

BOOK REVIEWS

Tropical Woody Rubiaceae, by E. Robbrecht. *Opera Botanica Belgica* Volume 1. 272 pp. Meise: Nationale Plantentuin van België. 1988. ISBN 90-72619-02-1. Softcover. No price given.

The premier issue of *Opera Botanica Belgica* is the first family-wide summary of the systematics of the Rubiaceae to appear in almost twenty-five years, bringing us up to date in virtually all areas of research bearing on the taxonomy of the fourth largest family of angiosperms (637 genera and roughly 10,700 species). Most of this well organized study describes and evaluates "characteristic features" (especially morphological and anatomical features) of Rubiaceae that have been, or might be, employed by taxonomists. Discussion extends to idioblasts, exudates, crystals, ariloids, ant and mite associations, bacterial and fungal interactions, pollination biology, dispersal biology, biogeography at the generic and tribal levels, and much more. The new classification follows from a re-evaluation of the characters as well as the taxonomic schemes proposed by Schumann (1891), Verdcourt (1958), and Bremekamp (1966). Dr. Robbrecht convincingly argues that division of the family into four subfamilies and more than forty tribes yields an improved alignment of morphological and anatomical data that is also supported by chemical and cytological information, as scanty as that often is.

Woody Rubiaceae are emphasized, but herbaceous (and mostly temperate) taxa are included in the proposed classification, which extends to the entire family. Herbaceous species are present in less than 20 percent of rubiaceae genera, and their repeated derivation from woody ancestors is evident. Another admitted bias is toward Old World (especially African) genera, and the subfamily Ixoroideae, which is where the author has much research experience, and where our knowledge of the family is thus relatively far advanced. Robbrecht's reliance on floristic as well as monographic research is evident throughout, and one senses that years of "routine" herbarium identifications have contributed substantially to his comprehensive view of character distribution in the family.

The discussion of "characteristic features" is presently the most reliable and accessible exposition of morphological and anatomical variation in the Rubiaceae. Terminology pertaining to trichomes, the wall structure of exotesta cells, colleters, and inflorescences is expanded and clarified. For example, the anomalous "hairs" on *Hillia* seeds are shown to be highly divided wings. The discussion is thorough and unambiguous, an exception perhaps being the distinction between "fang" and "climbing" hooks in some lianas (if indeed they are different structures), and the characterization of *Airosperma* as having corolla lobes contorted to the right, an error apparent in Schumann's original illustration where both left- and right-contorted corollas are figured.

The author often suggests the adaptive significance of characters, although

where data are slim the conclusions are necessarily tentative. Robbrecht does not over-speculate, and for a few systematically significant features—such as ovule number or exotesta cell anatomy—he advances no adaptive explanation. Is there a correlation between seed coat anatomy and fruit type, perhaps?

The taxonomic value or “reliability” of characters in distinguishing genera, tribes, and subfamilies is illustrated with reference to their use in prior systematic studies. The many characters deemed useful only at lower taxonomic ranks are, of course, those that exhibit strong homoplasy among the tribes. Other potentially useful characters, such as stipule ontogeny and vascularization, pollen, and fruit-production strategies, are still insufficiently known to be of much systematic value at the tribal level.

Homoplasious evolution is also strongly suggested for many characters when they are mapped against the author’s proposed classification in a series of Venn diagrams. This mapping method, where tribes are represented by circular shapes, allows the “placing” of taxa in the system without implying a specific phylogeny. Probable instances of convergence include reduction in the number of ovules per ovary locule and presence of raphid crystals—characters that served as the basis for subfamilial circumscription by Schumann (in the case of ovule number) and by Verdcourt and Bremekamp (for raphides). Other instances of convergent or parallel evolution include tetramerous flowers, a tendency for increase in flower parts (pleiomery), corolla lobe aestivation, dioecism and heterodistyly, and development of a stylar pollen-presentation mechanism. The parallel evolution of small fruits in both Old and New World Gardeniineae is an example of how data from floristic studies contribute to evolutionary hypotheses.

Robbrecht’s classification purports to delimit “natural” taxa, and is “evolutionary” in the sense that paraphyletic is accepted while polyphyletic is not; he considers phylogenetic classification of Rubiaceae to be an eventual goal. (Garcia Kirkbride’s (1982) phylogeny of Rubiaceae subfamilies based on two characters, and Bremer’s (1987) study of Argostemmateae and Hamelieae are among the very few explicitly cladistic investigations carried out for Rubiaceae.) Robbrecht emphasizes taxa that are “intermediate,” linking higher groups, when discussing relationships. He accepts the supposition (F. Hallé, 1967) that Ixoroideae are the most primitive subfamily, but further phylogenetic speculation is limited (indeed, “phylogeny” does not appear in the index), although evolutionary trends are hypothesized for nodal anatomy, stipules (four per node is primitive and rare), and habit (herbs are advanced). Placental evolution is outlined for Hedyotideae (from phyllospory to stachyosporry) and for Rubioideae (from pluriovulate to uniovulate placentas). For broader phylogenetic hypotheses, the available data base seems yet inadequate.

Looking for overall correlations among characters, Robbrecht abandons the single-character criteria previously employed to align genera and tribes. The result is a scheme that resembles Schumann’s classification in some important respects, but cannot be considered a return to the “classical” systems of the nineteenth century. Bremekamp’s small, segregate subfamilies are rejected, as is Verdcourt’s apparently unwarranted reliance on raphid crystals as the pri-

mary defining feature of Rubioideae. Two examples give an idea of the extent of Robbrecht's rearrangements, as well as the rationale informing them.

Subfamily Rubioideae contains, "without doubt, the most advanced members of the family," i.e., the largely herbaceous tribes. The subfamily includes all tribes assigned there by Bremekamp, except Knoxieae and Craterispermeae (moved to Antirheoideae), as well as Ophiorrhizeae (placed by Bremekamp in Urophyllloideae), and Pomazoteae (placed in its own subfamily by Bremekamp). While possession of raphids was essential for membership in Rubioideae in the systems of Verdcourt and Bremekamp, Robbrecht points out that it cannot stand alone as a defining feature, since species possessing raphides are manifestly related to others without them. Robbrecht identifies multiovulate and uniovulate tribes as comprising two major groups within the subfamily, the uniovulate group being the more "natural" (monophyletic?), but some Morindeae—usually with one ovule per cell—may sometimes have two. The Hedyotideae "indicates that a link between the two [tribal groupings] seems plausible. This same tribe seems to link the subfamily Rubioideae with the Cinchonoideae, viz. the Isertieae." The tribes Anthospermeae, Paederieae, Theligoneae, Spermacoceae, and Rubieae show a trend toward dry fruits as well as herbaceous habit.

Subfamily Antirheoideae is the most heavily emended of Bremekamp's and Verdcourt's subfamilies—by them restricted to tribe Guettardeae—but here greatly expanded to include Alberteae, Knoxieae, Vanguerieae, and Chio-cocceae, these last tribes distributed to other subfamilies by Verdcourt and Bremekamp on account of presence of raphides or appreciable endosperm. Robbrecht's Antirheoideae is essentially a reconstruction of Schumann's [supertribe] "Guettardinae," members of which "show so striking similarities in their flowers and fruits, that Bremekamp's and Verdcourt's dispersal of the "Guettardinae" over different subfamilies resulted, no doubt, in a more artificial classification." To this re-expanded subfamily Robbrecht also assigns the Retiniphyllae, Cephalantheae, and Craterispermeae.

The gaps in our rubiaceaceous knowledge are many and wide, and Robbrecht calls for survey-type studies to establish the limits of tribes Cinchoneae, Condamineae, Rondeletieae, and Isertieae. In the Antirheoideae, the tribal position of many genera is uncertain, and this is also true for Psychotrieae, where delimitation of the enormous *Psychotria* is a problem. Modern revisions are lacking for many genera, and our knowledge is uneven geographically. The least well known Rubiaceae are in Malesia and Madagascar, where groups often have an important bearing on an understanding of African and Asiatic taxa. Concerning Madagascar, the study of Rubiaceae is "practically dormant" while relentless deforestation results in the continuing loss of species. The study of Australian and New Caledonian Rubiaceae is said to be in a similarly quiescent state. In the *Flora Neotropica* series, a single monograph (on the three genera of Henriquezieae) has appeared—more quiescence.

Perhaps only a fragment of living tropical woody Rubiaceae will be saved for future investigation, but an enormous and hardly exploited resource of evolutionary data is already present in systematic collections. Robbrecht shows

us how those data can be extracted and what we should be looking for. As a minimal data set that should be assembled for the whole family (presumably for all genera) he suggests the following: presence or absence of raphides; anatomy of external hairs; corolla aestivation; data on floral biology; anatomy of seed exotesta; and pollen type (position, number, and type of apertures and features of the exine). This is, of course, far from what might be achieved with concerted and coordinated effort, namely an exhaustive, accessible, perfectly comparable, and thoroughly vouchered data base for Rubiaceae worldwide. The present study makes it plain that a lot of information can be gathered using the simplest techniques.

As a reference work, Dr. Robbrecht's monograph is excellent. In the exposition of his proposed classification, he gives the principal features of each suprageneric taxon, references to previous studies bearing on tribal classification, and a summary of geographical distribution. All included genera are listed for each tribe and subtribe. Among the appendices is a list of all accepted generic names and synonyms with tribal assignment—the first such published index in nearly a century. The bibliography of about 300 references includes the pages where each is mentioned in the text (a very useful feature), and in the subject index the main place of discussion is set in bold type. The taxonomic index also includes page references to Schumann, Verdcourt, and Bremekamp. Typographical errors are few, and I found only two cited references omitted from the bibliography. Commenting on the task of assembling and arranging so much material, the author admits that the Rubiaceae are “so vast a family that a single researcher cannot hope to gather all essential taxonomic data for an in-depth analysis.” But some researchers are evidently better equipped to do so than others. Addressing Volken's question of how Schumann's great productivity might be explained, Stafleu and Cowan (1985) suggest that “a really convincing and comprehensive answer is not possible.” Schumann's industry, and that of his successors in Rubiaceae systematics—Verdcourt, Bremekamp, and Robbrecht—is an inspiration.—S. P. DARWIN, Department of Biology, Tulane University, New Orleans, Louisiana 70118.

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Wayside Trees of Malaya, by E. J. H. Corner. ed. 3. Kuala Lumpur: The Malayan Nature Society, 1988. 2 volumes, 861 pp., 236 plates, & 260 figures. ISBN 967-99906-0-5. Hardcover. No price given.

Out of print for decades, that triumph of natural history, the *Wayside Trees of Malaya*, has now appeared in a new edition.

The *Wayside Trees* describes the commonly cultivated species and the frequently encountered indigenous trees of one equatorial country, but its value is global. Professor Corner pioneered the objective description of tree shape, bark morphology, and mode of growth. His observations on phenology and reproductive biology are still unexcelled; his narrative remains provocative and totally absorbing.

The form and content of the original 1940 edition remain essentially unchanged, though it is a little sad that the quality of printing has declined, particularly with respect to the illustrations. Nomenclature has been meticulously checked. The accounts of several families are now illuminated by the author's "Durian Theory," to which his researches on Malaysian trees gave birth. Other new information includes Hallé and Oldeman's on tree branching patterns, Koriba's on modes of growth, and Medway's on phenology. The essay on the natural history of figs is embellished with fascinating additions. The section on trees of local interest has been brought up to date and expanded with the author's astute eye and acerbic wit.

By and large the family and species descriptions stand firm also. This is because they remain based on opinion derived from Corner's own field observations within one country. Generally, his family and generic concepts are broader, and his species narrower than are currently common in the Far East, concepts that are under the spell of "Flora Malesiana." Nevertheless, the Bombacaceae are now separated from the Malvaceae, and the Moraceae and Ulmaceae from the Urticaceae (where *Streblus* becomes four genera); the Anisophylleaceae are retained; but *Ixonanthes* and *Erythroxylum* are kept together on the basis of their seed structure; *Irvingia* remains in the Simaroubaceae; the Chrysobalanaceae in the Rosaceae; and *Duabanga* and *Sonneratia* in Lythraceae. Various satellites of the Euphorbiaceae are retained in that family. The original generic definitions and names in such families as the Rosaceae (Chrysobalanaceae), Apocynaceae, Rubiaceae, and Leguminosae, where they have been under recent fissiparous scrutiny, have been maintained. Langsats and dukuns are placed in one species, as are the forms of *Allophylus*, but not those of *Pometia*. This is the work of someone who knows the plants and only makes changes when personally convinced.

Everywhere, Corner's continuing love of Malaya, its people, and its forests shines through the text. Considering the more than forty years of change of old forests to plantations, lanes to superhighways, and villages to cities that have elapsed, it is not surprising that many of the trees originally illustrated have gone. Amazingly, some also remain—it is always fascinating to learn how they

have survived. This should challenge the Malayan Nature Society to search for others that are still alive.

As testimony of the continuing value and majesty of this masterpiece to the public, the embarking graduate student, and the experienced scientist alike, the following is taken from a new passage in the introduction to the *Dipterocarpaceae*: "When we look upon the lowland forest or gaze up into its vaults, we see the canopy of dipterocarps whose sombre crowns compose very largely the ocean of trees that once covered the Malay Peninsula. . . . This glorious spectacle has been whittled away in the course of civilization, decimated this century by commercial logging, and now, with urban demand for agriculture, it is in danger of disappearing. Vast trunks thunder along highways to saw-mills, apparently from nowhere, and revenue accrues, but where can the citizen, the biologist, or the visitor see these fabulous giants—the most majestic trees that any land produces? One would have thought that such a national heritage should have been guarded zealously. There remain, fortunately, some tracts of this lowland forest preserved in catchment areas, national parks, forest reserves and game reserves though, as the shortage of timber increases, they may be deprived."—P. S. ASHTON, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138.



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