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Plant Morphology: The Historic Concepts of Wilhelm Troll, Walter Zimmermann and Agnes Arber

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Recent molecular systematic and developmental genetic findings have drawn attention to plant morphology as a discipline dealing with the phenotypic appearance of plant forms. However, since different terms and conceptual frameworks have evolved over a period of more than 200 years, it is reasonable to survey the history of plant morphology; this is the first of two papers with this aim. The present paper deals with the historic concepts of Troll, Zimmermann and Arber, which are based on Goethe's morphology. Included are contrasting views of 'unity and diversity', 'position and process', and 'morphology and phylogeny', which, in part, are basic views of current plant morphology, phylogenetic systematics and developmental genetics. Wilhelm Troll established the 'type concept' and the 'principle of variable proportions'. He has provided the most comprehensive overview of the positional relations of plant forms. Agnes Arber started from the universal dynamics of life and attempted to describe all structures as processes. She paid attention to 'repetitive branching', 'differential growth', and 'parallelism'. As a result she has recently been rediscovered by developmental botanists. Walter Zimmermann rejected any metaphysical influence on plant form and instead called for objective procedures. He was mainly interested in phylogenetic 'character transformation' and the 'reconstruction of genealogical lines'. Guided by the example of flower-like inflorescences, a future paper will deal with functional and developmental constraints influencing plant forms. Recent morphological concepts ('trialectical', 'continuum'/'fuzzy', 'process morphology') will be discussed and related to current morphological and developmental genetic research.

Key words: Plant form, plant morphology, natural philosophy, homology, phylogeny, Goethe, Troll, Arber, Zimmermann, typology, character transformation, differential growth, complementarity.

INTRODUCTION

Plant morphology deals with the phenotypic appearance or 'form' of plants. However, what is the form of a plant? Does it exist at all? Are our concepts adequate to explain what we call a plant form?

These questions are very old and were discussed in Greek antiquity and the Middle Ages. They have been answered either in the context of Aristotle's metaphysics or the Christian belief in Creation, always according to the spirit of the times (see Arber, 1950). Even today, during the age of evolutionary and molecular genetics, these questions are still pressing.

Two hundred years of plant morphology

Our knowledge of plants has increased dramatically in the last decades. Molecular techniques have promoted studies in phylogenetic systematics and developmental genetics. Plant forms have been analysed under the functional view of biomechanics and pollination ecology. The need to care for the world's natural heritage has enhanced studies in biodiversity. All these disciplines are either based on plant morphology or are closely related to it. Each of them deals with a different aspect of plant form. Diverse views and new findings require a reconsideration of the meaning, the content and the conceptual framework of plant morphology.

Since its introduction by Goethe in the late 18th century, modern plant morphology has had an eventful history. Many terms e.g. 'morphology', 'homology', and 'type' originate from pre-Darwinian times and are used today in different contexts. Goethe (1790) realised that the diversity of forms might be reduced to a number of 'archetypes'. To him, these archetypes represented abstract conclusions from his empirical observations [see Goethe's famous conversation with Schiller in Kuhn (1987 pp. 434–438)], but in the age of phylogenetic systematics they became transformed into ancestral types (see Arber, 1946). This confusion existed for a long time and might even persist today. For this reason, the relationship between morphological typology and phylogenetic grouping is re-examined in the present paper.

In Germany, discussion of typology and phylogeny is closely related to the names of Wilhelm Troll and Walter Zimmermann. Their bitter and often polemic controversy is well documented, and illustrates their conflicting views (see Nickel, 1996 pp. 58–60). Troll (1925, 1928) followed Goethe in taking the plant types to be ideas while Zimmermann (1930, 1937) only accepted types as natural groups having evolved from common ancestors. At the same time, Agnes Arber (1950) published *The natural philosophy of plant form*. She came from a perspective focused on the open growth of plants and the continuous change of plant forms during

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ontogeny. In having morphogenetic change in mind, she added a third aspect to the debate on morphology.

The historic concepts of Troll, Zimmermann and Arber (Fig. 1)

Agnes Arber (1879–1960), Walter Zimmermann (1892–1980) and Wilhelm Troll (1897–1978) were born in the last quarter of the 19th century and died at the ages of 81, 88 and 81, respectively. They were enthusiastic botanists, doing an immense amount of empirical work and writing important books (see selected references). However, although they were contemporaries, they followed completely different concepts and philosophies (Troll, 1925, 1928, 1951; Zimmermann, 1930, 1931, 1937; Arber, 1946, 1950; Hauke, 1996; Nickel, 1996). Troll and Arber were influenced by Goethe and followed metaphysical ideas by seeking the truth behind facts. In contrast, Zimmermann rejected any metaphysical influence on science. He was predominantly interested in phylogeny and in the evolutionary history of form. Troll and Zimmermann both intended to reduce the diversity of living forms and thus agreed in accepting types and groupings, while Arber focused on dynamic processes and thus could not accept static types for fundamental reasons. Zimmermann and Arber included morphology in biology, understanding it—in Arber's terminology—as a 'partial view' of the 'whole'. Troll, however, separated morphology from all analytical approaches and thus isolated German morphology for many years.

The aim of the present paper

The present paper is the first of two papers dealing with plant morphology. It summarizes selected historical views of plant form and re-examines the meaning of 'morphology'. A second paper is planned which will consider modern concepts including functional and genetic constraints on plant form.

The concepts of Troll, Zimmermann and Arber are historical views of plant form. As such they are part of current plant morphology, phylogenetic systematics and developmental biology (see Fig. 1). It is not only interesting to see how concepts have evolved and changed through the ages but it is also necessary to remember their historical roots (see Arber, 1950). Many misunderstandings and much confusion of terms have originated in historic disputes and interpretations. For this reason the present paper summarizes the three diverse historical concepts.

I do not attempt to summarize the entire work of the authors concerned; this would be beyond the scope of the present paper and, moreover, would require support by historians and philosophers of science. I focus predominantly on the controversial views concerning the antitheses of 'unity and diversity', 'statics and dynamics' and 'idealism and rationalism'. I comment briefly on Goethe's morphology before beginning the individual views because all three authors refer to Goethe's work. I endeavour to show that the different concepts are the result of different intentions, procedures and philosophies. Bearing this in mind we can learn from history that even objective research includes subjective elements and that different views can complement each other rather than being antithetic (see Rutishauser and Sattler, 1985).

ARCHETYPES AND METAMORPHOSIS: GOETHE'S MORPHOLOGY

Johann Wolfgang von Goethe (1749–1832) was not only a famous poet but also the founder of 'morphology'. For 200 years he has been honoured as one of the most outstanding and versatile men of his age and a great deal has been written about his work. The present summary of Goethe's fundamental influence on plant morphology is based mainly on the comments given by Steiner (1883), Troll (1928), Arber (1946), Froebe (1986) and Kuhn (1987, 1992).

Plant morphology

Goethe's interest in plants began with an ambition to identify the species around him. At first he was much

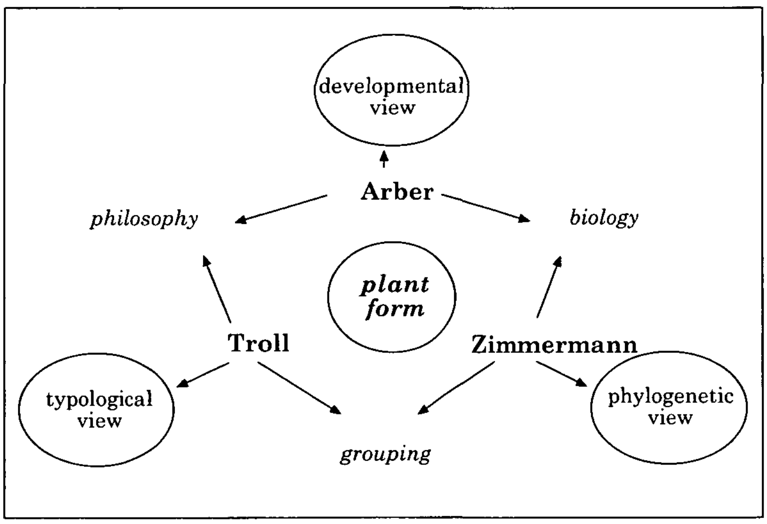

FIG. 1. The different approaches to the plant form of Arber, Troll and Zimmermann (see text).

impressed by the systematic studies of Linné, but then rejected his analytical approach. This rejection originated in him, as Goethe was a thoroughly spiritual and sensitive person whose philosophy of life was synthetic and holistic.

According to Goethe, analytical studies inevitably have to remain insufficient because living organisms are only complete as entities in themselves and not as fragments. To understand the entire organism it is imperative to also approach it from the synthetic point of view. Goethe introduced 'morphology' as an approach to both inorganic and organic entities. Correspondingly, plant morphology deals with the outer appearance of the entire organism (see Fig. 2).

In the present context two aspects of Goethe's view of plant morphology are particularly interesting: (1) Goethe's central idea was that a dynamic force was inherent in all organisms. He concluded that this dynamic process was life itself and therefore that all living organisms changed continuously. Thus, Goethe took plant form to be a changing unit and correspondingly asked morphology to study both the form and its change (see Fig. 2). (2) Goethe (see Malsch, 1959 p. 657) took morphology as a purely synthetic discipline instead of an analytical one. In this respect he contrasted it with physiology, not as an opposite but as a complement. Both disciplines agree in requiring botanists to disregard their personal feelings and to concentrate on the 'object under observation' (Goethe, 1793). However, empirical results remain incomplete as long as they are not combined with intellectual conclusions. Thus, Goethe's thought is characterized by the holistic approach of unifying objective sense and subjective perception.

Morphologie
(Johann Wolfgang von Goethe 1807)

Ruht auf der Überzeugung, daß alles was sei sich auch andeuten und zeigen müsse. Von den ersten physischen und chemischen Elementen an, bis zur geistigen Äußerung des Menschen lassen wir diesen Grundsatz gelten.
Wir wenden uns gleich zu dem was Gestalt hat. Das Unorganische, das Vegetative, das Animale, das Menschliche deutet sich alles selbst an, es erscheint als was es ist unserm äußern unserm inneren Sinn.
Die Gestalt ist ein Bewegliches, ein Werdendes, ein Vergehendes. Gestaltenlehre ist Verwandlungslehre. Die Lehre der Metamorphose ist der Schlüssel zu allen Zeichen der Natur.

FIG. 2. Goethe's explanation of 'morphology' (Kuhn, 1987 p. 349). Note his comprehensive and holistic approach to morphology and his dynamic view of form.

*The archetypal plant ('*Urpflanze*')*

Goethe admired nature for his entire life. He was fascinated by the diversity of forms and their dynamic changes and he often expressed his deep feelings in poems and letters. But he was also irritated by this diversity which apparently contradicted his holistic view. He became seriously interested in plants and tried to understand what unity might be behind the diversity. Goethe started to observe plants in detail. During his studies on seeds and seedlings in 1775/76, the idea arose that there must be some sort of 'archetypal plant' which all living plants might refer to. Goethe (1786/87) vividly described how he found this '*Urpflanze*' or 'archetypal plant' during his 'Italian journey'. Although he had first expected it to be a real plant (17.4.1787), he suddenly recognized that it was a pure idea of a plant. Goethe was overwhelmed by his finding and in particular by the simplicity of the underlying principle 'everything is leaf' (see letter to Charlotte von Stein, June 1787).

Goethe (1790) summarized his views in his famous botanical work *Versuch die Metamorphose der Pflanzen zu erklären* (An attempt to interpret the metamorphosis of plants; translated by Arber, 1946). The simple answer to his question concerning unity and diversity was given in the conclusion that the 'leaf' was the primary plant organ that underwent successive changes ['*Alles ist Blatt und durch diese Einfachheit wird die größte Mannigfaltigkeit möglich*'; Goethe in Kuhn (1987 p. 84)]. Goethe was, in fact, the first to state clearly that cotyledons, foliage leaves and floral organs were identical in being 'leaves'.

Goethe did not use the term 'leaf' as a foliage leaf, but as an idea, which is realised by diverse manifestations (see Arber, 1946 p. 81). Consequently, he applied the term to all lateral appendages of the growing apex in a similar manner for cotyledons up to carpels and *vice versa* but he took the 'leaf' itself to be immaterial (Fig. 4).

Metamorphosis

The primary unit of the plant form including the leaf itself, the internode below and the bud in its axil is repeated and

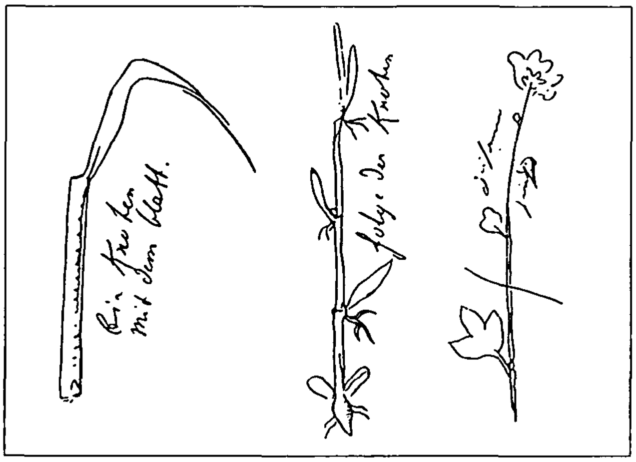

FIG. 3. Goethe's original illustration of 'the node with the leaf', the 'sequence of nodes' and the transition to flowering (from left to right) (after Schneckenburger, 1998).

continuously changed during the growth of a plant (Fig. 3). Goethe (1790) called this process of change 'metamorphosis'. He assumed that plant saps regulated the growth processes, which usually included three steps of metamorphosis: from seed to foliage; from bracts to flowers; and from carpels to fruits (Fig. 6A). The diversity of lateral appendages thus depends on metamorphosis which at all stages realises the underlying 'leaf' in a different form.

Goethe adopted the term 'metamorphosis' from ancient mythology in order to illustrate that all living forms are unstable and changeable (see Fig. 2). Only the 'type behind diversity' is fixed and permanent. Thus, in Goethe's view, metamorphosis is the process that realises diverse forms of an immaterial idea ('...*the process, by which one and the same organ presents itself to our eyes under protean forms, has been called the Metamorphosis of Plants*'; Goethe, 1790: § 4, translated by Arber, 1946 p. 91).

Goethe's use of the term metamorphosis differs from present usage which is rather restricted to the leaf sequence (Fig. 4). Nowadays, metamorphosis describes the gradual change of the foliage with age and thus might imply that carpels, for example, are taken to be modified leaves (Troll, 1937 p. 36). In Goethe's view, however, all forms are manifestations of one and the same underlying type. They merely illustrate the dynamic force of metamorphosis. Arber (1937 p. 173, 1946 p. 75) recognized this aspect of Goethe's view and preferred the term 'phyllome' to the term 'leaf' to indicate the equality in principle of all lateral appendages.

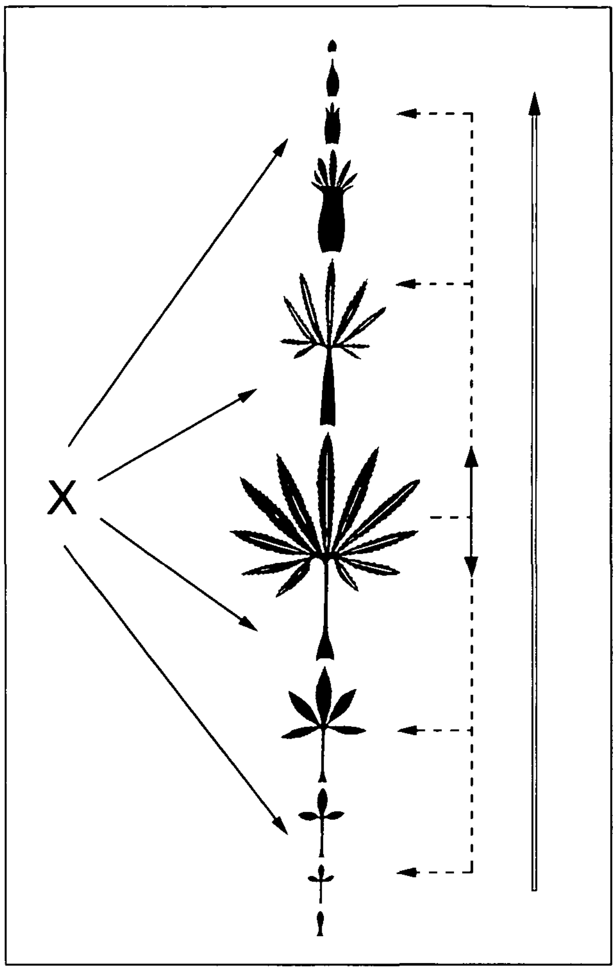

FIG. 4. Different views of leaf metamorphosis. The leaf sequence of *Helleborus foetidus* (Leistikow and Kockel, 1990) illustrates the usual application of the term 'metamorphosis' to the longitudinal and unidirectional series of leaves (double arrow). This view was shared by Zimmermann (1965). Troll (1954) referred to all leaves by the organization type (= foliage-leaf), from which they only differed in their proportions (dotted arrows). He agreed with Goethe (1790) in understanding 'metamorphosis' to be the variation of an underlying type. Goethe, however, did not derive the leaves from one another but took all to be equivalent (x). In his view, the series of leaves can be read in both directions (upwards and downwards). Arber (1950) also took all lateral appendages to be equivalent in being partial-shoots. For her, the diverse forms result from parallel development towards whole-shoot characters (solid arrows).

Goethe's metaphysical view of nature

Goethe's studies on plant morphology were embedded in his metaphysical view that nature was the 'personification of the universe' (e.g. Goethe, 1828): it is unity and ever changing diversity at the same time (Fig. 5).

Unity exists because all plant forms are manifestations of the one underlying type. This type never was and never will be realised in a single plant. It is static, immaterial and only exists as an intellectual construct. Diversity results from dynamics inherent in life. Individual plants are manifestations of the underlying type realised by means of metamorphosis, which constantly changes nature. In all cases the outer appearance of a plant depends on the stage of metamorphosis. The individual forms are real, material and can be studied empirically.

Diversity disguises the underlying unity. Thus, plant morphology must identify the 'type' behind the diversity. Comparative studies are therefore necessary to ascertain the degree of uniformity between organisms.

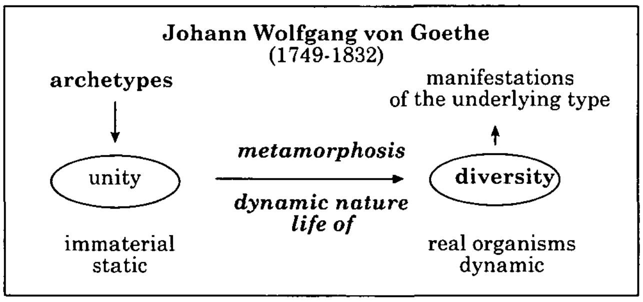

FIG. 5. Goethe's morphology is dominated by the view that immaterial archetypes exist in nature, which become realised in diverse manifestations by the process of metamorphosis. The dynamic force is life itself. Goethe's view thus includes metaphysical and dynamic aspects.

ORGANIZATION AND FORM: THE TYPOLOGICAL CONCEPT OF WILHELM TROLL

Troll's study of nature was inspired by Goethe's view of 'unity behind diversity' (Troll, 1928; Nickel, 1996). Troll's belief in a universal idea underlying nature corresponded to his profound faith in God and determined his empirical studies (Troll, 1950 p. 561). He devoted his entire life to

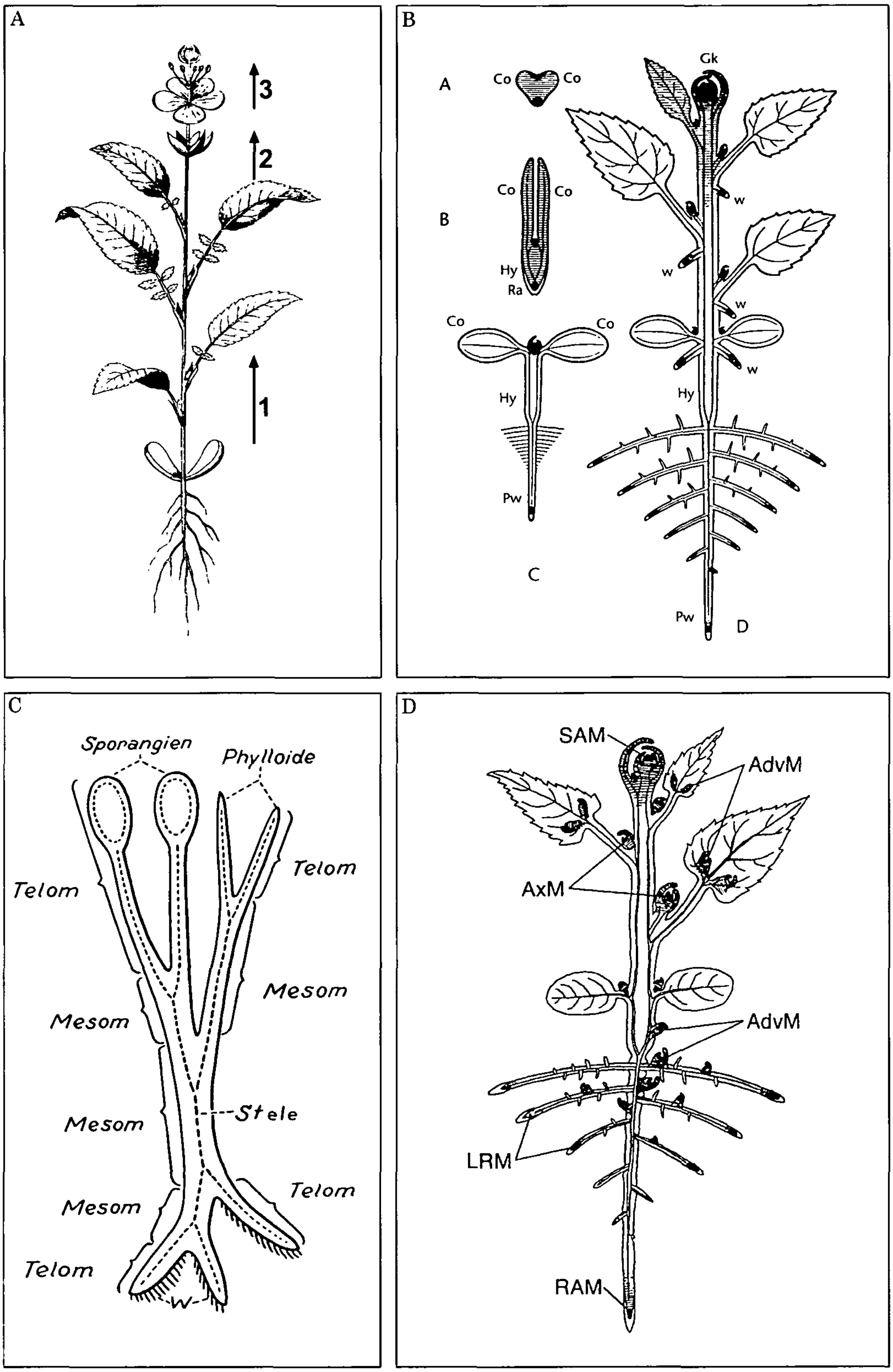

FIG. 6. Diverse reference systems used for the interpretation of the plant form. A, Annual plant illustrating Goethe's 'archetype' introduced by Schleiden (1850) (after Leistikow and Kockel, 1990; the arrows indicate the three steps of metamorphosis). B, The 'organization type' of the Angiosperm plant applied by Troll, who adopted the scheme from Sachs (1882) (Troll, 1954). C, The 'ancestral telome system' introduced by Zimmermann (only the terminal elements were called 'telomes'; the remaining ones were called 'mesomes'; Zimmermann, 1965). D, The compilation of vegetative leaf, root and shoot meristems (Kerstetter and Hake, 1997) is taken here as a tentative illustration of Arber's developmental view. AdvM, Adventitious meristem; A x M, axillary meristem; Co, cotyledon; Gk, terminal bud; tly, hypocotyl; LRM, lateral root meristem; Pw, primary root; Ra, radicle; RAM, root apical meristem; SAM, shoot apical meristem; w, stem-borne root.

comparative plant morphology and to the reduction of plant diversity to definite types.

Troll's philosophy had already matured when he published his remarkable book, *Organisation und Gestalt im Bereich der Blüte* (Floral organization and form; Troll, 1928). It deals with the analogy between flowers and inflorescences (Fig. 9) and illustrates the typological fundament of Troll's morphology.

*The organization type ('*Bauplan*')*

Flowers and inflorescences differ in their organization: the flower is usually seen as a condensed shoot bearing floral leaves, stamens and carpels whereas inflorescences are simple or compound shoot systems bearing several to many individual flowers. According to Troll, flowers and inflorescences differ in their organization ('*Bauplan*'), because they are manifestations of different organizational types (Troll, 1928 p. 25; Nickel, 1996 pp. 44–46).

Troll's 'organization type' corresponds to Goethe's idealistic archetype. It likewise represents the unity behind diversity and is recognized by positional principles (Troll, 1951 p. 376).

As regards the Angiosperms, Troll (1948 pp. 123–126; Fig. 6B) was convinced that they were composed of three basic organs ('*Grundorgane*'): roots, stems and leaves. Stems in contrast to roots are subdivided into nodes and internodes; leaves are only found at the nodes in a lateral position and lateral shoots always arise from the leaf's axil.

The leaf as one of the basic organs is characterized by the base, petiole and lamina (Fig. 7B: I). Each part may vary in its proportions, but all leaves can be compared by referring to the underlying type.

Troll (1964, 1969) was particularly interested in detecting types behind the diversity of inflorescences. He adopted the term 'synflorescence' from his academic teacher Karl von Goebel (1931 p. 2), but restricted it to those inflorescences whose lateral branches duplicate the main axis exactly. As the main axis either ends in a terminal flower (Fig. 8A: II) or in a non-flowering apex (Fig. 8A: I), only two types result: the monotelic and the polytelic synflorescence.

In the view of Troll, types are clearly distinguished from each other. For that reason transitional forms have to be forced into one of the given categories. A well-known and often discussed example is given by the phylloclade of *Ruscus* (Fig. 14D), which looks like a leaf but has the position of a lateral shoot (Arber, 1925 pp. 138–140, 1950 p. 97; Cooney-Sovetts and Sattler, 1986). Referring to the given basic organs and positional relations, Troll (1937 p. 347, 1951 p. 378) clearly identified it as a lateral shoot which only looked similar to a leaf (see Arber's diverging view below). A second example illustrating Troll's categorical view is his definition of 'pseudoterminal' flowers (Troll, 1964 p. 25). This term refers to a flower developing terminally which, for typological reasons, should be lateral. Examples are found in the monocotyledons in which terminal flowers occasionally determinate the actual indeterminate inflorescence. Troll explained this positional shift as congenital fusion which completely masks the underlying typological relations (see Arber's diverging view below).

Although Troll's typology was very successful, it remained controversial. Apart from the fundamental criticism concerning idealism (see Zimmermann's view below), the strict distinction of types has been questioned. This is particularly true for the huge diversity of inflorescences which, in many plant families, show transitions from the monotelic to the polytelic type (Fig. 8B; Weberling, 1989). Troll ignored transitional forms for many years. Only in his old age, when he had finished writing theoretical papers, is he said to have accepted transitional forms. Viewed today, it is somehow tragic that his principal field of interest (inflorescences) undermined his concept of distinct types and, to a certain extent, even his underlying philosophy.

A more modern view of Troll's 'types' is to see them as 'classes' characterized by sharp limits. Nowadays, what Troll called 'types' are seen as 'open types'. They have been compared with Gaussian curves, which do not exclude intermediate or abnormal forms (Froebe, 1971, 1986; Sattler, 1996). They are no longer considered ideas, but abstract models relating only to the real plants. This modern view of morphological types has become the most essential part of present morphological concepts (see Claßen-Bockhoff, 2001; Rutishauser and Isler, 2001) and will be discussed in a future paper.

The principle of variable proportions

Proceeding from the view that types are clearly separated units which include a variety of individual forms, Troll concluded that all structures that differ only in their proportions belong to one type. Referring to Goethe's metamorphosis, he called this rule the 'principle of variable proportions' (Troll, 1949 p. 494, 1951 p. 379).

Although Troll (1951 p. 379) included all structures differing in quantitative instead of qualitative characters into one type, he did not agree with the transformation theory introduced by d'Arcy Thompson (1917). This author started from the purely topographic view. He compared individual forms by projecting them into a Cartesian co-ordinate system and by describing them as mathematical functions. In this way he illustrated variable proportions among related species and analysed the spatial orientation of growth processes. Troll and d'Arcy Thompson agreed in comparing diverse forms within the limits of a given framework, the co-ordinate system and the type, respectively. They also agreed in arranging them in a series according to their degree of formal similarity. However, their concepts were rather different. While d'Arcy Thompson started from the analytic view and intended to measure diverse forms in a mathematically exact manner, Troll (1928 pp. 19, 25; 1937 p. 11) recognized the underlying type behind the varying forms.

In comparing individual forms, Troll predominantly took adult structures into consideration. He studied developmental stages only in order to detect characters of the adult form (Nickel, 1996 p. 47). Furthermore, he interpreted the individual forms by deriving them from the underlying type. For instance, he concluded that the growth form of cacti (Fig. 7A) could be derived from the Angiosperm type by reduction of foliage and transformation of the shoot into a water reservoir. Similarly, phyllodial

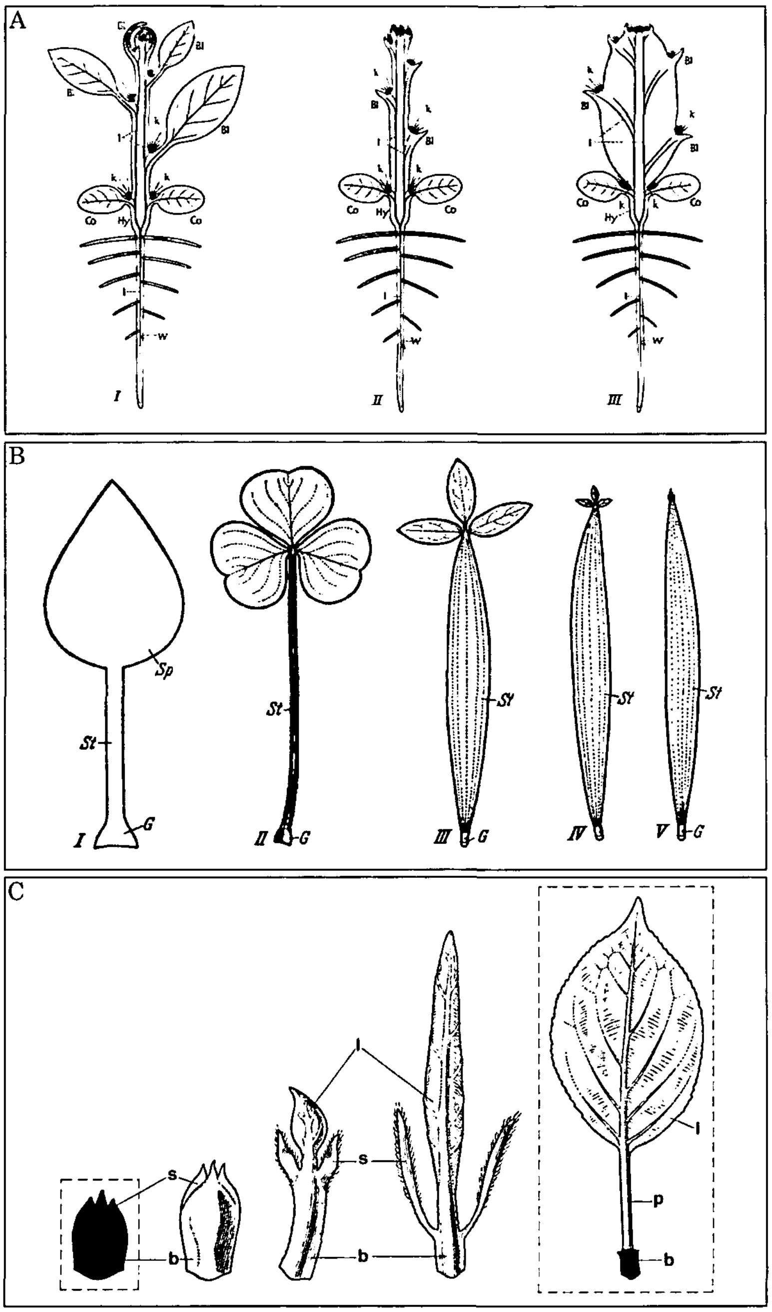

FIG. 7. Illustration of Troll's morphology using selected examples. A, The derivation of the cactoid growth form from the organization type of the Angiosperm plants (Nickel, 1996). B, The organization type of the foliage (I) and the illustration of the 'principle of variable proportions' by the leaves of *Oxalis acetosella* (II) and *O. bupleurifolia* (III-V) (Nickel, 1996). C, Detail of the leaf sequence of *Malus baccata* showing the bud scale (left), foliage-leaf (right) and transitional forms. According to Troll, the whole bud scale is homologous with the leaf base only (black), while Arber argues that the bud scale is equivalent to the whole foliage leaf (dotted frames) (after Troll, 1954). b, Base leaf; Bl, leaf; Co, cotyledon; G, leaf base; tly, hypocotyl; k, bud; l, vascular bundle (in A), lamina (in C); p, petiole; s, stipule; Sp, lamina; St, petiole; w, root .

leaves (Fig. 7B) have an enlarged petiole and a reduced lamina, while bud scales (Fig. 7C) have promoted the leaf base at the expense of the remaining leaf parts. Troll's static view of adult forms suggests that the scale leaf is homologous to the leaf-base of a fully developed foliage leaf. However, Arber (1950 p. 86) rejected this artificial procedure. She argued, as we do today, from the ontogenetic point of view, that a whole leaf could never be equated with an individual component of another leaf (Fig. 7C).

Homology and analogy

Referring to the example of flowers and inflorescences it is clear that forms belonging to the same type might be diverse while forms belonging to different types might be similar.

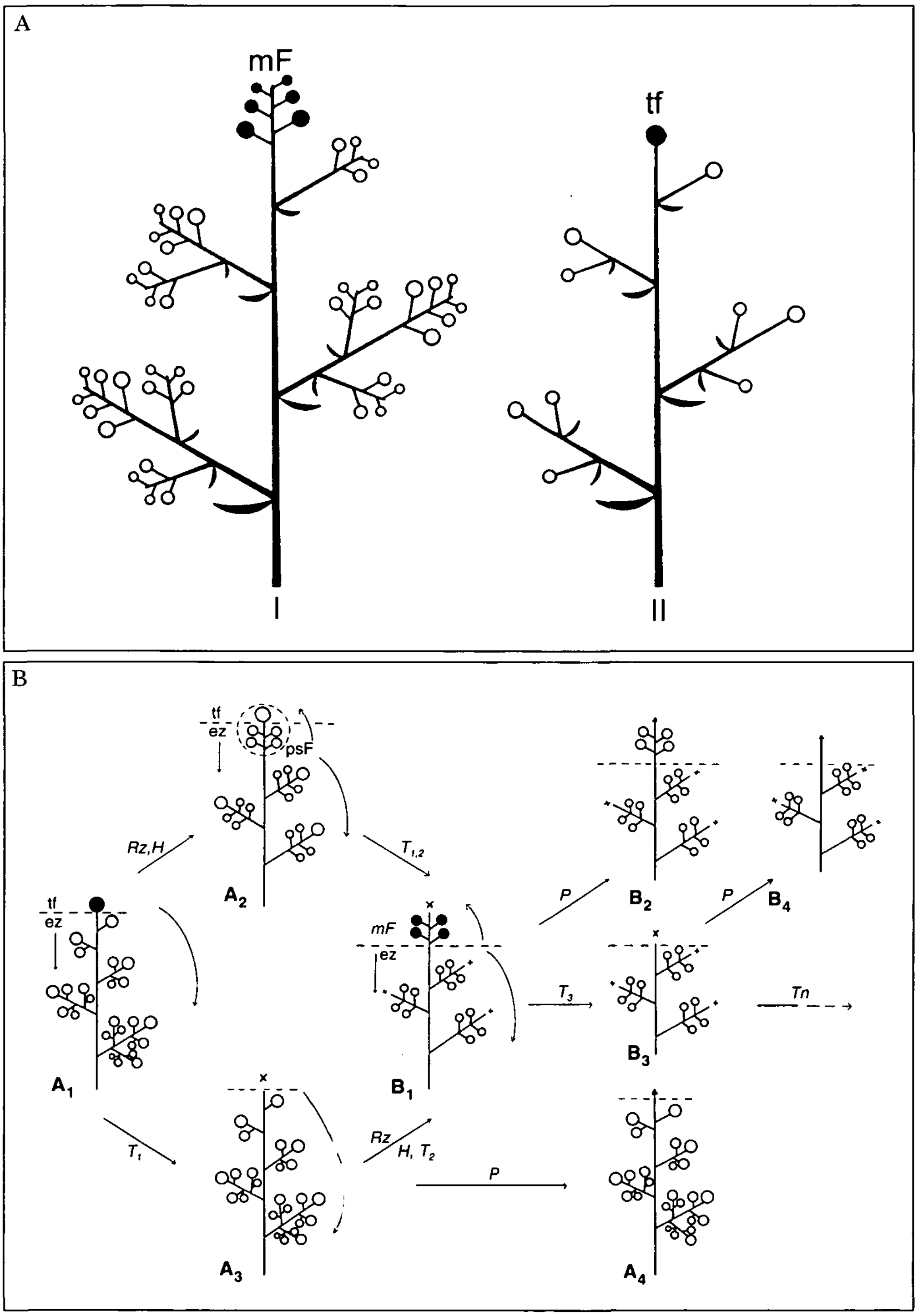

FIG. 8. Determinant and open types in inflorescence morphology. A, The two basic, originally sharply limited, types of polytelic (left) and monotelic (right) synflorescence (Troll, 1964). mF, Main florescence; tf, terminal flower. B, Schematic representation of the processes transforming monotelic synflorescences (A_1) into polytelic ones (B_1, B_3), with several transitional (A_2, A_3) and proliferating (A_4, B_2, B_4) forms (Claßen-Bockhoff, 2000). The main processes are homogenization (*H*), racemization (*Rz*), truncation (*T*), and proliferation (*P*). These processes show that the apparently limited types do in fact have intermediates between them. ez, Enrichment zone; psF, pseudo-florescence.

Troll referred to the terms 'homology' and 'analogy' to distinguish between 'identity in type' and 'similarity in outer appearance'.

The term 'homology' originates from pre-Darwinian times. Owen (1848) was the first to define homology clearly, as identity in structure. He strictly distinguished it from identity in function ('analogy'). Identical structures were originally recognized by their relative position within the organism, i.e. by purely morphological means. Since Darwin (1859), however, the terms homology and analogy

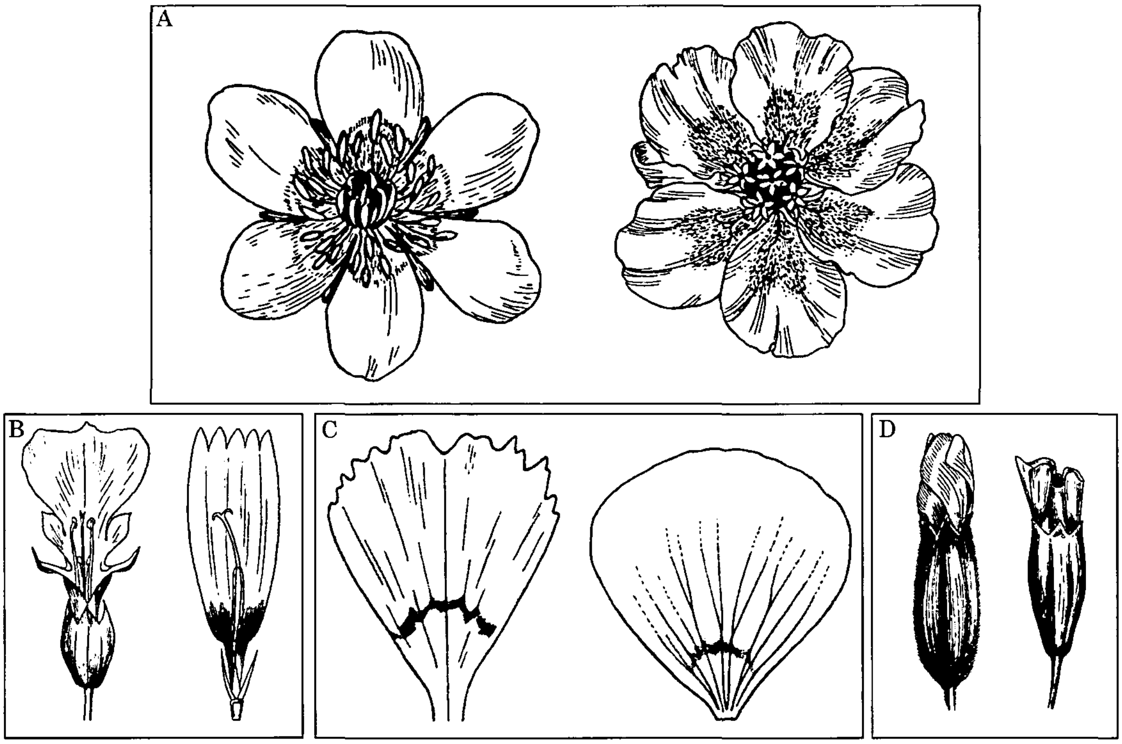

FIG. 9. Analogous similarity illustrating the 'Form type' *sensu* Troll. A, Flower of *Ranunuclus* (left) and the flower-like inflorescence of *Tagetes* (right) (Remane, 1956). B, Flower of *Teucrium scordium* (left) and the ray floret of *Catananche caerulea*. C, Petal of *Dianthus seguierii* (left) and the 'pseudopetal' (ray floret) of *Helianthemum chamaecistus* (right). D, Floral bud of *Melandrium rubrum* (left) and the prefloral capitulum of *Tagetes signata* (right) (B–D: Troll, 1928).

have been applied to phylogenetic and ecological aspects. Homologous structures in the phylogenetic sense originate from a common ancestral stock while analogous structures are similar because they are equally adapted to functional constraints (see Zimmermann's similar view below).

In view of the influence of ontogenetic and phylogenetic processes on form, Remane (1956 pp. 28–93) clearly illustrated that the criterion of 'identity in position' was no longer sufficient to detect homologies (in the phylogenetic sense). He added the 'criterion of specific quality' and the 'criterion of transitional forms' referring to unusual characters and developmental pathways, respectively.

However, Troll (1925 p. 557, 1950 p. 43) referred to the pre-Darwinian pure morphological meaning of the term homology and took identity in position to be the most important criterion. The individual manifestations of one type may show unequal growth of their parts but they always agree in having identical positions within the whole. They are thus morphologically identical and homologous. As organization is often masked by the design of the adult plants, homology has to be detected by comparative studies.

*The Form type('*Gestalt*')*

Analogous forms differ in organization but agree in their outer appearance (Fig. 9). Troll called the outer appearance '*Gestalt*', which is here translated as 'Form' (the capital letter indicating its specific meaning). In fact, Form is not merely the outer appearance; it is a philosophical concept.

According to his synthetic view, Troll (1928 p. 89) took Form to be a given entity, which for fundamental reasons is beyond any analysis. This means that a Form cannot be divided into parts without losing its identity. In the terminology of Arber (see below) it is a 'whole' and not only the additive result of parts. As morphology deals with Form, it is not an analytical discipline, and for that reason it differs fundamentally from physiology (Troll, 1925 pp. 559, 562). According to Troll, a synthesis between causal-analytical disciplines and typological morphology was impossible, and thus biology is a non-uniform science.

Although Troll was clearly influenced by Goethe, he differs from Goethe in this rigorous point of view. He also dissociated himself from his academic teacher Karl von Goebel (1898 p. 2) who took morphology to be only one of numerous views of biology. Goebel (1898 p. III) even expanded the meaning of morphology to unite it with the arising experimental disciplines. He included developmental and functional aspects and changed its name to 'organography' (Goebel, 1928 p. 1), thereby emphasizing that morphology was part of modern biology. Troll however could not accept this view, and resumed the tradition of idealistic morphology. Thus, he and his followers isolated German morphology for a long time.

According to Troll (1928), many examples of analogous similarity e.g. flowers and inflorescences, and marsupials and mammals, clearly illustrate that Form is independent of the underlying organization type. Troll (1928 pp. 89–93) supposed that an immanent 'urge to Form' ('*Gestaltungstrieb*') existed in nature, which found its expression in realising only a limited number of given Forms.

Troll (1928) found his view supported by his comparative studies on flowers and flower-like inflorescences (Fig. 9A). Unfortunately, he called the latter pseudanthia, although this term had already been used in another context (see Claßen-Bockhoff, 1991). He detected resemblance in minute details e.g. in similar shapes and colours of petals and ray florets (Fig. 9B–E). He concluded that structures were much more similar than necessary for an adaptation to pollinators and that, therefore, Form was likewise independent of functional constraints (Troll, 1928 pp. VII, 89).

Phylogeny and the 'gradation of types'

Typology, in Troll's view, is more a philosophy than a procedure. This is clearly documented in his discussion of typology, biosystematics and phylogeny (Troll, 1951). The task of systematics is to provide a system offering both a general view of the diversity of organisms and an image of their natural relationships. Referring to the morphological systems of his time which group organisms according to their similarity in organization, Troll (1951 p. 387) equated 'natural relationship' (*natürliche Verwandtschaft*) with 'identity in type' (*Übereinstimmung im Typus*). This conclusion followed naturally from his idealistic point of view, for Troll not only took the types to be strictly separated units, he also found them arranged in an hierarchical system. Leaflets are part of the lamina, leaves are part of the seed plant, and flowers are parts of an inflorescence. He, thus, generalized that the entire living world was manifested in a 'gradation of types' reflecting the natural order (Troll, 1951 p. 385). The corresponding hierarchy of systematic categories supported his view: differences in systematic categories correspond to differences in underlying types. Troll rejected the idea that systematic categories are the result of common descent, because his types are invariable constants. To him, only the unity in types could only be interpreted as the fundamental order in nature.

In contrast to systematics, phylogeny deals with the process of common descent. Although Troll (1951 p. 387) accepted the importance of evolutionary thinking, he argued that phylogenetic systems were impossible because processes and changes cannot be classified. Instead, morphological studies are always necessary to reconstruct phylogenies. Troll concluded that the natural order was only detectable by typology, and that phylogeny only provided systematics with the genealogical lines. In contrast to his contemporaries, Troll did not accept form-continua contradicting his type concept. Instead he argued that distinct changes must have happened in the course of evolution to produce discrete and discontinuous types (Nickel, 1996 p. 57).

Troll demanded that each natural classification should be based on types, not on single and arbitrary characters. He thus took typology to be the predominant and fundamental procedure of systematics (Troll, 1937 p. 48). It is clear that Troll's idealistic view, and particularly his view of individual forms having derived from given types instead of common ancestors, provoked heated disputes (see below).

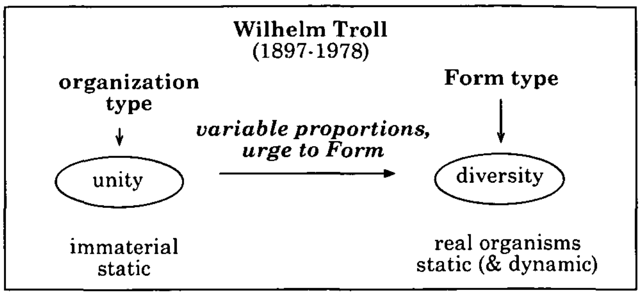

FIG. 10. Troll started from two given type categories: the organization and the Form type. The organization type is manifested in many real forms, which differ only in their proportions. The diversity of forms is limited by the Form type, and is realised by the 'urge to Form'. Troll's morphology is characterized by metaphysical, static and limited types. His idealistic view of typology should not be confused with the present procedure of typology, which corresponds to the generally accepted scientific procedure of abstraction.

Troll's typological view of nature

Troll's morphology reflects Goethe's dualistic view of a universal reference system ('organization type') and its many manifestations ('Form', *Gestalt*) (Fig. 10). However, it lacked Goethe's dynamics, as Troll did not focus on the process of change ('metamorphosis') but on the actual realization of a definite Form. His view was based on two static type categories: organization, which is a metaphysical idea, and Form, which is the perceivable form of an organism.

Unity in organization (homology) refers to given types which are detectable by comparative studies. The representatives of a type may be diverse in their outer appearance, but they always agree in the relative positions of their parts. Diversity results from both the principle of variable proportions (within one type) and the existence of different types. Because of the 'urge to Form', representatives of different types may look similar (analogy).

Today, Troll is one of the most controversial botanists in Germany. He is honoured by his followers and insulted by his opponents. At first, he was extremely successful. He made careful studies of many plants, documented their formal characters in clear diagrams and introduced reference systems for all parts of the plant (Troll, 1937, 1939, 1943). He provided the first general view on the diversity of plant form, and influenced German morphology for decades. At least 16 of his disciples have held a professorship in Germany and have passed on his typological concept. Later, typology lost its idealistic spirit (Froebe, 1971, 1986; Weberling, 1981 p. 313). It was reduced to a scientific procedure for abstracting general rules from the individual. From this point of view, typology is a necessary method for the study of plant form. Combined with drawing schemes (side-view, ground-view), it provides a general view of the diversity of plant form, and by no means contradicts phylogenetic thinking. Finally, Troll's idealistic spirit became so outdated, and even counterproductive, that in the age of increasing phylogenetic-thinking heated conflicts with his contemporaries became inevitable. These conflicts were promoted by Troll's rigid and uncompromising attitude, as well as by the separation of morphology from biology, by his demand for the predominance of typology, and particularly by the mixture of empirical findings and subjective ideas found in his work.

TELOMES AND ELEMENTARY PROCESSES: THE PHYLOGENETIC APPROACH OF WALTER ZIMMERMANN

Walter Zimmermann differed from Troll in several fundamental aspects. First, he turned against idealism, recommending a strict distinction between object and subject (Zimmermann, 1937 pp. 6–7). Second, he was a post-Darwinian phylogenist and tried to reconstruct the phylogeny of plants according to evolutionary theory. Thus, he was not looking for the 'archetypal' plant but for the 'ancestral' plant.

Objects and subjects

In response to the idealistic spirit pervading German science in his time (see above), Zimmermann (1937) clearly demanded an objective procedure for all aspects of scientific research. He did not refuse philosophy, and even confessed that research might always be partly subjective, but for practical reasons he tried to separate object and subject as far as possible (Zimmermann, 1930 p. VI).

Zimmermann (1937 p. 11) explained his view by making the distinction between natural regularities (*'Gesetzmäßigkeiten der Natur'*) and natural laws (*'Naturgesetze'*). While the first are observable and measurable, the latter are intellectual abstractions and, thus, non-existent in nature. Nevertheless, as far as natural laws only included relations that occurred in nature, Zimmermann accepted them as helpful generalizations and as a necessary part of the scientific procedure to gain knowledge.

According to Zimmermann (1937 pp. 31–39), abstract terms are absolutely necessary for communication, but may imply antithesis. He mentioned, for example, 'life and death', 'the whole and the parts', 'body and mind', which, in his opinion, do not exist as antitheses in nature but rather pervade and imply each other (see Arber's similar view below). They only appear as antitheses because practical issues have been mixed up with terms. Guided by the example 'the whole is more than its parts', Zimmermann explained his view. As the whole and the parts are not objects, but are actually terms, the question should instead be: 'Can we recognize different characters by looking at the whole and its parts, respectively?' Zimmermann (1931 p. 965) easily answered this question because cells, for example, contain different biological information to the entire organism. Referring to the question posed at the beginning of this paper, 'What is a plant form?', Zimmermann would likewise have modified it to: 'What can we learn about the characters of a plant form?'. The different formulation of the question clearly illustrates the different views on plant form held by Zimmermann and by Troll and Arber, respectively (see Fig. 1). Zimmermann (1937 pp. 7–8) gave preference to the rationalistic analysis

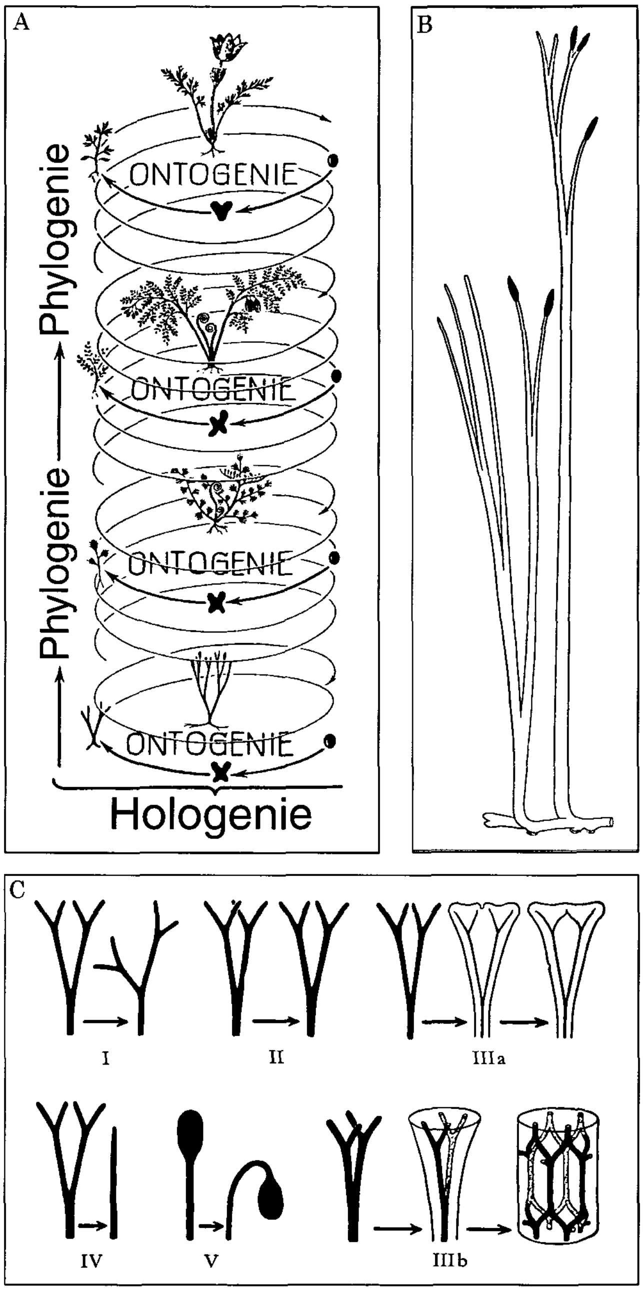

FIG. 11. Basic aspects of Zimmermann's phylogenetic view. A, The 'hologenetic spiral' illustrating the close relationship between phylogeny and ontogeny. B, Reconstruction of *Rhynia major* from the Devonian, which Zimmermann assumed to be the ancestral vascular plant. C, The five elementary processes causing character transformation in the course of evolution of vascular plants: I, overtopping; II, planation; III, fusion in both leaf (a) and stem (b) phylogeny; IV, reduction; V, incurvation (after Zimmermann, 1965).

as the only procedure, which achieves results depending only on the characteristics of the object under observation. Of course, it is necessary to pose adequate questions and hypotheses. This is particularly necessary for biology, which mediates between the inorganic world and the human subject. In this respect, biology is of central

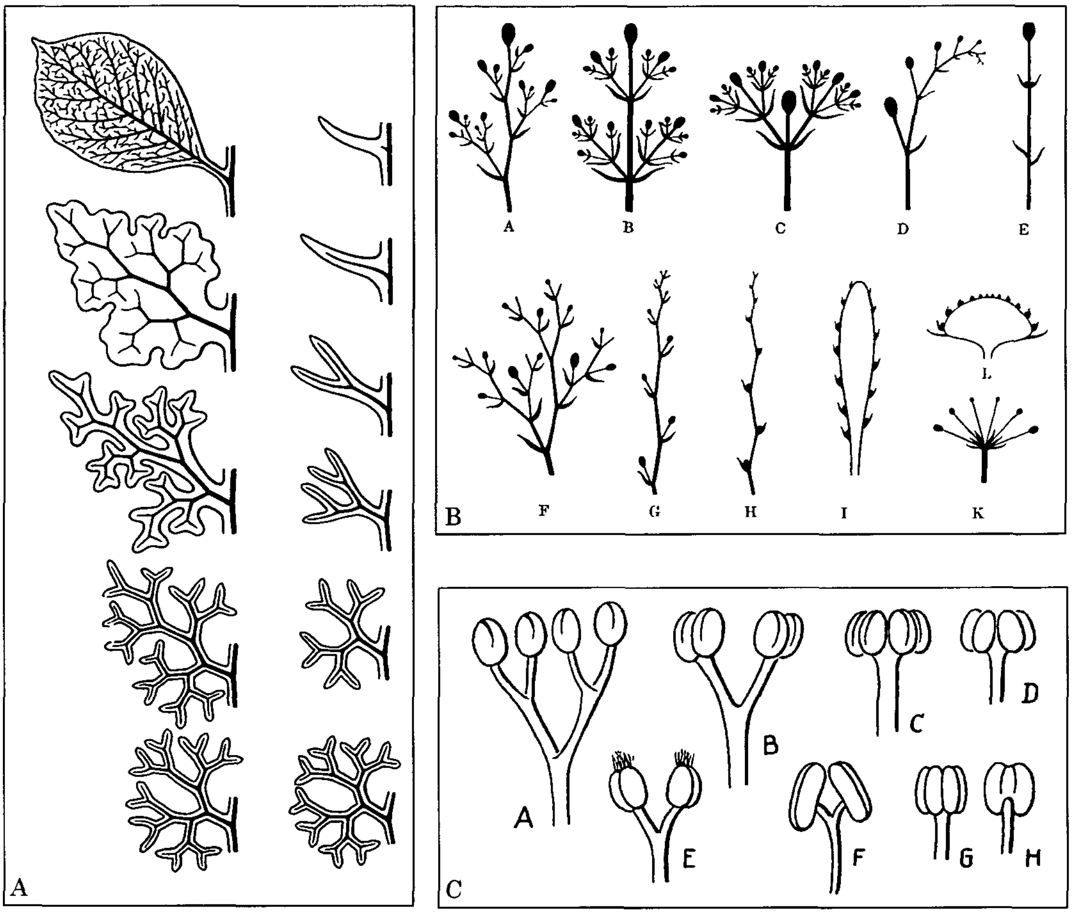

FIG. 12. The telome theory applied to the phylogeny of leaves (A), inflorescences (B) and stamens (C). A, Reconstruction of the leaf phylogeny in *Magnolia* (left) and in conifers (right) showing the assumed ancestral form (at the bottom), its recent form (top) and between them transitional forms caused by overtopping, planation, fusion and reduction. B, The diversity of inflorescences as the result of character transformation in the course of phylogeny: starting from the cymose panicle (A), assumed to be the basic form, all the remaining cymose (B–E) and racemose inflorescences (F–L) are derived by changes in internode length, overtopping, reduction and flowering sequence. C, Hypothetical evolution of Angiosperm stamens (D–H) from ancestral forms (A–C), which still illustrate their origin in a telome system (after Zimmermann, 1965).

importance because it provides a comprehensive view of the world (Zimmermann, 1937 pp. 3–4, 40–42). However, such a view is only possible if all biological disciplines, including morphology, are based on the same adequate procedures.

Morphology and phylogeny

Zimmermann's (1930 p. V) main interest was the change in plant form over the course of evolution. As phylogeny is based on morphology, Zimmermann also dealt with the history and significance of morphological studies. From his point of view, morphology was a very important discipline in pre-Darwinian times, but then lost its importance and is presently nothing but a resource for phylogenetical research.

Zimmermann (1930 pp. 7–12) summarized three historical stages in the science of morphology: a descriptive, an idealistic and an analytical stage. While idealistic morphology results in a subjective interpretation of empirical data, analytical morphology strictly distinguishes between the object under observation and the investigator (see above). Analytical morphology does not look for ideal types, but analyses plant forms by searching for form-building factors and ancestral forms. As every change in plant form is caused by physiological processes, morphology includes developmental physiology and is even related to genetic studies (Zimmermann, 1931 p. 976). Thus, modern morphology has changed from an irrational to an empirical-rationalistic discipline.

Starting from the undisputed view that the present diversity of plant form evolved, it is the task of phylogeny to identify ancestral forms and to reconstruct genealogies (Zimmermann, 1935 p. 98). It is also important to remember that evolution is a process closely combining ontogeny and phylogeny. Zimmermann (1935 p. 117, 1965 p. 31) explained his view by means of the 'hologenetic spiral' illustrating that each phylogenetic change is based on at least one ontogenetic change (Fig. 11A). Mutations modify determining factors relating to special characters, which then appear in the offspring in a changed form (Zimmermann, 1931 pp. 982–983). Such 'character transformations' represent the fundamental phylogenetic process. They have to be clearly distinguished from taxon phylogeny, which results from the knowledge of character transformations (Zimmermann, 1931 p. 967). The final aim of phylogeny is to present a taxon tree including all species and all steps of character transformation (Zimmermann, 1931 p. 982).

The telome theory

Zimmermann's principal work, *Die Phylogenie der Pflanzen* (The phylogeny of plants) was published in 1930. It includes both an introduction to the so-called 'telome theory' and the broad application of this theory to fossil and recent plants.

Starting from *Rhynia*-like fossils (Fig. 11B), Zimmermann introduced the supposed ancestral vascular plant, which was composed of only one element, the telome (Fig. 6C). In his view, telomes had a radial symmetry and the capacity for branching dichotomously. Adult organisms were three-dimensional telome systems bearing equivalent sterile telomes (phylloids) and fertile ones (sporangia). Zimmermann (1965 pp. 1–7) supposed that the present plant organs (shoots, leaves and roots) had evolved from telomes in the course of evolution. Thus, the term telome, which turns against the 'angiosperm-centred' view, is predominantly applicable to fossil plants (Zimmermann, 1965 p. 29).

Referring to De Candolle, Hofmeister, Potonié and others, Zimmermann (1965 pp. 8–25) listed six elementary processes which underly phylogenetic changes (Fig. 11C): overtopping (unilateral dominance), planation, fusion in both leaf and stem phylogeny (congenital switch of relative tissue positions), reduction, and incurvation (dorsiventrality). The sixth process is represented by longitudinal polarity, which is not however restricted to vascular plants (Zimmermann, 1965 p. 76).

The telome theory is a phylogenetic theory that illustrates the change of characters from a supposed ancestral form to modern forms (Zimmermann, 1965 p. 30). Since the present diversity is well known and the direction of the evolutionary process is clearly given by time, the main task is to find and to fix the ancestral form.

As regards vascular plants, Zimmermann (1930) introduced the telome system as the ancestral form and the elementary processes as changing elements. He applied his theory to an immense number of fossil and recent plants, and to all vegetative and reproductive plant structures (Fig. 12A and C). However, more recent paleobotanical discoveries and morphological concepts have restricted the validity of the telome theory (Stebbins, 1974 p. 144; Hagemann, 1976; Leistikow, 1990; Gifford and Foster, 1996 pp. 31–33).

Dealing with inflorescences, Zimmermann (1935) could not refer to fossils and thus had to infer the ancestral form indirectly from generally known facts. He demanded that the ancestral form must have been primitive in all characters and found the cymose panicle to agree best with this postulate. All other inflorescences might be derived from this form by the following elementary processes: inhibition of internode elongation; numerical reduction of lateral shoots and flowers; reduction of leaves; overtopping; differentiation; and changed flowering sequence (Fig. 12B). However, as ancestral inflorescences are still not known today, Zimmermann's concept remains hypothetical. It agrees with Troll's typology in referring recent forms to one reference, the assumed ancestral form and the type, respectively, and in naming the varying processes and proportion. However, it differs fundamentally in its intention to reconstruct phylogenetic character transformations instead of typological i.e. positional relations.

Character transformation

The present paper deals with morphological concepts. For this reason Zimmermann's important contributions to phylogenetic systematics are not reviewed here; they have been reviewed recently by Donoghue and Kadereit (1992) who clearly illustrated that many aspects of Hennig's phylogenetic systematics were based on Zimmermann's work. Instead, I focus here on those aspects of character transformation which affect morphological concepts.

According to Zimmermann (1965 p. 49), the elementary processes vary independently of each other, and appear in all possible combinations. Thus, diversity is caused by mutations, which change the phenotypic appearance. Though the elementary processes may be reversible in individual cases, there is a general tendency in the phylogeny of vascular plants to increase the differentiation of the plant body, the ability to settle in diverse niches and the amount of useful qualities (Zimmermann, 1930 p. 374, 1965 p. 56). In accordance with the theory of adaptation these general tendencies are caused by selection (Zimmermann, 1930 pp. 400, 421; see Arber's view of 'parallelism' below).

As mutations influence the complete ontogeny, it is not adequate to compare adult structures only. Furthermore, as the elementary processes vary independently and change only individual characters in the course of ontogeny, diversity occurs between closely related taxa and similarity between unrelated ones. Zimmermann (1965 p. 28) pointed out that the same character state might be both primitive and derived in different species and that the appearance of primitive character states must not be correlated with the primitive or derived state of the entire species. Hereby he described the phenomenon of mosaic evolution which was popularized as 'heterobathmy' by Takhtajan (1959).

Characters dating back to a common ancestral form are called homologous (Zimmermann, 1931 pp. 944, 989) whereas parallel and convergent structures are of polyphyletic origin (Zimmermann, 1930 p. 379). In contrast to the original meaning of homology (see above), the term in its phylogenetic sense relates not only to positional identities but also refers to processes and qualities. In fact, Albert *et al.* (1998) recently distinguished 'historical', 'process' and 'positional' homology.

As regards homologies, Zimmermann (1931 p. 993) highlighted the necessity of clearly fixing the ancestral form. The question of whether a tendril, for example, is homologous to a leaf or to a shoot can only be answered reasonably by referring to a plant whose organs have already differentiated. Otherwise, referring to the telome system, all structures would be homologous.

The recognition of polyphyletic character transformations also depends on the reference system. For example, the cactoid growth form illustrates convergent evolution because the common ancestor of the taxa concerned was not succulent (Zimmermann, 1930 p. 379). Only by referring to this ancestral form is it possible to infer that the similar growth form has evolved independently several times.

The necessity of grouping and the different meanings of 'type'

In view of the immense diversity of individuals, the fundamental task of biology is to group organisms, their parts and their life processes. Preconditions for that purpose are clear definitions and exact studies. Zimmermann (1931 pp. 961–963) rejected the mistaken belief that a form continuum should not be classified. Instead he argued that it would be better to exclude rare intermediate forms than to renounce sharp limits. In preferring grouping at the expense of natural continua he agreed with Troll and differed from Arber (see below).

Zimmermann (1931 pp. 942–950) distinguished three methods of grouping: artificial, idealistic and phylogenetic. The former relates to a special purpose and groups, for example, all assimilating structures. Thus, groupings consist of analogous forms. This method does not refer to phylogeny, but to some other criterion. The resulting groups are practical instead of natural.

The second way of grouping corresponds to the procedure of idealistic morphology. The types are based on metaphysical thinking and are principally unacceptable for modern botanists (see above).

The phylogenetic way is based on genealogy. It refers only to the objects and their natural relations and, thus, in Zimmermann's view it is the only relevant method for biology.

Zimmermann strictly distinguished types found by intuition from rational types corresponding to real objects. As regards both artificial and phylogenetic grouping, Zimmermann applied the term 'type' to both the type specimen of a plant collection and the supposed ancestral plant. Zimmermann did not reject typology as a procedure, but rejected the use of arbitrary types instead of practical ones. However, as we see it today, the above-mentioned practical types are no less arbitrary than the morphological ones. When we remove Troll's types from the context of his idealism, they prove to be practical types that refer to positional relationships and analogous similarities. They do not refer to an individual plant, but are abstract models of the objects concerned. Zimmermann himself accepted such abstract models in reconstructing phylogenies.

With regards to the different ways of grouping, Zimmermann (1931 pp. 970–975) held the opinion that they complemented rather than excluded each other. Particularly in those cases in which phylogenetic knowledge is lacking, he accepted artificial and idealistic groups as preliminary views. Although Zimmermann emphasized that in view of evolution the phylogenetic way was the only acceptable one, he mentioned the ingenious inspirations of Goethe and Hofmeister that were idealistic at first but were then proven correct by phylogenetic studies.

Rationalism vs. *idealism*

According to Zimmermann (1931 p. 972), phylogeny and morphology struggle for the same domain. That is, they both identify and compare characters. In doing this, they use different reference systems. Zimmermann only accepted the phylogenetic view and urged morphologists to stop asking questions that had already been answered phylogenetically. However, he did not take into consideration the fact that morphologists did not intend to reconstruct phylogeny but wanted to compare plant structures for a practical purpose.

Zimmermann consequently rejected both Troll's attempt to apply characters to immaterial types and 'intuition' as a relevant method. As regards intuition, Zimmermann (1931 pp. 952–956) distinguished between idealism and reconstruction. While idealistic morphologists refer to arbitrary types, phylogenists have to reconstruct genealogical lines. In so doing they are faced with the problem that phylogenetic lines are not directly observable and that only isolated data are available. Phylogenetic conclusions are inevitably abstract combinations (Zimmermann, 1931 p. 983); however, they refer to facts and therefore should not be confused with intuitive conceptions. Zimmermann's argumentation again opposed idealism, and not the typological procedure.

According to Zimmermann (1931 p. 950, 1937 p. 25), each grouping that ignores genealogical lines must be artificial. Having only the reconstruction of phylogeny in mind, Zimmermann was of course right. But with regard to the numerous aspects of plant form, including functional and developmental constraints, non-phylogenetic approaches may elucidate other characters of life. The best examples are recent studies dealing with epigenetic regulation and phenotypic diversity (see Schlichting and Pigliucci, 1998).

Zimmermann's phylogenetic view of nature

To understand the present diversity of plant forms, Zimmermann started from the evolutionary history of plants (Fig. 13). He was convinced that all vascular plants had evolved from a *Rhynia*-like ancestral plant. The original structural element, the telome, was transformed into the present plant organs over the course of evolution.

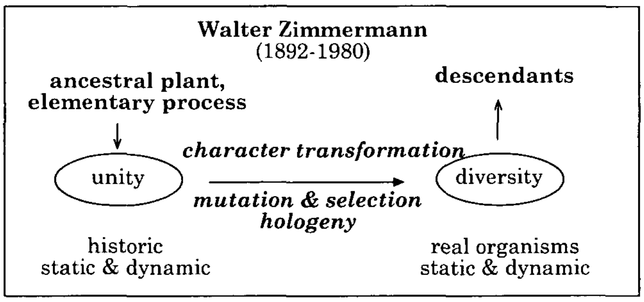

FIG. 13. Zimmermann started from the strictly phylogenetic view. The present diversity of vascular plants has evolved over time. The starting point was an ancestral plant, which became differentiated in the course of evolution by the processes of mutation and selection. Zimmermann focused on the change of forms, and declared himself against ideal types, but for practical reasons he accepted logical types and groupings.

While mutations by chance vary the genotype and modify ontogenetic processes, selection controls the resulting characters and turns the original form continuum into a discontinuous pattern.

Unity in organization results from common descent. There are only a few elementary processes underlying mutations. Homologous characters originate from a common ancestral structure, and are identifiable only by phylogenetic studies. The evolutionary processes of mutation and selection cause diversity. Depending on the living conditions, however, characters of different lines may look similar: they have then evolved convergently and in parallel.

Although Zimmermann always argued against idealism he was not completely free of it. His view of biology as the connecting agent of object and subject, his dream of a universal phylogenetic tree, the corresponding comprehensiveness of the telome theory, and the presentation of an abstract type (telome system) instead of the sought-for ancestral plant, illustrate that his views fell somewhere between idealism and rationalism (Zimmermann, 1935 p. 96, 1965 p. 209). Perhaps this is the reason why he got down to fundamental theoretical questions. He endeavoured to take idealistic elements out of morphology and phylogeny and to join these fields to modern biological disciplines.

PARTIAL-SHOOTS AND PARALLELISM: THE DYNAMIC CONCEPTS OF AGNES ARBER

In contrast to Troll and Zimmermann, Arber did not proceed from given types and phylogenetic constraints. Instead she aspired to independence, both in her way of life and in her mind (Arber, 1950; Hauke, 1996). She lived modestly and worked predominantly at home, raising her daughter alone after the early death of her husband. In 1950 she published her outstanding book, *The natural philosophy of plant form*, in which she discussed various aspects of plant form and morphology. Highly generalized, the two most important aspects of her view are that morphology has to be dynamic, and that all antitheses merge into a synthesis. In explaining and illustrating her views she gave detailed summaries of the diversity of morphological thought from Aristotle and Theophrastus to Albertus Magnus, Cesalpino, Jung, Malpighi, Grew, Goethe, De Candolle and her contemporaries Zimmermann and Troll. Thus, Arber's morphology is without doubt based on a broad historical-philosophical foundation.

Morphology as a partial-view

Like Troll, Arber (1946) was influenced by Goethe and was interested in his work throughout her life. She accepted his type concept, understanding it, as we do today, as a purely logical concept (1950 pp. 63–67). In her view, the type represents a fixed centre to which all structural variations might be applied. It has a timeless quality and must not be confused with a real ancestral plant. Likewise, morphological series are not temporal but logical constructs with no validity in time.

Arber preferred Goethe's dynamic view of an ever-changing nature to his type concept. Her view of morphology, therefore, clearly differed from that of Troll. Arber (1950) agreed with Troll in distinguishing the 'one' from the 'manifold' that is the 'unity of organization' and the 'diversity of individual forms', but she refused to accept either his idealistic view or his type concept.

Arber's understanding of morphology was based on biology as the comprehensive science of life (1950 p. 1). Among numerous different aspects of the living world, plant morphology deals with the specific aspect of plant form. According to Arber (1950 p. 3), the form itself can only be understood in relation to its function, as each action of a plant is reflected in either growth or discarding parts, both of which affect the outer appearance. Arber (1950 p. 4) concluded that '*morphology should comprehend and fuse both static and dynamic elements*'.

As regards morphology as a biological discipline, Arber clearly agreed with Zimmermann and differed from Troll. Arber (1950 p. 1) not only included morphology in biology but also pointed to the imperative necessity of combining all 'partial' views to the 'whole'. She did not accept antitheses such as 'form and function', 'typology and genealogy', 'morphology and physiology', but stated that: '*Each way of contemplating the plant—provided that it is a genuine and logical attempt to interpret well-attested facts—may have something of its own to offer, and what we need is a synthetic standpoint, combining the advantages of methods of analysis, which are usually treated as antagonistic*' (Arber, 1950 p. 71).

Static and dynamic aspects of the plant form

In the view of Arber (1950 p. 3), form in its wider connotation includes static and dynamic elements which are both aspects of the same unity. The static aspect is represented by the form in its narrower sense; for example, the outer appearance of a leaf. This leaf also represents a specific developmental stage within the plant's life cycle and thus is a process. In contrast to Troll, who only focused on the static aspects of morphology, Arber had a wider view. She followed Goethe and viewed life as a process. As forms are continuously changing units she tried to understand them from the dynamic point of view.

Arber (1950 pp. 7–71) accepted 'leaves', 'roots' and 'stems', but she refused to accept them as given types or basic organs. In her view, the organization types are neither real nor ideal, but purely intellectual constructs (Arber, 1950 p. 207). As logical principles they have their validity and are particularly helpful in describing structural variations and the idiosyncratic characters of leaves, stems and roots (Arber, 1950 p. 71), but they do not contribute to the fundamental interpretation of the plant body. Consequently, Arber (1950 p. 70) did not start from basic organs but from the dynamic character of plant life itself, i.e. from open growth and repetitive branching. Realising that each bud produced a new shoot which repeated the character of its parent shoot, Arber (1950 p. 71) concluded that the embryonic shoot with its apical and lateral meristems was the primary pattern of the above-ground plant body (Fig. 6D). All leaves, lateral shoots, stem-borne roots and hairs can be derived from it.

Compared to Troll and Zimmermann, Arber based her morphology on the dynamic aspect of plant form instead of the static one. She did this because she was interested in the developmental processes of plant growth. In contrast to Troll and Zimmermann, who used types for morphological and phylogenetic groupings, Arber minimized the use of typology. She never presented diagrams and schemes, which would have contradicted her dynamic view, but only illustrated individual plants and cross-sections. However, as scientific research is impossible without generalizations, Arber could not do without at least one type, the shoot, to which she referred all plant structures and developmental stages.

The partial-shoot theory

Unlimited growth of the apical meristem results in continuous production of fresh lateral meristems from which further growth may start. Lateral meristems firstly produce leaves then produce lateral shoots in a second step.

As regards the identity of leaves, Arber (1950 p. 74) referred to historical interpretations, particularly to Casimir de Candolle's (1868) interpretation of a leaf as an apically and adaxially inhibited branch. She introduced her 'partial-shoot-theory of the leaf' (Arber, 1950 pp. §VI–VIII) and compared her view with Zimmermann's telome theory which also postulated, though in a phylogenetic sense, that individual organs evolved from little differentiated ancestral forms.

According to Arber, shoots and leaves are not distinct units, but the leaf itself is a partial-shoot. This partial-shoot lacks radial symmetry because of its lateral origin and also lacks unlimited growth based on a premature cessation of the apical meristem (Arber, 1950 pp. 89, 124). However, the leaf-like shoot is nevertheless able to continue to grow by displacing the meristematic activity to basal and lateral parts. It resembles a shoot in: (1) giving rise to stipules and pinnae from lateral meristems; (2) showing radial symmetry in case of unifacial leaves; (3) including radial elements like the petiole, the midrib, and the rachis (Arber, 1950 p. 80); (4) presenting venation patterns similar to branching patterns (Fig. 14B); and (5) producing offspring (*Kalanchoe daigremontiana*), thus, leaves are partial-shoots whose whole-shoot characters are not fully expressed.

Arber not only took simple leaves to be partial-shoots, but also took compound leaves to be clusters of united partial-shoots. Each pinna and pinnula corresponds to a partial shoot (Fig. 14E). The close connection of different shoot-generations within the compound leaf is combined with a lack of their independent growth and a decrease in their meristematic activity, which finally ceases growth.

While the leaf has limited growth and a bifacial symmetry, the lateral shoot is radial and is able to continue growth like the primary shoot. Arber (1950 pp. 125–127) tried to explain this apparent contradiction by applying the partial-shoot theory to the axilliary bud. Fully realising the tentative character of her theory, she argued that the axilliary bud was a direct outcome of the leaf, that it was equivalent to two basal and dorsiventral leaf lobes which secondarily achieved radiality by union. The leaf, which is a partial-shoot, would thus achieve whole-shoothood in its offspring.

Repetitive branching and the 'urge towards whole-shoot characters'

According to Arber (1950 pp. 76, 134, 141), each element of the plant is a shoot or a partial-shoot: a leaf is a partial-shoot that shows reduced growth capacity; a root is a partial-shoot that lacks the capacity for producing sporogeneous tissue; and even trichomes are partial-shoots with shoot characters being more or less reduced. Thus, the plant is interpreted as a repetitively branched system that is alternately composed of 'leaves' and 'shoots', each being a shoot in different degrees of wholeness.

Referring to Spinoza, Arber took 'self-maintenance' to be the gist of life. It is expressed in both repetitive branching, which is self-continuance in time, and an 'urge towards whole-shoot characters', which is the realisation of inherent potentialities (Arber, 1950 pp. 77–79). According to Arber (1950 pp. 136, 176), the originally radial symmetry of sessile plants is only fully realised in the embryonic shoot. The independent growth of all lateral shoots is restricted by their relative position within the whole, their spatial density during ontogeny, and their union in a compound cluster. Partial-shoots can only compensate for their incompleteness by urging towards whole-shoot characters.

The urge towards whole-shoot characters is expressed, for example, by competition among different shoot generations. In general, the primary shoot dominates the lateral shoots, but there are many examples illustrating the contrary. According to Arber (1950 p. 94), the urge towards whole-shoot characters is evident in sympodial branching with its extreme in *Tilia* where the growth of lateral shoots elongates the stem (Fig. 14B). The urge to whole-shoot characters can also be seen in *Lathyrus aphaca* (Fig. 14C), which has assimilating stipules and rachis-tendrils, and in reproductive structures such as heart-shaped petals or paired pollen-sacs in which lateral parts dominate the inhibited apex.

The dominance of the lateral shoots over the parent shoot can also be found anatomically. In indeterminate inflorescences the uppermost flowers occasionally replace the apex and may then be supplied with vascular bundles like a terminal flower. The phylloclade of *Ruscus* (Fig. 14D) is an even more extreme example. According to Arber, it is a shoot-prophyll-complex in which the prophyll dominates its parent shoot. This is the reason why the adult structure appears leaf-like.

These examples illustrate how differently Arber and Troll interpreted the same structures. Troll always started from the relative position, while Arber focused on the dynamics of change. She wanted to understand the developmental processes behind different adult structures. In opening the door to genetics to elucidate the underlying mechanism, Arber (1925 p. 231) was ahead of her time (see Rutishauser, 2001).

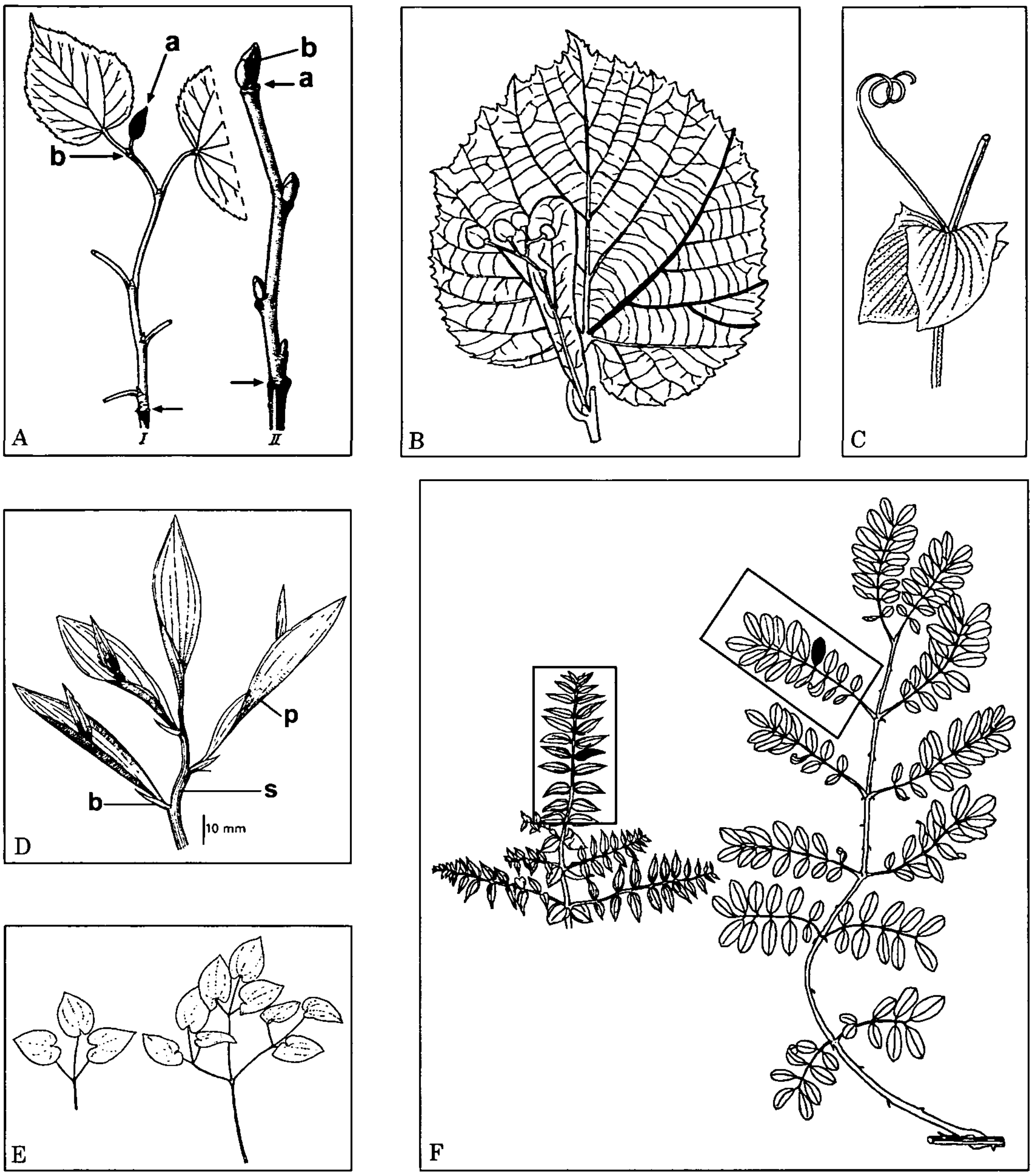

FIG. 14. Illustrations referring to Agnes Arber's *Natural philosophy of plant form*: A, *Tilia cordata*, shoot in spring (left) and in autumn (right) illustrating the dominance of the uppermost lateral bud (b) over the parent shoot (a). Arrows indicate scars of the preceding year's shoot. B, Foliage leaf of *Tilia tomentosa* (from below) showing the shoot-like branching pattern of the lateral veins (black). C, Foliage leaf of *Lathyrus aphaca*: the large assimilating stipules dominate the rachis-tendril. D, The phyllodes (p) of *Ruscus hypoglossum* are interpreted as leaf-like shoots by Troll and as prophyll-shoot complexes by Arber. b, Bract; s, stem. E, Compound leaves of *Epimedium* (garden hybrid) illustrating Arber's view of parallel-in-identity: each pinnula and pinna, respectively, is identical to a partial-shoot, whereas the whole leaf is identical to a cluster of several united generations of partial-shoots. The whole leaf in its simple form (left), has a parallel structure to an individual pinna of the more complex form (right). F, Similarity between the shoot system of *Coriaria myrtifolia* (left) and the compound leaf of *Caesalpinia japonica* (right) illustrating 'parallelism in configuration': the whole leaf (black) in *Coriaria* corresponds to one pinnula of *Caesalpinia* (black), the whole short shoot to one pinna (frame) and the whole shoot system to the whole compound leaf. (A: after Troll, 1954; B, E, F: after Arber, 1950; C: Sitte, 1998; D: Bell, 1991).

'Identity-in-parallel' and the universal process of 'parallelism'

Proceeding from the whole-shoot as the primary pattern of all plant structures and developmental processes, diversity is caused, according to Arber, by differential growth based on relative position as well as on developmental stage and inherent directiveness (Arber, 1950 pp. 167, 177, 208). Shoots, branching systems, inflorescences, leaves, compound leaves, floral leaves, and hairs are all identical in being whole or partial-shoots with different degrees of shoot characters (Fig. 14E). Arber (1950 pp. 76, 86) thus rejected the existence of 'organization types' and 'basic organs', and instead took the plant structures as specific developmental stages of the plant.

Arber (1950 p. 142) found compound and simple leaves, lobes and hairs to be 'identical-in-parallel'. '*To the compound leaf, the leaflet stands in the relation of* part *to* whole, *but it is also the* equivalent *of the compound leaf* as a whole, *though in another generation*' (Arber 1950 p. 142). The compound leaf merely differs from the simple one in being composed of several united generations of partial-shoots. Thus, the diverse appearance results from quantitative rather than from qualitative differences in development.

As Arber accepted the term 'leaf' only as a descriptive term, but interpreted all leaves as developmental stages, she avoided the use of the terms 'organization', 'homology' and 'analogy'. Instead she applied her view of 'parallelism' to them. According to Arber (1950 p. 159), parallelism is the universal process of change inherent in nature (Fig. 15). It is expressed in both repetition and change. Repetition in time corresponds to repetitive branching (rhythm) and repetition in space refers to symmetry (Arber, 1950 p. 176). Both change continuously in the process of ageing, and result in the present diversity of parallel identities.

Arber interpreted the diversity of 'leaves' as the result of 'parallelism in organization', thereby indicating that the form of equivalent partial-shoots (leaves) was modified in the course of repetitive growth (or 'metamorphosis'; see Fig. 4).

Repetitive growth may also result in similarity, for example between leaflets and leaves (Fig. 14E), shoot systems and compound leaves (Fig. 14F), and flowers and inflorescences (Fig. 9A). Arber applied the concept of 'identity-in-parallel' to these forms, interpreting them as being the result of 'parallelism in configuration'.

Arber (1950 pp. 159–161) discussed Troll's concept of 'organization' and 'Form' in detail. Although she did not accept the type concept, she emphasized that it was necessary to focus on the relation between organization and Form because analogous similarities were real. Furthermore, she argued that the type concept offered a way of realising the potentialities, which were implicit in the types. She did not, however, mention the usefulness of types in order to group diversity, possibly because this was not her

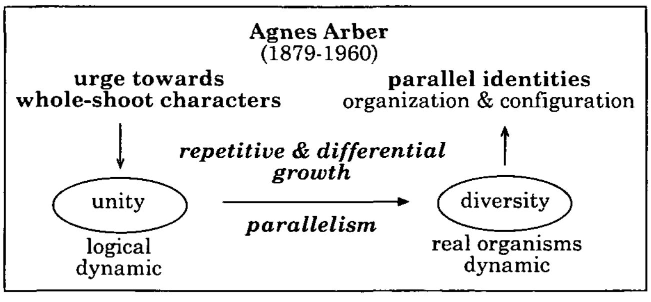

FIG. 15. Arber's view is characterized by processes: starting from the embryonic shoot the plant repetitively produces shoot generations, urging towards whole-shoot characters. Diversity is caused by differential growth. Pointing to the many examples of identity-in-parallel, Arber held the opinion that 'parallelism' is the universal dynamic principle underlying both phylogeny and ontogeny.

main interest. Arber (1950 p. 161) found that the synthesis of the apparent antitheses 'unity of type' and 'multiplicity of individual forms' was the process of 'parallel becoming'. She substituted the dynamic terms 'identity-in-parallel', 'parallelism in organization' and 'parallelism in configuration' for the static terms 'organization' and 'Form', 'homology' and 'analogy', and thus related Troll's terminology to her dynamic view (see Arber, 1954*a*).

Morphology and phylogeny

As regards phylogeny, Arber (1950 p. 64) expressed her deep scepticism about the methods applied. In view of a possible net-like interconnection of plant groups, she called into question whether the phylogenetic 'tree' might be the adequate image of evolution. Besides, she doubted whether the many examples of parallel evolution really were the result of mutation and selection (Arber, 1925 pp. 223–235). In her view, the universal tendency to parallel progression has been largely unnoticed in favour of Darwin's view of evolution.

Overall, Arber (1937 pp. 173–175, 1950 pp. 65–69) took the genealogical approach of phylogeny to be highly speculative and gave preference to the logical view of plant morphology. In her view, morphology and phylogeny not only differ from each other in using different reference systems, but particularly in the fact that genealogical series have a direction given by time whereas morphological series are purely logical ones (Arber, 1937 pp. 173–175). In this respect she again cited Goethe's view: '*But when we use this term* [leaf], *it must be with the reservation that we accustom ourselves to relate the phenomena to one another* in both directions. *For we can just as well say that a stamen is a contracted petal, as we can say of a petal that it is a stamen in a state of expansion*' (Goethe, 1790 § 120, translated by Arber, 1946). She pointed out that the concept of parallelism returned to Goethe's view, and demanded that we read morphological series in both directions.

Although morphology and phylogeny are different, they complement each other. According to Arber's holistic view, antitheses do not exist but always merge into a synthesis (Arber, 1950 p. 71). Morphological and analytical thought are partial-views of the 'whole' which is the totality of life. Likewise, empiricism and theory are inseparable elements for everyone seeking the truth. According to Arber's *Natural philosophy of plant form*, it is the aim of biology to unite subject and object, as well as science and philosophy, to a universal view of life (Arber, 1950 p. 208).

Arber's universal view of nature

According to Arber, plant forms are structures and processes at the same time. According to Zimmermann's telome theory, plants have become diverse in the course of evolution and presently appear as organisms with differentiated 'roots', 'stems' and 'leaves'. However, in Arber's view, these basic organs do not actually exist, but are only intellectual constructs. As logical types they are helpful to describe and detect the inherent potentialities of the plants, but do not explain the dynamics of form change (Fig. 15).

Starting from the open growth of plants and their repetitive branching, Arber concluded that the meristematic shoot was the principal pattern for all plant structures. Unity in organization results from shared whole-shoot characters. Diversity, on the other hand, results from repetitive and differential growth. Specific positional and growth conditions restrict the general 'urge towards whole-shoot characters' to different degrees, and thus result in diverse forms. Therefore, similar structures may also appear. They share either the same degree of partial-shoothood (parallelism in organization), or similar growth conditions (parallelism in configuration) but they are always caused by the dynamic force of parallelism.

Special attention has to be paid to Arber's concept of 'identity-in-parallel' and her view of 'the part and the whole' (see Kirchoff, 2001). According to Arber (1950 p. 158), the 'whole', for example a compound leaf, is not only composed of 'parts' in an additive manner, but each 'part' itself is a minute representation or 'microcosm' of the 'whole'. Arber (1954*b*, 1957) extended her view to the universe and, aged over 70 years, summarized her metaphysical philosophy of life. From electrons and atoms to biomes and the biosphere, all levels of the biological world are characterized by the relativity of being a part and a whole at the same time. Correspondingly, many 'partial' views are necessary to approach to the 'whole'. All partial views are equal and complementary to each other and all antitheses are neutralized by merging into a synthesis.

Arber shared the metaphysical spirit with Troll from whom she differed with regard to the type concept and the basic intention not to group forms but to understand their change. She shared the dynamic view with Zimmermann who, however, tried to reconstruct phylogenies in the sense of Darwin's theory of evolution. Arber focused on the developmental processes causing diversity and listed relative position, density in space and fusion as being among the fundamental processes of differential growth. Her independent thought has stimulated many morphologists and developmental genetists (see other papers in this issue), who have started to identify the underlying mechanisms—just as Arber suggested they do 50 years ago.

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