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Evo-devo and the search for homology (“sameness”) in biological systems[☆]

Rolf Rutishauser^{*}, Philip Moline

*Institut für Systematische Botanik der Universität Zürich, Zollikerstr.107,
CH-8008 Zürich, Switzerland*

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Abstract

Developmental biology and evolutionary studies have merged into evolutionary developmental biology (“evo-devo”). This synthesis already influenced and still continues to change the conceptual framework of structural biology. One of the cornerstones of structural biology is the concept of homology. But the search for homology (“sameness”) of biological structures depends on our favourite perspectives (axioms, paradigms). Five levels of homology (“sameness”) can be identified in the literature, although they overlap to some degree: (i) serial homology (homonymy) within modular organisms, (ii) historical homology (synapomorphy), which is taken as the only acceptable homology by many biologists, (iii) underlying homology (i.e., parallelism) in closely related taxa, (iv) deep evolutionary homology due to the “same” master genes in distantly related phyla, and (v) molecular homology exclusively at gene level. The following essay gives emphasis on the heuristic advantages of seemingly opposing perspectives in structural biology, with examples mainly from comparative plant morphology. The organization of the plant body in the majority of angiosperms led to the recognition of the classical root–shoot model. In some lineages bauplan rules were transcended during evolution and development. This resulted in morphological misfits such as the Podostemaceae, peculiar eudicots adapted to submerged river rocks. Their transformed “roots” and “shoots” fit only to a limited degree into the classical model which is based on

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^{*} Corresponding author. Tel.: +41 44 6348415.

E-mail address: rutishau@systbot.unizh.ch (R. Rutishauser).

either–or thinking. It has to be widened into a continuum model by taking over elements of fuzzy logic and fractal geometry to accommodate for lineages such as the Podostemaceae.

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Introduction

“Analysis of the structures, evolution and dynamics of systems is one of the main issues in theoretical biology today” (Breidbach et al., 2004, p. 1, excerpt from the editorial of “Theory in Biosciences”).

Aim of the paper

Developmental biology and evolutionary studies have recently entered into an exciting and fruitful relationship, known as evolutionary developmental biology (abbreviated “evo-devo”). Evolutionary biologists seek to understand how organisms have evolved and changed their shape and size. For this reason, the whole body and its subunits have to be compared with each other, either within the same organism (Fig. 1A and B) or between organisms that are (at least distantly) related to each other (Fig. 2A–D). Some developmental biologists then try to understand how alterations in gene expression and function lead to changes in body shape and pattern (Shubin et al., 1997; Hawkins, 2002; Wilkins, 2002). This opening towards evo-devo already influenced and still continues to change the conceptual framework of traditional biological disciplines such as comparative morphology and its search for homological structures, i.e., “sameness” (Bolker and Raff, 1996; Sattler and Rutishauser, 1997; Cronk, 2001, 2002; Kaplan, 2001; Bateman and Dimichele, 2002; Stuessy et al. 2003; Friedman et al., 2004). Various bauplan features became stabilized during the evolution of modular (metameric) organisms such as vascular plants, arthropods and vertebrates, and can be understood – at least to some degree – as adaptations to the environment (Raven and Edwards, 2001; Cronk, 2002; Gould, 2002; Schneider et al., 2002).

The following questions will be addressed in this paper:

- (1) What are the bauplans (body plans, archetypes) in multicellular plants and animals (Fig. 2A–D)?
- (2) Which homology criteria can be used to define bauplans in plants and animals, even when pertinent features are blurred or lost?
- (3) Which levels of homology (“sameness”) should be distinguished? And is phenotypic homology (including morphological correspondence) always caused by conserved gene expression patterns?
- (4) Case study from botany: How shall we label the transformed “roots” and “shoots” of the river-weeds (Podostemaceae), peculiar flowering plants living in river-rapids and waterfalls?

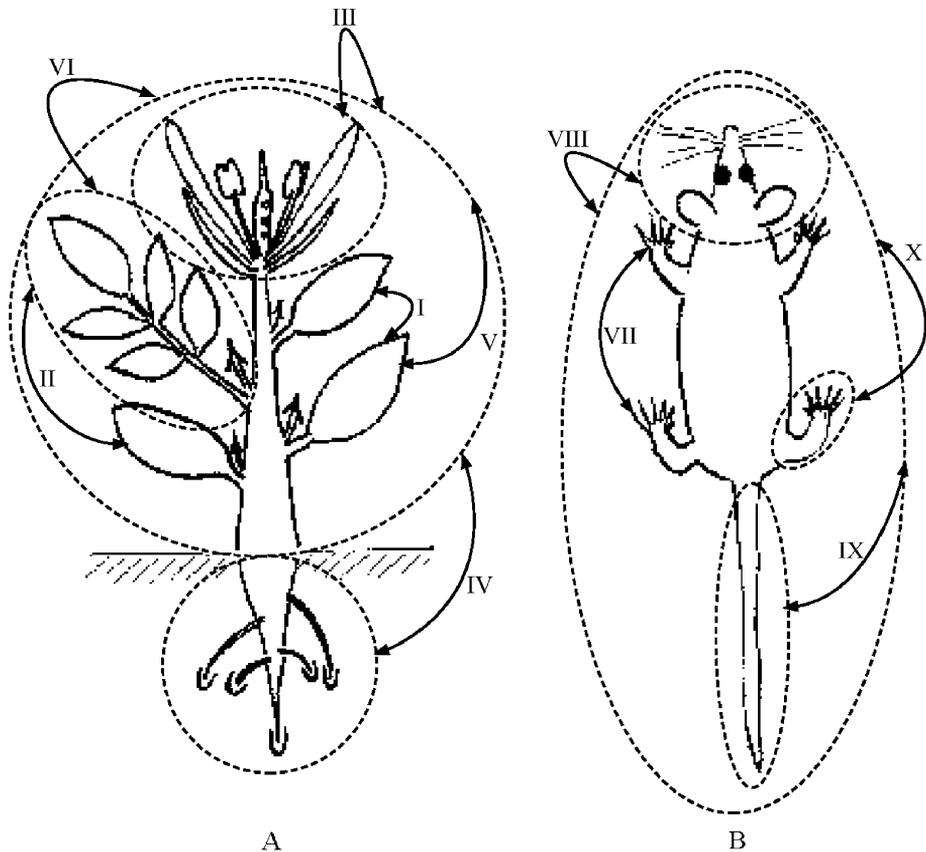


Fig. 1. (A)–(B) Bauplans (body plans, archetypes) of seed plants (A) and tetrapods (B), exemplified by rosid-like dicot and mouse, respectively. Roman numerals indicate levels of morphological comparison between the whole organism and its subsystems (organs, appendages, etc.). This allows one to recognize structural correspondence (including serial homology) which can be complete (100%) or partial: **I.** Seed plant: Comparison of two simple leaves along the same stem (shoot axis). **II.** Comparison of simple leaf and compound (pinnate) leaf. **III.** Comparison of flower and whole shoot*. **IV.** Comparison of branched taproot and whole shoot*. **V.** Comparison of simple leaf and whole shoot*. **VI.** Comparison of compound leaf (with axillary bud) and whole shoot*. **VII.** Mouse: Comparison of anterior and posterior limb (arm and leg). **VIII.** Comparison of head and whole mouse body*. **IX.** Comparison of tail and whole mouse body*. All comparisons marked with an asterisk (*) focus on part–whole relationships. They may allow one to observe self-similarity (including partial homology) according to the holographic paradigm (see text).

Perspectivism in structural biology and elsewhere

Although perspectivism is sometimes used in colloquial speech, it is not common in natural science including biology (Arber, 1950; Klaauw, 1966; Hassenstein, 1978;

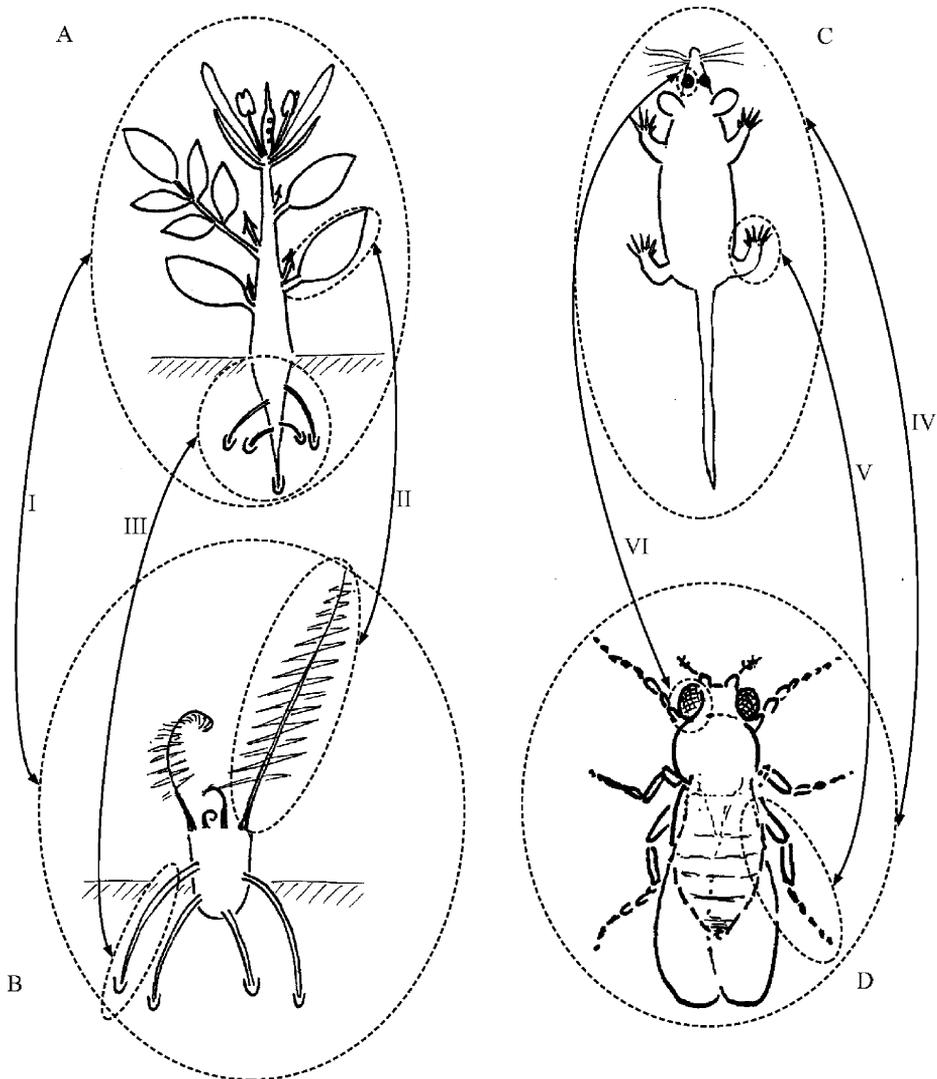


Fig. 2. (A)–(D) Bauplans (body plans, archetypes) of four different groups of multicellular organisms with modular construction. (A,B) Seed plants (A) and ferns (B), both members of vascular plants. (C,D) Tetrapods such as mouse (C) and insects such as fly (D), both members of Bilateria. Roman numerals indicate levels of morphological comparison between distantly related groups (taxa), for the whole organisms as well as their subsystems (organs, appendages, etc.). This allows to recognize structural correspondence and biological homology (“sameness”), at least on the molecular-genetic level: **I.** Comparison of the whole bodies of seed plant and fern. **II.** Comparison of the leaves (fronds) in seed plant and fern. **III.** Comparison of the root systems in seed plant and fern. **IV.** Comparison of the whole bodies of mouse and fly. **V.** Comparison of mouse limb and fly leg. **VI.** Comparison of the eyes in mouse and fly.

Sattler, 1986, 2001; Rutishauser and Isler, 2001; Rutishauser, 2005a). Perspectivism accepts every insight into nature as one perspective (but not the only one) to perceive and explain biological phenomena. Different perspectives (also called approaches, hypotheses, models) complement each other, rather than compete with each other, although not all of them are meant to be equal approximations of what really occurs in nature. Perspectivism in the sense of Woodger's (1967) *map analogy* is a heuristically promising option in structural biology: Different maps of the same terrain complement each other, each presenting a different aspect of reality. While looking for homologous structures and their underlying genetic networks in animals and plants, we should not just stick to a single perspective, but may switch between up to five levels (perspectives) of homology ("sameness") as summarized in Table 1. A botanical example: Structural categories in vascular plants such as "leaf", "stem" and "root" are simplified concepts reflecting certain aspects of their structural diversity (Figs. 3 and 4). Close to perspectivism is fuzzy logic (fuzzy set theory), in which concepts such as "leaf", "stem" and "root" are accepted with partially overlapping connotations, i.e., with fuzzy borderlines (Rutishauser, 1995, 2005a). Bernhard Hassenstein (1978) pointed out that life must be seen as injunction, i.e., as a concept that cannot be defined by a clear-cut set of properties. Illustrating this problem, he asked the question "How many grains result in a heap?" There is no clear-cut answer to such a question. It just depends on our perspective, if five, 20 or 50 grains are needed at minimum to get a "heap".

The search for "sameness" in biological systems

What is homology?

Homology is a central topic in structural biology, including comparative morphology. For a long time morphology of animals and plants was understood mainly as the search for bauplans (body plans, archetypes). How can plant structures be accepted as homologous or non-homologous due to their relative position within the bauplan (Fig. 1A and B)? The more complex the compared structures are, the easier will be our decision "homologous or not"! For example, "flowers" (with stamens and gynoecium) will be recognized as flowers, even when they are epiphyllous, i.e., expressed ectopically on leaves, or arising from endogenous buds along stems, as will be described in Podostemaceae (see "Case study", Fig. 7). Determination of whether two structures are homologous depends on the hierarchical level at which they are compared (Shubin et al., 1997). For example, bird wings and bat wings are analogous as wings, having evolved independently for flight in each lineage. However, at a deeper hierarchical level that includes all tetrapods, they are homologous as forelimbs, being derived from a corresponding appendage of a common ancestor. Nowadays, we are more flexible in finding homologies, because we have a phylogenetic framework for many clades, mainly due to molecular data. This improved situation enables us to distinguish homology ("sameness") at different morphological levels as well as homology ("sameness") at

Table 1. Levels of homology (“sameness”) in biological systems

Levels of comparisons	Levels of homology, including biological homology ^a	Underlying gene expression patterns & developmental pathways	Botanical examples (especially vascular plants)	Zoological examples (especially arthropods and vertebrates)
Comparison of multicellular structures (organs, systems, subsystems) within the same organism, showing modular construction	(A) Serial homology = iterative homology = homonymy , either complete or partial, leading to “mixed homologies”, e.g., “mixed shoot–leaf xidentity” (Baum and Donoghue, 2002)	Gene networks (GNW) and developmental pathways (DP) of repeated structures in modular organisms may match perfectly; GNW and DP of whole system (body) and sub-system may match according to holographic paradigm (see text)	<ul style="list-style-type: none"> - All leaves of a plant are homologous (Fig. 1A: relations I & II) - Flower is homologous to whole shoot^b (Fig. 1A: III) - Morphological correspondence of root and shoot (Fig. 1A: IV) - Morphological correspondence of leaf and whole shoot (Fig. 1A: V) 	<ul style="list-style-type: none"> - Anterior limb and posterior limb of mouse are homologous (Fig. 1B: relation VII) - Morphological correspondence of main mouse body and its head or tail^c (Fig. 1B:VIII & IX) - Morphological correspondence of mouse body and limb (as its part)^d
Comparison of multicellular structures (organs, systems, subsystems) in closely related taxa (i.e., species/genus/family level)	(B) Historical homology = “true” homology = phylogenetic homology , taxic homology, special homology, synapomorphy, “received” from common ancestor	Gene networks (GNW) and developmental pathways (DP) of homologous structures in related taxa may match (<i>this hypothesis has been validated for only a few systems!()</i>)	<ul style="list-style-type: none"> - Flattened “roots” of river-weeds (Podostemaceae, flowering plants) are homologous (Fig. 6A–L) - Leaves of <i>Ledermanniella</i> spp. are homologous (Fig. 7A–B) 	<ul style="list-style-type: none"> - Fish fin and tetrapod limb are homologous
	(C) Underlying homology = latent homology = homoiology , apomorphic tendency, homoplasmic tendency, parallelism, parallel evolution	GNW and DP of homologous structures in related taxa may match to some degree; but common ancestor did not exhibit this homologous character (because it was “somewhat genetically suppressed”)	<ul style="list-style-type: none"> - Crustose “roots” arisen at least three times in Asian and African Podostemaceae (Kita and Kato, 2004; Moline et al., in press) - More examples in Sanderson and Hufford (1996) 	<ul style="list-style-type: none"> - Bird plumage and stickleback armour as examples of evolution of similar features in different populations, based on similar genetic modifications (as reviewed by Shubin and Dahn (2004)
Comparison of multicellular structures (organs, systems, subsystems) in only distantly related (or seemingly unrelated) taxa	(D) Deep evolutionary homology = deep genetic homology = deep homology at the molecular genetic level	Master control genes (key regulatory genes) identical in different phyla, whereas cascade of downstream elements (GNW) and observable developmental pathways (DP) more or less dissimilar	<ul style="list-style-type: none"> - Formation of leaves (fronds) in seed plants and ferns only deeply homologous due to expression of KNOX genes^e (Fig. 2A–B: II) - Roots of lycophytes, ferns & seed plants may be taken as homologous or non-homologous^f 	<ul style="list-style-type: none"> - Hox genes^g along body axis in arthropods and vertebrates (Fig. 2C–D: relation IV) - <i>Pax6</i> as master control genes for eyes in arthropods and vertebrates (Fig. 2C–D: relation VI)

Table 1. (continued)

Levels of comparisons	Levels of homology, including biological homology ^a	Underlying gene expression patterns & developmental pathways	Botanical examples (especially vascular plants)	Zoological examples (especially arthropods and vertebrates)
Comparison of genes (or cells, subcellular elements, ...) in distinct taxa or same organism	(E) Molecular homology exclusively at gene level	Homologous genes as downstream elements that do not determine the phenotypic homology (“identity”) of an organ	- e.g., <i>rbcL</i> gene involved in RuBisCO synthesis (needed for photosynthesis)	- e.g., <i>Sonic hedgehog</i> gene in vertebrate limb bud versus neural tube ^b

^aBiological homology as an inclusive concept sensu Wagner (1989), Wagner (in Bock and Cardew, 1999) and Geeta (2003) comprises the homology levels (A)–(D). Phenotypic homology and morphological correspondence are less inclusive concepts, comprising only the homology levels (A)–(C), but usually excluding the homology levels (D) and (E).

^bSee Baum and Donoghue (2002, p. 64) on “inflorescence-flowers” when developmental programmes are mixed.

^cMinelli (2003, p. 575) presented developmental–genetic arguments in favour of the view that the vertebrate tail is of “appendicular nature”.

^dMinelli (2003, p. 574) gave evidence for the view that the holographic paradigm is also present in modular animals (arthropods, vertebrates): “It is possibly not by chance that segmented appendages are only present in animals whose main body is also segmented”... Minelli’s view comes close to what Bolker and Raff (1996) had in mind stressing the geographic (topological) conservation of body axes (see Cronk (2001) for definition of body axes in vascular plants).

^eSee Cronk (2001), Schneider et al. (2002), Kim et al. (2003), Friedman et al. (2004).

^fSee Cronk (2001), Schneider et al. (2002).

^gSee Shubin et al. 1997, Wilkins (2002, p. 299).

^hSee Bolker and Raff (1996), Shubin et al. (1997).

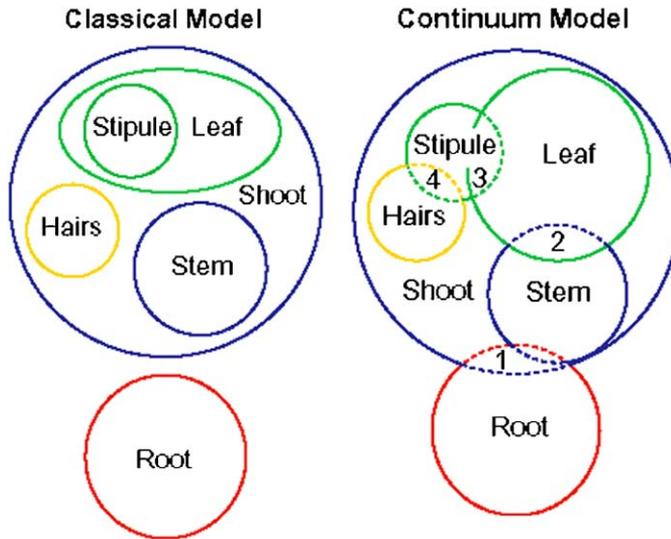
the molecular genetic level (Lankester, 1870; Remane 1956, both cited in Wagenitz, 2003; also Patterson, 1988; Hall, 1994; Sattler, 1994).

Five levels of homology

Five levels of homology (“sameness”) can be distinguished in modern evo-devo research: serial homology, historical homology, underlying homology, deep homology, and homology exclusively at gene level (e.g., Klaauw, 1966; Wagner, 1989; Shubin et al., 1997; Butler and Saidel, 2000; Minelli, 2003; Svensson, 2004). These five homology levels (or kinds of homology) will be presented below (see Table 1):

(A) *Serial homology*¹ = *homonymy*: Since Owen (1848, as cited in Wagenitz, 2003) we speak of serial homology when iterated parts (appendages, subunits) of the

¹Serially homologous organs on the morphological (phenotype) level are somewhat comparable to paralogous genes, i.e., gene homologues within the same genome (Patterson, 1988).



Figs. 3 and 4. Structural categories of vascular plants conceivable as mutually exclusive sets (classical root-shoot model) as well as fuzzy sets (continuum root-shoot model). In both schemes stem, leaf, stipule and hair are taken as subsets of the shoot. In the Classical Model (Fig. 3) the structural categories (organs, suborgans) belong to a hierarchical system of non-overlapping (“crisp”) sets. The Continuum Model (Fig. 4) is less hierarchical being consistent with the holographic paradigm (see text). In the latter scheme, the structural categories are seen as fuzzy sets with partially overlapping connotations. This allows one to perceive developmental mosaics (intermediates) between structures with seemingly different organ identities: **1.** Root–shoot mosaics, e.g., *Pinguicula* “roots” closely resembling *Utricularia* “stolons” (Rutishauser and Isler, 2001); **2.** Stem–leaf mosaics, e.g., indeterminate leaves of *Guarea* and *Chisocheton* (Fisher and Rutishauser, 1990; Fisher, 2002; Fukuda et al., 2003); **3.** Leaf–stipule mosaics, e.g., leaf-like stipules being equivalent to leaves in stipular position in *Galium–Rubia* group (Rutishauser, 1999); **4.** Stipule–hair mosaics, e.g., hair-like stipules and tufts of hairs in stipular sites in Brassicaceae, Leguminosae, Rubiaceae (Rutishauser, 1999). Note that additional structures known from vascular plants (e.g., leaflets, root hairs) are ignored in both schemes. Modified from Rutishauser and Isler (2001).

same organism are compared (illustrated in Fig. 1A and B: I and II, Fig. 1B: VII). This type of homology is also called iterative homology or homonymy (Patterson, 1988). Homonymy (“sameness”) of parts (limbs, leaves, etc.) is most obvious in animals and plants with a modular (metameric) construction. Hox genes are likely to be involved in the evolution of serial homology in arthropods and vertebrates (Shubin et al., 1997; Wilkins, 2002), whereas MADS-box genes seem to have played a similar role in the evolution of serial homology in seed plants, especially with respect to their floral organs (Theissen et al., 2002; Becker and Theissen, 2003). Comparing different members of a serial homology within a species may be informative regarding the developmental basis of their evolution (e.g., petals and stamens in flowering plants). Thus, serial homology

promotes understanding of mechanisms common to structures, i.e., their “biological homology” (Wagner, 1989; Geeta, 2003). The search for serial homology (homonymy) should also include comparisons between the whole body (system) and its subunits (subsystems). For example, the leaf shares a certain degree of “sameness” with the whole shoot (Fig. 1A: V–VI), and the mouse limb (Fig. 1B: X) shares a certain degree of “sameness” on a developmental and genetic level (such as Hox genes) with the whole body axis, as stressed by Minelli (2003): “It may be justified to look for correspondences between the appendages and the main body axis of the same animal, as the latter might be the source of the growth and patterning mechanisms which gave rise to the former”. The *holographic paradigm* (i.e., the acceptance of fractal properties) is relevant as an explanatory hypothesis for modular construction in organisms such as vascular plants, arthropods and vertebrates: The whole is built up of the parts in such a way that each part bears something of the whole within it. With respect to vascular plants this type of “serial homologies” between parts and the whole is included in the “continuum root-shoot model” (Fig. 4).

- (B) *Historical homology* = “true” homology²: This is the type of homology that most biologists have in mind when discussing homologous vs. non-homologous structures. Therefore, it has also been called “true” homology (Klaauw, 1966; Bolker and Raff, 1996) and taxic homology, meaning similarity (sameness) based on common origin/ancestry (Geeta, 2003). For newly gained characters historical homology equals synapomorphy (Patterson, 1988; Butler and Saidel, 2000; Telford and Budd, 2003). Various evolutionary and developmental biologists tend to restrict themselves to historical homology as the only “official” level of homology. For example, Nielsen and Martinez (2003) stated that “structures are homologous if they are derived from the same structure in their latest common ancestor”. In earlier days historical homology was also called homology *sensu stricto*, special homology and homogeny (e.g., Haeckel, 1866, Lankester, 1874, both cited in Wagenitz, 2003).
- (C) *Underlying homology* = *latent homology*: This type of homology gives emphasis to morphological correspondence (“sameness”) of similar structures in closely related taxa (e.g., species, genera, families) although the common ancestor did not exhibit this homologous character because it was “somewhat genetically suppressed” (Endress, 2003). Then, the “same” character occurs in parallel in several species within a larger lineage, due to “re-awaking” of retained homologous developmental mechanisms (see Meyer in Bock and Cardew, 1999). There are several synonyms (or nearly so) for this kind of “sameness” such as underlying synapomorphy, homoiology, parallel evolution, parallelism, apomorphic tendency, homoplastic tendency,³ canalized evolutionary potential

²“Truly” homologous organs (i.e., the “same” organ in different species) are somewhat comparable to orthologous genes, i.e., the “same” gene in different species.

³Although the term homoplasy is now usually understood as a synonym of all kinds of “non-homology”, we should keep in mind that the original meaning of “homoplasy” comprised “underlying homology” and “serial homology” (i.e., homology levels A and C of Table 1), as discussed by Sanderson and Hufford (1996) and Wray (in Bock and Cardew, 1999), and Gould (2002, p. 1074).

and homologous convergence (see Rutishauser and Isler, 2001; Rutishauser, 2005b and references therein). Developmental geneticists such as Bowman et al. (1999) concluded: “From a mechanistic standpoint, a homoplastic tendency could be explained by a genetic change occurring near the base of the lineage; this initial change would not result in morphological alterations but rather would predispose descendent taxa to exhibit morphological evolution due to subsequent genetic changes” (see a similar statement in Wilkins, 2002, p. 388). “Underlying homology” (including “parallelism”) should be clearly distinguished from (adaptive) “convergence”, although both concepts describe the repeated acquisition of similar traits in different lineages. Only parallelism involves the same genetic and developmental mechanism in closely related lines whereas convergence usually involves different mechanisms in unrelated (or only very distantly related) taxa.

- (D) *Deep evolutionary homology*⁴ = *deep homology at the molecular genetic level* (as proposed by Shubin et al., 1997; Wilkins, 2002): Although this level is often not clearly distinguished from level C (see above) it is important to stress the differences between them. In order to find “underlying homology” we have to compare closely related taxa (such as species within the same genus or sister genera). In order to find “deep homology at the molecular genetic level” distantly related taxa (phyla) such as ferns and seed plants (Fig. 2A and B), or arthropods and vertebrates (Fig. 2C and D) are compared. “Deep homology” points to the expression of homologous master genes (i.e., key regulatory genes) in these distantly related phyla. For example, Gould (2002, p. 1069) emphasized a “deep genetic homology” underlying and promoting the separate evolution of lens eyes in cephalopods and vertebrates: “Both share key underlying genes and developmental pathways as homologies”. Despite this “deep homology”, the resulting morphological structures are usually not thought to be homologous by structural biologists. For example, the “eyes” of arthropods, cephalopods and vertebrates are usually considered non-homologous, although *Pax6* generally acts as a master gene for eye development in the Bilateria (Bolker and Raff, 1996; Wilkins, 2002). Because appendage development in both arthropods and vertebrates depends on Hox genes, Wilkins (2002, p. 299) concluded as follows: “In the absence of morphological homology, there is “deep homology” at the molecular genetic level between insect appendages and vertebrate limbs”. “Deep evolutionary homology” may even apply to whole body plans of different phyla. For example, Gould (2002, p. 83) defended “the substantial validity of Geoffroy’s “crazy” comparison – the dorso-ventral inversion of the same basic body plan between arthropods and vertebrates” (see also Rieppel and Kearney, 2002; Minelli, 2003; Telford and Budd, 2003). And in botany already Hagemann (1976) asked the question whether the leaves of ferns and seed plants (both “euphyllophytes”) are homologous or not. Kim et al. (2003) have shown fundamental differences between KNOX gene expression in the compound

⁴Detlev Arendt (this volume) uses the term “molecular fingerprint” instead of “deep evolutionary homology”.

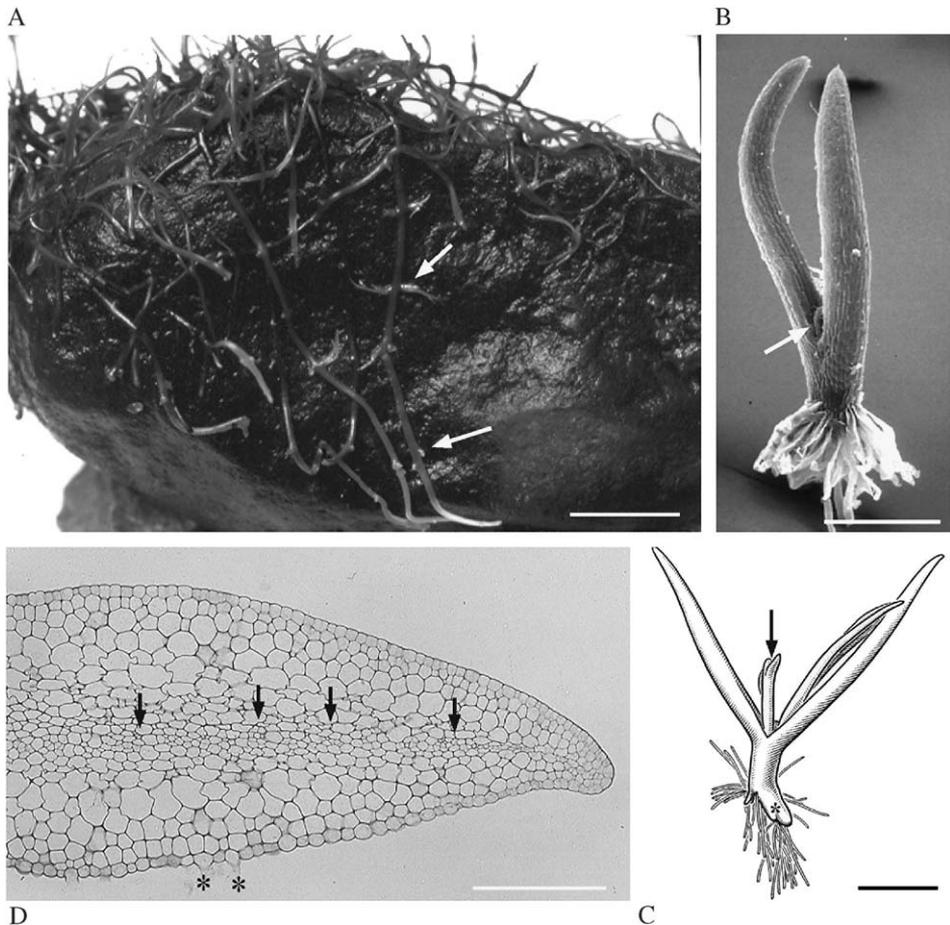


Fig. 5. Growth and development in Podostemaceae (river-weeds), flowering plants adapted to submerged river rocks. (A) *Podostemum ceratophyllum*. Submerged stone covered with green, thread-like creeping structures (“roots”). Arrows point to leafy shoots arising pairwise from endogenous buds along the “roots”. Scale bar = 15 mm. Photograph taken by R. Rutishauser, Eno River (North Carolina). (B) Seedling of *Marathrum schiedeanum* with two cotyledons and a rudimentary plumule (arrow) in between. Note bunch of adhesive hairs arising from the lower end of the hypocotyl (primary root pole lacking). Cultivated in Zurich Botanical Garden with seeds from Mexico. Scale bar = 200 μm . (C) Seedling of Venezuelan *Rhyncholacis* sp. The primary shoot (arrow) between the two cotyledons stops growth after the formation of few plumular leaves. The first stage of the creeping “root” is observable as exogenous outgrowth (asterisk) of the hypocotyl. Note presence of adhesive hairs. Redrawn from Grubert (1976). Scale bar = 500 μm . (D) Cross-section of mature ribbon-like “roots” of *Ledermanniella bowlingii* (SE Ghana). Arrow points to central layer with small-celled “vascular tissue” (usually not differentiated into xylem and phloem). Lower side with few epidermis cells elongating into adhesive hairs (see asterisks). Scale bar = 200 μm .

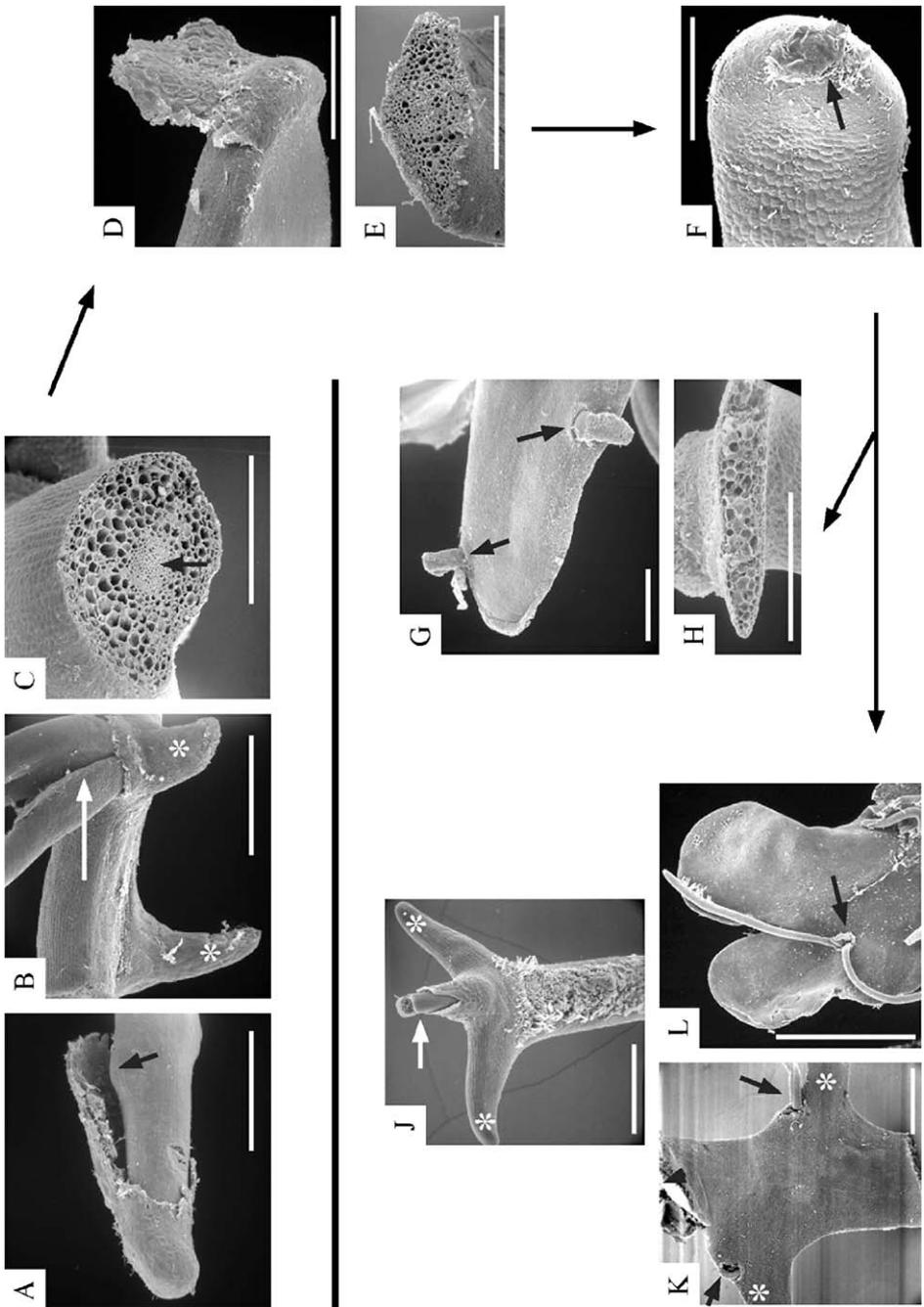
leaves of ferns and seed plants. This observation supports the hypothesis that the leaves of ferns and seed plants originated independently, thus they may not be historically (“truly”) homologous to each other (Schneider et al., 2002; Friedman et al., 2004).

- (E) *Molecular homology exclusively at gene level*: Evo-devo studies have identified many homologous genes and where they are expressed (Wilkins, 2002, see examples in Table 1). Most of them are downstream elements that do not determine the phenotypic homology (morphological correspondence) of an organ. They do not act as key regulatory genes for developmental processes and do not lead to “sameness” at the phenotypic level. Thus, most of these homologous genes (including orthologous vs. paralogous ones) may be of minor interest for evo-devo people who are in search of morphological correspondences (phenotypic homologies) and their underlying molecular mechanisms (Patterson, 1988; Butler and Saidel, 2000; Nielsen and Martinez, 2003; Svensson, 2004).

Synopsis of the five homology (“sameness”) levels

The reader should be aware that the five levels of homology as specified above are taken from the literature. Here we provide a synopsis of these homology levels,

Fig. 6. Creeping “roots” of Podostemaceae (subfamily Podostemoideae), arranged along a hypothetical transformation series. (A–C). Thread-like “root” of *Podostemum ceratophyllum* (Eastern North America). (A) Root tip covered by asymmetrical cap. (B) Lateral view of more developed root portion, with two exogenous finger-like holdfasts (asterisks). Arrow points to leafy shoot arising from endogenous bud along root flank. (C) Cross-section of mature, slightly flattened root, with vascular tissue in the center (arrow). Scale bars = 600 μm . (D–E). Ribbon-like root of *Cladopus queenslandicus* (NE Australia). (D) Root tip with hood-like cap. Scale bar = 200 μm . (E) Cross-section of mature ribbon-like root, with central vascular bundle. Scale bar = 600 μm . (F) *Farmeria metzgerioides* (Southern India). Tip of ribbon-like root with cap rudiment. Scale bar = 200 μm . (G–H). Free-floating ribbon-like root in *Polypleurum stylosum* (Southern India). (G) Apical region of broad ribbon-like root, seen from upper side. No cap observable. Arrows point to endogenous shoots (with first leaf each) next to root margin. Scale bar = 600 μm . (H) Cross-section of mature crustose root. Scale bar = 1 mm. (J–K). Ribbon-like roots without caps of *Zeylanidium* spp. (Southern India). (J) Narrow ribbon of *Z. subulatum*, seen from below. The mother root is determinate and gives rise to two exogenous daughter roots (asterisks). Arrow points to first leaf of endogenous shoot bud at the tip of the mother root. Note adhesive hairs on lower root surface. Scale bar = 600 μm . (K) *Zeylanidium lichenoides*. Nearly mature portion of broad ribbon-like root, seen from above. Arrowhead points towards root tip. Exogenous daughter roots (asterisks) arise in a zigzag pattern, with an endogenous shoot bud in each distal “axil” (arrows). Scale bar = 600 μm . (L) *Hydrobryum floribundum* (Southern Japan). Marginal region of lobed crustose (foliose) root, seen from above. Arrow points to first leaves of endogenous shoot arising from upper root surface. Scale bar = 2 mm. SEM graphs reproduced from Rutishauser (1997), but rearranged.



which are used and discussed by evo-devo people (Table 1). All these kinds of homology are caused by continuity of descent, usually equalling continuity of hereditary information (van Valen 1982, as cited in Wilkins, 2002, p. 165). Thus, their common basis is the recognition of highly conservative morphological patterns found either within the same modular organism or in a wide variety of taxa. The first three levels (A–C) of “sameness” (Table 1) emphasize morphological correspondence (phenotypic homology) of compared structures, whereas the last two levels D and E are kinds of homology at “deeper” genetic levels (including homologous genes). Levels D and E usually do not correspond to morphological correspondences (including organ identities) of phenotypes. Level A (serial homology) compares subunits within the same organism whereas levels B–D create homology statements by comparing structures in taxa which are related to a variable degree, e.g., members of related species, genera, families, or (especially level D) in very distantly related taxa such as members of different phyla: e.g., ferns vs. seed plants (Fig. 2A and B), arthropods vs. vertebrates (Fig. 2C and D). We should not restrict ourselves to only one homology level. We should always try to take into account several or all five levels of homology mentioned above. We should also consider partial (= mixed) homologies, developmental mosaics, and fuzzy organ identities (see continuum root–shoot model and “Case study” on Podostemaceae below, Figs. 4–7).

Biological homology as an inclusive concept

The four homology levels A–D may be understandable as subconcepts of “biological homology” which was proposed as a more inclusive homology concept (Table 1). According to Wagner (1989) two structures (from the same individual or from different individuals) are biologically homologous when “they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation”. Biological homology with its subconcepts A–D focusses on “structural sameness that allows to identify common processes that underlie this sameness” (Geeta, 2003). At levels A–C (with phenotypic homology usually obvious) the biological homology concept coincides with Butler and Saidel’s (2000) “syngeny” concept (meaning “same genesis”) that was proposed for sameness at the generative level, i.e., for similar structures that result from the same developmental pathways. The biological homology concept leads to a central question of evo-devo (Endress, 2003, p. 144): “Do morphological homologues have the same underlying molecular genetic machinery?” The following botanical example shows that structures that are homologous on the morphological level can arise from different genetic controls. It seems that the pinnae formation in compound (pinnate) leaves of many eudicots is correlated with *KNOX1* expression in leaf primordia (Kim et al., 2003; Kessler and Sinha, 2004). In contrast, in pea (*Pisum sativum*) and other members of the Leguminosae the formation of compound leaves instead depends on the expression of the *PEAFLO* gene which is the pea homologue of *FLORICAULA* and *LEAFY* from snapdragon (*Antirrhinum*) and *Arabidopsis*, respectively (Hofer et al., 2001). Moreover, pinnation in pea is independent of *PHANTASTICA* (*PHAN*), in contrast to *PHAN*-dependent pinnation in tomato. According to Tattersall et al.

(2005), gene expression patterns (also *KNOX* and *CRISPA*) indicate that the mechanism of pea leaf initiation is similar to what we see in *Arabidopsis* rather than in tomato. Numerous zoological examples of homologous structures based to some extent on different genes and different developmental processes are known (see, e.g., Butler and Saidel, 2000; Wilkins, 2002, also Wray in Bock and Cardew, 1999).

Traditional homology criteria

Any comparative morphological analysis is mainly a search for bauplans (body plans, archetypes) with the help of certain homology criteria. Three criteria are traditionally used, with the first one often accepted as more important than the two other criteria (see Remane, 1956, Eckardt, 1964, both cited in Wagenitz, 2003; also Rieppel and Kearney, 2002):

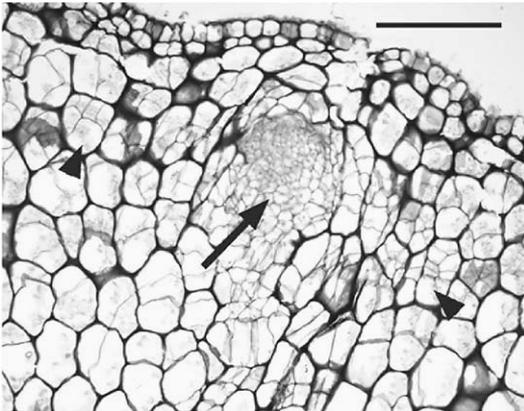
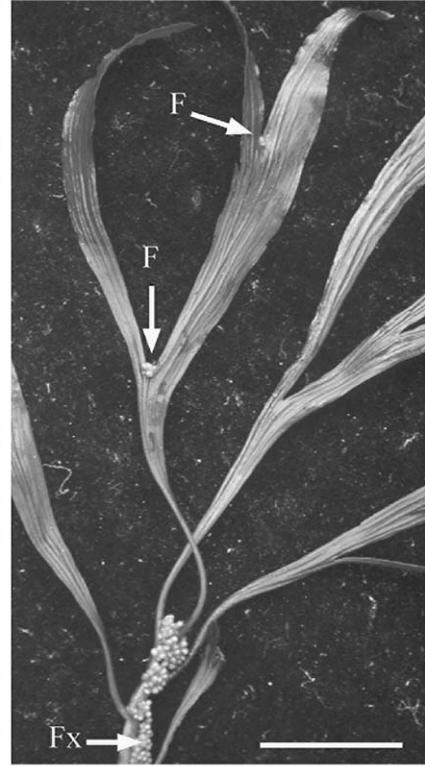
- (i) *Criterion of topological equivalence = position criterion*: Homologous organs often arise in similar or identical positions in organisms with modular (metameric) growth when different modules (segments) of the same organism or related taxa are compared. Organs which are homologous due to identical positions are called homotopous or positionally equivalent. In flowering plants this criterion is commonly used with respect to “axillary branching”, with leaves subtending daughter shoots (Fig. 1A). Topological equivalence (including same topological relation and/or connectivity) is often taken as the main homology criterion (Rieppel and Kearney, 2002). Cronk (2002, p. 5) confirms: “Whatever the cause, topological relations tend to be conservative, and for this reason the topological criterion is useful for assessing homology”. Nevertheless, heterotopic change occurs more often than is generally admitted (Bateman and Dimichele, 2002).⁵ This may be due to “ectopic expression of organ identity”, e.g., “leaves on leaves” and other kinds of epiphyly in vascular plants (Fig. 7A and B; see also the paragraph on “heterotopy, homeosis and ectopic expression of organ identity” below).
- (ii) *Criterion of special quality of structures*: Homologous organs often have identical or similar functions, as well as identical or similar parts (e.g., presence of caps and adhesive hairs in Podostemaceae roots, Fig. 6A). This criterion focuses (among other features) on the functions and complexity of an organ or another biological structure. When this criterion does not fit we may speak of “transference of function” or “exaptation” meaning that an organ takes over a new function (Hay and Mabberley, 1994). In contrast to multicellular animals the functions of a plant organ are often considered less important for the evaluation of its homology.

⁵Ectopic expression of organ identity coincides with the perhaps unnecessary new concept “homocracy” (as introduced by Nielsen and Martinez, 2003, and criticized by Svensson, 2004).

A



B



D

C

- (iii) *Criterion of linkage by intermediate forms = continuum criterion (including ontogenetic criterion)*: Organs, although looking different, may be accepted as homologous when intermediate or transitional forms are observable. For example, let us consider the odd “roots” in Podostemaceae (see “Case study” below): The continuum criterion makes it possible to accept the green crusts of derived members as root homologues along a hypothetical transformation series (Figs. 6A–L). When in other organisms and structures the continuum criterion does not work, this may be due to amalgamation (“hybridization”) of developmental pathways leading to “developmental mosaics” between organs normally assumed to have different identities (see below, Fig. 4: continuum model; also Weston, 2000).

Classical vs. continuum root-shoot models in vascular plants

In structural botany there are two seemingly opposing ways to perceive and conceive the bauplans and structural categories of vascular plants; the classical root–shoot model and the continuum root–shoot model (Figs. 3 and 4). Both perspectives (“schools”) have their own tradition and both have some roots in the morphological writings of Goethe (1790; as cited in Arber’s translation, 1946). Goethe’s typological–hierarchical view was continued as classical plant morphology (Fig. 3). Goethe’s holographic view was taken over as fuzzy (dynamic) morphology (Fig. 4). It is important to keep in mind that these two morphological “schools” do not exclude each other. They are best understood as complementary models, each one with its own predictive power. The classical model usually entails either–or thinking and conceptual realism whereas the continuum model reflects fuzzy logic, perspectivism, as-well-as thinking, and conceptual nominalism. In the following paragraphs we argue that both philosophical attitudes – the more reductionist “either–or philosophy” (Fig. 3) and the more holistic “as-well-as philosophy”



Fig. 7. Regeneration and endogenous flower formation in *Ledermanniella* spp. from tropical Africa. (A) *Ledermanniella bowlingii* (SE Ghana). Distal portion of mother stem (X) with leaves (L). Arrow points to epiphyllous daughter shoot. Distal end of stem X damaged, with regeneration of several daughter shoots (asterisk). Scale bar = 2 cm. (B–D). *Ledermanniella letouzeyi* (SW Cameroon) with short stem, forked leaves and many flower buds. (B) Flowering shoot, with densely arranged flower buds (Fx) along one stem sector. Note the foliage leaves which are forked once or twice, each segment lanceolate and provided with several parallel ribs. Additional flowers (F) are leaf-born (epiphyllous), arising from forks (angles) between leaf segments. Scale bar = 6 cm. (C) Stem basis with disc-like holdfast (asterisk) and many flowers along one stem sector, without being subtended by foliage leaves. Scale bar = 1 cm. (D) Cross-section of stem cortex. Arrow points to endogenous shoot bud, still surrounded by cortex of mother stem. Several parenchyma cells of stem cortex start to divide up into meristematic cells (as part of dedifferentiation, see arrowheads). Scale bar = 2 mm.

(Fig. 4) – are needed as heuristically valuable perspectives in order to progress in comparative plant morphology and developmental genetics.

- (1) *Classical root–shoot model as first and preliminary approach for the description of vascular plant bauplan*: According to the classical model (coinciding with “classical plant morphology”) the body of vascular plants is accepted as consisting of three main structural categories, i.e., root, stem and leaf. These organ types are seen as mutually exclusive sets which are non-homologous to each other. Overlaps between these structural categories are not possible. Especially for a clear leaf-stem distinction, the *position criterion* can be taken as the most useful criterion. This dismembering of a vascular plant into discrete structural categories or units (i.e., roots, stems and leaves) is often referred to as the *classical root–shoot model* (CRS model) or the shorter classical model (Fig. 3; Rutishauser and Isler, 2001; Rutishauser, 2005a). This model is useful as a perspective, or rule of thumb, because it is quite easy to handle and seems sufficient as a rough approach in most flowering plants. The classical model is also called the hierarchical view because “parts compose the whole, but the latter is not within the parts” (Sattler, 2001). The classical model was (and still is) often taken for granted in interpretations of the vascular plant bauplan (see Troll, 1939; Kaplan, 2001). Even morphological oddities as shown in the “Case study” on river-weeds (Podostemaceae) (Figs. 5–7) can be described to a certain degree using the classical root–shoot model!
- (2) *Continuum root–shoot model = fuzzy version of classical root–shoot model*: Numerous developmental geneticists working with vascular plants are quite aware of the shortcomings of the classical root–shoot model. For example, Sinha (1999) proposed a “leaf shoot continuum model” by giving emphasis on the partial repetition of the shoot developmental program within each leaf (with KNOX genes maintaining leaf indeterminacy). Several authors (e.g., Tsukaya, 1995; Sinha, 1999; Cronk, 2001; Hofer et al., 2001; Bharathan et al., 2002; Fukuda et al., 2003) have pointed to the fact that some vascular plants transcend the classical model with respect to leaves and shoots. Sinha’s “leaf shoot continuum model” can be understood as part of the more inclusive continuum root–shoot model = continuum model (Fig. 4) that was suggested already by Arber (1950), and further developed by Cusset (1994) and Sattler (1974, 1996). The continuum model accepts the same structural categories (plant organs) as the classical model, but allows them to have fuzzy (blurred) borderlines and intermediates, as suggested by developmental genetics and described at the morphological (phenotypic) level by, e.g., Sattler and Jeune (1992) and Lacroix et al. (2003). Thus, the classical model is a special case of the more comprehensive continuum model. Vergara–Silva (2003, p. 260) stressed the heuristic value of the continuum model in a recent essay on the importance of plant morphology for understanding evo-devo aspects as follows: “Distinct groups of genes that in principle act in one categorical structure, are actually also expressed in another, and ... the consequence that this overlapping pattern has on cell differentiation is an effective blurring of the phenotypic boundary between the structures

themselves”. The continuum model equals fuzzy morphology sensu Rutishauser (1995) and dynamic morphology sensu Lacroix et al. (2003).⁶ Honouring the famous plant morphologist and philosopher Agnes Arber (1879–1960), this type of morphological thinking was labelled as the “Fuzzy Arberian Morphology” = FAM approach (Rutishauser and Isler, 2001; Vergara-Silva, 2003). The continuum model is consistent with the *holographic paradigm*, i.e., the presence of self-similarity between the whole organism and its parts on the morphological as well as on the developmental level. This fact was stressed already by Arber (1950), and later by Kirchoff (2001) and Sattler (2001). The reiteration at different size scales (i.e., self-similarity) is reminiscent of fractal geometry, in which shapes are repeated at ever smaller scales (Prusinkiewicz, 2004).

The continuum model not only considers the developmental relationships of shoots (as the whole) and leaves (as their parts), but also similarities of *root and shoot*. Developmental geneticists have pointed out that there are groups of vascular plants (including among flowering plants), which do not always show a clear differentiation into root and shoot. They also stressed the fact that roots and shoots may have important regulatory mechanisms (including *CLAVATA* signalling pathways) in common (Raven and Edwards, 2001; Friedman et al., 2004; Birnbaum and Benfey, 2004). In a phylogenetic context the continuum model is consistent with the hypothesis that leaves are derived from stem-like (shoot-like) organs, at least in ferns and seed plants (Cronk, 2001; Friedman et al., 2004). The continuum model is also consistent with the phylogenetic hypothesis that in vascular plants the root may have evolved from an ancestral shoot (Raven and Edwards, 2001; Schneider et al., 2002).

Heterotopy, homeosis, and ectopic expression of organ identity

An organ or structure is called heterotopic when it develops in an unusual position of the body plan. Heterotopy violates the *position criterion*, i.e., the topological equivalence (= homotopy) of organs. Heterotopy often results from ectopic gene expression. For example, ectopic activation of the *Pax6* gene may even result in ectopic eyes on wings of the fruit fly (Butler and Saidel, 2000; Wilkins, 2002). Similarly, epiphyllous inflorescences and new shoots may arise along the rachis of compound leaves in various flowering plants such as tomato (Solanaceae), *Chisocheton* (Meliaceae) and *Ledermannia* (Podostemaceae, Figs. 7A and B; Dickinson, 1978; Fisher and Rutishauser, 1990; Fisher, 2002; Fukuda et al., 2003). The concepts “heterotopy”, “homeosis” and “ectopic expression of organ identity” have similar meanings (Baum and Donoghue, 2002; Cronk, 2002; Wagenitz, 2003).

⁶The continuum model is related to but not identical with Sattler’s (1994) “process morphology”. The continuum model retains structural categories (e.g., root, shoot axis, leaf) for the description and interpretation of the vascular plant body, whereas process morphology sensu Sattler replaces them by combinations of developmental processes (see also Lacroix et al., 2003; Rutishauser, 2005b).

These terms describe the transformation of body parts into structures normally found elsewhere according to the body plan. Homeosis is often seen as the phenomenon in which one structure is transformed into another homologous structure, e.g., leg and antenna in insects. As a phenotypic concept “homeosis” was recognized in different groups of organisms such as vascular plants already before the evo-devo times (as discussed by Sattler, 1988; Weston, 2000; Lacroix et al., 2003). Key regulatory genes (especially homeotic genes such as Hox, KNOX and MADS-box genes) and their ectopic expression are often involved in homeosis (Shubin et al., 1997; Theissen et al., 2002; Becker and Theissen, 2003). The biological homology concept (Table 1) lays emphasis on developmental modules (i.e., quasi-autonomous parts = QAPs) such as flowers (in angiosperms), limbs and eyes (in vertebrates and arthropods). Especially in mutants these modules (QAPs) may be induced out of their natural context. They are able to develop all their defining features in locations of the body where they usually do not occur, demonstrating that the development of the QAPs is locally controlled (see Wagner in Bock and Cardew, 1999).

Developmental mosaics, fuzzy organ identities and partial homology in vascular plants

According to the classical root–shoot model (Fig. 3) the various structural categories are crisp sets, perfectly excluding each other. The continuum root–shoot model (Fig. 4), however, accepts developmental mosaics of structural categories (“organs”) and, thus, fuzzy organ identities and mixed homologies between, e.g., root, shoot (including stem), leaf and their parts (Rutishauser, 1995, 1999; Sattler, 1996; Baum and Donoghue, 2002; Hawkins, 2002). Accepting structural categories as fuzzy sets, various structures in leaf position become understandable as developmental mosaics by giving equal weight to both the position criterion and the continuum criterion. Especially in vascular plants with odd morphologies there are developmental mosaics that can be seen as partially homologous to structures which – according to the classical model (Fig. 3) – have to be viewed as non-homologous (Sattler, 1974, 1996). Organs with partial (= mixed) phenotypic homologies show partially overlapping developmental pathways.⁷ Botanical examples are the “indeterminate leaves” of *Chisocheton* and *Guarea* (Meliaceae) and the stem–leaf indistinctness of vegetative organs in bladderworts (*Utricularia*) and allies (Lentibulariaceae), as discussed by Albert and Jobson (2001) and Rutishauser and Isler (2001).

⁷Be aware that the term “partial homology” has different meanings, depending on the homology level in focus! For example, Wagner (in Bock and Cardew, 1999, p. 34) claimed: “Partial homology is partial overlap in developmental constraints, not just a lower degree of similarity in appearance”. “Partial homologues” at the “deep evolutionary homology” level (Table 1) were also discussed by Abouheif as well as Wake (both in Bock and Cardew, 1999).

Case study: the peculiar architecture of “river-weeds” (Podostemaceae)⁸

“River-weeds” are specialists inhabiting river rapids and waterfalls of the tropics and subtropics

Podostemaceae is a family of 49 genera and c. 280 species worldwide (Ameka et al., 2003). Most species are found attached to rocks in river rapids and waterfalls and usually occur only in open high light areas (Fig. 5A). They are restricted to rivers that exhibit distinct high–low water seasonality. Most of the year Podostemaceae are submerged in turbulent, swift-flowing water, forming peculiar vegetative bodies which resemble lichens and bryophytes (especially liverworts) rather than flowering plants. These “river-weeds” show a high degree of structural plasticity and construction types not found elsewhere in the angiosperms (Bell, 1991; Rutishauser, 1997). Molecular data revealed that the Podostemaceae are eudicots (more exactly eurosids) and probably nested inside Clusiaceae as sister of subfamily Hypericoideae (see Gustafsson et al., 2002).

The usually annual life cycle of Podostemaceae

Only few podostemaceous members (including *Podostemum ceratophyllum*, Fig. 5A) are perennial, as long as they remain submerged. Most Podostemaceae, however, are annual, dying after having reproduced sexually with thousands of minute seeds (length 0.1–0.3 mm). At the beginning of the new rainy period (e.g., onset of monsoon in Southern India) the seeds stick to a submerged rock and germinate (Grubert, 1976). The seedling has two cotyledons and a plumule that usually stops growth after the formation of a few seedling leaves (Fig. 5B). The radicle pole of the seedling (hypocotyl) is covered by adhesive hairs, but never produces a primary root. After the formation of several adhesive hairs an exogenous lateral outgrowth of the hypocotyl (Fig. 5C) develops into the first creeping root, with or without root cap (calyptra) depending on the taxon (Sehgal et al., 2002; Suzuki et al., 2002). Most Podostemaceae continue to colonize the rocky substrate with thread- or ribbon-like roots that branch endogenously or exogenously. Adhesive hairs as well as holdfasts are reported to secrete a “super-glue”. Sticky biofilms produced by bacteria (including cyanobacteria) also help to attach the podostemaceous roots to the rocky substrate (Jäger-Zürn and Grubert, 2000). At the end of the rainy (monsoon) period the water level recedes, allowing the plants to flower in the air. Most podostemaceous members seem to be wind-pollinated (or cleistogamous); only neotropical and phylogenetically basal members belonging to

⁸The material and methods used have been described elsewhere in detail (Rutishauser, 1997; Ameka et al., 2003; Rutishauser et al., 2003; Moline et al., in press). The authors of the Podostemaceae species names mentioned here are as follows: *Cladopus queenslandicus* (Domin) C.D.K. Cook & R. Rutishauser, *Farmeria metzgerioides* (Trim.) Willis, *Hydrobryum floribundum* Koidz., *Ledermanniella bowlingii* (J.B. Hall) C. Cusset, *L. letouzeyi* C. Cusset, *Podostemum ceratophyllum* Michx., *Polypleurum stylosum* (Wight) J.B. Hall, *Zeylanidium lichenoides* (Kurz) Engler, *Z. subulatum* (Gardner) C. Cusset.

genera such as *Apinagia*, *Mourera*, *Rhyncholacis* and *Weddellina* are entomophilous, pollinated mainly by *Trigona* bees (Rutishauser and Grubert, 1999).

The classical root–shoot model for the description of the plant body in vascular plants

According to the classical model (Fig. 3) roots and shoots in vascular plants (especially seed plants) are distinguished as follows. There are four key features that help to distinguish *roots* from SHOOTS = LEAFY STEMS (root features in *italics*, shoot features IN CAPITALS): (i) *presence* vs. ABSENCE of a root cap (calyptra); (ii) *absence* vs. PRESENCE of exogenously formed leaves (scales); (iii) xylem and phloem in *alternating sectors* vs. xylem and phloem in the SAME AXIAL SECTORS (often as parts of COLLATERAL BUNDLES); (iv) *endogenous* vs. EXOGENOUS origin of lateral shoots.⁹

***Podostemum ceratophyllum* fits only to some degree into the classical root–shoot model**

If we use the classical root–shoot model (Fig. 3), as has already been done by, e.g., Rutishauser (1997) and Jäger-Zürn (2003), the description of *Podostemum ceratophyllum* is as follows. The creeping structures (“roots”) of this mainly North-American species are green, thread-like, attached to submerged rocks (Fig. 5A). They are slightly flattened and provided with an asymmetric multicellular cap, resembling the calyptra of typical roots (Fig. 6A, Rutishauser et al., 2003). The “roots” of *Podostemum ceratophyllum* have an oval outline when seen in transverse sections (diameter up to 2 mm, Fig. 6C). There is a central vascular bundle with inconspicuous xylem and phloem elements. Just behind the tip, protrusions arise along the “root” flanks that represent early stages of endogenous shoots. The first leaves of these endogenous shoots form while the shoot apex is still within the “root” cortex; they protrude by rupturing the cortex and epidermis. Additional appendages are finger-like exogenous outgrowths which act as holdfasts being directed to the surface of the rocky substratum (Fig. 6B). Each “root”-born shoot is first rosulate, with entire or forked leaves consisting of filiform to spatulate segments (Fig. 5A). After internode elongation and the formation of additional leaves the stems of *Podostemum ceratophyllum* reach a length of up to over 10 cm, depending on the population. Vegetative shoots start branching and produce the first flowers after the formation of 6–10 leaves. We can now apply the four key features for root–shoot distinction according to the classical model (Fig. 3): the presence of a cap and the endogenous formation of lateral shoots are characters indicating that the creeping filamentous structures of *Podostemum ceratophyllum* are homologous to the roots of other flowering plants. The slight dorsoventral flattening of the creeping structures in *Podostemum ceratophyllum*, their green colour, the presence of exogenous holdfasts

⁹Lateral roots along roots and stems, however, are initiated endogenously in most vascular plants.

along their flanks, and inconspicuous vascular tissue inside are somewhat unusual root features. Some of them are more typical for shoots (stems with leaves).

Creeping photosynthetic “roots” of Podostemaceae–Podostemoideae can be arranged along a hypothetical transformation series

In contrast to *Podostemum ceratophyllum* (Fig. 6A–C) the “roots” of various other Podostemoideae members are strongly flattened and crustose. We will call these flattened photosynthetic organs “ribbon-like roots”, even “crustose roots” when they are completely flattened and crustose, resembling foliose lichens. These ribbons may contain one or up to several vascular strands arranged in one plane (Fig. 5D, Rutishauser and Pfeifer, 2002; Koi and Kato, 2003). Root-born shoots in all species are initiated as endogenous buds, but the diversity in other structures throughout the family is enormous, with lateral roots arising from endogenous buds (*Farmeria*) or from exogenous buds (*Cladopus*) along the mother root. The root tips are provided with a dorsoventral hood-like cap (e.g., *Cladopus queenslandicus*, Fig. 6D). Or there is only a rudimentary root cap left (e.g., *Farmeria metzgerioides*, Fig. 6F). Ribbon-like roots often lack a cap; broad crustose roots always are devoid of caps (Fig. 6G–L). Crustose roots show marginal growth and exogenous branching (lobing) along their margins. Depending on the vigour of growth, the exogenous lateral outgrowths may be called “daughter roots” or “holdfasts”. Broad free-floating root-ribbons are typical for *Polypleurum stylosum* (Fig. 6G and H). They are attached to the rock by a proximal adhesive pad, resembling the seaweed *Fucus*. Endogenous shoots arise from the upper root surface, close to its margin. Ribbon-like to crustose roots that are completely attached to the rock by adhesive hairs are found in the Asian genera *Hydrobryum* and *Zeylanidium* (Fig. 6J–L). Narrow root ribbons, as typical for *Z. subulatum*, show a mother root that is determinate, giving rise to an endogenous shoot bud at its tip. Two exogenous daughter roots (again narrow ribbons) arise like the arms of a fork. They continue the colonization of the rock for a while, then they also stop growing (Fig. 6J, Hiyama et al., 2002). The broad ribbon-like roots of *Zeylanidium lichenoides* (width up to 5 mm) show exogenous daughter roots forming a zigzag pattern, with an endogenous shoot bud in each distal “axil” (Fig. 6K). In a few Asian podostemads, e.g., *Hydrobryum floribundum* (Fig. 6L) and *Zeylanidium olivaceum*, the “roots” are crustose (foliose), with a diameter of up to 10 (–30) cm and marginal meristem providing exogenous marginal lobes. Endogenous shoots arise from all over the upper root surface (Fig. 6L, Ota et al., 2001; Jäger–Zürn, 2003). Except for *Podostemum ceratophyllum* (Fig. 6A–C), all roots mentioned above belong to representatives from Asia and Australia (Fig. 6D–L). A similar variation of root architecture, however, can be found in African Podostemaceae, and to a lesser degree in American species. For example, *Ledermanniella bowlingii* (from Ghana) has broad root-ribbons (Fig. 5D, width up to 7 mm), showing exogenous branching into daughter roots (i.e., lateral lobes) with zigzag pattern (Ameka et al., 2003). One-flowered short shoots arise from endogenous buds along the root flanks, similar to the pattern shown for *Zeylanidium lichenoides* (Fig. 6K). A layer of small-celled “vascular tissue” (usually not

differentiated into xylem and phloem) is observable inside the broad ribbon-like root. Adhesive hairs (“root-hairs”) fix the root to the rock.

Do river-weeds possess roots at all?

The exposé above is based on the classical root–shoot model (Fig. 3) for describing and understanding bauplan(s). Nevertheless, there is an ongoing discussion whether podostemads have roots at all. A neutral solution for skeptics was (and still is) to get rid of the term “root” in Podostemaceae, as done by, e.g., Ota et al. (2001) and Sehgal et al. (2002). Instead, these authors have used the term “thallus”,¹⁰ a term usually restricted to the plant bodies of algae, lichens and liverworts. Dropping the term “root” in the Podostemaceae bauplan only means that these river specialists do not have typical roots, as we know them from other flowering plants. Ota et al. (2001) while describing the “roots” of *Hydrobryum* (Fig. 6L) concluded with the hypothesis: “The thalli, though remarkably different from typical roots of other angiosperms, might be extremely transformed roots.” The same interpretation (hypothesis) was favoured by other students of Podostemaceae architecture, e.g., by Troll (1939), Rutishauser (1997), Jäger–Zürn (2003) and Kita and Kato (2004), who also used terminological hybrids such as “thalloid root” or “root thallus”. In classical morphology studying plants and animals three criteria are favoured in order to evaluate homology (“sameness”) of structures within a taxon or clade (see above). Here we argue that based on the “criterion of linkage by intermediate forms” (e.g., Rieppel and Kearney, 2002) the green crusts of Podostemaceae such as *Hydrobryum* and *Zeylanidium* are homologous to the roots of other flowering plants. It is possible to arrange the “roots” of most podostemads along a transformation series (Fig. 6A–L). A progressive elaboration of the “root” is most obvious in Asian Podostemoideae, where it is accompanied by a size reduction of the root-born shoots (Rutishauser, 1997). The transformation series coincides with molecular data. According to molecular cladograms the Old-World Podostemoideae are derived from American taxa, with *Podostemum* being somewhat intermediate (Kita and Kato, 2001, 2004). Starting with thread-like roots, an enhanced dorsoventral flattening leads to ribbons, with or without adhesive hairs on the lower side. Crustose roots have arisen at least three times in parallel in Podostemaceae, twice in Asian podostemoids (*Hydrobryum*, *Zeylanidium*) and at least once in Africa (*Ledermanniella bowlingii* and allies, Fig. 5D; Kita and Kato, 2004; Moline et al., in press).

Endogenous shoot branching and epiphyllous outgrowths in Podostemaceae

The morphological description given above did not cover the shoots (i.e., stems and leaves) of Podostemaceae. We just learnt that “roots” of Podostemaceae can be

¹⁰The term “thallus”(from the Greek thállos, thallein, meaning “to sprout”) usually describes the undifferentiated stemless, rootless, leafless plant body which is characteristic of algae, fungi and liverworts (Wagenitz, 2003).

quite odd, i.e., morphological misfits when seen in the framework of the classical model. Do we have typical stems and typical leaves in podostemads? This seems to be the case for various podostemads, at least to some degree (Rutishauser, 1995, 1997). However, in several African Podostemaceae the “leaves” and “stems” do not behave as they should according to the classical model (Fig. 3). In *Ledermanniella bowlingii* (Ghana) there are epiphyllous shoots arising from leaves (Fig. 7A) whereas other new shoots arise from the damaged stem (as an example of regeneration). In *Ledermanniella letouzeyi* (Cameroon) epiphyllous flowers arise from the clefts (angles) of forked leaves (Fig. 7B). Many more flower buds in *L. letouzeyi*, however, are formed along the stem (Fig. 7B and C). This host of flowers is restricted to one stem sector, none of them being subtended by foliage leaves. A transverse stem section clearly shows that these flowers arise from endogenous sites inside the stem cortex (Fig. 7D), probably due to dedifferentiation of parenchyma cells. Endogenous flower formation along the stem is also known from other podostemads, e.g., *Indotristicha ramosissima* (Rutishauser and Huber, 1991). Close inspection of the epiphyllous flowers in *L. letouzeyi* (Fig. 7B) and related *Ledermanniella* spp. has shown that they also arise from endogenous buds inside the leaf tissue (Moline et al., in press).

Are river-weeds (Podostemaceae) “morphological misfits”?

The architectural rules given for the typical bauplan (body plan, archetype) of flowering plants are violated to a considerable degree in the river-weeds (Podostemaceae, Figs. 5–7): exogenous origin of daughter roots from mother roots, strong root flattening and loss of root-cap by adapting to submerged river rocks, (often) lack of axillary branching, instead endogenous origin of lateral shoots (especially flower buds) along the shoot axis, occurrence of daughter shoots and flowers in both sheaths of so-called “double-sheathed leaves” (i.e., a type of leaf insertion only found in Podostemaceae), even occurrence of epiphyllous flowers from the clefts of forked leaves. The acceptance of the continuum model (Fig. 4) is advantageous here as a complementary perspective for the morphological description and interpretation of the Podostemaceae. According to the continuum model “roots” (green crusts) of certain podostemads (e.g., Fig. 6L) may be seen as developmental mosaics, i.e., as organs combining elements (pertinent features) of roots and shoots (cf. Sehgal et al., 2002) while “stems” of other Podostemaceae with endogenous flower buds (e.g., Fig. 7D) imitate roots, at least to some degree. Developmental geneticists may eventually discover which key regulatory genes (including those defining “organ identity”) are really active in Podostemaceae and other morphological misfits in flowering plants. Vascular plants with bauplans that deviate strongly from the classical model (Fig. 3) were called “morphological misfits” by Bell (1991). However, Bell added that “misfit” is not the problem of the plant, but the problem of our inadequate thinking and concepts. In the expanded framework of the continuum model (Fig. 4) the podostemads are not “misfits”.

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