

Sattler's dynamic morphology: an acme or a reverie?

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Summary: Sattler's dynamic morphology is erroneously regarded as an alternative to typological (= essentialistic) morphology. When strictly applying its principles which are inconsistent, homologisation of any structure becomes impossible. This undermines the very nature of morphology which is intended for revealing correspondences between structures of different living beings. When we consider the semi-quantitative estimate of structural characters to be opposite to the homologisation of structures, Sattler's principles are generally not applicable because such an estimate needs regular appealing to structural standards (= merons) that are only established in typological morphology. Dynamic morphology is a part of typological morphology which aims to tackle the problem of revealing and precise scopes of application of merons.

Zusammenfassung: Sattlers 'dynamic morphology' wird fälschlicherweise als Alternative zur typologischen (=essentialistischen) Morphologie angesehen. Wendet man ihre Prinzipien, die inkonsistent sind, strikt an, wird die Homologisierung jeglicher Struktur unmöglich. Dies untergräbt genau den Kern der Morphologie, die gerade dazu bestimmt ist, Übereinstimmungen zwischen Strukturen verschiedener Lebewesen aufzuzeigen. Wenn wir eine semi-quantitative Bewertung struktureller Merkmale als Gegensatz zur Homologisierung von Strukturen betrachten, sind Sattlers Prinzipien meist unbrauchbar, denn eine derartige Bewertung benötigt eine geregelte Anwendung struktureller Standards (= 'merons'), die es nur in der typologischen Morphologie gibt. Die 'dynamic morphology' ist ein Teil der typologischen Morphologie, die das Ziel hat, das Problem der aufschlussreichen und exakten Anwendungsbereiche struktureller Standards zu lösen.

Keywords: plant morphology, dynamic morphology, typological morphology, fundamentals of morphology, merons

In 1966, Sattler challenged plant morphology which had been flourishing for about one and a half centuries. The criticised morphology is based on the idea of strict homology of every plant structure. It was repeatedly attacked thereafter by Sattler and his fellows (SATTLER 1984, 1988; RUTISHAUSER & SATTLER 1985, 1989; LACROIX & SATTLER 1994, etc.) to replace it by the new dynamic morphology, free of the strict dogma of homology. After more than 35 years of dynamic morphology, it is now time for a careful reflection.

Typological morphology versus dynamic morphology Aim and scope of typological morphology

Morphology, just as every science, is intended to discourse upon different phenomena realised as displays of some general laws. Plant morphology is based on such laws that can be recognised as types of structures/organs (e.g. phyllome, leaf, stamen etc.) (MEYEN 1978; LIUBARSKI 1996). Those are called merons (Greek μέρος for part) by MEYEN (1977, 1978). Constructing types of organs/structures (= set of merons) is a subject of a special scientific branch, called typology. Therefore, SATTLER (1966) considered the whole pre-Sattlerian morphology to be typological. Morphological treatment of a structure means revealing its homology, i.e. relating it to one of the accepted merons. The procedure is possible if only two prerequisites are a priori assumed to exist: (1) really obtainable, clearly delimited merons; the more distinctive merons are established, the more advanced is typological morphology. (2)

every structure under consideration can unequivocally be attributed to one meron. Otherwise, the homology of the concerned structure cannot be revealed with confidence and thus morphology would be useless.

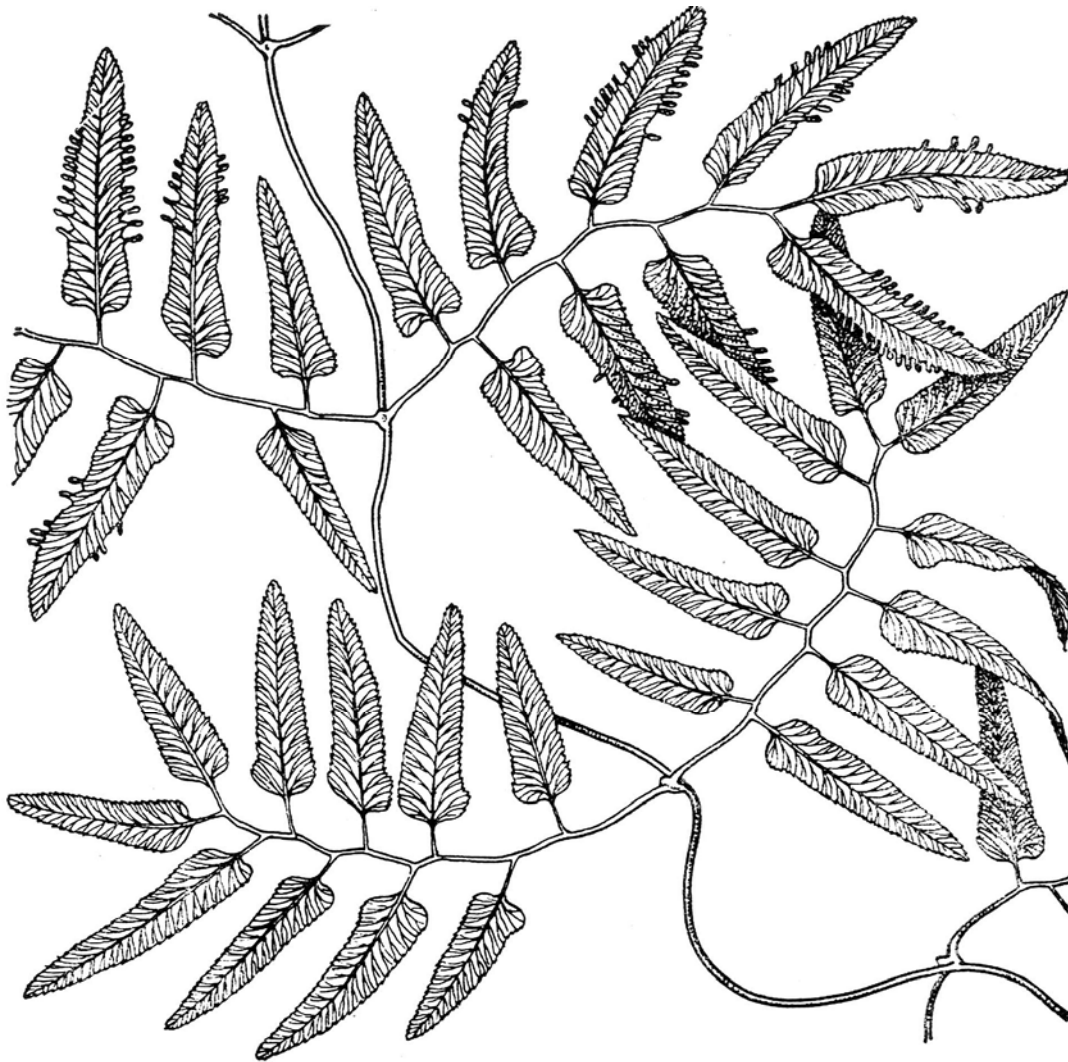


Figure 1: Part of the frond of *Lygodium volubile* (POPOVA 1980: fig. 105).

The vast majority of structures in higher plants can clearly be assigned to one of the merons which were already recognised in 19th century. These are, however, structures that combine characters of different merons. The above-ground organs of the fern *Lygodium japonicum* consist of a winding axis bearing paired, leaf-like appendages (fig. 1). The organ has an indeterminate apical meristem producing new pairs of appendages and internodes in between. Thus the organ looks like the typical shoot but its appearance is deceptive. It is attached to a subterranean rhizome, covered by uniform scales – none of which can be considered as a leaf. Though the ferns have no axillary branching, their branches are typically associated with their leaves (fronds). As there are no real leaves on the *Lygodium*'s rhizomes, its above-ground organs can be better considered as fronds which only simulate leafy shoots and differ from their counterparts in other ferns in highly prominent apical growth. Therefore, *Lygodium*'s

Sattler's dynamic morphology

fronds have characters of both, the typical leaf (position on the rhizome, slight dorsiventrality) and the typical shoot (indeterminate apical growth).

Combination of characters of different merons in a structure conceals its true homology. Special criteria are established to verify questionable homologies (REMANE 1952). The positional criterion, specificity criterion, and the criterion of transitional forms are now fully accepted, although some incongruity with logic principles were reported (MAMKAEV 1991). The major problem, however, is that these criteria normally yield concordant evidences only in the case of quite obvious homologies, while they produce inconsistent evidences in questionable ones (MAMKAEV 1991). When contradictory, the criteria must be sorted according to their reliability. An infallible method for sorting homology criteria could not be developed.

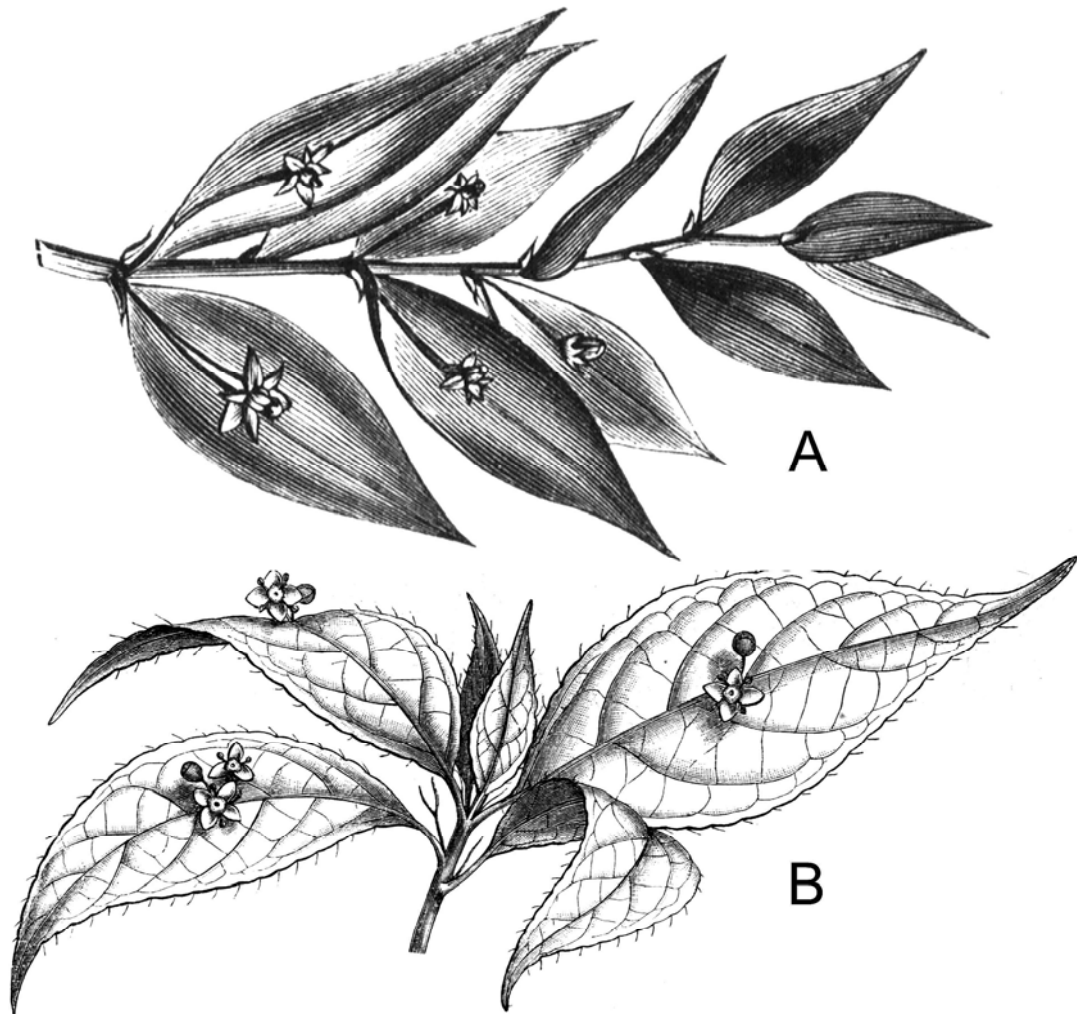


Figure 2: A) shoot of *Ruscus aculeatus* (ENGLER 1888: fig. 55); B) shoot of *Helwingia japonica* (HARMS 1898: fig. 82).

Foliage organs of *Ruscus aculeatus* and *Helwingia japonica* are rather similar (fig. 2). The two are elliptical, acuminate blades (petiolate in *Helwingia*) attached to axial organs and bearing an inflorescence on a surface. Nevertheless, their homologies are considered as quite different. The organ of *Ruscus* grows from the axil of a tiny scale developed on the supporting branch (position) and bears an inflorescence (specificity). Both characters are typical of the shoot. The

organ under consideration meets the positional and specificity criteria of the shoot in combination. Therefore it is undoubtedly a phyllomorphic modified shoot, the phylloclade. By contrast, the organ of *Helwingia* is a subtending structure of its axillary bud (position) which is typical of leaves; but it gives rise to an inflorescence in the middle of its adaxial face (specificity) which sharply contrasts with the leaf syndrome. The inflorescence provokes to interpret the foliage organ of *Helwingia*, analogously to *Ruscus*, as a phylloclade. But nobody would hesitate to recognize the organ as a somewhat unusual leaf. Then, the inflorescence has to be interpreted as a result of either heterotopy or (congenital) fusion of the inflorescence stalk and its subtending leaf. Thus, a botanist accepts evidence of the positional criterion and refuses the criterion of specificity. Is there any reason to do so? The positional criterion is sometimes thought to take priority over every other criterion of homology (REMANE 1956; MAMKAEV 1991). This is unlikely to be the real reason. If only the positional criterion takes priority over others, the flowers of the epiphyllous inflorescences in *Helwingia* could be interpreted as non-homologous to flowers of other Angiosperms. No botanist of sound mind would draw such a conclusion: *Helwingia*'s flowers are very similar to those inherent in plants of Cornales' affinity. So, a botanist rejects evidence of the positional criterion in favour of the evidence of the specificity criterion in this case.

This looks like a postulation of a hidden nature of structures or their 'essence' that can be guessed but never detected by analysis. Once having guessed the 'essence' a botanist inevitably juggles subconsciously with the criteria of homology to prove homology. Therefore, Sattler had some reasons to qualify pre-Sattlerian morphology as essential. Whether there is an 'essence' of a structure or something else, an arbitrary choosing of one or another criterion to prove 'guessed homology' does not meet the usual practice of modern science.

Moreover, there are structures that cannot be unequivocally homologised, neither with the axial nor with the appendicular organs. The vegetative body of some *Streptocarpus* species is a set of specific modules consisting of a nearly radially-symmetric basal part and a flat dorsio-ventral terminal one. The whole module looks like a petiolate leaf; that is why it is called 'phyllomorph' (JONG & BURTT 1975; JONG 1978). The junction of both parts is occupied by an intercalary meristem, forming the parts of the module. Besides, primordia of the inflorescence and/or new modules arise on the upper side of the module's basal part near its intercalary meristem. Modules of ferns of the families Psilotaceae and Stromatopteridaceae (BIERHORST 1971) are principally similar to the phyllomorphs of *Streptocarpus*. But, due to apical cell activity and basitonic to mesotonic branching, their basal, axial parts spread subterraneanly before they grow up to aerial, frond-like structures. No criterion is reliable to indicate homology of such modules because their different parts demonstrate characters of different merons. The modules of some *Utricularia* (Lentibulariaceae) species are rather axial structures, branching exogenously. They differ only in duration of their growth, extent of ramification, and presence/absence of trap bladders (RUTISHAUSER & SATTLER 1989). They can neither be considered as stems nor leaves nor roots (RUTISHAUSER & SATTLER l. c.). Therefore, any discussion about 'true' homology of both phyllomorphs and Utricularian modules is a waste of time.

In sum, typological morphology can be ineffective in homologising structures of many higher plants. Moreover, it prevents the botanists from realising adequate specificity of such organisms because it leads a morphologist to search for inexistent merons in plants instead of comprehending their real patterns (SATTLER 1966, 1984).

Sattler's dynamic alternative

The presented disadvantages of typological morphology stimulated SATTLER (1966) to propose the rejection of its Procrustean method of exact correspondence of a structure with a definite meron (i.e. precise homologisation of structures) in favour of balancing different characters of a structure in order to realise more adequately its pattern. Indeed, it is possible to construct a rather complete series from a typical shoot to a phyllomorphic shoot expressed in *Phyllanthus* (HAICOUR et al. 1989), an unusual, long growing compound leaf like one in Meliaceae (STEINGRAEBER & FISHER 1986) to a typical leaf (SATTLER 1966) – and even further to a leaf constituent and a trichome at an extreme (ARBER 1950). Though the majority of the members of this series can definitely be attributed to a meron, SATTLER (1966) claimed a gradual estimation of characters of the merons (displayed by structure) under consideration to be an appropriate method of morphology. Descriptions of structures according to dynamic vs. typological morphology are shown in table 1.

Table 1: Descriptions of structures according to dynamic vs. typological morphology. a) symmetry of an organ – dorsiventral 1 vs. radial 10; b) arrangement of the bundles – semicircular 1 vs. circular 10; c) bud in the axilla of the organ – present 1 vs. absent 10; d) subtending leaf/bract – present 10 vs. absent 1; e) apical growth – determinate 1 vs. indeterminate 10; f) abscission layer – present 1 vs. absent 10; g) secondary thickening – present 1 vs. absent 10. Grade 1 = appendicular organ; grade 10 = axial organ; grade 5 = intermediate.

	typological morphology	dynamic morphology						
		a	b	c	d	e	f	g
<i>Fagus sylvatica</i>	leaf	1	1	1	1	1	1	1
<i>Nymphaea alba</i>	peltate leaf	5	5	1	1	1	1	1
<i>Guarea guidonia</i>	untypical leaf	1	1	1	1	10	1	10
<i>Phyllanthus</i> spp.	phyllomorphic shoot	1	10	10	10	1	1	10
<i>Fagus sylvatica</i>	stem	10	10	10	10	10	10	10
<i>Utricularia macrorhiza</i>	?	10	10	10	1	1 or 10	10	1

The check list clearly shows the benefit of Sattler's method. It saves a morphologist from the trouble of futile disputing 'correct' homologies of structures with intermediate characters of different merons. Besides, this method enables a morphologist to set structures, like parts of Utricularian bodies, which are inevitably completely enigmatic when treated by the method of typological morphology. That's why Sattler's dynamic morphology is claimed to find easy solutions to problems that have been intriguing morphologists for ages.

Dynamic challenge with regard to conjoint structures

Many plants provide examples of conjoint structures whose assumed counterparts are separated in allied taxa. These are concaulescent or recaulescent shoots/inflorescences, syncarpous gynoeceums, sympetalous corollas, etc. All of them have traditionally been considered as fused, being derivatives from separated ones. However, the difficulty is that the fusion of initially separated structures, i.e. fusion per se, can be rarely observed during ontogeny, while the vast majority of conjoint structures develops as unseparable units from the very beginning.

Issue of typological morphology: congenital fusion

Two different types of fusion were assumed in the framework of typological morphology in the middle of the 19th century: postgenital fusion and congenital fusion (BARABÉ & VIETH 1979).

The postgenital fusion has always been interpreted as an observable process, a real uniting of separately arisen structures during ontogeny. This fusion seems to be characteristic of the (sym)plicate zone of the carpel with its conspicuous suture. Clear traces of former marginal epidermises of fused carpel margins are usually visible in cross-sections through the suture. Because of the real developmental merging of the surfaces of uniting organs or organ parts, often marked by the traces of their epidermises, SATTLER (1978) introduced the term 'surface fusion' instead of 'postgenital fusion.'

The congenital fusion, as established by PAYER (1857), is principally undetectable. A complex structure arises as a unit and shows neither suture nor remnants of presumably merged epidermises. Therefore, it is not an observable process but just a term of comparative morphology to indicate composed structures of a plant whose constituents have separate homologs in some other plants (BUCHET 1928). Payer's congenital fusion could be re-interpreted after Darwinism had conquered morphology. Evolution is thought to change both definitive structures and their development (REMANE 1952; DE BEER 1951; WADDINGTON 1942) making the latter shorter and more economic by eliminating unnecessary intermediate stages (SCHMALHAUSEN 1968). Then, the fusing structures could have progressed to a congenitally fused unit as a climax of the evolution of its development which does not recapitulate separate primordia of its constituents. If so, Payer's concept of the congenital fusion rather deals with evolutionary phenomena than with ontogenetic ones. Such an idea is adopted by some morphologists (BUCHET 1928; VOLGIN & TIKHOMIROV, 1980) but passionately argued by others (SATTLER 1978; BARABÉ & VIETH 1979).

The congenital fusion as stated by VAN TIEGHEM (1868) is radically different. The author distinguished fusion (*soudure*) and concrescence. The first is the development of one single unit originating from separated primordia which merge, showing no trace of initial epidermises of the fused parts. The latter originates from a common basis of separated rudiments which is a result of (1) intercalary growth of the tissue of the supporting organ that gives rise to the rudiments, or (2) lateral expansion and conjunction of rudiment bases followed by intercalary growth of the joint basis, or (3) both processes combined.

An intercalary growth of the tissue of a supporting organ is hardly distinguishable from that of the tissue of a joint basis of rudiments (BUGNON 1928b). The three *modi* recognised by Van Tieghem must be reduced to one: intercalary growth of tissue.

Both fusion and concrescence are potentially observable by investigation of the development of the structures concerned. That is why Van Tieghem's concept of congenital fusion does not meet Payer's concept of congenital fusion which is unobservable.

Both concepts are logically vulnerable. If the congenital fusion is a unobservable phenomenon, what is the reason for speaking about a fused, compound structure (BUGNON 1928b)? The limb of Crustaceans consists of two arms and a gill – contrary to the one-armed limb without gill of Uniramia. But no zoologist regards this structure as a unit of (congenitally) fused 2 limbs and 1 gill. The limbs of these two taxa are interpreted as differently patterned. If

Sattler's dynamic morphology

congenital fusion is an observable, intercalary growth of the tissue under separated primordia of organs, then no fusion takes place at all (BARABE & VIETH 1979) – the organs per se remain separated. Consequently, the term does not meet the literary sense of the word. Therefore, the concept of congenital fusion and congenitally fused organs has been proposed to be either completely rejected (BUGNON 1928a) or replaced with the semantically neutral concept of continuity and continuous structures (CLOS 1879; SATTLER 1977, 1978; GUÉDÈS 1979).

Sattler's solution: cutting the Gordian knot!

Congenital fusion is not a subject of scientific research within the framework of dynamic morphology because the latter is intended to tackle only empirically confirmed phenomena. That is why the morphologist must unsophisticatedly examine developmental processes which result in continuous structures. SATTLER (1977: fig. 2) listed the processes as follows:

- surface fusion which corresponds to postgenital fusion of typological morphology,
- heterotopy which is a changed site where the primordium arises,
- interprimordial growth which is a set of processes recognised as follows:
 - continued meristematic activity of a tissue between the emerged rudiments,
 - fusion of meristems of completely meristematic rudiments,
 - fusion of marginal meristems of rudiments,
 - initiation of new marginal meristems in between rudiments,
 - fusion of intercalary meristems situated under rudiment bases,
 - initiation of continuous intercalary meristem under all rudiments,
 - initiation of continuous intercalary meristem under occurred basal meristems of separated rudiments,
 - initiation of intercalary meristem in between rudiments,
 - expansion of intercalary meristem.

The list clearly shows that Sattler's ideas about continuous structures are inconsistent. Indeed, surface fusion and meristem fusion result both in the uniting of formerly separated structures during their development. The 'continuous structure' must therefore be an adequate name for such a unit. Intercalary growth does not really result in uniting structures. It has no connection with 'fusion' per se. Factually, intercalary growth produces a new structure (*sui generis*): the common pedestal which bears still separated structures on its top. The term 'continuous structure' is evidently inapplicable to such structures but Sattler paradoxically applies it in this case. Moreover, SATTLER (1977) did recognise the heterotopy that is a developmentally unobservable phenomenon. Therefore, it is detectable only by comparison of related taxa. Consequently, heterotopy is not a fact but a construct. As a construct, it is no more than a concept, quite comparable to Payer's concept of congenital fusion formulated in the framework of typological morphology. Thus, the acquired idea about heterotopy sharply contrasts with Sattler's principles of his dynamic morphology. That is why I do not think that dynamic morphology provides an ideal solution to the problem of conjoint structures.

Dynamic morphology: some advances, more doubts

Sattler's dynamic morphology is certainly an outcome of the positivistic paradigm which makes a scientist to concern him/herself with positive facts, excluding prejudiced theories and speculations. The mode is firmly believed to attain the scientific ideal of acquiring objective knowledge about nature. The mode is hardly feasible, however, because positive facts must be

a fiction as every fact must be a biased result of a paradigm (KUHN 1970). Therefore, dynamic morphology is obviously founded on a shaky basis.

Nevertheless, Sattler's programme is of utmost importance because it obscurely addresses an acute problem of natural science. Every law is applicable to a limited set of phenomena. Therefore, judging scope of a law is a *sine qua non* condition of scientific activity. It is especially important for biology dealing with a mammoth diversity of living beings. Biologists have still been ignoring the problem and many biological theories are kept as universal.

Plant morphologists have been recognising the universal organs, root, stem, and leaf since the middle of the 19th century. They have persistently been comparing every enigmatic structure of a plant to one of these three organs – even when a reasonable comparison is impossible. Sattler's proposal to refuse to homologise structures with any recognised meron, actually means that the scope of each meron does not cover the whole plant kingdom. Violent homologising of a structure with an accepted meron would result in a misinterpretation. Indeed, the patterns of the Lower Devonian plants, their diversity and position in plant classifications were all adequately realised only after botanists had applied a new meron, the telom with its specific ways of transformations (ZIMMERMANN 1959), instead of the three traditionally accepted organs of plants.

Sattler's programme is hazardous. The proclaimed gradual estimation of characters of different merons which are combined in the structure under consideration is not an alternative to homologising the structure in any way. Such an estimation would be made in the case of the availability of only a set of recognised standard merons. Otherwise, any comparison to get an estimation would be impossible. Sattler himself used merons of typological morphology to demonstrate his estimation method. Each standard is however not a positive fact but a construct. As a construct it depends on paradigms and theories which scientists adopt. That's why it is always biased. The comparison of objects with/to a standard is actually an essence of homologising. Therefore, the gradual estimation of characters of a structure is *de facto* a recondite application of a humiliated homology concept. Dynamic morphology is contradictory because it simultaneously rejects and applies strict homologies.

If refined with a refuted application of biased homologies, dynamic morphology is consistent but unable to estimate structural characters because it loses any standards for comparing structures. The solution would be an elaboration of a particular set of merons for each plant form. If so, the activity of Sattlerian morphologists would be rather similar to that of French zoologists in 18th century who used unequal terms for describing anatomies of man, horse, dog, etc. (KANAEV 1963).

Such a mode is only feasible on the condition that the number of objects under consideration is small. The more different living beings become the object of morphological research, the less practicable is the operation with an increasing number of meron sets. The very diverse living beings need a compact universal system of merons that would be applicable to every thing. This led to the establishment of a new science at the end of the 18th century: morphology. Morphology was aimed to establish procedures to standardize meron systems and to relate structures under consideration with a standard meron (v. GOETHE 1795, quoted by KANAEV 1955). The established procedure is traditionally called homologising. I believe that Sattler's proposal to reject the homologising plant structures in favour of sorting

characters into an infinitely variable continuum does not actually advance morphology but rather dismisses it.

The offered replacement of typological morphology by dynamic morphology is a sort of Utopia. As a consistent method, dynamic morphology would unavoidably demolish morphology per se. While inconsistent, it regularly needs hidden applications of concepts that have been formulated in typological morphology. That is why I do not consider Sattler's dynamic morphology as an alternative to typological morphology. It is a part of the well-known typological morphology which is especially aimed to precise the scopes of morphological laws resulting in special forms of merons.

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