Architecture and Phyllotaxis of
Anisophyllea disticha (Rhizophoraceae)

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Conspectus

Abstract

Anisophyllea disticha does not show distichous phyllotaxis. Erect (orthotropic) shoots with $\frac{2}{5}$ spiral phyllotaxis and radial symmetry give rise to tiers of sylleptic branches at regular intervals. The branches are horizontal (plagiotropic) and have marked dorsiventral symmetry. Their phyllotaxis is unique and consists of four ranks of alternately arranged leaves, two ranks of scale leaves on the dorsal side and two ranks of foliage leaves on the ventral side, dorsal and ventral leaves of the two ranks alternating regularly along the stem on opposite sides. Homology between the three kinds of leafy appendage is indicated by their constant unilacunar node, but dorsal (adaxial) scales on plagiotropic axes do not subtend axillary buds. The leaf arrangement is assumed to maximize photosynthesis and corresponds closely to ideal systems established by theoretical considerations.

Introduction

In the present study attention is drawn to some aspects of morphology and anatomy of a species of *Anisophyllea, A. disticha* (Jack)Baillon which allows a better comparison with its putative relatives. The genus *Anisophyllea* R. Br. ex Sabine includes about 25 species of trees and shrubs distributed primarily in tropical Africa, Ceylon, India and Southeast Asia (Ding Hou, 1958). Its relatively recent discovery in South America (Sandwith, 1952) where 3 species are presently known (Pires and Rodrigues, 1971) makes its known range almost pan-tropical. Species vary from treelets of the lower forest storey to tall, canopy trees.

The taxonomic position of *Anisophyllea* is somewhat controversial. Most authors have included it in the Rhizophoraceae, usually within a separate tribe
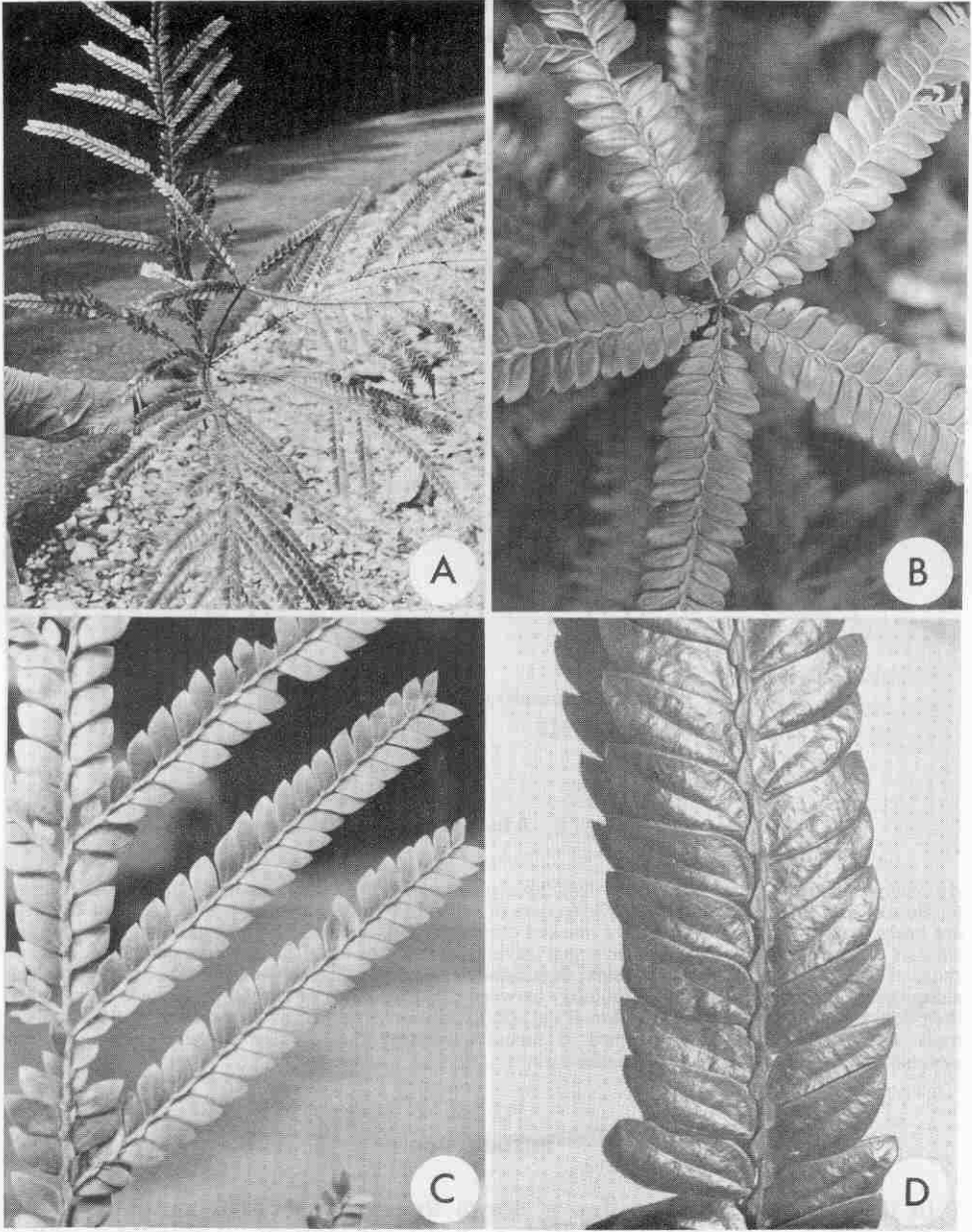
Plate 1. *Anisophyllea disticha*

    A. Habit of sapling, obliquely from above.

    B. Terminal tier of 5 plagiotropic branches from above, apex of orthotropic axis quiescent.

    C. Part of plagiotropic branch tier from above, with second-order branches.

    D. Detail of plagiotropic branch from above showing pronounced anisophylly.

    A and *C* from Ektachrome transparencies provided by Dr. J. B. Fisher (Kedah collection); *B* and *D* from Singapore collection.

Anisophylleae, together with *Combretocarpus, Polygonanthus* and *Poga*. These four genera differ from other members of the family in having alternate, exstipulate leaves (rather than opposite, stipulate leaves). The other three genera in the tribe have more limited distribution than *Anisophyllea: Combretocarpus* (1 sp.) is restricted to Sumatra and Borneo, *Poga* (1 sp.) to West Africa and *Polygonanthus* (2 spp.) to Amazonia (Pires and Rodrigues, 1971). This tribal aggregation is strongly supported by evidence from wood anatomy (van Vliet, 1976). A contrasted view is to segregate a separate family Anisophylleaceae (Schimp.)Ridl. (e.g. Takhtajan, 1969; Airy Shaw, 1973), but van Vliet points out similarities of the Anisophylleae to other Rhizophoraceae especially in its resemblance to the tribe Gynotrocheae.

It should be useful to establish the comparative phyllotaxis of members of the family, since the contrast between the tribes in this character is extreme. *Anisophyllea disticha* is significant in this respect because of the pronounced heterophylly of some of its axes which might represent a transition between the stipulate and exstipulate conditions, especially as the smaller leaves are often described as "stipule-like".

Anisophyllea disticha, "leechwood", is restricted to the Malay Peninsula, Sumatra and Kalimantan (Borneo) where it is a characteristic understorey treelet up to 7.5 m high occurring on a diversity of soils, ranging from swampy areas to drier granitic sands and ridges (Ding Hou, 1958). According to Hallé *et al* (1978, p. 200) the architecture of some *Anisophyllea* species represents an extreme expression of Massart's model, which refers to trees with an orthotropic, monopodial trunk which grows rhythmically and produces tiers of plagiotropic branches at regular intervals. *Anisophyllea disticha* in particular, stands apart from most other members of the genus in the extreme plagiotropy of the horizontal branches which are anisophyllous, with an apparent distichous series of scale leaves superimposed on the distichous foliage leaves (cf. Tay, 1977). This condition is occasionally found in *A. scortechinii* so that there is a possible phyletic link between *Anisophyllea disticha* and the rest of the genus (Ding Hou, 1958).

The present study establishes to what extent the phyllotaxis of the plagiotropic, anisophyllous branches is primary (i.e. determined by their method of inception at the shoot apex) or secondary (i.e. modified by later re-orientation through differential growth or torsions). Previous description has not addressed this problem (e.g. Ding Hou, 1958) and has not described microscopic details of anatomy of different leaf types (cf. Geh and Keng, 1974).

Materials and Methods

Two collections of fluid-preserved (FAA) material which included young orthotropic and plagiotropic axes were available for this study (J. B. Fisher, 5.vii.77, Kedah Peak, Malaysia and P. B. Tomlinson, 5.viii.82, Garden's Jungle, Singapore Botanic Gardens).

The distal 1 to 2 cm of a number of both types of axes were embedded in "Paraplast" and then serially sectioned at 8 μ with a rotary microtome. The sections

were mounted on slides and stained in safranin and fast green. In order to facilitate investigation of leaf development and nodal anatomy the individual sections were photographed in series through a Wild microscope with a Bolex movie camera, using the cinematographic drawing method described by Zimmermann and Tomlinson (1966).

Single transverse and longitudinal sections of mature leaves from these two collections were also prepared, using a sliding microtome to cut sections of 20-30 μ. These sections were mounted in glycerine and examined unstained. Finally, leaves from these collections were cleared in 5% alcoholic NaOH and examined unstained.

Diversity in external leaf size, form, and disposition was explored by examining the collections of *A. disticha* in the Harvard University Herbaria, which consisted mainly of plagiotropic axes.

Results

Architecture. Massart's model is well represented by this species in the orthotropic (trunk) axis which produces a tier of horizontal plagiotropic axes (branches) at wide regular, intervals (Plate 1A). There are usually 5 branches in each tier (Plate 1B). Our material did not include seedlings but the older trunk axis which we studied seems similar to the seedling axis described by Geh and Keng (1974). Germination is described as hypogeal and the plumule bears spirally-arranged scale leaves. Growth of the axis is rhythmic, eventually with the production of a tier of branches at the end of each of flush. We have had no opportunity to make extensive phenological studies but the apex of the orthotropic shoot immediately above the tier undergoes an extended period of rest before growth is renewed and the next vertical increment is made. Individuals within a population seem asynchronous with regard to flushing since orthotropic shoots at various stages of development can be found at any one time. Field study of marked individuals is needed, however, to monitor events precisely.

Leaves on orthotropic shoots are spirally-arranged with $\frac{2}{5}$ phyllotactic arrangement (Fig. 1A, 2A). At maturity the leaves are separated by extended internodes at the base of the shoot, but they are crowded towards the region of tier insertion. Leaves are scale-like, usually appressed to the stem and each subtends a minute lateral bud which normally undergoes no further development (Fig. 2D). Leaves towards the end of the flush are somewhat larger than those found at the beginning. Branches (Fig. 1A, arrows) are produced at the end of each flush by syllepsis (Hallé *et al.*, 1978), each branch subtended by a scale leaf. Usually five branches are produced i.e. one for each orthostichy in the phyllotactic spiral (Plate 1B). The subtending leaves apparently represent the last 5 leaves of the series produced by the apex of the orthotropic shoot before it undergoes rest. Although there is a short hypopodium, there is something of a transition in leaf size along the axis at its base (Plate 1B).

Branches extend almost horizontally and are markedly dorsiventral. They branch infrequently to produce daughter axes of a second and even third order which repeat

the plagiotropic organization (Plate 1C). Evidence for rhythmic growth of these plagiotropic axes is limited since the only articulations are the daughter branches themselves, which are usually produced in pairs from adjacent internodes (Plate 1A, C). No discrete terminal resting buds are produced and there is no regular fluctuation in size of the two kinds of leaf. Direct measurement of growth frequency is required to demonstrate rhythmic growth, if it exists.

Dorsiventrality is determined by phyllotaxis, as shown in serial sections of buds, with no secondary reorientation of leaves other than their separation by internodal extension (Fig. 2E-F). Leaves are four-ranked (Fig. 2E) and consist of two ranks of scale-leaves arranged alternately on the upper side of the branch (dorsal scales) and two ranks of larger foliage leaves on the lower side of the branch (ventral foliage leaves). The internodes between them are extended such that in an acropetal direction the sequence of leaves is – left scale – left foliage – right scale – right foliage – left scale . . . etc. (Plate 1D; Figs. 1B & 5A). In terms of the genetic spiral, the
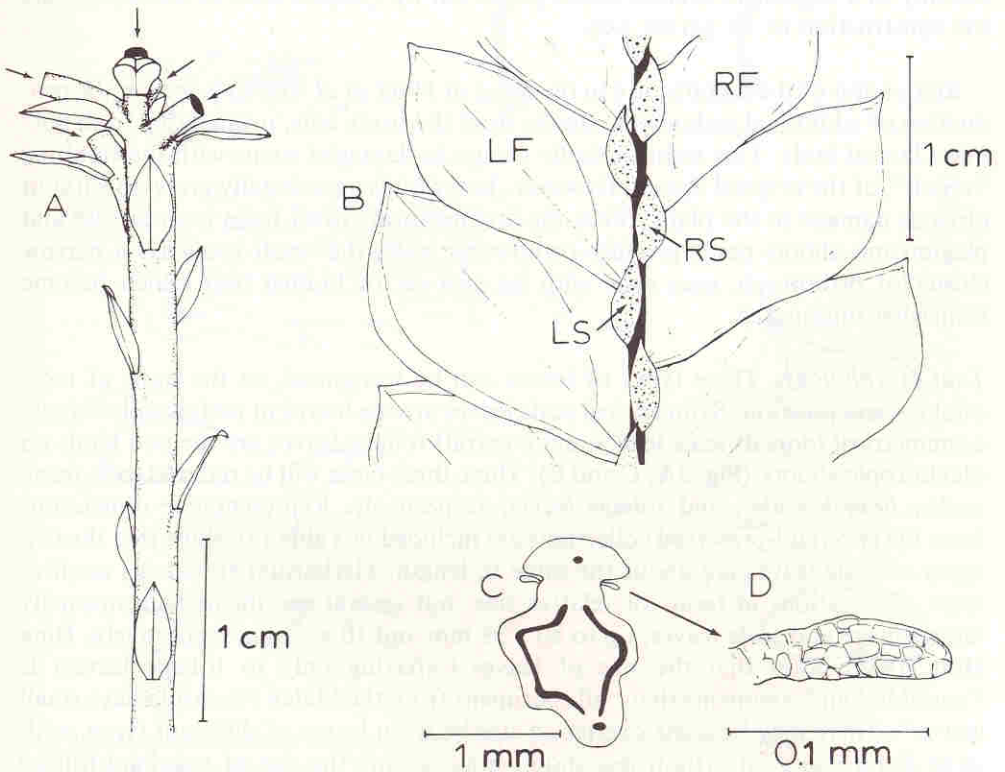

Fig. 1. *Anisophyllea disticha* (Singapore collection). Morphological details.
   A. Apex of orthotropic shoot; sylleptic branches forming terminal tier cut off (arrows).
   B. Detail of plagiotropic axis from above to show relative position of branch scales and foliage leaves; *LS*–left scale; *RS*–right scale; *LF*–left foliage leaf; *RF*–right foliage leaf; branch scale – stippled (cf. Fig. 4).
   C. T.S. trunk axis at level of insertion of trunk scale to show position of multiseriate gland; vascular tissue–solid black.
   D. Detail of multiseriate gland.

following values represent observed angular divergences proceeding acropetally
(n = 11):–

Sequence	Angle of Divergence
Left scale – left foliage	$46° \pm 13$
Left foliage – right scale	$180° \pm 0$
Right scale – right foliage	$314° \pm 13$
Right foliage – left scale	$180° \pm 0$

In Figure 5B, these four sequences are indicated by the numbered sequences 4-5,
5-6, 6-7, and 7-8, respectively.

Scale leaves subtend no axillary buds (Fig. 2K) whereas foliage leaves always sub-
tend at least one bud (Fig. 2I) which usually develops as an inflorescence, but occas-
sionally as a vegetative branch which grows out by syllepsis and, as stated, repeats
the construction of its parent axis.

Reiteration of the architecture in the sense of Hallé *et al.* (1978) is seen in the pro-
duction of additional orthotropic shoots from the trunk axis, presumably from dor-
mant lateral buds. This most typically occurs in damaged stems with the resulting
"repair" of the original crown. However, lower buds occasionally grow up without
obvious damage to the plant. Since the architectural crown-form is so precise and
plagiotropic shoots never produce orthotropic axes, the result is always a narrow
cluster of orthotropic axes each with its own set of branch tiers which become
somewhat internested.

Leaf morphology. Three types of leaves can be recognized on the basis of mor-
phology and position. Symmetrical scale leaves are the leaves of orthotropic shoots,
asymmetrical (dorsal) scale leaves and (ventral) foliage leaves are the two kinds on
plagiotropic shoots (Fig. 3A, C and E). These three types will be referred to as *trunk
scales, branch scales,* and *foliage leaves,* respectively. Representative dimensions
from the two fluid-preserved collections are included in Table 1 to show that the two
types of scale leaves are about the same in length. Herbarium specimens confirm
these observations in terms of relative size, but several specimens had unusually
large foliage and scale leaves, up to 80 x 35 mm and 10 x 5 mm, respectively. Ding
Hou (1958) notes that the size of leaves (referring only to foliage leaves) is
"variable" and comments that "all specimens from the Malay Peninsula have small
leaves". There may be some overlap in size between leaves of different types, with
large distal scales on orthotropic shoots approaching the size of proximal foliage
leaves on plagiotropic shoots. The two contrasted leaf types on plagiotropic shoots
always retain their relative size difference, with transitional forms restricted to the
branch base.

Mean length of foliage leaves in the two collections varied from 16 mm (Kedah
collection) to 25 mm (Singapore collection) and mean length was in both cases two
to three times greater than mean width. Both types of scale leaves in both collections
were about the same mean length, 5 mm, but trunk scales were fifty percent wider
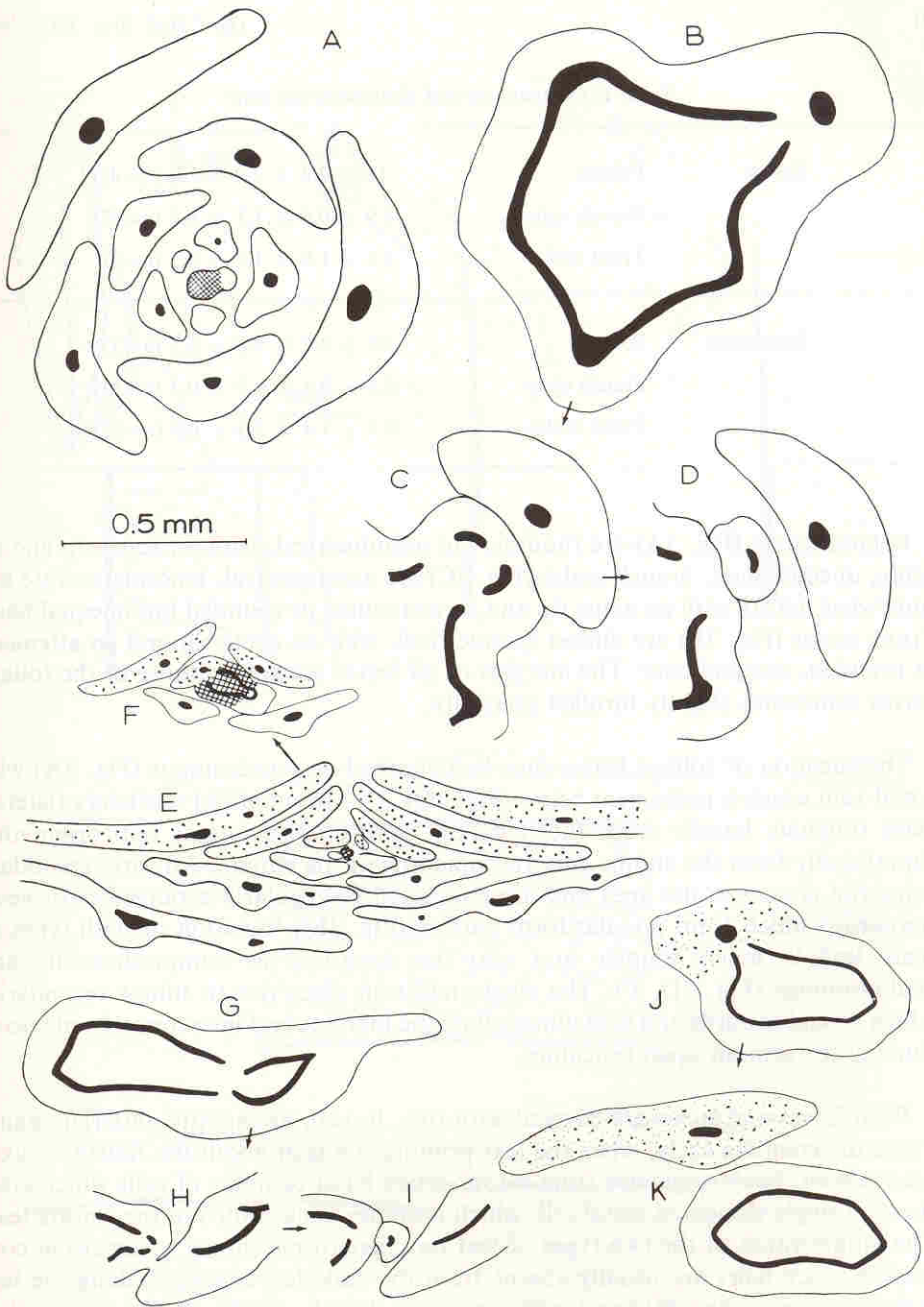than branch scales (cf. Fig. 3C and E).

Fig. 2. *Anisophyllea disticha* (Singapore collection). Phyllotaxis and nodal anatomy.
    A-D. Orthotropic shoot.
        A. T.S. bud 8 μ below shoot apex.
    B-D. T.S. three successive levels to show nodal anatomy.
        B. Leaf trace with single leaf gap. *C*. Branch traces from margin of leaf gap. *D*. Level of
        axillary bud.
    E-F. Plagiotropic shoot.
        E. T.S. bud at level of shoot apex.
        F. T.S. bud 64 μ below shoot apex.
    G-I. T.S. three successive levels to show: *G*. Departure of foliage leaf trace; *H*. Departure of
    bud trace.
    J-K. T.S. insertion of branch scale to show: *J*. Unilacunar node; *K*. Absence of bud.
    Vascular tissue – solid black; branch scale – stippled; axis – cross-hatched.

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Table 1. *Comparative leaf dimensions (in mm)*

Kedah	Foliage	$16 \pm 2.4 \times 7.0 \pm 1.3$ (n = 42)
	Branch scale	$4.9 \pm 0.6 \times 1.1 \pm 0.4$ (n = 47)
	Trunk scale	$5.2 \pm 1.8 \times 1.7 \pm 0.5$ (n = 7)
Singapore:	Foliage	$25 \pm 2.2 \times 9.0 \pm 1.1$ (n = 33)
	Branch scale	$5.3 \pm 0.4 \times 1.7 \pm 0.3$ (n = 33)
	Trunk scale	$5.5 \pm 1.4 \times 2.5 \pm 0.9$ (n = 17)

Foliage leaves (Fig. 3A) are rhombic but asymmetrical, with an acute tip and an acute, unequal base; branch scales (Fig. 3C) are asymmetrical, lanceolate-ovate but somewhat falcate with an acute tip and an acuminate or rounded but unequal base. Trunk scales (Fig. 3E) are almost symmetrical, with an acute tip and an attenuate or rounded, unequal base. The margins of all leaves are entire, those of the foliage leaves sometimes slightly inrolled abaxially.

The venation of foliage leaves may be described as acrodromous (Fig. 3A) with a mid-vein which is prominent below (Fig. 3G). Two pronounced secondary (lateral) veins originate basally from the mid-vein, with a third lateral vein originating suprabasally from the anodic or acroscopic side of the lamina. All three secondary veins run almost to the apex and are connected by regularly arranged cross-veins (tertiaries) which form a scalariform pattern (Fig. 3B). Venation of both types of scale leaf is much simpler and may be described as camptodromous and cladodromous (Fig. 3D, F). The single mid-vein gives rise to minor secondaries which extend towards and sometimes along the margins and interconnect only occasionally to form an open reticulum.

Both leaves and stems are covered with fine, brown, apparently uniseriate hairs. These differentiate early, when the leaf primordium is at about the fourth to sixth plastochron. Each originates from a four-celled basal complex of cells which gives rise to a single elongated distal cell, which becomes thick-walled in the mature leaf. The indumentum of the two types of leaf on plagiotropic shoots is somewhat contrasted, since hairs are usually absent from the scale leaves except along the leaf margins whereas the foliage leaves are quite densely hairy, on the surface but especially along the margins. Trunk scale leaves have frequent abaxial hairs, especially at the base of the lamina, as well as marginal hairs.

Multicellular clavate glands, in pairs or sometimes fours occur at the base of each type of leaf in a stipular position (Fig. 1C, D). They are not vasculated, and develop precociously so that they are conspicuous in the buds.

Leaf anatomy. Leaves of the three types are of comparable thickness, measured halfway between base and apex and mid-rib and margin, shown in Table 2, but mesophyll structure varies appreciably.
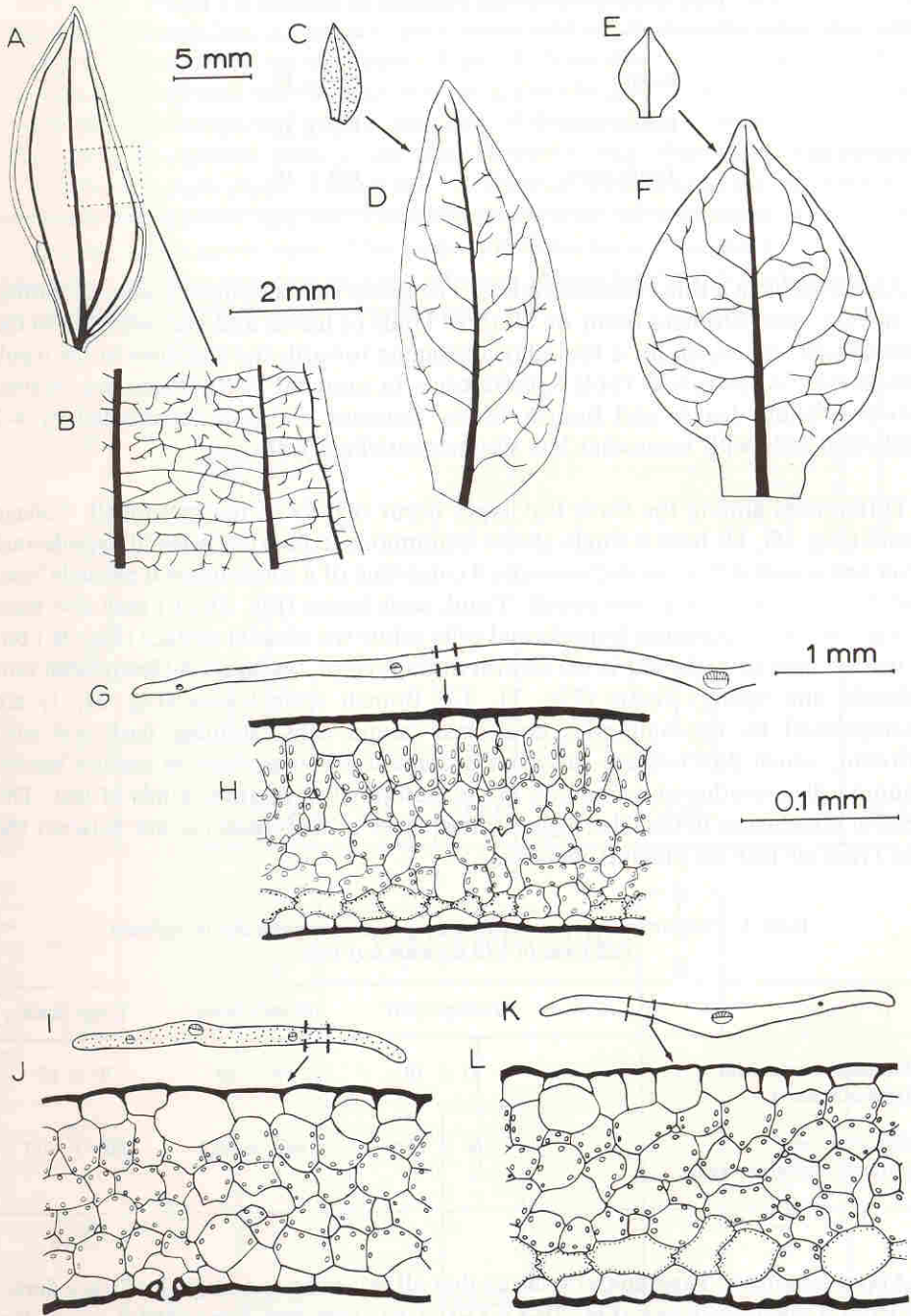
Fig. 3. *Anisophyllea disticha* (Singapore collection). Leaf anatomy.

 A-B; G-H. Foliage leaf.

 C-D; I-J. Branch scale.

 E-F; K-L. Trunk scale.

  A, C, E. Leaf outline showing major veins, from cleared specimens.

  B, D, F. Details of venation in same leaves.

  G, I, K. Outline of complete leaf (half-leaf in *G*).

  H, J, L. Detail of mesophyll anatomy.

  Colourless hypodermis – lumen dotted in *H* and *K*.

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Table 2. *Comparative Leaf Thickness* (in microns) (n = 10)

Foliage	130 ± 11
Branch scale	140 ± 18
Trunk scale	140 ± 19

All leaves have a thin, smooth cuticle. The epidermal cells have a sinuous outline in surface view. Stomata occur on all three kinds of leaves and are restricted to the abaxial surface, except for a few adaxial stomata towards the leaf apex in the trunk scale leaves. As shown in Table 3, differences in stomatal distributions are greatest between foliage leaves and branch scales. Stomata are each surrounded by 4-7 epidermal cells with somewhat less sinuous anticlinal walls.

Differences among the three leaf types occur mainly in the mesophyll. Foliage leaves (Fig. 3G, H) have a single almost continuous, colourless abaxial hypodermal layer and a well-differentiated mesophyll consisting of a single adaxial palisade layer and 2-4 layers of spongy mesophyll. Trunk scale leaves (Fig. 3K, L) may also have a single layer of colourless hypodermal cells below the abaxial surface (Fig. 3L) but in neither type of scale leaf is the central mesophyll of 2-4 layers differentiated into palisade and spongy tissue (Fig. 3J, L). Branch scale leaves (Fig. 3I, J) are distinguished by the numerous epidermal tannin cells, staining dark red with safranin, which differentiate early but become less conspicuous in mature leaves. Tannin cells are otherwise common in the mesophyll of all three kinds of leaf. The general conclusion is that the biggest differences in leaf anatomy are between the two types of leaf on plagiotropic axes.

Table 3. *Comparison of stomatal frequency and stomatal index in different leaf types (n = 10 for each leaf type).*

	Foliage Leaf	Branch Scale	Trunk Scale
Stomatal frequencies (stomata/mm^2)	93 ± 10	55 ± 18	70 ± 18
Stomatal index (stomata/epidermal cells)	.060 ± .008	.049 ± .012	.061 ± .013

Nodal Anatomy. Ciné-analysis shows that all leaves have a single leaf trace derived from a single leaf gap (Fig. 2B-D; G-I; J-K). Geh and Keng (1974) report the nodal anatomy for the family as "many-traced, trilacunar", and thereby imply that this also applies to *Anisophyllea disticha*. This is a curious discrepancy but it is possible that these authors refer to the two lateral traces from the upper margins of the leaf gap which are actually traces to the axillary bud and not the leaf (Fig. 2C, D; H, I).

Internode length. Evidence was sought to show that the scale leaves on plagiotropic shoots had a constant association with a foliage leaf, since this could relate to their interpretation as stipules. Figure 4 shows that in the Singapore population (lower histogram) there was an average greater length of the internode between a scale leaf and foliage leaf on the same side of the axis than between scale leaf and foliage leaf on opposite sides of the axis. However, this relationship was reversed in the Kedah sample (upper histogram). Herbarium specimens provided further examples of variation in spacing between the two types of appendage. In many examples, spacing is about equal. This leads to the conclusion that there is no constant association between the scale leaf and adjacent foliage leaf which might assist in an interpretation of the distinctive phyllotaxis.
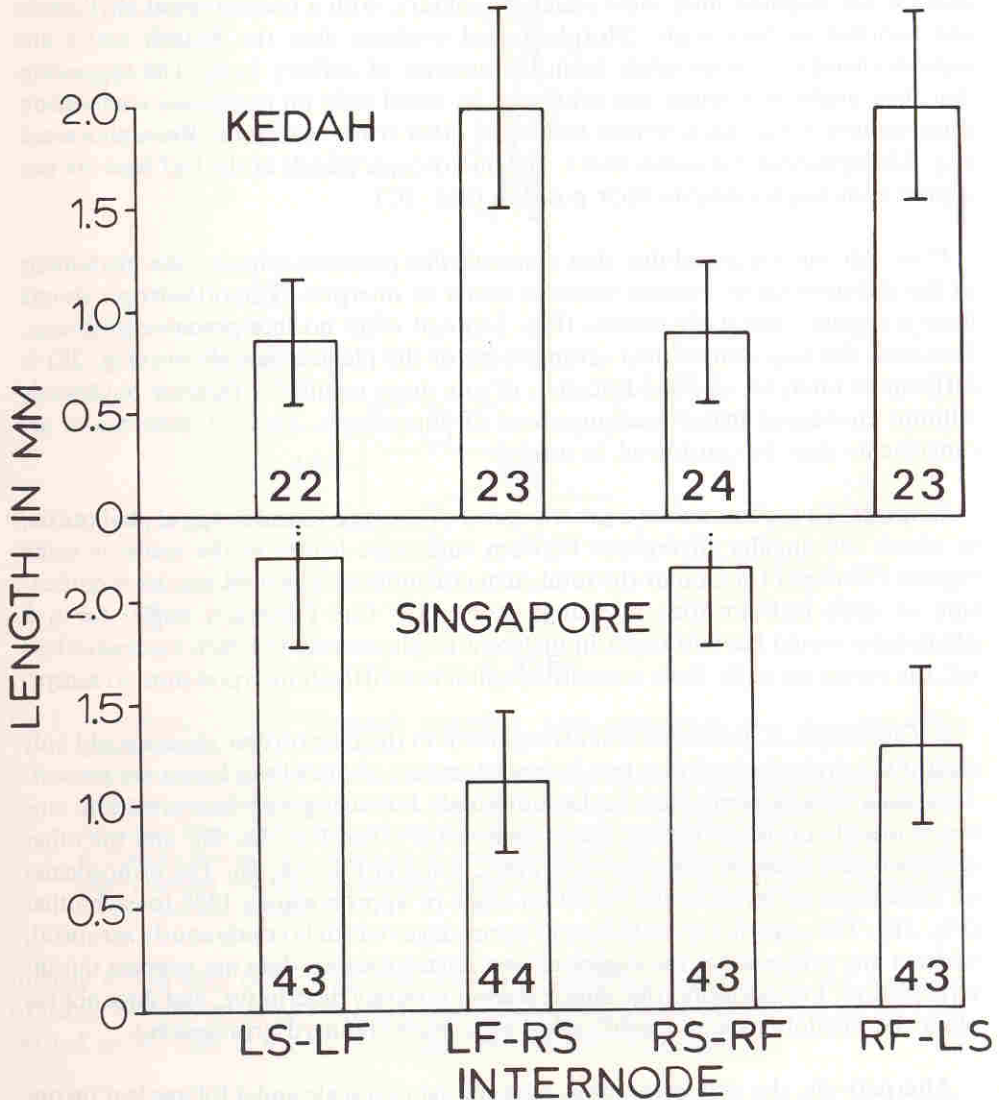

Fig. 4. *Anisophyllea disticha.* Histogram of average internode length along plagiotropic branch in two collections (Kedah, Singapore); vertical lines above bars represent standard error, numbers within bars represent sample size. Internodes are those between left scale and right foliage leaf (*LS-LF*); left foliage leaf and right scale (*LS-RS*); right scale and right foliage leaf (*RS-RF*) and right foliage leaf and left scale (*RF-LS*); cf. Fig. 2B.

Discussion

Phyllotaxy. Evidence from nodal anatomy demonstrates that the 3 kinds of leaves in *Anisophyllea* are homologous since they all have the same unilacunar, single-trace vascular configuration, and therefore cannot be regarded as referring to two categories, *viz.* leaf and stipule, even though accounts of the branch scale leaves have referred to them descriptively as either "stipule-like" (Ding Hou, 1958) or "appearing as stipules" (Corner, 1952). Nor are they consistently associated with foliage leaves in a way which might suggest that they are leaf-opposed stipules (Fig. 4). Further evidence is provided by the similar anatomy of scales on orthotropic and plagiotropic shoots (Fig. 3). The homology between trunk scales and leafy appendages is not disputed since these scales are solitary, with a normal spiral phyllotaxis and subtend axillary buds. Morphological evidence that the branch scales are stipules therefore comes solely from the absence of axillary buds. The suggestion that they might be stipular can otherwise be based only on out-group comparison since stipules are a characteristic feature of other tribes within the Rhizophoraceae (e.g. Rhizophoreae, Gynotrocheae). The microscopic glands at the leaf base are not stipule homologues despite their position (Fig. 1C).

If we rule out the possibility that *Anisophyllea* possesses stipules, the phyllotaxis of the different shoot systems becomes easier to interpret. The orthotropic shoots have a regular   spiral phyllotaxis (Fig. 2A) and offer no interpretative problems. However, the four-ranked leaf arrangement of the plagiotropic shoots (Fig. 2E) is difficult to interpret as a modification of any more regular or familiar phyllotaxis without envisaging major rearrangement of appendages. Each of these major arrangements may be considered in turn: –

1. *Spiral.* To accommodate a genetic spiral of the type found in spiral phyllotaxis, in which the angular divergence between successive leaves in the spiral is some regular Fibonacci fraction of the total stem circumference, would require modification of each leaf postion. A change from 144° (the Fibonacci angle) for a $\frac{2}{5}$ phyllotaxis would have to result in different displacements for each successive leaf (cf. the values on p. 8). Such a modified spiral is a difficult interpretation to accept.

2. *Distichous.* A distichous leaf arrangement in the plagiotropic shoots could only exist if it is hypothesized that two independent sets of distichous leaves are present. Two such arrangements can be hypothesized. Following one interpretation, one series would consist of foliage leaves (leaves 1-3-5-7 in Fig. 5A, B), and the other series would consist of scale leaves (leaves 2-4-6-8 in Fig. 5A, B). The orthostichies of these separate series would be set an angle of approximately 135° to each other (Fig. 5B). The sequence of initiation of appendages which is continuously acropetal, without any evidence for the suggested two separate series, does not support this interpretation. Furthermore, this interpretation is purely descriptive, and does not explain the phyllotaxis as a modification of a more standard arrangement.

Alternatively, the two series could each consist of a scale and a foliage leaf on opposite sides of the stem, that is one series of left foliage-right scale (leaves 1,2,5,6 in Fig. 5A, B) and the other of right foliage-left scale (leaves 3,4,7,8 in Fig. 5A, B). The orthostichies of the two series in this case would be set at an angle of approx-
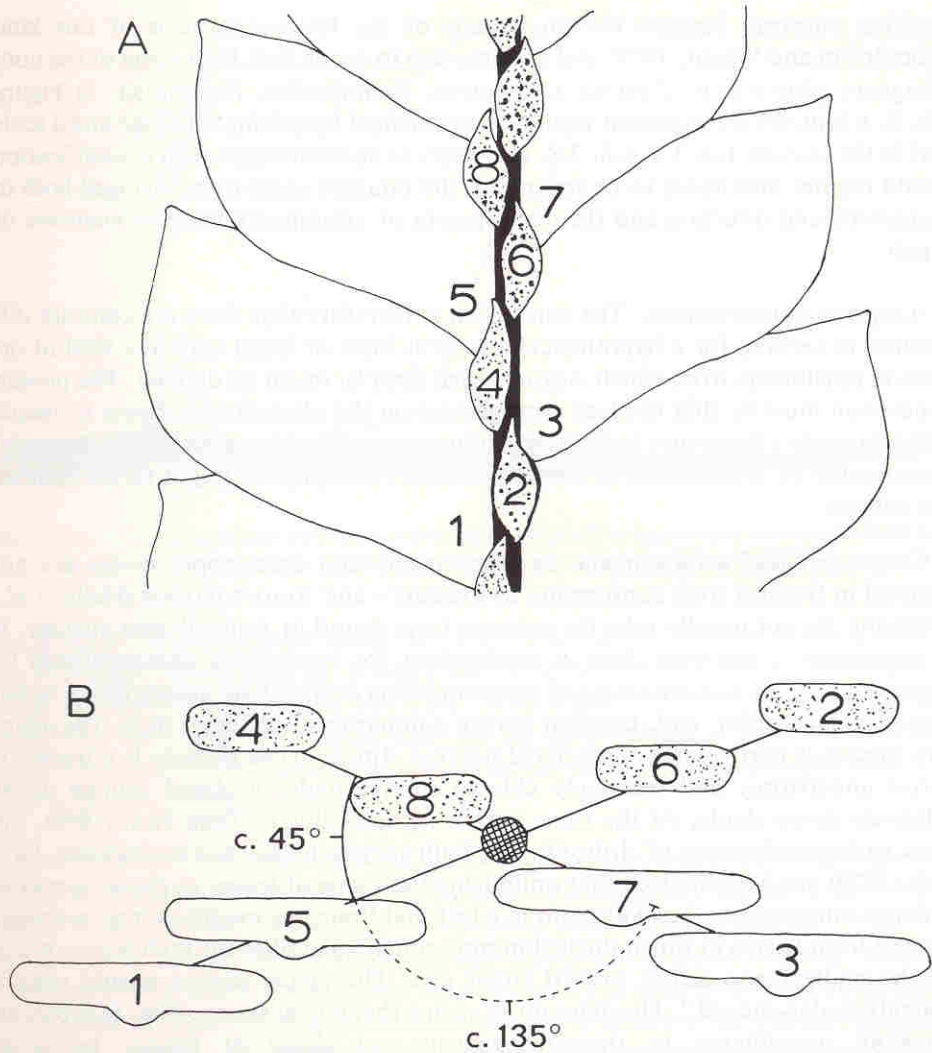
Fig. 5. *Anisophyllea disticha* (Singapore collection). Leaf arrangement on plagiotropic shoot (Diagrammatic).

    A. Plagiotropic axis from above, with foliar appendages (both foliage leaves and branch scales) numbered acropetally from 1 (oldest, basal) to 8 (youngest, distal). Odd-numbered appendages are foliage leaves; even-numbered appendages are branch scales (stippled).

    B. Diagram (not to scale) of axis (cross-hatched) shown in A, with the eight numbered appendages projected onto a transverse plane, in their four orthostichies. Angles between orthostichies are approximate (see text).

imately 45° to each other (Fig. 5B). This interpretation requires that the sequence of leaves of each series be interrupted alternately by 0,2,0,2, etc., leaves of the contrasted series. This is hardly a standard distichous arrangement.

    3. *Decussate and bijugate.* Particularly difficult problems exist if the phyllotaxis of the plagiotropic shoots is considered to be a modification of a system in which leaves are opposite with pairs either at right angles (decussate) or some other regularly repeating angle (bijugate). The last arrangement needs to be considered for com-

parative purposes because the phyllotaxis of the Rhizophoreae is of this kind (Tomlinson and Wheat, 1979) and it seems also to occur in at least some of the non-mangrove genera (e.g. *Carallia, Crossotylis, Gynotroches, Pellacalyx*). In Figure 5A, B, a bijugate arrangement would be represented by pairing a foliage and a scale leaf in the fashion 1-2, 3-4, 5-6, 7-8. However, to accommodate such a modification would require internodes to be separated, the bijugate angle to be changed both in magnitude and direction and the development of anisophylly between members of a pair.

Adaptive considerations. The conclusion is therefore that there are constant difficulties in seeking for a hypothetical ancestral form of shoot with any kind of orthodox phyllotaxis from which *Anisophyllea disticha* might be derived. The present conclusion must be that the leaf arrangement on the plagiotropic shoots is unique and represents a departure from those arrangements usual in angiosperms. A careful examination of architecture in other species of *Anisophyllea* might throw light on the subject.

Contrasted leaf arrangements on plagiotropic and orthotropic shoots are not unusual in tropical trees conforming to Massart's and Roux's models (Hallé *et al.*, 1978) but do not usually take the extreme form found in *Anisophyllea disticha*. It is reasonable to interpret them as mechanisms for maximizing photosynthesis by maximizing the surface area exposed and minimizing overlap both among leaves within one branch complex, and, between branch complexes of different tiers. The adaptive success is particularly appreciated because *Anisophyllea disticha* is a treelet of forest understorey and seemingly able to survive under a closed canopy under relatively dense shade, At the same time it is, according to Ding Hou (1958), the most widespread species of *Anisophyllea*, both geographically and ecologically. Givnish (1979) has hypothesized that optimizing the shape of leaves in planar arrays in order to minimize overlap will result in a leaf that "must be modified from a wedge-shaped form to one in which the leaf margin roughly parallels the midrib over much of the midleaf and tapers toward either end. The apical section should remain roughly wedge-shaped". His diagram of such a theoretical system (Fig. 6) shows an uncanny resemblance to the arrangement and shape of foliage leaves in *Anisophyllea disticha* (cf. Fig. 1B). Givnish suggests that this modification of leaf shape from wedge to parallelogram results in a more efficient "ribbon of photosynthetic tissue along the branch". *Anisophyllea disticha* seems not only to have brought this theoretical model to life, but to have improved upon it as well. Scale leaves further increase the surface area of the " ribbon of photosynthetic tissue" by patching the holes within it i.e. filling the gaps between the bases of the foliage leaves as well as covering the dorsal side of the branch. This interpretation does not, of course, rule out the possibility that the scale leaves have some other function not associated with photosynthesis. For example, they may be involved in close-packing of appendages within the dorsiventrally flattened shoot apex as a consequence of its apparently continuous growth.

Although the phyllotaxis of these plagiotropic branches may be unique within the angiosperms, the same leaf arrangement occurs in other groups. Several writers have commented upon the considerable similarity between species of *Selaginella* (section *Heterophyllum*) and *Anisophyllea disticha* (e.g. Corner, 1952). However, in *Selaginella* leaves are in pairs. Dengler (1983a, b) has recently described leaf
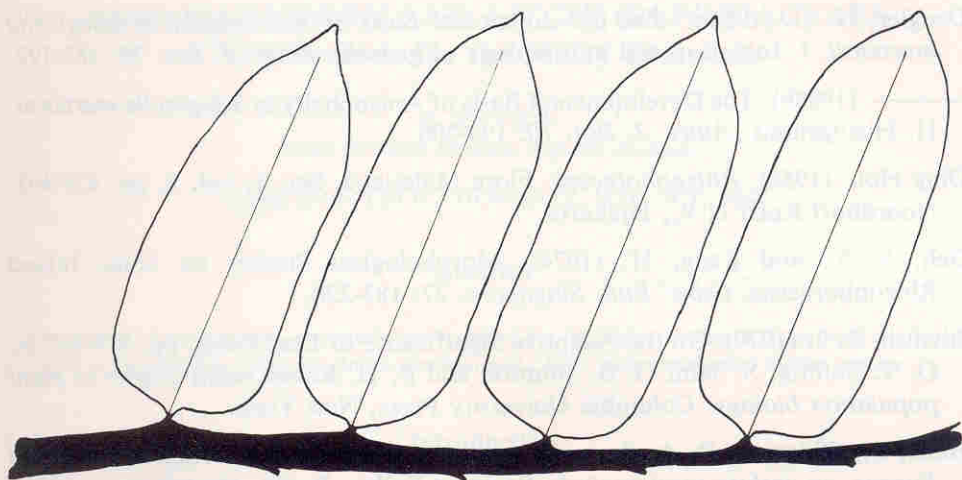
Fig. 6. Theoretical optimal leaf shape and display along one side of a horizontally orientated branch seen from above; leaves shown on one side of the branch only (after Givnish, 1979).

development in plagiotropic shoots of *Selaginella martensii* which shows a similar dorsiventrality determined by primary leaf arrangement. Her studies were undertaken to show that appendages which are "homologous" diverge considerably from each other very early in ontogeny and that the development of small dorsal leaves cannot be regarded as a simple truncating of the developmental process which occurs in larger, ventral leaves.

Our initial observations lead to the same conclusion in *Anisophyllea disticha* since dorsal and ventral leaves can be distinguished histologically within three to four plastochrons of their inception. At their third plastochron primordia which will develop into foliage leaves have six cell layers (at a point midway between longitudinal axis and margin) versus only five layers in scale primordia at the same developmental stage. Foliage primordia also show evidence of an abaxial ridge corresponding to the position of the midvein (Fig. 2E), and stain more densely with safranin than do scale primordia. Dengler's work (1983a, b) provides a model for the further investigation in developmental differences between contrasted leaf types in *Anisophyllea disticha*. Such an investigation would complement our initial observations and would contribute considerably to our understanding of the morphological plasticity of the vegetative parts of higher plants in response to limiting environmental circumstances.

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