, e.g. stomatal size and stomatal index, the occurrence of papillate stockades, etc.

Wherever data from anatomy conflicts considerably with a traditionally established taxonomic group it is likely that the latter is heterogenous and a re-evaluation of all the constituent species and their characteristics is in order. By application of this method the infrageneric classification can be established on a broader, firmer basis than otherwise possible. The concrete result of such application has been put forward as a new infrageneric scheme (Stone, 1974). In this system, eight subgenera are established (these are further grouped into four

unnamed groups of 3, 2, 2 and 1 subgenera respectively). Each subgenus consists of one or more (up to sixteen) sections. Altogether, 62 sections are recognized. These in turn are in some cases divided into subsections. There are 468 species accounted for, i.e. probably 90% of the total (the remainder are excluded temporarily as either probable synonyms or because data is quite insufficient for placement).

D. Cytology. — The predominant chromosome number found in *Pandanus* is 60 (somatic): but one tetraploid (*P. spiralis* R. Br.) is known. However, only some 30 species have been 'counted'. The foremost workers in this field have been Tjio, Harada, Cheah (1969) and the work is being continued by Jong. The only discovery of some taxonomic significance is that in some cultivars (e.g. *P. spurius* Miq.) some cells at least may be aneuploid (with such numbers as 59 or 61 chromosomes). So far however, there is no significant input from chromosome studies, but the work has probably not progressed far enough to be sure that this will remain true. It is at least potentially interesting that the one case of tetraploidy occurs at the margin of the generic distribution (Northern Territory, Australia) where it seems to be the case that habitat and climatic conditions are marginal. The karyotype analysis by Cheah shows that the chromosomes are very small. There may be 0-4 pairs of SAT-chromosomes, and many are short rods which are hardly discriminable.

E. Embryology. — *Pandanus* is peculiar in that the mature embryo sac in the few species so far studied, has a condition of supernumerary nuclei (over and above the usual eight): these nuclei, as was shown by Fagerlind (1940), migrate in from the surrounding tissue at a late stage. Recently this has been reconfirmed in two Malayan species (Cheah and Stone, 1975). The other genera of the family do not appear to show this phenomenon. The significance, if any, to taxonomy, has yet to be discovered. However, circumstantial evidence for a few species indicates that reproduction may be apomictic: it is conceivable that this is related to the 'nuclear migration' as first noticed by Campbell and demonstrated by Fagerlind, but this remains to be investigated.

F. Palynology. — The pollen morphology has yet to be investigated in detail. Present evidence suggests that some variation exists and thus some taxonomic information may arise from studies of pollen. It is hoped to investigate this with the Scanning-Electron Microscope now available in the University of Malaya.

#### IV. Synopsis of the infrageneric taxa of *Pandanus*<sup>1</sup>

##### Group 1

##### Subgenus 1. *Rykia*

Sections:

- |   |                         |                  |
|---|-------------------------|------------------|
| (1) <i>Rykia</i> (with subsections <i>Rykia</i> , <i>Bidens</i> , <i>Malaya</i> , <i>Multispina</i> , <i>Callicola</i> , <i>Atrodentata</i> , <i>Gressittia</i> ) | (2) <i>Asterodontia</i> | (7) <i>Kaida</i> |
|   | (3) <i>Hombromia</i>    |                  |
|   | (4) <i>Mydiophylla</i>  |                  |
|   | (5) <i>Rykiopsis</i>    |                  |
|   | (6) <i>Solmsia</i>      |                  |

##### Subgenus 2. *Lophostigma*

Sections:

- |                            |                          |                          |
|----------------------------|--------------------------|--------------------------|
| (1) <i>Lophostigma</i>     | (7) <i>Perrya</i>        | (13) <i>Bernardia</i>    |
| (2) <i>Megastigma</i>      | (8) <i>Cauliflora</i>    | (14) <i>Asterostigma</i> |
| (3) <i>Karuka</i>          | (9) <i>Barrotia</i>      | (15) <i>Tridens</i>      |
| (4) <i>Maysops</i>         | (10) <i>Liniobtutus</i>  | (16) <i>Cheilostigma</i> |
| (5) <i>Metamaysops</i>     | (11) <i>Brongniartia</i> |                          |
| (6) <i>Paralophostigma</i> | (12) <i>Veillonia</i>    |                          |

<sup>1</sup> See Stone (1974) for bibliographic citations.

Subgenus 3. *Kurzia*

Sections:

- |                          |                       |                        |
|--------------------------|-----------------------|------------------------|
| (1) <i>Kurzia</i>        | (5) <i>Curvifolia</i> | (9) <i>Kanehiraea</i>  |
| (2) <i>Microstigma</i>   | (6) <i>Involuta</i>   | (10) <i>Utilissima</i> |
| (3) <i>Jeanneretia</i>   | (7) <i>Marginata</i>  |                        |
| (4) <i>Pulvinistigma</i> | (8) <i>Cristata</i>   |                        |

**Group 2**

Subgenus 4. *Vinsonia*

Sections:

- |                           |                               |                          |
|---------------------------|-------------------------------|--------------------------|
| (1) <i>Vinsonia</i>       | (6) <i>Heterostigma</i>       | (9) <i>Acanthostyla</i>  |
| (2) <i>Barklya</i>        | (7) <i>Souleyetia</i> with    | (10) <i>Rykiella</i>     |
| (3) <i>Mammillarisia</i>  | subsections <i>Souleyetia</i> | (11) <i>Lonchostigma</i> |
| (4) <i>Dauphinensia</i>   | and <i>Sussea</i>             | (12) <i>Platyphylla</i>  |
| (5) <i>Stephanostigma</i> | (8) <i>Foullioya</i>          | (13) <i>Eydouxia</i>     |

Subgenus 5. *Martellidendron*

Sections:

- |                            |                       |
|----------------------------|-----------------------|
| (1) <i>Martellidendron</i> | (2) <i>Seychellea</i> |
|----------------------------|-----------------------|

**Group 3**

Subgenus 6. *Pandanus*

Sections:

- |   |  |                      |
|---|--|----------------------|
| (1) <i>Pandanus</i> , with Sub-<br>sections <i>Pandanus</i> ,<br><i>Austrokeura</i> , and<br><i>Insulanus</i> | (5) <i>Intraobtutus</i>  | (9) <i>Megakeura</i> |
| (2) <i>Fagerlindia</i>  | (6) <i>Australibrassia</i>   |                      |
| (3) <i>Elmeria</i>  | (7) <i>Semikeura</i> with<br>Subsections<br><i>Semikeura</i> and<br><i>Elaphrocarpus</i> |                      |
| (4) <i>Athrostigma</i>  | (8) <i>Excavata</i>  |                      |

Subgenus 7. *Coronata*

Sections:

- |                     |
|---------------------|
| (1) <i>Coronata</i> |
|---------------------|

**Group 4**

Subgenus 8. *Acrostigma*

Sections:

- |   |   |   |
|---|---|---|
| (1) <i>Acrostigma</i> , with<br>Subsections<br><i>Acrostigma</i> ,<br><i>Scabridi</i> ,<br><i>Dimissistyli</i> ,<br><i>Ornati</i> , | <i>Glaucophyllae</i> ,<br><i>Parvi</i> ,<br><i>Papilionati</i> ,<br><i>Alticolae</i> , and<br><i>Pumili</i> | (3) <i>Pseudacrostigma</i><br>(4) <i>Epiphytica</i> |
|   | (2) <i>Fusiforma</i>  |   |

**V. Future work needed.**

A. Functional significance of micromorphological-anatomical characters: The great variation in anatomical structure which correlates so well with classification, seems so far to resist an ecological or physiological explanation. For example, the more elaborate stomatal types (five in Tomlinson's, six or seven in Huyhn's)

suggest xeromorphy. Nonetheless, various species of *Pandanus* which are taxonomically unrelated and which have very different stomatal types, may occur sympatrically in exactly the same microhabitat, i.e. fresh-water swamps.

B. More precise developmental studies to determine the basis of different habit categories, as well as to provide a means to compare ontogeny in pandans with that in other plants.

C. Further cytological studies to determine if other examples of polyploidy exist, whether they correlate with classification and/or habitat, and whether they tend to cluster at the margin of the generic distribution as is apparently the case and would be expected theoretically on the basis of the evolutionary studies of e.g. Stebbins.

D. Palynological work as a basic survey and to correlate with taxonomy and with fossils, particularly to see whether palynomorphic form genera such as *Pandaniidites* can be in fact accepted as pandanaceous.

E. Distributional analysis as a partial basis of phylogenetic interpretation.

### References

- CHEAH, C. H. 1969. M.Sc. thesis, University of Malaya.
- 1973. Chromosome studies of *Pandanus*. *Bot. Jahrb. Syst.* **93**: 498–529.
- & B. C. STONE. 1975. Embryo sac and microsporangium development in *Pandanus*. *Phytomorphology* **25**: 228–238.
- FAGERLIND, F. 1940. Stempelbau und Embryosackentwicklung bei einigen Pandanazeen. *Annls Jard. bot. Buitenz.* **49**: 55–78.
- GINEIS, C. 1969. Étude anatomique de la plantule de *Pandanus* sp. *Bull. Inst. Fr. d'Afr. noir* **31 A**, 2: 325–339.
- GUILLAUMET, J. -L. 1973. Formes et development des 'Pandanus' Malgaches. *Webbia* **28**: 495–519, 6 figs., 10 pls.
- HALLÉ F. & R. A. A. OLDEMAN. 1970. *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux*. Masson & Co., Paris.
- 1975. Essay on the Architecture and Growth Dynamics of Tropical Trees. English translation by B. C. Stone. University of Malaya Press, Kuala Lumpur.
- HUYNH, K. -L. 1974. La morphologie microscopique de la feuille et la taxonomie du genre *Pandanus*. *Bot. Jahrb. Syst.* **94**: 190–256.
- KAM, Y. K. 1969. M.Sc. thesis, University of Malaya.
- 1971. Morphological studies in Pandanaceae III. Comparative systematic foliar anatomy of Malayan *Pandanus*. *Bot. J. Linn. Soc.* **64**: 315–351.
- & B. C. STONE. 1970. Morphological studies in Pandanaceae IV. Stomate structure in some Mascarene and Madagascar *Pandanus* and its meaning for infrageneric taxonomy. *Adansonia n.s.* **10**: 214–246.
- SOLLA, R. F. 1884. Contribuzione allo studio degli stomi delle *Pandanee*. *Nuovo G. bot. ital.* **16**: 172–182.
- STONE, B. C. 1974. Towards an improved infrageneric classification in *Pandanus* (Pandanaceae). *Bot. Jahrb. Syst.* **94**: 459–540.
- TOMLINSON, P. B. 1965. A study of stomatal structure in Pandanaceae. *Pacif. Sci.* **19**: 38–54.
- WARBURG, O. 1900. Pandanaceae, in A. Engler, *Das Pflanzenreich*, 3, **IV**. 9: 1–97. Engelmann, Leipzig.

## *Ternstroemia corneri* (Theaceae)

by

HSUAN KENG

*Department of Botany, University of Singapore*

In preparing a systematic account of the Malayan Theaceae for volume 3 of the *Tree Flora of Malaya*, I came across an obviously undescribed species of *Ternstroemia* from southern Johore. It is represented by several specimens collected by Professor E. J. H. Corner and others, all deposited at the Herbarium of the Botanic Gardens, Singapore, of which one (*Corner SFN 27840*) was sent to Kew as early as 1935 for identification and returned with an annotation sheet stating that it was "Not matched in Kew", signed by Mr. Fisher in 1936. Its large, obovate or oblanceolate leaves and ellipsoid fruits with a pointed apex are so characteristic that it can be readily differentiated from other large-fruited *Ternstroemia* species of Malaya and indeed those of the rest of the Malaysian region. The new species, dedicated to Professor Corner, is described below.

### *Ternstroemia corneri* H. Keng, sp. nov.

Arbor 12–20 metralis, ramulis teretibus. Folia coriacea, anguste obovata vel oblanceolata, 20–28 cm longa, 7–8.5 cm lata, apice rotundata vel mucronata, basi longa attenuata, margine integerrima, nervis 13–15 paribus; petiolis circa 1 cm longis, incrassatis. Flores solitarii, proxime positi, pedicellis 2–2.5 cm longis, bracteolis 2, suboppositis, lineo-lanceolatis, 5 mm longis, sepala 5–6, obovato-rotundata, 5–6 mm longa, petala 5–6, oblongo-obovata, 8–10 mm longa; stamina numerosa (circa 80), 5–7 mm longa, ovarium conicum, 2–4 mm longum, 2-loculare, loculis 2 plusve ovulatis. Fructus ellipsoideus vel anguste ellipsoideus, 4.5–5 cm longus et 2–2.5 cm diametro, seminibus 2–4.

Small to medium-sized tree, 12–20 m tall. Bark greyish, no stilt roots or buttresses. Branches and branchlets terete. Leaves 3–4 in a false whorl, coriaceous or thin coriaceous, narrowly obovate or oblanceolate, 20–28 × 7–8.5 cm; lateral veins 13–15 pairs; apex rounded or abruptly and bluntly mucronate; base long-attenuate; petiole 1 cm long, stout. Flowers solitary, in axils of fallen leaves, 2–2.5 cm across if fully expanded, peduncles 2–2.5 (–3) cm long; bracteoles 2, subopposite, a short distance below the calyx; sepals 5–6, obovate-rounded, 5–6 mm long; petals 5–6, oblong-obovate, 8–10 mm long; stamens about 80, in 3–4 series, the connective produced and pointed; ovary conical, 2–4 mm long, 2-loculate, with 2 ovules per locule, the style 2-forked. Fruit baccate, ovoid or narrowly ovoid, 4.5–5 cm long, 2–2.5 cm in diameter, seeds 2–4, ellipsoid, flattened.

Known only from southern Johore, Peninsular Malaysia, in lowland swamp forests.

Specimens examined: Johore, Sungei Berassau, Mawai-Jemuluang Road, *Corner SFN 28740* (Type) (in swamp forest), 6 February 1935; Sungei Sedili, *Corner* s.n. in March 1932 (a tree, up to 50 feet); Mawai, *Corner SFN 30888* (60 feet, leathery leaves, yellowish green beneath); Sungei Kayu, *Kiah SFN 32158*; Sungei Kayu, Mawai-Jemuluang Road, *Corner SFN 32245*; Mawai, *Nagadiman SFN 34736*; Sungei Gambut, *Corner SFN 36815* [all SING!].

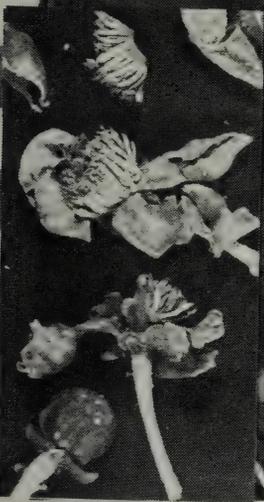
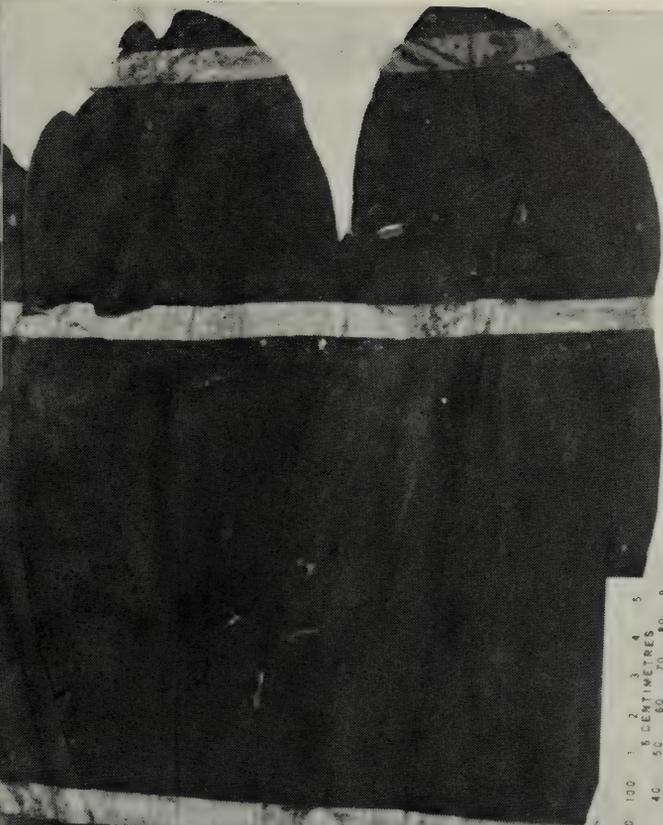
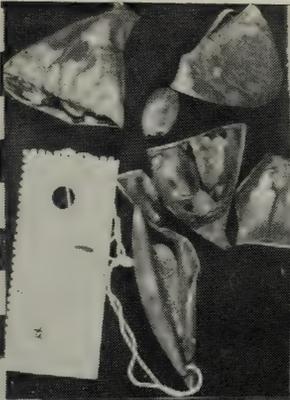
A simple dichotomous key to the four Peninsular Malaysian *Ternstroemia* species with larger flowers (over 1.5 cm across) and larger fruit (over 2 cm long) follows:

1. Normal leaves over 20 cm long; mature fruit distinctly ellipsoid and attenuate toward both ends, over 4.5 cm long ..... *T. corneri* H. Keng
1. Normal leaves less than 15 cm long; mature fruit rounded or ovoid, less than 3.5 cm long
  2. Flower (and fruit) stalk slender, 3.5–4 cm long; leaves elliptic obovate, 12–18 × 6–8 cm ..... *T. penangiana* Choisy
  2. Flower (and fruit) stalk stout, 1–1.5 (–2) cm long,
    3. Bracteoles immediately below and clasping the calyx; mature fruit ovoid-rounded, 3–3.5 × 2.5–3 cm; leaves elliptic to narrowly elliptic, 8–11 × 2.5–5.5 cm ..... *T. bancana* Miq.
    3. Bracteoles a short distance away and free from the calyx; mature fruit rounded, 2.5–2.75 cm across; leaves narrowly elliptic, 12–16 × 3.5–5 cm ..... *T. wallichiana* Engler

I am grateful to the Director of the Botanic Gardens, Singapore, for the herbarium and library facilities kindly provided and to Mr. D. Teow for the photographs reproduced in this paper.

*Facing plate: Ternstroemia corneri* H. Keng

A branch with unfolded flowers (type, *Corner SFN 28740*). *Upper inset*: fruits cut into halves showing the seeds (*Ngadiman SFN 34736*); *lower inset*: dissected flowers (type). All scales in cm.



CENTIMETRES		MILLIMETRES	
1	0	10	0
2	10	20	0
3	20	30	0
4	30	40	0
5	40	50	0
	50	60	0
	60	70	0
	70	80	0
	80	90	0
	90	100	0

HERIC HOEI BOE SINGAP  
*Hericia*  
 No. 28740

MALAY PENINSULA.  
 STATE OF JOHORE.

No. 28740  
 Date of February 1925  
 Collector

28740



# Thelypteridaceae Allied to *Phegopteris* in Malaya

by

R. E. HOLTTUM

Royal Botanic Gardens, Kew

## Summary

Following the revised scheme of genera in the family Thelypteridaceae proposed by the author in 1971, a revised account is here given of the genera *Macrothelypteris*, *Pseudophegopteris* and *Metathelypteris* in Malaya; these three genera, together with *Phegopteris* (sensu Ching 1963) appear to form a natural group. Some corrections to the nomenclature of the author's book *Ferns of Malaya* (1955) are made, with revised descriptions where necessary, and the addition of two species *Metathelypteris decipiens* (Clarke) Ching and *M. flaccida* (Bl.) Ching, not previously recorded for Malaya.

In my book on the ferns of Malaya (1955) I described 46 species of the family Thelypteridaceae, but (as stated on p. 236) no natural delimitation of genera had then been devised; those adopted were genera of convenience. It was clear to me that much more detailed observation of plants throughout the oriental tropics was necessary before a better arrangement of genera could be found. Subsequently R. C. Ching (1963) and K. Iwatsuki (1963-65) proposed new systems of classification, but both were mainly based on species of mainland Asia, whereas the family is far more diversified in the Malayan region and the Pacific. For the past eight years I have devoted most of my time and thought to a study of the family throughout the Old World, including Africa, with a glance also at the New World where A. R. Smith of Berkeley is attempting a similar survey. In 1971 I arrived at a new system of genera in the Old World, based on Ching's scheme but with considerable extensions. Since then I have prepared a series of monographs covering all species of individual genera; the series is not yet complete.

My present estimate is that Malaya has at least 54 species belonging to the family; this is about 10% of the total number of species in the Old World, with representatives of most of the genera; most of the missing genera have their main distribution in mainland Asia, but one of them is *Amauropelta* which is mainly American and extends across Africa to the Mascarene Islands.

The object of the present paper is to give a revised account of the Malayan species of a small group of genera which are distinguished by the following combination of characters which was first recognized by Ching: midrib of pinnae prominent but not grooved on the upper surface, and veins not reaching the margin. They also agree in having sori mainly exindusiate, and all genera except *Phegopteris* have some species with amply bipinnate fronds; such fronds do not occur in other genera of the family. I judge that the four genera form a natural group; if anyone wished to unite them, they would collectively bear the generic name *Phegopteris* (which in the strict sense of Ching does not occur in Malaya), but I prefer to maintain them as separate genera. They differ cytologically as follows: *Phegopteris*  $n = 30$ ; *Macrothelypteris* and *Pseudophegopteris*  $n = 31$ ; *Metathelypteris*  $n = 35$ . These numbers are based on several counts of plants from different sources, and of more than one species, in each case. Thus *Metathelypteris* has the same chromosome number as *Thelypteris* s.str., but the two groups differ in many ways and are certainly not closely related. *Phegopteris* has three species, two of them widely distributed in north temperate latitudes, one in southern China, extending to Tonkin

and Taiwan, with only one Malesian record, in Celebes; I found it to be easily maintained in cultivation at Penang, but it did not propagate itself from spores.

The name *Phegopteris* derives from *Polypodium phegopteris* Linn. It was first used as a generic name to distinguish terrestrial ferns which have exindusiate sori resembling those of *Polypodium*, and was used in the 19th century to cover various different groups of such ferns. The present limitation of the genus is due to Ching (1963: 312). Its distinctive characters are: stipe-scales with marginal acicular hairs but no such hairs on the surface; fronds simply pinnate, pinnae connected by a wing along the rachis, the wing forming semicircular lobes between pinnae.

In the following statement I have not attempted to give a full synonymy for each species, but I do give the following in all cases: (a) the basionym; (b) the name used in my book of 1955; (c) names used in conjunction with previous descriptions; (d) the correct name in *Thelypteris*, if such has been published. A full synonymy for *Pseudophegopteris* and *Macrothelypteris* will be found in my paper of 1969 cited below; it will be given for *Metathelypteris* when I prepare a monograph.

#### KEY TO THE GENERA IN MALAYA

Fronds simply pinnate; sori distinctly indusiate ..... 1. *Metathelypteris*

Fronds mostly bipinnate; sori exindusiate or with very small indusia:

Slender spreading acicular hairs consisting of several cells, abundant on lower surface of axes of frond; spores with a very fine raised reticulum not distinguishable with light microscope ..... 2. *Macrothelypteris*

Hairs on lower surface all unicellular; spores with a slightly raised surface reticulum of rather large meshes ..... 3. *Pseudophegopteris*

#### 1. *Metathelypteris* Ching 1963: 304. Holttum 1971: 26

Rhizome short, suberect. Fronds simply pinnate with deeply lobed pinnae (in two non-Malayan species bipinnate); veins often forked, not reaching margin; hairs on lower surface acicular or capitate, always unicellular; sori indusiate; no hairs or glands on body of sporangia.

*Distribution:* about 14 species, widely distributed but few of them anywhere abundant; San Thomé and Fernando Po; Madagascar; Ceylon; N.E. India to China and Japan; throughout Malesia on mountains; Solomon Islands.

Specimens from the islands of the Gulf of Guinea have been identified with the Madagascan *M. fragilis* (Bak.) Holtt. but may represent a distinct species. No specimens have been reported from Madagascar since the original specimen, a single frond, reached Kew in 1877. Another specimen, still undescribed and possibly originating from Nigeria, is the only evidence that plants of this genus now exist in mainland Africa. Only one species of the genus was described in Holttum 1955; two more are here added.

#### KEY TO THE MALAYAN SPECIES

Lobes of at least the lower pinnae lobed half-way towards costules or more deeply ..... 1. *M. flaccida*

Lobes of pinnae entire or crenate:

Pinna-lobes (except basal acroscopic lobe) entire; pinnae commonly to 6 × 2 cm; veins often simple in smaller pinna-lobes ..... 2. *M. decipiens*

Pinna-lobes of large pinnae crenate; pinnae commonly larger; almost all veins forked ..... 3. *M. dayi*

1. *Metathelypteris flaccida* (Bl.) Ching 1963: 306.

Basionym: *Aspidium flaccidum* Bl., Enum. Pl. Jav. (1828) 161. Racib. Fl. Btzg 1 (1898) 176.

Synonyms: *Lastrea flaccida* Moore, Ind. Fil. (1858) 92. Bedd., Ferns S. India (1864) t.250; Handbook (1883) 244. — *Dryopteris flaccida* (Bl.) O. Kuntze, Rev. Gen. Pl. 2 (1891) 812. v.A.v.R., Handb. Mal. Ferns (1908) 195. — *Thelypteris flaccida* (Bl.) Ching, Bull. Fan Mem. Inst. Biol. 6 (1936) 336.

Rhizome short, erect. Stipes to 25 cm or more long, pale, hairy in the groove; basal scales 3–4 mm long. Lamina 25 cm or more long, with rather widely-spaced subopposite pinnae, to 10 pairs, thin; basal pinnae narrowed towards base on basiscopic side. Largest pinnae of Malayan specimens 10 × 2.5 cm, acuminate, lobed almost to the costa; largest lobes lobed  $\frac{1}{2}$  way to costule or more deeply; costules to 4 mm apart; veins pinnate in the larger lobules of pinna-lobes, distal veins forked; lower surface of rachis, costae, costules, veins and surface of lamina bearing slender pale erect acicular hairs to  $\frac{3}{4}$  mm long; upper surface of costules and veins bearing scattered hairs as those on costa. Sori 1–3 in each lobule of a pinna-lobe, small; indusia thin with short acicular hairs.

*Distribution*: West Java (type); Sumatra (?); Malaya; Ceylon & S. India; N.E. India to West China.

In 1969 I found plants of this species on sheltered earth banks by a road at 5000 ft near Brinchang, Cameron Highlands; specimens were also collected somewhat earlier by Abdul Samat bin Ali (no. 363) on Maxwell's Hill, Perak. The Malayan specimens are all rather small and have shorter hairs on the lower surface than those from Java and from N.E. India. Prof. Manton found that in Ceylon the species occurs in both diploid and tetraploid forms (Phil. Trans. R. Soc. B, 238:137. 1954). Herbarium specimens from Ceylon at Kew can be separated into those with longer and with shorter, less abundant hairs on lower surface; the Cameron Highlands specimens correspond with the latter. It seems likely that this species will spread in northern Malaya as clearing provides suitable habitats.

2. *Metathelypteris decipiens* (Clarke) Ching 1963: 306.

Basionym: *Nephrodium gracilescens* (Bl.) Hook. var. *decipiens* Clarke, Trans. Linn. Soc. II, Bot. 1 (1880) 514, t.65, fig. 2.

Synonyms: *Lastrea gracilescens* var. *decipiens* Bedd., Handb. Suppl. (1892) 51. — *Thelypteris decipiens* Ching, Bull. Fan Mem. Inst. Biol. 6 (1936) 335.

Rhizome short-creeping or suberect with fronds closely tufted at its apex. Stipe 15–25 cm long, pale except for darkened base, very-short-hairy; scales narrow, 2 mm long, bearing short hairs. Lamina to 30 cm long, with about 12 pairs of free pinnae; basal pinnae sometimes a little reduced, often narrowed at the base on basiscopic side; texture thin. Largest pinnae on Indian specimens 9 × 2.5 cm, commonly 6 × 2 cm, on Malayan specimen 5 × 1.3 cm, short-acuminate with upcurved tip, lobed almost to costa; basal acroscopic lobe often enlarged and crenate, other lobes entire, slightly oblique, hardly falcate; costules to 3½ mm apart; veins to 6 pairs, those in acroscopic basal lobes mostly forked, in other lobes mostly simple; lower surface of rachis, costae and costules bearing scattered short hairs, also short brown linear scales; upper surface of costae densely hairy, scattered similar hairs on costules and veins. Sori medial or a little supramedial; indusium small, pale, with minute capitate hairs.

*Distribution*: Darjeeling district; Khasia Hills in Assam; in Malaya only found once on rocks in opening of mossy forest, by waterfall, Gunong Batu Brinchang, 6000 ft (Molesworth Allen 5005).

This species is very near *M. gracilescens* (Bl.) Ching, differing in broader pinna-lobes of the largest fronds, with acroscopic basal lobes enlarged and crenate, and in having some veins forked in the larger pinna-lobes. The Malayan plant matches specimens from the Khasia Hills very closely; it is not mentioned in the appendix to the second edition of my book. *M. gracilescens* (type species of the genus) has a wide distribution on mountains in the Malayan region (Sumatra, Java, Borneo, Philippines, New Guinea) also Taiwan and southern Japan; it has not yet been found in Malaya.

3. **Metathelypteris dayi** (Bedd.) Holttum 1976: 117.

Basionym: *Nephrodium dayi* Bedd., Journ. Bot. 25 (1887) 323.

Synonym: *Lastrea dayi* Bedd., Handb. Suppl. (1892) 54.

Misapplied name: *Thelypteris singalanensis* sensu Holttum 1955: 243, fig. 138.

I have no corrections or addition to the description of 1955, but here provide a correction of the name. The type of *Nephrodium singalanense* Bak. represents a Sumatran species distinct from the Malayan one; it has abundant minute capitate glandular hairs all over the lower surface and the fronds are thinner in texture, drying a darker green. It may be a forest plant, whereas the Malayan *M. dayi* grows in rather open places, not in full forest shade. A plant from Taiping Hills investigated by Prof. Manton proved to be tetraploid; the Sumatran *M. singalanensis* might be diploid.

*Distribution*: Sumatra, Malaya, West Java, Borneo, Philippines, New Guinea.

2. **Macrothelypteris** Ching 1963: 308. Holttum 1969: 25

Rhizome short, prostrate or suberect; scales at base of stipes narrow, thickened near their bases, with short acicular or capitate marginal and superficial hairs; fronds amply bipinnate-tripinnatifid with adnate pinnules; scales on rachis (if present) often with thickened bases, sometimes with marginal hairs, always with an acicular hair-tip, usually grading to septate hairs on distal parts of frond; sori small, with small indusia obscured by ripe sporangia; sporangia bearing capitate hairs; spores with a very fine surface-reticulum not distinguishable in detail with the light microscope, sometimes with slight wing-like outgrowths.

*Distribution*: about 9 species, from the Mascarene Islands to warmer parts of mainland Asia, throughout Malesia, widely in the Pacific. In Malaya only one species, which needs no new description but has an earlier name than that cited in Holttum 1955.

**Macrothelypteris torresiana** (Gaud.) Ching 1963: 310. Holttum 1969: 27.

Basionym: *Polystichum torresianum* Gaud. in Freycinet, Voy. Bot. (1824) 333.

Synonym: *Thelypteris torresiana* (Gaud.) Alston, Lilloa 30 (1960) 111.

Name in Holttum 1955: *Thelypteris uliginosa* (Kunze) Ching.

This species is at once distinguishable by its glaucous stipe with dark narrow basal scales and by the presence of slender acicular hairs more than 1 mm long and consisting of several cells, which take the place of scales on the lower surface of axes of the frond. It is distributed almost throughout the range of the genus and has also become established through human agency in various parts of the American tropics. It is not a common species in Malaya, except in the north, in open places in the lowlands, though easy to cultivate in Singapore.

It would not be surprising if *M. multisetata* (Baker) Ching, described from G. Matang near Kuching, Sarawak, and occurring at c. 3000 ft in the Padang Highlands of Sumatra, were to appear in open places on the mountains of Malaya. This species has larger fronds than *M. torresiana*, with reddish stipes and copious stiff spine-like scales throughout stipe and rachises.

### 3. *Pseudophegopteris* Ching 1963: 313. Holttum 1969: 12

Rhizome various, in the Malayan species erect, in *P. aurita* (Hook.) Ching long-creeping and slender. Stipe and rachis usually reddish, basal scales thin, red-brown when dry, edges not ciliate; scales on frond usually few, appressed, reduced to a single row of short cells with red transverse walls. Lamina usually large (smallest in the Malayan *P. rectangularis*), much longer than wide, with  $\pm$  reduced lower pinnae; in bipinnate fronds the lamina of pinnules adnate to pinna-rachis; hairs on frond acicular or short-capitate, always unicellular. Sori exindusiate, often spreading a little along the veins; sporangia sometimes bearing acicular hairs near annulus; spores pale, with a slightly raised reticulum of rather large meshes.

*Distribution*: 21 species, distributed from the islands of St Helena and San Thom  (Atlantic Ocean) to Hawaii; in Malesia only on mountains in open places.

The two Malayan species are named *Thelypteris oppositipinna* and *T. brunnea* in my book of 1955. Both names must be changed, and a new description of the latter is provided. The only other species which might occur in Malaya is *P. aurita* (Hook.) Ching, which was described from N.E. India and has been found on Mt Kinabalu and the highlands of eastern New Guinea; it might occur on the exposed upper parts of Gunong Tahan. In New Guinea this species was found to be tetraploid, but in Ceylon it is diploid.

#### *Pseudophegopteris rectangularis* (Zoll.) Holttum 1969: 19.

Basionym: *Polypodium rectangularis* Zoll., Syst. Verz. (1854) 37, 48.

Name in Holttum 1955: *Thelypteris oppositipinna* (v.A.v.R.) Ching.

*Distribution*: N.E. India; Sumatra, Malaya, Borneo, Java, at 3000–5000 ft.

The name *rectangularis* was based on a specimen from Java, the later name *oppositipinna* on a specimen from Sumatra; the species also received other names elsewhere (see Holttum 1969 for full synonymy). The few Malayan specimens have been found in rather dry exposed ground in or near stream-beds, whereas plants of *P. paludosa* (see below) grow in wet ground by streams. It would be interesting to transplant *P. rectangularis* to see whether different environmental conditions would cause it to vary from its normal characters as described and figured in my book.

#### *Pseudophegopteris paludosa* (Bl.) Ching 1963: 315. Holttum 1969: 23.

Basionym: *Polypodium paludosum* Bl., Fl. Jav. Fil. (1851) 192, t. 90.

Name in Holttum 1955: *Thelypteris brunnea* in part, excluding Indian plants.

Correct name in *Thelypteris*: *T. paludosa* (Bl.) K. Iwats., Acta Phytotax. Geobot. 19 (1961) 11.

Rhizome erect, massive in well-grown plants. Stipe 50 cm or more long glabrescent, reddish; basal scales to c.  $10 \times 2$  mm, very thin. Lamina to 120 cm or more long; free pinnae to c. 15 pairs, opposite, lower pinnae somewhat reduced and more widely spaced, basal pinnae 25 cm long on a frond with largest pinnae 33 cm; basal basiscopic pinnule or pinna-lobe longer than acroscopic. Pinnules broadly adnate to pinna-rachis, usually connected by a very narrow wing, grading distally to the deeply lobed apical part of the pinna; largest pinnules (apart from basal ones) about  $4 \times 1$  cm, deeply lobed, veins pinnate in the lobes; lower surface

of pinna-rachis and costae of pinnules bearing stiff spreading slender acicular hairs  $\frac{2}{3}$ – $\frac{3}{4}$  mm long, shorter and thicker hairs on upper surface. Sori usually 2 pairs in each pinnule-lobe, round or nearly so; sporangia lacking hairs near annulus.

*Distribution:* Malesia, Sumatra to New Guinea, on mountains at 4000–7000 ft, in open wet ground by streams; rather few collections.

When writing my book of 1955 I had only seen one plant of this species, which I found in an early clearing (for the trout hatchery) near Brinchang at Cameron Highlands in the 1930's; I also saw a plant collected by Mrs Allen at Fraser's Hill. As Mrs Allen has reported (Gard. Bull. Sing. 17: 260. 1958) the species increased greatly in the later large clearings at the Highlands, and I saw it growing abundantly by streams above Brinchang village in 1969; these Malayan plants certainly agree closely with specimens from the mountains of West Java, whence Blume had the type of his species.

The name *Thelypteris brunnea* applied to the Malayan species by me in 1955 was based on *Polypodium brunneum* Wall., published without a description in a list of the specimens in Wallich's herbarium. The earliest valid name for the Indian species is *Phegopteris pyrhorhachis* Kunze, based on a specimen from the Nilgiri Hills in southern India; the rhizome is somewhat prostrate and the fronds are never so large as in *P. paludosa*. In Ceylon Prof. Manton found both tetraploid and hexaploid forms of this species. Malayan plants of *P. paludosa* look very uniform at Cameron Highlands.

Mrs Allen remarked that she had found *P. rectangularis* and *P. paludosa* growing together, and it would not be surprising if intermediates were found. It should be noted that, apart from the great difference in size (which would not apply to young plants of *P. paludosa*) the two species differ constantly in the presence of stiff hairs on the sporangia *P. rectangularis* (see Holttum 1955 fig. 137) and their absence in *P. paludosa*.

The plants from Mt Kinabalu mentioned by Mrs Allen in her note on *Thelypteris brunnea* above-mentioned are *Pseudophegopteris aurita* (Hook.) Ching.

#### References to literature cited

- CHING, R. C. 1963. A re-classification of the family Thelypteridaceae from the mainland of Asia. *Acta phytotax. sinica* **8**: 289–335.
- HOLTTUM, R. E. 1955. A Revised Flora of Malaya, 2, Ferns of Malaya. Government Printer, Singapore.
- 1968. *Ibid.*, second edition, with appendix of corrections and additions.
- 1969. Studies in the family Thelypteridaceae, I. The genera *Phegopteris*, *Pseudophegopteris* and *Macrothelypteris*. *Blumea* **17**: 5–32.
- 1971. Studies in the family Thelypteridaceae III. A new system of genera in the Old World. *Blumea* **19**: 17–52.
- 1976. Some new records of Thelypteridaceae for the Philippines. *Kalikasan* **5**: 109–120.
- IWATSUKI, K. 1963–65. Taxonomy of the thelypteroid ferns, with special reference to the species of Japan and adjacent regions, Parts 1–4. *Mem. Coll. Sci. Kyoto Univ. B.* **30**: 21–51; **31**: 1–40, 125–197.

# Tremellales with Tubular Hymenophores Found in Singapore

by

A. DAVID<sup>1</sup>

&

M. JAQUENOUD

Laboratoire de Mycologie, associé au  
CNRS, Villeurbanne, France

Achlenstr. 30, CH-9016 St Gall.,  
Switzerland

## Summary

The authors describe a new species of pore-bearing Tremellales: *Aporpium hexagonoides*, and discuss a collection of a species closely related to *A. dimidiatum* David.

Until recently, the poroid Tremellales were only represented by a resupinate species, *Aporpium caryae* (Sw.) Teix. & Rog. In a recent paper (David, 1974), a new species was described from Guadeloupe and named *A. dimidiatum* David. The author believed that the existence of Tremellales in the form of polypores might be far less exceptional than had been previously supposed. This opinion was confirmed by a short stay in Singapore<sup>2</sup> in July 1974 devoted to the study of the island's polypores, when several poroid fungi with longitudinally divided hypobasidia were collected. On one hand the stay in Singapore was very profitable as far as the number of species collected was concerned, but on the other we were disappointed in the results of trying to culture them. From the spore samples made on the spot in Singapore, we should have got polysperous and monosperous mycelium on our return to Lyon, but only a low percentage of germinating spores were found, probably due to the 7-15 days' lapse before culturing. Are spores of equatorial species, developing in a climate which is always favourable for germination, particularly sensitive to drying out? The failure of the cultures, especially of monosperms, is to be regretted, because one specimen collected in Singapore shows, apart from its size, many characteristic features of *A. dimidiatum* described from Guadeloupe: no microscopic difference could be discerned. On the other hand other specimens certainly represent a new species —

## *Aporpium hexagonoides* David & Jaquenoud, sp. nov.

*Fructificationes* parvula<sup>3</sup>, solitaria, subdimidiata vel dimidiata, in statu recenti coriacea elastica; in statu sicco dura cornia, 2-3 cm lata, 1-1.8 cm ad radium, 0.3-0.85 cm crassa. *Facie superiore* (Plate 1b) applanata vel leviter convexa, albida ad marginem, alibi pallide ochracea, 10 YR 8/6 7/6 7/8,<sup>4</sup> molliter veluta (aut tomentosa) vel hispida in statu recenti; in arescendo corrugantur. Margine obtusa. *Facie inferiore* hymeniale (Plate 1a) pallide alutacea, 10 YR 8/2-2.5 Y 8/2. Pori magni, angulosi, plus minusve hexagonales, ca. 1 mm diam. Multi fascies hyphacei ex hymenio eminentes, sub lente visibiles. Tubuli contexto concolori neque aparte separati. *Systema hypharum* dimiticum: hyphae scaleticae

<sup>1</sup>Assisted by B. Dequatre, collaborateur technique du CNRS.

<sup>2</sup>We are much indebted to the Chairman, Nature Reserves Board, Singapore and to Dr Chang Kiaw Lan for all the help given to us during our stay in Singapore.

<sup>3</sup>We are very grateful to Dr. phil. H. Metzger, Professor at the Cantonal Grammar-School of St. Gall, for the Latin description.

<sup>4</sup>See "Code Munsell Book of Color" (1950), Baltimore, Maryland.

hyalinae (3-) 4-5  $\mu$  diam., crassis tunicatis usque ad 1  $\mu$  hyphae generativae hyalinae tenuiter tunicatae, 2-3  $\mu$  diam., cum articulis longissimis, ut fibulae rarae atque difficiles visu sunt (Fig. 1b). *Basidia* claviformia 20  $\times$  8  $\mu$ , longitudinaliter septata in parte superiore (Fig. 1a), 4 sterigmatis subulatis, 10-12  $\mu$  longis. *Basidiospores* hyalini, non cyanophili, non amyloidi, non dextrinoidi, subcylindrici, plus minusve depressi, cum regione apicali, Congo ammoniacali adhibito valde colorescente, 9-11  $\times$  4-5  $\mu$  (Fig. 1c). Inter basidia paraphysoidi subsunt simplices plus minusve ramosi.

Haec species facile cognoscitur, quod pori magni saepe hexagonoides fiunt. Praeterea ab utraque alia specie nota magnitudine basidiorum atque spororum differt, et quod probasidium non prius quam in partibus superioribus dividitur.

LY AD 1763 (holotypus in herbario A. David, Univ. Lugduni), ad truncum profunde in humo infossum, in margine silvae, Jungle Fall Valley Path, post casam, Bukit Timah Reserve, Singapore, 28.7.1974.

Fruiting bodies small, solitary, subdimidiate to dimidiate, leathery and flexible when fresh, hard and horny when dried, 2-3 cm long, radius of 1-1.8 cm, and 0.3-0.85 cm thick. *Upper surface* (Plate 1b) appanate to slightly convex, light ochraceous 10 YR 8/6 7/6 7/8 except towards the margin which is whitish, velutinous to hispid when fresh, becoming strongly radially wrinkled on drying. *Hymenial surface* pale brown between 10 YR 8/2 and 2.5 Y 8/2. Pores big angular, more or less hexagonal, about 1 mm. diam (Plate 1a). Numerous fascicles of hyphae emerging from the hymenium and visible under the hand-lens. Tubes and context concolorous and not distinctly separated. *Hyphal system* dimitic: skeletal hyphae hyaline (fig. 1b), 4-5  $\mu$  diam., with walls up to 1  $\mu$  thick. Generative hyphae hyaline, with thin walls, about 2-3  $\mu$ , with very long cells, so that the clamp connections are rare and difficult to see. *Basidia* clavate, 20  $\times$  8  $\mu$ , divided up longitudinally in the upper part (Fig. 1a), with 4 sterigmata which are subulate and 10-12  $\mu$  long. *Basidiospores* hyaline, neither cyanophilous, nor amyloid, nor dextrinoid, with thin walls, subcylindric, more or less depressed, with one apical region which can be dyed strongly with ammoniacal Congo, 9-11  $\times$  4-5  $\mu$  (Fig. 1c).

This species is easily recognizable by its big pores which are often hexagonal. It differs from the other two known species of *Aporpium* by the size of the basidia and of the spores, and by the fact that the probasidium is only divided up longitudinally in the upper part.

#### *Ecological and geographical distribution*

LY AD 1763 (holotype in the herbarium A. David, University of Lyon), on prostrate trunk, partly buried in the ground, at the edge of the forest, Jungle Fall Valley Path, behind the hut, Bukit Timah Reserve, Singapore. 28.7.1974. LY AD 1820 on section of a trunk, within the edge of the forest, McRitchie Jungle, Singapore. July 1974.

#### **An *Aporpium* sp. very similar to *A. dimidiatum***

This species, which we collected only once in Singapore presents so many similarities with *Aporpium dimidiatum* that we prefer to be cautious and not to make it a new species, at least for the time being. It differs from *A. dimidiatum* in the small size of its fruiting bodies, the smaller pores, and in being constantly sulcate. *Fruiting bodies*, many, small, dimidiate to effused-reflexed, solitary or more or less confluent in longitudinal stripes, 2.5-3 cm long, radius 1.5 cm, 0.7-8.0 cm thick, becoming very hard after drying. *Upper surface* convex, not hairy, but showing a fine tomentum under the hand-lens, beige to light rust 10 YR 8/3 7/3 7/4. Marginal area usually with 2-3 concentric grooves, the rest of the upper surface more or less scrobiculate. *Context* leathery, strongly zoned with brown

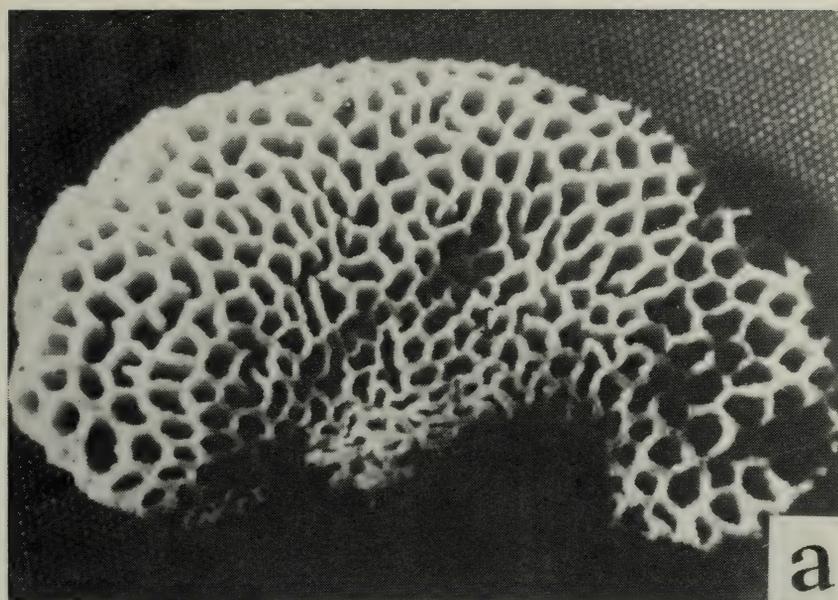


Plate 1. Fruitbody of *Aporpium hexagonoides* (x3)  
*a*: hymenial surface, *b*: upper surface.



stripes of cartilaginous consistency corresponding to growing layers. *Hymenial surface* greyish white, becoming brown when touched: (5-) 8-10 pores per mm. Microscopic characters: all identical to those of *A. dimidiatum*.

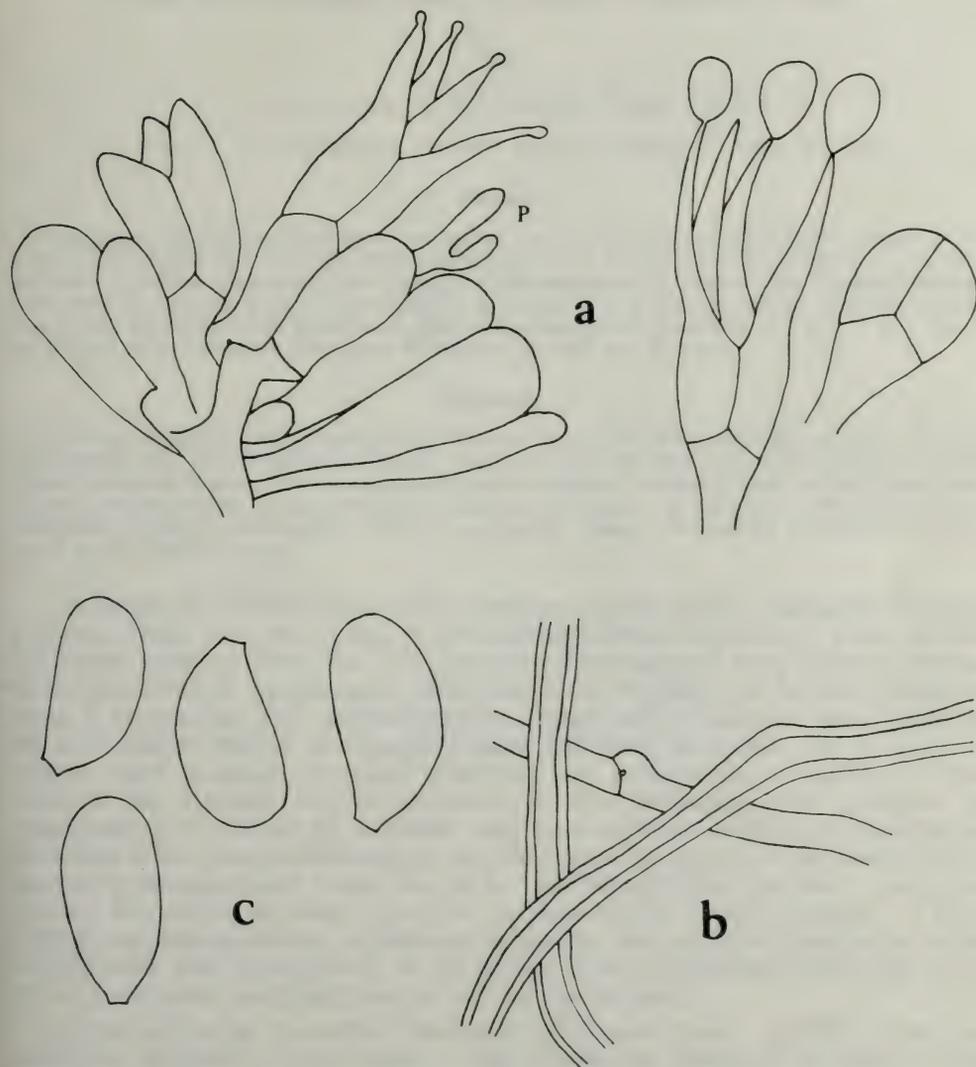


Fig. 1. *a*: fragment of the hymenium squashed after one night in ammoniacal Congo (x 2000)  
*b*: skeletal and generative hyphae (x 2000).  
*c*: spores (x 3000).

#### Reference

- DAVID, A. 1974. *Aporpium dimidiatum*, nouvelle tremellale porée. *Bull. trimest. Soc. mycol. Fr.* **90**: 179-185.



# Sur Un Nouveau Bolet Tropical à Spores Ornées

par

JACQUELINE PERREAU et ROGER HEIM

Laboratoire de Cryptogamie, Muséum National d'Histoire Naturelle, Paris

## Résumé

Originaire du Gabon, le *Boletus cornalinus* est un *Xerocomus* entièrement moucheté du même rose-pourpre que celui qui teinte les pores, tandis que la chair et les tubes se révèlent incarnats; il possède des spores brun jaunâtre à ornementation peu accentuée, d'irrégulièrement et densément fovéolée à verrucoso-cristulée. Il s'apparente à d'autres bolets appartenant aux sous-genres *Phylloporus* et *Xerocomus* dont certaines espèces montrent des spores non lisses; ses affinités plus lointaines pourraient se trouver du côté des *Piperati*.

## Summary

*Boletus cornalinus*, originating from Gabon, is a *Xerocomus* entirely spotted with the same purple rose colour that characterizes its pores, with the flesh and tubes being incarnate. Spores yellowish brown, finely ornamented; ornamentation irregularly and densely foveolated to verrucose-cristulate. Related to other Boletes, especially of subgenera *Phylloporus* and *Xerocomus* where some species exhibit non-smooth spores. Its remote affinities could be traced to the *Piperati* group.

À l'aube du XX<sup>ème</sup> siècle, on ne connaissait guère qu'une quinzaine de bolets à spores ornées avec, parmi eux, le cosmopolite *Boletus strobilaceus* Scop. ex. Fr. sur lequel Berkeley créa, dès 1851, le genre *Strobilomyces* et le *Boletus ananas* Curtis qui devint le type du genre *Boletellus* établi, en 1909, par Murrill. Actuellement, il est possible d'en compter plus de soixante-dix, découverts notamment au fur et à mesure que se développait l'étude des flores tropicales: ils se trouvent répartis dans plusieurs coupures génériques ou sous-génériques selon les conceptions des Auteurs sur la systématique des Bolétales. Bien qu'ayant la caractéristique commune de présenter une ornementation sporale, ces espèces se rattachent à des groupes différents au sein de l'ensemble formé par les champignons charnus à hyménophore tubulé et, si les indications tirées de leurs spores ne peuvent être seules décisives pour leur classement, du moins suggèrent — elles souvent des regroupements, affinités ou tendances; ainsi en est-il pour la forme de ces éléments, leur pigmentation et les particularités architecturales de leur paroi qui se manifestent essentiellement au niveau de l'exospore.

Tous ces bolets montrent justement une assez grande diversité dans les motifs de décoration exosporique: à côté de réseaux serrés et profonds, d'une ordonnance presque régulière, ou d'épaisses nervures longitudinales, on observe des verrues plus ou moins massives, des crêtes, des ailes élevées ou de fines stries, des nappes fovéolaires d'une extraordinaire variabilité, des réseaux contournés, incomplets ou formés d'amples alvéoles. Evidemment, selon les espèces, l'ornementation ne présente pas la même importance et apparaît parfois si faible qu'on la distingue à peine au microscope photonique et qu'il faut étudier ses détails en microscopie électronique à balayage.

Tel est le cas chez un bolet recueilli, à plusieurs reprises, par M. Gérard Gilles, dans la forêt de la Mondah, près de Libreville, au Gabon, forêt qui abrite une flore fongique particulièrement riche et intéressante, peu connue encore. Entièrement rose pourpré à incarnat, comme l'est la variété de calcédoine appelée cornaline, cette espèce nouvelle a reçu le nom de *Boletus (Xerocomus) cornalinus*.

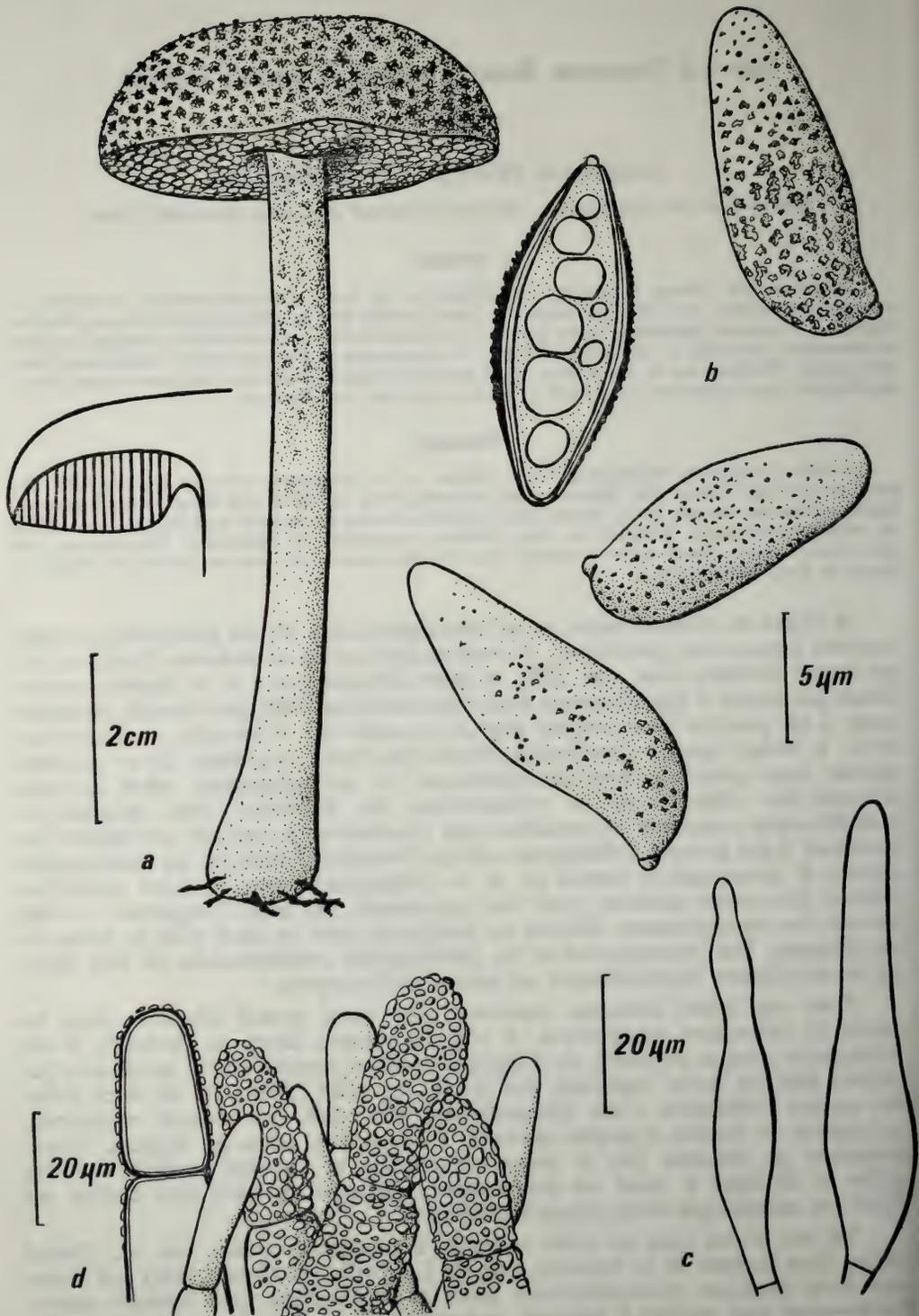


Fig. 1. *Boletus cornalinus*: a — Carpophore et coupe dans le chapeau; b — spores, dont une en coupe optique, vues au microscope photonique; c — pleurocystides; d — hyphes du revêtement pileïque.

## Description

### Caractères macroscopiques

*Chapeau* de 20–60 mm de diamètre et jusqu' à 20 mm d'épaisseur, convexe, puis convexe-aplati, régulier, sec, entièrement moucheté de flocons rose pourpré, vieux rose, rose vineux (Séguy 82 et 83)\* sur un fond plus clair, rosé (S 80), l'ensemble passant lors de la dessiccation à un brunâtre mêlé de tons rouillés-cuivrés; marge arrondie, très légèrement excédante, parfois de teinte plus pâle; revêtement non séparable.

*Chair* de 5 à 10 mm d'épaisseur, sèche, d'un blanc-rose pourpré, incarnat, proche de S 130, jaunissant à l'air en deux à trois minutes.

*Hyménophore* tubulé, horizontal ou faiblement ventru, échancré autour du sommet du pied selon des lamelles décourrentes en filet sur celui-ci; tubes longs de 5–15 mm, blanc rosé (S 130), immuables, mais devenant brun-jaune lorsqu'ils sont poudrés par la multitude des spores, à pores arrondis au début, puis subanguleux, assez réguliers, de 0,6–1 mm de diamètre, rose vineux (S 82), nettement plus vermillon (S 93–94) sur exsiccata.

*Pied* relativement grêle, de 50–100 mm de longueur, atteignant 6–8 mm de diamètre et 10 mm à la base vers laquelle il se dilate progressivement, fibreux, plein, entièrement couvert de flocons et de courtes fibrilles rose pourpré (S 82); la base est plus ou moins enveloppée d'un manchon de mycélium beige rosé d'où partent quelques rhizomorphes brun noirâtre assez gros et tenaces (Fig. 1, a).

*Couleur des spores en masse* : brun jaune.

*Odeur* inconnue.

*Saveur* légèrement acidulée.

### Caractères macrochimiques

NH<sub>4</sub>OH : instantanément jaune-brun verdâtre sur le revêtement et la chair — Acides : réaction nulle — FeSO<sub>4</sub> : immédiatement brunâtre sur la chair piléique — Iode (Réactif de Melzer) : réaction nulle sur la chair.

### Caractères microscopiques

*Basides* sub-ellipsoïdes, de 25–30 × 10–12 μm, portant quatre stérigmates effilés, peu arqués, longs de 5 μm en moyenne.

*Spores* de (13) — 13,5 — 15 × 4,5 — 5,5 — (6,2) μm, ellipsoïdes-fusifformes, longuement atténuées vers le sommet arrondi, subtilement aplati parfois; avec, à maturité, une dépression supra-appendiculaire accentuée, la face dorsale offrant souvent une convexité, puis une légère concavité juste au-dessus de l'appendice hilaire petit et subcylindrique; à gouttelettes lipidiques assez nombreuses; à paroi ornée, jaune brunâtre; non amyloïdes.

Au microscope photonique (Fig. 1, b), l'ornementation, peu accentuée, apparaît composée de multiples ponctuations délicates et de taches un peu arrondies ou étoilées-divariquées, parfois disposées en alignements, brunâtres ou jaune réfringent selon la mise au point. En coupe optique, cette ornementation se traduit par des échancrures festonnées dans une exospore colorée, alors qu'épispore et endospore sousjacentes demeurent d'épaisseur régulière. Toutefois, certaines spores montrent des plages pratiquement lisses.

Naturellement, les observations en microscopie à balayage précisent les détails d'un relief qui, dans ces conditions, se révèle moins masqué par la périspore et l'ectospore. En voyant les nombreuses fossettes ou anfractuosités plus ou moins fusionnées, isolant de petites crêtes contournées et irrégulièrement anastomosées ou des protubérances versiformes (Pl. I, A-D), on ne peut que penser aussitôt à une nappe fovéolaire. Toutes les caractéristiques de ce type ornemental sont

\* — E. Séguy — *Code universel des couleurs*. P. Lechevalier, Paris, 1936.

d'ailleurs réunies puisque l'on retrouve des plages de surface sporale lisses, surtout au sommet, ou à peine scrobiculées comme sur la zone entourant l'appendice hilaire (en B); à l'opposé, l'aspect déchiqueté et "cunéiforme" de la décoration se remarque sur toutes les photographies de la planche.

*Pleurocystides* fusiformes à sommet étiré-atténué, parfois capité, toujours émoussé (Fig. 1, c), de  $50-65 \times 12-15 \mu\text{m}$ ,  $4-5 \mu\text{m}$  au col, à paroi fine, à contenu jaune brunâtre, légèrement flexueuses, émergentes, relativement abondantes (5 à 7 par  $100 \mu\text{m}^2$ ).

*Cheilocystides* peu différenciées sur l'arête des tubes, larges de  $7-15 \mu\text{m}$ , très nombreuses et couvertes de granulations polygonales-arrondies, de  $0,2-0,5 \mu\text{m}$  de diamètre, rouge orangé vif très réfringent.

*Trame* des tubes de type *Phylloporus* et *Xerocomus*; hyphes hyalines, larges de  $5-7 \mu\text{m}$ , non bouclées, à peine divergentes.

*Revêtement piléique* constitué d'hyphes entrecroisées, incrustées, de largeur variable ( $5-16 \mu\text{m}$ ), étranglées aux cloisons et dont les articles terminaux, longs de  $30-35 \mu\text{m}$ , sont cylindracés ou clavulés.

Ces hyphes que l'on voit également en bouquets dans les flocons du pied, sont recouvertes de granulations semblables à celles observées sur les poils de l'arête des tubes. Dans les préparations montées avec  $\text{NH}_4\text{OH}$ , elles se révèlent seulement hyalines-réfringentes, car leur teinte rouge orangé vif disparaît sous l'action de ce produit (Fig. 1, d).

#### *Habitat et répartition géographique*

A terre, parmi les feuilles, en forêt ombrophile. Forêt de la Mondah, km 31.5, environs de Libreville, Gabon. Leg. Gérard Gilles, 13-10 et 10-11-1968, n° Div. Gab. 33 (type) — Autres récoltes : 20-10-1968, n° Div. Gab. 39 et 21-09-1969, n° Div. Gab. 33.

### ***Boletus (Xerocomus) cornalinus* Perreau et Heim, sp. nov.**

*Pileus* 20-60 mm latus, usque 20 mm crassus, convexus ad applanatum, omnino e purpureo-roseo ac vinoso floccosus, interstitiis dilute roseis. *Caro* incarnata, mox in aere flavescens, sapore acidulo. *Tubi* incarnati, postice breviores, semoti, lamellis decurrentes circum stipitis apicem; pori purpureo-rosei, subangulares. *Stipes* comparate gracilis, 50 - 100 mm longus, 6 - 8 mm diametro, basi leviter dilatatus, pileo concolor, mycelio isabellino, rhizomorphis umbrinis. *Sporae* (13) -  $13.5 - 15 \times 4.5 - 5.5 - (6,2) \mu$ , ellipsoideo-fusifformes, brunneolo-flavae, haud amyloideae, minutissime punctulatae, per microscopium electronicum ex irregulariter denseque foveolatis verrucoso-cristatae. *Pleurocystidia* numerosa,  $50 - 65 \times 12 - 15 \mu$ , elongato apice fusiformia, projicientia, brunneo-flavo succo impleta; *cheilocystidia* multis cinnabarinis  $\text{NH}_4\text{OH}$  decolorantibus granulis incrustata; hyphae cuticulares pilei stipitisque similiter tectae. *Hyphae* afibulatae. Ad terram in silva — Libreville, Gabon — leg. G. Gilles, 13-10 ac 10-11-1968, n° Div. Gab. 33 (typus PC).

La mise en évidence d'une ornementation sporale chez ce bolet africain aurait pu conduire à le placer dans le genre *Boletellus*; il ressemble en effet quelque peu aux *B. obscurecoccineus* (Höhn.) Singer et *B. cardinalicus* Heim et Perreau dont cependant les longues spores sont finement striées; par d'autres caractères, il paraîtrait se rapprocher du *B. purpurascens* Heinem. Or, tout récemment, E. J. H. Corner a suggéré que cette dernière espèce, à spores largement elliptiques et fortement verruqueuses, pourrait appartenir, ainsi que le *B. shichianus* (Teng et Ling) Teng à spores verruculeuses, au sous-genre *Punctispora* qu'il a établi avec, comme représentants, les *B. betula* Schw. et *B. punctisporus* Corner. Ces champignons possèdent précisément de grandes spores couvertes d'une nappe fovéolée

qui déploie toute la variabilité de détail qu'une telle décoration implique — toutefois, il s'agit simplement d'un phénomène de convergence, car le *B. cornalinus* s'éloigne d'eux par d'importantes différences liées à la réticulation du pied, la teinte jaune, puis olivacée de l'hyménophore, le bleuissement de la chair, etc . . .

Ces deux dernières caractéristiques se révèlent également propres à de nombreux *Xerocomus* dont s'écarte aussi notre espèce qui n'est pas sans évoquer cependant le *B. versicolor* Rostk. des régions tempérées; elle pourrait être, de plus près encore, comparée aux *B. puniceus* Chiu et *B. roseolus* Chiu, du Yunnan, aux *B. phoeniculus* Corner et *B. albipurpureus* Corner, de Malaisie. Avec ses hyphes incrustées, le *B. cornalinus* toucherait au groupe du *B. chrysenferon* St.-Amans et se rapprocherait légèrement de certains représentants tropicaux de cet ensemble, décrits notamment par E. J. H. Corner (*B. catervatus*, *B. satisfactus*) et qui offrent une chair jaunâtre ou blanche, immuable. L'existence d'incrustations sur les hyphes cuticulaires se montre d'ailleurs fréquente chez les bolets et M. Josserand a déjà noté pour le *B. porphyrosporus* [*Porphyrellus porphyrosporus* (Fr. et Hök) Gilb.], l'action dissolvante de l'ammoniaque sur le pigment "avec persistance de la masse primitivement pigmentée".

D'un autre côté, on peut noter certaines ressemblances entre le bolet gabonais et les *Xerocomus* à pores rouges de Nouvelle-Zélande [*X. macrobbii* McNabb peut-être, *X. nothofagi* McNabb et surtout *X. rufostipitatus* McNabb à chair crème] ou de Malaisie [*B. rubriporus* Corner, toutefois à chair bleuissante]. Enfin, et de même que pour ceux-ci, on peut penser, (car le *B. cornalinus* rappelle le *B. amarellus* Quélet), à des relations lointaines avec le groupe des *Piperati*, plus particulièrement avec des espèces nord-américaines telles que *Boletus pseudorubinellus* Smith et Thiers, *B. rubritubifera* Kauffman, *B. rubinellus* Peck; il faut remarquer pourtant que les réactions colorées obtenues sous l'influence de  $\text{NH}_4\text{OH}$  ou de  $\text{FeSO}_4$  ne concordent pas.

L'insertion d'une espèce à spores ornées dans le sous-genre *Xerocomus* ne peut guère surprendre puisque de nombreux *Boletellus*, dont les éléments sporaux apparaissent très finement costulés, se situent au voisinage immédiat de ce taxon et peut-être même en dépendent. D'autre part, si E. J. H. Corner mentionne l'existence probable d'une légère striation chez le *B. (Xerocomus) albipurpureus*, l'un de nous (J.P. 1965) signalait la présence de lignes, d'ondulations exosporiques chez le *B. subtomentosus* Fr. Grâce à des observations au microscope électronique à balayage, Moore et Grand 1970, ont montré, que les basidiospores du *Phylloporus rhodoxanthus* (Schw.) Bres. n'étaient pas lisses; leur surface porte, en effet, une multitude de protubérances fusiformes, enchevêtrées, souvent caténulées ou parallèles entre elles. De notre côté et avec cette même technique (J.P., inédit), des recherches ont permis d'examiner de façon plus précise le relief entrevu sur les spores de nombreux exemplaires de *B. subtomentosus*, mais aussi de le déceler chez le *B. parasiticus* Fr. : extrêmement peu accusé, il se manifeste en général par de délicates nervures ou par des saillies allongées, disposées en tous sens. Sur certaines spores, des fossettes, ainsi que des anfractuosités irrégulières sont visibles. L'agencement désordonné de petites crêtes en fuseau et à profil arrondi constitue un motif de décoration qui se révèle bien différent des nappes fovéolaires que l'on trouve chez le *B. cornalinus*; il ressemble fort, par contre, à celui observé sur les spores d'un champignon tout autre, *Hericium coralloides* (Scop. ex Fr.) S. F. Gray, chez qui la taille des protubérances est cependant plus grande.

Divers aspects d'architecture exosporique sont donc présents chez les *Xerocomus*; il est vraisemblable que d'autres seront décelés, reflétant et accentuant encore l'hétérogénéité de ce vaste sous-genre de bolets, mais sans doute l'examen de ces aspects aidera-t-il à la recherche d'une interprétation systématique plus naturelle de ce groupe.

## Notes Bibliographiques

- CHIU, W. F. 1948. The boletes of Yunnan. *Mycologia* **40**: 199–231.
- CORNER, E. J. H. 1970. *Phylloporus* Quél. and *Paxillus* Fr. in Malaya and Borneo. *Nova Hedwigia* **20**: 793–832, 8 fig., 8 pl.
- 1972. *Boletus* in Malaysia. Bot. Gardens, Govern. Print. Off., Singapore, 263 pp., 80 fig., 23 pl.
- 1974. *Boletus* and *Phylloporus* in Malaysia: further notes and descriptions. *Gdns' Bull. Singapore* **27**: 1–16, 1 fig.
- HEIM, R. & J. PERREAU 1963. Le genre *Boletellus* à Madagascar et en Nouvelle-Calédonie. *Revue Mycol.* **28**: 191–199, 6 fig., 1 pl.
- HEINEMANN, P. 1954. Flore Iconographique des Champignons du Congo, Bruxelles, 3ème fasc.: *Boletineae*: 49–80, 3 pl.
- JOSSERAND, M. 1952. La description des Champignons Supérieurs. P. Lechevalier, Paris, 338 pp.
- McNABB, R. F. R. 1967. The *Strobilomycetaceae* of New Zealand. *N.Z. Jl Bot.* **5**: 532–547, 3 fig.
- 1968. The *Boletaceae* of New Zealand. *N.Z. Jl Bot.* **6**: 137–176, 8 fig.
- MOORE, R. T. & L. F. GRAND. 1970. Application of scanning electron microscopy to basidiomycete taxonomy. *Proceedings IIIrd Ann. Scann. Electr. Microsc. Symp.*, Chicago, 7 pp., 33 fig.
- PERREAU-BERTRAND, J. 1961. Recherches sur les ornements sporales et la sporogénèse chez quelques espèces des genres *Boletellus* et *Strobilomyces* (Basidiomycètes). *Annls Sci. nat., Bot.*, 12ème série, **2**: 399–489, 35 pl.
- 1964. Complément à l'étude des ornements sporales dans le genre *Boletellus*. *Annls Sci. nat., Bot.*, 12ème série, **5**: 753–766, 5 pl.
- 1965. Structure membranaire et différenciations apicales chez les spores des genres "*Xerocomus*, *Boletellus*, *Heimiella* et *Strobilomyces*". *C. r. hebdom. Séanc. Acad. Sci., Paris* **260**: 4245–4248, 1 fig.
- 1974. Variations sur un thème ornemental: le réseau des basidiospores. Trav. myc. dédiés à R. Kühner, Numéro spécial, *Bull. Soc. Linn. Lyon* **43**: 327–338, 1 fig., 2 pl.
- PERREAU, J. & R. HEIM. 1969. L'ornementation des basidiospores au microscope électronique à balayage. *Revue Mycol.* **33** (1968): 329–340, 3 fig. 4 pl.
- SINGER, R. 1945. The *Boletineae* of Florida with notes on extralimital species. I. The *Strobilomycetaceae*. *Farlowia* **2**: 97–141, 1 pl.; II. The *Boletaceae* (*Gyroporoideae*). *Ibid.* 223–303, 1 pl.
- 1962. Agaricales in Modern Taxonomy. 2nd ed. J. Cramer, Weinheim, 915 pp., 73 pl.
- 1964. Boletes and related groups in South America. *Nova Hedwigia* **7**: 93–132, 4 pl.
- SMITH, A. H. & H. D. THIERS. 1971. The Boletes of Michigan. The University of Michigan Press, Ann Arbor, 428 pp., 133 fig., 157 pl.
- SNELL, W. H. & E. A. DICK. 1970. The *Boleti* of Northeastern North America. J. Cramer, Lehre, 115 pp., 87 pl.
- TENG, S. C. 1964. Champignons de Chine. Pékin, 808 pp.
- WATLING, R. 1970. *Boletaceae-Gomphidiaceae-Paxillaceae*. *British Fungus Flora Ag. and Boleti*. Royal Botanic Garden, Edinburgh, 125 pp., 108 fig.

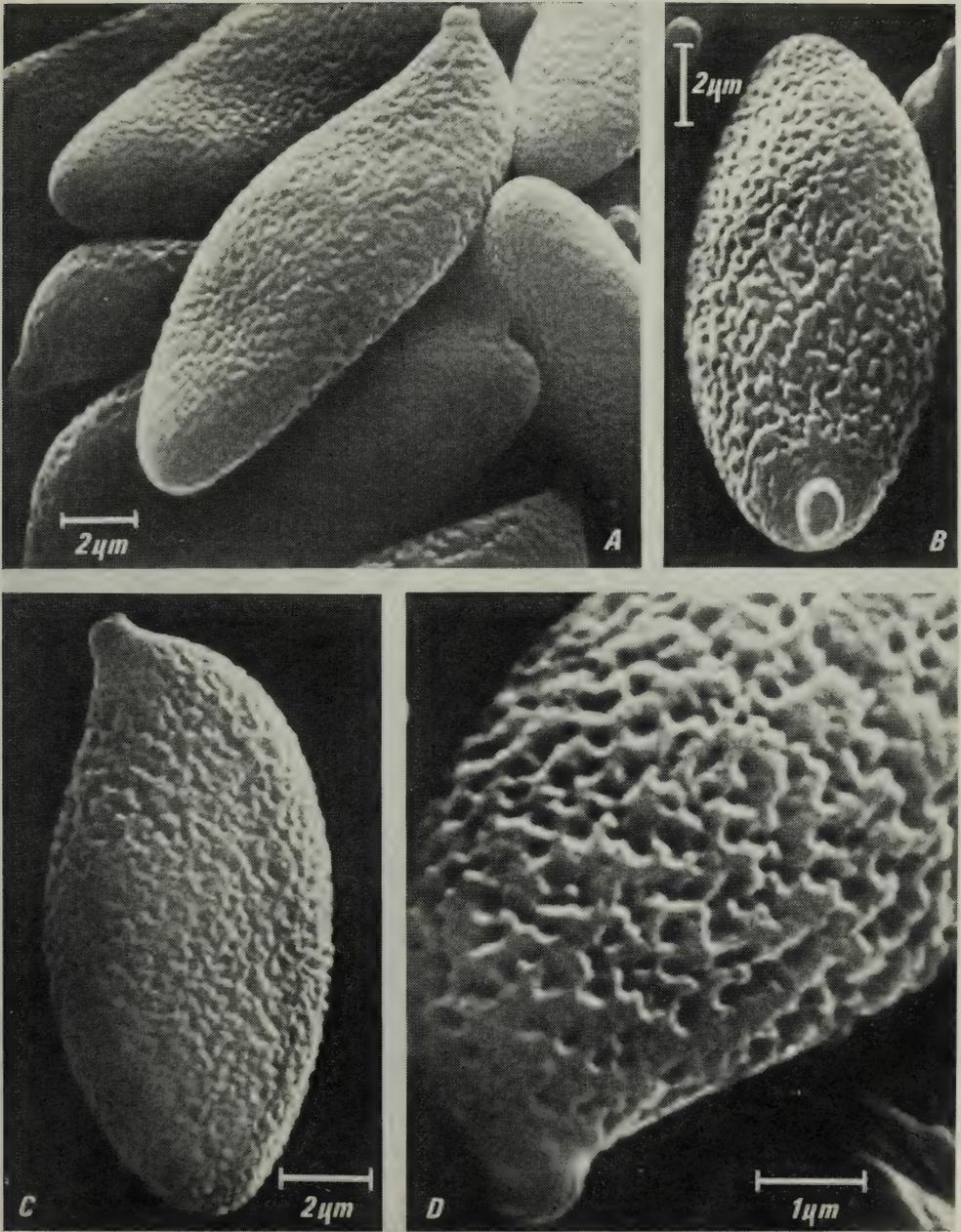


Planche I. Spores du *Boletus cornalinus* vues au microscope électronique à balayage.  
(Cl. Lab. Géol. Muséum, Paris)

- A — Divers aspects de l'ornementation fovéolée et verrucoso-cristulée;
- B — Spore en profil frontal, montrant une zone nettement fovéolée autour de l'appendice hilare;
- C — Spore en profil dorsi-ventral, à ornementation très déchiquetée, verruqueuse et cristulée;
- D — Détail de l'ornementation en nappe fovéolaire très densément creusée.



# Development of Primary Secretary Ducts in the Stem of *Mangifera indica* L. (Anacardiaceae)

by

A. FAHN and D. M. JOEL

*Department of Botany, The Hebrew University of Jerusalem, Israel*

## Summary

The development of primary secretary ducts of stems of *Mangifera indica* L. has been studied with the aid of the electron microscope. The duct cavity has been found to be formed lysigenously. The primary ducts start to develop in the young leaf primordia. There the future epithelial cells still contain very large central vacuoles. These cells envelope a single file of cells which disintegrate and initiate the duct cavity. In the stem the duct cavity enlarges by lysis of epithelial cells and neighbouring cells become epithelial. In open ducts wall-remains of disintegrated cells are found attached to the active epithelial cells.

## Introduction

Many early botanists with their excellent minds and with the aid of the then available equipment presented descriptions of the structure of cells and tissues, which, when examined many years later with the aid of the electron microscope, were usually found to be accurate. However, new embedding and sectioning techniques for light microscopy and the use of the electron microscope for anatomical investigations have in many cases added important new information to the understanding of developmental processes of cells and tissues.

The mode of initiation and development of cavities of internal secretary structures of plants has been dealt with mainly in early studies. Various investigators often held contradictory views as to whether cavities of specific ducts develop schizogenously, lysigenously or schizo-lysigenously (cf. Carr and Carr, 1970).

The ducts of the Anacardiaceae were examined by many researchers. The views on the manner of formation of the duct cavity in the different species and organs vary to a great extent (Müller, 1866-67; Sieck, 1895; Tschirch, 1900; Venning, 1948; Varghese and Pundir, 1964; Fahn and Evert, 1974). While studying the ducts of *Mangifera indica* and the way their cells produce and eliminate their secretary substance, we also tried to clarify the manner of duct cavity development in the different plant organs, with the aid of the electron microscope.

The present paper deals with the development of the primary shoot ducts.

## Material and Methods

Stem portions from the apical region and from mature internodes of one-year-old saplings of mango (*Mangifera indica* L.) were used for examination. The saplings were grown in a greenhouse at the Hebrew University of Jerusalem.

For light microscopy hand cut sections were used.

For electron microscopy small portions of tissues including ducts were fixed in 6% glutaraldehyde for 2 hours, postfixed in  $\text{OsO}_4$ , 2% for 2 hours (both in cacodylate buffer 0.1M pH 7.2), dehydrated in ethanol and embedded in Spurr's low viscosity embedding medium (Spurr, 1969). Sections were cut on LKB

ultrathome III, stained with uranyl acetate and lead citrate, and examined with a Philips 300 electron microscope.

### Observations

In the stems of mango (*Mangifera indica*) the primary secretory ducts occur in the phloem and pith (Plate 1, A-C). The mature duct consists, in cross section, of a cavity which is surrounded by a few concentric rows of cells which are more or less isodiametric or somewhat flattened and smaller than those of the neighbouring tissues. In the direction of the long axis of the duct they are elongated. No distinct intercellular spaces occur between these cells. The cells of the row neighbouring the cavity do not differ much from the cells of the other rows. They contain a large central vacuole and a thin layer of cytoplasm (Plate 2, A). In the duct cavity the secreted material is confined to its periphery. Most of the secreted material is exuded from the duct cavity during cutting of the stem and the fixation of the material.

The ducts start to differentiate in the shoot apex. In order to follow their development, successive sections, starting about 6 mm from the shoot tip and proceeding upwards, were examined. In the upper young region of the stem most of the cells neighbouring the duct cavity, the epithelial cells, are rich in cytoplasm and contain only a few very small vacuoles (Plate 2, B; Plate 4, A). The cytoplasm of these cells is dense, the ER is well developed. Parallel aligned ER elements have sometimes been seen to occupy a large part of the cytoplasm (Plate 4, A). The nuclei are relatively large. Plastids and mitochondria are numerous. Golgi bodies are occasionally observed in groups (Plate 3, A). Osmiophilic droplets are common and often in association with plastids and Golgi bodies (Plate 3, A; Plate 4, A, B). The process of secretion and sites of synthesis of the secretory substances in the cells will be treated in a separate article.

The duct cavity in the young portions of the stem is filled with electron dense secreted substances (Plate 4, B).

At the level of about 6 mm from the tip of the shoot apex single cells with a large vacuole and a very thin layer of cytoplasm are observed among the typical epithelial cells. Cell "a" in Plate 2, B gives the impression of joining the row of the densely stained epithelial cells after having divided from a cell situated behind them. In the gap where this cell is seen to join the epithelial cells, remnants of the back wall of an epithelial cell which has apparently undergone lysis can be seen. The region of the middle lamella between the wall of the joining cell and the remains of the wall of the disintegrated epithelial cell can clearly be observed.

In a section at a somewhat higher level (Plate 4, A), two small, narrow and deformed epithelial cells (d) with a dark disordered content are present. Between two unchanged epithelial cells a wide gap (g) can be seen in the same section. Part of the gap is occupied by electron dense material. One may assume that a cell which was in this place has disintegrated. Wall remains of the missing cell are seen attached to the neighbouring cell of the row surrounding the epithelial cells. In addition to outer cells joining the epithelial cells new cells are formed by anticlinal division of the epithelial ones. Between the cytoplasm of the epithelial cells and their walls, mostly in the region facing the duct cavity, large spaces occur containing vesicular and membranous structures, as well as very dark osmiophilic material (Plate 4, B). A thin layer of osmiophilic material often surrounds the entire cytoplasm.

In all sections, walls of the epithelial cells facing the cavity consist of two layers between which a distinct middle lamella can be seen. The middle lamella is swollen in many places (Plate 3, A, B). The layer closer to the cavity is irregularly fringed. This layer apparently represents remains of walls of the cells which have disintegrated.

The continuation of the stem ducts was followed in the leaf primordia situated less than 1 mm from the tip of the shoot apex. In the stem, before entering the primordia, the epithelial cells which are rich in cytoplasm were seen, in cross section, to surround a cell with a disintegrated protoplast (Plate 5A). In the leaf primordium itself the future epithelial cells contained large central vacuoles and thin layers of cytoplasm. As at the base of the leaf, at the site of the future duct cavity a single cell with a disintegrated protoplast was found in cross sections, at least up to one third of the height of the leaf primordium (Plate 5, B). In few places initial stages of disintegration were also observed in the cell wall.

### Discussion

Diverse views of the mode of development of the duct cavity in the Anacardiaceae have been held by different authors. Engler (1896) dealing with the family, McNair (1918) who investigated *Rhus diversiloba* Torr. and Gray, and Fahn and Evert (1974) who investigated the secondary phloem ducts of *Rhus glabra* Thunb. stated that the ducts develop schizogenously. Sieck (1895), who worked on stems and fruits of *Anacardium occidentale* L. reported that the ducts originate schizogenously, but that continued development is lysigenous. Such a mode of duct development in Anacardiaceae was also reported by Tschirch (1900). Venning (1948) came to the conclusion that the manner of development of duct cavities varies among plant organs being of schizogenous origin in stems and leaves of *Schinus* and fruits of mango of schizo-lysigenous origin in stems and leaves of *Spondias* and mango and of lysigenous origin in floral organs (with the exception of the ovary) in mango. Varghese and Pundir (1964) reported that in the pseudocarp of *Anacardium occidentale* the ducts develop lysigenously.

The present electron microscopical investigation on the primary secretory ducts of the stem of mango showed that the cavities of these ducts initiate and develop lysigenously. The stem ducts initiate in the leaf primordia situated very close to the tip of the shoot apex. In the centre of the developing duct there is a single file of cells. The cells of this file disintegrate, initiating the development of the duct cavity.

In the stem, the duct cavity enlarges by lysis of epithelial cells, and neighbouring cells become epithelial. A proof for lysis of cells may be found in that remains of additional cell walls can be seen on the surface of the epithelial cell walls facing the duct cavity. Between these remains and the intact epithelial cell walls a middle lamella with occasional swellings can clearly be observed. It can thus be concluded that the lysis of the wall starts from inside the cell and progresses towards the middle lamella. This differs completely from the manner of wall lysis during schizogenous development of intercellular spaces of duct cavities (Fahn and Benajoun, in preparation).

Fractures occurring in the separation zone of leaves were also reported to be a result of the dissolution of the middle lamellar region of cell walls (Sexton and Hall, 1974).

The succession of wall lysis as seen in the mango ducts differs also from that reported by Tschirch (1889) for gum duct formation. There, according to Tschirch, the disintegration of walls starts in the primary walls and then proceeds in the secondary wall. The wall lysis in the cells of mango stem ducts differs therefore basically in mode of succession from that occurring in schizogenous processes and lysigenous formation of gum ducts.

Concurrently with the further process of cell lysis radial (anticlinal) divisions of epithelial cells may apparently take place. However, the initial stage of duct formation is strictly lysigenous.

### Acknowledgement

The authors wish to thank The Department of Horticulture of the Volcani Institute at Bet Dagan for kindly supplying the seeds from which the mango saplings were grown.

### References

- CARR, D. J. & S. G. M. CARR, 1970. Oil glands and ducts in *Eucalyptus* l'Hérit. II. Development and structure of oil glands in the embryo. *Aust. J. Bot.* **18**: 191–212.
- ENGLER, A. 1896. Anacardiaceae. In: A. Engler and K. Prantl (ed.), Die natürlichen Pflanzenfamilien III, **5**.
- FAHN, A. & R. F. EVERT, 1974. Ultrastructure of the secretory ducts of *Rhus glabra* L., *Am. J. Bot.* **61**: 1–14.
- McNAIR, J. B. 1918. Secretory canals of *Rhus diversiloba*. *Bot. Gaz.* **65**: 268–273.
- MÜLLER, N. J. C. 1866-67. Untersuchungen über die Vertheilung der Harze, ätherischen Oele, Gummi und Gummiharze, und die Stellung der Sekretionsbehälter im Pflanzenkörper. *Jb. wiss. Bot.* **5**: 387–421.
- SEXTON, R. & J. L. HALL, 1974. Fine structure and cytochemistry of the abscission zone cells of *Phaseolus* leaves. I. Ultrastructural changes occurring during abscission. *Ann. Bot.* **38**: 849–854.
- SIECK, W. 1895. Die Schizolysigenen Sekretbehälter. *Jb. wiss. Bot.* **27**: 197–242.
- SPURR, A. R. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. *J. Ultrastruct. Res.* **26**: 31–43.
- TSCHIRCH, A. 1889. Angewandte Pflanzenanatomie, Band I. Urban & Schwarzenberg, Vienna.
- 1900. Die Harze u.d. Harzbehälter. Gebrüder Borntraeger, Leipzig.
- VARGHESE, T. M. & Y. P. S. PUNDIR, 1964. Anatomy of the pseudocarp in *Anacardium occidentale* L., *Proc. Indian Acad. Sci.* **59**: 252–258.
- VENNING, F. D. 1948. The ontogeny of the laticiferous canals in the Anacardiaceae. *Am. J. Bot.* **35**: 637–644.

### Facing Page

Plate 1. Micrographs of hand cut cross-sections of a stem, showing *A*, primary (phd) and secondary (sd) phloem ducts, × 120; *B*, one primary phloem duct, × 300; *C*, a pith duct (pd), × 300.

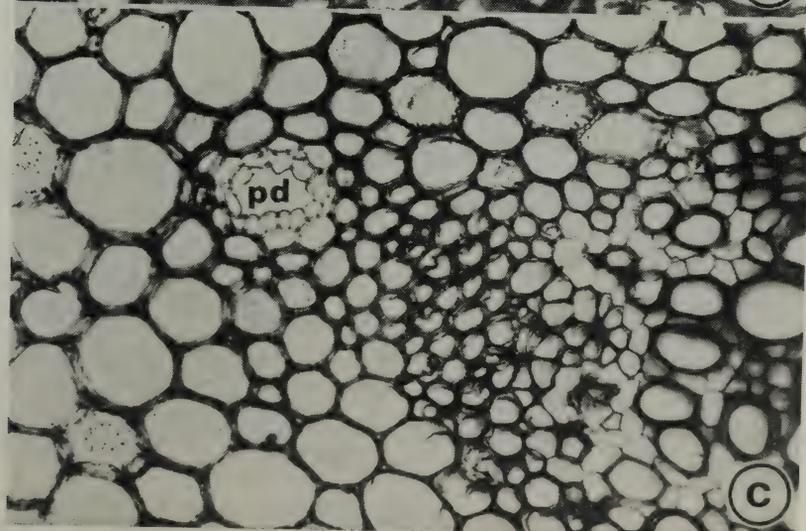
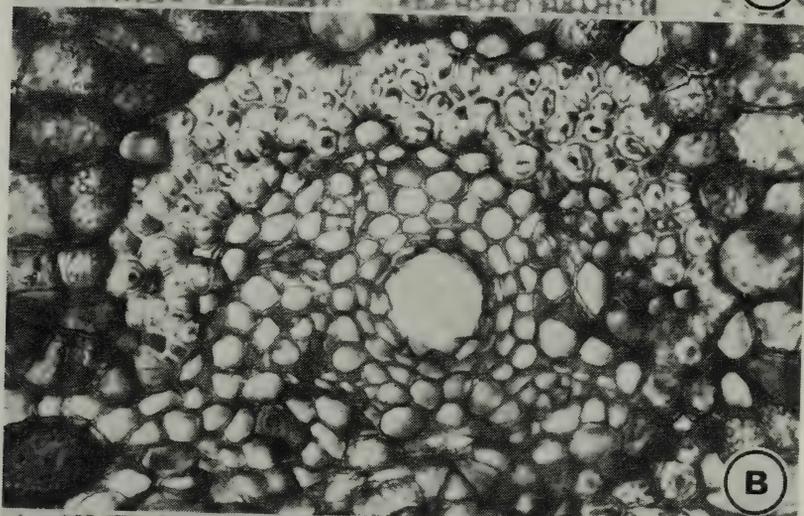
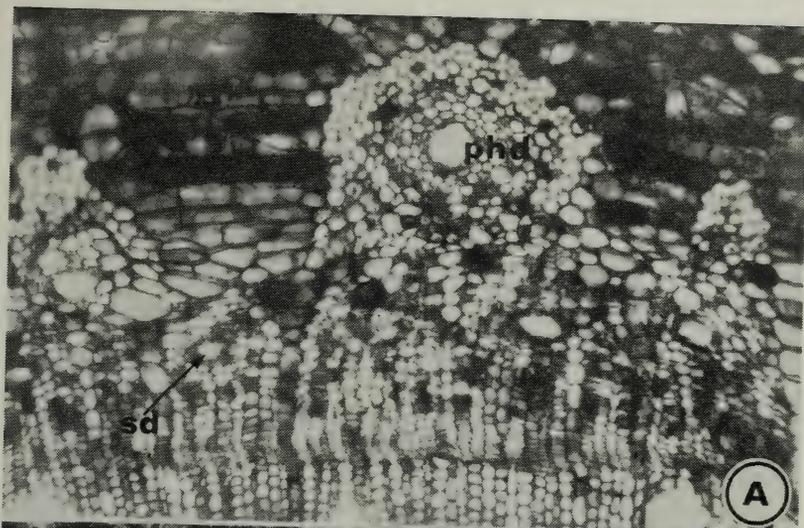




Plate 2. Electron micrographs of cross-sections of primary ducts. *A*, mature phloem duct; *c* — duct cavity, *wr* — wall remnant of disintegrating cell,  $\times 5000$ ; *B*, young pith duct showing a gap (*g*) in the epithelium apparently formed by disintegration of an epithelial cell. A neighbouring outer cell (*a*) is seen to join the gap,  $\times 4600$ .

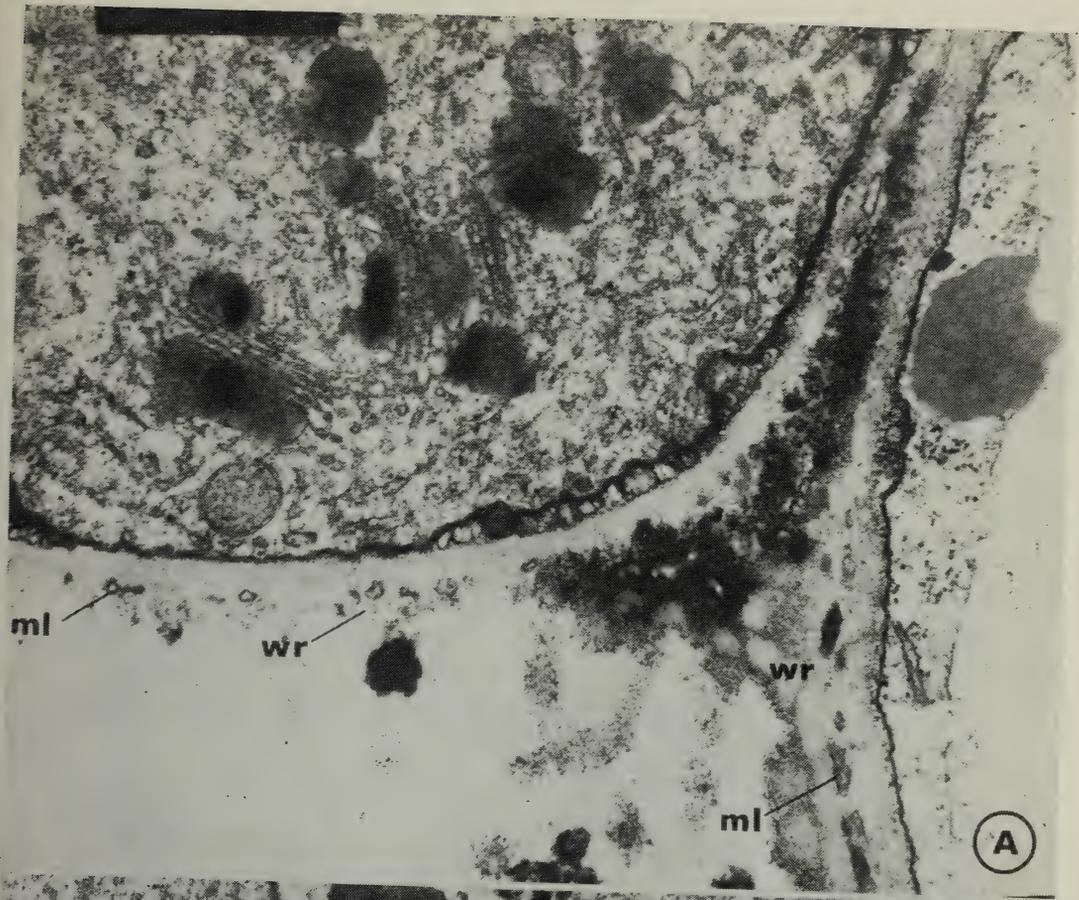


Plate 3. Electron micrographs of cross-sections of portion of young pith ducts showing, around the duct cavity, wall remains of disintegrated cells. ml — middle lamella, wr — wall remains. A,  $\times 40,000$ ; B,  $\times 30,000$ .

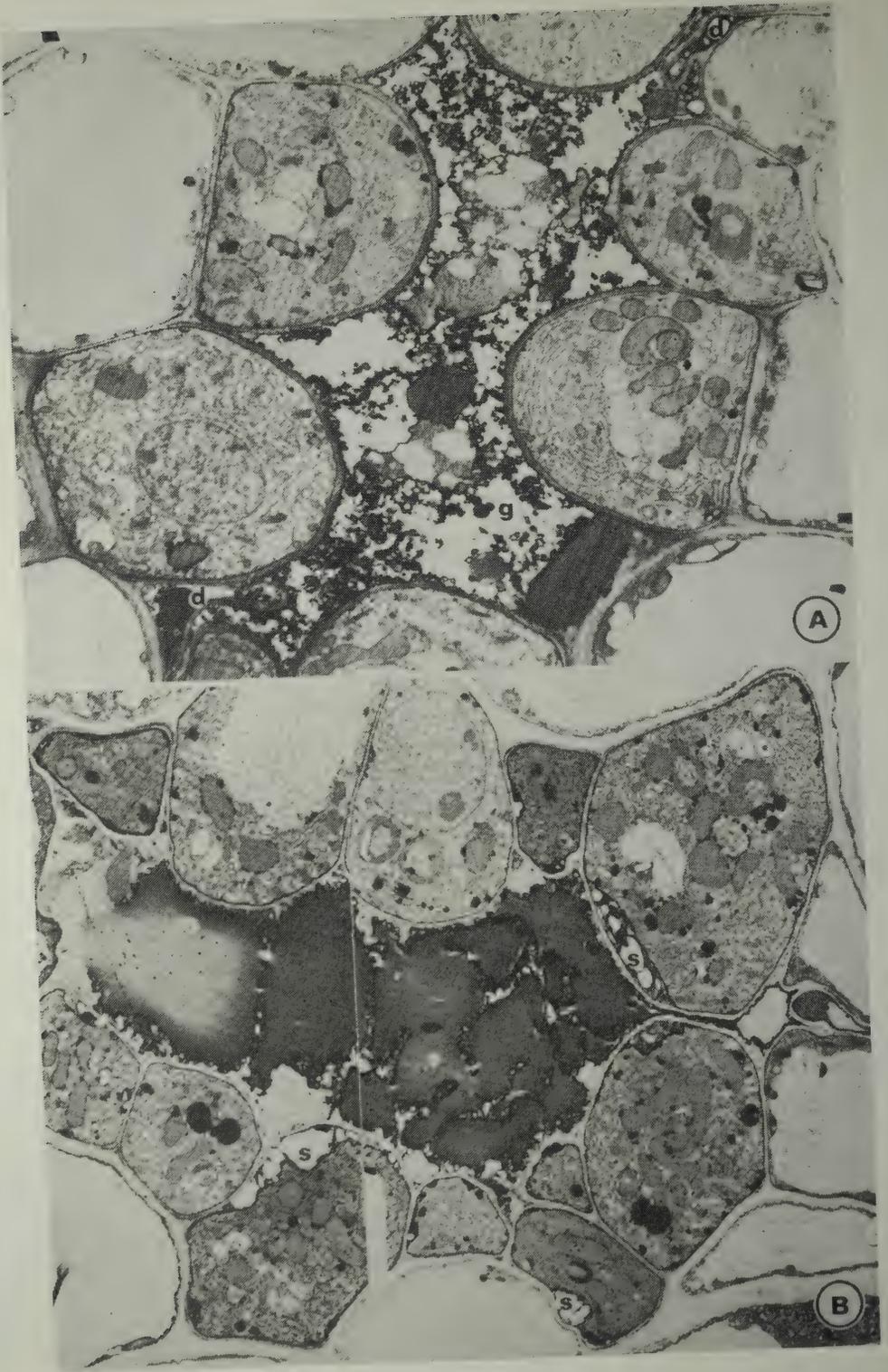


Plate 4. As in plate 3. *A*, showing 2 deformed cells (d) and a gap (g) in the epithelium,  $\times 4000$ ; *B*, showing in epithelial cells spaces (s), between protoplast and walls, filled with vesicular and lamellar structures,  $\times 3700$ .

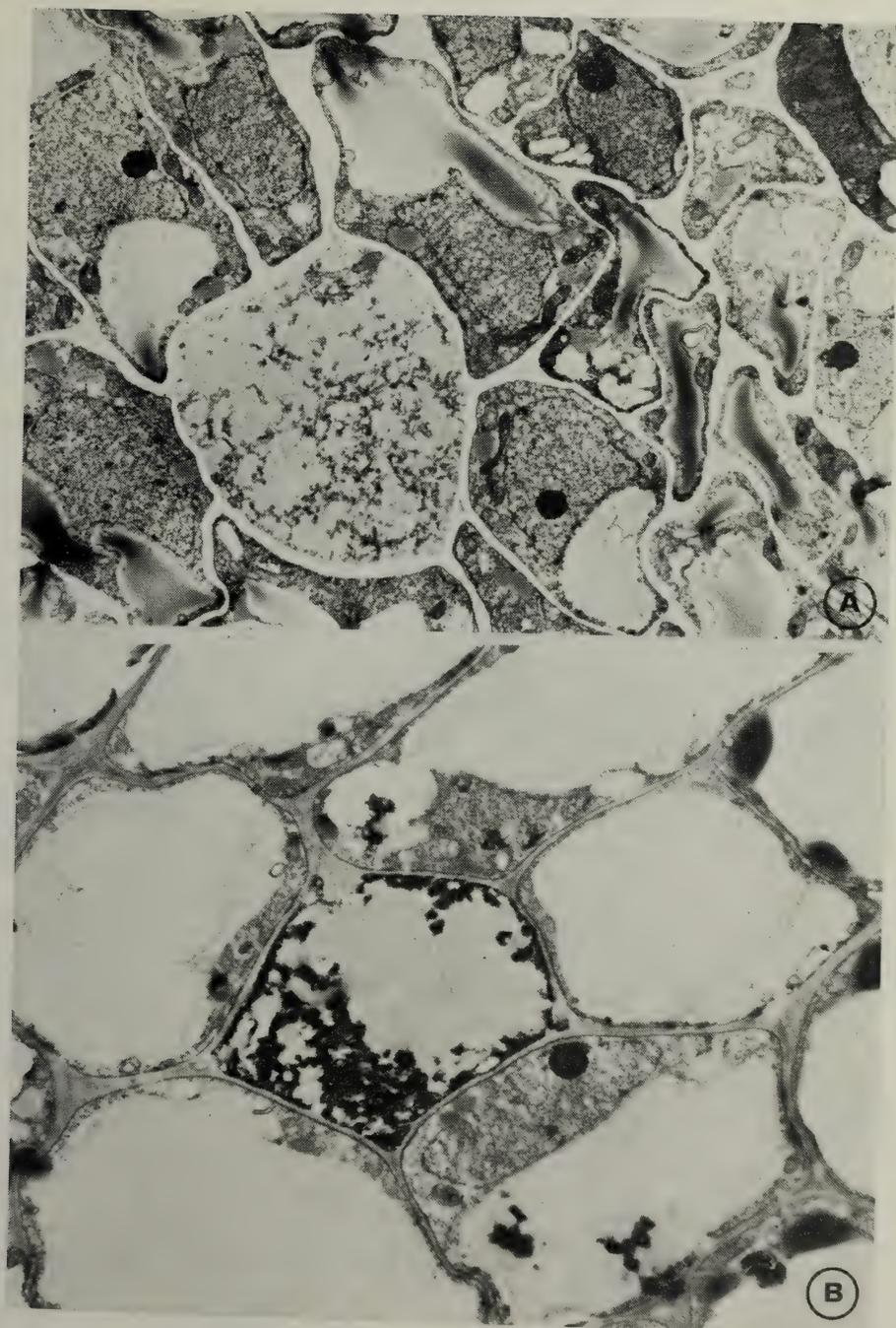


Plate 5. *A*, Electron micrograph of a cross-section of a pith duct close to the base of a leaf primordium.  $\times 5000$ ;  
*B*, A cross-section of the duct shown in *A* but in the leaf primordium.  $\times 5000$ .



# Girdling Vascular Bundles in Dicotyledon Flowers

by

KENNETH R. SPORNE

*The Botany School, University of Cambridge*

## Summary

For more than 35 years, girdling vascular bundles have been known to occur in the flowers of species belonging to nine families of dicotyledons. Further families are now added to the list, bringing the total to twenty. The occurrence of girdling bundles does not appear to have any special taxonomic or phylogenetic significance. Vascular patterns with girdling bundles are illustrated for members of eleven families.

The purpose of this paper is to draw attention to a phenomenon which is more widespread among dicotyledons than has hitherto been realized, namely, the occurrence within the floral receptacle of a horizontal girdling vascular bundle which connects the vascular bundles supplying the perianth members.

The term "girdling vascular bundle" was used by Saunders (1939) to describe such lateral interconnections in species belonging to the Cistaceae, Combretaceae, Lythraceae, Melastomataceae and Onagraceae. In four other families (Campanulaceae, Hydrocaryaceae, Rubiaceae and Valerianaceae) she mentioned lateral connections but did not refer to them as girdles. To judge from her books, and from the references quoted therein, Saunders (1939) must have looked at representatives of at least 168 families of dicotyledons. Having examined representatives of more than 150 families myself, I have been able to add a further eleven to the list of those with girdling bundles. Three of these (Leguminosae, Tropaeolaceae and Violaceae) have already been briefly described (Sporne, 1974). The other eight families are Begoniaceae, Caricaceae, Ericaceae, Flacourtiaceae, Gentianaceae, Loasaceae, Stylidiaceae and Tiliaceae, which bring to twenty the total number of families in which this phenomenon has been recorded.

As will subsequently become apparent, some distinction needs to be made between those girdles in which both the sepals and the petals are involved and those in which the petals alone are involved or the sepals alone. It is proposed to call the first type "composite girdles" and the second type either "simple corolla girdles" or "simple calyx girdles", respectively.

Vascular connections between the sepals and the petals in *Campanula* and *Lobelia* were mentioned by Henslow (1888), but the details of his description were not correct. Thus, in *Campanula medium* L., he stated that the vascular bundle intended for a sepal branches before reaching it and sends off two cords, one for each petal alternating with it, "so that each petal receives two cords, one from each adjacent sepal — a most unusual condition of things, for petals have almost invariably their own cords issuing from the pedicel." If this description were correct it would, indeed, be unusual, for I know of only one example of a flower whose petals derive their entire vascular supply from that of the sepals, viz. *Viola* (Sporne, 1974, fig. 52C).

Plate 1 is a photograph, taken in the late Autumn, of an old flower of *Campanula carpatica* Jacq. At this time in the year, the soft tissues of the flower have rotted away, leaving just the vascular skeleton. The crown-like composite girdle is clearly visible. Fig. 1 is a stylized vertical projection of the vascular system in *Campanula rotundifolia* L., (omitting the supply to the gynoeceum). Three

vascular bundles enter the base of the flower and branch, somewhat irregularly, in the wall of the inferior ovary, until near the top there are ten trunk bundles. Of these, five are on the sepal radii and, giving rise to the five stamen bundles (A),

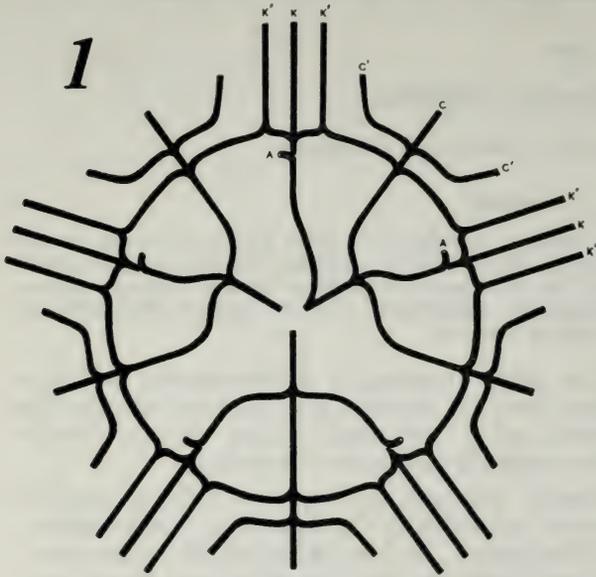


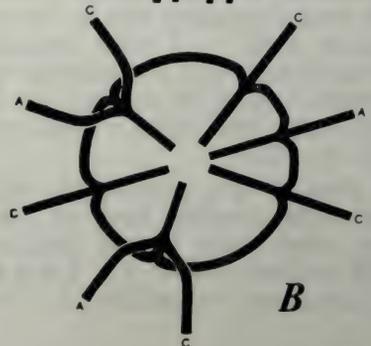
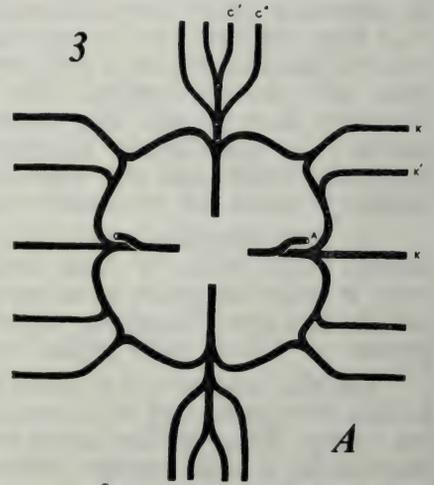
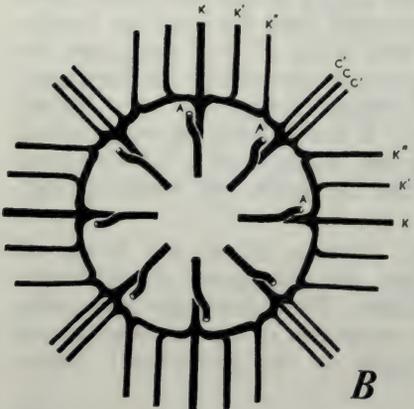
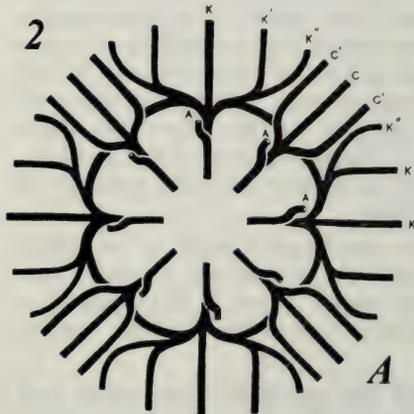
Fig. 1. *Campanula rotundifolia* L.

Fig. 2. A, *Fuchsia fulgens* Moç. and Sessé ex DC.

B, *Epilobium angustifolium* L.

Fig. 3. A, *Circaea lutetiana* L.

B, *Valeriana officinalis* L.



are continuous with the sepal mid-ribs (K). The other five trunk bundles are on the petal radii and continue into the petals, giving both the petal mid-rib (C) and the petal laterals (C'). Before the petal supply becomes distinct, however, all ten trunk bundles become connected by a horizontal girdle. It is from this girdle, and not from the sepal mid-rib, that the sepal laterals (K') have their origin. A similar composite girdling bundle has been figured by Mabberley (1973) for *Lobelia stricklandiae* Gilliland.

Fig. 2 illustrates the vascular system of two members of the Onagraceae, namely, *Fuchsia fulgens* Moç. and Sessé ex DC. and *Epilobium angustifolium* L. (Note that here, as in all the other illustrations, the vascular supply to the ovules and to the style is omitted.) In each of these two genera, there are eight trunk bundles in the wall of the inferior ovary, and a stamen bundle arises as a branch from each. They then become connected by a horizontal girdle which, in *Fuchsia*, is below the level of origin of the sepal and petal lateral bundles. In *Epilobium*, however, these lateral bundles have their origin in the girdle itself. *Circaea lutetiana* L. (Fig. 3A) also belongs to the Onagraceae, but has a much smaller flower than either *Fuchsia fulgens* or *Epilobium angustifolium*, yet it too has a horizontal girdle. There are four trunk bundles in the wall of the ovary, corresponding to the two sepals and the two petals, respectively. Each sepal receives five bundles, of which the laterals (K' and K'') are derived from the girdle. The petal laterals (C'') are, however, independent of it, as in *Fuchsia fulgens*.

*Valeriana officinalis* L. (Fig. 3B), also has a very small flower. Its calyx is represented merely by about twelve curled teeth, which receive no vascular supply at all. Six trunk bundles run up in the wall of the inferior ovary; two of them fork, to provide the total of eight needed for the five petals and the three stamens, and then a horizontal girdle is formed, for which the term "simple corolla girdle" is appropriate.

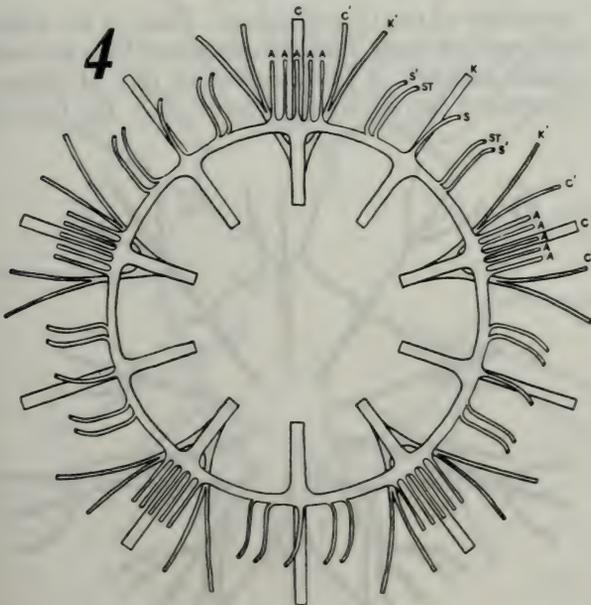


Fig. 4. *Loasa vulcanica* André.

Plate 2 illustrates the importance of clearing techniques when studying floral vascular systems. A horizontal slice through the apex of the inferior ovary of *Loasa vulcanica* André, was boiled for a few seconds in lactic acid (Sporne, 1948) and was then photographed by transmitted light. The vascular bundles show up as a silhouette, in which the horizontal composite girdle is clearly visible. A structure as complex as this would have been very difficult to envisage from a study of a series of microtome sections. Fig. 4 is a diagrammatic interpretation, based on several slices cut at slightly different levels. Opposite each of the five sepals there is a petaloid scale, receiving three vascular bundles (S and S') and inside each scale there are two staminodes (ST). The stamens (A) are in groups opposite the five petals. The sepal lateral (K') and the adjacent petal lateral (C') arise conjointly from the petal trunk bundle at a level slightly below that of the girdle.

is a petaloid scale, receiving three vascular bundles (S and S') and inside each scale there are two staminodes (ST). The stamens (A) are in groups opposite the five petals. The sepal lateral (K') and the adjacent petal lateral (C') arise conjointly from the petal trunk bundle at a level slightly below that of the girdle.

Fig. 5 shows part of the receptacular vascular system in *Mentzelia lindleyi* Torr. & Gray, which belongs to the same family as *Loasa*, namely the Loasaceae.

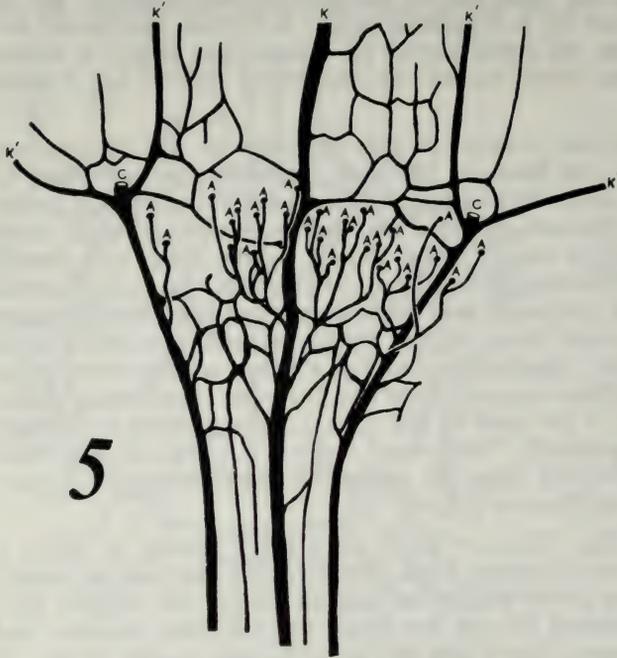


Fig. 5. *Mentzelia lindleyi* Torr. & Gray.

A portion of the receptacle was opened out flat and viewed from inside, after being cleared in lactic acid. The vascular system is strikingly different from that of *Loasa* for, instead of a single girdling bundle, there is an anastomosing system connecting the sepal and petal trunk bundles and from it the stamens receive their vascular supply. A similar arrangement occurs in *Mentzelia gronoviiifolia* Fisch. & Mey. Clearly, it would be unwise to generalize, on the basis of one genus within a family, about the occurrence of girdling bundles, for one can scarcely describe *Mentzelia* as having a girdle.

This is true also of various members of the Cucurbitaceae. Thus, in the edible cucumber, *Cucumis sativus* L., there are ten trunk bundles connected by a network of smaller bundles, while the vascular network of *Luffa cylindrica* (L.) M. Roem., is even more noticeable, especially after it has been retted to produce the familiar bathroom loofah. The Cucurbitaceae can scarcely be said to have a vascular girdle even though, from a physiological point of view, the vascular connections may be directly comparable.

*Stylidium graminifolium* Sw. ex DC, belonging to the Stylidiaceae, raises a similar problem. Running up in the wall of the inferior ovary, there are ten trunk bundles (Fig. 6), some of which are connected by horizontal bundles, while others are connected only by obliquely running bundles. Perhaps *Stylidium* should be described as having only a partial girdle.

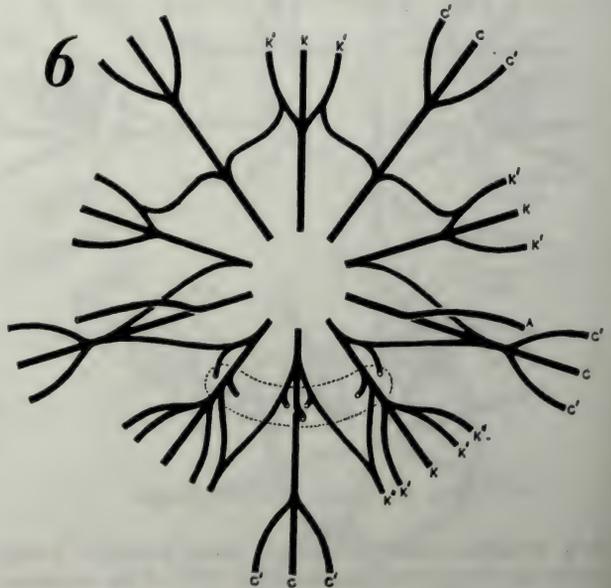


Fig. 6. *Stylidium graminifolium* Sw. ex DC. (The broken line represents a nectary.)

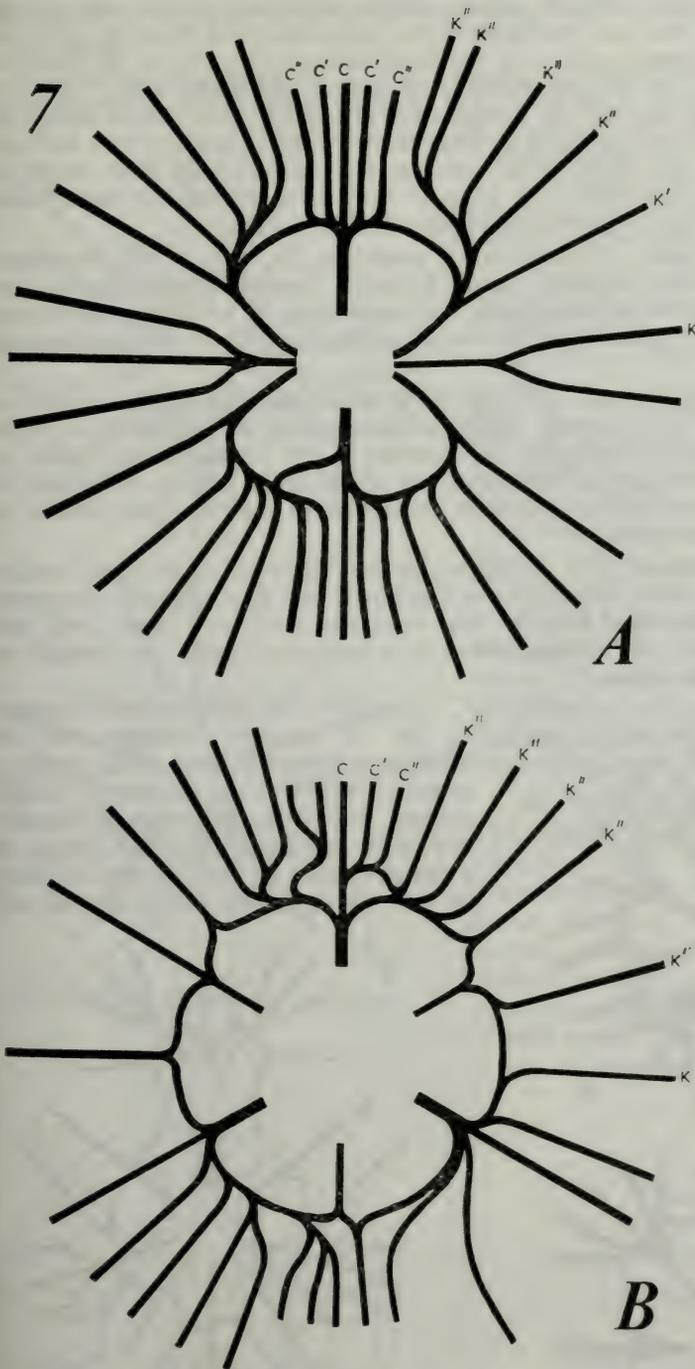


Fig. 7. *Begonia evansiana* Andr. A, staminate flower.  
B, pistillate flower.

The examples quoted so far have all been of hermaphrodite flowers. *Begonia evansiana* Andr. has unisexual flowers, and there is a well developed horizontal girdle in the pistillate flower, but only a partial one in the staminate flower. In each, there are two sepals and two petals. Fig 7A shows how, in the staminate flower, there are eight trunk bundles of which two lead directly into the sepal mid-ribs, while the remaining six become involved in two semi-circular partial girdles opposite the petals. The pistillate flower (Fig. 7B) has six trunk bundles in the wall of the inferior ovary which are connected by a complete horizontal composite girdle, from which petal laterals as well as sepal laterals originate.

Girdling bundles are more likely to occur in flowers where the perianth members are whorled, or even connate, rather than in those with spirally arranged perianth members. It is not surprising, therefore, that many examples of girdling bundles are found in flowers with inferior ovaries, where adnation, as well as connation may have occurred as a result of "intercalary concrescence" (a term suggested by Stebbins, 1974, which avoids the ambiguities of "fusion"). However, there are

also several families with superior ovaries whose perianths receive their supply from girdling bundles. Such an arrangement has been described (Sporne, 1974) for *Phaseolus*, in the papilionate section of the Leguminosae. It is also to be found in *Cassia floribunda* Cav., in the caesalpinoid section of the family (Fig. 8A). Ten trunk bundles enter the base of the flower, each giving rise to a branch supplying either a stamen (A) or a staminode (ST). They then become connected by a horizontal girdle, from which the sepal lateral bundles (K' and K'') have their origin. In passing, it should be noticed that the vascular bundles supplying the three lowermost stamens are peculiar in having a hollow cylinder of xylem.

Among the Ericaceae, *Rhododendron ponticum* L., has a well developed composite girdle. Ten trunk bundles radiate from the central cylinder. As they run horizontally in the disc-shaped receptacle, they each give off a stamen bundle and then all ten bundles are united by a horizontal girdle, from which the sepal laterals have their origin.

Fig. 9 (taken from Sporne, 1974, fig. 52A) illustrates the vascular system in *Tropaeolum minus* L. (The stamen supply is independent of the perianth supply and has, therefore, been omitted.) In this member of the Tropaeolaceae, there are ten trunk bundles in the base of the flower, of which three run the full length of the spur and back again. All ten are then connected by a girdle, from which the sepal laterals have their origin.

In *Sparmannia africana* L. f., belonging to the Tiliaceae, eight trunk bundles enter the base of the flower, four opposite the sepals and four opposite the petals. Despite the fact that the sepal bundles turn outwards at a much lower level than do the petal bundles, they all become united by a horizontal girdle, from which the sepal laterals have their origin.

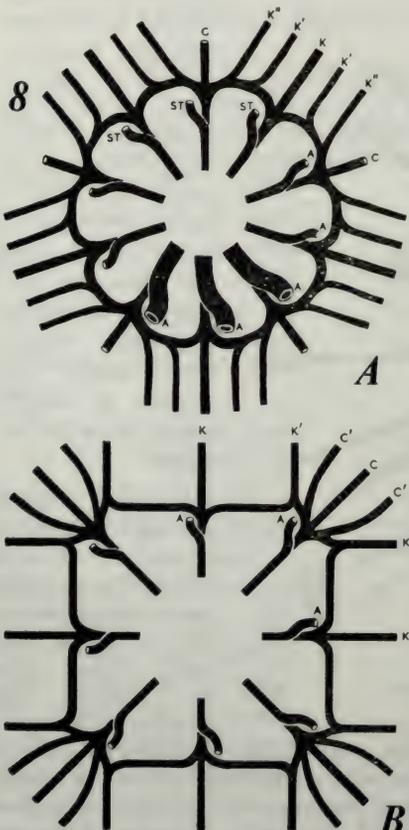


Fig. 8B is of *Heterocentron roseum* A. Br. & Bouché, belonging to the Melastomataceae. Although the ovary is superior, it lies at the bottom of a cup-shaped receptacle. Eight trunk bundles run up in this receptacle, each giving off a stamen trace before becoming linked by a composite girdle. This is not the only

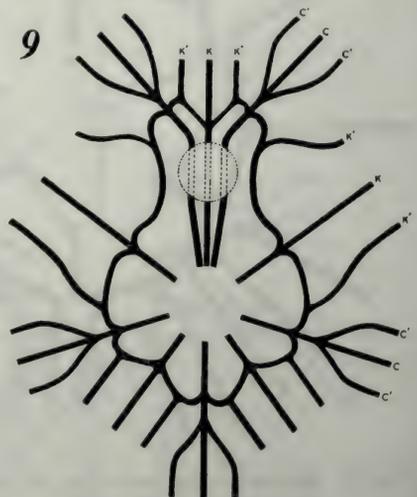


Fig. 8. A, *Cassia floribunda* Cav.  
B, *Heterocentron roseum* A.  
Br. and Bouché.  
Fig. 9. *Tropaeolum minus* L. (The broken lines represent the spur.)

link, however, for there are some anastomosing bundles in addition, below the level of the girdle.

*Passiflora quadrangularis* L. has a similar anastomosing network, but none of the connections is sufficiently large to justify the term "girdle". This arrangement is therefore equivalent to that in the Cucurbitaceae. Neither Passifloraceae nor Cucurbitaceae qualify for inclusion among those families with girdling bundles, as defined in this paper.

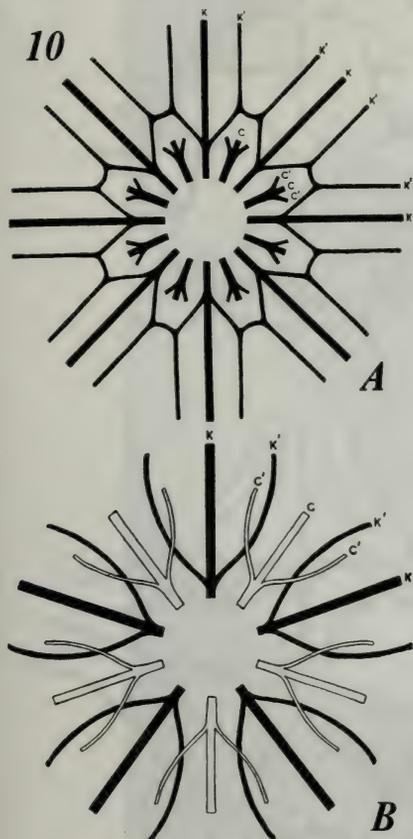


Fig. 10. A, *Blackstonia perfoliata* (L.) Huds.  
B, *Chironia linoides* L.

Fig. 10 illustrates two genera belonging to the Gentianaceae, one of which has a simple calyx girdle, while the other is completely without any lateral connections. The flower of *Blackstonia perfoliata* (L.) Huds., illustrated in Fig. 10A, was one with eight sepals. Each received a mid-rib (K) and lateral veins (K'); and each pair of adjacent laterals was joined by a short bridging bundle, so as to produce a "zig-zag" girdle. *Chironia linoides* L. (Fig. 10B) has pentamerous flowers in which the sepal supplies are completely independent of each other. *Centaurium minus* Moench, also belonging to the Gentianaceae, is variable in that bridges between adjacent sepal laterals are sometimes present and sometimes absent.

In *Phyllobotryon spathulatum* Muell. Arg., belonging to the Flacourtiaceae, the vascular supply to the three sepals is completely separate from that to the three petals, yet there are lateral connections in each system. Fig. 11A shows the calyx system, in which lateral connections form a partial girdle. Fig. 11B shows the corolla system, in which there are merely a few random interconnections.

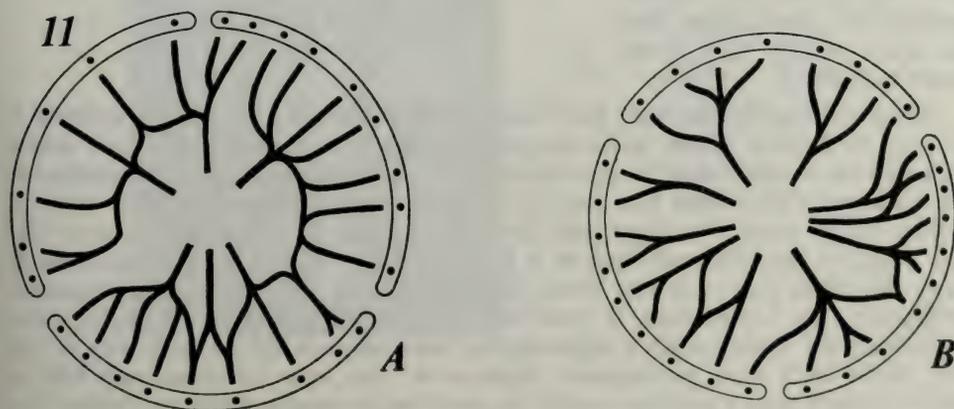


Fig. 11. *Phyllobotryon spathulatum* Muell. Arg. A, calyx. B, corolla.

The most remarkable vascular system that I have seen is that of *Carica papaya* L., illustrated in Fig. 12. The flowers are pentamerous and unisexual; and the perianth

members derive all their vascular supply from five trunk bundles. However, the way in which this happens in the staminate flowers is strikingly different from that in the pistillate flowers. Fig. 12A illustrates the vascular pattern of a staminate flower, in which there is a complete and simple calyx girdle, each sepal receiving a midrib (K) and two lateral veins (K'). The trunk bundle to each petal has its origin, not independently from the central cylinder, but runs for a short distance conjointly with a sepal trunk bundle; then, on becoming separate, it moves laterally on to a different radius. In the pistillate flower, illustrated in Fig. 12B, there is some variability, but mostly the petal trunk bundles arise conjointly with sepal trunk bundles, as in the staminate flower. However, the sepals receive many veins, the number varying from sepal to sepal, and only a partial girdle is formed. In passing, attention must be drawn to the stamen supply in the staminate flowers. The particular flower illustrated in Fig. 12A had five trunk bundles, which became connected by a partial girdle from which the ten stamen bundles had their origin (but the exact details vary from flower to flower).

What the significance may be of girdling bundles in floral vascular systems is not easy to discern. There have always been two schools of thought, one which holds that the course taken by vascular bundles is of great phylogenetic significance and the other which holds that vascular bundles develop where and when there is a physiological need. To those who hold the former view, Professor Corner has been heard to say "Go and look at a loofah", for of course it would be hard to justify the claim that each and every strand in such a network is of phylogenetic significance. Yet a reticulum, if described as such, might well be of phylogenetic significance, for it may fulfil a physiological need imposed by the large size of the fruit, which itself is of phylogenetic significance. Just as a reticulum may fulfil a need, so indeed may a girdling bundle, in providing alternative paths of conduction, analogous to closed vascular networks in stems.

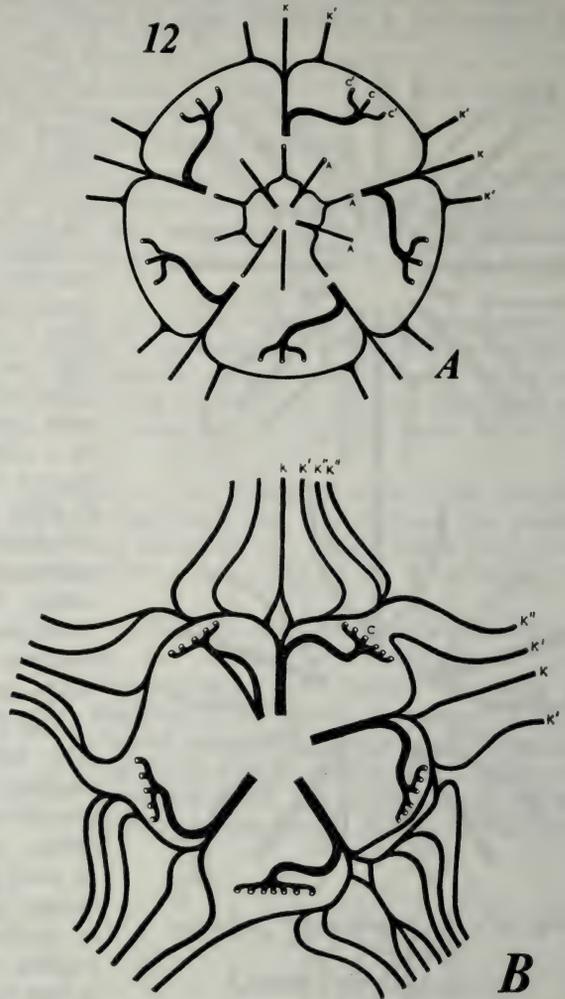


Fig. 12. *Carica papaya* L.  
A, staminate flower.  
B, pistillate flower.

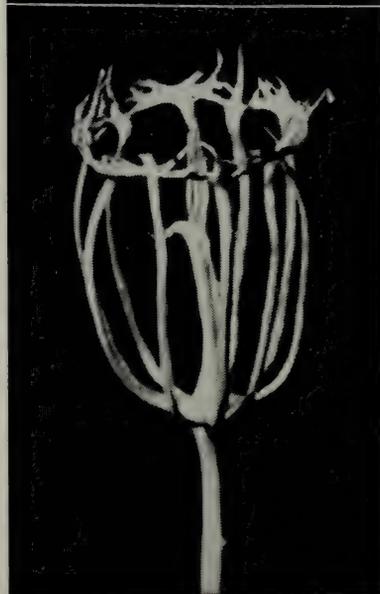
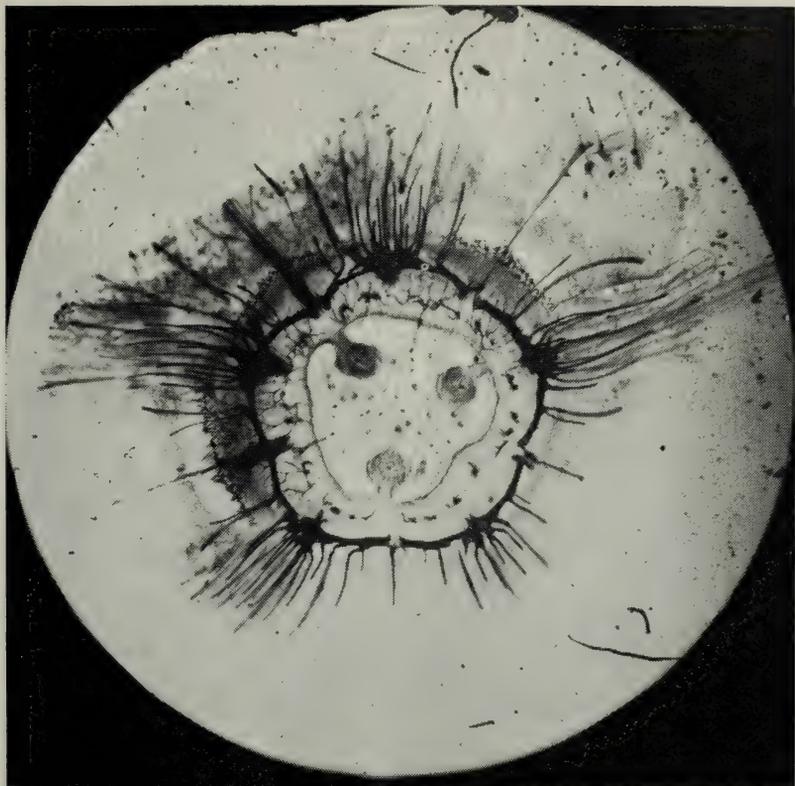


Plate 1. (above) *Loasa vulcanica* André., showing composite girdle.  $\times 20$ .

Plate 2. (below) *Campanula carpatica* Jacq. Vascular skeleton of flower.  $\times 3$ .



Too few examples have, so far, been described for any taxonomic significance to have come to light. Not only do many families of dicotyledons remain to be investigated, but so also do other species within those families which have been examined. We have, as yet, little idea of the variability that may exist from flower to flower on a single plant, or from individual to individual within a species. Summarizing our knowledge to date, one can say that girdling bundles occur in some members of six families in the Violales (Begoniaceae, Caricaceae, Cistaceae, Flacourtiaceae, Loasaceae and Violaceae), five in the Myrtales (Combretaceae, Hydrocaryaceae, Lythraceae, Melastomataceae and Onagraceae), two in the Campanulales (Campanulaceae and Stylidiaceae) and one family in each of the following: Dipsacales (Valerianaceae), Ericales (Ericaceae), Gentianales (Gentianaceae), Geraniales (Tropaeolaceae), Malvales (Tiliaceae) and Rosales (Leguminosae). In the taxonomic scheme of Cronquist (1968), these orders are placed in the Dilleniidae, Rosidae and Asteridae. There is none in the Magnoliidae, Caryophyllidae or Hamamelidae.

The families in which girdling bundles occur range from very primitive to very advanced. Thus the Flacourtiaceae have an advancement index of 22% (Sporne, 1969), while the Dipsacaceae are almost at the other extreme, with one of 94%. It is clear, therefore, that girdling bundles are poor indicators of evolutionary status.

One interesting fact emerges from a study of the vast literature dealing with floral vascular systems, and this is that morphologists who rely on microtome sections often fail to notice girdling bundles. A plea is, therefore, made for more frequent use of clearing techniques, for I have no doubt that those who use them will find that girdling bundles are much more widespread in their occurrence than has been realised. Then, eventually perhaps, their significance (be it taxonomic or phylogenetic) will become apparent. In the meantime, it would be wise to follow the advice of Carlquist (1970) and refrain from allowing interpretations to intrude into what should be purely descriptive work.

### Bibliography

- CARLQUIST, S. 1970. Towards acceptable evolutionary interpretations of floral anatomy. *Phytomorphology* **19**: 332-362.
- CRONQUIST, A. 1968. *The evolution and classification of flowering plants*. Nelson, London.
- HENSLOW, G. 1888. *The origin of floral structures through insect and other agencies*. Kegan, Paul and Trench, London.
- MABBERLEY, D. J. 1973. *The pachycaul species of Senecio and Lobelia in Africa*. Unpublished Ph.D. dissertation, University of Cambridge.
- SAUNDERS, E. R. 1937 and 1939. *Floral Morphology: a new outlook, with special reference to the interpretation of the gynaecium*. 2 Vols. Heffer, Cambridge.
- SPORNE, K. R. 1948. A note on a rapid clearing technique of wide application. *New Phytol.* **47**: 290-291.
- 1969. The ovule as an indicator of evolutionary status in angiosperms. *New Phytol.* **68**: 555-566.
- 1974. *The morphology of angiosperms*. Hutchinson, London.
- STEBBINS, G. L. 1974. *Flowering plants: evolution above the species level*. Arnold, London.



## Corner's Architectural Model

by

F. HALLÉ

& D. J. MABBERLEY

*Institut de Botanique  
Montpellier, France*

*Botany School, Oxford  
England*

Vegetatively unbranched trees with indeterminate apical growth and lateral sexuality belong to 'Corner's Model', as previously defined (Hallé & Oldeman, 1970). The papaya tree and the oil palm are familiar examples of this strange and probably very old strategy of growth. The monoaxial trunk, often thick in its primary tissues, is built by the activity of a single apical meristem; the leaves are large, often compound, and the internodes are short. Growth may be continuous or rhythmic; cauliflory is frequent in the Angiosperm examples. From an ecological point of view, they are mainly treelets of the tropical rain-forest undergrowth.

Although flowering before branching, these trees are not necessarily unbranched throughout their lives, e.g. old papaya trees produce branches from buds on the trunk; see also Plate I. This repetition of the original model, for each new branch behaves as did the first axis, is the 'réitération' of Oldeman (1974). Again, damage to the apex sometimes leads to the death of some species, e.g. *Cyanea carlsonii* Rock (Degener, Degener & Hörmann, 1969), but others can recover, as their axillary buds grow out, giving a branched tree.

Corner's Model is important in the tropics, as it occurs in nearly all the larger families of flowering plants. A list of 67 trees was published in 1970 by Hallé & Oldeman; now more than a hundred species are known to be monoaxial, but the present list is likely to expand rapidly in the coming years, with the increasing interest in, and knowledge of, tropical tree architecture.

### Taxonomic Distribution

The list below includes that of Hallé & Oldeman (1970: 21-5; 135), examples from which are indicated by an asterisk; bibliographic references to these are to be found in the original list.

### DICOTYLEDONS

#### ANACARDIACEAE†

*Semecarpus magnifica* K. Schum., New Guinea (F. Hallé, 1974)

*Semecarpus* sp., Malaysia, *Mabberley 1668* (Plate 1)

\**Trichoscypha ferruginea* Engl., Equatorial Africa

#### BALANOPACEAE

*Balanops pancheri* Baill., New Caledonia (J. M. Veillon, ined.)

#### BERBERIDACEAE

*Mahonia bealei* Carr., China; "Les Cèdres" Botanical Garden, Saint-Jean-Cap-Ferrat, France. 1973

† *Harpephyllum caffrum* Bern. exkr., grown from seed, has flowered at Oxford without branching, while this paper was in press.

## BIGNONIACEAE

- Colea lantziana* Baill., Madagascar, Tsimbazaza Botanical Garden, Tananarive. 1974  
*Colea nana* Perrier, Madagascar; Tsimbazaza Botanical Garden, Tananarive, 1974  
*Colea* sp., Madagascar, *Mabberley* 822 (1971)

## CAMPANULACEAE — LOBELIOIDEAE

- Brighamia rockii* St. John, Hawaii (St. John, 1969)  
*Cyanea aspleniifolia* (Mann) Hillebr., Hawaii (Rock, 1919)  
*Cyanea carlsonii* Rock, Hawaii (Degener, Degener & Hörmann, 1969)  
*Cyanea giffardii* Rock, Hawaii (Rock, 1919)  
*Delissea undulata* Gaud., Hawaii (Rock, 1919)

## CARICACEAE

- \**Carica papaya* L., Central America, now pantropical  
 \**Carica* sp., French Guyana

## COMPOSITAE

- \**Espeletia spicata* Sch. Bip. ex Wedd., S. American mountains

## CONNARACEAE

- \**Jollydora duparquetiana* (Baill.) Pierre, Equatorial Africa

## CUNONIACEAE

- Cunonia macrophylla* Brongn. & Gris., New Caledonia (J. M. Veillon, ined.)

## EUPHORBIACEAE

- \**Agrostistachys borneensis* Becc., Malaya and Borneo  
 \**Agrostistachys sessilifolia* Pax & Hoffm., Malaya (see F. Hallé, 1971)  
*Cleidion lasiophyllum* Pax & Hoffm., New Caledonia, (J. M. Veillon, ined.)  
*Euphorbia ankarensis* Boiteau, Madagascar (G. Cremers, ined.)  
*Euphorbia bupleurifolia* Jacq., South Africa (G. Cremers, ined.)  
*Euphorbia lophogona* Lam., Madagascar; "Les Cédres" Botanical Garden, Saint-Jean-Cap-Ferrat, France, 1973  
*Euphorbia moratii* Rauh, Madagascar (G. Cremers, ined.)  
 \**Pycnocomma angustifolia* Prain, West Africa (see F. Hallé, 1971)

## FLACOURTIACEAE

- Phyllobotryon spathulatum* Muell. Arg., (including \**P. soyauxianum* Baill.)  
 Equatorial Africa (Richards, 1952; Letouzey, Hallé and Cusset, 1969)

## GERANIACEAE

- Geranium canariense* Reuter, Canary Islands (Yeo, 1970)

## GESNERIACEAE

- Boea lanata* Ridl., Malaysia (Burt, 1964)

## LAURACEAE

- Litsea ripidion* Guill., New Caledonia (J. M. Veillon, ined.)



Plate I. *Semecarpus* sp., Mabblerley 1668 — Sepilok Forest Reserve, Sabah, Malaysia, 8 May 1974.



## LECYTHIDACEAE

*Barringtonia calyptrocalyx* K. Schum., New Guinea (F. Hallé, 1974)

\**Grias* sp., Brazil

## LEGUMINOSAE-MIMOSOIDEAE

*Pithecellobium hansemanii* (F. Muell.) Mohl, New Guinea (F. Hallé, 1974)

## LEGUMINOSAE-PAPILIONOIDEAE

*Angylocalyx oligophyllus* Bak.f., Tropical Africa (Mangenot, 1975)

*Sophora* sp., New Caledonia (J. M. Veillon, ined.)

## MALVACEAE

*Goethea strictiflora* Hook., Brazil; J. N. Maclet Botanical Garden, Tahiti, French Polynesia, 1973

## MELIACEAE

*Aglaia* sp., Malaysia, *Mabberley 1699* (1974)

*Chisocheton macranthus* (Merr.) Airy Shaw, Malaysia, *Mabberley 1718* (1974)

*Chisocheton medusae* Airy Shaw, Malaysia, *Mabberley 1680* (1974)

*Chisocheton polyandrus* Merr., Malaysia, *Mabberley 1688* (1974)

*Chisocheton princeps* Hemsl., Malaysia, *Mabberley 1561* (1974)

*Chisocheton setosus* Ridl., Malaysia, *Mikil SAN 30162* (1963)

*Dysoxylum urens* Val., Indonesia; Bogor Botanical Garden, 1972

\**Guarea richardiana* A. Juss., French Guyana

## MENISPERMACEAE

*Penianthus* sp. Gabon, *N. Hallé 4056* (1966)

## MORACEAE

\**Ficus theophrastoides* Seem., Solomon Islands

## MYRSINACEAE

*Oncostemon* sp., Madagascar (J. L. Guillaumet, ined.)

*Rapanea grandifolia* S. Moore, New Caledonia (J. M. Veillon ined)

*Tapeinosperma pachycaulum* St. & Whitm., Solomon Islands (Stone & Whitmore, 1970)

*Tapeinosperma cristobalense* St. & Whitm., Solomon Islands (Stone & Whitmore, 1970)

*Tapeinosperma* sp., New Ireland (M. Coode, ined.)

*Gen. dub.*, Rondonia, Brazil, *F. Hallé 2351* (1975)

## MYRTACEAE

*Jambosa acris* Panch., New Caledonia (J. M. Veillon, ined.)

## OCHNACEAE

\**Campylospermum duparquetianum* (Baill.) Van Tiegh., Tropical Africa

\**Campylospermum saclexii* (Van Tiegh.) Farron, Tropical Africa

\**Campylospermum subcordatum* (Stapf) Farron, Tropical Africa

\**Campylospermum zenkeri* (Engl.) Farron, Tropical Africa

## PITTOSPORACEAE

- \**Pittosporum ceratii* Guill., New Caledonia (J. M. Veillon ined.)

## PROTEACEAE

- Hicksbeachia pinnatifolia* F. Muell., Australia; Sydney Botanical Garden, 1972  
*Macadamia angustifolia* R. Viot, New Caledonia (J. M. Veillon, ined.)

## RUBIACEAE

- \**Bertiera simplicicaulis* N. Hallé, Equatorial Africa  
*Bikkia macrophylla* K. Schum., New Caledonia (J. M. Veillon, ined.)  
*Captaincookia margaretae* N. Hallé, New Caledonia (N. Hallé, 1973)  
*Coffea macrocarpa* A. Rich., Mauritius (G. Mangenot, ined.)  
*Gardenia conferta* Guill., New Caledonia (J. M. Veillon, ined.)  
\**Pentagonia gigantifolia* Ducke, Peru  
*Pseudomantalania macrophylla* J. F. Leroy, Madagascar (Leroy, 1973)

## SAPINDACEAE

- \**Chytranthus longiracemosus* Gilg ex Radlk., Tropical Africa  
\**Chytranthus mangenotii* N. Hallé & Assi, Tropical Africa  
\**Chytranthus pilgerianus* (Gilg) Pellegr., Gaboon  
\**Chytranthus welwitschii* Pellegr., Gaboon  
*Deinbollia* sp., Banco Arboretum, Ivory Coast, 1967  
*Jagera serrata* Radlk., Papua New Guinea, *Frodin & Mabberley UPNG 4305* (1974)  
\**Placodiscus bancoensis* Aubr. & Pellegr., Ivory Coast  
\**Radlkofera calodendron* Gilg, Gaboon

## SAPOTACEAE

- \**Delpydora gracilis* A. Chev., West Africa  
\**Delpydora macrophylla* Pierre, Equatorial Africa  
*Planchonella pronyensis* Guill., New Caledonia (J. M. Veillon ined.)

## SIMAROUBACEAE

- \**Brucea antidysenterica* Lam., Ivory Coast  
\**Eurycoma longifolia* Jack, Malaysia

## SOLANACEAE

- aff. *Solanum*, Acre, Brazil, *F. Hallé 2352* (1974)

## STERCULIACEAE

- \**Chlamydocola chlamydantha* (K. Schum.) Bodard, Tropical Africa  
\**Cola buntingii* Bak.f., West Africa  
\**Cola caricaefolia* (G. Don f.) K. Schum., West Africa  
\**Cola mahoundensis* Pellegr., Equatorial Africa  
*Herrania albiflora* Gaudot, Tropical America; Bogor Botanical Garden, 1972  
\**Ingonia digitata* (Mast.) Bodard, West Africa  
\**Theobroma mariae* K. Schum., Tropical America

## SYMPLOCACEAE

- Symplocos stravadioides* Brongn. & Gris., New Caledonia (J. M. Veillon, ined.)

THEOPHRASTACEAE

- \**Clavija lancifolia* Desf., French Guyana
- \**Clavija longifolia* (Jacq.) Mez, Tropical America

URTICACEAE

- Dendrocide moroides* (Wedd.) Chew, Australia; "Les Cèdres" Botanical Garden, Saint-Jean-Cap-Ferrat, France, 1975
- Obetia radula* (Bak.) B. D. Jackson, Madagascar, *Mabberley 752* (1971)

VERBENACEAE

- Oxera coriacea* Dubard, New Caledonia, *J. M. Veillon 2574* (1973)

VIOLACEAE

- \**Allexis cauliflora* (Oliver) Pierre, Equatorial Africa
- Neckia serrata* Korth., Indonesia, (Boerlage & Koorders, 1901)

MONOCOTYLEDONS

AGAVACEAE

- \**Nolina recurvata* Hemsl., Mexico

PALMAE (Corner's is the main architectural model within the family — see Corner (1966) and Whitmore (1973). The following is a short list of typical examples)

- Borassus aethiopum* Mart., Tropical Africa
- \**Cocos nucifera* L., pantropical
- Dypsis hildebrandtii* Becc., Madagascar; Tsimbazaza Botanical Garden, Tananarive, 1971
- \**Elaeis guineensis* Jacq., Tropical Africa
- Lodoicea maldivica* (Gmel.) Pers., Seychelles
- \**Mauritia flexuosa* Benth., Hook.f. Tropical America
- Oenocarpus distichus* Mart., Brazil
- \**Phytelephas macrocarpa* Ruiz & Pav., Colombia
- \**Roystonea oleracea* O. F. Cook, Central America
- Verschaffeltia splendida* H. Wendl., Seychelles

PANDANACEAE

- Pandanus danckelmannianus* K. Schum., Solomon Islands (Stone, 1972)
- Pandanus princeps* B. C. Stone, Madagascar (Stone, 1970; Guillaumet, 1973)

OTHER VASCULAR PLANTS, LIVING OR FOSSIL

FERNS

- \**Caulopteris* sp., fossil
- \**Hagiophyton* sp., fossil
- \**Megaphyton* sp., fossil
- \**Psaronius* sp., fossil
- \**Alsophila australis* R.Br., Tasmania

- \**Cyathea camerooniana* Hook., Tropical Africa
- \**Dicksonia* sp., Melanesia
- \**Thamnopteris schlechtendalii* (Eichwald) Brongniart, fossil

## PTERIDOSPERMS

- \**Eospermatopteris* sp., fossil
- \**Lyginopteris oldhamia* (Binney) Potonie, fossil
- \**Medullosa noei* Steidtmann, fossil

## CYCADS

- \**Cycadeoidea jenneyana* Ward, fossil
- \* ♀ *Cycas circinnalis* L., South East Asia
- \* ♀ *Cycas revoluta* Thunb., Asia
- \**Encephalartos laurentianus* De Wild., Zaïre
- \**Palaeocycas integer* (Nath.) Florin, fossil
- \**Williamsonia seawardiana* Sahni, fossil

## References

- BOERLAGE, J. G. & S. H. KOORDERS. 1901. Tabula LXXVI. *Neckia serrata* Korth. *Icon. Bogor.* 4: 1-3.
- BURTT, B. L. 1964. Angiosperm taxonomy in practice. *Syst. Assoc. Publ.* 6: 5-16.
- CORNER, E. J. H. 1966. *The Natural History of Palms*. Pp. 393. Weidenfeld & Nicholson, London.
- DEGENER, O, I. DEGENER & H. HÖRMANN. 1969. *Cyanea carlsonii* Rock and the unnatural distribution of *Sphagnum palustre* L. *Phytologia* 19: 1-4.
- GUILLAUMET, J. L. 1973. Formes et développement des *Pandanus* malgaches. *Webbia* 28: 495-519.
- HALLÉ, F. 1971. Architecture and growth of tropical trees exemplified by the Euphorbiaceae. *Biotropica* 3 (1) : 56-62.
- F. 1974. Architecture of trees in the Rain Forest of Morobe District. New Guinea. *Biotropica* 6 (1) : 43-50.
- HALLÉ, F. & R. A. A. OLDEMAN. 1970. *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux*. Pp. 178. Masson éd., Paris.
- HALLÉ, N. 1973. *Captaincookia*, genre nouveau monotypique néocalédonien de Rubiaceae — Ixoreae. *Adansonia* 13 (1) : 195-202.
- LEROY, J. F. 1973. Sur l'organisation et le mode de développement d'un très remarquable ensemble naturel de Rubiacées-Gardéniées à Madagascar. *C.r. hebdomadaire. Séanc. Acad. Sci. Paris* 277: 1657-1659.
- LETOUZEY, R., N. HALLÉ & G. CUSSET. 1969. *Phyllobotryae* (Flacourtiaceae) d'Afrique Centrale; variations morphologiques et biologiques; conséquences taxonomiques. *Adansonia* 9 (4) : 515-537.
- MANGENOT, G. 1957. *Angylocalyx oligophyllus* Bak. f. 1913. *Icones Pl. afr.* 4: 77.
- OLDEMAN, R. A. A. 1974. *L'architecture de la forêt Guyanaise*. O.R.S.T.O.M., Paris.

- RICHARDS, P. W. 1952. *The tropical rain-forest*. Cambridge University Press.
- ROCK, J. F. 1919. A monographic study of the Hawaiian species of the tribe Lobelioideae family Campanulaceae. *Mem. Bernice P. Bishop Mus.* 7 (2) : 1-394.
- ST. JOHN, H. 1969. Monograph of the genus *Brighamia* (Lobeliaceae). Hawaiian Plant Studies 29. *Bot. J. Linn. Soc.* 62: 187-204.
- STONE, B. C. 1970. Observations on the genus *Pandanus* in Madagascar. *Bot. J. Linn. Soc.* 63: 97-131.
- 1972. The genus *Pandanus* in the Solomon Islands with notes on adjacent regions. *Malaysian J. Sci.* 1 A: 93-132.
- STONE, B. C. & T. C. WHITMORE. 1970. Notes on the systematy of Solomon Islands plants and some of their New Guinea relatives. XI. *Tapeinosperma* (Myrsinaceae). *Reinwardtia* 8 (1) : 3-11.
- WHITMORE, T. C. 1973. *Palms of Malaya*. Pp. 148. Oxford University Press.
- YEO, P. F. 1970. *Geranium palmatum* group in Madeira and the Canary Isles. *J. R. hort. Soc.* 95: 410-414.



# Where and When Might the Tropical Angiospermous Flora Have Originated?

by

ROBERT F. THORNE

*Rancho Santa Ana Botanic Garden, Claremont, California 91711*

## Summary

The tropical angiospermous flora had its beginnings with the origin of the angiosperms in earliest Cretaceous time from some unknown, generalized gymnospermous ancestor, probably a still unrecognized group of Mesozoic pteridosperms. Over most of early and middle Cretaceous time, the angiosperms, early split into dicots and monocots, gradually became more prominent in tropical and later in temperate floras, with evolution by late Cretaceous in part into extant families and genera. The facts of present and past angiosperm distribution still point to southeastern Asia and attendant archipelagoes as the primary centre of preservation and probably the primary centre of origin of the most primitive living angiosperms. Other important centres for the development of the tropical angiosperm flora have been West Gondwanaland before its break-up, the upland shield areas of South America and Africa since their isolation from one another, Australasia, and to a much lesser extent the Greater Antilles and Mexican highlands.

## Introduction

The origins of the angiosperms are still obscure. When, where, and from what ancestral group they originated are still matters of much speculation and disagreement. We are much better supplied with negative information than with positive facts due to the incomplete nature of the fossil record and the almost universal extinction of the earliest angiosperms and their probable ancestors. However, expanding knowledge about the class Angiospermae enables us to narrow down considerably our choice of answers.

## Antiquity of the Angiospermae

The earliest guesses about the antiquity of the angiosperms were rather wild, ranging from the Cretaceous back at least to the Permian of late Paleozoic time. The earliest indisputable angiosperm remains, monosulcate angiosperm and tricolpate pollen, appeared in the fossil record in Barremian and Aptian time of the Lower Cretaceous less than 130 million years ago (Doyle, 1969, 1973; Wolfe *et al.*, 1976). Earlier fossil remains claimed to be angiospermous have been eliminated from consideration as belonging to other vascular plant classes or as having come from more recent strata than those to which they were first assigned (Scott, Leopold, and Barghoorn, 1960; Scott *et al.*, 1972). The complete absence of unequivocal angiosperm fossils from strata earlier than the Barremian, or possibly the Hauterivian, makes it gratuitous to assume a much earlier Jurassic or even Triassic origin for the angiosperms.

## Gradual Emergence of the Angiospermae

Another myth like early Mesozoic origins that should be set aside permanently for the early angiosperms is that they burst full-bloom in great numbers and variety upon the Early Cretaceous scene. We have enough fossil floras analyzed now that we can say categorically that the angiosperms very slowly gained prominence in

the world's floras of gymnosperms and ferns and even more gradually evolved into groups recognizable as extant families and genera. About 15 million years of slow angiosperm evolution took place before diverse angiosperm floras, like the Dakota, Potomac, and Cheyenne Sandstone floras, came into prominence by Upper Albian time, perhaps 112 million years ago (Wolfe *et al.*, 1976). Not until the Turonian and Senonian, 100 to 90 million years ago, were gymnosperm pollen and fern spores over-taken in abundance in the fossil record by angiospermous pollen. By late Senonian time, perhaps 70 million years ago, angiosperms had largely replaced the ferns and gymnosperms (Muller, 1970, Wolfe, 1974, Wolfe *et al.*, 1976). Possibly modern orders had appeared some tens of millions of years earlier. Many modern families and most extant genera have not been recognised from the fossil record until Tertiary times in the last 65 million years, and many taxa still have no acceptable fossil record.

### Probable Angiosperm Ancestors

Our knowledge of the morphology of various vascular plant classes has now enabled us to narrow down considerably those primitive vascular-plants groups that might have evolved into the early angiosperms. Pteridophytes, conifers, ginkgoes, cycads, gnetophytes, and the extinct Cordaitales and Bennettitales have now been removed from consideration, largely because they are more specialized in certain features than those archaic angiosperms now generally regarded as the most primitive living flowering plants (Eames, 1961; Cronquist, 1968; Takhtajan, 1969). The most primitive gymnosperms, the extinct Pteridospermae or seed-ferns, still remain as possible ancestors because of their generally primitive characteristics and their great diversity. Most recently Stebbins (1974) has revived rather unconvincingly the hypothesis that the angiospermous ovule is homologous with the seed-bearing cupule of the advanced Mesozoic pteridosperm order Caytoniales. However, the fossil Caytoniales, like the eliminated vascular-plant groups listed above, appear to be too specialized to pass as angiosperm ancestors. It seems more likely that some little-known, or probably still unrecognized, unspecialized group of Mesozoic seed-ferns evolved very early in the Cretaceous into the first angiosperms.

Where these long-extinct, unspecialized pteridosperms presumably evolved into recognizable angiosperms is also still controversial. At best, we can make an educated guess as to the probable centre of evolution of the Angiospermae by assembling what we know of the probable habitats of the earliest flowering plants and of fossil and extant distribution patterns of the most primitive living angiosperms.

### Tropical Character of the Angiospermae

Most angiosperm families are basically tropical in their adaptations and their geographic distribution. In an analysis of the 316 families accepted in my classification (Thorne, 1968, 1974), I have found 167 to have an exclusively or primarily tropical distribution, 106 a strong, or nearly equal, representation in both tropical and temperate zones, and only 43 an exclusively or largely temperate distribution. Of the 43 temperate families only four, Adoxaceae, Butomaceae *s.s.*, Hippuridaceae, and Myzodendraceae, each represented by a single genus, are primarily cool temperate in distribution, although two subfamilies, *Hectorelloideae* and *Tetrachondroideae* are essentially subantarctic in range. Every one of the 43 temperate families appears to be related to families that are primarily tropical and that are less specialized in many features, i.e., more primitive. If additional subfamilies are tallied with the families, 314 families and subfamilies are primarily tropical, 204 both tropical and temperate, and only 101 primarily temperate. The tropical bias of the Angiospermae thus is readily evident, approximately three to one. The families generally considered most primitive in the class are even more strikingly tropical. Analysis of the 95 families of the relatively primitive superorders Annoniflorae, Theiflorae, Rutiiflorae, and Hamamelidiflorae shows 57 primarily tropical and only 11 largely temperate, a ratio of more than five to one.

Angiosperm megafossil evidence, according to Axelrod (1959, 1970) indicates that the first recognizable flowering plants appeared from equable, warmer uplands first in lower middle latitudes at the beginning of the Early Cretaceous (Neocomian time), where they made up a very small percentage of the total vascular plant flora. At that time they were unrepresented in the megafossil record at high latitudes. As Axelrod graphically shows, they appeared at higher latitudes in progressively younger rocks until by late Cretaceous time they had in great variety largely replaced pteridophytes and gymnosperms even at higher, temperate latitudes. By Aptian time according to megafossils, angiosperms were present south of the equator only in lower latitudes. By the end of the Early Cretaceous in the Albian stage they had reached 70° N latitude but were only beginning to appear at middle latitudes (45° S) in the southern hemisphere (Axelrod, 1959). Fossil pollen evidence seems to support only in the broadest way this apparent poleward migration of early angiosperms (Doyle, 1969; Brenner, 1976; Hopkins, 1974). From this data, we can infer that the Angiospermae evolved in tropical areas, probably north of the equator.

### **Mesic Origins of the Angiospermae**

Perhaps even stronger than the fossil evidence are the inferences we can draw from extant archaic angiosperms, those relicts with vesselless xylem or with extremely primitive tracheid-like vessel elements that are long and narrow and have long scalariform perforation plates with usually more than 20 bars. These woody plants, like broad-leaved conifers, are essentially restricted to highly mesic sites with a minimum of seasonal water stress, primarily tropical montane forests or summer-wet temperate forests (Carlquist, 1975). This is a devastating argument against Stebbins' recently enunciated hypothesis (1974) that the first angiosperms were shrubby plants that evolved in response to a stressful warm climate with distinct dry and wet seasons. It was only as the angiosperms evolved xylem with greater conductive efficiency that they were able to invade and radiate rapidly in the hot tropical lowlands with their wide fluctuations in soil moisture and high insolation, and the temperate forests with more seasonal water stress (Carlquist, 1975). The extreme plasticity of both dicotyledons and monocotyledons allowed many of them rather early in their evolution to adapt to extreme habitats and unusual life-styles (Hickey, 1971; Doyle and Hickey, 1972; Doyle, 1973).

Thus the evidence from both fossil and extant primitive angiosperms indicates that they arose in continuously moist, tropical or subtropical uplands. Indeed, it is in just such montane areas today that we find the great majority of the angiosperms with a wide array of primitive features in flowers, pollen grains, seeds, and fruits as well as in stem anatomy, habit, and foliage. But we still have to decide which moist equable upland area is the probable original homeland of the primitive living Angiospermae.

### **Possible Centre of Origin of Primitive Angiosperms**

Southeastern Asia and its adjacent archipelagoes have most often been suggested by plant geographers as not only the most important centre of preservation but also as the likely "cradle" of the Angiospermae (Takhtajan, 1957, 1969; Thorne, 1963; Smith, 1970, 1973). Recently, however, the general acceptance of the theory of tectonic plate movement and sundering and floating apart of continents has caused some plant geographers to reconsider the problem with view to the suggested distribution of land masses during Cretaceous and early Tertiary times. Schuster (1972) and Raven and Axelrod (1974) favour Gondwanaland as the area from which the initial radiation of the angiosperms took place. The latter authors, on what often appears to be negative evidence, favour West Gondwanaland (South America and Africa as a unit), while claiming unconvincingly that the Oriental Region could not be the area of origin of the angiosperms because of its presumed composite Continental origin.

### Oriental Region

We should, therefore, examine the flora of the Oriental Region, which I define here as tropical southeastern Asia and the adjacent Indian-Western Pacific Ocean archipelagoes from Ceylon and Taiwan to tropical Queensland and Fiji. Few plant geographers would deny that this region has the world's most varied flora. Though smaller than the Ethiopian and Neotropical Regions, it possesses indigenous representatives of 433 major angiospermous taxa (families and additional subfamilies), 45 of them endemic, as compared to 366 major taxa, 38 endemic, for Madagascar and Africa south of the Sahara Desert, and 374, with 25 endemic, for all of South America including Fuegia. Among the most primitive angiosperms, the Annonales, Berberidales, Nymphaeales, and Hamamelidales, representation in the Oriental Region is even more overwhelming: 29 of 34 major annonalean, 15 of 18 berberidalean, 6 of 6 nymphaealean, and 11 of 11 hamamelidalean taxa. The same distribution pattern with the most primitive members of the taxon restricted to the Oriental Region is repeated in major taxon after major taxon. Takhtajan (1969) has given many examples. Some of the additional tropical groups that appear to have evolved primarily in southeastern Asia are the thealean *Dillenioidae*, Actinidiaceae, Dipterocarpaceae, Nepenthaceae, and *Planchonioideae*; Ericaceae; Symplocaceae; *Rafflesioideae*; Elaeocarpaceae; *Ficus*; *Gonystylus*; *Cardiopteris*; Rutaceae; Sabiaceae; *Acer*; Juglandineae; Fagales; Staphyleaceae; Daphniphyllineae; Crypteroniaceae; *Astronioideae*; *Cyrtandroideae*; Rhizophoraceae; Cornineae (except *Garrya*); Caprifoliaceae; orchidaceous *Apostasiodeae* and *Cypripedioideae*; Pandanaceae; and Zingiberaceae.

That the Oriental Region is of composite Continental origin may well be true. It is widely claimed that India-Ceylon split away from Africa and Madagascar at least 100 million years ago, colliding with Asia 45 m. y. BP, and that Australia broke away from Antarctica about 49 m. y. BP, arriving in its present position near Indonesia some 15 m. y. BP (Raven and Axelrod, 1975). Assuming that this time-table is correct, even 15 million years is surely more than adequate time to explain the widespread Indo-Malesian elements that dominate the rain-forest flora of tropical Queensland, New Guinea, and the other Melanesian islands. The flora of distinctive relicts of Australasia that Raven and Axelrod seem to attribute to Gondwanaland are more likely Oriental derivatives which have found a refuge in the isolated islands and highlands of Australasia. *Degeneria*, *Galbulimima*, and *Eupomatia* are very close relatives of the Magnoliaceae, of which all 12 genera and most of the perhaps 215 species are represented in mainland southeastern Asia or the Malay archipelago. The recently rediscovered *Idiospermum* of Queensland belongs to the Calycanthaceae (Thorne, 1974), whose other two genera, *Calycanthus* and *Chimonanthus*, are both represented in China. *Amborella*, *Austrobaileya*, and the Trimeniaceae have close relationships to the Calycanthaceae and to the Chloranthaceae and Monimiaceae, both heavily represented in the Indomalesian area. Possibly the Winteraceae, with chief centres of variation in New Guinea and New Caledonia may be autochthonous relicts of Australasia but they have relatively close affinities with the Oriental Illiciineae and Magnoliineae. The only two hamamelidalean genera of Queensland, *Ostrearia* and *Neostrearia* of the Hamamelidoideae, have undoubtedly reached northern Queensland, like *Distyliopsis* in New Guinea, from southeastern Asia, where their probable two closest relatives *Embolanthera* and *Maingaya* occur along with representatives of the other four subfamilies and a total of 15 of the 27 hamamelid genera, 4 more being found in temperate Asia. It is noteworthy that like the rain-forest angiosperm flora of New Guinea, New Caledonia, and tropical Queensland, most of the insect, land snail, oligochaete, avian, bat, and murid rodent faunas, at least of New Guinea and the tropical rain forests of Queensland, are derived from southeastern Asia or Malesia (Gressitt, 1956, 1961; Solem, 1958, 1959; Keast, 1959; Emerson, 1955; Mayr, 1972; Schodde and Calaby, 1972). For these reasons in my biogeographical subdivision of the Pacific islands (1963) I treated New Guinea, the Bismarck, Admiralty, and

Solomon Islands, wet tropical Queensland, and New Caledonia as the Papuan and Neocaledonian subregions of the Oriental Region. I do not think a Gondwanic origin of Australia-New Guinea has had much impact upon the majority of angiospermous elements of the tropical rain forests of Australasia.

### West Gondwanaland

The importance of West Gondwanaland and other tropical areas in the evolution of the tropical angiospermous flora must not be ignored, however. The Cretaceous angiosperms, according to the fossil record, radiated evolutionarily and geographically very widely and rapidly. Before West Gondwanaland disintegrated into the modern widely separate austral continents, it was probably the centre of origin of the tropical Annoniaceae; Scytopetalaceae; Sapotaceae; Euphorbiales; Geraniales; Caricaceae; Hydnoraceae; Chenopodiaceae; the rosalean Chrysobalanaceae, Connaraceae, *Caesalpinoideae*, *Mimosoideae*, and Podostemaceae; lilialean *Haemodoreae*, *Hypoxidoideae*, *Velloziaceae*, and Iridaceae; Areciflorae; and Musaceae, among others. A longer list can be gleaned from Raven and Axelrod (1974), but it must be used with caution since they claim a Gondwanic origin for taxa that are and were apparently meagrely represented there if at all.

### South America

After the break-up of Gondwanaland, the ancient shield areas of South America, especially the Guayana Highlands and Brazilian Planalto, appear to have contributed heavily to the development of such important tropical groups as the thealean *Bonnetioideae*, *Pelliceroideae*, Marcgraviaceae, Caryocaraceae, Sarracenaceae, Quiinaceae, and *Lecythidoideae*; Theophrastaceae; cistalean *Peridiscus*, *Leoniaceae*, and Loasaceae; Solanaceae; *Goupia*; Lissocarpaceae; tiliaceous *Tetralicoideae* and *Neotessmannioideae*; *Houmarioideae*; Polygalaceae; rutalean *Dictyomatoideae*, *Spathelioideae*, and *Alvaradoideae*; centrospermous Cactaceae, Rhabdodendraceae, and *Coccoloboideae*; rubiaceous Henriqueziaceae; Martyniaceae; Asteraceae; Cyclanthaceae; commelinalean Bromeliaceae, Pontederiaceae, Juncaceae, Commelinaceae, and Eriocaulaceae; and zingiberalean Heliconiaceae, Cannaceae, and Marantaceae.

### Africa

On the other hand, Africa seems to have contributed somewhat less to the origins of the tropical flora, perhaps because of the floristic depauperization that Raven and Axelrod (1974) emphasize so strongly. Certainly of African-Madagascan origin are the thealean Scytopetalaceae, Sarcolaenaceae, Sphaerosepalaceae, *Monotoideae*, Dioncophyllaceae, and *Napoleonoideae*; Huacaceae; Barbeyaceae; Didymelaceae; simaroubaeous *Kirkioideae* and *Balanitoideae*; Melianthaceae; centrospermous Aizoaceae and Didiereaceae; rosalean *Jollydoroideae*, *Montinioideae*, and Medusagynaceae; pittosporalean Bruniaceae; myrtalean Oliniaceae and Paenaceae; Pedaliaceae; Hoplestigmataceae; and lilialean *Cyanastroideae* and *Geosiridoideae*.

### Australasia

Although Australasia seems to receive little credit as an important centre of evolution from Raven and Axelrod (1974), it has contributed significantly to the origins of the tropical angiosperm flora. Among other groups that had their primary development if not their origin in Australasia are the Winteraceae; Epacridaceae; Goodeniaceae; Stackhousiaceae; *Akania*, Gyrostemonaceae; rosalean *Escalloniaceae*, Cunoniaceae, and *Davidsonia*; Pittosporaceae; Proteaceae; Casuarinaceae; myrtaceous *Leptospermoideae*; Haloragaceae; lamialean *Chloanthoideae* and *Prostantheroideae*; liliaceous *Xanthorrhoeaceae*; Restionaceae; Centrolepidaceae, and the poaceous *Micraioideae*.

### North America and Temperate Eurasia

North America and temperate Eurasia appear to have contributed few major groups to the tropical angiospermous flora, despite their formerly rich tropical floras. The highlands of Mexico and the Greater Antilles may have contributed to the tropical flora Cyrillaceae, Polemoniaceae, Fouquieriaceae, *Chitonoideae*, *Eriogonoideae*, Crossosomataceae, *Echeverioideae*, Garryaceae, and the liliaceous *Agavoideae*. The total elimination of tropical elements from Europe removes that area from consideration until the fossil record of its tropical epochs is better known.

### LITERATURE CITED

- AXELROD, D. I. 1959. Poleward migration of early angiosperm flora. *Science*, N.Y. **130**: 203–207.
- 1970. Mesozoic paleogeography and early angiosperm history. *Bot. Rev.* **36**: 277–319.
- BRENNER, G. J. 1976. Middle Cretaceous floral provinces and early migrations of angiosperms. Pp. 23–47. In C. B. Beck (Editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York. 341 pp.
- CARLQUIST, S. 1975. *Ecological Strategies of Xylem Evolution*. Univ. Calif. Press, Berkeley, Los Angeles, London. 259 pp.
- CRONQUIST, A. 1968. *The Evolution and Classification of Flowering Plants*. Houghton Mifflin, Boston. 396 pp.
- DOYLE, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic coastal plain and its evolutionary significance. *J. Arnold Arbor.* **50**: 1–35.
- 1973. Fossil evidence on early evolution of the monocotyledons. *Q. Rev. Biol.* **48**: 399–413.
- & L. J. HICKEY. 1972. Coordinated evolution in Potomac Group angiosperm pollen and leaves. (Abstract). *Am. J. Bot.* **59**: 660.
- EAMES, A. J. 1961. *Morphology of the Angiosperms*. McGraw-Hill, New York, Toronto, London. 518 pp.
- EMERSON, A. E. 1955. Geographical origins and dispersions of termite genera. *Fieldiana, Zool.* **37**: 465–521.
- GRESSITT, J. L. 1956. Some distribution patterns of Pacific Island faunae. *Syst. Zool.* **5**: 11–32, 47.
- 1961. Problems in the zoogeography of Pacific and Antarctic insects. *Pacif. Insects Monogr.* **2**: 1–94.
- HICKEY, L. J. 1971. Evolutionary significance of leaf architectural features in the woody dicots. (Abstract). *Am. J. Bot.* **58**: 469.
- HOPKINS, W. S. 1974. Some spores and pollen from the Christopher Formation (Albian) of Ellef and Amund Ringnes Island, and northwestern Melville Island, Canadian Arctic Archipelago. *Geol. Surv. Canada Pap.* **73–12**.
- KEAST, A. 1959. Australian birds: their zoogeography and adaptations to an arid continent. Pp. 89–114. In *Biogeography and Ecology in Australia*. Den Haag: W. Junk.
- MAYR, E. 1972. Continental drift and the history of the Australian bird fauna. *Emu* **72**: 26–28.

- MULLER, J. 1970. Palynological evidence on early differentiation of angiosperms. *Biol. Rev.* **45**: 417-450.
- RAVEN, P. H. & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Mo. bot. Gdn* **61**: 539-673.
- SCHODDE, R. & J. H. CALABY. 1972. The biogeography of the Australo-Papuan bird and mammal faunas in relation to Torres Strait. Pp. 257-300. In D. Walker (Editor), *Bridge and Barrier: The Natural and Cultural History of Torres Strait*.
- SCHUSTER, R. M. 1972. Continental movements, "Wallace's Line" and Indo-malayan-Australasian dispersal of land plants: some eclectic concepts. *Bot. Rev.* **38**: 3-86.
- SCOTT, R. A., E. S. BARGHOORN & E. B. LEOPOLD. 1960. How old are the angiosperms? *Am. J. Sci.* **258-A** (Bradley Vol.): 284-299.
- P. L. WILLIAMS, L. C. CRAIG, E. S. BARGHOORN, L. J. HICKEY, & H. D. MacGINITIE. 1972. "Pre-Cretaceous" angiosperms from Utah: evidence for Tertiary age of the palm woods and roots. *Am. J. Bot.* **59**: 886-896.
- SMITH, A. C. 1970. The Pacific as a key to flowering plant history. Univ. Hawaii, Harold L. Lyon Arboretum Lecture **1**: 1-27.
- 1973. Angiosperm evolution and the relationship of the floras of Africa and America. Pp. 49-61. In B. J. Meggers, A. S. Ayensu, & W. D. Duckworth (Editors). *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*. Smithsonian Inst. Press, Washington, D.C.
- SOLEM, A. 1958. Biogeography of the New Hebrides. *Nature* **181**: 1253-1255.
- 1959. Zoogeography of the land and fresh-water Mollusca of the New Hebrides. *Fieldiana, Zool.* **43**: 239-359.
- STEBBINS, G. L. 1974. *Flowering Plants, Evolution above the Species Level*. Harvard Univ. Press, Cambridge, Mass. xviii & 399 pp.
- TAKHTAJAN, A. L. 1957. On the origin of the temperate flora of Eurasia. *Akad. Nauk SSSR* **42**: 1635-1653.
- 1969. *Flowering Plants, Origin and Dispersal*. Transl. by C. Jeffrey. Oliver & Boyd, Edinburgh. 310 pp.
- THORNE, R. F. 1963. Biotic distribution patterns in the tropical Pacific. Pp. 311-354. In J. L. Gressitt (Editor), *Pacific Basin Biogeography*, Bishop Museum Press, Honolulu.
- 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. *Aliso* **6** (4): 57-66.
- 1969. Floristic relationships between New Caledonia and the Solomon Islands. *Phil. Trans. R. Soc. Lond.* **B 255**: 595-602.
- 1974. A phylogenetic classification of the Annoniflorae. *Aliso* **8**: 147-209.
- WOLFE, J. A. 1974. Fossil forms of Amentiferae. *Brittonia* **25**: 334-335.
- J. A. DOYLE, & V. M. PAGE. 1976. The bases of angiosperm phylogeny: paleobotany. *Ann. Mo. bot. Gdn* **62**: 801-824 (for 1975).



# On the Origin of the Sycomore Fig (*Ficus sycomorus* L.) in the Middle East

by

J. GALIL<sup>1</sup>, M. STEIN<sup>2</sup> & A. HOROVITZ<sup>3</sup>

## Summary

The distribution area of *Ficus sycomorus* can be divided into two distinct parts. The main area, in which trees produce viable seeds and grow spontaneously follows along the Eastern Coast of Africa, from South Africa to Sudan. The northern area, in which no seeds are produced and the trees are dependent on man for propagation, includes the Middle East and North Africa. In the present paper an attempt is made to elucidate the problem of origin of *F. sycomorus* plants in the northern area. These may be either remnants of prehistoric native populations which have lost their ability to set seed or secondary derivatives introduced into the area in remote times by man.

Remnants of fruit bat skeletons in caves from the Natufian period (9,000-7,000 B.C.) are taken as a possible indication for the presence of sycomore fig in the Middle East at an early date. Remnants of sycomore roots in the upper Nile Valley dating from the Badarian period (about 4000 B.C.) also support the assumption of a primary origin of the tree in the Middle East.

It is proposed that, due to loss of the specific pollinator at the dawn of civilization, the trees ceased to reproduce spontaneously. Instead they have since been propagated vegetatively by man for fruit and wood.

## Introduction

The sycomore fig *Ficus sycomorus* L. (Plate 1a) belongs to the Sudanian phytogeographical element. Today this species grows wild mainly in eastern parts of Africa, from Sudan and Ethiopia to South Africa (Kruger Park) with extensions into Yemen on the Arab Peninsula and into the Namib Desert in Southwest Africa (Fig. 1). The trees are most commonly found along stream banks, but also grow at other sites where the water table is high, as in the Mombasa area of Kenya. The pollinator of the sycomore fig, the wasp *Ceratosolen arabicus* Mayr (Agaonidae) occurs in these same areas, so that throughout eastern Africa the trees are fertilized and produce viable seed. Where conditions are favourable, one finds young plants of seed origin.

Outside its present main distribution area, the sycomore grows in various Middle Eastern localities (Rhodes, Cyprus, Lebanon, Israel, Egypt) and in North Africa (Libya and Algeria). In these secondary distribution areas (Fig. 1) also, the species occurs in wet habitats in the vicinity of streams and springs or in valleys and plains where the water table is high. In the Middle East the sycomore does not grow spontaneously. The pollinating wasp does not occur here and trees produce no seed.

The two sycophilous wasps which inhabit the syconia in this area, namely *Sycophaga sycomori* L. (Torymidae) and *Apocrypta longitarsus* Mayr (Torymidae), do not carry pollen on their bodies and cannot bring about pollination (Galil and Eisikowitch, 1968). The present day trees in the Middle East have all been planted by man.

<sup>1,3</sup> Tel Aviv University, Department of Botany, The Dr. George S. Wise Center for Life Sciences, Tel Aviv, Israel.

<sup>2</sup> Kfar Masaryk.

Sycamore figs have been domesticated in the Middle East for their juicy fruits which develop in great numbers, for their timber, and as shade trees. A number of cultivars can be distinguished which differ in fruit size and shape, in the length of the fruit stalk, and, most important, in their ability to produce parthenocarpic fruit (Galil, 1968). Two cultivated varieties (Kelabi and Roumi) are known in Egypt according to Brown and Walsingham (1917). In Israel the cultivated varieties are Belami and Razi. In Cyprus a fifth variety differing from the others is grown in addition to Belami.

The sycamore fig is not the only tropical plant extending into areas bordering the Mediterranean. About 100 tropical species of the Sudanian element occur in Israel alone (Grünberg-Fertig, 1966). Some of these are prominent trees which stand out in their surroundings. Most of these species are confined to the hot, sheltered Jordan Rift Valley; others grow in the also relatively warm coastal plain. Since these plants reproduce spontaneously and are in their majority of no economic value, they must have reached their present Middle-Eastern distribution without the aid of man. It is likely that most of them belong to a recent migratory wave which, aided by rising temperatures, moved northward from Africa after the end of the last glaciation (Galil, 1972).

Within the Sudanian element in the Middle East, the sycamore fig constitutes a special case: first, it has apparently been of special interest to man from early times on and second, it is not pollinated and lacks natural means of dispersal in its present Middle-Eastern and North-African distribution. In view of the above, the present study explores two main alternative questions. Has the sycamore fig moved to the Middle East spontaneously as a part of the wild Sudanian element and remained in the area after losing its reproductive capacity only because of the active help of man, or has man been entirely responsible for its northward transportation? In the present study these two alternative possibilities are explored.

### Lines of Investigation

Fossil equivalents of *Ficus sycomorus* or its close relatives are not available. Also a search for palynological evidence is futile since the pollen of the sycamore fig remains confined within the syconium and is not dispersed in the air. Accordingly, the present investigation relies on archaeological data only.

Egypt and later Palestine were important centres of early civilization. The organization of State in the Nile Valley, the concept of the immortal God-King, the unique cult of the dead and the invention of hieroglyphic writing provided the basis for the preservation of evidence on life in ancient Egypt and on the plants and animals which accompanied man. Information can be assembled from writings, paintings, ornaments, bass reliefs and remnants of dry plant parts found in tombs (Laurent-Taekholm, 1964). Because of the dry desert climate, such plant parts are well preserved and can often be identified with certainty. The sycamore fig is richly represented in these records.

Good sources of information on the sycamore fig in later periods are the Old and New Testament and the Talmud (Carmin, 1931; Galil, 1966). While the true identity of many Bible plants is controversial, that of the sycamore fig is universally accepted.

In addition to these direct sources of evidence, indirect methods may sometimes be helpful. In cases where the plant in question is connected with another organism whose remains are more amenable to preservation, the presence of the plant may sometimes be inferred from that of the second organism. Of course such deductions can be made only when the two organisms are closely linked. It appears that such links exist between the sycamore fig and the Egyptian fruit bat, *Rousettus aegyptiacus* Geoffroy, of which remnants have been found.

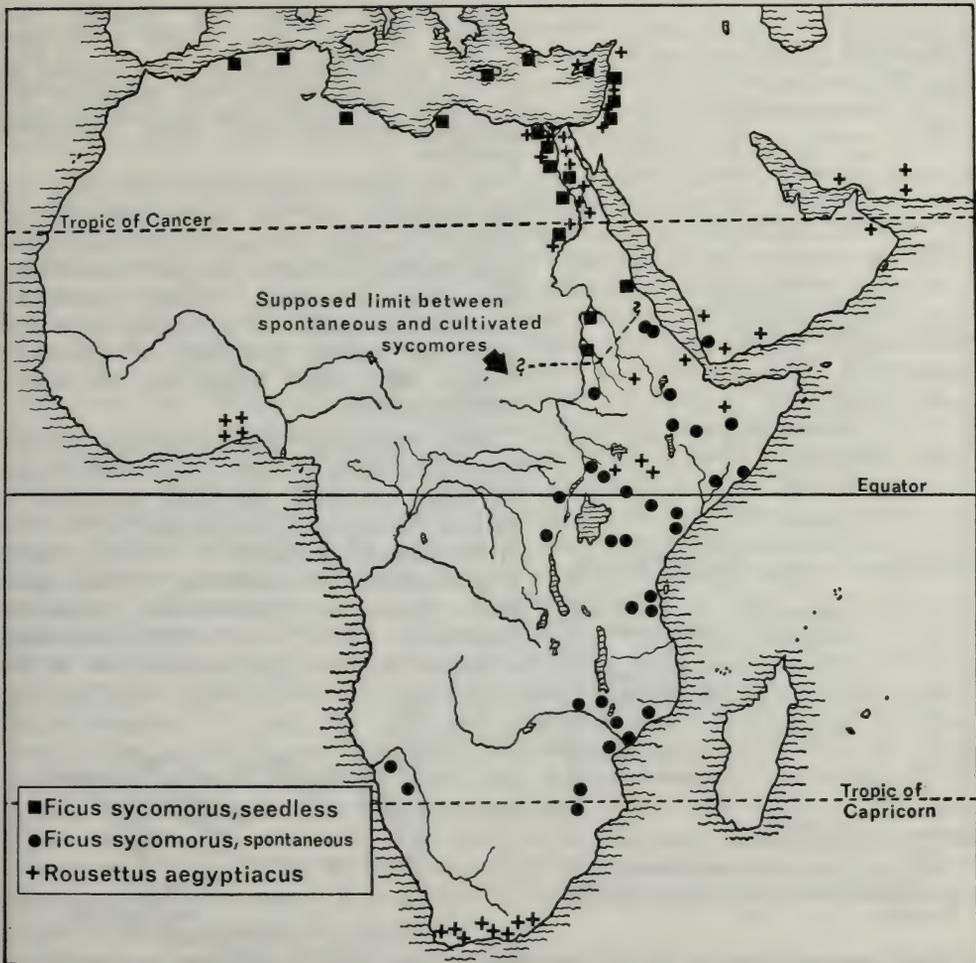


Fig. 1. Distribution map of seed producing and of seedless sycomore and of the Egyptian fruit bat (distribution of bat partly after Harrison, 1964).

### The Sycomore Fig in the Middle East in Retrospect

In Biblical times the sycomore tree was already widespread and well known in Palestine (Kings I, Chapter 10: 27; Chronicles II, Chapter 1: 15, Chronicles II, Chapter 9: 27). At around 1,000 B.C., King David appointed a curator responsible for the sycomores and olive trees in the plain of Lydda (Chronicles I, Chapter 27: 28). The prophet Amos (Amos, Chapter 7: 14) practiced the ancient method of gashing sycomore syconia in the hill area of Palestine. This gashing, by which ripening of the syconia is induced at an early stage prior to the emergence of the inhabiting wasps, makes the fruit more suitable for consumption (Galil, 1968). In the New Testament there is a reference to a tall sycomore tree in Jericho (Luke, Chapter 19: 4).

In ancient Palestine the sycomore tree was held in esteem mainly for its timber and less for its juicy fruit or shade yielding crown as was the case in the more arid Nile Valley. This is evident from Talmudic literature (100 B.C. to 400 A.D.), mainly the Mishna and Tosephta, in which many rules governing use of the tree and its products are found.

- EGYPT -		
c.1085 B.C.	NEW KINGDOM XVIII-XX DYN.	
c.1567 "	HATSHEPSUT	
c.1786 "	INTERM. PERIOD	
c.2181 "	MID. KINGDOM VII-XII DYN.	
c.2686 "	OLD KINGDOM III-VI DYN.	
c.3200 "	I-II DYN. ARCHAIC PERIOD [HISTORIC PER.]	
c.3400 "	LATE GERZEAN	
c.3600 "	EARLY GERZEAN MAADI	
c.4000 "	x AMRATIAN MERIMDA	
c.5000 "	x BADARIAN TASIAN	ISRAEL
c.7000 "	NEOLITHIC FAIYUM, A'	NEOLITHIC JERICHO PRE-POTTERY N.
c.9000 "	HELOUAN MESOLITHIC [PREHISTORIC PER.]	NATUFIAN MESOLITHIC

Fig. 2. Archeological periods in the Middle East, beginning with the Natufian.

XXth Dynasty (about 1,100 B.C.). All parts of the syconium, including the insects inhabiting it, were well preserved and could be identified. This syconium is at a late developmental stage and the female sycophilous wasps had already left it. However, the male wasps within the fruit could be identified. They are the same parasites which inhabit present-day syconia in the Middle East. There was no trace of the natural pollinator *Ceratosolen arabicus*, and the fruit contained no seeds.

One of the earliest sycamore findings comes from Petrie's excavations in the valley of the Royal Tombs at Abydos (Fig. 3). In his report, Petrie (1901) shows a drawing of a dried sycamore fruit, one of the numerous figs found strung together on threads in the tomb of Pharaoh Den Setui of the first dynasty (Fig. 2). Thus we may judge that throughout the historic period, the sycamore fig was very popular in Egypt.

In his well known book "Enquiry into plants", Theophrastus (372-287 B.C.) also gave a detailed account of the sycamore fig in Egypt and Cyprus. He described the gashing technique and other cultivation practices.

In the dynastic epoch of Egypt (Fig. 2), the sycamore tree was held in high favour. The fruit appears time and again among the food offerings in burial sites and in necklaces decorating mummies. Many household utensils were made of sycamore wood and numerous coffins prepared of sycamore boards have been found in the tombs (Wönig, 1897).

Well preserved leafy branches, woody parts and fruits (Lucas, 1948) which can be easily identified, are now deposited in various museums in Europe and U.S.A. The Archaeological Museum of Cairo contains a particularly rich collection of plant parts from pharaonic excavations (Laurent-Täckholm, 1964). Galil (1967) examined a fruit taken from the tomb of Ani of the



Fig. 3. Prehistoric settlements in the Middle East.

The earliest archeological records of the plant come from neolithic villages and burial sites along the Nile Valley in predynastic Egypt (Fig. 2). These records are few and sometimes uncertain. In an account of excavations at Mostagedda near Tasa and at Badari on the western bank of the Nile in Middle Egypt, Brunton (1937) brings a clear instance of two sycamore fruits found in a tomb of the Amratian period at the beginning of the fifth millennium B.C. (Fig. 2).

The Nile Valley lies 200-300 m below the western desert plateaux and the eastern desert which flank it. The seasonal floods and thus the cultivated ground do not extend over the entire width of the valley at all points. Between the cultivated areas and the eastern and western escarpments there are broad discontinuous strips of low non-irrigated and non-cultivated desert which are intersected by wadis that descend from the plateaux. Under the low present-day rainfall in the area (about 25 mm per annum at Cairo) these wadis are now dry. In the low desert strips along the valley, large roots leading to remnants of tree trunks have been unearthed. Brunton (1937) comments on such roots in Badarian levels of the Tasa and Mustagedda excavations, where they were found sometimes adjoining the cultivated land and sometimes at a distance from it and always deeply below the present desert soil surface. The roots excavated at these levels must have predated the Old Kingdom settlements since tombs of this period cut through the roots. Brunton concludes from presence of these roots that precipitations in the Nile Valley or water supply from the surrounding hills were higher in the fifth millennium B.C. than they are today. Similar accounts of roots from the same period are brought by Mond and Myers (1937), who also excavated in Middle Egypt at Aramant, near Luxor (Plate 1b) of today (Fig. 3). Here the settlements were at some distance from the cultivated land along the streams descending from the surrounding hills and the roots were found at about 12 m above the flood level of the period. Roots from these excavations are shown in Plate 1b. They evidently belong to a large tree whose trunk, however, has not been preserved. Sir Arthur W. Hill of Kew Gardens who examined these roots reported as follows: "The specimen of wood sent for identification appears to be that of *Ficus sycomorus*, although from its indifferent state of preservation, it is not possible to identify it with any degree of certainty". Another sample from the same level was identified as a species of *Acacia*.

Here too, it has been suggested that the trees belong to the Badarian period at the latest. In one of the Badarian cemeteries such roots were found in the rock on both sides of a burial chamber which cuts through them. This indicates that the trees must have predated the settlement.

### **The Fruit Bat as Evidence for Occurrence of Sycamore Fig in Natufian Palestine**

The fruits of the various *Ficus* species, which are juicy and comparatively poor in hard matter, are particularly well adapted to consumption by fruit bats. Biologists have commented on this link in different parts of the tropics. Williams (1928) has shown this in the Philippines and Ratcliffe (1938) in tropical Australia. Anderson and Jones (1967) note that the pantropical distribution of the fruit eating bats coincides with that of the genus *Ficus*. Ramirez (1971) notes that fruit bats do not occur in New Zealand and Hawaii, which lack native *Ficus* species.

One of the bats known to include *Ficus sycomorus* fruits in its diet is the Egyptian fruit bat, *Rousettus aegyptiacus* (Pteropodidae) (Plate 1c). As seen from Fig. 1, the distribution of this large tropical bat coincides roughly with the primary distribution of the sycamore fig. The East Mediterranean coast is at the northern limits of this distribution.

The fruit bat is active at night and shelters in caves, where it hangs by its legs upside down from ceilings, during daytime. Juicy tree fruits and the young shoots of various trees constitute its main food. It consumes and swallows soft fruits in their entirety; fruits with a hard pericarp or kernels are squashed in the mouth and the hard parts spat out. Frequently, the bat carries the fruits to one particular branch on a tree and consumes them there. Accumulated dropped seeds, and later seedlings, beneath such a point are clear indications for an "eating post". Each animal consumes about twice its body weight in fruits or shoots (about 250 g) in 24 hours. A daily food supply is necessary and two or three days of starvation suffice to kill the animal.

In Israel the spring to autumn diet comes largely from cultivated fruit trees (Fig. 4), causing serious damage to fruit growers. In the cold winter months the bats subsist in the area surveyed on fruits of ornamental china berry (*Melia azedarach* L.) and are also observed to nibble pods of the wild-growing and cultivated carob, *Ceratonia siliqua* L., which occasionally remain on the tree after ripening in the previous summer. The mandarin (*Citrus nobilis* Lour.) occasionally serves as another food source during the winter months. In Israel's coastal plain, bats suck the fruits empty of their contents, leaving the hollow peel on the trees. *Citrus* species with thicker peels, such as oranges and grapefruits, are not attacked.

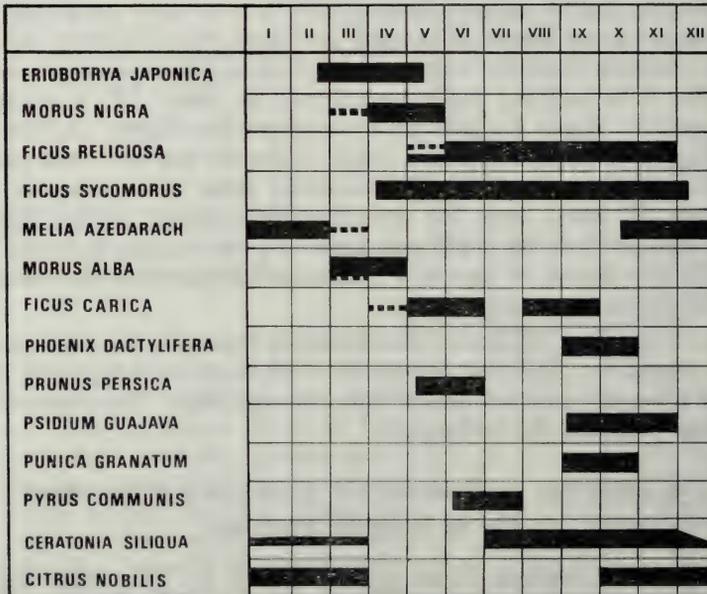


Fig. 4. Time table of present-day food plants of the fruit bat.

While today *R. aegyptiacus* has a large choice of fruits at its disposal in Palestine, this is unlikely to have been the case prior to fruit crop domestication. Native East Mediterranean trees and shrubs cannot supply an all-the-year-round diet. As far as they have juicy fruits, these ripen in autumn. Young leaves and shoots are only available in spring and early summer.

The sweet fruits of the tropical *Ziziphus spina-christi* Willd., which abounds in the coastal plain and warm valleys of Palestine are not consumed by the bat in nature, presumably because of the tree's thorny stipules.

As to the locally growing *Ficus* species, animals in captivity readily consumed the fruits of any of the cultivated species offered to them. In the wild state the fruit bat frequents the common fig, *Ficus carica* L. Since this tree bears crops two or three times a year, these figs are only available at intervals. This is not the case in *Ficus sycomorus*, which provides a continuous supply of food throughout the warmer months from alternately fruiting trees in the same neighbourhood. In the coastal plain of Israel trees have been observed bearing up to seven crops a year. *F. sycomorus* can thus bridge over gaps in fruit supply, even under present conditions. There is only a short fruitless interval during the coldest months of the year.

On the basis of what has been said, one would expect the bat to show an innate preference for *F. sycomorus* over other fruit trees which are today more abundantly available in the area surveyed. This hypothesis was tested in a number of experiments. In addition, a test of feeding response to carob was made, since the fruits of this local species are available during the cold months of food shortage.

Ten bats were kept in a wire cage which was darkened during daytime. They were trained to take their food from plates on a particular shelf. In some cases fruits were suspended by threads from the ceiling. The observations, although made by electric light, did not markedly interfere with the feeding activities of the bats.

*Experiment 1* (end of November). After sunset three plates were presented. One plate contained pieces of guava (*Psidium guajava* L.) and apple fruit; the second contained a mixture of guava and sycamore fruit pieces; the third contained only sycamore fruit. After an hour, all sycamore fruit had been consumed whereas the apple and guava had not been touched, by themselves or mixed with sycamore figs.

*Experiment 2* (end of January). Two plates were presented. One plate contained a mixture of apples, pears and tomatoes in 12% cane sugar solution; the second contained the same mixture with an addition of mashed sycamore fruit stalks (not fruits). On the following morning the first plate had remained untouched while most of the second plate had been emptied.

*Experiment 3* (end of January). Two plates containing 12% sucrose solution were presented to bats which had been starved for three hours in a separate cage. To one plate mashed tender sycamore leaves and shoots were added. On confrontation with the food plates the bats immediately approached the plate containing leaves and shoots. On the following morning that latter plate was empty while the plate containing only cane sugar solution had remained untouched.

*Experiment 4* (February). Eight ripe carob pods were soaked in water and suspended in the case at a height of 2 m from the ground. A bowl with drinking water was placed on the feeding shelf. Bats that had been kept on half their normal rations throughout the preceding day and had not been fed at all for several hours prior to the experiment were released into the cage. After two hours, four of the fruits had been nibbled at and broken to pieces. Although the carob pods were approached, broken into pieces and even carried to eating posts, they were hardly eaten. These pods are too dry to be consumed by the bat and therefore of no dietary value.

The experiments with sycamore fig demonstrate a definite preference for all parts of this species over other fruits. The sycamore tree may thus have been an indispensable wild food plant which could sustain the fruit bat during the greater part of the year in pre-agricultural Palestine. Accordingly, it is difficult to explain the presence of the bat in the Middle East of that time without simultaneous occurrence of *F. sycomorus* in the area. It is feasible that the animal's northward

movement from its primary distribution area in tropical Africa (Fig. 1) has been closely linked with the northward migration of *F. sycomorus*, the fig providing sustenance for the bat and the bat serving as an agent of seed dispersal.

The oldest known pictures of flying foxes are wall paintings found at Beni Hasan and date from the twelfth Dynasty, about 2,000 B.C. (Allen, 1939). These are of no great help for the elucidation of our problem. But since the bat lives in caves, there are good chances for the preservation of its skeleton, which thus can serve as indirect evidence for the occurrence of *Ficus sycomorus*. Fortunately, such records are available for a period which predates the earliest archaeological traces of the plant, namely from the Natufian level (about 9000-7000 B.C.).

The Natufian mesolithic civilization is indigenous to an area extending from Central Lebanon through Palestine to Helouan in Egypt (Fig. 3). Records of this civilization of wide-spectrum food gathering, small game hunting, and fishing have been found in different parts of Israel, mostly in caves (Garrod and Bate, 1937) but also in open places (Kenyon, 1971). Parts of skeletons of the fruit bats have so far been found in two of the caves. Haas (1952) has described *R. stekelesi*, a species very close to the recent form, from the Upper Natufian level of the Abu Usba cave, on Mt. Carmel. Also a single molar of *R. aegyptiacus* was detected in the Natufian deposits of the Hayonim cave on the western slopes of the Lower Galilee mountains by Bar Yoseph and Chernov (1966).

It is noteworthy that in earlier Palaeolithic levels in the same caves no remnants of the fruit bat have been found. The scarcity of these remnants in the Natufian caves, in spite of the favourable conditions for preservations existing there, indicates that even in this era the populations of the bat in Palestine were very meagre. It is very possible that their establishment was hampered by insufficient food supply, especially in the winter.

### Discussion

The alternatives posed in the introduction, namely whether *F. sycomorus* moved spontaneously to the Middle East with the Sudanian element or whether it was brought here by man can now be reviewed. Since there are indications that the sycomore fig may have been in the area already in Natufian times, as early as the eighth millenium B.C., the primary question is whether man at that time was already versed in plant cultivation practices and could transport plants over distances.

It is generally accepted that the Middle East and the neighbouring countries were the cradle of agriculture in the Old World. Van Zeist (1970), who studied the plant findings at Tel Mureybit in the Euphrates Valley, Syria, from the period of 8050-7542 B.C., described seeds and fruit of 18 species of wild plants, including wild einkorn (*Triticum boeoticum* Boiss.), wild barley (*Hordeum spontaneum* Koch) and various pulses. At Ali Kosh (Deh Luran plain, Iranian Kurdistan), cultivated plant remnants of the period 7500-6750 B.C., including einkorn (*T. monococcum* L.) and emmer (*T. diccoccum* Schubl.) were found. These are a clear indication of agriculture (according to Renfrew, 1969). The earliest remains of cultivated plants in the area of Palestine in the prepottery neolithic A level of Jericho (about 7000 B.C.) include carbonized seeds of einkorn and emmer, as well as various possibly cultivated pulses (Hopf, 1969). It is noteworthy that this Neolithic level in Jericho overlies a clear Natufian layer (Kenyon, 1971).

As to the beginnings of agriculture in Palestine, Stekelis (1966) regards the Natufian sickles and mortars as evidence for plant cultivation. Accordingly, he puts the beginning of the Neolithicum at about 9000 B.C. and includes the Natufian period in it. Yet that culture is generally regarded as mesolithic and pre-agricultural. According to Kenyon (1971), the Natufian was still a food gatherer, hunter

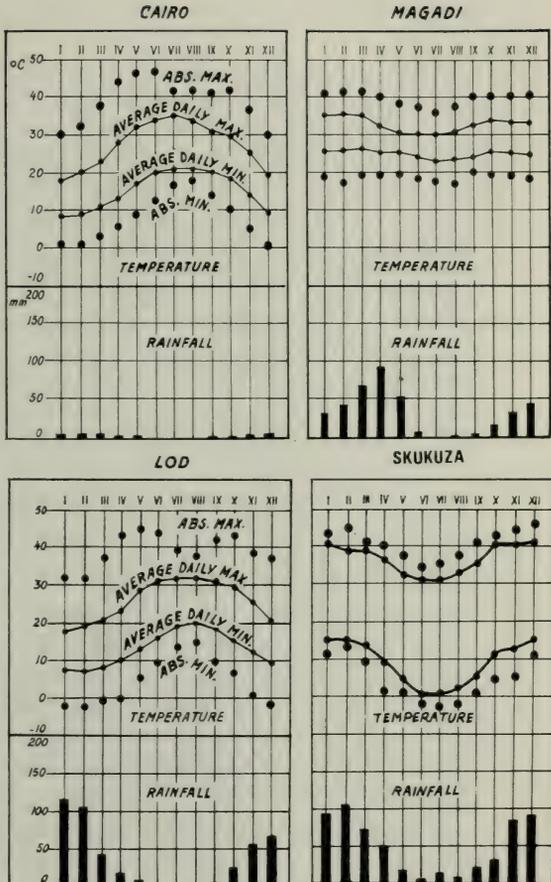
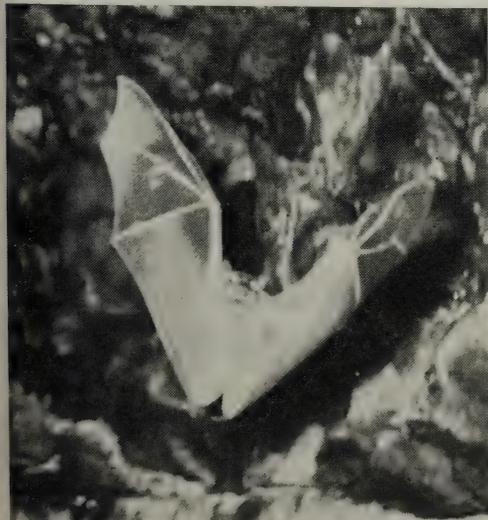
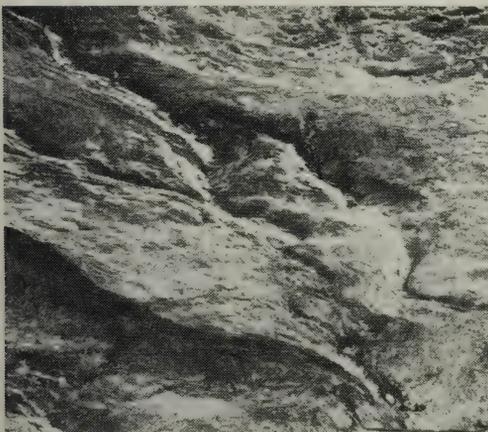


Plate 1.

- Left top: a. Sycamore tree.
- centre: b. Sycamore roots from the Badarian period (after Mond and Myers, 1937).
- bottom: c. Fruit bat.
- Right: d. Climate curves of Cairo (Egypt), Magadi (Kenya, East Africa), Lod (Israel) and Skukuza (Kruger Park, South Africa).



and fisherman and the tools found were used for cutting and pounding wild cereals.

The plant findings of the early Neolithic in Jericho indicate an advanced stage of plant domestication. Arduous and long-continuing processes of selection must have preceded this period. Even if no clear evidence for agriculture in the Natufian period is as yet available, probings into plant cultivation must have been made in this period. It is feasible that intensive harvesting of wild plants and their preparation for consumption with the aid of especially designed tools led eventually to the sowing of these plants near the settlements to ease collection. Unfortunately, as long as man did not promote the selection of cultivated plants, e.g. non-brittle cereals, no real indication of agriculture can be expected. Furthermore, Natufian levels have so far not revealed remnants of the wild plants harvested and processed with the tools detected in that level. Possibly some of the wild seeds found at Tel Mureybit, but whose native habitat at that time was at a considerable distance north of the settlement (van Zeist, 1970), were similarly sown by man. According to van Loon (1968) some microliths found at Tel Mureybit show Natufian influence.

Another possibility must be taken into account, which is relevant to the distribution of the sycomore in the area in ancient times. In addition to seed agriculture there are also early traces of dates, grapes and common figs (*F. carica*) in the area. Already in the pre-pottery A Neolithic level of Jericho carbonized pips of *Ficus* cf. *carica* have been found (Hopf, 1969). Western (1971) reports on *Ficus* charcoals from the same level. It is important to determine finally whether these findings belong to the deciduous common fig or to the evergreen sycomore. If they belong indeed to *F. carica*, this species must have been native to Palestine and not introduced from South Arabia or Iran as is claimed by Werth (1932) and Condit (1937). If, on the other hand, the remnants represent *F. sycomorus* this would be of great help for the elucidation of the problem posed in the present paper.

The common fig as well as the sycomore can be vegetatively propagated from branches stuck into the ground under suitable conditions. This type of plant propagation appears to be more simple and easier than seed propagation in which the difference between propagule and the grown plant is much greater. There is no conclusive evidence as to whether propagation by vegetative parts (vegeticulture) or seed propagation was the earliest type of plant cultivation in the Middle East (Harris, 1969). It must be taken into account that in this region there are several suitable habitats for vegetative propagation by branches stuck into the soil. These include muddy swamps along the flooded areas of the Nile and sandy soils on a high water table along the coastal plain of Palestine, in which branches can root readily.

There are few references as to the domestication of the sycomore fig in botanical literature. The German botanist Schweinfurth (1910 p. 34) attempted to elucidate the origin of the early Egyptians by tracing the natural distribution of two of their sacred trees that were planted in temple gardens, *Mimusops schimperi* Hochst., Sapotaceae and *Ficus sycomorus*. According to Schweinfurth, the two species grow wild in the southwestern hilly parts of the Arab Peninsula and in northern Ethiopia, i.e. on the two sides of the Red Sea. Since he found no genuinely wild-growing specimens of these species in Egypt, nor in the Upper Nile reaches, which support a tropical Sudanian flora today, he concluded that the incipient Egyptians brought these alien plants with them from their country of origin in Arabia. While the sycomore fig became well established in its new habitats, *Mimusops schimperi*, the "Persea" of the Greeks, became increasingly rare after the Hellenistic-Roman period and almost disappeared in the Islamic period.

It appears that Schweinfurth was unaware of the distribution of *Ficus sycomorus* in equatorial and southern East Africa. Also his theories on the origin of the Egyptian are questionable. Archaeologists and anthropologists hold that the population of the Nile Valley is a heterogeneous group of elements part of which occupied the Nile Valley already in Paleolithic times and that invasion took place not only from the south but also from Libya in the west. Moreover, it is unnecessary to evoke migrations of the ancient Egyptians to account for south-to-north movements of the sycomore fig. For example, northward migrations of the Central African Ishango tribe from Lake Edward in Congo to Khartoum, and further north along the Nile Valley are believed to have taken place in the Mesolithicum (de Heinzelin, 1962). Here this Central African civilization could have come into contact with the southern outpost of the Natufian civilization at Helouan.

Another proof of possible contacts between the Natufian culture and more southern areas is indicated by occurrence of shells of the tropical mussel *Cypraea moneta* in Natufian levels of the Carmel caves in northern Palestine (Garrod and Bate, 1937). The northern limit of the natural distribution of this mussel is the Gulf of Oman, far to the south.

Yet the transportation of living plants by man at such remote times is so far an open question. Data on the transplantation and shipping of plants appear in the archaeological record only relatively late. On the walls of the burial palace of Egyptian Queen Hatshepsut (XVIII Dynasty, ca. 1480 B.C.) in Deir el Bahari near Thebes, paintings depict a delegation to Punt (Somaliland) loading a vessel with living spice plants (Hepper, 1967). Dixon (1969) notes that in all likelihood living plants were transported by ancient Egyptians also at much earlier periods. However, no definite data are available.

It appears that in late Pleistocene and early Holocene the climate was humid in the Sudan and Ethiopia. Also the present area of the Sahara desert must have been more humid at that time and neolithic settlements have been found in areas which are most inhabited today. According to Moreau (1963, 1966), the maquis of the North African shores extended further south and the Sudanian vegetation moved northwards. At least in western North-Africa no desert barrier remained between the Mediterranean and Ethiopian territories. Wide desert areas remained in the east, but here the Nile Valley with its periodic floods constituted a bridge between the Mediterranean and Sudanian vegetations and a south-to-north route for the advance of tropical plants.

Childe (1953) describes the vegetation along the Nile at the last pluvial period as follows: "Today the country south of Cairo is virtually rainless and would be utter desert save for the annual irrigation by the Nile flood. But in the pluvial period conditions must have been very different. The valleys of the wadis running in from the high desert must have been clothed with spring grasses, including quite possibly wild cereals and this herbage must have nourished herds of wild asses, barbary sheep, urus, antelopes, etc. To find floristic and faunistic environment comparable to that encountered by the most ancient Egyptians one must travel far upstream into the monsoon zone. On the White Nile the traveller will find, growing wild, plants that survived in historical Egypt only in gardens". It is likely that the sycomore fig which is part of the tropical element in Ethiopia and Sudan was among the species growing in the Nile Valley in those times.

The flourishing vegetation along the Nile described by Childe must have become impoverished gradually with the drying of the climate, but even in Badarian times, at the dawn of history, the vegetation was still richer than today as evidenced by the remnants of large trees and their roots.

As long as *F. sycomorus* bore viable seeds, migrating fruit-eating birds and bats, especially those which migrate from south to north at the onset of the warm season (such as *Oriolus oriolus*) could have been instrumental in moving the plant

northwards. When the climate became drier, the flooded areas along the Nile became restricted and the sides of the valley bed changed into low desert, the tropical vegetation retreated to suitable niches.

The present absence of the sycamore fig's natural pollinator in its Middle Eastern distribution remains the central question. Did *Ceratosolen arabicus* disappear because of any change in climate? Climates in the Middle East are markedly different from the climate of the tropical savannas, the native habitat of the sycamore fig.

Different precipitation regimes or absence of summer rains do not appear to be of any significance, since the sycamore occupies humid habitats. Temperature differences might be more critical. In the tropical savanna, temperatures are high throughout the year and show no diverging seasonal and diurnal extremes (see Magadi in Plate 1d). The Mediterranean and desert climates are far less equable. In winter temperatures fall below zero (see Cairo and Lod). However, the possibility that the Middle Eastern temperature extremes which are withstood by the sycamore fig might be too great for its pollinator is ruled out by climatic data from Kruger Park in Southwest Africa. Temperature extremes in this park (see Skukuza), which occupies southern hemisphere latitudes analogous to those of Middle Egypt, are greater than in the Middle East. Yet in the park area the sycamore fig is pollinated regularly and sets seed. Young plants of seed origin are observed in the park (personal communication from the nature conservator of Kruger Park, Mr. P. van Wyk).

Another possible explanation for the absence of pollinators throughout the secondary distribution area of *F. sycomorus* is loss of compatibility between the wasp and new cultivars, resulting from selection and vegetative reproduction for many centuries. A clear sign of degeneration in these plants is the production of various types of parthenocarpic fruits found in the cultivated varieties (Galil, 1968). It is well known that many cultivated plants grown continuously from roots or stems lose their fertility and cannot produce seeds any longer.

To test this point, two attempts have been made to inhabit syconia of *F. sycomorus* in Israel by *C. arabicus* wasps, brought from Kenya. Both attempts failed and no oviposition took place. Yet this is not conclusive evidence for incompatibility of local modern cultivars and the pollinator since in both cases wasps were introduced into syconia near the end of the active season of plant and insect under local conditions.

Investigation of the sycamore figs and their sycophilous wasps in Sudan, especially at the limit between the wild growing and cultivated trees (Fig. 1) may help in the elucidation of the problem. Unfortunately, there is very little information on either the tree or its pollinators in this area in the scientific literature. For our study, reports on the pollinator *Ceratosolen arabicus* are more valuable than purely botanical information. The dependence of the wasp on the sycamore figs is so narrow that in practice the presence of this sole pollinator can be taken as evidence for the presence of the tree.

The most pertinent of the few available data are as follows: *Sycophaga sycomori*, the specific parasite of *F. sycomorus* is reported from Nubia (Sudan) on the southern bank of the Nile, near Abu Simbel. As already mentioned, this wasp is wide spread throughout the whole distribution area of the sycamore fig, including Egypt and Palestine, and does not pollinate the flowers. The pollinator *C. arabicus* is not mentioned from that place.

A former Arab resident of Khartoum (Sudan) confirmed that the sycamore is extensively cultivated in the surroundings of the city and gashing is practiced there for raising the quality of the fruit. Locally the sycamore fruit are called "those of stripped cheeks" after the wide fissures, typical of the ripe fruit sold in the market. Thus the sycamore figs growing along the Nile in North Sudan appear to be cultivated seedless varieties as in the Middle East.

The pollinator *C. arabicus* is reported (various authors, including Wiebes, 1968), from various parts of Eritrea (Keren, Ghinda) and Ethiopia (Addis Ababa, Caschei, Masi). Undoubtedly, the trees growing there are pollinated normally and produce seeds.

In spite of the meagre and incomplete information, the impression of a transition between the spontaneous and the cultivated types of *F. sycomorus* somewhere in Sudan is obvious. It appears likely that in desert Moslem northern Sudan, which was under Egyptian influence for a long time, the same or similar selected varieties of cultivated sycomores are grown as in Egypt. On the other hand, in the woodland savannas of southern Sudan, with its negro-nilotic pagan and partially christianized population, the tree is still spontaneous.

Since in desert northern Sudan every piece of irrigated ground on which sycomores could survive is in high demand, it is likely that all wild-growing trees there were removed by farmers and replaced by useful selected cultivars. Thus a more or less sharp boundary between the wild and cultivated types of *F. sycomorus* must have formed, corresponding to the vegetational and ethnic dividing line between the northern and southern Sudan. Of course the above hypothesis needs verification by detailed surveys of the area.

### Conclusions

Because of the antiquity of the sycamore in the Middle East, any decision between the two alternatives posed in the introduction remains speculative. The question is whether the reasonable possibility that in the Natufian period man already made the first steps in plant cultivation and propagation from seeds and from branches, and the clear evidence of cultural connections between Palestine and tropical Africa at those times — provide sufficient ground for assuming that the tree was deliberately brought from the south by man. Perhaps the lack of any archaeological or geological remnants of the fruit bat in levels below the Natufian, i.e. before the onset of agriculture, even in hot and humid periods, supports such a supposition. One of the authors of the present paper tends to accept this idea.

The other two authors believe, together with many prehistorians, that Natufian man was not sufficiently advanced for carrying plants along great distances. The presence of the sycophilous parasite *Sycophaga sycomori* within the figs throughout the Middle East indicates that the movement of the trees from south to north must have taken place step by step.

The follow-up of the changes of climate and movement of vegetation during late Pleistocene and early Holocene provides a sufficient basis for the conclusion that the sycamore fig could have reached its secondary distribution area together with other components of the last migration wave and that it started its existence in the Middle East as a spontaneous, wild-growing plant. Only afterwards, perhaps at the early Neolithicum or even later when man started to cultivate plants and select them, cultivars were developed which lacked their compatibility with the pollinator and consequently lost their ability to produce viable seeds.

The clear dividing line between wild growing and cultivated sycomores in Sudan is due to man's interference and is in fact an ethnic and cultural boundary.

Evidence for the presence of *F. sycomorus* in the Middle East in ancient times is far from satisfactory, especially since the data supporting the presence of the plant in Natufian Palestine are based on an indirect method of enquiry. But all possible sources of information have not been exhausted. The only fig from Pharaonic tombs which was searched for the presence of pollinators and seeds belongs to a comparatively recent period (XX Dynasty, about 1100 B.C.). It appears that the sycamore of that time was already identical with the recent form. Studies of additional figs from earlier dynasties should provide critical information.

The identity of *Ficus* pips and charcoals found at the pre-pottery Neolithic layer of Jericho with either *F. carica* or *F. sycomorus* should be established. Soil samples and coproliths from Natufian caves should be searched for presence of *F. sycomorus* seeds. Seed findings from earlier periods could provide the basis for a more definite decision as to the origin of the sycomore fig in the Middle East.

### Acknowledgments

The authors are indebted to Prof. E. J. H. Corner (Cambridge), Mr. N. Hepper (Kew) and Mr. J. Roth (Shaar Agolan, Israel) who have kindly read the manuscript and offered many helpful suggestions; thanks are also due to Mr. S. Shaeffer for the illustrations and Mr. A. Shuw for the photographic work.

### References

- ALDRED, C. 1965. Egypt to the end of the Old Kingdom. Thames and Hudson, London.
- ALLEN, G. M. 1939. Bats. Dover Publications, New York.
- ANDERSON, S. and J. Knox JONES, Jr. 1967. Recent mammals of the world. Ronald Press, New York.
- BAR YOSEF, O. & E. TCHERNOV. 1966. Archaeological finds and the fossil faunas of the Natufian and microlithic industries at Hayonin cave (Western Galilee, Israel). *Israel J. Zool.* **15**: 104-140.
- BROWN, Th. W. & F. G. WALSINGHAM. 1917. The Sycomore fig in Egypt. *J. Hered.* **8**: 3-12.
- BRUNTON, G. 1937. Mostagedda. Quaritch, London.
- CARMIN, J. and D. SCHEINKIN. 1931. The fauna of Palestinean plants. 2. *Ficus sycomorus* Linn. *Bull. Soc. ent. Égypte* **15**: 164-187.
- CONDIT, I. J. 1947. The Fig. Waltham, Mass., U.S.A.
- DIXON, D. M. 1969. The transplantations of Punt incense trees in Egypt. *J. Egypt. Archaeology* **55**: 55-65.
- GALIL, J. 1966. The sycomore tree in the civilization of the Middle-East. *Nature and Country* **8**: 306-318, 335-338 (Hebrew).
- 1967. Sycomore wasps from ancient Egyptian tombs. *Israel J. Ent.* **2**: 1-10.
- 1968. An ancient technique for ripening sycomore fruit in East Mediterranean countries. *Econ. Bot.* **22**: 178-190.
- 1972. On the origin of the savanna vegetation in Israel. *Nature and Country* **14**: 139-145 (Hebrew).
- GALIL, J. and D. EISIKOWITCH. 1968. On the pollination ecology of *Ficus sycomorus* in East Africa. *Ecology* **49**: 259-269.
- GARROD, D. A. E. 1942. Excavations in the cave of Shukbah, Palestine, *Proc. prehist. Soc.* **8**: 1-5.
- GARROD, D. A. E. & D. M. A. BATE. 1937. The stone age of Mount Carmel. Clarendon Press, Oxford.
- CHILDE, V. GORDON. 1953. New light on the most ancient East. Grove Press, New York.

- GRÜNBERG-FERTIG, J. 1966. Phytogeographical-analytical study in the flora of Palestine. Thesis submitted for the degree Doctor of Philosophy, The Hebrew University, Jerusalem.
- HARRIS, D. R. 1969. Agricultural systems, ecosystems and the origin of agriculture. In the symposium on "Domestication and Exploitation of Plants and Animals", ed. P. J. Ucko and G. W. Dimbleby, pp. 3-15. Duckworth, London.
- HARISSON, D. L. 1964. The mammals of Arabia. Benn, London.
- de HEINZELIN, J. 1962. Ishango. *Scient. Am.* **206**: 105-118.
- HEPPER, F. N. 1967. An ancient expedition to transplant living trees. *J. R. hort. Soc.* **92**: 435-438.
- HOPE, M. 1969. Plant remains and early farming in Jericho. In the symposium on "Domestication and Exploitation of Plants and Animals", ed. P. J. Ucko and G. W. Dimbleby, pp. 355-359. Duckworth, London.
- KENYON, K. 1971. Archaeology of the Holy-Land. Benn, London.
- LAURENT-TAECKHOLM, V. 1964. Faraos blomster. Natur och Kultur, Stockholm.
- van LOON, M. N. 1968. The Oriental Institute excavations at Mureybit, Syria. *J. Near Eastern Studies* **27**: 265-82.
- LUCAS, A. 1948. Ancient Egyptian materials and industries. Arnold, London.
- MOND, R. & O. H. MYERS. 1937. Cemeteries of Armant I. The Egypt Exploration Society, London.
- MOREAU, R. E. 1963. Vicissitudes of the African biomes. *Proc. zool. Soc. Lond.* **141**: 395-421.
- MOREAU, R. E. 1966. The Bird faunas of Africa and its islands. Academic Press, New York, London.
- PETRIE, W. M. F. 1901. The Royal Tombs. The Egypt Exploration Fund, London.
- RAMIREZ, W. B. 1970. Host specificity of fig wasps (Agaonidae). *Evolution* **24**: 680-691.
- RATCLIFFE, F. 1938. Flying fox and drifting sand. Chatto and Windus, London.
- RENFREW, J. M. 1969. The archaeological evidence for the domestication of plants. In the symposium on "Domestication and exploitation of plants and animals", ed. P. J. Ucko and G. W. Dimbleby, pp. 149-172. Duckworth, London.
- SCHWEINFURTH, G. 1910. Ueber die Bedeutung der "Kulturgeschichte". *Bot. Jb.* **45**, Beibl. **103**: 28-38.
- STEKELIS, M. & G. HAAS. 1952. The Abu Husba cave. *Israel Explor. J.* **2**: 15-47.
- STEKELIS, M. 1966. The Yarmuqian Civilization. Shaar Hagolan.
- THEOPHRASTUS (372-287 B. C.). Enquiry into plants. Translated by A. Hort, 1916. Heinemann, London.
- WERTH, E. 1932. Die wilde Feige im östliche Mittelmeergebiet und die Herkunft der Feigenkultur. *Ber. dt. bot. Ges.* **50**: 539-557.

- WESTERN, A. C. 1971. The ecological interpretation of ancient charcoals from Jericho. *Levant* **3**: 31-40.
- WILLIAMS, F. X. 1928. Studies in tropical wasps, their hosts and associates. *Bull. Hawaiian Sug. Plrs Ass. Exp. Stn. Ent. Ser.* **19**: 1-179.
- WÖNIG, F. 1897. Die Pflanzen in Alt-Aegypten. Heitz, Leipzig.
- WIEBES, J. T. 1968. Fig wasps from Israeli *Ficus sycomorus* and related East-African species. *Zoöl. Meded., Leiden* **42**: 307-320.
- Van ZEIST, W. 1970. The Oriental Institute excavations at Mureybit, Syria. *J. Near Eastern Studies* **29**: 167-176.



# A Short History of Fig Wasp Research

by

J. T. WIEBES

*Department of Systematic Zoology and Evolutionary Biology  
University of Leiden, The Netherlands*

For convenience, the history of fig wasp research may be divided into four periods. Mayer's "Zur Naturgeschichte der Feigeninsecten" (1882) appears to present the first natural break. On the one hand, in giving a comprehensive review of older literature, it is the conclusion of its period. On the other hand, in being one of a number of contemporaneous reports on exotic fig wasps and, above all things, as a precursor to Mayr's paper of 1885, it also is the opening of a new era. In a way, Grandi's revision of the Agaonidae described by Mayr, and its accessory world catalogue (1928d), would form a similar stage half a century later. Between the two, past the times that scientists merely looked all wonder at figs and their wasps, we find the period in which the warp of fig wasp taxonomy was stretched. Some of the weft, it is true, was of very unequal capacity.

After 1928 we find more than a quarter-century of miscellaneous reports, waifs and strays in comparison with Grandi's synthesis. Then, in the fifties, a new activity arises with a gradual shift of interest to the symbiosis of figs and wasps, its mechanism and evolution.

In the present review I shall not confine myself to data on the Agaonidae. In the survey of our knowledge of fig wasp biology, we cannot dispense with their Torymid mess-mates. An outline of their nomenclatorial history is included in the first chapters. For data on pre-Linnean literature, and for a more complete discussion of eighteenth-century papers, I here refer to Mayer's review of 1882: their biological significance is negligible.

## **Wonder** (the period before Mayer, 1882)

In the "Systema Naturae", Linnaeus named two fig insects viz., *Cynips psenes* from oriental *Ficus carica* and *C. sycomori* from the sycomore fig of Egypt. These insects were generally misidentified until a hundred years later largely, it would seem, because of the confusion created by Linnaeus himself.

Linnaeus' pupil Hasselquist (1757), in his itinerary of a voyage to Palestine, described *Cynips ficus* and *C. caricae* from *Ficus carica*, and *C. cycomori* from *F. sycomorus* (see table 1 for a concise survey of the nomenclatorial history). These descriptions, with only a few small alterations, were repeated in the second part added to the German translation of the "Iter" (1762). In the meantime Linnaeus, presumably having decided that *Cynips ficus* and *C. caricae* probably were the two sexes of one species, united them under the name *Cynips psenes*. The original description of *C. ficus* "corpus totum rufum" and thus, implicitly, the description of *C. psenes*, did not seem to fit the shiny black insect Gravenhorst (1829) described as *Blastophaga grossorum*: the nomenclatorial outcome of a pronounced sexual dimorphism.

Linnaeus (1758) redescribed *Cynips sycomori* and unfortunately added a character of the Agaonidae "antennae ... basi crasso-conicae". This, and the inadequate labels of the specimens in the Linnean Cabinet (Saunders in Waterhouse, 1881), led Westwood (1840) to the description of *Blastophaga sycomori*, which soon proved to be identical with *C. psenes* (see Loew, 1843). Genuine *C. sycomori* was renamed *Sycophaga crassipes* Westwood (1840) although Forskal, as early as 1775, knew both sexes of what he rightly named *Cynips sycomori*.

There remain *Cynips caricae*, and *Ichneumon ficarius* Cavolini, 1782. Loew (1843), "auf Linné's Autorität", accepted the identity of *Cynips ficus* and *C. caricae*, but according to Waterhouse (1881) the two must certainly be considered distinct species. Confusion was complete when Saunders (1883a: 20) listed three species of *Blastophaga* viz.,

- sp.1. *B. ficus*, Hasselq.; *C. psenes*, Linn.; *B. sycomori*, Westw.
- sp.2. *B. caricae*, Hasselq.; *C. psenes*, Linn.
- sp.3. *B. grossorum*, Grav.

Half a year later, Saunders (1883c) alluded *Cynips caricae* to *Idarnella* Westwood (*Idarnodes* Westwood, both names of 1883: a, and c, respectively) for which, however, *Philotrypesis* Förster (1878) proved to be an older name. Except for Mayer, 1882 (and later, myself: Wiebes in China, 1962) no one seems to have recommended the use of the specific epithet *ficarius* as used by Cavolini, 1782. In a way, Westwood (1883c: vii) did, but he regarded *ficarius* distinct from *caricae*.

Table 1. Survey of the nomenclatorial history of *Blastophaga psenes*, *Philotrypesis caricae* and *Sycophaga sycomori*.

	<i>Blastophaga psenes</i> (Linnaeus, 1758)	<i>Philotrypesis caricae</i> (Linn. in Hass., 1762)	<i>Sycophaga sycomori</i> (Linnaeus, 1758)
Linn. in Hass., 1757	<i>Cynips ficus</i>	<i>Cynips caricae</i>	<i>Cynips sycomori</i>
Linnaeus, 1758	← <i>Cynips psenes</i> →		<i>Cynips sycomori</i>
Linn. in Hass., 1762	<i>Cynips ficus</i>	<i>Cynips caricae</i>	<i>Cynips sycomori</i>
Forskal, 1775			<i>Cynips sycomori</i>
Cavolini, 1782	<i>Ichneumon psenes</i>	<i>Ichneumon ficarius</i>	
Gallesio, 1820	<i>Chalcis psenes</i>	<i>Chalcis centrinus</i>	
Gravenhorst, 1829	<i>Blast.grossorum</i>		
Westwood, 1840		<i>Blast.sycomori</i>	<i>Sycophaga crassipes</i>
Loew, 1843	← <i>Blast.psenes</i> →		<i>Sycophaga sycomori</i>
Förster, 1878		<i>Philotrypesis longicauda</i>	
Saunders, 1878	<i>Blast.grossorum</i>	<i>Blast.psenes</i>	<i>Sycophaga crassipes</i>
Waterhouse, 1881	<i>Blast.grossorum</i>	<i>Blast.ficus</i>	<i>Sycophaga sycomori</i>
Westwood, 1882	← <i>Blast.psenes</i> →		<i>Sycophaga crassipes</i>
Mayer, 1882	<i>Blast.grossorum</i>	<i>Ichneumon ficarius</i>	<i>Sycophaga sycomori</i>
Saunders, 1883a	<i>Blast.grossorum</i>	<i>Blast.caricae</i>	<i>Sycophaga crassipes</i>
Saunders, 1883c		<i>Idarnella caricae</i>	
Westwood, 1883c		<i>Idarnodes caricae</i>	
		<i>Idarnodes ficarius</i>	
Mayr, 1885	← <i>Blast.grossorum</i> →		<i>Philotrypesis caricae</i>
			<i>Sycophaga sycomori</i>

It took two recent decisions (1964, Opinion 694; 1974, Opinion 1018) to validate *Philotrypesis caricae* (Linnaeus in Hasselquist, 1762) as the name of the common inquiline of *Ficus carica*, in the same sense as it had been used by Mayr (1885).

Grandi (1921b, 1930) and Joseph (1958). In the opinion of 1964, *Blastophaga psenes* (Linnaeus, 1758) was validated as the name for the pollinating insect.

Dalman (1818) expressed his wonder in the name of the fig insect he described from Sierra Leone: *Agaon paradoxum*. *Agaon* was taken as the basis of the family name by Walker (1846), after Westwood recognized the affinities of *Agaon* and *Blastophaga* and, like Latreille (1825), classified them with the Chalcididae. Billberg (1820) as well as later Schulz (1906) emended *Agaon* to *Agaum*; Kieffer (1911) would create a synonym *Courtella* (see Wiebes, 1968b).

It is unfortunate that the specimens recorded by Coquerel (1855) from La Réunion cannot now be found, and are probably lost. Three out of four of his species from *Ficus terragena* (probably, the same as *F. mauritiana* Lam.) are types of generic names viz., *Sycocrypta* with *S. coeca*, suppressed in Opinion 682 (1963) for *Ceratosolen* Mayr, 1885; *Apocrypta* with its type *A. perplexa*, and with *A. paradoxum* which belongs to *Sycophaga* Westwood, 1840; and *Chalcis explorator*, which was taken by Ashmead (1904a) as the type of *Apocryptophagus*: most probably it is one of the Sycoryctini, and not *Idarnes* as Walker (1871b: 60) suggested, nor *Sycophaga* as Westwood (1883b: 379) had it.

Motschulsky's (1863) material I have seen in the Moscow Natural History Museum. *Platyscapa frontalis* belongs to *Waterstoniella* Grandi, 1921a; *Platyneura testacea* most probably is a species of *Parakoebelea* Joseph, 1957a. Validation of the older names would create nomenclatorial changes in the Agaonidae and Torymidae.

From the West Indies Walker (1843) described *Idarnes carme*, which seems to be the same as *Tetragonaspis* Mayr, 1885 (as Mayr supposed but could not decide from Walker's description). This leaves the Old World species of "*Idarnes*" without a generic name (see Wiebes, 1966a: 155-156; 1968a: 310-311), but see the suggestion by Gordh (1975: 439) that *Idarnomorpha* Girault (1915b) could serve. Compare, however, also Hill (1967d: 94), who listed *Idarnomorpha* as a synonym of *Otitesella* Westwood! The type of *I. carme* is a female specimen in the British Museum (Natural History), from which the head was already lost when Westwood (1883a: 37, note) studied it; now it seems to be completely lost, and a neotype had to be designated (Gordh, 1975: 426-427). In the same 1843 paper Walker described *Paphagus* (Walker, 1871b: 65, "*Paphagus Sidero* ... belongs to the Agaonidae"), which was also by Mayr (1885: 151) mentioned as if he supposed it to be a fig wasp. Ashmead (1904a: 319, 499) cited it as one of the Pteromalidae. More confusion was created by Walker's description of wasps destructive to the fig in India, originally in 1871 (b), and again (posthumously) with different names in 1875 (see Patton, 1884; Wiebes, 1967e: 400-402).

In all, by the time Mayer wrote his review, there were known eighteen fig wasps, be they under twenty-four names. Most of these were known in one sex only, but they represented a fair sample of all but one of the larger groups now recognized (see table 2). Their host figs, as far as then known, belong to *Urostigma* (*Ficus benghalensis* from India), *Ficus* (*F. carica*), and *Sycomorus* (*F. sycomorus* from Egypt, and *F. mauritiana* from La Réunion).

Although Linnaeus (Hegardt, 1749) already explained the process of caprification by supposing that the insects brought the farina from the wild fig, which contained male flowers, to the domestic fig, which contained only female flowers (see Westwood, 1840: 215), several authors doubted or opposed this explanation. Mayer (1882, partly basing himself on Solms, 1882) extensively dwelled on this point. Most of his views on *Ficus carica* were corroborated by data from Grandi (1920a, 1929a), Buscalioni & Grandi (1936, 1938), and Joseph (1958), and will be discussed in a later chapter.

Table 2. Fig wasps known in 1882.

AGAONIDAE	proper name	reference
-see table 1-	<i>Elastophaga psenes</i> (L., 1758)	Joseph, 1958: 201
<i>Agaon paradoxum</i> Dalman, 1818	<i>Agaon paradoxum</i> Dalman	Wiebes, 1968b: 346
<i>Sycocrypta coeca</i> Coquerel, 1855	<i>Ceratosolen coecus</i> (Coquerel)	Opinion 682, 1963
<i>Platyscapa frontalis</i> Motschulsky, 1863	<i>Hateretoniella frontalis</i> (Motsch.)	(new comb.)
TORYMIDAE, Sycophaginae		
-see table 1-	<i>Sycophaga sycomori</i> (L., 1758)	Wiebes, 1968a: 311
<i>Idarnes carme</i> Walker, 1843	<i>Idarnes carme</i> Walker	Gorán, 1975: 425
<i>Apoerypta paradoxa</i> Coq., 1855	<i>Sycophaga paradoxa</i> (Coquerel)	Westwood, 1883b: 379
<i>Platyneura testacea</i> Motschulsky, 1863	<i>Parakoebelia testacea</i> (Motsch.)	(new comb.)
<i>Apoerypta perplexa</i> Coquerel, 1855	<i>Apoerypta perplexa</i> Coquerel	Westwood, 1883b: 379
<i>Chalcis explorator</i> Coquerel, 1855	<i>Apocryptophagus explorator</i> (Coq.)	Ashmead, 1904a: 238
<i>Idarnes stabilis</i> Walker, 1871	} <i>Sycoscapter stabilis</i> (Walker)	Wiebes, 1967e: 407
<i>Idarnes orientalis</i> Walker, 1875		
-see table 1-	<i>Philotrypesis caricae</i> (L. in Hass.)	Joseph, 1958: 201
<i>Idarnes transiens</i> Walker, 1871	} <i>Philotrypesis transiens</i> (Walker)	Opinion 1018, 1974
<i>Polarisa lutea</i> Walker, 1875		
<i>Sycobia bethyloides</i> Walker, 1871, ♀	<i>Walkerella temeraria</i> Westwood	Wiebes, 1967e: 402
<i>Idarnes pteromaloides</i> Walker, 1871	} <i>Micranisa pteromaloides</i> (Walker)	Wiebes, 1967e: 404
<i>Micranisa</i> Walker, 1875		
TORYMIDAE, Epichrysomallinae		
<i>Sycobia bethyloides</i> Walker, 1871	} <i>Sycobia bethyloides</i> Walker	Joseph, 1957a: 128
<i>Agrianisa myrmecoides</i> Walker, 1875		
EURYTOMIDAE, Eudecatominae		
<i>Sycophila megastigmoides</i> Walker, 1871	} <i>Sycophila megastigmoides</i> Walker	Burks, 1969: 119
<i>Pseudisa smicroides</i> Walker, 1875		
<i>Sycophila decatomooides</i> Walker, 1871	} <i>Sycophila decatomooides</i> Walker	Burks, 1969: 119
<i>Icanisa decatomooides</i> Walker, 1875		

### Warp and Woof (from Mayer, 1882 to Grandi, 1928d)

Before 1882 only a few shipments of tropical or subtropical fig insects were sent to Europe. Then, in 1882, Mayer reported on the collections made by Solms, that is, taken from figs in European herbaria or collected in Java, or brought from Egypt by Schweinfurth and Valentiner; moreover, Fritz von Müller (1886–1887) sent several samples from Brazil. Thus began the stream of shipments to Europe, and to America, where research was soon to start.

I shall now discuss some works of more general importance viz., those by Mayr (1885), Ashmead (1904a) and Grandi (1916–1917). Table 3 contains the classification of most of the genera discussed below; a more complete list of the Sycophaginae was presented by Hill (1967d: 92–96).

Mayr distinguished between three categories of fig insects viz., gall makers (according to Mayr: probably all "Agaoninen", certainly those of the genus *Blastophaga*), Hymenoptera parasitic upon larvae and pupae of the gall makers, and visitors ("Feigenbesucher") such as ants and fruit flies. Next to several genera of

the modern family Agaonidae, the first group also contained *Crossogaster* and *Sycophaga* (inclusive of *Apocrypta*!). It is now known (Galil, Dulberger & Rosen, 1970) that at least *Sycophaga sycomori* does cause "gall-tissue" in *Ficus sycomorus*. It was mainly the female morphology (the facial groove and other characters related to the way of entering the fig receptacle) that characterized the Agaoninae in Mayr's restricted sense (with Walker, the Agaonidae contained all fig wasps). Undoubtedly, Mayr classified his Agaoninae with the Chalcididae. In 1906, Mayr added new records and descriptions.

Table 3. Fig wasp classifications by Saunders, Mayr, Ashmead and Grandi compared.

Saunders, 1883a	Mayr, 1885	Ashmead, 1904a	Grandi, 1928d	recent names
SYCOPHAGIDES				
Prionostomata <sup>1)</sup>	"Agaoninen"	AGAONIDAE	AGAONINAE	AGAONIDAE
		Agaoninae	Agaonini	Agaoninae
Agaon	Agaon	Agaon	Agaon	Agaon
			<i>Alfonsiella</i>	<i>Alfonsiella</i>
			<i>Allotrioxoon</i>	<i>Allotrioxoon</i>
			<i>Elisabethiella</i>	<i>Elisabethiella</i>
Pleistodontes	Pleistodontes	Pleistodontes	Pleistodontes	Pleistodontes
	Tetrapus	Tetrapus	Tetrapus	Tetrapus
Eupristina	Eupristina	Eupristina	Eupristina	Eupristina
Sycocrypta				
	<i>Ceratosolen</i>	<i>Ceratosolen</i>	<i>Ceratosolen</i>	<i>Ceratosolen</i>
<i>Kradibia</i>				
Blastophaga	Blastophaga	Blastophaga	Blast. s. str.	Blastophaga s.l.
		<i>Eisenia</i>	<i>Secundeisenia</i>	
			<i>Pegoscapus</i>	<i>Pegoscapus</i> <sup>2)</sup>
			<i>Julianella</i>	
			<i>Valentinella</i>	
			<i>Liporrhopalum</i>	<i>Liporrhopalum</i>
Platyscapa		Sycophaginae		
		Platyscapa		
			<i>Waterstoniella</i>	<i>Waterstoniella</i>
				TORYMIDAE
				Sycophaginae
Heplostomata <sup>1)</sup>			Sycophagini <sup>3)</sup>	
	<i>Crossogaster</i>	<i>Crossogaster</i>	<i>Crossogaster</i>	<i>Crossogaster</i>
<i>Sycophaga</i>				
<i>Apocrypta</i>	<i>Sycophaga</i>	<i>Sycophaga</i>	<i>Sycophaga</i>	<i>Sycophaga</i>
<i>paradoxa</i>				
<i>perplexa</i>		<i>Apocrypta</i>	<i>Apocrypta</i>	
	---	TORYMIDAE	TORYMIDAE	<i>Apocrypta</i>
		Idarninae	Idarnini	
	<i>Goniogaster</i>	<i>Goniogaster</i>	<i>Goniogaster</i>	
SYCOLACIDES				
<i>Idarnes</i> etc.	<i>Idarnes</i> etc.	<i>Idarnes</i> etc.	<i>Idarnes</i> etc.	<i>Idarnes</i> etc.

<sup>1</sup> These names are emendations of Prionastomata and Aploastomata, respectively (Saunders, 1883b).

<sup>2</sup> Hill (1967d: 91), following Waterston (1920a), gave preference to *Secundeisenia* Schulz (1906) over *Pegoscapus* Cameron (1906). According to Ramirez (1970a: 11), the date of publication of Cameron's paper is June 1st, while Schulz (1906: 356) cited *Eiseniella* Ashmead (July 13th, 1906), showing that *Secundeisenia* postdates *Pegoscapus*.

<sup>3</sup> Various genera, now classified with Otitesellini and Sycocini, omitted.

It may be noted that Saunders, as late as 1883 (a: 11–20; b: v–vi), when he divided Walker's Agaonidae into phytophagous "Sycophagides", and other, presumably parasitic types, classified the former with the Cynipidae. The latter, considered to have "no tribal affinity with *Agaon*", were named "Sycolacides". Westwood, in 1882 as in 1840, allocated *Agaon* to the Chalcididae. The Haplostomata of Saunders, being the group that might prove to be parasitic, were excluded from the Agaonidae by Patton (1884: xvi): "should they prove to be sycophagous the term Sycophagides should be retained for them, as the genus *Sycophaga* is included; otherwise Saunders' term Sycolacides may be employed".

Ashmead (1904a) classified *Agaon* etc. in the nominate subfamily of the Agaonidae; Saunders' Haplostomata, and also *Platyscapa* and *Crossogaster*, formed the subfamily Sycophaginae. Most of the parasitic types were classified in the Torymid subfamily Idarninae; some others in Monodontomerinae (*Physothorax*, *Plesiostigma*; compare a recent paper by Burks, 1969) or in Miscogasteridae (*Aepocerus*; see Mayr, 1906: 180–181). Ashmead's treatment of the Chalcidoidea set the stage for a long time to come; Schmiedeknecht (1909) duplicated this classification in his volume of the "Genera Insectorum", but considered the Chalcid flies a family instead of a superfamily. In this, Grandi at first followed Schmiedeknecht.

While the fig wasps formed only a small part of the amount treated by Ashmead, Grandi (from 1916 onwards) in an impressive series of major publications, specialized on these smaller groups. He described many species and genera from Africa (1916a, 1917b), Australia (1916b), Ceylon and India (1916c), Java (1917a), the Americas (1919), etc. In so doing, or in separate publications, he provided morphological descriptions of *Blastophaga* (1920a) and *Tetrapus* (1925a), now classified in two subfamilies of the Agaonidae; of *Sycophaga*, *Apocrypta* (males only) and *Crossogaster* (1916a), *Philotrypesis* (1921b), and *Otitesella* (1922b) — examples of five out of the six tribes now recognized in Sycophagine Torymidiae — and *Neosycophila* (1923d), a genus of the subfamily Epichrysomallinae. Thus, except for the tribe Sycoryctini and the subfamilies Toryminae and Eudecatominae, all major types were dealt with! In 1928 (d), Grandi revised the Agaonidae from Mayr's collection, and he published a world catalogue of the group.

In Grandi's opinion, *Sycophaga*, *Apocrypta* and *Crossogaster* formed the Agaonine tribe Sycophagini (i.e., Saunders' Haplostomata), while the other parasites were part of Ashmead's subfamily Idarninae of the Torymidiae (with *Goniogaster* Mayr, the female of *Apocrypta*; see, however, Grandi, 1923d: 113, note). Among the Idarninae, Grandi (e.g., 1925b) distinguished between the "Idarnini veri" and two biological groups containing *Otitesella* and related genera, and *Neosycophila*. Much later (1952a, 1955b), he would again note on these groups, and in 1963 (c) he considered my proposition (Wiebes, 1961b) to include the Sycophaginae with the Idarninae. Anticipating a later discussion of the recent classification of fig wasps, I here include table 4 to provide a synopsis of the larger groups.

Table 4. Classification of fig wasps.

Agaonidae
Agaoninae
Blastophaginae
Torymidiae
Toryminae (e.g., <i>Physothorax</i> )
Sycophaginae
Sycophagini
Apocryptini
Sycoryctini
Philotrypesini
Otitesellini
Sycoecini
Epichrysomallinae
Eurytomidae
Eudecatominae (e.g., <i>Sycophila</i> )

Grandi was particularly interested in the morphological adaptations of insects to special conditions. The various groups of fig wasps and their adaptations were

to be compared with the modifications in groups such as mining insect larvae. The *Neosycophila*-wasps, developing in rather superficial galls from which the mature females and males escape directly to the outside, were considered to possess no adaptive deviations from a normal Chalcid morphology. The females of *Otitesella* and related genera too, were considered rather normal. Their males, however, and those of most other groups now classified with the Sycophaginae (Sycocini excepted), are apterous and also otherwise aberrant. The females of most Sycophaginae (not the *Otitesellini* and *Sycocini*) have long ovipositors and in many instances the gaster can be lengthened by telescoping the segments, or the one or two last segments are tubularly lengthened (these characters would later serve as differential characters of several tribes).

The females of the Agaonidae are characterized by the depression of the head; the presence of a facial groove; the reduction of the mouth-parts, although special mandibular appendages are developed; the modification of the proximal antennal segments; the armature of the fore and hind tibiae. (Grandi did not know the function of the pollen pockets.) The males have atrophied mouth-parts; no ocelli; reduced antennae situated in grooves; no wings; etc. Some of these characters were also found with some *Otitesella*-like females (i.e., the modern *Sycocini*; not our *Otitesellini*!) and, in the male sex, also with the "Idarnini veri": Grandi rightly considered these attributes correlated with the way of entering the fig receptacle (females), or with the life within the receptacle (males). For these modifications, which were on several occasions profusely discussed and illustrated (Grandi, 1923a, 1925b, 1929c, 1936c, 1958a, 1959, 1961b), Grandi suggested several ways of origin viz., involutions, rudimentations or disappearance of (parts of) organs, or hypertelic development, displacement, and transformation, and also the development of new (parts of) organs. Some, although always connected with the function the organs have to perform "generally do not seem to be necessary, often not even useful, sometimes even a hindrance (if not disgenic)" (Grandi, 1959: 223). What Grandi seemed to imply is that not all modifications were of apparent importance to the individual or specific existence of the bearer: "e quindi, apparentemente, non vantaggiose alla specie" (1925b: 311). To understand much better, however, the pros and cons of any particular modification (or rather, its function in the composite syndrome in which several modifications coincide), much more would have to be known of the behaviour of the wasps in symbiosis.

Before mention will be made of Grandi's important observations on *Blastophaga psenes* and *Philotrypesis caricae*, which will be the main theme of the next chapter, I shall now discuss the papers by Froggatt (1901) and Pemberton (1921) on Australian *Pleistodontes froggatti*, and by Baker (1913) and Williams (1928) on some Philippine wasps. Actually, Froggatt's paper was not the first on the biology of insects living in figs, and he could refer to several papers on capricification e.g., by Cunningham (1889) on the fertilization of *Ficus roxburghii* (*F. auriculata* Lour.), Howard (1899) and Eisen (1891) on attempts to introduce *Blastophaga psenes* into California as a pollinator for *Ficus carica*. Cunningham described the flowers of *F. auriculata*, and the effects of the presence of insects upon them: he concluded that it is not pollination that causes development, but the irritation following the act of oviposition. The same observation was made by Treub (1902) for *Ficus hirta* of Java, although here some germination of pollen grains was observed. In California, some of the fig growers considered the process of capricification of no practical value, but only the survival of an ancient custom blindly handed down from father to son in Mediterranean regions. Yet, in many places the wasps were successfully introduced (see table 5; Ramirez, 1970b, table 2 listed figs introduced in absence of Agaonidae: they did not set seed).

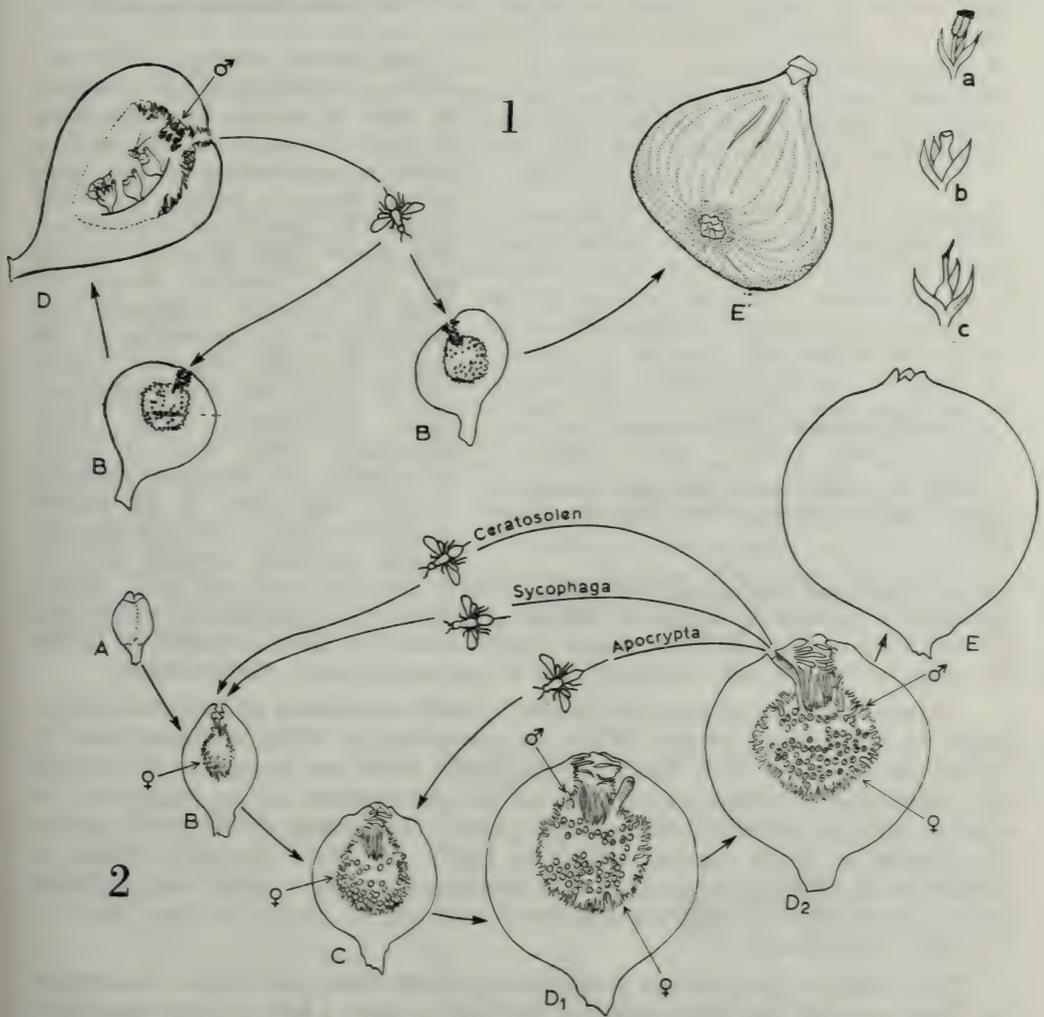
Table 5. Fig wasps introduced with their hosts.

fig	from	pollinator	brought by	introduced to	date	result	selected references
<i>F. carica</i>	? Asia <sup>1)</sup>	<i>Blast. psenes</i>	? Phoenicians	Mediterranean	? 1400 B.C.	+	Eisen, 1901: 16-20
<i>F. carica</i>	"Asia Minor"	<i>Blast. psenes</i>	H.E. Van Deman	California	1890	-	Swingle, 1908: 181
<i>F. carica</i>	Smyrna	<i>Blast. psenes</i>	James Shin	California	1891 (twice)	-	Swingle, 1908: 181
<i>F. carica</i>	Smyrna	<i>Blast. psenes</i>	Thomas Hall	California	1892	-	Swingle, 1908: 181
<i>F. carica</i>	"Asia Minor"	<i>Blast. psenes</i>	A.C. Denotovitch	California	1895	-	Swingle, 1908: 181
<i>F. carica</i>	Naples	<i>Blast. psenes</i>	W.T. Swingle	California	1898	-	Swingle, 1899: [8], 1908: 181
<i>F. carica</i>	Algeria	<i>Blast. psenes</i>	W.T. Swingle	California	1899	+	Swingle, 1899: [8], 1908: 181
<i>F. carica</i>	?	<i>Blast. psenes</i>	?	Australia	?	+	Robson, 1911; Savage, 1924
<i>F. carica</i>	?	<i>Blast. psenes</i>	?	Retoria	?	+	Waterston, 1920a: 128
<i>F. macrophylla</i>	Australia	<i>P. froggatti</i>	F.M. [uir]	Hawaii	1921*	+	Muir, 1922: 12; Wiebes, 1963b: 307
<i>F. rubiginosa</i>	Australia	<i>P. imperialis</i>	?	Hawaii	1922	+	Timberlake, 1923: 200
<i>F. alba</i>	?	[ <i>Blastophaga</i> ]	[Fosberg]	Hawaii	ca. 1930	+	Corner, 1958: 18
<i>F. fistulosa</i>	?	[ <i>Ceratosolen</i> ]	[Fosberg]	Hawaii	ca. 1930	+	Corner, 1958: 18
<i>F. religiosa</i>	East Asia	<i>P. quadriceps</i>	?	Israel	?	+	Galil & Eisikowitch, 1968c: 356

<sup>1</sup> The observation that the entomofauna of the sycones of *Ficus carica* is more complete in India than elsewhere (i.e., it harbours there a species of *Sycosapteridea* not found in Europe, Mayr, 1885: 153; Joseph, 1957a: 119), adds to the probability of Asia being its homeland.

*Ficus macrophylla*, the fig observed by Froggatt and Pemberton, is different from the edible fig in that it is monoecious, bearing male, female and gall flowers in one syconium (fig. 2). In other species, male and female flowers occur in separate figs e.g., in *Ficus carica* and *F. nota* (studied by Baker and Williams) (fig. 1; dioecious figs). The entrance of the female *Pleistodontes* wasps through the narrow ostiole of *Ficus macrophylla* was described by Pemberton (1921) as a forward-reaching movement to fix the tips of the hook-like mandibles into the tissue in front and then, in lowering them, to draw the whole body forward over a short distance. The saw-like serrations of the mandibular appendage prevent the head from slipping back. Usually up to five or six wasps will successfully enter a single receptacle, and immediately begin egg-laying. The larva hatching from the egg, matures and pupates within the gall-flower. The wing-less males hatch first out of their galls, and they start in search for a gall containing a female; they fertilize the females by inserting the tip of the abdomen through a hole gnawed in the galls. The females leave the fig by boring a hole through the wall of the receptacle at any point. In doing so they become covered with pollen from the ruptured male flowers which, unlike in many other species of *Ficus* where they are concentrated around the ostiole, are not confined to any particular part of the fig. "Much of this pollen must be brushed from the wasp's body during the short but strenuous trip — to the young fig —, yet sufficient is carried over to secure ample pollination for a great many female flowers" (Pemberton, 1921: 306): it was not noted how the pollen is being transported, and this would remain unknown until 1969!

Many of the details described for *Pleistodontes froggatti* were identically observed for *Ceratosolen notus* and the dioecious *Ficus nota* (see Baker, 1913), and for *Blastophaga psenes* and *Ficus carica* (the former, however, does possess pollen pockets, just as does *P. froggatti*, but these are completely lacking in the latter). Important differences are found in the place where the females leave the receptacle, which is through the ostiole in *Ficus carica* and *F. nota* (where it is often enlarged by the males). Williams (1928: 11-13) listed a number of instances of males enlarging the ostiole or tunnelling close to it. Later we shall learn how important this kind of male behaviour can be.



Figs. 1 & 2. Cycles of dioecious (*Ficus carica*, fig. 1) and monoecious figs (*F. sycomorus*, fig. 2), and their wasps (*Blastophaga* indicated in fig. 1; three with names added in fig. 2). The letters correspond with those used in the text (p. 220); a, ♂; b, short-styled, and c, long-styled ♀ flowers. Adapted from Wiebes (1965a) and Galil & Eisikowitch (1968a).

In comparison with 1882, by 1928 the number of known fig wasps was greatly augmented. For a paper by Van der Vecht (1973), I once computed these numbers of the Agaonidae: they were depicted in a graph reproduced here (fig. 3).

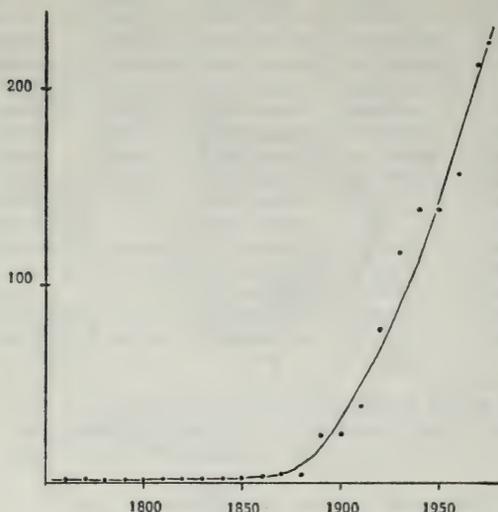


Fig. 3. Trend curve for the number of known Agaonid species. From Van der Vecht (1973).

#### Waifs and Strays (thirty years of miscellaneous reports)

The period between 1928 and 1958 is characterized by a number of small papers on fig wasps from all parts of the world. As such, it forms a continuation of the series already begun by Grandi, Waterston (1914–1921, mainly on new African and some Indo-Malayan forms), etc. Special mention should be made of Grandi's important contributions to the knowledge of the fauna of South America (1934, 1936b, 1938a; see also Hoffmeyer, 1932; Mangabeiro Filho, 1937; Blanchard, 1944) and of Ishii's descriptions of Japanese parasites (1934). Also some of the papers by Girault (1913–1939) fall into this period, and they certainly may be

named waifs and strays (see De Santis, 1961)! Between 1951 and 1957, Risbec published a number of papers on African and Malagasy Chalcidoidea; see Wiebes (1970a) for a revision of the fig wasps. Joseph started his series of papers on Indian fig wasps in 1952; it was concluded later in cooperation with Abdurahiman.

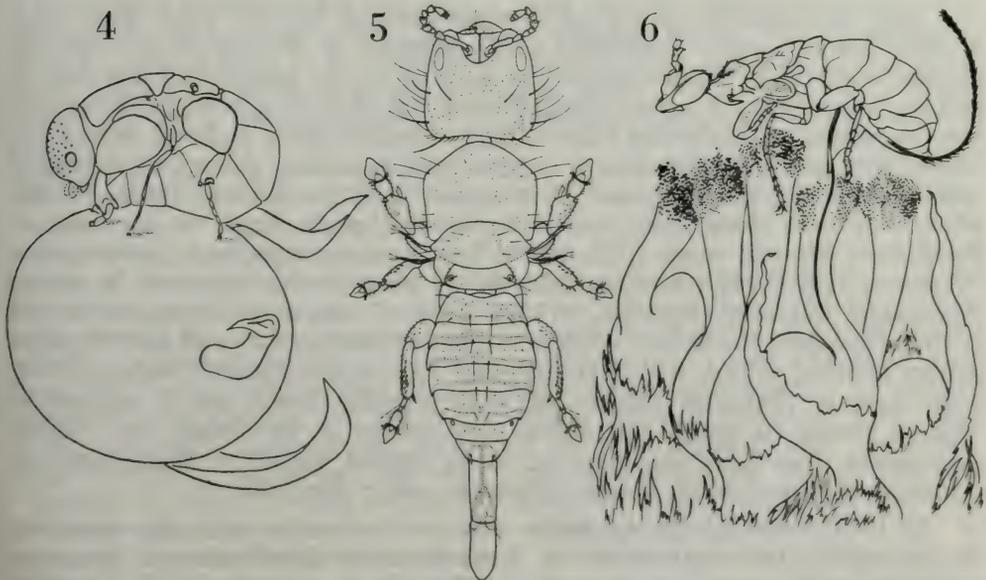
As mentioned in the previous chapter, Grandi contributed an important monograph on *Blastophaga psenes* (1920a, second edition in 1929a, additional note in 1935a). In 1936 and 1938, Buscalioni & Grandi wrote two papers on the biology and cultivation of *Ficus carica*, and on the development of its receptacles, in relation with the pollinator *Blastophaga psenes*. The parasite *Philotrypesis caricae* was treated in 1921b (second edition in 1930). In 1961b, Grandi published in English on his findings; some of the data mentioned here were taken from that summary. Joseph (1958) combined additional notes on *B. psenes* and new data on *P. carica*, in his thesis.

The males of *Blastophaga psenes* emerge from their galls before the females do. They approach the galls containing the females, gnaw a hole with the mandibles, introduce the tubularly lengthened last segments of the gaster, and fertilize the females while they are still in their galls (fig. 4). Each male copulates with several females (the sex ratio is 9–18 males for 100 females), and dies within the cavity of the fig. The females, after having left their gall through the hole made by the male, on their way to the ostiole pass the region of the male flowers where they become dusted with pollen. The scales of the ostiole of the D-phase fig (see fig. 1) easily yield and allow the females a passage out. The scales lining the ostiole of the B-phase figs, where the females now go, offer more resistance: the wasp wedges its head under the free edge of the outer scales, then goes on laboriously through the scales and in this process, loses its wings and parts of the antennae and legs. The number of females found in the cavity of the young figs seems to vary e.g., Condit (1918: 539) mentioned eighteen, Grandi (1929a: 109) found no more than four. In the cavity of a gall-fig (see fig. 1), the female may oviposit in as many as 300–400

flowers (in the ovary, between the nucellus and the integument); for some variation, see Grandi (1929a: 113). At the same time a small quantity of fluid from the acid gland is injected into the endosperm, causing its proliferation into nourishing tissue for the wasp larva. The larva passes through two larval stages and a prepupa before the pupal stage; complete development takes two-and-a-half, two, or seven months, depending on the generation falling in spring, summer, or winter, respectively (on the number of generations, see Joseph, 1958: 212–216).

The actions of the females inside the edible or (young) seed-figs are very similar to those described above; however, as the long-styled flowers have the ovaries out of reach of the wasp ovipositor, the females finally perish after their futile attempts to perpetuate the species but not before pollination has been accomplished (see a good account in Condit, 1947: 42–46).

After considering all facts, wrote Buscalioni & Grandi (1936: 117; translated from Italian): the symbiosis of *Blastophaga* and our *Ficus* is rather complex, and, through the intervention of Man, has developed into an association of three partners. The *Blastophaga* and the caprifig can be explained exclusively as a parasitic action on the ovules; Man, by practising deceit (“mercé un inganno”), succeeded in exploiting the insect, compelling it to enter the receptacles of the domestic fig, the flowers of which, long-styled by cultivation, escape infection by the insect [end of citation]. It is true that there is a complicated sequence of different types of receptacles on the wild fig tree viz., a winter form with mainly gall flowers and some male; a summer form with a mixture of gall and female flowers, or with female flowers only; and an autumn form with gall flowers only, in which the wasps overwinter. Without entering a further discussion here, I suggest there is nothing in which the symbiosis of *Ficus carica* and *Blastophaga psenes* fundamentally differs from symbioses of other dioecious figs and their pollinators. As will be shown below, in comparison with many, it even is a rather simple instance of mutualistic symbiosis.



Figs. 4–6. Three figures of great historical interest: 4, *Blastophaga psenes*, male mating with female in gall; 5, *Philotrypesis caricae*, male; 6, *Ceratosolen arabicus*, female ovipositing and pollinating. From Grandi (1920a, 1921b) and Galil & Eisikowitch (1969a).

The generations of *Philotrypesis caricae* are much the same as in *Blastophaga psenes*. The following account is for a great part taken from Joseph (1966: 401-402). Copulation of males and females mostly takes place outside the gall, soon after the female is liberated by the male from the ovary in which it developed. A single male copulates with several females (sex ratio, 50–60 males for 100 females). The oviposition will be discussed in the next chapter; about fifty eggs are laid by a single female. It seems that the factor determining the oviposition is the presence of the acid secreted by the *Blastophaga*. At the beginning, the larva of both *Blastophaga* and *Philotrypesis* feed on the endosperm, but later the *Blastophaga* is starved by the *Philotrypesis* — or may be weakened by some toxic secretion produced by the *Philotrypesis*. This explains much of the unisexual variation in size of the imagines, as the quantity of food left for the *Philotrypesis*-larva depends on whether the *Blastophaga* is being killed early or late in the second instar. This may also influence the sex ratio: it has been suggested that haploid males are able better to survive partial larval starvation than do diploid females.

### Wasps in Symbiosis (the period after Joseph, 1958)

In my opinion, Joseph's doctor's thesis (Joseph, 1958), discussed in the previous chapter, opened a new period in the history of fig wasp research. Joseph knew the edible fig and its symbionts as well as Grandi did, but he moreover gained an intimate knowledge of the biology of the tropical forms and their parasites. Many proved new to science, and thus it took Joseph, as it later did also me as well as Hill and Ramirez, much time to describe the new genera and species: a task still unaccomplished. Gradually, however, a new classification of fig wasps arises, enabling a comparison of the classification of *Ficus* and the underlying hypotheses (Corner, 1965, 1967–1975) with the phylogenetic classification of the wasps.

### THE POLLINATORS

Soon, the specificity of the relationships between figs and wasps (here taken in the restricted sense: Agaonidae only) appeared to be very strict. This was already surmised by Grandi earlier, but it could not be proved before a botanist and an entomologist, in a joint effort, studied a great many species. Corner started this cooperation with Van der Vecht (1959; collections made in Java), from whom I took over the entomological part. I started with a revision of the Indo-Australian species of *Ceratosolen* Mayr and *Pleistodontes* Saunders (Wiebes, 1963a, b). Hill, who collected in Hong Kong, and later also in Uganda, began on a revision of Hong Kong figs and wasps (Hill, 1967a, b, d), and monographed *Liporrhopalum* Waterston (Hill, 1969). Ramirez collected fig wasps in the Americas; he revised *Pegoscapus* Cameron (Ramirez, 1970a). Later, I would add revisions of the genera *Alfonsiella* Waterston (Wiebes, 1972b), *Elisabethiella* Grandi and *Nigeriella* Wiebes (Wiebes, 1974a), *Agaon* Dalman and *Allotriozoon* Grandi (Wiebes, 1974c), while those of *Deilagaon* Wiebes and *Waterstoniella* Grandi are in preparation. This, it should be noted, still leaves large groups to be revised e.g., African *Ceratosolen*, *Eupristina* Saunders, the many species united in *Blastophaga* s.l., American *Tetrapus* Mayr. Large collections exist: see table 6.

In 1973, I divided the Agaonidae into two subfamilies viz., Agaoninae and Blastophaginae; later again in 1974a, I compared the classification of the genera with that of their host groups of *Ficus*. This led to a suggestion of a possible classification of the figs into a number of groups different from those used by Corner (1965) but coinciding with the (supposedly phylogenetic) groups of the wasps (see table 8). One example will be discussed at the end of this chapter.

Table 6. Important collections of fig wasps made since 1950.

provenance	collector	<i>Ficus</i> by	some references
Asia, Australasia	Corner	Corner	Corner, 1958, 1963c
"	Bishop Museum	-	Wiebes, 1976
India	Joseph	Joseph	Joseph, 1952 ff.
Indonesia, mainly Java	Van der Vecht	Corner	Wiebes, 1961b ff.
N. Borneo (Kinabalu)	Corner	Corner	Corner, 1964
Philippine Is.	Wiebes & Pancho	Corner	Wiebes, 1965a, 1974a
"	Noona Dan	-	Petersen, 1966
Hong Kong	Hill	Hill	Hill, 1967a, d
Solomon Is.	Corner	Corner	Corner, 1967
"	Noona Dan	-	Petersen, 1966
Malagasy	Blommers	Blommers	Wiebes, 1974c
La Réunion	Etienne	Cadet	-
East Africa	Galil	Galil	Wiebes, 1964b, 1968a
Uganda	Hill	Hill	Wiebes, 1972b, 1974c
Guinea (W. Africa)	Lamotte & Roy	-	Joseph, 1959a
Nigeria	Medler	Mrs. Medler	Wiebes, 1972a ff.
Central America	Ramirez	Ramirez	Ramirez, 1970a
"	Ramirez, Gordh	Ramirez, Gordh	Gordh, 1975

Ramirez (1974) took another course, basing himself on the same old table (Wiebes, 1963a: 101, table 2) and host catalogue (Wiebes, 1966b) as revised later by Hill (1967c: 427, table), but he added an interesting discussion of many concurrent characters of Agaonid genera and *Ficus*-subgenera and sections. This new approach became possible, as new data were known on the biology of figs and wasps.

As usual in biology for too long a time, the one instance of *Blastophaga psenes* and *Ficus carica* taken from the temperate region, was considered to present a good example of the symbiosis of figs and wasps in general. The situation in the edible fig, however, appeared to be quite simple compared to the pollination process in several tropical species. In *Blastophaga psenes*, the pollen is passively carried on the body of the female wasp ("topocentric pollination" *sensu* Galil, 1973a). As Galil and his coworkers, in many papers of very high standard from 1965 onwards, have shown, the situation is not always as simple in other *Ficus* species, where "ethodynamic pollination" may occur. There proved to be a considerable variation in structure and behaviour of the pollinators of different species of *Ficus*. Unique organs used as containers by various species of wasp, for transporting pollen from male figs to young receptive female figs (c.f. fig. 6), were independently but almost simultaneously, recorded by Ramirez (7.ii.1969, "corbiculae"), Galil & Eisikowitch (9.v.1969, "pollen pockets"), and Chopra & Kaur (3.vi.1969, "pollen stuck to the epimeral region of the mesothorax"). In common consent of Galil, Ramirez, and Eisikowitch (1973: 176, note), the name "corbiculae" is used for the pollen-carrying organs on the fore coxae ("coxal corbiculae" *sensu* Ramirez), while for the more complicated thoracal organs the term "pockets" is used ("sternal corbiculae" *sensu* Ramirez). In spite of numerous structural differences between the syconia of dioecious and monoecious figs, the two may have several biological features in common (Galil, 1973b: 309). In table 7 I list the species of fig and pollinator on which we have information concerning the pollination process (except for some discussed above), with the literature-references added. As in previous sections, in the following compilation of what is known on fig-wasp behaviour in various figs, some important parts are verbally taken from the original reports.

Table 7. Pollination and/or oviposition behaviour described for monoecious (m) and dioecious figs (d).

UROSTIGMA	pollinator	references
<i>Ficus macrophylla</i> (m)	<i>Pleistodontes froggatti</i>	Froggatt, 1901; Pemberton, 1921
<i>Ficus religiosa</i> (m)	<i>Blastophaga quadraticeps</i>	Galil & Eisikowitch, 1965, 1968c, 1971; Galil & Snitzer-Pasternak, 1970; Galil, Zeroni & Bar Shalom, 1973; see also Johri & Konar, 1956
<i>Ficus costaricana</i> (m)	<i>Pegosecapus estherae</i> <sup>1)</sup>	Galil, Ramirez & Eisikowitch, 1973
<i>Ficus hemsleyana</i> (m)	<i>Pegosecapus tonduzi</i>	Galil, Ramirez & Eisikowitch, 1973
PHARMACOSYCEA		
<i>Ficus</i> spp. (m)	<i>Tetrapus</i> spp.	Ramirez, 1970a
FICUS		
<i>Ficus carica</i> (d)	<i>Blastophaga psenes</i>	Grandi, 1920a, 1929a; Joseph, 1958
<i>Ficus hirta</i> (d)	<i>Blastophaga javana</i>	Treub, 1902
<i>Ficus auriculata</i> (d)	<i>Ceratosolen emarginatus</i>	Cunningham, 1889 <sup>2)</sup>
<i>Ficus nota</i> (d)	<i>Ceratosolen notus</i>	Baker, 1913; Williams, 1928
<i>Ficus hispida</i> (d)	<i>Ceratosolen s. solmsi</i>	Lee & Tan, 1973
<i>Ficus fistulosa</i>	<i>Ceratosolen hewitti</i>	Galil, 1973b
SYCOMORUS		
<i>Ficus racemosa</i> (m)	<i>Ceratosolen fusciceps</i>	Chopra & Kaur, 1969 <sup>3)</sup>
<i>Ficus sycomorus</i> (m)	<i>Ceratosolen arabicus</i>	Galil, 1966; Galil & Eisikowitch, 1968a, b, 1969a, 1971, 1974

<sup>1</sup> See Ramirez (1970a) for further details on *Pegosecapus*-behaviour.

<sup>2</sup> I am not sure that Cunningham's observations refer to this species of wasp.

<sup>3</sup> *Ficus tsiela* with *Maniella delhiensis*, *Ficus virens* with *Blastophaga vaidi* [sic!], and *Ficus carica* with *Blastophaga psenes* were also mentioned but no details were given.

Galil & Eisikowitch (1968a: 262-265, fig. 6) distinguished between the developmental phases of *Ficus sycomorus* as follows (see fig. 2):

*Phase A (pre-female)*. — young syconium prior to the opening of the ostiole.

*Phase B (female)*. — ostiolar scales loosen, female flowers ripen, sycophilous wasps penetrate into the syconium and oviposit into the ovaries; pollination of the female flowers.

*Phase C (inter-floral)*. — wasp larvae and fig embryo's develop within their respective ovaries; ovaries occupied by the larvae are transformed into galls.

*Phase D (male)*. — male flowers mature, wasps reach the imago stage, fertilized female wasps leave the syconia via channels bored by the males.

*Phase E (post-floral)*. — both the syconia and the seeds inside them ripen.

*Ceratosolen arabicus* and the monoecious *Ficus sycomorus* (see Galil & Eisikowitch, 1968a, b, 1969a, b, 1974). — In two phases viz., the female phase B and the male phase D, the sycophilous wasps are active within the syconium. In the last-mentioned male phase, the male flowers at first remain closed, while the male wasps emerge from their galls, puncture the walls of the female galls and impregnate the females within. Then, the males assemble at the upper part of the syconium: at the end of the first day, the amount of liquid in the syconium decreases and the stamens gradually protrude from their perianths at the male zone of the fig around the ostiole.

In the morning of the second day, the male wasps start working at the male flower zone: they clasp the anthers and tumble down into the cavity of the fig while still holding the anthers between the legs. At the same time, the female wasps start to emerge from their galls, they approach the cut anthers and grasp them. With the mandibles and with the scapes of the antennae, a female widens the narrow dehiscence slit of the anther, and with the aroliola of the fore leg lifts

pollen on to the ventral surface of the body. Then, the wasp curves the thorax so that the covering membranes of the pollen pockets stand out along their inner suture: a wide opening now leads into the pocket. The pollen is shoved into the pocket with the combs of the fore coxae.

In the mean time, the males have made tunnels, one to three per syconium, in the male flower zone close to the ostiole. Through these tunnels, the females eventually emerge, their pockets loaded with pollen.

The pollination act in *Ficus sycomorus* is here described after Galil & Eisikowitch (1969a), while some details were taken from their 1974 paper. Immediately upon entering the young syconia at the female phase (B), the female of *Ceratosolen arabicus* starts ovipositing into the pistils, one after the other. Toward the end of the oviposition, the fore legs of the wasp fold back until the arolia reach the lower margin of the pockets (fig. 6). Then, the tarsi touch the stigmata below, and so bring the pollen grains on them.

*Ceratosolen hewitti* and the dioecious *Ficus fistulosa* (see Galil, 1973b). — Here the wasp-releasing D-phase male figs and receptive B-phase figs of both sexes grow on different trees. The behaviour in the D-phase does not differ essentially from that of *C. arabicus* in *F. sycomorus*. Also the behaviour of the females on the short- and long-styled female flowers (in different figs) is almost identical, although eggs are not likely to be laid through the long-styled pistils of the female flowers.

*Blastophaga quadraticeps* and the monoecious *Ficus religiosa* (see Galil & Eisikowitch, 1965, 1968c; Galil & Snitzer-Pasternak, 1970, 1971; Galil, Zeroni & Bar Shalom, 1973). — The behaviour of the wasps is somewhat different from that in *Ceratosolen arabicus* in that the males, after the copulation act, do not cut the anthers as the *Ceratosolen*-wasps do. The fertilized females remain in their galls for many hours. In the mean time, the males bore the exit holes, and only afterwards do the females begin to emerge. In a series of beautiful experiments, Galil and coworkers proved that it is the replenishment of the internal atmosphere by air from outside the syconium — lowering the CO<sub>2</sub>-content to less than 3-4 percent — that enables the females to leave their galls. At the same time, this lower CO<sub>2</sub>-content inactivates the male wasps. The diagram of fig. 7 illustrates the reciprocal relationships (after Galil, Zeroni & Bar Shalom, 1973: 1122, fig. 7).

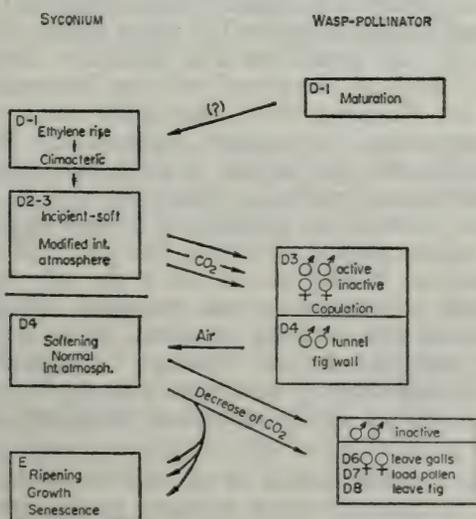


Fig. 7. Reciprocal relationships between the fig and the pollinator in *Ficus religiosa*. From Galil, Zeroni & Bar Shalom (1973).

Now, the females approach the still intact anthers and — here as in *Ceratosolen arabicus*, with the antennal scapes and the mandibles — crumble the pollen. The fore tarsi touch the anthers, and the pollen pockets are loaded. Also the unloading of the pollen and the act of pollination, in the B-phase young figs, are the same for *Blastophaga quadraticeps* and *Ceratosolen arabicus*.

*Pegoscapus tonduzi* (and *P. estherae*) and the monoecious *Ficus hemsleyana* (and *F. costaricana*) (see Galil, Ramirez & Eisikowitch, 1973) — The wasps of most species of the genus *Pegoscapus* do not have thoracal pollen pockets only, but coxal corbiculae as well. As in *Ficus religiosa*, the female wasp after leaving its gall, approaches the male flower and pushes its head between the pistils in search for open anthers. The flagella of the antennae are pressed into the anther, while the scapes keep open the dehiscence slit. In these species again, the pollen is taken with the fore arolia and brought on the mesosternum, where the pollen pockets not being completely covered as in the previously mentioned species, receive the pollen as it is shoveled in with the coxal comb. Also the coxal corbiculae act as pollen containers during the transport to a young fig, after the females have left the D-phase syconium through exit holes gnawed by the males.

The pollination act by *P. estherae* was divided by Galil, Ramirez & Eisikowitch, into the following steps. 1, preparatory step: oviposition; 2, combing of pollen from pockets to corbiculae: pollination now starts; 3, transfer of pollen from coxal corbiculae to the arolia of the fore legs; and 4, pollination proper: the striking of the fore tarsi on each other, and shaking off the pollen on the stigmata below.

I discussed the data on pollination in *Ficus* at some length, because they are of the greatest interest for the understanding of the symbiosis of figs and wasps. Hopefully, this compilation will stimulate further research and completion of our, as yet very incomplete, knowledge of the situation in many groups: "so as to obtain a broader view of the evolution of the interrelations between the figs and their pollinating wasps" (Galil, Ramirez & Eisikowitch, 1973: 183).

At this time, the taxonomic implications are not yet very clear. On the one hand, the shape and structure of some of the organs used in emerging from the galls, pollination within figs, or in entering the young syconia, were used for the distinction of the two subfamilies of the Agaonidae (Wiebes, 1973) viz., the elongate head and the subvertical orientation of the female mandible (Agaoninae); the ventral crenulations (Agaoninae) or ridges (Blastophaginae) on the mandibular appendage, which is rigidly (Blastophaginae) or rather loosely connected (Agaoninae) to the mandible proper; the prominent and articulate elongation of the third antennal segment, more distinctly developed with the Blastophaginae than with the Agaoninae; etc. (but see Ramirez, 1974, who finds other connections). On the other hand, in one genus (e.g., *Pegoscapus*, *Pleistodontes*, *Waterstoniella*) pollen pockets and/or corbiculae may be present in some but absent in other species, indicating that a resemblance in pollination behaviour may be the result of convergent evolution. *Tetrapus* seems to be primitive in several aspects (Ramirez, *in litt.*) e.g., it lacks external pollen-carrying structures (the pollen is eaten, and carried in the digestive tract; Ramirez, 1970b), and it also is the only Agaonid not breaking wings and antennae while entering the young syconium. Also in *Pleistodontes*, the condition without pockets may well be primitive, while their presence (e.g., in *P. froggatti*, *imperialis*) may be a derived character. In some of the Blastophaginae, however, the external pollen-carrying structures seem to be secondarily lost (e.g., in some *Waterstoniella*), or are in the process of being lost (as in *Waterstoniella masii*).

What is needed for a reconstruction of the coevolution of figs and wasps, is a more complete survey of character-states in many groups, permitting of a phylogenetic analysis. The groups to be prospected include all symbionts of the fig, inquillines and parasites (in short: mess-mates) as well as pollinators. The symbioses, then, are taken as the taxonomic units of the phylogenetic classification, while the

wasps (with all their features) are treated as the characters of the symbiosis. Although some classification on the tribal level was recently suggested, and accepted by students of fig insects (see table 4), the knowledge of the mess-mates is as yet very scanty<sup>1</sup>). A survey of some, mostly biological data is presented below.

### THE MESS-MATES

#### Agaonidae

The symbioses of figs and wasps have other partners than pollinators and plants. Recently, it became known that some of the Agaonidae behave as cuckoos: laying eggs without preparing food (i.e., pollinating the flowers!). The first and best known instance is *Ceratosolen galili* in *Ficus sycomorus* (see Wiebes, 1964b, 1968a; Galil & Eisikowitch, 1968a, 1969a). The female has pollen pockets and its behaviour during oviposition is quite similar to that of *Ceratosolen arabicus*: the pockets are always empty, however, and pollination movements have not been observed. In a way, its behaviour is similar to that of *Sycophaga sycomori* (at least, its place in the symbiosis is). In my opinion, *C. galili* is not closely related to *C. arabicus*. This poses the question as to the evolution of its relationship with the sycomore fig. As seen from its pollen pockets, *C. galili* in a previous evolutionary stage acted as a pollinator, but to which fig? If it is conceivable that two species of fig merge, keeping one of the pollinators as such while the other is lost or develops into a food-parasite; or that a species of wasp switches from its "own" fig to another, to act as a parasite — what about the supposed phylogenetic specificity of figs and wasps?

Several instances of supposed parasitic Agaonidae are now known, mainly from Africa. A previously recorded case of an Indo-Malayan fig harbouring two Agaonidae (Wiebes, 1966c) should be reconsidered in the light of our new knowledge. Also the instance of two species of *Pegoscapus*-symbionts of *Ficus tuerckheimii* in Costa Rica (Ramirez, 1970a) should be reinvestigated. Some more species of *Ceratosolen* seem to belong to the group of *C. galili* e.g., *flabellatus*, which lives in the syconia of *Ficus capensis* next to what I suppose to be the legitimate partner (*C. capensis*). Some species of *Alfonsiella* are sometimes found in figs evidently pollinated by other wasps (i.e., *Elisabethiella*; Wiebes, 1972b): a male of *Alfonsiella* was found next to one of *Elisabethiella* in *Ficus salicifolia* by Mayr (1885: 192), and it was mistaken for an apterous form of *Crossogaster triformis* (see Grandi, 1928d: 206-210; Wiebes, 1975). More often than not, however, the species of *Alfonsiella* are found quite alone, and they do have pollen pockets.

#### Toryminae

*Physothorax*, from figs of section *Americana*, was recently recognized as one of the Toryminae (Burks, 1969). The females have long ovipositors, with which they pierce the fig receptacle from the outside (Butcher, 1964: 237). There are winged as well as wingless (or brachypterous) males.

#### Sycophagini

*Sycophaga sycomori* is one of the Sycophagini, a tribe of the Torymidae Sycophaginae (see table 4). *Sycophaga* contains a number of species all of which, as far as known or assumed from their morphology, enter the figs of African *Sycomorus* through the ostiole to oviposit. *S. sycomori* is able to induce the formation of parthenogenetic nourishing tissue for its larva. This tissue, however, originates in the nucellus and not in the endosperm as in *Ficus carica* (see references in Grandi, 1929a: 112) or in *Ficus religiosa* (Johri & Konar, 1956).

<sup>1</sup>Hill (1967d: 95) listed ten genera as "incertae sedis". Some of these were mentioned above (viz., nos. 1, 2, 6, 7, 8, 9): which leaves only four unplaced viz., *Critogaster* Mayr (American parasites of *Tetrapus*), *Dynatogmus* Mayr from Africa, *Heterandrium* Mayr (American parasites of *Pegoscapus*) and *Pseudidarnes* Girault from Australian *Malvanthera*.

The behaviour of *Sycophaga sycomori*, and its effects on the structure and development of *Ficus sycomorus*, were discussed by Galil, Dulberger & Rosen (1970; see also the papers by Galil & Eisikowitch mentioned with *F. sycomorus*, above).

The females of most Sycophagini have long ovipositors, and they oviposit from the outside of the fig, through the peel. Ansari (1966: 80-82, *Parakoebelea*; 1967: 380-381, "*Idarnes*") described the process of egg-laying in Sycophagine wasps (see fig. 8a, b). After locating a proper place on the surface of the fig, the female moves forward in order to bring the distal end of the ovipositor near the selected place. Holding the fig firmly with its legs, the female moves its ovipositor forward and backward till the surface of the fig is punctured; then, the insect creeps backward, pushing the ovipositor (guided by the valves, from which it gradually dislodges proximally) into the fig receptacle. Usually, one egg is deposited into each gall flower, but in some cases two eggs were laid: it is worth mentioning that Ansari recorded the finding of two specimens viz., a male and a female developing within a single gall — in my opinion, this record wants confirmation. The males of the Sycophagini are rather aberrant. Grandi (1916a: 227-228, figs. 32, 1; 36, 2; etc.) described the peculiar transverse division of the head into two parts, the anterior of which bears the eyes, the antennae, and the sockets for the mandibular condyles. The gaster bears very long, laminate excrescences of the spiracles of the eighth urotergite. The morphology of the male *Idarnes* (*Ganosoma* in Mayr's sense) recently redescribed by Gordh (1975: 408-412), shows that its relationship to the Old World Sycophagini cannot be very close as e.g., the head is relatively normal, and the spiracles of the eighth urotergite have no excrescences.

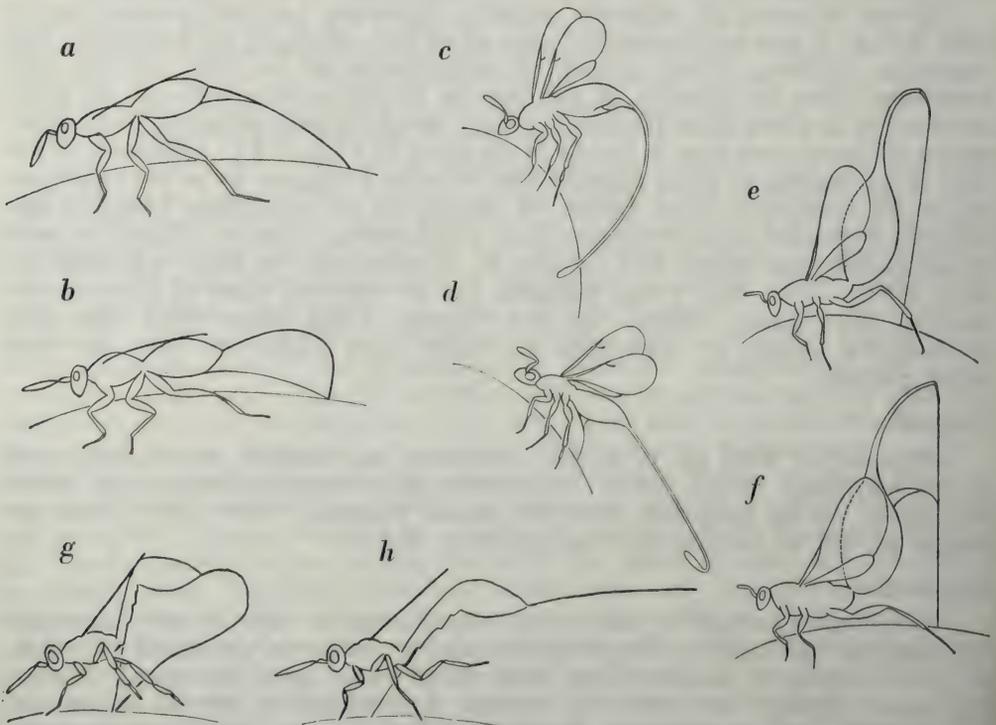


Fig. 8. Some stages in the process of oviposition in Sycophagini (a, b), Sycoryctini (c, d), Philotrypesini (e, f), and Apocryptini (g, h). Adapted from Joseph (1953a, 1958) and Ansari (1966, 1967).

Ansari used the term "cleptoparasite" for the wasps discussed, and Hill (1967c: 431) suggested that the species of *Eukoebelea* are phytophagous and compete with the Agaonidae for the ovule endosperm. In young receptacles of

*Ficus nota* in the Philippines, I saw *Eukoebelea* ovipositing (? no eggs observed!) before *Ceratosolen* had entered the fig.

*Eukoebelea* has been recorded from sections *Neomorphe* and *Sycocarpus*, and from subgenus *Sycomorus* (see the plant groups mentioned in table 8); the genus *Idarnes* is restricted to section *Americana* (see Gordh, 1975), while the Old World species alluded to this group have a rather wide host-spectrum; *Parakoebelea* is known from Indian and African *Sycomorus* (and one species from section *Conosycea*?); while *Sycophaga* only occurs in African *Sycomorus*. In general, most Sycophagini ("Idarnes" excluded) appear to be living in figs pollinated by Agaonidae of the genus *Ceratosolen*, and by those of *Pegoscopus*.

#### *Apocryptini*

Again, reference should be made to the paper by Ansari (1967). *Apocrypta westwoodi*, like all congeners, is peculiar in having the female gastral segments keeled, permitting of a telescoping lengthening of the gaster. The insect, in drilling a hole through the peel of the fig, raises its hind pair of legs, and the ovipositor is pushed in, beneath the body of the wasp (fig. 8g). The ovipositor gets lodged in the grooves formed by the gastral sternites. Now the legs are relaxed; the valves still guide the ovipositor until, after thrusting a considerable length of the ovipositor, the wasp suddenly pulls out the valves, which now rest over the fig or swish in the air (fig. 8h). The male (Grandi, 1916a: 264-273) is slender, and has large — although never protruding — spiracular peritremata of the eighth urotergite.

The species seem to be restricted to *Ceratosolen*-harbouring figs viz., *Neomorphe*, *Sycocarpus* and *Sycomorus*. Presumably, *A. longitarsus* parasitizes (or lives as an inquiline with) *Sycophaga sycomori* in Israeli *Ficus sycomorus* (Galil & Eisikowitch, 1968b: 757). It is peculiar, and well worth further research, that some related forms from African figs are much larger and more robust, in the same relation to normal *Apocrypta* as *Parakoebelea* stands to *Eukoebelea*.

#### *Sycoryctini*

The Sycoryctini form a large tribe, the internal relationships of which are not very clear. In the Sycoryctini, the apparent gaster ends with the eighth urotergite, and the ninth is tubularly lengthened covering the valvulae almost to the tips (forming a "tail"). Joseph (1953c: 67-69) described the process of oviposition for *Sycoscapteridea* (fig. 8c, d). When the female feels a particular spot to be suitable, the tip of the "tail" is brought in contact with the surface, which is pierced. As the insect creeps backward, the ovipositor, dislodged from the sheathing "tail", is thrust into the fig. After oviposition, the wasp pulls out the ovipositor in an interesting manner: it slowly raises the gaster by straightening its bent legs and gently pulls out the ovipositor stage by stage, while slowly creeping forward till the whole ovipositor is out of the fig. The males are less depressed or slender than in the Sycophagini or Apocryptini, respectively; the head is not divided into two parts, and the spiracular peritremata are not prominent, nor very large.

The Indo-Australian genera were keyed by Wiebes (1967e: 173). They are generally found throughout the subgenera *Urostigma* and *Pharmacosycea* (both, Old World species only), and *Ficus*, but not occurring in all species. Hill (1967c: 431) noted that they may well be parasites of the Agaonidae or even of the other Sycophaginae, as they are noticeable smaller than the other wasps in their respective fig faunas.

#### *Philotrypesini*

The cleptoparasite of *Blastophaga psenes* in *Ficus carica* is a member of this tribe; its oviposition-behaviour was studied by Joseph (1958) while earlier observations, with a figure of ovipositing female wasps, were given by Lichtenstein (1919,

figs. 2–3). With the females of the *Philotrypesini*, the eighth and ninth gastral segments are modified, and they form part of a "tail"; moreover, the ovipositor proper and its valves are rather long. Here again, as in the *Apocryptini*, the gaster is raised high, and the wall of the fig is pierced almost beneath the body of the wasp (fig. 8e, f). Then, the ovipositor is dislodged from its sheath. According to Joseph (1958: 225), the valves remain at the point of insertion of the ovipositor, and they are not kept backward as Lichtenstein (1919: 316) recorded; only in case of disturbance, the valves are kept "en position de repos". The males of *Philotrypesis* (fig. 5) show some superficial resemblance to those of the *Sycoryctini*, but they may — among other things — be easily distinguished by the emarginate ventral stomal edge. Some species have fully winged ("homomorphic") males, and several intermediate forms may occur in one sample (for these and other variations, see Grandi, 1930: 53-71).

The species occur in Old World groups of *Urostigma*, *Oreosycea* and *Ficus*. *Sycomor* has no *Philotrypesis*.

#### *Otitesellini*

The females have a short ovipositor, and for that reason are supposed to oviposit from within the fig receptacle. Some have special features evidently related to the way of entering the fig e.g., rasp-like regions on the thorax (*Eujacobsonia*), stout teeth or spines on the legs (*Grasseiana*, *Lipothymus*), etc. The males are peculiar by their oversized heads and mandibles, and they superficially resemble those of *Philotrypesis*. The hosts are found in the Old World groups of *Urostigma* (*Malvanthera* excluded), *Oreosycea*, in a few species of *Sycidium*, and one of *Sycocarpus*. For a review, see Wiebes (1974d: 161).

#### *Sycoecini*

Several of these were formerly classified with the *Sycophaginae* in the old sense, until Hill (1967d: 94–95, 98) erected a separate tribe for their reception. The females have several adaptations for penetrating the fig ostiole, especially in various appendages to the mandibles or the fore tibiae (see also the remarks on *Seres*, by Ramirez, 1974: 774, 776). The males are alate. The distribution of the group is disjunct, one genus (*Diaziella*, see Wiebes, 1974b) occurring in the Philippines (presumably in some figs of section *Conosycea*), while all others are African (host figs of section *Galglychia*, and one in section *Urostigma*).

#### *Epichrysomallinae*

Several genera, some of which with a complicated taxonomic history having been classified with several Chalcidoid families, were recently united in this subfamily (see Hill, 1967d: 96–98). Since then, three new genera were added viz., *Parasycochia* and *Sycobiomorphella* by Abdurahiman & Joseph (1967b), and *Sycophilomorpha* by Joseph & Abdurahiman (1969). The species occur mostly in *Urostigma*-figs, but one was recorded from *Ficus ampelas*, another from *F. tinctoria* (both, section *Sycidium*): it is on these that some biological data are available. Females and males of *Neosycophila omeomorpha* Grandi (see 1923d), both fully winged, develop in large galls of *Ficus tinctoria gibbosa*, which they eventually leave to the outside of the receptacle. Grandi (p. 114) stated as a peculiarity (for fig wasps!) that the male has not developed any "incarico per la liberazione della sua compagna" with which, of course, it mates outside the fig.

#### *Eudecatominae*

Of the fig wasps not belonging to either the *Agaonidae* or the *Torymidae*, this is the most important group. Many species were described from figs of the subgenus *Urostigma*, from Asia as well as from South America: these include several, originally classified with *Decatoma* (some differential characters of *Eudecatoma* and *Sycophila*, as most are now named, were given by Burks, 1971: 7). Boucek (1974: 268) noted that there seems to be little information about whether the

sycophilous species are really confined to figs, as several others do develop in various galls on other plants, or are clearly associated with insects in grass stems. Joseph (1959b: 92) suggested a "cleptoparasitic" way of life for *Decatoma fici* in *Ficus virens*; Hill (1967c: 431) noted that *Sycophila* are probably phytophagous gall-formers, although they could be parasitizing the Epichrysomallinae. The structure of the female reproductive system was discussed by Copland & King (1972).

### THE FIGS

In the lowland tropics of Asia and Australasia, the abundance of fig-species is a good measure of the richness of the environment in plant and animal life (Corner, 1967: 24, see also p. 32 ff.). *Ficus* is mainly defined by its syconium (i.e., in my opinion, by blastophagy), and this conceals the fact that *Ficus* has greater diversity in vegetative mechanism than any other genus of flowering plant and, indeed, of most families. From this basis, one expects a rather clear picture of the taxonomic subdivision of the genus, once the species are described and the synonymies revealed. Much as *Ficus* can be taken as an example of the phylogenetic history of its biota, the classification of its hymenopterous symbionts should conform. Indeed, most of the series and sections as defined by Corner (1965), prove to be paralleled by groups of wasps, especially those of the pollinating Agaonidae. The larger subdivision of *Ficus* in four taxonomic sections, however, is not in all parts reflected in the composition of the wasp fauna (table 8).

Table 8. The classifications of figs and wasps compared.

<i>Ficus</i>	Agaonidae	
	Agaoninae	Blastophaginae
<b>UROSTIGMA</b>		
<i>Urostigma</i>	<i>Elisabethiella</i> <sup>1)</sup>	<i>Blastophaga</i>
<i>Leucogyne</i>		<i>Maniella</i>
<i>Conosycea</i>		<i>Blastophaga</i> , <i>Eupristina</i> , <i>Parapristina</i> , <i>Waterstoniella</i> , <i>Deilagaon</i>
<i>Stilpnophyllum</i>	<i>Pleistodontes</i>	<i>Blastophaga</i>
<i>Malvanthera</i>		<i>Elastophaga</i> <sup>1)</sup>
<i>Galoglychia</i>		
<i>Americana</i>		<i>Pegoscapus</i>
<b>PHARMACOSYCEA</b>		
<i>Pharmacosycea</i>	<i>Tetrapus</i>	
<i>Oreosycea</i>		<i>Blastophaga</i> , <i>Dolichoris</i>
<b>FIGUS</b>		
<i>Ficus</i>		<i>Blastophaga</i>
<i>Rhisocladus</i>		<i>Blastophaga</i>
<i>Kalosyca</i>		<i>Blastophaga</i>
<i>Sinosyctidium</i>		?
<i>Syctidium</i>		<i>Lipornhopalum</i> , <i>Ceratosolen</i>
<i>Adenosperma</i>		<i>Ceratosolen</i>
<i>Neomorpha</i>		<i>Ceratosolen</i>
<i>Syocarpus</i>		<i>Ceratosolen</i>
<b>SYCOMORUS</b>		<i>Ceratosolen</i>

<sup>1</sup> One species only; these records need confirmation. Several other, solitary, records of figs and wasps of uncertain classification are omitted.

A notable discrepancy, here discussed as one example of the joint effort of botany and entomology to arrive at an integrated classification, is found in the group pollinated by *Ceratosolen*-wasps viz., sections *Adenosperma*, *Neomorpha* and *Sycocarpus* of subgenus *Ficus*, and subgenus *Sycomorus*. Also with the mess-mates, three of these groups are exclusively characterized by the presence of one genus viz., *Apocrypta*, while one, *Sycomorus*, is characterized by the presence of *Sycophaga* (in Africa) and the absence of *Philotrypesis*. Some of the species classified with *Ceratosolen* (but none of *Apocrypta* and *Sycophaga*), are members of the entomofauna of other fig sections e.g., section *Sycidium* (*Ficus minahassae* with *Ceratosolen pygmaeus*; *F. pungens* with *C. nanus*); section *Ficus* (*F. pseudopalma* with *C. bakeri*); section *Oreosyceae* (*F. pritchardii* with *C. marshalli*). Ramirez (1974), referring to his unpublished thesis, combined these species and groups, as well as *F. rivularis* ("probably pollinated by a *Ceratosolen* wasp"), all in a heap (subgenus *Sycomorus* in his sense). When I classified *Ceratosolen marshalli*, *nanus*, and *pygmaeus* (Wiebes, 1963a: 8–9, 85; two other species, from figs of section *Sycocarpus*, were tentatively placed in the same species-group), I did not know *Liporrhopalum*. Now, having at hand Hill's revision of *Liporrhopalum*, many of its characteristic features lead me to a reevaluation of the three putative *Ceratosolen*'s. Not all connections are clear yet, mainly because most groups of *Blastophaga* s.l. are still not revised, but I cannot now be as certain as I was twelve years ago, of any apparent affinity with *Ceratosolen*. As to the botanical place of *Ficus pritchardii*, a "problem is that, as a monoecious species [it] should belong in one of the subgenera *Urostigma*, *Pharmacosyceae* or *Sycomorus*. It fits none and finds no aberrant alliance with any of their species" (Corner, 1970b: 401).

*Ficus pseudopalma* (as well as *F. rivularis*) differs from the rest of section *Ficus* markedly enough to require a separate taxonomic series (Corner, 1969b: 326); on p. 56 of 1967, Corner stated: "if *F. pseudopalma* had an entire perianth, which seems a detail, it would be close to *F. dammaropsis*" (section *Sycocarpus*). In the same paper of 1969 (b, fig. 5) Corner illustrated the intricate relationships between sections *Ficus* and *Sycocarpus*. In this diagram, *Auriculisperma* and *Sycocarpus* are derived from an ancestral *Ficus*, which also sends offshoots to section *Ficus* (with *Pseudopalmeae* as one of the early branches) and, separately, to *Rivulales*. It does not show *Sycomorus*, some species of which harbour wasps immediately related to those from *Neomorpha* (e.g., *F. oligodon* and *F. auriculata* with *Ceratosolen emarginatus*). *F. oligodon*, it should be noted, was formerly classified with *Sycocarpus* (subsection *Pomifera*) because of its saccate perianth covering the ovary: a prime respect in the classification of the genus (Corner, 1962: 395). In *Sycomorus*, the one Indo-Australian species (viz., *F. racemosa*) is peculiar in not having a symbiont of the genus *Sycophaga*, which is present in all African species; the figs are monoecious, while the *Ficus* sections mentioned above are dioecious.

In my opinion, as also published in 1973 (p. 24–25), the entomological evidence suggests a reclassification of the figs although this should wait, I hasten to add, until the evidence is more conclusive! The interplay of characters, as recorded in *Ficus*, may possibly be unravelled by the characters of the wasps. As our present knowledge of *Ceratosolen* indicates, the old classification of *Neomorpha* with *Sycomorus* appears to be confirmed, and its close alliance with *Sycocarpus* (*Covellia*) corroborated. This is not to suggest that the origin of *Sycocarpus* is to be sought in modern *Neomorpha* (Corner, 1962: 395, contradicted this), but they may form sister-groups which, of course, is what is meant by "alliance" or "taxonomic relationship". The monoecious condition found in *Sycomorus* as well as in a species of *Papuasyceae*, may indicate the primitive state, whereas *Neomorpha* and *Sycocarpus* (etc.) may represent the derived dioecious condition. The pollinator of *Ficus pseudopalma*, in my opinion, gives away a close connection with primitive *Sycocarpus*, while the absence of *Apocrypta* from its entomofauna, may point to an early branching.

The completion of a laborious task is still before us: the inventory of the fig fauna, and the apprehension of the relations between figs and wasps. The combinations of characters then, once seen in a phylogenetic context, recognized as indicators of monophyletic groups of taxa and, eventually, understood in their biological meaning, may be used as arguments for a classification of their bearers: figs and wasps in symbiosis.

### References

For convenience, this list includes only the references not given in Hill's (1967d: 107-124) bibliography, a few corrections (indicated by an asterisk), and additions to that bibliography. It is supposed to be complete up to and including most of the year 1975.

- ABDURAHIMAN, U. C. & K. J. JOSEPH. 1967a. Contributions to our knowledge of fig insects (Chalcidoidea: parasitic Hymenoptera) from India (New Series) 1. Notes on some new and interesting fig-insects.— *Oriental Insects* **1**: 1-19.
- 1967b. *Idem* 2. New fig insects from Delhi and correction of a mistaken identification.— *Bull. Ent. Loyola Coll.* **8**: 48-57.
- 1975a. Three new Chalcidoidea (Hymenoptera) from India.— *Oriental Insects* **9**: 99-109.
- 1975b. New fig insects (Hymenoptera: Chalcidoidea) from India: three Torymids parasitic on Agaonids.— *Entomophaga* **20**: 73-80.
- ANSARI, M. H. 1967. The process of egg laying in Idarninae (Chalcidoidea: Hymenoptera).— *Ind. J. Ent.* **29**: 380-384.
- BALTAZAR, C. R. 1966. A catalogue of Philippine Hymenoptera (with a bibliography, 1758-1963).— *Pacific Ins. Monogr.* **8**: 1-488.
- BOUCEK, Z. 1974. On the Chalcidoidea (Hymenoptera) described by C. Rondani.— *Redia* **55**: 241-285.
- BURKS, B. D. 1969. Redefinitions of two genera of Chalcidoids from figs, with new Florida species (Hymenoptera).— *Florida Ent.* **52**: 115-122.
- 1971. A synopsis of the genera of the family Eurytomidae (Hymenoptera: Chalcidoidea).— *Trans. Am. ent. Soc.* **97**: 1-89.
- CASTELLANOS, A. 1944. La especie de Ficus del noroeste Argentino.— *Lilloa* **10**: 483-491.
- CHOPRA, R. N. & H. KAUR. 1969. Pollination and fertilization in some Ficus species.— *Beitr. Biol. Pflanzen* **45**: 441-446.
- COPLAND, M. J. W. & P. E. KING. 1972. The structure of the female reproductive system in the Eurytomidae (Chalcidoidea: Hymenoptera).— *J. Zool. (London)* **166**: 185-212.
- COPLAND, M. J. W., P. E. KING & D. S. HILL. 1973. The structure of the female reproductive system in the Agaonidae (Chalcidoidea, Hymenoptera).— *J. Ent. (London) (A)* **48**: 25-35.
- CORNER, E. J. H. 1967. Ficus in the Solomon islands and its bearing on the post-Jurassic history of Melanesia.— *Phil. Trans. R. Soc. Lond. (B)* **253**: 23-159.
- 1969a. The complex of Ficus deltoidea; a recent invasion of the Sunda Shelf.— *Ibid.* **256**: 281-317.
- 1969b. Ficus sect. Adenosperma.— *Ibid.* **256**: 319-355.
- 1970a. Ficus subgen. Ficus. Two rare and primitive pachycaul species.— *Ibid.* **259**: 353-381.
- 1970b. Ficus subgen. Pharmacosycea with reference to the species of New Caledonia.— *Ibid.* **259**: 383-433.
- 1975. Ficus in the New Hebrides.— *Ibid.* **272**: 343-367.
- CROIZAT, L. 1968. The biogeography of the tropical lands and islands east of Suez-Madagascar: with particular reference to the dispersal and form-making of Ficus L., and different other vegetal and animal groups.— *Atti Ist. bot. Lab. Crittogam. Univ. Pavia (6)* **4**: 1-400.
- 1969. A proposito di alcune critiche di E. J. H. Corner.— *Ibid.* **5**: 181-190.
- EISEN, G. 1901. The fig: its history, culture and curing, with a descriptive catalogue of the known varieties of figs.— *Bull. Div. Pomol. U.S. Dept. Agric.* **9**: 1-317 [Bibliography: 295-301].

- FORSKAL, P. 1775. *Flora aegyptiaco-arabica*: 1–32, i-cxxvi, 1–220.
- GALIL, J. 1966. [The sycamore tree in the civilization of the Near East].— *Teva VeAretz* **8**: 306–318, 338–355 [Hebrew].
- 1967. Sycamore wasps from ancient Egyptian tombs.— *Israel J. Ent.* **2**: 1–10.
- 1968. An ancient technique for ripening sycamore fruit in East Mediterranean countries.— *Econ. Bot.* **22**: 178–190.
- 1973a. Topocentric and ethodynamic pollination.— In N. B. M. Brantjes (Ed.), *Pollination and dispersal*: 85–100.
- 1973b. Pollination in dioecious figs. Pollination of *Ficus fistulosa* by *Ceratosolen hewitti*.— *Gdns' Bull., Singapore* **26**: 303–311.
- GALIL, J., R. DULBERGER & D. ROSEN. 1970. The effects of *Sycophaga sycomori* L. on the structure and development of the syconia in *Ficus sycomorus* L.— *New Phytol.* **69**: 103–111.
- \*GALIL, J. & D. EISIKOWITCH. 1965. [Pollination of the flowers of *Ficus religiosa* L.].— *Teva VeAretz* **7**: 1–16 [Hebrew].
- 1968a. On the pollination ecology of *Ficus sycomorus* in East Africa.— *Ecology* **49**: 259–269.
- 1968b. Flowering cycles and fruit types of *Ficus sycomorus* in Israel.— *New Phytol.* **67**: 745–758.
- 1968c. On the pollination ecology of *Ficus religiosa* in Israel.— *Phytomorphology* **18**: 356–363.
- 1969a. Further studies on the pollination ecology of *Ficus sycomorus* L. (Hymenoptera, Chalcidoidea, Agaonidae).— *Tijdschr. Ent.* **112**: 1–13.
- 1969b. Note on pollen transport, pollination and protection of ovaries in *Ficus sycomorus*.— *New Phytol.* **68**: 1243–1244.
- 1971. Studies on mutualistic symbiosis between syconia and sycophilous wasps in monoecious figs.— *Ibid.* **70**: 773–787.
- 1974. Further studies on pollination ecology in *Ficus sycomorus* ii. Pocket filling and emptying by *Ceratosolen arabicus* Mayr.— *Ibid.* **73**: 515–528.
- GALIL, J., W. RAMIREZ B. & D. EISIKOWITCH. 1973. Pollination of *Ficus costaricana* and *F. hemsleyana* by *Blastophaga estherae* and *B. tonduzi* (Agaonidae) in Costa Rica.— *Tijdschr. Ent.* **116**: 175–183.
- GALIL, J. & Y. SNITZER-PASTERNAK. 1970. Pollination in *Ficus religiosa* L. as connected with the structure and mode of action of the pollen pockets of *Blastophaga quadraticeps* Mayr.— *New Phytol.* **69**: 775–784.
- 1971. Note on pollination in *Ficus religiosa* L.— *Ent. Ber., Amst.* **31**: 123–124.
- GALIL, J., M. ZERONI & D. BAR SHALOM. 1973. Carbon dioxide and ethylene effects in the co-ordination between the pollinator *Blastophaga quadraticeps* and the syconium in *Ficus religiosa*.— *New Phytol.* **72**: 1113–1127.
- GALLESIO, G. 1820. *Pomona italiana*. Parte scientifica fasc. 1 contenente il trattato del fico: 81–103.
- GAUD, S. M. & L. F. MARTORELL. 1973. New insect records for Puerto Rico.— *J. Agric. Univ. Puerto Rico* **57**: 247–254.
- GIRAULT, A. A. 1917. Some new Australian chalcid-flies, mostly of the family Encyrtidae (Hymenoptera).— *Insector Inscit. menstr.* **5**: 29–37.
- GORDH, G. 1975. The comparative external morphology and systematics of the neotropical parasitic fig wasp genus *Idarnes* (Hymenoptera: Torymidae).— *Univ. Kansas Sci. Bull.* **50**: 389–455.
- GRANDI, G. 1967. La vita straordinaria degli insetti dei fichi.— *Scientia* **7** (102): 7.
- \*HASSELQUIST, F. 1757. *Iter Palaestinum*. Eller Resa til Heliga Landet forrattad ifran År 1749 til 1752, med Beskrifningar Ron, Anmarkningar ofver de markvardigste Naturalier: i-xiv, 1–619.
- 1762. *Reise nach Pälästina in den Jahren von 1749 bis 1752*. Auf Befehl Ihro Majestät der Königin von Schweden herausgegeben von Carl Linnæus: 1–17, 1–606.
- \*HEGARDT, C. 1749. *Ficus*.— In Caroli Linnæi *Amoenitates Academicæ* 1 (2): 23–54.
- HILL, D. S. 1967d. Figs (*Ficus* spp.) of Hong Kong: i-viii, 1–130 [Bibliography: 107–124].
- 1969. Revision of the genus *Liporrhopalum* Waterston, 1920 (Hymenoptera Chalcidoidea, Agaonidae).— *Zool. Verh.* **100**: 1–36.
- 1971. Wasps and figs.— *New Scient. & Science J.*: 144–146.

- HOWARD, L. O. 1899. The present status of the caprifig experiments in California.— *Bull. Div. Ent. U.S. Dept. Agric. (n.s.)* **20**: 28–35.
- \*JOSEPH, K. J. 1957a. Contributions to our knowledge of fig insects (Chalcidoidea: parasitic Hymenoptera) from India vii. Descriptions of fifteen new and revision of some old species.— *Ann. Soc. ent. France* **125**: 97–133.
- 1966. Taxonomy, biology and adaptations in fig insects (Chalcidoidea).— *Proc. 2nd All-India Congr. Zool.* **2**: 400–403.
- 1967. Newer trends in the taxonomy of the fig-inhabiting Chalcidoidea.— *Bull. nat. Inst. Sci., India* **34**: 257–262.
- JOSEPH, K. J. & U. C. ABDURAHIMAN. 1968. Descriptions of six new species of Decatoma (Chalcidoidea: Eurytomidae) from *Ficus benghalensis* L.— *Oriental Insects* **2**: 63–87.
- 1969. Contributions to our knowledge of fig insects (Chalcidoidea: Hymenoptera) from India 4. Further descriptions of new fig insects from *Ficus benghalensis* L.— *Ibid.* **3**: 37–45.
- LATREILLE, P. A. 1825. Familles naturelles du règne animal: i–vi, 1–570.
- LEE, S. S. & C. H. TAN. 1973. Fig wasps (Hymenoptera, Chalcidoidea).— *Malay. Nat. J.* **26**: 112–119.
- LICHTENSTEIN, J. L. 1919. Note préliminaire au sujet de *Philotrypesis caricae* Hass.— *Bull. Soc. ent. France*: 313–316.
- NIKOLSKAJA, M. N. 1954. [Blastophaga-pollinator of the fig].— *Priroda, Leningrad* **5**: 107–108 [Russian].
- PETERSEN, B. 1966. The Noona Dan Expedition, 1961–62. Insects and other land arthropods.— *Ent. Medd.* **34**: 283–304.
- PRINCIPI, M. M. 1971. Guido Grandi e la sua opera.— *Boll. Ist. Ent. Univ. Bologna* **30**: 1–24.
- RAMIREZ B., W. 1969. Fig wasps: mechanism of pollen transfer.— *Science* **163**: 580–581.
- 1970a. Taxonomic and biological studies of neotropical fig wasps (Hymenoptera: Agaonidae).— *Univ. Kansas Sci. Bull.* **39**: 1–44.
- 1970b. Host specificity of fig wasps (Agaonidae).— *Evolution* **24**: 680–691.
- 1974. Coevolution of *Ficus* and Agaonidae.— *Ann. Missouri Bot. Gdn* **61**: 770–780.
- ROBSON, T. B. 1911. Blastophaga in Australia.— *Rural Calif.* **35**: 307.
- SANTIS, L. de. 1971. La fauna de Chalcidoideos de America del Sur.— *Bol. Soc. ent. Peru* **6**: 59–63.
- \*SAUNDERS, S. S. 1883a. Descriptions of three new genera and species of fig insects allied to *Blastophaga* from Calcutta, Australia, and Madagascar; with notes on their parasites and on the affinities of the respective races.— *Trans. ent. Soc. London*: 1–27.
- 1883b. [Characterization of fig insects].— *Proc. ent. Soc. London*: v–vi.
- \*————— 1883c. On the *Cynips caricae* of Hasselquist and other fig-insects allied thereto; with descriptions of a new species from Australia.— *Trans. ent. Soc. London*: 383–392.
- 1883d. [Exhibition of both sexes of *Ichneumon ficarius* . . .].— *Proc. ent. Soc. London*: xxxi–xxxii.
- SAVAGE, C. G. 1924. Smyrna fig culture.— *J. S. Austr. Dept. Agric.* **28**: 401–421.
- SISSON, R. F. 1970. The wasp that plays cupid to a fig.— *Nat. Geographic* **138**: 690–697.
- TREUB, M. 1902. L'organe femelle et l'embryogénèse dans le *Ficus hirta* Vahl.— *Ann. Jard. bot., Buitenzorg (ser. 2)* **3**: 124–157.
- VECHT, J. van der, 1973. Insekten zonder tal: een uitdaging.— *Versl. Ned. Akad. Wetensch. Amst. (Nat.)* **82**: 41–48.
- WALKER, F. 1846. List of the Hymenopterous insects in the collection of the British Museum, part 1: 1–100.
- WATERHOUSE, C. O. 1881. Remarks on the types of *Cynips psenes* and *Cynips sycomori* in the Linnean Collection.— *Proc. ent. Soc. London*: xli–xlii (and reply by Saunders: xlii–xliv).
- WESTWOOD, J. O. 1883c. [Further descriptions of insects infesting figs; errata].— *Trans. ent. Soc. London*: vii.
- WIEBES, J. T. 1967a. Indo-Malayan and Papuan fig wasps (Hymenoptera, Chalcidoidea) 5. Description of *Otitesellini* (Torymidae).— *Proc. Acad. Sci. Amst. (C)* **70**: 121–136.
- 1967b. *Idem* 6. The genus *Eujacobsonia* Grandi (Torymidae).— *Zool. Meded., Leiden* **42**: 107–115.

- 1967c. *Guadalia vissali* nov. gen., nov. spec., a new fig wasp from the Solomon Islands (Hymenoptera, Torymidae, Otitesellini).— *Ent. Ber., Amst.* **27**: 214–218.
- 1967d. Polanisa Walker, 1875 (Insecta, Hymenoptera): proposed suppression under the plenary powers.— *Bull. zool. Nomencl.* **26**: 319–320; **31**: 24–26 (1974, Opinion no. 1018).
- 1967e. Redescription of Sycophaginae from Ceylon and India, with designation of lectotypes, and a world catalogue of the Otitesellini (Hymenoptera Chalcidoidea, Torymidae).— *Tijdschr. Ent.* **110**: 399–442.
- 1968a. Fig wasps from Israeli *Ficus sycomorus* and related East African species (Hymenoptera, Chalcidoidea) 2. Agaonidae (concluded) and Sycophagini.— *Zool. Meded., Leiden* **42**: 307–320.
- 1968b. Species of *Agaon* from Congo (Kinshasa), with notes on synonymy (Hymenoptera, Chalcidoidea).— *Proc. Acad. Sci. Amst. (C)* **71**: 346–355.
- 1968c. A new *Pleistodontes* (Hymenoptera Chalcidoidea, Agaonidae) from Rennell Island.— *Nat. Hist. Rennell Isl.* **5**: 115–117.
- 1969a. Preliminary report on a collection of fig insects (Hymenoptera Chalcidoidea) from *Ficus gnaphalocarpa*.— *Mém. Inst. fond. Afr. noire* **84**: 401–402.
- 1969b. *Philosycus*, a new genus of fig wasps allied to *Otitesella* Westwood (Hymenoptera Chalcidoidea, Torymidae).— *Ann. Mus. R. Afr. centr., in 8, Zool.* **175**: 439–445.
- 1969c. Hymenoptera Agaonidae, with an introductory chapter on West African fig wasps.— *Ibid.* **175**: 449–464.
- 1970a. Revision of the Agaonidae described by J. Risbec, and notes on their Torymid symbionts (Hymenoptera, Chalcidoidea).— *Zool. Meded., Leiden* **45**: 1–16.
- 1970b. Vijgen en vijgewespen.— *In* K. H. Voous (Ed.), *Biosystematiek*: 180–206. 240–242.
- 1971. A new record of *Allotriozoneon prodigiosum* Grandi, and description of its symbionts (Hymenoptera, Chalcidoidea).— *Mém. Inst. fond. Afr. noire* **86**: 367–383.
- 1972a. A new species of *Agaon* from Nigeria (Hymenoptera, Chalcidoidea).— *Ent. Ber., Amst.* **32**: 122–124.
- 1972b. The genus *Alfonsiella* Waterston (Hymenoptera, Chalcidoidea, Agaonidae).— *Zool. Meded., Leiden* **47**: 321–330.
- 1973. Phylogenetic specificity of figs and fig wasps.— *In* N.B.M. Branjes (Ed.), *Pollination and dispersal*: 21–25.
- 1974a. *Nigeriella*, a new genus of West African fig wasps allied to *Elisabethiella* Grandi (Hymenoptera Chalcidoidea, Agaonidae).— *Zool. Meded., Leiden* **48**: 29–42.
- 1974b. The fig wasp genus *Diaziella* Grandi (Hymenoptera Chalcidoidea, Torymidae Sycocini).— *Proc. Acad. Sci. Amst. (C)* **77**: 295–300.
- 1974c. Species of *Agaon* Dalman and *Allotriozoneon* Grandi from Africa and Malagasy (Hymenoptera Chalcidoidea, Agaonidae).— *Zool. Meded., Leiden* **48**: 123–143.
- 1974d. Philippine fig wasps 1. Records and descriptions of Otitesellini (Hymenoptera Chalcidoidea, Torymidae).— *Ibid.* **48**: 145–161.
- 1975. Fig insects from Aldabra (Hymenoptera, Chalcidoidea).— *Ibid.* **49**: 225–236.
- 1976. Indo-Malayan and Papuan fig wasps (Hymenoptera, Chalcidoidea) 7. Agaonidae, mainly caught at light.— *In* preparation.

## The Taxonomist's Dilemma

by

V. H. HEYWOOD

*Department of Botany, Plant Science Laboratories  
University of Reading, England.*

Taxonomists, or at least the services they provide, are suddenly in demand. This is not quite the same as saying that taxonomy has regained its earlier popularity — indeed there are signs that in some of the developed countries the number of students going on to seek taxonomic training is decreasing after reaching a peak in the 1960's. Teaching and research schools are in some cases being run down and in some major European universities they are non-existent. Likewise many important museums and herbaria are understaffed and the accumulation of unidentified material is often of massive proportions.

The pressure for an increase in the number of taxonomists stems largely from the growing and realistic appreciation of both the extent and pace at which man has been consuming, destroying, modifying and deteriorating our global environment, and in particular our plant resources which form the very base of the life-support systems of our planet (Heslop-Harrison, 1975), and from the initiatives that have been proposed to combat this. The most important recognition of the dangers facing plant life, and of the consequences for man if urgent steps are not taken to moderate them, comes from the United Nations Conference on the Human Environment held in Stockholm in 1972 and the ensuing recommendations 39-45 of the Declaration on the Human Environment dealing with plant and animal resources, their survey and conservation. If one considers the main recommendations, they cover survey of plant genetic resources, preparation of inventories, field exploration and collecting, conservation in nature and in gardens and seed banks. To those of us who work as practising taxonomists this sounds all too familiar, since it is a fair summary of the kinds of activities in which we and previous generations of taxonomists have been engaged for the past two centuries. What does the taxonomist do if not explore plant resources in the field throughout the world and produce checklists, Floras, keys and monographs, which are essentially inventories with a greater or lesser amount of detail? Yet the role of taxonomy is not explicitly recognized. Conservation, resources, ecology have become accepted words, even today understood by governments, but taxonomy still does not have a familiar ring and the term classification still retains a pejorative gloss. A similar failure to appreciate the role of taxonomy was a characteristic of the International Biological Programme, yet the evidence of the urgent need to extend floristic exploration, especially in areas at high risk such as the tropics, sub-tropics, islands and areas of Mediterranean climate, was fully available. Among those to draw attention to the need to study the tropical floras, Corner was prominent as early as 1946. His appointment to a professorship of Tropical Botany by the University of Cambridge was a belated recognition of both the importance of his work and his personal standing, but his pleas for action went largely unheard by governments and international agencies.

Explicit recognition of the need for an expansion of taxonomic work was given at the 18th General Assembly of the International Union of Biological Sciences in 1973, which passed resolutions recommending that special attention be

given to the improvement of the services providing for the identification of animal and plant species, as well as to the improvement of the flow of information on taxonomic data to all other relevant disciplines, and requesting that the Executive Committee point out to the national adhering organizations the great importance of the training of biological taxonomists. Similar resolutions have been passed by congresses and symposia but it would be unrealistic to expect any substantial action to be taken by governments especially in the present economic climate. The problems of supply and training of taxonomists have already been alluded to briefly and will be discussed further below.

It is against the above background that taxonomists work today; not a particularly comforting one. It contrasts with previous generations of taxonomists who worked with a high degree of tranquillity, not faced with an agonizing series of choices of techniques, priorities, philosophies.

In the post-Linnean period, as the exploration of new territories in various parts of the world gathered momentum and material flowed into botanic gardens, herbaria and museums, taxonomy rapidly progressed from being essentially a codification of folk biologies, and mainly West European, to a world-wide system of classification and communication for biology. The fact that this fundamental change in the nature of taxonomy had taken place was scarcely realized at the time (Heywood, 1974). Indeed one of the unfortunate consequences of the acceptance of Darwinian evolutionary theory was that attention was diverted from the practical data-processing role of taxonomy to an almost obsessive compulsion to seek evolutionary interpretations of taxonomic data and to place all organisms in their correct place on so-called phylogenetic trees. This preoccupation with evolutionary explanation has, quite understandably, continued to the present day: in the age of evolutionary biology it could scarcely be otherwise. What has seldom been assessed is what the effect on practical classification has been. To the extent that comparative data have been deliberately discarded or ignored in favour of supposedly phylogenetically significant features, and thereby departing from the principles of classification based on maximum co-variation or correlation of characters, it is arguable that taxonomy has been greatly retarded. This, combined with the tendency to decry the importance of taxonomy as an information system, may well have set classificatory taxonomy back ten or twenty years. Today when we have powerful tools for the study of phylogeny, such as numerical cladistics, and powerful new classes of data, such as amino acid sequences of cytochromes *c* and plastocyanins, we are in a situation where we have to consider seriously whether we can afford to devote a major effort to this kind of study, or whether we should concentrate our energies and resources on floristic exploration and writing Floras and monographs. Similarly we must ask whether detailed study of micro-characters by scanning electron microscopy, chemical features by gel electrophoresis, chromatography, etc., or the population structure of temperate species of no known or potential economic, ecological or agronomic importance, can be justified.

To answer that we must continue to do both is to sidestep the dilemma that faces us today. What then has happened that has forced us into this situation? Quite simply, our predecessors, after earlier naive assumptions as to the numbers of the world's biota, came to realize that the task facing them in exploring, describing and understanding the world's flora and fauna was virtually limitless, but that it would only be a matter of time before the basic inventorying would be complete. The great museums and herbaria were established and collections were amassed from region after region as part of an apparently never-ending process. For political-historical reasons, floristic exploration and Flora-writing was a feature associated with imperialism and colonialism as regards the under-developed, largely tropical, parts of the world and no global assessment of progress was ever seriously made.

It is only in the course of the last five to ten years that we have come to realize that the end is in sight and that we have achieved much less than we had realized. This new situation has arisen because of expanding world populations and increased expectations as regards living standards, with all the consequent destruction of natural vegetation, especially tropical forest, which is basically non-renewable, for living room, cultivation, industrialization, etc. The statistics are horrifying and sufficiently well documented to need no repetition here. The almost inevitable outcome will be massive world-wide extinction of the world's most interesting and economically valuable floras and their replacement, where there is space still available by some form of secondary and relatively uniform vegetation.

The probability that about 85% of the world's extant organisms have not yet been described need not concern us here: there never was any possibility that they would or even should all ever be discovered and named. The position concerning higher plants is on the face of it much more satisfactory — it is estimated that about 250,000 species of angiosperms have been recognised and that only 10-20,000 still remain to be discovered and described. Unfortunately we know very little about the great majority of the quarter million species apart from some of their basic morphology and some distributional and ecological data. For only a tiny minority do we possess details of their karyology, population structure, chemical constituents, breeding system, etc.

What makes the situation so serious is not the eventual outcome but the alarmingly rapid rate at which species by the hundred and thousands and indeed whole ecosystems, are either disappearing or becoming threatened. While we can make estimates such as those which suggest that up to 20,000 angiosperm species are threatened or even in danger of extinction, our impotence is triple in that (1) the majority are in tropical or sub-tropical areas of the world, (2) we do not have the means of taking action on a sufficiently massive scale to avoid the inevitable extinction of a high percentage of them due to lack of funds and trained manpower, not to mention sociological and political factors, and (3) we have no means of knowing, even were the resources available to tackle the problem, exactly which species are in greatest peril.

Despite the valiant efforts of the IUCN and its Threatened Plants Committee to identify and catalogue the threatened species. It is only in cool temperate and perhaps Mediterranean regions where this will be achieved in time.

The immensity of the problem in the tropics is such that the action needed is vastly in excess of the manpower and resources available or likely to become available in the near future and we can only hope that a sufficient number of national parks and reserves can be established and maintained so as to allow us to retain for future generations some reasonably representative samples of the floristic richness and resources of the various countries and regions concerned. In addition to such natural reserves, it is necessary to establish seed banks and living resources centres, especially in scientifically organized Botanic Gardens as discussed at the Kew Conference held in September 1975 sponsored by the NATO Eco-Sciences Panel. Such action is already being organized by various international agencies for cultivated plants and their wild relatives, which is a big enough task in itself, but it must be extended to deal with at least some of the wild species to which no economic importance is at present attached. Just how such species should be selected is a major problem since, as indicated above, our detailed knowledge of large parts of tropical floras is so limited that we cannot in many cases say which of them are threatened.

In the light of the situation a positive response is needed from the taxonomic community, yet all too often the reaction is either that the problem is so vast that nothing any individual taxonomist can do will have any effect, or that the whole question is one for politicians, economists, and governments, not scientists.

I believe that this is unduly pessimistic an attitude to take. The taxonomist is often uniquely qualified to know what the situation is in a particular area and a great deal could be done by devoting effort to identifying areas or species at high risk and further by assembling this information for general use. One urgent task is to make a world survey, country by country of the floristic situation — what the size of the flora is, how far it has been studied, what Floras are available, are in preparation or are being planned, what the manpower situation is, which countries are involved, what assistance is needed. Surveys of this kind have been undertaken for Europe through the *Flora Europaea* organization, for the Mediterranean through the CNRS symposium on the Mediterranean basin held in Montpellier in June 1973 and through a working party of the OPTIMA organization and for all Africa south of the Sahara by AETFAT.

There is a widespread feeling amongst taxonomists that they should have freedom to work on any group no matter what the overall situation might be. At the risk of being highly unpopular, I feel that such an attitude is today somewhat arrogant, especially when one considers that most taxonomists are employed from public funds. Very few scientists today have such freedom of choice and I believe that taxonomists today should seriously consider whether there is not some positive action they could take to help in a small way to alleviate the situation outlined above. It is easy enough to append signatures to resolutions and to lament the perils facing the world's flora but this is hypocritical if at the same time research programmes are undertaken without regard to these considerations. It would not be difficult to compile a list of taxonomic groups deserving high priority either because they contain many threatened species or because they are of economic importance, and have not been adequately studied or revised. Closer collaboration, for example, between taxonomists and agronomists and plant breeders should be urged in areas such as exploration of genetic resources, collecting material for seed banks and living collections.

There are two further areas which should make claims on our time — education and training. Our first concern should be to try and educate our colleagues by explaining patiently the need for what seems to them quite routine and unspectacular research. To a large extent our own insistence that we are all evolutionary biologists concerned with the solution of what to the outsider may seem quite parochial problems has been largely responsible for our failure to convince our colleagues of the seriousness of the threats facing plant resources today. However intellectually stimulating the search for evolutionary ancestors may be, it has diverted attention from the real-life situation. For too long, conservation has been left in the care of the prophets of doom, rather than accepting our own responsibilities to present the hard facts in a realistic way. If we, as taxonomists, with our own intimate knowledge cannot get the message across, then who will?

Training of taxonomists prevents a whole series of problems. Those of us with the facilities and staffing have a moral responsibility to accept the rôle of training, as best we can, taxonomists for those countries where qualified staff are distinguished by their scarcity. Our aim should be to train the teachers so that they can take over the tasks in their own land. At the same time we should resist attempts by government to restrict our rôle in this area because of temporary economic difficulties.

Finally we should draw attention to the consequences if we do not take action on a large enough scale. It is not just the tropical countries but the whole of mankind that will suffer if we are to do too little, too late. We have a responsibility not only to ourselves but to future generations.

Professor Corner was one of the first to draw attention to the taxonomist's dilemma. If we have any criticism to make it is that he did not from his wisdom plead the case with even greater eloquence than he did.

**References**

- HESLOP-HARRISON, J. 1975. Man and the endangered plant. *International Year Book 1975*: xii-xvi.
- HEYWOOD, V. H. 1974. Systematics — the stone of Sisyphus. *Biol. J. Linn. Soc.* **6**: 169-178.



# On the Style of Floras: some general considerations\*

by

D. G. FRODIN

*Herbarium*

*University of Papua New Guinea*

## Summary

The most satisfactory style for a Flora at the present time should be one of conciseness and practicality, with "correctness and clearness of method and language [being] the first qualities requisite," to quote Bentham (1874, p. 50). This should be inventory, identification, and provision of essential data. Large-scale flora projects, of which there are perhaps too many on the stage today, should be examined very carefully; in many cases their bulk (and cost) may defeat any real usefulness or impact, and their basis is shaky, leaving many to be terminated incomplete or only completed after more than a generation. Such incomplete works, with which the pages of floristic bibliographies are replete, are ultimately of less value than one which may be more modest but is complete, and in fact should perhaps be viewed as a wasting of botanists' time and resources. Furthermore, with the EDP-IR communications, and media revolutions (the full impact of which has yet to be felt in systematic biology), it may be questioned whether much of the specialized data found in large-scale floras need be tied up in the print medium but could better be handled in other, less familiar ways; at the same time, such methods would lead to fewer losses than is usually the case at present in translating taxonomic and floristic research into conventional floras. The FNA represented a step in the right direction, but it faced public relations problems and an unfavourable administrative climate and it may have been too big a step at that time and place. Some smaller but similar projects are still under way in other parts of the world and it is these "guinea-pigs" that will be watched with interest in the next few years. However, there is still plenty of scope for the more modest, concise work, which, because less time is usually taken in production, stands a better chance in the present economic climate of gaining support and carrying through to completion, although technically it might be less "prestigious". It is thus to be hoped that works such as *Flora Europaea*, *Flora of Turkey*, *Flora Iranica*, and the *Tree Flora of Malaya* will be successfully completed in the next decade, and others like them undertaken, even for lesser-known tropical regions. There is also, in my view, scope for good annotated enumerations, preferably with keys; the recent *Prodromus einer Flora von Südwestafrika* is a good example.

The completion of a revised and expanded version of my Guide to standard floras of the world, which first appeared in a limited cyclostyled edition in 1964, has provided the opportunity to make a review of the purpose, design, and content of floras, manuals and enumerations; additional stimulus for this has come from a series of recent articles dealing with various aspects of the subject (Fisher, 1968; Heywood, 1973; Shetler, 1971; Taylor, 1971; Watson, 1971). These in turn resulted from a consideration of the "information explosion" in systematics (see also Anonymous 1974), the introduction of the new methodologies of taxometrics (numerical taxonomy) and EDP-IR during the 1960's and early 1970's, the progress of *Flora Europaea*, the development of the Flora North America Program (before its termination in 1973), and the increasing demands on the systematics profession made by other biologists (notably ecologists) and by "environmental scientists." Together, these papers represent the first major reconsideration of the principles and the style of floras and other floristic works for a century or more, with a few exceptions (van Steenis, 1954; Davis & Heywood, 1963). The present review gives

---

\* This essay was originally intended to be one of the introductory chapters to my forthcoming *Guide to standard Floras of the world*, but had to be omitted for lack of space. It is presented here as a separate work.

a summary of these contributions and traces the historical development of Flora-writing as well as analyzing current trends and making some suggestions for the future.

#### HISTORICAL SURVEY

Most of the more important floristic works in current use around the world by and large adhere to principles gradually laid down in the mid-19th century and succinctly summarized by Bentham (1861, 1874) and de Candolle (1880). Bentham's principles are contained in the first five aphorisms of his "Outlines of Botany", which appeared in nearly all of the colonial floras in the series issued from the Royal Botanic Gardens, Kew, as well as some contemporary works such as Hillebrand's *Flora of the Hawaiian Islands*. Their influence was widespread and lasting, and because the first three are particularly apropos to the present discussion I repeat them here:

"1. The principal object of a Flora of a country, is to afford the means of determining (i.e. ascertaining the name of) any plant growing in it, whether for the purpose of ulterior study or of intellectual exercise.

2. With this view, a Flora consists of descriptions of all the wild or native plants contained in the country in question, so drawn up and arranged that the student may identify with the corresponding description any individual specimen which he may so gather.

3. These descriptions should be clear, concise, accurate, and characteristic, so as that each one should be readily adapted to the plant it relates to, and to no other one; they should be as nearly as possible arranged under natural divisions, so as to facilitate the comparison of each plant with those nearest allied to it; and they should be accompanied by an artificial key or index, by means of which the student may be guided step by step in the observation of such peculiarities or characters in his plant, as may lead him, with the least delay, to the individual description belonging to it."

The second part of the fifth aphorism is also of some interest and is likewise quoted:

"The botanist's endeavours should always be, on the one hand, to make as near an approach to precision as circumstances will allow, and, on the other hand, to avoid that prolixity of detail and overloading with technical terms which tends rather to confusion than clearness. In this he will be more or less successful. The aptness of a botanical description, like the beauty of a work of imagination, will always vary with the style and genius of the author."

The first of these aphorisms clearly reflects Bentham's view of a flora; and it was in this spirit that much of the "Kew Series" of colonial floras was prepared, as with the contemporary floras of the British Isles prepared by him and by Hooker (these latter, even today, are still appreciated for their method and conciseness). Bentham's principles, with modifications, also gave rise through the example of Torrey's and Gray's classic works on North American plants of the late 1830's and 1840's to the standard format of many current North American Floras and manuals. Other major works of the period strongly influenced by these principles — as acknowledged by their authors — were Miquel's *Flora indiae batavae* (1855-59), Boissier's *Flora orientalis* (1867-88), and Willkomm & Lange's *Prodromus florum hispaniae* (1861-93).

In kindred spirit to the concisely descriptive floras of the Anglo-American (and Franco-Swiss) "school", but with somewhat different methodology and aims, there arose the Continental "manual-key". This represented a substantially

independent development, stemming from the simple dichotomous analytical keys devised by Lamarck for the first edition of his *Flore française* in 1778 (Voss, 1952; quoted in Radford et al., 1974). Lamarck intended this work to be nothing more than a handy means of plant identification (Stafleu, 1971), and all manual-keys which have appeared since then have been motivated by this principle. In such works, the format of separate keys (or synoptic devices) and descriptions typical of works of the Anglo-American "school" was bypassed in favour of diagnostic analytical keys which (in later years) also variously incorporated brief, partly symbolic notes on habitat, distribution, life-form, phenology, karyotypes, etc. As the 19th century progressed, bringing with it greatly improved means of transportation and more leisure, the manual-key style became very widespread in Europe, often going under the name of "excursion-flora." Through Central European influence, this kind of flora penetrated to Russia and eventually became an ubiquitous feature in the comprehensive network of regional floras which developed in the Soviet Union from the 1920's onwards. (The Russian term for such works is *opredelitel'*, sometimes translated as "the keys" or "determinator" but better rendered in English, I feel, as "manual-key", being more expressive and idiomatic.) However, no matter where they are produced, manual-keys are to a large extent based on more comprehensive "research" or "creative" floras; because of their largely derivative nature and (in some parts of the world) periodic issue to meet public demand, they (along with local descriptive manuals) have been termed "routine" floras (van Steenis, 1954; Davis & Heywood, 1963). As a style, the manual-key is not often seen outside Europe of the Soviet Union; good recent examples by non-Continental authors include *Flora of the Sydney Region* by Beadle et al. (2nd ed., 1972) and *Flora of the Pacific Northwest; an illustrated manual* by Hitchcock and Cronquist (1973).

An interesting link between the two "schools" was provided by the floras written by Bentham (and those influenced by him). Although these works were basically concisely descriptive, like most of those written by the de Candolles, the Hookers, Torrey and Gray, Bentham consistently used analytical keys in place of (or in addition to) the synoptical devices which characterized the works of the other authors (and those influenced by them). This reflects the strong influence of the *Flore française* of Lamarck (by 1815 under de Candolle's authorship), with its analytical keys (or "indexes", to use Bentham's term), and other French works during Bentham's formative years as a botanist (1817-26), which were spent in France (Bentham, 1974). By contrast, J. D. Hooker apparently believed that such keys made things too easy in that students would pay little attention to diagnoses and descriptions. This view may well have been shared by A. de Candolle, who failed to mention them in his *La Phytographie* of 1880 (van Steenis, 1954).

The next major development in floristic writing to be considered here is the detailed semi-monographic flora, which also had its origins in the mid-19th century. It seems likely that the motivating forces for such works were prestige (something which also lay behind the many sumptuous sets of "scientific results" of voyages and expeditions in this period) and a belief that a flora should act as a detailed compendium and repository of information about the plants of an area and not solely as a practical handbook for identification and essential information. In other words, it should be a specialized kind of encyclopaedia, with sub-monographic accounts containing detailed descriptions, synonymy, specimen citations, extensive notes, and (often) illustrations in large plates. This concept of a flora seems to have arisen (or taken strongest hold) in the Central European intellectual sphere, and cannot fail to have been influenced by the Germanic predilection for detail rather than conciseness. It was here that the Linnean system persisted longest, due largely to the strength of the scholastic tradition (and the *ex cathedra* professorial system) and the continuing demand for general compendia of the plant kingdom (Bentham, 1874). The first truly original systematic work in Central Europe which

professed a "natural" system was Endlicher's *Genera plantarum* (1836-40). Soon after, Endlicher joined forces with von Martius to work on the first "modern" semi-monographic flora, the king-sized *Flora brasiliensis*, begun in 1840. In this way, the endemic mania for large compendia was shifted into significant new channels, the results of which were to have a major influence over the next two generations.

The greatest flora of the 19th century dragged its detailed pages slowly on for 66 years, a time span exceeding that of most British colonial floras of the same period, and was for long a dominant factor in European phytography. As with *Flora Europaea* a century later, its organization consisted of editors, technical co-workers ("Privatassistenten"), and numerous specialist contributors. Amongst the many botanists so involved, there were three — Eichler, Engler, and Urban — who brought the Berlin "school" of systematics into being after 1870 and imbued it with the *Weltanschauung* and scholarship which were to make it so influential. All had been, or were actively, editors or co-workers or both on *Flora brasiliensis*. Under the general direction of Engler after 1889, the Berlin "school" came to specialize in large-scale monographic works, detailed series of regional revisions, plant-geographical studies, and related contributions, culminating in that supreme monument of German systematics, *Die natürlichen Pflanzenfamilien* (1887-1915; 2nd ed., 1926+, not completed). Contemporaneously with much of *Flora brasiliensis*, but on the domestic front, there was another large-scale work, the Reichenbachs' *Icones florum germanicarum* (1834-70).

In spite of all this effort, and the stimulus provided by the development of the German colonial empire after 1880, few, if any, concise practical works ever appeared; there was nothing comparable to the "Kew Series" or the range of regional manuals in North America. Indeed, the influence of the Berlin school under Engler led to a very widespread emphasis on synthetic work, and less attention was paid to floras in the late 19th and early 20th centuries, at least in Europe (Davis & Heywood, *l.c.*, p. 33.) One example of a German colonial flora is Schumann and Lauterbach's *Die Flora der deutschen Schutzgebiete in der Südsee* (1900-05) for German New Guinea, Micronesia, and Samoa. This is essentially an enumeration, containing a useful repository of geographical and other data but lacking in methodical organization and largely innocent of keys. It is all but useless for identification and cannot be compared with a work such as Merrill's *Flora of Manila* (1912). Perhaps, indeed, the Central European predilection for detail was of such a nature as to have precluded (or retarded) the development of a practical philosophy towards floras, at least outside Central Europe and its many "excursion-floras." Writing in 1874 of German botany, Bentham remarked, "The country abounds in those plodding minds which revel in the working out of minutiae of detail, and, to find their way, are satisfied with a sexual, alphabetical, or any other artificial index . . ." A similar lack of method also marred much of von Mueller's writings on the Australian and New Guinean floras, and the same could be said of some Dutch works on the East Indies. In France, no characteristic "school" developed apart from the influences of Lamarck and the de Candolles and, indeed, few important floras appeared under French auspices in the mid- and late 19th century. The suppression of any chair at the Sorbonne or the Paris Museum specifically responsible for systematics and classification between 1853-73 and the associated loss of the Delessert Herbarium to Geneva in 1869 were serious setbacks (Leandri, 1967) and present French activity in the writing of floras is largely a development of the 20th century and one showing few original features.

The final key development in floristic writing to be considered here was the annotated enumeration or checklist. These began to appear from the late 19th century onwards as an outgrowth of the "synopsis" or "systema vegetabilium", and are essentially catalogues. Generally they were viewed as an interim measure, so that something of the results of floristic research could be made available to the

public in a concise, easily prepared form, or as works in which much descriptive detail was considered unnecessary, such as local or insular florulas. While the majority of such works cover relatively small areas, there have also been produced a goodly number of extensive annotated enumerations for large, often botanically poorly known areas, especially in the tropics. Notable examples of large enumerations include *Enumeration of Philippine flowering plants* (Merrill, 1923-26); *Conspectus florae angolensis* (Carrisso et al., 1937+ ); *Enumeratio spermatophytarum aethopicum* (Cufodontis, 1953-72); and *Catalogus florae domingensis* (Moscoso, 1943). Many of the authors/editors lacked the means and/or time to prepare full descriptive works but believed some kind of consolidated publication, even if imperfect, was necessary. While they have been criticized by some writers, such works should be regarded as better than no consolidated work at all, and in many cases have fared, or may fare, better than semi-monographic floras.

The preferred contents of floristic works have been well summarized for our time by Blake and Atwood (1942, p. 8-9) and Davis and Heywood (*l.c.*) and need not be reiterated here. The question of content has also been considered by van Steenis (1954) and Brenan (1963). The most important additions and refinements to the standardized formats of Flora-writing have been in the areas of nomenclature, ecology, chorology and distribution, mapping, karyology, critical commentary, and illustration. The findings of palynology and comparative phytochemistry have left their imprint largely above the species level. In general, it may perhaps be said that standards with regard to content have gradually improved in the years since World War II.

On the other hand, the present century has by and large witnessed a concomitant — and perhaps inevitable — increase in the bulk (and cost!) of Floras and, often, a decrease in utility. There has perhaps also been a tendency in many cases not to think out clearly the aims and purpose of a given floristic project. Such trends have been deplored by van Steenis (*l.c.*) who believed that “recent Floras often differ considerably from Bentham’s scheme”. Davis and Heywood (*l.c.*) further note that there are a number of works called “Flora” which contain keys but no descriptions, as well as some with descriptions but no keys; instances of such works still may be found amongst even very recent floristic literature. Some floras contain an exceptional amount of non-phytographic matter and must be viewed more as encyclopaedias than as practical manuals. In this connexion, it is interesting to note that very few writers after 1880 (and until recent years) appear to have seriously reconsidered the philosophy and methodology of floras, despite their great importance as a means of phytographic communication (van Steenis, *l.c.*; Heywood, 1973). Perhaps, as van Steenis notes, the older writers (especially Bentham) “had at the time exhausted the subject in such an admirable way that nobody found occasion to discuss it any further.” He noted that Diels in his *Methoden der Phytographie* of 1923 did not give special attention to this question — a curious omission in view of the large contributions to floristic literature by German and Central European botanists but perhaps explicable in view of the relative lack of concern with method and conciseness in so many of these works.

Since World War I, and even more so since the last war, there has been a distinct tendency towards the creation of large-scale, multi-author flora series for many countries or regions where knowledge of the plant life is imperfect in one way or another, particularly in the tropics. In addition, with an increasing amount of material to be covered as well as increasing specialization, more and more of the larger floras have been issued in serial parts, without regard to systematic order. Some of these become partial substitutes for serious monographs, for which there seem today to be few satisfactory publication outlets and which in some quarters appear to have a low academic “status” (cf. Jacobs, 1969). In many botanical circles today, it seems that large-scale floristic projects have become

"fashionable", the rise and fall of the Flora North America Program notwithstanding, and the resulting floras have a certain "prestige" value. A number of these have been set up for smaller, mostly politically delimited units (mainly within the tropics), despite the advice of van Steenis who believed that large-scale "creative" floras should be written with reference to large, natural botanical regions such as Malesia. Most larger botanical institutes in North America, Europe, and (to a lesser extent) elsewhere presently have one or more of these projects under way. Some of these works are meaningful, and as they progress represent real contributions to knowledge, although perhaps in some cases progressing too slowly; examples include *Flora Malesiana*, *Flora Iranica*, *Flora Neotropica*, *Flora SSSR*, and some of the African floras. Others are too detailed or otherwise long-winded, too grandiose, cover unnecessarily small areas, or have an insecure basis. The length of time taken, or likely to be taken, to complete many of these works is quite considerable; this in itself raises questions about financing as well as individual and institutional motivation (de Wolf, 1963, 1964). The time-span of *Flora brasiliensis* has already been mentioned; other examples are the *Flora of Peru* (40 years, still incomplete and interest fading); *Flora capensis* (74 years, with a 31-year break from 1865 to 1896); *Flora of Tropical East Africa* (23 years and quite some way from completion); *Flora Polska* (56 years, although all but complete); *Flora SSSR* (30 years); and *Flora Malesiana* (27 years, only some 30-40% completed, and some families unlikely to be published). For these and other reasons, De Wolf has questioned the wisdom of many large-scale projects, suggesting instead that more attention be paid to the preparation of "concise" works (although the objection would be raised that for many little-known regions, a substantial amount of basic monographic and revisionary work is required in connection with a flora project and this must be expressed in some way in the published flora, because there may be no alternative). Fortunately, some over-elaborate works have been discontinued; a notable example is *Genera et species plantarum argentinorum* (1943-56). I consider, however, that the whole question of large-scale floras should be looked at more closely, with a view to making further cuts and consolidations and storing a considerable percentage of data outside the print medium (or at least outside the realm of the standard flora).

#### FLORAS AT THE PRESENT TIME

At the beginning of this paper, I noted that in recent years there has been an information explosion in systematics, from which Floras have not been spared. The impact of this, together with the introduction of EDP-IR methods, has led to considerable recent discussion of the content and style of floras and the philosophy and methodology of flora-writing — the first substantial debate for some 100 years in this area, with only very few key contributions in the intervening period. As this is very much a current issue, which Heywood (1973) believes to be of "crisis" proportions, it seems useful to consider the progress and problems of Flora-writing at the present time and to make some suggestions about the future, with particular reference to infra-tropical regions.

The continued acceptance — perhaps uncritically — of long-standing and stereotyped formats and sets of questions for floras and related works by generations of botanists is not only evidence of their general utility but also a reflection of the conservatism inherent in much of the taxonomic profession; in other words, tradition has perhaps been as strong a force as any intrinsic merit in these parameters. Taylor (1971) states that these are some 200 years old but as I have shown in this paper the design principles and content of most present-day descriptive works are largely based on principles laid down between 1830 and 1860 (with manual keys and enumerations (or catalogues), as well as ligneous Floras, evolving later to meet particular needs or to cope with difficult situations like the inventorying and classification of Floras of humid tropical regions).

An examination of the relevant literature cited at the beginning of this paper as well as personal observations suggest that at present there are essentially two views, both of long standing and to some extent at odds, concerning the central purpose of descriptive floras. This, in some way, parallels van Steenis's view that most floras are "dualistic" in nature, i.e. they attempt to serve two different ends, the one archival or encyclopaedic, the other for identification (van Steenis, 1962). He argued that this problem could be resolved in north temperate regions, but not in the tropics. A similar theme has been central to the current ongoing discussion.

The first philosophy — one which sees Floras as tools for identification — harks right back to the first aphorism of Bentham quoted early in this paper. The relative value of this philosophy has again been emphasized by Heywood (1973) as well as indirectly by Watson (1971). Heywood suggests that Floras should address themselves to the following questions about the plants of an area:

- (a) what there is,
- (b) how they may be recognized, and
- (c) where they may be found

and that this involves keys, descriptions, auxiliary data, and necessary nomenclatural apparatus. It is argued that Floras were not necessarily intended to serve as sources of strictly comparative data. This philosophy is in general also adhered to by Brenan (1963) in his review of the rôle of Floras in developing countries.

The second philosophy — in which floras are seen as essentially archival or encyclopaedic — has its roots in the *Flora brasiliensis* tradition, is exemplified in many large-scale flora projects today, and considers that floras should be "a physical repository of descriptive data about plants which are organized and formatted, usually in book form, so as to answer to time-tested set of prescribed questions . . ." (Shetler, 1971).

The differences between these two philosophies as related to developments in the 19th century have already been discussed, with several examples. In our own day, the first philosophy is well exemplified by *Flora Europaea*, which will ultimately deal with some 15,000 species in five quarto volumes. Other examples of recent floras where an attempt has been made at conciseness are *Flora iranica*, *Flora of Turkey*, *Flowering plants of Jamaica*, *Prodromus einer Flora von Südwestafrika*, and *Flora of West Tropical Africa* (2nd ed.) as well as many smaller descriptive floras and manuals.

In this connexion, it may be noted that the longest time that will have been taken for these projects is about 25 years (*Flora Europaea*), something hardly ever achieved by most of present-day large-scale flora projects, which in most cases will take anywhere from 20 to 40 or more years to complete (cf. De Wolf, 1963). In addition, the creation of large-scale works, involving lengthy research and preparation and sometimes interinstitutional cooperation, involves a considerably greater investment of time and manpower (averaging 50 species per year per taxonomist) as opposed to the production of "concise" works (averaging 250 species per year per taxonomist) (De Wolf, 1964).

Sometimes the two philosophies are confused. In the "Introductory Notes" to the Flora of Papua New Guinea Concise Handbook Project (of which nothing has yet been published) it is stated that, in order to make available "information" on the flora (which is presently very scattered apart from what is available in *Flora Malesiana*), the sponsoring institutions have "embarked on a project to produce, in a handbook format, a *concise* Flora . . ." By contrast, the one sample family treatment seen suggests that the work, even with some information previously relegated to "technical supporting papers", will be somewhat encyclopaedic in nature; four pages of text are required to deal with three species. This is hardly "concise" in the sense of the Benthamian tradition or the *Flora of Turkey*

but more like the *Flora of Guatemala* or even *Flora Malesiana* — both essentially large-scale works in the von Martian tradition. In our days, relatively few concise floras for tropical regions have been successfully completed and published, and some are still marred by awkward formats; apart from the *Flora of West Tropical Africa*, mention can be made of *Flora of Java* (1963-68), *Flowering plants of Jamaica*, and *Tree flora of Malaya* (1972+), still in progress but with good prospects for early completion). All of these are (or will become) widely-used standard works and will be of more real value than many grander but unfinished floras.

Fisher (1968) has called attention to the proliferation of data which faces systematic botanists today. This has had an effect on large-scale independent monographic work, particularly in large families (Jacobs, 1969), and it has become more convenient in many cases to do this work through the medium of large-scale regional or national Floras, there being fewer independent outlets or special monographic series than was the case in past decades. Fisher has also drawn attention to weaknesses in verbal descriptions, stressing the importance of illustrations; this has special relevance to the humid tropics where there are so many different kinds of plants to be considered and where the perception of most people is much more visually than literarily oriented. This point has been clearly recognized by the author of such Asian works as *Cay-co mien-nam Viêt-Nam* (Pham, 1970-72), *Iconographia cormophytorum sinicarum* (Anonymous 1972+), and *Choson singmul myongchip* (Chông, 1956-57). These are all atlas-floras comprising small figures and parallel text, with analytical keys playing a supporting rôle; although they are modelled on "Western" atlas-floras, I believe that something of the Asian (and particularly Chinese) botanical tradition has also played a rôle in their creation. Some of them are also relatively "concise" as Floras, here owing something to the traditions of Bentham and his contemporaries.

Watson (1971) has called for just a return to the Benthamian tradition of "concise" Floras, and makes the significant suggestion that the kind of information which now tends to go into elaborate "archival" Floras is more appropriate to other kinds of taxonomic publication or for storage and retrieval through data banks or other non-print media. Believing that the two philosophies of Flora-writing — the information/archival and the practical — should be separated and that a given work should follow one or the other, Watson considers that many Floras are confused in this respect and in the end represent unhappy compromises, failing in both areas; they are neither useful sources of comparative data nor practical tools for identification (and still expensive!), and have not conceded that under present conditions these functions must be virtually separated. He concludes by stating that "we have all these advantages [computerization, philosophical analysis, masses of data, etc.], yet have more difficulty in getting to grips with real problems than Bentham did."

A step in the direction suggested by Watson was taken by the development after 1968 of the FNA Program (Shetler, 1971; Shetler et al., 1973). This was to be a relatively sophisticated information storage-and-retrieval system which would be linked with a concise conventional flora in some 5-6 volumes in the manner of *Flora Europaea*; the production of a hard-copy flora was viewed in part as a recognition of the strength of convention and tradition in Flora-writing. However, the project was killed in 1973 as a result of administrative pressures on science and internal and external politics; it later became evident that the new methodology threatened to become the master rather than the servant of the operation (Shetler, 1974) and at this writing it is a moot point whether EDP-IR will become a really effective tool in Flora-writing in the way hoped for by its advocates. Some smaller projects are, however, under way, e.g. for Vera Cruz, Mexico (Gómez-Pompa & Butanda 1973; Gómez-Pompa & Nevling 1973) and in South Africa (Hall, 1974) and it is these upon which attention will be focused in the years to come. Related schemes involve the complete encoding of essential data from the specimens in

the Queensland Herbarium at Brisbane and the South African National Herbarium at Pretoria; from these it may eventually be possible to produce *inter alia* preliminary floristic catalogues for these areas.

#### FUTURE DEVELOPMENT

The above references to the introduction of EDP-IR methodology — claimed to be the most important change to the philosophies of Flora-writing for a century — lead naturally to the final question: what of Floras in the future? The impact of new methodologies could eventually bring about the revolution hoped for by their advocates, but firstly some key philosophical (and practical) questions must be resolved.

Floras today, as Watson has noted, are often confused in their philosophy and are deficient in many ways as a result. Most of them, unless they are really elaborate, large-scale works with a consistent format and standard of information content, are of little use for comparative data because of the pull of traditional essentialist conventions in the writing process; most authors still see identification as a principal aim (supplemented by limited information of relatively general interest such as habitat, distribution, life-form, phenology and karyotypes) but in many cases are obliged, or feel obliged, to include more comprehensive information, resulting in a confusion of objectives. Keys are often highly selective, too, and in floras where the manual-key format prevails (such as *Flora of Java*) it becomes very difficult to extract useful comparative data.

What, then, might be the best way to resolve the apparent impasse? Firstly, there should be much more effort given in planning new projects to the *philosophy and objectives* of the proposed work as well as to the *means, manpower, and motivation* available (especially for larger works which may take, even in a concise form, many years to complete). Secondly, more concern should be given to the standardization of data accumulation and organization and the avoidance of the losses that occur when work is published. In this, connexion, much depends upon continuing improvements in EDP-IR methodology, further introduction of data-processing in herbaria and in individual research, and an improved political understanding of the value of such methods in systematic publication (and their limitations!).

Personally, I believe that the best rôle for a Flora as such today remains the practical one: inventory, identification and essential related data. To the "essential data" of Bentham's time there should now be added that from ecology and karyology (cf. van Steenis, 1954) as well as plenty of illustrations. In addition, there should be a clear indication of where taxonomic or biosystematic problems occur as has been so well handled in *Flora of New Zealand* by Allan *et al.* (1961, 1971). If lesser-known areas are involved (as is the case with most of the humid tropics), it may be desirable to expand supporting data and commentary (including citations) somewhat, as is being done with the *Flora of Turkey* (which, in my opinion, is one of the best of current larger floras dealing with lesser-known areas and one very kindred in spirit to the famous "Kew Series" of the 19th century). In addition, concise floras should always have references to standard monographs, revisions, floras and other contributions under each family and genus heading.

By contrast, large-scale floras should be viewed as having an entirely separate function; they should not be undertaken except for large natural regions such as Malesia or for very large political entities such as the U.S.S.R. They should perhaps even be run as open-ended serials rather than as "closed" works, as was done with *North American Flora* some years ago and is being done with *Flora Neotropica*. Furthermore, much of the archival function of such works, with their

often elaborate synonymy, could be assumed by non-print media and EDP-IR systems (as was envisioned by the FNA Program), doing away with the need for storing much relatively specialized data in increasingly costly print media; instead, such information could be generated in microcard or microfiche form (readers are now becoming relatively inexpensive and widespread) or as processed output. Detailed information in this form could then be used for the preparation and publication in print media of conventional "concise" floras (as well as for the production of major systematic treatments).

For some little-known areas where time or local conditions may not permit the preparation of more extensive works, I believe it desirable to continue to produce annotated enumerations or checklists. These should preferably be in the manner of Merrill's *Enumeration of Philippine Flowering Plants*, though if keys can be added, so much the better. Such a format would have perhaps been the best method at the present time for a complete listing of the Papuan flora. An excellent example of what can be done in a relatively short time for a comparatively little-known areas with limited manpower is *Prodromus einer Flora von Südwestafrika* (Merxmüller et al., 1966-72), previously referred to. There is no room, however, for improperly annotated or unannotated checklists.

In many tropical regions (and developing countries generally) careful consideration should be given to making the results of systematic botanical work readily available to the public — in other words, to the concomitant preparation of works which will have a wide impact and can be seen to be useful. Atlas-Floras such as those already noted, where most or all species are illustrated, may have a greater audience than more conventional works. Keys should be simple and practical; descriptions should be concise, clear, and provide the essentials (easier if illustrations are used consistently). In these areas, it will only be a small number of persons who would prefer a detailed treatment, and this could be provided from other sources. Where the total flora is very large (and comprehensive works often correspondingly costly, especially in local terms), there is also scope for a number of works of more limited scope. Thus continuing attention should be given to forest floras and tree books (which often have considerable public appeal) as well as works on grasses, weeds, etc. One humid tropical country, Malaysia Barat (Malaya), is particularly well supplied with such partial works. For teaching purposes, it may often suffice to have a compact, illustrated school-manual covering a range of more easily accessible species (van Steenis, 1962). One of the finest of tropical manuals ever published remains E.J.H. Corner's *Wayside trees of Malaya* (2nd ed., 1952); this is considered a favourite by my students in New Guinea because of its interesting text, many illustrations, and clear keys. This should be revised and updated, and more of its kind (there being lamentably few in the tropics) should be written. In New Guinea, because the "official" botanists have been interested more in specialized, mostly technical floristic works than in books aimed at local people, the University Herbarium at Port Moresby has commenced work on a series of illustrated teaching booklets on the local flora, each dealing with a given habitat or life-form.

There will certainly be instances where it is necessary or desirable to make encyclopaedic information readily available on a given group (or groups) of plants. In these cases, this is better done outside the realm of floras, i.e. as separate publications or in serials. The best systematic encyclopaedia ever produced was *Die natürlichen Pflanzenfamilien*, and it would be highly desirable if the means and manpower could be found to complete the second edition of this work or undertake a new version in English. However, it should avoid becoming too bogged down in detail, a fault shown by the second edition here and there. Much of such detail could better be handled by non-taxonomic publications (Heywood, 1973) such as *Biology and Chemistry of the Umbelliferae*.

## References

- ANON. 1974. Trends, priorities, and needs in systematic and evolutionary biology. *Syst. Zool.* **23**: 416-439 (also in *Brittonia* **26**: 421-444).
- BENTHAM, G. 1861. Outlines of Botany. In his *Flora hong-kongensis*, pp. i-xxxvi. Reeve & Co., London.
- 1874. On the recent progress and present state of knowledge of systematic botany. *Rept Brit. Assoc. Adv. Sci. 1847*: 27-54.
- BLAKE, S. T. & A. C. ATWOOD. 1942 *Geographical guide to the floras of the world*, I. 336 pp. (U.S.D.A. Misc. Publ. 401.) Washington.
- BRENAN, J. P. M. 1963. The value of floras to underdeveloped countries. *Impact* (Paris).
- DE CANDOLLE, A. 1880. *La Phytographie*. Masson, Paris.
- DAVIS, P. H. & V. H. HEYWOOD. 1963. *Principles of angiosperm taxonomy*. Oliver & Boyd, Edinburgh & London.
- De WOLF, G. P., Jr. 1963. On the Flora Neotropica. *Taxon* **12**: 251-253.
- 1964. On the sizes of floras. *Ibid.*, **13**: 149-153.
- FISHER, F. J. F. 1968. The role of geographical and ecological studies in taxonomy, In Heywood, V. H. (ed.). *Modern methods in plant taxonomy*, pp. 241-259. Academic Press, London & New York.
- GÓMEZ-POMPA, A., and C. A. BUTANDA (eds.) 1973. *El uso de computadoras en la Flora de Vera Cruz*. Instituto de Biología, Dept. de Botánica, U.N.A.M., Mexico City.
- GÓMEZ-POMPA, A., and L. I. NEVLING. 1973. The use of electronic data-processing methods in the *Flora of Veracruz* program. *Contr. Gray Herb.* **203**: 49-64.
- HALL, A. V. 1974. Museum specimen record data storage and retrieval. *Taxon* **23**: 23-28.
- HEYWOOD, V. H. 1973. Ecological data in practical taxonomy. In his *Taxonomy and ecology*, pp. 329-347. Academic Press, London & New York.
- JACOBS, M. 1969. Large families — not alone! *Taxon* **18**: 253-262.
- LEANDRI, J. 1967. La fin de la dynastie des Jussieu et l'éclipse d'une chaire au Muséum (1853 à 1873). *Adansonia, n.s.* **7**: 443-450.
- SHETLER, S. G. 1971. Flora North America as an information system. *BioScience* **21**: 524, 529-532.
- 1974. Demythologizing biological data banking. *Taxon* **23**: 71-100.
- SHETLER, S. G. et al. 1973. *A guide for contributors to Flora North America (FNA)*. Provisional ed. 28 pp., appendices (*Flora North America Rpt.* 65) Washington.
- STAFLEU, F. A. 1971. *Linnaeus and the Linnaeans*. (Regnum Veg. 79.) Utrecht: I.A.P.T.
- Van STEENIS, C. G. G. J. 1954. General principles in the design of Floras. In *Huitième Congrès International de Botanique, Paris, Rapp. et Comm.*, sects. 2,4,5,6, pp. 59-66. Paris.

- 1962. The school flora as a medium for instruction in the tropics. *proc. Ninth Pacific Sci. Congr.*, **4** (Botany): 139–140.
- TAYLOR, R. A. 1971. The *Flora North America* Project. *BioScience* **21**: 521–523.
- VOSS, E. G. 1952. The history of keys and phylogenetic trees in systematic biology. *J. Sci. Labs. Denison Univ.* **43**: 1–25 (quoted from Radford, A.E., et al. 1974. *Vascular plant systematics*, p. 523. Harper & Row, New York).
- WATSON, L. 1971. Basic taxonomic data: the need for organisation over presentation and accumulation. *Taxon* **20**: 131–136.

# This World We Live in Will Be Only as Beautiful as You and I Make It

by

EDWIN A. MENNINGER

P.O. Box 107, Stuart, Florida 33494, U.S.A.

The beauty of the landscape might be defined as a visual loveliness that excites and exhilarates the senses pleurably or exalts the mind or spirit. It is not necessarily confined to colour, though often augmented or brought out by contrasts of light and dark, or emphasized by colourful patterning, or affected by lighting displays. The contour of a mountain may be beautiful, or the depth of a yawning chasm may awaken a deep and almost overwhelming awe of the magnificence spread before the eye.

But the landscape of man-created communities throughout the world is too often lost in a maze of lawns and trees with their predominating blanket of green. This uninterrupted sameness is worsened in the warm areas of the earth where spring flowers are just a memory and autumn leaf colouring is unknown.

In Florida where I live and in similar warm areas throughout the world, the beauty of our landscape depends solely on how and where brilliant colours are utilized to brighten, decorate or emphasize the eye's acceptance of surroundings that are perpetually green. Untold numbers of lakes, waterways, sounds, estuaries, and nearly a thousand miles of ocean beaches create unexcelled natural beauty of their kind, especially when accentuated with light and shadow with the help of sun and moon, and can even achieve a wild sort of beauty with the aid of tempestuous winds. Sunrise and sunset provide the only colour overtones in these natural surroundings, usually fleeting, often magnificent. But, by and large, the natural landscape in Florida is an eternal, unending, unchanging vastness of green with nothing but daylight to bring its values to the eye. For without the eye, how can there be any physical beauty? There is a spiritual beauty known to all of us, but that develops in a world apart from material things and knows neither sunlight nor shadow. The physical landscape requires colour to achieve the ultimate in beauty.

Ponce de Leon must have been dreaming when he christened his discovery Florida — the land of flowers. There were no flowers, nothing but a vast expanse of green. It is easy to understand why people reaching California are overwhelmed by "the splendor of poppy fields ablaze in the sun of May." The gorgeous blue-bonnets of Texas are an eye-filling sight at their peak. And even in midsummer on the Kansas plains, the sight of the sunflowers, "tawny and gold and brown," is more magnificent than many other wild flower colonies. But in Florida, Ponce de Leon found no such display because there was none.

In the south end of the State, where Ponce de Leon never arrived, there are two native trees with beautiful flowers — the Geiger tree (*Cordia sebestena* L.) with quantities of burnt-orange blossoms among the evergreen leaves, blooming off and on several times a year; and the Lignum Vitae (*Guaiaecum officinale* L.) with the richest sky-blue starlike flowers all up and down the branches, a breath-taking

sight. The Geiger tree is sparingly cultivated half way up the state, but the Lignum Vitae is too slow growing to be useful as an ornamental and is almost never seen out of its native tropics.

Along the north line of Florida, by the Georgia-Alabama border, two beautiful native flowering trees add sparkle to the landscape — the Southern Magnolia (*Magnolia grandiflora* L.) and the Fever tree or Maiden's Blushes (*Pinckneya pubens* Michx) with its gorgeous Rhododendron-like flowers, but Ponce de Leon did not see these either. He saw green trees and lots of them.

Many books are available today with literally thousands of colour photographs of the gorgeous flowers to be found in all parts of the world, and available to each one of us for our personal experience and enjoyment, if we only make the effort.

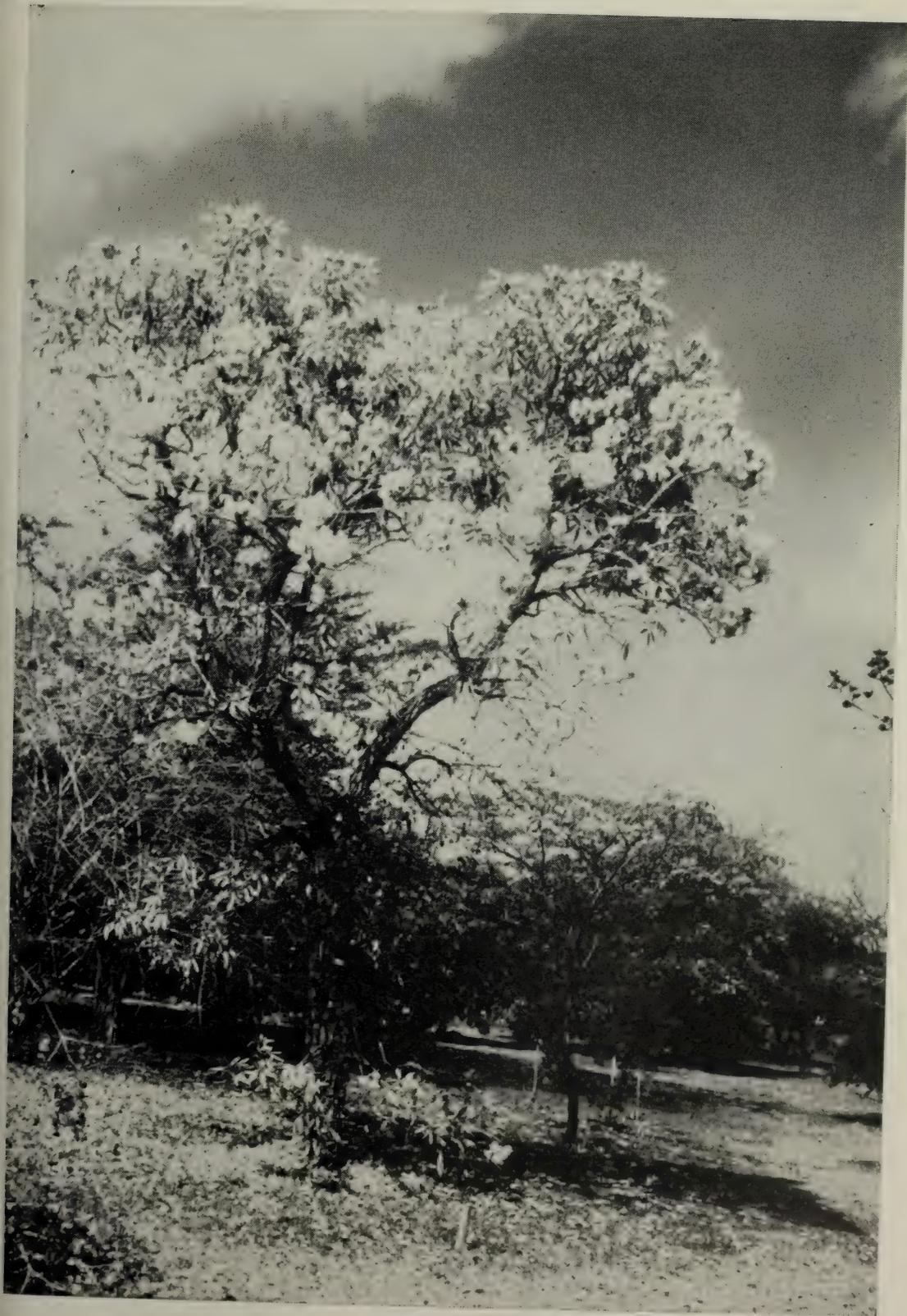
B. Y. Morrison, genius of the world of azaleas, long head of the U.S.D.A. Bureau of Plant Introduction, and kingpin of the American Horticultural Society for many years with both his pen and his purse, wrote the foreword in this author's book on *Flowering Trees of the World* in which 425 colour plates depict some of the most beautiful. Morrison was a dreamer too and he dreamed big. He wrote in part:

"It is true, perhaps, that many of the trees shown will be of no value to many a reader as plants for his garden, and that some may never even find a single place in these United States where they may repeat the miracle of their flowering. Does that matter too much? No, a thousand times no, for a mere examination of the pictures alone will open one's eyes to beauty and urge on one's zeal toward new efforts to know and experience, within the possible realm of one's own garden life, things he had never dreamed of.

"In this day and age, dare one dream? A thousand times yes, for without a dream there is no vision, and without vision, the people perish."

Hawaii is the classic example of how beauty on the landscape is born in the hearts of the people who live there. Like Florida, Hawaii has no native flowering trees that are outstandingly beautiful in blossom, except *Clermontia* and a few *Hibiscus*, and these are seldom seen. Yet the world has come to think of Hawaii as the ultimate in floral beauty. Why? Because the beauty which lies in the hearts of the Hawaiian people has found expression by the planting of millions of beautiful flowering trees which, in a fertile volcanic soil, pour out their spectacular flowers in eye-filling displays. The trees that bear them are from other warm countries, not from Hawaii. The gorgeous shower trees (*Cassia* sp.) are native to India. The magnificent *Plumeria* trees (which Floridians insist on calling "Frangipani") are natives of Mexico. One Hawaiian garden has 72 kinds of *Plumeria* trees; can you imagine such a spectacle? Some of these have blossoms 6 inches across! Flowers of *Plumeria* are particularly useful in making leis because they do not wilt when picked. The Hawaiian people hang bouquets around the necks of visitors and natives, mix moonlight and the music of steel guitars and chorus voices, to convince the guests that here is a flower heaven. We have the same moonlight in Florida; all we need is more beauty in our hearts.

Yes, no doubt about it, Ponce de Leon was dreaming. Four hundred years before our time he caught a glimpse of the magnificent spectacle that Florida would become when flowers of every size and hue from every warm country on earth would come here to make their home and add their beauty and colour to an indescribably lovely landscape. He saw the beauty that man could and would





create, and it is this vision of long ago that is gradually taking place on the Florida peninsula. Flowering trees by the millions, flowering shrubs undreamed of except by Ponce de Leon, flowering vines and untold numbers of groundlings with bright blossoms — all these are the details of a landscape that you and I are striving to create.

What matters the location? Be it Florida or England or New Zealand or Kenya, the beauty of the landscape is born of the beauty in our hearts and the surroundings of each one of us will be, can be, must be magnificent. Each one of us should ask ourselves: "What am I doing today to make my home, my city, my State more beautiful?"



## Index to Latin names

*Generic and specific names in roman type are synonyms; new names proposed in this book are in bold type.*

- Acacia*, 50, 120, 195  
*Acanthaceae*, 74-6, 110  
*Acanthococcus* sp., 59, 61  
*Acer*, 186  
*Actinidiaceae*, 186  
*Adenium*, 75  
*Adoxaceae*, 184  
*Aegilops*, 123  
*Aeonium*, 48  
*Aepocereus*, 212  
*Agathis borneensis*, 93  
    *dammara*, 92, 97 (& fig. 9)  
*Aglaia* sp., 177  
*Agaon*, 209, 211-2, 218, 227  
    *paradoxum*, 209-10  
*Agaonidae*, 207, 209, 211-3, 216 218, 222-7  
*Agaoninae*, 211-2, 218, 222, 227  
*Agaonini*, 211  
*Agaum*, 209  
*Agavaceae*, 179  
*Agavoideae*, 188  
*Agrianisa myrmecoides*, 210  
*Agropyron*, 123  
*Agrostistachys borneensis*, 176  
    *sessilifolia*, 176  
*Aizoaceae*, 187  
*Akania*, 187  
*Alfonsiella*, 211, 218, 223, 227  
*Allexis cauliflora*, 179  
*Allotriozoon*, 211, 218, 227  
*Alnus*, 110  
*Aloe capitata* var. *cipolinicola*, 48  
*Alsophila australis*, 179  
*Alstonia*, 22  
*Amaryllidaceae*, 123  
*Amborella*, 186  
*Amorphophallus*, 76  
*Anacardiaceae*, 68, 96, 131, 161, 163, 175  
    *Anacardium occidentale*, 163  
    *pumilum*, 61  
*Ancylanthus rubiginosus*, 69  
*Andira inermis*, 61  
*Andryala* spp., 50  
*Angiospermae*, 183 *et seq.*  
*Angylocalyx oligophyllus*, 177  
*Anisophyllea quangensis*, 69  
*Anisoptera*, 128-9, 132 *et seq.*  
*Anneslea*, 109  
*Annona stenophylla*, 68  
*Annonaceae*, 68, 90, 96, 132  
*Annonales*, 186  
*Annoniflorae*, 184  
*Annonineae*, 187  
*Aploastomata*, 211  
*Apocryta*, 209, 211-2, 215-fig. 2, 225, 228  
    *longitarsus*, 191, 225  
    *paradoxa*, 209-11  
    *perplexa*, 209-11  
    *westwoodi*, 225  
*Apocryptini*, 212, 224-fig. 8g-h, 225-6  
*Apocryptophagus*, 209  
    *explorator*, 210  
*Apocynaceae*, 68, 90, 96  
*Aporpium caryae*, 151  
    *dimidiatum*, 151 *et seq.*  
    **hexagonoides**, 151 *et seq.*  
*Arachnoidea*, 68  
*Araliaceae*, 68  
*Araucaria*, 20, 110  
*Arbutus andrachne*, 17  
*Areciflorae*, 187  
*Argostemma*, 74, 79  
*Arisaema*, 75  
    *anomalum*, 75  
    *filiforme*, 76  
    *fimbriatum*, 75  
    *umbrinum*, 76  
*Armoracia*, 123  
*Arthropodium*, 20  
*Arthropoda*, 112  
*Artocarpus*, 4, 35  
    ser. *Angusticarpus*, 37  
    *anisophylla*, 37  
    sect. *Artocarpus*, 37  
    subg. *Artocarpus*, 35-6 (& fig. 1a-e)  
    ser. *Cauliflori*, 37  
    sect. *Duricarpus*, 37  
    *elasticus*, 36 (& fig. 1f), 37-8  
    *fulvicortex*, 36 (& fig. 1h-i), 37  
    *heterophyllus*, 16, 35, 37-8  
    *hispidus*, 36 (& fig. 1a-d)

- ser. *Incisfolii*, 37  
*integer*, 35, 37-8  
   var. *silvestris*, 37  
*kemando*, 37  
*lanceifolius*, 37  
*multifidus*, 37  
*peltatus*, 36 — fig. 1f-g  
   subg. *Pseudojaca*, 35-8 (& fig. 1f-i)  
*rigidus*, 37  
 ser. *Rugosi*, 36-7  
*sericicarpus*, 37  
 spp., 29  
*styracifolius*, 37  
*tamaran*, 37  
*teysmannii*, 37  
*Arundo donax*, 17  
*Aspidium flaccidum*, 147  
*Aster*, 49  
   *multiflorus*, 49  
   *novae-angliae*, 49  
 Asteraceae, 187 (see also Compositae)  
 Asteridae, 173  
*Astragalus*, 128  
*Austrobaileya*, 186  
*Avicennia marina*, 16  
*Baikiaea*, 67  
   *plurijuga*, 67  
*Balanitoideae*, 187  
*Balanocarpus*, 128  
 Balanopaceae, 175  
*Balanophora*, 106  
*Balanops pancheri*, 175  
*Bambusa arundinacea*, 17  
 Barbeyaceae, 187  
*Barringtonia*, 111  
   *calyptrocalyx*, 177  
*Begonia*, 75-7, 79  
   *evansiana*, 167 (& fig. 7)  
 Begoniaceae, 165, 173  
*Bencomia*, 48  
 Bennettitales, 184  
 Berberidaceae, 175  
 Berberidales, 186  
*Bertonia*, 78  
*Bertiera simplicicaulis*, 178  
 Bignoniaceae, 176  
   *Bikkia macrophylla*, 178  
*Blackstonia perfoliata* 171 (& fig. 10A)  
*Blastophaga*, 209-12, 214, 215 fig. 1, 217-8,  
   227-8  
   *caricae*, 208  
   *ficus*, 208  
   *grossorum*, 207  
   *javana*, 220  
   *psenes*, 208-9, 213-4, 216-20 (& fig. 4), 225-6  
   *quadraticeps*, 214, 220-2  
   *sycomori*, 208  
   *vaidi*, 220  
 Blastophaginae, 212, 218, 222, 227  
*Boea lanata*, 176  
 Boletales, 155  
*Boletellus*, 155, 159  
*Boletus*, 4  
   *albipurpureus*, 159  
   *amarellus*, 159  
   *ananas*, 155  
   *catervatus*, 159  
   *chrysenteron*, 159  
   *cornalinus*, 155 et seq.  
   *parasiticus*, 159  
   *phoeniculus*, 159  
   subg. *Phylloporus*, 155 et seq.  
   'Piperati', 155, 159  
   *porphyrosporus*, 159  
   *pseudorubinellus*, 159  
   *puniceus*, 159  
   *roseolus*, 159  
   *rubinellus*, 159  
   *rubriporus*, 159  
   *rubriubifera*, 159  
   *satisfactus*, 159  
   *strobilaceus*, 155  
   *subtomentosus*, 159  
   *versicolor*, 159  
   subg. *Xerocomus*, 155 et seq.  
 Bombacaceae, 90, 96, 131  
*Bombax*, 22  
   *valetonii*, 29  
 Bonnetioideae, 187  
*Borassus aethiopum*, 179  
*Brachylaena*, 50-1  
   *neriifolia*, 51  
*Brachystegia russelliae*, 68  
*Brackenridgea arenaria*, 69  
*Brassica*, 123  
*Brighamia rockii*, 176  
 Bromeliinae, 187  
*Brucea antidysenterica*, 178  
 Bruineae, 187  
*Bupleurum*, 48  
*Burmannia longifolia*, 76  
   *sphagoides*, 76  
 Burmaniaceae, 76  
 Burseraceae, 90, 96  
 Butomaceae, 184  
*Byrsonima verbascifolia*, 61  
 Cactaceae, 48, 123, 187  
*Caesalpinia*, 111  
   *pulcherrima*, 14  
*Calamus* sp., 120  
*Callicarpa saccata*, 120  
*Caloncoba suffruticosa*, 68  
*Calophyllum*, 111  
 Calycanthaceae, 186  
*Calycenthus*, 186  
*Campanula*, 48, 165  
   *carpatica*, 165, pl. 1 opp. 172.  
   *medium*, 165  
   *rotundifolia*, 165, 166 fig. 1

- Campanulaceae, 42 et seq., 123, 165, 173  
   *Lobelioideae*, 45, 176  
 Campanulales, 173  
*Campsis*, 113  
*Campylospermum duparquetianum*, 177  
   *sacleuxii*, 177  
   *subcordatum*, 177  
   *zenkeri*, 177  
*Canavalia*, 111  
 Cannaceae, 187  
*Canthium*, 69  
 Caprifoliaceae, 186  
*Captaincookia margaretae*, 178  
*Cardioteris*, 186  
*Carica papaya*, 172 (& fig. 12), 176  
   sp., 176  
 Caricaceae, 165, 173, 176  
 Caricaceae, 187  
*Carlina*, 48  
*Caryocar brasiliense* subsp. *intermedium*, 61  
 Caryocaraceae, 90, 96, 187  
 Caryophyllidae, 173  
*Cassia*, 59  
   *floribunda*, 170 (& fig. 8A)  
*Cassytha*, 116  
*Casuarina*, 111  
 Casuarinaceae, 114, 187  
*Caulopteris* sp., 179  
 Caytoniales, 20, 184  
*Cecropia*, 120-1  
*Ceiba pentandra*, 29  
 Celastraceae, 68, 90, 96  
*Celosia cristata*, 117  
*Celsia*, 128  
 Centrolepidoceae, 187  
*Ceratonia, siliqua*, 196 (& fig. 4)  
*Ceratosolen*, 211, 214-5 (& Fig. 2), 218, 225,  
   227-8  
   *arabicus*, 191, 194, 201-2, 217 fig. 6, 220-3  
   *bakeri*, 228  
   *capensis*, 223  
   *coecus*, 210  
   *emarginatus*, 220, 228  
   *flabellatus*, 223  
   *fusciceps*, 220  
   *galili*, 223  
   *hewitti*, 220-1  
   *marshalli*, 228  
   *nanus*, 228  
   *notus*, 214, 220  
   *pygmaeus*, 228  
*Ceroxylon*, 48  
 Chalcididae, 209, 211-2  
 Chalcidoidea, 212, 216  
 Chalcis centrinus, 208  
   *explorator*, 209  
   *pseus*, 208  
*Chamaeclitandra henriquesiana*, 68  
 Chenopodiaceae, 187  
*Chimonanthus*, 186  
*Chironia linoides*, 171 (& fig. 10B)  
*Chisocheton*, 20  
   *macranthus*, 177  
   *medusae*, 177  
   *polyandrus*, 177  
   *princeps*, 177  
   *setosus*, 177  
*Chlamydocola chlamydantha*, 178  
 Chloranthaceae, 186  
*Chrysanthemum*, 48  
 Chrysobalanaceae, 68, 90, 187  
*Chrysophyllum soboliferum*, 61  
*Chytranthus longiracemosus*, 178  
   *mangenotii*, 178  
   *pilgerianus*, 178  
   *welwitschii*, 178  
*Circaea lutetiana*, 166 fig. 3A, 168  
*Cissus fragilis*, 75  
 Cistaceae, 165, 173  
*Citrus nobilis*, 196 (& fig. 4)  
   spp., 196  
*Clarkia*, 115  
*Clavaria*, 3  
*Clavija lancifolia*, 179  
   *longifolia*, 179  
*Cleidion lasiophyllum*, 176  
*Clerodendrum*, 111  
   *buchneri*, 69  
   *fistulosum*, 120  
   *lanceolatum*, 69  
   *milne-redheadii*, 69  
   *pusillum*, 69  
   *triplinerve*, 69  
 Cochlospermaceae, 68  
*Cochlospermum insigne*, 59, 61  
   *tinctorium*, 68  
*Cocos nucifera*, 179  
*Codiaeum variegatum*, 117  
*Coffea macrocarpa*, 178  
*Cola buntingii*, 178  
   *caricaefolia*, 178  
   *mahoundensis*, 178  
*Colea lantziana*, 176  
   *nana*, 176  
   sp., 176  
*Colubrina*, 111  
 Combretaceae, 68, 96  
*Combretum*, 61  
   *argyrotrichum*, 68  
   *brassiciforme*, 68  
   *harmsianum*, 68  
   *lineare*, 68  
   *paniculatum*, 61  
   *platypetalum*, 68  
   *relictum*, 68  
   *sericeum*, 61, 68  
   *viscosum*, 68

- Commelinineae, 187  
 Compositae, 42 et seq., 110, 123, 176  
     *Cichorieae*, 49  
 Connaraceae, 176, 187  
     *Jollydoroideae*, 187  
*Conyza vernonioides*, 50  
 Cordaitales, 184  
*Cordia*, 50, 111  
     *sebestana*, 251  
 Cornineae, 186  
*Cornus mas*, 16  
*Cosmianthemum*, 74  
*Cotylanthera*, 76  
*Cotylelobium*, 128-9, 132 et seq.  
 Courtella, 209  
*Crambe*, 48  
 'Crassocephalum', 46-7  
*Critogaster*, 223  
*Crossogaster*, 211-2  
     *triformis*, 223  
 Crossosomataceae, 188  
 Cruciferae, 123  
 Crypteroniaceae, 186  
*Cryptosepalum exfoliatum*, 68  
     *maraviense*, 68  
*Ctenolophon*, 110  
*Cucumis sativus*, 168  
 Cucurbitaceae, 96, 129, 168, 171  
*Cunonia macrophylla*, 176  
 Cunoniaceae, 176, 187  
*Cussonia corbusieri*, 68  
*Cyanea aspleniifolia*, 176  
     *carlsonii*, 175-6  
     *giffardii*, 176  
*Cyathea*, 48  
     *camerooniana*, 180  
 Cycadaceae, 110  
*Cycadeoidea jenneyana*, 180  
*Cycas*, 111  
     *circinnalis*, 21, 180  
     *revoluta*, 180  
 Cyclanthaceae, 187  
 Cynipidae, 212  
*Cynips caricae*, 207-8  
     *cycomori*, 207-8  
     *ficus*, 207-8  
     *psenes*, 207-8  
     *sycomori*, 207-8  
*Cynopterus brachyotis*, 29  
 Cyperaceae, 63  
*Cyperus*, 111  
*Cypraea moneta*, 200  
 Cyrillaceae, 188  
*Cyrtandra*, 74, 78-9  
     *mirabilis*, 74  
     *penduliflora*, 75  
     *radiciflora*, 74  
     *splendens*, 78  
*Dacrydium pectinatum*, 92-3  
 Daphniphyllineae, 186  
*Davidsonia*, 187  
*Decatoma*, 226  
     *fici*, 227  
*Degeneria*, 186  
*Deilagaon*, 211, 227  
*Deinbollia fanshawei*, 69  
     sp., 178  
*Delissea undulata*, 176  
*Delpydora gracilis*, 178  
     *macrophylla*, 178  
*Dendriopoterium*, 48  
*Dendrocacalia*, 51  
*Dendrocalamus strictus*, 17  
*Dendrocnide moroides*, 179  
*Desmodium*, 111  
*Diazella*, 226  
 Dichapetalaceae, 68  
*Dichapetalum bullockii*, 68  
     *cymosum*, 66, 68  
     *rhodesicum*, 68  
 Didiereaceae, 187  
*Didissandra*, 74  
 Didymelaceae, 187  
*Didymocarpus*, 74, 78-9  
     *gracilipes*, 75  
     *malayanus*, 75  
*Digitalis*, 48  
     *purpurea*, 77  
 Dilleniaceae, 68  
     *Dillenoioideae*, 186  
 Dilleniidae, 173  
 Dioncophyllaceae, 187  
*Diospyros batocana*, 66  
     *chamaethamnus*, 66, 68  
     *galpinii*, 68  
     *lycioides*, 68  
     *virgata*, 68  
 Dipsacales, 173  
 Dipterocarpaceae, 4, 127 et seq., 186  
     *Dipterocarpoideae*, 128  
     *Monotoideae*, 128, 187  
*Dipterocarpus*, 128-9, 131 et seq.  
*Distyliopsis*, 186  
*Dodonaea*, 111  
*Dolichoris*, 227  
*Doona*, 128-9, 132 et seq.  
*Dossinia marmorata*, 78  
*Dracontomelum mangiferum*, 20  
*Drosophila*, 130  
*Dryobalanops*, 128 9, 132 et seq.  
     *beccarii*, 91-3  
*Dryopteris flaccida*, 147

- Duabanga grandiflora*, 29  
*Durio*, 4, 25-6  
   *acutifolius*, 26  
   *beccarianus*, 26  
   *dulcis*, 26  
   *grandiflorus*, 26  
   *graveolens*, 26, 32  
   *griffithii*, 26  
   *kutejensis*, 26  
   *lowianus*, 32  
   *malaccensis*, 26, 32  
   *oxleyanus*, 26  
   *pinangianus*, 26, 32  
   *testudinarum*, 26  
   *wyatt-smithii*, 26  
   *ziberthinus*, 25 et seq.  
*Dynatogmus*, 223  
*Dypsip hildebrandtii*, 179  
*Dysoxylum urens*, 177  
Ebenaceae, 68  
Echeverioideae, 188  
Echinodermata, 112  
*Echium* spp., 48, 50  
*Ehretia*, 50  
Eisenia, 211  
*Ekebergia pumila*, 68  
*Elaeis guineensis*, 179  
Elaeocarpaceae, 21, 186  
*Elatostema*, 74  
*Elephantorrhiza elephantina*, 66, 68  
   *obliqua*, 66, 68  
   *woodii*, 68  
*Elisabethiella*, 211, 218, 223, 227  
*Elymus*, 123  
*Embolanthera*, 186  
*Encephalartos laurentinus*, 180  
*Endospermum*, 22  
   spp., 120  
*Entada dolichorrhachis*, 68  
   *nana*, 68  
*Eonycteris spelaea*, 25, 29  
*Eospermatopteris*, sp., 180  
Epacridaceae, 187  
Epichrysomallinae, 210, 212, 226, 227  
*Epilobium angustifolium*, 166 fig. 2B, 168  
*Episcia reptans*, 78  
*Epithema*, 77  
Ericaceae, 123, 165, 170, 173, 186  
Ericales, 173  
*Eriobotrya japonica*, 196 fig. 4  
Eriocaulineae, 187  
Eriogonoideae, 188  
*Eryngium* spp.,  
*Erysimum*, 48  
*Erythrina*, 111  
   *baumii*, 59, 68  
   *zeyheri*, 66, 68  
Escalloniodeae, 187  
*Espeletia* spp., 42, 50-1  
   *spicata*, 176  
*Eucalyptus*, 61  
*Euclea crispa*, 59, 60 fig. 1, 68  
*Eudecatoma*, 226  
Eudecatominae, 210 2, 12, 226  
*Eugenia angolensis*, 69  
   *capensis*, 69  
   *pusilla*, 66, 69  
*Eujacobsenia*, 226  
*Eukoebelea*, 224-5  
*Euphorbia*, 111  
   *ankarensis*, 176  
   *bupleurifolia*, 176  
   *lophogona*, 176  
   *moratii*, 176  
   spp., 48  
Euphorbiaceae, 90, 96, 176  
Euphorbiales, 187  
*Eupomatia*, 186  
*Eupristina*, 211, 218, 227  
*Eurycoma longifolia*, 178  
Eurytomidae, 210, 212  
Fagaceae, 132  
Fagales, 186  
*Ficus*, 4, 13, 46, 57, 122-3, 130, 186  
   sect. *Adenosperma*, 227-8  
   *alba*, 214  
   sect. *Americana*, 223, 225, 227  
   *ampelas*, 226  
   *auriculata*, 213, 220, 228  
   sect. *Auriculosperma*, 228  
   *benghalensis*, 13, 15, 209  
   *capensis*, 223  
   *carica*, 16, 196 fig. 4, 197, 199, 203, 207-9,  
     213-7 (& fig. 1), 219-20, 223  
   sect. *Conosycea*, 225-7  
   *costaricana*, 220, 222  
   *dammaropsis*, 228  
   sect. *Ficus*, 220, 227-8  
   subg. *Ficus*, 209, 220, 225-8  
   *fistulosa*, 214, 220-1  
   sect. *Galoglychia*, 226-7  
   *hemsleyana*, 220, 222  
   *hirta*, 213, 220  
   *hispidia*, 220  
   sect. *Kalosyce*, 227  
   sect. *Leucogyne*, 227  
   *macrophylla*, 214, 220  
   sect. *Malvanthera*, 223, 226-7  
   *mauritanica*, 209  
   *monahasae*, 228  
   sect. *Neomorphe*, 225, 227-8  
   *nota*, 214-220  
   *oligodon*, 228  
   sect. *Oreosyce*, 226-8  
   sect. *Papuasycea*, 228  
   sect. *Pharmacosyce*, 220, 225, 227  
   subg. *Pharmacosyce*, 227  
   subsect. *Pomifera*, 228  
   *pritchardii*, 228  
   *pseudopalma*, 228  
   ser. *Pseudopalmae*, 228

- pungens*, 228  
*pygmaea*, 69  
*racemosa*, 220, 228  
*religiosa*, 196 (& fig. 4), 220, 223  
 sect. *Rhizocladus*, 227  
 ser. *Rivulares*, 228  
*rivularis*, 228  
*roxburghii*, 213  
*rubiginosa*, 214  
*salicifolia*, 223  
 sect. *Sinosycidium*, 227  
 spp., 195, 214, 217-20, 222, 227  
 sect. *Stilpnophyllum*, 227  
 sect. *Sycidium*, 226-8  
 sect. *Sycocarpus*, 225-8  
*sycomorus*, 191 et seq., 207, 209, 211, 215  
 fig. 2, 220-1, 223-225  
 subg. *Sycomorus*, 209, 220, 223, 225-8  
*terragona*, 209  
*theophrastoides*, 177  
*tinctoria*, 226  
 var. *gibbosa*, 226  
*tseila*, 220  
*tuerckheimii*, 223  
 sect. *Urostigma*, 226  
 subg. *Urostigma*, 209, 220, 225-8  
*verruculosa*, 69  
*virens*, 220, 227
- Fimbristylis*, 111  
 Flacourtiaceae, 68, 96, 165, 171, 173, 176  
 Fouquieriaceae, 188  
*Freycinetia*, 137  
*Fuchsia fulgens*, 166 fig. 2A, 167  
*Gaertnera*, 109  
*Galbulimima*, 186  
*Ganosoma*, 224  
*Garcinia buchneri*, 68  
*Gardenia conferta*, 178  
*subacaulis*, 69  
*Garrya*, 186  
 Garryaceae, 188  
 Gentianaceae, 165, 171, 173  
*Gentianoideae*, 49  
 Gentianales, 173  
 Geraniales, 173, 187  
 Geraniaceae, 176  
*Geranium canariense*, 176  
*Gerrardanthus*, 75  
 Gesneriaceae, 76-8, 123, 176  
*Cyrtandroideae*, 186  
*Ginkgo*, 110  
*Goethea strictiflora*, 177  
*Gomphostemma*, 74  
*Goniogaster*, 211  
*Gonostylus*, 186  
 Goodeniaceae, 187  
*Gossypium*, 16, 114  
*arboreum*, 114  
*thurberi*, 114  
*Goupiia*, 187
- Gramineae, 123  
*Micrairoideae*, 187  
*Grasseiana*, 226  
*Grewia decemovulata*, 69  
*falcistipula*, 69  
*herbacea*, 69  
*Grias* sp., 177  
*Guaiacum officinale*, 251  
*Guarea richardiana*, 177  
*Guettarda*, 111  
 Guttiferae, 68, 90, 96  
 Gyrostemonaceae, 187  
*Haemodoreae*, 187  
*Hagiophyton* sp., 179  
 Haloragaceae, 187  
 Hamamelidales, 186  
 Hamamelidaceae, 173  
 Hammelidiflorae, 184  
*Hamamelidoideae*, 186  
 Haplostomata, 211, 212  
*Harmsioplanax*, 19-20  
*Harpephyllum caffrum*, 175  
*Hectorelloideae*, 184  
*Hedychium*, 75, 76  
*cylindricum*, 76  
*Hedysarum*, 44  
*Heeria nitida*, 68  
*Heliciopsis*, 20  
*Heliconioideae*, 187  
*Heridium coralloides*, 159  
*Hernandia*, 111  
*Herrania albiflora*, 178  
*Heterandrium*, 223  
*Heterocentron roseum*, 170 (& fig. 8B)  
 Hexacorallia, 112  
*Hibiscus*, 111  
*Hicksbeachia pinnatifolia*, 178  
 Hippuridaceae, 184  
*Hopea*, 128-9, 132 et seq.  
 Hoplestigmataceae, 187  
*Hordeum spontaneum*, 198  
 Houmiriaceae, 90, 96  
*Houmiriodeae*, 187  
*Hoya*, 120  
 Huacaceae, 187  
*Hugonia gossweileri*, 68  
*Hydnophytum*, 120  
 Hydnoraceae, 187  
 Hldrocaryaceae, 165, 173  
*Hypoxidoideae*, 187  
 Icacinaceae, 96  
*Ichneumon psenes*, 208  
*ficarius*, 208  
*Idarnella caricacae*, 208

- Idarnes*, 209, 211, 224-5  
*carne*, 209-10  
*orientalis*, 210  
*pteromaliodes*, 210  
*stabilis*, 210  
*transiens*, 210  
 Idarninae, 211-2  
*Idarnodes caricae*, 208  
*ficarius*, 208  
*Idarnomorpha*, 209  
*Idiospermum*, 186  
*Ilex*, 110  
 Illiciineae, 186  
*Impatiens duthieae*, 75  
*flanaganae*, 75  
*mirabilis*, 75  
*Ingonia digitata*, 178  
 Insecta, 112  
*Ipomoea*, 111  
 Iridaceae, 187  
*Geosiridoideae*, 187  
*Isanisa decatomoides*, 210  
*Ischaemum*, 111  
*Isoglossa*, 75  
 Ixonanthaceae, 68  
*Jacaranda decurrens*, 61  
*Jagera serrata*, 178  
*Jambosa acris*, 177  
*Jollydora duparquetiana*, 176  
 Juglandineae, 186  
*Julianella*, 211  
 Juncaceae, 187  
*Knema*, 21  
*Knightia*, 110  
*Korthalsia*, 120  
*Kradibia*, 211  
 Labiatae — *Prostantheroideae*, 187  
*Landolphia gossweileri*, 68  
*Lansea edulis*, 68  
*gossweileri*, 68  
*Katangensis*, 68  
*virgata*, 68  
*Lastrea dayi*, 148  
*flaccida*, 147  
*gracilescens* var. *decipiens*, 147  
 Lauraceae, 90, 96, 116, 132, 176  
*Laurus nobilis*, 16  
 Lecythidaceae, 68, 90, 96, 177  
*Lecythidoideae*, 187  
*Napoleonoideae*, 187  
*Planchonioideae*, 186  
 Leguminosae, 90, 96, 111, 131, 165, 170, 173  
*Caesalpinioideae*, 68, 187  
*Mimosoideae*, 68, 177, 187  
*Papilionoideae*, 68, 177  
*Leptactina benguelensis*, 69  
*Licania dealbata*, 61  
*Limonium*, 48  
 Linaceae, 68  
*Linariantha*, 74  
*Biporrhopalum*, 211, 218, 227-8  
*Lipothymus*, 226  
 Lissocarpaceae, 187  
*Litsea ripidion*, 176  
 Loasa, 168  
*vulcanica*, 167 (& fig. 4), pl. 2 opp. 172  
 Loasaceae, 165, 168, 173, 187  
*Lobelia*, 22, 41 et seq., 165  
*assurgens*, 50  
*bambuseti*, 45, 49  
*deckenii*, 45, 46  
 subsp. *keniensis*, 45  
*dortmanna*, 51  
*giberroa*, 45, 49  
 subsect. *Haynaldiana*, 45 et seq.  
*nicotianifolia*, 45, 47  
 subsect. *Nicotianifoliae*, 45 et seq.  
*nubigena*, 45  
*rhynchopetalum*, 41 fig. 1, 45, 47, 49  
 sect. *Rhynchopetalum*, 42 et seq.  
 subsect. *Rueelliana*, 45 et seq.  
*stricklandiae*, 167  
*sumatrana*, 45, 46  
*telekii*, 45, 46  
*urens*, 50  
*wollastonii*, 45, 49-50  
*Lodoicea maldavica*, 179  
 Loganiaceae, 68  
 Loranthaceae, 114  
*Luffa cylindrica*, 168  
*Lupinus alopecuroides*, 48  
*Lyginopteris oldhamia*, 180  
 Lythraceae, 165, 173  
*Macadamia angustifolia*, 178  
*Macrothelypteris*, 145 et seq.  
*multisetata*, 149  
*torresiana*, 148-9  
*Magnistipula sapinii*, 68  
*Magnolia grandiflora*, 252  
 Magnoliaceae, 186  
 Magnoliidae, 173  
 Magnoliineae, 186  
*Mahonia bealei*, 175  
*Maingaya*, 186  
 Malpighiaceae, 68  
 Malvaceae, 114, 177  
 Malvales, 173  
*Mangifera indica*, 16, 161 et seq.  
*Maniella*, 227  
*delhiensis*, 220  
*Mapania*, 78  
 Marantaceae, 187  
 Marcgraviaceae, 187  
*Marquesia*, 128  
 Martyniaceae, 187  
*Mastixiodendron*, 109

- Matthiola incana*, 16  
*Mauritia flexuosa*, 179  
*Medeola*, 73  
*Medullosa noei*, 180  
 Medusagynaceae, 187  
*Megaphyton* sp., 179  
 Melastomataceae, 49, 120, 165, 173  
   *Astronioideae*, 186  
   *Chitonoideae*, 188  
*Melia azedarach*, 196, 196 fig. 4  
 Meliaceae, 68, 131, 177  
 Melianthaceae, 187  
 Menispermaceae, 177  
*Mentzelia gronoviifolia*, 168  
   *lindleyi*, 168 (& fig. 5)  
*Mercurialis*, 73  
*Metasequoia*, 110  
*Metathelypteris*, 145  
   *dayi*, 146, 148  
   *decipiens*, 145-7  
   *flaccida*, 145-7  
   *fragilis*, 146  
*Metroxylon*, 20  
*Micranisa*, 210  
   *pteromaloides*, 210  
*Mikaniopsis*, 50  
*Mimulopsis*, 75  
*Mimusops schimperi*, 199  
 Miscogasteridae, 212  
 Monimiaceae, 109, 186  
 Monodontomerinae, 212  
*Monophyllaea*, 77, 116  
   *glauca*, 78  
*Monoporandra*, 128, 129, 132 *et seq.*  
*Monotes*, 128  
*Montinioideae*, 187  
 Moraceae, 35, 69, 90, 96, 177  
*Morinda*, 111, 116  
   *angloensis*, 69  
*Morus alba*, 196 fig. 4  
   *nigra*, 196 fig. 4  
*Musa*, 16  
 Musaceae, 187  
*Myosotis*, 50  
 Myristicaceae, 21-2, 90, 96  
*Myrmecodia*, 120-1  
 Myrsinaceae, 177  
 Myrtaceae, 69, 90, 96, 177  
   *Leptospermoideae*, 187  
 Myrtales, 173  
 Myzodendraceae, 184  
*Napoleona gossweileri*, 68  
*Naucleaeae*, 116  
*Neckia*, 74  
   *serrata*, 179  
*Nectarinia johnstonii johnstonii*, 44  
*Neostrearia*, 186  
*Neosycophila*, 212-3  
   *omeomorpha*, 226  
 Nepenthaceae, 186  
*Nepenthes*, 117, 120  
*Nephrodium dayi*, 148  
   *gracilescens* var. *decipiens*, 147  
   *singalanense*, 148  
*Nigeriella*, 218, 227  
*Nolina recurvata*, 179  
*Nothofagus*, 110  
 Nyctaginaceae, 96  
 Nymphaeles, 186  
*Nypa*, 110  
*Obetia radula*, 179  
*Ochna confusa*, 69  
   *katangensis*, 69  
   *leptoclada*, 69  
   *macroculyx*, 69  
   *manikensis*, 69  
   *mossambicensis*, 69  
   *pygmaea*, 69  
   *richardsiae*, 69  
   *schweinfurthiana*, 62  
 Ochnaceae, 69  
*Ochthocosmus candidus*, 68  
 Octocorallia, 112  
*Octomeles*, 22  
*Oenocarpus distichus*, 179  
 Olacaceae, 90, 96  
*Olea europaea*, 16  
 Oleaceae, 114  
 Oliniaceae, 187  
 Onagraceae, 165, 167, 173  
*Oncostemon* sp., 177  
 Orchidaceae, 117, 121  
   *Apostasioideae*, 186  
   *Cypripedioideae*, 186  
*Oriolus oriolus*, 200  
*Oroxylon indicum*, 29  
*Ostrearia*, 186  
*Otitessella*, 209, 212-3  
 Otitessellini, 211-3, 226  
*Otomys orestes orestes*, 44  
*Oxera coriacea*, 179  
*Oxytropis*, 128  
 Pachynocarpus, 128  
*Pachypodium*, 48  
*Pachystigma pygmaeum*, 69  
 Paenaeaceae, 187  
*Palaeocycas integer*, 180  
 Palmae, 73, 96, 179  
 Pandanaceae, 73, 137, 179, 186

## Pandanales, 137

*Pandanus*, 4, 111, 137 *et seq.*

- sect. *Acanthostyla*, 141, 138
- sect. *Acrostigma*, 141
- subg. *Acrostigma*, 141
- subsect. *Acrostigma*, 141
- subsect. *Alticolae*, 141
- sect. *Asterodontia*, 140
- sect. *Asterostigma*, 140
- sect. *Athrostigma*, 141
- subsect. *Atrodentata*, 140
- sect. *Australibrassia*, 141
- subsect. *Austrokeura*, 141
- sect. *Barklya*, 141
- sect. *Barrotia*, 140
- sect. *Bernardia*, 140
- subsect. *Bidens*, 140
- sect. *Brongniartia*, 140
- subsect. *Callicola*, 140
- sect. *Cauliflora*, 138, 140
- sect. *Cheilostigma*, 140
- sect. *Coronata*, 141
- subg. *Coronata*, 141
- sect. *Cristata*, 141
- sect. *Curvifolia*, 141
- danckelmannianus*, 179
- sect. *Dauphinensia*, 141
- subsect. *Dimissistyli*, 141
- subsect. *Elaphrocarpus*, 141
- sect. *Elmeria*, 141
- sect. *Epiphytica*, 141
- sect. *Excavata*, 141
- sec. *Eydouxia*, 141
- sect. *Fagerlindia*, 141
- sect. *Foullioya*, 141
- sect. *Fusiforma*, 141
- subsect. *Glaucophyllae*, 141
- subsect. *Gressitia*, 140
- sect. *Heterostigma*, 141
- sect. *Hombroonia*, 140
- subsect. *Insulanus*, 141
- sect. *Intraobtusus*, 141
- sect. *Involuta*, 141
- sect. *Jeanneretia*, 141
- sect. *Kaida*, 140
- sect. *Kanehiraea*, 141
- sect. *Karuka*, 140
- sect. *Kurzia*, 141
- subg. *Kurzia*, 141
- sect. *Liniobtusus*, 140
- sect. *Lonchostigma*, 141
- sect. *Lophostigma*, 140
- subg. *Lophostigma*, 140
- subsect. *Malaya*, 140
- sect. *Mammiliarisia*, 141
- sect. *Marginata*, 141
- sect. *Martellidendron*, 141
- subg. *Martellidendron*, 140
- sect. *Maysops*, 140
- sect. *Megakeura*, 141
- sect. *Megastigma*, 140
- sect. *Metamaysops*, 140
- sect. *Microstigma*, 141
- subsect. *Multispina*, 140
- sect. *Mydiophylla*, 140
- subsect. *Ornati*, 141
- sect. *Pandanus*
- subg. *Pandanus*, 141
- subsect. *Pandanus*, 141
- subsect. *Papilionatae*, 141

sect. *Paralophostigma*, 140subsect. *Parvi*, 141sect. *Perrya*, 140sect. *Platyphylla*, 141*princeps*, 179sect. *Pseudoacrostigma*, 141sect. *Pulvinistigma*, 141subsect. *Pumili*, 141sect. *Rykia*, 140subg. *Rykia*, 140subsect. *Rykia*, 140sect. *Rykiella*, 141sect. *Rykiopsis*, 140subsect. *Scabridi*, 141subsect. *Semikeura*, 141sect. *Seychellea*, 141*sigmoideus*, 138sect. *Solmsia*, 140sect. *Souleyetia*, 141subsect. *Souleyetia*, 141*spiralis*, 137, 140sect. *Stephanostigma*, 141subsect. *Sussea*, 141sect. *Tridens*, 138, 140sect. *Utilissima*, 141sect. *Veillonina*, 140sect. *Vinsonia*, 141subg. *Vinsonia*, 141*Paphagus*, 209*sidero*, 209*Paphiopedilum*, 78*Parakoebelea*, 209, 224-5**testacea**, 210*Parapristina*, 227*Parashorea*, 128-9, 132 *et seq.**Parasyccobia*, 226*Parinari*, 67*capensis*, 59, 63-6 (& fig. 3), 68*curatellifolia*, 59, 66*obtusifolia*, 61*Paris*, 73, 108*Parkia*, 29*Paropsia brazzeana*, 69*Passiflora quadrangularis*, 171

## Passifloraceae, 69, 171

*Pavetta pygmaea*, 69

## Pedaliaceae, 187

*Pegoscapus*, 211, 218, 222-3, 225, 227*estherae*, 220, 222*tonduzi*, 220, 222*Pellicierioideae*, 187*Penianthus* sp., 177*Pentacme*, 128, 132'*Pentacorallia*', 112*Pentagonia gigantifolia*, 178*Peridiscus*, 187*Petasites*, 51*Phaseolus*, 170*Phegopteris*, 145 *et seq.**pyrrhorhachis*, 150*Phoenix dactylifera*, 196 fig. 4

- Philotrypesini, 212, 224 fig. 8e-f, 225  
*Philotrypesis*, 212, 226, 228  
   *caricae*, 208, 210, 213, 216, 217 fig. 5, 218  
   *longicauda*, 208  
   *transiens*, 210  
*Phragmites australis*, 17  
*Phyllanthus*, 59  
*Phyllobotryon spathulatum*, 171 (& fig. 11) 176  
*Phylloporus rhodoxanthos*, 159  
*Physothorax*, 212, 223  
*Phytelephas macrocarpa*, 179  
*Pinckneya pubens*, 252  
 Pinaceae, 116  
*Pithecellobium hansemannii*  
 Pittosporaceae, 178  
 Pittosporineae, 187  
*Pittosporum ceratii*, 178  
*Placodiscus bancoensis*, 178  
*Planchonella pronyensis*, 178  
*Platanus*, 113  
*Platyneura testacea*, 209  
*Playtyscapa*, 211-2  
   *frontalis*, 209-10  
*Pletocomia*, 19  
*Pleistodontes*, 211, 214, 218, 222, 227  
   *froggatti*, 213-4, 220, 222  
   *imperialis*, 214, 222  
*Plesio stigma*, 212  
*Podophyllum*, 73  
 Podostemaceae, 187  
*Poinciana pulcherrima*, 14  
*Polanisa lutea*, 210  
 Polemoniaceae, 188  
 Polygalineae, 187  
 Polygonaceae, 76  
   *Coccoloboideae*, 187  
*Polygonum*, 29  
*Polypodium*, 146  
   *brunneum*, 150  
   *paludosum*, 149  
   *phegopteris*, 146  
   *rectangulare*, 149  
*Polystichum torresianum*, 148  
*Pongamia*, 111  
 Pontederiaceae, 187  
*Porphyrellus porphyrosporus*, 159  
*Prainea*, 35, 38  
*Primula vulgaris*, 77  
*Prionastomata*, 211  
*Protea*, 63  
   *angolensis*, 69  
   *heckmanniana*, 69  
   *madiensis*, 63  
   *paludosa*, 69  
   *trichophylla*, 69  
 Proteaceae, 69, 114, 178, 187  
*Prunus persica*, 196 fig. 4  
*Psaronius* sp., 179  
*Pseuderanthemum*, 74  
*Pseudidarnes*, 223  
*Pseudomantalania macrophylla*, 178  
*Pseudophegopteris*, 145 et seq.  
   *aurita*, 149-50  
   *paludosa*, 149-50  
   *rectangularis*, 149-50  
*Psidium guajava*, 196 fig. 4, 197  
*Psorospermum mechowii*, 68  
*Psychotria* spp., 69  
 Pteridospermae, 184  
*Pteropus vampyrus*, 29  
*Punica granatum*, 196 fig. 4  
*Puya*, 48, 51  
   *ramondii*, 48  
*Pycnocomia angustifolia*, 176  
*Pygmaeothamnus conrescens*, 69  
   *zeyheri*, 69  
*Pyrus communis*, 196 fig. 4  
*Quercus*, 110  
   *ilex*, 16  
 Quinaceae, 187  
*Radlkofera calodendron*, 178  
*Rafflesia*, 106  
*Rafflesioideae*, 186  
 Ranales, 109  
*Rapanea grandiflora*, 177  
*Raphanus*, 123  
*Rauvolfia nana*, 68  
*Resia*, 75  
 Restionaceae, 187  
 Rhabdodendraceae, 187  
 Rhamnaceae, 69  
*Rheum nobile*, 48  
*Rhizophora mucronata*, 16  
 Rhizophoraceae, 69, 111, 186  
*Rhododendron ponticum*, 170  
*Rhus diversiloba*, 163  
   *glabra*, 163  
   *kirkii*, 68  
 Richetia, 128  
 Rosaceae, 90, 96, 121  
   *Pomoideae*, 114  
 Rosales, 173  
 Rosidae, 173  
*Rousettus aegyptiacus*, 192, 193 fig. 1, 195-6,  
   198  
   *stekelesi*, 198  
*Roystonea oleracea*, 179  
 Rubiaceae, 69, 76, 96, 109, 123, 165, 178  
   *Henriquesioideae*, 187  
*Ruellia*, 78

- Rutaceae, 186  
   *Dictyolomatoideae*, 187  
   *Spathelioideae*, 187  
 Rutiflorae, 184  
 Sabiaceae, 186  
*Salacia bussei*, 68  
   *kraussii*, 68  
   *luebbertii*, 68  
 Sapindaceae, 69, 96, 131, 178  
 Sapotaceae, 90, 96, 132, 178, 187  
 Sapotinae, 187  
*Sararanga*, 137  
 Sarcolaenaceae, 187  
 Sarraceniaceae, 187  
*Saussurea gossipiphora*, 48  
*Scaevola*, 111  
*Schinus*, 163  
 Scrophulariaceae, 117, 123  
 Scytopetaliceae, 187  
 Scytopetalineae, 187  
 Secundeisenia, 211  
*Selaginella*, 78  
*Semecarpus magnifica*, 175  
   sp., 175, pl. 1 opp. 176  
*Senecio*, 22, 41 *et seq.*  
   *asperulus*, 50  
   *bonariensis*, 50  
   *brassica*, 43-4, 46  
   sect. *Crociserides*, 44 *et seq.*  
   subg. *Dendrosenecio*, 42 *et seq.*  
   *gigas*, 43  
   *hypargyraeus*, 50  
   *johnstonii*, 43  
     subsp. *barbatipes*, 43-4  
     subsp. *refractisquamatus*, 43  
   *keniodendron*, 43-4, 50  
   *leucadendron*, 43  
   *mannii*, 21, 43, 47  
   *maranguensis*, 50  
   *redivivus*, 43  
*Senecioneae*, 45  
*Seres*, 226  
*Shorea*, 128-9, 132 *et seq.*  
   *albida*, 92-3  
*Simaroubaceae*, 96, 131, 178  
   *Alvaradoideae*, 187  
   *Kirkioideae*, 187  
*Sloanea*, 21  
 Solanaceae, 178, 187  
*Solanum*, 116  
 aff. *Solanum*, 178  
*Sonchus*, 48-9  
*Sonerila*, 74, 79  
   *borneensis*, 78  
   *tenuifolia*, 78  
*Sonneratia*, 111  
*Sophora*, 111  
   sp., 177  
 Sparganiaceae, 137  
*Sparmannia africana*, 170  
 Sphaerosepalaceae, 187  
*Sphedothamnus angolensis*, 68  
*Spilanthes*, 111  
*Spondias*, 163  
 Stackhousiaceae, 187  
 Staphyleaceae, 186  
*Staurogyne*, 76  
*Steenisia*, 75  
*Stemona*, 108  
 Stemonoporus, 128-9  
 Sterculiaceae, 178  
*Streptocarpus molweniensis*, 77  
*Strobilanthes*, 75  
   *cernuus*, 75  
   *kunthianus*, 75  
*Strobilomyces*, 155  
*Strophanthus angusii*, 68  
*Strychnos gossweileri*, 68  
 Stylidiaceae, 165, 173  
*Stylidium graminifolium*, 168 (& fig. 6)  
*Sycobia bethyloides*, 210  
*Sycobiomorphella*, 226  
 Sycocrypta, 209, 211  
   *croeca*, 209-10  
 Sycococini, 211-3, 226  
 Sycolacides, 211-2  
*Sycophaga*, 209, 211-2, 215 fig. 2, 223, 225, 228  
   *crassipes*, 208  
   *paradoxa*, 210  
   *sycomor*, 191, 202, 208, 211, 223-5  
 Sycophagides, 211-2  
 Sycophaginae, 210-3  
 Sycophagini, 211-2, 223-5 (& fig. 8a-b)  
*Sycophila*, 212, 226-7  
   *decatomoides*, 210  
*Sycophilomorpha*, 226  
 Sycoryctini, 209, 212, 224-6 (& fig. 8c-d)  
*Sycoscapter stabilis*, 210  
*Sycoscapteridea*, 214, 225  
 Symplocaceae, 178, 186  
*Symplocos*, 110  
   *stravadioides*, 178  
*Syzygium guineense* subsp. *huillense*, 69  
*Tabebuia argentea*, pl. opp. 252  
*Tacazzea*, 75  
*Tamarindus indica*, 17  
*Tapeinosperma pachycaulum*, 177  
   *crystalense*, 177  
   sp., 177  
 Tapiphyllum spp., 69  
 Tecophilaeaceae-Cynastroideae, 187  
*Terminalia*, 21, 22, 111  
   *mollis*, 63

- Ternstroemia*, 144  
*bancana*, 144  
*corneri*, 143 *et seq.*  
*penangiana*, 144  
*wallichiana*, 144  
*Tetracera masuiana*, 68  
*Tetrachondroideae*, 184  
*Tetragonaspis*, 209  
*Tetrameles*, 22  
*Tetrapus*, 211-2, 218, 222-3, 227  
*spp.*, 220  
*Thalassiophyta*, 3  
*Thamnopteria schlechtendahlilii*, 180  
Theaceae, 4, 109, 143  
Theiflorae, 184  
Thelypteridaceae, 145 *et seq.*  
*Thelypteris*, 145  
*brunnea*, 149-50  
*decipiens*, 147  
*flaccida*, 147  
*oppositipinna*, 149  
*paludosa*, 149  
*singalanensis*, 148  
*torresiana*, 148  
*uliginosa*, 148  
*Theobroma mariae*, 178  
Theophrastaceae, 179, 187  
Tiliaceae, 69, 165, 170, 173  
*Neotessmannioideae*, 187  
*Tetralicoideae*, 187  
Torymidae, 209-11, 226  
Toryminae, 212, 223  
*Tournefortia*, 111  
*Trechus*, 45  
Tremellales, 4, 151  
*Tricalysia cacondensis*, 69  
*suffruticosa*, 69  
*Trichilia quadrivalvis*, 64 (& fig. 3), 65, 68  
*Trichoscypha ferruginea*, 175  
Trimeniaceae, 186  
*Tristania*, 109  
*Triticum*, 123  
*boeoticum*, 198  
*dicocum*, 198  
*monococum*, 198  
Tropaeolaceae, 165, 170, 173  
*Tropaeolum minus*, 170 (& fig. 9)  
Typhaceae, 137  
Typhales, 137  
Umbelliferae, 76, 121  
*Uncaria*, 116  
*Upuna*, 128  
*borneensis*, 128  
Urticaceae, 179  
*Valentinella*, 211  
*Valeriana officinalis*, 166 fig. 3B, 168  
Valerianaceae, 165, 173  
*Vateria*, 128-9 132 *et seq.*  
*Vatica*, 128-30, 132 *et seq.*  
*Vellozioidae*, 187  
*Verbascum*, 128  
Verbenaceae, 69, 179  
*Chloanthoideae*, 179  
*Verschaffeltia splendida*, 179  
*Viola*, 165  
Violaceae, 96, 165, 173, 179  
*Leonioideae*, 187  
Violales, 173  
Vochysiaceae, 96  
*Walkerella temeraria*, 210  
*Waterstoniella*, 209, 211, 218, 222, 227  
*frontalis*, 210  
*masii*, 222  
*Wedelia*, 111  
*Welwitschia*, 42  
*Whiteodendron moultonianum*, 93  
*Williamsonia sewardiana*, 180  
Winteraceae, 186-7  
*Xanthorrhoea spp.*, 48  
*Xanthorrhoeideae*, 187  
*Xerocomus macrobbii*, 159  
*nothofagi*, 159  
*rufostipulatus*, 159  
*Xerospermum intermedium*, 19  
*Yucca brevifolia*, 51  
*spp.*, 48  
Zingiberaceae, 74, 186  
*Ziziphus jujuba*, 16  
*spina-christi*, 196  
*zeyherana*, 69

## ERRATA

- In the running head of pages 15 to 266, 1976 should read 1977  
p. 25, in abstract line 10 from bottom for *dehiscense* read *dehiscence*  
pp. 27, 29, 31, 33, in running head, for *Zibethinus* read *zibethinus*  
p. 61, line 7, for *et al* read *et al.*  
p. 64, line 5 for *C. Dc.* read *C.DC*  
p. 70, line 8, for *Act. a* read *Acta*  
line 9, for 3: (1) read 3 (1).  
p. 79, for *MOORE, H.J.* read *MOORE, H.E.*

**PUBLICATIONS OF THE BOTANIC GARDENS  
SINGAPORE**

---

1. **The Agricultural Bulletin of the Malay Peninsula (Series I).**  
Only Nos. 3, 5, 7, 8 and 9 available, at 20 cents each.
  2. **The Agricultural Bulletin of the Straits and F.M.S. (Series II).**  
Vols. 1-10, 1901-1911, monthly issues.  
Many parts available.  
Price: \$5 per volume, 50 cents per part.
  3. **The Gardens' Bulletin, Straits Settlements (Series III).**  
Vols. 1-11, 1912-1947.  
Vol. 1 (1-5) January-May 1912 issued under title of **Agricultural Bulletin of the Straits & F.M.S.**  
Prices on application.
  4. **The Gardens' Bulletin, Singapore (Series IV).**  
Vols. 12-27, 1949-1971. Vol. 28 Pt. I in print.  
Price: Vol. 13 Pt. I (New impression) \$12 per copy, \$20 per vol.  
Vols. 12 & 14 \$13 per vol.  
Vol. 15 \$20 per vol.  
Vols. 16-25 \$25 per vol. Individual parts vary in price.  
Vol. 26 (Pt. I \$18; Pt. II \$18); 27 (Pt. I \$18; Pt. II \$8.50);  
28 (Pt. I \$18); 29 (\$30); Vol. 30 & Gardens' Bulletin Supplement  
1 in press.  
Frequency: Parts are published as materials become available.
  5. **Materials for a Flora of the Malay Peninsula, Monocotyledons.**  
Parts 1, 2 and 3 remain available.  
Price: \$10 per set, \$5 per part.
  6. **Annual Reports.**  
1909-1972.
  7. (a) **Malayan Orchid Hybrids by M. R. Henderson and G. H. Addison.** \$15.  
(b) **Malayan Orchid Hybrids, Supplement I by G. H. Addison.** \$21.
  8. **A Revised Flora of Malaya.**  
(a) Vol. 1, Orchids, by R. E. Holttum. \$30 (3rd ed. 1972 Impr.).  
(b) Vol. 2, Ferns, by R. E. Holttum. \$20 (2nd ed., 1968).  
(c) Vol. 3, Grasses, by †H. B. Gilliland. \$30 (1971).
  9. **Boletus in Malaysia by E. J. H. Corner.** \$50 (1972).
- Items 1-6 obtainable from the Commissioner, Parks & Recreation Department,  
Botanic Gardens, Cluny Road, Singapore 10.
- Items 7-9 obtainable from Singapore National Printers (Pte) Ltd, Upper Serangoon  
Road, Singapore 13.

*Prices quoted are in Singapore Dollars  
Overseas postage is extra*





