TRACES OF ANCIENT DICHOTOMIES IN ANGIOSPERMS

(A contribution to our Knowledge of Phyllospory and Stachyospory)

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Introduction.

It is a generally accepted concept nowadays that dichotomy is the most primitive type of ramification in land plants. Recently Lam (1948) briefly reviewed the literature of this subject in the light of the telome theory. He recalled that the dichotomies of fern leaves are to be regarded as homologous to the dichotomies of stems in more primitive plants and enumerated a number of more or less haphazardly collected cases in higher plants, of which the most probable interpretation is that they are traces of such ancient dichotomies, betraying their original relation to a branch system.

In his paper, Lam discriminated between such traces in vegetative and in reproductive parts and he arrived at the provisional conclusion that traces of ancient dichotomies in the vegetative parts should particularly occur in what he termed the 'phyllosporous' plants, and that those of the reproductive parts are particularly found in the 'stachysporous' groups.

At his instigation I made an attempt to collect some more data in this respect, especially regarding the leaves, but also the perianth and the reproductive organs of the Angiosperms, a subject which hitherto seems to have practically been given no attention. Readily following this suggestion I looked first of all through my own and another private collection of dried plants from the Netherlands, together containing some 3000—4000 specimens in which all families of some importance are well represented. For the families wanting in our flora, I based my investigations both on living material in the Leiden Botanic Garden and on dried material preserved in the 'Rijksherbarium'. In addition, I looked through the complete Engler and Prantl, "Die Natürlichen Pflanzenfamilien".

Yet, though no important group of Angiosperms is likely to have escaped my attention, my work does by no means pretend to be complete or exhaustive. If, despite this, the number of cases mentioned underneath is comparatively small, this should be attributed to two causes; the first is that I mainly paid attention to leaf venation and that only distinct dichotomies of the stronger nerves were given attention; and the second is that only a very small portion of the numerous genera which were
looked over, provided me with positive results, which intimates that dichotomy remains a rare phenomenon in the Angiosperms.

**Axes.**

Regarding traces of dichotomies in main or lateral axes, stems, rhizomes and roots, I have found little in addition to what was mentioned already by Lam. I may only add the following cases.

Next to the dichotomous rootlets in Conifera which are inhabited by a mycorrhiza fungus, I found the same phenomenon in the cycadaceous *Dioon edule* (fig. 1) and Engler and Prantl mention it in *Encephalartos hildebrandti*. It is stated by them that these rootlets are invariably inhabited by a fungus and by endophytic blue-green algae, which are not found in normal, i.e. non-dichotomous rootlets. The dichotomous ones develop near the soil surface; they are negatively geotropic and sometimes protrude into the air.

Analogous cases are found in some saprophytic *Orchidaceae*, e.g. *Epipogon* (cf. Schröter, 1904, pl. 19, fig. 5) and *Coralliorhiza* (cf. Wettstein, 1935, fig. 689), and *Burmanniaceae*, viz. *Sarcosiphon episcopalis* (fig. 2). No doubt similar structures are to be expected in other saprophytical Angiosperms whose roots (or rhizomes) are inhabited by a mycorrhiza fungus.

As far as stem dichotomies in Angiosperms are concerned I can only add to previously given instances that Troll (1937) cites 1) dichotomy in the rhizome of *Nuphar* and that Velenovsky (1913) stated dichotomy, accompanied by an angular leaf, in the stem of *Alstroemeria brasilienensis*.

It may be recalled here that stem dichotomies, mostly (always?) with angular leaves, in the Angiosperms thusfar are only known in the Monocotyledones (*Palmae, Amaryllidaceae*) and the *Nymphaeaceae*. In some cases they are quite normal, in others however (*Cocos, Arenga*) they seem to develop as a consequence of some damage inflicted upon the growing point.

**Leaves.**

In a fern leaf with open venation we regard the nerves as remnants of an ancient ramification system. In the Ferns with closed venation and in the Angiosperms, secondary connections between the nerves darken the picture. However, traces of the original ramification system remain visible, especially in the stronger nerves. Some of these ramifications are from our present point of view traces of ancient dichotomies.

A remarkable fact in the Angiosperms is that the aquatic life is not only accompanied by a reduction of the number of weaker nerves, but often the leaves are also reduced to the main venation or nearly so. In the ramification of the aquatic leaves we find both splendid dichotomies and monopodial ramification.

The following cases of dichotomy have come to my knowledge; in my enumeration I followed the system given by Wettstein (1935).

1) The original publication (Glück, 1924) was unavailable to me.
DICOTYLEDONEAE.

Monochlamydeae.

In the greater part of this group the leaf venation is of the advanced monopodial (pinnate) type, without any traces of dichotomy.

An exception, however, is formed by the Proteaceae in which the leaves of many genera (Simsia; Grevillea; Hakea, figs. 3—4) show segmentations and (or) venations of a primitive type, with many apparent dichotomies. Particularly interesting in this respect is the leaf of Franklandia fucifolia (fig. 5) which is up to six times dichotomously divided and forms a splendid example of what Troll (1937) calls cruciate dichotomy. This leaf closely resembles the branching system of Psilotum and the like.

Some weak traces of dichotomy are found in the nerves of Chenopodiaceae and Polygonaceae, e.g. in those of Polygonum convolvulus (fig. 6).

No distinct traces of dichotomies were found in the Euphorbiaceae, but very neat ones in Buxus (fig. 7), however, with many transverse connections.

Dialypetalae.

Numerous beautiful traces of dichotomy are found in the leaf venation of the Polycarpicae.

Ranunculaceae — Batrachium (figs. 8—9), Eranthis hiemalis (fig. 10), Nigella damascena (fig. 11), Anemone pusilla (cf. Zimmermann, 1939, figs. 13, 20, 23).

Berberidaceae — Berberis thunbergii (fig. 12); note the sympodial main nerve, as far as I am aware a rare phenomenon in the Angiosperms.

Nymphaeaceae — Cabomba aquatica, aerial and aquatic leaves (figs. 13—14); Nuphar luteum (fig. 15), with only very few lateral connections. In Nymphaea such connections are more numerous.

Aristolochiaceae — Main nerves strictly dichotomous in Asarum europaeum (fig. 16). The same type, but slightly more advanced, is found in Aristolochia.

Ceratophyllaceae — Ceratophyllum, aquatic leaves up to 3 times dichotomous (fig. 17).

Rhoeadaceae, Gutierrezales, Myrtales — No evident traces of dichotomies have been detected by me in these orders, even not in Myriophyllum, whose leaves are monopodially nerved throughout.

Parietales — Distinct traces of dichotomy only in Droseraceae, e.g. in Drosera binata in which the leaves are twice furcate (cf. Lam, 1948, fig. 6), and in Drosera intermedia and rotundifolia (figs. 18—19). Weak traces of dichotomy are furthermore found in Begonia.

Rosales: Papilionaceae — neat dichotomous nerve endings are found in Trifolium (fig. 20) and Medicago (fig. 21).

Podostemaceae — numerous dichotomously segmented leaves are found in this group of aquatic plants, e.g. in Mourera weddelliana (many times furcate), Pohlia laciniata, Inversodicraea (fig. 22), Macropodiella and Winklerella (fig. 23). In the related Hydrostachyaceae the leaves are monopodially segmented.
Columniferae, Gruinales, Terebinthales, Celastrales, Rhamnales — no traces of dichotomy found.

Umbelliferae — Some traces of dichotomies are found in Umbelliferae and Araliaceae, e.g. in Anethum graveolens (fig. 24), Apium inundatum and Hedera helix f. arborescens (fig. 25). In most Umbelliferae however, even in the aquatic leaves, the main ramification is pinnate and therefore monopodial.

Sympetalae.

In the Sympetalae cases of distinct dichotomy of stronger nerves seem to be rare. I found it in the following cases:

Primulaceae — Cyclamen (fig. 27) shows the type of Aristolochia. The aquatic leaves of Hottonia palustris, however, are quite monopodial.

Of the Tubiflorae only Utricularia and Genlisea (Lentibulariaceae) show traces of dichotomies.

In the Scrophulariaceae Limnophila shows transitional stages between monopodially nerved aerial leaves and aquatic leaves with dichotomous ultimate segments. Much the same condition is found in Bidens (Compositae). Both cases are pictured by Goebel (1933, figs. 1648—1649).

MONOCOTYLEDONEAE.

Monocotyledonous leaves are generally parallel-nerved; even in the very basis no traces of dichotomy could be discovered in the adult leaf. Properly speaking, this is a surprising condition in a group with so many primitive characters. Maybe an investigation of the ontogeny will reveal dichotomies in early stages, comparable to those of e.g. Agathis and Podocarpus.

Quite another type, however, is found in the Araceae, in which Amorphophallus shows a primitive type of leaf (fig. 28). Each of the main parts of the leaf blade is forked, each daughter branch of a fork showing a very neat sympodial system.

Possibly the leaf venation of some other Araceae (fig. 29) bears some relation to this ramification.

Perianth.

Dichotomous venation seems to be much more frequent in the perianth leaves than in vegetative phyllomes. Particularly the petals of the majority of the Angiosperms show the phenomenon very clearly and only few species seem to be without any traces of dichotomous venation.

The most primitive condition being, of course, dichotomous venation without or with only a few lateral connections, I mainly looked for that type. It may be recorded in the following cases:

DICOTYLEDONEAE.

Monochlamydeae.

In the Monochlamydeae only the group with larger flowers, viz, the Centrospermae, was examined. In the Caryophyllaceae the petal nerves of Cerastium and some Dianthus species are dichotomous; in Saponaria
there are some lateral connections and this character is still more advanced in such genera as Coronaria, Melandrium, etc.

In the Caryophyllaceae a great number of genera have bilobate petals e.g. Melandrium, Silene, Stellaria, Malachium, Cerastium, etc. This condition is possibly to be interpreted as a dichotomy. A peculiar condition is found in Dianthus monspessulanus (fig. 30), in which the petals are multifid and the segments are once or twice dichotomous.

**Cactaceae** — In Echinocactus petals the dichotomous nerves are not or hardly laterally connected; in Echinopsis these connections are few and in Phyllocactus phyllanthoides they are numerous.

**Dialypetalae.**

Very neat dichotomies are found in some Ranunculaceae, e.g. the petals of Ranunculus (fig. 31). In other genera lateral connections occur, sometimes so many as to convert the venation into a reticulate one (Caltha).

In the Nymphaeaceae the petals of Nymphaea show lateral connections; in Nuphar these lead to a reticulate venation.

In the Cruciferae, e.g. in Matthiola incana (fig. 32) the nerves make connections near the margin.

In the petal nerves of the Papaveraceae, the Parietales (incl. the Begoniaceae), the Saxifragaceae and the Rosaceae (among which Fragaria and Potentilla), lateral connections occur, and these may sometimes lead to a reticulate venation (Papaver, Rosa).

In the Papilionaceae I found beautiful dichotomies in Onobrychis (fig. 33). In other species e.g. Lathyrus the nerves make cross connections.

Whatever there is of dichotomous petal nerves in the Myrtales, Colum- niferae, Gruinales, Terebinthales and Umbelliferae, is invariably accompanied by lateral connections.

**Sympetalae.**

Dichotomous petal nerves are found in Pirola (fig. 34). In such Ericaceae as Rhododendron the venation was found to be reticulate.

Very neat dichotomies, however, are found in the petals of many Primulaceae e.g. Hottonia palustris (fig. 35), Lysimachia vulgaris and particularly in Cyclamen (fig. 36). In Primula cross connections blur the picture.

The same is true in the Tubiflorae, Contortae, Rubiales and Cucurbitales. Particularly in the Boraginaceae, Solanaceae, Scrophulariaceae, Orobanchaceae and Labiatae the venation is reticulate.

**Oleaceae** — Forsythia viridissima (fig. 37) shows neatly dichotomous petal nerves; in Jasminum nudiflorum the nerves show some lateral connections.

**Compositae** — Reticulate venation in the petals is the general condition.

**Dialypetalae.**

The petal nerves are connected near the margin e.g. Anthemis mixta (fig. 38).
MONOCOTYLEDONEAE.

The venation of the perianth of the Monocotyledones is generally dichotomous. As instances I may mention here Alisma (fig. 39), Fritillaria meleagris (fig. 40), Tulipa (fig. 41), etc. Of the Iridaceae the perianth venation in Crocus is dichotomous, in Iris pseudacorus, however, reticulate. Cannas has dichotomous venation with lateral connections.

In the Orchidaceae the nerves are sometimes strictly dichotomous, e.g. in Orchis morio (fig. 42), sometimes reticulate e.g. in Dendrobium.

Stamens.

Branched 'filaments' occur in a number of families and several of these are probably best interpreted as remains of a dichotomous branching system. As has been pointed out by Lam (1948, p. 139) a general intérpretation is not yet possible. The intrinsic value of phyllosporous stamens, i.e. microsporophylls, and of stachyosporous ones, i.e. supposed sporangium-bearing axes; their mutual relation; the origin and significance of basifix, introrse (dorsifix) and extrorse (ventrifix) anthers; these all are as many unsolved problems in the New Morphology. The cases mentioned underneath are therefore given without much critical comment. It is realised that their individual significance may widely differ from one case to another. Moreover several cases are unsufficently known. Also and particularly in this field, ontogenetical investigations seem essential for a good understanding.

In general we can say that there are stamens of which we are inclined to call their filaments 'forked', and others in which we tend to use the expression 'connate'. Without extensive research it will, in some cases, be difficult or even impossible to decide which term should be chosen. It is true that 'forked' seems the more descriptive and therefore the more neutral of the two. On the other hand, the interpretation of an ancient dichotomy is lurking behind it. 'Connate' presupposes some secondary process of which there is no proof without an investigation of the ontogeny.

However, it seems not too far-fetched to consider a very general type of Angiosperm stamen as a stalk — whether an axis or a reduced leaf — with two pairs of sporangia on top. In these we might see two subsequent dichotomies and this interpretation is certainly confirmed by those cases in which either branch of a filament bears a bisporangiate theca instead of a tetrasporangiate anther. In other cases, however, either branch apparently bears a full anther, but these certainly require a closer investigation.

The first-named type, with two separate thecae is extant in Betula (cf. Lam, 1948, fig. 6), Carpinus (cf. Wettstein, 1935, fig. 403) and Corylus. The second type, with a tetrasporangiate anther on top of each branch, is found in Salix (cf. Lam, 1948, fig. 6). Here the bifurcation, if any, may be situated quite near the insertion (S. cinerea; cf. Lam, 1948, fig. 6) or about halfway up (S. incana, fig. 43) or immediately below the sporangia (S. glauca, fig. 44). In some species with normally unforked or nearly unforked filaments (S. caprea, cinerea, fragilis, incana,
repens) there are occasional records of furcate filaments (var. monadelpha) and this is one of those cases in which it seems impossible to choose between 'forked' and 'connate'.

A family in which many cases of branched filaments occur is that of the Euphorbiaceae. Some of these branchings are dichotomies. I mention Maprounea brasiliensis (the ultimate ramifications only), Lasiococca and Ricinus. In Ricinus and Maprounea each ultimate branch bears a theca, in Lasiococca, however, an anther. In Ricinus (cf. Lam, 1948, fig. 6) I found a flat laterally attached structure which Lam with apparent conviction (or for the lack of better) interpreted as an angular leaf (l.e., p. 119).

Similar organs seem to occur in a number of Podostemaceae, e.g. in Mniopsis saldanhana (fig. 46). The lateral structure in these cases has been interpreted as a reduced perianth leaf. This may be correct, but even then its position would probably stamp it as an angular leaf to the bifurcation of the filament.

More dubious cases are found in such families, in which stamens are known to grow in bundles, e.g. in the Malvaceae, Bombacaceae, in Pandanus, and possibly in some other groups. In most of these cases secondary connections will probably play an important part and their ultimate interpretation will have to wait until much more essential data are available. A remarkable fact is that in the Malvaceae, Bombacaceae and Guttiferae the ultimate ramifications bear single thecae.

Stigmata.

Without venturing to give an interpretation we may state here that forked stigmata are known to occur in Mirabilis viscosa (Nyctaginaceae), Begonia (cf. Lam, 1948, fig. 6), Carica (Caricaceae) and many Euphorbiaceae, e.g. Agithamnia (fig. 47), Erismanthus (fig. 48), Ricinus (fig. 49), Jatropha and Epiprinus. Since stigmata probably are phyllome-tips in any case, their eventual dichotomy is not surprising at all. (Nor would it be if they were axes, for that matter).

Teratologies.

Spontaneous teratologies are largely depending on their numerical occurrence. If they are rare enough, they are considered 'abnormal', if they are less rare, they are considered a part of the genotypical variability — which they are in any case, if the time factor is included in the picture, as they cannot be but based upon the potentialities incorporated in the plant.

Only few of the above-mentioned instances may be called teratologies e.g. the var. monadelpha in some Salix species. Teratologies are particularly interesting in case they probably may be interpreted as atavisms e.g. in the stem dichotomies of Arenga and Cocos.

Next to these there are many records of bifurcations in stems and leaves that probably proceed from damages of the growing point and have no phylogenetical value at all.
Conclusions.

It may be asked what is the bearing of traces of dichotomy in various organs in the Angiosperms on our opinion about the system, particularly in connection with Lam's groups of *Phyllosporae* and *Stachyosporae*.

If it may be assumed that the structures described above are dichotomies or traces of dichotomies, and this is hardly doubtful; if the dichotomies found in the Angiosperms are homologa of those in the Ferns; and if therefore, in the Angiosperms, dichotomy is to be considered a primitive character, the following conclusions might have some importance.

1. Stem dichotomy is often (always?) accompanied by an angular leaf.

2. The fact that in a few groups (*Euphorbiaceae*, *Podostemaceae*) forked filaments are provided with a lateral structure at one side of the bifurcation might stamp these bifurcations as stem dichotomies and the plants therefore as stachyosporous.

3. Lam's thesis that traces of dichotomy are particularly found in the vegetative parts of the *Phyllosporae* and in the generative ones (filaments) of the *Stachyosporae* (in his provisional delimitation) has–partly been confirmed, but there are some noteworthy exceptions.

   It is true that the more primitive type of venation is abundant in the obviously phyllosporous *Polycarpiceae*, but it is wanting or almost wanting in many other orders (*Rhoeadales*, *Guttiferae*, *Myrtales*). A remarkable fact is that some *Papilionaceae* show very neat nerve dichotomies, whilst the related *Rosaceae* do not. In the *Parietales* only the *Droseraceae* and, though less obviously, *Begonia* show nerve dichotomies. In the *Umbelliflorae* there are some traces, but they are weak, even in the aquatic leaves of some *Umbelliferae*.

   Dichotomy of the stronger nerves is not found in the *Monocotyledoneae*. This is surprising on account of their obvious relationship with the *Polycarpiceae*. Maybe nerve dichotomies are hidden in the most basal part of the leaf, maybe the fact is due to other peculiarities of the parallel-nerved leaf. Anyhow, a very striking exception is made by the *Araceae* in which a very primitive type of ramification is found in the leaf of *Amorphophallus*. Possibly the leaf venation of other *Araceae* has some relationship to this ramification.

   In the *Sympetalae*, dichotomous venation occurs in the, possibly stachyosporous, *Primulaceae* (but not in the aquatic leaves of *Hottonia*). Some other traces are restricted to aquatic leaves, e.g. *Utricularia* (*Lentibulariaceae*), *Limnophila* (*Scrophulariaceae*) and *Bidens* (*Compositae*).

   In the *Monochlamydeae* dichotomous nerves are practically wanting; the main exceptions being the *Proteaceae* and *Buxus*, whose systematic positions are often regarded as doubtful.

   With some hesitation I make the following conclusions: According to their venation type the *Proteaceae* differ from the greater part of the stachyosporous *Monochlamydeae*; possibly they are phyllosporous really.

   The allegedly stachyosporous *Primulaceae* show some instances of primitive venation. This separates them from the greater part of the *Monochlamydeae*, but not from the *Polygonales* and *Centrospermae*.

   The allegedly stachyosporous *Araceae* also show traces of primitive leaf venation; possibly they are phyllosporous really.
4. Dichotomy seems to be furthered by environmental stimuli, such as endophytic Fungi and Algae (roots or rhizomes of Cycadaceae, Coniferae, Orchidaceae, Burmanniaceae), aquatic life (leaves of Cabomba, etc.), and perhaps insectivory (leaves of Drosera) and saprophytism (Monotropa).

As to the influence of aquatic life, the potentiality to the dichotomous type of ramification should of course be primarily extant, but even in plants in which the aerial leaves are monopodially veined, the aquatic ones often show gradual transitions to dichotomy (Limnophila, Bidens, Umbelliferae).

On the other hand the aquatic leaves of Hottonia palustris are monopodially branched but the aerial leaves of Cyclamen show dichotomous nerves.

On considering leaf venation from the viewpoint of organogeny, it should be constantly borne in mind that venation is a character most likely to be subject to ontogenetical and phaenotypical modifications. This is the principal reason, why in this comparing investigation only the more evident cases have been considered.

5. Petal venation, being much oftener dichotomous, is therefore less significant. It seems as if the leaves in the reproductive region are more conservative in this respect.

However, dichotomous petal venation without lateral connections (open venation) only occurs in the following groups: Centrospermae, Ranunculaceae, Papilionaceae, Primulaceae, Pirolaceae, Oleaceae and the greater part of the Monocotyledoneae.

6. As long as so few essential and fundamental facts concerning the Angiosperm stamens are known, it is useless to try and interpret the few cases of dichotomy in the filament, the more so since apparent dichotomy and secondary coalescence cannot be discriminated without a thorough ontogenetical investigation.

The cases of furcate filaments can be arranged in the following groups: Betulaceae; Salix; Euphorbiaceae and Podostemaceae; Malvaceae and Bombacaceae; Pandanus.

In the Euphorbiaceae and Podostemaceae occasional ‘angular leaves’ are found which seem to support both the interpretation of a dichotomy and the state of stachyospory.

It is difficult to say what relation the bundled filaments (often with a theca instead of an anther on top) in such families as the Malvaceae and Bombacaceae may have to those mentioned earlier. The often mentioned relation to the Euphorbiaceae seems not impossible.

7. Furcate stigmata are few in number. No conclusions whatever can be based on so scarce a material.

8. It provisionally seems that the distribution of phyllospory and stachyospory in the Angiosperms is more intricate than was originally conceived. Further investigations in this field are urgently needed.
Literature.

Schötter, C., 1904. Taschenflora des Alpenwanderns.
Zimmermann, W., 1930. Die Phylogenie der Pflanzen.
Legend to the figures

(s. dried material; v. living material; alc. alcohol material).

Roots and rhizomes — 1. Dioon edule, roots, v. — 2. Sarcosiphon episepalis, rhizome, after BECCARI from WETTSTEIN.


Stamens — 43. Salix incana, after HEIMANS, HEINSIUS and THIJSSE. — 44. Salix purpurea, after HEIMANS, HEINSIUS and THIJSSE. — 45. Maprounea brasiliensis, after WETTSTEIN. — 46. Mnepopsis saldanahome, after ENGEL and PRANTL.

Stigmata — 47. Argithamnia candida, after ENGEL and PRANTL. — 48. Erithanthhus sinensis, after ENGEL and PRANTL. — 49. Ricinus communis, after WETTSTEIN.