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THE SEEDS OF DICOTYLEDONS

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VOLUME 1

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CONTENTS

VOLUME 1

Preface	page vii	5 Seed-evolution	48
PART ONE		The primitive dicotyledonous seed, 48; the evolution of the dicotyledonous seed, 48; unitegmic seeds: the origin of Sympetaleae, 49; Convolvulaceae, 50; arillate and sarcotestal seeds, 52; seed-size, 52; a Myristicalean start, 55; seed-progress, 57; transference of function, 58; the origin of the angiosperm seed, 58; neoteny again, 59	
1 Material and method	i	PART TWO	
2 Seed-form	3	Descriptions of seeds by families 65	
The bitegmic anatropous seed, 4; campylotropous seeds, 4; obcampylotropous seeds, 4; hilar seeds, 4; pre-raphe seeds, 4; orthotropous seeds, 5; the dorsal raphe, 5; perichalazal seeds, 5; pachychalazal seeds, 5; alate seeds, 6; pleurogrammatic seeds, 7		Acanthaceae, 65; Aceraceae, 65; Actinidiaceae, 65; Adoxaceae, 66; Aextoxicaceae, 66; Aizoaceae, 66; Akaniaceae, 67; Alangiaceae, 67; Amaranthaceae, 67; Anacardiaceae, 67; Ancistrocladaceae, 68; Annonaceae, 68; Apocynaceae, 70; Aquifoliaceae, 73; Araliaceae, 73; Aristolochiaceae, 73; Asclepiadaceae, 74	
3 Seed-coats	8	Balanitaceae, 75; Balsaminaceae, 75; Basellaceae, 75; Begoniaceae, 75; Berberidaceae, 75; Betulaceae, 76; Bignoniaceae, 76; Bixaceae, 76; Bombacaceae, 78; Bonnetiaceae, 82; Boraginaceae, 82; Bretschneideraceae, 83; Bruniaceae, 83; Burseraceae, 83; Buxaceae, 84; Byblidaceae, 84	
Testa and tegmen, 8; multiplicative integuments and overgrown seeds, 8; factors in the formation of seeds, 9; description of the seed-coats, 9; exotestal seeds, 10; mesotestal seeds, 11; endotestal seeds; crystal-cells and raphid-cells, 11; exotegmic seeds with a palisade, 13; exotegmic seeds with fibres, 14; exotegmic tracheidal seeds, 17; endotegmic seeds, 18; undifferentiated seed-coats, 18; cell-form, 19; aerenchyma and stomata, 19; the vascular supply of the seed, 20; hairs, 22; chalaza, 22; aril, 23; sarco-testa, 24		Cactaceae, 85; Callitrichaceae, 85; Calycanthaceae, 85; Campanulaceae, 85; Canellaceae, 86; Cannabiaceae, 86; Cappariaceae, 86; Caprifoliaceae, 88; Caricaceae, 89; Caryocaraceae, 89; Caryophyllaceae, 90; Casuarinaceae, 91; Celastraceae, 91; Ceratophyllaceae, 95; Cercidiphyllaceae, 95; Chenopodiaceae, 95; Chloranthaceae, 95; Circaeasteraceae, 97; Cistaceae, 97; Clusiaceae, 97; Combretaceae, 103; Compositae, 104; Connaraceae, 105; Convolvulaceae, 110; Coriariaceae, 111; Cornaceae, 111; Corynocarpaceae, 111; Crassulaceae, 111; Crossosomataceae, 111; Cruciferae, 111; Cucurbitaceae, 112; Cunoniaceae, 115; Cynocrambaceae, 115	
4 Criticism of the arrangement of dicotyledonous families into orders	25	Daphniphyllaceae, 116; Datisceae, 116; Degeneriaceae, 116; Didiereaceae, 117; Dilleniaceae, 117; Dioncophyllaceae, 119; Dipsacaceae, 119; Dipsotercarpaceae, 119; Droseraceae, 121	
Magnoliales–Ranales, 25; Ranunculales, 27; Theales–Guttiferae–Dilleniales, 28; Bixales–Violales, 30; Rutales–Sapindales, 30; Celastrales, 32; Cappariadales–Cruciales–Rhoecadales, 32; Euphorbiales–Malvales–Thymelaeales–Tiliales, 33; Geraniales–Malpighiales–Polygalales, 35; Hamamelidales–Rosales–Leguminosae, 35; Rhamnales–Proteales, 36; Lythrales–Myrtales, 37; Cucurbitales–Passiflorales, 38; Aristolochiales–Nepenthales–Rafflesiales–Sarraceniales, 40; Araliales–Cornales–Caprifoliaceae, 40; Centrospermae, 41; Tamaricales, 42; Amentiferae, 42; Piperales, 43; summary of positive contributions, 44; classification of bitegmic dicotyledonous seeds, 45			

CONTENTS

Ebenaceae, 122; Elaeagnaceae, 124; Elaeocarpaceae, 124; Elatinaceae, 128; Ericales, 128; Erythroxylaceae, 128; Escalloniaceae, 129; Eucommiaceae, 129; Euphorbiaceae, 129; Eupomatiaceae, 143; Eupteleaceae, 143	aceae, 216; Phrymaceae, 216; Phytolaccaceae, 217; Piperaceae, 217; Pittosporaceae, 218; Plantaginaceae, 218; Platanaceae, 218; Plumbaginaceae, 218; Podophyllaceae, 218; Podostemaceae, 219; Polemoniaceae, 220; Polygalaceae, 220; Polygonaceae, 222; Portulacaceae, 222; Primulaceae, 222; Proteaceae, 222; Punicaceae, 224
Fagaceae, 143; Flacourtiaceae, 143; Fouquieriaceae, 147; Frankeniaceae, 147; Fumariaceae, 147	Rafflesiaceae, 224; Ranunculaceae, 224; Resedaceae, 226; Rhamnaceae, 226; Rhizophoraceae, 227; Rosaceae, 228; Rubiaceae, 231; Rutaceae, 232
Garryaceae, 147; Gentianaceae, 148; Geraniaceae, 148; Gesneriaceae, 149; Glaucidiaceae, 149; Gonystylaceae, 149; Goodeniaceae, 150; Grossulariaceae, 151	Salicaceae, 237; Salvadoraceae, 237; Santalales, 237; Sapindaceae, 238; Sapotaceae, 248; Sarraceniacae, 249; Saururaceae, 249; Sauvagesiaceae, 249; Saxifragaceae, 250; Schisandraceae, 250; Scrophulariaceae, 250; Scyphostegiaceae, 251; Scytropetalaceae, 252; Selaginaceae, 252; Simaroubaceae, 252; Solanaceae, 254; Sonneratiaceae, 255; Sphenocleaceae, 256; Stachyuraceae, 256; Stackhousiaceae, 256; Staphyleaceae, 256; Sterculiaceae, 258; Styliidiaceae, 265; Styracaceae, 265; Symplocaceae, 265
Halorrhagaceae, 151; Hamamelidaceae, 151; Hernandiaceae, 152; Hippocastanaceae, 152; Hydnoraceae, 153; Hydrangeaceae, 153; Hydrophylaceae, 153; Hypericaceae, 153	Tamaricaceae, 265; Theaceae, 265; Thymelaeaceae, 270; Tiliaceae, 271; Tovariaceae, 274; Trapaceae, 274; Tremandraceae, 274; Trigoniaceae, 274; Trochodendraceae, 274; Tropaeolaceae, 275; Turneraceae, 275
Icacinaceae, 154; Illiciaceae, 154; Ixonanthaceae, 154	Ulmaceae, 275; Umbelliferae, 275; Urticaceae, 276
Juglandaceae, 155; Julianaceae, 156	Valerianaceae, 276; Verbenaceae, 276; Violaceae, 276; Vitaceae, 277; Vochysiaceae, 280
Krameriaceae, 156	Winteraceae, 280
Labiatae, 156; Lacistemaceae, 156; Lactoridaceae, 156; Lardizabalaceae, 156; Lauraceae, 157; Lecythidaceae, 159; Legnotidaceae, 161; Leguminosae, 161; Leitneriaceae, 173; Lentibulariaceae, 173; Limnanthaceae, 173; Linaceae, 173; Loasaceae, 174; Lobeliaceae, 175; Loganiaceae, 175; Lythraceae, 176	Zygophyllaceae, 282
Magnoliaceae, 177; Malpighiaceae, 179; Malvaceae, 180; Marcgraviaceae, 182; Martyniaceae, 182; Melastomataceae, 182; Meliaceae, 185; Melianthaceae, 193; Menispermaceae, 193; Monimiaceae, 194; Moraceae, 197; Moringaceae, 197; Myricaceae, 198; Myristicaceae, 198; Myrsinaceae, 202; Myrtaceae, 202	
Nandinaceae, 205; Nepenthaceae, 206; Nyctaginaceae, 206; Nymphaeaceae, 207; Nyssaceae, 207	References 284
Ochnaceae, 208; Olacaceae, 209; Oleaceae, 209; Onagraceae, 209; Opiliaceae, 210; Orobanchaceae, 210; Oxalidaceae, 210	Index 305
Paeoniaceae, 211; Pandaceae, 212; Papaveraceae, 212; Parnassiaceae, 215; Passifloraceae, 215; Pedali-	The Figures are in Volume 2

PREFACE

Open a book on flowering plants and find how little there is about their seeds! The subject is abstruse with little to commend it unless for the identification of the seeds of commerce but, pursued botanically, it is absorbing, penetrating and illuminating. From seeds came the plants which made fruits (angiosperms) and those which added flowers (anthophytes). Modern theories of the origin of these plants dwell on flowers. The fruit was the subject of the durian-theory. I turn now to their source in seeds.

When the late Professor Kwan Koriba came from Kyoto to Singapore in 1942 to direct the Botanical Gardens during the war, we turned in our confinement to the botany of trees. In 1945 when lies, starvation and chaos were around, we discovered this interest. We did not know of Netolitzky's book, which I have since studied and re-studied. I have pondered why such genius has passed unrecognized. His book on the seed-structure of angiosperms summarizes knowledge up till the end of 1923; no detail has escaped; the erudition is profound; and he came to the brink of the discovery that seed-structure should be the basis of the natural classification of flowering plants. Perhaps the terse descriptions and the sketchy illustrations failed to convey the message. Probably the weight of authority overwhelmed him. Engler, Wettstein, Warming, Lotsy, Hallier and other great exponents of classification failed to perceive the importance of the researches into seed-structure which French, German and Italian schools had begun to explore last century.

How to follow, for there is still an enormous amount of research to be undertaken, I have contemplated. A modern encyclopedia might be planned but parts exist, knowledge is inadequate, and patience would be unrewarded. It is possible to continue, however, where Netolitzky left off. I have built, then, on his text and borne in mind

five considerations. (1) There is great pleasure in discovering how a seed is made; it is the most elaborate part of the plant. (2) Families have characteristic seeds by which they may be related in orders. (3) Compared with monocotyledons, the orders of dicotyledons are unsatisfactory, but they have the greater variety of seed-structure. (4) Conviction calls for ample illustration. (5) A prototype must have existed for this variety if, as the intricacy of their seeds seems to prove, angiosperms were monophyletic.

The outcome is an account of the seed in those families of dicotyledons for which there is something known about the microscopic structure; the pocket-lens description is totally inadequate. It is illustrated mainly from my researches on tropical seeds, these being the less known. There is an attempt to prove the importance of microscopic structure in the ordinal classification of families, a consideration of the prototype, and a general introduction. The presentation has largely been reversed for the very reason that, in all systems of dicotyledonous classification, on which the botany of flowering plants depends, the grouping of families into orders is uncertain, even arbitrary and artificial, and for the most part unsatisfactory; most orders do not fit the precision in seed-structure which Netolitzky exposed. The family becomes of necessity the unit of description though some families are at fault. Descriptions have been assembled, therefore, in the last but major section of the work where the arrangement is alphabetical. To have assembled them by similarity in seed-structure, though ideal, would have been bewildering because there would be constant distraction through reference to an index; Vitaceae would come near Magnoliaceae with Winteraceae as far away as alphabetically; Convolvulaceae would follow Paeoniaceae; Proteaceae would accompany Papaveraceae; Cruciferae would not go with Cappariaceae, nor

Geraniaceae with Linaceae; thus one can appreciate Netolitzky's desistance. Moreover the time is not ripe. The seeds of many families are too little known or too problematic, e.g. Droseraceae. Before this main section there comes, therefore, the criticism of the customary orders. Here, with so much detail under review, it is necessary to pass continually to and fro between the orders and the families which they are supposed to embrace. I tried various methods to facilitate this perpetual motion and found none more satisfactory than the alphabetical; it does not burden the mind.

Lack of knowledge and of space have forced me to forgo an attempt to define generic differences. Even in such well-studied families as Rosaceae and Scrophulariaceae too few species have been examined, and where, as with Cruciferae, there is more certainty, the modern text can be cited.

Seed-studies begin with the ovule and end with germination. Flower and fruit pass in review. Ovary and pericarp must be sectioned. Vascular bundles must be traced. Lignification, suberization, cutinization and mucilagization must be investigated, as well as cell-contents; all contribute to the hardening of the seed-coat which becomes its character. It is easy to stray into a multitude of problems from floral to physiological and biochemical evolution. I have left these in other hands and concentrated on the gross form of the seed, its cellular construction, vascular supply, and general lignification. The chemical characters may be as important but it soon becomes clear that, for the moribund tissues of the seed-coat, no ordinary stains or reagents are discriminatory enough in the common round of anatomy. A palisade so characteristic as the outer epidermis of the Leguminous seed or the hypodermis of the Convolvulaceous seed may or may not be lignified, and yet it is the family character. Probably the seed-coat of *Eucalyptus* has been examined in greatest detail but it affords no chemical satisfaction.

The first reaction will be to suppose that I have exaggerated the importance of seed-structure. With increasing familiarity it will be realized that seed-structure is a prime inheritance. Its histological detail expresses genetic character. The many variations cannot be ascribed to environmental selection. The profoundly different seeds of crucifer, mallow, speedwell and chenopodium arrive on the same waste ground. The profoundly different seeds of *Magnolia*, *Sterculia*, *Garcinia* and *Tabernaemontana*

sprout together on the floor of the tropical forest. Drupes and nuts protect seeds with thick outer lignification, yet the intrinsic details of the seed-structure may be retained, e.g. *Canarium*, *Elaeocarpus*, *Grewia*, *Scaevola* and *Terminalia*. Magnoliaceous seeds are complicated, those of Sympetalae are simplified. The main trend in seed-evolution has been simplification by reduction in complexity and size, e.g. *Myristica* compared with *Begonia* or *Bellis*, as palm to orchid. Embryologists have established the advance from the bitegmic to the unitegmic ovule and from the crassinucellate to the tenuinucellate. Simplification becomes the theme, and from the whittling away of the Magnolialean complexity there emerges the idea of a complicated prototype. Palaeobotany would not be able to recognize a primitive dicotyledonous seed. In a recent paper (Boumann 1971) phyletic emphasis has been laid not so much on the final structure of the seed-coat as on the manner in which the integuments may arise in the ovule. Both matters are important but, since the final structure of the differentiated integument is so much more explicit, it cannot be discarded.

This work is also a vindication of that part of the durian-theory which discovered a primitive factor in the arillate seed. The conclusion has been derided through prejudice and ignorance, but what is laughed at commonly comes to be taken seriously. All along the evidence accumulates in favour of the primitive envelope; it is woven into these pages in the continual effort to show that classification without seed-structure is unsound and, consequently, our knowledge of the evolution of flowering plants.

It is a pleasure to thank the many botanists who have supplied me with material, in particular H.K. Airy Shaw, J. A. R. Anderson, P. S. Ashton and F. Hallé. On two short visits to Ceylon in 1968 and 1972, I was enabled to collect a large number of critical seeds through the kindness of Professor B. A. Abeywickrama and his colleagues Dr Dassanayake and Dr Balasubramaniam of the University of Ceylon; indeed this work, begun in Singapore, has matured in Ceylon. Many slides have been prepared for me in the last three years by P. Mohana Rao, of the University of Delhi. With E. C. Bate-Smith I have had numerous discussions on the biochemical classification of flowering plants; the subject is beyond most provincial schools of botany but of increasing concern to the chemist (Bate-Smith 1972).

PREFACE

ix

Dr Gh Dihoru, of the Institut de Biologie 'Tr. Savulesiu', Bucharest, has kindly supplied me with the following notes on the life of Netolitzky; they are taken from the obituary by Popovici (1947). Netolitzky was born at Zwickau, Bohemia, on 1 October 1875 and died in Vienna on 5 January 1945. He was a student in the universities of Prague, Strassburg and Vienna where, as a junior assistant from 1 January 1896 to 31 August 1899, he took his doctorate in medicine in 1899. He moved to the University of Innsbruck, 1 November 1899 to 30 April 1904, then to the University of Graz, 1

May 1904 to 31 January 1910. From 14 February 1910 to 30 September 1912 he was an assistant in the chemistry of foodstuffs at the University of Cernaui. In 1912 he became an associate professor of the University and in 1919 was made Professor of Pharmacognosy and Plant Anatomy, and Director of the Institute of Plant Anatomy and Physiology. As pensioner in 1940, he entered a professorship at the University of Iasi before he retired to Vienna in the capacity of Professor of Pharmaceutical Medicine. A profound knowledge of botany illuminates his writings.

E.J.H.C.

TO THE MEMORY OF
DR FRITZ NETOLITZKY
(1 OCTOBER 1875–5 JANUARY 1945)

Professor of Pharmacognosy and Plant Anatomy in the University of Cernauți, Rumania
Professor of Pharmaceutical Medicine in the University of Vienna