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Plants are used to having identity crises

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Macroscopic nature is never really anomalous. Abnormalities, like other exceptional cases, at least show incontestably, what the plants *can* do.

Arber 1950: 6

However, regardless of how much faith one has in anatomical definitions, they should not be taken as more than a means of communication prior to subsequent genetic analysis.

Scheres *et al.* 1996: 963

Truth, except as a figure of speech, does not exist in empirical science.

Brower 2000: 18

INTRODUCTION

Our green and living world is a continuum in space and time. This view is well expressed in the ‘continuum model’ proposed by botanists and biophilosophers such as Arber (1950) and Sattler (1996). As an opposite view we may accept the green world around us as consisting of discrete units on several hierarchical levels. This view is called here the ‘discontinuum model’ or the ‘classical model’ because it has been the predominant view in biological textbooks for decades. Branching and repetition of developmental units (e.g. cells, meristems, modules, leaves, phytomers) are omnipresent as developmental processes in multicellular plants. These processes resemble the process of segmentation in various metazoan phyla, also occasionally leading to fuzzy borderlines between consecutive developmental units (Minelli and Fusco 2004, Prusinkiewicz 2004, Rutishauser and Moline 2005). Perspectivists studying plants accept structural and developmen-

tal categories such as cells, meristems, modules, leaves and phytomers as mind-born, simplified concepts reflecting certain aspects of the structural diversity (Sattler and Rutishauser 1990, Hay and Mabberley 1994). The best choice is to combine the heuristic advantages of both the continuum and the classical model by accepting the living world (especially the green one) as a heterogeneous continuum where typical forms are more frequent than intermediate ones. The present chapter focuses on unusual plant forms outside or beyond the geneticist's lab.

Classical model

A striking feature of vascular plants (i.e. seed-plants and ferns) is their apparent morphological simplicity. During the life cycle of a typical flowering plant, only three vegetative organ systems (leaves, stems and roots) and four reproductive organ systems (sepals, petals, stamens and carpels) are formed (Sattler 1996, Soltis *et al.* 2005, Endress 2006). According to the classical model the various structural categories are crisp sets, perfectly excluding each other. For example, for a clear leaf–stem distinction the relative position of an organ is taken as the most useful criterion (Rutishauser and Moline 2005).

Continuum model

Developmental geneticists (e.g. Tsukaya 1995, Jackson 1996, Sinha 1999, Hofer *et al.* 2001) have pointed to the fact that some vascular plants transcend the classical model. The continuum model accepts the same organ systems as the classical model, but allows them to have fuzzy (blurred) borderlines and intermediates, as described by, for example, Sattler and Jeune (1992) and Lacroix *et al.* (2003). This approach coincides with the fractal paradigm in that the whole is repeated in the parts to some extent, or the holographic structure where the whole can be retrieved from a part of it (Sattler 2001). For example, the continuum model accepts developmental mosaics of plant organs and mixed homologies between root, shoot (including stem), leaf and their parts (Rutishauser 1995, 1999, Sattler 1996, Baum and Donoghue 2002, Hawkins 2002). Developmental mosaics can be defined by giving equal weight to both the position criterion and the criterion of linkage through intermediate forms (Rutishauser and Moline 2005).

Organ identity

An organ in multicellular animals and plants is a part of a living organism with a certain set of functions besides its positional and constructional characters. In the context of plant developmental genetics 'organ identity' means the developmental fate of an uncommitted primordium. This term is used in zoology (e.g. Blochlinger *et al.* 1991) and botany as well. 'Organ identities' can be defined by morphological criteria and by their gene expression pattern, including organ identity genes that sculpt, for instance, the structure of angiospermous flowers (Yu *et al.* 1999, Soltis *et al.* 2005, Theissen 2005, Endress 2006, Jaramillo and Kramer 2007). The 'organ identity' concept is closely related to the concept of 'homology'; both have multiple and sometimes conflicting meanings, as reviewed by Sattler (1994), Bock and Cardew (1999), Brower (2000), Rutishauser and Moline (2005), and Theissen (2005). 'Organ identity' as a concept is also used outside the reproductive zone. The vegetative body of vascular plants thus shows primordia that are committed during early development to take over organ identities such as 'leaf identity' or 'root identity'. Acquisition of organ identity often happens progressively rather than at once (Sylvester *et al.* 1996, Bey *et al.* 2004). In some ferns and aberrant flowering plants ('morphological misfits') such as *Utricularia* the commitment of a primordium (meristematic area) to become a 'leaf' or 'shoot' (including 'stem') can be considerably delayed (Steeves *et al.* 1993, Rutishauser and Isler 2001).

MULTICELLULAR PLANTS HAVING IDENTITY CRISES ON VARIOUS LEVELS

The concept of an identity crisis is better known in psychology and sociology where it describes a condition of disorientation and role confusion as a result of conflicting pressures and expectations. Within the past few years the term 'identity crisis' has been adopted by developmental geneticists (Elledge 1996, Geuten *et al.* 2006, Lugassi *et al.* 2006). They have started to understand pattern repetition (reiteration) better at different levels of structural complexity. Multicellular plants such as angiosperms are used to having identity crises on various levels, from cells to meristems and organs and even beyond. Identity crises, however, are not the problem of the plants, but of our inadequate thinking and concepts.

Cell identity crisis

Cells in multicellular organisms acquire different identities in an ordered spatial arrangement: ‘How do cells learn about their identity?’ is a question asked by Scheres (2001: 112). Cell theory identifies the cell as the elementary unit from which all living organisms are constructed. In contradiction of cell theory, cells of higher plants are neither physically separated nor structurally independent. Plasmodesmata (i.e. cell-to-cell channels) connect each plant cell to its neighbours, aiding the exchange of proteins, RNAs and other molecules. Thus, higher plants are nowadays accepted as being both multicellular and supracellular. This view coincides with Tsukaya’s (2002: 33) ‘neo-cell theory’: ‘Each cell is also controlled by factors that govern the morphogenesis of the organ of which the cells are a part.’ Baluska *et al.* (2004) admit: ‘This identity crisis of the “cell” is not simply a problem confined to plants, as nanotubular intercellular bridges are also generated “de novo” between animal cells.’

Meristem identity crisis

Meristems in vascular plants are tissues primarily concerned with the formation of new cells by division. They are responsible for making roots, shoots (including stems and leaves) and (in seed plants) also flowers. The term ‘meristem identity’ is used to characterise the growth phases of a shoot apical meristem (SAM), with vegetative meristem, inflorescence meristem and floral meristem as three possible ‘identities’. Involved in the change of meristem identities in flowering plants (such as *Antirrhinum* and *Arabidopsis*) are *FLO*-like genes such as *FLORICAULA* and *LEAFY* (inflorescence meristem identity). Also responsible for floral meristem identity are MADS-box genes such as *SQUAMOSA* (*Antirrhinum*) and *APETALA1* (*Arabidopsis*), whereas MADS-box genes such as *AGAMOUS* and *PLENA* are involved in floral meristem determination (Theissen 2000, 2005). In *Arabidopsis* the switch from one meristem identity to the next means a change of identities of lateral appendages. For example, Parcy *et al.* (1998) described the conversion of vegetative to floral meristems in *Arabidopsis* as follows: ‘After floral induction in wild-type *Arabidopsis*, primordia that would otherwise have become leaves develop into flowers instead.’ A similar situation is found in *Nymphaea* and *Nuphar* (Nymphaeaceae) which share an extra-axillary mode of floral inception in the shoot (i.e. rhizome) apical meristem. Some leaf sites along the ontogenetic spiral are occupied by floral primordia

lacking a subtending leaf or bract. This pattern of flower initiation in leaf sites is repeated inside the ‘branching flowers’ of *Nymphaea prolifera*, a species occurring in Central and South America (Figures 11.1B, 11.2A, 11.2B). Instead of producing a single flower, an individual floral meristem of certain angiosperms (wild-type plants or mutants) can branch continuously giving rise to a complex inflorescence with many flowers. This process is called floral reversion and is found in, for example, *Arabidopsis* when floral meristems switch back to an indeterminate state and restart as a shoot apical meristem (Stahl and Simon 2005). Floral reversion also occurs in *Nymphaea prolifera*: each ‘branching flower’ first produces some perianth-like leaves, then it switches back to SAM identity forming the rhizome tip (Figure 11.1B, 11.2A, 11.2B). This switch is repeated up to three times giving rise to a branched complex of more than 100 sterile flowers serving as vegetative propagules (Grob *et al.* 2006).

There are developmental parallels between the flower level (as a subsystem) and the inflorescence level (as a system) in various groups of angiosperms. Baum and Donoghue (2002: 64) used the double-term ‘inflorescence-flowers’ when developmental programs of both flower and inflorescence are mixed. By examining MADS-box genes Yu *et al.* (1999) have shown that gene activities found during flower initiation are also found during early development of the head-like inflorescences of Asteraceae. This could explain why simple flowers and compound ‘flowers’ (i.e. inflorescences) are in certain taxa quite similar to each other – ‘a resemblance sometimes carried into the minutest details of form and coloration’ (Arber 1947: 233).

Floral organ identity crises

Developmental geneticists began to use the term ‘organ identity’ in botany while studying the genes that determine the developmental fate of flowers and their appendages (Coen 1999, Theissen 2000, 2005). For example, ‘complete’ bisexual flowers are observable in the eudicot *Clerodendrum minahassae*, a member of the eudicot family Verbenaceae (Figure 11.1D). Four whorls of organs are distinguishable: sepals, petals, stamens and carpels (the latter fused into a superior ovary). *Clerodendrum minahassae* adds ‘petalness’ to its sepals *after* anthesis in order to attract birds for fruit dispersal. In *Mussaenda* and *Warszewiczia* (both Rubiaceae) one out of five sepals is transformed into a showy, bract-like organ, serving as an optical signal for the whole inflorescence (Figure 11.1E).

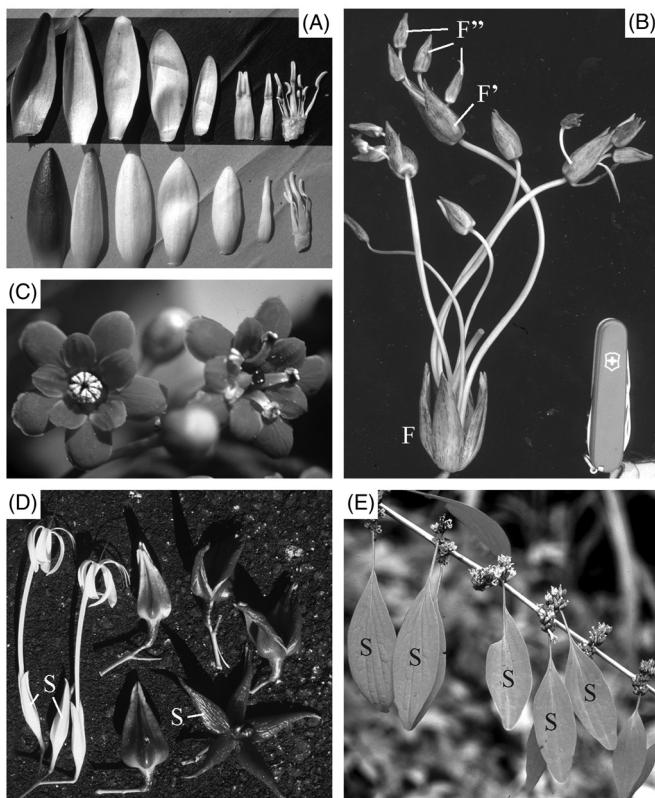


Figure 11.1 Flowers and their parts having identity crises. A, *Nymphaea tuberosa* (Nymphaeaceae). Continuum of identities in floral organs.

Upper row seen from ventral (inner) side, lower row seen from dorsal (outer) side. Outermost four perianth members as sepals green outside, followed by several completely white petals. Innermost petals turning into yellowish petaloid stamens, inner stamens yellow with narrow filaments. B, *Nymphaea prolifera* (Nymphaeaceae). Mother flower (F) branching into daughter flowers (F') and grand-daughter flowers (F''), acting as vegetative propagules.

(For anatomical and developmental details see Figure 11.2.) C, *Jacquinia pungens* (Theophrastaceae). Two flowers, with male stage on the left, female stage (ovary visible) on the right. There are two pentamerous whorls of red ‘petals’: the outer whorl equals the ‘true’ corolla, the inner whorl is equivalent to five petaloid staminodes. D, *Clerodendrum minahassae* (Verbenaceae). Temporal continuum of flower shape from anthesis to fruit maturation. Anthetic flowers white, with long corolla tube and five petal lobes. After anthesis the perianth is dropped. The five sepals (S, white during anthesis) become firm and turn into a spreading red star surrounding the nearly black fleshy fruit. Thus, the calyx is adding ‘petalness’

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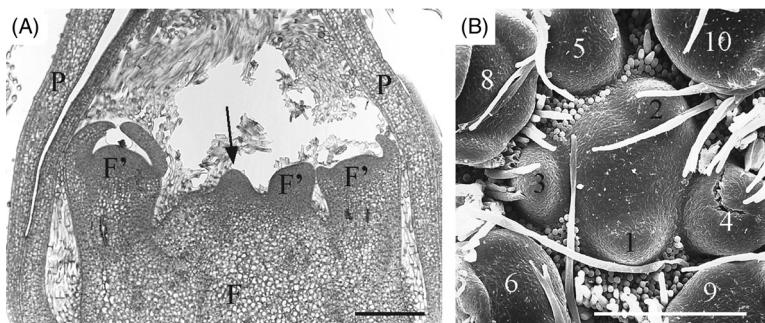


Figure 11.2 *Nymphaea prolifera* with meristem identity crisis of branching flowers (see overview Figure 11.1B). A, Longitudinal section of mother flower (F) with daughter flowers (F'). Note perianth (P) of mother flower. Arrow points to obliquely cut young leaf primordium next to apical meristem. Scale bar = 200 µm (reproduced from Grob et al. 2006). B, Top view on central portion of mother flower (perianth removed). The flower centre behaves like a shoot apical meristem, showing lateral primordia (1–10) along an ontogenetic spiral (site 7 is out of the frame). Most sites (4–6, 8–10) are occupied by floral primordia without any subtending leaves. Dorsiventral shape of primordia 1 and 3 (next to apical meristem) reveals their leaf identity. Hemispherical primordium 2 is the first stage of another young flower. Scale bar = 200 µm (reproduced from Grob et al. 2006).

Geuten et al. (2006) used the term ‘floral organ identity crisis’ or, more specifically, ‘petal identity crisis’ while focusing on the developmental genetics of petaloid sepals and the evolution of petaloidy in *Impatiens* (Balsaminaceae) and related eudicots. In basal angiosperms such as *Nymphaea* there is a continuum of forms (a ‘morphoclone’) bridging sepals, petals and stamens. In, for example, *N. tuberosa* (Figure 11.1A) there are intermediates between typical sepals (green outside), typical petals (completely white) and typical stamens (yellow, with anthers fixed to thread-like filaments). Do these sepals and petals suffer from an identity crisis? Endress (2006: 7) seems to agree for *Nymphaea*: ‘Therefore, it makes more sense to speak of tepals and to use the modifiers sepaloid tepals and petaloid tepals.’ Fuzziness of floral organ identity gene action in various angiosperms is described by Soltis et al. (2005: 190). They

Caption for Figure 11.1 (Cont.) after anthesis. E, *Warszewiczia coccinea* (Rubiaceae). The flower clusters along the twig are provided with flag-like leaves (red, 6 cm long) which are modified sepals (S). Photograph by P. Peisl (Zurich).

concluded: 'Morphology, developmental data and genetic data may provide conflicting evidence of homology (organ identity) and yet ultimately a more complete, and complex, view of a structure.' This is in agreement with a combinatorial notion of homology, such as suggested, for example, by Minelli (1998). Developmental mosaics between sepals, petals and stamens are acceptable because these kinds of floral appendages are usually taken as modified leaves. Arber (1950: 55) summarised the history of this idea: 'We may indeed agree with Goethe and deCandolle that petals and stamens show so much affinity that it is evidently reasonable to group them together. The petals will then be regarded as transition members between the vegetative and the actively reproductive parts of the floral shoot.'

Many angiosperms produce petaloid stamens, i.e. showy floral organs which according to their relative position in the developing flower are stamens and not petals. Jaramillo and Kramer (2007) call this phenomenon 'a decoupling of position from the morphological similarity of the structures in question.' For example, flowers of *Jacquinia pungens* (Figure 11.1C) have two pentamerous whorls of petaloid structures, with 'true' petals forming the outer whorl and petaloid staminodes forming the inner one (Walker-Larsen and Harder 2000). In *Costus* (related to ginger), 'true' sepals and petals are rather inconspicuous whereas the showy and broad lip (attractive for pollinators) is formed by the fusion of five staminodes (i.e. sterile stamens) (Figure 11.3A–D; Kirchoff 1991).

Although stamens and carpels are often said to be homologous structures, both being sporophylls, they are basically different in some respects. According to Endress (2006: 9) 'an ovule can also be compared with a stamen in some way, and the carpel is then more complex.' Nagasawa *et al.* (2003) described double mutants of rice (*Oryza*) having 'organs with unknown identity'. They are 'neither stamens nor carpels, but have partial floral identity.'

Leaf identity crisis: leaf–shoot indistinction

Some vascular plants transcend the classical model with respect to leaves and shoots (Cronk 2001, Hofer *et al.* 2001, Bharathan *et al.* 2002). For example, compound leaves of *Chisocheton* (Meliaceae) with indeterminate apical growth and three-dimensional branching due to epiphyllous shoots are developmental mosaics sharing growth processes with whole shoots. 'Indeterminate leaves' in *Chisocheton* and *Guarea* (Meliaceae) and examples of leaf–shoot indistinction in bladderworts

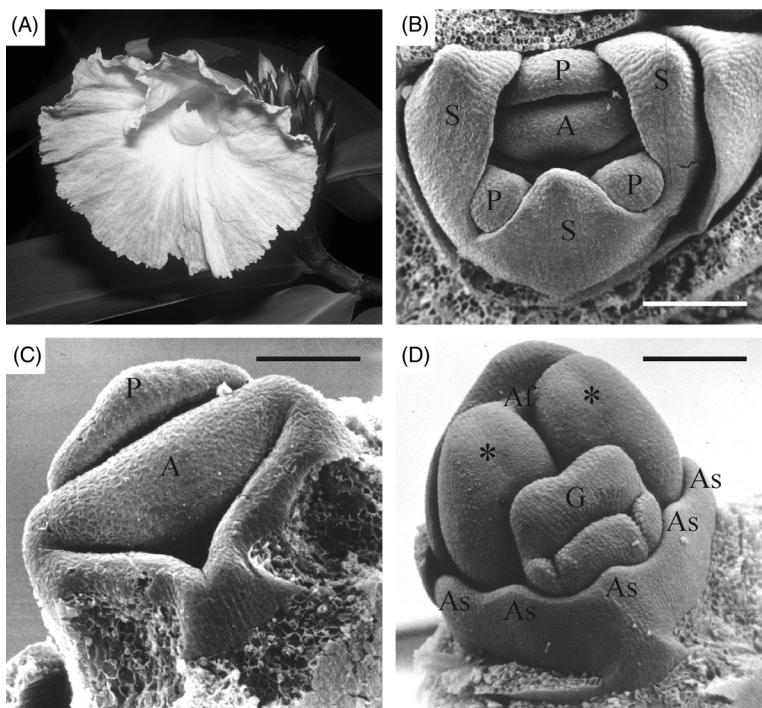


Figure 11.3 *Costus* (Costaceae) with petaloid androecium having an identity crisis. A, *Costus* sp.: frontal view of flower in anthesis, showing prominent white petaloid lip resulting from fusion of five staminodes. There is only one fertile stamen per flower. The ‘true’ sepals and petals are inconspicuous and hidden. Photograph by P. Peisl (Zurich). B–D, *Costus cuspidatus*. Flower development as shown by scanning electron micrographs before and after removal of sepals (S) and petals (P). The androecium arises as a collar-like girdling primordium (labelled A). Its prominent dorsal portion develops into the only fertile stamen (Af) with two anther halves (asterisks). The less prominent lateral and ventral portions of the girdling primordium have teeth equalling the five staminodal teeth (As) that will form the showy androecial lip. G = stigma (gynoecium). Scale bars = 200 µm.

(*Utricularia*, Lentibulariaceae) were presented by Rutishauser (1999), Rutishauser and Isler (2001), Fisher (2002) and Fukuda *et al.* (2003). Epiphyllous flowers are also known from African Podostemaceae (river-weeds) which are angiosperms adapted to waterfalls (Figure 11.5A; Rutishauser and Moline 2005).

Induction of leaves directly from leaves occurs in maize mutants (Schichnes *et al.* 1997), and induction of ectopic shoot meristems on leaves is known from *Arabidopsis* mutants (Byrne *et al.* 2003).

A genetically well-understood example illustrating the switch from leaf identity to shoot (or stem) identity is the *Hooded* mutant of *Hordeum vulgare*, also called hooded barley (Yagil and Stebbins 1969): the subtending leaf ('lemma' = bract) produces one or more ectopic spikelets on the awn. Molecular studies (e.g. Reiser *et al.* 2000) have elucidated that the hooded phenotype of barley is caused by misexpression of a *knox* gene. Williams-Carrier *et al.* (1997) suggested that the inverse polarity of the ectopic spikelets seen in the *Hooded* mutant of barley and transgenic *KNOTTED1* plants of maize results from the homeotic transformation (conversion) of the lemma awn into a reiterative inflorescence axis. Hooded barley is therefore an example of conversion of organ identity. In a phylogenetic context the above-mentioned cases of leaf–shoot indistinction are consistent with the hypothesis that leaves are derived from stem-like (or shoot-like) organs, at least in most ferns and seed-plants (Cronk 2001, Friedman *et al.* 2004).

We should also consider the identity question for tiny, scale-like leaves (1–2 mm long) of aquatic angiosperms such as Podostemaceae. For example, the moss-like leaves of *Tristicha* and allies lack vascular tissue completely (Rutishauser 1995). Thus, there are good reasons for doubt about their leaf identity: where is the borderline between scale-like hairs (trichomes) and rudimentary leaves?

Stipule identity crisis: stipule–leaf indistinction

Typical stipules are two lateral appendages of the leaf base. Leaf blade and stipules usually arise from a common primordial bulge at the shoot apex. Stipules occur in many dicot families (e.g. Fabaceae, Rosaceae) whereas they are absent in most monocots. Charlton (1991) found in *Azara microphylla* (Flacourtiaceae) a homeotic replacement of the stipule by a leaf. The same phenomenon is observable in pea (*Pisum sativum*) mutants such as *cochleata* (Yaxley *et al.* 2001). There are tendrils forming the blades as well as tendrils arising from stipular positions, a situation not known from any wild-type member of Fabaceae (Marx 1987, Hofer *et al.* 2001). In the *afila* (*af*) mutant all primary pinnae are replaced by a bunch of tendrils, whereas the stipules are not altered. A gene known to interact with the *af* gene is *sinuate leaf* (*sil*), which results in undulating margins of both leaflets and stipules. When combined with *af*, *sil* plants have adventitious tendrils arising from clefts in the distal portion of the stipule (Figure 11.4A, B; Marx 1987). Thus, pertinent characters of the leaf blade can be ectopically expressed in stipular sites. Or, as said by Yaxley *et al.* (2001), these

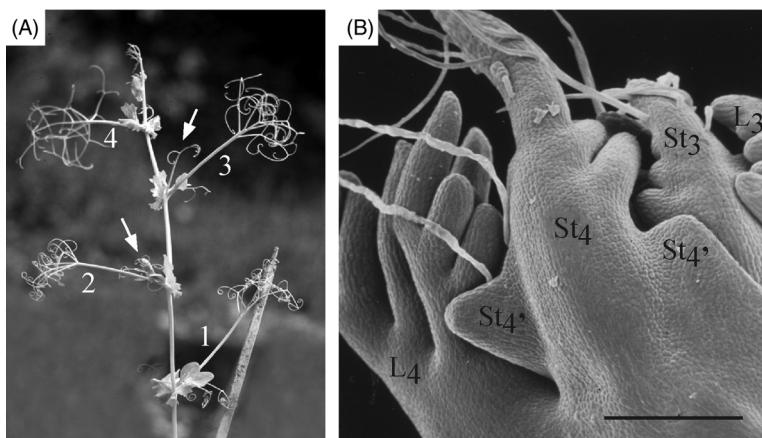


Figure 11.4 *Pisum sativum* (Fabaceae) ‘afila’/‘sinuate leaf’ (af/sil) double mutant, cultivated at the Botanical Garden Zürich from seeds received from G. A. Marx B777-188-(4) (fixed 3.10.1985). Stipules are changed into a more compound leaf-like identity. A, climbing shoot with compound leaves (1–4), each one associated with two leafy stipules. All leaflets of the blade are replaced by a bunch of tendrils (as typical for the af mutant). Moreover, af/sil plants have adventitious tendrils (arrows) arising from a cleft in the distal portion of each stipule. B, growing shoot tip of af/sil plant, showing two young leaves (including stipules). The blade of leaf 4 (L4) consists of primordial tendrils. The associated stipule (St4) gives rise to an upper portion again forming tendrils and two lateral stipular lobes (St4'). Scale bar = 200 µm.

mutants ‘change stipules into a more “compound leaf-like” identity’. More examples of ectopic expression of leaf identity in stipular position are mentioned in Rutishauser and Sattler (1986), and Rutishauser (1999). Stipules in flowering plants are, by definition, restricted to the leaf base. However, a few mutants in *Arabidopsis* and pea are known to have supernumerary stipules which are ectopically expressed as part of the leaf blade or rachis (Tattersall *et al.* 2005). The so-called stipels at the base of the lateral leaflets in the compound leaves of the garden bean (*Phaseolus vulgaris*) may be understood as ectopically expressed supernumerary stipules (Arber 1950, Rutishauser and Isler 2001).

Stem identity crisis

Stems are the carriers of leaves and flowers in seed plants. Stems and roots are usually cylindrical and provided with apical meristems

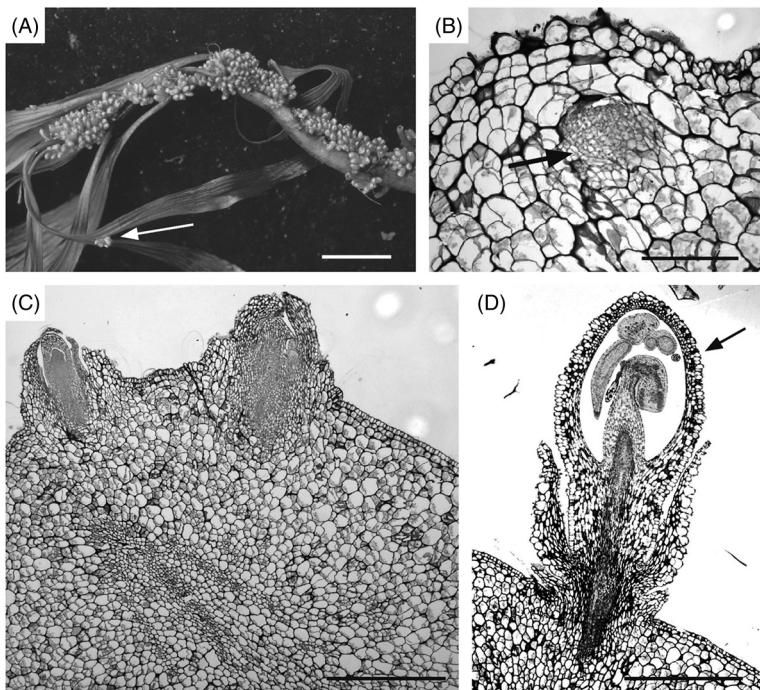


Figure 11.5 Endogenous flower formation along leafy stems of *Ledermaniella letouzeyi* (Podostemaceae = river-weeds). Do they suffer from an identity crisis? A, Elongate flowering shoot with forked leaves and many flower buds arising along the stem. Arrow points to epiphyllous flowers in cleft of forked leaf blade. Scale bar = 2 cm. B, 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). Scale bar = 200 μm . C–D, Later developmental stages with endogenous flower buds penetrating the stem periphery. Each flower is protected by a sac-like cover = spathella (arrow), as typical for most Podostemaceae. Scale bars = 1 mm.

whereas typical leaves are dorsiventrally flattened and lacking an apical meristem. Stems and leaves result from the production of a chain of phytomers as reiterative units, each unit consisting of the node with the leaf attached, its axillary bud (if present) and a stem unit (internode) (Sylvester *et al.* 1996, Jaramillo and Kramer 2007). Thus, a stem may be understood as a composite structure (i. e. having ‘compound identity’), consisting of the basal portions of the phytomers as developmental units. Stems and roots are usually distinguished by the position of outgrowing lateral shoots. In stems, lateral shoots (twigs) arise from

exogenous buds along the stems, subtended by a leaf or bract in seed-plants. Endogenous shoot buds (without a subtending leaf) usually arise from roots and not from stems. There are, however, examples of endogenous flower bud origin along the stems in African Podostemaceae such as *Ledermannia letouzeyi* (Figure 11.5A–D). Most flowers are initiated inside the stem cortex (owing to dedifferentiation) and penetrate the stem periphery prior to anthesis. This is a peculiar solution to increase flower numbers along stems *ad infinitum*. The flowers in these aquatic angiosperms can be viewed as developmental modules (i.e. quasi-autonomous parts, QAPs) induced out of their natural context. They develop all their defining features in locations of the body where they usually do not occur, demonstrating that development of the QAPs is locally controlled (Wagner in Bock and Cardew 1999, Rutishauser and Moline 2005). Thus, *Ledermannia letouzeyi* and other African podostemads have a natural capacity to regenerate flowers from the adult stem cortex (see Xu *et al.* 2006).

Root identity crisis: root–shoot indistinction

Typical roots of vascular plants are non-photosynthetic, endogenously branching organs with an apical meristem protected by a cap. Developmental geneticists have pointed out that there are vascular plants that do not always show a clear differentiation into root and shoot. They have also stressed the fact that roots and shoots may have important regulatory mechanisms (including CLAVATA signalling pathways) in common (Scheres *et al.* 1996, Byrne *et al.* 2003, Birnbaum and Benfey 2004, Friedman *et al.* 2004, Stahl and Simon 2005). Lacking a better term for ‘relevant organogenetic properties’, Barlow *et al.* (2001) have spoken of properties of ‘rootiness’ guiding an uncommitted primordium towards the ‘root’ developmental pathway whereas properties of ‘shootiness’ are needed for the primordial commitment towards ‘shoot’ (i.e. leafy stem) development.

Root–shoot indistinction is consistent with the phylogenetic hypothesis that in vascular plants the root evolved from an ancestral shoot (Raven and Edwards 2001, Schneider *et al.* 2002). Thus, it becomes understandable that various flowering plants such as the river-weeds may suffer from a root identity crisis (Figure 11.6A–G; Rutishauser and Moline 2005). The Podostemaceae are peculiar angiosperms confined to tropical waterfalls and river-rapids. Their ‘roots’ (or what are usually called ‘roots’) are fixed to submerged rocks mainly with adhesive hairs (Figure 11.6A). Most podostemaceous roots are

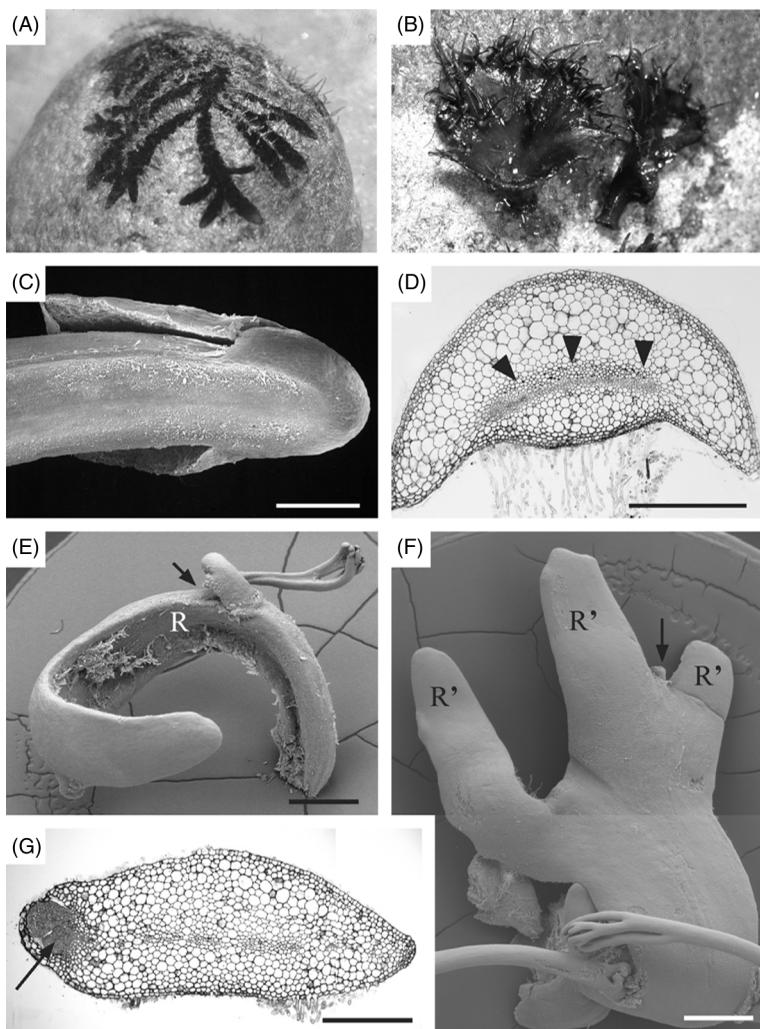


Figure 11.6 Podostemaceae (river-weeds) as flowering plants adapted to tropical waterfalls. Their roots are green, flattened and fixed to the rock. These roots are used to having an identity crisis. A–B, *Griffithella hookeriana* (S India) with root polymorphism: Roots are 1 cm broad ribbons and completely attached to the rock, or they are 2 cm high cups and fixed to the rock with a foot only. Needle-like leaves arise from endogenous buds along the root margins. C–D, *Thelethlyax minutiflora* (Madagascar) with ribbon-like root. C, Root tip with asymmetrical cap, seen from below. D, Dorsiventral cross-section of ribbon-like root with concave lower side (fixed to the rock) and convex upper side. Arrow-heads point to lens-shaped vascular tissue replacing the central cylinder of typical roots.

(Cont.)

dorsiventrally flattened, forming ribbons or even broad crusts resembling foliose lichens. They are green and photosynthetic. They contain a lens-shaped vascular complex (Figure 11.6D) or a planar network of inconspicuous vascular bundles (Figure 11.6G). In various Podostemaceae the roots are provided with an asymmetrical cap (Figure 11.6C). The ribbon-like roots of other podostemads even lack such a cap and branch exogenously into daughter roots (Figures 11.6E, 11.6F). In the South Indian *Griffithella*, for example, the roots are highly polymorphic; there are either broad ribbons (Figure 11.6A) or cup-like structures with an anchoring foot (Figure 11.6B). Arber (1950: 134) came to the conclusion: ‘The urge toward whole-shoot characters, which we have recognised in the leaf, may be detected, though less frequently, in the root. The root-thallus of the podostemads sometimes shows remarkably shoot-like features . . .’. This ambiguity of root organisation may explain why there are botanists who avoid the term ‘root’ for the flattened structures in Podostemaceae, using instead more neutral terms such as ‘thallus’ or even seemingly contradictory terms such as flattened ‘stem’ (Ota *et al.* 2001, Sehgal *et al.* 2002, Koi and Kato 2003).

Difficulties in distinguishing ‘root identity’ and ‘shoot identity’ (leafy stolons) are also known from Lentibulariaceae such as bladderworts (*Utricularia*) and butterworts (*Pinguicula*). Usually it is said that *Pinguicula* has roots and the sister genus *Utricularia* lacks them. However, *Utricularia* stolons may have arisen from what are called ‘roots’ in *Pinguicula* just by adding exogenous leaves to the root surface, as proposed by Rutishauser and Isler (2001). This would explain the high degree of similarity of the stolons (stems) of various bladderworts with the roots of some butterworts: lack of calyptra (root-cap), positive geotropic growth and ‘awkward’ phyllotaxis patterns found in bladderwort stolons, e.g. orthomonostichy with all leaves arranged along a single stem sector. Genes homologous to WUSCHEL in *Arabidopsis* may be involved in the ectopic induction of leaf development when *Pinguicula* ‘roots’ turn into *Utricularia* ‘stolons’ (see Gallois *et al.* 2004).

Caption for Figure 11.6 (Cont.) Scale bars = 250 µm and 500 µm, respectively. E–G, *Stonesia ghoguei* (Cameroon) with narrow to broad ribbons, lacking root caps. Roots (R) branch exogenously giving rise to daughter roots (R'). Arrows point to shootlets arising from endogenous buds along the root margin. Vascular root tissue (as shown in cross-section) is divided up into a planar network. Scale bars = 1 mm (E, F) and 300 µm (G).

CONCLUDING REMARKS

An organ or structure is called heterotopic when it develops in an unusual position within the body plan. Concepts such as 'heterotopy', 'homeosis', 'homocracy' and 'ectopic expression of organ identity' coincide with the concept of 'quasi-autonomous parts' which can be induced out of their natural context (Sattler 1994, Shubin *et al.* 1997, Wagner in Bock and Cardew 1999, Baum and Donoghue 2002, Svensson 2004, Rutishauser and Moline 2005, Jaramillo and Kramer 2007). All these concepts describe the transformation of parts into structures normally found elsewhere according to the body plan. Developmental geneticists are invited to study some of the abovementioned plants in order to explain the decanalisation (relaxation) of their body plans as compared with typical vascular plants. Which key regulatory genes (including homeotic genes such as KNOX and MADS-box genes) are involved in the identity crises of these plants?

Vergara-Silva (2003: 260) gave a preliminary explanation for the frequently occurring identity crises of meristems and organs in vascular plants: '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.'

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