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BOOK REVIEW

The Seeds of Dicotyledons: by E. J. H. CORNER. Cambridge University Press, London, 1976. In two volumes. Volume 1: ix + 311 pp. £15. Volume 2: 552 pp. (647 figures). £25.

Corner's early work on tropical fruits, which led to his well-known durian theory of the origin of trees (*Ann. Bot. Lond.* 1949 *ns* **13**, 367), convinced him of the importance of the structure of fruits and seeds in identifying the true relationships of flowering plants. Present systems of classification rely on the structure of the flower—an organ whose structure is prejudiced by the needs of pollination, only secondarily reflecting the intrinsic characteristics of the organism. Seeds, on the other hand, are characteristic of families; "every natural family of dicotyledons has a characteristic seed". The family becomes of necessity the unit of description, although some families, as at present recognised, are in this respect at fault.

With this premise, Corner began more than 30 years ago assiduously collecting information about the structure of dicot seeds, and the present work is the result of this massive investigation. He was immensely encouraged by the discovery some time later of a book, published in 1926, by F. Netolitzky, then professor of plant anatomy and pharmacognosy in Cernauti, Rumania, on the anatomy of angiosperm seeds, which coincided remarkably with the conclusions he himself had come to, and to which he gives handsome acknowledgement.

The feature of the seed which both authors emphasis as involved in this relationship is the microscopic structure of the seed-coat. The prototype dicot seed has two integuments, which derive from the two integuments of the ovule. To avoid the ambiguity that arises when the integuments of the ovule and seed are called by the same names, Corner refers to those of the ovule as the outer and inner integuments, the produce of the former then becomes the *testa*, that of the latter the *tegmen*. Seeds with characteristic testa can be called *testal*, those with characteristic tegmen *tegmic*. When both are present the seed-coat is *bitegmic*; when only one persists, *unitegmic*.

In order to fulfil its function of protecting the embryo, the seed-coat has to be thickened and strengthened, and this is achieved by sclerification of layers of cells in one or other of the integuments. In either case, it is sometimes the outer epidermis that is thickened, sometimes the inner epidermis, and, in the case of the testa, sometimes an intermediate layer, the mesoderm, the particular layer so modified being, in most instances, characteristic of the family. Thus there are five basically different types of thickening, and these form the starting-point of Corner's analysis. Examples of some of the smaller "alliances" so revealed are: *Bitegmic mesotestal*: Rosaceae, Hamamelidaceae, Buxaceae, Myrtaceae, Melastomaceae; *Unitegmic mesotestal*: Rosaceae, Araliaceae, Cornales, Caprifoliaceae; *Bitegmic endotegmic*: Nandinadeae, Saururiaceae, Piperaceae, Podostemaceae, Rafflesiaces; *Unitegmic endotegmic*: Peperomiaceae, Hydnoraceae, Santalaceae.

Further subdivision of larger groups is achieved by consideration of finer anatomical detail of the cellular structure of the individual thickened layer. The result is the division of the dicots into groups of families having like characters of the seedcoat, and the next step is to consider the phylogenetic relationships between these groups. The composition of many of these groups is familiar in the ordinal arrangement of present systems, but there are also many unexpected conjunctions and disjunctions, so that the retention of the rank and title of "order" for these alliances would be misleading.

One of the largest of these groups is that of the Sympetalae, nearly all of which are unitegmic exotestal. Another large group is a varied one of 34–35 families of "advanced and diversified floral characters", but having in common the general character of a fibrous exotegmen, which is so distinctive and remarkable that Corner is inclined, in spite of these diversities, to regard them as monophyletic. The Amentiferae form part of another large and rather varied group of families with exotestal thickening. The Lythrales-Myrtales are dispersed, some with fibrous endotegmal, others with mesotestal, thickening.

The question, now, is how these alliances fit into present day concepts of the phytochemical relationships of plants. Since there is, of course, no commitment to a chemical system of classification, no conflict of interest is involved, but there are stronger pointers towards the incorporation of chemical data in any revision of current systems. There are two features of Corner's approach which are of particular interest to the phytochemist. The first is the idea that the seed characters may provide a sounder basis for systematic classification than floral or adult vegetative characters. Chemically, this has already been shown to be true of the herbaceous Leguminosae, in which the seed of every species examined had the primitive leucoanthocyanidin character which only a chosen few of the leaves and flowers possess (*Qual. Plant Mat. Veg.* 1959, **5**, 189). Leguminosae have, also, one of the more distinctive seed-coats. Thus the seed reveals the true status of the family which the adult form of the plant in most instances conceals. Altogether too little is known, however, about the chemistry of seed-coats to be able to pair off the information which Corner now provides with comparable information from the chemical standpoint.

The second is that in the process of evolution the cellular layers are reduced in number from the full complement in the Magnoliales and other woody families to the unitegmic condition in many of the Sympetalae. A similar situation prevails in respect of the chemistry of the plant. The "regular" phenolic constituents, for instance, found in the less advanced families are progressively modified, substituted or lost, the Sympetalae again being the most affected. Within the limited area of the dicot system in which they occur, the iridoid compounds show similar trends. It will be interesting, in view of this parallelism, to see whether the alliances suggested by

Corner bear any facultative relationship to those indicated by chemical similarities. To be able to do this it will be necessary, however, to collect information about the chemistry of the seed-coats themselves. At present most of the information concerns the leaves and other vegetative tissues.

The position of the Magnoliales is especially relevant. Chemically they are distinct in the poverty of trihydroxyflavonoids, the absence of ellagitannins and iridoids, and the frequent presence of isoquinoline alkaloids. Corner distinguishes them by placing them in a class of their own with prototypic seed-coat structure. Within this order, so conserved, however, Schisandraceae and Illiciaceae *may be relics of the mesotestal ancestry of the Hamamelidales, Rosales, Myrtales and Theales*, and it is interesting that in the Magnoliales it is in these two families, and only in these, that trihydroxyflavonoids occur.

The evidence that Corner provides casts doubt on the naturalness of orders as commonly defined. He devotes a whole chapter to criticism of the arrangement of dicot families into orders, remarking that *the unsatisfactory nature of ordinal classification is proved by the number of systems that have been proposed.* For purposes of classification and meaningful discussion, however, some superfamilial ranking has to be devised, and Corner himself of necessity uses currently accepted ordinal concepts for the discussion of his own results. Except for Magnoliales, however, he recognises no assemblage of corresponding rank, referring to the groups of families having the same seedcoat characters simply as "alliances". The question then is, how will the information he provides be assimilated into plant systematics? Not, it may be assumed, in the manner advocated by Omar Khayyam! The answer may be along the lines adopted by Dahlgren (*Bot. Notis.* 1975, **128,** 119) in his handling of the iridoid constituents. Their occurrence cuts across a number of taxonomic boundaries, both familial and ordinal, and to accommodate them he removes *Hydrangea* and *Escallonia* from Saxifragaceae and *Sambucus* from Caprifoliaceae, and together with other components erects a new, more comprehensive order, Cornales. This is then included, along with Ericales, Sarraceniales and Eucommiales (all of which contain iridoids) in a super-order, Cornanae, and this in turn is accommodated in close relationship with the other iridoid containing superorders Gentiananae (which includes Rubiaceae) and Lamianae, so that they occupy a well-circumscribed area in a diagram on inter-ordinal relationships. In this case, of course, the redistribution of families is relatively modest, but his spatial arrangement brings together several groups of orders hitherto regarded as widely separated. The same overall arrangement also accommodates in close proximity most of the families containing ellagitannins. It seems likely, therefore, that some at least of the features of the present work might be similarly assimilated into current systems without too much difficulty.

Examples of some phytochemically interesting conjuctions which catch the eye are: Combretaceae (much ellagitannin) with Rutaceae (without); Polygalaceae with Cruciferae (both with much sinapic acid); Proteaceae (now more usually associated with Rosales) with Papaveraceae; Dipterocarpaceae (much ellagitannin) with Malvales (without); and Melianthaceae (much ellagitannin) with Ranalean families (without). Most of the first-named in these conjunctions are variously—in fact dubiously—placed by modern systematists, and it will be interesting to see if Corner's contribution will help in bringing agreement closer.

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