THE OPTIONS OF PLANT ORGANISMS FOR THE DEVELOPMENT OF NEW TYPES OR TYPOGENESIS IN PLANTS

por

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Resumen

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Este artículo trata sobre el método morfológico comparativo (tipología) combinado con estudios de desarrollo para mejorar el conocimiento de las relaciones filogenéticas entre diversas formas de plantas. El método se ilustra con dos ejemplos; el primero alude a las relaciones filogenéticas existentes entre las hepáticas y los helechos, casi todos de tipo-repens abierto. El segundo ilustra la relación más compleja existente entre las angiospermas primitivas, tipo árbol, las cuales retornaron a la condición de arbusto o hierba perenne y aun a la de plantas delgadas tipo-repens abierto. El tipo del sinflorescencia característica de las angiospermas desempeña un papel central en este desarrollo aun si se suprime esta última etapa.

Palabras clave: tipogénesis, plantas.

Abstract

The presented paper deals with the comparative morphological method (typology) combined with developmental studies as a means for understanding phylogenetic relations between different plant forms. This method becomes illuminated by two examples. The first are the phylogenetic relations between liverworts and ferns from which many follow the open repens-type. The second illuminates the much more complicated relations'between the primitive, tree-like angiosperms which returned via shrubs and herbal perennial plants to the delicate plants of the open repens-type. The angiospermic synflorescence-type plays a central role in this evolutionary pathway even if it becomes relinquished by the last step.

Key words: plants, typogenesis.

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Classic comparative plant morphology, as Wilhelm Troll left us behind in his magnificent work, needs more attention and further critical development to play its essential role in modern biology. This should be done in steady exchange with those experimental sciences to which typology provides the organismic basis. Comparative morphology allows not only a first insight into the relations between the organisms of a common type, but has beyond that the capacity to give insight into the relations between different types, i.e. to find out the different pathways for possible typogeneses. The so-called synthetic theory of evolution denies this (see **Reif *et al.*** 2000). But in my opinion this theory is indeed in many respects insufficient to solve especially macroevolutionary problems as long, as the organisms are seen only as objects of environmental influences, i.e. mutation and selection as the factors driving evolution (**Weingarten,** 1993:280). The typological construction cannot be changed in any direction, but only in such a way that life of the modified organism is warranted. This makes the organism a subject in evolution, which offers only certain developmental options for constructive changes. The knowledge of these allows to predict possible typogeneses (**Hagemann,** 2000). Therefore, the organism, which is the entity of life, must be placed in the center of biology for understanding typogenesis.

Another correction of the theoretical fundaments of plant biology is also urgently needed, namely the classic cell theory, which estimated cells of higher plants as its "elementary organisms" (**Brücke,** 1861, **Sitte** 1998:2, 36). So-called land plants, such as bryophytes, pteridophytes, and seed plants, have a phragmoblastemic structure. I introduced the term "phragmoblastem" for the type of tissue of all these plants (**Hagemann,** 1982, 1992). It expresses that cell divisions in land plants produce by no means individualized living units, as the term "elementary organisms" suggests. Instead of this, cell division means the integration of new cell walls into the growing plant organism. This integration becomes realized by the phragmoplast, which becomes etsablished by the persisting spindle apparatus together with a dense ER-network between the daughter nuclei after mitosis. The remaining spindle elements are further used for transport of Golgi-vesicles containing the wall materials. They become fused on the periphery of the centrifugally growing cell plate and this again conserves thousends of plasmodesmata passing the cell plate (Fig. 1). On the one hand, the protoplast permeating the wall system of the whole plant, behaves as a unit, as is on the other hand the wall skeleton of the plant. Thus, cell division in higher plants provides subdivision without interrupting the organismic unit. This
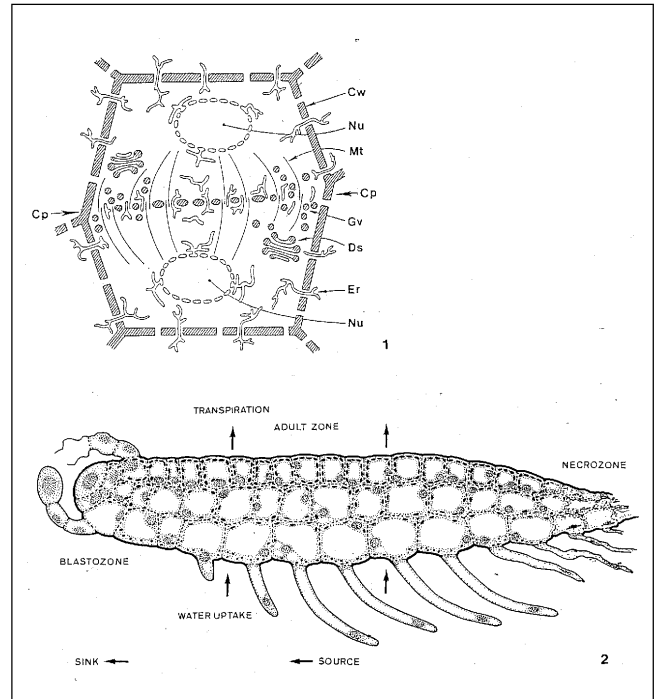
Figures 1-2: 1. Phragmotomy of a plant cell, the basis of the phragmoblastem. Cw cell wall with plasmodesmata, Nu nucleus, Mt microtubuli of the phragmoplast, Cp cell plate, Gv Golgi vesicles, Ds dictyosome, Er endoplasmatic reticulum connected through plasmodesmata. **2**. Open repens-type of a simple, thalloid liverwort or fern gametophyte with its functional zones.

is the solution of the problems occuring with organismic growth.

The vegetation body of small primitive land plants has an open, frondose, dorsiventral, and polar structure, such as those of Metzgeriales, e.g. *Pellia epiphylla* or the gametophytes of ferns, such as *Stenochlaena tenuifolia* (Figs. 3-4). They represent, what I have called the open, frondose repens-type, an evergrowing and everdying plant creeping endlessly over the ground (Hagemann 1999, 2000; Fig. 2). Such an organism expresses its polarity by its growing pole and dying pole. The first is represented by the blastozone, the second by its necrozone (**Hagemann & Gleissberg**, 1996). Blastozones are those parts of apical meristems which are responsible for primary morphogenesis, i.e. the establishment of the primary organismic form elements of the plant body. The frondose thallus is formed by a marginal blastozone growing horizontally. It forms under the influence of gravity a leaf-like structure with different dorsal and ventral sides. Prevailing thickening growth of the central blastozone forms a winged midrib. The polarity between the blastozone and the necrozone together with gravity, light,
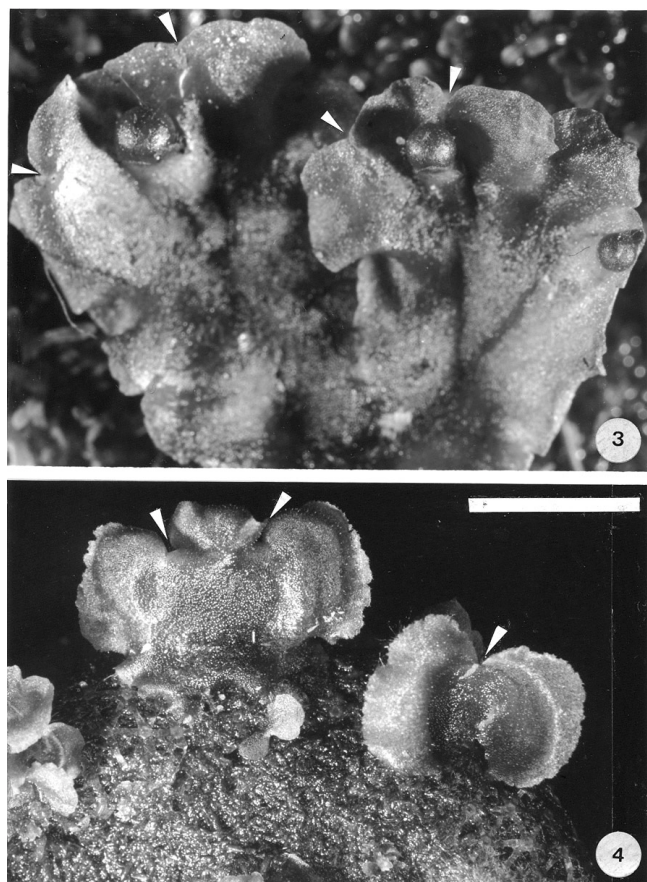
Figures 3-4: 3. *Pellia epiphylla* after several dichotomies from above with three sporogonia, which develop on the bases of the midlobes between two branches. The situation of the smallest sporogonium is not clearly visible. **4**. Two gamentophytes of *Stenochlaena tenuifolia*, unbranched plant (right hand side) and once branched (blastozones marked by arrow heads, bar = 5 mm).

and water supply engenders a lot of differences between the poles, dorsal and ventral sides, photosynthesis and storage sites. The resulting gradients cause transport of substances (moving of materials) between sources and sinks, such as water transport in the wall system between the ventral and the transpiring dorsal side. Metabolites move between photosynthetic active tissues on the light exposed, adult dorsal side and the blastozones, meristems and storage sites as the sinks for those products. Thus, tissue differentiation is the consequence of certain claimes to organismic regions. Those effects, which dominate local tissues, cause their specific differentiation, e.g. transport of metabolites cause procambium differentiation, and later vascular bundles with more specialized transporting tissues. The organism, not the single cell, decides on tissue differentiation by special usage of certain tissue zones in the growing organism.

After the establishment of the primary form, the tissue of the blastozone -the promeristem (**Sussex & Steeves**, 1967, **Esau**, 1977:272, **Sachs**, 1991:131)- enters a phase of accelerated growth with the effect of declining cell dimensions in the so-called transition zone **Popham**, 1951, **Esau,** 1965:96, **Stevenson**, 1976). Within the transition zone tissue differentiation begins with the establishment of the primary histogenes, as are the protoderm, procambium, and the quickly extending groundhistogen (**Sachs**, 1991:131) which produce during further growth the final tissue organization of the adult vegetation body (final histogenesis: Hagemann 1999). In our gametophytic examples inner histogenetic differentiation stays in a simple condition without the differentiation of procambium, which may occur in other examples of Metzgeriales, such as *Metzgeria, Pallavicinia* or *Hymenophytum* (**Hagemann,** 1999). But in *Pellia* and *Stenochlaena* gametophytes the protoderm differentiates certain appendages, as are trichomes, rhizoids, and gametangia (Figs. 2-4).

One of the most important processes of primary morphogenesis is blastozone fractionation which produces dichotomous branches and leaves of ferns and seed plants. Dichotomous branching can easily be observed in the gametophytes of *Stenochlaena* (Figs. 4 and 5-8). Blastozone fractionation is a mutual effect between growth of the blastozone and growth in the transition zone beneath the first. The marginal blastozone is clearly marked by its big marginal initials (Fig. 5). Especially in the flanks of it the marginal tissue, included the marginal cells, become rather quickly subdivided, thus producing the lateral thallus wings. This transition is also seen beneath the marginal blastozone, although the transition tissue is not as extremely small-celled, as it is in the flanks. This is the consequence of rapid extension of the ribs ground tissue. During growth the blastozone dilatates, until it reaches double width. In this moment the fractionation can be observed. The transition zone integrates the center of the blastozone and divides it into two equal fractions (Figs. 6-7). The tissue of the central transition zone grows out as a small-celled midlobe between two equal blastozones. The midlobe contains the two opposed inner wings of the two resulting thallus branches (Fig. 8). After the fractionation, the plant grows in the form of an Y with two marginal blastozones. But after some time, when the progressing necrozone of the plant reaches its branching point, the process turns out as a vegetative (clonal) multiplication of the organism.

In shoot differentiation blastozone fractionation leads to the isolation of leaf marginal blastozones from the ra-
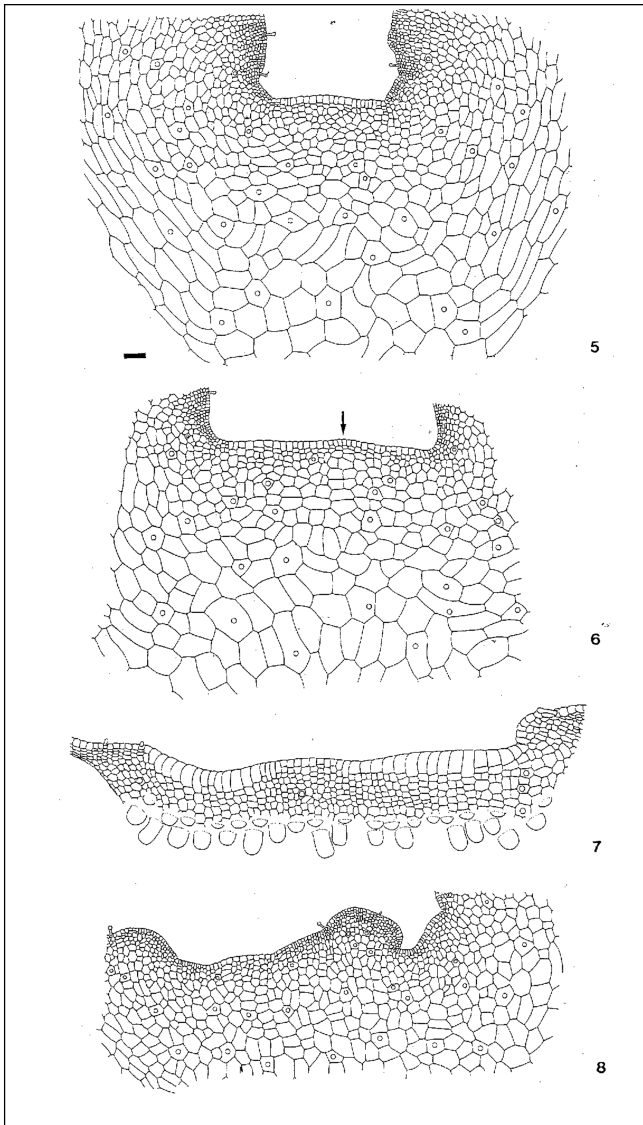
Figures 5-8. Gametophyte of *Stenochlaena tenuifolia*: blastozone fractionation. **5**. normal blastozone seen from above. The median part with isodiametric cells under extension growth is the thickened costa. On the flanks the "prosenchymatic" wings are seen which push the wings around the apical sinus. **6**. Cor-roborated blastozone starting the fractionation, seen from above. The extending ground parenchyma of the costa expands fan-like. Beneath the central part of the blastozone periclinally extending ground parenchyma with predominating anticlinal wall integration can be observed. Below this region in the center of the midrib, prosenchymatic extension of central tissue begins (arrow). Above this region, the blastozonal cells become smaller and the blastozone somewhat vaulted. **7**. The blastozone shortly later seen from underneath showing the necks of the youngest archegonia. The small-celled midlobe is now clearly outlined. Its marginal initials have not assumed extension growth. **8**. The midlobe has grown and includes new parts of small-celled blastozone tissues from the flanks. Marginal glands signalize histogenetic differentiation. Circles mark the position of glandular hairs. (bar = 100 µm, from Hagemann 1999).

dial shoot blastozone (Figs. 9-11). The radiallity of the shoot is the consequence of vertical growth, which withdraws the shoot from the effect of crossing gravity in the situation of horizontally growing plants. The nearly radial condition of the apical blastozone has a lobed outline (Fig. 11). The fractionation of the leaf blastozones leaves gaps in the margin of the shoot blastozone which slowly become filled up. This can easily be demonstrated by the apical blastozone of *Dryopteris filix mas* (Figs. 9-10). The blastozone is crowned by a three-sided apical initial and changes on its basis into the cup-shaped transition zone. The oldest blastozone lobes reach far beyond the transition zone (Fig. 9), which then grows outwards interrupting the oldest parts of the lobe from the stem blastozone by extreme, small-celled transition tissue. The crescent-shaped leaf blastozone has thus reached independency (Fig. 10). The fractionation process demonstrates convincingly that the usual hypothesis of the developmental physiologists, such as **Wardlaw** (1968: 131), **Steeves** (1961), **Steeves & Sussex** (1989:134, **Steeves et al.,** 1993), namely that leaf sites begin their existence as radial growth centers, is not in accordance with the organization of the shoot apex (**Hagemann,** 2002). The differentiation of a leaf initial with two cutting faces begins already before the fractionation is accomplished. The small-celled transition zone above the leaf primordium produces the leaf gap (Fig. 11). Already before the fractionation, the shoot blastozone lobes have induced the procambial histogene which after the fractionation followes further growth of the marginal leaf blastozone. This coherency of organismic form differentiation can never be understood from the viewpoint of the classic cell theory. After the constitution, the marginal blastozone formes the wave-like acrorvergently curved leaf primordium, which produces on its part a medially positioned and endogenously growing first root primordium (Figs. 10-11).

All construction elements, such as the leaves, stems, and roots of the cormus-type, as do the bones of the vertebrate skeleton, have constant positional relations with one another (Fig. 15). This was already discovered by J.W. v. **Goethe** (1790, s. 1982), who argued "Dagegen ist das Beständigste der Platz" ("most constantly is the position"). He developed thus typology, i.e. the identification of the positional relations between the construction elements, as the fundamental method of the comparative morphology. Identity of position was later termed "homology" by **Owen** (1848). Contrary to this, Owen defined equally formed construction elements with different positional relations as "analogous". **But Darwin** (1859) defined more precisely "nonhomologous" organs, which are formed
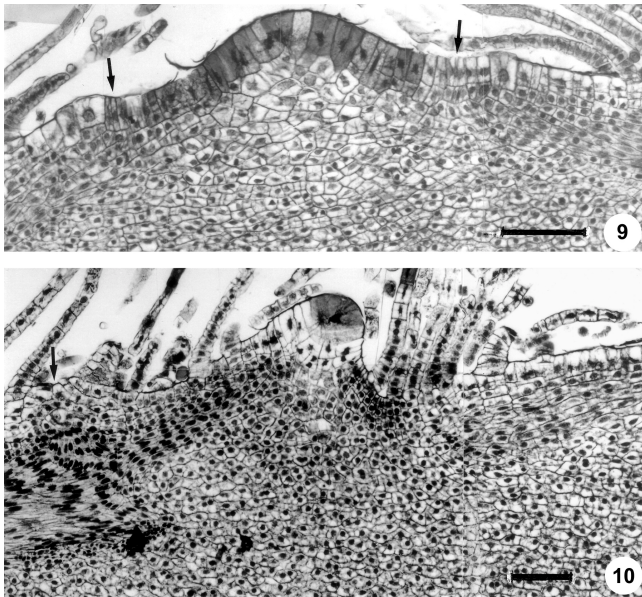
Figures 9-10: *Dryopteris filix mas*. **9.** Radial section of the shoot apex. Shoot apical blastozone with apical initial and the two youngest leaf blastozones with their apical initials which become separated by small-celled fractionation zones. These had been separated from the shoot blastozone by the upwards spreading, cup-shaped transition zone beneath the blastozone lobes (arrows). **10.** Young leaf blastozone with a remarkable, strong procambial strand and starting growth of the first root (arrow), whose initial gets just its tetrahedral form (bars = 100 μm, from Hagemann 2002).

Figure 11: Sketch drawn from a series of cross sections through the apical dome of *Dryopteris filix mas*. 1 - 9 The youngest leaves, -1 - -4 prospective leaf sites in the stem blastozone which is marked by a stippled line and its apical cell. It has a lobed outline as a consequence of the fractionations between stem and leaf blastozones. Leaf gap parenchyma: cross-hatched. The procambial tissue is directed to the leaf primordia and surrounds even the prospective leaf sites which may be understood as attraction centers of transport of metabolites. The first root of a leaf becomes differentiated just below above the gusset beneath the leaf primordium (arrow beneath leaf 4). The inclined line marks the course of the sections of Figs. 9-10 (from Hagemann 2002).

convergently by equal function as analogous. Classic examples are the axillary branches of Asparagaceae (phyllocladia) which have taken over the function of foliage leaves (Figs. 12-13).

How does the method of typology work? I shall try to answer this question in my further report by means of two examples. I have already used the cormus-type (Fig. 15). Plants of this type are the cormophytes: ferns and seed plants. The latter comprise Gymnospermae and flowering plants resp. Angiospermae. The differentiation of the shoot system into a green vegetative basis and a terminal flower resp. an inflorescence was defined by **Wilhelm Troll** (1964) as the synflorescence. Already **Goethe** (1790) developed the hypothesis that flowers are reproductive shoots. Above a vegetative shoot division with green trophophylls the shoot is continued in a terminal flower with reproductive leaves on a contracted stem division. The sequence of leaves in the flower is: sepals, petals, stamens, and carpels. As a rule, the latter use up the shoot blastozone and thus, the shoot becomes closed. This type of a flowering shoot is best represented *Magnolia kobus* (Fig. 14). In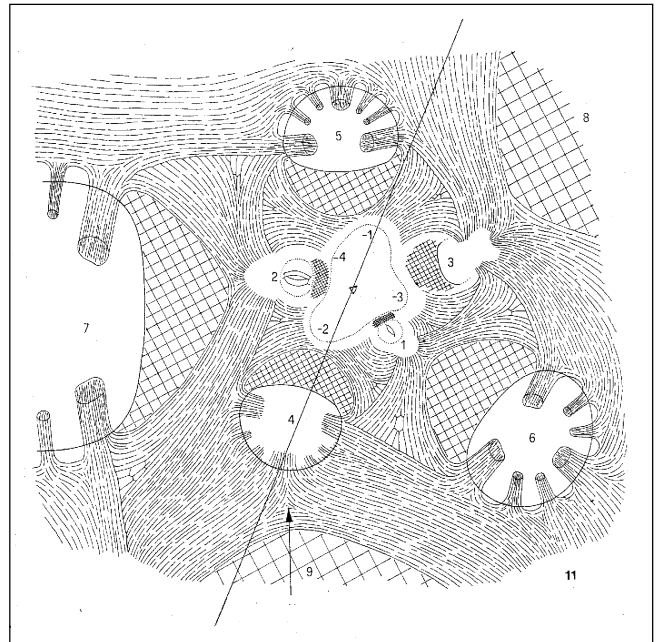novation of the System occurs by lateral branches developing in the axils of the trophophylls in an acrotonous sequence and this in turn provides a sympodial branch system in *Magnolia*, because the uppermost, strongest buds will repeat their mother shoot. But such furthering of the uppermost branches provides the option of proleptic branching sensu **Müller-Doblies & Weberling** (1984), i.e. during the same vegetation period the branches develop simultaneously with their mother shoot which occurs as a rule in tropical regions. If the axillary blastozones start growth simultaneously with their subtending leaf, then their early activity has an inhibiting influence on the growth of this leaf which stays in the condition of a bract. This I have termed the simultaneous branching type which characterizes synflorescences (**Hagemann**, 1990). The consequence is the branching type of the synflorescences (**Troll** 1964/69), whose most primitive ones are the "monotelic synflorescences" (Fig. 16) (**Weberling & Troll,** 1998: 423 ff). This
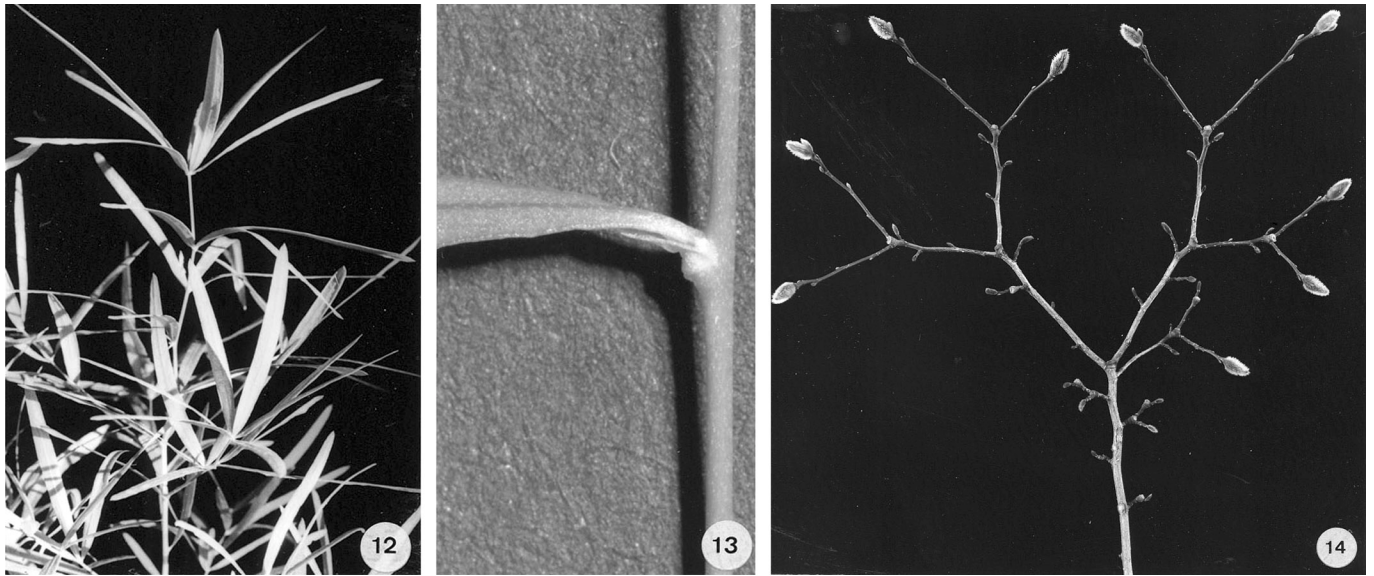
Figures 12-14: 12-13. *Asparagus falcatus*: Shoot system with leaf-like phyllocladia (12). **13** Shoot axis with a scale-leaf ubtending a phyllocladium (from Hagemann 2000). **14**. *Magnolia kobus*: branch system of an older tree in early spring. The yearly growth units produce acrotonic axillary buds and terminate in a big flower bud. Only the two biggest, uppermost buds continue the branch system with fertile growth units. The older growth units terminate in a big scar left behind by the flowers (from Hagemann 1990).
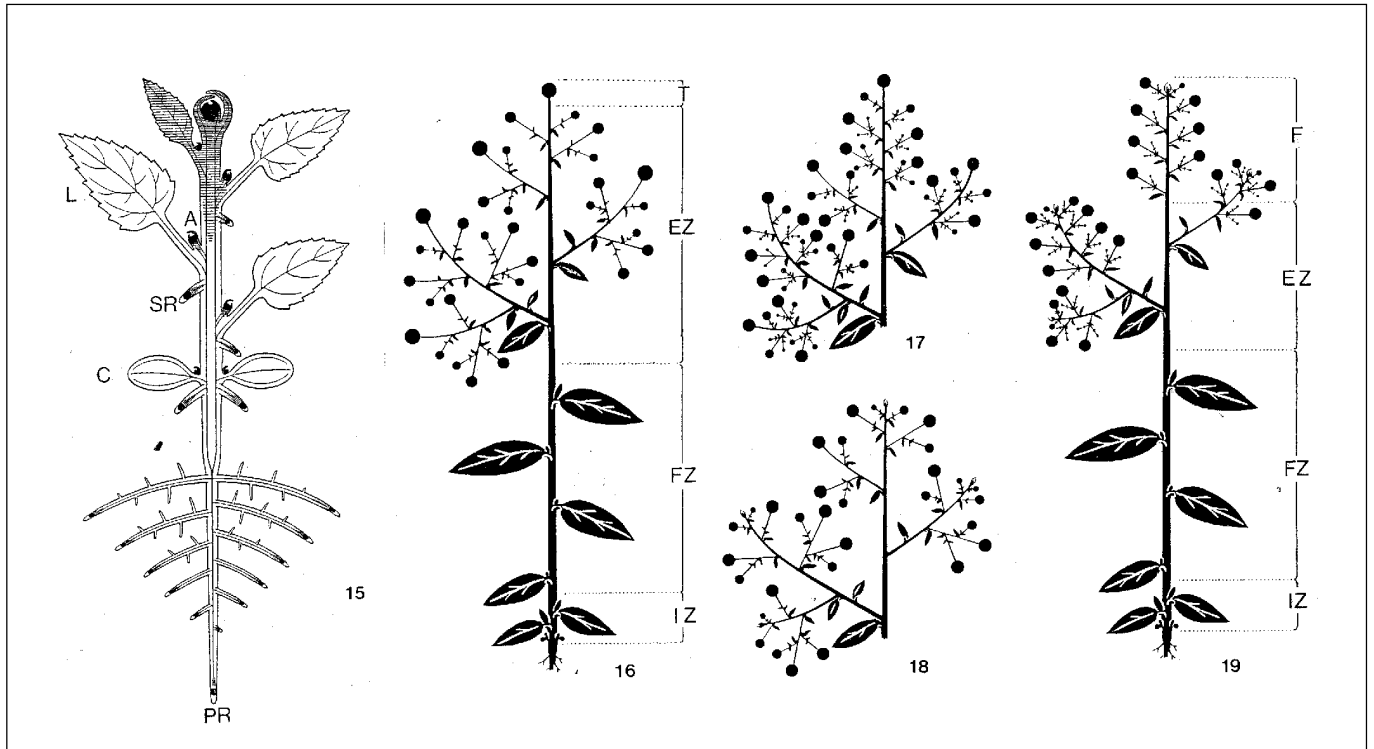

Figures 15-19: 15. So-called "Urpflanze" after Troll (1959:19). Shoot blastozones and root meristems black, PR branched primary root, C cotyledons, L leaves, A axillary buds, SR shoot-born roots. **16-19** monotelic and polytelic synflorescences. **16**. Type of the monotelic synflorescence, **17**. differentiated enrichment zone of a monotelic anthoblast, **18**. truncated monotelic anthoblast, **19**. polytelic synflorescence. IZ Innovation zone, FZ frondose zone, IZ + FZ trophotagma, EZ enrichment zone, T terminal flower, F florescence, EZ + T resp. EZ + F = anthotagma (Hagemann 1975).

is best represented by Rosaceae, such as *Rubus fruticosus* (Fig. 20). This is not only realized as observed in annual growth units of shrubs and many trees, but also in a lot of herbaceous plants, such as herbaceous Rosaceae and most Ranunculaceae. These plants develop a subterranean catalyptic innovation zone, the green, upright stem zone and further upwards the flowering zone becomes closed by the terminal flower (Fig. 16). The simultaneously growing branches were called "enrichment shoots" or "paracladia", which repeat the main shoot above their insertion. Thus, the synflorescence included the vegetative basal zone producing the catalyptic innovation shoots (**Müller-Doblies & Weberling**, 1984), the paracladial zone (enrichment zone), and the terminal flower. All parts of the synflorescence below the terminal flower were united under the term "Unterbau" or the "hypotagma" **Troll** (1964:181). **Mora-Osejo** (1987) introduced for the flowering zone including the terminal flower the term "anthotagma" and for the vegetative zone the term "hypotagma", and exchanged later the latter term later into "trophotagma" (**Hagemann,** 1990, **Mora-Osejo & Gonzáles,** 1995) to avoid confusion with Troll's terminology. Thus, the type of the angiospermous monotelic synflorescence is a whole shoot system with its vegetative and innovative part, the trophotagma, and its reproductive part, the anthotagma. Innovation shoots are the founders of new generations of such synflorescences.

Thus, a type visualizes the organismic construction ("organization type") of a given plant without answering causal relations. However, typology is an indispensible, propaedeutical means for causal questioning in as much, as the topographical conditions in the organism finally regulate development and differentiation step by step. Already early in his book "Vergleichende Untersuchungen über Organisation und Gestalt im Bereich der Blüte" ("Comparative Studies on the Organization and Organismic Form within the Flower") **Troll** (1928) differentiated between the plants "organization type" and the type of its "Gestalt". The "gestalt-type" he understood as a recurrrent type of form, i.e. he used it as an expression for the manifestation of equal forms in case of a different origin, e.g. the form of a "blossom" like that of *Rubus fruticosus* with calyx, corolla, androecium, and gynoecium, *Chrysanthemum leucanthemum*, a capitulum engendered by an involucrum, ligulate flowers and a disk of tubular flowers, or even a double capitulum like those by **Troll** (1928) used examples of *Syncephalantha decipiens* or *Myriocephalus gracilis* developed from densely aggregated capitulae which develop the ligulate flowers only in peripheral position of the whole aggregation (Figs. 21-26). The gestalt-type includes convergent forms which may develop from homologous or

Figures 20-23: 20-21. *Rubus fruticosus*: monotelic synflorescence, the terminal flower opens first (20). Flowers in anthesis and postfloration showing calyx, corolla, androecium and gynoecium (21). **22-23**. *Chrysanthemum leucanthemum* flower head from below and above with involucrum and ray flowers (22) resp. ray flowers and tubular (disk) flowers (23) (original).
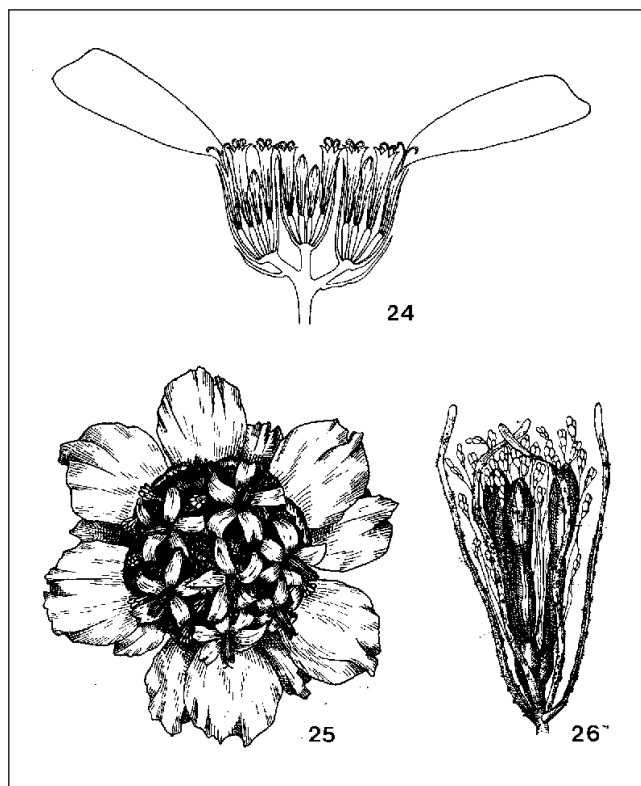
**Figures 24-26.** Secondary flower heads. **24**. *Syncephalantha decipiens* with a terminal head and **25-26**. *Myriocephalus gracilis*: secondary flower head from above (25) and a single flower head (26). (24 from Weberling 1989; 25,26 from Troll 1928).

analogous construction elements. Therefore, Troll distinguished between homologous and analogous convergences (**Hagemann**, 1977). In place of these terms, today the terms "parallelism" and "homoplasy" have been adopted (**Sanderson & Hufford**, 1996). Thus, in our examples, the gestalt-type is based on homoplasy and this means, the construction elements of the gestalt-type - the calyx of *Rubus* and the involucrum of *Chrysanthemum* are analogous construction elements in respect to their organization-types but homologous construction elements in the frame of the gestalt-type. Unfortunately, in his later practice, Troll worked only with the organization-type, as is usual in comparative morphology.

It was by far overlooked that a system of different categories of types, such as the organization-type and the gestalt-type are, offers a chance to discover phylogenetic relations existing between them. I think, Troll was aware of this but in consequence of his aversion to phylogenetic speculations, he delayed again and again the discussion of such problems. The necessity to change again the terminology of his synflorescence typology, to make the relations between the two types –monotely and polytely– really clear, was to hard a task for him. I shall refer to that later, when the relations between different synflorescence types will be treated.

Because the Gestalt-type may have originated from different organization-types, comparing of the latter shows up the possible ways for typological changes. An enlarged spectrum of different type categories may thus be useful as a tool for the demonstration of typological connections. As the "life-type" I see the wellknown antithetic change of generations, which were described first by **Hofmeister** (1851). The life-cycles of bryophytes, pteridophytes, and seed plants are different regarding life and reproduction of the haploid and diploid generations. All these plants have different haploid and diploid individuals. The life-type comprises both generations which seem to represent different types, certainly often only extremely reduced. This allows to perceive the morphological relations between the heteromorphous generations. Also different "types of development" exist in land plants. Therefore, the typological sketches of these should provide one with informations about the growing regions and their relations to the produced organs, i.e. the blastozones, necrozones, intercalary and cambium-like meristems, as e.g. demonstrates a diagramm of a developing dicotyledonous seed plant (**Troll**, 1973: 19) or of a fern (**Weber**, 1953: 7) (Figs. 14, 27). I shall now demonstrate the practice of such comparative typology at hand of the phylogenetic relations between the types of
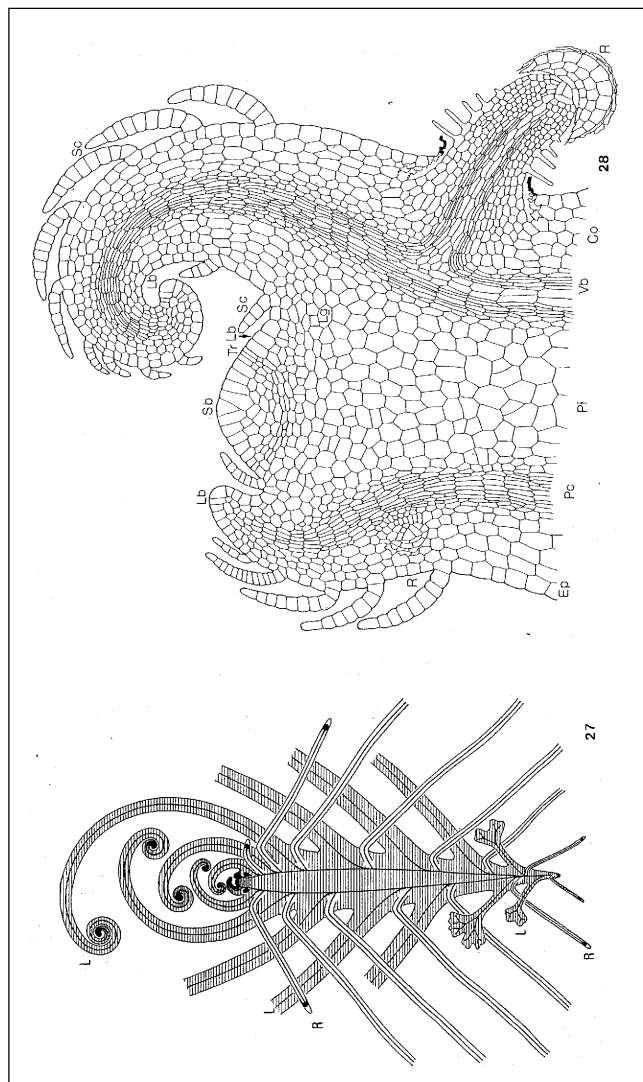
Figures 27-28: 27. Cormus-type of a tree fern according to Weber (1953). **28**. Anatomical aspect of the cormus-type (original). A shoot axis, L leaf, R root, Sb shoot blastozone, Lb leaf blastozone, Sc scale, Tr transition zone, Lg leaf gap, Ep epidermis, Vb vascular bundle, Pc procambium, Pi pith, Co cortex.

bryophytes and ferns and between the different types of angiospermous synflorescences.

At first, I present the life types of a frondose liverwort and a fern (Figs. 3, 4, 27-30). Their frondose gametophytes are of the same open repens-type and both produce the same appendages: trichomes and rhizoids in comparable positions. Both are able to branch dichotomically (Figs. 3-4). Gametophytes of liverworts, such as *Fossombronia tuberifera* –minutely depicted by **Goebel** (1930: 783)– and ferns, such as *Anogramma leptophylla* (**Hagemann** 2000),

conincide also in other special structures, e.g. in producing small tubers for storage of starch and in both cases these may serve as marsupia (Figs. 31-33). The gametangia of bryophytes and ferns are structurally the same. But a single, meaningful difference is their position. In *Pellia*, as in other liverworts, archegonia are produced on the upper side of the plant, in ferns on the lower side near the marginal blastozone (Figs. 29-30, 42-44). This lends ferns the option that their diplonts breaking through the archegonia will directly contact the soil what is impossible for the sporogonium of bryophytes (Figs. 29, 30, 34).

Contrary to the haplonts, the diplonts of bryophytes and ferns are totally different. The sporogonium of a liverwort lacks a blastozone and therewith a vegetation body at all. It is nothing more than a spore capsule with auxiliary means serving nourishment (the foot), exposition (seta), and spore release (capsule opening mechanisms and elaters) which become exclusively differentiated and developed inside the archegonium. After spore release the sporogonium dies. The gametophyte continues growth and produces new sporogonia every year again.
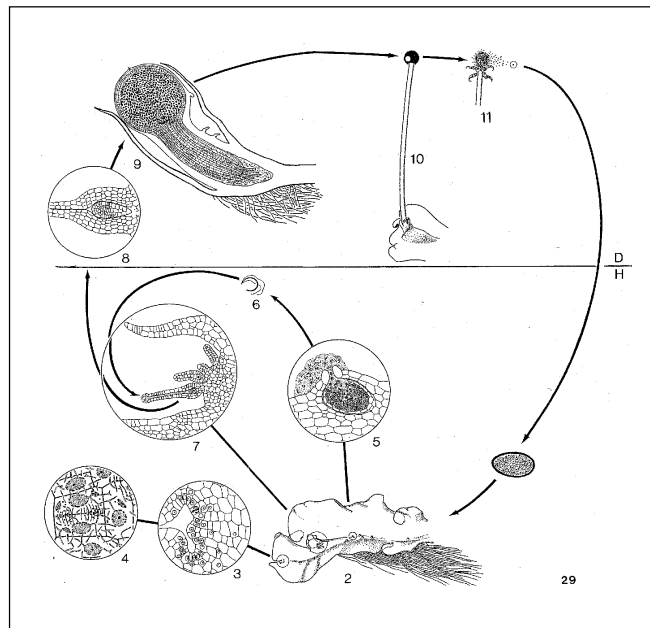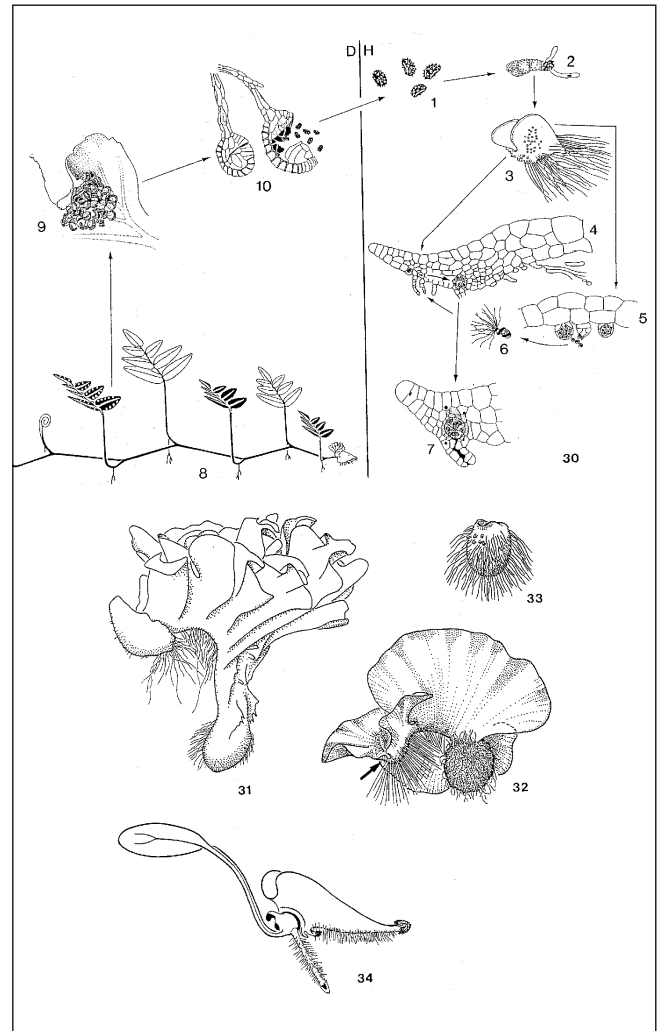
The fern sporophyte, as the homologon of the sporogonium in the life-type, is a rooted shoot, i.e. it represents the cormus-type which is in case of vertical growth a radial tree-like, in case of a more slender, creeping repens-type a dorsiventral vegetation body (Figs. 27, 28, 35, 36).

Figures 30-34: Life-type of a fern (*Hypolepis*). H. Haplontic phase, D diplontic phase. 1 Spores, 2 young gametophyte, 3 fertile gametophyte with archegonia and antheridia, 4 gametophyte with archegonia (longisection of its midrib), 5 section of a wing with antheridia, 6 androgamete underway to an archegonium, 7 developing embryo in the archegonium venter. 8 young sporophyte, 9 marginal sorus, 10 ripe sporangia releasing spores (from Hagemann 2000). **31.** *Fossombronia tuberifera* with a young, developing tuber and an old one which has produced the plant. **32-33.** *Anogramma leptophylla*: gametophyte developed from a shrinking tuber with a fresh developing tuber growing down into the ground (32, arrow), 33 old underground tuber with a group of archegonia and a marginal blastozone. **34.** Sketch of a fern sporophyte originating from a gametophyte. The young sporophyte has its shoot apical blastozone, a first leaf with a root merging into the soil, and a second leaf primordium. (31 after Goebel 1930, 32-33 from Hagemann 1992a, 34 original).

Figure 29: Life-type of *Pellia epiphylla*. H Haplontic phase, D diplontic phase. 1 Multicellular spore, 2 fully developed gametophyte with fractionating blastozone (3) and phragmotomy of a blastozone initial (4), antheridium extruding male gametes (5, 6), archegonium sorus (7), developing young sporogonium in a fertilized archegonium (8), embryotheca containing a ripe sporogonium (9) during winter, encovered by the midlobe (underside) and the involucrum (upperside). The archegonial neck, venter, and the soral receptaculum - bearing some not fertilized archegonia - form the embryotheca which encloses the sporogonium totally. Elongated seta exposing the capsule (10) and opened sporangium releasing the spores (11) (original).

The stems have an open blastozone producing the marginal leaf blastozones by fractionation, as already observed in *Dryopteris filix mas* (Figs. 9-11). The plagiotropous leaves (croiziers) become exposed to light and have a closed development using up their blastozone after a maximal phase of corroberation. Their pinnate dorsiventral form and their development resembles the gametophyte organization. But latest, when the necrozone of the stem reaches the leaf insertion, they have to die together with the roots which originated basally on the young leaf (Figs. 27, 28, 35, 36). Roots grow endogenously with a subterminal meristem which takes its origin outside the leaf trace connecting the leaf with the stem bundle system (Figs. 10, 28, 38). The root meristem produces

tissue in all directions around its growth center during its life. The root meristem is an inner center of thickening growth which wins the connection with the leaf trace via the induction of a root procambial strand. But inner thickening growth surroundet by permanent tissues around it must rupture the latter, at first the outer cortex of the shoot. The root enters the soil. It is easy to understand that continuation of its central thickening growth must cause the older surrounding tissues to rupture steadily around the periphery of the root. The rupturing ring zone divides the calyptra from the root body, whose future outer layer differentiates as the rhizodermis, whereas the calyptra dissolves steadily on its surface, thus giving the rhizodermis free (Figs. 28, 38). Therefore, it is free of a cuticula and not comparable with the epidermis of the shoot. The rhizodermis differentiates rhizoids which are called the root hairs. The columella of the calyptra functions as storage tissue for starch. Growing older it becomes replaced by fresh tissues from the calyptrogene, whereas the older tissues reach the periphery of the calyptra, where they become dissolved producing voluminous masses of mu-
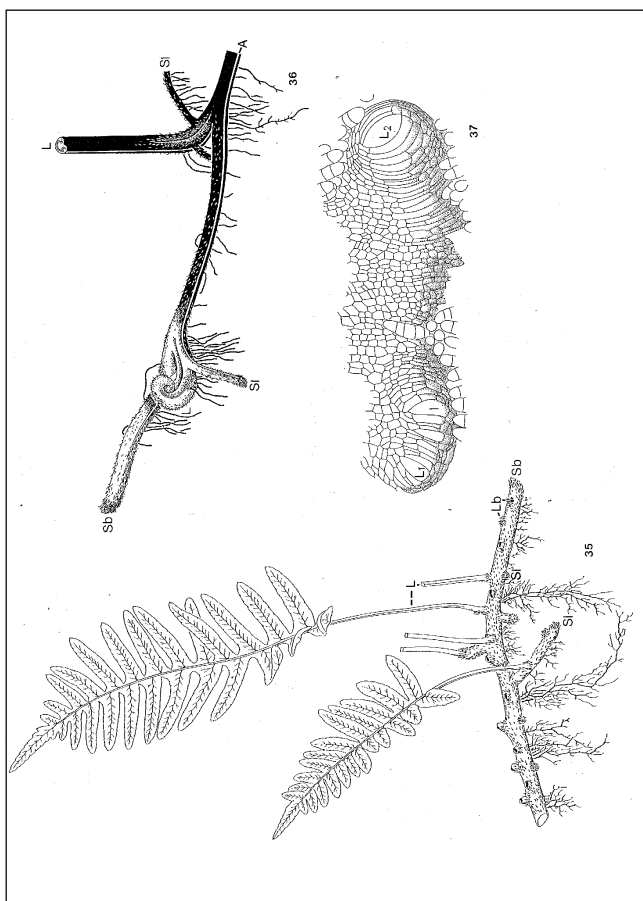
Figures 35-37: 35. Open repens-type of *Polypodium vulgare*. The rhizome with its shoot blastozone (Sb), distichous leaves (L) and leave buds (Lb) on the upper side and lateral shoots (Sl) in its flanks. **36**. Rhizome of *Hypolepis repens* with longitudinally orientated leaves (L) and a marginal aerophore with stomata (A) which is continuous with the blades underside. Lateral shoots arise on the leaves horizontally orientated bases early from the aerophore. Sb Shoot blastozone. **37**. *Pteridium aquilinum*: rhizome blastozone with two-sided marginal initial (I) and two leaf primordia (L₁ and L₂), (from Hagemann 1976).
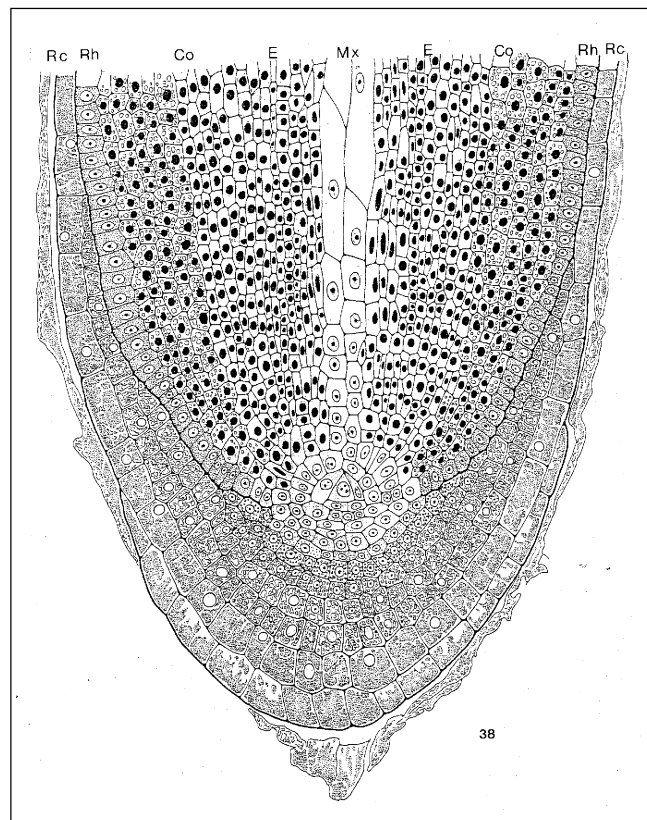

Figure 38: Root meristem from *Dryopteris filix mas* with central initial, root cap (Rc), rhizodermis (Rh), future endodermis (E), cortex (Co), and metaxylem initials (Mx), (original).

cilage under considerable pressure. Therewith it widens the future root channel through the soil and at the same time feeds symbiontic organisms like procaryonts and fungi in the so-called rhizosphere. **Goebel** (1930: 865) had already drawn attention to the fact that marsupia of certain liverworts, which penetrate deeply into the soil, such as *Lethocolea drummondii*, develop the same organization as root tips do in cormophytes. This suggests the hypothesis that tuberous structures, such as seen in *Fossombronia tuberifera* or *Anogramma leptophylla*, have the option to change into roots, if their growth becomes concentrated to an inner center, which continues growth, whereas the cortex becomes ruptured (Figs. 32-33). The simple and primitive tubers have an epidermis with rhizoids and these in turn provide the tubers with water. If the structure becomes ruptered, the epidermis becomes replaced by a rhizodermis which produces root hairs with the same function (**Hagemann**, 1997, 2000). Such a hypothesis is also supported by the fact that the position of the first roots of a fern sporeling have a comparable positional relation to the blastozones of their first leaves. This is easily to observe in longitudinal sections of the embryo (Figs. 39-41).

The fern sporophyte produces the same appendages as the gametophyte: trichomes mostly in the form of scales, rhizoids which are produced in certain ferns on their rhizomes, and leaf bases, and in form of the root hairs. Sporangia are produced in most ferns on the underside of the leaves, which is again comparable with the position of gametangia on the underside of the prothalli, where archegonia develop near the growing blastozone (Figs. 42-44).

Although the fern leaf is comparable with the gametophyte, it is not homologous with it, because as a whole, the gametophyte is homologous with the cormus (Figs. 4, 27-28). In consequence of this, the whole cormus must be a differentiated thallus. This causes the idea that most primitive ferns must have had a thalloid vegetation body, such as have their gametophytes. The fact that early fern gametophytes were not preserved in the fossil record allows the conclusion that comparable delicate sporophytes had undergone the same fate. But as models for the type of such a diploid "pteridothallus", recent Hypolepidaceae must be taken into consideration (Fig. 36) (**Hagemann,** 1976). Their rhizomes are contracted like the rachis links of their leaves which have a continuous margin. The leaf margins are continued on the rhizomes which in case of *Pteridium aquilinum* grow by a marginal blastozone terminated by an apical initial with two cutting faces (Fig. 37). The whole plant is thus constructed like a heavily branched, single, open fern leaf.

Typologic comparison thus shows: the fern sporophyte can easily be developed from a fern gametophyte. This disposes on the options for all changes which are needed for the development of the cormophytic type. The type of the bryophytic sporogonium lacks a blastozone and in consequence a vegetation body. It is a structure of its own originating in the archegonium venter not as its own plant, in case of Ricciaceae not even as a sporangium because the venter of the archegonium itself serves as the "angium" for the spores. Contrary, the fern sporangium has a homologous position and structure with the gametangia of its gametophyte. Thus, it seems impossible for me to develop a fern sporophyte typologically from a bryophytic sporogonium, as traditionally is hypothesized by palaeobotanists and the so-called telome theory (**Zimmermann**, 1959: 98ff, compare **Kenrick & Crane**, 1997:226ff).

The second example will be the gestalt-type of the angiosperm synflorescences. As is wellknown, Troll created two different organization-types: the monotelic and the polytelic synflorescence (Figs. 16-19) (**Troll**, 1964). **Weberling** (1961) had already in the second half of the 50th in tenacious discussions convinced his admired teacher that between these two organization-types must exist phylogenetic relations. But Troll´s aversion against phylogenetic speculations made these discussions difficult. We, i.e. Froebe, Mora-Osejo, Kunze, and all the other pupils of Troll of that time were interested participants of these exiting discussions, which convinced **Troll** (1963) finally. So he announced in his fundamental work on inflorescences (1964:156) that he intends to describe the phylogenetic relations between the synflorescence types. Unfortunately, he died before his work was finished. Weberling (**Weberling & Troll,** 1998) edited his legacy and mentioned a lot of convincing examples, which underlined the phylogenetic relations between the two synflorescence-types in the concluding chapter.

I have already mentioned the organization of the monotelic synflorescence. Its anthotagma is terminated by an apical flower, as all its paracladia of different orders are. Thus, its enrichment zone is made up of paracladia which repeat the acropetally following synflorescence (Fig. 20). Polytelic synflorescences lack terminal flowers, i.e. their axes have open ends (Figs. 45-49). The flowers of these synflorescences are presented in open terminal aggregations of racemic or thyrsic construction which replace the terminal flower Figs. 46, 48). This is especially striking in case of the Asteraceae, such as *Ligularia dentata* (Fig. 49). The paracladia of this type again repeat the main axes above their insertion, i.e. the paracladia of this type are termi-
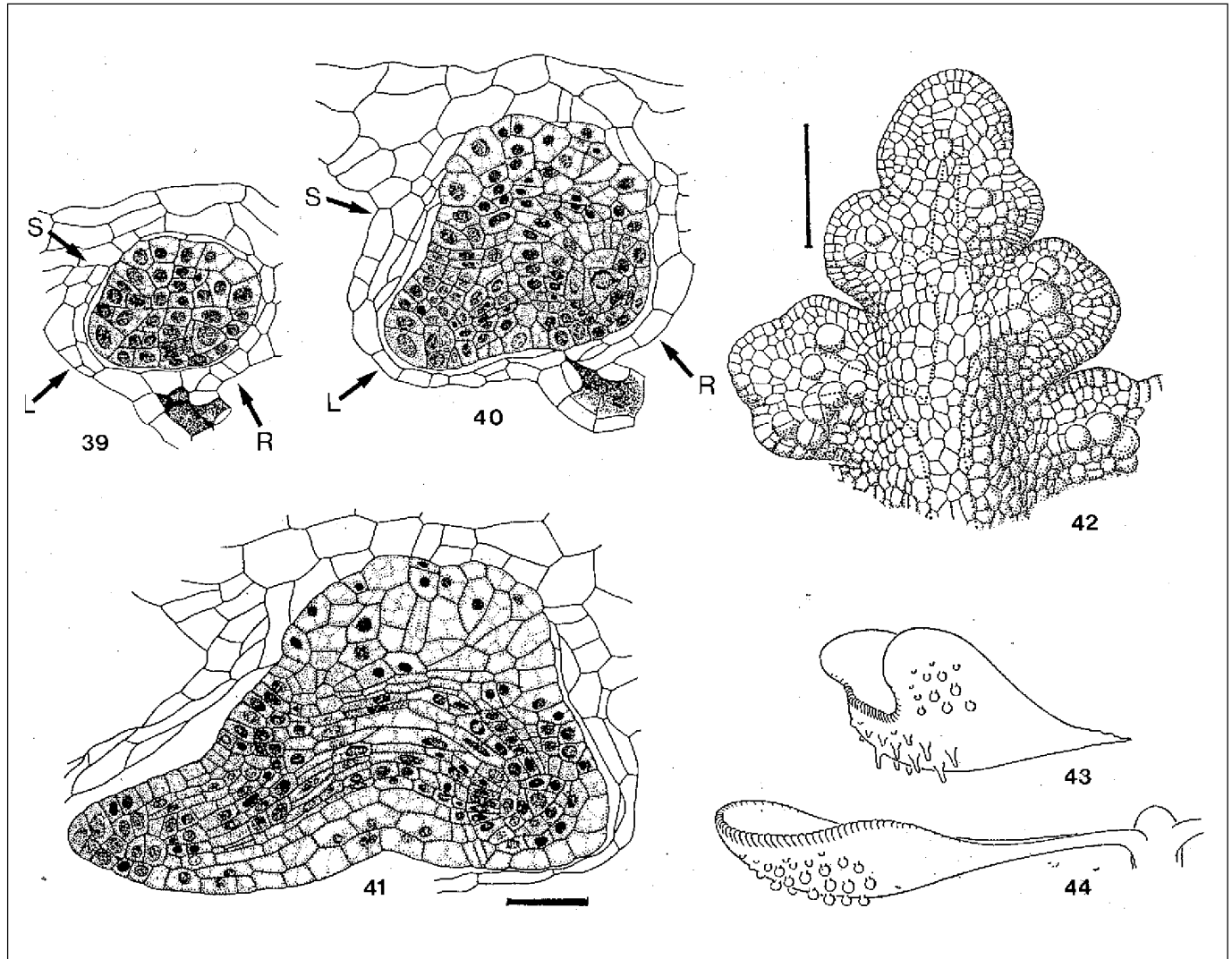
Figures 39-44. Three stages of embryo development of *Pityrogramma sulphurea*. Shoot, leaf, and root initials (S, L, R with arrows) can already be observed **39.** The first leaf primordium with its root primordium becomes more prominent **40.** Only in Fig. **41** the shoot blastozone becomes prominent before the second leaf primordium will be seen. **42** Development of sporangia in the sporophyte of *Anogramma chaerophylla* in subblastozonal position - their initials are clearly seen - is comparable with the position of the archegonia in the gametophytes (compare Figs. 7 and 33) (bar = 100 μm). **43-44:** The subblastzonal position of gametangia, especially archegonia on the gametophytes **(43)** and the position of the sporangia on the underside of the fern leaf blastozone **(44)** are also comparable (Figs. 39 - 41 after Vladesco 1935 and v. Guttenberg 1966), 42 - 44 original).

nated by florescences ("coflorescences"). Thus, all paracladia are throughout open branches, even if they may be reduced to a single florescence in axillary positions, as in case of the monotelic synflorescence the smallest paracladia are single axillary flowers. The resemblance between the two organization-types is surprizing and thus, it is consequent to speak of a common gestalt-type.

Three independently occuring developmental steps are necessary to transform the monotelic synflorescence into a polytelic one and all these are easily realized options for change. 1. The loss of the terminal flowers leads to open main axes and paracladia (Fig. 18). Troll called a synflorescence with such open axes "monotele Rumpfsynfloreszenz", a truncated synflorescence and the process was called by **Maresquelle & Sell** (1965) and **Sell** (1969) "truncation". 2. The differentiation of the enrichment zone into a basal "special enrichment zone" and a terminal zone with equal short paracladia of single flowers or dichasial short paracladia, such as seen in *Adenophora*

Figures 45-48: 45-47. *Lysimachia vulgaris*. The airial shoot with a green trophotagma (45), its partly frondulose upper part of the anthotagma with its racemic florescence and the downwards following paracladia (46), subterranean innovation zone with innovation buds producing new synflorescences (47). 48. *Scrophularia nodosa* with a thyrsic florescence and coflorescences (compare Fig. 19, original photographs).

liliiflora (Fig. 53). This "homogenization" of a terminal zone is combined with "racemization", i.e. with acropetal anthesis which characterizes a racemose construction (Fig. 53). The latter process may be the consequence of continued acropetal flower production which on its part prevents the differentiation of a terminal flower (Figs. 46-48). These two first processes together are already decisive for the transformation of the monotelic into the polytelic synflorescence. 3. The third process, which completes the Gestalt-type of the polytelic with that of the monotelic synflorescence is called "disjunction" of the florescences by elongation of their basal internodes, which expose the florescences like the single terminal flowers of the monotelic synflorescences in such a way, as it is observed in *Ligularia dentata* (Fig. 49). The typogenetic constructional options for changing the monotelic into the polytelic organization-type are thus truncation, homogenization, racemization and disjunction, terms which were proposed by **Maresquelle & Sell** (1965) and **Sell** (1976), see also **Kunze** (1989).

Again we observe that typogenesis of the polytelic synflorescence is a complex event with different developmental changes which must play together. This is the more amazingly, as such macroevolutionary events are by no means singulary events in plant evolution. The same processes can be observed in many families and orders in angiospermes, where these parallel events occur with the consequence that in all these groups monotelic synflorescences change into polytelic ones. **Troll** 1964 - 1969, **Troll & Weberling** (1989), **Weberling & Troll** (1998) have shown this in more than 20 families. This demonstrates the fact that such typogeneses occur lawfully, if certain types are reached, i.e. if the monotelic organization-type in a family is verified, then it is a question of time, when polytelic species come into existence. This allows to predict this evolution, if it is not yet reached in a given monotelic family.

Moreover, these typogenetic processes reiterate. Polytelic synflorescences become again truncated. Their enrichment zone of the second order will again be differentiated in an enrichment zone of the third order and a homogenized upper end. Sell (1969, 1976, 1982) has shown that polytely until the third order occurs in different families, such as the Acanthaceae, Myrtaceae and others. **Troll** (1928) has already shown that such recurrence plays its role in Asteraceae with flower heads of the second and third order replacing terminal flowers, florescences and florescences of higher orders. This can easily be observed in the genera *Sencio* and *Ligularia* (Figs. 49-52). **Kunze** (1989) proposed to speak of polytelic synflorescences of a second resp. third order.

In case of such consecutive typogeneses, which are accomplished in the frame of a gestalt-type, previous construction elements of a given organization-type become differentiated to reestablish the construction elements of the new organization-type. This means, the next order construction elements cannot be homologous but must be analogous construction elements in the different organization-types. This is confusing, as was already stated by **Kunze** (1989). Therefore, it is difficult to understand that Troll designated the enrichment zone of the monotelic and polytelic synflorescence with equal terms. Even, if


Figures 49-52: 49. *Ligularia dentata*. The anthoblast is a secondary synflorescence (polytelic synflorescence), whose racemic florescence is condensed into a flower head (compare Figs. 22, 23). All other heads are coflorescences of higher orders. 50. *Senecio tanguticus* has a differentiated secondary synflorescence. 51. *Ligularia stenocephala* has a racemic open florescence of the third order. 52. shows its open, died end (all original).

they look alike, they are not homologous. This can be avoided, if one goes a step further than Kunze. Thus, the monotelic synflorescence becomes a synflorescence of the first order, polytely of the first order sensu Kunze then will become a synflorescence of the second order and consequently all polytelic synflorescences of higher orders then will be such of the third, fourth, fifth, etc. orders. Each construction element, as are all the enrichment zones, paracladia, or terminal members will the be unequivocally identifiable by their order in the organization-type. All construction elements with equal orders are homologous, all those with different orders will be analogous. This again underlines that it is impossible to decide about homology resp. analogy of construction elements, unless the classification of the type in question is not cleared.

In my report, I introduced the gestalt-type of the open repens-type, which is realized in frondose liverworts and fern gametophytes. This type is followed again by most cormophytic fern sporophytes, as *Hypolepis* or *Polypo-*

dium species demonstrate (Figs. 35-36). Polytelic synflorescence-types in angiospermes posses again the options for the recurrence of the open repens-type. I like to show this at hand of the genus *Lysimachia* of the Primulaceae. *L. vulgaris* is a sympodial rhizome geophyte (Figs. 45-47). Its innovation buds originate in the axils of subterranean rhizome scales. These will grow out in next spring and develop as a polytelic synflorescence, i.e. a synflorescence of the second order. Above the innovation zone the green trophotagma unfoldes with a zone of inhibited axillary buds (Fig. 19: FZ). In the anthotagma, axillary buds develop simultaneously in the axils of some green, but smaller leaves, which upwards become smaller bracts until a racemic florescence terminates the above ground shoot division (Fig. 45). Later the necrozone of the mother shoot isolates the renewed synflorescences, which produce on their part a subterranean innovation zone. What are now in such plants the options for the recurrence of the open repens-type? These are 1. the open axes which might prolifer-
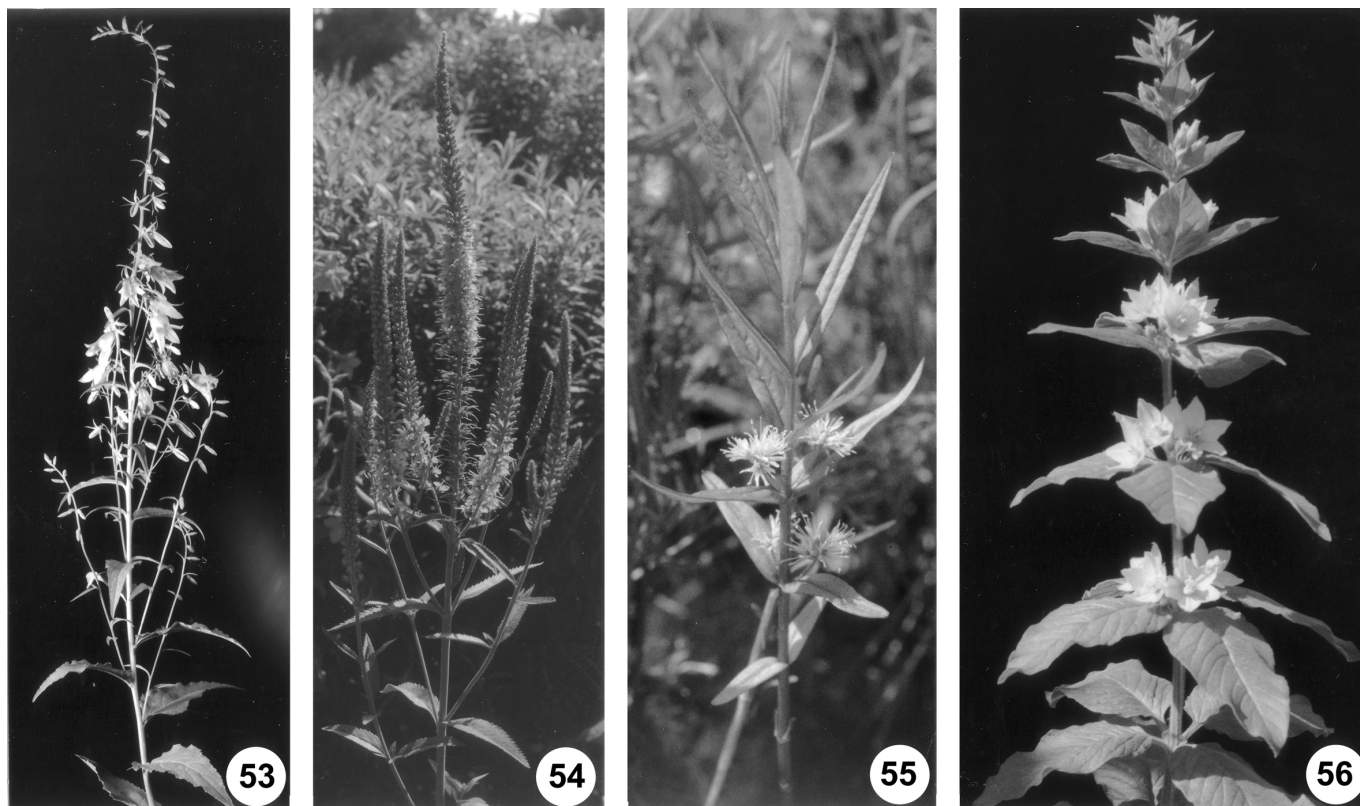
Figures 53-56: 53. *Adenophora liliiflora* demonstrates homogenization and racemization, but all axes of the differentiated branches are closed by terminal flowers which are a little further developed than their nearest lateral flowers. 54. *Pseudolysimachion longifolium* with racemic florescences. 55. *Lysimachia thyrsiflora*: proliferating upright shoot with coflorescences in the axils of its lower frondose leaves. The enrichment zone proliferates without producing a florescence. 56. *Lysimachia punctata* presents a proliferating florescence without an enrichment zone. Its florescence becomes enriched by descending serial flowers (original photographs).

ate, as can be observed in *Lysimachia thyrsiflora* (Fig. 55). 2. The development of a frondose anthotagma, i.e. instead of bracts, the anthotagma develops foliage leaves which do not longer inhibit the development of flowers in their axils. Is this already the case in the enrichment zone of the second order of *L. vulgaris*, this phenomenon progresses further upwards into the florescence as can be seen in *L. punctata*, where it may also proliferate (Figs. 46, 56). 3. If the shoot system reduces secondary thickening and gets a slender habit creeping above the ground, then the habit of *L. nummularia* results which 4. produces roots on each node of its decussate leaves (Fig. 57). Thus, the slender shoot becomes rooted in the soil, overwinters and continues to grow next spring together with its vegetative axillary shoots. In June the growing shoots develop single flowers instead of vegetative axillary shoots and in the following summer they continue to grow vegetatively again. In *Lysimachia nummularia* the frondose florescence proliferates. Thus, the flowering section of the shoot develops from the florescence with single flowers in the axils of its leaves as already observed in *L. punctata* (Fig. 56). It should be remarked here that *L. thyrsiflora* has replaced its green trophotagma by a terminal, frondose proliferation zone which is homologous to the florescence. Thus, the enrichment zone follows directly on the innovation zone by the production of axillary coflorescences (Fig. 55). The open repens-type may also be formed from the enrichment zone. This is observed in many other families, such as the Scrophulariaceae, i.e. the relationship of *Veronica* (Figs. 54, 58). *Pseudolysimachion longifolium* (= *Veronica longifolia*) has a normal polytelic synflorescence with a terminal florescence and some coflorescences in its enrichment zone (Fig. 54). Whilst *V. filiformis* has the same construction, as seen in *Lysimachia nummularia*, i.e. this plant produces single flowers in the axils of its frondose leaves, the frondose main axis of *V. officinalis* produces racemic coflorescences in the axils of its leaves (Fig. 58). These plants may therefore be compared with *Lysimachia thyrsiflora* (Fig. 55). When the shoot systems of *L. nummularia* and *Veronica officinalis* grow by their terminal blastozones, they die from behind by their progressing necrozone and isolate the vegetative branches thus accomplishing vegetative multiplication. The typogenesis of the open repens-type can be observed in several different families of the angiosperms. With the recurrence of the open repens-type the plants leave irretrievably the gestalt-type of the synflorescence.

It would now be of importance for me to know, how far such phylogenetic considerations will also be possible in tropical plants. Mora-Osejo has developed very
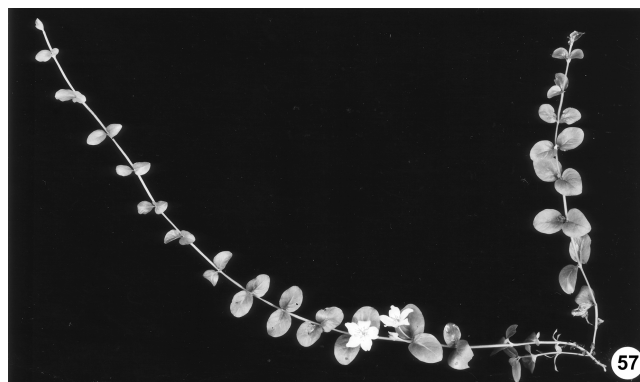
Figures 57-58: 57. *Lysimachia nummularia* has reached the open repens-type by continued proliferation of a frondose florescence. 58. *Veronica officinalis* reaches again the open repens-type by means of a proliferating, homogenisized enrichment zone producing coflorescences. The behavior of *Lysimachia thyrsiflora* (Fig. 55) may serve as a model which is found also in other families and in the genus *Veronica* (original photographs).

fruitful ideas on the gestalt-types of tropical rain forest plants, which he termed "holocaulons" and "anthocaulons". The latter are especially characteristic for a lot of paramo plants, such as the genera of *Espeletia, Paepalanthus*, and *Plantago*. These are interesting gestalt-types. Certainly, such types cannot grow really endless because as trees or vertically growing rosettes, they have their limits on account of mechanical reasons. But in case of the small rosette-like *Plantago* species as are *Plantago media, P. major, P. lanceolata* even potential, open, vertically oriented rosettes have come into existence. Their necrozone works below the ground and shootborn roots of freshly growing and flowering parts draw the plants steadily downwards into the soil, thus filling up the gap resulting from the rotting basal parts with the living rosettes (**Weberling & Troll**, 1998:406

ff). The resulting type is really a potentially endless growing, vertical anthocaulon.

I think, with aids of a consequent typologic system of different categories of types, such as gestalt-types, organization-types, life-types, and developmental types, etc., it must be possible to find out the ways of evolution, which can be used by plant organisms changing the type. This allows to understand phylogeny as an organismic process directed by the constructional options, which make such changes for plants possible, i.e. understanding the organism as a subject in evolution. In my opinion, all existing types of plants can be linked together with one another. Thus, we learn to understand the phylogenetic relations between all important plant types. Resulting phylogenetic hypotheses may then be prooved by modern molecular methods which per se may mesure relationship, but fail to understand it.

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