Developmental Genetics and Morphological Evolution of Flowering Plants, Especially Bladderworts (*Utricularia*): Fuzzy Arberian Morphology Complements Classical Morphology

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This review compares new developmental models on flowering and other vascular plants with evolutionary hypotheses formulated by Agnes Arber (1879–1960) and like-minded botanists. Special emphasis is laid on philosophical basics such as perspectivism, pluralism about evolutionary modelling, continuum way of thinking, and fuzzy logic. Arber's perspective is best labelled as *Fuzzy Arberian Morphology* (FAM Approach). Its proponents ('FAMmers') treat structural categories (e.g. 'roots', 'shoots', 'stems', 'leaves', 'stipules') in vascular plants as concepts with fuzzy borderlines allowing intermediates (including transitional forms, developmental mosaics). The FAM Approach complements *Classical Plant Morphology* (ClaM Approach), which is the traditional approach in botany. ClaM proponents ('ClaMmers') postulate that the structural categories of vascular plants are regarded as concepts with clear-cut borderlines and without intermediates. However, during the evolution of vascular plants, the root-shoot distinction and the stem-leaf distinction have become blurred several times due to developmental changes, resulting in organs with unique combinations of features. This happened, for example, in the bladderworts (*Utricularia*, Lentibulariaceae). When focusing on the 'leaf', the FAM Approach is identical to Arber's 'partial-shoot theory of the leaf' and Sinha's 'leaf shoot continuum model'. A compound leaf can repeat the developmental pathway of the whole shoot, at least to some degree. For example, compound leaves of *Chisocheton* (Meliaceae) with indeterminate apical growth and three-dimensional branching may be seen as developmental mosaics sharing some growth processes with whole shoots! We focus here on the FAM Approach because this perspective is especially promising for developmental geneticists studying flowering and other vascular plants.   © 2001 Annals of Botany Company

Key words: Review, body plan, developmental mosaics, leaf development, history of botany, homeosis, homeotic genes, Lentibulariaceae, morphological evolution, process morphology, stipules, *Utricularia*, flowering plants.

INTRODUCTION

Agnes Arber (1879–1960), a giant in the history of botany (1)

The year 2000 was the 50th anniversary of the publication of Agnes Arber's book, *The natural philosophy of plant form* (1950). This book, and many of her earlier publications, were milestones on the way to a more open and dynamic approach to plant morphology and developmental genetics, summarized in Sattler's (2001) contribution in this issue of *Annals of Botany*. Since Arber's death in 1960, new methods and perspectives have allowed a more dynamic and a more holistic approach to the study of plant form. Nevertheless, some of Arber's hypotheses survived the decades and are still refreshing our minds while we look for new ideas about the evolutionary development of vascular plants. This review covers examples from Agnes Arber's works (published between 1920 and 1957) as well as more recent publications giving credit to Arber's perspective, which is called Fuzzy

Arberian Morphology (= FAM Approach). 'Arberian' refers to Agnes Arber and her way of thinking[1]. A special focus will be on papers published by Gérard Cusset, Rolf Sattler and their colleagues propagating 'continuum morphology', which is closely related to the FAM Approach (e.g. Sattler, 1996). New results in comparative morphology and developmental genetics speak in favour of the heuristic value of the FAM Approach, as will be shown in this review. In her writings, Agnes Arber anticipated various new explanatory models for vascular plant development proposed by molecular geneticists. The fuzzy meaning of structural categories in *Utricularia* and other vascular plants will be discussed, putting emphasis on the heuristic value of Arber's 'partial-shoot theory of the leaf'. Cross-references allow the reader to browse through the 29 sections [labelled 1–29] to get the most out of this paper.

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[1]We use the adjective 'Arberian' similarly to already existing terms such as 'Aristotelian' (according to the philosophical school of Aristotle), 'Darwinian' (in the sense of Charles Darwin and his followers), or 'Victorian' (pertaining to Queen Victoria).

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FIG. 1. A lesson in perspectivism and as-well-as thinking. Street-car in the city of Zürich announcing 'I am also a ship' (see section 3). [Copyright by Zürcher Verkehrsverbund, Zürich, Switzerland.].

'The algorithmic beauty of plants'—Repetition and self-similarity (to some degree) (2)

Branching and repetition of developmental units (cells, meristems, modules) are omnipresent in the plant kingdom. Mathematical algorithms based on fractal geometry and L systems allow branching patterns to be simulated (e.g. Prusinkiewicz and Lindenmayer, 1990). Examples of self-maintenance and auto-reproduction at the cellular and meristem level are provided by Barlow *et al.* (2001). At higher levels, the complex organization of branching in flowering plants can be understood as the repetition of modules. Instead of producing a single flower, an individual floral meristem can branch continuously giving rise to a complex inflorescence with many flowers (Fig. 2: *Nymphaea prolifera*). Developmental geneticists are gaining a better understanding of pattern repetition (reiteration) at different levels of structural complexity. Thus, there are developmental parallels between flower level (as a subsystem) and inflorescence level (as a system). 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 in certain taxa simple flowers and compound 'flowers' (i.e. inflorescences) are quite similar to each other—'a resemblance sometimes carried into the minutest details of form and coloration' (Arber, 1947 p. 233).

Arber was convinced that the principle of repetition is found everywhere in multicellular plants. Focusing on vascular plants, Arber was puzzled by the fact that some steps of the developmental pathway of a whole shoot (i.e. leafy stem) can be repeated within a compound leaf. According to Arber (1950 p.125) 'a typical leaf is a shoot in which the apex is limited in its power of elongation and in its radiality'. Thus, Arber (1941, 1950) proposed the partial-shoot theory of the leaf in vascular plants, based on ideas already formulated in the 19th century (see flowchart of ideas in Fig. 40). This theory was recently discussed under the label 'leaf shoot continuum model' (Sinha, 1999; Hofer *et al.*, 2001). It is consistent with Fuzzy Arberian Morphology (Table 1; see section 21). Compound leaves may repeat in each part what they have already produced as

a developing whole. This can be observed in individuals of *Sambucus nigra* (Fig. 3) and *Phellodendron amurense* (Fig. 4) when some or all first order leaflets (pinnae) repeat the branching pattern of the normally once-pinnate leaf. Arber (1941, 1950) described many examples of vascular plants showing repetition during growth and development. The repeated unit can be totally identical to the one already formed (i.e. complete repetition of a developmental pathway), or the structures formed afterwards may repeat the preceding ones only to some degree (i.e. partial repetition of a developmental pathway) while deviating in other features. Arber's work already implies the holographic paradigm: the whole is built up of the parts in such a way that each part bears something of the whole within it, as stressed 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 (McLellan, 1999).

PHILOSOPHICAL BASICS

Perspectivism and the advertisements in the Zürich public transport system (3)

If you visited Zürich in 2000 and 2001 you would have seen street-cars bearing the message: 'I am also a ship' (Fig. 1). Travelling on Lake Zürich, you may have been puzzled by ships announcing: 'I am also a train'. Riding local trains to the suburbs, you could also have read the notice on the engine: 'I am also a bus'. Not understanding the figurative meaning of these sentences, foreign tourists may have wondered whether the Swiss were crazy. No! They had just learnt a lesson in 'as-well-as thinking'! The metaphorical meaning of these sentences is obvious. As a passenger on the Zürich public transport system you need just a single ticket which is valid for all types of public transport. You can switch between street-cars, buses, trains and ships as long as your ticket is valid. The philosophical background of the Zürich public transport advertisements is known as perspectivism, which coincides with as-well-as thinking. The concepts 'street-car' and 'ship' are overlapping when the same ticket allows the use of either means of transport

in the Zürich area. Under these circumstances, the street-car is able to claim: 'I am a ship as well as a street-car' (Fig. 1).

Although perspectivism is often used in colloquial speech, it is not common in natural science including biology (Hassenstein, 1978; Sattler, 1986). Perspectivism accepts every insight into nature as one perspective (but not the only one) to see and explain biological phenomena. Different perspectives (also called approaches, models) complement each other, rather than compete with each other, although not all of them are meant to be equal approximations to what really occurs in nature. In everyday life we often oscillate between two philosophical perspectives, depending on the circumstances. We may feel very healthy or very sick once in a while, or we may feel just slightly sick. Then we realise that there is no clear borderline between the concepts 'healthy' and 'sick'. Nobody doubts the fuzzy connotations of these terms. Perspectivism was anticipated by Arber (1950, 1954, 1957) and earlier philosophers who stressed the 'coincidence of contraries'. This term describes the somewhat astonishing situation that even biologists are allowed to label phenomena of living organisms (e.g. a 'leaflet' of vascular plants) with seemingly contradictory terms. Arber (1957 p. 70) was aware of the difficulties in explaining perspectivism, postulating that "the expression 'coincidence of contraries'... is (perhaps) best explained by saying that in general it involves getting beyond the Law of Contradiction" (see next section). Perspectivism is closely related to as-if-ism[2], pluralism, conceptual nominalism (Brower, 2000), and Woodger's (1967) map analogy (see section 5).

Either-or philosophy in biology and other natural sciences (4)

In contrast to perspectivism there is the view based on conceptual realism (essentialism) assuming that structural categories are immanent in life, forming crisp or distinct sets, i.e. terms with non-overlapping connotations and without intermediates. This school of thought, common in biology and other natural sciences, coincides with 'either-or thinking' as expressed by Aristotle's Law of Contradiction ('A cannot be both A and not-A'), which is the basis of all ordinary discursive-logical reasoning (Arber, 1957 p. 70; Rutishauser and Sattler, 1985). Either-or thinking is also known as nothing-but thinking[3], according to which the street-car in Zürich is only allowed to admit: 'I am nothing but a street-car'. Similarly, either-or thinking may have led certain botanists to propose that 'the plant is nothing but leaf' (Coen, 1999 p. 57), citing one of Goethe's views. A similar view was also proposed by other botanists with regard to the whole vegetative plant body (apart from the inflorescences) in *Utricularia* (see section 27).

[2]As-if-ism (or shorter asifism): We may use a term as if it referred to a real entity, but we should never confuse such a concept (model, metaphor) with reality (see section 15).

[3]Nothing-but thinking: 'A is nothing but A' is a shorter version of Aristotle's Law of Contradiction: 'A is not both A and not-A'. Dobzhansky *et al.* (1977) and Sattler (1986) have discussed the shortcomings of the 'nothing-but' fallacy in science.

Either-or approaches in biology and other scientific disciplines assume that the perceived structures and processes in nature must always fit into a set of mutually exclusive categories. According to this view intermediates between categories do not exist. This view coincides with the 'Law or Principle of the Excluded Middle', which is another axiom of Aristotelian logic, namely that 'A is either B or not-B' (Arber, 1957 p. 70; Kosko and Isaka, 1993; Williams, 1995). Classical plant morphology of vascular plants is often consistent with either-or thinking, especially when intermediates (i.e. developmental mosaics) are excluded from structural categories such as 'leaf', 'shoot' (i.e. leafy stem) and 'root' (Figs 38, 40, Table 1). Sattler (1986 p. 75) suggested the following: 'May be ... most of the practising biologists are conceptual realists or have a tendency towards this position. Thus, to them entities such as 'genes', 'cells', 'organs', 'organisms', and 'species' are real (i.e. natural kinds)'. Arber (e.g. 1957) was quite aware of the shortcomings of any either-or approach in science.

The supremacy of perspectivism over either-or philosophy in plant morphology (5)

This paper deals with the 'science of plant form', mainly comparative plant morphology. In this domain, many scientists tend to avoid perspectivism. In the following chapters it should become obvious that both philosophical attitudes (the more holistic 'as-well-as philosophy' and the more reductionistic 'either-or philosophy') were and are needed as heuristically valuable perspectives in order to progress in comparative plant morphology and developmental genetics. Awareness, however, is growing among botanists and developmental geneticists that perspectivism in the sense of Woodger's (1967) map analogy may be an option that is heuristically promising: different maps of the same terrain such as 'vascular plants' complement each other, each presenting a different aspect of reality. No single map can represent all aspects of a region (Sattler, 1986 p. 76; Brower, 2000). Perspectivists studying vascular plants accept structural categories such as 'leaf' and 'stem' as mind-born, simplified, concepts reflecting certain aspects of the structural diversity (Rutishauser and Sattler, 1985, 1986, 1989; Sattler and Rutishauser, 1990; Hay and Mabberley, 1994). Close to perspectivism is fuzzy logic, in which concepts such as 'leaf' and 'stem' are accepted with partially overlapping connotations and fuzzy borderlines. If a compound leaf (Fig. 4) could speak, it might say: 'I am a shoot as well as a leaf'. Again, a 'leaflet' or a 'stipule' might say: 'I am *equivalent* to the whole leaf to which I belong as well as a *part* of it' (Fig. 37). This seemingly paradoxical view was called 'identity-in-parallel' by Arber (1950 p. 143). These statements summarize what Arber had in mind with her partial-shoot theory of the leaf (see sections 21–23; also Hofer *et al.*, 2001; Kirchoff, 2001).

The following quote from the molecular geneticists Scheres *et al.* (1996) may serve as a philosophical starting point of developmental biological work: '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'. Similarly, systematists such as Gift and Stevens (1997) stressed the importance of 'taxonomic psychology' stating that 'the relationship among characters, their subdivision into states, and the world as we see it is the central point. We make many silent assumptions about what is significant or not as we delimit states from the welter of individual observations we obtain, and so those states may not relate in a direct or simple way to the organisms we study'. The metaphorical meaning of scientific concepts in comparative morphology and developmental genetics of plants will be discussed in sections 15 and 16.

COMPARATIVE PLANT MORPHOLOGY AS A BIOLOGICAL DISCIPLINE

Botany began with comparative plant morphology (6)

Agnes Arber was an enthusiastic historian of botany, in contrast to many of her contemporaries. Already the young Agnes Arber (1925 p. 223) regretted that 'little heed seems to be paid to the degree to which the very nature of man's mind directs his thought along roads which his predecessors have travelled in the past, and which his posteriority will tread again and again' (e.g. Fig. 40, Table 1). When, in this review, we focus on a phenomenological approach to form
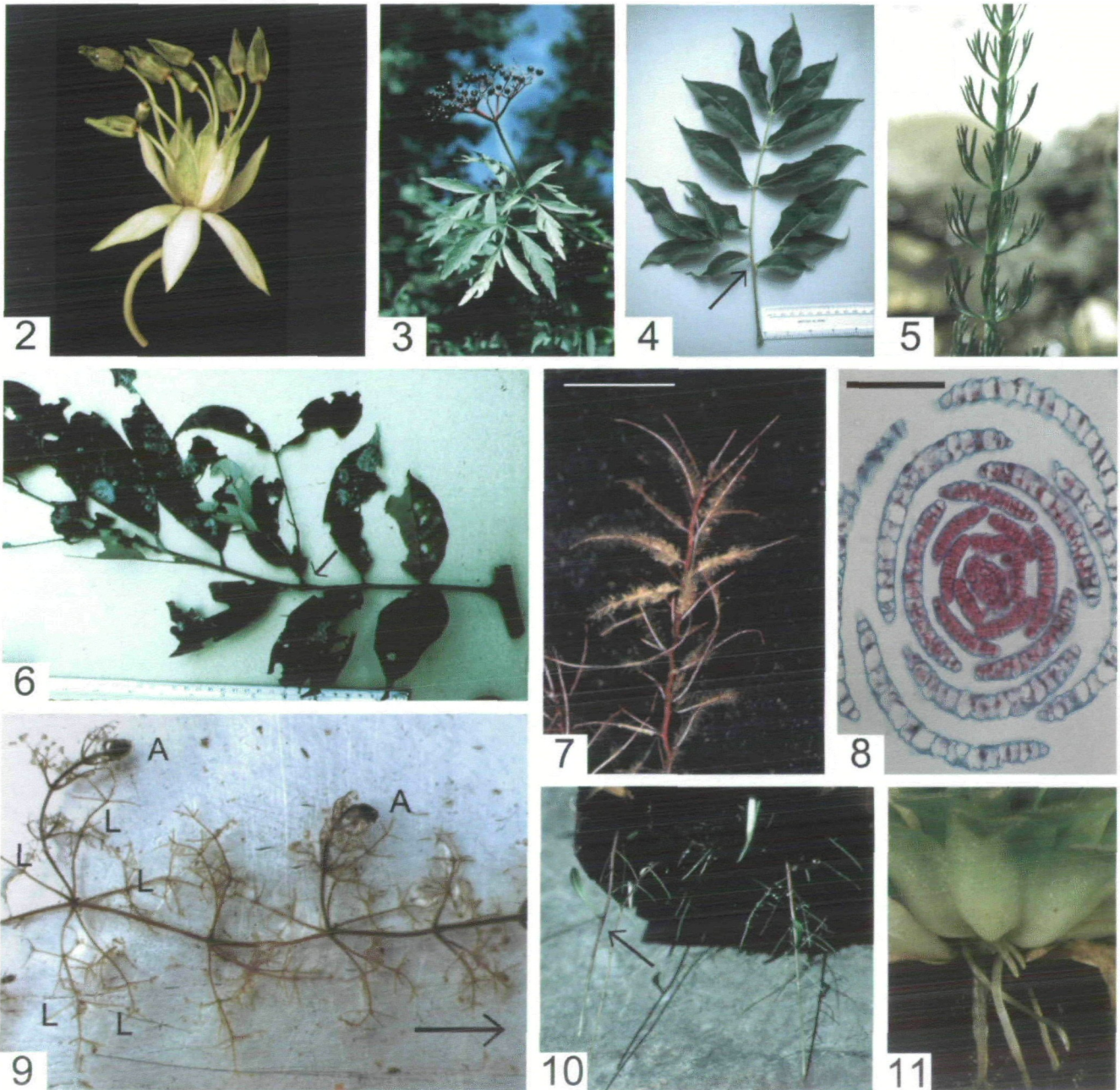
Figs 2–11. Caption over page.

and development in biology (i.e. an approach not analysing gene activities), we use the term 'comparative morphology'. Comparative plant morphology describes the shape of developing plants in space and time. It has a long tradition, presumably going back to the Greek Theophrastus (born 370 BC). Comparative plant morphology was revived by Johann Wolfgang Goethe and his contemporaries such as J. Jung, I. Kant and L. Oken (see Arber, 1946; Heusser, 2000). Traditional text-books on comparative morphology of land plants (mainly vascular plants) fill thousands of pages and are still worth studying (e.g. Hofmeister, 1868; Sachs, 1875; Goebel, 1928–1933; Troll, 1937–41; Kaplan, 1998). Comparative plant morphology and anatomy are the foundation for solving many taxonomic, developmental and evolutionary problems (Sattler and Rutishauser, 1997; Stevens, 2000). New disciplines such as molecular systematics and developmental genetics also depend on the findings of comparative morphological analyses in order to better understand body plans (bauplans, blueprints) and biological pattern formation. Thus, an exact description of all morphological and morphogenetic phenomena is a basic prerequisite for molecular genetics.

Homology in comparative morphology and phylogenetic analysis (7)

'Homology is the soul of phylogenetic analysis. Assessing homology is what morphologists and systematists spend much of their time on' (Qiu and Palmer, 1999). 'Characters are considered to be homologous if they are derived from a common ancestor' (Reiser et al., 2000). These two statements by molecular systematists and developmental geneticists point to the very heart of comparative plant morphology because 'all hypotheses of homology rely on observed morphological similarities' (Weston, 2000). However, do we really know exactly what we mean when we say that two objects are homologous or non-homologous? The term 'homology' has various definitions and different meanings in morphology and non-molecular systematics (Arber, 1937; Wardlaw, 1965; Donoghue, 1992; Hall, 1994; Sattler, 1994; Albert et al., 1998; Stevens, 2000; see also Table 1, and section 13). Any comparative morphological analysis—with the exception of process morphology (see section 24)—is mainly a search for body plans (bauplans) with the help of certain homology criteria. Three criteria are used traditionally (Eckardt, 1964): (1) Position criterion = homotopy: homologous organs often arise in similar or identical positions in organisms with modular 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. (2) Special qualities: homologous organs often have identical or similar functions, as well as identical or similar parts. (3) Continuum criterion: although they may look different, organs may be accepted as homologous when intermediate or transitional forms are observable. Arber (1950 p. 55) summarized the history of this idea using floral appendages as an example: '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. Possibly the word *transition* [her italics] is out of place, and we are dealing, actually, with a *mixture* [again her italics] of characters in varying proportions'.

Comparative plant morphologists tend to belong to two seemingly opposing morphological schools (8)

In structural botany there are two main ways to perceive and conceive of vascular plants using structural categories and developmental processes (Figs 38–40, Table 1, see sections 9 and 10). Both schools have their own long tradition and both have some roots in the morphological writings of Goethe (1790; see Arber's 1946 translation).

FIGS 2–11. Organs and/or sub-organs with fuzzy identity in various flowering plants. Fig. 2. *Nymphaea prolifera* Wiersema (Nymphaeaceae). Mother flower with internal daughter flowers. The reversion of floral meristem identity back to inflorescence meristem identity is constitutional in this species. Instead of fertile flowers, only sterile tuberous flowers are formed; they act as vegetative propagules. [Photograph taken by R. Rutishauser; Pantanos de Centla, Tabasco, Mexico.] Fig. 3. *Sambucus nigra* L. (Caprifoliaceae). Infrutescence and double-pinnate leaf. This twig belongs to a mutant with double-pinnate instead of once-pinnate leaves. [Photograph taken by R. Bolli; E Switzerland.] Fig. 4. *Phellodendron amurense* Rupr. (Rutaceae). Compound leaf of mutant phenotype showing double pinnation instead of normal once-pinnate leaves. Arrow points to lowermost first-order leaflets along rachis with branched lateral pinnae that arise from the 'pseudo-axils' of the first-order leaflets. [Photograph taken by D. Suter; Botanic Garden Edinburgh, Scotland.] Fig. 5. *Carum verticillatum* (L.) Koch (Apiaceae). Portion of upright leaf (total length 20 cm) above water level. The pinnae along the main rachis are arranged as if they were verticillate leaves along a stem. This is due to transversal orientation of the subdivisions of paired first-order pinnae. [Photograph taken by R.Rutishauser; Extremadura near Caceres, SW Spain.] Fig. 6. *Chisocheton tenuis* Stevens (Meliaceae). Basal portion of mature once-pinnate leaf arising from the stem (on the right). Arrow points to an epiphyllous shoot arising from the rachis of the leaf. [Photograph taken by J.B. Fisher; Eastern Highlands District, Papua New Guinea.] Figs 7 and 8. *Indotristicha ramosissima* (Wight) Royen (Podostemaceae—Tristichoideae). Fig. 7. First-order shoot with reddish floating stem and feather-like photosynthetic appendages (ramuli). Each ramulus (total length 2–3 cm) with reddish to bright brown scales (some of which have already dropped). Fig. 8. Cross-section of young ramulus tip, with scales (one cell thick) scattered around the apical meristem. Scale bars = 2 cm and 100 μm, respectively. [Photographs taken by R. Rutishauser; river Netravati near Belthangadi, Karnataka, S India.] Fig. 9. *Utricularia purpurea* Walter (Lentibulariaceae). Central portion (length 7·5 cm) of floating water-shoot with superposed, pentamerous leaf (L) whorls. Every second whorl with extra-axillary daughter shoot (A) along upper (dorsal) stolon sector. Arrow points towards the distal end of the water-shoot. Note whorled arrangement of the pinnae (leaf segments) repeating the whorled phyllotaxy of the whole shoot. [Photograph taken by R. Rutishauser; Lac de Lucerne, Québec, Canada.] Fig. 10. *Utricularia longifolia* Gardner (Lentibulariaceae). Cultivated in hanging pot, seen from below. Root-like stolons break through the bottom of the pot and show positive geotropism. The stolons are branched exogenously and are provided with a few entire leaves (arrow). [Photograph taken by R. Rutishauser; Botanical Garden of Zürich, Switzerland.] Fig. 11. *Pinguicula moranensis* H.B.K. (Lentibulariaceae). Close-up of rosette with leaves and unbranched cap-less roots arising from the abaxial leaf bases. [Photograph taken by R. Rutishauser; Botanical Garden of Zürich, Switzerland.]

Goethe's typological-hierarchical view was continued as Classical Plant Morphology (ClaM Approach) for example by Troll (1937–41) and some of his students. Goethe's holographic view was taken over as Fuzzy Arberian Morphology (FAM Approach) by Arber (1941, 1950), Cusset (1986, 1994), Sattler (1996, 2001) and their school

(see review by Weston, 2000). The ClaM Approach mainly depends on conceptual realism and either-or thinking whereas the FAM Approach is mainly based on perspectivism and continuum thinking (Figs 38 and 39, see sections 4 and 5). Here we have to bear in mind that neither morphological school excludes the other. They
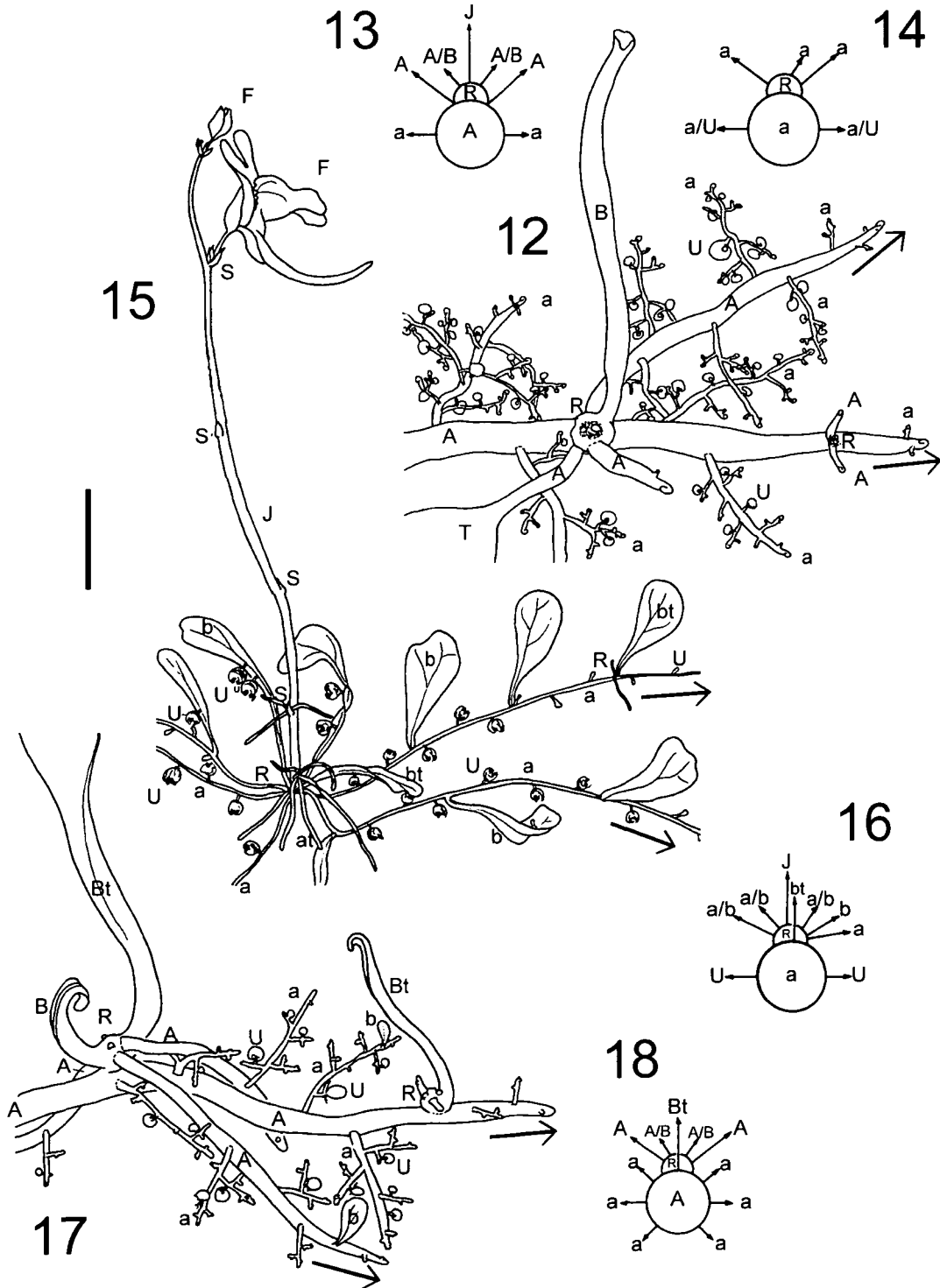
FIGS 12–18. Caption over page.

should be understood as complementary perspectives (each one with its own predictive power). A scheme intended to present the history of both the ClaM and FAM Approach shows who is standing on whose shoulders (Fig. 40). For example, Agnes Arber (1879–1960) as the first female giant in the history of botany stands on the shoulders of Wilhelm Hofmeister (1827–1877) who was recognized as 'one of the true giants in the history of biology' by Kaplan and Cooke (1996).

Classical Morphology (ClaM Approach) of vascular plants (9)

There is a long tradition of the use of crisp structural categories for the description of body plans and their dynamics in plants and animals. According to the ClaM Approach, the body of vascular plants is accepted as consisting of three main organ types, i.e. 'root', 'stem' and 'leaf'. These three organ types are seen as non-homologous to each other, i.e. overlaps between these structural categories are excluded in the framework of the ClaM
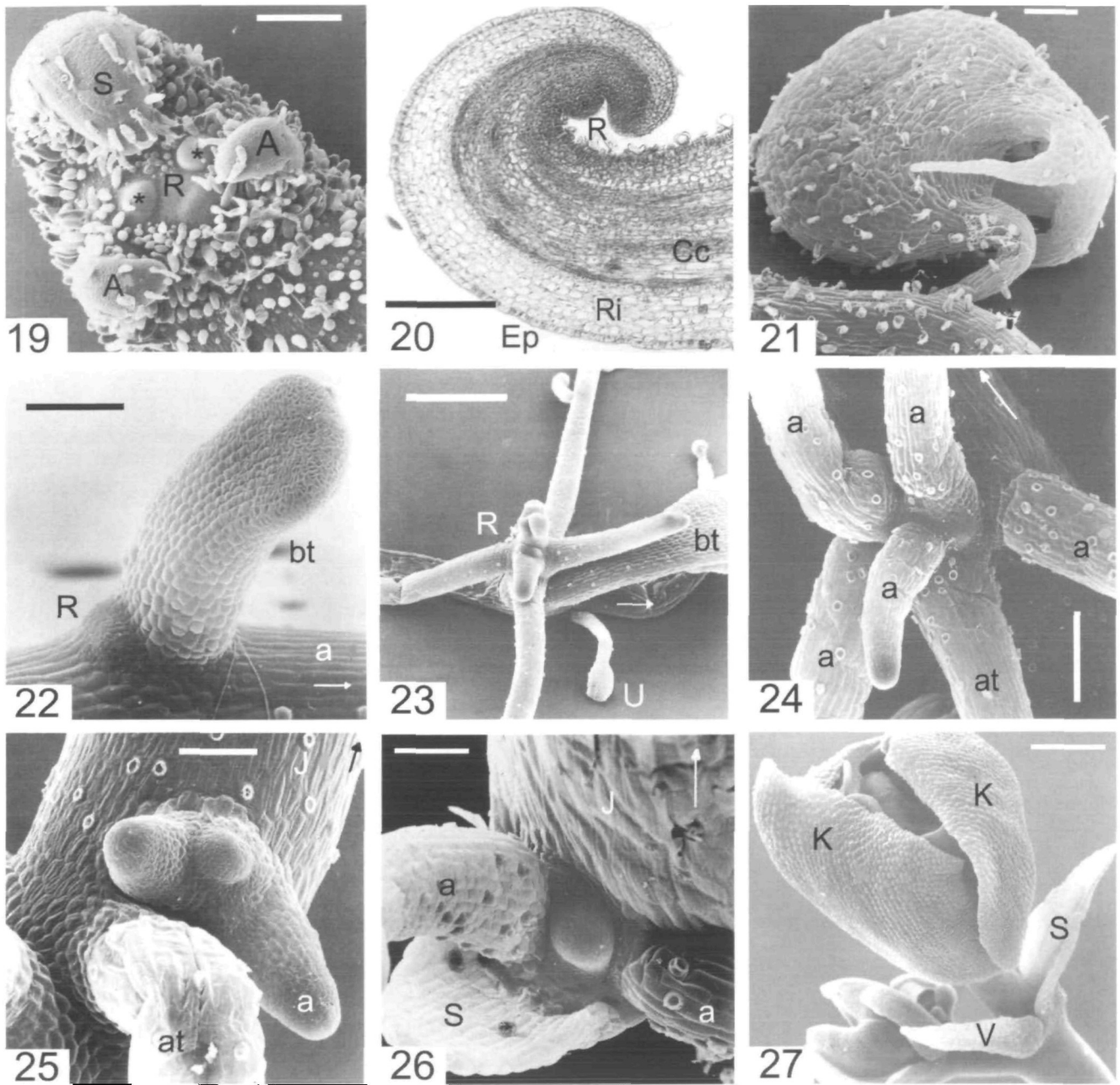
Approach (e.g. Troll, 1937–41; Troll and Dietz, 1954; Kaplan, 1998). Especially for a clear leaf-stem distinction, the position criterion is taken as the only useful criterion by many proponents of the ClaM Approach. Dismembering a vascular plant into discrete structural categories or units (i.e. 'roots', 'stems' and 'leaves') in this way is also known as the classical root shoot model (CRS model) or the 'classical model' for short (Figs 38, 40, Table 1). This model is useful as a perspective, or rule of thumb, because it is quite easy to handle with our discursive-logical way of thinking (Arber, 1957; Rutishauser and Sattler, 1985; Sattler, 1986; Rutishauser and Huber, 1991). The ClaM Approach is also called the hierarchical view because 'parts compose the whole, but the latter is not within the parts' (Sattler, 2001). The ClaM Approach was often taken for granted, especially during the first half of the 20th century. This explains why Arber (1954 p. 81), as the proponent of the alternative FAM Approach, complained: 'The leaf was a concept which one could not, as it were, get behind. When, however, the ban was lifted, and the leaf lost the privileged position accorded to it as an organ *sui generis*, the way was open towards interpreting it'. ClaM proponents do not have problems accepting developmental mosaics (intermediates, transitional forms) between various structural categories (sub-types) as long as they belong to the same organ type. For example, developmental mosaics between petals and stamens are acceptable as long as both kinds of floral appendages are taken as metamorphosed leaves or phyllomes (Goethe, 1790; Arber, 1950; Albert et al., 1998; see section 7: continuum criterion). Various developmental geneticists are aware of shortcomings of the ClaM Approach. For example, Tsukaya (1995), Jackson (1996), Sinha (1999) and Hofer et al. (2001) have pointed to the fact that some vascular plants transcend the ClaM Approach. Thus, the FAM Approach may be a heuristically valuable alternative for broad-minded developmental geneticists (see next section; also Figs 38–40, Table 1).

Fuzzy Arberian Morphology[4] (FAM Approach) of vascular plants (10)

There is an alternative morphological school which is based on perspectivism (see section 5). Honouring Agnes Arber, we call this complementary perspective 'Fuzzy Arberian Morphology' (= FAM Approach). Arber (1946) was aware that this type of thinking can be traced back to Charles Gaudichaud (1841), Casimir deCandolle (1868) and Julius Sachs (1875), and even further back to Johann Wolfgang Goethe (1790) and some of his contemporaries (Fig. 40; see Cusset, 1994; Webster and Goodwin, 1996; Heusser, 2000). Like Arber (1941, 1950), 'Goethe thought that subdivided leaves represent a striving to become nearer complete in the sense that each leaf tried to become a shoot'

FIGS 12–18. Portions of mature plants of three *Utricularia* spp. (bladderworts, Lentibulariaceae). [Plants grown in the Botanical Garden of Zürich; drawings by J. Brugger.] Figs 12–14. *Utricularia alpina* Jacq.: epiphytic species from Venezuela. Fig. 12, Portion of vegetative plant body. Arrows indicate the growth direction of the coiled tips of thick stolons (A). The extra-axillary rosettes (R) arise from the dorsal sector of thick stolons and consist of thick daughter stolons (A) and leaves (B) with coiled tips. Branched thin stolons (a) are inserted along the flanks of the thick stolons (A). Figs 13 and 14, Schematical cross-section of thick stolon (A) and thin stolon (a), respectively, showing outgrowths along dorsal (upper) sector different from those along stolon flanks. Figs 15 and 16. *Utricularia sandersonii* Oliver: terrestrial species from South Africa. Fig. 15. Portion of plant body with vegetative structures and inflorescence; for abbreviations see above. Arrows point towards the tips of thread-like stolons (a). All leaves are inserted in a single row (monostichy) along the upper stolon sector. There is one leaf (bt) that serves as a subtending leaf per rosette, with bt more distal than the axillary rosette (i.e. inverse axillary branching). The rosettes (R) consist of stolons (a) and leaves (b) and finally terminate with an inflorescence (J). Traps (U) arise from the stolon flanks (a) and from the lower side of some leaves. Fig. 16. Schematic cross-section of a stolon (a) with dorsal rosette (R) continuing into inflorescence (J). Figs 17 and 18. *Utricularia longifolia* Gardner: terrestrial or lithophytic species from Brazil. Fig. 17. Portion of vegetative plant body. Arrows point to straight tips of thick stolons (A). The rosettes (R) arising from the dorsal sectors of thick stolons consist of thick stolons (A) and leaves (B), the latter with coiled tips. Along the flanks of a main stolon (A) there are branched thin stolons (a). Fig. 18. Schematic cross-section of thick stolon (A), showing outgrowths along dorsal (upper) sector different from those along stolon flanks. There is one leaf (Bt) that serves as a subtending leaf per rosette, with the subtending leaf more distal than the axillary rosette (inverse axillary branching). *Utricularia alpina* and *U. longifolia* have two sizes of stolons (A, a) and two sizes of leaves (B, b). *U. sandersonii* has only thin stolons (a) and small leaves (b). Note that stolons (A or a) and leaves (B or b) occupy equivalent sites within the rosette (R). A, Thick stolon (diameter more than 1 mm); a, Thin stolon (diameter 1 mm or less); at, subtending stolon (replacing subtending leaf); A/B or a/b, sites in rosettes which can be occupied by a stolon or a leaf; B, big leaf (often more than 5 cm); b, small leaf (less than 3 cm); Bt and bt, big and small subtending leaves, respectively (with inverse axillary branching); F, flower; J, inflorescence; R, rosette (short shoot); S, bract; T, stolon tuber; U, trap (bladder, utricule). Bars = 5 mm (Figs 12, 15 and 17).

[4]Fuzzy Arberian morphology is related but not identical to Sattler's (1992, 1994) 'process morphology'. Be aware that other botanists (e.g. Weston, 2000) take these models as synonymous. According to our understanding, Fuzzy Arberian Morphology retains structural categories (e.g. 'leaf') for the description and interpretation of the plant body whereas 'process morphology' replaces them by combinations of developmental processes (see section 24 and Table 1).

FIGS 19–27. Developmental morphology of two *Utricularia* spp.: epiphytic *U. alpina* from Venezuela (Figs 19–21) and terrestrial *U. sandersonii* from South Africa (Figs 22–27). [Plants grown in the Botanical Garden of Zürich; all figures except for Figs 20 and 21 reproduced from Brugger and Rutishauser, 1989. Fig. 19. *Utricularia alpina* Jacq. Scanning electron micrograph (SEM) of distal portion of thick stolon with coiled tip (S), seen from dorsal (upper) side. The first outgrowths of a rosette (R) are observable, consisting of two opposite daughter stolons (A) and a central portion with primordial bumps (*) whose 'organ identity' is not yet determined. Note the abundant hairs. Bar = 150 μm. Fig. 20. Longitudinal section of thick stolon with coiled meristematic tip (apical meristem) and young rosette (R, similar to Fig. 19) along convex (= dorsal) stolon sector. Central cylinder (Cc) of prospective vascular tissue, surrounded by differentiating parenchymatous cortex (Ri) and epidermis (Ep). Bar = 150 μm. Fig. 21. Mature stalked trap, arising from capillary stolon branch, with two unbranched antennae covering the lateral areas of the basal mouth. Bar = 100 μm. Fig. 22. *Utricularia sandersonii* Oliver. Young leaf (bt) subtending rosette bud (R) in proximal ('wrong') axil. Arrow points towards distal end of mother stolon (a) that carries both leaf and axillary bud along dorsal sector. Bar = 100 μm. Fig. 23. Later developmental stage of rosette (R) arising from proximal ('wrong') axil of subtending leaf (bt). Arrow points towards distal end of mother stolon. Most outgrowths of this rosette develop into daughter stolons. Note stalked trap (U) arising from lateral sector of mother stolon. Bar = 500 μm. Fig. 24. Additional rosette at base of inflorescence stalk, arising from distal ('right') axil of subtending stolon (at). Arrow points towards inflorescence tip. Rosette consists of five additional stolons (a), the youngest (with meristematic tip observable) arising from the rosette centre. Bar = 150 μm. Fig. 25. A young rosette stage at base of inflorescence stalk, arising from distal ('right') axil of subtending stolon (at). Arrow points towards inflorescence tip. Largest rosette outgrowth (a) probably acquiring stolon identity. Bar = 100 μm. Fig. 26. Subtending bract (S) with stolons (a) arising from distal ('right') axil along inflorescence stalk (J). Arrow points towards inflorescence tip. Bar = 100 μm. Fig. 27. Young inflorescence (raceme) with large flower bud in the axil of subtending scale (S). Note prophyll (V) at the base of flower stalk. Younger flower bud observable on lower left. K, sepals. Bar = 150 μm.
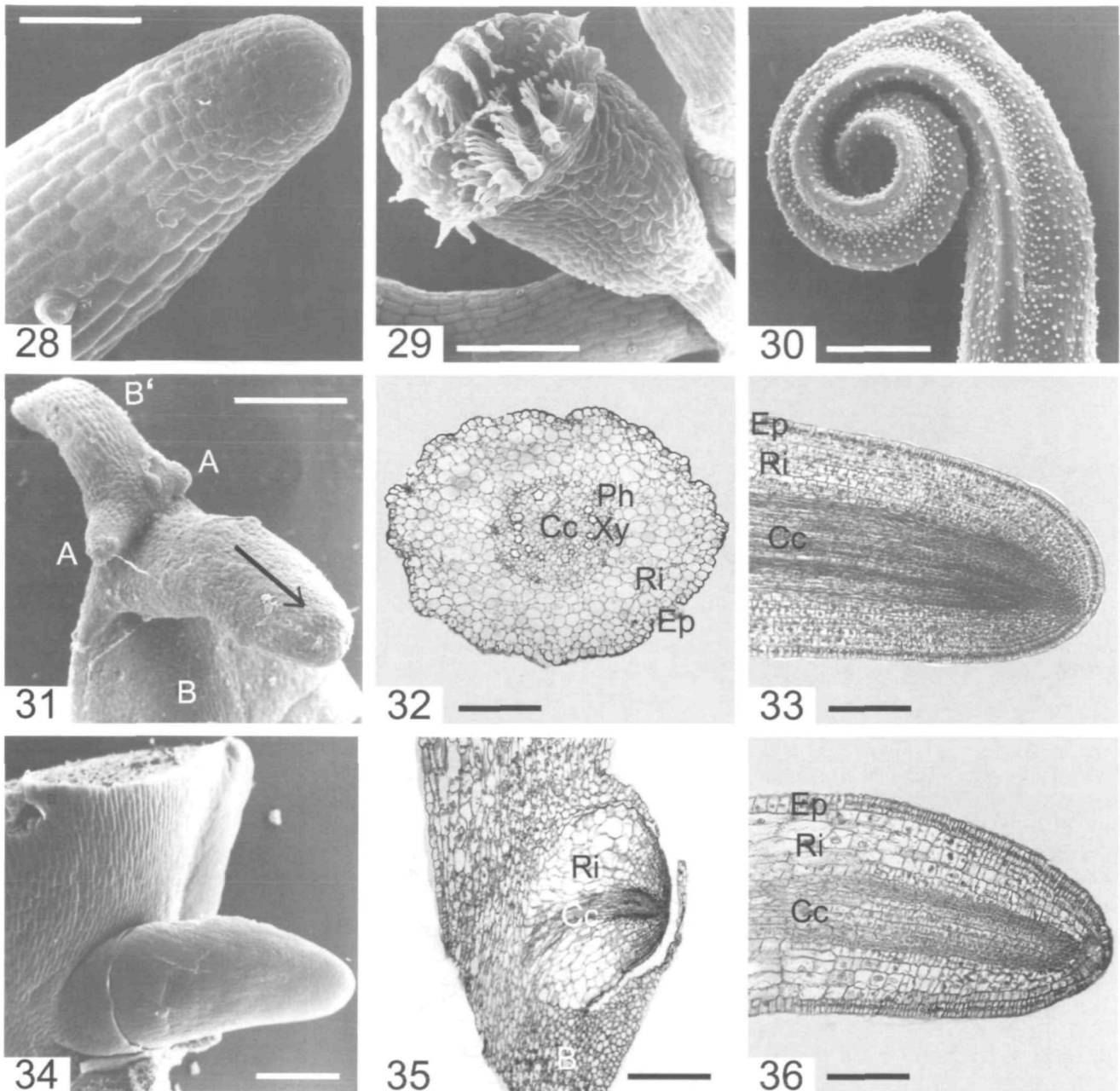
FIGS 28–36. Developmental morphology of two *Utricularia* spp.: terrestrial *U. livida* from South Africa (Figs 28 and 29); terrestrial or lithophytic *U. longifolia* from Brazil (Figs 30–33); as compared to *Pinguicula moranensis* from Mexico (Figs 34–36). [Plants grown in the Botanical Garden of Zürich; Figs 31 and 34 reproduced from Brugger and Rutishauser, 1989.] Fig. 28. *Utricularia livida* E. Meyer. Straight stolon tip. Bar = 40 μm. Fig. 29. Mature stalked trap, terminal mouth with radiating, comb-like rows of stipitate glands. Bar = 200 μm. Fig. 30. *Utricularia longifolia* Gardner. Coiled blade region of 4-cm-long young leaf. Bar = 500 μm. Fig. 31. Elongating tip of 3-cm-long leaf blade (B) acquiring stolon identity after the leaf was removed from the mother plant. Arrow points towards meristematic tip that continues as stolon. Note adventitious bud with young leaf (B') and two primordia that may grow into daughter stolons (A). Bar = 300 μm. Fig. 32. Cross-section of thick stolon. Epidermis (Ep) and parenchymatous cortex (Ri) surround ectophloic central cylinder (Cc), with xylem (Xy) and phloem (Ph) elements. Bar = 500 μm. Fig. 33. Longitudinal section of straight stolon tip. Note central cylinder (Cc) of prospective vascular tissue, surrounded by young parenchymatous cortex (Ri) and epidermis (Ep). Bar = 100 μm. Fig. 34. *Pinguicula moranensis* H.B.K. Young root arising from abaxial (dorsal) side of leaf base (see Fig. 11). Note endogenous origin of root with collar of leaf tissue surrounding root insertion. Bar = 300 μm. Fig. 35. Longitudinal section of root primordium breaking through cortical tissue of leaf base (B). Note prospective vascular cylinder (Cc) and differentiating parenchymatous cortex (Ri). Bar = 150 μm. Fig. 36. Longitudinal section of root tip lacking root cap. Note central cylinder (Cc) of prospective vascular tissue, surrounded by young parenchymatous cortex (Ri) and epidermis (Ep). Bar = 100 μm.

(Ryder, 1954 p. 267). Central to Fuzzy Arberian Morphology is the assumption that structural categories and developmental processes conceivable in plants often have fuzzy borderlines (i.e. overlapping connotations). This view is known as the continuum root shoot model or the 'continuum model'. It is based on fuzzy set theory (Fig. 39,
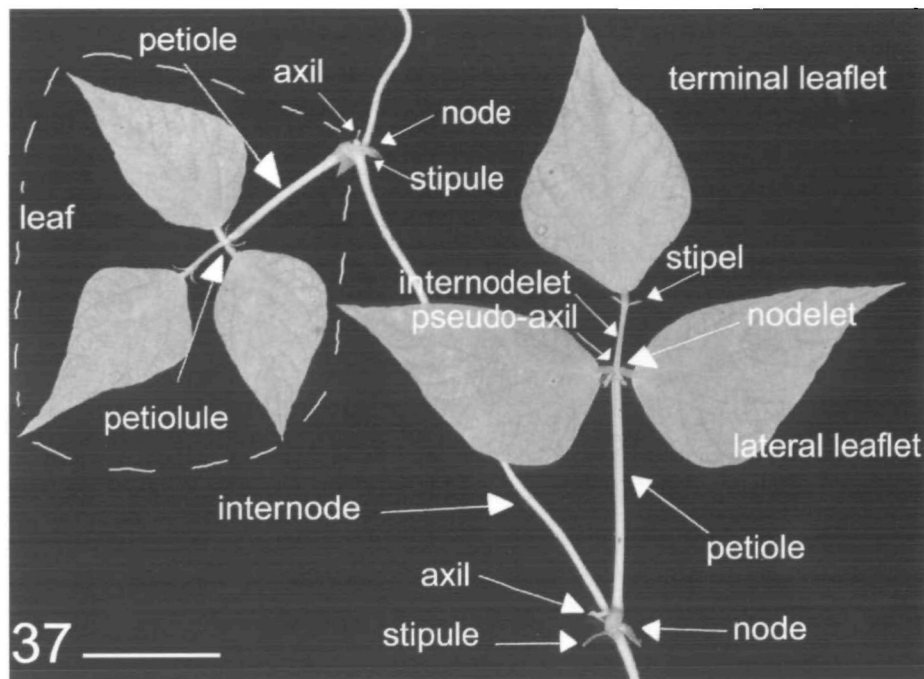
FIG. 37. Two trifoliolate leaves attached to stem portion of *Phaseolus vulgaris* L. (Garden bean, Leguminosae). The terms chosen for the various organs and sub-organs (as proposed by Arber, 1941, 1950; Sinha, 1999) point to the validity of the holographic paradigm (see sections 2 and 20): The SHOOTS are partially repeated by the parts of the compound leaf. The following pairs of structural categories are 'identical-in-parallel' according to Arber: *NODE - nodelet*; INTERNODE - *internodelet*; AXIL - *pseudo-axil*; LEAF - *leaflet*; PETIOLE - *petiolule*; STIPULE - *stipel*. Bar = 2 cm.

Table 1; Sattler, 1986; Rutishauser, 1995). The FAM Approach coincides with Sattler's continuum morphology and the holographic paradigm because the whole is repeated in the parts to some extent, or—occasionally—the whole can be retrieved from a part of it (Weston, 2000; Sattler, 2001; see also section 2). The FAM Approach accepts a partial overlap of the connotations for structural categories in vascular plants such as 'roots', 'shoots' (i.e. 'leafy stems') and 'leaves' (Fig. 39). Thus, their borderlines are fuzzy or blurred. When focusing on 'leaves' of vascular plants, the FAM Approach is equivalent to Arber's partial-shoot theory of the leaf (see sections 21–23).

The three homology criteria traditionally used in Classical Morphology are also useful within the framework of Fuzzy Arberian Morphology in order to understand the body plans of vascular plants. Violations of these criteria (especially violations of the position criterion), however, are handled more easily by taking the FAM Approach: (1) Position criterion = homotopy: in flowering plants this criterion is commonly used with respect to 'axillary branching', with leaves subtending daughter shoots (see section 18). When this criterion does not fit, we speak of heterotopy. This may be due to 'ectopic expression of organ identity', including 'leaves on leaves' and other kinds of epiphylly (see section 17). (2) Special qualities: this criterion covers (among other features) the functions of a plant part ('plant organ'). When this criterion does not work we may speak of 'transference of function' or 'exaptation' meaning that an organ takes on new functions (Hay and Mabberley,

1994; Graham *et al.*, 2000). In contrast to zoology, the functions of a plant organ are not always considered as important for the evaluation of its 'homology' (see section 16). (3) Continuum criterion: when this criterion does not work it may be due to amalgamation[5] of developmental pathways leading to 'developmental mosaics' between 'organs' normally assumed to have different 'identities' (Fig. 39).

The FAM Approach accepts developmental mosaics and, thus, partial homology[6] between, e.g. 'root', 'shoot' (i.e. leafy stem), 'leaf' and its parts (Rutishauser, 1995; Sattler, 1996) whereas the ClaM Approach excludes the existence of partial homology and developmental mosaics between these categories or 'organs', or considers them rare and unimportant (Figs 38–40, Table 1). Total homology (i.e. 1:1 correspondence) is mainly based on the position criterion (i.e. homotopy) which is taken as more important than the other two criteria by proponents of the ClaM Approach (e.g. Kaplan, 1998 p. 79; see sections 9 and 16). Using the FAM Approach, 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 somewhat aberrant

[5]Sattler preferred the term 'hybridization of developmental pathways' (see Weston, 2000).

[6]The concept of 'partial homology' (or 'structural similarity') resembles that of some molecular biologists who speak of two sequences as being 50 % homologous (i.e. 50 % identical) if they share 50 % of their aligned nucleotides (Weston, 2000).

vascular plants ('morphological misfits'), there are developmental mosaics which can be seen as partially homologous to structures which—according to the ClaM Approach—have to be viewed as non-homologous. Organs which are partially homologous to each other show partially overlapping developmental pathways (as illustrated in Fig. 39). The explanatory power of the FAM Approach will be shown for the 'leaf' of vascular plants in general (sections 18–24), as well as for bladderworts (*Utricularia*) that will serve as a case study (sections 25–29).

FROM COMPARATIVE PLANT MORPHOLOGY TO DEVELOPMENTAL GENETICS

Molecular developmental genetics—the new approach (11)

In the first half of the last century (i.e. during Agnes Arber's life), it was not possible to imagine the superb experimental tools that are now available to geneticists for molecular analysis of animal and plant development. Developmental genetics is a modern biological discipline that analyses development and evolution of living organisms with the help of mutations, gene transfer and localization of gene expression. Developmental geneticists are on the way to designing new plants, and using genetic tools for the improvement of crops and forest plants (Jackson, 1996; Howell, 1998; Westhoff *et al.*, 1998; Pidkowich *et al.*, 1999, Theissen, 2000). Thus, a goal of molecular developmental research is the 'ability to rationally design plants for human needs' (Meyerowitz, 1998). The general question is tackled: 'How do simple groups of embryonic cells develop into complex and highly structured organisms, or parts of organisms?' Meyerowitz (1998) realistically admits that 'the answers are only beginning to be known'. Clearly, the role of homeotic genes in the evolution of plant body plans needs to be explored. These genes encode transcription factors similar to bacterial repressor proteins and appear to be taxonomically ubiquitous and very ancient (Niklas, 2000). Examples of homeotic genes relevant to plant development are the *knotted*-like homeobox genes (abbreviated to '*knox* genes'), the MADS box genes and the *FLO(RICAULA)*-like meristem identity genes (see sections 14, 16, 17 and 23). Homeotic genes are undoubtedly important to our understanding of plant body plans. However, no gene acts in isolation. The ability of homeotic genes to potentially define or transform body plans is expressed within a complex genetic and epigenetic milieu of which we are currently incompletely aware (Beurton *et al.*, 2000; Niklas, 2000).

Mutants everywhere (12)

The wealth of plant forms outside the geneticist's laboratory is overwhelming. Various morphological switches are due to single-gene (monogenic) mutations (see Hilu, 1983; Gottlieb, 1986; Burtt, 1994). Among the outstanding examples are simple one-step mutations (e.g. *FLORICAULA*, *unifoliata*) that alter the number,

Classical Model   **Continuum Model**

38   39
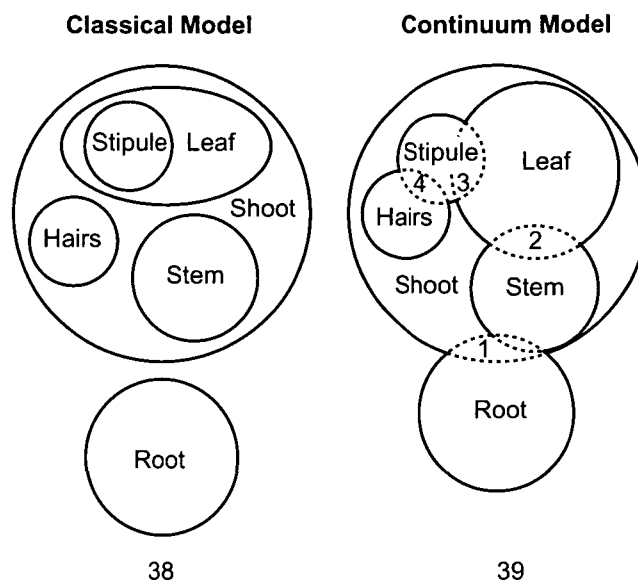
FIGS 38 and 39. Structural categories of vascular plants as conceived according to the Classical Model (i.e. Classical Morphology = ClaM Approach) and the Continuum Model (i.e. Fuzzy Arberian Morphology = FAM Approach). Note that some structures of vascular plants (e.g. leaflets, root-hairs) are omitted in the schemes. In the Classical Model (Fig. 38), the structural categories (organs, sub-organs) belong to an hierarchical system of non-overlapping sets (see sections 4 and 9). The Continuum Model (Fig. 39) is less hierarchical and is consistent with the holographic paradigm (see sections 3 and 10; Fig. 37). In this model, the structural categories are seen as a morphocline of fuzzy sets with partially overlapping connotations, allowing the perception of developmental mosaics (intermediates) between structures with different 'organ identities': 1, Root-shoot mosaics (e.g. *Pinguicula* 'roots' and *Utricularia* 'stolons', see sections 25–29); 2, stem-leaf mosaics (e.g. so-called 'leaves' of *Guarea* and *Chisocheton*; see section 22); 3, leaf-stipule mosaics (e.g. leaf-like 'stipules' being equivalent to 'leaves' in stipular position in *Rubia-Galium* group and *Azara*, see section 20); 4, stipule-hair mosaics (e.g. hair-like 'stipules' and tufts of hairs in stipular sites in Brassicaceae, Leguminosae, Rubiaceae; Rutishauser, 1984; Rutishauser and Sattler, 1986).

position, symmetry, and fusion of vegetative or floral parts (Hofer *et al.*, 1997; Coen, 1999). Some of these natural mutant phenotypes had already been studied by Arber (1934), e.g. the hooded *Hordeum trifurcatum* mutant 'Nepaul barley' (see section 23). Some naturally occurring mutants have been analysed recently by molecular geneticists. For example, Williams-Carrier *et al.* (1997) and Cubas *et al.* (1999) were successful in characterizing the molecular switches leading to naturally occurring mutants in *Hordeum* (with epiphyllous flowers in addition to normal ones) and *Linaria* (with polysymmetric flowers instead of monosymmetric ones). It may be stimulatory for developmental geneticists to consider some of Arber's concepts while studying naturally occurring mutants. Arber (1950 p. 6) wrote: 'Macroscopic nature is never really anomalous. Abnormalities, like other exceptional cases, at least show incontestably, what the plants *can* do'. Some examples of parallel evolution probably depend on the mutation of orthologous ('homologous') genes (see sections 13 and 14).

FUZZY ARBERIAN MORPHOLOGY
= FAM APPROACH
e.g. Continuum Root-Shoot Model:
root, stem and leaf as overlapping
developmental pathways

CLASSICAL PLANT MORPHOLOGY
= ClaM APPROACH
e.g. Classical Root-Shoot Model:
root, stem and leaf as
rigidly discrete units

FUZZY ARBERIAN MORPHOLOGISTS
= FAMMERS, e.g. Gérard Cusset,
Rolf Sattler, Bernard Jeune,
Christian Lacroix, Rolf Rutishauser

DEVELOPMENTAL GENETICISTS
e.g. Julie Hofer,
Neelima Sinha,
Hirokazu Tsukaya

CLASSICAL PLANT
MORPHOLOGISTS
= ClaMMERS

AGNES ARBER 1879 - 1960
FIRST ♀ GIANT IN
HISTORY OF BOTANY

Wilhelm Troll
1897 - 1987

Karl von Goebel
1855 - 1932

Casimir de Candolle
1836 - 1918

Wilhelm Hofmeister
1827 - 1877

Julius Sachs
1832 - 1897

Alexander Braun
1805 - 1877

Aug.-Pyr. de Candolle
1778 - 1841
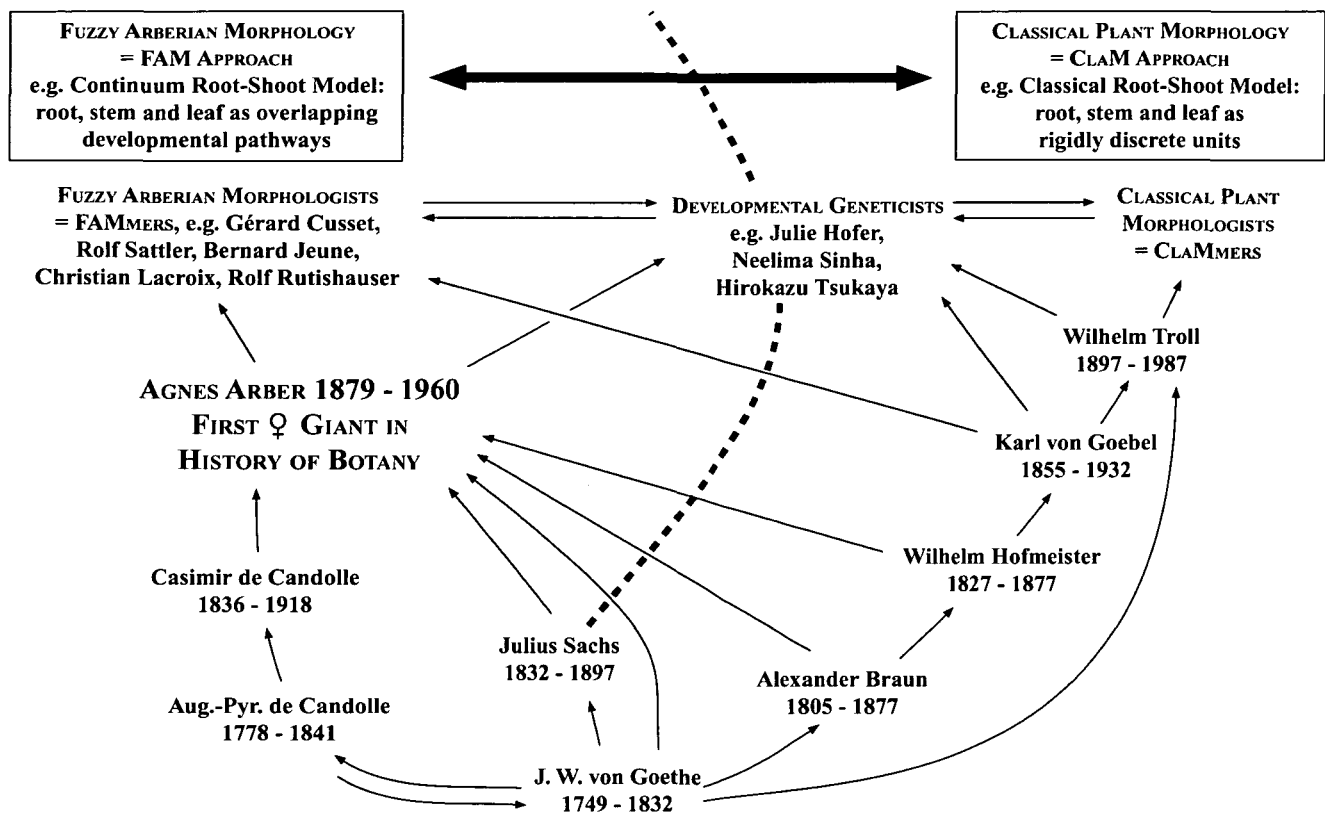
J. W. von Goethe
1749 - 1832

FIG. 40. History of two alternative approaches (perspectives, theoretical models) for the description and interpretation of the body of vascular plants. The continuum root-shoot model coincides with Fuzzy Arberian Morphology (FAM Approach) whereas the classical root-shoot model coincides with Classical Plant Morphology (ClaM Approach; see sections 8–10). Neither 'morphological school' excludes the other. They should be understood as complementary perspectives (each one with its own predictive power). This 'flow chart of morphological thoughts' shows who is standing on whose shoulders. Agnes Arber (1879–1960), as the first female giant in the history of botany, stands on the shoulders of earlier giants such as Wilhelm Hofmeister (1827–1877). Only a few botanists' names are mentioned here (see Rutishauser and Sattler, 1985 for another survey). The developmental geneticists mentioned have already published arguments in favour of the FAM Approach although they normally use the crisp terminology of the ClaM Approach (see section 23).

Parallel evolution = Vavilov's law and the genetic basis of evolutionary trends and homoplastic tendencies in related taxa (13)

Related taxa (genera, species) often show similar evolutionary trends (tendencies) due to genetic similarities (Wardlaw, 1965 p. 380; Takhtajan, 1991). Related taxa may vary their body plan along identical lines giving rise to seemingly homologous structures or features although the common ancestor probably did not possess them. This situation is known under various synonyms such as 'parallel evolution', 'parallel variation', 'homologous variation' or 'Vavilov's law'[7]. Parallelism in closely related taxa (Kubitzki et al., 1991) and 'homoiology' as an analogy on a homologous basis (Hahn and Weibel, 1996) are again concepts closely related or identical to parallel evolution. Using the cladistic terminology, various examples of

[7]According to Arber (1925 p. 224) Vavilov's law (1922) had its forerunners in the 19th century, with similar statements in publications by Naudin (1856), Duval-Jouve (1865) and Darwin (1868) [for these early publications see literature list in Arber, 1925].

parallel evolution have also been labelled as clade specific patterns of homoplasy (Hufford, 1997) or as homoplastic tendencies (Bowman et al., 1999). Vavilov (1922) showed that parallel evolution occurs, not only in species belonging to the same genus, but also in species of related genera, e.g. the switch from a fragmenting to a non-fragmenting spike-axis which occurred several times during cereal evolution (as reviewed by Arber, 1925 p. 227). Parallel evolution in related taxa may be seen as parallelism on a similar genetic background, i.e. due to a genetic predisposition such as the presence of orthologous genes with equivalent mutations.

Arber, especially in her early papers, did not use the term 'gene' (hereditary factor) as it is commonly used today (Maienschein, 1992; Beurton et al., 2000). Instead, she used terms such as 'deep-seated character' or 'inherent character' (Arber, 1925). These terms are metaphors (i.e. figures of speech, see section 15) and have nothing to do with a belief in teleology (Lennox, 1992; Hofer et al., 2001). The metaphors preferred by Arber only reflect the state of genetics during her lifetime. Three years after Vavilov's

TABLE 1. *Classical Plant Morphology and Fuzzy Arberian Morphology as two complementary 'morphological schools' for understanding body plans (bauplans) of vascular plants (see text, also Figs 38–40)*

	CLASSICAL PLANT MORPHOLOGY = ClAM APPROACH (see section 9)	FUZZY ARBERIAN MORPHOLOGY = FAM APPROACH (see section 10)
Complementary models, perspectives		
Users may be called...	ClAMMERS (see Fig. 40)	FAMMERS (see Fig. 40)
Philosophical background (axioms, assumptions)	• Law of Contradiction (Arber, 1957 p. 70) • Conceptual realism, essentialism (Sattler, 1986 p. 75): Only one hypothesis reflects reality • Crisp logic • Either-or thinking (see section 4) • Hierarchical view	• Coincidence of Contraries (Arber, 1957 p. 70) • Map analogy (Sattler, 1986 p. 76): Perspectivism + as-if-ism allow switching between different models • Fuzzy logic (Rutishauser, 1995, 1999) • As-well-as thinking (see section 3) • Holographic view
Models for vascular plant bodies (incl. synonyms)	• Classical model (Sattler, 1986 p. 103) • Classical root-shoot model model (Troll, 1937–41; Rutishauser and Huber, 1991) → Fig. 38	• Continuum model (Sattler, 1986 p. 106) • Partial-shoot theory of the leaf (Arber, 1950) = leaf shoot continuum model (Sinha, 1999) → Fig. 39
Homology	Only 1 : 1 correspondence (i.e. complete homology) accepted; position criterion favoured, continuum criterion neglected	Complete and partial homology acceptable; equal weight is given to both position criterion and continuum criterion
Predictive power, heuristic value	• Easy to handle because in accordance with our common discursive-logical reasoning • Developmental mosaics (intermediates) between structures of same homology ('organ identity') can be understood	• Search for genetic similarities between structures with seemingly different homologies (i.e. different 'organ identities') • Developmental mosaics (intermediates, transitional stages) between organs of different homologies can also be understood
Shortcomings	• Danger of confounding model with reality • Developmental mosaics (intermediates, transitional series) between structures of different homologies are excluded	• Fuzzy logic and perspectivism are difficult to communicate in terms of structural categories because of their ambiguous or overlapping connotations
How to overcome the shortcomings?	• Use FAM Approach as complementary model • Accept the holographic paradigm: A part may repeat the whole (Sattler, 2001)	• Go over to process thinking (process morphology): replace structural categories by combinations of developmental processes (Sattler, 1996; see sections 19 and 24)

(1922) seminal paper, Arber (1925 p. 231) was aware of this deficit: 'It seems to me that the tendency to progress in a certain definite direction is as much an inherent character of a given race, as are the features of its chemistry and morphology. It is the geneticists who have cleared the ground for this idea, for their work has opened our eyes to the fact that we have not fully analysed the characters of an individual organism until we are acquainted, not only with its observable features, but also with its potentialities if bred from... That these tendencies in evolution should so often lead to parallel developments, need not to surprise us'. While studying multiple independent alterations of floral structure (i.e. loss of petals and stamens) in the brassicaceous genus *Lepidium*, the developmental geneticists 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'.

Examples of parallel evolution (homoplastic tendencies) in related groups (14)

There are many recurrent forms and changes of form in vascular plants, especially angiosperms (Burtt, 1994). Only a few examples of parallel evolution (i.e. evolutionary trends which are obviously based on a similar genetic background) will be mentioned here: (1) Epiphyllous shoots as described for various mutants in arabidopsis are also found in the wild type of other brassicaceous taxa, e.g. in *Cardamine pratensis* (Troll, 1941 p. 1137; Dickinson, 1978). They may be due to changes of orthologous *knox* genes in arabidopsis and related genera (Chuck *et al.*, 1996; see also section 11). (2) In arabidopsis, the A class mutant *apetala1-1* of the MADS box gene family shows abnormal inflorescences with the flowers replaced by complex structures composed of several individual flowers (Bowman, 1994; Coen, 1999; Theissen, 2000). Arber (1931) herself described similar developmental switches in inflorescences of *Nasturtium officinale* (watercress) which is a close relative of arabidopsis. She wrote: 'Late in June, 1929, I found, near Cambridge, fruiting racemes of the Watercress, in which some of the lowest flowers had evidently been abnormal, for the receptacle below each siliqua bore the remains of 1–4 small supernumerary flowers... During that summer I found it in three localities about Cambridge'. Arber observed in watercress what could be orthologues (or phenocopies?) of the *apetala1-1* mutation in arabidopsis (see e.g. Bowman, 1994; Howell, 1998). (3) The evolutionary switches to cauliflower-like inflorescences in arabidopsis and *Brassica oleracea* var. *botrytis* depend on orthologous MADS box genes such as '*Cauliflower*' (Kempin *et al.*, 1995; Purugganan *et al.*, 2000; Theissen *et al.*, 2000). (4) In various families of the advanced eudicots (i.e. Lamiales and allies within asterids), there is an evolutionary trend from monosymmetric (zygomorphic) to polysymmetric (actinomorphic) flowers or *vice versa*. These shifts may be caused by mutations in *cycloidea*-like genes (Luo *et al.*, 1996; Donoghue

et al., 1998; Coen, 1999; Cubas *et al.*, 1999; Endress, 1999; Ree and Donoghue, 1999; Citerne *et al.*, 2000).

Parallel evolution ('parallelism') can also be found among a larger taxonomic group (Wake, 1991; Endress, 1992; Baas and Wheeler, 1996; Hufford, 1997). Agnes Arber mentioned examples of parallel evolution where we cannot yet speculate on their genetic basis. Arber (1925 p. 150) wrote on 'dropper' formation that occurs in Liliaceae *sensu lato* (e.g. *Tulipa, Gagea, Erythronium*), orchids (e.g. *Ophrydeae*) and other monocots: 'A curious feature of the life-history of the Tulip is the lowering of the bulb into the soil, year by year, during the period of immaturity. This descent is accomplished by means of a tubular organ, the 'dropper' or 'sinker', which carries the terminal bud inside its tip'. Arber (1925 p. 155) concluded: 'The occurrence of dropper formation, in Monocotyledons so distinct from one another in affinities as the Orchids and Liliaceae, is an instance of the parallelism between the cohorts...' [see also Tillich (1998) on stolon-like droppers in monocots].

Metaphors in developmental genetics and elsewhere in biology (15)

'Truth, except as a figure of speech, does not exist in empirical science' (Brower, 2000 p. 18). A figure of speech (metaphor) presupposes a similarity of two things and denotes one of them by signifying the other, as if they were identical. Metaphors are often used as convenient descriptive terms in order to become understandable, in biology as well as in other disciplines (Keller, 1995). Arber (1937, 1954 p. 122) discussed the value of metaphors in biology to some extent: 'It can scarcely be denied that the use of pictorial imagery in thinking is a fundamental need of the human mind'.

Developmental geneticists often use metaphors. For example, genes (especially homeotic genes, master genes) may be regarded as responsible for 'developmental control', 'developmental programming' and 'leaf designing' (Sussex, 1989; Jackson, 1996). Regulatory genes such as homeobox genes (e.g. *HOX* genes, *knox* genes) and MADS box genes have been called 'molecular architects of body plans' in animals and plants, respectively (McGinnis and Kuziora, 1994; Theissen and Saedler, 1998). For example, the MADS box genes act to some degree as molecular architects of the floral body plans in vascular plants (Parcy *et al.*, 1998; Hasebe and Ito, 2000; Theissen, 2000; Theissen *et al.*, 2000). Metaphors like 'molecular architects of body plans (bauplans)' may overemphasize the role of genes because they imply the existence of developmental programmes due to control genes (e.g. homeobox genes, MADS box genes) with specific effects on pattern formation (see Beurton *et al.*, 2000 for other critical comments). The wild-type function of these genes is necessary for the correct formation of the body plan. Developmental geneticists such as Theissen and Saedler (1998) admit: "Plants as well as animals have no 'molecular architects of body plans' in a strict sense. However, they have many genes that substantially contribute to development. ... Not all genes which, upon mutation, affect the formation of the body plan, may actually control its formation". There are other geneticists

and also biophilosophers (e.g. Mueller, 1994; Griesemer, 2000) who accept that genes do not directly determine supracellular patterns of cell differentiation.

The best solution is to take over the perspectivist's approach by using metaphors (concepts, models) as if they existed in nature in order to give them explanatory power, but never confounding model and reality (Arber, 1954 p. 79; see more on as-if-ism in section 3). With respect to comparative morphology of vascular plants, this means that organs such as 'root', 'stem', 'leaf', 'stipule' in the vegetative phase and organs such as 'sepal', 'petal', 'stamen' and 'carpel' in the reproductive phase of flowering plants are at best metaphors, i.e. convenient descriptive terms approaching reality to some degree. This is also the case with the term 'organ identity' and similar developmental genetic concepts as will be shown in the next section.

Organ identity and meristem identity (16)

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. According to the ClaM Approach, 'roots', 'stems' and 'leaves' are the three basic organs of vascular plants. However, other structural categories of plants, such as 'stipules', 'leaflets' and 'hairs' can also be called organs (or sub-organs) because they may have certain functions, e.g. secretion of mucilage or photosynthesis (Figs 37 and 38). In terms of molecular developmental genetics, 'organ identity' means the developmental fate of an uncommitted primordium. 'Organ identity' equals 'morphological significance' and 'morphological nature'. These are terms which have been used by comparative morphologists for a long time. 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[8] (see reviews by Albert *et al.*, 1998; Meyerowitz, 1998; Theissen and Saedler, 1998; Coen, 1999; Theissen, 2000). 'Organ identity' as a concept is also used outside the reproductive zone. Thus, the vegetative body of vascular plants shows primordia that are committed during early development to take over organ identities such as 'leaf identity' or 'root identity' (Poethig, 1997). In a developing leaf primordium, Gleissberg *et al.* (2000) and Scanlon (2000) even distinguished 'sub-organ identities' which can be delimited along three axes (gradients). They are called 'marginal identity', 'adaxial identity' and 'abaxial identity' (see section 24).

A term related to organ identity is 'meristem identity' which is used to characterize the growth phases of a shoot meristem, with vegetative meristem, inflorescence meristem and floral meristem as three possible 'identities' (Theissen, 2000). In certain plants such as arabidopsis, the switch from one meristem identity stage to the next means a switch between lateral appendages of different identities. 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'. Involved in the change of meristem identities in flowering plants are *FLO*-like genes such as *FLORICAULA* and *LEAFY* in *Antirrhinum* and arabidopsis, respectively (see sections 11 and 23).

Concepts like 'organ identity' and 'meristem identity' are related to either-or philosophy as long as we accept that such concepts really exist in nature (conceptual realism). According to Fuzzy Arberian Morphology, however, the identity of an organ such as 'root', 'stem' or 'leaf' can be fuzzy, as will be shown in sections 21–29. When a leaf part such as a 'leaflet' is repeating the developmental pathway of the whole leaf, Arber (1950) used the term 'identity-in-parallel' (see section 5; Fig. 37). There are also fuzzy borderlines between complex organs and organ complexes. Rutishauser (1999) presented various cases where whorled organs in vascular plants have fuzzy identities. This leads to the view that somewhat similar organs (including their primordial stages) may have overlapping identities, i.e. only partially identical developmental pathways[9].

'Organ identity' can be defined by morphological criteria or by its gene expression pattern, including organ identity genes that sculpt, e.g. the structure of angiospermous flowers (Meyerowitz, 1998; Yu *et al.*, 1999; Theissen, 2000). Occasionally, the organ identity is converted during development. For example, leaf parts behaving as stems will be described in sections 23 (*Hordeum* mutant) and 25–27 (*Utricularia*, Fig. 31).

We still know little about the relevant organogenetic properties with which an uncommitted primordium or an initial stage consisting of one or a few meristematic cells only has to be 'imbued' in order to accomplish organogenesis. Lacking a better term for 'relevant organogenetic properties', Barlow *et al.* (2001) speak of properties of 'rootiness' guiding an uncommitted primordium towards the developmental pathway 'root', whereas properties of 'shootiness' are needed for primordial commitment towards 'shoot' (i.e. leafy stem) development. Acquisition of organ identity (e.g. leaf identity) may occur progressively or at once (Poethig, 1997). In some ferns and aberrant flowering plants ('morphological misfits') such as *Utricularia*, the commitment of becoming a 'leaf' or 'stolon' (i.e. stem) can be delayed considerably (Rutishauser and Sattler, 1985; Brugger and Rutishauser, 1989; Steeves *et al.*, 1993). It is sometimes difficult to even distinguish 'root identity' and 'shoot identity' (leafy stolons) in Lentibulariaceae such as *Pinguicula* and *Utricularia* (see sections 28 and 29).

Heterotopy, homeosis and ectopic expression of organ identity (17)

An organ or structure is termed heterotopic when it develops in an unusual ('wrong') position on the body plan. Heterotopy violates the position criterion, i.e. the positional equivalence (= homotopy) of organs (see sections 7 and 10). Heterotopy often results from ectopic gene expression and, thus, ectopic expression of organ identity (Clark, 1997; see section 23). For example, epiphyllous inflorescences and

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[8]'Appendages' in vascular plants are lateral organs with determinate growth.

[9]This situation coincides with partial homology (see section 10).

shoots may arise along the rachis of compound leaves in various dicotyledons such as tomato and *Chisocheton* spp. (Fig. 6; Sattler, 1975; Dickinson, 1978; Fisher and Rutishauser, 1990; Fukuda *unpubl. res.*). Heterotopy, complete homeosis and ectopic expression of organ identity have a nearly identical meaning. These terms describe the transformation of body parts into structures normally found elsewhere according to the body plan (Okada *et al.*, 1996). 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' has been recognized on different taxonomic levels, especially in vascular plants (Cooney-Sovetts and Sattler, 1986; Sattler, 1988; Charlton, 1991; Kirchoff, 1991; Barabé and Lacroix, 2000; Weston, 2000). Regulatory genes (especially homeotic genes) and their ectopic expression are often involved in homeosis (Okada *et al.*, 1996; see sections 11 and 23). In wild type flowering plants there are many examples where homeotic replacement of structure A by structure B is suggested to have occurred. For example, Charlton (1991, 1998) found a homeotic replacement of the stipule by a leaf in *Azara microphylla* (Flacourtiaceae). Other examples of homeotic replacement of stipules by leaves (i.e. ectopic expression of 'leaf identity' in stipular position) are mentioned in section 20. Until now we have only spoken about complete homeosis. A wider definition of homeosis (= homeotic transformation) was given by Sattler (1994 p. 438) as 'the total or partial replacement of one part by another of the same organism'. Partial replacement leads to developmental mosaics and partially homologous organs (see sections 10 and 21–29).

WHAT IS A TYPICAL 'LEAF'? HOW CAN IT BE DISTINGUISHED FROM A 'SHOOT' (LEAFY STEM), A 'LEAFLET' OR A 'STIPULE'?

A typical 'leaf' (18)

'Leaf' and 'stem' are the two organ types of a 'shoot' in vascular plants. 'Leaf', 'stem' and 'root' may be understood as adaptive peaks of terrestrial vascular plants: a bipolar axial system (with roots and stems) guarantees fixation in the soil and optimal exposure of the foliage leaves as light collectors (Stebbins, 1974 p. 125; Niklas, 1997; see section 28). We cannot answer the question 'What is a leaf?' without asking similar questions such as: What is a shoot? What is a stem? What is a leaflet? What is a stipule? These questions cover structural categories which are used with some arbitrariness to describe and understand the body plan of vascular plants. Julius Sachs (1875) realised this when he emphasized: "The morphological conceptions of 'stem' and 'leaf' are correlative; one cannot be conceived without the other ... The expressions 'stem' and 'leaf' denote only certain relationships of the parts of a whole—the 'shoot'" (as cited in Arber, 1950 p. 71). In spite of these difficulties, several botanists have tried to define or describe a 'leaf' in vascular plants (e.g. Hofmeister, 1868; Goebel, 1933; Troll, 1939; Hagemann, 1970, 1984; Rutishauser and

Sattler, 1985; Cusset, 1986; Steeves and Sussex, 1989). More recently, developmental geneticists have also claimed to have difficulties in 'defining' typical leaves of vascular plants. For example, Jackson (1996) asked and answered the following question: 'Given the immense variation in leaf architecture, how do we define a leaf? The only defining feature may be that all leaves are initiated as dorsiventral or flattened primordia from a shoot apical meristem'. Scanlon (2000) presented a similar leaf definition: 'At least two developmental characters define most if not all leaves: namely (1) leaves arise from a relatively large number of progenitor 'founder cells' recruited from the periphery of the shoot apical meristem; (2) leaves are dorsiventrally asymmetrical (bifacial) at their inception'.

The nine criteria given below may be useful to define or describe typical leaves, at least in flowering plants (which are by far the largest group of vascular plants). This definition (or circumscription) is useful in the framework of both the Classical Approach and Fuzzy Arberian Morphology (Figs 38–40):

(1) A leaf is usually divided into a base (sheathing or not), a petiole (stalk) and a green blade (lamina, simple or compound) which is normally the main site of photosynthesis (Figs 3–6). Many families (especially dicots) are characterized by additional basal outgrowths, so-called stipules (Fig. 37; Hofer *et al.*, 1997, 2001; Scanlon, 2000; see section 20).

(2) A leaf usually shows a dorsoventral symmetry with respect to the shape of cross-sections, as well as arrangement of photosynthetic tissue, vascular bundles and other anatomical features. Thus, typical green leaves are broader than thick, so that relatively little tissue is needed to present a large area to incident light—clearly an adaptation to their role in photosynthesis and transpiration (Givnish, 1987; Dengler, 1994; Dengler and Kang, 2001). Less typical leaves are, however, centric or unifacial showing radial symmetry, e.g. cylindrical phyllodes of *Acacia* spp. (Arber, 1925: her Fig. 85; Sattler *et al.*, 1988; Bell, 1991; Kaplan, 1998; Gleissberg *et al.*, 2000).

(3) The leaflets in typical compound leaves are arranged in one plane or nearly so (e.g. *Phaseolus*, Fig. 37). Less typical compound leaves, however, show verticillate leaflet arrangement (e.g. *Carum verticillatum*, Fig. 5; *Utricularia purpurea*, Fig. 9; Eberwein, 1996; Rutishauser, 1999).

(4) In compound leaves with many lateral leaflets along the main rachis, leaflet initiation can occur in an acropetal, basipetal or bidirectional order (Hagemann and Gleissberg, 1996; Rutishauser and Sattler, 1997; Gleissberg and Kadereit, 1999). Leaf inception at the shoot tip, however, nearly always occurs in an acropetal order. There are only a few examples known in flowering plants of shoots with intercalary or basipetal leaf initiation, e.g. inflorescences of *Mourera*, shoots of *Acacia verticillata* and allies (Rutishauser, 1999; Rutishauser and Grubert, 1999; see section 22).

(5) The leaf normally originates as a transversely oriented primordium on the periphery of the shoot apical

meristem (Jackson, 1996; Clark, 1997; Scanlon, 2000). Becoming separated from the apex, the leaf seems to arise as an appendage from the stem node (often with a broad leaf sheath). Leaves, however, may also be seen as parts of phytomers, i.e. constructional units containing a stem portion (Howard, 1974; Rutishauser and Sattler, 1985; Brutnell and Langdale, 1998; Howell, 1998). Less typical leaves can be initiated while a proper shoot meristem is lacking (Schichnes *et al.*, 1997).

(6) Growth duration: a typical leaf is an organ of limited apical growth. The apical meristem of foliage leaves in many angiosperms is differentiated early during organogenesis, in contrast to typical stems (shoots) that show an indeterminate apical growth or nearly so. Less typical leaves, however, show a long-lasting apical growth, e.g. *Chisocheton* and *Guarea* (Meliaceae; Fisher and Rutishauser, 1990; Fukuda *unpubl. res.*).

(7) The typical leaf has at least one shoot bud in its axil, giving rise to axillary branching which is especially typical of seed plants among vascular plants (see also section 24). Restriction of lateral shoot formation to leaf axils may have several advantages: e.g. protection in early development, and optimal nutrient supply by the subtending leaf (see Goebel, 1928 p. 107; Niklas, 1997, 1998). Contrasting this axillary branching, the 'pseudo-axils' of the leaflets in a typical compound leaf are usually empty (e.g. *Phaseolus*, Fig. 37). However, there are various exceptions to this rule that show epiphyllous buds and shoots (e.g. *Chisocheton tenuis*, Fig. 6). Foliage leaf axils of various seed plants (especially cycads, palms) are often empty (Fisher and Maidman, 1999).

(8) Life spans of leaves are often shorter than those of the associated stems, especially in deciduous trees and shrubs growing in seasonal climates (Chabot and Hicks, 1982).

(9) The vascular pattern (including orientation of xylem and phloem) has often been used to identify the morphological significance of doubtful leaves and leaf-like shoots such as the phylloclades of the Asparagaceae (Arber, 1925; Cooney-Sovetts and Sattler, 1986; but see Dengler and Kang, 2001).

The leaf definition (i.e. circumscription) given above fits for many vascular plants, especially for typical flowering plants, including model organisms such as maize, tobacco and arabidopsis which are preferentially studied by developmental geneticists. They are looking for 'a single underlying theme to plants' which may be epitomized by the 'leaf' (Coen, 1999 p. 57). According to Tsukaya (1995), 'a full understanding of the leaf is essential for a full understanding of plant morphology'. One may continue by asking which of the features mentioned above are really diagnostic, distinguishing 'leaf' and 'shoot', or 'leaf' and 'stem', just to find out that there are none. Each feature normally taken as typical for leaves (or so-called leaves) can, in exceptional cases, also be realised in whole shoots (including stems). The reverse also seems to be true (for more details see Sachs, 1875 p. 136; Rutishauser and Sattler, 1985). Therefore, it is not surprising that Arber

(1930 p. 308–309) concluded: 'If we once accept the fact that 'stem' and 'leaf' are no more than convenient descriptive terms, which should not be placed in antithesis as if they corresponded to sharply opposed morphological categories, the problem of their delimitation and of their differentiating characters vanishes into thin air'.

There are plants (especially aquatic plants) where the above-mentioned 'leaf definition' clearly fails. For example, the so-called ramuli in the rheophytic *Indotristicha ramosissima* (Podostemaceae) are photosynthetic appendages along the stem (Fig. 7). They arise like leaves (i.e. not subtended by other leaves or scales). Each ramulus (length up to 2–3 cm) consists of many scales (one cell thick) which are radially spread around the ramulus axis (Fig. 8). Depending on the perspective (ClaM *vs.* FAM Approach), the ramuli can be interpreted as short shoots (in leaf sites), as compound leaves (with radial leaflet arrangement) or as developmental mosaics combining both shoot and leaf features (see Rutishauser and Huber, 1991; Rutishauser, 1997 and references cited therein). Even more difficult is the interpretation of 'leaves' and 'shoots' (i.e. leafy stems) in *Utricularia* (Figs 9 and 10), as will be shown in sections 25–29. Both 'leaves' and 'stems' are interrelated notions describing structures that belong together. Certain developmental characteristics or cascades of gene expressions may be shared by leaves and stems in various vascular plants (e.g. *Chisocheton* and *Guarea*; see section 22). Once we know more about the genes and the epigenetic modifiers that control the developmental pathways of compound leaves as compared to their associated stems, we may better estimate the degree of overlap between these developmental pathways.

Quantification of developmental mosaics between 'leaves' and 'stems' (19)

How can developmental mosaics be quantified in terms of the FAM Approach? A quantification may be especially useful for developmental mosaics between plant structures with different 'organ identities' (see section 16) because this gives an estimation of the degree of overlap of seemingly non-homologous developmental pathways. Empirical studies have revealed the appropriateness of fuzzy logic and the FAM Approach for the quantification of developmental mosaics (e.g. Jeune and Sattler, 1992, 1996; Jeune and Lacroix, 1993; Cusset, 1994; Hay and Mabberley, 1994; Sattler, 1994). This will be discussed using the '*leaf*' and the 'STEM' of flowering plants as examples. The '*leaf*' is a fuzzy set combining some processes and topological relations whereas the 'STEM' is another fuzzy set combining a different set of processes and topological relations (Sattler and Jeune, 1992; Cusset, 1994; Rutishauser, 1995). Three of the main distinguishing criteria are summarized as follows (leaf features in *italics*; stem features in SMALL CAPITALS): (1) growth duration: *determinate (limited)* vs. INDETERMINATE (UNLIMITED); (2) growth distribution including acquisition of a certain symmetry type: *dorsiventral (bilateral)* vs. RADIAL (AXIAL); and (3) positioning of meristems and primordia: *extra-axillary and axillant* vs. AXILLARY AND NON-AXILLANT. Using multivariate analysis, specifically

principal component analysis, Jeune and Sattler (1992) were able to calculate the distances between atypical plant structures such as '*leaves*' and ·STEMS· of *Utricularia foliosa* and the centroids of typical '*leaf*' and typical ·STEM·. Jeune and Sattler's papers may be seen as a way of quantifying developmental mosaics and other atypical plant structures according to fuzzy logic. The distances given by Jeune and Sattler are estimations of the degree to which e.g. *Utricularia* leaves are typical '*leaves*' and the degree to which they resemble typical ·STEMS· (see sections 25–27). The quantification of partial homology and developmental mosaics, however, is still in its infancy (Sattler and Jeune, 1992; Cusset, 1994). This may be the reason why many botanists and developmental geneticists still hesitate to take the FAM Approach and the related process morphology (see section 24) as explanatory models allowing predictions beyond the ClaM Approach (Table 1).

'Stipules' and 'leaves' (20)

Comparative plant morphologists have collected many data on the structure and development of stipules—nodal or basal appendages that accompany leaves in various vascular plants (mainly dicots, rarely monocots and other vascular plants). Stipules are either short-lived, with a role in bud protection and mucilage production only, or else they are leafy and persistent, resembling the associated leaves. Stipules are typically present in many dicotyledonous families, e.g. Leguminosae (Fig. 37; Weberling, 1967; Sattler *et al.*, 1988; Rutishauser, 1999; Hofer *et al.*, 2001). Arber (1941 p. 100) pointed out: 'Any sound theory of the leaf must recognise the fact that certain elements of the leaf in the angiosperms may have a diversified origin, and hence cannot always be neatly homologised from family to family'. This statement seems to be justified especially for stipules. There are two main interpretations of stipules, as summarized by Rutishauser (1999) and Dickison (2000 pp. 252–254): (1) according to the classical leaf-stipule concept (Fig. 38, i.e. ClaM Approach), stipules are accepted as outgrowths (parts) of a leaf or leaves nearby (Eichler, 1861; Sinnott and Bailey, 1914); (2) according to the modified leaf-stipule concept (Fig. 39, i.e. FAM Approach), stipules can be accepted as more or less independent nodal appendages (additional leaf-like outgrowths) which are only positionally associated with leaves. They can be viewed something like a lateral repetition of the leaf or leaves nearby (Croizat, 1960; Rutishauser and Sattler, 1986). This second model is a heuristic aid in dicotyledonous families such as Cunoniaceae, Leguminosae and Rubiaceae. In various members of these families stipules arise as separate primordia from the shoot apical meristem, only positionally associated with leaf primordia (Rutishauser and Dickison, 1989; Rutishauser, 1999). There is developmental evidence in favour of both the classical and the modified leaf-stipule concept, i.e. both the ClaM and FAM Approach. These approaches are, thus, best seen as complementary views. Stipules either arise on the flanks of the leaf primordium, or from primordia spatially independent of, but concomitant with, the leaf primordium. Leaves in most vascular plants have at least one vascular bundle (= leaf trace) connected

to the vascular tissue of the stem whereas stipules may be served by separate stipular traces and/or by vascular branches of the leaf traces (Rutishauser, 1984; Rutishauser and Sattler, 1986; Dickison, 2000).

In various dicotyledons, the stipules closely resemble the associated leaf. The FAM Approach (continuum model) allows the acceptance of leaf-stipule intermediates as developmental mosaics (Fig. 39): The conceptual border-line between leaf and stipule is fuzzy in various taxa, such as whorl-forming Acacias in Leguminosae, and the *Rubia-Galium* group in Rubiaceae (Rutishauser, 1984, 1999; Rutishauser and Sattler, 1986). The interfoliar stipules (with empty axils) of *Rubia cordifolia* are copies of the leaves (with axillary buds) of the same whorl. Both leaves and leaf-like stipules have the same cordate shape, provided with a stalk. Putting it differently but meaning the same, Cronquist (1968 p. 65) proposed a homeotic stipule → leaf transition within the *Rubia-Galium* group: 'In species with four equal leaves at a node, the stipules have lost their identity as stipules and become leaves like other leaves, except the probable absence of axillary buds... The situation in *Galium* should serve as a warning against too formal and rigid an approach to evolutionary morphology'. The repetition of the leaf development program in stipular sites is also found in *Azara* (Flacourtiaceae) and explained by Charlton (1991, 1998) as naturally occurring homeotic replacement of 'stipules' by 'leaves' (see section 17). Similar homeotic mutants are known from *Pisum* with leaf-like structures in stipular sites (Hofer *et al.*, 2001). In certain dicots (e.g. Leguminosae, Rubiaceae), stipules form 'mor-phoclines' grading from leaf-like to hair-like structures (as indicated in Fig. 39; Rutishauser and Sattler, 1986). Arber (1950 p. 141) wrote: 'Stipules grade from members recalling fully developed foliage-leaves, down into hair-like bodies. The extreme of reduction is seen in certain crucifers, which are generally described as exstipulate, but which actually develop minute, non-vascular, paired structures at the base of the leaf, the stipular nature of which can scarcely be doubted' (see section 23 on rudimentary stipules in arabidopsis).

ARGUMENTS IN FAVOUR OF THE PARTIAL-SHOOT THEORY OF THE LEAF (AS PART OF THE FAM APPROACH)

Introductory remarks (21)

Sinha (1999) and Hofer *et al.* (2001) reviewed new results of molecular genetics of leaf development in angiosperms. These authors are among the first developmental geneticists to credit Agnes Arber and her partial-shoot theory of the leaf (Figs 39 and 40). This theory, as part of the FAM Approach (Fig. 39), has some heuristic value and predictive power. The main tenets of the partial-shoot theory of the leaf are as follows: (1) There is a certain degree of fuzziness between the 'shoot' as a whole and a 'leaf' as its part: '... the leaf is a shoot, though an imperfect one' (Arber, 1941 p. 87). Especially compound leaves of many vascular plants can be considered to be partially equivalent to shoot systems. Thus, the developmental pathway of the whole

shoot is partially repeated during the development of its leaves. (2) The leaf axis (with petiole, nodelets and internodelets[10]) of a compound leaf may be seen as partially homologous to the stem (with nodes and internodes) of a whole shoot, whereas the leaflets (with petiolules) partially correspond to the whole leaf (with petiole). In certain compound leaves even the stipules are repeated within the leaf, forming stipels at the base of leaflets (e.g. *Phaseolus*, Fig. 37). (3) In terms of developmental genetics, the partial-shoot theory of the leaf implies (or predicts) that a set of developmental genes expressed in the shoot and its apical meristem are also expressed in each single leaf during apical growth and leaflet inception (see section 23).

Leaf shoot continuum model (as proposed by Sinha, 1999) may be a more adequate term for what was called the partial-shoot theory of the leaf by Arber (1941, 1950). The term 'continuum' allows also the opposite view, i.e. to see the shoot as a partial leaf. Arber (1950 p. 87) was aware of this possibility. She wrote: 'The distinction between the two-dimensional leaf and the three-dimensional shoot is … by no means absolute. The tendency to radiality and the tendency to dorsiventrality coexist both in shoot and leaf, though the relative emphasis on these tendencies varies … the shoot being predominantly radial, but with an underlying trend towards dorsiventrality, and the leaf being predominantly dorsiventral, but with an underlying trend towards radiality'.

Comparative morphological evidence in favour of the partial-shoot theory of the leaf (22)

Some of the arguments given below were presented and illustrated by Arber herself (e.g. 1941, 1950). All of them depend on comparative morphological and developmental studies. Several papers in favour of the partial-shoot theory of the leaf have been published during the last 20 years, mainly by Rolf Sattler, Gérard Cusset and their collaborators. The reader should be aware that verification of the FAM Approach does not mean falsification of the ClaM Approach. Both are complementary models; each one allows some predictions and has some shortcomings (Figs 38–40, Table 1, see sections 8–10). We focus here on the FAM Approach because this view is still ignored in most botanical text-books:

(1) There are arguments in favour of the partial-shoot theory of the leaf given by paleobotanists. Some elements of the partial-shoot theory resemble the 'telome theory' and related ideas on the evolutionary origin of the foliage leaves (called megaphylls, euphylls) in vascular plants[11]. 'Megaphylls' are the leaves of the euphyllophytes (i.e. the major clade of vascular plants), comprising ferns, *Equisetum* and seed plants, but no lycophytes (Pryer *et al.*, 2001). Paleobotanists (e.g.

Kenrick and Crane, 1997; Graham *et al.*, 2000) proposed two distinct modes of origin for leaves, giving rise to microphylls (scales) in lycophytes and megaphylls (fronds) in euphyllophytes such as ferns and seed plants. Many botanists accept the hypothesis that during land plant evolution, megaphylls (including fronds and prefronds) were derived from branched axial organs ('telome trusses') by flattening ('planation'), congenital fusion and a switch to determinate growth[12] (Zimmermann, 1953, 1959; Stewart and Rothwell, 1993; Kato and Imaichi, 1997; Kurmann and Hemsley, 1999; Classen-Bockhoff, 2001; Sussex and Kerk, 2001). Prefronds, as found in early vascular plants such as the extinct progymnosperms (e.g. *Archaeopteris*), are three-dimensionally branched structures and are seen as phylogenetic precursors of compound leaves, especially fronds of modern ferns.

(2) All additional arguments mentioned below are provided by comparative morphologists studying the developmental patterns of modern-day plants. For example, developmental mosaics between leaves and shoots are described for various recent ferns, e.g. *Gonocormus* (*Trichomanes* group) with shoot buds developing from the rachis (Hébant-Mauri, 1990). To label a fully meristematic primordium as 'leaf' is to label it according to its presumptive developmental fate ('organ identity') under undisturbed conditions (see sections 16 and 17). However, surgical or chemical treatment may change the developmental fate of what was supposed to become a leaf. In some ferns at least (e.g. species of *Dryopteris, Hypolepis, Osmunda*), such experimentally induced changes include the developmental switch from a leaf (frond) primordium to a shoot (rhizome) bud and *vice versa* (Steeves and Sussex, 1989; Steeves *et al.*, 1993). Natural examples of shoot or flower development from primordia occupying leaf sites are known in flowering plants such as *Nymphaea* (Cutter, 1958), arabidopsis (Parcy *et al.*, 1998) and *Utricularia* (see Fig. 31, section 26).

(3) Leaves of most vascular plants are initiated sequentially as transversely inserted primordia. They arise at a shoot apical meristem which maintains itself in the process as an organized unit of undifferentiated dividing cells (see section 18; Medford *et al.*, 1992; Smith and Hake, 1992). Similarly, young compound leaves of angiosperms such as *Apium repens* (Apiaceae), *Rhus typhina* (Anacardiaceae) and *Murraya koenigii* (Rutaceae) are provided with a meristematic leaf tip which may be called the leaf apical meristem. These taxa show an acropetal mode of initiation with leaflet primordia which are inserted transversely at the leaf apical meristem. Thus, they resemble leaf initiation at the shoot apical meristem (Sattler and Rutishauser, 1992; Lacroix and Sattler, 1994; Lacroix, 1995).

[10]The terms 'nodelets' and 'internodelets' were already proposed by Arber (1941, 1950).
[11]Arber (1950 p. 78) was herself convinced that the partial-shoot theory 'has no phylogenetic implications'. She added: 'There is no need to assume that the leaf passed ancestrally through a complete-shoot phase'.

[12]Note that these evolutionary processes have their counterpart during leaf development, with e.g. 'planation' (during phylogeny) corresponding to 'adaxialization' (during ontogeny); see section 24, also Gleissberg *et al.* (2000).

(4) Although typical compound leaves show determinate growth, a few 'leaves' are known to have an apical meristem and (nearly) indeterminate growth. Field studies in tree-forming Meliaceae such as *Chisocheton* and *Guarea* have revealed that the leaves may show seasonal apical growth for several years. The leaf apical meristem seems to contribute cells and leaflets in a manner similar to the shoot apical meristem producing leaves (Mueller, 1983; Steingraeber and Fisher, 1986; Steeves and Sussex, 1989; Fisher and Rutishauser, 1990; Miesch, 1990; Miesch and Barnola, 1993; Fukuda *unpubl. res.*, 2001). Both shoot tips and leaf tips of *Chisocheton* and *Guarea* show seasonal flushing. Each time the shoot apical meristem adds new leaves, the leaf apical meristem also initiates new leaflets. Thus, the meristematic leaf tips and the meristematic shoot tips react to the same endogenous or environmental stimuli. Moreover, the leaf axis (i.e. petiole and rachis) increases in diameter due to secondary thickening with wood production. In addition, certain species of *Chisocheton* produce epiphyllous shoots (*Ch. tenuis*, Fig. 6) or epiphyllous inflorescences (*Ch. pohlianus*; Stevens, 1975). Thus, compound leaves of *Chisocheton* and *Guarea* have developmental routines resembling whole shoots.

(5) Leaf inception does not normally use up the whole shoot apical meristem. Exceptions to this rule are terminal leaves which are also called non-appendicular leaves because they do not arise as lateral appendages. Arber (1928) described terminal leaves in the grass *Gigantochloa*. Troll (1937) observed terminal leaves in seedlings of other monocots. Terminal leaves are also found in certain Podostemaceae (eudicots) such as *Mourera fluviatilis* where the terminal leaf of the spike-like inflorescences is initiated first and all other bracts are incepted in basipetal sequence along two rows (Rutishauser and Grubert, 1999). This pattern (terminal appendage first, then basipetal inception of lateral appendages) is very unique for shoots whereas it is quite common for imparipinnate leaves in many flowering plants (e.g. *Polemonium caeruleum*; Hagemann, 1970, 1984; Rutishauser and Sattler, 1997; Gleissberg and Kadereit, 1999).

Developmental genetic evidence in favour of the partial-shoot theory of the leaf (23)

According to molecular genetics, various developmental mosaics found in vascular plants are due to ectopic expression of organ identity and the activity of homeotic genes (see section 17). Changes of control functions can cause developmental processes originally expressed in one organ to appear in another (i.e. homeosis). There are many original publications and reviews on the molecular basis of leaf development with support of the partial-shoot theory of the leaf (e.g. Tsukaya, 1995; Chuck *et al.*, 1996; Rutishauser and Sattler, 1997; Sinha, 1999; Hofer *et al.*, 2001; Fukuda *unpubl. res.*, 2001). The prediction based on Arber's theory is that some genes would be involved in the elaboration of both shoot axes (including vegetative stem

and floral axes) and compound leaf axes (including petiole and rachides):

(1) As early as 1929, Uittien reported that in some plants the same genes may influence both stem length and leaf length (e.g. in *Chelidonium*). He found a correlation of stem (inflorescence) length and leaf length for numerous other angiosperms (e.g. *Wisteria sinensis*). New findings point to the same fact. Some mutants of arabidopsis have the same defect in the petiole and in the stem. According to Tsukaya *et al.* (1995), the *acaulis* 2 mutant has a defect in the elongation of the inflorescence axis, the flower stalks (pedicels) and the leaf petioles, but leaf blades are of normal size. Tsukaya (1995 p. 407) concluded that the petiole should be considered separately from the leaf blade, as an axial organ more similar to the stem. According to him, 'leaves share some common features with stems'.

(2) Compound leaves in pea (*Pisum sativum*) have been likened to reproductive determinate shoots. Hofer *et al.* (1997, 2001), Hofer and Ellis (1998) and Gourlay *et al.* (2000) have described the developmental genetics of the pea leaf from the viewpoint that considers it as a determinate lateral shoot somewhat comparable to a flower or a floral shoot. This parallel is based on the recent cloning of the pea leaf mutation *unifoliata*. This gene regulates both compound leaf and flower morphogenesis in pea. *Unifoliata* is the orthologue of the floral meristem identity genes *FLORICAULA* (*FLO*) from *Antirrhinum* and *LEAFY* (*LFY*) from arabidopsis. All three are important representatives of the *FLO*-like meristem identity genes which are required for the transition from inflorescence to floral meristems (i.e. conversion of meristem identity). In their absence, the inflorescence programme is continuously reiterated (cf. Fig. 2; see section 16; reviews by Hasebe and Ito, 2000; Theissen, 2000). According to Sinha (1999), it can be hypothesized that the function of *FLO*-like genes in developing leaves may be restricted to species with compound leaves, since loss-of-function mutations at *FLO/LFY* in *Antirrhinum* and arabidopsis do not show any abnormalities in leaf development. Thus, at least in pea and some other flowering plants, the compoundedness (branching) of a leaf may be due to the expression of shoot-specific genes in the leaf (Hofer *et al.*, 1997, 2001; Tsukaya, 1998; Sinha, 1999).

(3) Hareven *et al.* (1996) concluded from developmental genetic experiments that the compound leaf in tomato is formed not by a 'simple-leaf' developmental program that is reiterated, but, instead, by a unique 'compound-leaf' developmental program (see reviews by Rutishauser and Sattler, 1997; Brutnell and Langdale, 1998; Reiser *et al.*, 2000). Jackson (1996) added: 'Perhaps one should consider the tomato leaf as sharing characteristics of both shoot and leaf identities, an idea that has been proposed for other compound leaves'. Mutants that fail to maintain the shoot apical meristem and axillary meristems in tomato initiate apical meristems at the junctions (i.e. pseudo-axils[13]) between the petiolule

[13]See Fig. 37 for clarification!

and rachis. The mutation can be phenocopied by overexpressing homeobox genes (Janssen *et al.*, 1998) or pruning off all axillary and terminal meristems (Miesch, 1990). Sinha (1999) wrote: 'This suggests that the tomato compound leaf has some stem-like features and may be an intermediate structure between simple leaves and stems, although this finding may not be generalizable, and compound-leafed species will have to be evaluated case by case'.

(4) Leaflets of compound leaves can be accompanied by outgrowths from the leaflet insertion areas. These so-called 'stipels' resemble stipules and may be interpreted as echo-like repetitions of the leaf developmental pathway in each leaflet site (Arber, 1950). They arise at the insertion area of leaflets whereas stipules are inserted at the leaf basis (e.g. *Phaseolus*, Fig. 37). Stipels are restricted to some dicotyledons which also possess stipules (see section 20). Normally, stipels are small teeth, scales or glands at the insertion area of the leaflets, with two stipels at the base of the terminal leaflet, and one stipel per lateral leaflet. In arabidopsis, the *KNAT1* mutant possesses stipels which were called 'stipules' by Chuck *et al.* (1996). Wild-type arabidopsis lacks stipels although rudimentary stipules at the leaf base are present[14]. Chuck *et al.* (1996) described shoot-like features of the lobed leaves in arabidopsis that resulted from expression of the homeobox gene *KNAT1*. These findings suggest that *knox* genes may also have played a role in the evolution of stipules and stipels of compound leaves (see sections 11 and 14).

(5) Ectopic expression of a gene refers to its expression outside the usual domain (Westhoff *et al.*, 1998). Concepts with similar or identical meaning as ectopic expression of 'organ identity' are heterotopy and homeotic transformation (Sattler, 1975; Weston, 2000; see section 17): organs or other biological structures arise in positions not predicted by the body plan. Ectopic expression of homeotic genes such as *knox* genes has been engineered in barley, maize, tobacco and arabidopsis, and results in the alteration of cell fates and, in the most extreme cases, in the formation of shoots on leaves. Based on these observations it was proposed that *knox* genes have a role in maintaining cells of the shoot apical meristem in an undifferentiated state. Presumably, overexpression or ectopic expression of *knox* genes in regions of the leaf blade prevents cells from perceiving, or responding to positional information that confers 'leaf identity' and, instead, they adopt the 'identity of shoot meristems' (Chuck *et al.*, 1996; Brutnell and Langdale, 1998; Reiser *et al.*, 2000; see next paragraph, and sections 16 and 17).

(6) Arber (1934) described and illustrated Nepaul barley (*Hordeum trifurcatum*) as an example of a shoot-bearing leaf. It shows epiphyllous spikelets arising from the awned lemma. By examining their relative positions, Arber (1934 p. 312) concluded that the

lemma[15] (bract) 'which is a *leaf* member, behaves to the accessory spikelet in all respects as if it were that spikelet's parent *axis* [her italics]. And so we return–as we so often must–to the standpoint of Goethe (1790), whose morphological insight led him long ago to recognise the fertility which lies hidden in a leaf'. The very same situation is found in the *Hooded* mutant of *Hordeum vulgare* which was described later by Stebbins and Yagil (1966) and Yagil and Stebbins (1969): the lemma (bract) produces one or more ectopic spikelets on the awn. Molecular studies (Müller *et al.*, 1995; Reiser *et al.*, 2000) have elucidated that the *Hooded* phenotype of barley is caused by misexpression of the *knox* gene *Hvknox3*. Williams-Carrier *et al.* (1997) suggested that the inverse polarity of the ectopic spikelets seen in the *Hooded* mutant of barley and transgenic *KN1* plants of maize results from the homeotic transformation of the lemma awn into a reiterative inflorescence axis. These are examples of conversion of organ identity: a leaf part (the awn) is converted into a shoot axis. Similar conversions are known from *Utricularia* as will be shown in sections 25–29 (e.g. Fig. 31).

(7) Let us again consider the role of meristems in stem tips and leaf tips. Leaf initiation at the shoot apical meristem and leaflet initiation at the leaf apex may be modulated by the same or similar internal (biochemical) effectors (e.g. Cusset, 1986; Jeune and Lacroix, 1993). The same regulatory genes may be expressed in both types of meristems. Additional arguments in favour of homologous roles of shoot apical meristems and leaf apical meristems in flowering plants and ferns may be available when cell lineage and molecular analyses have been made in stem and leaf tips of plants with acropetally developing pinnate leaves. Most clonal and molecular analyses published to date only cover shoot apices (e.g. Medford *et al.*, 1992; Poethig and Szymkowiak, 1995; Poethig, 1997; Gleissberg *et al.*, 2000), whereas such studies on meristematic leaf tips with acropetal leaflet initiation are still lacking, except for that by Fukuda (*unpubl. res.*).

Process morphology[16] (24)

Both the ClaM and FAM Approach have shortcomings because both depend on the recognition and definition (crisp or fuzzy) of structural categories (Table 1). Process morphology (process thinking) may be a way of overcoming these shortcomings because it allows the replacement of structural categories by process combinations ('developmental routines'). This is an alternative way to describe plant development by giving emphasis to the observable developmental processes rather than sticking to structural categories such as 'leaf' and 'stem' and their organ identities (Sattler, 1992, 1994). The central tenet of Sattler's approach is that organisms are not structures that *have* developmental processes, they *are* developmental

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[14]For scanning electron micrographs showing arabidopsis leaves with rudimentary stipules see Bowman (1994).

[15]Arber (1934 p. 312) used here the term 'flowering glume' as synonymous to 'lemma'.

[16]See footnote 4.

processes (Sattler and Rutishauser, 1990, 1997; Weston, 2000; Kirchoff, 2001). Process morphology allows whole plants to be seen as combinations of developmental processes instead of more or less arbitrarily assigning plant parts to categories such as 'root', 'stem' and 'leaf'. Structural descriptions (i.e. ClaM and FAM Approach) and dynamic descriptions in terms of process morphology are complementary, as exemplified by Sattler and Rutishauser (1990) in *Utricularia* spp. (sections 25–29). Parameters for process morphology with respect to vascular plant development are growth duration, symmetrization (e.g. acquisition of dorsoventral symmetry), positioning, branching, tropism, rhythm, reiteration and senescence. Process combinations ('developmental routines') are canalized during land plant evolution, leading to body plans (Zimmermann, 1953, 1959; Jeune and Sattler, 1992, 1996; Graham *et al.*, 2000; Niklas, 2000; Classen-Bockhoff, 2001). With regard to evolution, the question is as follows: How and why have process combinations changed during ontogeny and phylogeny?

Various developmental geneticists seem to be aware of the advantages of process morphology. Much architectural diversity in vascular plants results from the varied growth patterns of apical and axillary meristems (Sussex and Kerk, 2001). A suite of developmental processes leads from the leaf primordium to the mature leaf. Tsukaya (1998 p. 113) subdivided leaf morphogenesis of arabidopsis and *Antirrhinum* into subsequent processes (phases). He admitted: 'The mechanisms regulating each process of morphogenesis, such as leaf determination, establishment of dorsoventrality and polarity recognition, remain unknown. Molecular genetics seems to prove the most suitable approach to such processes and should allow us to dissect the relevant developmental pathways into genetically programmed, unit processes'. Developmental geneticists are gaining a better understanding of developmental processes leading to flattened dorsoventral leaves. For example, adaxialization is a fashionable concept explaining leaf development. It is a developmental process in vascular plants that leads from an uncommitted primordium to a flattened leaf with dorsoventral symmetry. Thus, adaxialization is a step towards acquisition of 'leaf identity'. The lamina may be seen as an adaxial character of the leaf primordium (e.g. Sylvester *et al.*, 1996; Brutnell and Langdale, 1998; Sinha, 1999; Gleissberg *et al.*, 2000; Hudson, 2000; Byrne *et al.*, 2001). *Phantastica* (*phan*) mutants of *Antirrhinum* lack the adaxializing (= lamina broadening) function. Instead of a flattened lamina, *phan* mutants possess centric = unifacial (i.e. radially symmetric, needle-like) leaves with abaxial characters around their circumference (Waites and Hudson, 1995; Scanlon, 2000; Byrne *et al.*, 2001). According to Gleissberg *et al.* (2000), 'unifacial, abaxialized leaf sectors can form by a localised and controlled downregulation of a factor conferring adaxial identity'. Adaxialization of the young leaf seems to be a prerequisite for axillary branching. In seed plants and some other vascular plants, daughter shoot meristems develop as axillary buds in close association with the adaxial leaf base at the junction of leaf and stem (see section 18). Thus, the 'adaxial leaf domain' renders competency to

develop axillary buds (Scanlon, 2000). McConnell and Barton (1998) described the mutation *phabulosa-1d* in arabidopsis. This dominant mutation affects leaf polarity such that adaxial characters develop in place of abaxial leaf characters, including ectopic shoot meristems on the undersides of leaves, while well developed leaf blades are lacking. Altered leaf polarity, including upside-down positioning of the lateral branch and subtending leaf, occurs as a developmental idiosyncrasy in certain *Utricularia* species (e.g. *U. longifolia, U. sandersonii*; Figs 15, 17, 22 and 23, see section 26).

CASE STUDY: MORPHOLOGICAL EVOLUTION IN *UTRICULARIA* (BLADDERWORTS) AND THE HEURISTIC VALUE OF THE FAM APPROACH

Introductory remarks (25)

Flowering plants with body plans that deviate strongly from the ClaM Approach and the classical model may be called 'misfits' (Bell, 1991). However, Bell adds that 'misfit' is not the problem of the plant, but the problem of our inadequate thinking and concepts. Morphological misfits do not fit into the ClaM Approach which is useful as a rule of thumb in many other groups of flowering plants. Misfits are found in various aquatic vascular plants such as the Lemnaceae (duck-weeds) and the Podostemaceae (river-weeds; Rutishauser, 1995, 1997; Lemon and Posluszny, 2000). Extreme morphological misfits are also found in the bladderworts (*Utricularia* spp.) which belong to the Lentibulariaceae. All 214 *Utricularia* species are provided with sucking traps (Figs 21 and 29) which only act in water, although several species do not live as submerged aquatics (Taylor, 1989; Jobson *et al.*, 2000). Many species are able to live as terrestrial members on moist soil (e.g. *U. livida, U. sandersonii*, Fig. 15; *U. longifolia*, Fig. 17) or as epiphytes on trees (e.g. *U. alpina*, Fig. 12). The terrestrial and epiphytic species became secondarily released from the aquatic environment (Brugger and Rutishauser, 1989; Cook, 1999). Their traps catch prey in wet soil, in water-filled holes or even in cisterns of bromeliad rosettes (Taylor, 1989).

Species of *Utricularia* show various examples of developmental mosaics between structural categories which are called for convenience 'leaf' and 'stem', even in this paper. In certain aquatic members such as *U. purpurea* (Fig. 9), the developmental pathway of the whole shoot is repeated within each compound leaf to an astonishing degree (Rutishauser, 1999). This, together with other observations, led Goebel (1891) to the somewhat exaggerated conclusion that a primordium in *Utricularia* can grow into any organ such as a trap, leaf, green shoot (i.e. leafy stem), anchorage shoot, or inflorescence. This generalization is only partly appropriate. Nevertheless, the developmental and positional constraints in *Utricularia* deviate considerably from the rules used in Classical Morphology. *Utricularia*'s plant body, thus, may be better understood within the conceptual framework of Fuzzy Arberian Morphology (compare sections 9 and 10, Table 1).

Nine rules for a better understanding of Utricularia *body plans (26)*

To summarize what is already known of the morphological and developmental peculiarities (idiosyncrasies) in *Utricularia*, nine 'rules' are formulated which are based mainly on the studies of Brugger and Rutishauser (1989), Rutishauser and Sattler (1989), Sattler and Rutishauser (1990) and Rutishauser (1993, 1999):

(1) The orthodox distinction of 'root', 'stem' and 'leaf' is transcended throughout the genus *Utricularia*. For descriptive purposes, the flat, determinate, photosynthetic organs may be called 'leaves', whereas the cylindrical, indeterminate structures carrying rosettes and other organs may be labelled 'stolons'[17] (i.e. elongated leafy stems; Figs 9–10 and 12–33). In aquatic species such as *U. aurea* and *U. foliosa*, the 'leaves' and the various types of 'shoots' (e.g. floating photosynthetic ones) and the inflorescences may be interpreted as partially homologous to each other. These structural categories share as 'fuzzy sets' some but not all developmental processes (Jeune and Sattler, 1992; Sattler and Jeune, 1992; Rutishauser, 1993). This situation in *Utricularia* is also known as 'leaf-shoot indistinction' due to a 'relaxed body plan' (Albert and Jobson, 2001; Jobson and Albert, 2001).

(2) In certain *Utricularia* spp. the meristematic stolon tips are coiled towards the dorsal (= upper) side (i.e. the side pointing towards the sky and away from the soil). This is the case in many aquatic species such as *U. aurea, U. australis, U. foliosa, U. macrorhiza* and *U. purpurea*, as well as in various terrestrial and epiphytic species such as *U. alpina* (Figs 19 and 20) and *U. dichotoma* (Reut and Fineran, 2000). However, other species such as *U. livida, U. longifolia* and *U. sandersonii* have straight stolon tips (Figs 24, 28, 33). Also, growing leaf tips can be coiled in *Utricularia* spp. Coiled leaf tips (i.e. circinate vernation) are found in species with straight stolon tips such as *U. longifolia* (Fig. 30) as well as in species with coiled stolon tips such as *U. alpina* and *U. foliosa*. Thus, shoots and leaves of various *Utricularia* species behave like fern leaves, showing prolonged apical growth and circinate vernation.

(3) Bladders may arise from stolons as well as from leaves in terrestrial species such as *U. sandersonii* (Figs 15, 16 and 23). In other terrestrial to epiphytic species (e.g. *U. longifolia, U. alpina*) the traps are restricted to thin stolons (Figs 12–14 and 16–18). In aquatic species (e.g. *U. foliosa, U. purpurea*) bladders are parts of the dissected leaves.

(4) Normal axillary branching along the stolons is lacking in most species. Branching occurs without a subtending leaf, i.e. extra-axillary (e.g. in *U. alpina, U. purpurea*; Figs 9, 12, 19 and 20), or the positions of leaf and axillary branches can be interchanged along the mother stolon (stem): the subtending leaf points towards the distal end of the mother stolon whereas the axillary

[17]Also called 'runners' by Kaplan (1998) and 'runner stolons' by Reut and Fineran (2000).

shoot bud points towards the proximal end of the mother stolon (e.g. in *U. dichotoma, U. longifolia* and *U. sandersonii*; Figs 15, 17, 22 and 23; Reut and Fineran, 2000). This upside-down position of lateral branch and subtending leaf may also be called 'inverse axillary branching' (see section 24).

(5) The stolons have different morphogenetic potential which depends not only on the sector and the diameter of the stolon but also on the systematic group (Taylor, 1989). The stolons of the three species illustrated in Figs 12–18 show different dorsoventral patterns of lateral appendages (as described in more detail in the legends). Most structures arise along the dorsal (upper) stolon sector, including leaves and buds (rosettes) of daughter stolons, additional leaves and inflorescences. The lateral stolon sectors (flanks) may produce appendages different from those along the dorsal side. In terrestrial and epiphytic species there are thin stolons or bladders = utricules which arise along the flanks (Figs 13, 14, 16 and 18). In aquatic *Utricularia* spp. such as *U. aurea, U. australis, U. foliosa* and *U. macrorhiza*, the flank positions are occupied by dissected, bladder-bearing leaves whereas the dorsal stolon sector forms only thread-like respiratory shoots ('air-shoots') and inflorescences (Taylor, 1989; Sattler and Rutishauser, 1990). The ventral stolon sector of most species is free of appendages.

(6) The appendages within the vegetative rosettes along the upper stolon sector may often be arranged in an irregular phyllotactic pattern, e.g. in *U. sandersonii* (Figs 23 and 24). In other species such as *U. alpina*, the rosette formation follows a strict regular pattern: firstly, formation of two opposite primordia which always develop into thick daughter stolons; secondly, formation of three bumps which are arranged in a triangle (Fig. 19).

(7) The developmental fate ('organ identity') of the various primordia in a rosette is not fixed in early development. Thus, the rosette outgrowths (leaves or stolons) are interchangeable to some degree, depending on the species and the rosette position. For example, the two bumps labelled with asterisks (*) in Fig. 19 (*U. alpina*) may grow into two stolons, or into two leaves, or into a stolon and a leaf (see quantitative analysis in Brugger and Rutishauser, 1989). Conversion of organ identity in *Utricularia* is even possible in a very late stage of leaf or stolon development. Occasionally the tip of a nearly mature leaf can continue its growth and become a stolon again (e.g. *U. longifolia* with conversion leaf → stolon in Fig. 31). The reverse switch is also possible: in certain *Utricularia* spp. a stolon can become determinate and flat, forming a terminal leaf (Troll and Dietz, 1954).

(8) Inflorescences usually arise from rosettes which are positioned along the dorsal (upper) stolon sector (Figs 13, 15 and 16). During the switch from the vegetative rosette phase to inflorescence formation, *Utricularia* species usually return to the typical angiosperm body plan with spirally arranged bracts along the inflorescence axis (peduncle) and normal axillary branching leading to a raceme (Fig. 15). In aquatic

Utricularia species, the additional appendages at the peduncle base may form a few anchorage shoots (so-called 'rhizoids'), or in a few species such as *U. aurea*, may also form a whorl of floats (Rutishauser, 1993).

(9) The transition back to the normal axillary branching (i.e. a proximal leaf with a branch in its distal axil) occurs gradually (e.g. in *U. sandersonii*, Fig. 15): firstly, axillary branching occurs but with a stolon (not a leaf) as subtending organ (Fig. 25); secondly, typical bracts occur as subtending organs but axillary products consisting of stolons only (Fig. 26); finally, the typical cormophytic constellation with bracts, bracteoles and axillary flowers (Fig. 27).

The plant body of Utricularia *is best interpreted according to Fuzzy Arberian Morphology (FAM Approach) (27)*

Taylor (1989 p. 6), the excellent monographer of the genus *Utricularia*, was aware of the problems with organ delimitation and definition in this genus. He wrote: 'For taxonomic and descriptive purposes, whatever their true or theoretical nature, it is desirable to have a consistent terminology for the various organs'. Similarly, we have used the concepts 'leaf', 'stolon' (stem or runner) and 'shoot' (leafy stem) in the nine rules given above. Agnes Arber (1920) in her early book on water plants used the concepts 'leaf' and 'shoot' for descriptive purposes only. Arber (1920 pp. 103–106) argued in a matter that coincides with Fuzzy Arberian Morphology: '... but it now remains to consider how far current morphological conceptions can be applied to so anomalous a genus as *Utricularia*. There has probably been more controversy about the morphological nature[18] of the different organs of these plants, than about such problems in the case of any other Angiosperm ... In this genus the distinction habitually drawn by botanists between stem and leaf, breaks down completely. The bladder is probably best interpreted as a modification of part of the 'leaf', but even if this be conceded, it does not carry us far, since the nature of the 'leaf' itself still stands in dispute. By some authors, the entire vegetative body, apart from the inflorescence axis, has been regarded as a root system, while others view it either as wholly axial or as consisting of stems and leaves. A view which has received considerable prominence, is that the entire plant is a much divided leaf[19], but if this be so, it must, as Goebel (1891) has pointed out, be admitted that this 'leaf' possesses many characters which we are accustomed to stems alone: long continued apical growth, as well as power of bearing leaves and axillary branches and of developing in more than one plane. The fact that adventitious shoots are produced on the leaves of other Lentibulariaceae is, however, favourable to this view (Goebel, 1904). The unique plasticity of the *Utricularias* is indicated by the many observations on regeneration phenomena in the genus, which show that almost any part of these plants can produce new shoots at will ... As

illustrations of the numerous abnormalities on record, it may be noted that an inflorescence-bract sometimes develops into a water-leaf or even an entire water-shoot, while a bladder rudiment may develop into a water-shoot. In the development of the seedling, the primary leaves may be replaced by stolons'[20]. Arber (1920 pp. 106–107) concluded as follows: 'In general, the only safe conclusion to be drawn from a study of the available evidence regarding the nature of the organs in the Bladderworts, seems to be that—in the present state of our ignorance—the attempt to fit so elusive a genus into the Procrustean bed of rigid morphology, is doomed to failure. It is probably best, as a purely provisional hypothesis, to accept the view that the vegetative body of the *Utricularias* partakes of both stem nature and leaf nature[21]. How such a condition can have arisen, historically, from an ancestor possessing well-defined stem and leaf organs, remains one of the unsolved mysteries of phylogeny'. Arber was probably satisfied with this 'fuzzy' conclusion. To our knowledge, she never mentioned *Utricularia* again in all her books and publications after 1920!

Despite Arber's thought-provoking comments, many 20th century botanists went on to interpret the vegetative body of *Utricularia* spp. in the framework of Classical Plant Morphology. The resulting contradictory interpretations clearly show the shortcomings of the ClaM Approach (as reviewed in Brugger and Rutishauser, 1989; Sattler and Rutishauser, 1990; Rutishauser, 1999). For example, the shoots of *Utricularia purpurea* (Fig. 9) were interpreted as having no leaves at all (Schmucker and Linnemann, 1959). Troll and Dietz (1954) concluded similarly with respect to the shoots of terrestrial and epiphytic *Utricularia* species. According to them, the so-called 'leaves' of *U. longifolia* (Fig. 17) are nothing but 'phylloclades', i.e. phyllomorphic shoots. Kaplan (1998) came to the opposite conclusion that in *Utricularia* (all species?) the whole vegetative body is a much divided, indeterminate leaf that is provided with epiphyllous inflorescences.

The distinction of 'roots' from 'shoots' in vascular plants, especially in Lentibulariaceae (28)

There are four key features which are normally used to distinguish *roots* from SHOOTS = LEAFY STEMS (root features in *italics*, shoot features in SMALL CAPITALS): (1) *presence* vs. ABSENCE of a root cap (calyptra); (2) *absence* vs. PRESENCE of exogenously formed leaves (scales); (3) xylem and phloem in *alternating sectors* vs. xylem and phloem in the SAME AXIAL SECTORS (often as parts of COLLATERAL BUNDLES); (4) *endogenous* vs. EXOGENOUS origin of daughter axes[22]. These four key criteria are used in comparative morphology (e.g. Sattler and Jeune, 1992; Cusset, 1994;

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[18]'Morphological nature' equals 'organ identity' according to modern molecular genetic literature (see section 16).

[19]Kamienski (1877) is cited in Arber (1920) as an early proponent of this view. A modern proponent of this view is Kaplan (1998).

[20]See Goebel (1891, 1928), Brugger and Rutishauser (1989), Kaplan (1998).

[21]Arber's interpretation is identical to the acceptance of developmental mosaics between 'leaves' and 'stems' of more typical angiosperms (see section 10). It may be also called 'leaf-shoot indistinction' (see section 26).

[22]Daughter roots along roots and stems, however, are initiated endogenously in most vascular plants.

Hagemann, 1999) and developmental genetics (e.g. Scheres *et al.*, 1996). It is widely believed that all members of the lentibulariaceous genera *Utricularia* and *Genlisea* have lost their 'roots' completely whereas the sister genus *Pinguicula* still has 'roots' (e.g. Troll, 1939 p. 1858; Schmucker and Linnemann, 1959; Reut and Fineran, 2000; Albert and Jobson, 2001; Jobson and Albert, 2001). However, the stolons of various *Utricularia* species (e.g. *U. longifolia, U. sandersonii,* Figs 10 and 31–33) strongly resemble the roots of *Pinguicula* (e.g. *P. moranensis;* Figs 11 and 34–36; Brugger and Rutishauser, 1989). Firstly, the meristematic tips of *Utricularia* stolons as well as *Pinguicula* roots lack a calyptra (Figs 33 and 36); secondly, both show a central cylinder with a random arrangement of phloem and xylem elements (i.e. no collateral bundles, Fig. 32); thirdly, both *Pinguicula* roots and *Utricularia* stolons may show positive geotropic growth (Figs 10 and 11). There are two remaining differences between *Pinguicula* roots and *Utricularia* stolons: *Pinguicula* roots arise endogenously from cortical tissue of the leaf bases and do not carry leaves (Figs 11, 34 and 35) while *Utricularia* stolons arise as exogenous buds (e.g. Figs 24, 25 and 31) and have the morphogenetic capacity to produce leaves from exogenous primordia.

The evolutionary breakdown of the typical angiosperm body plan in Lentibulariaceae—Utricularia *'stolons' and* Pinguicula *'roots'[23] have overlapping developmental pathways (29)*

As mentioned above, the roots of *Pinguicula* are more similar to stolons of *Utricularia* than to typical roots of angiosperms outside the Lentibulariaceae. This fact allows us to propose the following prediction which must be tested by genetic analysis: in spite of their different labelling, *Utricularia* 'stolons' and *Pinguicula* 'roots' share pertinent developmental processes which may be due to the expression of orthologous regulatory (homeotic) genes in both kinds of cylindrical organs. Accepting *Pinguicula* as a genus more basal than *Utricularia* within the Lentibulariaceae, we may hypothesize that the so-called 'roots' of a *Pinguicula*-like ancestor 'learnt' how to make exogenous 'leaves'. This evolutionary novelty (i.e. key innovation) gave rise to a multitude of stolon types in *Utricularia*. Such a hypothesis may also explain the downwards growing 'root-like leaves' (in German: 'Wurzelblätter') of *Genlisea* (18 spp.) which also belongs to the *Genlisea-Utricularia* clade (Reut, 1993; Jobson *et al.*, 2000).

Many botanists believe that both *Genlisea* and *Utricularia* do not have roots at all (Kaplan, 1998 and references therein). The evolutionary breakdown (or decanalization) of the typical angiosperm body plan may have arisen in a *Pinguicula*-like ancestor that returned to an aquatic habitat. As aquatic plants, the ancestor became released from pressures of the more sele ··ve terrestrial environment. Thus, the ancestral form had no need to retain typical

'roots', 'stems' and 'leaves', which may be viewed as peaks of a terrestrial fitness landscape (Stebbins, 1974; Niklas, 1997; Cook, 1999). Instead, the resulting aquatic genera *Genlisea* and *Utricularia* evolved different body plans which are better suited for life in water and wet mud, i.e. as solutions of an aquatic fitness landscape (Niklas, 1997). In the framework of the FAM Approach, the deviating body plans in Lentibulariaceae are due to the amalgamation of the developmental pathways which are called 'leaves', 'stems' and 'roots' in the terrestrial ancestors of the *Genlisea-Utricularia* clade, and not only by root loss (Brugger and Rutishauser, 1989). This view, however, leads to the additional question of why epiphytic *Utricularia* species, i.e. taxa that have left again the aquatic or wet terrestrial environment, still retain some of the developmental idiosyncrasies of their aquatic ancestors. Moreover, the unusual body plans of the *Genlisea-Utricularia* clade are restricted to the vegetative growth phase. During their reproductive growth phase they all return to the typical angiosperm body plan with normal axillary branching and often spiral phyllotaxy (Fig. 15; Sattler and Rutishauser, 1990). Thus, the decanalization of the body plan in Lentibulariaceae is probably partly genetically fixed and partly environmentally triggered (cf. Hay and Mabberley, 1994). According to Jobson and Albert (2001), *Utricularia* features such as 'rootlessness, asymmetrical phyllotaxy and leaf-shoot indistinction resemble phenotypes of known auxin transport mutants, suggesting that one or few genes of large effect could underlie bladderwort developmental release'. New developmental genetic studies may finally show whether the hypothesis of 'root loss' (as proposed again by Albert and Jobson, 2001) or that of 'exogenous leaf formation by transformed roots' best explains the evolution of the unique body plans of the *Genlisea-Utricularia* clade from ancestral asterids with a typical angiosperm body plan!

There are other groups of vascular plants (especially some water plants) that do not show a clear differentiation into 'roots', 'stems' and 'leaves', at least not during their vegetative growth. In ferns and seed plants, 'there are a number of cases in which roots become transformed into shoots at the apex by throwing off their root caps and forming leaves' (Goebel, 1905 pp. 226–227, as cited in Kaplan, 1998). Evolutionary breakdowns of any clear root-stem-leaf differentiation also occurred in *Lemna* and allies (Araceae), in various Podostemaceae and in epiphytic filmy ferns (Arber, 1920; Goebel, 1928 p. 127; Troll, 1937 p. 255; Rutishauser and Sattler, 1985, 1989; Rutishauser, 1997; Schneider, 2000; for other examples see Cusset, 1994).

CONCLUSIONS

In the 20th century, comparative plant morphology has undergone fundamental conceptual, theoretical and philosophical changes. These changes lead to different questions and may redirect the course of research in evolutionary botany and developmental plant genetics. Agnes Arber's oeuvre is still worth reading. It opens our eyes to the assumptions (axioms) on which biological sciences are regularly based. In this paper we have drawn special

[23]As-if-ism allows labelling of the 'rooting' cylindrical, leafless organs of *Pinguicula* as 'roots' although they seem to be more similar to *Utricularia* stolons than to typical roots of asterid angiosperms (see section 3).

attention to the idea of a dynamic continuum in the body plans of vascular plants. We do not claim that Classical Plant Morphology (i.e. ClaM Approach) has been devoid of dynamic or continuum thinking. It has, however, been constrained by the assumption of a more or less rigid categorical framework (Fig. 38). Fuzzy Arberian Morphology (i.e. FAM Approach, including 'continuum morphology') transcends this constraint to a great extent because mutually exclusive structural categories are replaced by peaks in a heterogeneous continuum; structural categories in many vascular plants are fuzzy sets with less frequent developmental mosaics in between (Fig. 39; Sattler and Rutishauser, 1997). Process morphology, as proposed by Sattler (1992, 1994), is even more radical by getting rid of all arbitrarily assigned plant parts and using instead combinations of developmental processes. Comparative plant morphology with its three complementary ways of model thinking—ClaM Approach, FAM Approach and Process Morphology—is a strong biological discipline that is relevant to related fields such as developmental genetics, molecular systematics and evolutionary biology. Special emphasis is given in this paper to the concept of 'leaf' as a structural category in vascular plants. Arguments are added in favour of the FAM Approach, especially in favour of Arber's partial-shoot theory. The genus *Utricularia* (Lentibulariaceae) with its aquatic, terrestrial and epiphytic members serves as a case study. The ClaM Approach fails in *Utricularia* and other vascular plants with deviating morphologies.

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