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Leaf Morphology in the *Umbelliferae*: Rachis Unifaciality, Stipels and Pinna Insertion

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With 2 Figures

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Summary

GUÉDÈS M. 1984. Leaf morphology in the *Umbelliferae:* Rachis unifaciality, stipels and pinna insertion. — Phyton (Austria) 24 (2): 257—272, 2 figures. — English with German summary.

Although pinnae of compound leaves mostly lie in the plane of the rachis, which would be the blade plane if the leaf were simple, pinnae in the *Umbelliferae* may lie in planes perpendicular to that of the rachis. As their margins are continuous with those of the rachis up- and downwards, the upper rachis margin then runs horizontally above and close to the base of the pinna to connect with the abaxial pinna margin. This horizontal margin stretch may develop part of the pinna blade, which is thus folded inwards at its insertion. Even when the pinnae lie in the rachis plane, they may be curved or folded horizontally at their insertion and the upper rachis margin may run in a loop in the pinna axil, its course being underscored in *Conium maculatum* by developing membranous scales or stipels, especially on turning into and coming from the axil. Such scales are reminiscent of the stipels of Thalictrum (*Ranunculaceae*). When the rachis is unifacial in the *Umbelliferae,* its morphologically adaxial surface may nonetheless become apparent at pinna insertions (*Foeniculum vulgare*). Petiole and rachis unifaciality as well as marginal loops at pinna insertion are probably advanced features in the *Umbelliferae,* and may help to make clearer the phylogenetic status of various taxa. The bearing of anatomy on unifaciality is discussed and it is concluded that external morphology should be primarily resorted to in ascertaining unifaciality, especially in the Umbelliferous leaves.

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Zusammenfassung

Guédès M. 1984. Blattmorphologie der *Umbelliferae:* Rhachis-Unifazialität, Stipellen und Fieder-Insertion. — Phyton (Austria) 24 (2): 257—272, 2 Abbildungen. — Englisch mit deutscher Zusammenfassung.

Während Fiedern zusammengesetzter Blätter meist in der Ebene der Rhachis liegen (was im Falle eines ungeteilten Blattes der Blatt-Ebene entsprechen würde), können die Fiedern bei den *Umbelliferae* auch in Ebenen senkrecht zu derjenigen der Rhachis stehen. Gehen die Ränder dieser Fiedern in diejenigen der angrenzenden Rhachisabschnitte über, so läuft der Rhachisrand oberseits dicht an der Basis der Fieder horizontal entlang, um sich mit dem abaxialen Fiederrand zu verbinden. Entwickelt dieser horizontale Rand-Abschnitt einen Teil der Fiederspreite, so ist diese an der Ansatzstelle einwärts gefaltet. Auch wenn die Fiederspreite in der Rhachis-Ebene liegt, kann sie an der Ansatzstelle horizontal gekrümmt oder gefaltet sein; der Rhachisrand ober der Fieder kann eine Schleife in der Fiederachsel bilden und sein Verlauf kann bei *Conium maculatum* insbesondere dort, wo der Rand in die Schleife in der Fiederachsel einbiegt und sie wieder verläßt, durch die Ausbildung häutiger Schuppen oder Stipellen betont sein. Solche Schuppen erinnern an die Stipellen bei *Thalictrum* (*Ranunculaceae*). Ist die Rhachis bei Umbelliferen unifazial, kann ihre morphologische Oberseite an den Insertionstellen der Fiedern dennoch erkennbar sein (*Foeniculum vulgare*). Unifazialität von Blattstiel und Rhachis, ebenso wie Rhachisrand-Schleifen im Bereich des Fiederansatzes, sind wahrscheinlich abgeleitete Merkmale der *Umbelliferae* und können zum Klären der phylogenetischen Position mancher Taxa beitragen. Nach Diskussion vermeintlicher Beziehungen zwischen anatomischem Bau und Unifazialität wird festgestellt, daß, besonders bei Umbelliferen-Blättern, in erster Linie äußere morphologische Merkmale zum Nachweis der Unifazialität verwendet werden sollten.

The compound leaves of the *Umbelliferae* may have a partly or sometimes mostly unifacial main rachis, that is one bounded all round by its morphologically lower (dorsal) surface (Troll 1934, 1935, 1939; Kaplan 1970). Unifaciality is often found only at the lower segments of the rachis, with the petiole then also unifacial. Even when mostly unifacial, the rachis is bifacial upwards. If the lateral rachides or leaflets are bifacial, both margins of each may meet at or just above the insertion of the leaflets or lateral rachides on the main unifacial rachis, or alternatively the insertion of bifacial leaflets or rachides may involve the freeing of the margins of the main unifacial rachis at its 'node', and their continuity there with those of the lateral members.

A unifacial rachis may be viewed as one with its margins fused along its mid-ventral generatrix. Such a fusion indeed occurs at the juncture of the bifacial sheath and the unifacial petiole. Both margins may separate again just below the lowermost 'node' of the main rachis and be produced into the lower margins of the pinnae or lateral rachides. The upper margins of the latter then either merge just above the 'node'

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if the first rachis 'internode' again is unifacial, or proceed along it on both sides as its own margins if it is bifacial.

Insertion of the leaflets or lateral rachides of compound pinnae in compound leaves is generaly vertical, the plane of these lateral members thus being confounded with, or parallel to, that containing the rachis margins, and the whole rachis if this is flat. In the *Umbelliferae*, however, TROLL 1934, 1939 observed that pinnae may be inserted horizontally, with their plane perpendicular to the rachis one at least at insertion. As they are bifacial, this implies that the rachis margin above makes an abaxial turn above the pinna insertion to connect with the abaxial pinna margin. Although TROLL perfectly understood that, he does not seem to have actually observed the relevant margin segment. I wish to demonstrate it, and also to explain how pinnae may have a horizontal folded, V-shaped insertion and how an even more complicated W-shaped horizontal course of rachis margins at pinna insertion may occur, with the two lower shanks of the W bearing the leaflet.

Another feature that appears to have escaped attention in Umbelliferous leaves is the occurence of stipels. Broadly understood, these are any appendage of the margins of compound leaves at the junction of the rachis and leaflets or lateral rachides. They may assume the shape of small leaflets, membranous scales, glands or big hairs with all possible intermediates, and are nearly always at only the lower margin juncture of a petiolule .They are a common feature of the *Leguminosae*, occuring as glands or hairs even in some taxa where they are supposed to be lacking (GUÉDÈS & DUPUY 1981). As a rule, their connection with the margins is obvious. In *Thalictrum* of the *Ranunculaceae*, however, there are ventral but also dorsal stipels at the nodes of a compound leaf whose main and lateral rachides apparently are unifacial, so without any apparent margins. I was led to postulate that the ventral fused margins of these rachides in actuality are freed at the rachis nodes and makes loops in the axils of lateral rachides. On part of their course they develop the stipellar membranes. The dorsal ones are seated at the top of the axillary loops and accordingly are bent adaxially (GUÉDÈS 1968). Similarities between the leaves of the *Ranunculaceae* and *Umbelliferae* have long been pointed out (BITTER 1897) and that remarkable margin course will now be evidenced in one of the *Umbelliferae* as well, leading to the W-shaped rachis margins at pinna insertion just alluded to.

Observations

Conium maculatum L.

Although a widely known plant, the hemlock displays remarkable leaf features that seem to have passed unnoticed, and still are perhaps

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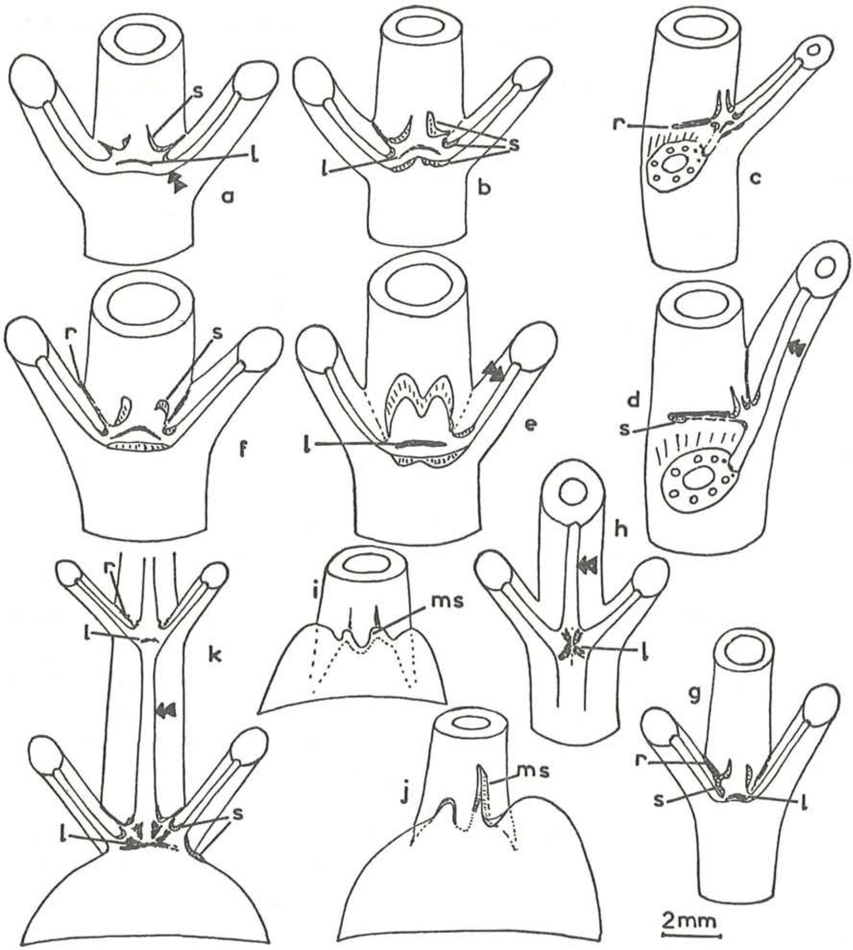

Fig. 1. *Conium maculatum.* — a—g Lowermost rachis nodes with lateral rachides of various lower leaves, ventral views, except c—d, lateral views (b—c same leaf). — h Second rachis node, ventral view. — i—j Transition zone from base to petiole in two lower leaves, ventral views. — k Upper leaf with no petiole and sheath margins proceeding as lower margins of lateral rachides. — l ligule, ms median stipule, r axillary ridge, s stipel. — Arrows denote leaf margins. See text for further explanations

unique in the *Umbelliferae*. Plants used for this study were gathered along the Loire (right bank) in Tours, France.

The leaves in the lower half of the stem have a unifacial petiole, topping a sheath whose margins accordingly meet ventrally in a median stipule. Upper leaves have a shorter petiole which is bifacial, then no

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petiole at all, their sheath margins becoming continuous with the lower margins of their lowermost pair of secondary rachides (Fig. 1 k).

In all leaves, stipellar membranes are obvious at the insertion of this first pair of rachides, so at the lowermost node of the main rachis. They are more or less developed, the longest may be hardly a millimeter in height, but commonly they are several mm long. In the upper leaves, the lower stipellar scales may prolong the sheath margins, which evidences their belonging to margins (Fig. 1 k).

Stipels are seen in very precise locations at the first node of the main rachis. Not all possible locations are always occupied at a given node, but at their completest, stipellar formations are as follows.

Just below the rachis node, the unifacial petiole frees its ventral margins into a cross-zone (Fig. 1 b, e—f; 2 a). This is a horizontal stretch of the leaf margins that were fused lower down, and it develops a stipel (Fig. 1 b, e—f) that is commonly notched in the middle (Fig. 1 b, e), that is, its two halves, belonging to the right and left margins of the petiole are partly free. This stipel may be nearly lacking, appearing as a mere ridge atop the petiole (Fig. 1 a). In any case, the stipel or ridge is continuous with the lower margins of the lateral rachides, which are always bifacial, although their ventral surface is far narrower than their dorsal one. The lateral rachides, moreover, have their ventral surface nearly adaxial (Fig. 1 a—k) as usual with lateral leaflets or rachides. In this way their lower margin connects easily with the cross-zone atop the petiole at all, their sheath margins becoming continuous with the lower directly be produced into the margins of the bifacial first internode of the main rachis, which are displaced adaxially as a result of the relative reduction of the ventral surface.

This is however not so. The upper margin of a lateral rachis develops a stipel at its insertion on the main rachis, but this is commonly bent towards the axil of the lateral rachis, rather than joining the overlying main rachis margin (Fig. 1 a—d, 2 a on the right). The stipel developed by the upper margin of the lateral rachis entering the axil is more often than not prolonged there (Fig. 1 d) as an axillary ridge which may bear a further, dorsal stipel within the axil (Fig. 1 d, 2 a). The latter, when present, is shorter and thicker than the ventral stipels. The axillary margin then turns around to come back to the ventral side, running very close to the previous shank, in a hair-pin-like manner (Fig. 1 d). The proximal shank (against the main rachis) is a thicker ridge than the distal one, and may also develop a thick dorsal stipel (Fig. 2 a). It is this proximal shank of the axillary loop that develops a ventral stipel on becoming continuous with the margin of the main rachis (Fig. 1 d, 2 a). Fig. 2 a on the right depicts that remarkable

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course of the junction between the upper margin of a lateral rachis and the corresponding margin of the main rachis.

The proximal margin in the rachis axil apparently runs at the base of the proximal ridge (Fig. 1 d), for the ventral stipel clearly joins the ridge there rather than on its top.

Instead of two parallel axillary ridges, a single massive ridge is often seen in the axils of the lowermost lateral rachides (Fig. 1 b, g on the left; 2 a on the left). Then there may be two stipels meeting on the ventral end of this ridge, the one continuous with the upper margins of the lateral rachis, the other with the margin of the main rachis (Fig. 1 b). Commonly, however, both stipels are themselves continuous, escalating or rather stepping over, the ridge end (Fig. 1 g on the left), thus making it clear that the leaf margin here runs along the girth of the ridge end, then shallowly hollowed out beneath the stipel arc. This is easily accounted for by admitting that both shanks of the hair-pin like margin ridge are now fused into a single axillary pipe with the two upper ventral stipels at the rachis axil now continuous around the pipe brim. The pipe, moreover is in fact solid on most of its length. Comparison of both sides of Fig. 2 a will make this obvious.

In lower leaves, the margins of the lowermost rachis internode, as opposed to those of the lateral rachides, are not underlined by longitudinal ridges. That the rachis, however, is bifacial, seems to result from the stipels not meeting above the insertion of the lateral rachides, but rather initiating an upward course (Fig. 1 a—d, f—g). Only below the second rachis pair may the margins of the first internode become apparent (Fig. 1 h), and margins are then obvious as ridges on further internodes. In upper leaves with no petiole (Fig. 1 k) the margins of the first internode of the main rachis are apparent, which may support the bifacial interpretation of the first rachis internode in lower leaves.

In only one leaf, the first rachis internode was found to be unifacial, the ventral upper stipels merging in each other between it and the axils of lateral rachides (Fig. 1 e).

In all leaves, besides the stipels that underscore the course of leaf margins, the lowermost rachis node develops a ventral ligule, i. e. an outgrowth of its ventral surface, just above the cross-zone stipel (Fig. 1 a—c, 2 a). This ligule is low and thick, with short hairs. It is sometimes very close to the cross-zone, and when the latter is absent (Fig. 1 g), it can be mistaken for it. The ligule is also present on leaves without a petiole, whose lower margins of lateral rachides prolong the sheath ones (Fig. 1 k).

At the second and further rachis nodes, there are no stipels or only very rudimentary ones. Axillary ridges are also lacking or obsolescent. When they occur, as sometimes happens at the second node, the margins

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of the lateral rachis join those of the upper internode of the main rachis without any loop in to the axil, so the situation must be as in Fig. 1 g. The ligule may be present at these upper nodes, but as a rule it is replaced by four ridges from the ventral surface, joining the junctures of the margins of the main lateral rachides with the centre of the "crossroads" of the ventral surfaces of these rachides (Fig. 1 h).

That the petiole is unifacial even when there is no cross-zone stipel atop it (Fig. 1 a, g) is further borne out by the sheath margins meeting at the junction of the sheath and petiole. They may meet on a nearly horizontal line, but very often their meeting line is made into an upside-down W through intercalary growth on both sides of the middle (Fig. 1 i) and in such instances, the margins may be obscure in the middle (Fig. 1 j). The petiole, nevertheless, is still unifacial as it has a cross-zone just below the first rachis node.

In the uppermost leaves still with a petiole, this becomes bifacial. Both sheath margins somewhat ascend parallely along its ventral zone without merging. They underline the petiole margins at this level. Petiole margins then become obscure as the organ is rounded in section, but at the first rachis node, there is no cross-zone. Only the ligule is now to be seen, although upper lateral stipels are commonly present, especially at the upper margins of lateral rachis and at the margins of the first internode of the main rachis, immediately above the node.

Some of these leaves, however, still seem to display a cross-zone atop their petiole, as a ridge rather than a stipel, and yet their sheath margins do not meet ventrally, behaving as those of the leaves with bifacial petioles. In such cases, I believe the petiole still to be unifacial, with sheath margins basically arranged as in Fig. 1 j, but with the downward, near-median shanks of the inverted W obscure, so that these margins seemingly behave as those of a bifacial petiole. Unifaciality here seems to be obvious from the occurence of a cross-zone topping the petiole. It cannot be excluded, however, that petiole margins merely become indistinct while still running along the petiole, drawing to each other to fuse somewhere up it, so that the upper portion of the petiole is unifacial and topped by a cross-zone.

Even when unifacial on account of lacking obvious margins and evidencing margin fusion below and above it, the petiole never has a closed ring of bundles, and so displays no ventro-median bundle opposite its dorsal bundle. Unifacial leaf portions without a ventro-median are common in many families.

Rachis and pinna insertion in other genera

No similar stipels were found in Umbellifers scanned in this respect, and no indication of them were found in the literature, but interesting

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features cropped up in examining leaf and rachis insertion in some very common species.

In *Foeniculum vulgare* L., the petiole and first rachis internode are unifacial (Troll 1939: 1618). I found that in upper leaves with short petioles, the lateral rachides at the first node of the main rachis may also be unifacial (Fig. 2 b). Then the second internode of the main rachis again was unifacial, though with bifacial lateral rachides atop it, at the second node (Fig. 2 c). Only the third internode became bifacial (Fig. 2 d).

The insertion of bifacial rachides on the main rachis is such that they are nearly horizontal, if the main rachis is maintained vertical. They are also much flattened dorso-ventrally (Fig. 2 c—e) and the upper (back) margins of lateral rachides must run a nearly horizontal course in the axil of the lateral rachis to join the corresponding margin of the main rachis (Fig. 2 d—e). That horizontal margin stretch is orientated as the axillary ridges of *Conium*. It is the more obvious as it demarcates the green dorsal surface of the main rachis from the whitish ventral surface of the lateral rachis. The lower (ventral) margin of the lateral rachis is directly continuous with the relevant margin of the next lower internode of the main rachis.

In *Heracleum sphondylium* L., leaflets or pinnae are folded horizontally at their insertion on the rachis (Fig. 2 f—g). Both of their halves make up a solid very short petiolule, then their lower half is freed and widers more than the upper one. The latter may fail to develop a blade for 0.5—1 cm next to the insertion (Fig. 2 f on the right), so that the leaflet has a sizeable flattened petiolule with its lower margin foliarized. This happens at the upper leaflets on a rachis.

In upper cauline leaves of *Sium latifolium* L. (living lower cauline leaves were unavailable to me at the time when these observations were made) are interesting in two respects. Besides their marginal teeth, the leaflets have a more elongate tooth at their insertion, where their lower (ventral) margin merges in the corresponding margin of the rachis internode below (Fig. 2 h). This tooth may deserve being called a stipel even more than stipellar membranes of *Conium*, and it is closely similar to the stipels of other compound leaves which are but the lowermost second-order leaflet on the first-order ones, located at the insertion of the latter on the leaf rachis. Moreover, leaflets of *Sium latifolium* are folded horizontally at insertion much like those of *Heracleum*, but their upper insertion shank is far shorter than the lower one (Fig. 2 h), so that the folding is far less apparent.

Even more interesting, the margin of the rachis internode above the upper insertion shank is not immediately continuous with the end of the latter. Rather, it proceeds backwards horizontally closely above this

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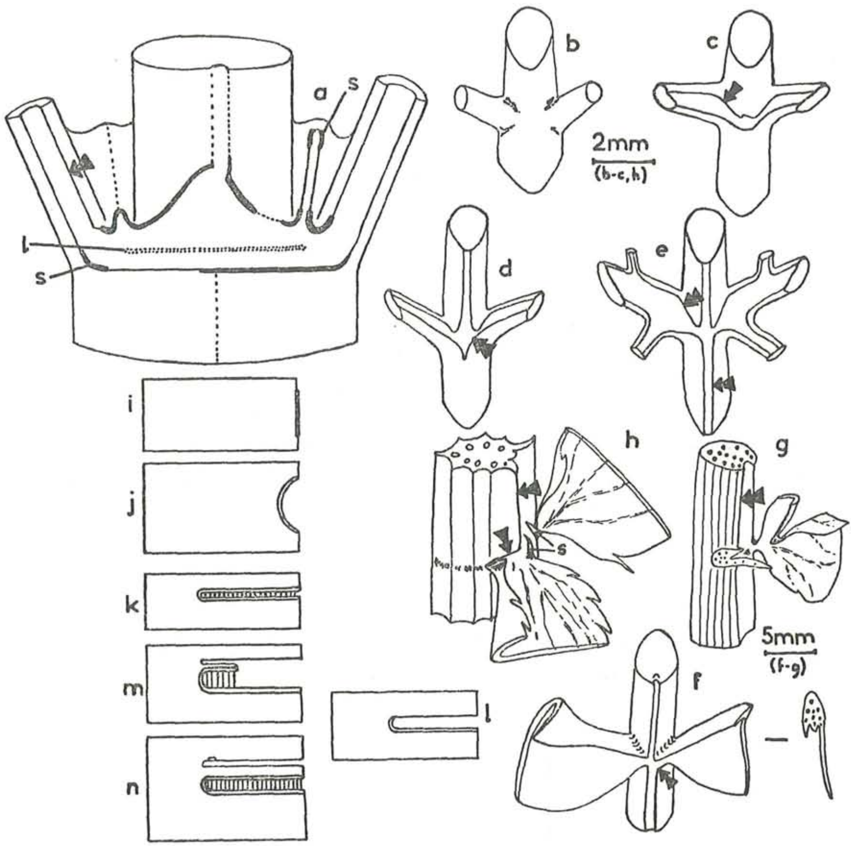

Fig 2. — a Interpretive scheme of lowermost rachis node of a *Conium* leaf, ventral view. Heavy lines: stipels, dotted lines: lines of margin fusion or obliterated margins. Arrows indicate apparent margins. Main rachis is assumed to be bifacial on the right, with its margin lateral, and unifacial on the left with its margin on the middle line (compare Fig. 1 e). — b—e *Foeniculum vulgare*. Insertion of lateral rachides of upper leaf, ventral views, b first rachis node; c—e second to fourth nodes. — f—g *Heracleum sphondylium;* leaflet insertion, lateral (a) and ventral (f) views. Right leaflet in f is dissymetrical at insertion (see corresponding right scheme) as are both leaflets in g. — h *Sium latifolium* Leaflet insertion in an upper cauline leaf, lateral view. — l ligule, s stipel.

i—n Schemes of pinna insertion, lateral views, margins of main rachis at right, vertically, double lines denote insertion lines of leaflets or lateral rarachides; when this is folded both shanks are fused at insertion, and the area in between is hatched on the schemes. A margin loop may occur above insertion (m—n); i conventional leaflet; j light back bending of insertion line; k horizontal folding of insertion line (compare f); l light back folding with horizontal connecting shank (compare c—e); m half-folding with overlying loop of main margin (compare h); n horizontal folding with overlying loop (*Conium maculatum*, although lateral rachis of *Conium* is rounded)

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shanks up to the level of the bottom of the V-shaped insertion, then turns about even more closely, to merge at last in the tip of the upper shank (Fig. 2 h, m).

According to Troll 1935, the lower cauline leaves of *S. latifolium* have a rachis that is unifacial in its lower two thirds. In upper cauline leaves, the rachis is wholly bifacial. Leaflet insertion on the unifacial rachis remains to be studied. It may be that the lower margins of both leaflets at a node abut on each other in a cross-zone, and even that leaflet blades are continous on this zone.

Discussion

Pinna insertion, leaf segmentation and phylogeny

These observations provide a direct confirmation of Troll's (1934, 1939) interpretations as to the horizontal or sub-horizontal insertion of pinnae in the *Umbelliferae* and corresponding course of leaf margins. The one Troll postulated is directly observed in *Foeniculum*. The insertion of leaflets in *Sium* and secondary rachides in *Conium maculatum* is even more complicated, with axillary loops. These are closely similar to margins loops in *Thalictrum* (Guédès 1968) although lateral rachides of *Thalictrum* are unifacial, as is the main rachis.

A series can be set up of increasingly complicated modes of insertion of pinnae in the *Umbelliferae.* We may start from the vertical insertion of a flat pinna (Fig. 2 i) where a vertical segment of the rachis margin directly proliferates into a leaflet or lateral rachis. This segment may become more or less curved (Fig. 2 j), then frankly folded into a horizontal U or V (Fig. 2 k: *Heracleum sphondylium*). Both shanks of the U in effect bound the insertion surface of a solid petiolule but are spread open above as the leaflet blade unfolds (Fig. 2 f). If only the lower shank of the U proliferates as a lateral rachis (Fig. 2 l), the condition in *Foeniculum vulgare* is reached. Besides the lower shank the „root" of the upper one may also proliferate, thence the arrangement in *Sium latifolium* (Fig. 2 m) where the upper shank does not directly connect with the upper rachis margin: rather the latter first reaches horizontally a little above and up to the bottom (dorsal end) of the U or V, then turns about and comes back to join the upper shank. Finally, in *Conium maculatum,* the lateral rachis also is inserted through a horizontal U-shaped area and the upper margin of the main rachis behaves somewhat as in *Sium,* but has to run a whole horizontal narrow U just above the far larger U-shaped insertion (Fig. 2 n).

It is tempting to view this series as mirroring phylogeny. Vertically inserted pinnae (Fag. 2 i) occur in many more or less primitive plants often with rather thin rachides, such as the *Rosaceae* and *Saxifragaceae.* They might well be the primitive Umbelliferous condition.

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The *Heracleum*-type insertion with folded horizontal leaflets is still basically similar though probably more advanced. It is reminiscent of the insertion of the pinnae that arise through postgenital splitting of a continuous pleated blade in certain palms (*Phoenix*). Such comparisons of course can only be purely morphologic, yet they serve to emphasize the basically similar developmental potentialities in widely different taxa.

The horizontal location of the pinnae is probably a derivative condition. Only the lower shank of the horizontal V of the *Heracleum*-type folded insertion then proliferates into a pinna, so the *Foeniculum* condition is reached (Fig. 2 l). It is remarkable that in *Foeniculum* the petiole and rachis also become partly unifacial, probably another advanced feature in the *Umbelliferae*, even though leaf peltation, hence petiole unifaciality, is recorded in primitive Angiosperms as early as the mid-Cretaceous (Albian: Doyle & Hickey 1976).

Finally marginal loops at insertions on the main rachis, such as occur in *Sium* and especially *Conium* also seem to be derivative traits. In *Conium* (Fig. 2 n) the *Heracleum* condition is retained with a margin loop superimposed. In *Sium* (Fig. 2 m) it might be that starting from the latter arrangement, the upper shank of the U insertion and the lower shank of the superadded loop have retreated. It might also be that a superimposed loop first appeared after the upper shank of a *Heracleum*-type insertion had receded, so that no ancestor to *Sium* would ever have occured with any *Conium* arrangement. Again in *Conium* and lower cauline leaves of *Sium* marginal loops are correlated with unifaciality of the petiole and lower rachis.

Conium is advanced in other respects, especially in lacking vittae and developing a secretory endocarp layer. *Foeniculum* is also advanced in its capillary leaflets and lack of calyx teeth, bracts and bracteoles. *Sium* is very peculiar in its adaptation to aquatic biotopes, secondary multiplication of vittae and highly distinctive petiole. The latter may be short and supplemented by the lowermost rachis internode, the lower pair of pinnae being reduced or obliterated (*Sium erectum* Huds., Troll 1935). The petiole may also be totally lacking and at most replaced by the lowermost rachis internodes, whose leaflets are disappeared (*Sium latifolium,* Troll 1935). When these are lacking, their potential location is still made obvious by the occurence of septa at the levels of the lowest rachis nodes. Such a septum may occur at mid sheath in *S. latifolium,* whose cauline leaves may have a full or reduced leaflet pair there, in which case they have not even a spurious petiole. Sheath leaflets may also occur as tiny appendages (Troll 1935).

This underlines the homology of the sheath and rachis, the former simply being a flat rachis, but their similarity is no doubt a recent

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evolutionary development in *Sium*. Ancestral leaves had no well defined sheats but they got one long before the *Umbelliferae* becames differentiated. The usual, ancestral condition in the *Umbelliferae* thus is a clear-cut sheath without leaflets. The ability to produced leaflets, however, is retained in potentia and manifested again by such genera as *Sium* and *Carum*, advanced among the *Umbelliferae*. *Carum carvi* L. develops laciniate 'leaflets' or 'stipules' at the insertion of the sheaths of its upper leaves on the stem. These appendages in fact are neiter leaflets nor stipules since they are located at the bottom of the sheath. They may be unique in Angiosperms and do not mirror any ancestral condition. *Carum* is an advanced genus with hardly any calyx teeth, bracts or bracteoles, and generally with narrow leaflets that are inserted horizontally (Troll 1934, 1939).

In the *Ranunculaceae*, *Thalictrum* is certainly a very advanced genus, and it seems to be the only one with margin loops and rachis unifaciality. Such neglected features of vegetative gross morphology, rather than being despised probably because they need no sophisticated instruments to be evidenced, should be given their due share of consideration when trying to reconstruct phylogeny.

What is unifaciality?

Misunderstandings, I am afraid, have become rampant as regards the unifaciality concept. Kaplan 1970 is to be congratulated for trying to introduce it to American botany, but quite contrary to his assertion (Kaplan 1970: 121), Troll & Meyer 1955 never stated that the bi- or unifacial condition of a phyllome portion has something to do with the activity of marginal and rounding meristems respectively. Troll was very clear that an organ portion may be unifacial and flat or bifacial and rounded in outline, even though most unifacial organs are rounded and most bifacial ones are flat. The rounding meristem of unifacial organs is generally active but may be inhibited, and bifacial organs may become rounded through the activity of a ventral meristem.

A similar misconception led to Hagemann's (1970) claim that, as unifacial petioles are at first flat, they are initiated in a bifacial condition, becoming unifacial as time passes and they get rounded through their 'ventral' meristem. In Troll's view, on the contrary, the flat unifacial petiole is already unifacial, with no ventral surface, which is why it develops cross-zones below and above. Its rounding is a subordinate development.

Troll's view seems to me the right one (Guédès 1979). A unifacial phyllome portion is one with a single morphological surface all round, as a rule the outer (dorsal) one (epiunifaciality), very rarely the inner

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(ventral) one (hypounifaciality). When it passes into a bifacial, conventional portion the margins of the latter cannot proceed along the petiole, as this has no margins. They meet horizontally in a cross-zone or meet at angle on the ventral side (epiunifaciality) or sometimes the dorsal one (hypounifaciality).

This has no bearing on the flat or rounded outline of the unifacial portion. Blade margins are seen meet in cross-zones atop very flat unifacial petioles such as those of lower leaves of *Ginkgo* shoots (Guédès 1966).

The rounded condition, which is not indicative of unifaciality, bears a relation to the rounding of the arc vascular bundles in the phyllome portion. If this is unifacial and rounded, its bundles will curve in a circle with the most lateral ones, now medio-ventral, often fused into a ventro-median bundle. A phyllome portion, however, may well be unifacial and rounded in outline without its most ventral bundles merged into a ventro-median. When a phyllome portion is unifacial but flat, the bundles remain more or less along a tangential line, because those ventral bundles that would close the circle either do not develop, when the organ remains narrow, or develop laterally, when it is extended through lateral p s e u d o -marginal meristems.

A bifacial and flat phyllome portion also has its bundles in a tangential line, but a bifacial and rounded portion commonly has a seemingly closed circle, of bundles. In the latter, however, the most ventral bundles are n o t the morphologically most lateral ones, but are branches from more centrally located bundles. This is readily apparent when the transition from a bifacial and flat portion, especially the leaf-base or sheath, to the rounded bifacial petiole is studied. The most lateral bundles from the sheath that enter the petiole do n o t pass to the ventral side of the latter. They remain lateral, while bundles that branch off from more or less centrally-located bundles of the sheath take a medio-ventral location in the petiole. As they commonly become inverted, the bundle circle in the petiole assumes the shape of an inrolled line, which it is not. Such spurious bundle circles of course are n o t indicative of unifaciality.

Kaplan 1970 did not pinpoint the difference between the leaf of *Lilaeopsis occidentalis* Coult. & Rose, with a unifacial rachis whose vascular arc seems truly inrolled, although no true ventro-median bundle is present, and that of *Oxypolis greenmanii* Math. & Const., whose rachis also is unifacial, but with a morphologically open vascular arc of bundles. In contradistinction to *Lilaeopsis,* whose ventral bundles in the rachis are branches from marginal sheath bundles entering the blade, and do not occur in the bifacial sheath, the ventral rachis bundles of *Oxypolis* are branches from sheath bundles midway between the median bundle and the margins, and are already present in the bifacial

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sheath (Kaplan 1970, Fig. 1 A—D, K—Q). They cannot point to the (otherwise obvious) unifaciality of the rachis-blade, since they are present in the obviously bifacial sheath.

In point of fact, when the outmost sheath bundles to pass into the petiole are far from sheath margins, and distal branches from them are responsible for closing the vascular circle of the blade ventrally, as occurs in *Lilaeopsis*, this may or may not be indicative of unifaciality of the latter. It may happen that the branches closing the vascular circle merely correspond to the intercalary branches from more dorsal bundles that close the circle in rounded bifacial petioles. This is obvious in *Aquilegia* where the petiole has a vascular circle closed as in *Lilaeopsis* but still displays two margins, and so is bifacial (Guédès 1972). The same might apply to *Lilaeopsis*, so that in neither *Oxypolis* nor *Lilaeopsis* would anatomy point to unifacialty, even though rachides in these genera indeed are unifacial.

All this being so, nothing can be said as to the unifacial condition of a phyllome portion from studying its histogenesis, since no distinction can then be made between a true and spurious marginal meristem, or between the rounding meristen of a unifacial portion and the ventral meristem of a bifacial one. And the occurence of a closed circle of bundles is indicative of unifaciality only when closure occurs at the level of the portion under consideration through nearing and often fusing of the most distal bundles on both sides in the adjacent bifacial portion.

As emphasized previously (Guédès 1979), outer morphology is thus the main or only fast criterium of unifaciality. If margins are to be seen along a phyllome portion that are continuous with the sheath and/or blade margins, that portion is bifacial whether or not it is flat and has a closed vascular circle. If margins of the sheath and/or blade are seen merge in a cross-zone or at an angle, the portion above, below or between the cross-zone(s) is unifacial whether or not it is rounded and has a closed vascular circle. The unifacial portion is bounded at both ends by a cross-zone, unless the latter is directly inserted on the stem without any mediating leaf-base (*Ginkgo* leaf) or is a terminal unifacial blade or apical blade mucro.

In *Conium* margins are not apparent all along most of the rounded internodes of the rachis but at both ends of them they are underlined by the stipellar membranes which run parallel to each other (Fig. 1 a—c, f), and the internodes are in all probability bifacial. It might be thought, however, that a unifacial segment occur at mid-internode where margins are obliterated. This could only be demonstrated if margins could be induced to develop by some experimental treatment. They then would be seen merge at two cross-zones or angles above and below the

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unifacial segment. If alternatively my interpretation is borne out, they will simply run along the whole internode. Only exceptionally are margins seen merge in a cross-zone above the first (lowest) rachis node (Fig. 1 e) and then the overlying internode is unifacial.

In well-developed leaves, the petiole is unifacial with cross-zones above and below, evidenced by the sheath margins and stipels. The cross-zone below is commonly distorted into an inverted W-shaped figure (Fig. 1 i—j) and in smaller upper leaves the petiole is bifacial, without cross-zones. No petiole or rachis segment has a ventro-median bundle, whether or not it is unifacial: unifaciality is never translated anatomically.

Conium is also interesting in illuminating the distinction between a ventral true ligule from the ventral phyllome surface, and mid-ventral stipel from phyllome margins at the upper cross-zone of the unifacial petiole. The stipel occurs only when the petiole is unifacial, whereas the ligule is apparent also when it is bifacial (Fig. 1 a—c, k), and similar ligular outgrowths also occurs at upper rachis nodes, where no cross-zones are ever formed.

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Recensio

FRAHM Jan-Peter & FREY Wolfgang 1983. Moosflora. Mit 108 Abbildungen von J. DÖRING. — In: Uni-Taschenbücher 1250. — Kl. 8°, 522 Seiten; brosch. — Verlag Eugen Ulmer Stuttgart. — DM 29,80; ISBN 3-8001-2463-7.

Die neue Moosflora in der bekannten UTB-Reihe soll nach den Ausführungen der Autoren im Vorwort an die Stelle der „Moosflora von Südwestdeutschland" von Karl BERTSCH treten. Der Rahmen ist auf alle Moose der Bundesrepublik Deutschland erweitert worden, sodaß das Werk auch in den Nachbarländern (mit Ausnahme der Hochalpen) benutzt werden kann. Die Verfasser streben sicheres Bestimmen für den Anfänger und leichtes Nachschlagen von diagnostisch wichtigen Merkmalen für den Fortgeschrittenen an.

Am Anfang stehen kurze Abschnitte über das System der Moose, über Sammeln und Präparieren, weiters Schemazeichnungen diagnostisch wichtiger Merkmale, ein Verzeichnis der Fachausdrücke und eines der Autoren sowie Hinweise auf weiterführende Literatur.

Dann folgt ab p. 26 der Hauptteil, in dem die Moose in systematischer Folge aufgeführt sind, mit bis zu den Arten führenden Bestimmungsschlüsseln; die zahlreichen Abbildungen (jede der 108 Abb. besteht aus einer Anzahl Einzelfiguren) veranschaulichen die zum Bestimmen wichtigen Merkmale. Alle Taxa werden, über die in den Schlüsseln genannten Merkmale hinaus, durch Beschreibungen charakterisiert, denen bei den Arten Standorts- und Verbreitungshinweise angefügt sind.

Es ist erfreulich, daß der beliebte „BERTSCH" eine Nachfolge gefunden hat und damit in veränderter Form wieder eine handliche und preisgünstige Moosflora für den mitteleuropäischen Raum zur Verfügung steht. Leider sind die Seiten 31 und 34 verwechselt worden.

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