species of the genera *Haumaniastrum* (*8*) and *Crotalaria* (*9*) have been reviewed. Hyperaccumulators have been recently defined as plant species with a specified elemental content, which in the case of nickel is >1000 μg/g on a dry weight basis (*10*). Until now, the highest recorded copper concentration has been that of *H. robertii* (*2*), although further research (*8*) has shown that it contains considerably more cobalt than copper.

A survey of the copper content of various plants collected from Shaba Province, Zaïre (Table 1), carried out by atomic absorption spectrophotometry, has revealed the existence of a new hyperaccumulator (using the same 1000 μg/g criterion as for nickel): *Aeolanthus biformifolius* De Wild. (Labiatae). This species, which was previously only known from the vicinity to the Luiswishi Mine, has a very marked ability to accumulate copper. We have, however, recently discovered this dwarf perennial growing at the old "Mine de l'Étoile" and at the Ruashi Mine, both in the vicinity of Lubumbashi. From its present known distribution, it must be considered as endemic to the southern part of the Shaban Copper Belt.

There is a seasonal variation in the copper content of individual plant organs of *A. biformifolius*. Concentrations are lowest at the beginning of the rainy season and then increase rapidly with the development of the new corm, which is fully mature by the end of the rainy season some 3 months later. *A. biformifolius* should be considered as a copper flower for the southern part of the Shaban Copper Belt, since it appears to be confined to substrates rich in copper.

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Tree Branch Angle: Maximizing Effective Leaf Area

Abstract. *In a computer simulation of branching pattern and leaf cluster in* Terminalia catappa, *right and left branch angles were varied, and the effective leaf surface areas were calculated. Theoretical branch angles that result in maximum effective leaf area are close to the values observed in nature.*

The shape or geometry of a living tree has been related to its adaptive strategy for light interception (*1, 2*). The woody framework of branches presents the photosynthetic surface, the leaves, to sunlight in a manner that is primarily, but not totally, related to the photosynthetic efficiency of the leaf and the distribution of light in the environment of the tree. Horn (*1*), on theoretical grounds, has established two basic types of leaf distribution: the monolayer with leaves densely packed in a single layer, and the multilayer with leaves loosely scattered among many layers. Understory trees and forest floor species tend to be monolayered; canopy tree and pioneer species tend to be multilayered. Among crop plants, the shape of the leaf canopy (as determined by branch and leaf arrangement) directly affects light interception and, hence, productivity (*3*). In the simpler system of an individual leaf, the biophysical and adaptive significance of shape and orientation have been studied (*4*). Although the bifurcation ratio (a measure of the degree of branching) was shown to be greater in evergreen broadleaved trees than in deciduous ones (*5*), there are no published studies that quantitatively relate the parameters of tree branching to the interception of light by the leaf surface. The greatest obstacle to investigations of the adaptive function of branching pattern has been the three-dimensional complexity of tree branches and the varying orientation of the leaves borne by them. We present the finding that, in at least one tree species, the natural limits placed on branching and the asymmetry of branch angles observed in nature are, in fact, very close to theoretical values which maximize the effective leaf surface area (the horizontal projection of the leaf area), a feature with obvious adaptive value.

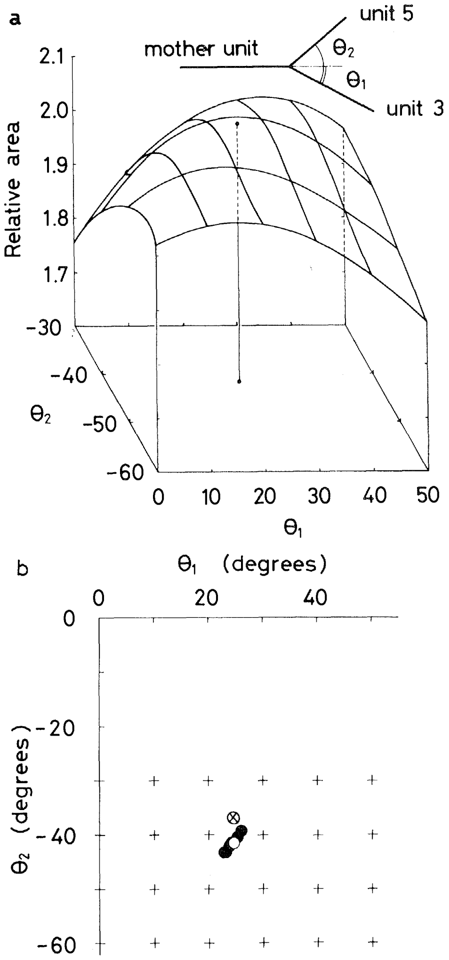

Fig. 1. (a) The effective leaf area versus θ_1 and θ_2. Conditions of the simulations are the same as Fig. 2. The maximum effective leaf area is shown by a vertical line indicating the optimal θ_1 and θ_2. Inset: explanation of branch angles θ_1 and θ_2. (b) Comparison of the actual θ_1 and θ_2 (⊗) with the optimal values derived from simulation in Fig. 2c. The conditions of the simulation are the same as Fig. 2. Results obtained with the six different values for the leaf disk radius between 0.7 and 0.9 (●), instead of 0.8 (○), are shown.

The tropical tree *Terminalia catappa* L. (Combretaceae) has certain architectural features that make it ideal for quantitative studies of branch pattern and leaf surface area. Its distinctive pattern of growth and development, *Terminalia*-branching, is widespread among tropical dicotyledonous trees (*6*). The tree, basically, consists of an erect leader axis with tiers of three to five lateral branches that result from periodic outgrowth of axillary buds and form a characteristic pagoda shape to the crown. The older lateral branches are horizontal and dorsoventrally flattened. Each lateral branch complex is composed of a repeating series of branch units, and each of these bears a cluster of horizontal leaves at its distal end (*7*). Therefore, most of the leaf surface of the tree is presented as a series of flattened layers, each one equivalent to a monolayer; these are well spaced along the trunk. Branching in *Terminalia* has already been studied quantitatively, and average values of different morphological parameters have been calculated (*8*). These ac-

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tual values and observed natural limitations to branching were combined with a previous theoretical model for treelike bodies (*9*) to develop a reliable computer simulation of tree geometry for this species (*10*). The treelike bodies in the original, theoretical model were developed with only two parameters, the ratio of mother to daughter branch unit lengths and the asymmetry of forking. Such asymmetric branching was substantiated in *Terminalia*. When two new branch units (unit 3 and unit 5) arise from the distal end of a previous unit (mother unit) there is a regular asymmetry in the branch angles (θ_1 and θ_2, respectively) (Fig. 1a). The cluster of seven to ten leaves at the end of each unit can be approximated by a horizontal disk at that point. Taking the shape and length of the leaves into account, we found that a constant radius of 0.8 times the length of the longest distal unit gave a reasonable approximation of the effective surface area of a leaf cluster, the area in horizontal projection (*11*). Our earlier simulation (*10*) showed that the natural limitations imposed on the degree of bifurcation increase the effective (that is, fully exposed) surface area of a branch, although the absolute area decreases. This was especially true when a branch tier simulation consisted of five branches, a number that occurs frequently in vigorous trees. Using an improved simulation procedure in which the total area of the branch tier is divided into Dirichlet domains (*12*), we calculated the effective leaf surface areas when θ_1 and θ_2 were varied (*13*). Representative drawings of such simulations with three orders of branching are presented in Fig. 2 (*14*). The area is plotted against θ_1 and θ_2 (Fig. 1a). The maximum area occurs when θ_1 and θ_2 are 24.6° and −41.4°, respectively (Fig. 2c). In nature, the observed values are 24.4° and −36.9°, respectively (*15*). Maximum surface area results when the angle between units 3 and 5 ($|\theta_1| + |\theta_2|$) is about 66°, whereas the observed angle is about 61°. The differences between calculated and observed values are probably not significant, considering the variation of the observed values (*15*). Several other values for disk radii (between 0.7 and 0.9, instead of 0.8) were also used for computing optimum values for θ_1 and θ_2 (Fig. 1b).

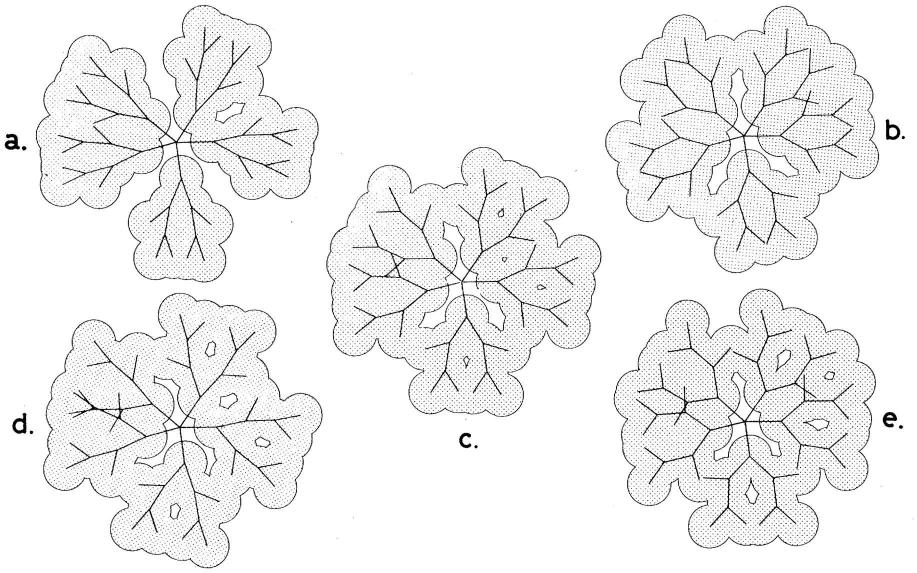

Fig. 2. Variation of the effective leaf area of a branch tier depending on the branch angles, θ_1 and θ_2. The tier of the five lateral branch complexes is simulated with three orders of bifurcation according to the rules of *Terminalia*-branching (*10*). The divergence angle of the first branch unit of each branch complex equals 138.5°. The sign of the branch angles of the first branch unit in each successive branch complex alternates (*14*). The ratios of branch lengths of units 3 and 5 to that of their mother unit are 0.94 and 0.87, respectively. The radius of the leaf disk approximation is 0.8 where the length of the longest distal branch unit is unity. Simulations of the branch tiers are projected on a horizontal plane. θ_1 and θ_2, respectively, are as follows: (a) 10° and −30°; (b) 40° and −30°; (c) 24.6° and −41.4°; (d) 10° and −50°; and (e) 40° and −50°. Maximum effective leaf area is (c).

The above results show that the observed branch angles result in the maximum effective leaf surface possible for a branch system that follows this pattern of branching. In addition, the natural constraints on bifurcation of lateral branches result in a greater effective leaf area per leaf cluster than when branching is unrestrained (*10*). This indicates that branching pattern in *Terminalia* is correlated with efficient presentation of leaf surface to direct sunlight rather than simply with maximum total leaf surface. We presume that the maximum effective use of full sunlight is an important adaptive feature in *Terminalia*, and that branch angles have been evolutionarily selected for this feature. Our presumption is reasonable for a species that grows naturally in open habitats of sandy beaches in southeastern Asia. Each branch tier is well-illuminated since there is little shading by the distant and alternating branch complexes of the other tiers. Unfortunately, there is no information on photosynthetic rates for this species. The pagoda shape of the tree means that the tree is essentially made up of a conical stack of monolayers, at least in the young tree. It is unclear how this relates to Horn's concepts of plant succession (*1*) since it combines features of both the monolayer and the multilayer.

Branch angles and ratios of sequential mother to daughter branch unit lengths are known to determine directly the overall geometry of a tree and seem to be intrinsic characteristics of a species (*9*). One such intrinsic characteristic, branch angle, is shown here to be adapted to the maximum and most efficient presentation of leaf area to sunlight. However, it would be too simplistic to relate observed parameters of tree architecture to optimal values of one biologically important characteristic such as effective leaf area. Even if we can define a group of parameters which are sufficient for the complete description of a tree, we still lack the necessary biophysical information to assign all or even the most significant biological function to any particular parameter, for example, exposure to sunlight, mechanical stability, or heat exchange, or their interactions. Nevertheless, the correlation of a known parameter (branch angle) to the maximum value of an obviously basic function (exposure to sunlight) is an important contribution to our understanding of the adaptive geometry of trees.

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13. The calculations were carried out by an electronic digital microcomputer with a disk memory (P652 and DAS 604, Olivetti). Simulations were drawn by an x-y plotter (WX535, Watanabe Sokuki, Tokyo).
14. The signs of θ_1 and θ_2 of the first bifurcation are reversed in each sequential lateral branch of the tier. All later bifurcations, however, follow the rules of the *Terminalia* simulation (*10*). The change in initial symmetry occurs in nature. We are presently investigating the effects of such natural symmetry changes.
15. The following are the means and standard deviations calculated for 65 bifurcations observed in nature: $\theta_1 = 24.4°$, $s_1 = 5.94°$; $\theta_2 = -36.9°$, $s_2 = 6.92°$; $|\theta_1| + |\theta_2| = 61.3°$, $s_{1+2} = 7.30°$. The previously published values for θ_1 and θ_2, 27° and −35°, respectively, were based on a more limited sample of bifurcations (*8*, *10*).
16. We thank J. E. Eckenwalder and P. F. Stevens for reading the manuscript. Supported in part by NSF grant DEB77-13953.

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Brachiopods: Biomechanical Interdependences Governing Their Origin and Phylogeny

Abstract. *The adaptive advantage of epibenthic articulate brachiopods over inarticulate forms resulted from a modification of the mechanics of shell opening from an indirect hydraulic system to a direct muscular one. As a consequence, the articulate brachiopods were able to reduce the complex muscular system of the ancestral inarticulates, freeing two-thirds of the space within the shell for enlargement of the feeding apparatus. The original hydraulic mechanism of the inarticulate brachiopods most likely evolved from the hydrostatic skeleton of metameric lower invertebrates, probably polychaete-like annelids, as shown by a biomechanical analysis. The transitional stages between such annelids and inarticulate brachiopods are presented and explained as adaptive improvements in body construction.*

The vast majority of brachiopods, or lamp shells, are epibenthic, sessile, suspension feeders. This relatively uniform way of life permits an easier comprehension of the structure and function of their morphology than of that in many other groups of organisms. Moreover, they are well suited for analysis of the biomechanics of each morphological feature and the interaction or interdependence of the individual parts of the apparatus comprising such biological systems as shell opening and feeding. A more detailed understanding of the biomechanics of these systems is fundamental for a better comprehension of the evolutionary history of the brachiopods, including their origin from lower invertebrates and the major phylogenetic changes within the group.

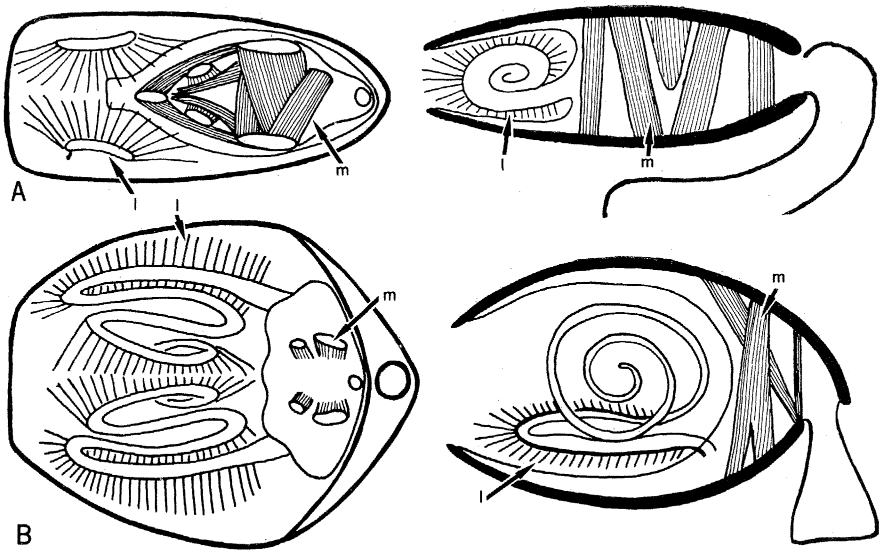

Fig. 1. Schematic representation of (A) an inarticulate brachiopod (*Lingula*) and (B) an articulate brachiopod (*Magellania*) in dorsal and lateral views to show the differential relationships between muscle (*m*) volume and mantle cavity volume with the contained lophophores (*l*). [Modified from figures of several authors (*15–17*)]

The major evolutionary advance within the lamp shells is expressed by the two major subgroups, namely, the primitive Inarticulata (brachiopods with valves not rigidly hinged to one another) and the advanced Articulata (those having a hinge of interlocking teeth and sockets between the valves). A comparison of the muscular systems and the lophophores (food gathering and respiratory apparatus) of typical representatives from both groups (Fig. 1) shows that in the Inarticulata most of the space within the shell is occupied by muscles and coelomic cavities, while in the Articulata the anterior two-thirds of the shell interior is occupied by the lophophore. Two questions come to mind immediately. Why do these differences exist, and how can the direction of evolutionary change be ascertained within the lamp shells?

The answer to both questions lies in the mechanism of shell opening in the two groups and in the consequences of the modification of this mechanism for the rest of the morphology of the brachiopods. The muscular system that opens the shell in the Articulata has been described and is understood clearly, but little has been written about the morphology and function of the shell-opening mechanism in the Inarticulata. An examination of the anatomy of the latter revealed that they open their valves by an indirect hydraulic system. They lack directly acting opening muscles such as those of the Articulata. Instead, the Inarticulata possess a set of longitudinal muscles that run obliquely through the body and have one end attached to the posterior end of the ventral valve and the other end inserting into the soft body of the animal (Fig. 2). On contraction, these muscles pull the body into the posterior part of the shell. Because of the constant volume of the fluid-filled coelom, the body swells in other directions. Lateral swelling is prevented by two partitions (the gastroparietal and ileoparietal "bands") in association with the laterally positioned longitudinal muscles; consequently, the body can expand only dorsoventrally and hence forces the shell open. Harmful deformation of the body and lateral shifting of the valves are prevented by a complex muscular system. Such a system is indispensable in the few inarticulates (lingulids) that burrow with a valve-shifting mechanism (*1*). However, for all epibenthic brachiopods, any evolutionary change that permitted a reduction of the muscular-coelomic apparatus and a consequent enlargement of the mantle cavity with its lophophores

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