

Leaf ontogeny and morphology in *Acacia* Mill. (Mimosaceae)

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Introduction

Leaves are the primary organs of photosynthesis in most higher plants. Despite their common function they display a spectacular diversity of form and structure. For several centuries botanists have attempted to define and explain the wide variety of leaf shape and size found within and between individuals. Various factors have been identified that influence variation within individuals: external factors such as mineral nutrition, light intensity and day length, and internal factors such as plant physiological age and the position on the plant at which the leaf arises (Ashby 1948). Developmental processes must mediate these influences, and molecular biology is just beginning to grasp the complexity of the interactions involved (e.g. Tsiantis & Hay 2003; Fleming 2005; Tsukaya 2006).

The classical model of plant morphology divides plants' bodies into four discrete types of organs. These are the phyllome (leaf), caulome (stem), rhizome (root) and trichome (numerous sources, see Rutishauser & Sattler 1985). All plant structures are considered to be modified versions of these basic units (e.g. flower petals are modified leaves). Leaves, as phyllomes, differ from other classical plant structures in several ways. They are formed as lateral organs from the shoot apical meristem and generally exhibit determinate growth and dorsiventral symmetry.

Leaves can be classified into two basic forms: simple with a single blade region, or compound with multiple connected blade regions. Compound leaves are widespread and are believed to have arisen numerous times in angiosperms with multiple reversions to simple leaves (Champagne & Sinha 2004). Two hypotheses have been proposed to explain the homology of compound leaves, and have been debated for fifty years. The first follows the precepts of classical morphology and suggests that the whole compound leaf is the equivalent of a simple leaf, with leaflets arising as subdivisions of the blade (e.g. Troll 1939). In this view toothed, lobed, pinnate and bipinnate leaves represent increasing levels of dissection. The second hypothesis of compound leaf homology equates each individual leaflet to a simple leaf and the entire structure as a 'partial shoot' (Sattler 1992).

Abstract

The recently redefined genus *Acacia* consists of more than 1000 species, nearly all of which are endemic to Australia. *Acacia* foliage is highly variable and all species exhibit heteroblastic leaf development to some extent as seedlings, with a typical progression from pinnate to bipinnate leaves in the first few seedling nodes followed in most species by the transition to phyllodes. Although phyllodes occur in several plant families, the *Acacia* phyllode is unique and its structure, development and the genetic processes involved in its formation are not well understood. Despite its significance for classification, the developmental homology of this character remains uncertain. Modern microscopy and molecular genetic studies into leaf morphology and development suggest the concepts of process morphology may allow a different way of interpreting the foliage changes exhibited by *Acacia* species.

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Early studies of plant development focused on identifying 'initial' cells that were the progenitors of certain cell types, tissues and organs, and using this knowledge to reveal structural homology. This "zoocentric" outlook viewed cells as gaining a certain identity or fate that was passed on to all daughter cells. The variability of plants confounded attempts to identify these 'initials' (e.g. Boke 1940 [*Acacia* Mill.]; Pray 1957 [3 monocot genera]; Denne 1966 [*Trifolium* L.]). Plant cells have greater general potency and thus their cellular identities do not become so fixed during ontogeny as in animals, but rely more upon hormone gradients across tissues and intercellular signalling.

The occurrence of structures that could not be satisfactorily categorised under the classical model led to the concept of continuum morphology. This model describes a continuous field of possible structures in which the classical forms are the extreme types, between which occur a range of intermediate structures (Sattler

& Jeune 1992; Sattler 1996). The 'partial shoot' theory suggests that the compound leaf is an intermediate structure somewhere in the continuum between a leaf and a shoot (for another example of continuum morphology using *Acacia* see Sattler et al. 1988). This also implies a combination of developmental processes particular to each type of organ, in this case the dorsiventral symmetry and determinate growth of leaves and the stem-like production of lateral organs (Sattler 1992). Considering organs as combinations of processes, and the continuum of plant form as a continuum of process combinations is the essence of process morphology. This concept allows direct comparison of the development of differing organs and a deeper understanding of plant growth. In order to understand leaf form and evolution, including the phyllode, we must identify the processes involved in leaf development, and the differences between simple and compound leaves are fundamental to this subject.

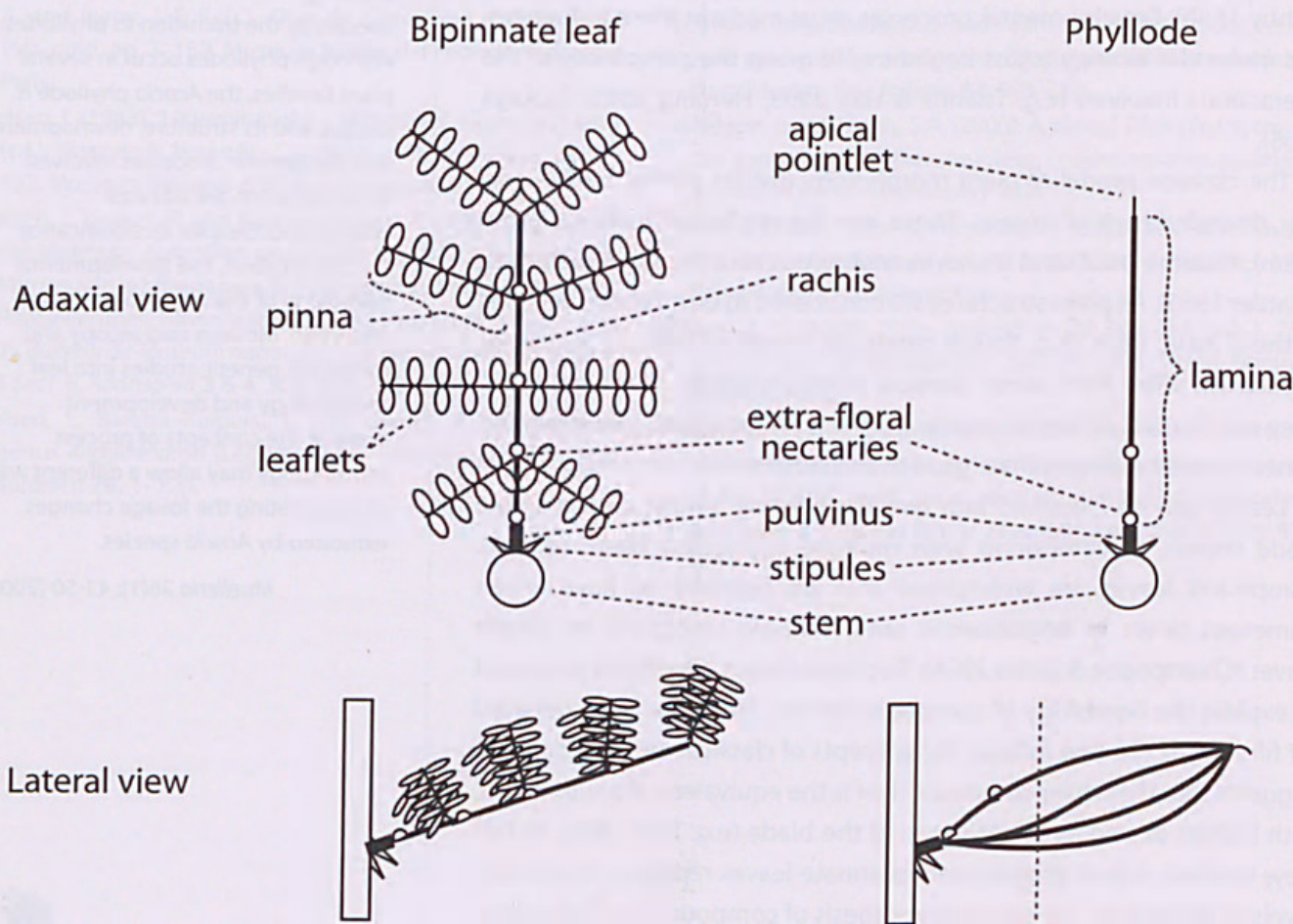


Figure 1. Typical external morphology of bipinnate leaves and phyllodes in the genus *Acacia*.

Acacia foliage and the history of the phyllode

Acacia is the most speciose genus of vascular plants in Australia and has a complex taxonomic history. Vegetative characters have had a prominent role in the infra-generic classification due to the similarity of floral features throughout the genus. *Acacia* foliage is highly variable and all species exhibit heteroblastic leaf development to some extent as seedlings. A typical progression goes from pinnate to bipinnate leaves in the first few seedling nodes followed in most species by the transition to phyllodes. Of the currently described and accepted species of *Acacia*, approximately 70 have bipinnate compound leaves at maturity and more than 900 have phyllodes (Maslin 2003).

Phyllodes and compound leaves of *Acacia* share several common features (Fig. 1) with rare exceptions. They both bear an axillary bud, have stipules that are usually caducous, and at least one extra-floral nectary

located on the adaxial edge of the rachis or phyllode. They have a small apical pointlet at the tip, and a pulvinus at the base, but unlike other Mimosoid genera the pulvini of *Acacia* appear to be incapable of seismonastic (response to touch) and nyctinastic (response to light intensity) movements (Wilkinson 1983). While the compound leaf includes a petiole, rachis, pinnae and leaflets, the phyllode consists of the pulvinus and a photosynthetic zone, loosely termed the lamina. The lamina is vertically flattened in most species, although some are terete, horizontally flattened or reduced to scales. In some species the pulvinus is absent, in which case the phyllodes are decurrent. Two striking anatomical features of the phyllode are the isobilateral lamina symmetry and the opposing pairs of vascular bundles that comprise the major veins (Fig. 2).

The homology of the *Acacia* phyllode has caused much debate among morphologists and taxonomists in the last two centuries. Willdenow (1806), in his

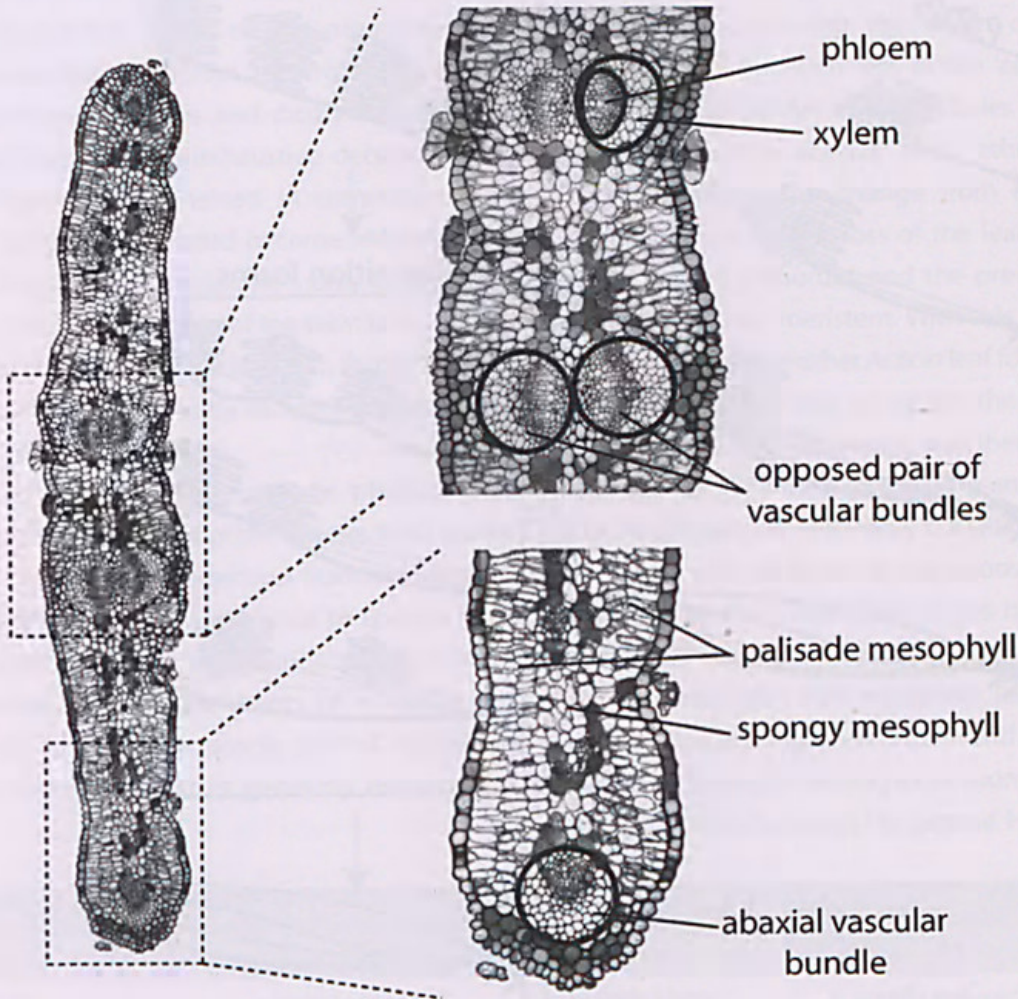


Figure 2. Transverse section of a phyllode (dotted line through phyllode on Fig. 1) showing significant points of anatomy.

classification of *Acacia* based on foliage types, referred to it as a 'simple leaf'. The term "phyllodium" appears to originate from Candolle (1813), literally meaning 'like a leaf', implying that it fulfilled the functions of a leaf yet was not a leaf, nor was it a photosynthetic stem (cladode, phylloclade or cladophyll). A variety of transitional forms occur between the seedling bipinnate leaves and mature phyllodes present in the phyllodinous Australian acacias (Fig. 3a). Reinke (1897) interpreted these as indicating that the mature structure was in fact derived from the petiole of a pinnate leaf. In his discussion of plant vegetative structures, Goebel (1905) stressed the importance of the arrested leaf primordium to the concept of a phyllode; i.e. if an apparently primitive vegetative structure is a phyllode, and so derived and reduced from a true leaf, there must be a remnant arrested leaf primordium at its apex. In Goebel's view,

without an arrested leaf primordium the structure must either be a true leaf or a primitive enation. Some of the earliest work on *Acacia* phyllodes states that they are completely lacking an arrested leaf primordium (Hildebrand 1875) but Goebel (1884; 1905) and Mann (1894) considered this to be incorrect, and that what appeared to be a leaf primordium could always be observed at the apical tip of a developing phyllode. This structure was variously named the arrested true leaf primordium or the terminal seta, depending on the author's opinion of its homology. Many settled upon the neutral term 'apical pointlet', simply referring to its location and appearance, rather than any implication of origin.

Various publications from the 1870s to the 1970s expressed two different views concerning the precise homology of the *Acacia* phyllode and the apical pointlet

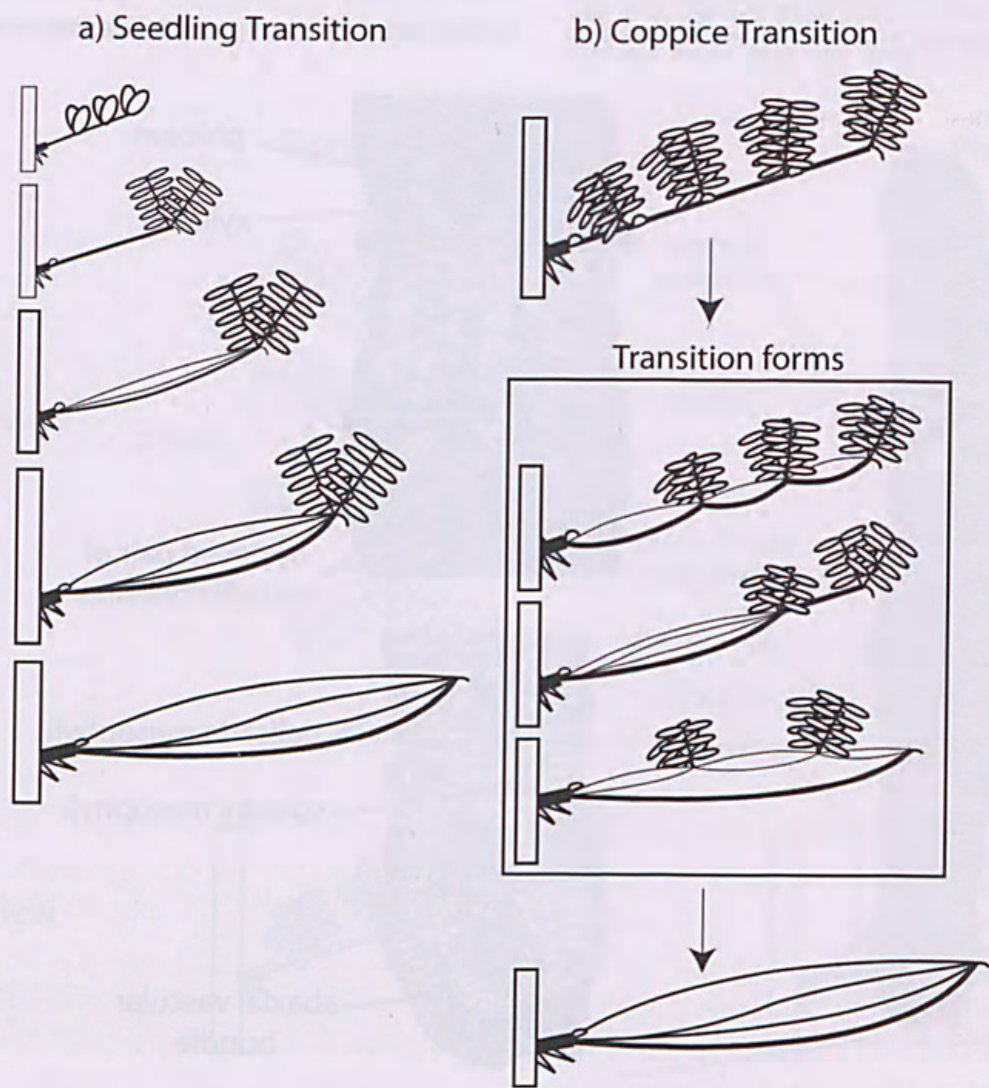


Figure 3. a) Typical heteroblastic leaf progression of an *Acacia* seedling; b) typical heteroblastic leaf progression in *Acacia* coppice reversion shoots.

at its tip. Mann (1894), Reinke (1897), Arber (1918), Peters (1925), Troll (1939) and Vassal (1970) regarded the phyllode as having developed from only the petiole of a bipinnate leaf. Bentham (1875), Preston (1902), Fletcher (1920) and Catalano (1934) thought that the petiole and the rachis were involved in the formation of the phyllode. Bentham (1864, 1875) and Goebel (1895, 1905, 1928, 1932) supported both hypotheses at different times. Goebel, Mann and Troll considered the apical pointlet of the phyllode equivalent to the whole lamina of a foliage leaf, and Catalano thought that the apical pointlet must be an aborted terminal leaflet. All these conclusions were predominantly based upon external form and development. The petiole hypothesis arose primarily from observations of seedling transitions that display a uniform development of phyllode lamina below the pinnae. It was called into question by work on coppice reversion shoots with much more irregular lamina development (Fig. 3b), which suggested the petiole-rachis homology. Arber (1918) differed from this trend and supported the petiolar hypothesis based on the organization of the mature vasculature bundles, noting the similarity to monocotyledonous leaves and dicotyledonous leaf bases and petioles. Despite exhaustive debate on this topic, both hypotheses remained in common usage. This issue is further complicated because although it is clear that in English the petiole refers only to the stem of a leaf, one of the earliest uses of the term is in an early German herbal by Leonhart Fuchs (1541, Rutishauser, R. pers. comm.) where he explicitly includes the bipinnate leaf rachis in its definition.

Outside the genus *Acacia*, the term ‘phyllode’ has been applied to a number of other species with leaves that consist only of tissues derived from the petiole. Troll (1939) applied the term ‘phyllode’ to species from the Crassulaceae, Apiaceae and Oxalidaceae, and Arber (1918) proposed the phyllode theory of monocot leaf origin. Neither of these proposals gained significant support and today the term is generally restricted to acacias.

Boke (1940) performed the first histogenetic study of phyllode morphology using *Acacia longifolia* (Andrews) Willd. He attempted to identify cell lineages and discrete meristems that determined the form of adult phyllodes with limited success. In the shoot apical meristem he found the layers of tunica to be variable and not always distinct from the corpus, nor did they have identifiable initials. He also failed to find initial cells for leaf primordia in any layer of the tunica, instead identifying multiple divisions in many layers occurring almost simultaneously. These observations lead him to suggest that a more dynamic view of the morphology and terms was necessary.

The majority of Boke’s work consisted of detailed observations of cell division in developing phyllodes. He described a leaf sub-apical meristem that produced the early lengthening of the phyllode primordium, and the early maturation of the abaxial tissues combined with the appearance of an adaxial meristem. He described how this meristem produced the vertically expanded phyllode. In explaining the origin of this meristem Boke referred to much less active ‘adaxial meristems’ he considered similar in the petioles and leaf axes of non-phyllodinous acacias and other angiosperms. Boke considered the change from bipinnate foliage to phyllodes to be the loss of the leaf blade meristem and/or leaflet primordia, and the precocious action of a discrete adaxial meristem. With this idea established, he did not examine other *Acacia* leaf forms in depth, but rather applied the idea to explain the leaf morphology of *A. dealbata* Link (bipinnate; was then *A. decurrens* var. *dealbata* (Link) F.Muell. ex Maiden) and *A. melanoxylon* R.Br. (phyllodinous with slow transition). He described the range of leaf forms as variations in the ‘strength’ of each meristem. Bipinnate leaves had ‘strong’ leaflet primordia; phyllodes had a strong adaxial meristem; and intermediates had moderate leaflet primordium ‘strength’, producing a few pinnae and moderate adaxial meristem ‘strength’ causing expansion of the axis below and sometimes between the pinnae. He concluded that

Table 1. Hypotheses of phyllode homology in <i>Acacia</i> .			
Bipinnate leaf structure	Petiole hypothesis	Rachis hypothesis	Lamina hypothesis
Petiole	phyllode blade	phyllode blade	greatly reduced
Rachis	apical pointlet	phyllode blade	phyllode blade
Pinnae & Leaflets	apical pointlet	absent	phyllode blade

the phyllode was the equivalent of the petiole-rachis of a pinnate foliage leaf.

Boke observed the presence of an apical pointlet not only on the phyllodes, but also on the pinnate and transition leaves of this species, on the bipinnate leaves of *A. decurrens* Willd., and on all foliar types in *A. melanoxylon*. Boke (1940) concluded that as an apical pointlet occurred in pinnate, bipinnate, transition and phyllodinous leaves, it could not represent an aborted lamina. It was simply the physical apex, or at most an abortive terminal leaflet. Argument on this topic appears to have been suspended for many years, although the petiole hypothesis persisted in texts (McLuckie & McKee 1954; Debenham 1971).

Boke's study showed detailed development of a phyllode for the first time, rather than simply drawing conclusions from adult structures. He clarified that phyllode expansion was adaxial, not in both directions as previously thought; however his preconceptions of discrete meristems caused him to overlook the possibility of a link between what he called the increasing strength of the adaxial meristem and decreasing strength of the leaflet primordia, and the fact that both meristems occurred on the adaxial surface. This was due to the lack of comparison to juvenile pinnate and bipinnate leaf development, a problem that was only remedied 40 years later by Donald Kaplan.

Kaplan (1975) carried out the first detailed investigation of the development of bipinnate *Acacia* leaves using coppice reversion shoots of *A. melanoxylon*. He discovered that the petiole was actually produced by late intercalary divisions, after the formation of the rest of the leaf. He detected no sign of lamina suppression in favour of petiole expansion; rather he observed a reduction of late intercalary divisions – actual suppression of the petiole such that it is almost absent in mature phyllodes. He concluded that the phyllode is the positional homologue of the bipinnate leaf lamina. This led Kaplan (1980) to perform the first comparative developmental analysis of *Acacia* foliage in an attempt to reconcile the disparate interpretations of this structure. He observed that previous studies of phyllode ontogeny were either done at a superficial organogenetic level or were not sufficiently comparative to determine structural equivalences. He examined the growth and

development of seedling leaves to mature foliage in four species (*A. longifolia*, *A. pravissima* F.Muell, *A. verticillata* Willd. and *A. melanoxylon*) using transverse and radial longitudinal sections. Through observations of the timing and location of growth and differentiation he identified the stages and processes involved in formation of pinnate, bipinnate and transition leaves as well as phyllodes.

Kaplan identified two separate and seemingly independent processes occurring in the heteroblastic leaf development of acacias. The first and most obvious was the change from dissected to simple blade morphology. The second change was the progressive increase in lamina length and decrease in petiole length. The dramatic shift to simple blade form generally obscured the second trend. Kaplan proposed that this was largely responsible for the conflicting opinions of phyllode homology. In studies using coppice reversion shoots the second trend (increase in lamina length/decrease in petiole) is well advanced; reduction in dissection is the only transition occurring and the lamina homology of the phyllode has been apparent. Studies of seedling transition leaves observed both changes occurring simultaneously and thus the phyllode appeared to be in the position of the petiole as the number of pinnae was reduced and the rachis expanded.

Kaplan and Boke similarly concluded that the phyllode was the equivalent of the bipinnate lamina, but had very different ideas about the development of the structure. Boke believed that the different foliage forms were controlled by the switching on and off of discrete meristems. Kaplan regards the change from dissected to simple lamina to be a congenital suppression of the pinnae primordia, but the vertical mode of growth to be the same in the two types of foliage (pinnae arising adaxially, phyllodes expanding adaxially), hence his use of the term 'positionally equivalent'. It is the difference between viewing form structurally (meristem type A produces organ type A, meristem B produces organ B), and interpreting it by the processes which create and maintain it (a background of vertical expansion, with an overlaying process of varying levels of dissection).

The concepts of the rachis and petiole of the bipinnate acacia leaf, and their respective contributions to the development of the phyllode, have been the

sticking point of morphological argument about the phyllode for more than 100 years. The differences between the petiole and the rachis are few. Although the anatomy has not been adequately investigated, externally they appear identical. The petiole is only distinguished from the rachis as the portion of the leaf axis between the pulvinus and the first pair of pinnae. In regard to the development, Kaplan (1980) found late intercalary divisions produced the petiole; however the same could be said of the rachis. If the same process produces both the petiole and the rachis, then it is a mistake to attempt to subdivide the leaf axis into these separate structures. Identifying the full combination of processes that underpin the development of a 'phyllode' from initiation to maturity, and determining how these differ from the processes in other leaves may bring further insight.

Historically, morphological investigation has relied on establishing homology of classical components. In the case of the phyllode these have been the petiole, rachis, lamina and various meristems. Modern developmental genetics is identifying genes and gene families that operate in different domains, allowing a new conceptual framework for leaf morphology. Gene families such as YABBYs and Class III HD-ZIPs have been identified (see Bowman *et al.* 2002) that are responsible for establishing adaxial and abaxial cell identity, and consequently lamina outgrowth. Class I KNOTTED-like homeobox (KNOX) genes are expressed throughout the shoot apical meristem and play a role in the maintenance of meristem identity and cell indeterminacy, but have also been identified as playing a role in leaf complexity (Bharathan *et al.* 2002). These observations are directly relevant to the processes responsible for creating and maintaining structures, avoiding the classical reliance on the transformation of one structure into another. Process homologies can be established by comparing the identities and expression patterns of key regulatory genes in species from different plant families, and comparisons made between their expression patterns. These techniques give us a new opportunity to reappraise *Acacia* phyllodes and bipinnate foliage by directly investigating the actual developmental process involved in their creation.

Conclusion

Three hypotheses of *Acacia* phyllode homology have been proposed since Candolle first used the term 'phyllodium' (Table 1). The petiole hypothesis arose primarily from observations of seedling transitions and has been called into question by later work on coppice reversion shoots that suggested the petiole-rachis homology; however both have remained in common usage. Boke proposed the hypothesis that the phyllode was equivalent to the entire bipinnate leaf but derived from a different meristem. Kaplan supported the lamina equivalence of the phyllode blade but disagreed with the developmental pathway proposed by Boke.

Through all these investigations the goal has been to identify the homology of the 'endpoint', the phyllode, when compared to other plant structures. The hypotheses of structural homology themselves have led to our understanding that the phyllode is functionally and positionally a leaf. The *Acacia* phyllode may not strictly be a 'phyllode', yet it is markedly different from a "normal" foliage leaf and this difference is worthy of study. Process morphology is revealing the details of plant growth and allowing comparisons between apparently disparate organs. It is not names and labels, but ultimately the progress of ideas, facilitated by new approaches and better models, that will help us comprehend the phyllode's strangeness and deepen our understanding of plant form.

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