Wulfenia **9** (2002): 73–76

Wulfenia

Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

On the problem of homologization of prophylls and cotyledons

Vladimir V. Choob

Summary: 'Prophyll' is a term, created for the first one (or two) phyllomes of any lateral axis. Initially the prophylls were considered as homologues of cotyledons, thus prophylls were often used for phylogenetic speculations. German botanists have contributed greatly to the problem of prophylls. The placement of prophylls is conservative (at least in families of Angiosperms). They have a certain position relatively to the mother shoot and to the subtending leaf. Correspondingly, the prophyll characters may be applied to the reconstruction of the shoot system relations in ambiguous cases. Despite of the position conservatism, we have found the variability in the prophyll placements along the shoots of some *Ranunculus* species. According to our opinion, prophylls and cotyledons fail the positional criterion of homology, but they have a common character – they are the beginners of leaf series of their shoots. Consequently, the prophylls and the cotyledons may be considered as the initial points for the phyllotaxis. Plants use these phyllomes for the formation of the spatial pattern of the leaf helix. It is important to stress, that prophylls and cotyledons have a functional similarity, but this cannot be regarded as a phylogenetic similarity.

Zusammenfassung:.Der Begriff „Vorblatt" wurde zur Bezeichnung des ersten Blattes (der ersten zwei Blätter) an Seitenachsen eingeführt. Anfänglich wurden Vorblätter als homolog zu Keimblättern betrachtet, folglich wurden Vorblätter auch für phylogenetische Überlegungen herangezogen. Deutsche Botaniker steuerten viel zur Problematik der Vorblätter bei. Die Platzierung der Vorblätter ist konservativ (vor allem bei den Angiospermen-Familien). Sie haben eine bestimmte Position zur Hauptachse und zum Tragblatt der Achse. Demgemäß können Vorblatt-Merkmale zur Rekonstruktion von Sprosssystem-Beziehungen in unklaren Fällen herangezogen werden. Trotz der Unveränderlichkeit der Lage konnten wir Variabilität der Vorblatt-Positionen entlang der Sprosse einiger *Ranunculus*-Arten finden. Nach unserer Meinung, verfehlen Vorblätter und Keimblätter das Homologiekriterium der Lage, besitzen aber ein gemeinsames Merkmal – sie sind der Anfangspunkt der Blatt-Serie ihrer Sprosse. Als Konsequenz daraus können Vorblätter und Keimblätter als Anfangspunkte der Phyllotaxis angesehen werden. Pflanzen verwenden diese Blätter zur Formung des räumlichen Musters der Blatt-Spirale. Es ist wichtig zu betonen, dass Vorblätter und Keimblätter funktionell zwar ähnlich sind, dass daraus aber keine phylogenetische Ähnlichkeit ableitbar ist.

Keywords: prophyll, cotyledon, leaf morphology, homologization

The idea of the homologization of the lateral shoots and the main shoot has a long history. Since the 19th century morphologists use the term 'prophyll' sensu Turpin (cit. by TOMLINSON 1970) to point out the homology between the cotyledon (first leaf of the main axis) and the first leaf on the lateral axis. As a matter of fact, the majority of Monocots possess a single adaxial prophyll, whereas in Dicots we find two prophylls in transversal position. The prophylls often differ in shape from the following leaves on the same shoot.

In German literature, the term 'prophyll' (Vorblatt) was further developed and accumulated the fundamental knowledge on the organ position in flowering plants. EICHLER (1875) was the first, who noticed, that the number of prophylls sometimes does not correlate with the plant division into Monocots and Dicots. He referred to *Ranunculus lingua* as an example of Dicots with a single adaxial leaf. As an example of Monocots with two transversal prophylls he described fam. Amaryllidaceae. However, EICHLER erroneously interpreted two inflorescence bracts as the first pair of leaves on the lateral axis, because he shared the viewpoint of

IRMISCH (1860) on the monopodial bulb construction in Amaryllidaceae. Later it was proved, that amaryllidaceous bulbs are sympodial and the inflorescence terminates the axis, correspondingly the bracts cannot be referred to prophylls (MÜLLER-DOBLIES, 1971).

At Eichler's time the position of prophylls was calculated from the structure of the axial system. Morphologists practically did not use the position of prophylls (as primary data) to establish the architecture of the axial system, although it is principally possible (CHOOB 1999).

A detailed theoretical and practical examination of prophylls with special emphasis to Monocots was undertaken by GOEBEL (1923) and his student RUTHER (1918). According to their theory, the prophyll in Monocots evolved from two phyllomes by their fusion. This hypothesis was supported by following observations: 1) bidentate shape of prophyll apex in many Monocots, and 2) its adaxial position. Accepting this speculation, one has to conclude, that Monocots are evolutionary younger than Dicots. Moreover, if the homologization of prophylls and cotyledons is correct, one can extrapolate, that the ancestral cotyledonary leaf of Monocots was a product of two cotyledons (SKVORTSOV & KOSTINA 1994).

Careful observations by RUTHER (1918) revealed that prophylls in Monocots sometimes lack two teeth on the apex; moreover, this organ was placed in different angles relatively to the subtending leaf and parent axis. She demonstrated the significant diversity in prophyll shape. In order to classify this diversity, RUTHER introduced the new terms 'Niederblattvorblatt' ('cataprophyll' – similar to cataphylls), 'Laubblattvorblatt' ('photoprophyll' – similar to green leaves) and 'Hochblattvorblatt' ('bracteoprophyll' – similar to bracts). Since RUTHER's work, the difference in organ shape between prophylls and other leaves appeared to be not so important. RUTHER (1918) gives examples of transversal (in Commelinaceae), and even of abaxial (in *Tofieldia*) position of the first leaf of the lateral shoot. In order to argue the complex two-phyllome nature of prophylls in Monocots, she found two shoots, developed in the axil of one prophyll in some Gramineae.

Later TOMLINSON (1970) made a critical revision of the term 'prophyll'. According to his view, prophylls do not differ from the other leaves in structure, their position is very variable, thus there is no reason to use a special term for the first one or two leaves of the lateral shoot. TOMLINSON (1970) proposed to refuse the term 'prophyll', because it is 'just a leaf'.

Despite of TOMLINSON's hypercriticism, the position of the first leaves is often used as a tool for establishment of interrelation in axial system, especially in difficult cases. For instance, when internodes are shortened, the vascular anatomy gives poor results and investigators fail to observe the spatial relation between vascular bundles, when it is objectively difficult to distinguish the lateral and the main axis. TROLL (1954) and his proponents actively used the term; 'prophyll' appeared to be a very pragmatic generalization with great vitality in works on plant morphology. In spite of this, the theoretical basis for prophylls was not changed, until now: prophyll is assumed to be a homologue of cotyledon and it is of great value for the creators of different evolutionary scenario.

The hypothesis of the origin of prophylls by fusion of two phyllomes (RUTHER 1918; SKVORTSOV & KOSTINA 1994) has no valid argumentation. Really, in some Monocots two (or more) buds occur in the axil of one prophyll. Nevertheless, we cannot draw a conclusion, that the number of the lateral shoots indicate a complex leaf, composed of several phyllomes. We have observed up to 7(!) collateral buds in the axil of one prophyll in *Zephyranthes candida.*

Following the proposed logics, we would come to a paradox conclusion, that one prophyll in this species is the result of a fusion of 7 leaves! If one will accept the number of buds in the axil as a valid argument for prophyll evolution scenario, one has to claim that every foliage leaf in *Allium sativum* is the result of a fusion of 3 to 8 (or more) leaves.

The bidentate prophyll apex is another argument to be discussed. According to our observations (CHOOB & MAVRODIEV 2001) in Commelinaceae, the structure of the apical region of prophylls is in strict correlation with the direction of the lateral shoot growth. Thus, intravaginal shoots, growing parallel to the parent axis, have bidentate prophylls with two keels. If the lateral shoots are extravaginal (i.e. growing perpendicular to the mother shoot), the teeth and keels on the prophylls disappear. We have changed the direction of growth experimentally (when extravaginal shoots could grow parallel only), and the prophyll became keeled and bidentate. We hypothesized, that the specific shape of prophylls in Monocots is directed by the parent shoot, when the prophylls have close mechanical contact in early development. Correspondingly, two teeth and keels ultimately point to the main axis, whereas the position of the bud in the axil of prophylls may be variable.

It is important to note, that in some other Monocots the prophyll could be divided into two lobes by strong mechanical pressure of the surrounding organs. In Amaryllidaceae *Haemanthus albiflos* (IRMISCH 1860) and *Ungernia* (MÜLLER-DOBLIES & MÜLLER-DOBLIES 1978) have distinctly two-lobed prophylls. In *Narcissus campernelli*, IRMISCH (1860) depicted two lobes of a prophyll as separate phyllomes. The pressure may have an effect even on foliage leaves (not prophylls). For example, we observed a leaf with two laminas in *N. triandrus* cv. 'Hawera' (CHOOB & KOZHEVNIKOVA 2000).

In many families the position of the first leaves on lateral shoots appeared to be a rather conservative character. An exception from this rule is *Ranunculus lingua* and other species of *Ranunculus* with simple leaves (*R. flammula*, *R. amplexicaulis* etc.). A single adaxial prophyll, described by EICHLER (1875), is typical for lateral shoots, born at the base of the main axis. The shape is typical for Monocots: two teeth on the apex and keels. In spite of this, in the inflorescence region, the first pair of leaves is orientated transversally (similar to *Ranunculus* species with dissected leaves). In the intermediate zone between the basal part and the inflorescence the prophylls remarkably change their placement. Toward the inflorescence the first prophyll moves from adaxial to transversal position. The keels disappear, because the prophyll looses the contact with the parent axis. The internode between the first and the second leaf shortens, and as a result, we see two transversal prophylls (nearly on the same node) instead of one adaxial prophyll.

We should underline, that several species of *Ranunculus* with simple leaves have two cotyledons, whereas in the basal part of axial system their shoots possess one single prophyll. The direct homologization of the prophyll and cotyledon is not grounded well enough. It is clear that the typical transversal position of prophylls appear due to a gradual rotation of the lowermost phyllomes in the leaf series of lateral shoots. The second prophyll is homologous to the second leaf (but not to a part of a single prophyll, as it was proposed in the 'fusion hypothesis'), and the internode between the transversal prophylls is reduced to zero.

If the prophylls are not homologous to cotyledons (as it was assumed by the creators of the term 'prophyll' – TURPIN and others), do we have any reason to distinguish the prophylls from the leaf series of the lateral shoots? The point is, prophylls have a unique position in leaf

series: they have no foregoing node. In this sense the usage of the terms 'hypopodium' and 'hypocotyl' (TROLL 1954) for the lowermost portion of any axis is legitimate. For cotyledons we are unable to point out organs, homologous to the subtending leaf or parent axis, which have strong influence on the development of prophylls. Despite of this, prophylls and cotyledons have similar functions: they serve as starting points of the phyllotaxis. Every plant taxon has its typical characters in initiation of lateral axis leaf series. These characters are more or less conservative. The investigation of the prophyll position is governed by the principles of leaf spiral formation. At the same time, cotyledons are the basic point for the phyllotaxis on the main axis, and the principles of leaf spiral development are the same in lateral and main shoots.

Thus we have to change the initial sense of the term 'prophyll'. In spite of our failure to homologize prophylls and cotyledons, both organs initiate the spatial pattern of the leaf spirals. Prophylls and cotyledons have a common function in plant development.

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Address of the author:

Dr. Vladimir V. Choob
Department of Plant Physiology, Biological Faculty
Moscow State University
Vorobjevy Gory
119992 GSP2, Moscow
Russia
E-Mail: choob@ru.ru