

# MAIN RESULTS OF THE "TELOME THEORY"

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## ABSTRACT

The telome theory as a representative of the "New Morphology", i.e. as a phylogenetic theory, describes the historical phylogenetic process. This process forms in the first period of development the "Urtelome" (Thalassiophyta, Rhyniaceae). In the second period these "Urtelome" change to the recent Kormophyta. Only a few elementary processes participate in this immense change. In the first period, beginning with the unicellular stage, five cytological elementary processes formed the "Urtelome" (TEXT-FIG. 3): (1) connection of cells, (2) differentiation of meristem = origin of polarity, (3) rotation of cell axis, (4) shifting of chief phases in alternation of generations and (5) differentiation of different permanent tissues. The exterior form changes accordingly from the state of "Urtelome" to the recent shoot through five elementary processes (TEXT-FIG. 8): (1) planation, (2) overtopping, (3) syngensis, (4) reduction and (5) incurvation.

During these and other phylogenetic processes the exterior form does not change immediately, as does the genotype. Visible forms arise ontogenetically out of this changed genotype. According to the "Law of Recapitulation" the ontogenetically youngest stages relatively often recapitulate the phylogeny. In particular the Palaeontology, if statistically applied, offers sure proofs for the change of single features in phylogeny ("Merkmalsphylogenie").

## INTRODUCTION

THE telome theory, as it is called, is a theory which tries to connect the fossil and living plants by their phylogenetical relations. Misconceptions that have arisen from it are due to differences in morphologic outlook rather than in languages. These great differences in morphologic concepts have been recently characterized by the Dutch botanist Lam (1948) as the antithesis of "Old" and "New Morphology". The "Old Morphology", which is sometimes called "idealistic", has been "Angiosperm-centred"; that means it started from Angiosperm-like "Urpflanzen" (primordial plants, Archetypes) and tried to deduce therefrom the other plants.

By contrast the telome theory as representative of the "New Morphology" is explicitly a phylogenetic theory, i.e. it proceeds from real ancestors and tries to describe the historical phylogenetic process as accurately as possible. This historical process trans-

forms the outward shape as well as the internal structure and the course of ontogeny. The telome theory, thus, combines phylogenetic research on external shape, on anatomy ("stelar theory") and on ontogeny (e.g. alternation of generations). Such phylogenetic knowledge is to be attained only by close co-operation of the study of fossil and recent plants. The main proof of the telome theory is in the fossils which, in the earliest epochs, show the predominance of the ancestral forms and later, by numerous "connecting links", the gradual approach to the present state. We complete the evidence of fossils by findings from recent organisms.<sup>1</sup> This is indispensable especially for the oldest chapter of evolution until telomes came into existence. As an example one may mention the occurrence in the early Palaeozoic of the different types of habit as evident from Table I.

This succession of types is a definite proof of the predominance of the Rhynia-type at the outset of terrestrial plants, which are thus the phylogenetically primordial plants of our land-flora (ZIMMERMANN, 1950).

As the telome theory is not "Angiosperm-centred", the term "telome"<sup>2</sup> became necessary, since in earliest land-plants the "typical" organs of Angiosperms, viz. leaf, shoot, root, etc., were still missing. If, nevertheless, I occasionally illustrate ancient stages by reference to present organisms, this is meant in the sense of "Merkmalsphylo-

1. On co-operation of phylogenetic methods, see Zimmermann, 1943.

2. Telomes in a broader sense are the undifferentiated elements in the organization of the oldest land-plants. We distinguish:

- (a) telomes in a restricted sense, i.e. single-nerved terminal "branches" from the last ramification to the tip of the plant,
- (b) mesomes, i.e. corresponding parts between two ramifications. According to their function and inner organization the telomes are either vegetative telomes (phylloids) or fertile telomes (sporangia).

A term like "telome" has to be clear and intelligible, so as not to evoke misunderstandings on the anatomic relations. For the word "branch", moreover, a "not Angiosperm-centred" term is missing. The German word "Trieb" is rather close to such a neutral term.

TABLE I — MORPHOLOGICAL TYPES (% OF SPECIES)

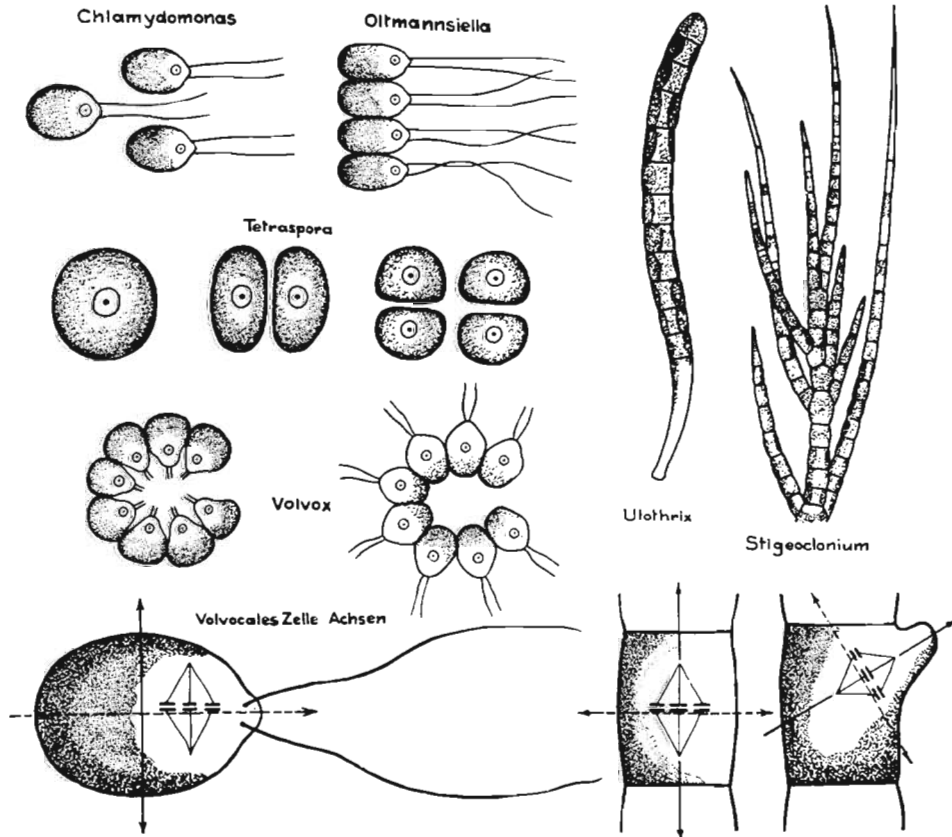
GEOLOGICAL FORM	RHYN. TYPE	PSILOPHYTON TYPE	MIKROPHYLL TYPE	HEMIKORNOPHYTA	KORMOPHYTA
Upper Devonian	74	73	6	26	61
Middle Devonian	16	8	16	39	21
Lower Devonian	38	22	21	19	0
Australian Silurian	85	0	15	0	0
N. European „	88	12	70	0	0

genie" (semophygeny): in particular features recent plants sometimes represent the ancient type.

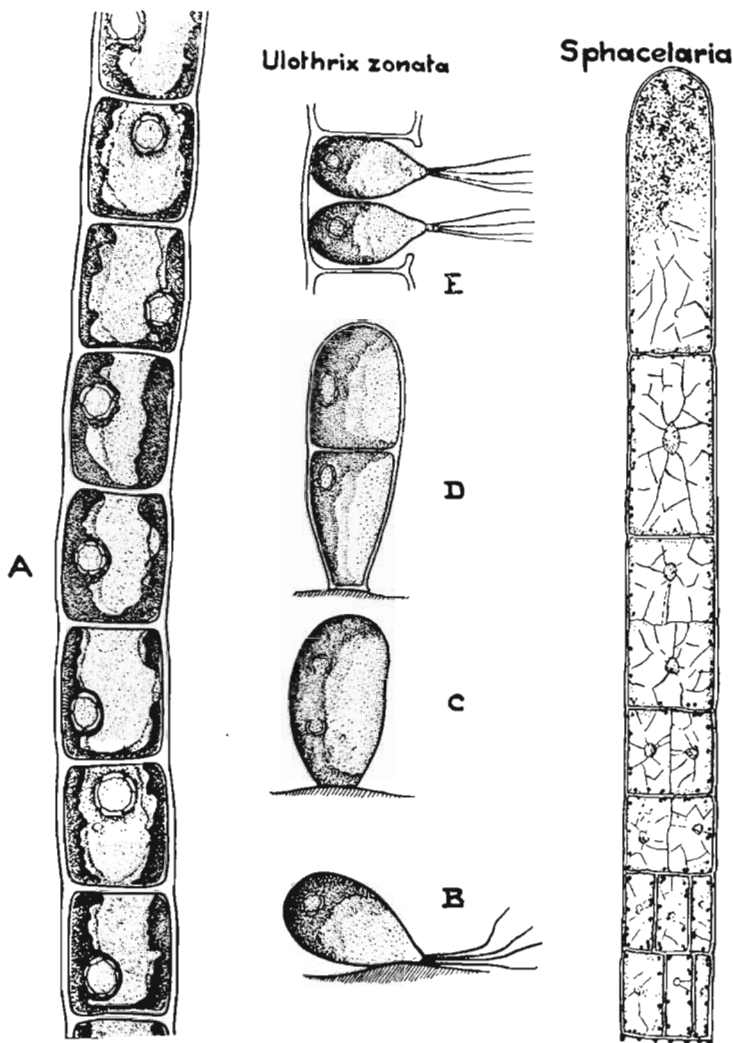
In the foreground of our considerations we put the "main line" of descent to the Angiosperms, starting from unicellular stages. It is surprising that the manifold configuration within this "main line" and in related forms derives merely from combinations of a few "elementary processes". The term "elementary processes" implies that these elements of evolution proceed in ontogeny and phylogeny independently of each other.

This is proved by a free combination of various phases of elementary processes in the final stage of development in spite of common ancestors.

I am deeply indebted to investigations of my predecessors who partially belonged to the "Old Morphology" and who, from Goethe and De Candolle to Hofmeister, Pringsheim, Van Tieghem, Celakowsky, Bower, Potonié, Lignier, Ch. and P. Bertrand, Tansley, Church, Schoute, Eames, Kidston, Lang, Sahni, Halle, Florin and others, laid the foundations for the telome



TEXT-FIG. 1 — Preliminary stages of telome formation. Left: Volvocales, right: Ulotrichales.



TEXT-FIG. 2 — Formation of filaments. A-E, ontogeny of *Ulothrix*, E slightly diagrammatic; right: *Sphacelaria*.

theory. But the narrow frame of a short summary forbids a detailed account of the historic development of the telome theory or the inclusion of many examples.

#### THE ORIGIN OF TELOMES

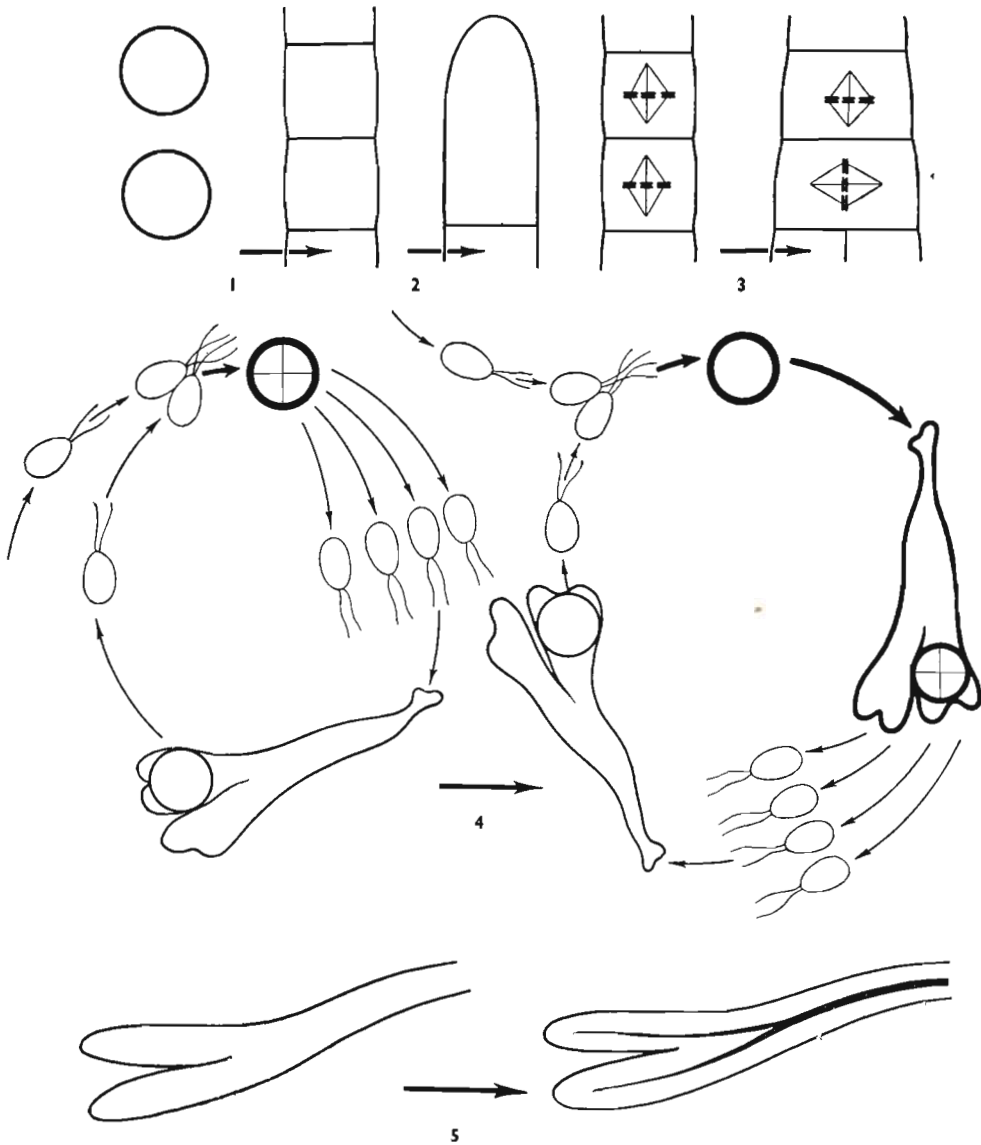
In this part the development from unicellular stages to telomes (thallus of *Thalassiophyta*)<sup>3</sup> is described.

*Stage of unicellular plants* — We start from single cells proved to have existed as far back

3. In the sense of Church, without, however, agreeing with all his views.

as the Precambrian as result of a long evolution. As we see from later stages (e.g. the flagellated reproductive cells of the "main line"), a polar organization of the cell was acquired at some time or other. This stage, for instance, is nowadays represented by *Chlamydomonas* (TEXT-FIG. 1). Moreover, in the possession of chlorophyll *a* and *b* *Chlamydomonas* represents such an archetype, while the possession of pyrenoids may be a specialization of *Chlamydomonas* and other Volvocales.

In order to understand the following the knowledge of cell axes is essential (see TEXT-FIG. 1, bottom, left):



TEXT-FIG. 3 — The five elementary processes leading to telomes.

(a) *Axis of division*, morphologically marked by the connecting line from flagellum-pole to chromatophore, physiologically marked by its position in the plane of division.

(b) *Axis of growth*, position vertical to axis of division, morphologically marked by the position of the nuclear spindle, physiologically marked by the direction of compensating main growth following cell division.

*Elementary processes on the road to telomes:*  
 first elementary process: "interconnection of cells" (TEXT-FIG. 3, No. 1) —

(a) Other elementary processes apart, we find in mobile stages a loose connection by plasma or gelatinous coating as in the marine Volvocales genus *Oltmannsiella* (TEXT-FIG. 1, top, middle).

(b) In plants attached to the bottom we find interconnection of cells by solid walls. This form of the first elementary process is characteristic of "typical" plants, in which the cells are connected by a joint cell-wall of the daughter cells following cell division. The *Ulothrix* filament (TEXT-FIGS. 1, right,

& 2) is an example, without rotation of axis or other elementary processes. The position of the axis of the germ cell is retained during the whole development of the filament to the new formation of the germ cells. The longitudinal cell division becomes the transverse division of the filament. The filament stage of algae is one of the oldest types of plant habit (testified already in the Precambrian).

*Second elementary process: rotation of cell axes* (TEXT-FIG. 3, No. 3) —

(a) Without combination with the third elementary process, observed in the *Schizomeris* stage of *Ulothrix*, the monosiphonous filament may become polysiphonous. That means the new cell walls are no longer placed parallel to each other but are orientated in all directions of space. Certainly an abundant formation of three-dimensional tissue is possible only by combination with the third elementary process.

(b) Rotation of the axis and localized growth produced branching of the filament (compare *Stigeoclonium*, TEXT-FIG. 1, right, other Chaetophoraceae or hairs in higher plants). By interweaving of branched filaments, plants — sometimes many yards long and 2-3 ft. thick — as far back as the old Palaeozoic plants like *Prototaxites* are formed.

*Third elementary process: differentiation in apical cell<sup>4</sup>, meristemal tissue and permanent tissue* (TEXT-FIG. 3, No. 2) — The apical cell developed in Pheaeophyceae probably over the stage of a trichothallos growth according to Text-fig. 3, No. 5, in the "main line", perhaps directly by concentration of growth on the terminal cell.

*Combination of the second and third elementary process* —

(a) *Rotation of axis in meristemal tissue but not in apical cell* — *Sphacelaria*-type: In the apical cell and the first segment the position of the axis in the monosiphonous filament is retained (TEXT-FIGS. 2, 4). By rotation of the axis the filament later becomes polysiphonous; in *Stypocaulon*, *Dictyota* and others a real growth continues for some time. The existence of *Chara* proves that within the limits of our "main line", i.e. within the Chlorophyceae, a similar transition form occurred.

4. Even in cases where no single apical cell as a "Scheitelgrosszelle" is directly discernible, in the long run only one single cell or its descendants can maintain themselves at the apex.

(b) *Rotation of axis in apical cell* — *Equisetum*-type: Rhythmic oscillation of the axis in the apical cell leads to two, three or more angular apical cells (*Fontinalis*, TEXT-FIG. 4). This type we find mainly in combination with a "Scheitelgrosszelle" (large apical cell). It seems uncertain how far this type is characteristic of the "main line".

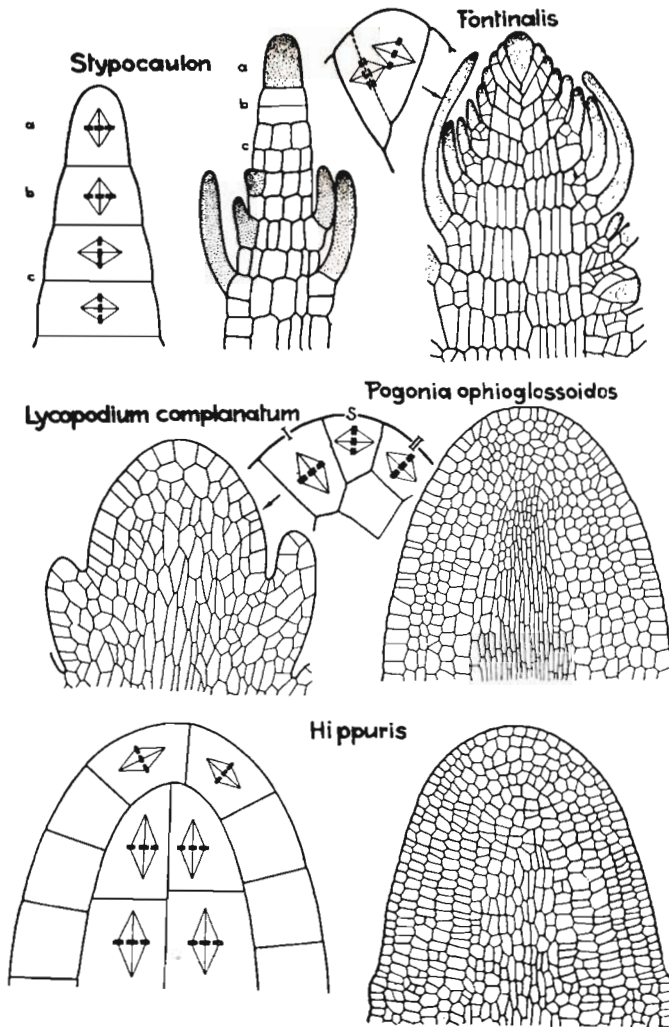
*Lycopodium*-type — A "Scheitelgrosszelle" is missing. In the apical cell and its descendants, which are very similar to each other, a varying position of the axis leads to a multi-cellular growing point as demonstrated by the presence of growing points in fossil Rhyniaceae and many recent growing points, *Psilotum*, *Lycopodium*, Coniferae, *Filices euporangiatae*, etc. (see TEXT-FIG. 4). The same is to be assumed for the main ancestors of the Rhyniaceae, viz. the Thalasssiophyta. By this position of the axis in the growing point the three-dimensional growth of a simple telome is caused as indicated in the following table:

AXIS OF DIVISION	AXIS OF GROWTH	RESULTING POSITION OF CELL WALL	RESULTING GROWTH
Periclinal	Anticlinal	Anticlinal	Growth in length
Anticlinal	Periclinal	Periclinal	Increase in thickness

In general, however, we find combinations and intermediate forms of both positions of the axes.

*Angiosperm*-type — Additionally we mention the manifold formation of the growing point, exhibiting all sorts of intermediate stages to the *Lycopodium*-type. In *Hippuris*, for instance, we find a new constant position of the axis to be called inverted to that of *Sphacelaria*. The tunica-layers which, due to a periclinal axis of division, are differentiated in an early stage of the embryo, are characterized by anticlinal axes of division, while in the corpus a periclinal axis of division predominates. Here, too, the particular forms of the growing points differ by distinct participation of the various transitional forms.

(c) *Dichotomy* — If not only a single apical cell but also a sister cell (strictly speaking, two descendants of the original apical cell resulting from longitudinal division of the apical cell) are equally favoured in growth, the bifurcation of telomes results. No differentiation taking place, the two telomes are alike (isotomy).



TEXT-FIG. 4 — Growing points.

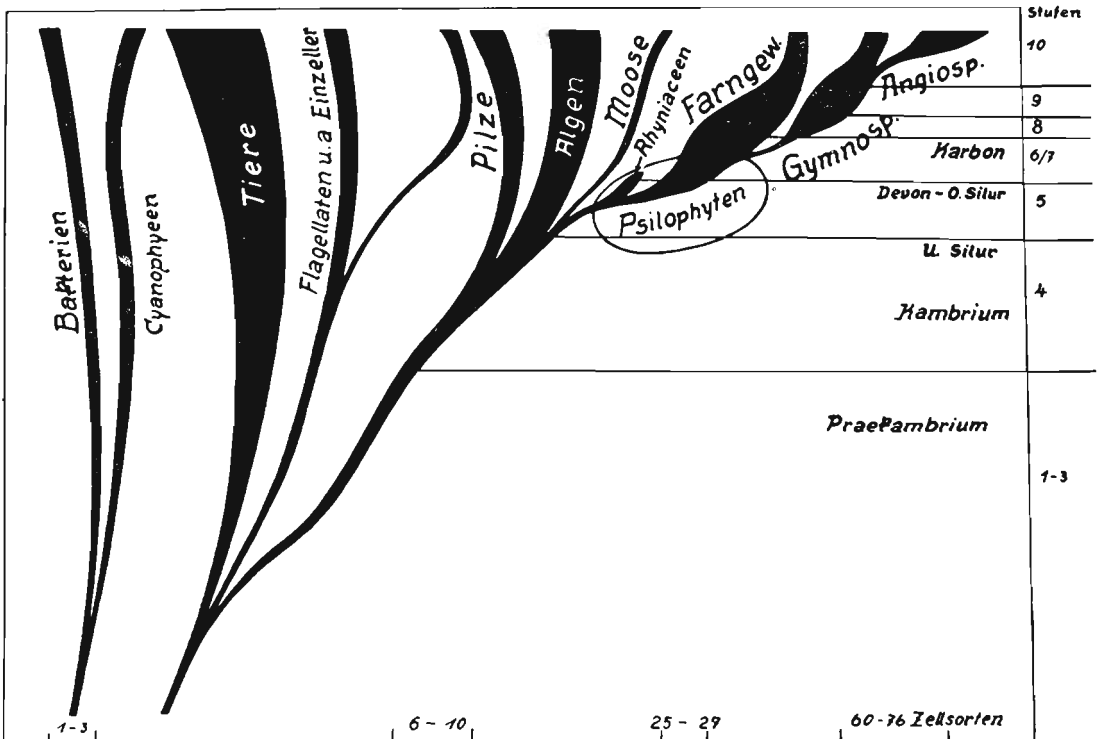
*Fourth elementary process: shifting of chief phases in alternation of generations* (TEXT-FIG. 3, No. 4) — According to general consensus of opinion the original stage was probably the haploid type (as represented by Volvocales), i.e. only the zygote was diploid. By postponement of meiosis into the mother-cells of agametes the isomorphic alternation of generations results: isomorphic haploid gametophyte and diploid spermatophyte (TEXT-FIG. 6).

A similar postponement of meiosis into the gametangium produces the diploid type (only the gametes haploid, as in Diatomeae, Siphonales, Fucales, Metazoa, etc.).

*Fifth elementary process: differentiation of different permanent tissue* (TEXT-FIG. 3, No. 5) particularly of a sclerenchymatic central bundle, which makes the telomes tear-proof.

*The Structure of Thalassiphyta* (TEXT-FIG. 5) — We can deduce the structure of Thalassiphyta from common features of the immediate predecessors of the early land-plants (the marine algae) as well as of their descendants (the Rhyniaceae themselves and the present sea-weeds, especially from the littoral zone).

For instance, all fossil sea-weeds, preserved from the Cambrian and Ordovician, consisted of undifferentiated bifurcated telomes, as far



TEXT-FIG. 5 — Genealogical tree of the world of organisms.

as they were branched at all. Furthermore, they frequently had a central bundle of mechanical tissue as is common in recent seaweeds.

The fact that the spores in the oldest land-plants were formed throughout in telomes, implies a similar arrangement in the Thalasiosiphyta. Moreover, from the alternation of generations in the Archegoniatae (including the Psilophyta) we must conclude that this form of reproduction pertained already to the ancestors. However, in consequence of an aquatic life, some special features may have been different at that time: planospores instead of air-spores, isomorphous instead of heteromorphous alternation of generations.

Finally, general phylogenetic rules permit such indirect deductions. I have in mind the rule according to which differentiated organizations evolved from the undifferentiated, or according to which the common characters of phylogenetically more comprehensive groups are more original than those restricted to phylogenetically restricted groups.

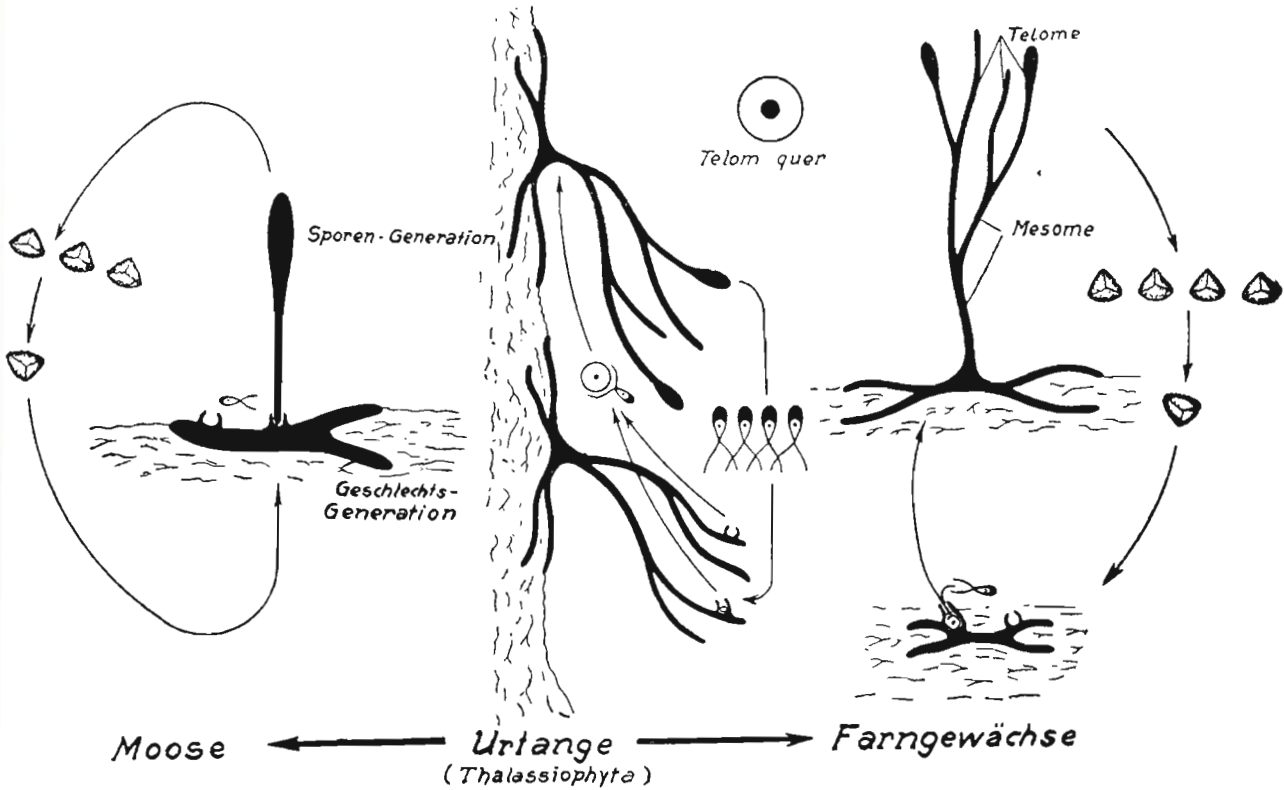
According to all this evidence the Thalasiosiphyta, owing to their original form and the five elementary processes, were constructed as follows:

1. From the common ancestral type (as transmitted to a great extent by *Chlamydomonas*) they assumed

- the habit of living in a liquid medium (probably the sea),
- the differentiation of the cell in nucleus, cytoplasm and green chromatophores (e.g. chlorophyll *a* and *b*),
- alternation of generations, derived of the haploid type (meiosis originally in the zygote),
- ability to move the cell by means of flagella.

2. The cells were connected by common cell walls, formed during cell division (first elementary process).

3. As division of labour (perhaps owing to sessile habit) the contrast between meristemical apical cell and permanent tissue resulted. Following irregular rotations of the cell axis the apical cell, together with its



TEXT-FIG. 6 — Change from isomorphic alternation of generations in Thalassiophyta (centre) to the heteromorphic alternation of generations in Rhyniaceae (right) and in mosses (left).

originally meristematic descendants, formed a three-dimensional growing point, which became a simple telome (second and third elementary process).

4. By rhythmically repeated longitudinal divisions of the apical cell — while both parts retained their permanently embryonal character and their special growing capacity — the telome became isotomously furcated.

5. By postponement of meiosis into the sporangia an isomorphic alternation of generations resulted (fourth elementary process, TEXT-FIG. 6, middle).

6. A central sclerenchymatous bundle made the telomes tear-proof (fifth elementary process).

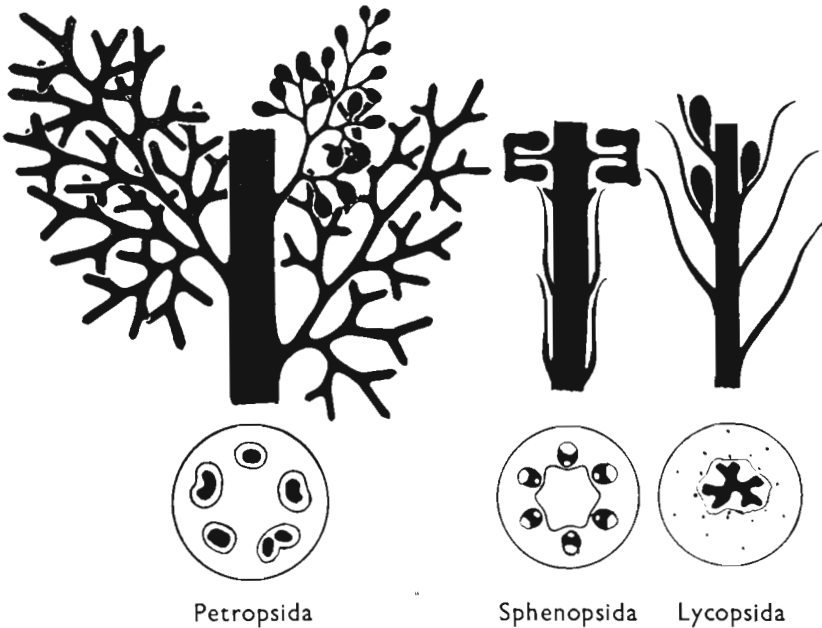
The independence of these elementary processes is proved by the fact that they can occur in multiple combinations. At present such combinations are still existing and it is characteristic that less developed types (like unicellular stages and filaments) dominate in ontogenetically juvenile stages.

#### THE ROAD FROM THALASSIOPHYTA TO EARLY LAND-PLANTS

1. Early land-plants are represented from Upper Silurian to Middle Devonian by Rhyniaceae (*Hostimella*-like forms, *Hicklingia*, *Taenioocrada*, *Zosterophyllum*, *Rhynia*, *Horneophyton*, leafless *Psilophyton* species and others). They originated from Thalassiophyta-like forms by developing a heteromorphic alternation of generations. That means the sporophyte was comparatively large while the gametophyte remained small and always thallophytic.<sup>5</sup> Even the sporophyte temporarily retained the thallophytic structure of merely undifferentiated archetelomes which rose by negative geotropism (TEXT-FIG. 6, right). Thus a distinction between shoot and leaf did not yet exist. Equally the anatomy remained very simple. The central

5. In contrast to the sporophyte, the gametophyte in the first land-plants and ensuing Pteridophytes remained small to safeguard spermatozoic fertilization.





TEXT-FIG. 7 — Kormophytic types.

sclerenchyma fibres became the central tracheide bundle of the protostele (TEXT-FIG. 6, top, middle). Around this central xylem elongated parenchymatic cells differentiated as forerunners of the phloem. Furthermore, we discern stomata on the aerial parts, root hairs on the basal parts.

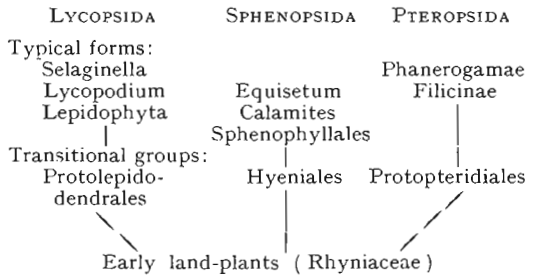
2. As organs of propagation we find terminal sporangia in these land-plants which produced air-spores; their formation by meiosis is proved by the tetrads. Of the gametophyte we have no direct knowledge. Since, up till now, no fossil remains of it have been found — in contrast to the excellent preservation of the sporophyte — we may assume great fragility of the gametophyte. This corresponds to the delicate constitution of the gametophyte in the descendants of early land-plants, the Pteridophyta.

3. Parallel to the Rhyniaceae the Bryophytes developed from thalassiohytic forms by relative dominance of the gametophyte. The sporophyte became parasitically dependent on the gametophyte and was accordingly reduced to a single fertile telome. Since the gametophyte needs water for the fertilization of the spermatozoa, the Bryophytes, in contrast to the Pteridophyta, remained close to the earth and often preserved their thallophytic structure. The time of origin of Bryophy-

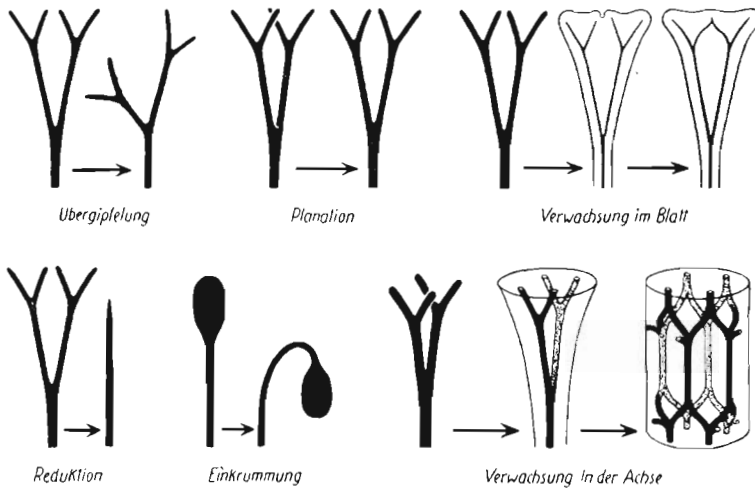
tes is yet exactly to be ascertained. Probably they became terrestrial plants later than the early land-plants, approximately in the Carboniferous. The exact date of the transformation of the isomorphic alternation of generations to a heteromorphic one is still unknown. Probably it is linked to the transition to land.

**THE DEVELOPMENT OF THE KORMOPHYTIC HABIT**

1. From the syntelome (Telomstände) of the early land-plants the Kormophyta derived by differentiation of the sporophyte in at least three parallel groups. Their relation is explained by the following genealogical table:



2. The development of Kormophyta is easier to understand if we start from the various



TEXT-FIG. 8 — The five elementary processes in the course of development from early land-plants to "typical" Kormophyta.

"types" within the Kormophyta (TEXT-FIG. 7). According to the later members of the evolutionary sequence we distinguish:

First type, Lycopsida: leaves small and alternate, sporangia in the axils of sporophylls, actinostele.

Second type, Sphenopsida: leaves small and verticillate, sporangia in peltate sporophylls, eustele.

Third type, Pteropsida: leaves large and (originally) alternate, sporangia on pinnate (and derived) sporophylls, polystele (in ferns) or eustele (in Angiosperms).

3. To form the group of "Psilophyta", we may combine with the Rhyniaceae the transition groups like the Protolpidodendrales (*Protolpidodendron*, *Barrandeina*, *Duisbergia*, *Baragwanathia*, *Drepanophycus* and perhaps *Asteroxylon* or *Thursophyton*, respectively), the Hyeniales and the Protopteridiales (*Protopteridium*, *Rhacophyton condrusorum*, *Aneuropteris*, *Cephalopteris*, *Cladoxylon* and *Pseudosporochnus*). They have much in common, for instance the predominance of forked leaves even in groups which later on have but simple needle-like foliage or pinnate leaves. Nevertheless, in these three transitional groups the tendency towards the "typical" form of the descendants is already evident.

4. The transformation of the Rhyniaceae habit to that of the "typical" Kormophyta results from very few elementary processes (TEXT-FIG. 8), viz.:

(a) *Overtopping* (*Übergipfelung*). From the furcated and thus equivalent telomes and mesomes this process produced

- (i) the contrast in shoots between axis and leaves,
- (ii) the corresponding contrast in leaves between rachis and leaflets.

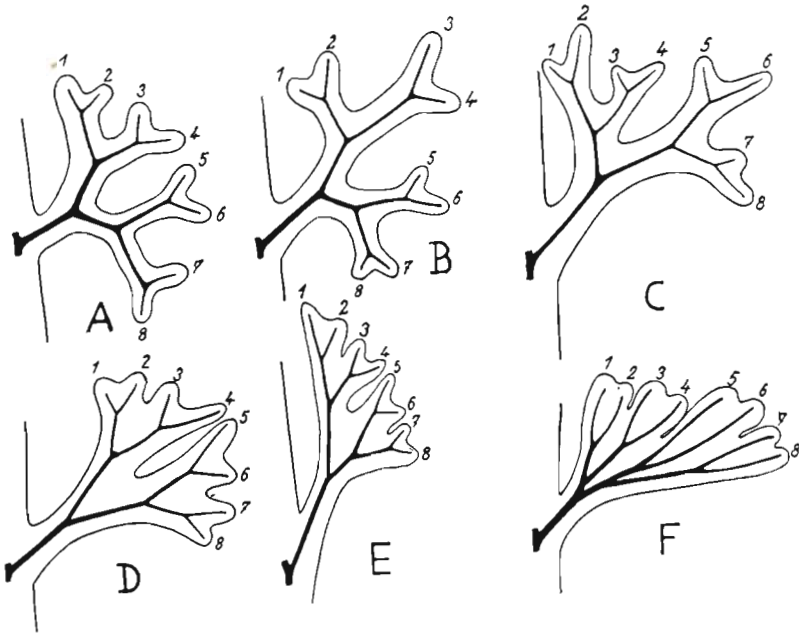
Following the development of the shoot by overtopping, the leaves and leaflets are arranged alternately as proved by fossils.

(b) *Planation* caused the telomes and mesomes to array themselves in a plane. It concerns particularly the leaves. Furthermore, as secondary modification, ramifications (including leaf position) may become arranged in one plane (e.g. flabellate *Lepidodendrons*, *Selaginella*, *Iris*, *Ravenala* and other Monocotyledons, etc.). Planation is a special case of organ dislocation, which is also evident in variations of leaf arrangement.

(c) *Syngenesis* (*Verwachsung*) connected the telomes and mesomes by (i) parenchyma, or by (ii) their steles.

Syngenesis within the leaf led either to forked veining with "open" venation (TEXT-FIG. 8), if only parenchymatic syngenesis occurred, or else to the pinnately veined leaf, if overtopping took place. Furthermore, by anastomosing of steles net veining of the leaves resulted, appearing since the Upper Carboniferous.

The transformations within the stem, as indicated by Text-fig. 8, bottom right,



TEXT-FIG. 9 — Six forms of overtopping.

correspond completely. The various stele types of the stelar theory result from a differentiated syngeneses of the branching stele. Thus the stelar theory is an anatomical component of the telome theory or else a parallel to the part of the telome theory that is restricted to the external morphology of organs. Mere parenchymatic fusion leads to the polysteles (in an "open" form, e.g. peculiar to some *Selaginella* stems). Frequently, however, especially in the stems of ferns and Angiosperms the "strands" of the stele (meristele) anastomose corresponding to a system of vascular bundles, as in Text-fig. 8, bottom, right. Here, too, the cross-sections of the stem show the polysteles or, in corresponding modification, the eusteles. But syngeneses in the stem can go still further, either in a radial direction, leading to the actinosteles (see cross-section of the stem in TEXT-FIG. 7, bottom, right) or in a tangential direction leading to the siphonosteles or solenosteles ("adelphosteles" of Van Tieghem<sup>6</sup>). It is significant that only the

metaxylem is regularly involved in such syngeneses, whilst the protoxylem still represents the original furcated, open structure of early land-plants.

As a rule only the metaxylem participates in such syngeneses, while the protoxylem is not connected and shows the original open-furcated structure of ancient land-plants.

(d) *Reduction* and

(e) *Incurvation* (Einkruemmung) or, generally speaking, the unequal growth of the tissue on two opposite flanks of the organ.

(f) *Longitudinal differentiation*, for example the differentiation of various forms of leaves in a shoot, mostly in combination with other elementary processes. For example, in the first leaves we rarely find the more advanced phases of elementary processes: the first leaves of ferns are furcated, etc.

the siphonosteles as an intermediate link between protosteles and polysteles or eusteles. The reason for this alteration lies chiefly in fossil transmissions. In the primary stele structure of archaic Pteropsida, in particular from Devonian and Lower Carboniferous, the polysteles dominate so evidently that its direct joining to the protosteles seems assured. This is maintained in spite of the much later (perhaps Permian) Osmundales siphonosteles, particularly as their derivation from a polysteles or eustele, respectively, is simple.

6. This concept of the stelar theory is in accordance with the ruling form of the stelar theory which I supported myself at an earlier time (e.g. 1930, FIG. 27) inasmuch as it acknowledges the protosteles as the primary type of the stelar structure. However, it differs from it by no longer regarding

To these 5 or 6 forming elementary processes *anatomic transformations* are added. For instance, the leaf tissue may differentiate dorsiventrally, the polystele may transform into an eustele by the centripetal metaxylem and the phloem becoming parenchyma and the centrifugal metaxylem becoming secondary xylem, etc.

5. *Overtopping* occurs in various forms, for instance in leaves (TEXT-FIG. 9) besides:

(A) the *archetype* without overtopping: the telomes are equivalent as in pinnules of the Upper Devonian genus *Archaeopteris*;

(B) the *katadromic oscillating overtopping* (Pendeluebergipfelung), prevailing in palaeozoic pteridophylls and in the pinnate leaves of dicotyledons (*Pulsatilla*). This predominance of the katadromic overtopping, contrasted with the prevailing anadromic overtopping in present fern fronds, is an independent proof of the overtopping concept;

(C) the *anadromic oscillating overtopping*, predominating in present fern fronds (*Polypodiaceae*);

(D) the *symmetric fastigate overtopping* (Dachuebergipfelung), e.g. in the Carboniferous genus *Odontopteris*;

(E) the *asymmetric (katadromic) fastigate overtopping*, found in the genus *Rhacopteris* (related to *Archaeopteris*) from Upper Devonian and Carboniferous;

(F) the *asymmetric (anadromic) fastigate overtopping*, like (C) represented by present fern fronds, e.g. in pinnules of *Adiantum*.

It is significant that the overtopping forms in leaf and shoot axis correspond to each other. In plants exhibiting katadromic pinnate leaves, we have axillary ramification, that means the lowest leaf of a lateral branch is as a "Tragblatt" ("bearing leaf") placed too on the katadromic or outward side of the shoot. In the Polypodiaceae with anadromic overtopping of the leaves the relation between "bearing leaf" and lateral branch is often inverted: the lateral branches originate from below the "bearing leaf" which thus stands on the anadromic side.

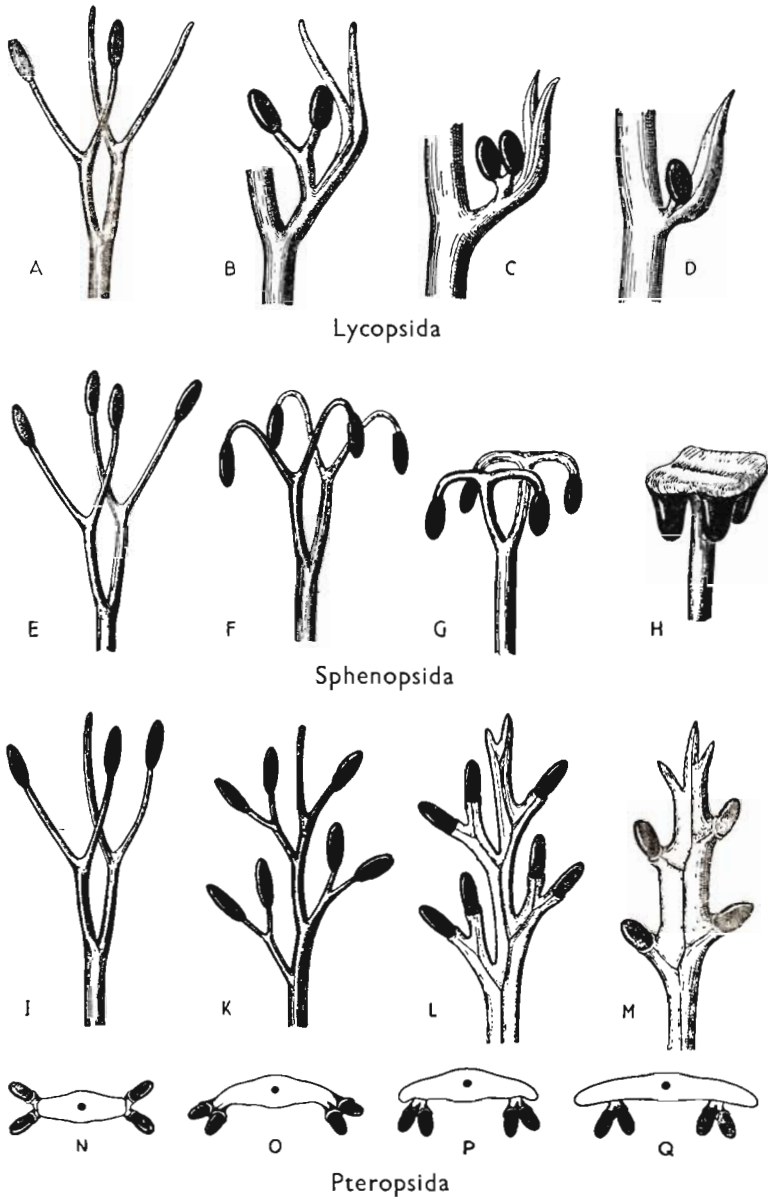
6. The independence of the different elementary processes is demonstrated especially at the beginning of phylogenetic transformation in the transitional groups leading to the Kormophyta (Protolpidodendrales, Hyeniales and Protopteridiales). Here frequently only the one or the other elementary process comes into existence, although in a very incomplete manner.

7. For instance in the earliest Lycopsidea (in the Protolpidodendrales) overtopping is restricted to the formation of a shoot axis with attached leaves. The Protolpidodendrales (*Protolpidodendron*, *Barrandeina* and others) thus still possess furcated leaves or they demonstrate clearly (like *Drepanophycus*), according to investigations of Halle, the syngeneses of the furcated leaves with the shoot axis. In this way within the "type" of Lycopsidea only the tips of the furcated leaves remain free. Moreover, the bifurcated arms of the actinostele in *Asteroxylon* (similar to TEXT-FIG. 7, bottom right) clearly indicate the fusion of syntelomes, as the protostelic leaf traces detach from the bifurcated arms of the actinostele.

8. Transitional groups leading to the Sphenopsida, the Hyeniales, likewise still have furcated leaves just as the adjoining oldest representatives of the "typical" Sphenopsida, like *Asterocalamitaceae* and *Sphenophyllaceae*. If, incidentally, in the latter the bifurcated leaves fused with the shoot axis the original triradiate actinostele occasionally became hexaradiate. Characteristically 3 (or a multiple of 3) groups of protoxylems dominate in Sphenopsida.

9. The Protopteridiales are marked by less distinct or sporadic elementary processes. Thus in *Pseudosporochnus Krejci* the modification is limited to a compression of the bifurcations into one point (by reduction of the bearing mesomes) by which a crown results, while the other elementary processes are scarcely represented, e.g. the terminal telomes are by no means adjusted in one plane. Similar facts concern species of *Protopteridium* and some Palaeozoic Coenopteridales, linked by transitional genera, where "typical" leaves, arranged in one plane, are still missing.

10. Moreover, especially in the leaves of Pteropsida, we may particularly well observe the *interchanging co-operation of the elementary processes*. By mere oscillating overtopping there arises the pinnate leaf with alternate leaflets as in Text-fig. 7, left. Opposite pinnules result by rhythmic reduction of each second mesome. Syngeneses converts the bifurcated leaf into a furcatedly veined leaf (as in *Ginkgo*) and the pinnate leaf in a pinnately veined leaf. Just here countless modifications exist, if, for instance, only the last pinnules fuse as is the case in many ferns. Thus the Palaeozoic Pteridophylls *Neuropteris*, *Pecopteris*, *Alethopteris* form a flowing sequence according to the



TEXT-FIG. 10 — Development of sporophylls.

pinnule fusing merely in itself (*Neuropteris*) or furthermore with the bearing basis (*Pecopteris*) or with a broadened basis (*Alethopteris*) respectively.

11. The *organs of reproduction* are modified by the same elementary processes as the vegetative organs (TEXT-FIG. 10). For instance the sporophyll of the Lycopsidea is reduced to a single-veined leaf with an

axillary sporangium. It is characteristic of the Protolipidodendrales to be still in possession of the transitional forms corresponding to Text-fig. 10, B (only the sporangia being already reduced to one). Thus they still have a common stalk for sporangium and furcated leaf. The Psilotales too, similar to Text-fig. 10, C, represent such a transitional form.

In the Sphenopsida the Hyeniales show merely incurvation of the stalks of sporangia, corresponding to Text-fig. 10, F. Only later, in the Equisetales, syngensis of the mesomes to a shield-like plate is added (TEXT-FIG. 10, H).

In the Pteropsida a predominantly oscillating overtopping leads to a pinnate sporophyll. If the mesomes fuse laterally with each other, the pinnately veined sporophyll with marginal sporangium results. Further syngensis and incurvation produce, for instance, the different types of ovaries (see ZIMMERMANN, 1930, FIG. 231). Here, too, very simple elementary processes are involved though the variety in evolution of synsporangia (Sporangienstaende) especially in the Pteropsida is very large.

An elementary process specific of fertile organs is the unequal expansion of the upper and lower sides, to be summed up by the elementary process of incurvation. It leads, for example, to a dislocation of the sporangia to the lower side (less often to the upper side) of sporophylls. On the other hand, we find planation less in sporophylls than in trophophylls. Planation is missing in Sphenopsida and Lycopsidea, whilst in Pteropsida the sporophyll is frequently modified by planation, particularly if it became a scale of a cone or (as in many recent ferns) simultaneously serves as trophophyll. But in some ("stachyospermic") Pteropsida the synsporangia *in toto* retain the original radial symmetry, likewise some parts of the sporophyll in "phyllospermic" Pteropsida show this primitive morphological trait. This has led to many disagreements of a morphological kind since such more or less radial forms like sori, placenta, scale complex of conifers, Bennettitalean and Ginkgo flower, "Ophioglossalean leaf", stamen of Angiosperms, ovule and others do not really harmonize with either the type of leaf or that of the shoot. But phylogenetically these derivations from the type are easy to understand, since elementary processes like planation modify organs only in case the transformation is of ecological advantage, for instance, in the formation of an assimilating leaf surface or in the scales of a cone protecting the sporangia, etc.

12. The independence of the elementary processes is proved by the fact that they affect the different organs in a different way. In consequence, according to the "biogenetic

law", juvenile stages frequently show less advanced transformations than mature stages. Certainly there are numerous cases to be observed in which single elementary processes in juvenile organs do not become manifested. Thus in the first leaves of ferns regularly no overtopping occurs, they are furcated. Furthermore, overtopping is missing in many embryos of Pteridophyta and Phanerogams, as well as, for instance, at the growing points of *Psilolum* in spite of the remarkable contrast of axis and leaf in the adult stage. But, at the same time, stages of widely different elementary processes may combine as is often seen in recent plants. For instance, fern fronds especially from the Palaeozoic demonstrate clearly how some parts of the frond retained primitive traits (furcation and unconnected telomes) while others exhibit advanced features. The immense richness in the form groups designated as Pteridophylls rests on the changing combination of the elementary processes (see ZIMMERMANN, 1938). Another typical instance of changing combinations of elementary processes is the different combination of vegetative and generative organs in Pteridosperms.

If according to the *New Morphology* we as natural scientists aim to describe the natural process, it is evident that ontogeny and phylogeny are not identical, and that we may at best draw conclusions from ontogeny on phylogeny by means of the "biogenetic law". Further, the causal problems of phylogeny (Darwinism, Lamarckism, the orthogenesis theory, etc.) can be solved scientifically only by an analysis of evolution. It is significant that the macrophylogenetic development of types is to be traced back to microphylogenetic processes which are partly to be handled as mutations in experiment.

13. Naturally all elementary processes are holo-genetic actions. For instance, overtopping is really due to a change of the genotype (mutations) by which the ontogeny is altered, thus, usually the growing point of the axis overtops the embryonal stage of lateral organs. Thus objections often raised, according to which the assumptions of overtopping, syngensis and other phylogenetical processes are said to be wrong since these elementary processes from the outset are not enacted at the growing point, are really beside the point of this whole question.

14. The main value of the telome theory and, besides fossil findings, at the same time

its most important argument of proof, is its general validity and uniformity. The telome theory not only applies to "typical" organs—that means to such organs as are classified according to classical morphology under the

notion of leaf, shoot, axis, stem, root—but all forms of Kormophyta are to be traced back to the varying combinations and the different degree of manifestation of a few modifying processes.

#### REFERENCES

- HALLE, T. G. (1933-40). De utdoeda vaexterna. "Vaexternas Liv." **4**: 449 & **5**: 1. *Stockholm*.
- LAM, H. J. (1948). The New Morphology. *Acta biotheoretica*.
- ZIMMERMANN, W. (1930). Phylogenie der Pflanzen. *Jena*.
- Idem (1934). Research on Phylogeny of Species and single characters. *American Naturalist*, **68**: 381
- Idem (1938). Phylogenie der Pteridophyten. *Manual of Pteridology*. *The Hague*. S.558.
- Idem (1938a). Telomtheorie. *Biologie*. **7**: 385.
- Idem (1943). Die Methoden der Phylogenetik, in Heberer: Evolution der Organismen, p.20. *Jena*.
- Idem (1945). Hauptergebnisse der Telomtheorie. (Als MS vervielf.)
- Idem (1945a). Palaeobotanik. *Handbuch der Biologie*. **4**: 252.
- Idem (1948). Grundfragen der Evolution. *Frankfurt*.
- Idem (1948a). Stammesgeschichtliche Entwicklung unserer Heilpflanzen. *Suedd. Apothekerzeitung*. **88**: 399.
- Idem (1949). Geschichte der Pflanzen. *Stuttgart*.
- Idem (1950). Ueber Urpflanzen und Urlandpflanzen Naturw. Rundschau, p. 259.