

POLYMEROUS LEAF WHORLS IN VASCULAR PLANTS: DEVELOPMENTAL MORPHOLOGY AND FUZZINESS OF ORGAN IDENTITIES

Rolf Rutishauser¹

Botanischer Garten und Institut für Systematische Botanik, Universität, Zollikerstrasse 107, 8008 Zürich, Switzerland

In vascular plants there are at least eight ways to develop polymerous whorls, i.e., whorls with four or more leaves. Six ways are presented and compared with literature to estimate organ identity (morphological significance) of the leaflike whorl members. New shoots (also seedlings) may start with dimerous or trimerous whorls. Then leaf number per whorl rises as follows: (1) Many taxa add more leaves per whorl continuously with increasing size of the apical meristem (e.g., *Equisetum*, *Hippuris*). (2) Taxa provided with interpetiolar stipules replace their stipules by leaves (e.g., *Galium* and allies). (3) Taxa with the capacity to form compound leaves shift basal leaflets around the whole node (e.g., *Linnophila*, probably also *Ceratophyllum*). Various whorled plants start shoot development with leaf inception along a helix, which is continued into the whorled region. Then polymerous whorls develop as follows: (4) *Acacia longipedunculata* forms helically arranged fascicles instead of single leaves before the production of complete whorls. (5) *Acacia baueri* and *Acacia verticillata* add supernumerary leaves between a first series of helically arranged leaves. (6) *Hydrothrix* produces an annular bulge around the node of each first-formed leaf. All additional leaves of a whorl arise on this annular bulge. Leaf identity of whorl members cannot be defined unequivocally in whorls with asynchronous (i.e., nonsimultaneous) development, dorsoventral distribution of lateral buds, and/or fewer vascular traces than leaves per node. It is heuristically stimulating to accept structural categories (e.g., shoot, leaf, leaflet, stipule) as fuzzy concepts, as developmental pathways that may overlap to some degree, leading to developmental mosaics (intermediates). For example, the whorled leaves of *Utricularia purpurea* resemble whole shoots, corroborating Arber's partial-shoot theory.

Keywords: anisophylly, aquatic angiosperms, continuum morphology, functional significance, nodal vascular pattern, subapical leaf inception, systematics, Leguminosae, Lentibulariaceae, Pontederiaceae, Rubiaceae, Scrophulariaceae.

Charles Sanders Peirce (1839–1914), America's most innovative philosopher, ... held that all that exists is continuous, and such continuums govern knowledge. (McNeill and Freiburger 1993, p. 28)

Introduction

What Is a Whorl?

The *American Heritage Dictionary* gives the following definition: in plants a whorl is "an arrangement of three or more parts, as leaves or petals, radiating from a single organ or node." Thus, the term "whorl" is used to describe a ringlike arrangement (or tier) of organs, especially leaves along stems. In a more strict sense, a whorl is a full cycle of organs that can be delimited from preceding and subsequent cycles. The organs of a cycle may appear simultaneously or in a rapid sequence (Endress 1987, 1992; Ronse Decraene and Smets 1997). It is not always possible to clearly distinguish between verticillate and spiral patterns. For example, shoot apices of *Huperzia squarrosa* (Lycopodiaceae) show spirally arranged leaves (with divergence angles of ca. 65.5°) that are synchro-

nized into pentamerous whorls (Rutishauser 1998). Several botanists (e.g., Goebel 1913a; Schoute 1936; Millet et al. 1961; Loiseau and Grangeon 1963; Kwiatkowska 1995, 1999) distinguished between true whorls and false whorls (pseudo-whorls) using different definitions. Schoute (1922, 1925) added other terms such as "growth whorls" and "binding whorls." I avoid these terms and use instead the descriptive terms "synchronous whorls" and "asynchronous whorls."

In synchronous whorls all leaves are initiated simultaneously (figs. 1–4). Many vegetative whorls, however, are asynchronous whorls where the leaves of each whorl arise nonsimultaneously (figs. 5–9). The different types of whorled phyllotaxis (with k leaves per whorl) can be labeled according to the angles between successive whorls. According to Jean (1994) and Zagórska-Marek (1994), the k -merous (multimerous) systems consist of alternating (or superposed) whorls with all leaves arranged along straight lines (orthostichies), whereas k -jugate (multijugate) systems are golden-sectioners. Their successive whorls are spirally twisted and show divergence angles of $137.5^\circ/k$. Alternating and spirally twisted dimerous whorls

¹ Fax 0-1-6348403; e-mail rutishau@systbot.unizh.ch.

are typical for decussate and bijugate phyllotaxis patterns, respectively (Rutishauser 1998). Green et al. (1998) proposed that distichy as found in grasses, e.g., should be called “whorled phyllotaxis,” with one leaf per whorl. Thus, vegetative whorls of vascular plants may consist of $k = 1-30$ leaves or even more.

Where Do Whorls Occur among Vascular Plants?

Nearly all dicot seedlings start with a dimerous whorl of cotyledons. Many dicots continue with decussate (or tricussate) phyllotaxis in the vegetative phase or switch to spiral (helical) patterns (Kwiatkowska 1995). Other dicots form polymeric whorls with $k \geq 4$ leaves (figs. 2–8). Verticillate phyllotaxis is less frequent in monocots. Whorls are found in various Hydrocharitaceae (e.g., *Hydrilla*; Cook 1996b) and in a single Pontederiaceae (*Hydrothrix*, fig. 9; Rutishauser 1983). Many angiosperms (especially eudicots and monocots) have their flower appendages arranged in whorls. In flowers, in contrast to the vegetative region, the organ identities change abruptly from whorl to whorl (Irish 1998). The diameter and the time lapse of appearance of successive organs (plastochron) may be different between floral whorls (Endress 1992). Outside the angiosperms, leaf whorls are present in some ferns (e.g., *Salvinia*), fern allies (e.g., *Equisetum*, fig. 1), and gymnosperms (e.g., *Juniperus*; Namboodiri and Beck 1968).

Organ Identity

Research on whorls in plants has a long tradition (e.g., DeCandolle 1827; Braun 1831; Hofmeister 1868; Delpino 1883; Schoute 1913). These and more recent publications help us to recognize organ identity (morphological significance) of the whorl members. Traditional botanists asked questions about homology and morphological significance of plant structures. Since the arrival of molecular developmental genetics, the term “organ identity” is used instead. Organ identity means the developmental fate of a primordium. Acquisition of organ identity (e.g., stamen or carpel in flowers) may happen progressively or abruptly (Wolpert et al. 1998). Whorl subunits along stems of vascular plants may be described as “leaves.” In this article I use the term “leaf” as a purely descriptive concept. However, please see Rutishauser and Sattler (1985, 1986, 1997), Rutishauser (1995), Poethig (1997), Hofer and Ellis (1998), and Hudson (1999) for discussions on questions like What is a leaf? What does leaf identity mean? and How can we distinguish leaves from shoots (including stems), leaflets, or stipules?

Aims of This Study

This article gives an overview of leaf whorls outside the floral region. Because it is mainly a review article, information from the literature will be presented in the “Results,” while the “Discussion” will focus on general aspects of leaf whorls. The various types of whorled phyllotaxis are distinguished according to differences in early development and their vascular supply. Nine case studies serve as examples for different pathways of leaf whorl formation in vascular plants. Except for *Equisetum* (fig. 1), all case studies focus on flowering plants (figs. 2–9). I restrict myself to plants with polymeric whorls

that are at least tetramerous (with $k \geq 4$ leaves). Each case study contains a paragraph entitled “Hypotheses on Organ Identity.” What I call a leaf in the nine case studies may turn out to be a “true” leaf, a leaflet (leaf segment), a stipule, a whole shoot, or even a developmental mosaic, depending on the taxon. “True leaf” (phyllome) stands for an appendage whose leaf identity is obvious for many botanists. According to continuum morphology and fuzzy morphology, structural categories in plant morphology are labels for developmental pathways that overlap, leading to intermediates, i.e., developmental mosaics. Whereas continuum morphology *sensu* Sattler (e.g., 1996) gives emphasis on the intermediacy of these structures, fuzzy morphology allows labeling with seemingly contrasting terms (Rutishauser 1995). The seemingly contradictory hypotheses on organ identity of whorl members are complementary perspectives adding different aspects to what we conceive of as shoot (stem), leaf, leaflet, and stipule in vascular plants (Arber 1950; Rutishauser and Sattler 1985, 1986). The functional significance of leaf whorls and explanatory models for whorl morphogenesis will be discussed at the end.

Material and Methods

The original data are mainly based on fixed material. Several plants were cultivated at the Botanic Garden of the University of Zurich (BGUZ). Voucher specimens for each species are deposited at Z/ZT unless specified otherwise:

Acacia baueri Benth. subsp. *aspera* (Maiden & Betche) Pedley (Leguminosae): Blue Mountains, New South Wales, Australia. C.U. Kramer 9995, October 7, 1986.

Acacia hippuroides Heward ex Benth.: Australia, northern West Australia. K.F. Kenneally 9525, September 6, 1985.

Acacia longipedunculata Pedley: Australia, Queensland, 2 km northwest of Irvine bank. J. De Campo, October 26, 1983 [BRI 297140].

Acacia verticillata (L'Héritier) Willdenow: Australia, Victoria, 40 km north of Melbourne. A. Drinnan s.n., September 15, 1985.

Ceratophyllum submersum L. (Ceratophyllaceae): cultivated at BGUZ.

Cruciata glabra (L.) Ehrendorfer (Rubiaceae, tribe Rubieae): Italy, Sardinia.

R. Rutishauser 8112025, April 11, 1981.

Equisetum fluviatile L. (Equisetaceae): cultivated at BGUZ.

Equisetum hyemale L.: Switzerland, forest near Zurich. Rutishauser s.n., April 26, 1982.

Equisetum telmateia Ehrh.: Switzerland, roadside near Lake of Constance. Rutishauser s.n., April 17, 1981.

Galium rubioides L. (Rubiaceae): cultivated at BGUZ.

Hippuris vulgaris L. (Hippuridaceae or “Scroph II clade”): cultivated at BGUZ.

Hydrothrix gardneri J.D. Hooker (Pontederiaceae): cultivated at BGUZ; seeds from Eastern Brazil, Ceará, pond near Icó. Bogner 1222.

Limmophila indica (L.) Druce (Scrophulariaceae): South India, Kerala, Malappuram District. Rutishauser & Huber 8915124, November 16, 1989.

Phuopsis stylosa (Trinius) Jackson (Rubiaceae): cultivated at BGUZ.

Utricularia purpurea Walter (Lentibulariaceae): Canada, Quebec, Lac de Lucerne near Ste-Marguerite. Rutishauser s.n., September 23, 1984.

The material used for this study was fixed and preserved in formalin–acetic acid–ethyl alcohol (FAA) or 70% ethyl alcohol. For scanning electron microscopy, the dissected shoot tips were critical-point dried and sputter-coated (Au-Pd). Most of the micrographs were taken with a Cambridge S4 scanning electron microscope at 20 kV.

Results

Synchronous Leaf Whorls

Equisetum fluviatile, *Equisetum hyemale*, and *Equisetum telmateia* (Equisetaceae) (Fig. 1)

General description. *Equisetum* (15 spp.) is the only extant genus within the Sphenopsida that flourished from Carboniferous to Cretaceous (Stewart and Rothwell 1993). A horizontal rhizome gives rise to aerial stems. The minute leaves of each whorl are parts of a common tubular sheath that is 3–12 mm long, depending on the species (fig. 1B, 1D). The

leaf tips form teeth around the margin of the sheath. They are usually without chlorophyll, photosynthesis being carried out entirely by the green stems. The stems are more or less ridged. Each ridge corresponds to a leaf in the node (sheath) above, and the ridges in successive internodes normally alternate with one another (Bierhorst 1959; Sporne 1966; Boureau 1971; Foster and Gifford 1989; Hauke 1990).

Meristic variation. Depending on the species and its developmental phase, *Equisetum* has three to 36 leaves per whorl (Braun 1831, p. 358). In the embryo three leaves are typically formed at the first node (Wardlaw 1965). The lowermost whorls of lateral buds are tubular sheaths with fimbriate margins where it is impossible to clearly distinguish individual leaves (fig. 1F; Rutishauser and Sattler 1987). As the young sporophyte or lateral shoot grows, the shoot meristem enlarges and progressively larger numbers of leaf primordia are formed at each whorl. Most species increase leaf number per whorl along a shoot and finally decrease it again. For example, the whorls of *Equisetum fluviatile* and *Equisetum hyemale* have (4–)10–30 teeth (fig. 1B, 1D). The green stems of *Equisetum telmateia* have (6–)15–36 teeth per whorl (Daviero et al. 1996). In the upper stem zone and along lateral branches the leaf

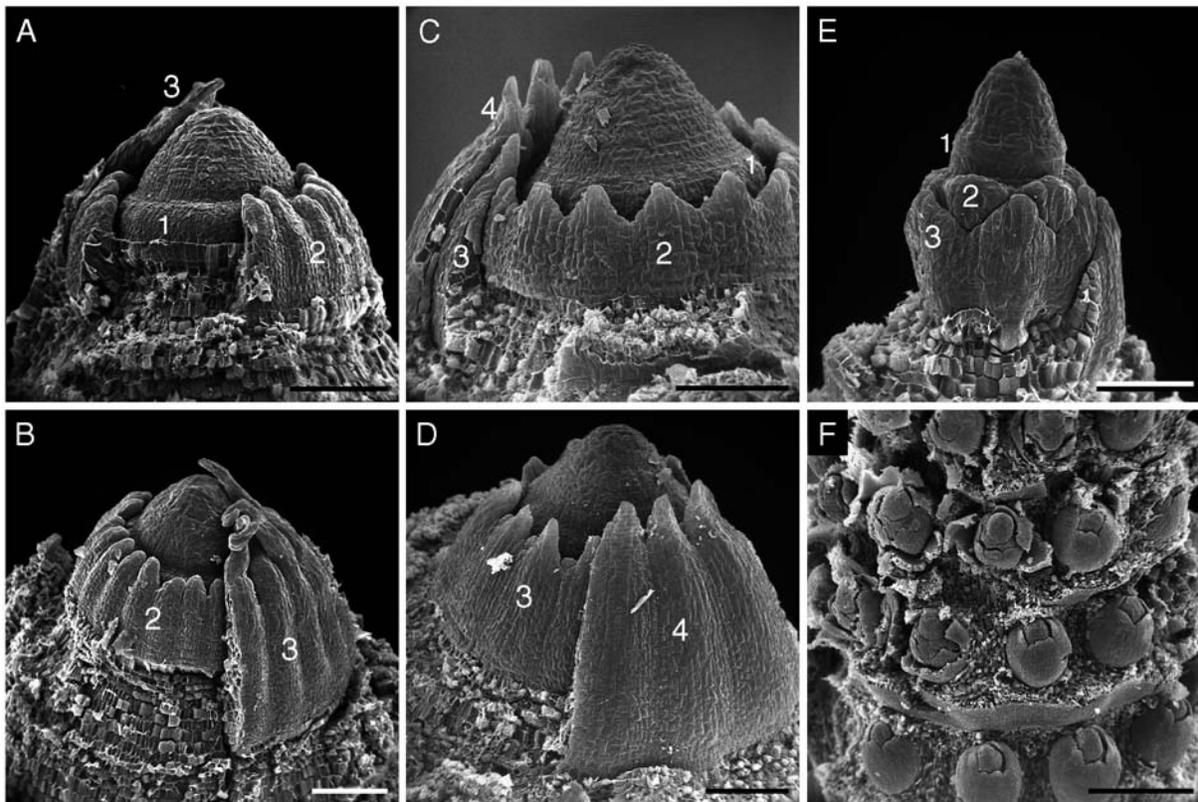


Fig. 1 Developmental morphology of *Equisetum* (Equisetaceae) leaf whorls. A, B, *Equisetum hyemale*. C, D, *Equisetum fluviatile*. E, F, *Equisetum telmateia*. A–D, Apical meristems of two vigorous aerial shoots. Apical dome surrounded by the youngest whorls (partially removed). Whorl formation starts with an annular bulge (1) that later forms the tubular sheath with an apical ring of teeth (2–4). Bars = 100 μ m. E, Apical meristem of aerial shoot toward cessation of growth, with hexamerous alternating whorls (2–3). Youngest whorl (1) as annular bulge. Bar = 100 μ m. F, More proximal region of vigorous aerial shoot. Leaf sheaths of four successive whorls totally removed. Lateral shoot buds arranged in alternating whorls. Bar = 400 μ m. Arabic numerals represent the order of appearance of leaves; the lowest number represents the most recent leaf or whorl formed.

number per whorl may decrease again, down to six (fig. 1E) or even three. Only *Equisetum scirpoides* shows a restriction to (3–)4 leaves per whorl throughout (Johnson 1933). Bierhorst (1959, 1971), who studied meristic variation of leaf number in nine *Equisetum* species, found that changes between successive whorls occur in ca. 40% of the nodes. Where differences in leaf number occur, the departures from perfect alternation are pronounced.

Whorl development and positions of shoot buds. Growth at the shoot meristem takes place following the activity of the tetrahedral apical cell. Despite the spiral sequence of cutting off daughter cells, subsequent growth results in whorled phyllotaxis (Sporne 1966). An annular bulge is formed at the shoot meristem before the initiation of the individual leaf primordia (fig. 1A, 1C, 1E; Hofmeister 1851, 1868; Golub and Wetmore 1948; Hauke 1985). In a later stage, the upper region of the annular bulge around the apical dome starts to divide into several teeth at a time when the common sheath is elongating (fig. 1B, 1D). Also, the sporophyll whorls of *Equisetum* start their development as concentric rings around a conical apical meristem (Foster and Gifford 1989). There is no axillary branching in *Equisetum*. Lateral bud primordia (also with an apical cell) arise in the angle between the tubular sheath and the stem on radii between the leaves. As in leaf whorls, these extra-axillary bud primordia are arranged in alternating whorls or nearly so (fig. 1F). Helical phyllotaxis with leaves detached from each other is not known in *Equisetum* and its fossil allies (Stewart and Rothwell 1993). In teratological cases of helically twisted shoots (i.e., biastrepsis), the leaves of a shoot zone form a continuous helical sheath (Milde 1852; Page 1968; Bierhorst 1971).

Vascular supply. The vascular system of the *Equisetum* stem is without parallel in the plant kingdom today (Sporne 1966). Schmid (1982, p. 905) called it “perforated ectophloic siphonostele.” At the nodes, the vascular bundles are connected by a continuous cylinder of xylem, from which the leaf traces and branch traces (in the radii between) have their origin. The internodal bundles are arranged in a ring and seem to represent leaf traces extending to the node below (Bierhorst 1959, 1971; Boureau 1971). The tubular sheaths (fig. 1F) of the lowermost whorls of lateral buds are not vascularized (Johnson 1933).

Two hypotheses on organ identity. (1) Hofmeister (1851, p. 90) and Duval-Jouve (1864) thought that each whorl of *Equisetum* is equivalent to one subdivided leaf. This first hypothesis points to the fact that *Equisetum* whorls result from a single nodal primordium (annular bulge) that breaks into a number of smaller units after it has been initiated. (2) Popular for *Equisetum* whorls is the “one tooth = one leaf tip” equation (Braun 1831, p. 351; Hofmeister 1868; Page 1972; Hauke 1990). This hypothesis is compatible with commonly held views on the evolution of the sphenopsids. Leaf morphology in early fossil equisetaleans suggest that the microphylls of modern *Equisetum* probably evolved by reduction of mega-phyll-like precursors, so-called sphenophylls (Stewart and Rothwell 1993; Kenrick and Crane 1997).

Leaf whorls in related fossil Equisetales (Sphenopsida). Whorled phyllotaxis was already present in Carboniferous equisetaleans that had prominent forked sphenophylls (Good 1971). In *Asterophyllites* there were up to 40 leaves per whorl,

each leaf forming a needle of 5–40-mm in length. *Neocalamites* (Triassic and Lower Jurassic) had as many as 80–100 slender leaves attached to each node (Stewart and Rothwell 1993).

Hippuris vulgaris (Hippuridaceae or “Scroph II Clade”) (Fig. 2)

General description. *Hippuris* (two spp.) is a circumboreal genus of mainly amphibious plants (Cook 1996b). The plants produce simple, linear leaves arranged in symmetrical whorls at regular intervals. Erect and normally unbranched stems arise from a sympodially branching rhizome (Irmisch 1854; Glück 1911; Arber 1920). Heterophylly is observable as variation in number of leaves per whorl and in leaf shape and size. Terrestrially developed leaves are darker green, shorter, and thicker than submerged assimilating ones (McCully and Dale 1961; Kane and Albert 1987; Goliber 1989). The flowers of *Hippuris* are relatively small and reduced (Reeves and Olmstead 1998). They are sessile and borne singly in the axils of aerial leaves (fig. 2A; Cook 1978, 1996b).

Meristic variation. There are (2–)4–12(–16) leaves per whorl (Goebel 1928; Schoute 1936; McCully and Dale 1961; Loiseau and Grangeon 1963). Seedlings start with dimerous whorls, while the first whorl of vegetative lateral buds is often trimerous. Rhizomes and basal portions of erect shoots carry alternating whorls of three to four scales (Velenovsky 1907, p. 557; Jeune and Cusset 1971). Leaf number increases (fig. 2A) and reaches the maximum between the sixteenth and the twentieth nodes. Vanhecke (1982) focused on the occurrence of forked leaves (“double leaves”) in erect shoots. Their frequency seems to depend on the population studied and on the degree of instability in phyllotaxis. Forked leaves are often associated with increasing leaf numbers.

Whorl development and the positions of shoot and floral buds. The apical meristem of the establishing erect shoot is first hemispherical (fig. 2A) and then dome shaped (fig. 2B). Each whorl is initiated simultaneously. Successive whorls are normally alternating. Slight irregularities, however, occur (arrowhead in fig. 2C). When an aerial shoot is ready for flowering, all leaf primordia start to divide into an abaxial lobe (subtending bract) and an adaxial lobe (floral meristem; fig. 2B). A switch from verticillate to spiral phyllotaxis has rarely been observed in *Hippuris* (Schoute 1913, 1938).

Vascular supply. As in other aquatic angiosperms, the stem vascular tissue (stele) is a solid cylinder lacking parenchymatous pith and leaf gaps (Schenck 1886; Lance-Nougarede and Loiseau 1960; Napp-Zinn 1973/1974). Each leaf of a *Hippuris* whorl receives its own trace from the stele, or two adjacent leaves of a whorl are supplied by a forked common trace (fig. 2D; McCully and Dale 1961; Loiseau and Grangeon 1963).

Hypothesis on organ identity. Most botanists since Braun (1831, p. 351) accepted the view that each whorl member is a “true” leaf, although two neighboring leaves may share a vascular trace.

Leaf whorls in related taxa. According to new molecular data, the small families Hippuridaceae, Callitrichaceae, and Plantaginaceae have been merged with a part of the former Scrophulariaceae into a newly circumscribed family (“Scroph II clade”) that should be called “Antirrhinaceae,” according

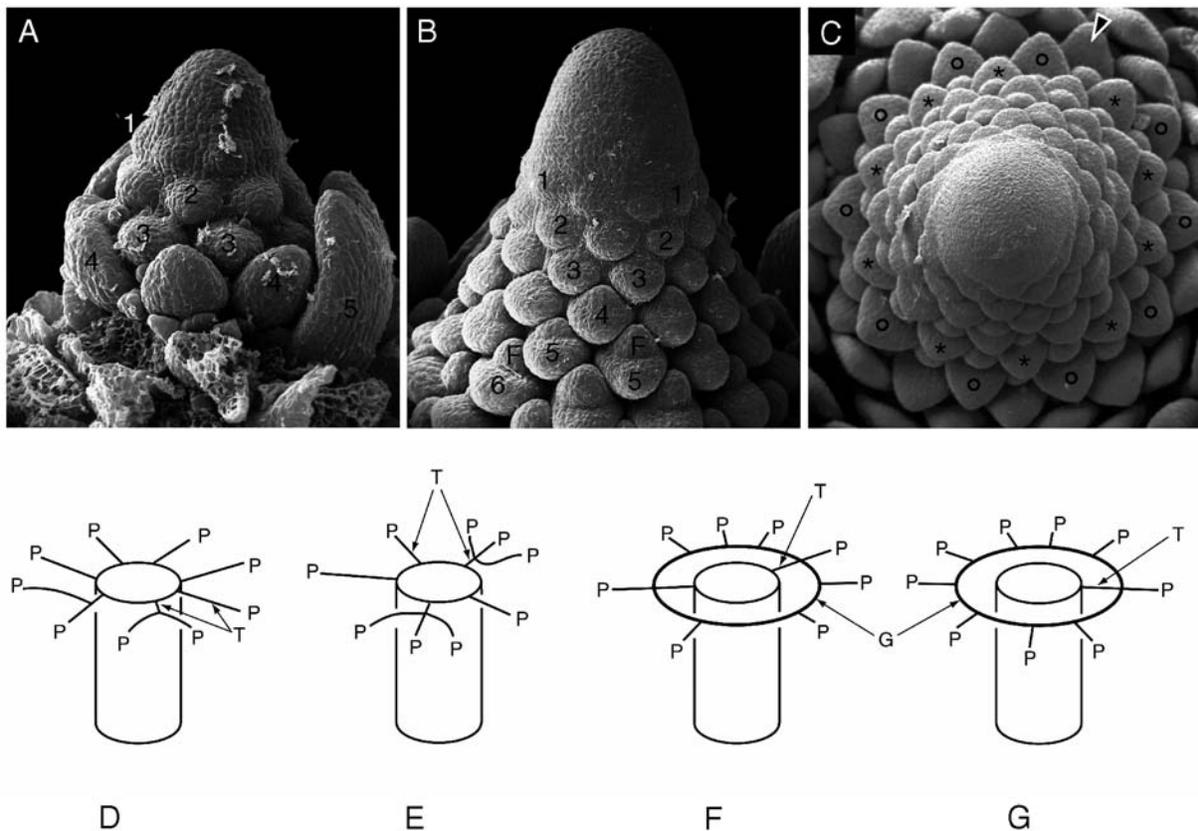


Fig. 2 Developmental morphology of *Hippuris vulgaris* (Hippuridaceae) leaf whorls and comparison with vascular supply in other angiosperms. A–D, *Hippuris vulgaris*. E, *Platytheca galioides* (Tremandraceae). F, *Phuopsis stylosa* and other Rubieae (Rubiaceae). G, *Hydrothrix gardneri* (Pontederiaceae). A, Apical meristem of young aerial shoot, with alternating 8-merous leaf whorls (1–5). Bar = 100 μ m. B, Another shoot meristem with 10-merous leaf whorls (1–6). Each primordium is dividing into an abaxial lobe (leafy bract) and an adaxial lobe (F = floral primordium). Bar = 100 μ m. C, Top view of same shoot meristem. Two successive and alternating whorls marked with o and asterisk. Arrow points to extra-large gap. Bar = 100 μ m. D–G, Schematic drawings of 9-merous leaf whorls of four different angiosperms. There are fewer vascular traces (T) from the stele than leaves (P) per whorl. *Phuopsis* and *Hydrothrix* are provided with a girdling vascular bundle (G). Arabic numerals represent the order of appearance of leaves; the lowest number represents the most recent leaf or whorl formed.

to Reveal et al. (1999). Dimerous whorls (i.e., decussate and bijugate phyllotaxes) are found in *Callitriche* and *Plantago* subgenus *Psyllium*. For example, *Plantago arborescens* and *Plantago webbii* produce trimerous to pentamerous whorls with synchronous development (Rutishauser 1998). Whorled phyllotaxis is also found in Scrophulariaceae such as *Linaria*, e.g., *Linaria verticillata* and *Linaria anticaria* with whorls of three to eight leaves. The Scrophulariaceae also possess genera having clearly asynchronous whorls (e.g., *Limnophila*, fig. 5).

Ceratophyllum submersum (Ceratophyllaceae) (Fig. 3)

General description. Molecular and morphological data suggest that *Ceratophyllum* (ca. four spp.) is a basal angiospermous genus that has no close relatives (Chase et al. 1993; Les 1993; Angiosperm Phylogeny Group 1998). The cosmopolitan genus lives entirely submerged. The elongated, periodically branched stem bears whorls of leaves that are 2–4 cm long and forked (1)–2–4 times. *Ceratophyllum* is monoecious and hypohydrophilous, with the ratio of female and male flowers being usually male biased and variable (Les 1993). Flowers

have a whorl of three to 12 bracts serving as a perianth (Cook 1996b). Female flowers contain a single carpel. The three to 46 stamens of male flowers are arranged in trimerous or tetramerous whorls or in irregular spirals following Fibonacci and Lucas patterns (Rutishauser and Sattler 1987; Endress 1994b). *Ceratophyllum submersum* is similar to the remaining species with respect to vegetative growth (Turlier 1972; Sehgal and Mohan Ram 1981; Wilmot-Dear 1985).

Meristic variation. The leaves are arranged in alternating whorls or nearly so. There may be two to 12 leaves per whorl, but usually there are seven to 10. The first whorls of seedlings are dimerous (de Klercker 1885; Velenovsky 1907; Arber 1920; Les 1985), whereas lateral vegetative buds start with (4)–6–8 leaves per whorl, with the two transversal leaves being more vigorous than the others. Leaf number increases in higher whorls. Toward cessation of shoot growth, the leaf number per whorl again decreases. Pearl (1907) published a biometric analysis of intraindividual variability of leaf number per whorl. From a total of 2328 examined whorls Pearl (1907) found a mean of 8.7 ± 1.2 leaves per whorl. There were 175 whorls

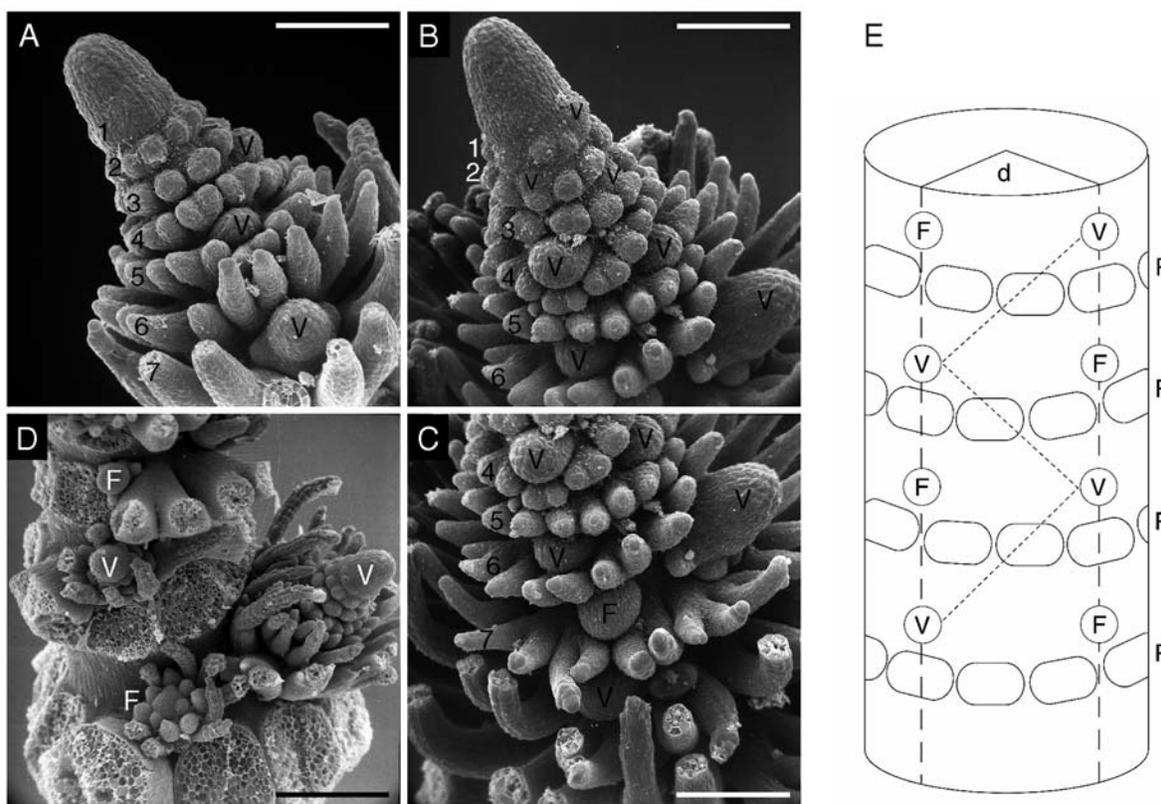


Fig. 3 Developmental morphology of *Ceratophyllum submersum* leaf whorls (Ceratophyllaceae). *A*, Distal part of vegetative shoot with apical meristem, annular bulge of whorl (1), and six successive whorls (2–7) showing bifurcating leaf primordia. *V* = vegetative lateral buds. Bar = 100 μm . *B*, *C*, Distal and subdistal parts of flower-forming shoot with apical meristem and seven successive whorls (1–7). Vegetative buds (*V*) alternating along two sectors. *F* = extra-axillary flower bud. Bar = 100 μm . *D*, Insertion area of three successive leaf whorls, with axillary vegetative buds (*V*) and extra-axillary male floral buds (*F*). Bar = 200 μm . *E*, Leaf and bud arrangement in *Ceratophyllum* along flowering shoot. *P* = insertion area of four successive and alternating leaf whorls. Lateral buds along two orthostichies with divergence angle $d = 70^\circ\text{--}90^\circ$; axillary vegetative buds (*V*) along zigzag line, extra-axillary flower buds (*F*) between. Arabic numerals represent the order of appearance of leaves; the lowest number represents the most recent leaf or whorl formed.

with five or six leaves, 753 whorls with seven or eight leaves, 1350 whorls with nine or 10 leaves, and only 50 whorls with 11 or 12 leaves. Thus, the variation in leaf number is markedly skewed.

Whorl development and positions of shoot buds. The shoot meristem of *Ceratophyllum* is an elongate cone with a slight curvature away from the sector with the favored lateral buds (fig. 3A, 3B; Strasburger 1902; Schaeppi 1935; Troll 1937; Turlier 1972). The first sign of a new whorl is an annular bulge (1 in fig. 3) around the shoot meristem. Individual hemispherical leaf primordia are formed on the annular bulge during whorl plastochron 2. Each leaf primordium starts to divide dichotomously during whorl plastochrons 3–5 (fig. 3A, 3B). Whorl development is often somewhat disturbed by the precocious inception of lateral buds. Vigorous vegetative buds appear as early as the subtending leaf primordium (fig. 3B). There is only one vegetative bud per leaf whorl. Along a single stem, all vegetative buds are arranged along a zigzag line, i.e., along two orthostichies that are occupied alternatively (fig. 3A–3D). They are normally oriented toward the water surface in more or less horizontally floating shoots, with intersection

angles ca. $70^\circ\text{--}90^\circ$ (fig. 3E; Schaeppi 1935; Raynal-Roques 1981). Along the zigzag line the vegetative buds occasionally show periodic growth promotion. For example, the vegetative bud of every third whorl may grow more vigorously than those between (fig. 3B, 3C; Rutishauser and Sattler 1987). At the onset of flowering no striking change in overall morphology occurs. The inconspicuous flowers (*F* in fig. 3) arise mainly along the same orthostichies as the vegetative buds (fig. 3E). Because of the alternation of successive leaf whorls, the flower buds occupy extra-axillary positions, i.e., the radii between two leaves (fig. 3C–3E). Such a flower arrangement may have some advantages for hypohydrophilous pollination (Strasburger 1902). Vigorous flowering shoots occasionally have additional (up to four) flower buds within each whorl (Arber 1920; Raynal-Roques 1981). While *Ceratophyllum* shows synchronous whorl development along established stems, the first whorls of axillary buds are clearly asynchronous. Two opposite leaves in the transversal plane are initiated before the remaining whorl members (fig. 3A).

Vascular supply. The vascular system of *Ceratophyllum* stems consists of a solid central cylinder (fig. 2D), which is

similar to other aquatic angiosperms such as *Hippuris* (de Klercker 1885; Schenck 1886; Arber 1920; Jones 1931; Napp-Zinn 1973/1974). According to Schneider and Carlquist (1996), this central core of conductive tissue mainly contains phloem but no obvious xylem elements. Again similar to *Hippuris*, each leaf of a *Ceratophyllum* whorl receives its own trace or (more rarely than in *Hippuris*) two adjacent leaves are supplied by forks of a common trace from the stele (Schaeppi 1935; Loiseau and Grangeon 1963; Loiseau 1969).

Three hypotheses on organ identity. (1) Most botanists accept that a *Ceratophyllum* whorl consists of seven to 10 “true” leaves. (2) Schaeppi (1935) concluded that each whorl is identical to two opposite leaves with basal leaflets around the node. He pointed to the fact that the two rows of vegetative buds along the seedling axis are in the same planes as the two cotyledons and the first pair of leaves. Thus, according to Schaeppi (1935), *Ceratophyllum* is characterized by sectorial anisoclady. (3) Braun (1831, p. 351) and Raynal-Roques (1981) postulated that the *Ceratophyllum* whorls may be derived evolutionarily from nodes with only one compound leaf. This complex leaf with a ringlike and short sheath divides precociously into seven to 10 forked subunits that become equally spaced around the node. The position of each vegetative bud equals the median plane of the original leaf, whereas all flowers arise from accessory buds. According to this view, *Ceratophyllum* is provided with a dorsoventral version of distichous phyllotaxis.

Utricularia purpurea (Lentibulariaceae) (Fig. 4)

General description. The genus *Utricularia* (214 spp.) is well known because of animal-catching traps (Sculthorpe 1967; Taylor 1989). *Utricularia purpurea* and its two sister species of section *Vesiculina* are submerged herbs in both Americas. They have mainly rose pink flowers, whorled phyllotaxis, and traps borne terminally on the leaf segments (fig. 4A). *Utricularia purpurea* is free floating (planktonic), with shoots 20–100 cm long. Along the main axis there are tetramerous to hexamerous whorls of leaves (fig. 4A). Each leaf is subdivided into whorled leaflets. All daughter shoots are inserted along the stem sector toward which the young shoot tip is coiled. Thus, I will call it the concave sector of the dorsoventrally organized stem. This side faces the water surface in horizontally floating shoots (Arber 1920; Lloyd 1942).

Meristic variation. The species of *Utricularia* section *Vesiculina* have two to seven leaves per whorl (Taylor 1989). The whorls along the stem of *U. purpurea* consist of four to six leaves, whereas the leaflet whorls along the leaf rachis are tetramerous (or dimerous). The daughter shoots first form one tetramerous leaf whorl. With the second whorl, the shoot buds normally switch to pentamerous (fig. 4A) or hexamerous whorls.

Whorl development and positions of shoot buds. The leaves and shoots (stems) grow acropetally. The leaves cease whorl formation after two or three nodes, while the indeterminate shoots continue to do so. Whole shoots and compound leaves result from developmental pathways that overlap considerably. Both produce subunits in a verticillate and acropetal order. Both have meristematic tips curved or coiled to some degree (Rutishauser and Sattler 1989). Both successive leaf

whorls and successive leaflet whorls are superposed (fig. 4A–4D). Daughter shoot buds occur in every second leaf whorl along the upper (concave) sector of the stem. They are extra-axillary, i.e., not subtended by a leaf (V in fig. 4A, 4B). The shoot bud is delayed when compared to the leaf primordia of the same whorl (fig. 4E).

Vascular supply. Stems and leaf axes (rachides) have a solid vascular cylinder without central pith (typical for many aquatics). At each stem node one vascular trace departs to each leaf and, if it is present, to the extra-axillary shoot bud (fig. 4B).

Three hypotheses on organ identity. (1) The determinate whorl members of *U. purpurea* and allies (section *Vesiculina*) are “true” leaves, while the delayed but indeterminate member (V in fig. 4A, 4E) is a shoot bud (Troll 1939; Taylor 1989). (2) Contrasting with this view, Lloyd (1933, 1942) concluded that *U. purpurea* and allies have no leaves, these being represented by verticillate branches. Similarly, Godfrey and Wooten (1981) described *U. purpurea* as having “bladder bearing branchlets in whorls.” (3) Combining both interpretations, Rutishauser and Sattler (1989) interpreted the leaves of *U. purpurea* as developmental mosaics partially homologous to whole shoots. This is according to Arber (1920, p. 107), who accepted “the view that the vegetative body of the Utricularias partakes of both stem and leaf nature. How such a condition can have arisen, historically, from an ancestor possessing well-defined stem and leaf organs, remains one of the unresolved mysteries of phylogeny.”

Leaf whorls in related taxa. Whorl formation is known from other Utricularias. For example, *Utricularia aurea*, *Utricularia stellaris*, and other members of the large section *Utricularia* have a whorl of two to five inflated appendages (floats) at the base of the peduncle (Taylor 1989; Rutishauser 1993). The scales and bracts above the float whorl are normally arranged along a Fibonacci helix.

Asynchronous Leaf Whorls

Limnophila indica (Scrophulariaceae) (Fig. 5)

General description. *Limnophila* (36 spp.) has 13 aquatic species that occur in the warm Old World and (some naturalized) in North America (Philcox 1970; Raynal and Philcox 1975; Cook 1996a, 1996b). Some aquatic species (e.g., *Limnophila heterophylla*, *Limnophila indica*, and *Limnophila sessiliflora*) are heterophyllous. They have finely divided submerged leaves. The emergent erect shoots of, e.g., *L. indica*, have toothed lanceolate leaves that are normally arranged in alternating pairs (i.e., dimerous whorls, fig. 5J). A few polymerous whorls may show transitional leaves (fig. 5F; Mohan Ram and Rao 1982). The submerged stems carry polymerous whorls of leaves that are pinnately divided into threadlike segments (fig. 5H). Abscisic acid (ABA) induces typical aerial leaves and flowers even on submerged nodes of *L. indica* (Mohan Ram 1991).

Meristic variation. In *L. indica* there are 12–14 leaves (leaflets) per vigorous submerged whorl whereas aerial stems may occasionally have 2(–4) leaves per node. In other *Limnophila* species the submerged nodes have up to 19 whorl members. In some *Limnophila* species also the emerged nodes

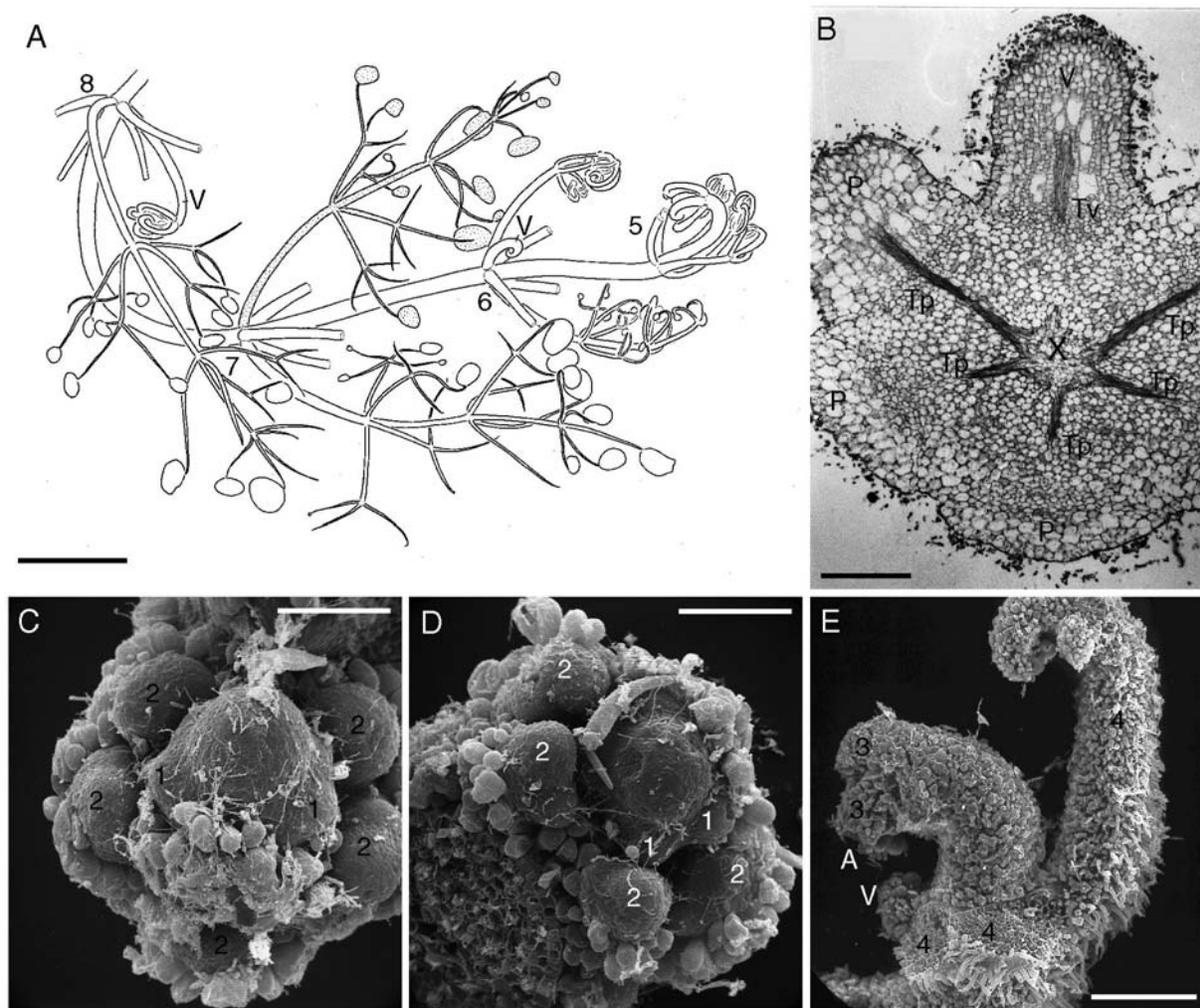


Fig. 4 Developmental morphology of *Utricularia purpurea* leaf whorls (Lentibulariaceae). *A*, Distal portion of 25-cm-long shoot. Leaves in pentamerous whorls; whorl 6 and 8 with extra-axillary shoot (*V*). Each leaf (one of them dotted) with three whorls of leaflets; traps at tips of leaf segments. Bar = 5 mm. *B*, Cross section of node with pentamerous leaf whorl (*P*); *X* = stele (vascular cylinder); *T_p* = leaf trace; *T_v* = additional trace providing extra-axillary shoot bud (*V*). Bar = 300 μ m. *C*, *D*, Coiled shoot tip with apical meristem, seen from two opposite sides; youngest whorl (*1*) superposed to next pentamerous whorl (*2*). Bar = 50 μ m. *E*, Another coiled shoot tip with whorls of coiled leaves (*3*, *4*; partly removed). *A* = shoot meristem; *V* = extra-axillary shoot bud of whorl *4*. Bar = 200 μ m. Arabic numerals represent the order of appearance of leaves; the lowest number represents the most recent leaf or whorl formed. (Adapted from Rutishauser and Sattler 1989.)

regularly have more than two leaves. For example, 5–8-merous whorls are typical for emerged stems of *L. sessiliflora*, whereas its submerged whorls consist of six to 10, or even more, leaves (Yang and Yen 1997). In *Limmophila hippuridoides* both submerged and emerged leaves (leaflets) are entire. The number of leaves per whorl is diminished continuously from nine at submerged whorls to three above (Philcox 1970).

Whorl development and positions of shoot buds. Early developmental stages of submerged whorls of *L. indica* and allies show a two-lobed annular bulge around the shoot meristem (*1* in fig. 5*B*; Goebel 1933; Schaeppi 1935; Turlier and Bugnon 1974). The subdivision of the two-lobed annular bulge occurs successively, first within the median plane and later around the whole node (fig. 5*B*–5*D*). The median leaves are

the first to develop filiform leaflets. Primordial leaflet shape is similar to the shape of young leaves around the node. Later the filiform leaflets elongate and terminate with bristles (fig. 5*D*–5*F*). Leaf pairs of aerial shoots arise as two opposite bulges at the shoot meristem (fig. 5*G*). There is only one vigorous vegetative bud per whorl (fig. 5*A*). A second opposite vegetative bud is present but often is much smaller. All favored vegetative buds in *Limmophila* are arranged along a helix. This situation is known as helical anisoclady (Loiseau 1965; Raynal and Philcox 1975; Raynal-Roques 1981).

Vascular supply. Each whorl is provided with two opposite traces entering the stele in the median plane, i.e., in the plane of the opposite buds and first-formed whorl members (fig. 5*I*). The two traces are trunk bundles that branch with

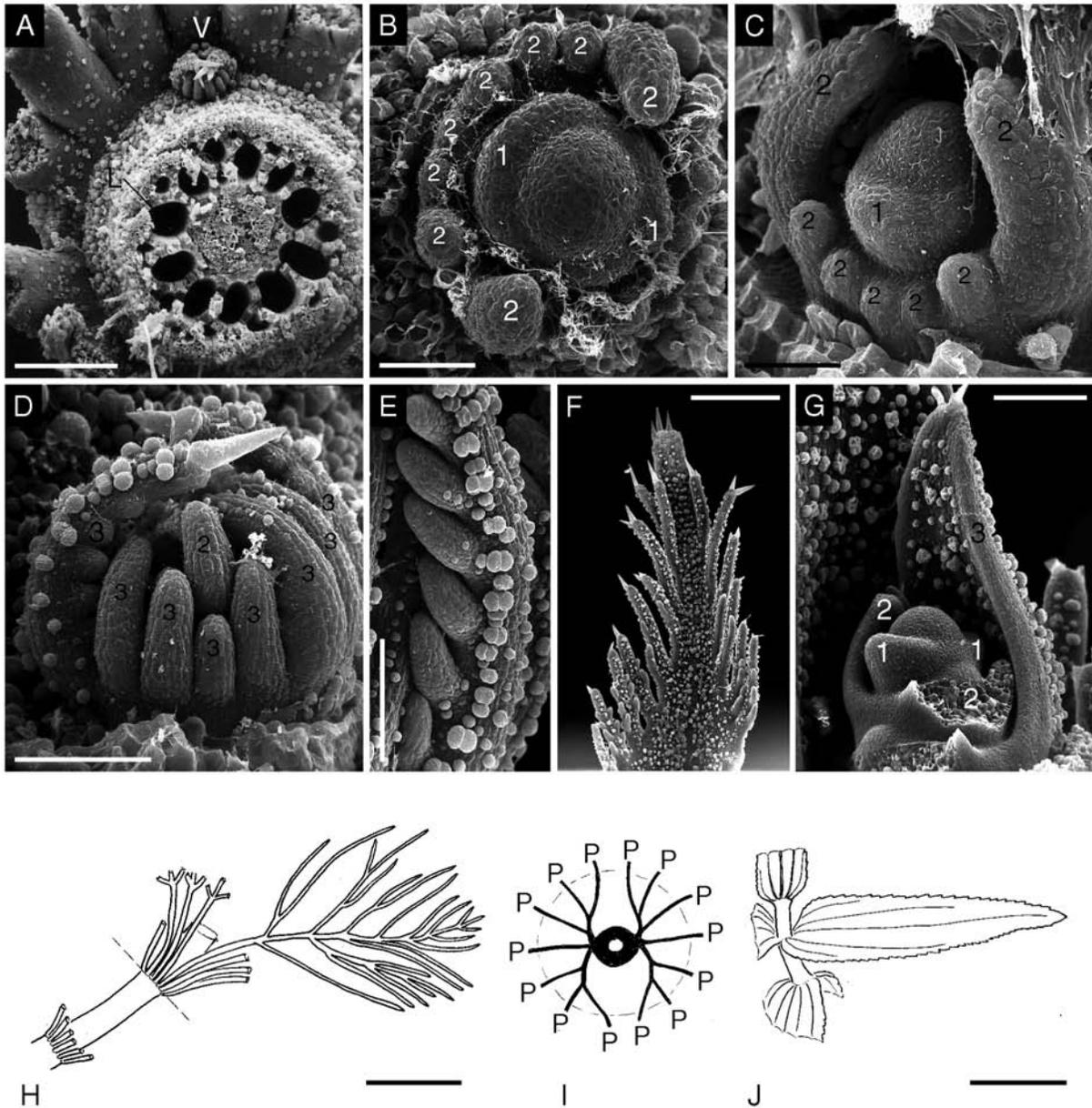


Fig. 5 Developmental morphology of *Limmophila indica* leaf whorls (Scrophulariaceae). *A*, Cross section of submerged stem just above insertion level of mature whorl. *V* = lateral bud; *L* = cortical lacunar system. Bar = 400 μm . *B*, *C*, Two apical meristems of submerged shoots, with two-lobed annular bulge (1); next older whorl (2) with two large leaf primordia (opposite) and delayed primordia between. Bar = 40 μm . *D*, Whorl during plastochron 3. Bar = 100 μm . *E*, Submerged leaf with outgrowing leaflets or segments. Bar = 100 μm . *F*, Tip of transitional leaf (immature). Bar = 300 μm . *G*, Tip of aerial shoot, with apical meristem and decussate arrangement of entire leaves (1–3). Bar = 100 μm . *H*, Submerged stem portion with polymerous whorls of pinnate leaves. Bar = 1 cm. *I*, Vascular supply in stem node of 14-merous leaf whorl (*P*). *J*, Aerial stem portion with leaf pairs. Bar = 1 cm. Arabic numerals represent the order of appearance of leaves; the lowest number represents the most recent leaf or whorl formed.

pedate pattern into as many daughter bundles as there are leaves (*P*) in a whorl (Schaeppi 1935; Turlier and Bugnon 1974).

Two hypotheses on organ identity. (1) Several botanists accept all whorl members of submerged shoots as “true” leaves (e.g., Philcox 1970; Mohan Ram and Rao 1982; Cook 1996a, 1996b). (2) According to Goebel (1913a), Schaeppi (1935),

Turlier and Bugnon (1974), Raynal and Philcox (1975), and Raynal-Roques (1981), the two whorl members subtending a bud are the terminal leaflets of two compound leaves that produce all additional whorl members. Turlier and Bugnon (1974, p. 2750) explained the formation of polymerous whorls in *Limmophila* by the process of precocious leaf branching (“ramification résolutive”) around the shoot meristem (node).

This process is explained as “le fractionnement d’une masse tissulaire, non encore organiquement structurée, en plusieurs foyers d’activité qui s’individualisent en engendrant chacun un primordium distinct.” Thus, what is called a multimerous leaf whorl according to hypothesis 1 is accepted as a leaf pair with basal leaflets according to hypothesis 2.

Leaf whorls in related taxa. As in *Linnophila*, the related Madagascan genus *Hydrotriche* (four spp.) also shows 3–20-merous leaf whorls and helical anisoclady (Cook 1996b). Raynal-Roques (1979) explained the *Hydrotriche* whorls as equivalent to two compound leaves. *Linnophila* and *Hydrotriche* are relatives of *Gratiola* (tribe Gratioleae within Scrophulariaceae) and may end up as members of the same “Scroph II clade” as *Hippuris* and *Plantago* (fig. 2; Reeves and Olmstead 1998).

*Galium rubioides and Allies (Rubiaceae,
Tribe Rubieae) (Fig. 6)*

General description and positions of shoot buds. Within the large family Rubiaceae, the Rubieae normally have two tetramerous or pentamerous alternating whorls of petals and stamens (fig. 6F), while a calyx is either lacking or strongly reduced (Pötter and Klopfer 1987). The tribe Rubieae is also characterized by vegetative whorls consisting of four to 12 leafy appendages (Bremekamp 1966; Rutishauser 1985). Normally these leaves are linear to lanceolate, with one or three parallel veins (fig. 6C). In *Rubia cordifolia*, however, there are tetramerous whorls of petiolate, cordate leaves (fig. 6A). In most Rubieae, only two leaves per whorl have axillary buds. These bud-bearing leaves are called P-leaves. All additional whorl members (labeled as P'-leaves) lack an axillary bud (fig. 6F). Along inflorescence axes the P'-leaves may be reduced, whereas the P-leaves subtend cymes. Helical anisoclady is typical for the Rubieae and other Rubiaceae. One of the two axillary buds per whorl is often more vigorous than the other one. All favored buds are arranged along a helix with a divergence of $\leq 90^\circ$ (Rutishauser 1981; Rutishauser et al. 1998).

Meristic variation. The first whorl of many Rubieae seedlings consists of four leaves, with two opposite P-leaves somewhat bigger than the two P'-leaves between. In several Rubieae the number of P'-leaves increases along the stem (e.g., up to six to 10 in *Galium verum*), whereas the number of P-leaves is fixed to two. In a few Rubieae (e.g., *Phuopsis stylosa*, *Rubia fruticosa*), the number of P-leaves per whorl occasionally is three (Rutishauser 1985). Rubieae such as *Galium palustre* and *Rubia peregrina* oscillate between four and five leaves in successive whorls. This instability in phyllotaxis is combined with an increased tendency to form forked (two-tipped) P'-leaves (Takeda 1916; Troll 1939). Forked leaves are rare in Rubieae with constant leaf number, e.g., in the regularly tetramerous whorls of *Galium boreale*.

Whorl development. Each whorl starts as a somewhat cornered annular bulge surrounding the shoot meristem (1 in fig. 6B, 6E). In *Cruciata glabra* (fig. 6F) the P'-leaves show a delayed outgrowth as compared to the P-leaves. *Phuopsis stylosa* has 6–9-merous whorls. Two opposite corners are more prominent in these whorls that show asynchronous development. The P-leaves are initiated first and the P'-leaves of the same whorl develop later; this can be seen during plastochron

2 (fig. 6E). A similar asynchronous whorl formation is typical for other Rubieae, with five to 10 leaves per node, e.g., *Galium aparine* and *Galium spurium* (Pötter and Klopfer 1987). The P-leaves of consecutive whorls deviate from the opposite-decussate arrangement to a variable degree. Decussation of the P-leaves is identical to superposition of tetramerous whorls consisting of two P-leaves and two P'-leaves, as found in *C. glabra* (fig. 6F). In contrast, the tetramerous whorls of *Galium rubioides* (fig. 6B, 6C) are alternating, or nearly so. This variation in phyllotaxis is correlated with the absence or presence of developmental differences between the P-leaves and the P'-leaves. In *G. rubioides* there are almost no developmental differences between P-leaves and P'-leaves in early development (fig. 6B). Successive tetramerous whorls (including their favored axillary buds) are spirally twisted and show divergence angles of 50° – 75° (Nägeli 1858). *Asperula cynanchica*, however, shows strongly asynchronous whorl development. The successive tetramerous whorls show divergence angles between 68° and 80° with respect to the favored axillary buds. Thus, the tetramerous whorls of *A. cynanchica* deviate from exact superposition (90°) only by values of 10° – 22° (Franke 1896; Schoute 1938). A switch from whorled to helical phyllotaxis (i.e., Fibonacci patterns) is rare in Rubieae; it can be observed along the inflorescence axis of *Phuopsis stylosa* (Rutishauser 1985).

Vascular supply. Most members of the Rubieae have two traces per node (fig. 2F). These traces occupy the same median sectors as the two bud-bearing P-leaves. All P'-leaves are supplied by branches from a girdling vascular bundle (Jeune 1980). *Galium rubioides* and *Galium kinuta* are exceptional because all four whorl members get their own traces from the stele (fig. 6D; Fukuda 1988).

Four hypotheses on organ identity. (1) Many morphologists (e.g., DeCandolle 1827; Braun 1831; Eichler 1861; Hofmeister 1868; Franke 1896; Takeda 1916; Troll 1939) accept only the two P-leaves of a whorl as “true” leaves. The remaining whorl members (P'-leaves) are interpreted as interpetiolar (interfoliar) stipules. (2) According to an alternative view, all whorl members in the Rubieae represent leaves (Croizat 1960, p. 913; Wardlaw 1965; Bremekamp 1966). Cronquist (1968, p. 65) proposed a homeotic stipule \rightarrow leaf transition within the Rubieae: “In species with four equal leaves at a node, the stipules have lost their identity as stipules and become leaves like other leaves, except the probable absence of axillary buds. ... The situation in *Galium* should serve as a warning against too formal and rigid an approach to evolutionary morphology.” (3) Rudimentary-stipule hypothesis: groups of colleters (glandular hairs) are present in the gaps between all leaves (P and P'; fig. 6E). These colleters, frequent in Rubieae, may be accepted as rudimentary stipules. Thus, the P'-leaves are homologous to P-leaves (Rutishauser 1985; Bell 1991). (4) The P'-leaves may be interpreted as intermediates (developmental mosaics) between leaves and stipules. This view implies a morphological continuum ranging from typical leaves to typical stipules. According to this continuum approach, the P'-leaves in Rubieae repeat the developmental pathways of the P-leaves to a variable degree, depending on the species (Jeune 1980; Rutishauser 1985).

Leaf whorls in related taxa. Various Rubiaceae increase the number of P-leaves per whorl. For example, *Phyllis nobla*

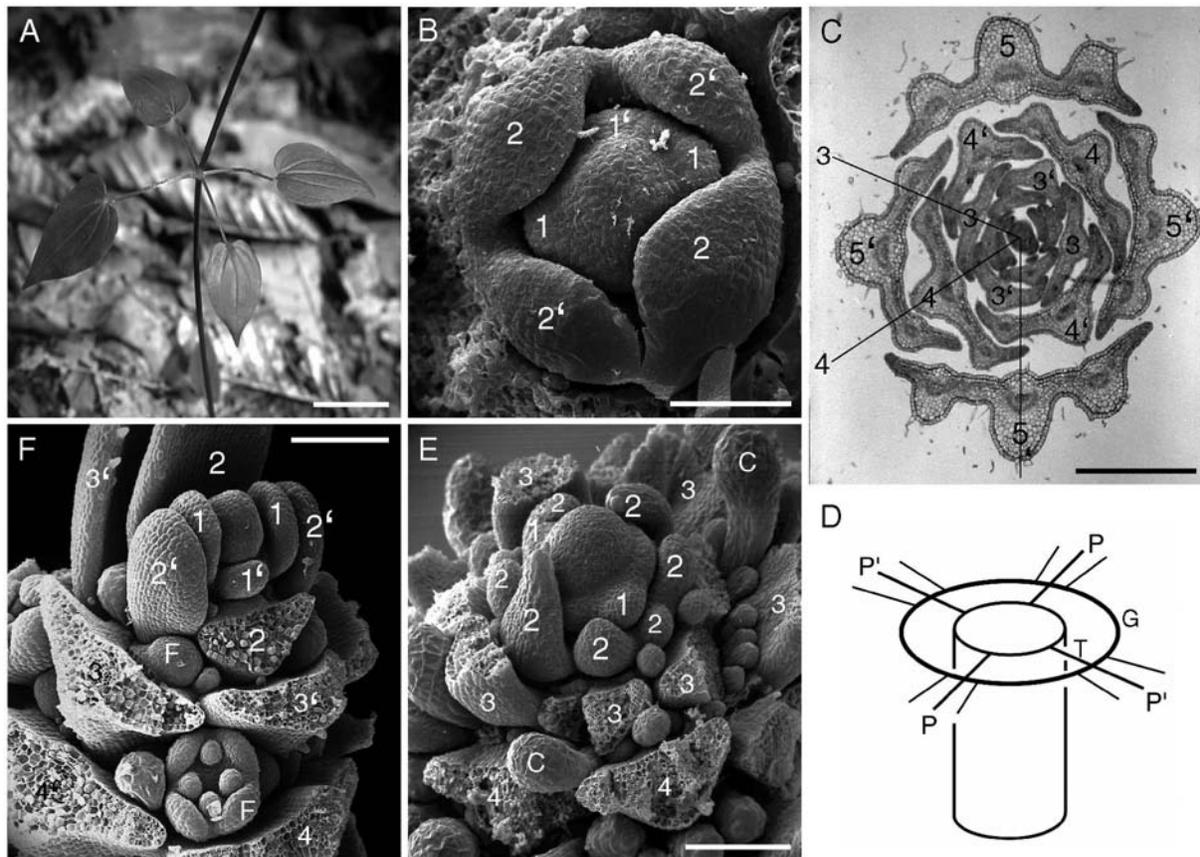


Fig. 6 Developmental morphology of leaf whorls in the tribe *Rubieae* (Rubiaceae). *A*, *Rubia cordifolia*. *B–D*, *Galium rubioides*. *E*, *Phuopsis stylosa*. *F*, *Cruciana glabra*. *A*, Tetramerous whorl with petiolate heart-shaped leaves. Bar = 2 cm. *B*, Shoot tip with apical meristem and two tetramerous alternating whorls; slightly asynchronous development with primordia size $1 > 1'$ and $2 > 2'$. Bar = 100 μm . *C*, Cross section of shoot tip with tetramerous whorls of slightly unequal leaves $3 > 3'$, $4 > 4'$, and $5 > 5'$. Alternation of successive whorls with divergence angle of 50° – 60° . Bar = 500 μm . *D*, Vascular supply of tetramerous whorl with four vascular traces (*T*) and girdling vascular bundle (*G*) supplying axillating leaves (*P*) and those (*P'*) without buds. *E*, Shoot meristem with two-lobed annular bulge (*1*); next outer whorl (*2*) 8-merous with two large leaf primordia (opposite) and smaller ones between. Older whorls (*3*, *4*) removed except colleters (*C*). Bar = 100 μm . *F*, Shoot meristem and two tetramerous superposed whorls; clearly asynchronous whorl development with primordia size $1 > 1'$ and $2 > 2'$. Next outer whorls with eccentric floral buds (*F*) in axils of leaf *3* and *4*; *3'* and *4'* are leaves without buds. Bar = 100 μm . Arabic numerals represent the order of appearance of leaves; the lowest number represents the most recent leaf or whorl formed. (Fig. 6A photographed by the author in southern India.)

(tribe Anthospermeae) regularly has three to four P-leaves per whorl. Other rubiaceae genera with sometimes more than two P-leaves per whorl are, e.g., *Bouvardia*, *Cephalanthus*, *Coffea*, *Gardenia*, *Hamelia*, *Houstonia* (Rutishauser 1985). *Limnosipanea spruceana*, an aquatic from tropical South America, has four to six leaves per whorl, whereas another species (*Limnosipanea ternifolia*) is normally 3-verticillate (Velasquez 1994; Cook 1996b).

Acacia hippuroides, *Acacia longipedunculata*, and *Allies* (Leguminosae) (Fig. 7)

General description and positions of shoot buds. Most Australian species of *Acacia* (wattles = *Racosperma*, ca. 900 spp.) show pinnate leaves only during the seedling stage. Afterward they switch to phyllodes (rachis leaves) that are needle-like or laterally flattened (Troll 1939; Howard 1974; Kaplan

1984; Sattler et al. 1988; Bell 1991). Whorls of phyllodes and stipules occur in at least two sections of the phyllodinous *Acacias*, including the following species that will be described in this and the following paragraph: *Acacia hippuroides* (fig. 7A–7D), *Acacia longipedunculata* (fig. 7E, 7F), and *Acacia baueri* (fig. 8E, 8F) belong to section *Lycopodiifoliae* (all forming low shrubs), whereas *Acacia verticillata* (fig. 8A–8D) is a shrubby species of section *Juliflorae* (Pedley 1972, 1978/1979; Simmons 1981). In these four species there is often a single lateral bud in each of one or two whorls. Lateral buds of successive whorls are arranged along a helix. *Acacia hippuroides* and *A. longipedunculata* may have up to three to four lateral buds per whorl, each subtended by a phyllode (Rutishauser 1986).

Meristic variation. The whorls of *A. hippuroides* consist of 10–19 phyllodes; those of *A. longipedunculata* contain

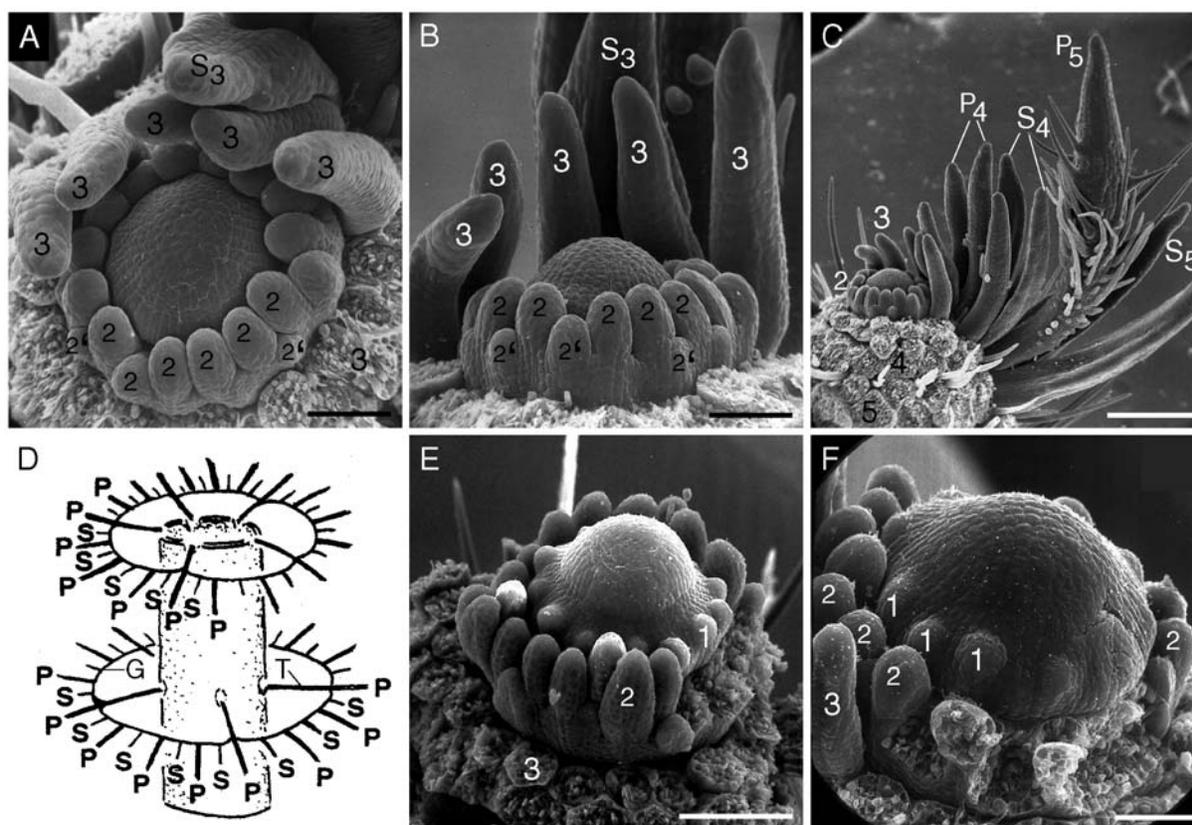


Fig. 7 Developmental morphology of phyllode whorls in *Acacia* sect. *Lycopodiifoliae* (Leguminosae). A–D, *Acacia hippuroides*. E, F, *Acacia longipedunculata*. A, B, Two different views of shoot tip. Shoot meristem is surrounded by annular bulge of new whorl; whorl 2 consists of inner ring of phyllode primordia (2) and delayed outer stipule primordia (2'). 3 and S₃ are phyllodes and stipules of whorl 3. Bar = 50 μm. C, Older whorls (3–5) of same shoot tip (appendages removed except one sector). P₄, P₅ and S₄, S₅ = phyllodes and stipules of whorls 4 and 5. Bar = 200 μm. D, Vascular supply of two successive whorls. Each whorl with 10–19 phyllodes (P), same number of stipules (S); only four to six common traces (T) arise from the stele and supply a girdling vascular bundle (G). E, F, Two shoot meristems with two primordial phyllode whorls (1, 2). 3 = phyllode of next whorl. Bars = 100 μm. Arabic numerals represent the order of appearance of leaves; the lowest number represents the most recent leaf or whorl formed.

15–27 phyllodes. There is about the same number of setaceous interfoliar stipules as phyllodes per whorl. In these two species and other members of section *Lycopodiifoliae* the number of phyllodes in each whorl is never less than five to nine, as observed in *Acacia galioides* (Pedley 1972). Seedlings do not have complete whorls yet. Incomplete or half-whorls are arranged along a helix in seedlings of, e.g., *A. longipedunculata* (Rutishauser and Sattler 1986).

Whorl development. A ring of bumps is the first sign of a new whorl around the shoot meristem. Soon a ringlike platform or shoulder becomes distinguishable from the inner apical region (fig. 7E, 7F). The arrangement of these bumps around the shoot meristem is not always regular. Along the shoulder, a few bumps are inserted higher up than others (1 in fig. 7E, 7F). During the second whorl plastochron additional bumps (2') appear outside and between the already developed wreath of primordia (2 in fig. 7A, 7B). During whorl plastochrons 3–4 the outer whorl primordia (prospective stipules) accelerate their growth in length. This contrasts with the behavior of the inner cycle of bumps that always develop into phyllodes (fig. 7A–7C).

Vascular supply. *Acacia hippuroides*, *A. longipedunculata*, and other species of sect. *Lycopodiifoliae* possess a unique vascular pattern within the nodes. The number of vascular traces (trunk bundles) is lower than that of the phyllodes. For example, in *A. hippuroides* only four to six trunk bundles leave the stele within a node, whereas there are five to eight trunk bundles per whorl in *A. longipedunculata* (Rutishauser and Sattler 1986; Sattler et al. 1988). Branches of the trunk bundles form a girdling bundle and supply all whorl members, phyllodes, and stipules (fig. 7D). Even *A. galioides*, with five to nine phyllodes per whorl, has fewer traces than phyllodes; only three to five trunk bundles are observable per node (Buscalioni and Catalano 1927). Lateral buds (if present) occupy the sectors of the trunk bundles.

Four hypotheses on organ identity. (1) Each phyllode may be accepted as a “true” leaf, sharing an interfoliar stipule with its leafy neighbor (Pedley 1972). (2) All whorl members (including the so-called stipules) may be interpreted as having leaf identity; the colleters (glandular hairs) between them are accepted as rudimentary stipules (Rutishauser and Sattler 1986). (3) Buscalioni and Catalano (1927) proposed that in

whorl-forming Acacias, including *A. galioides*, the number of trunk bundles indicates the number of compound leaves per whorl. Thus, each phyllode whorl of *A. hippuroides* consists of four to six “true” leaves. (4) It is best to accept that interpretations 1–3 approximate nature to some degree, but probably none of them fully reflects nature. Continuum morphology allows the recognition of a morphocline comprising pinnate leaves, phyllodes, stipules, and collectors, including intermediates between them (Rutishauser and Sattler 1986).

Acacia baueri and *Acacia verticillata*
(Leguminosae) (Fig. 8)

General description. The classification of *A. baueri* and *A. verticillata* is explained in the previous case study. The phyllodes in both species can be verticillate or scattered. The existence of two subspecies in *A. baueri* with different phyllotaxis patterns shows that the capacity to form whorls is genetically determined: *A. baueri* subsp. *baueri* has regular or oblique whorls consisting of five to 10 phyllodes, whereas subsp. *aspera* has all phyllodes irregularly scattered along the stem (Pedley 1972). Similarly, the phyllodes of *A. verticillata* are some-

times whorled (with six to 12 phyllodes per whorl) and sometimes scattered (fig. 8D). In *A. baueri* and *A. verticillata* there are two types of phyllodes occurring along the same twig: few P-phyllodes have setaceous stipules and subtend axillary buds. The second phyllode type (called exstipulate, or E-phyllode) is more frequent. These E-phyllodes normally lack stipules and axillary buds. At maturity, the E-phyllodes closely resemble the P-phyllodes in both species. Adaxial nectaries are present in both P- and E-phyllodes of *A. baueri*, whereas the nectary is lacking in E-phyllodes of *A. verticillata*. Seedlings of *A. verticillata* have their first (and compound) leaves arranged along a helix (1–5 in fig. 8C). They are all provided with two stipules and an axillary bud. The same helix continues with P-phyllodes (e.g., 6–10 in fig. 8C, 8D) into the area of the needle-like phyllodes (Kaplan 1980). All E-phyllodes are inserted at and between the levels of the P-leaves, forming complete and incomplete whorls.

Meristic variation. The E-phyllodes of *A. baueri* outnumber the P-phyllodes by the factor 3–9. In *A. verticillata* there are six to 26 times as many E-phyllodes as P-phyllodes (Del-pino 1883; Rutishauser 1986). Contrasting with *A. baueri*,

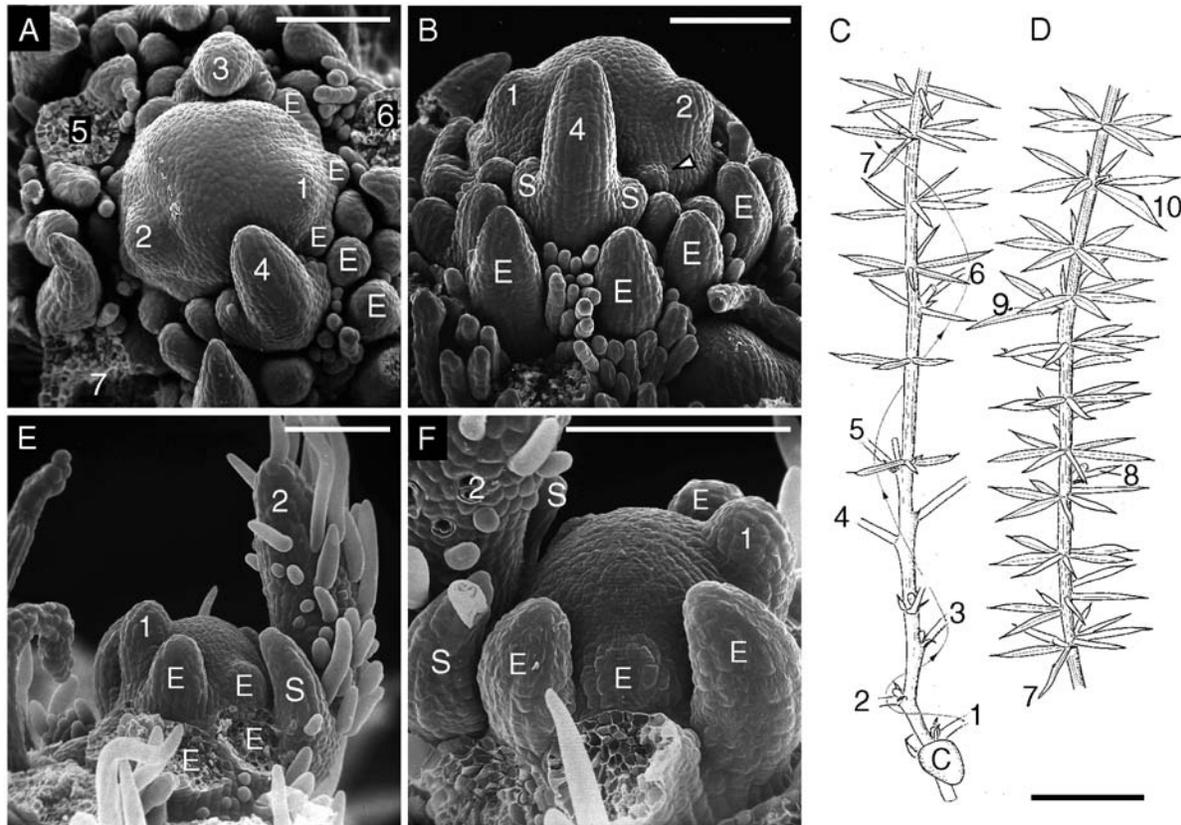


Fig. 8 Developmental morphology of two *Acacia* spp. with phyllode whorls or irregularly scattered phyllotaxis (Leguminosae). A–D, *Acacia verticillata*. E, F, *Acacia baueri* subsp. *aspera*. A, B, Two shoot meristems, with stipulate helically arranged P-phyllodes (1–7) arising at shoot meristem and exstipulate E-phyllodes arising lower down in subapical zone. S = stipules of P-phyllode (4). Arrowhead points to initial E-phyllode. Bars = 100 μ m. C, D, Seedling axis, with cotyledons (C) and petioles of pinnate seedling leaves (1–5). The generative helix continues with P-phyllodes (6–10); additional E-phyllodes in whorls or nearly so. Bar = 1 cm. E, F, Two views of shoot tip, with distichously arranged P-phyllodes (1, 2); E-phyllodes arise between them. S = stipules of P-phyllode (2). Bar = 100 μ m. Arabic numerals in A, B, E, and F represent the order of appearance of leaves; the lowest number represents the most recent leaf or whorl formed.

not all *A. verticillata* whorls possess a P-phyllode. Sometimes there are one to three sterile whorls consisting of E-phylloides only between two whorls with a P-phyllode each (fig. 8D). In *A. verticillata* the divergence angles between consecutive P-phylloides are often close to 137.5° but occasionally $\geq 145^\circ$ (Kaplan 1980; Rutishauser and Sattler 1986). Spirodistichy or exact distichy of P-phylloides (with divergence angles approximating 180°) is common in *A. baueri* (fig. 8E, 8F).

Whorl development and positions of shoot buds. There are two waves of phyllode formation: first a series of P-phylloides and then a series of E-phylloides (fig. 8A, 8B, 8E, 8F). The P-phylloides arise as prominent hemispherical primordia (1–2) at the apical meristem, soon accompanied by two stipular primordia (*S* in fig. 8). They show helical or (spiro-)distichous phyllotaxis. E-phylloides, however, are initiated as slightly (*A. baueri*) or considerably smaller hemispherical primordia (*A. verticillata*) later and some distance down the flanks of the shoot meristem, i.e., in subapical zones at and between the insertion levels of the three youngest P-phylloides.

Vascular supply. Each phyllode of *A. baueri* and *A. verticillata* is supplied by its own trace(s) from the stele. The P-phyllode (with stipules and axillary bud) is provided with three traces that are associated with a conspicuous stelar gap. The single traces to the E-phylloides leave the stele separately, associated with inconspicuous gaps (Dormer 1944). In *Acacia* spp. with compound stipulate leaves and helical to distichous phyllotaxis, the nodes are trilacunar, i.e., provided with three gaps according to the number of leaf traces (Kaplan 1980; Sharma and Pillai 1985).

Four hypotheses on organ identity. (1) The E-phylloides (lacking axillary buds and stipules) of *A. verticillata* were interpreted as additional stipules by Braun (1831, p. 352) and Hofmeister (1868). Similarly, Kaplan (1984, p. 68) concluded that in *A. verticillata* the E-phylloides are “more closely homologous with metamorphosed stipules than with the foliage leaf axis itself.” (2) Velenovsky (1913, p. 95) and Goebel (1913a, 1928, 1933) considered both P- and E-phylloides in *A. verticillata* as leaf homologues that differ in their early growth rates. Rutishauser (1986, 1988) extended this hypothesis also to *A. baueri*, where E-phylloides are even more similar to P-phylloides. The E-phylloides may be viewed as additional leaves that repeat the developmental pathway of the P-phylloides. (3) Delpino (1883) hypothesized that the E-leaves in *A. verticillata* are “pseudophylloides,” i.e., a new category of appendages homologous to neither P-leaves nor stipules. (4) Continuum view: the three interpretations 1–3 become different perspectives of the same hypothesis when we accept that P-leaves, E-leaves, and stipules are structural categories with overlapping developmental pathways, i.e., members of the same morphocline. E-leaves in both *A. baueri* and *A. verticillata* can be explained as slightly abbreviated versions of P-leaves, whereas the stipules in these species deviate to a higher degree (Rutishauser 1986; Rutishauser and Sattler 1986).

Leaf whorls in related species. Whorl formation in Australian *Acacias* (*Acacia* subgenus *Heterophyllum*) is typical for most members of section *Lycopodiifoliae* (Pedley 1972, 1978/1979). *Acacia riceana*, a close relative of *A. verticillata*, has an irregularly scattered or an almost whorled phyllotaxis. Certain Australian *Acacias* form fascicles and incomplete whorls rather than complete ones. Examples are *Acacia brunioides*,

Acacia conferta, *Acacia gordonii*, *Acacia minutifolia*, and *Acacia subternata*, all of which belong to section *Phyllodineae* (Velenovsky 1913, p. 95; Pedley 1978/1979; Simmons 1981; Rutishauser 1986; and R. Rutishauser, unpublished results).

Hydrothrix gardneri (*Pontederiaceae*) (Fig. 9)

General description. *Hydrothrix* is a monotypic genus of the *Pontederiaceae* (Cook 1996b). It grows in northeastern Brazil as a submerged herb with elongate stems and filamentous leaves arranged in whorls (fig. 9A). Each whorl consists of a single main leaf (P) with a membranous ochrea (i.e., a cuplike stipule) that encircles the node. All other leaves (E) of the same whorl are borne inside this ochrea (fig. 9D, 9F). They lack a prominent ochrea. At the base of each E-leaf a minute axillary stipule is present. The P-leaves of successive whorls are arranged along a helix with divergence angles of ca. 160° , i.e., in a spirodistichous pattern (fig. 9E: 6–9). The E-leaves are evenly distributed in one to two rings around the whole node. All filamentous leaves (P and E) are slightly flattened and face, with their broader side, toward the node center (fig. 9E; Rutishauser 1983). Whorl formation, as described for *Hydrothrix*, is not known from other monocots.

Meristic variation. There are seven to 30 leaves per whorl. The lowermost nodes of lateral shoots may consist of a P-leaf and only zero to three E-leaves (Goebel 1913b).

Whorl development and positions of shoot buds. Only the P-leaves are initiated at the shoot meristem. They arise as semicircular bulges (1 in fig. 9B). Then the collar-like ochrea of the young P-leaf encircles the node (2 in fig. 9B, 9C). Inside this, a horseshoe-shaped bulge is formed (R_3 in fig. 9B, 9C). During plastochron 4 this bulge surrounds the whole node, leading to an asymmetric ring that is the site for the formation of all E-leaves. The first E-primordia are observable on rings R_4 and R_5 (fig. 9B, 9C). In the following plastochrons, additional E-leaves are initiated in an acropetal (centripetal) direction (fig. 9D: E_5 , E_6). When the plant starts flowering, it switches from monopodial to sympodial growth. The main shoot axis becomes determinate and forms a terminal flower pair. The penultimate P-leaf then subtends an axillary bud above its whorl-forming ring. This axillary bud will form the next sympodial unit or module (Rutishauser 1983).

Vascular supply. In each node there is one vascular trace oriented in the same radius as the single P-leaf. All E-leaves of a whorl are supplied by branches from a girdling vascular bundle that is attached to the only trace (figs. 2G, 9E).

Two hypotheses on the relative position of the E-leaves. (1) Only the P-leaves (one per whorl) are inserted along the long shoot axis. All E-leaves of a whorl belong to an axillary short shoot subtended by a P-leaf and with annular insertion around the long shoot axis (Goebel 1913b; Arber 1920). (2) The E-leaves of a whorl belong to the same shoot axis as the P-leaf. The annular bulges are intercalated in subapical zones of the shoot tip and give rise to all E-leaves (Rutishauser 1983, 1988).

Discussion

Functional Significance of Whorled Phyllotaxis

Functional significance of whorled phyllotaxis for terrestrial plants. The role of dorsoventral floral whorls in plant pol-

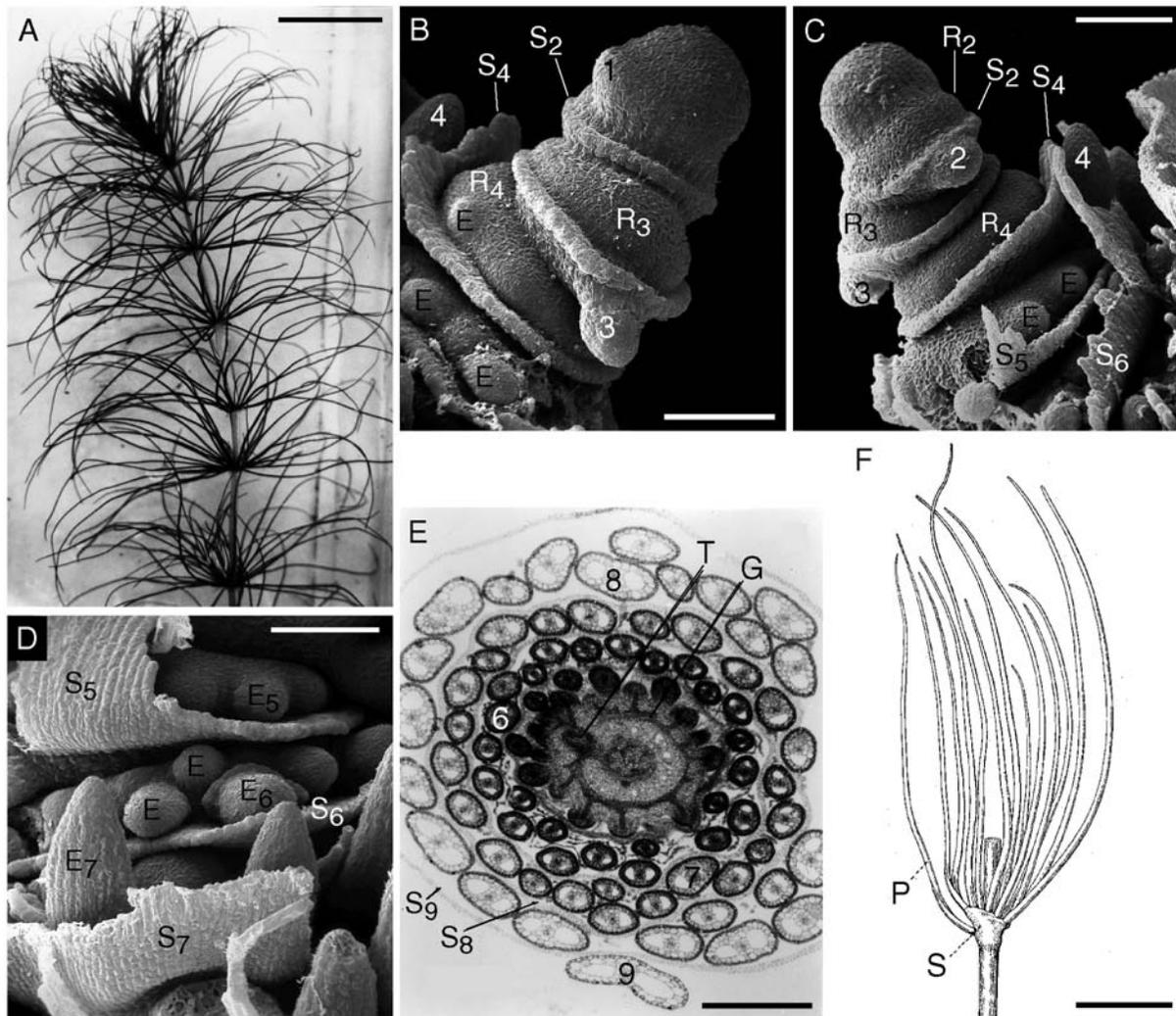


Fig. 9 Developmental morphology of *Hydrothrix gardneri* leaf whorls (Pontederiaceae). *A*, Submerged shoot with polymerous whorls of filamentous leaves. Bar = 1 cm. *B*, *C*, Two views of vegetative shoot tip. 1–4 = primordial main leaves, arranged along a helix, with collar-like ochreas S_2 – S_6 . Annular bulges (R_2 – R_4) giving rise to whorls, which are soon provided with leaf primordia (*E*). Bar = 70 μ m. *D*, More proximal portion of shoot tip, with partially removed ochreas (S_5 – S_7) of three successive whorls. The annular bulges initiate whorl-forming leaves (E_5 – E_7). Bar = 70 μ m. *E*, Cross section of vegetative shoot tip. Main leaves (6–9) along spiral, S_5 and S_9 are the ochreas of leaves 8 and 9. Note girdling vascular bundle (*G*) and single trace (*T*) from central stele. Bar = 100 μ m. *F*, Mature whorl consisting of P-leaf (*P*; with ochrea, *S*) and additional 12 leaves. Bar = 5 μ m. Arabic numerals represent the order of appearance of leaves; the lowest number represents the most recent leaf or whorl formed. (*A*–*E* adapted from Rutishauser 1983; *F* reproduced from Goebel 1913*b*.)

linator systems is reviewed by Neal et al. (1998). What is the functional (adaptive) significance of whorled phyllotaxis outside the floral region? According to Niklas (1998), vertical shoots with alternating whorls optimize their “fitness landscapes” for light harvesting. Tubular sheaths in jointed plants such as *Equisetum* (fig. 1) and Casuarinaceae give mechanical strength to the next internode that elongates as a result of a basal meristem. Whorl formation in these plants may also be a prerequisite for leaf reduction, while the stem bears most of the photosynthetic tissue (Boureau 1971). This phenomenon is a way of reducing water loss in xeric conditions, although *Equisetum* presents an interesting association of xeromorphic and hygromorphic stem characters (Sporne 1966; Daviero et

al. 1996; Spatz et al. 1998). Australian Acacias are adapted to dry and hot climates (Simmons 1981). The four studied whorl-forming *Acacia* species (figs. 7, 8) have stiff needle-like leaves (phyllodes). It is not obvious why they form phyllode whorls while most other Australian wattles show spirally arranged phyllodes (Rutishauser 1986).

Hippuris syndrome and functional significance of whorled phyllotaxis for aquatic angiosperms. There is convincing evidence that all aquatic angiosperms evolved from terrestrial ancestors. Cook (1996*b*, 1999) assumes that the evolutionary switch from terrestrial to aquatic life happened more than 200 times during the evolution of land plants (embryophytes). Thus, there are many cases of parallel evolution (including

convergences, homoplasies) among aquatic angiosperms (Arber 1920; Cusset and Jeune 1975; Raynal-Roques 1981). Many flowering plants of ponds and lakes evolved in parallel highly dissected leaves or leaf parts that are arranged in tiers similar to the leaf whorls of *Hippuris*. This was called *Hippuris* syndrome by Cook (1978). Tiers of linear or threadlike photosynthetic structures may be seen as best suited to life in slowly flowing water, as a means to optimize O₂ and CO₂ exchange as well as buoyancy. Tiers are important and whorls are a simple answer. The *Hippuris* syndrome is found, e.g., in *Aldrovanda*, *Ceratophyllum*, *Hippuris*, *Hydrothrix*, *Limnophila pro parte*, *Megalodonta*, *Myriophyllum*, *Rotala pro parte*, *Utricularia purpurea*, and allies (figs. 2–5, 9). They all grow as submerged herbs in ponds and lakes. Four of them (*Hippuris*, *Limnophila*, *Megalodonta*, *Myriophyllum*) are heterophyllous and show clearly different leaves above water level (Sculthorpe 1967; Kane and Albert 1987; Mohan Ram 1991). Because the Rubiaceae (especially Rubieae) have many terrestrial species with whorled leaves (fig. 6), one expects them to be preadapted for an aquatic life. But this is not so, except for the rubiaceous *Limnosipanea spruceana* (tropical South America) that is aquatic and shows a *Hippuris*-like habit (Cook 1978, 1996b).

Fuzziness of Organ Identities

The “leaf” as a composite structure. A typical megaphyllous “leaf” in vascular plants (especially seed plants) is a dorsoventral organ of limited growth, borne on the stem and having a bud in its axil. The “leaf” consists of various components with different developmental pathways, e.g., blade and stipules. Cell clones forming a leaf are interdependent and are controlled by alternative and/or synergistic gene sets (Tsukaya 1995, 1998; Jackson 1996; Poethig 1997; Lyndon 1998b). Dorsoventral leaf polarity and axillary bud formation are correlated phenomena, as shown by *Arabidopsis* mutants having reverse leaf polarity (McConnell and Barton 1998). The geneticists’ view coincides with the phylogenetic perspective that the megaphyllous “leaf” of vascular plants is a composite structure including its axillary bud (Arber 1950). The “leaf” of extant vascular plants probably has multiple origins. Fossil data suggest that the microphylls of *Equisetum* and the megaphylls (including prefronds) of ferns and seed plants are homologous to lateral branches or telome trusses, but it is likely that some pertinent features of megaphylls (e.g., planation, webbing, dorsoventral symmetry, determinate growth, reduction) evolved independently in these groups (Croizat 1960; Howard 1974; Stewart and Rothwell 1993; Kenrick and Crane 1997). As an evolutionary reminiscence, some components of the modern “leaf” in extant vascular plants (especially ferns and seed plants) are partially homologous to those of the “shoot” (or “stem”), as proposed by Arber’s (1950) partial-shoot theory. Thus, it may be difficult or arbitrary to clearly distinguish structural categories such as “shoots” (including “stems”), “leaves” (including “leaflets”), and “stipules” (Rutishauser and Sattler 1985).

What is a stipule? Stipules are additional nodal appendages next to the leaf insertion. There are often two stipules per leaf (e.g., in *Acacia baueri* and *Acacia verticillata*; fig. 8). Stipules arise either on the flanks of the leaf primordium or

from primordia spatially independent but concomitant with the leaf primordium (Rutishauser and Sattler 1986; Grimes 1996). As compared to associated leaves, stipules often show a precocious development, with a stop in growth clearly prior to the leaf itself. Stipules can be green and persisting as long as the leaf itself, or they can be caducous when serving for bud protection only. Stipules are typical for several dicots and a few monocots, as shown in figures 6–9. Many botanists since Eichler (1861) accepted stipules as basal subunits of the leaf itself. However, it is heuristically better to accept stipules of various dicotyledonous families (e.g., Cunoniaceae, Leguminosae, Rubiaceae) as additional nodal outgrowths that may repeat the developmental pathway of a leaf nearby (Rutishauser and Sattler 1986; Pötter and Klopfer 1987). Especially interfoliar (interpetiolar) stipules placed in the radii between whorled leaves can be viewed as lateral repetition of a leaf of the same node (Rutishauser 1985; Rutishauser and Dickison 1989).

What is a leaflet? Many dicots have compound leaves with subunits that are called “leaflets,” “pinnae,” or “leaf segments.” According to Arber’s partial-shoot theory (1950), compound leaves repeat the developmental pathways of whole shoots. New results from developmental genetics corroborate this theory (Tsukaya 1995; Hofer and Ellis 1998). Thus, a leaflet is partially homologous to a whole leaf, whereas petiole and rachis are partially homologous to the shoot axis (stem). This phenomenon is obvious in *U. purpurea* (fig. 4). Shoots (stems) and leaves of *U. purpurea* and other Utricularias have overlapping developmental pathways, leading to a considerable degree of fuzziness of “leaf” and “shoot” (including “stem”) as structural categories (Sattler and Rutishauser 1990; Rutishauser 1993). This fuzziness is also found in Meliaceae (especially *Chisocheiton* and *Guarea*), with nearly indeterminate pinnate leaves and epiphyllous shoots (Fisher and Rutishauser 1990). Moreover, compound leaves of Podostemaceae, Polemoniaceae, and other dicots resemble whole shoots with respect to transversal leaflet insertion and three-dimensional leaf branching (Sattler and Rutishauser 1992; Rutishauser 1995; Rutishauser and Sattler 1997). The principle of repetitive branching (i.e., repetitive meristem division) makes it understandable that structures already produced at the shoot meristem are, like an echo, occasionally repeated within a compound leaf (Arber 1950).

Complementarity of morphological interpretations. Contradictory models in structural botany are often complementary views with different heuristic values and different “contents of truth” (Arber 1954, 1957; Rutishauser and Sattler 1985, 1986, 1987, 1989). In the nine case studies (figs. 1–9) it is not obvious which organ identity (morphological significance) the whorl members really have. This is because evolutionary processes in plants transcended structural categories (Sattler 1992, 1994, 1996; Sattler and Rutishauser 1997). When we use structural categories for plant description, we have to be aware of their fuzzy connotations (Rutishauser 1995). When we try to clearly define them, we should allow different hypotheses as complementary views. Thus, the more or less contradictory hypotheses on organ identity mentioned in this article “owe their apparent opposition merely to the standpoint from which they are regarded” (Arber 1957, p. 68). They result from thinking on opposite sides of a logical

gap. The acceptance of a complementary relationship between two or more apparently contradicting views is the first step toward a dialectic synthesis into a new predictive model. The complementarity idea in this broad sense is part of Bertalanffy's (1975) epistemological perspectivism.

Symmetry of Whorl-Forming Shoots

Alternating versus superposed whorls. Alternating whorls arise successively at the shoot meristem and show equal numbers of leaves, with the leaves of the upper whorl occupying the sectors exactly between the leaves of the lower whorl. Equidistance and alternation are parts of "Hofmeister's rule" (Braun 1831, p. 360; Hofmeister 1868; Schoute 1913; Leins and Erbar 1997). *Hippuris* and *Galium rubioides* are examples for nearly alternating whorls (fig. 2A–2C; fig. 6B, 6C). In terms of Hofmeister's rule, all whorl members around the apical meristem determine the primordial positions of a new whorl.

Superposed whorls have their organs arranged in the same radii and violate Hofmeister's rule. Superposition of whorls (also known as "sectorial cohesiveness" or "in-line" production of organs) is observable in several flowers, e.g., superposition of tepals and stamens in *Basella* and *Berberis* (Lacroix and Sattler 1988; Endress 1992, 1994b). Superposition of stamens with perianth members is the most frequent case of "sectorial cohesiveness." This phenomenon is occasionally the result of the fact that stamen and perianth members originate from a common primordium.

Superposed leaf whorls are very rare in vascular plants outside the floral region of angiosperms. Several fossil allies of *Equisetum* had sphenophylls and sporophylls arranged in superposed whorls (e.g., *Archaeocalamites*, *Asterophyllites*; Bierhorst 1971; Boureau 1971; Stewart and Rothwell 1993). Superposed leaf whorls are also observable in *U. purpurea* and allies (fig. 4C, 4D) where superposition is developmentally correlated to two factors: (1) the floating shoots are dorsoventral systems with respect to circinate shoot tips and branching and (2) the distance between superposed successive whorls is large and, thus, the time lapse (plastochron) between them may last longer than what we know from alternating whorls (fig. 4C, 4D; Rutishauser 1998).

The Rubieae provide several examples of intermediates between alternating and superposed whorls (Fukuda 1988). Different degrees of spiral twisting are observable in species with tetramerous leaf whorls. *Cruciata glabra* (fig. 6F) and *Asperula cynanchica* are examples of nearly superposed whorls, whereas *G. rubioides* shows nearly alternating whorls (fig. 6B). The more similar the four whorl members are during development, the better they approach exact alternation in successive whorls.

Synchronous versus asynchronous whorls. Synchronous whorls are observable as a ringlike arrangement during inception around the shoot meristem. A synchronous whorl consists of a single cycle of organs that are initiated simultaneously. There is an obvious time lapse (plastochron) between successive whorls. Synchronous whorls may originate from an annular bulge (*Equisetum*, *Ceratophyllum*) or may start development with a cycle of free leaf primordia (*Hippuris*, *U. purpurea*; figs. 1–4). Synchronous leaf whorls often form tubular sheaths, e.g., *Equisetum* and Casuarinaceae such as *Al-*

locasuarina verticillata (Flores 1980; R. Rutishauser, unpublished results).

Vascular plants reveal a variety of asynchronous whorls. The primordial subunits of an asynchronous whorl are initiated nonsimultaneously (e.g., spirally) around the shoot meristem. Thus, it may be difficult to decide which leaf primordia around a shoot meristem will finally form a whorl as a result of uneven internode elongation. Examples of asynchronous whorls are presented in figures 5–9. Asynchronous leaf whorls in monocots and some dicots often arise as so-called growth whorls (Schoute 1922, 1936). In growth whorls the whorled appearance is a result of an uneven distribution of internode elongation. For example, in species of *Anagallis*, *Euphorbia*, *Fritillaria*, *Lilium*, *Peperomia*, *Polygala*, and *Polygonatum* the leaves are initiated along a spiral. *k*-merous growth whorls are formed when every *k*th internode elongates and all other internodes stay short (Velenovsky 1907, p. 570; Kwiatkowska 1995, 1999). Thus, asynchronous whorls (especially growth whorls) are developmentally related to spiral or irregular modes of phyllotaxis.

Many examples of synchronous and asynchronous whorls (with and without common tube) are found in floral perianth whorls (Endress 1994a; Erbar and Leins 1997). Asynchronous floral whorls often show organ inception according to a 2/5 spiral (e.g., various Caryophyllaceae; Rutishauser 1981; Lyndon 1998a, 1998b; Ronse Decraene et al. 1998).

Temporary versus permanent anisophylly. In the asynchronous whorls presented in figures 5–9, size differences between whorl members are observable during early development, while they reach similar size and shape at maturity. This type of hidden anisophylly was also called temporary anisophylly by Loiseau (1969: *anisophyllie discrète, anisophyllie temporaire*). Anisophylly as such, i.e., permanent anisophylly, is present when the mature leaves of a whorl still have different size. There are several examples of sectorial and permanent anisophylly that are combined with dorsoventral shoot symmetry, decussate phyllotaxis, and occasionally sectorial anisoclady: *Anisophyllea*, *Elatostema* (including *Pellionia*), *Herniaria*, *Columnnea* (including *Pentadenia*), *Selaginella*, and *Strobilanthes* (including *Goldfussia*) (Goebel 1928; Troll 1937; Schoute 1938; Champagnat 1949; Rutishauser 1981; Dengler 1991, 1999; Charlton 1998). The leaves of anisophyllous whorls may differ also in size and shape. For example, the trimerous leaf whorls of *Salvinia* consist of two floating entire leaves and one submerged and highly dissected leaf (Croxdale 1978; Lemon and Posluszny 1997).

From anisophyllous to mixed whorls. The whorl members are described in "Results" as having leaf identity. Contrasting hypotheses, however, show that whorl members may have another organ identity. For example, what is called "leaf" in the whorls of certain vascular plants may also be interpreted as a whole "shoot" (in *U. purpurea*), as a "leaflet" or "leaf segment" (in *Limnophila* and *Ceratophyllum*), or as a "stipule" (in *Acacia* spp. and Rubieae). When whorls are accepted as consisting of subunits with different organ identity (e.g., leaves and stipules), they may be called mixed whorls rather than anisophyllous whorls. Obvious mixed whorls are found in *U. purpurea* because an extra-axillary shoot bud occupies the site of the sixth leaf in a whorl (fig. 4). Another mixed whorl is found in *Theligonum* (Rubiaceae), where a whorl consists of

a leaf, two stipules, and one to two male flowers on the opposite side of the node (Rutishauser et al. 1998).

Positioning of lateral buds and shoot symmetry. Axillary branching is typical for most angiosperms but is lacking in many ferns and fern allies. Lateral buds in extra-axillary positions, i.e., in the radii between two adjacent leaves, are observable in *Equisetum* (fig. 1), *U. purpurea*, and (with respect to flower buds) in *Ceratophyllum*. Extra-axillary positioning of lateral buds in *Ceratophyllum* and *Utricularia* is developmentally correlated with dorsoventral polarity of their submerged plagiotropous shoots (figs. 3, 4). Most lateral buds in both taxa are arranged along the upper stem sector (facing the sky). There is only a slight curvature of the elongate shoot meristem in *Ceratophyllum* downward, while the shoot tips of several *Utricularia* spp. (including *U. purpurea*) are strongly coiled upward (Brugger and Rutishauser 1989; Sattler and Rutishauser 1990). In whorled plants with radial symmetry there may be as many lateral buds as whorl members, e.g., in *Equisetum* and (with respect to axillary flower buds) also in *Hippuris* (figs. 1, 2). When there are only two buds per whorl, they may show unequal size, with all favored buds arranged along a helix. Helical anisoclady of axillary buds is typical for, e.g., *Limnophila* and allies, *Galium* and other Rubieae, and various Caryophyllaceae such as *Sagina* (figs. 5, 6; Champagnat 1949; Loiseau 1969; Rutishauser 1981, 1998). Also, in the cases with only one axillary bud per whorl (*Acacia* spp., figs. 7, 8; *Hydrothrix*, fig. 9), helical or distichous bud arrangement can be observed.

Axillary branching as observable in most seed plants may be explained by McConnell and Barton's (1998) cyclic model for shoot development: in plants with axillary branching, shoot meristems make leaves that, in turn, are responsible for generating new shoot meristems in their axils. More elaborate developmental models than those reviewed by Schmitz and Theres (1999) are needed to explain the extra-axillary positioning of all or some lateral buds in *Equisetum*, *Utricularia*, and *Ceratophyllum*.

Developmental Control of Whorl Morphogenesis

Geometrical correlations. Polymerous whorls are only possible with narrow leaf insertions. For typical synchronous whorls the maximal leaf arc (leaf insertion angle) is $360^\circ/k$, when k is the leaf number per whorl. The number of leaves or floral organs within a whorl is a function of the apical meristem size at the time the leaves are initiated (Bierhorst 1959; McCully and Dale 1961; Wardlaw 1965; Running et al. 1998). Consequently, polymerous whorls (with $k \geq 4$ leaves) are only possible when the shoot meristem is much larger than the single leaf primordium. A geometrical mean to estimate the size ratio of leaf primordium and shoot meristem is the plastochron ratio (Richards 1951; Lyndon 1998b; Rutishauser 1998).

Computer simulation of whorled phyllotaxis. Although computer simulation models of whorl formation (based on various mechanisms) are beyond the scope of this article, their relevance should be noted. In the models proposed by Harrison (1982), Meinhardt (1982), and Meinhardt et al. (1998) each whorl is taken as a new developmental unit (phytomer) in which a sequence of morphogenetic processes is repeated. They

are mainly based on morphogen waves, including activator-inhibitor mechanisms. Harrison and Meinhardt et al. produced computer simulation models for whorls that start with an annular bulge before the outgrowth of separate whorl appendages, e.g., in the marine green algae *Acetabularia*. Here whorl formation is probably a result of both differential growth and biophysical factors (Serikawa and Mandoli 1998). The simulated morphogenetic cascade is similar to what is also observable in *Equisetum* shoot tips (fig. 1). Simulation models are also useful for understanding whorl formation in taxa where the leaves arise as separate primordia from the shoot meristem (e.g., in *Hippuris*, fig. 2). The individual leaves in whorls are at a small distance from each other, while the distance between the whorls is larger. This different spacing cannot be explained by lateral inhibition mechanism. Thus, Meinhardt et al. (1998) search for a factor determining stem length. Biophysical models add another perspective to our understanding of whorls and forked primordia. Green et al. (1998) postulated physical buckling instability as a result of differential growth of the apical surface. Similarly, Douady and Couder (1998) simulated the formation of whorled patterns and their coexistence with spiral patterns using biophysical parameters. More detailed models are needed to explain all modes of whorl formation. These models will explain once the fuzziness of organ identities in the whorls presented in figures 1–9.

Nodal vascular patterns with fewer traces than leaves. Terrestrial dicots (e.g., *Acacia*, *Galium*) have stems with eusteles, i.e., a ring of more or less interconnected strands or a hollow vascular cylinder with leaf gaps and parenchymatous pith (fig. 7D; Beck et al. 1982; Schmid 1982). The eustele is best suited for aerial axes with respect to mechanical support and secondary thickening. Many flowering plants secondarily acquired a life in water (Cook 1999). Their eusteles were reduced to a central cylinder consisting of vascular and mechanic tissue only, but with almost no parenchymatous pith (Arber 1920; Lance-Nougarède and Loiseau 1960; Sculthorpe 1967; Howard 1974; Schneider and Carlquist 1996). This reduced eustele as found, e.g., in *Ceratophyllum*, *Hippuris*, *Hydrothrix*, and *U. purpurea*, is best suited for tension and twisting in the aquatic environment (fig. 4B, 9E).

Commonly in vascular plants, a leaf receives at least one trace from the stele of the shoot axis. This is the case in, e.g., *Equisetum* and *A. verticillata* (Dormer 1944; Kaplan 1980). There are, however, various whorled plants with fewer traces than leaves per whorl. *Ceratophyllum*, *Hippuris*, and *Hydrothrix gardneri* are aquatics with a reduced number of traces (fig. 2D, 2G; fig. 9E). Also, terrestrial angiosperms may have a reduced trace number as compared to the leaf number per whorl, e.g., most members of Rubieae, *Acacia* sect. *Lycopodiifoliae*, and also Tremandraceae such as *Platytheca galioides* (fig. 2E, 2F; fig. 7D; van Tieghem 1906; Rutishauser 1985). Whether a leaf is provided with its own trace or shares it with the leaves nearby is not a question of its organ identity or morphological significance. It is a question of developmental differences during whorl formation (Sachs 1991). For example, the tetramerous whorls of *G. rubioides* have four independent traces. Two of them may be accepted as stipular traces (fig. 6D). Various whorled taxa possess stem nodes with a girdling vascular bundle that connects the remaining trace(s) with all leaves of a whorl (fig. 2F, 2G; fig. 6D; fig. 7D; Hanstein 1857).

Girdling vascular bundles in combination with fewer traces than appendages per whorl are also found in flowers such as *Loasa* and *Viola* (Sporne 1974, 1977). Computer simulations of stelar architecture similar to those by Stein (1993) and Roth et al. (1998) may be a tool for understanding also the occurrence of girdling vascular bundles and common trunk bundles in leaf whorls of various angiosperms.

Apical versus subapical leaf inception in angiosperms. The apical meristem (or apical dome) is normally a hemispherical tip of the shoot apex distal to the youngest leaf primordia (Lyndon 1998b). In vegetative shoots of most vascular plants, only the apical meristem produces new leaves. In other words, most vascular plants show apical leaf inception only. This rule is taken for granted by many botanists, including developmental geneticists (Jackson 1996). This rule, however, is not valid in *A. baueri* and *A. verticillata*, with two waves of leaf (phyllode) formation within the same shoot tip (fig. 8). The exstipulate E-leaves arise between and below the youngest stipulate P-leaves, i.e., in a subapical region. In other words, leaves already produced at the shoot meristem are repeated in subapical but still meristematic zones. Thus, the leaf-forming area of the apical meristem looks like a star (or octopus) with morphogenetic arms as residual meristems that initiate secondary leaves between and below already present primary leaves (Rutishauser 1986; Rutishauser and Sattler 1986). Subapical leaf inception (including basipetal leaf inception) is a rare pattern during the vegetative phase of vascular plants. Only a few additional examples can be mentioned: *Gunnera chilensis* (Gunneraceae) and *H. gardneri* (fig. 9; Rutishauser 1983, 1988). Repeated initiation of new leaves between and below already present ones is also found in the thalloid stems of *Marathrum schiedeanum* and in the spikelike inflorescences of *Mourera fluviatilis* (both Podostemaceae; Rutishauser and Grubert 1999; Rutishauser et al. 1999). Subapical or, more specifically, centrifugal primordial inception, however, is typical for various eudicot flowers with polymerous androecia (Hofmeister 1868; Rutishauser 1993; Endress 1994a; Leins and Erbar 1997; Ronse Decraene and Smets 1997; Rutishauser and Grubert 1999).

Developmental mechanisms in the evolution of polymerous leaf whorls. *Equisetum* and *Ceratophyllum* belong to isolated families with whorled phyllotaxis throughout. Thus, whorled phyllotaxis is genetically fixed here. In other taxa with whorl-forming members (e.g., *Acacia*, *Myriophyllum*), there are close relatives with helical or irregularly scattered patterns. A comparison of their developmental morphologies and nodal vascular patterns helps to elucidate whorl evolution. There are at least eight ways for vascular plants to develop polymerous whorls, i.e., whorls with four or more leaves. Only six of them are described in this article.

When young plants (shoots) start with dimerous and trimerous whorls (i.e., decussate and tricussate phyllotaxis), they have four options for rising leaf number per whorl: (1) The common way is to increase leaf number continuously with increasing size of the apical meristem: first four, then five and more leaves per whorl (e.g., *Equisetum*, *Hippuris*, figs. 1, 2). (2) In a few taxa with decussate phyllotaxis, two successive leaf pairs form a tetramerous whorl because every second internode does not elongate, e.g., in Caryophyllaceae such as

Silene stellata and *Polycarpea nivea* (Velenovsky 1907, p. 570; Rutishauser 1981). (3) Taxa provided with leaf pairs and interpetiolar (interfoliar) stipules replace stipules by leaves or leaf-stipule intermediates (e.g., *Galium* and other Rubiaceae-Rubieae, fig. 6). (4) Taxa with the capacity to form compound leaves shift basal leaflets (pinnae) around the whole node (e.g., *Limnophila* and probably *Ceratophyllum*, figs. 3, 5; also *Bauera*; Dickison and Rutishauser 1990).

Various whorled plants start shoot development with leaf inception along a helix. They continue with spiral leaf inception into the whorled region. On the basis of this generative helix there are another four options to realize polymerous whorls: (5) Some taxa with spiral inception of all leaves form *k*-merous whorls by elongating every *k*th internode only (e.g., *Huperzia*, *Lilium*, *Polygonatum*; Velenovsky 1907, p. 570; Rutishauser 1998; Kwiatkowska 1999). These whorls were called growth whorls and binding whorls by Schoute (1922, 1925). (6) Shoots of *Acacia longipedunculata* show helically arranged fascicles or half-whorls as intermediate steps before producing complete whorls (fig. 7; Rutishauser and Sattler 1986). (7) *Acacia verticillata* and *A. baueri* add supernumerary leaves between a first series of helically arranged leaves (fig. 8). (8) *Hydrothrix* produces annular bulges in the axils of the first-formed leaves. All additional whorl-forming leaves arise from these annular bulges (fig. 9).

Exceptionally, two of the eight whorl-forming modes may be found in the same species. For example, Kwiatkowska (1999) observed both modes 2 and 5 as whorl-forming modes in *Peperomia verticillata*.

Conclusion

The developmental mechanisms mentioned above suggest that different pathways are obscured under the heading “polymerous whorls” (including “multimerous” and “multijugate whorls” *sensu* Jean 1994). Symmetry, growth pattern, and vascular supply of whorl members do not constitute criteria that allow assignment of their organ identities to mutually exclusive categories such as “shoot” (including “stem”), “leaf” (including “leaflet”), and “stipule.” Comparative morphologists and molecular developmental geneticists are challenged to investigate the self-organizing processes and the underlying genetic and physiological mechanisms in the shoot meristem. How do these processes and mechanisms interact when whorls are formed with, e.g., girdling vascular bundles, common trunk bundles, or even fuzzy organ identities?

Acknowledgments

The technical assistance (with scanning electron microscopy, production of plates) of U. Jauch (Institut für Pflanzenbiologie, Universität Zürich) and A. Bernhard is gratefully acknowledged. I also thank A. Bernhard, C. D. K. Cook, P. K. Endress, B. Isler Rutishauser (Zürich), D. Barabé (Montreal), D. Kwiatkowska (Wroclaw), D. Les (Storrs), and H. Tsukaya (Tokyo) for valuable comments on the manuscript. I appreciate the financial support from the Georges-und-Antoine-Claraz-Schenkung (Switzerland) for some collecting trips.

Literature Cited

- Angiosperm Phylogeny Group 1998 An ordinal classification for the families of flowering plants. *Ann Mo Bot Gard* 85:531–553.
- Arber A 1920 Water plants: a study of aquatic angiosperms. Reprinted in 1972, Cramer, Lehre.
- 1950 The natural philosophy of plant form. Reprinted in 1970, Hafner, Darien, Conn.
- 1954 The mind and the eye. Cambridge University Press, Cambridge.
- 1957 The manifold and the one. Reprinted in 1967, Theosophical, Wheaton, Ill.
- Beck CB, R Schmid, GW Rothwell 1982 Stelar morphology and the primary vascular system of seed plants. *Bot Rev* 48:691–815.
- Bell AD 1991 Plant form: an illustrated guide to flowering plant morphology. Oxford University Press, Oxford.
- Bertalanffy L 1975 Perspectives on general system theory: scientific-philosophical studies. Braziller, New York.
- Bierhorst DW 1959 Symmetry in *Equisetum*. *Am J Bot* 46:170–179.
- 1971 Morphology of vascular plants. Macmillan, New York.
- Boureau E 1971 Les sphénophytes: biologie et histoire évolutive. Librairie Vuibert, Paris.
- Braun A 1831 Vergleichende Untersuchung über die Ordnung der Schuppen an den Tannenzapfen als Einleitung zur Untersuchung der Blattstellung überhaupt. *Nova Acta Acad Carol Leop* 15:195–402, 34 pls.
- Bremekamp CEB 1966 Remarks on the position, the delimitation, and the subdivision of the Rubiaceae. *Acta Bot Neerl* 15:1–33.
- Brugger J, R Rutishauser 1989 Bau und Entwicklung landbewohnender *Utricularia*-Arten. *Bot Helv* 99:91–146.
- Buscalioni L, G Catalano 1927 Il problema della fillotassi nelle Acacie verticillate. *Malpighia* 30:466–471.
- Champagnat P 1949 Ramification à régime rythmique et anisophyllie chez les végétaux supérieurs. *Lilloa* 16:161–191.
- Charlton WA 1998 Pendulum symmetry. Pages 61–87 in RV Jean, D Barabé, eds. *Symmetry in plants*. World Scientific, Singapore.
- Chase MW, DE Soltis, RG Olmstead, D Morgan, DH Les, BD Mishler, MR Duvall et al 1993 Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcL*. *Ann Mo Bot Gard* 80: 528–580.
- Cook CDK 1978 The *Hippuris* syndrome. Pages 163–176 in HE Street, ed. *Essays in plant taxonomy*. Academic Press, London.
- 1996a Aquatic and wetland plants of India. Oxford University Press, Oxford.
- 1996b Aquatic plant book. 2d ed. SPB Academic, The Hague.
- 1999 The number and kinds of embryo-bearing plants which have become aquatic: a survey. *Perspect Plant Ecol Evol Syst* 2: 79–102.
- Croizat L 1960 Principia botanica. 2 vols. L. Croizat, Caracas.
- Cronquist A 1968 The evolution and classification of flowering plants. Thomas Nelson, London.
- Croxdale JG 1978 *Salvinia* leaves. I. Origin and early differentiation of floating and submerged leaves. *Can J Bot* 56:1982–1994.
- Cusset G, B Jeune 1975 L'eau et la morphogenèse foliaire des Dicotylédones. Actes du 100e Congrès national des Sociétés savantes, Paris 2:283–294.
- Daviero V, B Meyer-Berthaud, R Lecoustre 1996 A morphometric approach to the architecture and ontogeny of the extant sphenopsis *Equisetum telmateia* Ehrh. *Int J Plant Sci* 157:567–581.
- DeCandolle AP 1827 Organographie végétale. 2 vols. Déterville, Paris.
- de Klercker JEF 1885 Sur l'anatomie et le développement de *Ceratophyllum*. Bihang Kongl. Svenska Vetenskaps-Akademiens Handlingar 9(10):1–23.
- Delpino F 1883 Teoria generale della fillotassi. *Atti R Univ Genova* 4:1–345, 16 pls.
- Dengler NG 1991 Patterns of leaf development in anisophyllous shoots. *Can J Bot* 70:676–691.
- 1999 Anisophylly and dorsiventral shoot symmetry. *Int J Plant Sci* 160(suppl):S67–S80.
- Dickison WC, R Rutishauser 1990 Developmental morphology of stipules and systematics of the Cunoniaceae and presumed allies. II. Taxa without interpetiolar stipules and conclusions. *Bot Helv* 100: 75–95.
- Dormer KJ 1944 Some examples of correlation between stipules and lateral leaf traces. *New Phytol* 43:151–153.
- Douady S, Y Couder 1998 The phyllotactic patterns as resulting from self-organization in an iterative process. Pages 539–570 in RV Jean, D Barabé, eds. *Symmetry in plants*. World Scientific, Singapore.
- Duval-Jouve J 1864 Histoire naturelle de *Equisetum* de France. Bailière, Paris.
- Eichler AW 1861 Zur Entwicklungsgeschichte des Blattes mit besonderer Berücksichtigung der Nebenblatt-Bildungen. PhD thesis. University of Marburg.
- Endress PK 1987 Floral phyllotaxis and floral evolution. *Bot Jahrb Syst* 108:417–438.
- 1992 Evolution and floral diversity: the phylogenetic surroundings of *Arabidopsis* and *Antirrhinum*. *Int J Plant Sci* 153(suppl):S106–S122.
- 1994a Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge.
- 1994b Evolutionary aspects of the floral structure in *Ceratophyllum*. *Plant Syst Evol Suppl* 8:175–183.
- Erbar C, P Leins 1997 Different patterns of floral development in whorled flowers, exemplified by Apiaceae and Brassicaceae. *Int J Plant Sci* 158:S49–S64.
- Fisher JB, R Rutishauser 1990 Leaves and epiphyllous shoots in *Chiosobeton* (Meliaceae): a continuum of woody leaf and stem axes. *Can J Bot* 68:2316–2328.
- Flores EM 1980 Shoot vascular system and phyllotaxis of *Casuarina* (Casuarinaceae). *Am J Bot* 67:131–140.
- Foster AS, EM Gifford 1989 Comparative morphology of vascular plants. 3d ed. WH Freeman, San Francisco.
- Franke M 1896 Beiträge zur Morphologie und Entwicklungsgeschichte der Stellaten. *Bot Zeitung* 54:33–60.
- Fukuda Y 1988 Phyllotaxis in two species of *Rubia*, *R. akane* and *R. sikkimensis*. *Bot Mag Tokyo* 101:25–38.
- Glück H 1911 Biologische und morphologische Untersuchungen über Wasser- und Sumpfgewächse. Pt 3. Die Uferflora. G Fischer, Jena.
- Godfrey RK, JW Wooten 1981 Aquatic and wetland plants of southeastern United States. University of Georgia Press, Athens.
- Goebel K 1913a Morphologische und biologische Bemerkungen. 21. Scheinwirtel. *Flora* 105:71–87.
- 1913b Morphologische und biologische Bemerkungen. 22. *Hydrothrix gardneri*. *Flora* 105:88–100.
- 1928 Organographie der Pflanzen, insbesondere der Archeogoniaten und Samenpflanzen. 3d ed. Vol 1. Fischer, Jena.
- 1933 Organographie der Pflanzen, insbesondere der Archeogoniaten und Samenpflanzen. 3d ed. Vol 3. Fischer, Jena.
- Goliber TE 1989 Regulation of leaf development in heterophyllous aquatic plants. *Curr Top Plant Biochem Physiol* 8:184–206.
- Golub SJ, RH Wetmore 1948 Studies of development in the vegetative shoot of *Equisetum arvense*. I. The shoot apex. II. The mature shoot. *Am J Bot* 35:755–781.
- Good CW 1971 The ontogeny of carboniferous articulates: calamite leaves and twigs. *Palaeontogr Abt B Palaeophytol* 133:137–158.
- Green PB, CR Steele, SC Rennich 1998 How plants produce pattern:

- a review and a proposal that undulating field behavior is the mechanism. Pages 359–392 in RV Jean, D Barabé, eds. *Symmetry in plants*. World Scientific, Singapore.
- Grimes J 1996 Branch apices, heterochrony, and inflorescence morphology in some mimosoid legumes (Leguminosae: Mimosoideae). *Telopea* 6:729–748.
- Hanstein J 1857 Über gürtelförmige Gefäßstrang-Verbindungen im Stengelknoten dicotyler Gewächse. *Abh Konigl Akad Wiss Berl* 1857:77–98.
- Harrison LG 1982 An overview of kinetic theory in developmental modeling. Pages 3–33 in S Subtelny, PB Green, eds. *Developmental order: its origin and regulation*. AR Lyss, New York.
- Hauke RL 1985 The transition from vegetative to reproductive growth of shoot apices of holoheterophytic species of *Equisetum*: phenology, morphology, and anatomy. *Can J Bot* 63:2430–2438.
- 1990 Equisetaceae. Pages 46–48 in K Kubitzki, KU Kramer, PS Green, eds. *The families and genera of vascular plants*. Vol 1. Springer, Berlin.
- Hofer JMI, THN Ellis 1998 The genetic control of patterning in pea leaves. *Trends Plant Sci* 3:439–444.
- Hofmeister W 1851 Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen. W Engelmann, Leipzig.
- 1868 *Allgemeine Morphologie der Gewächse*. W Engelmann, Leipzig.
- Howard RA 1974 The stem-node-leaf continuum of the Dicotyledoneae. *J Arnold Arbor Harv Univ* 55:125–181.
- Hudson A 1999 Axioms and axes in leaf formation. *Curr Opin Plant Biol* 2:56–60.
- Irish VF 1998 Floral developments in *Arabidopsis*. *Plant Physiol Biochem* 36:61–68.
- Irmisch T 1854 Bemerkung über *Hippuris vulgaris* L. *Bot Zeit* 12: 281–287.
- Jackson D 1996 Plant morphogenesis: designing leaves. *Curr Biol* 6: 917–919.
- Jean RV 1994 *Phyllotaxis: a systemic study in plant morphogenesis*. Cambridge University Press, Cambridge.
- Jeune B 1980 Croissance des feuilles et stipules du *Galium palustre* L. subsp. *elongatum* (Presl) Lange et valeur phylogénique de ces données de morphogénèse. *Adansonia* 19:451–465.
- Jeune B, G Cusset 1971 A propos de la ramification de l'*Hippuris vulgaris* L. *Bull Soc Bot Fr* 118:627–638.
- Johnson MA 1933 Origin and development of tissues in *Equisetum scirpoides*. *Bot Gaz* 94:469–494.
- Jones EN 1931 The morphology and biology of *Ceratophyllum demersum*. *Univ Iowa Stud Nat Hist* 13:11–55.
- Kane ME, LS Albert 1987 Abscisic acid induces aerial leaf morphology and vasculature in submerged *Hippuris vulgaris* L. *Aquat Bot* 28:81–88.
- Kaplan DR 1980 Heteroblastic leaf development in *Acacia*: morphological and morphogenetic implications. *Cellule* 73:135–203.
- 1984 The concept of homology and its central role in the elucidation of plant systematic relationships. Pages 51–70 in T Duncan, TF Stuessy, eds. *Cladistics: perspectives on the reconstruction of evolutionary history*. Columbia University Press, New York.
- Kenrick P, PR Crane 1997 The origin and early diversification of land plants: a cladistic analysis. Smithsonian Institution Press, Washington, D.C.
- Kwiatkowska D 1995 Ontogenetic changes of phyllotaxis in *Anagallis arvensis* L. *Acta Soc Bot Pol* 64:319–325.
- 1999 Formation of pseudowhorls in *Peperomia verticillata* (L.) A. Dietr. shoots exhibiting various phyllotactic patterns. *Ann Bot* 83 (in press).
- Lacroix C, R Sattler 1988 Phyllotaxis theories and tepal-stamen superposition in *Basella rubra*. *Am J Bot* 75:906–917.
- Lance-Nougarede A, J-E Loiseau 1960 Sur la structure et le fonctionnement du méristème végétatif de quelques angiospermes aquatiques ou semi-aquatiques dépourvues de moelle. *C R Hebd Seances Acad Sci* 250:4438–4440.
- Leins P, C Erbar 1997 Floral developmental studies: some old and new questions. *Int J Plant Sci* 158:S3–S12.
- Lemon GD, U Posluszny 1997 Shoot morphology and organogenesis of the aquatic floating fern *Salvinia molesta* D.S. Mitchell, examined with the aid of laser scanning confocal microscopy. *Int J Plant Sci* 158:693–703.
- Les D 1985 The taxonomic significance of plumule morphology in *Ceratophyllum* (Ceratophyllaceae). *Syst Bot* 10:338–346.
- 1993 Ceratophyllaceae. Pages 246–250 in K Kubitzki, JG Rohwer, V Bittrich, eds. *The families and genera of vascular plants*. Vol 2. Springer, Berlin.
- Lloyd FE 1933 The structure and behavior of *Utricularia purpurea*. *Can J Res* 8:234–252.
- 1942 *The carnivorous plants*. Chronica Botanica, Waltham, Mass.
- Loiseau J-E 1965 Anisocladie hélicoïdale et hélices foliaires multiples chez quelques angiospermes. Pages 367–389 in *Travaux dédiés à L. Plantefol*. Masson, Paris.
- 1969 *La phyllotaxie*. Masson, Paris.
- Loiseau J-E, D Grangeon 1963 Variations phyllotaxiques chez *Ceratophyllum demersum* L. et *Hippuris vulgaris* L. *Bull Soc Bot Fr Mem* 1963:76–91.
- Lyndon RF 1998a Phyllotaxis in flowers and in flower reversion. Pages 109–124 in RV Jean, D Barabé, eds. *Symmetry in plants*. World Scientific, Singapore.
- 1998b *The shoot apical meristem: its growth and development*. Cambridge University Press, New York.
- McConnell JR, MK Barton 1998 Leaf polarity and meristem formation in *Arabidopsis*. *Development* 125:2935–2942.
- McCully M, HM Dale 1961 Variations in leaf number in *Hippuris*: a study of whorled phyllotaxis. *Can J Bot* 39:611–625.
- McNeill D, P Freiberger 1993 *Fuzzy logic: the discovery of a revolutionary computer technology and how it is changing our world*. Simon & Schuster, New York.
- Meinhardt H 1982 *Models of biological pattern formation*. Academic Press, London.
- Meinhardt H, A-J Koch, G Bernasconi 1998 Models of pattern formation applied to plant development. Pages 723–758 in RV Jean, D Barabé, eds. *Symmetry in plants*. World Scientific, Singapore.
- Milde J 1852 Beiträge zur Kenntnis der Equiseten. *Nova Acta Leopold* 1852:559–612.
- Millet B, Y Courtot, L Baillaud 1961 Sur les faux-verticilles. *Ann Sci Univ Besancon Bot*, 2d ser, 17:73–78.
- Mohan Ram HY 1991 Biology of aquatic flowering plants. *Proc Indian Natl Sci Acad B* 57:95–108.
- Mohan Ram HY, S Rao 1982 In vitro induction of aerial leaves and of precocious flowering in submerged shoots of *Limnophila indica* by abscisic acid. *Planta* 155:521–523.
- Nägeli K 1858 Das Wachstum des Stammes und der Wurzel bei den Gefäßpflanzen und die Anordnung der Gefäßstränge im Stengel. *Beitr Wiss Bot Leipzig* 1:1–158.
- Namboodiri KK, CB Beck 1968 A comparative study of the primary vascular system of conifers. II. Genera with opposite and whorled phyllotaxis. *Am J Bot* 55:458–463.
- Napp-Zinn K 1973/1974 *Anatomie des Blattes*. 2A. Entwicklungsgeschichtliche und topographische Anatomie des Angiospermenblattes. Borntraeger, Berlin.
- Neal PR, A Dafni, M Giurfa 1998 Floral symmetry and its role in plant-pollinator systems: terminology, distribution, and hypotheses. *Annu Rev Ecol Syst* 29:345–373.
- Niklas KJ 1998 Light harvesting “fitness landscapes” for vertical shoots with different phyllotactic patterns. Pages 759–773 in RV Jean, D Barabé, eds. *Symmetry in plants*. World Scientific, Singapore.

- Page CN 1968 Spiral shoots in the great horsetail, *Equisetum telmateia* Ehrh. Proc Bot Soc Br Isles 7:173–176.
- 1972 An interpretation of the morphology and evolution of the cone and shoot of *Equisetum*. Bot J Linn Soc 65:359–397.
- Pearl R 1907 Variation and differentiation in *Ceratophyllum*. Carnegie Inst Wash Publ 58:1–136.
- Pedley L 1972 A revision of *Acacia lycopodiifolia* A. Cunn. ex Hook. and its allies. Contrib Qld Herb 11:1–23.
- 1978/1979 A revision of *Acacia* Mill. in Queensland. Pts 1, 2. *Austrobaileya* 1:75–337.
- Philcox D 1970 A taxonomic revision of the genus *Limnophila*. Kew Bull 24:101–170.
- Poethig RS 1997 Leaf morphogenesis in flowering plants. Plant Cell 9:1077–1087.
- Pötter U, K Klopfer 1987 Untersuchungen zur Blatt- und Blütenentwicklung bei *Galium aparine* L. (Rubiaceae). Flora 179:305–314.
- Raynal A, D Philcox 1975 *Limnophila ceratophylloides* and *L. fluviatilis*, two heteromorphic African species. *Adansonia*, 2d ser, 15: 225–238.
- Raynal-Roques A 1979 Le genre *Hydrotriche* (Scrophulariaceae). *Adansonia*, 2d ser, 19:145–173.
- 1981 Contribution à l'étude biomorphologique des angiospermes aquatiques tropicales: essai d'analyse de l'évolution. PhD thesis. University of Montpellier.
- Reeves PA, RG Olmstead 1998 Evolution of novel morphological and reproductive traits in a clade containing *Antirrhinum majus* (Scrophulariaceae). Am J Bot 85:1047–1056.
- Reveal JL, WS Judd, RG Olmstead 1999 Proposal to conserve the name *Antirrhinaceae* against *Plantaginaceae* (Magnoliophyta). Taxon 48:182.
- Richards FJ 1951 Phyllotaxis: its quantitative expression and relation to growth in the apex. Philos Trans R Soc Lond B Biol Sci 235: 509–563.
- Ronse Decraene LP, EF Smets 1997 A floral ontogenetic study of some species of *Capparis* and *Boscia*, with special emphasis on the androecium. Bot Jahrb Syst 119:231–255.
- Ronse Decraene LP, EF Smets, P Vanvinckenroye 1998 Pseudodiplostemony, and its implications for the evolution of the androecium in the Caryophyllaceae. J Plant Res 111:24–43.
- Roth A, V Mosbrugger, A Wunderlin 1998 Computer simulations as a tool for understanding the evolution of water transport systems in land plants: a review and new data. Rev Palaeobot Palynol 102: 79–99.
- Running MP, JC Fletcher, EM Meyerowitz 1998 The *WIGGUM* gene is required for proper regulation of floral meristem size in *Arabidopsis*. Development 125: 2545–2553.
- Rutishauser R 1981 Blattstellung und Sprossentwicklung bei Blütenpflanzen unter besonderer Berücksichtigung der Nelkengewächse (Caryophyllaceen s.l.). Diss Bot 62:1–165.
- 1983 *Hydrothrix gardneri*: Bau und Entwicklung einer eigenartigen Pontederiacee. Bot Jahrb Syst 104:115–141.
- 1985 Blattquirle, Stipeln und Kolleteren bei den Rubieae (Rubiaceae) im Vergleich mit anderen Angiospermen. Beitr Biol Pflanz 59:375–424.
- 1986 Phyllotactic patterns in phyllodinous Acacias (*Acacia* subg. *Heterophyllum*): promising aspects for systematics. Bull Int Group Study Mimosoideae 14:77–108.
- 1988 Exceptions to acropetal leaf initiation in vegetative shoots of angiosperms. Am J Bot 75:44–45. (Abstract.)
- 1993 The developmental plasticity of *Utricularia aurea* (Lentibulariaceae) and its floats. Aquat Bot 45:119–143.
- 1995 Developmental patterns of leaves in Podostemaceae as compared to more typical flowering plants: saltational evolution and fuzzy morphology. Can J Bot 73:1305–1317.
- 1998 Plastochrone ratio and leaf arc as parameters of a quantitative phyllotaxis analysis in vascular plants. Pages 171–212 in RV Jean, D Barabé, eds. Symmetry in plants. World Scientific, Singapore.
- Rutishauser R, WC Dickison 1989 Developmental morphology of stipules and systematics of the Cunoniaceae and presumed allies. I. Taxa with interpetiolar stipules. Bot Helv 99:147–169.
- Rutishauser R, M Grubert 1999 The architecture of *Mourera fluviatilis* (Podostemaceae): developmental morphology of inflorescences, flowers, and seedlings. Am J Bot 86:907–922.
- Rutishauser R, A Novelo R, CT Philbrick 1999 Developmental morphology of New World Podostemaceae: *Marathrum* and *Vanroyella*. Int J Plant Sci 160:29–45.
- Rutishauser R, LP Ronse Decraene, E Smets, I Mendoza-Heuer 1998 *Theligonum cynocrambe*: the developmental morphology of a peculiar rubiaceae herb. Plant Syst Evol 210:1–24.
- Rutishauser R, R Sattler 1985 Complementarity and heuristic value of contrasting models in structural botany. I. General considerations. Bot Jahrb Syst 107:415–455.
- 1986 Architecture and development of the phyllode-stipules whorls in *Acacia longipedunculata*: controversial interpretations and continuum approach. Can J Bot 64:1987–2019.
- 1987 Complementarity and heuristic value of contrasting models in structural botany. II. Case study on leaf whorls: *Equisetum* and *Ceratophyllum*. Bot Jahrb Syst 109:227–255.
- 1989 Complementarity and heuristic value of contrasting models in structural botany. III. Case study on shoot-like “leaves” and leaf-like “shoots” in *Utricularia macrorhiza* and *U. purpurea* (Lentibulariaceae). Bot Jahrb Syst 111:121–137.
- 1997 Expression of shoot processes in leaf development of *Polemonium caeruleum* as compared to other dicotyledons. Bot Jahrb Syst 119:563–582.
- Sachs T 1991 Pattern formation in plant tissues. Cambridge University Press, Cambridge.
- Sattler R 1992 Process morphology: structural dynamics in development and evolution. Can J Bot 70:708–714.
- 1994 Homology, homeosis and process morphology in plants. Pages 423–475 in BK Hall, ed. Homology: the hierarchical basis of comparative biology. Academic Press, New York.
- 1996 Classical morphology and continuum morphology: opposition and continuum. Ann Bot 78:577–581.
- Sattler R, D Luckert, R Rutishauser 1988 Symmetry in plants: phyllode and stipule development in *Acacia longipedunculata*. Can J Bot 66:1270–1284.
- Sattler R, R Rutishauser 1990 Structural and dynamic descriptions of the development of *Utricularia foliosa* and *U. australis*. Can J Bot 68:1989–2003.
- 1992 Partial homology of pinnate leaves and shoots: orientation of leaflet inception. Bot Jahrb Syst 114: 61–79.
- 1997 The fundamental relevance of morphology and morphogenesis to plant research. Ann Bot 80: 571–582.
- Schaepfi H 1935 Untersuchungen über die Blattentwicklung bei *Ceratophyllum*, *Cabomba* und *Limnophila*. Planta 24:755–769.
- Schenck H 1886 Vergleichende Anatomie der submersen Gewächse. Bibliotheca Botanica. Abhandlungen aus dem Gesamtgebiete der Botanik 1:1–67, 10 pls. Theodor Fischer, Kassel.
- Schmid R 1982 The terminology and classification of steles: historical perspective and the outlines of a system. Bot Rev 48:814–931.
- Schmitz G, K Theres 1999 Genetic control of branching in *Arabidopsis* and tomato. Curr Opin Plant Biol 2:51–55.
- Schneider EL, S Carlquist 1996 Conductive tissue in *Ceratophyllum demersum* (Ceratophyllaceae). SIDA Contrib Bot 17:437–443.
- Schoute JC 1913 Beiträge zur Blattstellungslehre. I. Die Theorie. Recl Trav Bot Neerl 10:153–325.
- 1922 On whorled phyllotaxis I. Growth whorls. Recl Trav Bot Neerl 19:184–206.
- 1925 On whorled phyllotaxis. II. Late binding whorls of *Pep-eromia*. Recl Trav Bot Neerl 22:128–172.

- 1936 On whorled phyllotaxis III. True and false whorls. *Recl Trav Bot Neerl* 33:670–687.
- 1938 On whorled phyllotaxis IV. Early binding whorls. *Recl Trav Bot Neerl* 35:415–558.
- Sculthorpe CD 1967 *The biology of aquatic vascular plants*. Edward Arnold, London.
- Sehgal A, HY Mohan Ram 1981 Comparative developmental morphology of two populations of *Ceratophyllum* L. (Ceratophyllaceae) and their taxonomy. *Bot J Linn Soc* 82:343–356.
- Serikawa KA, DF Mandoli 1998 An analysis of morphogenesis of the reproductive whorl of *Acetabularia acetabulum*. *Planta* 207: 96–104.
- Sharma KC, A Pillai 1985 Stem-node-leaf continuum in *Acacia*. *Feddes Repert* 96:279–284.
- Simmons MH 1981 *Acacias of Australia*. Thomas Nelson, Melbourne.
- Spatz HC, L Koehler, T Speck 1998 Biomechanics and functional anatomy of hollow-stemmed sphenopsids. I. *Equisetum giganteum* (Equisetaceae). *Am J Bot* 85:305–314.
- Sporne KR 1966 *The morphology of pteridophytes*. Hutchinson, London.
- 1974 *The morphology of angiosperms*. Hutchinson, London.
- 1977 Girdling vascular bundles in dicotyledon flowers. *Gard Bull (Singap)* 29:165–173.
- Stein WE 1993 Modeling the evolution of stelar architecture in vascular plants. *Int J Plant Sci* 154:229–263.
- Stewart WN, GW Rothwell 1993 *Paleobotany and the evolution of plants*. 2d ed. Cambridge University Press, Cambridge.
- Strasburger E 1902 Ein Beitrag zur Kenntnis von *Ceratophyllum submersum* und phylogenetische Erörterungen. *Jahrb Wiss Bot* 37: 477–526.
- Takeda H 1916 Some points in the morphology of the stipules in the Stellatae, with special reference to *Galium*. *Ann Bot (Lond)* 30: 197–214.
- Taylor P 1989 *The genus Utricularia: a taxonomic monograph*. Kew Bull Addit Ser 14.
- Troll W 1937 *Vergleichende Morphologie der höheren Pflanzen*. Vol 1, no 1. Borntraeger, Berlin.
- 1939 *Vergleichende Morphologie der höheren Pflanzen*. Vol 1, no 2. Borntraeger, Berlin.
- Tsukaya H 1995 Developmental genetics of leaf morphogenesis in dicotyledonous plants. *J Plant Res* 108:407–416.
- 1998 Genetic evidence for polarities that regulate leaf morphogenesis. *J Plant Res* 111:113–119.
- Turlier M-F 1972 Recherches sur l'organogénèse foliaire précoce. 1. Deux espèces-types pour les ramifications dichotome et latérale (*Ceratophyllum demersum* L. et *Myriophyllum spicatum* L.). *Rev Gen Bot* 79:297–308.
- Turlier M-F, F Bugnon 1974 Structure du point végétatif caulinaire et ramification foliaire chez le *Limnophila sessiliflora* Bl. (Scrophulariaceae). *C R Acad Sci Paris, ser D*, 278:2747–2750.
- Vanhecke L 1982 Double-leaves in *Hippuris* and their significance for phyllotaxis. Pages 37–48 in JJ Symoens, SS Hooper, P Compere, eds. *Studies on aquatic vascular plants*. Royal Botanical Society of Belgium, Brussels.
- van Tieghem P 1906 Sur les verticilles foliaires hétérogènes. *J Bot (Morot)* 20:103–109.
- Velasquez J 1994 *Plantas acuaticas vasculares de Venezuela*. Universidad Central de Venezuela, Caracas.
- Velenovsky J 1907 *Vergleichende Morphologie der Pflanzen*. Vol 2. Rivnac, Prague.
- 1913 *Vergleichende Morphologie der Pflanzen*. Vol 4. Rivnac, Prague.
- Wardlaw CW 1965 *Organization and evolution in plants*. Longmans, London.
- Wilmot-Dear M 1985 *Ceratophyllum* revised: a study in fruit and leaf variation. *Kew Bull* 40:243–271.
- Wolpert L, R Beddington, J Brockes, T Jessell, P Lawrence, E Meyerowitz 1998 *Principles of development*. Current Biology, London.
- Yang Y-P, S-H Yen 1997 Notes on *Limnophila* (Scrophulariaceae) of Taiwan. *Bot Bull Acad Sin* 38:285–295.
- Zagórska-Marek B 1994 Phyllotaxic diversity in *Magnolia* flowers. *Acta Soc Bot Pol* 63:117–137.