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

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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., Limnophila, 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 Freiberger 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 synchronized into pentameric 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°/k. Alternating and spirally twisted dimerous whorls
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 tricusrate) 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., Hydrodrilla; Cook 1996b) and in a single Pontederiaceae (Hydrotrix, 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., De Candolle 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, 1992); 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 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 bymale* 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

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**Fig. 1** Developmental morphology of *Equisetum* (Equisetaceae) leaf whorls. A, B, *Equisetum bymale*. 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 μm. E, Apical meristem of aerial shoot toward cessation of growth, with hexameric alternating whorls (2–3). Youngest whorl (1) as annular bulge. Bar = 100 μm. 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 mm. 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 ephelophytic 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 equisetales suggests that the microphylls of modern *Equisetum* probably evolved by reduction of megaphyll-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 equisetales 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). Heterophyll 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 (Velenovský 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-Nougarède 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
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 pentameric 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 monoeccious 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 = 200 μm. D, Insertion area of three successive leaf whorls, with axillary vegetative buds (V) and extra-axillary male floral buds (F). Bar = 100 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°–90°; 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°–90° (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 hypophysophilous 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 Klerck 1883; 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 ten “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 anisocladly. (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 ten 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 hexameric 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 pentameric (fig. 4A) or hexameric 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 whorls 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) Contrast 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 polymorphic whorls may show transitional leaves (fig. 5F; Mohan Ram and Rao 1982). The submerged stems carry polymorphic 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
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 *Limnophila 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. 5B; 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. 5B–5D). 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. 5D–5F). Leaf pairs of aerial shoots arise as two opposite bulges at the shoot meristem (fig. 5G). There is only one vigorous vegetative bud per whorl (fig. 5A). A second opposite vegetative bud is present but often is much smaller. All favored vegetative buds in *Limnophila* are arranged along a helix. This situation is known as helical anisoclad (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. 5I). The two traces are trunk bundles that branch with
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 *Limnophila* 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 Limnophila, the related Madagascan genus Hydrotriche (four spp.) also shows 3–20-merous leaves and helical anisoclady (Cook 1996b). Raynal-Roques (1979) explained the Hydrotriche whorls as equivalent to two compound leaves. Limnophila and Hydrotriche are relatives of Gratiola (tribe Gratiolaeae 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 (Bremerkamp 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 petioleate, 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 ≤90° (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 other two. All favored leaves are between. In several Rubieae the number of P-leaves increases along the stem (e.g., up to six to ten 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 (I in fig. 6B, 6E). In Crucizita 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 plastochnon 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 (Cronquist 1968, p. 65) proposed a homeotic trans-stipule 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, Crucita 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 rubiaceous 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 Lycopodiifolae (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 phylloide (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 (20). 3 and S1 are phyllodes and stipules of whorl 3. Bar = 50 μm. C, Older whorls (3–5) of same shoot tip (appendages removed except one sector). Pn, P1, and Sn, S1 = 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). S = phyllose 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 galoides (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. 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. galoides, 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 phylloide whorl of *A. hippuroides* consists 
of four to six “true” leaves. (4) It is best to accept that interpret-
ations 1–3 approximate nature to some degree, but prob-
ably none of them fully reflects nature. Continuum morphol-
ogy allows the recognition of a morphcline comprising 
pinnate leaves, phyllodes, stipules, and collers, 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 phy-
llodes in both species can be verticillate or scattered. The ex-
pistence 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. *as-
pera* has all phyllodes irregularly scattered along the stem (Ped-
ley 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 phylloide type (called exstipulate, or E-phyll-
loide) is more frequent. These E-phyllodes normally lack stip-
ules 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 ar-
ranged along a helix (1–5 in fig. 8C). They are all provided 
with two stipules and an axillary bud. The same helix contin-
ues 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* outnum-er 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,*
not all *A. verticillata* whors possess a P-phyllode. Sometimes there are one to three sterile whors consisting of E-phyllodes only between two whors with a P-phyllode each (fig. 8D). In *A. verticillata* the divergence angles between consecutive P-phyllodes are often close to 137.5° but occasionally ≥145° (Kaplan 1980; Rutishauser and Sattler 1986). Spirodistichy or exact distichy of P-phyllodes (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 phylloide formation: first a series of P-phyllodes and then a series of E-phyllodes (fig. 8A, 8B, 8E, 8F). The P-phyllodes 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-phyllodes, 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-phyllodes.

**Vascular supply.** Each phylloide 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-phyllodes 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-phyllodes (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-phyllodes are “more closely homologous with metamorphosed stipules than with the foliage leaves that repeat the developmental pathway of the P-phyllodes.” (2) Velenovsky (1913, p. 95) and Goebel (1913a, 1928, 1933) considered both P- and E-phyllodes 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-phyllodes are even more similar to P-phyllodes. The E-phyllodes may be viewed as additional leaves that repeat the developmental pathway of the P-phyllodes. (3) Delpino (1883) hypothesized that the E-leaves in *A. verticillata* are “pseudophyllodes,” 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 morphoclone. 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 *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 whors 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 filamen-

tous leaves arranged in whors (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, 9E). They lack a prominent ochrea. At the base of each E-leaf a minute axillary stipule is present. The P-leaves of successive whors 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, in fig. 9B, 9C). During plastochnon 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 R1 and R2 (fig. 9B, 9C). In the following plastochnons, additional E-leaves are initiated in an acropetal (centripetal) direction (fig. 9D: E5, E6). 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 whors 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 S₂–S₆. Annular bulges (R₁–R₄) giving rise to whorls, which are soon provided with leaf primordia (E). Bar = 70 μm. D, More proximal portion of shoot tip, with partially removed ochreas (S₅–S₇) of three successive whorls. The annular bulges initiate whorl-forming leaves (E₁–E₇). Bar = 70 μm. E, Cross section of vegetative shoot tip. Main leaves (6–9) along spiral, S₁ and S₂ are the ochreas of leaves 8 and 9. Note girdling vascular bundle (G) and single trace (T) from central stele. Bar = 100 μm. F, Mature whorl consisting of P-leaf (P; with ochrea, S) and additional 12 leaves. Bar = 5 μm. 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 1913b.)

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 (phylodes). It is not obvious why they form phylloidal whorls while most other Australian wattles show spirally arranged phylodes (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 (1996b, 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*, *Limnotheca 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*, *Limnotheca*, *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 Rubiae) 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 *Limnosiptana 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 doroventral 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 (Tsu-kaya 1995, 1998; Jackson 1996; Poethig 1997; Lyndon 1998b). Doroventral 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., plation, webbing, doroventral 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 “leaflet,” “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 *Chisocheton* 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 rubioideae 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 “sectoral 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 “sectoral 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 tetrmerous leaf whorls. Crucia glabra (fig. 6F) and Asperula cymanchica are examples of nearly superposed whorls, whereas G. rubioideae 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 Alcastrusarla 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, Frictillaria, Lilium, Peperomia, Polygala, and Polygonatum the leaves are initiated along a spiral. k-merous growth whorls are formed when every kth 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: anisophylie declares, anisophylie 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 sectoral and permanent anisophylly that are combined with dorsoventral shoot symmetry, decussate phyllotaxis, and occasionally sectorial anisoclad: Anisophyllea, Elatostema (including Pellionia), Herniaia, Columinea (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 submersed 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 Theligionum (Rubieae), 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 plagirotropous 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 Caryophylllaceae 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.** Polymorous whorls are only possible with narrow leaf insertions. For typical synchronous whorls the maximal leaf arc (leaf insertion angle) is 360°/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, polymorous whorls (with k ≥ 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 (Sericawa 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 is 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. *Lycopo- diolae*, 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 1998). 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 (phylloide) 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 schiedeana* and in the spikelike inflorescences of *Mourea 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 De Craene 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 tricuspidate 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 *Polycarpaea 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-Rubiaceae, fig. 6). (4) Taxa with the capacity to form compound leaves shift basal leaflets (pinnae) around the whole node (e.g., *Linnophila* 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?

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