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THE SCIENCE OF PLANT MORPHOLOGY: DEFINITION, HISTORY, AND ROLE IN MODERN BIOLOGY[1]

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As a scientific discipline, plant morphology is 211 yr old, originated by Goethe in 1790. It is a discipline that has largely been Germanic in practice. Because it took its origins from the study of the natural history of plants and the United States is principally an engineering society, the discipline of plant morphology in its pure form has never been widely practiced in this country. What has been labeled ''plant morphology'' in the United States has served largely as a handmaiden for systematics, using morphological characteristics to carve up diversity into its systematic subunits. Because the heart of plant morphology as a science is a focus on the convergences rather than the homologies in a phylogenetic sense, the German tradition of plant morphology is a unifying science that focuses on fundamental themes that transcend systematic boundaries. This paper traces the history of the science of plant morphology through the lineage of its principal practitioners: Goethe, Hofmeister, von Goebel, and Troll. It also evaluates the principles of plant morphology by applying them to the phyletically diverse Pteridophytes, showing that contemporary members of that group exhibit levels of shoot organization comparable to that of seed plants and discusses the implications of these findings.

Key words: Goethe; Hofmeister; megaphyll; microphyll; plant morphology; primary thickening growth; Pteridophytes; systematics; Troll; von Goebel.

Although the Pelton Award is made for meritorious work in the field of experimental morphology of plants, I consider the latter as a particular approach within the broader and older discipline of plant morphology. In recent times there has been no clear statement of what the science of plant morphology is and how such emphases relate to the science as a whole. It is not clear to many practitioners that plant morphology itself represents a valid scientific discipline. Due to historical declines in the interest and teaching of plant morphology, it has come to be viewed largely as a provider of characters for systematic circumscription, hence virtually synonymous with plant systematics. Given that contemporary systematics has put a greater emphasis on molecular rather than morphological data, the time seems ripe to reevalute plant morphology and what its role can and should be in modern plant biology.

In this article I attempt to clarify the concept of plant morphology as a discipline, review its historical heritage, and discuss how it relates to and differs from systematics. I show that plant morphology is a scientific discipline with its own principles, from which predictions can be made about the unknown. I illustrate some of these general principles and their application by evaluating them in a phyletically heterogeneous plant group, the pteridophytes, which previously had been interpreted largely by models from fossil rather than contemporary plants.

THE SCIENCE OF PLANT MORPHOLOGY

The principal reasons the science of plant morphology is virtually unknown and did not make an impact in the Anglo-American regions of the world are mainly cultural and historical. Plant morphology is largely a German science that never was prominent in the United States. The German tradition of plant morphology took its origins from the study of the natural history of plants. Because the United States is principally an engineering society, concerned more with the tools of science than with its theory, philosophy, and history, we have never had a comparable natural history tradition. Because it required the use of a particular tool (microscopy), plant anatomy, which focuses on the cell and tissue levels of organization, received greater emphasis and scientific credibility in this country than did plant morphology. This difference in emphasis is reflected especially in the difference in conception of what has been called ''plant morphology'' in the United States compared to this concept in Germany. Following the tradition established by Coulter and Chamberlain of the University of Chicago (Coulter and Chamberlain, 1901), plant morphology in the United States was defined as the study of the anatomical and cytological features of the life histories of plants expressed in a taxonomic framework. Hence, the emphasis was on the microscopic details of vascular plant reproduction and systematic relationships with the focus of the German tradition relegated to brief accounts of the plant's habit.

In the context of our country's emphasis on tools and techniques rather than philosophy, this microscopical/life-history conception of plant morphology doubtless was seen as being more rigorous than the seemingly less precise study of form relationships based on external morphology, i.e., the German tradition. A series of influential textbooks exemplifying and promoting this Anglo-American conception of plant morphology developed through the years, including the most recent editions of Bold, Alexopoulos, and Delevoryas (1987); Gifford and Foster (1989); and Scagel et al. (1984). These works not only reinforced this life-history emphasis in research and ped-

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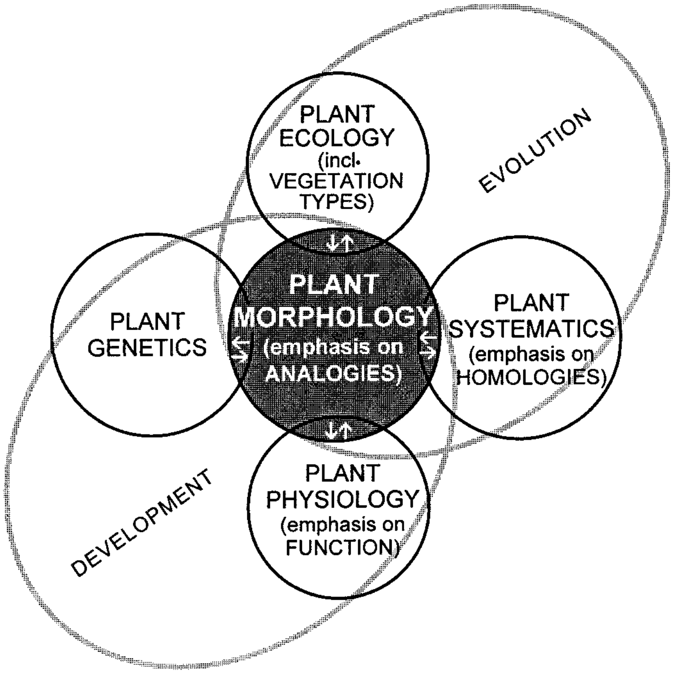

Fig. 1. Diagram of the relationship of plant morphology (shaded circle) to plant systematics, ecology, genetics and plant physiology (open circles). The larger synthetic fields of development and evolution are circumscribed by the fainter ovals. Arrows indicate the mutual influences between fields.

Figure Abbreviations: AB, axillary bud or branch; Co, cotyledon; CZ, cryptophilic zone; DLB, decurrent leaf base; E, soil boundary; Hy, hypocotyl; In, internode; L, lamina; La, labium; Li, ligule; LB, leaf base; LL, lower leaf zone; N, node; P_1–P_4, sequence of leaf primordia in the bud proceeding from the youngest to the oldest; Pet, petiole; PR, primary root; PS, primary shoot; PZ, photophilic zone; RB, renewal bud; RC, root cap; S, stipule; Sp, sporangium; SR, shoot-borne root; TB, terminal bud; UL, upper leaf zone.

agogy of vascular plants, but also resulted in a similar emphasis in the study of the bryophytes (Schofield, 1985), algae (Bold and Wynne, 1985), and fungi (Moore-Landecker, 1990).

In contrast to this American conception of plant morphology, the German tradition can be characterized as the science of form relationships with the emphasis on the term relationships expressed at the whole plant and organ levels of organization. The contrast of plant morphology with systematics is illustrated in Fig. 1, where the field of plant morphology is illustrated as a central sphere that overlaps tangentially with systematics but is not equivalent to it. The arrows between the two fields indicate the mutual exchange of information and influence that occurs between them, as with the other disciplines shown. Despite this overlap, however, plant morphology and systematics are two different disciplines with different centers of gravity. In systematics, the emphasis is on the homologies in a phylogenetic sense, whereas in morphology, the emphasis is on the analogies or convergences in a phylogenetic sense. The principles of morphology transcend the systematic boundaries. Thus the two disciplines operate in opposite directions. Systematics uses morphological characteristics to carve diversity into its taxonomic subunits, whereas plant morphology uses diversity to deduce fundamental themes regardless of the systematic affinities. Hence, from first principles, systematics can be characterized as a dividing discipline, whereas plant morphology is a unifying discipline.

Systematics is not the only discipline that plant morphology serves. Figure 1 shows three other fundamental fields (plant ecology, genetics, and physiology), and dual arrows also indicate the mutual influences between these areas. Given that the origins of plant morphology are traceable to the interest in plant natural history, it would be expected that it would have a connection with ecology and related vegetation analysis. In fact, historically, the great plant morphologists were also the great plant geographers and ecologists (e.g., Schimper, Kerner, Warming, Troll, Meusel, and Rauh). Similarly, plant morphology has had significant historical connections with plant physiology. The inseparable relationship between form and function has meant that, like ecologists, many plant morphologists of the past were also the noted plant physiologists (e.g., Hofmeister, von Goebel, Sachs, Troll). While it is obvious that plant morphology would contrib-

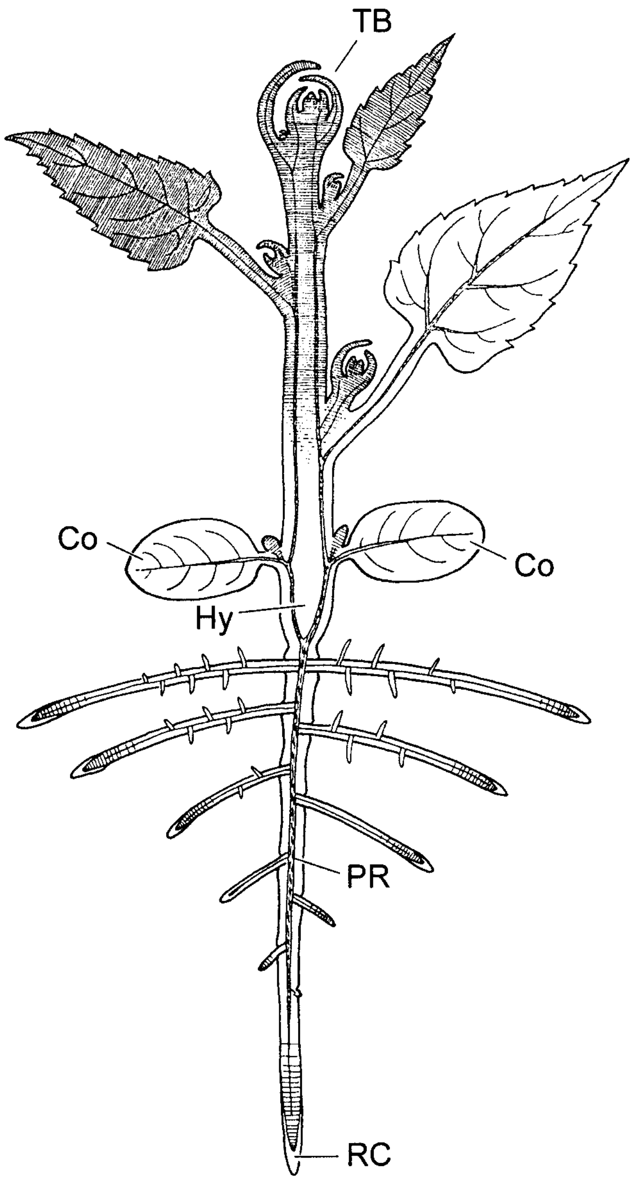

Fig. 2. Idealized median longisection through the body of a dicotyledonous flowering plant, illustrating the relationship between the distal shoot system and proximal root system. Shaded areas represent regions undergoing growth with the greatest density of shading indicating regions of most intense meristematic activity. (Reproduced with permission from Troll, 1937–1943.)

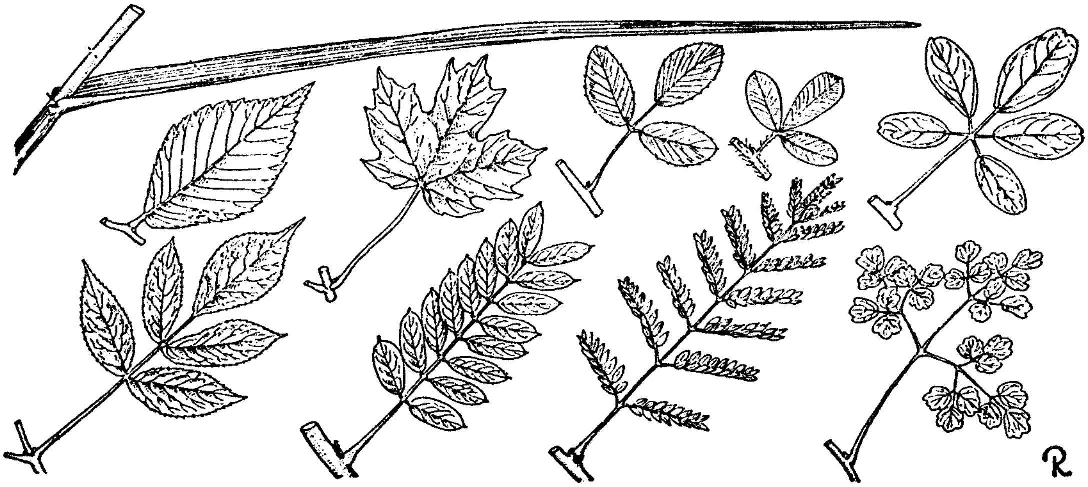

Fig. 3. Leaf parts and types, found particularly in angiosperms. (Reproduced from Lawrence, 1955.)

ute to plant genetics in the characterization of the phenotype, workers in molecular genetics increasingly have been concerned with the causal aspects of plant morphogenesis. Today, in fact, most investigators work at the interfaces between plant morphology and these other disciplines. This is a result of the shifting fashions of science, not an indication that there are no more unresolved problems in plant morphology.

Not only can plant morphology be delimited horizontally from other biological disciplines but it also can be vertically delimited from other levels of biological organization. The discipline of plant morphology encompasses the whole plant down to the organ level of organization (Fig. 2). While it occasionally uses the anatomical level of organization as morphological markers, it can only legitimately do so with histological characteristics that are correlated developmentally with morphogenesis or form generation. It has been demonstrated that the plant's morphology is an emergent property relative to its anatomy; i.e., the two levels of organization can be relatively independent and the anatomical level does not determine the morphological level (Kaplan and Hagemann, 1991;

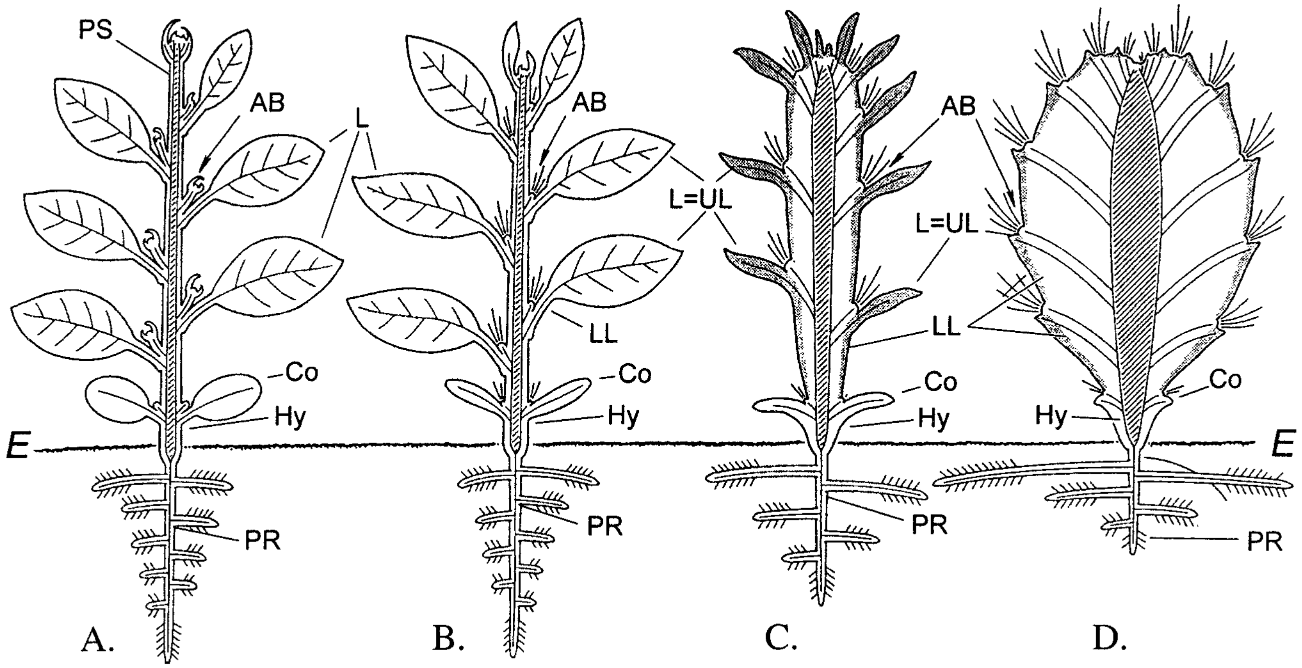

Fig. 4. Spectrum of morphology between conventional herbaceous dicotyledon (A) and a barrel cactus-type (D) illustrated as idealized median longisections of their plant bodies. (A) An herbaceous dicotyledon, showing typical, fully developed foliage leaves, each subtending an axillary bud. (B) A *Pereskia*-type "leafy cactus," showing large laminate leaves subtending axillary short shoots (areoles) that bear spine leaves, which are diagnostic for family Cactaceae. (C) *Cylindropuntia*-type cactus, exhibiting leaves with reduced, cylindrical blades that subtend each of the axillary, spine-bearing areoles. The shoot axis also exhibits marked primary thickening in the cortex region associated with enlargement of decurrent leaf bases (cushions or podaria). (D) *Ferocactus,* a barrel-type cactus, showing marked primary thickening in its cortex and corresponding reduction of the upper leaf zone (lamina-petiole homologue) into an inconspicuous projection and elaboration of the leaf base as a prominent projection. (Reproduced with permission from Rauh, 1979.)

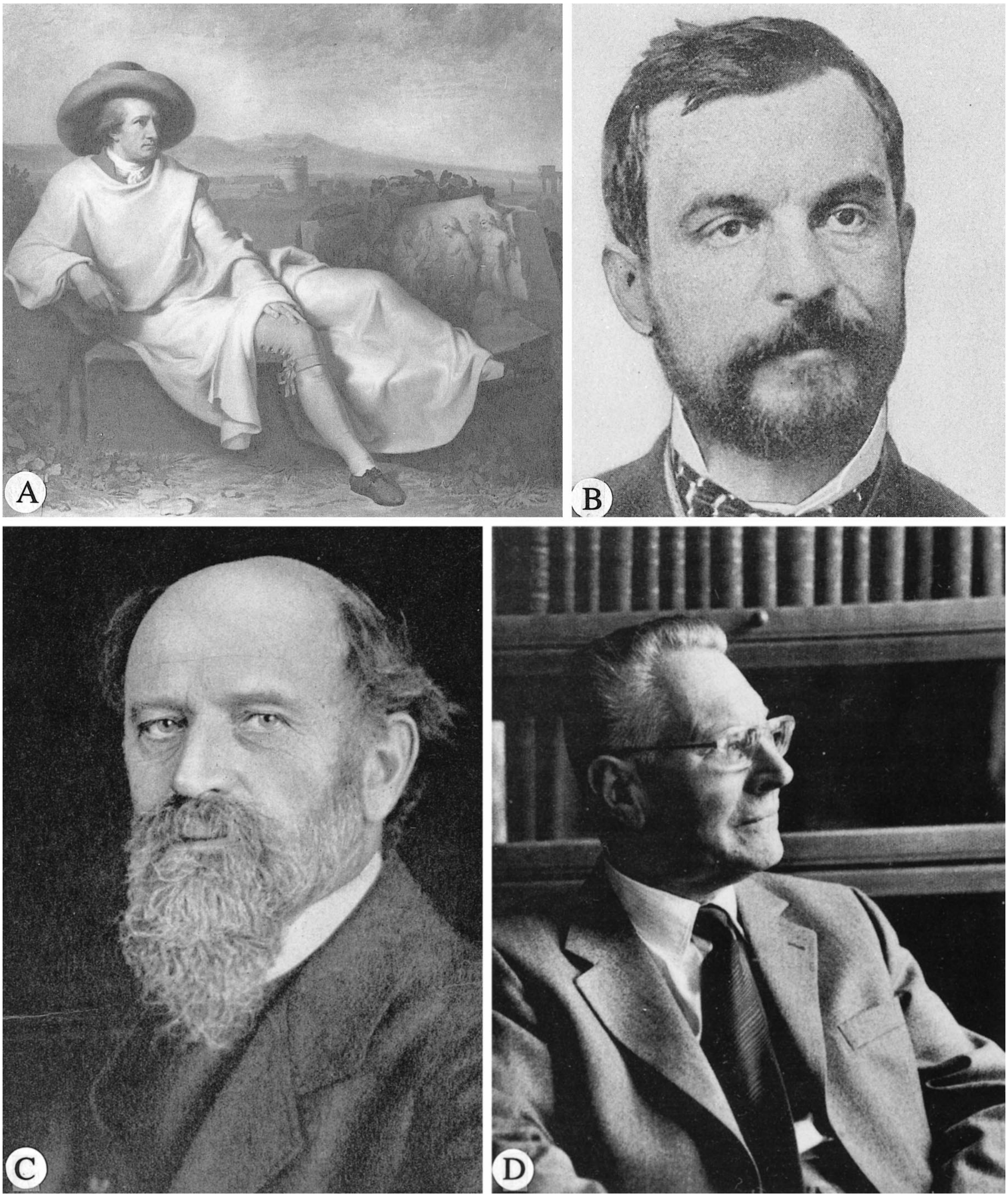

Fig. 5. Principal figures in the history of plant morphology. (A) Johann Wolfgang von Goethe as depicted by Tischbein during Goethe's travels in Italy (reproduced with permission from Mueller and Engard, 1952). (B) Wilhelm Hofmeister (reproduced from von Goebel, 1905). (C) Karl von Goebel (reproduced from Bergdolt, 1942). (D) Wilhelm Troll (reproduced with permission from Nickel, 1996).

Cooke and Lu, 1992; Kaplan, 1992). Similarly, the next higher level of organismal organization, growth habit, is an emergent property relative to the plant's morphology (Kaplan and Groff, 1995). For example, members of the cactus family (Cactaceae) are characterized by an idiosyncratic shoot morphology (see Fig. 4). However, this distinctive shoot form does not limit the variety of growth habits cacti exhibit; one can find cacti growing as trees, shrubs, cushion plants, vines and even plagiotropic, rhizomatous forms (Rauh, 1979).

We can conclude that the science of plant morphology can be circumscribed by both its emphasis in a comparative framework and its distinctive level in the hierarchy of biological organization. Once it is effectively delimited, its central role in biology and its fundamental contribution to the biological sciences become clear.

In order to more effectively characterize plant morphology I shall contrast it with what has been called ''phytography'' because there has been a tendency to confuse the two. Phy-

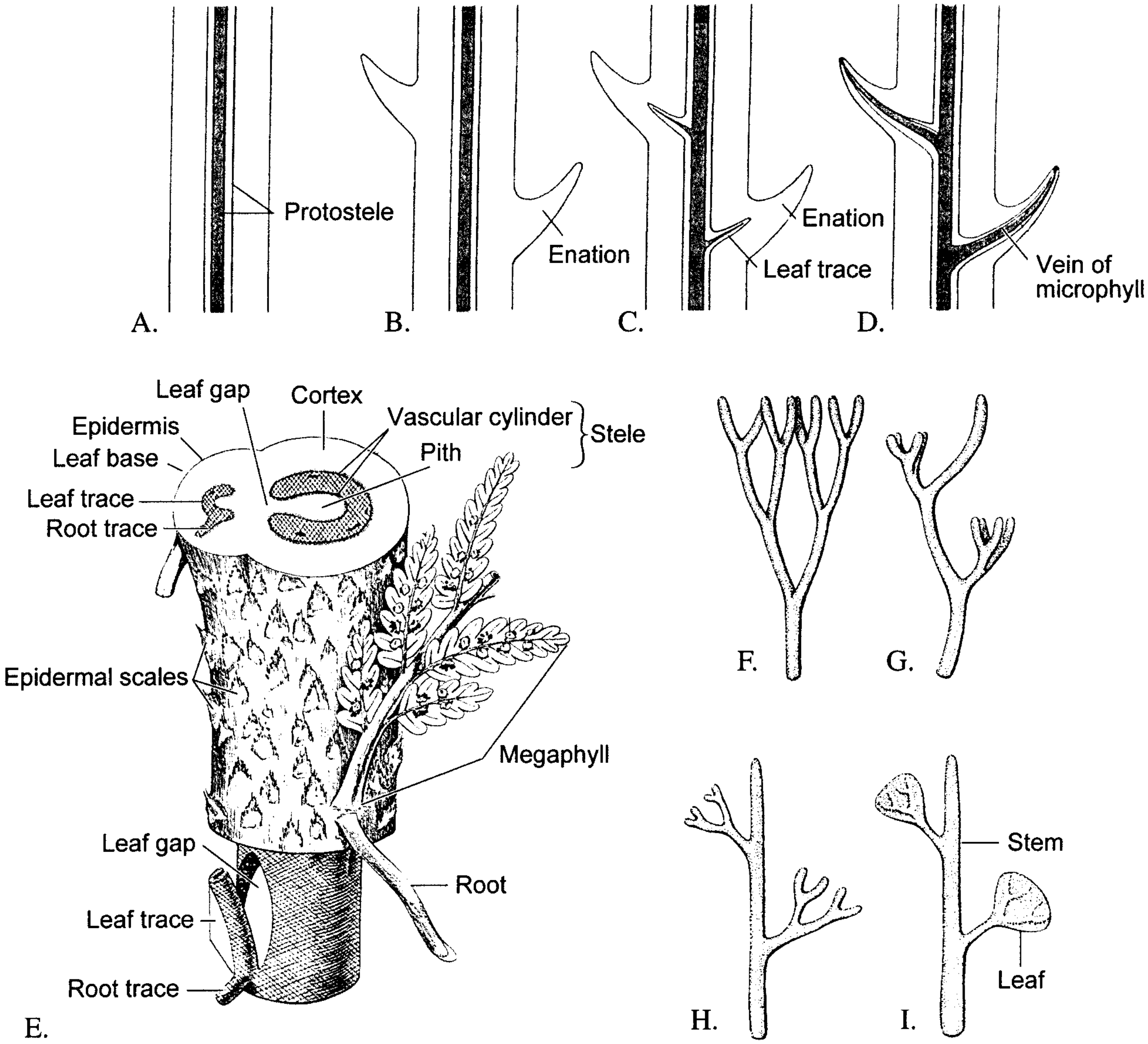

Fig. 6. Structure and evolutionary theories of the origin of microphyllous and megaphyllous leaves from leafless, rhyniophyte axes. (A–D) Longisectional diagrams illustrating the origin and evolution of microphylls as interpreted by the enation theory. (A) Leafless, protostelic axis of *Rhynia.* (B) Primitive enations devoid of leaf traces as illustrated by *Psilotum.* (C) Stage showing termination of leaf traces at the bases of enations. (D) Typical microphyll with leaf trace running unbranched as the midvein into each leaf. (E) Model of morphology and vascular anatomy of a small portion of a fern shoot, showing the frond as a megaphyll and the fact that the divergence of its leaf trace is associated with a leaf gap. (F–I) Hypothetical stages in the evolution of megaphyllous leaves from dichotomously branched axes of a *Rhynia*-like ancestor, according to the telome theory. (F) Isotomous branch system of rhyniophyte ancestor. (G) Unequal dichotomy or overtopping. (H) Dichotomous branching of primitive megaphylls in one plane (planation). (I) Union of forked divisions of megaphylls (webbing) to produce megaphyll with flat, dichotomously veined lamina. (A–D, F–I reproduced with permission from Gifford and Foster, 1989; E, reproduced with permission from Jeffrey, 1917.)

tography refers to the naming of plants and/or plant parts. It is what has been termed ‘‘descriptive botany.’’ For example, in the drawing of different leaf parts and types illustrated in Fig. 3 from Lawrence’s introductory taxonomy book (Lawrence, 1955), the application of the descriptive terms to each leaf or blade type is what comprises phytography. By contrast, plant morphology seeks to understand the common denominator that underlies or links these seemingly diverse and unrelated leaf forms. The plant morphologist comes to these conclusions of structural relationship by the comparative study of plant form between species and along the length of the metameric organism (serial homology or ‘‘homonomie’’) as well as by the study of organogenesis and experimentally induced variants, which supply additional, often cryptic clues about structural relationship. Thus, from the outset and at its very core, plant morphology is a comparative discipline concerned with the connectivity or linkages between characteristics, not their isolated expression. And while plant morphology is not obligately tied to phylogenetic formulations of form relationships, these linkages in character expression are, in my opinion, the most compelling evidence that the diversity of plant form we see on the earth today is the result of evolution.

As an example of the kind of linkages in form that plant morphology characterizes, Fig. 4 shows a spectrum of flow-

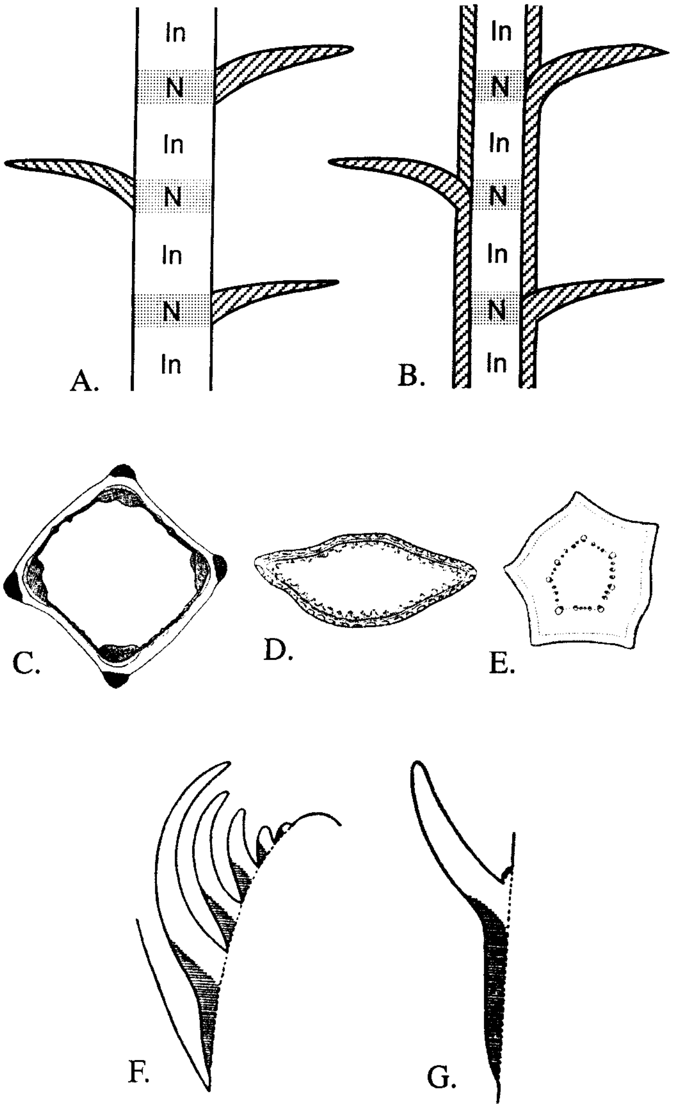

Fig. 7. Relationship of leaf to stem in vascular plants. (A) Traditional model showing leaf insertion restricted to the nodes and stem tissue expressed in the internodes. (B) Actual model where leaf insertion extends along the length of each "internode" in the form of a decurrent leaf base. (C–E) Transections of internodes of shoots with different phyllotactic patterns, illustrating how the transectional outline of the internode reflects the pattern of leaf insertion. (C) Transection of the shoot of the mint *Stachys silvaticus* exhibiting a square stem as a result of its opposite and decussate phyllotaxis. (Reproduced with permission from Troll and Rauh, 1950.) (D) Elliptical transectional outline of an internode of *Muehlenbeckia platyclados* its shape a result of its distichous phyllotaxis. (E) Polygonal internodal outline in *Euphorbia pteroneura* as a result of its helical phyllotaxis. (F) Idealized median longisection of a shoot tip showing the theoretical origin of decurrent leaf bases as a result of elongation of the point of leaf insertion (shaded) with the associated internode. (G) Idealized median longisection of an individual leaf that has a decurrent base as the result of abaxial leaf base elongation with the associated internode. ([D–G] reproduced with permission from Troll, 1937–1943.)

ering plants, extending from a typical herbaceous dicotyledon (Fig. 4A) through three members of the cactus family (Cactaceae), ending with a typical, barrel-type cactus (Fig. 4B–D). Cactaceae are of particular interest because contemporary representatives display all manner of intermediates between leafy cacti, such as *Pereskia* and *Pereskiopsis* (Fig. 4B), and those with varying degrees of leaf reduction, such as in *Opuntia* (Fig. 4C) and *Ferocactus* (Fig. 4D) (Rauh, 1979), making morphological connections easy to deduce.

From these figures it can be deduced that the divergence of the shoot in species such as the barrel cactus from the more typical dicotyledonous shoot morphology involves a reduction in the degree of expression of the upper leaf (lamina–petiole) zone in favor of the development of the lower leaf zone as a decurrent leaf base or podarium accompanied by a marked increase in axis primary thickening (compare Fig. 4D with 4A–C). Hence, what might appear to be a radical departure in plant form can be shown to occur within a stereotypical organizational theme or "Bauplan" within the Cactaceae. That parallel changes in morphology have occurred in independent phyletic lines (e.g., Euphorbiaceae, Asclepiadaceae) reflects the basic morphological principles that are repeated in contemporary plants regardless of their systematic affinity. The characterization of these morphological themes and the principles they represent is the central goal of plant morphology as a basic science.

Finally, a corollary to a form relationship concept of plant morphology is that the concept of homology in this context refers simply to structural correspondences and not commonality of descent (Kaplan, 1984). Such an agnostic outlook toward plant structural correspondences does not preclude their phylogentic application, but insures that structural correspondences will be more soundly determined because they have to be self-standing rather than resting on a phylogentic argument.

Because a science, just like an organism, is profoundly affected by its evolutionary history, in the next section I describe how the heritage of plant morphology has resulted in the development of its philosophical perspectives and analytical tools for evaluating plant form. Then I shall apply these perspectives and tools to the challenging problem of how to interpret shoot organization in different pteridophyte groups.

HISTORICAL HERITAGE OF PLANT MORPHOLOGY

This brief account of the history of plant morphology focuses less on dates and discoveries and more on the most influential figures, their contributions to the discipline, and the impact their different attitudes and emphases had on the different directions the science took during its history. My principal goal in reviewing this history is to try to determine why plant morphology as a science has become eclipsed in modern times and what contributions this rich heritage can make to contemporary biology.

Despite its history of over two centuries, German plant morphology has had only four principal figures who were significant in its development: Johann Wolfgang von Goethe, Wilhelm Hofmeister, Karl von Goebel, and Wilhelm Troll. I now look at these gentlemen individually and collectively to have some sense of the path of development of plant morphology and the reasons it took the directions it did.

Johann Wolfgang von Goethe (1749–1832)—The celebrated German literary dramatist and poet Johann Wolfgang von Goethe also had strong interests in the sciences, having contributed not only to plant morphology, but also to the study of color, mineralogy, and animal skeletal morphology among many other fields (Fig. 5A) (Mann, Mollenhauer, and Peters, 1992). Goethe originated the term "morphology," and more significantly, its methodology, i.e., comparative morphology or typology. His most significant contribution was the perspective

Fig. 8. Decurrent leaf base expression in the shoots of (A) *Buxus sempervirens* and (B) *Taxus baccata.*

that despite all the organographic diversity that flowering plants exhibit, one could deduce a fundamental organizational theme or ''Bauplan'' that linked this morphological variety. Moreover, Goethe theorized that knowing the fundamental ''Bauplan'' of an organism enabled one to predict plant forms that had not been discovered (Mueller and Engard, 1952). Because these perspectives were originally published in 1790 in Goethe's book *Versuch die Metamorphose der Pflanzen zu erklären* (''An Attempt to Explain the Metamorphosis of Plants''; Goethe, 1790) the origin of plant morphology as a discipline can be dated by the appearance of his pivotal publication.

Because today we tend to take such things for granted, it is hard for us to appreciate how revelatory Goethe's perspectives were. Because of its pre-Darwinian origins and largely theoretical nature, Goethe's approach was later derogatorily labeled ''idealistic morphology,'' by the phylogeneticists of the post-Darwinian period. Unfortunately, this dichotomy between pure or idealistic and phylogenetically oriented morphology represented an unnecessary tension that persists to varying degrees to this day (Troll, 1937–1943). Nevertheless, a significant range of research was carried out by idealistic morphologists, such as Alexander von Braun, who continued the Goethean tradition into the latter part of the 19th century. However, since Darwinian evolution simply supplied the explanation for the origin of many of the homologies determined by the Idealistic School, there actually was no conflict between these different points of view.

Wilhelm Hofmeister (1824–1877)—Undoubtedly the most notable figure in the history of plant morphology was Friederich Wilhelm Benedikt Hofmeister (Fig. 5B). Known principally as the discoverer of the alternation of generations and for his fundamental studies of plant embryology, Hofmeister

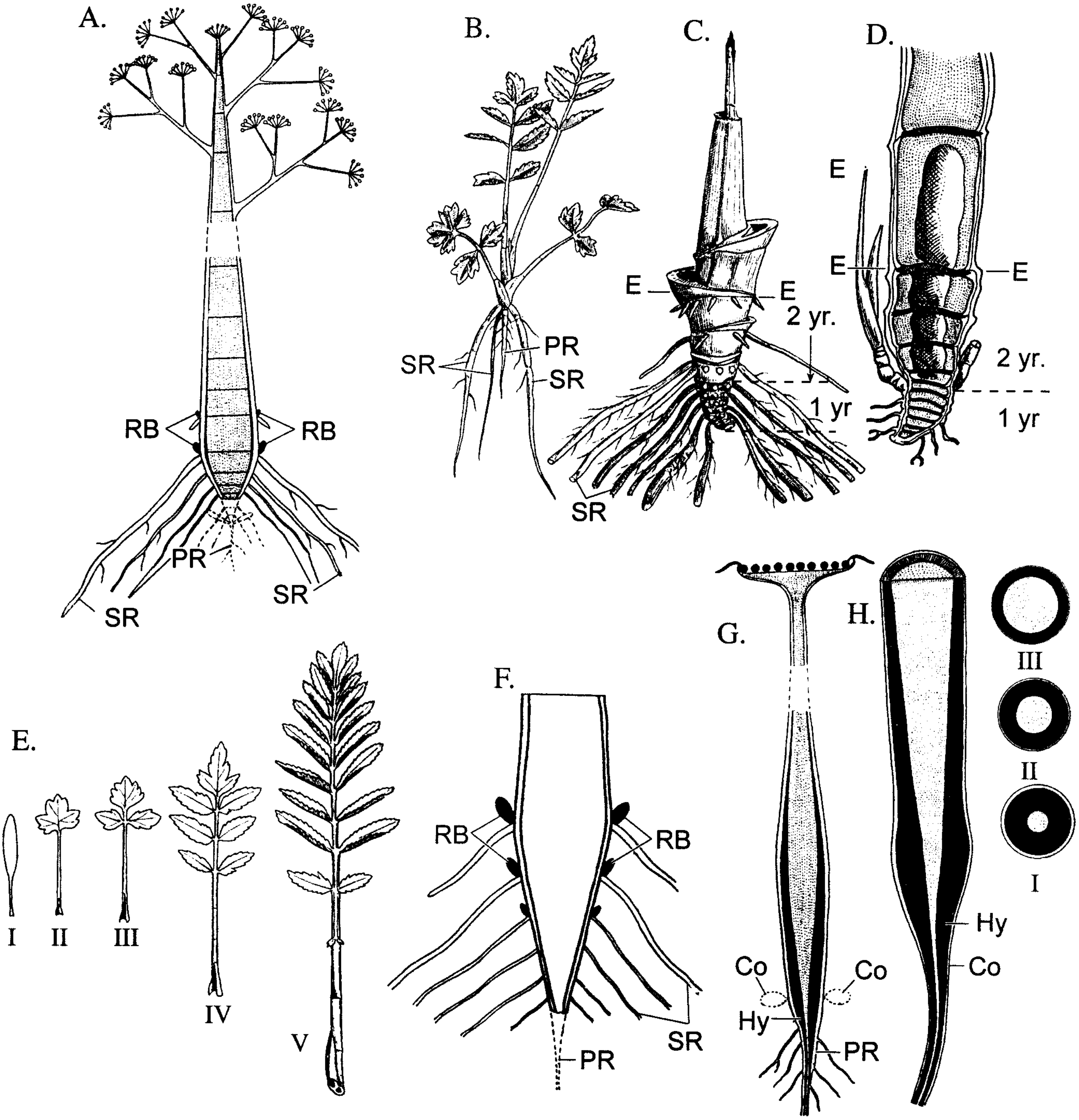

Fig. 9. Primary thickening rhythm "Erstarkungswachstum" in shoots of dicotyledonous angiosperms. (A) Scheme of shoot development of the aquatic plant *Sium latifolium*, showing the marked increase in axis diameter in the vegetative phase of development and a decrease in axis diameter in the reproductive phase, producing the obconic form of its shoot base. (B–D) Stages in the ontogeny of *Sium latifolium*. (B) Seedling plant showing structure and position of primary leaves. (C) Base of the plant at the beginning of the second year. The newly added growth is indicated by the arrows. (D) Detail of the base of a flowering plant. (E) Leaf series in *Sium latifolium*: E_{I}, cotyledon; E_{II} and E_{III}, primary leaves; E_{IV}, foliage leaf from the zone of the beginning of thickening; E_{V}, foliage leaf from the region of maximal axis thickening. (F) Diagrammatic median longisection of an idealized axis showing the correlation between lateral bud (black) and shoot-borne root development and the degree of thickening of the axis. (G–H) Diagrammatic median longisections of the shoot of *Helianthus annuus*, showing a primary thickening rhythm partially masked by secondary xylem formation but still evident in the shape of the pith. $H_{I\text{–}III}$ are transections from proximal to distal regions of the shoot. Cortical tissue is open, pith tissue is stippled and xylem tissue (primary and secondary) black. (Redrawn with permission from Troll and Rauh, 1950.)

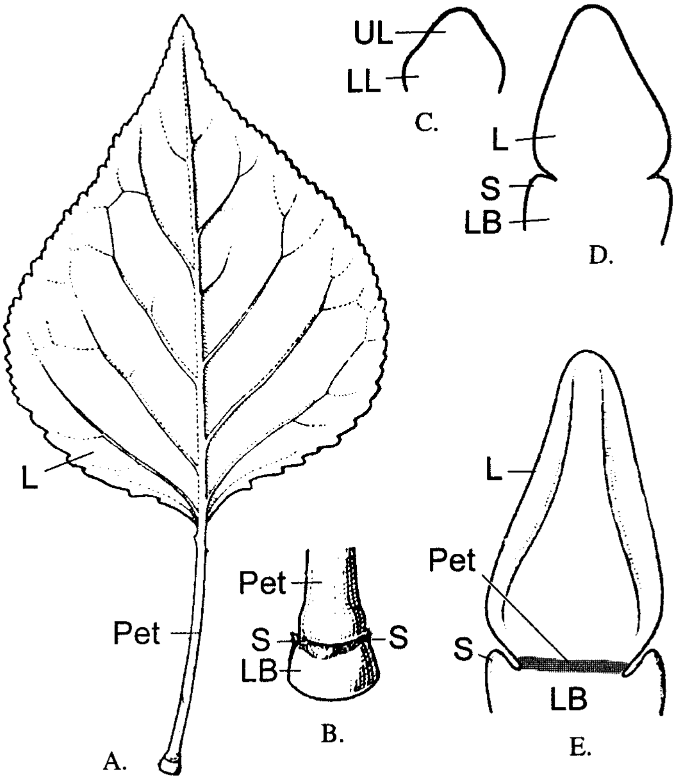

Fig. 10. Leaf morphology and development in *Prunus siberica.* (A) Mature leaf as seen from the abaxial side, showing its differentiation into a simple, distal lamina, an intervening petiole, and a leaf base. (B) Detail of the junction of petiole and leaf base, showing the remains of the stipules. (C–E) Stages of development showing morphological differentiation into upper and lower leaf zones (C and D respectively), followed by origination of stipules from the margins of the lower leaf zone (E). Primordial petiole zone indicated by hatching at the base of the upper leaf zone in (E). (Reproduced with permission from Troll, 1937–1943.)

is equally significant for having sired the most notable lineage of German plant morphologists. Since we have already devoted an extensive article to his life and contributions (Kaplan and Cooke, 1996), I will summarize here his relevance to the science of plant morphology.

Hofmeister was an autodidact in botany and stands as one of the real geniuses in the history of botanical science. He had no university education, much less a Ph.D. degree, but ultimately was appointed Professor of Botany at Heidelberg at age 39. The fact that he was self-taught also explains the sharp separation between him and the idealistic morphological tradition that preceded him. Whereas the idealistic morphologists were concerned with the relationship of plant forms to one another, Hofmeister asked why plants exhibit these form relationships, i.e., what is the causal basis for this morphological diversity? To these questions he brought an impressive arsenal of tools and perspectives from physics and chemistry, all of which he also taught himself. As one of the earliest plant biophysicists, Hofmeister was so far ahead of his time that he was not understood by his contemporaries or many who followed him (Kaplan and Cooke, 1996).

Hofmeister's principal contribution to the field of plant morphology was his book *Allgemeine Morphologie der Gewächse* [''General Morphology of (Plant) Growth,'' Hofmeister, 1868], published as part of the series entitled the ''Handbook of Physiological Botany'' (*Handbuch der Physiologischen Botanik*) of which Hofmeister was the general editor. Even the title's emphasis on plant growth underscored its dynamic, developmental focus, representing a revolutionary break with the idealistic morphological tradition (Troll, 1937). Hofmeister not only presented a fundamentally analytical view of the developmental basis underlying the diversity of plant form, but also biophysical interpretations of a range of phenomena including phyllotaxis and the effects of gravity and light on a plant's morphology. Although it was not an easy book to read or understand, it had a great influence on changing the outlooks of subsequent practitioners and was the first modern treatise on plant morphology, presaging the great tradition of plant morphogenesis that was to be expressed later in the 20th century.

Karl von Goebel (1855–1932)—Karl Ritter Eberhard von Goebel was a disciple of Hofmeister (Fig. 5C). Von Goebel, born in Billigheim in the state of Baden near Heilbronn, where his father owned a machine factory, would attend the University of Tübingen. Initially, following the wishes of his mother, he studied theology and philosophy. However, he switched to botany after coming under the influence of Hofmeister, who had come to Tübingen as Professor of Botany from Heidelberg in 1872. Had Hofmeister been in better health during his time at Tübingen, it is likely that von Goebel would have done his doctoral work with him. However, von Goebel moved in 1876 to Strasbourg, where he completed his doctorate with Heinrich Anton de Bary (Speta, 1997). In spite of this brief exposure, Hofmeister would be a lasting influence on von Goebel's career and von Goebel would write extensively about Hofmeister (von Goebel, 1926). It was his contact with Hofmeister that led von Goebel to develop his interest in morphology, especially its causal aspects, and in the study of cryptogamic plants. His knowledge of the algae, fungi, and plant anatomy was enhanced by his experience with DeBary.

Besides Hofmeister, the other significant influence on von Goebel's development was the great physiologist anatomist Julius von Sachs at Würzburg, whom von Goebel served as an assistant from 1878 through to his habilitation in 1880. Sachs' influence was expressed in von Goebel's experimental approaches to plant morphogenesis as well as his interest in physiological explanations of plant form. Sachs became a lifelong friend of von Goebel, and the two carried on an extensive correspondence until Sachs' death in 1897 (Bergdolt, 1942).

Von Goebel occupied a succession of academic posts, proceeding from Strasbourg in 1881 to the University of Rostock from 1882 to 1886, and the University of Marburg from 1886 to 1891, when he received the call to Munich. At the University of Munich, von Goebel created the world famous Botanical Garden and Botanical Institute at Nymphenburg and established it as a center for the training of plant morphologists.

In contrast with Hofmeister, whose plant collecting activities were restricted largely to central Europe, von Goebel was an inveterate world traveler, traveling to India and Java in 1885–1886, to Australia and New Zealand in 1898–1899, to North America in 1905, and to Brazil in 1913. In 1925, at age 70, he made a second journey to Java (Speta, 1997). During these trips von Goebel collected a tremendous diversity of plant species, greatly expanding the range of phenomena that had been accounted for in previous morphological treatises. Von Goebel had an eye for detail and a synthetic perspective that allowed him to place phenomenology in the context of whole-plant diversity. Not only did his knowledge cover vascular plant

Fig. 11. Upper portion of the shoot axis of *Heracleum lanatum*, showing the upper cauline vegetative leaves, and the progressive distal reduction of the shoot axis and the bracts as a transition is made to the terminal umbel.

diversity worldwide, but also the cryptogams, especially the bryophytes. In fact, to this day, von Goebel's account of the bryophytes in his *Organographie der Pflanzen* (Organography of Plants) stands as the most comprehensive account of their comparative morphology (von Goebel, 1928–1933).

Although he published numerous individual papers, Goebel's morphological legacy was his monumental treatise Organography of Plants, a three-volume work that appeared in three editions between 1898 and 1933 (von Goebel, 1898–1901, 1913–1923, 1928–1933), including an English translation in 1900 (von Goebel, 1900–1905). Because of its English translation, von Goebel's perspective and influence would be

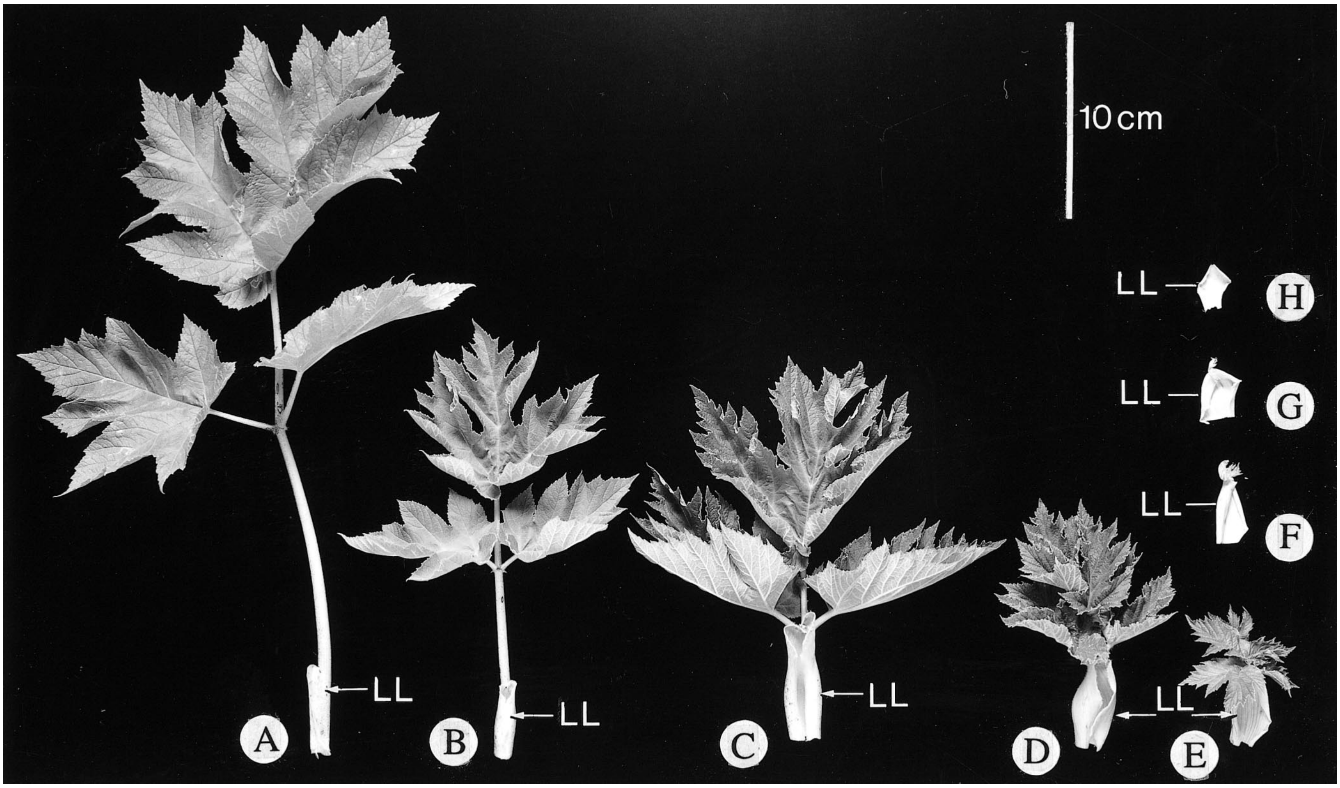

Fig. 12. Successive leaves in their acroscopic sequence of insertion along the length of the shoot of *Heracleum lanatum.* This sequence shows the progressive reduction of the upper leaf zone derivatives (lamina and petiole) in favor of the lower leaf zone derivative (median stipulate leaf base).

wider than that of either Hofmeister, who preceded him, or Wilhelm Troll, who followed him. Von Goebel purposely called his work ''Organography'' to underscore its causal orientation and hence avoid the stigma of ''idealistic morphology.'' Furthermore, the goal of organography was to distinguish those features of plant form that could be understood as adaptations to environmental (external) conditions from those that were a result of inner, presumably genetic, bases. Reflecting his experience with Sachs, he emphasized the functional aspects of plant organs as well as their form relationships. In some of his deductions on the causal significance of a plant's morphology von Goebel would invoke rather vague physiological explanations, such as nutritional or hormonal (integrative) causes, and these, coupled with simple but naive experiments, represented the weaker elements of his legacy. However, the fact that he questioned why plants took the form they did ultimately made him the spiritual father figure of plant morphogenetic research in the 20th century.

By the time that von Goebel was a young Ph.D., Darwinian evolution had made its impact. Remarkably, in his own plant morphology treatise Hofmeister (1868) had already fully assimilated Darwin's *Origin of Species* (Kaplan and Cooke, 1996). Hence, in von Goebel's era, phylogenetic interpretations of plant morphology came to supersede those of idealistic morphology. Von Goebel nevertheless maintained a healthy skepticism toward such phylogenetic speculation. While he was inclined toward physiological explanations of the many variants in plant morphology, he also was highly critical of the simplistic adaptationist interpretations that were rampant in that era. Such skepticism toward phylogenetic theorizing and the adaptive mode of much of plant structure would be passed on to his disciples, resulting in an even sharper reaction from people such as Wilhelm Troll.

Wilhelm Troll (1897–1978)—Of the four major figures in German plant morphology, the most complicated and controversial was Wilhelm Julius Georg Hubert Troll, a doctoral student of von Goebel at Munich (Fig. 5D). Troll was the son of a psychiatrist-neurologist Theodor Julius Troll and was born in Munich but raised in the fore-alpine region south of Munich (in Gabersee, near Wasserburg/Inn) (Nickel, 1996). In these natural areas and the Bavarian Alps Wilhelm and his younger brother Karl developed their intense interests in nature and in plants in particular. Karl Troll became one of the premier plant geographers, ultimately becoming more famous than his brother Wilhelm.

Wilhelm Troll completed his doctorate with von Goebel in Plant Morphology at the University of Munich in 1921. He then served as an assistant to von Goebel in the Botanical Institute, becoming habilitated in 1925. From 1928 to 1930 he participated in the Sunda Expedition to Malaysia, principally studying root structure and function in mangrove vegetation. In 1932, he was appointed Ordinarius Professor and Director of the Botanical Garden at the Martin Luther University in Halle and served in that capacity until 1945, near the end of World War II. Because Halle ultimately came to be located in the DDR (East Germany), Troll and a whole host of East German intellectuals were moved by the U.S. forces to the west zone just in advance of the Russian occupation in July 1945. From July 1945 to January 1946 Troll obtained an interim teaching position at the Gymnasium school in Kircheimbolanden/Pfalz. Finally, in May 1946, he was appointed Ordinarius

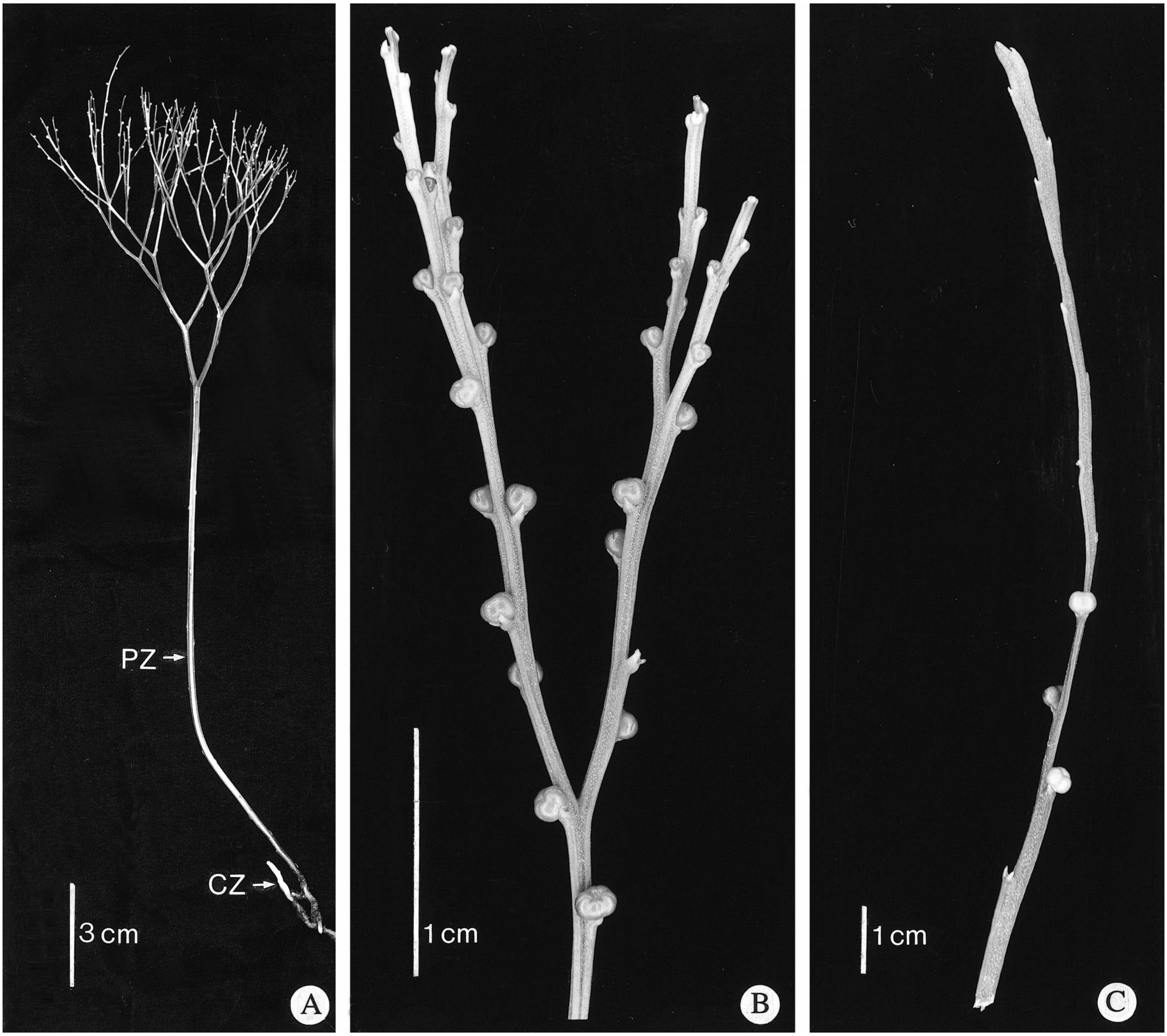

Fig. 13. Shoot morphology in *Psilotum nudum.* (A) A whole shoot, showing the difference between the degree of regularity of branching in the proximal cryptophilic and distal photophilic zones as well as the change in axis diameter along the length of the shoot. (B) Detail of the distal fertile region of the shoot showing bifid sporophylls bearing enlarged synangia on their adaxial surfaces. Decurrent leaf ridges are also evident along the length of the shoot. (C) Divergent shoot development. This specimen exhibits vegetative proliferation wherein vegetative growth of the shoot is renewed after declining to the minimal axis diameter in the distal fertile region of the shoot. Not only does this shoot regain the maximum diameter, but it also shows a symmetry and phyllotactic change from radial symmetry with tristichous phyllotaxis to bilateral symmetry with distichous phyllotaxis.

Professor and Director of the Botanical Institute and Botanical Garden of the newly reconstructed University of Mainz in West Germany. He retired in March 1966 and worked as an emeritus Professor until his death on 28 December 1978 at age 81 (Nickel, 1996). Thus, Troll's life and career spanned the most tumultuous era in German history, including the two World Wars, and the nature of his career and perspectives must be evaluated against that background.

Prior to his full-time entry into the University of Munich, Wilhelm Troll served in the German Army as a lieutenant on the Western Front in World War I, from 1916 to 1918. Like many Germans, this experience had a devastating affect on him that no doubt influenced many of the scientific perspectives he would develop. He withdrew from his native Catholicism and, like many in this postwar period, developed a reaction against industrial materialism, mechanism in science, and the tendencies of contemporary science to focus on narrowly circumscribed, mathematically based problems (Nickel, 1996). This disillusionment engendered a desire to return to a more romantic era of Germany's past, to holism and the idealistic morphology of Goethe.

Von Goebel was fond of saying that only those phenomena could be called morphological that could not yet be explained physiologically (''*morphologisch das sei, was sich physiolo-*

gisch noch nicht erklären lasse''; cited in Nickel, 1996). Troll, however, did not feel that one could deal with morphology causally. He believed that one could only deal with description and presentation (''Darstellung''), but that morphological relationships or typologies were not susceptible to explanation or causal analysis. Troll, like Goethe, saw the central goal of morphology as the analysis of diversity and the deduction of types. This typological approach was basically an intuitive process that would be evident to the investigator once he or she had analyzed the spectrum of form variants. Like Goethe, Troll believed that the types were real, not just abstractions, and that they stood behind the diversity that one saw in the physical world. In many ways, Troll held a platonic view of the biological world.

Troll felt that the pinnacle of morphology would be knowing the diversity of forms so well that one could predict morphologies that had not yet been discovered or described (Troll, 1928). The best analogy for Troll's goal of plant morphology is the development of the equivalent of the Periodic Table in chemistry. According to such a perspective, the range of variants could be derived from the type by quantitative variations in growth distribution, a point of view represented by Goethe's principle of variable proportions (Troll, 1949). In fact, Troll's idealistic morphological accounts of the variations in plant form in his treatises (Troll, 1937–1943) are very reminiscent of D'Arcy Thompson's theoretical derivations of differences in animal morphology (Thompson, 1917). Many of Troll's constructs were purely hypothetical and not tested by actual developmental studies. In a few cases, they turned out to be wrong because they were based on the false assumption that all developmental changes were strictly quantitative in nature, when in fact qualitative changes in development can also be significant (Kaplan, 1980). Thus, while Troll's idealistic morphological theorizing can be useful pedagogically, in other instances it can be misleading. Nevertheless, because he used variations in development as an underpinning of his typological deductions, Troll's treatises and papers are a useful resource for information on comparative plant development.

Troll's typological approach became especially murky with reference to questions of phylogeny. From von Goebel he inherited a skepticism toward the more simplistic phylogenetic deductions of the time. He had also developed his own skepticism about relying on fossil plants for a definitive picture of plant evolution; he saw the fossil record as being too fragmentary and lacunate to be able draw any valid phylogenetic conclusions from it. Such views put Troll at loggerheads with the noted German paleobotanist/phylogenist Walter Zimmermann, the author of the telome theory (Zimmermann, 1965). The two carried on a polemical debate in the literature (Zimmermann, 1930, 1937, 1953, 1959, 1968; Troll, 1937–1943) without resolution because of its partisan nature.

In reality, Troll's views on Darwinian evolution were complex. Looking at his typological philosophy superficially, with

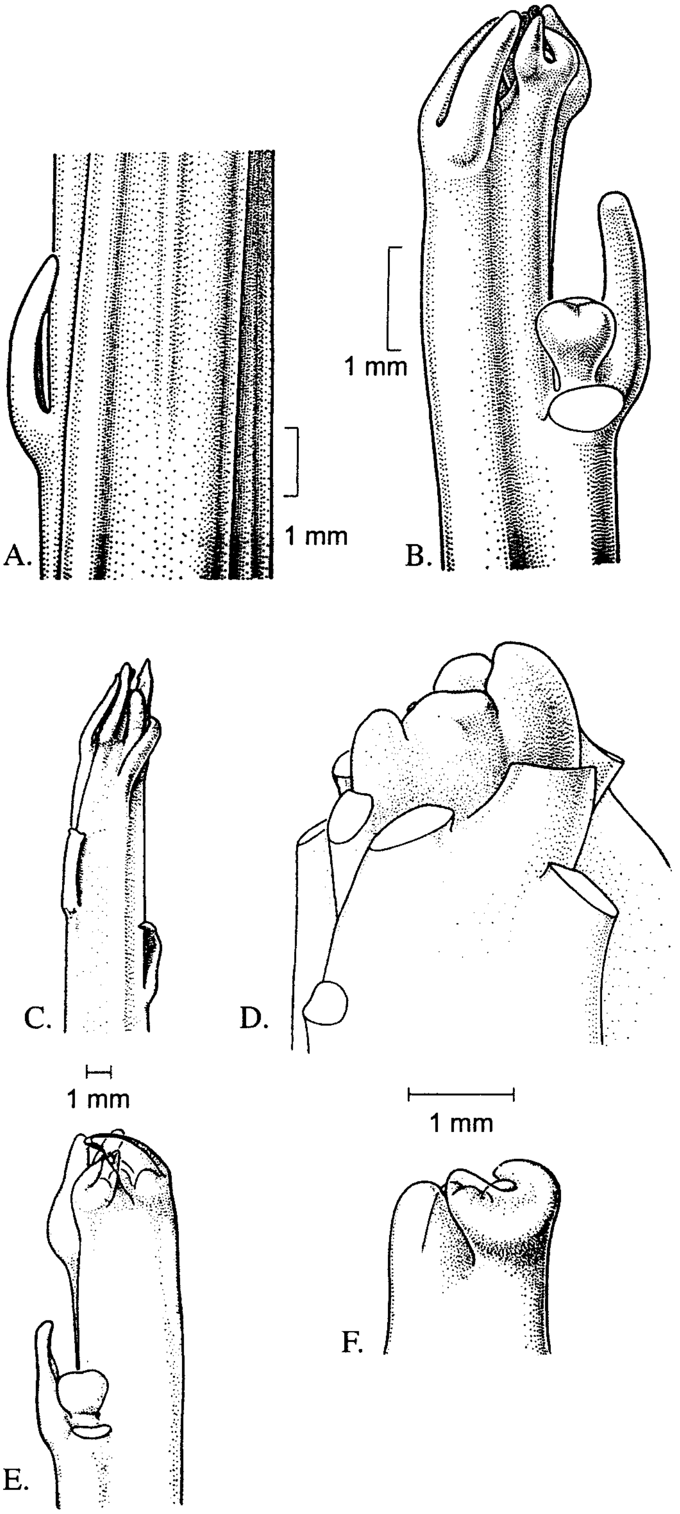

Fig. 14. Details of shoot thickening and relationship of leaf to axis development in *Psilotum nudum.* (A) Portion of vegetative shoot in the phase of maximal axis thickening, showing the greater number of decurrent leaf ridges associated with the higher phyllotactic fraction in this proximal part of the photophilic shoot as well as a simple scale leaf borne at these strictly vegetative nodes. (B) Detail of the distal fertile region of the shoot showing bifid sporophylls bearing typical, trisporangiate synangia on their adaxial surfaces. One of the two leaflets on the lower right sporophyll has been cut away to expose the young synangium on its adaxial surface. Note also the fewer decurrent ridges associated with the narrower axis diameter and lower phyl-

←

lotactic fraction in this distal fertile region of the shoot. (C, D) Low- and high-magnification views of the shoot tip of the sterile, vegetative region of the shoot, showing the relationship of the volume of the shoot apex to the leaf primordia initiated from it. (E–F) Corresponding views of the relationship of leaf primordium size to shoot apex volume in the distal, fertile region of the shoot. ([A–B] reproduced with permission from Siegert, 1967; [C–F] reproduced with permission from Siegert, 1969.)

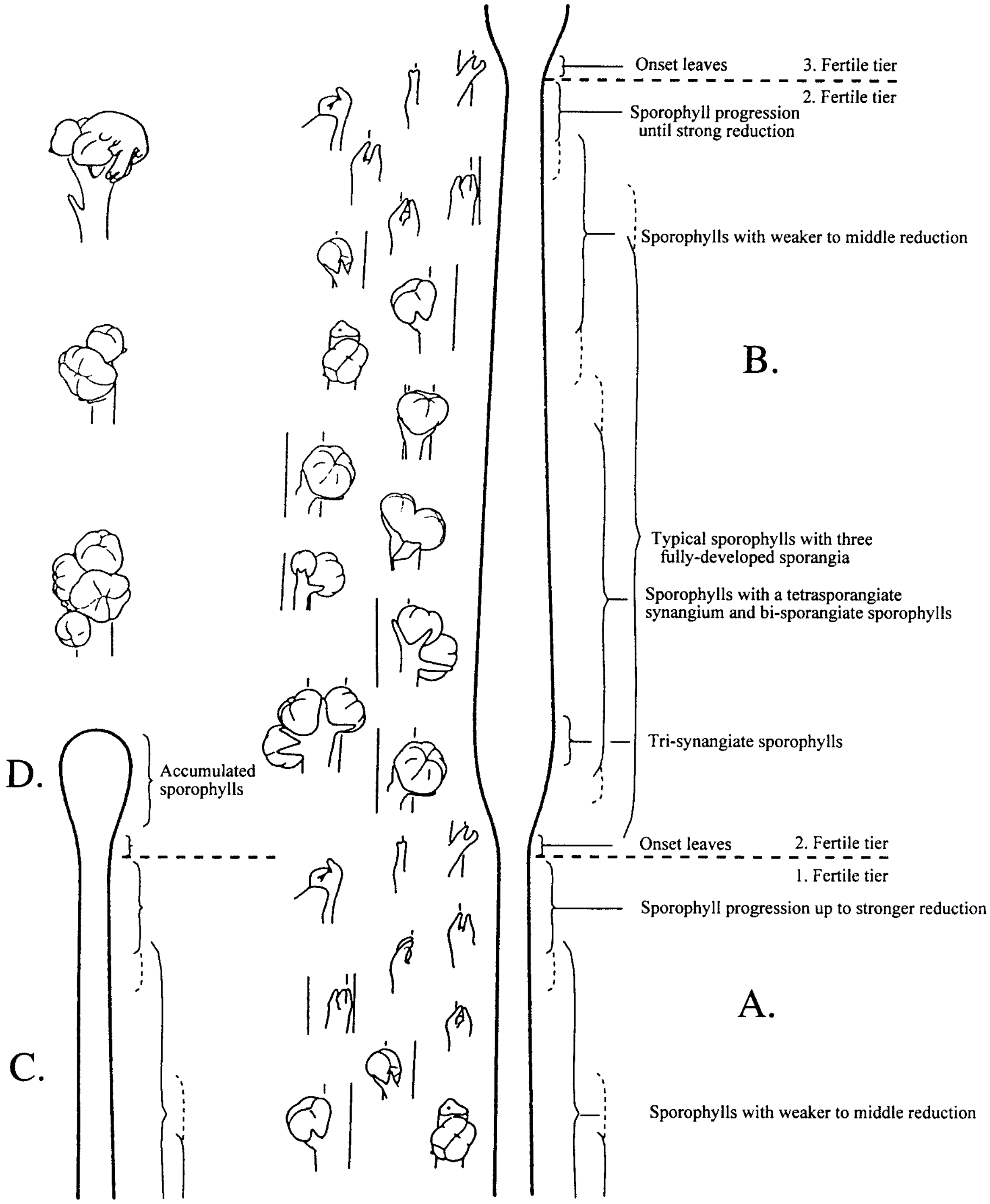

Fig. 15. Proliferated shoot leaf succession for *Psilotum nudum,* showing the range of leaf and sporophyll types correlated with axis diameter in proliferated shoots. In the middle right of this figure is a diagram of a proliferated axis reflecting the fluctuating changes in shoot axis diameter. To the left of the first fertile tier (A) is the compressed termination of the axis (D). The horizontal, dashed lines indicate the boundary between the respective shoot generations or tiers (A–D). The brackets shown to the right of each axis segment give the boundaries of the respective sporophyll morphologies shown to the left of each of the shoot tiers. (Reproduced with permission from Siegert, 1973.)

its quasi-religious overtones, it would be easy to paint him as anti-evolutionary, and there are some who have done so (Eyde, 1975). However, in reality, Troll conceded that evolution was the best explanation we have of the succession of forms found in the earth's history (Nickel, 1996). Darwin's recognition of the basic unity of type in different groups served as a point of harmony between Troll and Darwin (Troll, 1925). They differed, however, in their views about what this unity of type represented. Darwin felt it reflected the commonality of descent, whereas Troll considered it to be a form principle that was more fundamental than geneology. Because he saw his typologies as fundamental natural expressions, Troll felt that classification systems could be built upon them. Furthermore, since they involved a consideration of entire organisms and the integration of their form relationships, Troll believed the typologies were more significant than the individual, isolated characteristics upon which systematists tended to base their conclusions.

While Troll conceded that natural selection did play a role in the origin of some characteristics of organisms, he did not believe that it could explain all of the variations in form. Certainly, modern views of structural evolution would incorporate the idea that the organizational theme or ‘‘Bauplan’’ of the organismal group in question have to be taken into account in any consideration of plant evolution (Kaplan and Groff, 1995). Thus, Troll inveighed against a strictly random conception of the evolutionary process.

Interestingly, Troll postulated that major jumps in the evolution of forms could occur, as opposed to the gradualism represented in Darwin's views. Eldredge and Gould's theory of ‘‘punctutated equilibrium’’ (Eldredge and Gould, 1972; Gould and Eldredge, 1977) would have found some resonance with Troll, even though their philosophies were very different. Despite starting from altogether different first principles and being colored by an element of skepticism about the simplistic features of phylogenetic thinking and Darwinian dogmatism, Troll's views of plant phylogeny are not as extreme as they might seem.

Like von Goebel and Hofmeister, the central point of Troll's contributions and perspectives were contained in his major, multivolume treatise entitled *Vergleichende Morphologie der höheren Pflanzen*, (Troll, 1937–1943) (‘‘Comparative Morphology of Higher Plants’’). Whereas von Goebel tried to distance his own work from its idealistic morphology predecessors by calling it ‘‘organography,’’ Troll's naming of his treatise ‘‘comparative morphology’’ was intended to express his return to that idealistic tradition. If von Goebel's treatise was impressive for its time in terms of the breadth and depth of its coverage, Troll's was even more so. Troll's work was more complete and comprehensive than von Goebel's and also better organized and more clearly written. Whatever questions one might have about Troll's scientific philosophy, one could never fault him as a didactor and empiricist. The quality and clarity of his artwork and photography set new standards. These same high standards of description and illustration would characterize Troll's work for his entire career. A testimonial to their high quality is the great number of modern, non-German texts that have drawn upon Troll's figures long after his works were out of print (e.g., Gifford and Foster, 1989).

Troll's comparative morphology treatise, an amalgamation of his own research and the work of others, was the most comprehensive to date. The formal work was intended to be a programmatic presentation of the complete range of vascular plant morphology, both vegetative and reproductive. Only the first three volumes dealing with vegetative morphology were published. Volume I dealt with vegetative shoot morphology, Volume II dealt with vegetative leaf morphology, and Volume III with the morphology of roots and root systems. The original intention was to follow with volumes on reproductive shoots ending with seed and seedling morphology. Unfortunately, World War II interrupted the work.

Troll's principal activity in his postwar position in Mainz was the continuation of this programmatic work, beginning with inflorescence morphology. Unfortunately, Troll's contributions in this area became so excessive in detail and quantity (he is reputed to have studied literally thousands of species in >300 families; Troll, 1969) that he never completed the remainder of the program. Not even his most active disciple, Focko Weberling, was able to complete the inflorescence program, so massive and extensive was this undertaking. Fortunately, Troll did publish a more compact overview in his companion volumes entitled *Praktische Einführung in die Pflanzenmorphologie* (‘‘Practical Introduction to the Morphology of Plants’’), which appeared as a two volume work (Troll, 1954, 1957) and covered the more general aspects of flower, fruit, and inflorescence morphology in economic plants (Troll, 1957).

In the final analysis, despite having a number of notable disciples, Troll's idiosyncratic philosophy was not practiced or promoted actively by his students. His students tended to represent much more conventional perspectives and made syntheses with other areas of interest. The only long-term benefit of Troll's typological orientation was his belief that only way to deduce types was through the rigorous and accurate characterization of nature. Thus, Troll's lasting contributions were his exceptionally detailed, lucidly presented comparative studies of plant morphology and his effective organization of the subject. While it was good to have such an extensive subject represented by a single, uniform perspective, the negative side has been that such an exhaustive treatment gives the impression that everything has been studied and therefore the subject of plant morphology is closed. Nothing could be further from the truth. No matter how extensively a given discipline may be studied by an individual, the work of that person is restricted to a particular time in history. With the advent of new technologies and accompanying new perspectives, every discipline, regardless of its age, is subject to revision. No matter how empirically based they may have been, Troll's contributions contain uncertainties that need to be revisited if for no other reason because they were colored by his distinct philosophical biases.

Today most of the tradition of plant morphology has died out in Germany, with only a handful of Troll's former students, such as Focko Weberling, Albrecht Siegert, Wolfgang Hagemann, Hans Froebe, and Weberling's student Thomas Stützel, carrying on any semblance of this heritage.

Historical conclusions—Having reviewed the major figures in the history of German plant morphology and their contributions to the development of the field, I now want to return to the original question of why the field became eclipsed. Given the fundamental nature of the contributions of these notable figures, why hasn't this science made a greater impact on contemporary plant biology?

Clearly there are a variety of reasons, some obvious and others subtle. One of the most obvious reasons is the language barrier. Even if investigators do have some facility with German, their tendencies will be to focus on a particular set of facts or descriptions in these large treatises and to shy away from the broader, more philosophical expositions in them. This is due in part to the fact that the historical and/or philosophical presentations are more difficult to read and involve grammatical and interpretive nuances that can be beyond the German reading ability of the average Anglo-American morphologist. As a result, many of the broader interpretive issues or frameworks from this German heritage tend not to receive any consideration in this country. This situation is further exacerbated by the recent declines and almost complete disappearance of requirements for foreign language skills in Ph.D. programs in the United States. Therefore, is it any wonder that there is no critical assessment or understanding of Troll's philosophical perspectives among contemporary non-German botanists?

Another obvious barrier to the penetration of this German conception into our U.S. scientific culture is the aforementioned emphasis on tools and technology here, in contrast to the philosophically grounded approaches of Europe. Moreover, with the advent of molecular techniques in this decade, this gulf has become even wider because plant morphology as a discipline is grounded in organismal biology and the latter has virtually disappeared from view. Once we have sequenced all of the relevant plant genomes and have come to realize that such sequence data leaves many questions in organismal biology unanswered, we may finally appreciate that organisms are valid and fundamental biological units worthy of our attention. Then morphology may finally be appreciated and respected as a key to the understanding of plant organismal biology.

The broad historical trends of plant morphology, have followed the general path of any science: description of phenomena, classification of those phenomena, and the investigation of the causal linkages between phenomena. These developments have received different degrees of emphasis in the respective practitioners. For example, both Goethe and Troll were concerned more with the classification and integration of morphological phenomenology and Goebel and Hofmeister more with the causal aspects. During the development and progressive refinement of the subject, however, all of its past practitioners have contributed to both the causal and descriptive areas of the science.

With the current emphasis on genetics in biology, plant morphology today focuses more on the causal aspects of plant form. Even though the mode today is to focus on selected ''model systems'' because of their greater ease of experimental manipulation, in fact, you cannot derive general principles from such model systems. Such principles can only be derived from the type of broad, comparative investigations plant morphology traditionally has provided. Instead of seeing exhaustive treatises like Troll's as the endpoint in the development of the subject, they should be seen as starting points in the development of a more integrated view of plants as organisms.

And while today plant morphology may play a less fundamental role in mapping out phylogenies than it has in the past, it can play a significant role in evolutionary biology in general. Not only can it help elucidate the developmental basis for the evolution of form in the respective plant groups (Kuzoff, Hufford, and Soltis, 2001), but it also can be significant in giving evolutionary biologists a clearer picture of ''developmental constraints'' (Smith et al., 1985) and their role in the evolution of morphology and its adaptive significance.

Similarly, the great record of plant morphology can be of significance to the paleobotanists in their characterization of the evolution of plant form. While it is true that the interpretation of ancient extinct vascular plants should not be biased by the study of contemporary representatives alone, neither should fossil plants be studied without a full understanding of the morphological principles underlying the diversity of contemporary plants. Since the study of fossils has tended to be biased toward anatomical data, the context of contemporary plant morphology has not been used sufficiently to determine the actual morphological status these extinct groups show. In the next section I illustrate the problems with the latter approach and the insights from the study of contemporary plants that plant morphology can provide for the study and interpretation of the broad patterns of structural evolution in vascular plants.

THE PROBLEMATICAL STATUS OF PTERIDOPHYTE MORPHOLOGY

The most important legacy from this history of plant morphology is a set of fundamental principles of shoot organization and development derived from the study of a broad array of vascular plants, especially seed plants. In order to illustrate these principles I shall apply them to the interpretation of the morphology of the shoots of Pteridophytes, better known in the past as the ferns and fern allies.

Pteridophytes are linked only by a common life-history pattern: a heteromorphic alternation of generations, between a dominant, free-sporing sporophyte and a free-living but highly reduced gametophyte (Gifford and Foster, 1989). Because the pteridophytes are not a natural group, the morphological correspondences they exhibit are indicative of fundamental principles and thus provide a good illustration of the goals of plant morphology as a discipline. All members of this group (Psilopsida, Lycopsida, Sphenopsida, and Filicopsida) have a more extensive representation in the fossil record than among contemporary plants, and interpretation of their morphology has been based largely on fossil rather than contemporary plant models. However, despite their ancient phyletic lineages and phylogenetic heterogeneity, we now want to ask whether contemporary pteridophytes exhibit the same basic shoot organizational principles as those exhibited by seed plants or whether they exhibit ancient morphological properties that are not to be found in any other contemporary plants.

A REEVALUATION OF LEAF MORPHOLOGY IN THE PTERIDOPHYTES

An example of the type of interpretation that has suggested a contrast in shoot organization between pteridophytes and seed plants involves the morphology of their leaves. Two different leaf types have been recognized in Pteridophytes: ''microphylls'' and ''megaphylls.'' Microphyllous (small) leaves have been defined as appendages supplied by a single, unbranched vein. Since, in the classical microphyll, this single leaf trace extends from a protostele, its departure is not associated with a leaf gap (Fig. 6D). By contrast, megaphyllous leaves have been characterized as not only being larger, but also having a complex, much-branched venation whose leaf trace departure is associated with a leaf gap (Fig. 6E). Traditionally, species in Psilopsida, Lycopsida, and Sphenopsida have been considered to have microphyllous leaves, whereas the ferns (Filicopsida) and all seed plants have been considered to have megaphyllous organs (Gifford and Foster, 1989).

Underlying this difference in leaf homology is the assumption that microphylls and megaphylls have had different phylogenetic origins. The microphyll is considered to have originated as an epidermal scale or emergence from the protostelic axis of a primitively leafless, rhyniophyte ancestor (Fig. 6A, B). Once this appendage had grown out it was vascularized secondarily by an unbranched trace, which became the unbranched midvein in the freely projecting part of the leaf (Fig. 6C, D). Because such stem outgrowths were considered to be homologous with emergences or enations, the interpretation of their phylogenetic origin was called the Enation Theory (Fig. 6A–D).

By contrast, megaphylls have been considered to have originated by a process of cladification (derivation from branch systems) from isotomous, dichotomizing, rhyniophyte ancestors (Fig. 6F), including processes of anisotomy or ''overtopping'' (Fig. 6G), followed by planation (Fig. 6H) and webbing to form laminate leaves (Fig. 6I). This interpretation, which was formalized as the Telome Theory by Walter Zimmermann (1930), has been the prevailing view of the evolutionary origin of megaphyllous organs. The complex venation of the megaphyll leaf product was thus seen as an evolutionary fusion and planation product of a number of protostelic axes (Fig. 6F–I). The appeal of Zimmermann's theory was that it explained the origin of both the morphological and anatomical features of megaphyllous leaves.

Regardless of how firmly entrenched the concepts of microphyll and megaphyll may be in the literature, there are numerous contradictions and inconsistencies that make these concepts questionable and indefensible from the viewpoint of comparative morphology. In the first place, as concepts, they are anatomically, not morphologically based. Given that it is the vascular tissue, particularly the xylem, which tends to be best preserved in fossil plants, it is understandable that the practicing paleobotanist would focus on the vascular strands in defining organ natures and morphology. Anatomical perspectives tend to imply that the vascular system determines the organ's morphogenesis. However, contemporary studies of the relationship of histogenesis (tissue differentiation) to morphogenesis have demonstrated either the independence of these processes or that the morphogenesis is the primary process with histogenesis following form development (Hagemann, 1967; Kaplan and Hagemann, 1991, 1992; Cooke and Lu, 1992; Kaplan, 1992; Kaplan and Cooke, 1997). Thus, while anatomical characters may be the only source of organ definition in many fossil specimens, they can no longer be seen as more basic than the morphology. Whether an organ is or is not a leaf is defined not by its vasculature, but by other, subtler, more fundamental morphological relationships, i.e., basic dorsiventrality of the leaf organ and its distinctive meristem distribution in relation to this symmetry pattern (Kaplan and Groff, 1995).

Regardless of these fundamental considerations of organ determination, within the examples of microphyllous and megaphyllous leaves, each of the criteria are either conflicted or contradicted in each of the major plant groups to the point that it is difficult to distinguish microphylls from megaphylls among contemporary vascular plants. For example, Wagner, Beitel, and Wagner (1982) have described species of *Selaginella* (*S. adunca* and *S. schaffneri*) as having complex dichotomous to reticulate venation patterns in what otherwise have been considered to be classic microphyllous leaves.

Conversely, ferns in the genera *Lygodium*, *Gleichenia*, and all of the filmy ferns (Hymenophyllaceae) have large, dissected fronds with complicated venation, but their stems are protostelic without leaf gaps. Hence, on the basis of their vascular supply, they would not qualify as megaphylls even though other features of their morphology and anatomy make them classical examples of megaphyllous appendages. And while the univeined appendages of *Equisetum* suggest that they are microphyllous leaves, its fossil representatives, such as species of *Sphenophyllum*, have more elaborated leaves with dichotomous venation (Taylor and Taylor, 1993). These species illustrate the lack of correlation between anatomical and morphological features of an organ and underscore that the anatomical features cannot be substituted for morphological characteristics in drawing morphological conclusions.

One could, with equal justification, ask why the linear, univeined leaves in many conifers are not microphylls. The principal reason is that morphologists know that species of *Araucaria*, *Agathis*, and *Podocarpus* have larger leaves with elaborate dichotomous venation and hence assume that the simple, univeined conifer needle has been derived by reduction.

Even the concept of leaf gap in so-called megaphyllous plants (ferns and seed plants) is conflicted and difficult to define. For example, Beck, Schmid, and Rothwell (1982), in a thorough review of stelar structure, have shown that the primary vascular system in the majority of seed plants consists of a longitudinal system of leaf trace sympodia, the leaf traces of which are impossible to distinguish from their sympodial continuations because every axial component ultimately supplies a leaf and itself can be considered a leaf trace. Furthermore, it is largely in those closed sympodial systems with lateral interconnections between adjacent sympodia that a parenchymatic gap is circumscribed above the point of departure of the leaf trace. Such parenchymatic regions appear even more gaplike in those shoots that form secondary vascular tissues from cambial activity. Nevertheless, it is clear from the review of Beck, Schmid, and Rothwell (1982) that the basic configuration of the primary vascular systems of microphyllous and megaphyllous plants do not differ fundamentally from one another, hence the supposed presence or absence of leaf gaps is not a basic distinction between these leaf types.

Even present views of the phylogeny of microphylls and megaphylls are conflicted. While most contemporary texts in morphology and paleobotany accept the difference in derivation (Fig. 6A–D, F–I), Zimmermann (1930) proposed that microphylls were derived from megaphylls by a process of evolutionary reduction rather than by two different phylogenetic origins (enation vs. cladification). Since he was the author of the telome theory, it would be expected that Zimmermann would see the megaphyll as the fundamental leaf type. However, given the lack of a valid distinction between these leaf types, if any phylogenetic interpretation has any validity, Zimmermann's derivation of microphyllous from megaphyllous leaves would seem more credible than their derivation from enations.

The problem with both the enation and the telome theories is that they are gap-filling theories, or hypotheses. There is gap between levels of plant organization, that of the leafless rhyniophyte like plant body and that of leafy shoots. Both the enation and telome theories attempt to bridge this gap by inventing a set of intermediates between these two character states (Fig. 6B, C and Fig. 6G, H). The problem is that the fossil plants discovered after this theoretical derivation are then slotted into the theory rather than being used to test and challenge it. Because these two theories have a phylogenetic slant, in contrast to the typologies of idealistic morphology, they have been taken more seriously than Troll's models because they have been viewed as having been based in a more concrete reality (Zimmermann, 1931, 1953). In fact, Zimmermann's theory is as hypothetical and as much a case of idealistic morphology as Troll's typologies based on contemporary plants. It is just that Zimmermann pushed his type back earlier in time and based it on the morphology of a particular, seemingly concrete fossil form. Given their fundamental similarities, it is ironic that Troll and Zimmermann should have become such arch antagonists.

Finally, Wardlaw (1957) demonstrated that so-called ‘‘microphyllous’’ leaves in pteridophytes are initiated in the same phyllotactic patterns as shoots of their megaphyllous counterparts and that the details of their initiation from their shoot apical meristems are indistinguishable from those of megaphyllous leaves in ferns and seed plants. Thus, there is little legitimate basis for distinguishing microphylls from megaphylls among any contemporary plants in terms of their position or developmental pattern.

Regardless of the phylogenetic theories that have been in vogue, when members of so-called microphyllous and megaphyllous contemporary vascular plants groups are compared morphologically, they are nearly impossible to distinguish morphologically. They are simply ‘‘leaves,’’ whether they represent evolutionary homologies or analogies between their respective groups. Because both microphylls and megaphylls are inseparable components of their shoots, the evolution of leaf morphology must be evaluated in the context of the shoot as a whole and not as isolated organ types. Because the phylogenetic basis for their recognition is so tenuous and theoretical, I think it is best that this distinction between leaf types in vascular plants be abandoned until we have more convincing evidence of a true distinction between them.

A REEVALUATION OF SHOOT MORPHOLOGY IN THE PTERIDOPHYTES

Fundamental principles of shoot organization as deduced from seed plants—Given that the prevailing interpretation of the relationship of leaf morphology between pteridophytes and seed plants seems questionable, I want to look at other basic features of shoot morphology in contemporary pteridophytes to see if they exhibit any primitive features that differ fundamentally from those of contemporary seed plants. In order to provide the criteria for comparison, I first review the principles of seed-plant shoot organization that come from the long history of plant morphology we have just traced. The fundamentality of these principles is further reinforced by demonstrating their expression in all of these pteridophyte groups.

Principle I: Relationship of leaf to stem—The shoots of higher plants are typically characterized as being differentiated into nodes and internodes. The nodes, by definition, are the sites of leaf insertion, whereas the internodes are considered to be the stem units that typically elongate between the points of leaf insertion. The model for such a clear delineation between node and internode is illustrated in Fig. 7A. However, a more accurate model of leaf–stem relationships is illustrated in Fig. 7B. Here, leaf insertion is not localized at the node. Each internode is not just stem, but a compound structure consisting of decurrent leaf bases, that run along the length of the internode below it (Fig. 7B). These decurrent leaf bases corticate the shoot axis, and the photosynthetic tissue one sees at the periphery of a stem transection is actually leaf tissue that is adnate with the shoot axis.

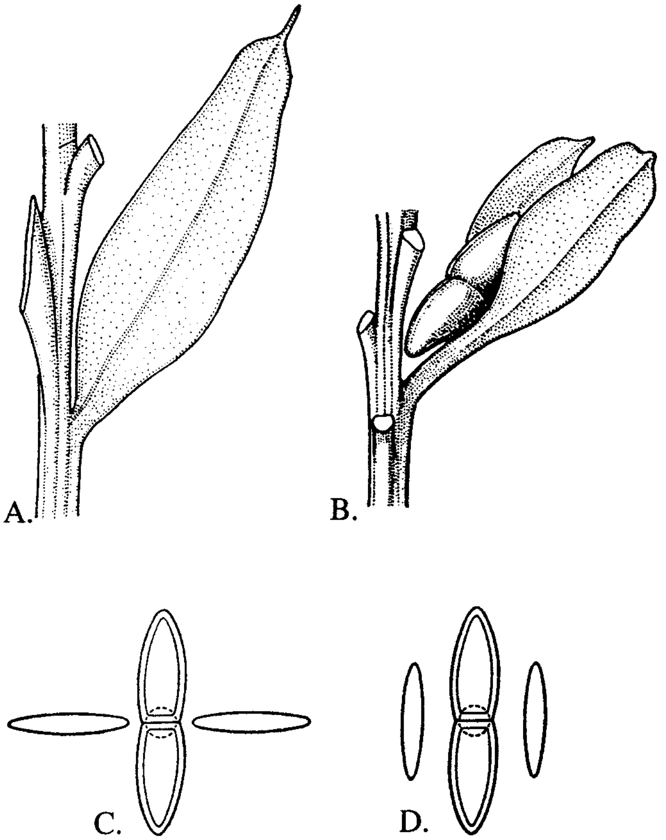

Fig. 16. Morphology and leaflet orientation of sporophylls in *Tmesipteris tannensis.* (A) Shoot axis with vertically oriented vegetative leaf without a significant petiole; all of the other leaf blades have been cut off. (B) Sporophyll, consisting of two sterile, vertically planated leaflets bearing a bilobed synangium on its adaxial surface. In contrast with the vegetative leaf, the sporophyll has a distinct petiole (compare with A). (C, D) Theoretical transectional diagrams showing the orientation of the leaflets if they each were homologous with an individual vegetative leaf (C) and if they were leaflet homologues of a single fertile leaf (D). (Reproduced with permission from Siegert, 1967.)

Because leaf and axis components are inseparable, one uses the term ‘‘shoot’’ to refer to this compound, axial unit. Figure 8(A, B) shows the decurrent leaf bases evident along the lengths of the internodes in *Buxus sempervirens* (Buxaceae) (Fig. 8A), an angiosperm shrub, and *Taxus baccata* (Taxaceae) (Fig. 8B), a gymnospermous shrub. Even if a marginal seam is not conspicuously delimiting the decurrent leaf base along the length of the internode, it is doubtless true that all internodes are corticated along their length by leaf base tissue. When a leaf abscises, only the lamina/petiole region of the leaf (upper leaf zone) falls leaving its decurrent leaf base (lower leaf zone) clothing the axis. According to such a conception of shoot organization, the shoot is not clearly delineated into ‘‘nodes’’ and ‘‘internodes’’ but between the locus of leaf projection and its subjacent basal extension. Hence, the leaf component, not the stem, is the dominant element of the shoot and Goethe’s aphorism ‘‘Alles ist Blatt’’ (‘‘Everything is leaf or foliar’’) (Goethe, 1790) seems even more insightful.

If the point of leaf insertion, in fact, is not restricted to the nodes but runs along the length of what traditionally has been called the internode, then one could predict that the transectional shape of an internode will reflect the pattern of phyllotaxis of its shoot. In fact, this is the case. For example, in shoots with an opposite and decussate phyllotaxis, as found in many mints, internodes are square as a consequence of the four diagonal orthostichies of leaf insertion (Fig. 7C). By contrast, internodes in shoots with a two-ranked or distichous

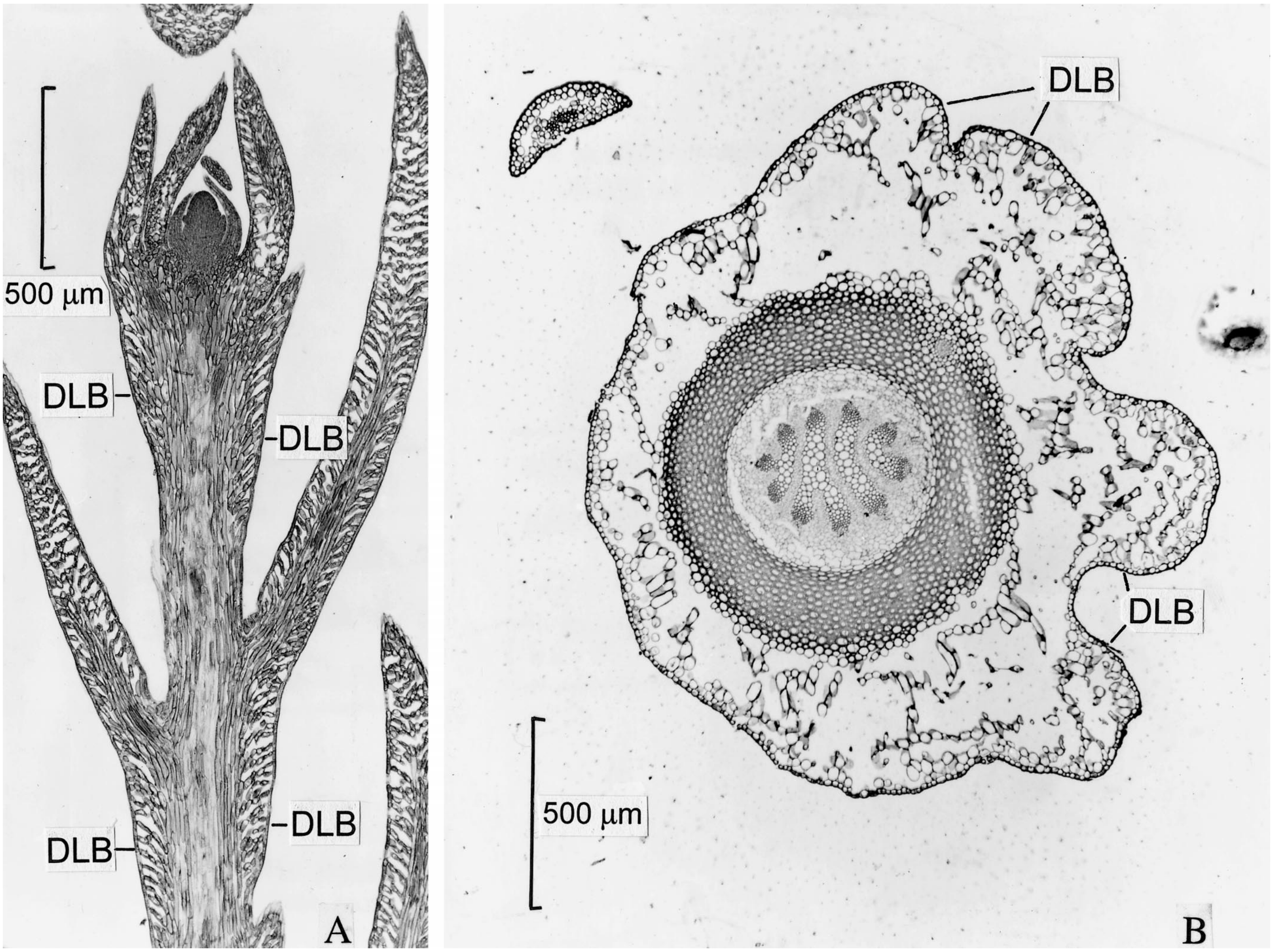

Fig. 17. Shoot morphology in *Lycopodium.* (A) Near-median longisection of the shoot tip, including the shoot apical meristem and youngest leaves of *Lycopodium* sp. (most likely *L. complanatum*), showing leaves with decurrent leaf bases, which elongate in conjunction with elongation of the axis and have the same histology as the freely projecting blade region. (B) Transection of the axis of *L. complanatum,* showing that the cortical tissue, as shown in longisection in (A), is part of the decurrent leaf bases. ([A] from a commercial microscope slide made by Triarch, Ripon, Wisconsin, USA.)

phyllotaxis have a bilaterally symmetrical or elliptical shape, reflecting their alternate pattern of leaf insertion (Fig. 7D). Internodes with a helical or polystichous phyllotaxis exhibit a polygonal outline, reflecting the fact that leaves are inserted at an infinite number of radii around the shoot's circumference (Fig. 7E).

Leaf insertions extend along the length of an internode because the leaves are initiated from the periphery of the shoot apex before there is any significant extension of the internodes. Since the incipient internode is such a short region (only a couple of cell diameters high), a part of the leaf base is inevitably included with shoot elongation (shaded areas in Fig. 7F, G). Thus the shoot axis, represented in its purest form by the central pith region, is always corticated by surrounding leaf tissues (Fig. 7G).

In passing, it should be noted that these deductions on leaf–stem relationship can only be observed in the region of the shoot where the primary body is retained unchanged. If secondary growth occurs, then the contribution of leaves to the transection of the shoot axis will either be obscured or lost. This is not a problem with the contemporary pteridophytes we characterize below because none of them exhibit any secondary growth.

Principle II: Rhythms of primary thickening growth (''Erstarkungswachstum'')—A second principle in the growth of the shoots of seed plants is an ontogenetic rhythm in shoot primary thickening that has been termed ''Erstarkungswachstum'' or ''strengthening growth'' by the Germans (Troll and Rauh, 1950). The German word ''Erstarkungswachstum'' actually refers both to the ontogenetic increase in stem diameter and to the decrease in the distal, flowering region of a shoot, especially in herbaceous annual plants (Fig. 9A) (Troll and Rauh, 1950). In this regard, Tomlinson and Zimmermann's (1966) use of the term ''establishment growth'' for ''Erstarkungswachstum'' seems even less appropriate because of the functional, adaptational connotations of the term ''establishment.'' In fact, the obconical shape of young shoot regions, by itself, is not a mechanically sound construction. Without an augmentation of mechanical support, either in the form of shoot-borne prop roots or secondary growth, such an inverted cone axis would not be stable. Thus, it is more accurate to use

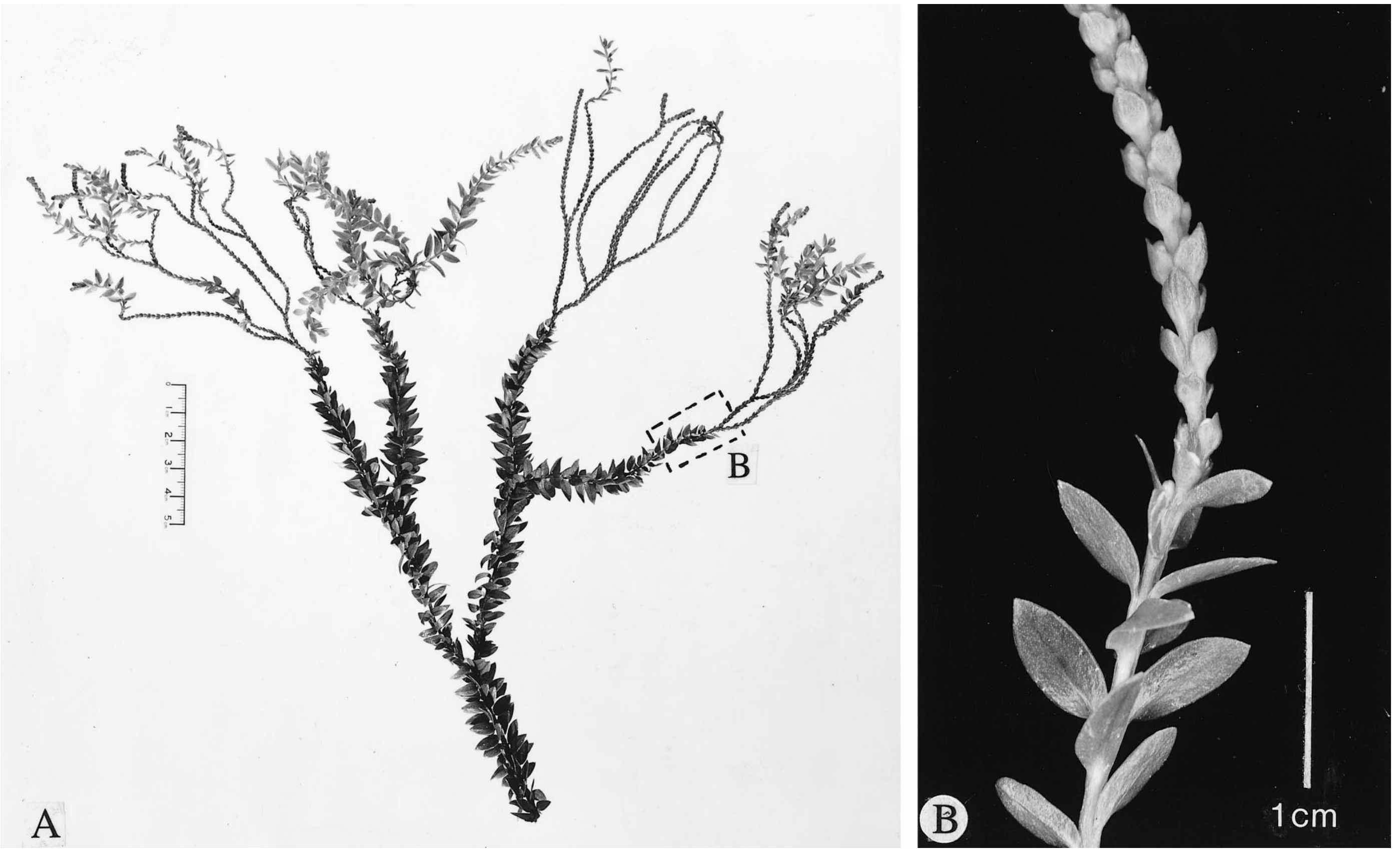

Fig. 18. Sporophyll and trophophyll transitions and morphology in *Huperzia phlegmaria.* Distal portion of the shoot, showing isotmous branching in both the proximal vegetative region and in the distal strobili. Note that this species also shows regular reversions to vegetative growth at the tips of many of the strobilus branches. (B) Detail of transition between vegetative proximal region and the sporophyll-bearing base of a cone segment, corresponding to region (B) delimited in (A).

a neutral, purely descriptive term, such as ''Erstarkungswachstum'' or primary thickening rhythm for this aspect of shoot development.

Troll and Rauh (1950) have shown that such an ontogenetic cycle in primary thickening is characteristic of ferns and all seed plants, whether they undergo secondary thickening or not. The obconic shape of the base of the shoot axis is most evident in the shoots of pteridophytes and monocotyledonous angiosperms because they lack the secondary growth that masks this inverted cone form at the base of shoots of gymnosperms and dicotyledons. However, Troll and Rauh (1950) have illustrated the occurrence of obconic young axes in aquatic dicotyledons such as *Oenanthe aquatica* and *Sium latifolium* (Apiaceae) because they also show so little secondary xylem formation (Fig. 9A–D). Even in dicotyledons, such as *Helianthus annuus* (Asteraceae), which has a substantial amount of secondary xylem at the base of its shoot, the obconical shape of its primary axis is preserved in the shape of its pith (Troll and Rauh, 1950) (Fig. 9G, H).

While the obconic axis shape is characteristic of the earliest phases of shoot ontogeny, sooner or later this primary thickening impulse reaches a maximum and is followed by a decrease in axis diameter, usually coinciding with the onset of the reproductive phase (Fig. 9A). Correlated with these changes in axis diameter are corresponding increases and decreases in the maximal diameter of the shoot apex (Troll and Rauh, 1950). Although it has been traditional to interpret the changes in the diameter of the shoot apex as the cause of changes in dimensions of the subjacent axis (Steeves and Sussex, 1989), it is virtually impossible to distinguish cause and effect between the shoot apex and axis in the intact plant. For these reasons, their relationship is best left as a correlation.

Other characteristics that also change in correlation with the primary thickening rhythm are leaf and lateral bud size and complexity. For example, in the leaf series in *Sium latifolium* shown in Fig. 9E, the primary leaves that follow the simple spatulate cotyledons (Fig. $9E_{I}$) have palmately dissected and ternate blades and are inserted at the narrowest shoot nodes (Fig. $9E_{II,III}$). As shoot axis diameter increases, leaves inserted at the wider nodes become correspondingly longer, with a greater number of pinnae in their blade sectors (Fig. 9B, E_{IV}), reaching their maximum length and pinna number in the widest part of the shoot (Fig. $9E_{V}$). Conversely, as the axis becomes narrower in the distal, reproductive region, the structure of the leaves, expressed as floral bracts, become reduced and simpler, but not necessarily in a way identical to the simplified primary leaves in the juvenile region of the shoot (see Figs. 11, 12).

Axillary buds borne at the widest nodes of the shoot axis also tend to be larger, and they also are the buds from which renewal growth will occur (Fig. 9F and D, respectively). I (Kaplan, 1973) have demonstrated such a correlation between lateral bud size and stem diameter in the rhizomatous shoots of *Acorus calamus* (Acoraceae). I showed that all the buds, regardless of size, contain the same number of leaves and leaf primordia (about ten). The differences in bud size reflect differences in sizes of the axillary meristems and their leaf products. Thus, the entire shoot system shows an integration of all of its components in this thickening process.

If a given species initiates roots from its shoot axis, the number of roots initiated will also show a correlation with this primary thickening rhythm; shoots with narrow diameter axes will have a smaller circumference and will form fewer roots per node than those with a larger stem diameter (Troll and Rauh, 1950) (Fig. 9F and C, respectively).

Collectively, all of these changes in shoot morphology, including the ''Erstarkungswachstum'' of the axis, are an expression of the heteroblastic development of the shoot as a whole (Allsopp, 1967). Heteroblastic development usually has been described in terms of differences in leaf morphology because it is the most obvious expression of change in shoot form. But the evidence of a spectrum of integrated events (leaf and axis development as well as differences in bud and root development) underscore that this heteroblastic change is a whole-organism phenomenon and not restricted to an individual organ component of the shoot (Troll and Rauh, 1950; Allsopp, 1967).

Principle III: Developmental segmentation of leaf primordia and their relationship to heteroblastic changes in mature leaf morphology—Eichler (1861) recognized that the earliest differentiation of a leaf primordium after its initiation from the shoot apex is into a broader, axis-encircling proximal region that he called the lower leaf zone (''Unterblatt'') and a distal, typically narrower and freely projecting region that he called the upper leaf zone (''Oberblatt'') (Fig. 10C, D). Typically, the upper leaf zone differentiates into the lamina and petiole regions of the leaf (Fig. 10D, E, and A respectively), whereas the lower leaf zone differentiates into the leaf base and its appendages (the stipules), if these are developed (Fig. 10D, E, A, and B respectively). The extent to which the upper and lower leaf zones are differentiated from each other may vary between species. Where upper and lower leaf zones are clearly distinguishable, one can see in the heteroblastic leaf series a developmental articulation between these two different leaf zones where successive leaves show differing degrees of upper and lower leaf development.

In many members of the parsley family (Apiaceae), for example, the leaf base region is sharply set off from the upper leaf zone by differences in color and venation. For example, in the cow parsnip *Heracleum lanatum,* the aerial shoot exhibits a primary thickening rhythm, bearing leaves of differing degrees of elaboration correlated with axis diameter (Fig. 11). All of its leaves have sheathing to median stipulate leaf bases (Figs. 11, 12), and as one follows the leaf series distally from the basal rosette to the inflorescence region, successive appendages show a progressive reduction of the upper leaf zone (Fig. 12A–E) and the cauline bracts consist of the lower leaf zone either predominantly or exclusively (Fig. 12F–H). Thus, not only does the heteroblastic sequence of leaves change in size and degree of elaboration but also in terms of the proportions between these major zones of the leaf.

Shoot organization in principal pteridophyte groups—Having characterized the three basic principles of seed-plant shoot organization and development, I now want to determine if these concepts are also expressed in members of each of the of the major groups of contemporary Pteridophytes.

Psilopsida—Because of the seemingly simple, inconspicuous nature of its leaves, the isotomous nature of its aerial shoot branching and lack of roots, and its isomorphic alternation of generations, *Psilotum* has been seen by many paleobotanists and plant morphologists as a living ''rhyniophyte'' (Rouffa, 1971, 1978; Stewart and Rothwell, 1993). Certainly, at a superficial level *Psilotum* would seem to simulate those ancient fossil plants (Fig. 13A). However, a more critical analysis of its morphology and shoot organization reveals that despite its seeming simplicity, *Psilotum* exhibits the same level of organization as that of seed plants. Had the more elaborated morphology of its related genus *Tmesipteris* been studied thoroughly before that of *Psilotum*, the latter would have been more accurately interpreted because *Tmesipteris* would have provided the appropriate context. Because species of *Tmesipteris* are more exotic than those of *Psilotum*, and because many investigators saw *Psilotum* as a rhyniophyte, *Psilotum* has been the focus, rather than its more elaborated relative. However, the critical and comprehensive studies of Albrecht Siegert on *Psilotum* (Siegert, 1964, 1965, 1967, 1969, 1970, 1973) provide fundamental information on the morphology and development of *Psilotum nudum* that decisively refutes this rhyniophyte bias.

The shoot of *Psilotum nudum* is differentiated into a plagiotropic, subterranean, nonphotosynthetic region called the ''cryptophilic zone'' and an orthotropic, photosynthetic sector called the ''photophilic zone'' (Siegert, 1964) (Fig. 13A). The typically subterranean cryptophilic axes are devoid of leaves, but bear rhizoids, whereas the photophilic shoots bear reduced, scale-type leaves (Fig. 13A). The cryptophilic zone also differs in the irregularity of its branching, as contrasted with the regular, cruciate dichotomy in the distal region of the photophilic zone (Fig. 13A). Siegert (1964) has noted that sporophylls in *Psilotum* tend to be restricted to the ultimate branches of the photophilic shoot (Fig. 13A). However, he has also shown examples where sporophylls occur distal to the final branching point.

In contrast with the leafless cryptophilic zone, *P. nudum*'s photophilic shoots bear leaves along their length, even though they may be inconspicuous (Fig. 13A, B). Figure 14 (A, B) shows the details of the simple scale leaves borne at the base of the photophilic shoot (Fig. 14A) and a sporophyll from the distal, fertile region (Fig. 14B). The sterile leaf typically is awl-shaped and trough-like at its point of insertion (Fig. 14A). By contrast, the fertile leaf has two lobes, each of which resembles the reduced blade of the sterile leaf, but bearing a trisporangiate synangium on its adaxial surface (Fig. 14B). Like the shoots of seed plants, both sterile and fertile appendages have decurrent leaf bases along the length of the shoot axis below the point of blade insertion (Figs. 13B, 14A, B). Using Eichler's (1861) terminology, the freely projecting region of a sterile leaf would correspond to its upper leaf zone, whereas the decurrent ridge would correspond to its lower leaf zone.

Siegert (1964) has shown that the shoots of *P. nudum* exhibit a distinct primary thickening rhythm or ''Erstarkungswachstum,'' which we have described for the shoots of seed plants. Furthermore, correlated with this cycle of axis thickening are changes in size and degrees of elaboration of the appendages borne on those shoot regions. The region of max-

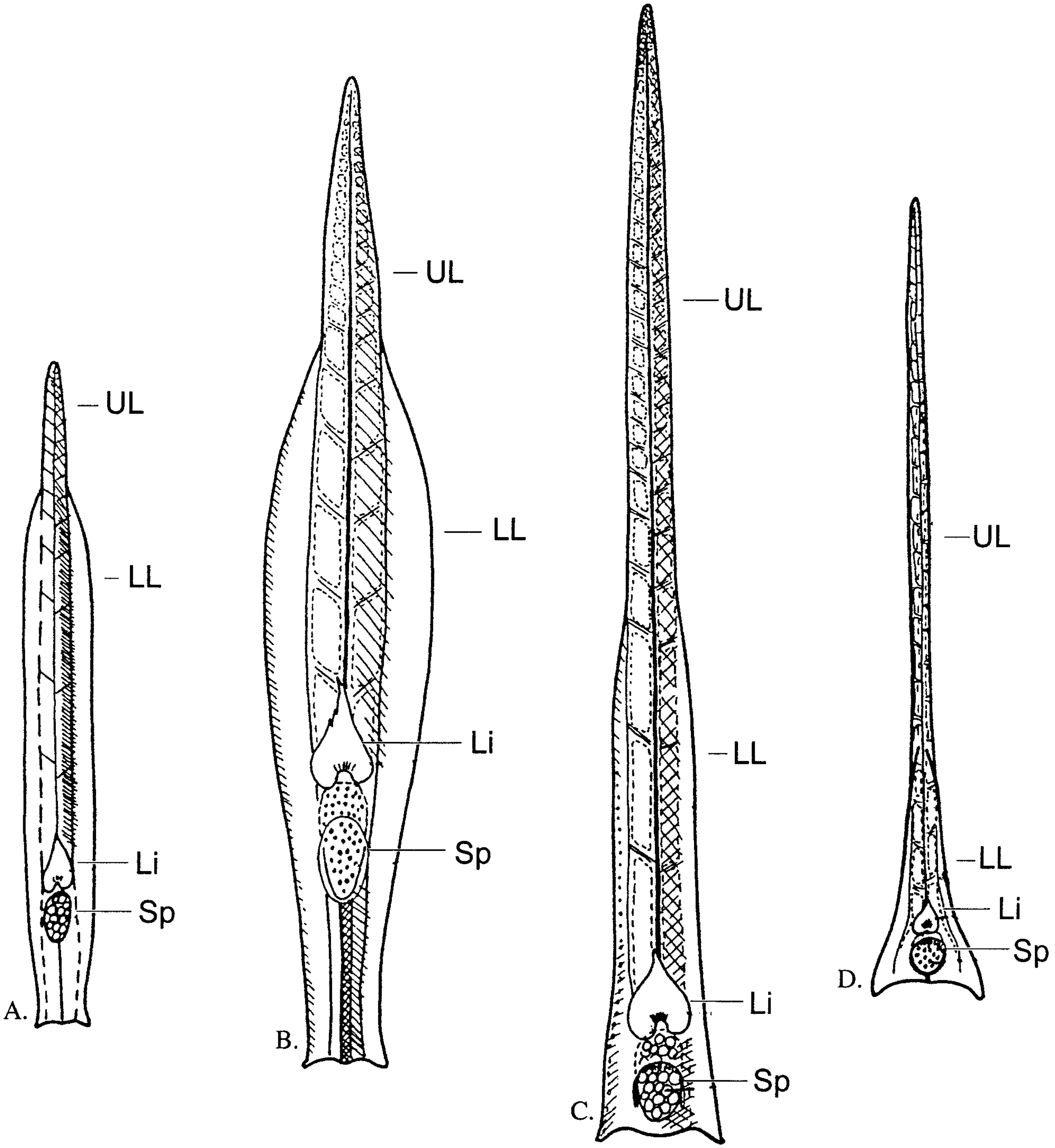

Fig. 19. Comparative morphology of sporophylls in members of Isoëtaceae, showing the relationship between the distal projecting blade region and the proximal sheathing base as well as the position of the ligule and sporangium on the adaxial surface of each leaf. Drawings semidiagrammatic and not to absolute scale. (A) *Stylites gemmifera.* (B) *Isoëtes andina.* (C) *Isoëtes novogranadensis.* (D) *Isoëtes lacustris.* (Drawings contributed by Dr. W. Hagemann from an unpublished book manuscript and reproduced with permission.)

imal thickening typically occurs in the transition between the cryptophilic and photophilic zones at the site where the stem undergoes its change from a plagiotropic to orthotropic growth (Fig. 13A). From that point to the distal extremity of the photophilic zone, the diameter of the shoot typically declines (Fig. 13A, B).

This distal narrowing of the shoot axis is expressed in the changes in phyllotaxis along its length. For example, the basal region of the photophilic shoot will bear six to nine ribs or phyllotactic orthostichies (Fig. 14A). As these axes narrow distally, the phyllotactic fraction becomes reduced to the one third or tristichous pattern characteristic of the fertile region of the shoot (Fig. 14B). Hence, as one proceeds distally in this primary thickening cycle, the greatest proportion of aerial shoot diameter is made up of the decurrent leaf ridges instead of the central stem region of the axis. This decrease in stem

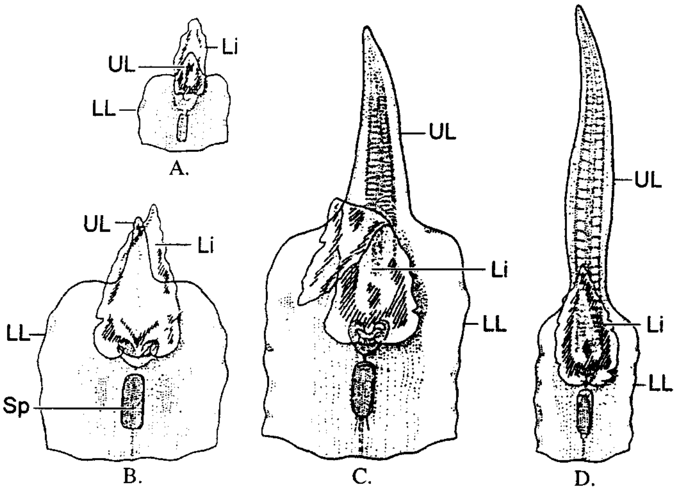

Fig. 20. Stages of sporophyll development as seen in dissected leaf stages of *Isoëtes andina.* Leaves as observed from the adaxial surface so that the changing proportions between upper and lower leaf zones and ligule can be seen in successively older (larger) leaf development stages. (Reproduced with permission from Kubtzki and Borchert, 1964.)

diameter is thus a consequence not only of branching, but also of the size of the leaf primordium relative to the volume of the shoot apex (Fig. 14D, F). In the maximal phase of shoot development, leaf primordium size is small relative to apical volume (Fig. 14C, D), whereas in the distal fertile region, the relationship is the opposite (Fig. 14E, F).

Normally, determination of each ultimate photophilic branch is associated with this progressive dwindling of the diameter of the shoot apex. However, quite often the shoot tip will proliferate, producing an axis that is markedly thickened compared with the region that preceded it. For example, the specimen shown in Fig. 13C exhibits a shoot segment with the typical reduction of axis diameter associated with the end of the fertile region of a photophilic branch. However, instead of terminating growth, its meristem has reverted to vegetative development, forming scale leaves in a distichous rather than the tristichous pattern that preceded it. More significantly, however, this proliferated shoot segment shows a progressive increase in axis diameter, regaining the maximum diameter characteristic of the more proximal fertile shoot regions (Fig. 13C).

Siegert (1964, 1969, 1970, 1973) has shown that such reversions to vegetative growth, but without the aforementioned marked change in phyllotaxis and symmetry of the example in Fig. 13C, is quite common in photophilic shoots of *P. nudum.* In these instances, there can be two to three tiers of fertile shoot segments, separated by one or more unitipped sterile appendages that Siegert has called ‘‘onset’’ leaves (‘‘Anlaufblätter’’) (Siegert, 1964). Each successive tier is characterized by an increase in axis diameter, followed by its narrowing (Fig. 15). Correlated with these changes in axis diameter are corresponding changes in the size and degree of elaboration of the sporophylls borne on these shoot segments. For example, the first fertile tier exhibits the narrowest axis diameter (Fig. 15A). Following a short zone of normal sporophyll formation, there is a zone of moderate to weak development of sporophylls ending in very reduced or what Siegert terms ‘‘hypoplasious’’ sporophylls (Fig. 15A).

The bifid onset leaf marks the beginning of the second fertile tier. The axis of the second tier undergoes the greatest increase in diameter and forms the most elaborated (‘‘Hyperplasious’’) sporophylls with up to three synangia and four sporophyll lobes per appendage (Fig. 15B). As the diameter of the axis of the second tier declines, normal trisporangiate sporophylls are formed, followed again by reduced sporophylls (Fig. 15B). The third fertile tier again begins with a bifid onset leaf, repeating the cycle of fully developed sporophylls and ending in reduced sporophylls (Fig. 15C). If a fourth tier is formed, the axis is again dilated, but the sporophylls are aggregated together because of the lack of internodal elongation (Fig. 15D). In this region of terminal sporophyll aggregation, the synangia exhibit various degrees of fusion and distortion (Fig. 15D).

The regular occurrence of sporophylls bearing two and even three synangia on their adaxial surface refutes previous suggestions that the synangium in *Psilotum* actually terminates a lateral branch and that the two lobes of the sporophyll are homologous with individual sterile leaves (e.g., Bierhorst, 1956). In addition to evidence from these variant sporophyll morphologies, Siegert (1967) noted that branch and leaf primordia in *Psilotum* are not only distinctive from inception but also occupy different positions in the shoot.

Siegert (1967) also pointed out that adaxial insertion of synangia in Psilotaceae is even more convincingly demonstrated in *Tmesipteris.* The blade surfaces in both the sterile and fertile leaves in *Tmesipteris* differ from those of *Psilotum* because of their distinctive vertical planation or flattening in the median rather than the usual transverse plane (Fig. 16A, B). The bisporangiate synangium of *Tmesipteris* is inserted on the adaxial surface of the sporophyll, not its apex (Fig. 16B). Siegert (1967) indicated that if each of the leaflet lobes of the sporophyll of *Tmesipteris* were the homologue of an individual sterile leaf, with their median flattening, they would exhibit the orientation shown in Fig. 16C. Instead, they show the orientation shown in Fig. 16D, which is the same as that of the sterile, vegetative leaf (compare Fig. 16B with A).

This use of *Tmesipteris* to help understand the morphology of *Psilotum* illustrates how much more definitive morphological interpretations of *Psilotum* could be if comparisons were made between these two genera rather than depending exclusively on the more enigmatic, reduced *Psilotum.*

An example of previous attempts to squeeze the morphology of *Psilotum* into a rhyniophyte model is the paper by Rouffa (1971) on what he termed an ‘‘appendageless’’ variant of *P. nudum.* According to Rouffa, this form seemed to bear no appendages and its synangia were clustered at the tips of its branches, reminiscent of an ancient, *Rhynia*-type morphology.

Rouffa’s deductions seem to have been made without a knowledge or understanding of Siegert’s previous investigations. Critical examination of Rouffa’s figures demonstrates that while superficially this form may seem appendageless, it is not leafless. All of its shoots have decurrent leaf bases of wild-type *Psilotum* and these leaf bases fall into the same phyllotactic pattern as wild-type *P. nudum.* Since these decurrent bases are developmental expressions of the lower leaf zone, it is the upper leaf zone or lamina region that is reduced. In fact in some of Rouffa’s specimens, a reduced, stublike upper leaf zone is evident at the summit of each decurrent base. Because he accepted Bierhorst’s (1956) branch homology of the synangium, Rouffa (1971) referred to these reduced laminae as ‘‘branch stubs’’ on the assumption that they rep-

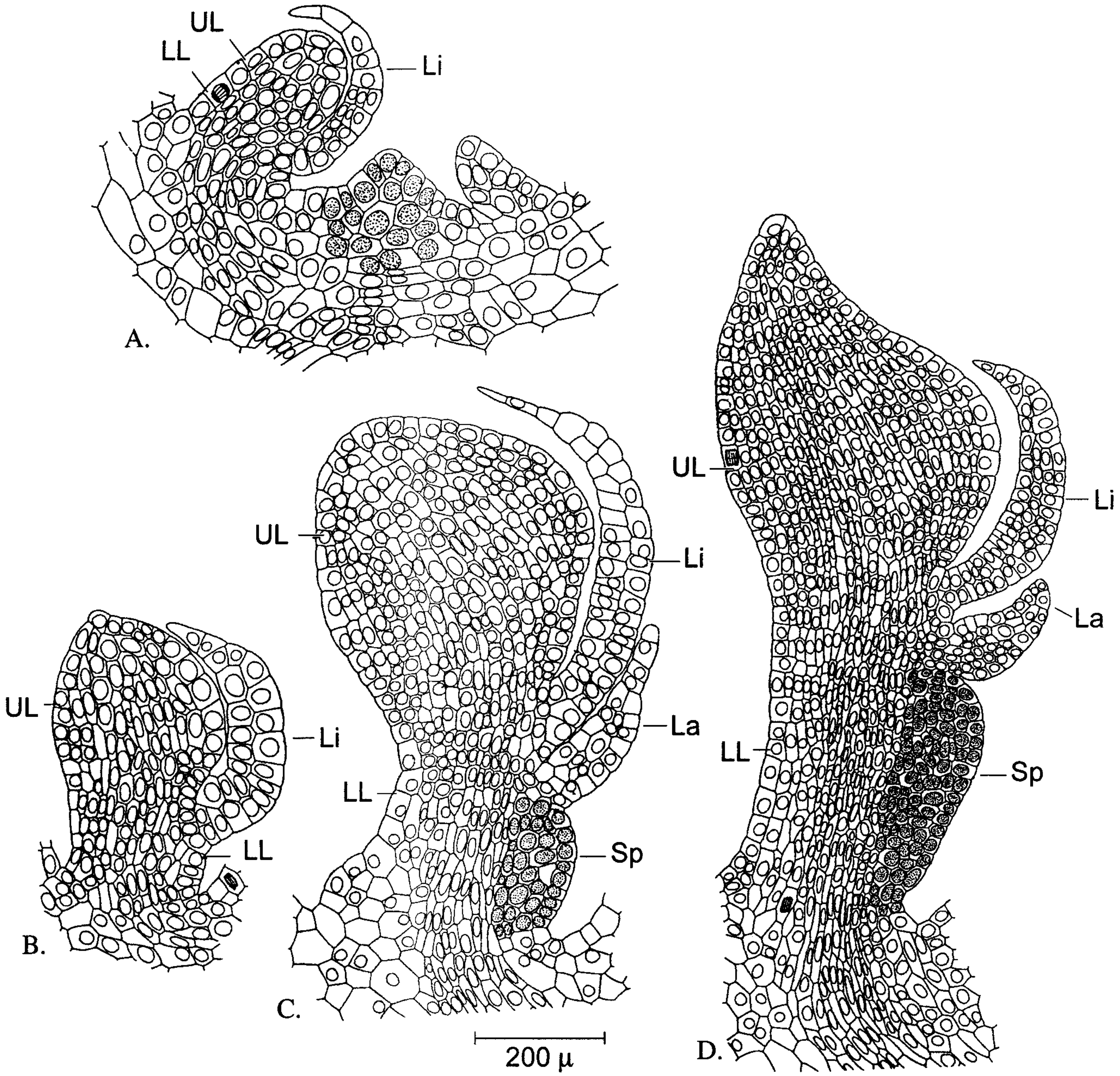

Fig. 21. Median radial longisections of successive stages of sporophyll development in *Isoëtes lacustris.* (A) Leaf ~100 μm long. (B) Leaf ~200 μm long. (C) Leaf ~400 μm long. (D) Leaf ~550 μm long. (Drawings contributed by Dr. W. Hagemann from an unpublished book manuscript and reproduced with permission.)

resented variously arrested branch outgrowths. Since Siegert (1967) convincingly demonstrated that shoot branches and leaves in *Psilotum* occupy different positions in its shoot system, it is clear that these ''branch stubs'' are not branch, but leaf homologues.

There are a host of xeromorphic species (e.g., *Rhipsalis* in Cactaceae) in which the upper leaf zone is reduced or even absent and only the leaf base region is expressed. Given the marked degree of phenotypic plasticity exhibited by species of *Psilotum,* such an ''appendageless'' variant is not surprising. Since its synangia are normally borne on the lamina surface, if the lamina is reduced, the synangia will not be developed on the elongated axes. The terminal region is thus the only zone where synangia are developed in this variety, comparable to the normally occurring sporophyll aggregation that Siegert (1973) has characterized (Fig. 15D).

Thus, despite the predominance of previous interpretations suggesting *Psilotum* is a living rhyniophyte, critical modern studies on the organization and developmental patterns of its shoot indicate that both genera of Psilotaceae exhibit a shoot organization like that of seed plants. Not only is the leaf component an integrated element of the shoot as indicated by its decurrent leaf bases, but also its regular changes in size and complexity correlate with the cycles of primary thickening growth, as in all vascular plants (Troll and Rauh, 1950). Regardless of what its phyletic history may have been, the or-

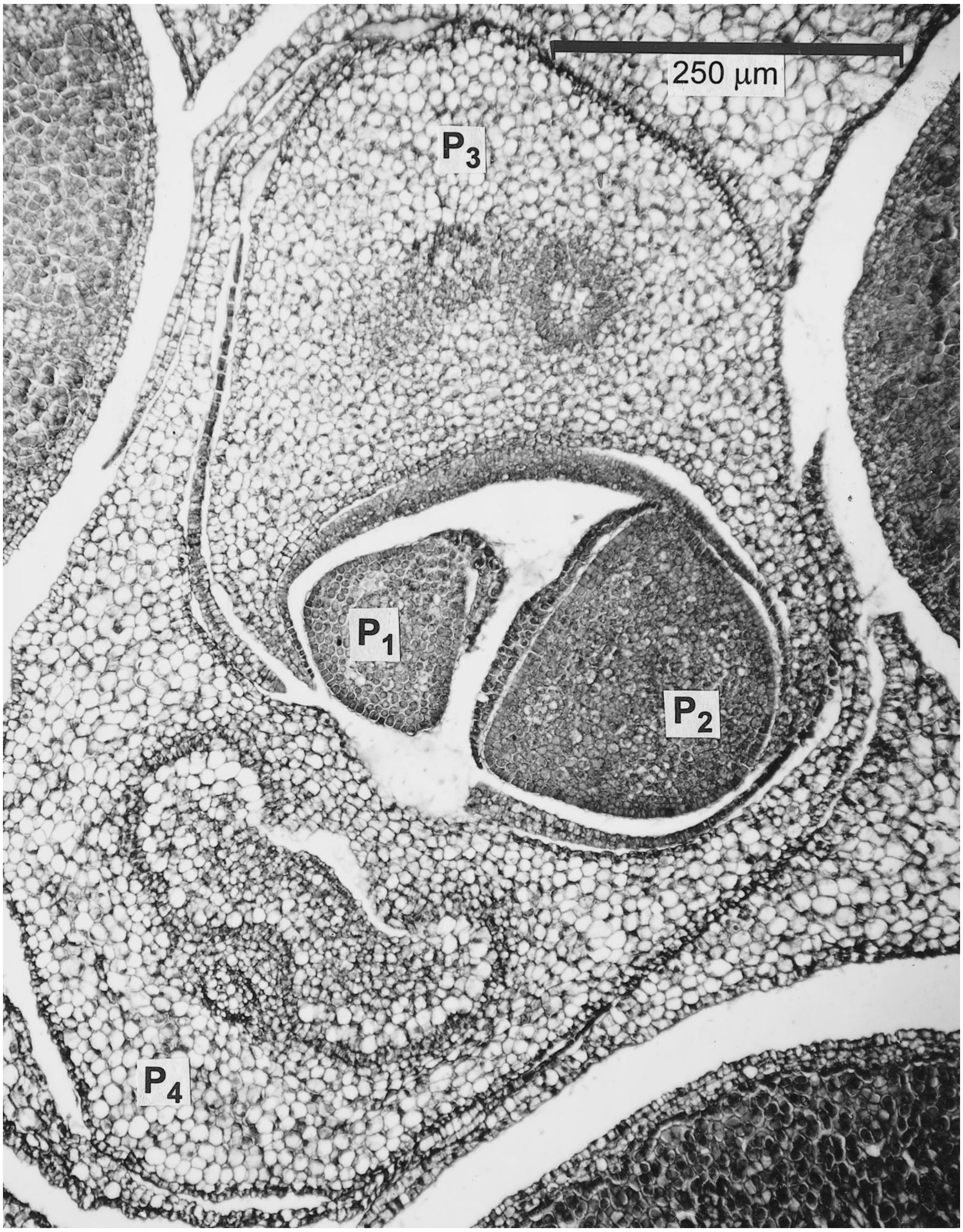

Fig. 22. Transection of the terminal bud of the shoot of *Isoëtes melanopoda,* showing successive leaves in a helical phyllotaxis. The youngest leaves visible (P_1 and P_2) are cut through the future lamina region (upper leaf zone), whereas the older leaves (P_3 and P_4) are cut through the sheathing base region (lower leaf zone).

ganizational level of *Psilotum* is comparable to that of other vascular plants of a wide range of affinities. Moreover, the simplified nature of its leaves is suggestive of an evolutionary reduction rather than an enation homology.

Lycopsida—The clubmosses in the genera *Huperzia, Lycopodiella, Lycopodium, Phylloglossum, Selaginella, Isoëtes,* and *Stylites* differ from the Psilopsida in their development of roots and larger and more elaborate leaves. Like the whisk ferns (Psilopsida), Lycopsida traditionally have been viewed as being primitively microphyllous. Despite this traditional characterization, like members of Psilotaceae, they exhibit features of shoot and leaf morphology that contradict these views.

All members of the homosporous Lycopodiaceae have decurrent leaf bases just as we have described for seed plants and *Psilotum.* Figure 17A, for example, shows a portion of a longitudinal section of the shoot of a species of *Lycopodium* (most likely *L. complanatum*). Its decurrent leaf bases are evident and exhibit the same histology as their freely projecting blades (Fig. 17A). The transection of a so-called ‘‘internode’’ of *L. complanatum* gives a similar image; it is impossible to distinguish the cortex of this axis from the leaf base region of the appendages because they are one and the same (Fig. 17B). Given that the so-called leaf cushions that persisted on the trunks of fossil arborescent lycopods such as *Lepidodendron* and *Sigillaria* (Stewart and Rothwell, 1993) are also decurrent leaf bases, the expression of the same characteristic in living lycopods suggests that this organizational feature may have had its origin early in lycopod evolution.

Transitions observed between the photosynthetic, leaf-bearing (i.e., trophophylls), vegetative region of its shoot and the sporangia-bearing reproductive region of shoots of *Huperzia* are similar to the transitions between foliage leaves and inflorescence bracts we have noted above in the transitions between vegetative and reproductive regions of flowering plant shoots (Fig. 12). For example, shoots of *H. phlegmaria* commonly exhibit several cycles of reversions from vegetative shoot to cone formation and then back to vegetative shoot development (Fig. 18A). Figure 18B shows a detail of a transition between the trophophyllic and sporophyllic regions of a shoot of the type shown in Fig. 18A. Here it can be seen that in transition to the sporophyll, the projecting lamina region becomes reduced in successive leaves until it is evident only as a small, spike-like protrusion, projecting from the widened sporophyll leaf base region, which barely encloses its adaxial sporangium (Fig. 18B). Like many vaginate bracts in angiosperm reproductive shoots, in the cone of *Huperzia phlegmaria* its sporophylls are similarly vaginate organs in which the lower leaf zone is enlarged and its upper leaf zone or lamina equivalent is reduced.

An even more marked example in Lycopsida of the fact that variations in leaf morphology are due to differing degrees of expression between upper and lower leaf zones of their leaf primordia is exhibited by members of the family Isöetaceae-*Isoëtes* and *Stylites.* Figure 19A–D illustrates sporophyll morphology in *Stylites gemmifera* (Fig. 19A) and three species of *Isoëtes* (Fig. 19B–D). Each of these leaves is differentiated into a distal, projecting lamina or upper leaf zone equivalent (UL Fig. 19A–D) and a proximal leaf base or lower leaf zone equivalent evident as a membranous sheath (LL Fig. 19A–D). The boundary between upper and lower leaf zones can be demarcated by the transectional outline between the narrow, projecting upper leaf zone and its broader leaf base region: the upper leaf zone tends to be thickened, subunifacial to nearly triangular in outline, whereas the leaf base appears strictly bifacial with broad membranous wings (see Fig. 22). Both the ligule and large sporangia are borne on the adaxial surface of the sheathing base (Fig. 19).

Each of the four sporophylls illustrated shows a different proportion of upper to lower leaf zone length. In both *Stylites gemmifera* and *Isoëtes andina,* the leaves have a relatively short upper leaf zone and a sheathing base comprising two-thirds or more of the total leaf length (Fig. 19A, B). In *Isoëtes novogranadensis,* upper and lower leaf lengths are nearly equal (Fig. 19C), whereas in *I. lacustris,* the lower leaf zone is significantly shorter than the upper leaf blade (Fig. 19D). It is clear that the central, lacunate rib region of the leaf is continuous from the upper leaf zone through the lower leaf zone (Figs. 19A–D). This is an example where the anatomical level of organization is independent of the morphological level in the same organ. This observation reinforces the conclusion that histological characteristics cannot be substituted for morphological characteristics in drawing morphological conclusions.

Evidence for the validity of the delineation of upper leaf and lower leaf zones in the mature leaves of species in Isoëtaceae described above comes from the study of the youngest stages of leaf morphogenesis, when these two regions are defined. Figure 20A–D shows the developmental stages of young, whole leaves of *Isoëtes andina* (Kubitzki and Borchert, 1964). At the earliest stage of development, enlargement of the lower leaf zone is more extensive than the upper leaf zone (Fig. 20A). Not only is the lower leaf zone significantly longer and wider than the upper leaf rudiment projecting from it distally, but the upper leaf is completely covered by the ligule, which is significantly longer at this stage (Fig. 20A). In its precocious rate of extension, the ligule is reminiscent of stipules in angiosperm leaves (Troll, 1937–1943). Once the ligule has reached its final length, the upper leaf zone continues to elongate (Fig. 20B, C) and ultimately extends beyond its ligule (Fig. 20D), dwarfing it in the mature leaf (Fig. 19B).

One of the reasons upper and lower leaf zones are more sharply delimited in the early stages of development in *I. andina* is that the broader, more rectangular shape of the lower leaf zone delineates a longitudinal boundary between it and the upper leaf zone early in sporophyll development (Fig. 20A–C). However, as the upper leaf zone projects more extensively, the distal margins of its sheath are drawn upward at a less acute angle (Fig. 20D), foretelling its more gradual transition to the upper leaf in the mature sporophyll (Fig. 19B).

Histological sections of early stages of leaf development in *I. lacustris* and *I. melanopoda* further substantiate this early differentiation of these primordial leaf zones in sporophyll development. For example, Fig. 21A–D shows median longisections of successive stages of early development of the sporophylls of *I. lacustris.* From the earliest stage shown, the point of ligule insertion occurs below the boundary between upper and lower leaf zones (Fig. 20A). Characteristically, at this early stage, precocious elongation of the ligule has caused it to be swept back over the leaf apex, covering it almost completely (as seen in the leaf dissections, compare Fig. 21A with Fig. 20A). However, at this early stage, the upper leaf zone is already characterized by the greater thickening growth that sets it off from its leaf-base region (Fig. 21A) and that becomes more accentuated in later stages of development (Fig. 21B–D). The thickening growth of the upper leaf zone is both adaxial and abaxial, associated with radially oriented cell lineages derived from the protoderm on both sides of the leaf (Fig. 21B–D). In this marked radial growth, the young leaf stages of *Isoëtes* resemble unifacial leaves in the monocotyledons, which have upper leaf regions that undergo growth predominantly in volume, in contrast with the surface growth of their sheathing bases (lower leaf zones) (Kaplan, 1975). However, the lower leaf zone of *Isoëtes lacustris* only undergoes thickening growth when it initiates its massive sporangium from the adaxial surface of its basal sheath (compare Fig. 21C, D with B). Once the apex of the upper leaf zone becomes attenuated, the basipetal wave of leaf maturation sets in and the meristematic activity of the leaf becomes displaced basally, in a classic case of basiplastic leaf differentiation, with the proximal sheath being the last zone of the leaf to reach its full length (Fig. 21D).

Transections of successively older leaves of *I. melanopoda* illustrate the marked difference in shape and growth mode of the upper and lower leaf zones. In Fig. 22, transections through primordia P_1 and P_2 pass through the upper leaf zones of their leaves, showing their bifacial (dorsiventral) outline, whose growth in volume is emphasized over growth in surface. As shown by the sections through leaves P_3 and P_4, that are cut though the lower leaf zone or future sheathing base (Fig. 22), transectional growth in the lower leaf zone is more in surface than in volume. In these successive stages of sheath devel-

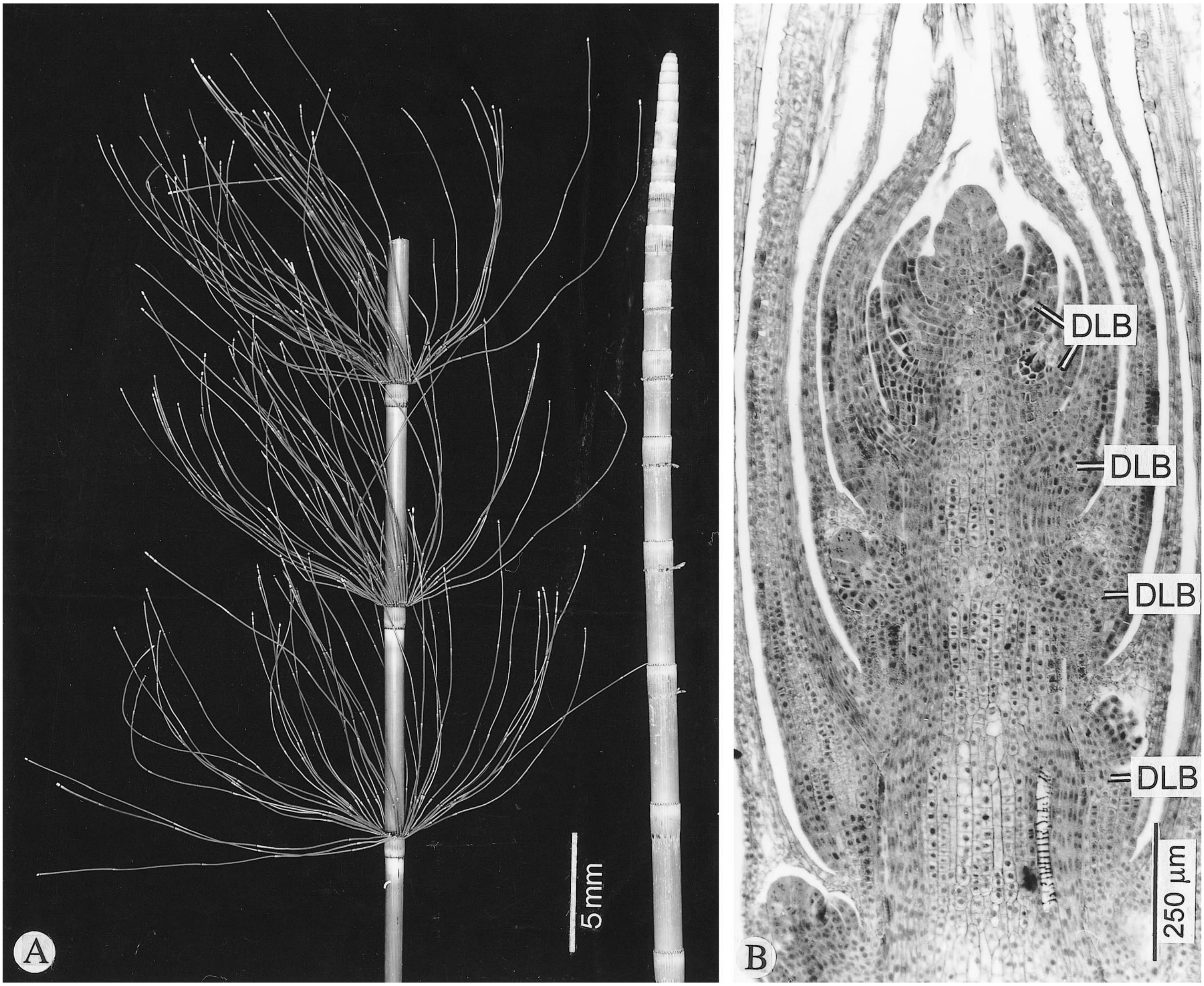

Fig. 23. Shoot morphology and development in *Equisetum.* (A) Aerial shoot segments of *E. myriochaetum,* showing the delimitation into nodes and internodes, with reduced leaf whorls inserted at each node. These aerial shoots assume a ''horsetail'' appearance as a result of the extensive outgrowth of lateral branches at each node. (B) Median longisection of the shoot tip of *E. arvense,* showing the expression of decurrent leaf bases that elongate with the ''internodes.'' ([B] from a commercial microscope slide made by Triarch, Ripon, Wisconsin, USA.)

opment, the marginal wings wrapped around the periphery of the younger leaves are attenuated into a thin, biseriate to uniseriate margin, showing the marked marginal extension that characterizes the leaf base in contrast to its upper leaf blade homologue. Thus, while upper and lower leaf zones grade into one another in mature sporophylls (Fig. 19C and D), they are clearly distinct in their longitudinal extent and transectional growth in early stages of leaf development.

Given that the leaves of *Isoëtes* and *Stylites* exhibit morphogenetic processes that resemble those in unifacial leaves in seed plants and also show a range of variation as a result of differential extension between upper and lower leaf zones, it is difficult to see these organs in *Isoëtes* as being microphyllous or enation homologues. The application of the microphyll vs. megaphyll dichotomy to the interpretation of their morphology seems inappropriate, whether they have a single vein or not. Because certain species of *Isoëtes* can exhibit large leaves with an equivalent degree of regional differentiation and developmental complexity, they demonstrate how such rigid, phylogenetic conceptions can be a limitation rather than an aid in assessing the evolutionary status of the morphology of these organisms.

Sphenopsida—This is another pteridophytic group whose representation in the fossil record is more extensive than among contemporary plants (Taylor and Taylor, 1993). Today it is represented only by the genus *Equisetum,* comprising some 15 species worldwide (Mabberley, 1997).

Among the diagnostic features of vegetative shoot morphology in *Equisetum* are its clear differentiation into nodes and internodes and its leaves, arranged in a whorled phyllotaxis and united into a common sheath. The only indication of the number of leaves comprising a vegetative whorl is the number of teeth at the summit of its leaf sheaths (Fig. 23A).

Although the sporophylls in the strobilus region of a shoot are free from one another, they also occur in a whorled phyllotaxis. The shoot system consists of subterranean, plagiotropic, rhizomatous axes bearing orthotropic, aboveground aerial branches that ultimately bear the cones. Roots typically are confined to the rhizomatous portion and are initiated only from the lateral branch primordia, not from its main axes (de Janczewski, 1876–1877). Thus, its roots are not only shoot-borne but, more precisely, lateral shoot-borne.

Since shoots in *Equisetum* do not undergo secondary growth, their primary thickening rhythm is evident. It is expressed by the changing diameter of the axis along the length of the shoot and in the number of leaves and branches per node. *Equisetum,* like all the species we have described here, also has decurrent leaf bases. From a superficial perspective, with their seemingly clear delineation into nodes and internodes (Fig. 23A) one would expect shoots in *Equisetum* to exemplify the shoot model shown in Fig. 7A, but in fact they show the shoot organization illustrated in Fig. 7B.

The organization of its shoot can be seen in the median longisection of the shoot of *E. arvense* in Fig. 23B. The portion of each leaf whorl that projects from the axis is the leaf sheath with its summital teeth (cf. Fig. 23B with 23A). However, below their point of insertion is a cushionlike protrusion corresponding to the decurrent leaf base. As the so-called internode elongates, this leaf base region extends with it, differentiating into the chlorenchyma, which corticates the axis (Fig. 23B). Hence, like all of the other species we have characterized in this article, what has been described as cortical tissue of the stem of *Equisetum* is actually leaf tissue adnate to its central axis.

From a traditional phylogenetic viewpoint, because of their simple, univeined nature (Fig. 23A), leaves in the vegetative region of the shoot of *Equisetum* have been considered microphyllous. However, the peltate sporophylls in the strobilus region of its shoot have been considered to be megaphyllous. Cone appendages in *Equisetum* traditionally have been called sporangiophores rather than sporophylls because they have been interpreted as originating from fertile telome systems, which, in the course of evolution, became recurved and reduced to form their characteristic peltate configuration (Stewart and Rothwell, 1993). The problem with such theories is that serial appendages along the length of an individual shoot would then have two different phylogenetic origins. Such a contradiction lies either in the spurious distinction between microphylls and megaphylls or in a misunderstanding of the morphological relationships between sterile and fertile appendages in *Equisetum,* or both. By demonstrating the regular occurrence of intermediates between sporophylls and vegetative leaves in *Equisetum,* it can be shown that these contradictions in appendage morphology and evolution result from misinterpretations of appendage homology in *Equisetum.*

Page (1972) has noted that within a clone of *Equisetum,* aerial shoots exhibit approximately the same number of nodes, regardless of whether the shoot is strictly vegetative or has both sterile and fertile (cone-bearing) regions. Appendages in both fertile and sterile regions occur in clear whorls. Since the internodes are short in the strobilus, a fertile shoot has a greater number of nodes in its cone region than in the subjacent vegetative region. Conversely, the strictly vegetative shoots are longer because their internodes are elongated, even though their node number is the same. This concept is illustrated in Fig. 24. All three shoots diagrammed have 29 nodes. In shoot A, 22 nodes are fertile and seven are vegetative (including the annulus or basal node of the cone) (Fig. 24A). In shoot B, ten nodes are fertile and 19 are sterile (Fig. 24B), whereas in shoot C, all 29 are sterile (Fig. 24C). Such equivalences in numbers along a given aerial shoot suggest a serial homology between the vegetative and reproductive appendages of an aerial shoot.

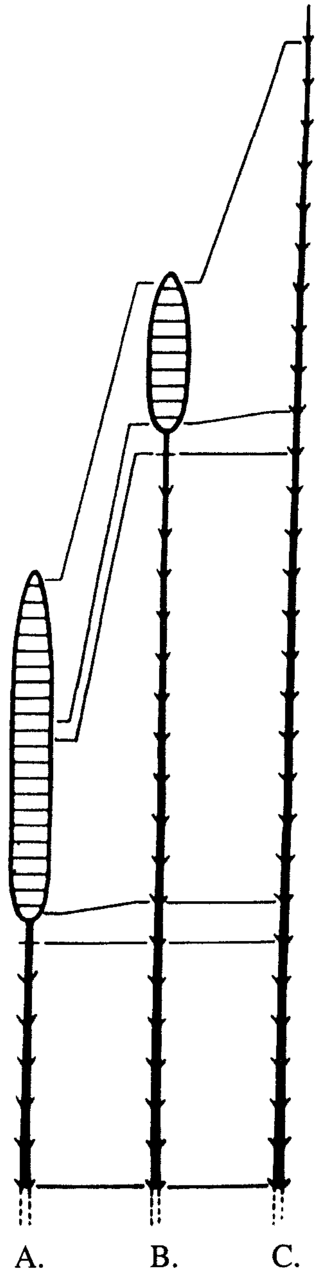

Fig. 24. Diagram illustrating the relationship between fertile and vegetative shoot regions in *Equisetum.* (A) Twenty-two units are fertile, one is an annulus and six are vegetative nodes. (B) Ten units are fertile, one is an annulus and 18 are vegetative. (C) All 29 nodes are vegetative. (Reproduced with permission from Page, 1972.)

A homology between sporophylls and trophophylls in *Equisetum* is indicated by the intermixing of vegetative and reproductive appendages in the cones of some species, as well as by the more gradual transitions between the two phases, as seen in some strobili. For example, in the cone of *E. telmateia* illustrated in Fig. 25A, the strobilus has reverted to vegetative

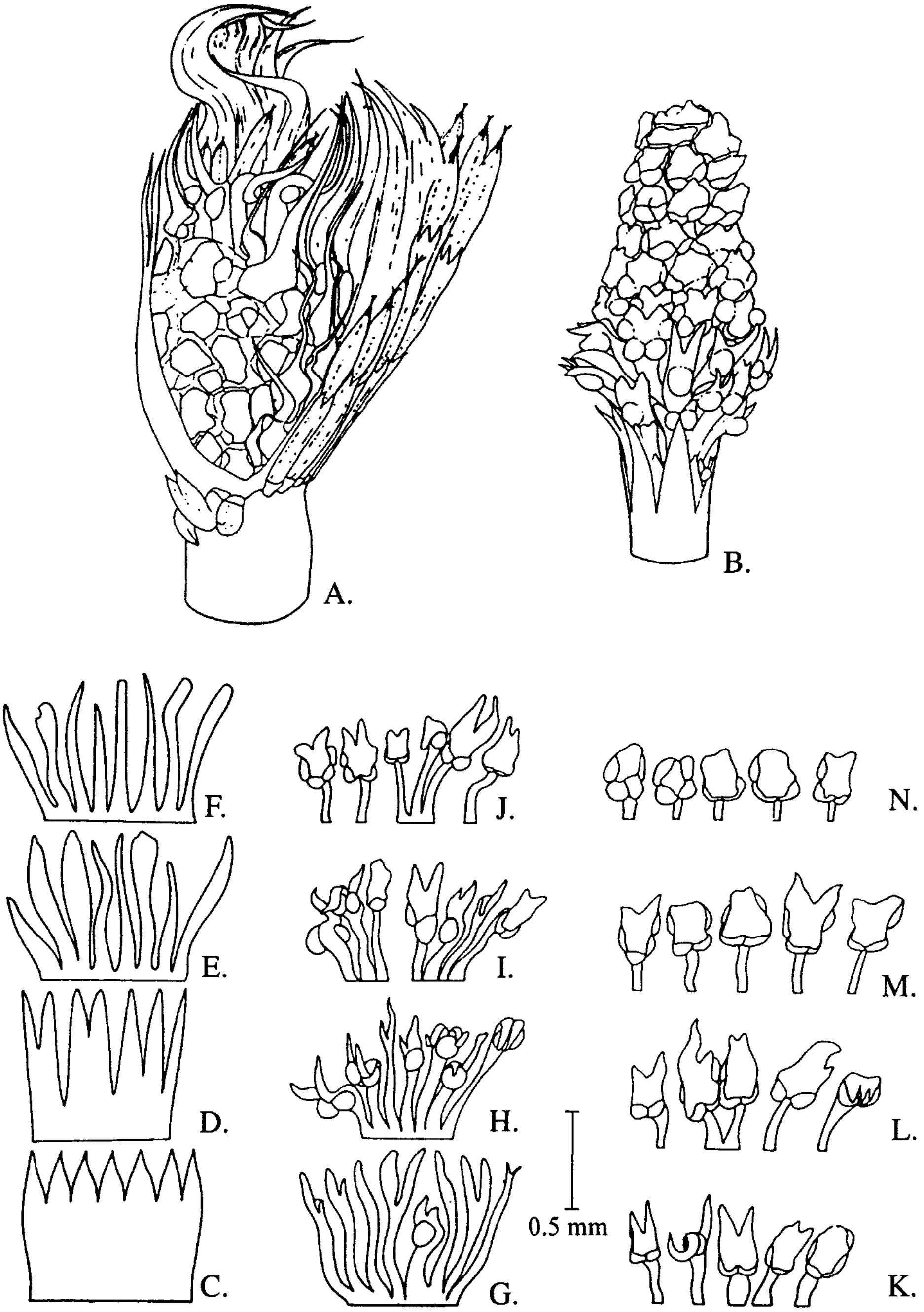

Fig. 25. (A) Aberrant cone of *Equisetum telmateia* showing retention of vegetative characteristics throughout one side of the strobilus. (B) Strobilus of *E. palustre,* showing the slow transition from vegetative to reproductive organs. (C–N) Appendages of the cone of *E. palustre* shown in (B) dissected off and laid out in a single plane to show the homologies between trophophylls and sporophylls. (Reproduced with permission from Page, 1972.)

growth at its apex and the appendages on one side are vegetative, whereas those in the same whorls around the rest of the cone are reproductive (Fig. 25A).

Such a homology is reinforced in cones such as those of *E. palustre* (Fig. 25B), which exhibit a more gradual transition with a greater number of intermediate stages between the vegetative and sporangia-bearing leaves. In Fig. 25C–N, the full range of transitions of this cone are laid out in a single plane so that homologies between vegetative and reproductive organs are clear. In the vegetative series, the leaves become increasingly individualized as free lobes, as a result of growth in the lobe part instead of in the common base (Fig. 25C–F). In addition, many of the individual lobes become bifurcated at their apices, and this apical dichotomy is expressed in the sterile, apical regions of the fertile, sporangial-bearing sporophyll transition forms (Fig. 25G–K). Also, in the transition forms, the sporophylls become increasingly individualized and separated from one another and have only a short common sheath (Fig. 25E–H). This is true in the transitions where their petioles are mostly separate (Fig. 25I, J) and in those where their sporophylls are free and able to effect sporangial separation for dehiscence and spore dispersal (Fig. 25K–N). From these serial changes it can be seen that the petiole or stalk of the sporophyll is derived from the subdivided common sheath of the vegetative leaf whorl (Fig. 25C–J).

This leaf series also shows that the first sporangia to be differentiated are the basalmost pair and that as the sporangia-forming blade region of the sporophyll is expanded laterally and distally, additional sporangia arise laterally and distally (Fig. 25J–N). The degree of distinction of the sporophyll petiole from the sporangia-bearing blade is increased by the hypopeltate (abaxial) expansion of the blade, seemingly eliminating the continuity between the blade and base that would indicate the homology of the stalk in the fully differentiated sporophyll (Fig. 25K–N).

It can be concluded that each sporophyll in *Equisetum* is homologous with an entire individual vegetative leaf, not just a portion of it. The sporophyll blade that bears the sporangia is comparable positionally to the distal portion of a vegetative leaf, and its petiole corresponds to the basal portion of the vegetative leaf or that part that is united into the sheath. Other than bearing sporangia, the principal divergence of the sporophyll from its trophophyll homologue is that it develops a hypopeltate (abaxial) blade extension that serves to seal the cone and protect the developing sporangia from desiccation until they are ripe and ready to release their spores.

Hence, *Equisetum* serves as effective a challenge to the concepts of microphyll vs. megaphyll as any of the pteridophytes we have noted. If intermediates occur between organs that have been classified into each of these categories, then the categories are no longer valid. Such examples emphasize what the study of contemporary plants can contribute to the study of organ phylogenies that may not be obtainable from fossils.

GENERAL CONCLUSIONS

Using the principles of seed-plant shoot organization as criteria for judging the evolutionary status of the shoots of contemporary Pteridophytes, in representatives of each of these major groups we see the same shoot organizational features as contemporary seed plants. Members of all the pteridophytic groups exhibit leaf–stem relationships expressed by decurrent leaf bases as well as a fundamental, ontogenetic rhythm in axis thickening correlated with changes in the size and degree of elaboration of the leaf component of the shoot. Moreover, depending upon the degree of regional elaboration of their leaves, their heteroblastic changes in leaf morphology exhibit the same basic articulation between upper and lower leaf zones (e.g., *Isöetes*) as we find in seed plants. From this survey we can conclude that none of the members of these living Pteridophytes seem to retain an ancient, rhyniophyte-type of body organization.

The seeming generality of this high degree of shoot organization in contemporary Pteridophytes suggests that this type of shoot organization could have had its inception much earlier in vascular plant evolution than currently thought. While our usual thinking is to hypothesize a number of steps between one character state and the next (as in the telome and enation theories; Fig. 6), the evolution from leafless rhyniophyte axes to those of a typical leafy shoot organization might have been a relatively simple, one-step organizational change, not involving a series of intermediates. As a result of biophysical/biomechanical constraints, once land plants developed certain degrees of stature and self-standing orthotropic growth, then present leaf–stem relationships and leaf elaboration could have been correlated with this basic change in habit. Such perspectives would then be in harmony with our view that evolutionary changes in plant morphology are expressed in the organism as a whole rather than in individual organs one at a time, as has been thought traditionally.

This survey of shoot morphology in pteridophytes illustrates the kind of unique perspectives that the principles of plant morphology, which cut across phylogenetic lines, bring to the understanding the major features of plant evolution. Such perspectives have the potential to complement the current emphasis on plant phylogeny and further illuminate our understanding of plant structural change.

LITERATURE CITED

ALLSOPP, A. 1967. Heteroblastic development in vascular plants. *In* M. Abercrombie and J. Brachet [eds.], Advances in morphogenesis, vol. 6, 127–171. Academic Press, New York, New York, USA.

BECK, C. B., R. SCHMID, AND G. W. ROTHWELL. 1982. Stelar morphology and the primary vascular system of seed plants. *Botanical Review* 48: 691–815.

BERGDOLT, E. 1942. Karl von Goebel. Ein deutsches Forscherleben in Briefen aus Sechs Jahrzehnten 1870–1932. Ahnenerbe-Stiftung, Berlin, Germany.

BIERHORST, D. W. 1956. Observations on aerial appendages in Psilotaceae. *Phytomorphology* 6: 176–184.

BOLD, H. C., C. J. ALEXOPOULOS, AND T. DELEVORYAS. 1987. Morphology of plants and fungi, 5th ed. Harper and Row, New York, New York, USA.

BOLD, H. C., AND M. J. WYNNE. 1985. Introduction to the algae, 2nd ed. Prentice Hall, Englewood Cliffs, New Jersey, USA.

COOKE, T. J., AND B. LU. 1992. The independence of cell shape and overall form in multicellular algae and land plants: cells do not act as building blocks for constructing plant organs. *International Journal of Plant Sciences* 153: S7–S27.

COULTER, J. M., AND C. J. CHAMBERLAIN. 1901. Morphology of spermatophytes. D. Appleton, New York, New York, USA.

DE JANCZEWSKI, E. 1876–1877. Recherches sur le développment des bourgeons dans les Prêles. *Memoire Societe Nátionale Science Naturel de Cherbourg* 20: 69.

EICHLER, A. W. 1861. Zur Entwicklungsgeschichte des Blattes mit besonderer Berücksichtigung der Nebenblattbildungen. Ph.D. dissertation, University of Marburg, Germany.

ELDREDGE, N., AND S. J. GOULD. 1972. Punctuated equilibria: an alternative to phyletic gradualism. *In* T. J. M. Schopf [ed.], Models in paleobiology, 82–115. Freeman, Cooper, and Co., San Francisco, California, USA.

EYDE, R. H. 1975. The foliar theory of the flower. *American Scientist* 63: 430–437.

GIFFORD, E. M., AND A. S. FOSTER. 1989. Morphology and evolution of vascular plants, 3rd ed. W. H. Freeman, New York, New York, USA.

GOETHE, J. W. 1790. Versuch die Metamorphose der Pflanzen zu erklären. Ettinger, Gotha, Germany.

GOULD, S. J., AND N. ELDREDGE. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* 3: 115–151.

HAGEMANN, W. 1967. Die Gestaltung als determinierendes Prinzip bei der Entwicklung des Pflanzenkörpers. *Mathematische und Naturwissenschaftliche Unterricht* 20: 289–297.

HOFMEISTER, W. 1868. Allgemeine Morphologie der Gewächse. Handbuch der Physiologischen Botanik. Wilhelm Engelmann, Leipzig, Germany.

JEFFREY, E. C., 1917. The anatomy of woody plants. University of Chicago Press, Chicago, Illinois, USA.

KAPLAN, D. R. 1973. Comparative developmental analysis of the heteroblastic leaf series of axillary shoots of *Acorus calamus* L. (Araceae) *La Cellule* 69: 251–290.

KAPLAN, D. R. 1975. Comparative developmental evaluation of the morphology of unifacial leaves in the monocotyledons. *Botanischen Jarbücher Systematik* 95: 1–105.

KAPLAN, D. R. 1980. Heteroblastic leaf development in *Acacia*: morphological and morphogenetic implications. *La Cellule* 73: 135–203.

KAPLAN, D. R. 1984. The concept of homology and its central role in the elucidation of plant systematic relationships. *In* T. Duncan and T. F. Stuessy [eds.], Cladistics: perspectives on the reconstruction of evolutionary history, 51–70. Columbia University Press, New York, New York, USA.

KAPLAN, D. R. 1992. The relationship of cells to organisms in plants: problem and implications of an organismal perspective. *International Journal of Plant Sciences* 153: S28–S37.

KAPLAN, D. R., AND T. J. COOKE. 1996. The genius of Wilhelm Hofmeister: the origin of causal-analytical research in plant development. *American Journal of Botany* 83: 1647–1660.

KAPLAN, D. R., AND T. J. COOKE. 1997. Fundamental concepts in the embryogenesis of dicotyledons: a morphological interpretation of embryo mutants. *Plant Cell* 9: 1903–1919.

KAPLAN, D. R., AND P. A. GROFF. 1995. Developmental themes in vascular plants: functional and evolutionary significance. *In* P. C. Hoch and A. J. Stephenson [eds.], Experimental and molecular approaches to plant biosystematics, 111–145. Missouri Botanical Garden, St. Louis, Missouri, USA.

KAPLAN, D. R., AND W. HAGEMANN. 1991. The relationship of cell and organism in vascular plants. *BioScience* 41: 693–703.

KAPLAN, D. R., AND W. HAGEMANN. 1992. The organism and plant cells in light of Goethe's comparative morphological method. *In* G. D. Mann, D. Mollenhauer, and S. Peters [eds.], In der Mitte zwischen Natur und Subjekt. Johann Wolfgang von Goethe's Versuch, die Metamorphose der Pflanze zu erklären 1790–1990, 93–117. Waldemar Kramer, Frankfurt, Germany.

KUBITZKI, K., AND R. BORCHERT. 1964. Morphologische Studien an *Isoëtes triquetra* A. Braun und Bemerkungen über das Verhältnis der Gattung *Stylites* E. Amstutz zur Gattung *Isoëtes* L. *Berichte der deutschen botanischen Gesellschaft* 77: 227–234.

KUZOFF, R. K., L. HUFFORD, AND D. E. SOLTIS. 2001. Structural homology and developmental transformations associated with ovary diversification in *Lithophragma* (Saxifragaceae). *American Journal of Botany* 88: 196–205.

LAWRENCE, G. H. M. 1955. An introduction to plant taxonomy. Macmillan, New York, New York, USA.

MABBERLEY, D. J. 1997. The plant-book, 2nd ed. Cambridge University Press, Cambridge, UK.

MANN, G., D. MOLLENHAUER, AND S. PETERS. 1992. In der Mitte zwischen Natur und Subjekt. Johann Wolfgang von Goethe's Versuch, die Metamorphose der Pflanze zu erklären 1790–1990. Waldemar Kramer, Frankfurt, Germany.

MOORE-LANDECKER, E. 1990. Fundamentals of the fungi, 3rd ed. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

MUELLER, B., AND C. J. ENGARD. 1952. Goethe's botanical writings. University Press of Hawaii, Honolololu, Hawaii, USA.

NICKEL, G. 1996. Wilhelm Troll (1897–1978): Eine Biographie. *Acta Historica Leopoldiana* 25: 1–240.

PAGE, C. N. 1972. An interpretation of the morphology and evolution of the cone and shoot of *Equisetum*. *Botanical Journal of the Linnean Society* 65: 359–397.

RAUH, W. 1979. Kakteen an ihren Standorten. Paul Parey, Berlin and Hamburg, Germany.

ROUFFA, A. S. 1971. An appendageless *Psilotum*. Introduction to aerial shoot morphology. *American Fern Journal* 61: 75–86.

ROUFFA, A. S. 1978. On phenotypic expression, morphogenetic pattern and synangium evolution in *Psilotum*. *American Journal of Botany* 65: 692–713.

SCAGEL, R. F., R. J. BANDONI, J. R. MAZE, G. E. ROUSE, W. B. SCHOFIELD, AND J. R. STEIN. 1984. Plants: an evolutionary survey. Wadsworth, Belmont, California, USA.

SCHOFIELD, W. B. 1985. Introduction to bryology. Macmillan, New York, New York, USA.

SIEGERT, A. 1964. Morphologische, enwicklungsgeschichtliche und systematische Studien an *Psilotum triquetrum* Sw. I. Allgemeiner Teil. Erstarkung und primäres Dickenwachstum der Sprosse. *Beiträge zur Biologie der Pflanzen* 40: 121–157.

SIEGERT, A. 1965. II. Die Verzweigung (mit einer allgemeinen Erörterung des Begriffes ''Dichotomie''). *Beiträge zur Biologie der Pflanzen* 41: 209–230.

SIEGERT, A. 1967. III. Das Blatt aus der Sicht der Homologien. *Beiträge zur Biologie der Pflanzen* 43: 285–328.

SIEGERT, A. 1969. IV. Die Bildungsabweichungen der Sporophylle. *Beiträge zur Biologie der Pflanzen* 46: 45–71.

SIEGERT, A. 1970. IV. Die Bildungsabweichungen der Sporophylle. *Beiträge zur Biologie der Pflanzen* 46: 435–459.

SIEGERT, A. 1973. IV. Die Bildungsabweichungen der Sporophylle (Schluss). *Beiträge zur Biologie der Pflanzen* 49: 291–319.

SMITH, J. M., R. BURIAN, S. KAUFFMAN, P. ALBERCH, J. CAMPBELL, B. GOODWIN, R. LANDE, D. RAUP, AND L. WOLPERT. 1985. Developmental constraints and evolution. *Quarterly Review of Biology* 60: 265–287.

SPETA, F. 1997. Wurzeln: Einblicke in verborgene Welten. Katalog der Ausstellung der Land Oberösterreich, Oö Landesmueum, Linz, Austria.

STEEVES, T. A., AND I. M. SUSSEX. 1989. Patterns in plant development, 2nd ed. Cambridge University Press, Cambridge, UK.

STEWART, W. N., AND G. W. ROTHWELL. 1993. Paleobotany and the evolution of plants, 2nd ed. Cambridge University Press, Cambridge, UK.

TAYLOR, T. N., AND E. L. TAYLOR. 1993. The biology and evolution of fossil plants. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

THOMPSON, D. W. 1917. On growth and form. Cambridge University Press, Cambridge, UK.

TOMLINSON, P. B., AND M. H. ZIMMERMANN. 1966. Anatomy of the palm *Rhapis excelsa* III. Juvenile phase. *Journal of the Arnold Arboretum* 47: 301–312.

TROLL, W. 1925. Gestalt und Gesetz. Versuch einer geistesgeschichtlichen Grundlegung der morphologischen und physiologischen Forschung. *Flora* 118/119: 536–565.

TROLL, W. 1928. Organisation und Gestalt im Bereich der Blüte. Julius Springer, Berlin, Germany.

TROLL, W. 1937–1943. Vergleichende Morphologie der höheren Pflanzen. Erster Band: Vegetationsorgane. Teil I–III. Gebrüder Borntraeger, Berlin, Germany.

TROLL, W. 1949. Die Urbildlichkeit der organischen Gestaltung und Goethes Prinzip der ''variablen Proportionen.'' *Experientia* 5: 491–495.

TROLL, W. 1954. Praktische Einführung in die Pflanzenmorphologie, 1. Teil: Der vegetative Aufbau. Gustav Fischer, Jena, Germany.

TROLL, W. 1957. Praktische Einführung in die Pflanzenmorphologie, 2. Teil: Die blühende Pflanze. Gustav Fischer, Jena, Germany.

TROLL, W. 1969. Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers, Band 2. Teil 1: III Abschnitt: Monotele Synfloreszenzen. Gustav Fischer, Stuttgart, Germany.

TROLL, W., AND W. RAUH. 1950. Das Erstarkungswachstum krautiger Dikotylen, mit besonderer Berücksichtigung der primären Verdickungsvorgänge. *Sitzungsberichte der Heidelberger Akademie der Wissenschaften.* Mathematisch- naturwissentschaftliche Klasse. Jahrgang 1950. 1 Abhandlung. 1–86.

VON GOEBEL, K. 1898–1901. Organographie der Pflanzen, 1st ed., parts 1 and 2. Gustav Fischer, Jena, Germany.

VON GOEBEL, K. 1900–1905. Organography of plants. English translation (by I. Balfour). Parts 1 and 2. Oxford University, Oxford, UK.

VON GOEBEL, K. 1905. Wilhelm Hofmeister. *Plant World* 8: 291–298.

VON GOEBEL, K. 1913–1923. Organographie der Pflanzen. 2nd ed., parts 1–3. Gustav Fischer, Jena, Germany.

VON GOEBEL, K. 1926. Wilhelm Hofmeister; the work and life of a nineteenth century botanist with biographical supplement by. C. Ganzenmüller (née Hofmeister). Ray Society, London, UK.

VON GOEBEL, K. 1928–1933. Organographie der Pflanzen. 3rd ed., parts 1–3. Gustav Fischer, Jena, Germany.

WAGNER, W. H., JR., J. M. BEITEL, AND F. S. WAGNER. 1982. Complex venation patterns in the leaves of *Selaginella*: megaphyll-like leaves in Lycophytes. *Science* 218: 793–794.

WARDLAW, C. W. 1957. Experimental and analytical studies of pteridophytes XXXVII. A note on the inception of microphylls and macrophylls. *Annals of Botany* New Series 21: 427–437.

ZIMMERMANN, W. 1930. Die Phylogenie der Pflanzen. Gustav Fischer, Jena, Germany.

ZIMMERMANN, W. 1931. Arbeitsweise der botanischen Phylogenetik und anderer Gruppierengswissenschaften. *In* E. Aberhalden (ed.), Handbuch der biologischen Arbeitsmethoden, Abt. IX, Teil 3, Heft 6. Urban und Schwarzenberg, Berlin, Germany.

ZIMMERMANN, W. 1953. Evolution. Die Geschichte ihrer Probleme und Erkenntnisse. Karl Alber, Freiburg, Germany.

ZIMMERMANN, W. 1959. Die Phylogenie der Pflanzen, 2nd ed. Gustav Fischer, Stuttgart, Germany.

ZIMMERMANN, W. 1965. Die Telomtheorie. Gustav Fischer, Stuttgart, Germany.

ZIMMERMANN, W. 1968. Evolution und Naturphilosophie. Duncker und Humblot, Berlin, Germany.