

TWENTYFOURTH
SIR ALBERT CHARLES SEWARD MEMORIAL LECTURE

THE TENDENCY CONCEPT: A VIEW ILLUSTRATED
BY THE PRINCIPAL EVOLUTIONARY STEPS IN
THE PLANT KINGDOM

BY

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TO start this 24th Sir Albert Charles Seward Memorial Lecture I should like to give you a definition of my tendency concept (Jonker, 1976) as this developed in my mind during a career of 45 years of research in plant taxonomy, palaeobotany and palynology, and 25 years in teaching, supervising and the training of students.

A tendency is expressed in the course of evolution by a genesis of similar phenomena in different, and not closely related taxa, which phenomena developed independently within the different taxa, and, moreover often in different geological periods.

To give a few examples:

1. A tendency to develop cauloid, phylloid and often rhizoid parts, i.e. an outward differentiation of the plant body into stems, roots and leaves or similar parts.

It manifests itself in e.g.

CHLOROPHYTA — Siphonales: a good example is the genus *Caulerpa*, which is a diplontic alga and a coenocyte;

PHAEOPHYTA — Laminariales: a good example is the genus *Laminaria*, i.e. in a diploid sporophyte;

SOME RHODOPHYTA — Ceramiales, especially in the families Delesseriaceae, Rhodomenaceae and Ceramiaceae, i.e. both in the haploid gametophyte and in the diploid tetrasporophyte;

Devonian algae or perhaps transitional forms between algae and Tracheophytes, with flabelliform leafy parts, of still unknown affinities and unknown life cycles. A good example is the genus *Germanophyton*.

BRYOPHYTA — Musci, i.e. in the haploid gametophore. In this taxon the expression of this tendency was initiated in the Carboniferous.

All Tracheophytes, Psilophyta excepted, i.e. in the diploid sporophyte. In the Tracheophytes the expression of this tendency became manifest in the early Devonian.

2. Another example is the tendency to heterospory in Pteridophytic divisions (Lycopodiophyta, Equisetophyta, Pterophyta) starting in Middle and Late Devonian times, after the above divisions arose from Psilophytic ancestors and after those divisions had developed into separate, independent taxa. In the Lycopodiophytes this tendency expressed itself for the first time in the Upper Devonian or Lower Carboniferous; in the Equisetophytes there was a short spell of heterospory during the Carboniferous; in the eusporangiate *Primo-filices* it was first apparent in the Middle or Upper Devonian; and finally in leptosporangiate ferns (Marsileales and Salviniiales) in the Triassic or Jurassic.

3. A third example concerns the tendency to angioovuly and angiospermy. It finds its expression in an encasement of the ovules and seeds respectively, and results in the development of ovaries and fruits. We find it expressed, in the Jurassic in the Caytoniales, in the Lower Cretaceous in the Angiosperms, probably in the Tertiary in the Coniferous genus *Juniperus*. It is expressed in the Conifer genus *Araucaria* in yet another way. We even see an expression of this tendency, in the Upper Cretaceous, in the order Marsileales, i.e.

leptosporangiate ferns. Ferns do not develop seeds but here the equivalents of the seeds, the sori, are encased.

These three examples throw a new light on a number of the important evolutionary steps: while to some extent similar, they originated independently and were often concerned with quite different phenomena. Here I may state that the tendency concept is not identical with — or another term for — phenomena known as convergence or parallelism, as is apparent from the examples I have just mentioned. The expression of the same tendency in different taxa does not, in all cases, lead to morphologically identical plants or organs. It is not, like parallelism, a result of similar

environmental circumstances or the same way of living, e.g. the external habits of fishes on the one hand and porpoises or dolphins on the other, to quote a striking zoological example. Our first mentioned case — the differentiation into stems, leaves and roots — included both submerged algae and landplants.

Using this tendency concept I should now like to follow the evolution of land plants up to the most-advanced seed plants we know: the Angiosperms. We have to start away back in Middle Devonian times, when the Pteridophytic taxa that arose from a Psilophytic stock had developed into independent, no longer closely related divisions of the plant kingdom (Table 1).

TABLE 1 — TENDENCY SEQUENCE STARTING FROM HOMOSPOROUS PTERIDOPHYTES

I (heterospory)	megasporangia containing megaspores (which germinate)	microsporangia containing microspores (which do not germinate)
II (reduction of the number of megaspores in a megasporangium)	each megasporangium containing a single functional megaspore	—————
III (pre-integument and prepollen)	<p><i>Macrophyllous</i></p> <p>a. megasori and microsori</p> <p>b. megasorus consisting of a single megasporangium</p> <p>c. the indusium encloses the megasporangium as a pre-integument, forming together a preovulum</p>	<p><i>Microphyllous</i></p> <p>the megasporophyll or part of it encloses the unisporous as a pre-integument, forming together a preovulum</p> <p>prepollen (does not germinate)</p>
IV (integument and pollen)	<p>ovules → seeds</p> <p>a. mature seed containing a primary endosperm</p> <p>b. mature seeds containing an embryo</p>	<p>pollen (germinates)</p> <p>a. Pollen I: distal germination giving rise to a pollen tube of the haustorial type</p> <p>b. Pollen II: distal germination giving rise to a pollen tube of the sperm-carrying type</p>
V (angiovully and angiospermy)	<p>ovary → fruit</p> <p>double fertilization</p>	<p>c. Pollen III: germination not necessarily distal → more than one aperture</p>

The tendency that meant a first step in the direction of seed plants was the tendency to heterospory, which found its expression in the origin of microsporangia containing microspores, and megasporangia containing megaspores. I better exclude from these considerations the Equisetophyta, which indeed showed, in the Carboniferous, a heterospory of short duration. In my opinion, however, this division did not include ancestors to the seed plants. This leaves the Lycopodiophyta and the early ferns, i.e. a microphyllous and a macrophyllous group, as possible ancestors. In my opinion both groups gave rise to seed plants. I consequently reject the concept that all seed plants are to be derived from the so-called Pregymnosperms, which group I prefer to regard as the order Protopteridiales of the early ferns. I object to the term Pregymnosperms as it contains and expresses an unproved, unprovable, improbable, and dangerous hypothesis. Within this order Protopteridiales the tendency to heterospory and some of the following tendencies found expression, as in numerous other taxa, a matter which will be discussed in the following section.

The heterospory in the heterosporous Lycopodiophytes does not differ in any fundamental way from that in heterosporous ferns. In both cases it resulted, apart from the micro- and megaspores, in a reduction of the gametophyte which is most strongly pronounced in the microprothallus which consists of only a few vegetative cells and one or two antheridia. This remains enclosed by the microspore wall which means that microspores do not germinate, as distinct from isospores. After decay and liquefaction of the prothallial cells and antheridium wall and, to some extent, a decay of the microspore wall the antherozoids are released. I do not regard this as germination, as contrasted with Chaloner's view (Chaloner, 1967, 1970, 1976). He uses the term germination in the sense

of any emergence of cell contents from the spore wall. In my opinion the germination of a seed means the emergence of the seedling, and the germination of a Pteridophytic spore the emergence of the prothallus (Jonker, 1974, 1976).

Megaspores, however, do germinate, i.e. part of the multicellular prothallus becomes exposed, even though it does not become a truly independent gametophyte such as is found in most homosporous Pteridophytic taxa.

The next step in the sequence towards seed plants is revealed in the tendency to a reduction in the number of functional megaspores in the megasporangium to a single one. This tendency finds a similar expression in both microphyllous and macrophyllous taxa. Often four spore initials are formed but only one of them develops into a mature megaspore. In the case of the Lower Carboniferous fern *Stauropteris burntislandica*, (Surange, 1952; Chaloner, 1958) two megaspores developed and as such might be considered an initial phase in the manifestation of this tendency. We see it expressed in some Carboniferous Lycopodiophytes and Equisetophytes (esp. *Calamocarpon*). In the macrophyllous taxa it is to be expected, though not known with certainty, in a number of Upper Devonian Protopteridiales, and it is fully expressed in all species of the Marsileales and Salviniiales.

There is no counterpart to this in the microsporangium, i.e. the tendency to a reduction in the number of spores to ultimately a single functional one, only finds expression in the megasporangium.

The third tendency that we meet on our way to the seed plants manifests itself in a loose casing surrounding the unisporous megasporangium. I refer to this casing as pre-integument. As in the previous stages this tendency is repeated in different taxa in different geological periods and, moreover, finds a different expression in

the microphyllous and macrophyllous taxa. It is not expressed in the Equisetophyta, since in *Calamocarpon* the outer layers of the megasporangium itself develop into a solid coat. As this is not a novel structure we cannot regard it as a pre-integument.

In microphyllous taxa such as the Carboniferous strobilus *Lepidocarpon* (Lepidodendrales), and in some related genera, we observe a sporophyll which loosely encloses a unisporous megasporangium as a bottle-shaped pre-integument with a micropyle-like open neck. A similar pre-integument is also to be found in the Carboniferous genus *Miadesmia* (Selaginellales) but in this case the pre-integument is not formed by the sporophyll but by a lateral outgrowth of the latter, the velum. The apical part of the pre-integument is provided with tentacles which trapped the microspores, demonstrating that also pollination was effected.

In macrophyllous taxa the situation characterized by a single sporangium in the axial or on the adaxial side of the sporophyll, is not met with: the pre-integument originated in a quite different way. We may use the situation in the genus *Azolla* to obtain an idea of the nature of the macrophyllous pre-integument. In the Salviniaceae we observe that the megasorus of *Salvinia* (Salviniaceae), consisting of unisporous megasporangia, is enclosed by an indusium. In *Azolla* (Azollaceae) this megasorus is reduced to a single megasporangium though other sporangia may be formed initially. The inferior indusium encloses the megasporangium during the development of the latter as a loose pre-integument which closes finally at its top, forming a more or less micropyle-like apex. It suggests that in macrophyllous taxa the pre-integument might be homologous to an indusium.

The Salviniaceae, however, are not known before the Upper Cretaceous, while we know from papers by Long (1962) and

Pettitt and Beck (1968) that as early as Late Devonian and Early Carboniferous times pre-integuments existed as inferior whorls of scales—each one of which was often provided with a vascular bundle—surrounding and often partly enclosing—as a cupula—the unisporous megasporangium. In the latter another three spore initials sometimes started development. It may be questioned whether this cupule, of which the scales are often connate to their bases to both the megasporangium and to one another, is homologous to an indusium. Perhaps we may compare the situation to that in the Marattiales in which the inferior indusium consists of scales, which are either free from the sorus or connate to one another and to the sorus. The sporangia in a sorus are, in that case, fused to form a synangium. The Marattiales which display a soral casing to some extent are, however, homosporous which means that the expression of the tendency now under consideration does not go hand in hand with the tendencies to heterospory and to reduction in the number of spores, or with the reduction of the number of sporangia in a sorus.

I refer to a unisporous megasporangium enclosed by a pre-integument as a preovulum.

The microspores of the preovulate plants, like those in the Pteridophyta, did not germinate, which means that the reduced microprothallus and antheridium remained enclosed in the spore wall. Antherozoids were discharged proximally, either by decay of the spore wall or via slits in the trilete mark. So far they do not differ from microspores of other heterosporous plants mentioned above. However, in addition they often show 'pollen characters' with regard to wall structure and ornamentation. Above all they were transported to the preovules before releasing the antherozoids. In microphyllous preovules this took place in or near the micropyle-like apex. In macrophyllous plants in which the preovule

has, in most cases, no micropyle, this occurred on the megasporangium which is often provided with a beak-like process, the salpinx. For this microsporal condition we apply Renault's term prepollen.

The next step is the formation of true ovules by a fusion of the pre-integument and the megasporangial wall, leaving only an open micropyle, in microphyllous plants. In macrophyllous plants this tendency manifests itself in a fusion of the pre-integumental scales into a closed coat and the fusion of the latter with the megasporangium wall, leaving no more than an open micropyle. The pre-integument has evolved into an integument, the proovule into an ovule. After pollination and fertilization the integument becomes a solid testa, i.e. the ovule becomes a seed.

This all means that the integument of microphyllous seed plants (e.g. Conifers), which evolved from the megasporophyll or an outgrowth (velum) of it, is radically distinct from the macrophyllous integument which evolved from an indusium. This was already postulated by Hagerup (1933) as early as 1933. Other opinions apparently exist with regard to this matter for, according to Pettitt (1970) "it has been suggested rightly or wrongly that the cupule evolved into the angiospermous carpel".

We have now reached the stage of gymnospermous seed plants and we may distinguish two substages. In Cycadperms and Ginkgoperms the mature seed, i.e. a seed that is released by the mother plant, contains a primary endosperm with a well-developed pollen chamber. In the more advanced Gymnosperms (and in Angiosperms as well) the mature seed contains an embryo.

Again we may observe a microsporal counterpart with the tendency to form ovules and seeds. The microspores now become true pollen, i.e. they germinate by a distal extrusion of a pollen tube, which is no more than a prolonged microprothallial cell.

In the first substage, parallel with the development of mature seeds containing a primary endosperm, the distal germination gives rise to a haustorial pollen tube, while the antherozoids are released proximally as in microspores and prepollen. In the second substage of gymnospermy, parallel with the development of seeds containing an embryo, there is a distal germination only and no proximal emergence of antherozoids; the pollen tube is of the sperm-carrying type. The tendency to form pollen tubes of the latter type is to be observed, consequently, in both microphyllous and in macrophyllous seed plants.

The next tendency is that to angiospermy and consequent angiospermy, which finds its expression in an envelopment of the ovules and seeds. In my introduction I have already mentioned the manifestation of this tendency in different taxa in different geological periods. It reached its full development in the Angiosperms and, in this subdivision of the Spermatophyta, goes together with the phenomenon of double fertilization. In Angiosperms the envelopments of ovules and seeds are called ovaries and fruits respectively. It is highly probable that the ovary varies in character and origin in the different angiospermous taxa, which is in accordance with our definition of tendencies, but this problem will not be discussed in the present context.

The basal phylogenetic problems in the Angiosperms: monophyletic or polyphyletic, phyllospermy or stachyospermy, the homologies in the ovaries, the carpel and stigma problem, etc. are very complicated and there is by no means agreement with regard to the different concepts. These problems go far beyond the scope of this paper. I only want to emphasize the different evolutionary tendencies regarding ovaries, fruits and seeds within the Angiosperms. These are expressed in sequences from e.g. apocarpny to coenocarpny, superior ovaries to inferior ovaries, unilocular to plurilocular

ovaries, large seeds with fleshy testae to small dry seeds, etc. These tendencies are apparent in different lines of Angiosperm phylogeny, which is in accordance with my tendency concept.

The same applies to microsporial tendencies. The tendency which led to gymnospermy coincided with a microsporial tendency leading to true pollen, i.e. microspores showing a distal germination giving rise to a pollen tube, either haustorial or sperm carrying. The primitive microsporial condition in Angiosperms is expressed in the same type of pollen: a single distal aperture which is either a colpus (sulcus) or a pore (ulcus); the pollen tube is of the sperm-carrying type. Pollen evolution in Angiosperms is characterized by the successive formation of more and more apertures; their arrangement is then no longer distal but equatorial and finally pantoaperturate. The ornamentation sequence is, according to palaeo-palynological data (Laing, 1976) from psilate via the occurrence of detached structural elements to tectate, though some modern pollen-morphogeneticists assume an inverse sequence (Walker & Skvarla, 1975; Walker & Doyle, 1975; Walker, 1976). I shall abstain from entering into a discussion on this controversy in this particular paper. The evolutionary sequence with regard to the relation between polar axis and equatorial diameter is

apparently from pertransverse (peroblate) via adequate (spheroidal) to pererect (perprolate).

The microsporial sequences mentioned here are expressions of tendencies as well, such as to be found in different taxa and in different, parallel evolutionary lines within the Angiosperms. However, unlike the situation encountered in the Gymnosperms there is little or no correlation with the megasporangial tendencies in Angiosperms, or with other flower-morphological tendencies such as leading from choripetaly to sympetaly. The various different but non the less obvious tendencies that we meet with in the Angiosperms are apparently completely independent of one another. Along with the still meagre fossil data, it is this lack of correlation which make the study of the phylogeny of the different angiospermous taxa so extremely complicated and difficult.

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