# "FUSION" AND "CONTINUITY" IN FLORAL MORPHOLOGY*

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ABSTRACT. The concept of "fusion" is analyzed in terms of its intension and extension. It is shown that this concept has been misapplied to describe non-fusion processes such as shifting (heterotopy), meristem extension, and *de novo* formation of common meristems. In order to avoid such transgressions of the domain of applicability of "fusion", it is proposed to use the concept of "continuity". This latter concept has the further advantage that it can be used in the absence of detailed developmental data which are still lacking in the majority of taxa. Continuity may result from the following very diverse ontogenetic and/or phylogenetic processes: "surface fusion" (traditionally known as "postgenital fusion"), "shifting" (leading to "heterotopy"), and "interprimordial growth". The latter in turn is very diverse and includes meristem fusion (as an ontogenetic fusion), *in situ* inception of a common meristem or growing region instead of separate ones in the ancestral form (as a phylogenetic fusion), and the non-fusion processes of (ontogenetic) meristem extension and (phylogenetic) *de novo* formation of meristems. It is pointed out that "ontogenetic fusion" is not synonymous with "postgenital fusion" and that the concepts of "congenital fusion" and "phylogenetic fusion" also have different meanings.

The diversity of floral construction is enormous. We ask: by what kind of processes has it arisen? It certainly is a challenge to provide an exhaustive set of non-overlapping concepts of processes that are necessary and sufficient to generate the existing diversity. It is even more challenging to develop such a set of processes for which it can be shown that they actually occur(red) during the evolution of plants. I am not pursuing this arduous task in this communication. I rather intend to focus on one process which has been considered to be of utmost importance, namely fusion. It is probably no exaggeration to state that this process—as it has been understood and applied to floral morphology—has been held to produce greater variation in floral structure than any other process. According to traditional interpretations, fusion has produced such diverse structures as calyx and corolla tubes, androecial tubes and walls of syncarpous ovaries, walls of inferior ovaries, hypanthia, adnation of stamens to the perianth or gynoecium, etc. Consequently, the morphological and systematic literature abounds with terms such as coalescence, adnation, concrescence, connation and unification all of which refer to the origin of complex structures by means of fusion. It is obvious that the notion of fusion figures prominently in the construction of taxonomic keys and the diagnosis of many taxa at all ranks. Systematists indeed rely heavily on the usage of the term fusion, equivalent terms, or sub-categories of the term such as 'coalescence' and 'adnation'.

Since the concept of "fusion" has been used so widely and has led to a number of difficulties, it becomes important to analyze its meaning, i.e. its intension (=connotation) and its extension (=domain of applicability). With regard to its intension, "fusion" has been defined as "a merging of diverse elements into a unified whole" (*Webster's New Collegiate Dictionary*).

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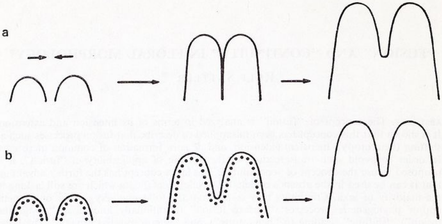

FIG. 1. Surface fusion (fig. 1a) and meristem fusion (fig. 1b) may lead to nearly indistinguishable mature structures. Meristems are dotted. Arrows indicate ontogenetic changes.

Examples of elements that may fuse are developing organs which fuse by appression of their surfaces (postgenital fusion in the sense of 'surface fusion'; fig. 1a) or meristems (i.e. meristematic regions of developing organs) whose activity becomes extended and thus leads to one continuous ("fused") meristem instead of separate ones (fig. 1b). The latter fusion has been termed 'meristem fusion' (Hagemann 1970, 1973). If subclasses of meristems are distinguished, one may differentiate between the fusion of marginal, submarginal and intercalary meristems. Meristems generally are not as clearly discernable as the surfaces of organs. Therefore, the concept of fusion applied to meristems may create problems and ambiguities that are inherent in the notion and delimitation of meristems.

The fusion of elements may occur in different contexts and time dimensions. Traditionally, fusion during ontogeny (ontogenetic fusion) is distinguished from fusion during phylogeny (phylogenetic fusion). Unfortunately, ontogenetic fusion has been equated with postgenital fusion (in the sense of surface fusion) and phylogenetic fusion with congenital fusion (see, e.g., Cusick 1966). From what has been said above, it is obvious that this equation is not necessarily correct [as Cusick (1966) already suspected]. Ontogenetic fusion may be surface fusion (i.e. postgenital in the traditional sense) or meristem fusion, a process that traditionally has been subsumed under the category of congenital fusion. On the other hand, congenital fusion may be phylogenetic fusion, yet it has been applied to a range of processes that are non-fusion processes (see below); furthermore, one may point to a series of a gradual increase in amount and intensity of postgenital fusion during phylogeny and thus envisage changes in postgenital fusion also as a phylogenetic fusion.

Since we are forced to give up the equation of postgenital with ontogenetic fusion on one hand, and congenital with phylogenetic fusion on the other hand, we end up with two pairs of concepts instead of one. One might argue that these two pairs of concepts can be used independently and to some extent this will most probably be the case. Some typologists most likely, will

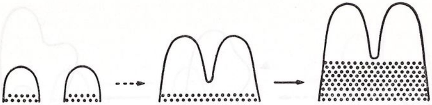

FIG. 2. Phylogenetic fusion. Separate meristems of the ancestral form are replaced by a common meristem that arises *in situ*. Meristems are dotted. Dashed arrow refers to phylogenetic changes, solid arrow to ontogenesis.

continue to use "congenital fusion" in a sense which is rather different from that of phylogenetic fusion, i.e. in a sense that does not necessarily imply any fusion at all, but simply allows them to adhere to the classical model of plant construction even in cases that contradict it from an empirical point of view. An example would be the so-called fusion of inflorescence and subtending leaf of *Phyllonoma* which was shown to result from an epiphyllous inception of the inflorescence (Dickinson & Sattler 1974). The excellent work of Jong (1970) and Jong & Burtt (1975) on the growth patterns in *Streptocarpus* also should be quoted in this regard.

Since the concept of congenital fusion refers to a very heterogeneous range of processes some of which like the one just mentioned are non-fusion processes, I think it is best to eliminate the concept in its broad (traditional) meaning from an empirically oriented morphology. One could, of course, redefine it in a narrower sense so that it becomes synonymous with meristem fusion. However, such a redefinition might lead to confusion. It appears preferable to use the term 'meristem fusion'. Another redefinition in a special phylogenetic sense might, however, prove to be useful. In that sense it would refer to cases in which separate structures of an ancestral form are replaced by one (unified) structure (fig. 2). Such a redefinition of congenital fusion as phylogenetic fusion would amount to an elimination of the original concept of congenital fusion. If the term 'congenital fusion' is retained for this new concept, confusion may arise. The term 'phyl(ogen)etic fusion' is preferable in this regard.

The concept of postgenital fusion also could be eliminated or it could be used in a narrow sense as an equivalent to "surface fusion" (not "ontogenetic fusion"). Generally, the concept of postgenital fusion has been used in the sense of surface fusion, but the literal meaning and definition often has suggested a broader meaning in the sense of ontogenetic fusion. Thus, there has been a certain discrepancy between the usage and definition of the term. I succumbed to this ambivalence in a previous publication (Sattler 1974, p. 30). In that publication, I used the term 'postgenital fusion' in the ontogenetic sense, but I had only surface fusion in mind disregarding meristem fusion which also is observable during ontogeny and represents therefore a fusion in an empirical sense.

As a correction to what I wrote in that previous publication (Sattler 1974, p. 30, no. 4), I propose now to use the terms 'surface fusion' and 'meristem fusion' on one hand as fusions that occur during ontogeny, and the term 'phyl(ogen)etic fusion' as a fusion that occurs during phylogeny. I should add

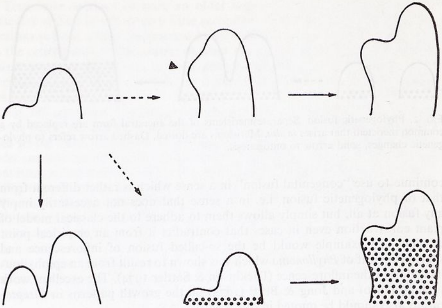

FIG. 3. Phylogenetic shifting of primordial inception (see arrowhead) may lead to the same or similar mature construction as, for example, phylogenetic fusion. Dashed arrows indicate phylogenetic changes, whereas solid arrows refer to ontogenetic events. Meristems are dotted.

at once that I still have some doubts with regard to the status of "phylogenetic fusion". It is not a fusion in the sense of a materially continuous process that could be observed by a witness of evolution. In order to describe phylogenetic fusion one has to rely on a comparative scheme of the plants under consideration, i.e. one has to know the homologies of the "fused" and separate structures. Thus, even if we knew the phylogeny of the plants, we would still be thrown back into very complex methodological problems of homologization. Even typology in one way or another may be relevant in this context. Without going into any detail on the methodological problems of establishing phylogenetic fusions, I should at least point out that vascularization and even intermediate forms are not necessarily reliable indicators of fusion (see, e.g. Schmid 1972; Dickinson & Sattler 1975).

Phylogenetic fusions do not necessarily entail ontogenetic fusions. However, ontogenetic fusions also may be considered phylogenetic fusions, at least in cases where successive ontogenies show increasing fusion. This increase from one ontogeny to the next may be interpreted as phylogenetic fusion.

The best established fusions are surface fusions. Phylogenetic fusions generally are the most debatable ones, whereas meristem fusions are intermediate between the two with regard to the strength of their empirical foundation. In a previous publication (Sattler 1974) I admitted only surface fusions as "fusions". It seems to me now that meristem fusions also have to be included into the category of "fusion", although meristem fusions may be continuous with non-fusion processes, as the meristems become less and less

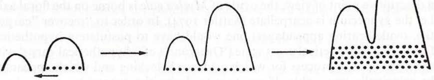

FIG. 4. Meristem extension from one primordium to the adjacent one.

applicable. Special attention is called for in these cases and broader quantitative concepts of the time-space distribution of growth may eventually render fusion an obsolete concept in this regard. Finally, one may consider including phylogenetic fusions into the category of "fusion", but one should realize that these fusions are problematical for several reasons and that phylogenetic fusions are a different kind of fusion. A different term might be appropriate to underline the difference.

I have to return now to the distinction between the connotation of a concept and its domain of applicability. What I have indicated in terms of the connotation of the concept of fusion can be stated in different ways in terms of its domain of applicability. The crucial point is that many plant morphologists and systematists have been using the concept of fusion beyond its domain of applicability. In other words: the concept of fusion has been misused. First of all, the process of phylogenetic shifting (leading to heterotopy) has been mistaken for phylogenetic fusion. Yet the two processes are quite distinct (fig. 3), although they may lead to the same mature construction. It follows that evolutionary events have been misinterpreted in a number of cases. What has been said to result from phylogenetic fusion, actually was produced through phylogenetic shifting, i.e. heterotopy (Sattler 1975; Dickinson, in press). Shifting may occur with regard to the inception of primordia (e.g., the inflorescence primordium in epiphyllous inflorescences such as *Phyllonoma*: Dickinson & Sattler 1974) or with regard to meristematic zones (e.g., Bugnon 1958). Secondly, the concept of fusion has been misused by applying it to the process of meristem extension (Sattler 1977). Meristem extension which has not yet been studied sufficiently, also can lead to new associations of organs which in the mature state may be incorrectly interpreted as the result of fusion (fig. 4). Thirdly, *de novo* formation of common meristems at the base of primordia may give rise to structures which may give the false impression of fusion products (fig. 5). Obviously, the addition of a new structure is quite a different process than that of the fusion of pre-existing structures. The walls of certain inferior ovaries may have been produced by such *de novo* meristems, although this again has not been demonstrated unequivocally.

It is understandable why the concept of fusion has been applied beyond its domain. First of all, as I pointed out above, it can be used (i.e. misused) to uphold the schema of classical morphology in certain cases when the observations do not fit it. For example, the concept of fusion can be used (i.e. misused) to postulate ovule-bearing appendages (i.e. carpels) where they don't occur. This has been shown in *Myrica gale* (Macdonald & Sattler 1973) as well as in other taxa. In *Myrica gale* the floral apex is directly transformed into the terminal (basal) ovule. No ontogenetic fusion is involved. Thus, from a descriptive point of view, the ovule of *Myrica gale* is borne on the floral axis, i.e. the gynoecium is acarpellate (Sattler 1974). In order to "recover "carpels (i.e. ovule-bearing appendages) one would have to postulate a hypothetical fusion of a hypothetical cross zone ('Querzone') of a hypothetical carpel with the floral apex, a process for which evidence is lacking and which appears to be principally impossible. If we want to derive the gynoecium with a basal ovule from an ancestral carpellate condition, we would have to postulate that "the site of ovular emergence has been shifted away from a demonstrably foliar position" (Burtt 1961). This postulate is at least theoretically possible on the basis of our knowledge of floral morphogenesis. If we accept this view, then we would have to conclude that in *Myrica* as in a number of other Angiospermous taxa the "foliar carpel has been superseded" (Burtt 1961).

The second reason why the concept of fusion has been applied beyond its domain is a rather innocent yet common one. Very often the development of structures that are associated with each other is not known. Therefore, one cannot tell whether the apparent association is the result of fusion, heterotopy, meristem extension or *de novo* formation of meristems. If we consider, for example, the mature flowers of *Lythrum salicaria* in which the petals are inserted high up on the calyx tube, we cannot tell whether this condition was produced by heterotopy (as it was demonstrated by Cheung & Sattler 1967), meristem fusion, meristem extension, or *de novo* formation of meristems. Since systematists who devise keys for the identification of plants usually deal with mature structures (and prefer to use mature structures for obvious practical reasons), they are in a difficult position with regard to the concept of fusion. One might argue that they are bound to extend the concept of fusion to doubtful cases (unless a developmental investigation is undertaken). Yet, this is not true. Another concept and another term that do not necessitate the misuse of the concept of fusion have been available for a long time. This

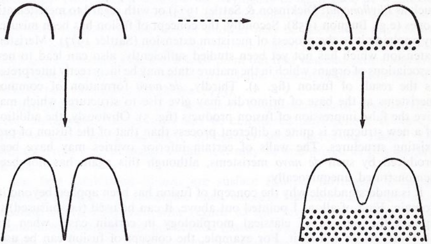

FIG. 5. Phylogenetic *de novo* formation of a basal meristem (dashed arrow). Solid arrows refer to ontogenetic changes. Meristems are dotted.

concept and term are that of "continuity" proposed nearly a hundred years ago by Clos (1879). I do not know why "continuity" has not been generally accepted. It overcomes the problems that have been caused by the questionable use of the concept of fusion.

"Continuity" is a relative concept, i.e. it can be used in a relative sense. Fundamentally, all organs of a plant are continuous with each other. One can, however, use the concept of continuity in such a way that it refers to all those phenomena that were meant by the concept of fusion including the transgression of the semantic domain of the latter. In other words: "continuity" can be looked upon in such a way that it refers to the results of surface fusion, meristem fusion, meristem extension, *de novo* formation of meristems, and shifting (heterotopy). In still other words: "continuity" can be used for all those cases which the systematist generally describes as fusions which, however, may or may not be fusions. Thus, "continuity" is a concept which describes what is observable without implying false or unknown developmental data or doubtful phylogenetic hypotheses. The following example will illustrate how the concept is applied. Primordia of floral appendages are always continuous with the floral axis. However, in sympetalous flowers, the petals are continuous with each other *above* the floral axis. Daniel & Sattler (in press) have shown that in *Solanum dulcamara* the inception of the corolla tube results from meristem fusion. Thus, we can interpret at least the early stages of corolla tube development of *Solanum dulcamara* as a process of meristem fusion. In many other plants sympetalous corollas are also observed. But we don't yet know whether they are also formed by meristem fusion. All we can really say at this time is that there is *continuity of petals above the receptacle.*

One might argue that the systematist uses the term 'fusion' in the sense of "continuity" and that for practical purposes it doesn't make any difference which term is used. One could go further and object that my conclusions are only of a semantic nature substituting one term for another without touching the core of morphological description and interpretation. I disagree with this criticism for a number of reasons. 1. "Continuity" refers to an end result whereas fusion is a process. Process and product are definitely not identical, although one leads to the other. It is crucial—as has been pointed out above—that the same product may result from different processes: fusion as well as non-fusion processes. 2. The general use of the term 'fusion' is misleading and untenable because it may imply false evolutionary origins of the structures in question. 3. False ideas about origins may lead to distorted ideas about relationships and to unnatural classifications. 4. Thus, the general use and misuse of the term 'fusion' may undermine the goals of systematics and evolutionary botany (except in a very practical sense). 5. Furthermore, it may obscure our knowledge of certain plant structures and their ontogenetic and phylogenetic origin. For example, when we apply the term 'fusion' to structures whose development is not sufficiently known, we may gain the impression that the processes of their development and/or evolution are understood. In fact, they may be quite doubtful or even the contrary of fusion. If we use the concept of continuity instead, we admit that all we know is what we observe and we immediately pose the question: how did this continuity arise ontogenetically and/or phylogenetically? Nothing is obscured. Paths for future investigation are opened up. Thus, the introduction and use of the concept "continuity"—far from being just a different word for fusion—is relevant to issues of ontogenetic and phylogenetic processes, phylogenetic relationships, phenetic and phylogenetic classification. Furthermore, it uncovers problems and connections that could not be seen before. All of these issues concern realities and not just semantics.

In two other articles (Sattler 1977; Daniel & Sattler, in press) I have summarized the processes that may lead to continuity. They are the following:

I. Surface fusion (equivalent to the traditional usage of the concept of postgenital fusion) (fig. 1a).

II. Interprimordial growth (Sattler 1973) including the borderline case in which interprimordial growth approximates primordial growth (e.g. ring primordia).

  1. Meristem fusion (Hagemann 1970, 1973), i.e. ontogenetic fusion of marginal, submarginal or intercalary meristems, or fully meristematic primordia (fig. 1b).
  2. Meristem extension (which is related or even equivalent to Hagemann's "Meristeminkorporation") (fig. 4).
  3. *In situ* inception of common meristems which may be equivalent to separate meristems in the ancestral form (=phylogenetic fusion) (fig. 2), or *in situ* inception of *de novo* meristems (fig. 5).

III. Shifting of primordial inception (leading to heterotopy) (Zimmermann 1959) (fig. 3).

For the majority of apparently associated (so-called "fused") plant structures we do not know by which of the above processes they were formed. Yet, we can at least describe them objectively in terms of continuity. We cannot hope, though, that soon all the morphological and systematic literature will be rewritten in terms of the concept of continuity instead of that of fusion. But we should at least realize when we encounter the term 'fusion' that we are dealing with a phenomenon of continuity which may or may not have resulted from fusion.

The concept of fusion cannot occupy the central place that it has held for a long time in morphology and systematics. "Continuity" is the comprehensive concept that encompasses the broad domain to which the concept of fusion has been applied and misapplied. Fusion is only one among several processes that ontogenetically and phylogenetically lead to continuity.

Through a recognition of the limitations of the concept of fusion and an elaboration of non-fusion processes that falsely have been subsumed under the category of fusion, I hope to make a contribution to "a morphology which is more flexible and accords greater recognition to the changes which may have taken place within the Angiosperms" (Burtt 1961, p. 572).

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