

couveringi and *P. gordonii* as valid species in a distinct subgenus was previously advocated by Andrews alone. The phylogenetic implications of this assessment are clear, and the chapter should promote critical testing of the hypotheses.

Chapter 9 is devoted to *Ramapithecus*. New finds in the Siwaliks and the discovery of the generalized hominid species *Australopithecus afarensis* imply that the hominid status of *Ramapithecus* may be less secure than Simons and Pilbeam suggest here. Pilbeam's newer interpretations (*Nature* 270, 684 [1977]), written later than chapter 9, are far more concordant with the evidence. They effectively make this chapter a historical curiosity.

Howell's chapter "Hominidae" is a book within a book. Its 95 pages (many in reduced print) and bibliography of 656 entries reveal an attention to detail that draws on years of personal study of the original fossils. Its systematic content will surely kindle debate.

In contrast, the chapter on Carnivora by Savage is disappointing. Its admitted shortcomings include superficial, secondhand treatment of the Plio-Pleistocene carnivores and judgments "made from intuition rather than from experience" (p. 250). The combination of Copen, Maglio, Madden, and Beden fares much better in its expert treatment of the proboscideans. The observation that isolated Plio-Pleistocene elephant molars are often insufficient for precise biostratigraphic correlation is particularly significant. Harris furnishes a fine chapter on deinotheres and barytheres. Churcher and Richardson deliver a chapter on Equidae containing a handy keyed species list and series of site maps.

Cooke and Wilkinson's chapter on Suidae and Tayassuidae uses a valuable discussion of the modern African pigs to introduce the fossils. Cooke's reconstruction of Plio-Pleistocene suid phylogeny has converged dramatically with that of White and Harris (*Science* 198, 13 [1977]). Reference to the latter work appears in Howell's chapter but is curiously absent from Cooke's. Hamilton's review of Cervidae and Palaeomerycidae is in fascinating contrast to the traditional approaches taken by many other contributors. The benefits of his Hennigian methodology are familiar, but the costs are tellingly illustrated as he is left grappling with parallelism, convergence, and fragmentary fossils. Gentry's effort on Bovidae could have been a detailed and complex account, but he donates a solid, lucid, and compact interpretation of the

evolution of this family. Maglio attempts a final synthetic chapter on patterns of African mammal evolution but faces a frustrating statistic—by his own account probably over 80 percent of Africa's former mammal taxa are undiscovered.

The book is full of fascinating and enjoyable detail ranging from Meyer's biblical citations concerning hyracoids to Patterson's description of skeletal specializations in the aardvark. Bits of humor are also found scattered among the dusty bones. Simons, Andrews, and Pilbeam describe 1907–08 Fayum fossil collector Richard Maarkgraf as being alone or with one assistant in the desert and "always traveling on camelback." In obvious reference to a modern fieldworker with considerably more *National Geographic* exposure they add parenthetically, "We have no way of knowing whether or not he smoked a pipe while riding about" (p. 123).

If a common theme characterizes this volume it is the need for much more research. Enormous gaps in our knowledge of African mammal evolution remain. Both larger and smaller gaps must be bridged before we can effectively begin to test the implications of the quotation from Charles Darwin on phyletic gradualism that prefaces the book.

Evolution of African Mammals should remain a major source of data for years to come. It will foster paleontological research because it so accurately defines our knowledge. Its ultimate success should therefore be measured by how soon its chapters need major revision.

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The Formation of Trees

Tropical Trees and Forests. An Architectural Analysis. F. HALLÉ, R. A. A. OLDEMAN, and P. B. TOMLINSON. Springer-Verlag, New York, 1978. xviii, 442 pp., illus. \$62.50.

An architectural analysis implies an understanding of the precise manner in which a structure is assembled. This book achieves just such an understanding with a far-reaching approach that is not confined to tropical trees and forests but is applicable to temperate trees, shrubs, lianes, and herbs, indeed to all types of plants and plant communities. The book represents a breakthrough in the understanding of the nebulous concept of plant "form." It brings together for the first time in English the tenets of

botanical architecture contained principally in the work of Hallé and Oldeman published in 1970 and that of Oldeman published in 1974, along with isolated ideas and specialized terminology from earlier literature.

The authors demonstrate convincingly that the trunk and branches of any tree develop according to a highly organized basic model, which represents its inherited architecture. A tree as it grows from a seed will undergo a set sequence of branching and may present at this stage a rather formal and symmetrical appearance, which some trees maintain into the adult phase (firs, "pagoda trees," and the monkey puzzle). More usually, however, the architecture of an individual tree becomes modified, and to the casual observer more confusing, by continued reduplication of the initial model. Environmental factors (damage or enhanced light conditions, for example) cause dormant buds to develop, initiating a new sequence of branching organized in exactly the same manner as that of the model developed from the seed. The authors term this process of elaboration "reiteration." The concepts of model and of reiteration, then, allow both an understanding of the apparent complexity of most mature trees as individuals and an insight into the dynamics of the growth of a forest.

The book falls into three sections, although they are not delimited as such in the table of contents: general morphology, individual tree structure, and forest structure. Many general aspects of the morphology and morphological development of trees are introduced, together with the various features of tree growth that differentiate between the models to be described in the heart of the book. In reading this first section, particularly chapter 2, the reader will have to brush up his or her vocabulary in order to follow the subsequent arguments. Contrasting pairs of characters applied to meristem, bud, and shoot development abound. Thus we find preformation and neoformation, primary and secondary orientation, continuous and diffuse growth, monopodial and sympodial growth (compare Corner, 1940), basitonic and acrotonic development (compare Champagnat, 1965), single modules and relay axes (compare Prevost, 1967), apposition and substitution growth (compare Koriba, 1958), prolepsis and syllepsis, plagiotropic and orthotropic branches, and so on. Admittedly, the use of these terms avoids a lot of tedious description, but the reader will need to keep one finger permanently in the ex-

tensive glossary in which some 160 terms used in the book are explained. We learn, for example, that a treelet is a small tree. (In addition to the glossary, there are complete subject, species, and author indexes.) Among the fairly numerous minor faults throughout the book, the occasional transpositions of paired characters are ones that certainly puzzle the reader.

The central part of the book is devoted to a detailed study of the architectural models of tree growth that were first recorded in Hallé and Oldeman's 1970 publication. Twenty-three models are described, each identified by the name of a botanist who has, perhaps unwittingly, contributed to the knowledge of the structure of trees whose developmental sequence of branching conforms to that particular model. The bamboos, for example, mostly demonstrate McClure's model, the pleonanthic palms Corner's model. (The authors' interpretation of "tree" is very broad.) A reasonable justification for naming the models in this manner is presented. The models are mostly distinguished according to their various features as follows:

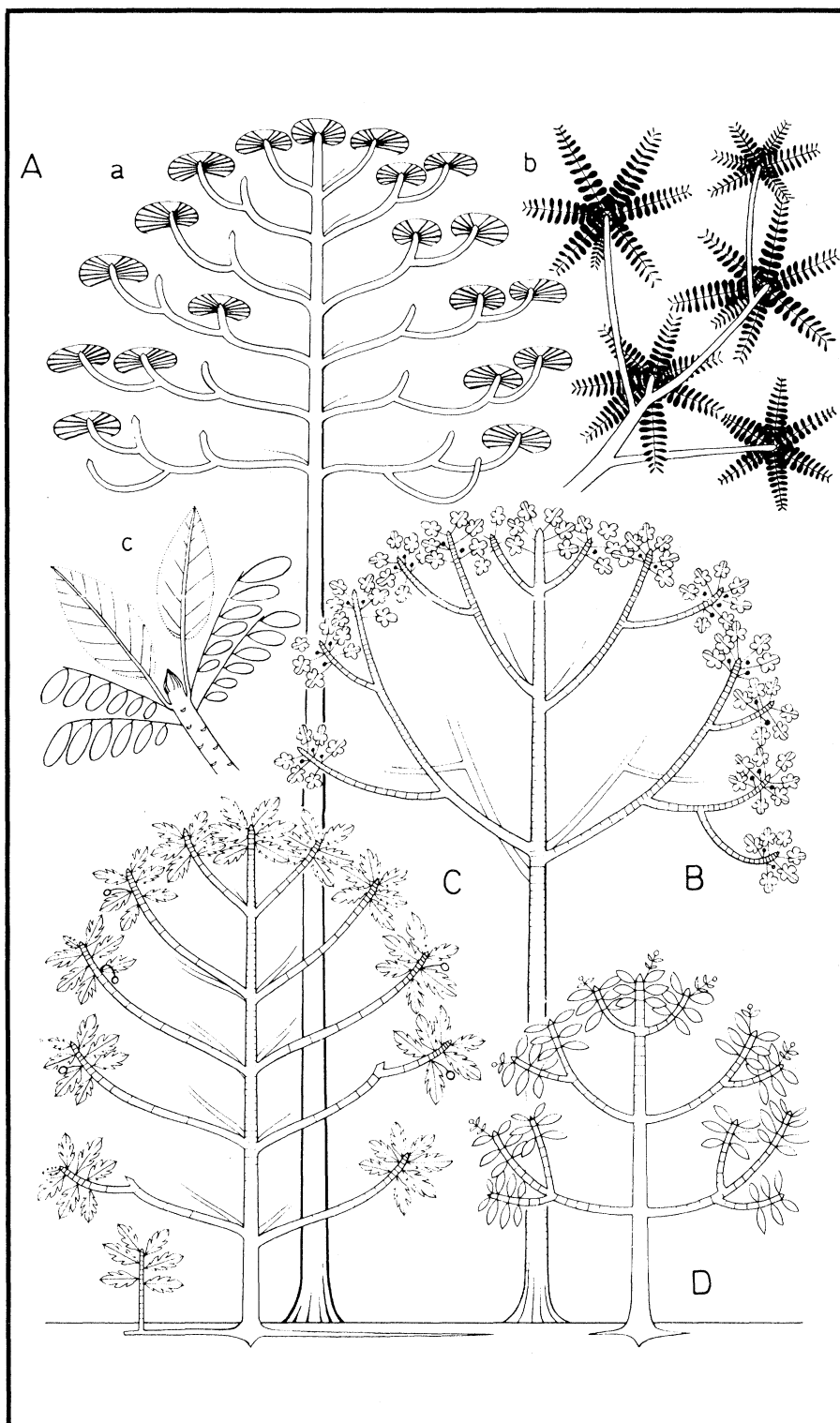
- Unbranched Trees such as palms.
- Branched Trees that have varying combinations of dichotomous features such as sympodial or monopodial trunk, branches or both, continuous or rhythmic growth, terminal or lateral inflorescence, and orthotropic or plagiotropic branches.
- Branches
 "mixed" Trees in which an axis develops vertically as part of the trunk and then sideways as a branch, with vertical growth continued by a lateral bud.

Each model is defined and illustrated with examples and numerous photographs and excellent diagrams—the clear diagrams are one of the delightful features of the book. Due consideration is given to details of variations, but it is emphasized that the models are intended to function as a fundamental guide to tree construction, not as mere pigeonholes for classifying tree types. Each model is discussed in terms of its possible "strategy." The ecological implications of the differences between the various models give rise to many intriguing questions; the ability to describe the form of trees in a real manner is so new that the authors'

comments on the ecological strategy of trees must be speculative. An illustrated dichotomous key is included, which emphasizes the importance of development in the concept of the model.

The authors continue by discussing reiteration, which they define as "any modification of the tree's architecture

not inherent in the definition of its model and which is occasioned by damage, environmental stress or supra-optimal conditions" or, more simply, "effectively a second tree, showing the same model has been substituted for (or added to) the first." A young tree will present an initially uncluttered model that will become



Examples of one model (Rauh's) of tree architecture. (A) General architecture, disposition of newly expanded leaves, and axillary flowering of *Entandrophragma utile* (Dawe) Sprague. (B) *Macaranga aleuritoides* F. von Muell. (C) *Artocarpus incisa* Thumb. (D) *Kalanchoë beharensis* Drake. [From *Tropical Trees and Forests*]

more and more elaborate as it gains reiterations.

Having established this basic and novel understanding of the dynamics of tree growth, the authors proceed to consider trees in their environment. There is considerable discussion of the general topic of energetics and a preoccupation with height-diameter ratios and volume-surface relationships, with the emphasis on qualitative rather than quantitative data. It is quite clear, however, that the authors' understanding and interpretation of the forest springs from many hours of thought in the forest rather than in an armchair. Just as the growth of a single tree is seen as a continuous process of developmental adjustment, so is the growth of the forest. Profile and plan diagrams of a number of forest plots are presented at static moments in time, as is conventional, but it is stressed that the forest is a dynamic structure and that the trees within it may be recognized as "trees of the past, trees of the present, and trees of the future" depending upon their status, that is, their future growth potential. The trees of the future constitute a "set" of the future, suppressed by the set of the present (although they may all be the same age), marking time until favorable conditions lead to an increase in growth. The authors maintain that the concept of "succession" oversimplifies the process; any apparent layering that is seen is a passive phenomenon of a transitory nature. The details of individual tree growth presented earlier in the book now begin to make additional sense. We are reminded that as a tree reaches its prime as a tree of the present the accumulating reiterations become progressively smaller; the location of the lowest reiteration usually corresponds to the location of the lowest branch on the tree, this point being designated the morphological inversion point of the tree. This leads to a recognition of the morphological inversion surface within a forest with an influence on microclimate and hence to an ecological inversion surface representing a particular balance of light and humidity.

The book is full of such refreshingly new ways of considering the tree and the forest, and it demands to be read a little at a time, slowly and repeatedly. The shape of a plant is fundamental to its existence, and the understanding of tree shape has itself been a slow process of growth, reiteration, and eventual blossoming.

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A Tropical Flora

Flora of Barro Colorado Island. THOMAS B. CROAT. Stanford University Press, Stanford, Calif., 1978. x, 944 pp., illus. \$55.

Western science has developed primarily in the north temperate zone, and the consequences for environmental biology have been profound; many of the earth's richest biomes are the least known. Though travel in the tropics has contributed significantly to the development of biological concepts, intensive long-term studies there have been rare. Until recently, relatively few biologists and very few research centers have been permanently located in species-rich tropical environments. One of the most important of such centers in the American tropics has been Barro Colorado Island, formed when the Panama Canal was built. Research on the island over the last 50 years has contributed significantly to our knowledge of the tropics. An important prerequisite for many kinds of research in an evergreen tropical environment is access to up-to-date information regarding the vascular plants. These plants form much of the community's structure, and they are its primary energy brokers. With the publication of Croat's long-awaited flora we now have the higher plants of this island at our fingertips.

Though only 15.6 square kilometers in area, Barro Colorado Island has by current count 1369 species of higher plants in 704 genera. Each of these species is keyed, described, and discussed in some detail in Croat's flora. The descriptions and keys are supplemented by over 550

of the author's photographs. The keys are well constructed and should offer no problems to someone with minimal botanical training, and there is a unique bonus. Near the end of the book are 47 pages devoted to a key to woody plants lacking both flowers and fruit. This key covers about 700 species and, considering how infrequently some woody plants produce flowers and fruit, should be one of the most useful parts of the book. At least one copy of the book has already been taken to Colombia for use in identifying lowland rain forest trees there. Small areas in lowland Colombia and Barro Colorado Island probably share more than 70 percent of their woody genera, enough for the key to those plants to be of considerable help. In fact, the keys should be useful over a wide area of lowland evergreen middle America.

The flora makes available much new information based largely on field observation. The 60-page introduction, which includes considerable information on flowering and fruiting phenology both for individual species and for the assemblage as a whole, will be useful in planning research projects and selecting species for study. Confusion of closely similar species and separation of "species" that are only parts of a single polymorphic population have been especially serious problems in the species-rich tropics. This book will help avoid these pitfalls and give both community ecologists and biologists working with specific taxa a better foundation on which to begin. A good bibliography, maps, and data on pollination and dispersal round out the volume.



Elaeis oleifera. [From *Flora of Barro Colorado Island*]