

On the character "carpel-form" : trends in the development of the Magnoliata pistil

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On the character "carpel-form". Trends in the development of the Magnoliatae pistil

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ABSTRACT

CRESENS, E. M. & E. F. SMETS (1992). On the character "carpel-form". Trends in the development of the Magnoliatae pistil. *Candollea* 47: 373-390. In English, English and French abstracts.

In our research methodology "types" (characters and character-states) are distinguished from "non-types". It is demonstrated that Leinfellner's main forms of expression of the peltate carpel are non-types. The character "carpel-form", which is complementary to Leinfellner's approach of carpel morphology, is defined. The various ways in which pistils become visible during ontogeny provide a basis for delineating the leptate, pseudoleptate and coenoleptate carpel-form as character-states. In addition to this characterization a semophyletic scheme which visualizes initial trends in the development of the pistil of the *Magnoliatae* is proposed. A preliminary Dahlgrenogram, showing the distribution of the three character-states is also presented.

RÉSUMÉ

CRESENS, E. M. & E. F. SMETS (1992). Le caractère "forme-de-carpelle". Tendances du développement pistillaire des Magnoliatae. *Candollea* 47: 373-390. En anglais, résumés anglais et français.

Dans notre stratégie de recherche, nous proposons une distinction entre "types" (caractères et états-de-caractère) et "non-types". Il est démontré que les plus importantes formes d'expression de la théorie des carpelles peltées de Leinfellner doivent être considérées comme "non-types". En complément à l'approche de Leinfellner nous avons défini un nouveau caractère, "forme-de-carpelle". Les différentes formes que présentent les pistils dans l'ontogénèse permettent la délimitation des états-de-caractères; c.à.d, les formes-de-carpelles leptée, pseudoleptée et coenoleptée. Nous proposons également un schéma sémphylétique, visualisant les modes initiaux de développement des pistils des *Magnoliatae*. De plus un Dahlgrenogramme préliminaire, montrant la répartition des trois états-de-caractère est présenté.

1. Introduction

In this paper some tentative results of our character-research on the gynoecium of the *Magnoliatae* are presented. Character-research aims to discover types, the term by which we denote features with predictive and discriminative value, viz. characters and character-states. The term "nontype" (formerly called "apparent type"; CRESENS & SMETS, 1989) refers to inadequately characterized features. Indeed, whereas "types" are more appropriate for delineating and justifying the higher taxa, "nontypes" must not be used for this purpose because they lead to artificial classifications.

Character-research requires three methodological steps: (1) the predictive value, or systematic relevance, of generally used characteristics is determined by examining distributional plots on Dahlgrenograms. When this leads to the thesis that the available characterizations do not exhibit an acceptably homogeneous pattern¹ a second step is required; (2) one should propose alternative characterizations and, eventually, reshape the types until they fulfill the needs with regard to the predictive value. It must be clear that the second step is repeated when a recharacterization also leads to an unacceptably heterogeneously shaded Dahlgrenogram; (3) the new types can be used to evaluate and to increase the predictive value of both the classification system and the other types. Hence, synthesis will cause that the system of classification will be more useful, i.e. its predictive value will be increased. Moreover, the system can be more adequately justified on the basis of the occurrence (absence or presence) of types.

2. Character-research and peltate carpel theory — complementary viewpoints?

2.1. Peltate carpel theory

On the classical account, the gynoecia are made up out of carpels which bear and enclose the ovules. On the basis of the degree of carpel fusion, a distinction is made between choricarpous and coenocarpous gynoecia. Choricarpy denotes to a set of monocarpellate pistils which represent the individually closed carpels. Coenocarpy is used to indicate that the pistil comprises laterally fused carpels. In the traditional framework the terms "carpel" and "monocarpellate pistil" are interchangeable. Indeed, it seems reasonable to state that pluricarpellate pistils — according to a process of mental dissection — are fused monocarpellate pistils. For example, one assumes that the primordial pluricarpellate pistil consists out of laterally fused horseshoe-shaped monocarpellate pistil primordia. This explanation of coenocarpy leads to the acceptance of choricarpous and coenocarpous gynoecia as part-for-part homologizable structures; e.g. the septae of a pluricarpellate pistil and the lateral flanks of monocarpellate pistils are considered as homologous parts (see also PURI, 1952, 1961, about the "double nature" of placentae and septae in pluricarpellate pistils). Such ideas of homologization can be found in the work of EAMES (1931), LAWRENCE (1951) and many other investigators. These authors postulate, from a phylogenetic point of view, that the primitive carpel is a sessile foliar leaf homologue producing ovules associated with its margin.

Since the more distal and the more proximal parts of sessile leaves do not exhibit fundamental morphological differences, it becomes understandable that routine comparisons were established mainly on the basis of a few cross-sections through pistils. Leinfellner (many publications, see further) opposed such horizontal homologization and stressed the importance of making a complete series of cross-sections through a pistil in order to obtain all structural information needed for the comparative work. The author draws attention to the fact that the pistil is a three dimensional whole; as a consequence the whole of its three dimensional shape must be used for determining homologies. This stands in close connection with the fact that Leinfellner — in accordance with the viewpoint of idealistic morphology — elaborated Troll's typological thinking and also considers carpels to be ovuliferous peltate leaf homologues.

TROLL (1932) postulates three types of carpel shape, viz. the manifestly peltate, the latently peltate and the epeltate carpel shape. According to the author the manifestly peltate and latently peltate carpels always evolve in a more or less scutelliform fashion. The epeltate carpels allegedly differ from the manifestly and latently peltate carpels because they show no peltate organization in any stage of their development. EAMES (1961: p. 223) writes: "Peltate form in the carpel is assumed to have arisen by the turning upward (ventrally) of the basal lobes of the lamina and their fusion, margin to margin, as in the formation of peltate leaves. Where the two marginal meristems meet, they unite, forming a transverse meristem, the cross-zone". Indeed, the *typus* of peltate leaves

¹If the observed heterogeneity is small or "acceptable", there is more reason to believe that this heterogeneity should be imputed rather to the occurrence of homologous convergencies (HAGEMANN, 1977), to the failure of the classification system, or to the heterogeneity inherent to the system of classification, than to inadequate characterizations (e.g. presence of unknown analogous convergencies).

and peltate carpels are, according to TROLL (1932) identical. Hence, both structures are homologous. Moreover, according to TROLL (1932) the unifacial inception of the petiole is the major characteristic of the peltate leaf forms (cf. BAUM, 1952b; HAGEMANN, 1970). The occurrence of a cross-zone (Querzone) would then be of secondary importance. As it is believed that the vascular leaf anatomy supports the distinction between unifacial and bifacial leaf parts, the characteristics distinguishing between the peltate and the epeltate carpels are also based on the vascular anatomy of the carpel (TROLL, 1932; SPROTTE, 1940). LEINFELLNER (1950: p. 404) states that the three carpel shapes can be deduced from one basic form, viz. "die eines peltaten, mehr oder weniger schlauchförmigen Blattes". According to this author, only the carpel lamina is important for the interpretation of the pistil, as the petiole (i.e. the unifacial part of the "Oberblatt") is usually absent and the leaf base has fused with the sessile lamina. So, a clear arrangement of the carpel primordia in lamina, carpel petiole and leaf base is mostly absent (see also HAGEMANN, 1975). Later, Leinfellner and Baum identified transitional forms (see below) between Troll's peltate and epeltate categories, which strengthened the idea that both peltate and epeltate carpels have one and the same *typus*, viz. that of peltate leaves.

Roughly speaking, peltate carpel theory *sensu* Leinfellner and Baum recognizes two major phenetic trends according to which the morphological variation of carpels can be tracked down (Fig. 1). Firstly, it assumes that the plicate region of a manifestly peltate carpel (Fig. 1a) is subject to reduction. This leads to extreme manifest peltation (Fig. 1a'). Secondly, the loss of fertility and the complete reduction of the ascidiolate zone brings us to latently peltate (Fig. 1b) and epeltate (Fig. 1c) carpels. Notice, however, that the term "latent peltation" is used not only for the carpels with a rudimentary, yet still clearly recognizable sterile ascidiolate zone (see BAUM, 1952b), but sometimes also to designate the extreme forms where the cross-zone, though its growth is inhibited, still yields a median basal ovule (see ECKARDT, 1957; LEINFELLNER, 1969c).

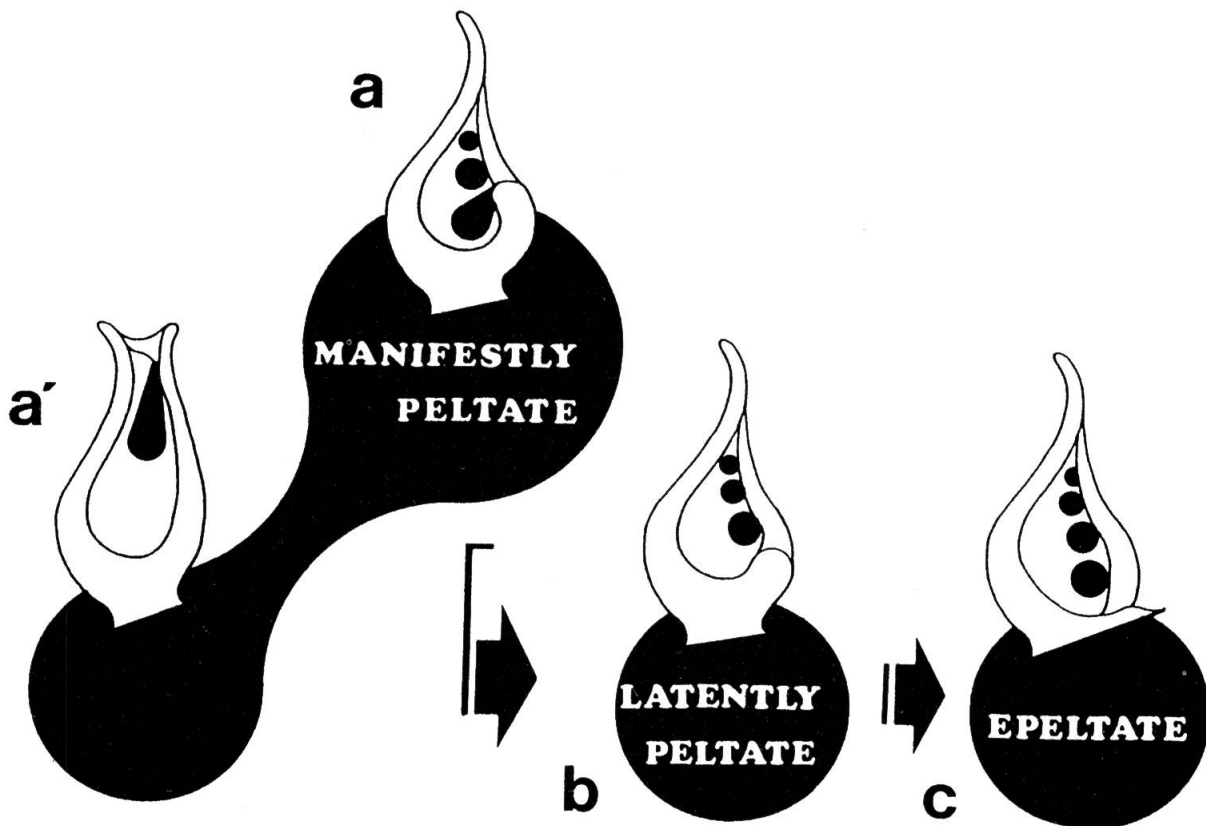


Fig. 1. — Relations among Leinfellner's manifestly peltate, latently peltate and epeltate carpels.

Zone-for-zone homologization of all magnoliophytinean pistils is an inherent feature of Leinfellner's conceptualization (e.g. all ascidiate zones are treated on a par). Since peltate carpel theory assumes that coenocarpy results from congenitally fused monocarpellate pistils, with or without participation of the receptacle, also pluricarpellate pistils (hemisyncarpous, eusyncarpous gynoeceia) can be interpreted in terms of the manifestly peltate, latently peltate and epeltate carpel shapes (BAUM, 1949; BAUM & LEINFELLNER, 1953; LEINFELLNER, 1950, 1969b, 1972a, b, 1973a, b).

The observation of the existence of peculiar monocarpellate pistils which can be interpreted as transitional forms (semipeltate carpels, e.g. in *Ranunculaceae* and *Proteaceae*: BAUM, 1952a, b, 1953a, b; see also LEINFELLNER, 1969c; modified peltate carpels: LEINFELLNER, 1969c, d, 1970a) between some of the three higher mentioned "basic" shapes, cause peltate carpel theory to appear as universal. In contrast with manifest peltation and latent peltation the cross-zone of the semipeltate carpel is not localized at the (imaginary) boundary line between the unifacial petiole and the bifacial lamina of the carpel but it is situated on the carpel petiole. Hence, the ventral slit and the ovarian cavity continues on the superior part of the carpel petiole (BAUM, 1953b). The cross-zones of the semipeltate carpels develop later than in the latently peltate carpels and still later than in the manifestly peltate carpels (see also LEINFELLNER, 1969c). According to BAUM (1952b, 1953a) the development of the cross-zone is inhibited because its inception and growth are postponed to a later ontogenetic stage and not because of growth limitations after its inception. In epeltate carpels no cross-zone at all would arise. The "modified peltate carpels" (LEINFELLNER, 1969d, 1970a) on the other hand — being those where the ventral slit continues onto the adaxial wall (cross-zone), and in some cases also onto the carpel petiole without a complete opening of the ascidiate zone — constitute the link between the manifestly peltate carpels and the latently peltate carpels with a fertile cross-zone (LEINFELLNER, 1969c).

So, LEINFELLNER (1950, 1951) managed to give a comprehensive interpretation of pistil morphology by postulating that all magnoliophytinean carpels are essentially peltate with a U-shaped placentation. He recognizes the manifestly peltate, latently peltate and epeltate carpels and puts them in a morphological array on which the distinction between choricarpy and coenocarpy can be superimposed. Moreover, Leinfellner's carpel shapes are consistent with observable morphological differences.

What we wanted to find out is whether the forms of expression of the peltate carpel theory are predictive towards the system of classification. The answer might be particularly valuable because previous character-research revealed that the types of degree of carpel fusion and the classical placentation types do not possess high predictive value (SMETS, 1984; CRESENS, 1986; CRESENS & SMETS, 1989). Indeed, all those "types" show unacceptably scattered distributional patterns on shaded Dahlgrenograms; a phenomenon that we attribute to the failure of recognizing homoplastic similarities.

2.2. The distribution of the carpel shapes

For evaluating the predictive value of characteristics the Dahlgrenogram already proved to be a useful instrument (SMETS, 1984, 1986; RONSE DECRAENE & SMETS, 1987; many contributions of Dahlgren and others). On the basis of data available from literature we constructed the plot in Figure 2. We wish to point out that families are interpreted as being *manifestly peltate* if carpels occur with: (1) a reduced though still fertile cross-zone (latently peltate sensu ECKARDT, 1957 and LEINFELLNER, 1969c); (2) either a reduced plicate and a fertile ascidiate zone, or a peltate and an ascidiate zone that are both fertile; (3) a clearly developed U-shaped placenta of which the basal part does not produce ovules. The families having carpels with a sterile and rudimentary, though still recognizable ascidiate zone are represented as being *latently peltate*. Following the same principles, the carpels of the hemisyncarpous and the eusyncarpous gynoeceia (LEINFELLNER, 1950) are interpreted as being *manifestly* or *latently* peltate. Hence, pluricarpellary pistils with a sterile and rudimentary synascidiate or hemisynascidiate pistil zone, are indicated as being latently peltate. If there is a manifestation of a rudimentary synascidiate or hemisynasci-

diate zone which is, however, fertile¹ then the carpel shape is represented as being manifestly peltate. This also holds true for the pistils with a free central placenta, if there are indications of a rudimentary compartmentalization of the bottom of the single locule (e.g. *Primulaceae*, GUÉDÈS, 1979). In accordance with the peltate carpel theory, the carpel shape of the *Myricaceae* (MACDONALD, 1979; MACDONALD & SATTLER, 1973), *Balanaphoraceae*, *Viscaceae*, *Loranthaceae* and *Santalaceae* (see McLEAN & IVIMEY-COOK, 1956; EAMES, 1961) must be indicated as being manifestly peltate (cf. WILSON & JUST, 1939; BAUM & LEINFELLNER, 1953).

In addition to the articles quoted the following ones were also very useful for shading the diagram (Fig. 2) : ECKARDT (1937, 1956, 1971), SCHAEPPPI & STEINDL (1950), BAUM & LEINFELLNER (1951), LEINFELLNER (1952, 1965, 1966a, b, c, d, e, 1967a, b, 1968, 1969a, 1970b, 1971), SCHAEPPPI & FRANK (1962), GUT (1966), KLOPFER (1968, 1970), SCHAEPPPI (1972, 1975), ROHWEDER & ENDRESS (1983) and HOFMANN & LUDEWIG (1985).

The admissibility of interpreting Leinfellner's manifestly peltate, latently peltate and epeltate carpel shapes as character-states of a character "carpel peltation" finds its origin in the fact that from the moment descriptive terms become part of general botanical vocabulary they, unintentionally(?), get a phylogenetic connotation. One should be aware of such default assumptions. Therefore it is worthwhile to investigate whether or not it is justified to baptize a term as character or character-state, which should imply that it possesses predictive value. Moreover, BAUM (1952b) does not exclude the possibility that the conceptual transformation series between the peltate carpel shapes also reflects semophylysis. We recall BAUM's (1952b) note about the "Morphologischen Reihe" in which the monocarpellate pistil of *Grevillea thelemanniana* is derived from a "manifest peltaten Karpell" via a hypothetical "gestieltes latent peltates Karpell" (the disappearance of the stalk will cause the *Grevillea* pistil to become sessile or, in other words, epeltate) : "Ich betone ausdrücklich, dass hier die morphologische, also typologische, Ableitung innerhalb der rezenten² Karpelle gemeint ist. Die phylogenetische Karpellentwicklung kann wohl, muss aber nicht mit ihr übereinstimmen" (BAUM 1952b: footnote 3, p. 194).

With respect to the distributional patterns in Figure 2 the following observations are self-evident: (1) the three types are strikingly widespread and (2) most orders and superorders are characterized by the occurrence of more than one of the types. We can conclude that the occurrence of the types of carpel peltation is very heterogeneous and that their predictive value is insignificant, if existing at all. Even at taxonomic levels below that of the family we are confronted with heterogeneity. For instance, within the *Ranunculaceae*, manifestly peltate (*Thalictrum* L., *Anemone* L., *Clematis* L., *Ranunculus* L.), latently peltate (*Helleborus* L., *Aconitum* L., *Aquilegia* L.) as well as transitional forms to epeltate forms (*Eranthis* Salisb. and *Cimicifuga* Wernischek) occur (TROLL, 1932; BAUM, 1952a, 1953a). Similar trends have been observed in the *Fabales* (cf. LEINFELLNER, 1969c, d, 1970a), the *Scrophulariales* (viz. *Bignoniaceae*; cf. LEINFELLNER, 1972b, 1973a, b) and the *Magnoliales* (cf. LEINFELLNER, 1969b). Even within one gynoecium, both peltate and epeltate forms can be found. The gynoecia of some *Magnoliaceae* (VAN HEEL, 1981), *Ranunculaceae* (BAUM, 1952a; VAN HEEL, 1983), *Calycanthaceae* (VAN HEEL, 1984) and *Winteraceae* (VINK, 1970) illustrate this phenomenon.

Since both peltate and epeltate carpels occur in related groups with monocarpellary pistils, it is necessary to caution against a typological and phylogenetic interpretation of the peltate and epeltate development (ENDRESS, 1983). Though the "nontypes" of peltate carpel theory do reflect certain morphological differences, they lack the additional evolutionary dimension for being predictive³. Hence, in answer to Baum's question about the semophyletic foundation of the morphological array manifestly peltate — latently peltate — epeltate (BAUM, 1952b), we must say that, for the angiosperms as a whole, this series cannot be placed against a semophyletic background.

¹"Fertile" means that one or more erect ovules occur, either implanted in median position on the simple cross-zone or rising from the "fused" cross-zones (see e.g. BAUM & LEINFELLNER, 1953; LEINFELLNER, 1953; ECKARDT, 1955; BUXBAUM, 1961; ROHWEDER, 1965).

²We really do not understand why "Ableitung innerhalb der rezenten Karpelle" should have nothing to do with semophylysis. Indeed, semophylysis and the predictivity of types stand in close relation.

³We agree with SATTLER (pers. comm.) that both approaches to pistil morphogenesis are complementary in many respects.

From a methodological viewpoint, the chain of reasoning inherent to peltate carpel theory and idealistic morphology in general, only permits to draw comparative morphogenetic conclusions within a purely phenetic domain. Peltate carpel theory becomes problematic when one tries to attribute semophyletic significance to the postulated morphoclines. For example, an answer to the question if the coenocarpous arrangement arose independently and according to several semophyletic lineages from ancestors with choricarpous gynoecia made up out of either peltate, latently peltate or epeltate monocarpellate pistils looks meaningless from the viewpoint of peltate carpel theory. Possibly, LEINFELLNER (1950) suggests that manifestly peltate pistils first passed through the array choricarpy — hemisyncarpy — eusyncarpy and that in each stage the carpels may develop into extreme manifestly peltate structures on the one hand, and into latently peltate and epeltate structures on the other. In conclusion, gradualism (e.g. "Prinzip der variablen Proportionen") is an interesting tool for establishing descriptive terms or nontypes which indicate morphological variation. However, the acceptance of gradualism is inappropriate for explaining the morphological variation, which is exemplified by the scattered distributional patterns of the peltate carpel shapes on the diagram.

When one still wants to use peltate carpel theory for semophyletic purposes one must realize the following implications. Firstly, only uni-state characters can be distinguished (in this case, the character "carpel peltation" with its only character-state "peltate"; the character "ovule implantation"¹ with the single state "U-shaped") which are not useful for predicting systematic relations within the angiosperms. Secondly, if one sticks to attribute a semophyletic dimension to gradualism (sensu peltate carpel theory), there is no reason at all to justify the acceptance of nontypes such as the manifestly peltate, the latently peltate and the epeltate carpel type. Hence, the "Prinzip der variablen Proportionen" explains the success of peltate carpel theory (the delineation of good nontypes) but also points to the main shortcoming of the theory because high predictive characters and character-states cannot be defined. Additional critical remarks on peltate carpel theory can be found in LORCH (1963) and SATTLER (1974).

3. The character carpel-form

3.1. Semophyletic representation

We are convinced that it is possible to delineate highly predictive gynoecial characters and character-states complementary to the useful descriptive terms and nontypes mentioned above. The various ways in which pistils become visible during ontogeny provide a basis for postulating three mutually exclusive sets of ontogenetic pathways. Accordingly, we have defined the new character "carpel-form" which refers to the earliest ontogeny of pistils. It comprises the following states: the *leptate*, the *pseudoleptate* and the *coenoleptate* carpel-form². In order to clarify why each of these states is referred to as a set of interrelated morphogenetic events we will use the scheme in Figure 3 with the major organizational levels and the relationships among those levels.

In our opinion one has to juxtapose the early development of the bitegmic ovule of *Gnetum* with its third envelope and the earliest development of unicarpellate gynoecia occurring in several taxa with a primitive status such as *Laurales*, *Annonales*, *Corynocarpales*, and so on. According to TAKASO & BOUMAN (1986) the outer envelope of *Gnetum* is initiated as two lateral primordia. These primordia realize continuity and engirdle a residual convex apex which will be transformed into a bitegmic ovule. Similarly, in many primitive angiosperms with (plesiomorphous) unicarpellate gynoecia consisting of one "terminal" monocarpellate pistil, gynoecium development starts when a concave support with a more or less pronounced basis is formed (e.g. *Chloranthaceae*,

¹This connotation is preferred by VAN HEEL (pers. comm.) to denote the concept "placentation".

²We have coined the term "leptate" — an anagram of the term "peltate" — in the same way as the term "tepal" has been derived from "petal" (JACKSON, 1965). The term "leptate" might be a rather infelicitous choice as it might appear to stand in relation to the Greek "leptos" (HOFMANN, pers. comm.) or might overstress a terminological relationship with peltate carpel theory (VAN HEEL, pers. comm.). Despite the suggestions that the term "leptate" would have outlived its usefulness — even before it became accepted — the term will be retained since a better terminology awaits a more accurate knowledge about the ontogenetic and semophyletic processes involved.

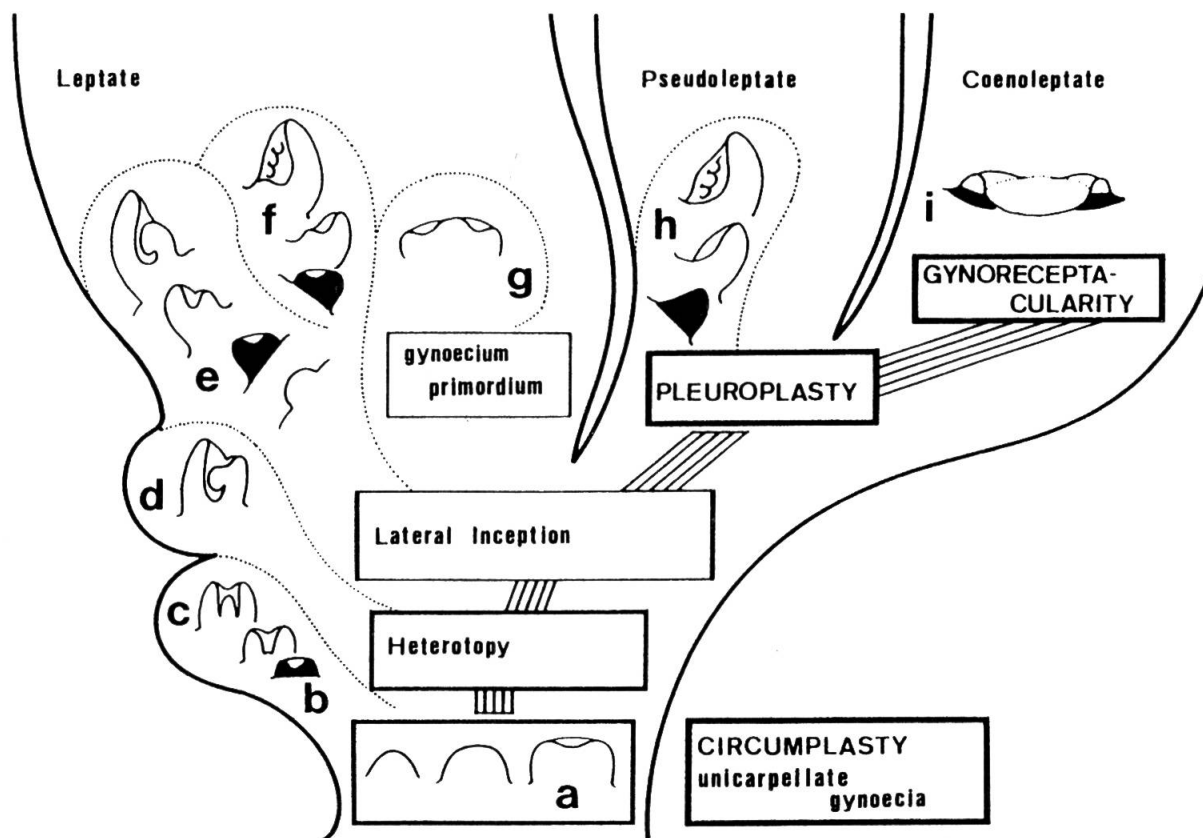


Fig. 3. — Semophyletic scheme visualizing some trends in the pistillary development of the *Magnoliatae*; the black parts in 3b, 3e, 3f and 3h represent the pistil primordia on which pistillary primordia become initiated; the black parts in 3i refer to the gynoreceptacular zone; see text for further explanation.

ENDRESS, 1987; *Lauraceae*, ENDRESS, 1972; *Corynocarpaceae*, PHILIPSON, 1987; see Fig. 3a, 4a). Hence, we can apply the concept *monocarpellate pistil primordium* to this ascidiform structure with its circumferential rim. The way in which the ascidiform primordium becomes visible is designated as *circumplastic inception*. The circular rim first attains permanency, the primordium being initially radial symmetrical. The circumplastic stage can be followed by a *biparous*¹ developmental stage. The biparous developmental stage mostly starts with the initiation of two growth centers or *pistillary primordia*² on the circular rim (Fig. 3b, 4a), an adaxial and an abaxial pistillary primordium (Fig. 3e, 3f, 4a). Since both pistillary primordia will develop in a specific way (in some cases even completely independent from each other; see Fig. 4a) we introduce the term "biparous".

The similarity between *Gnetum* and primitive circumplastic magnoliophytinean pistils is overwhelming. Indeed, in *Gnetum* the two "pistillary" primordia arise in lateral position on a convex dome (designated as a caulomatic structure because no obvious incision arises on the axis beneath the point of attachment, and because the residuum is in line with the axis). In the primitive angiospermous pistils under consideration the pistillary primordia arise on a concave support, viz. the carpel primordium in the traditional sense. The link between *Gnetales* and *Magnoliophytina* (viz. the homologization of the phyllomatic primordia arising on the convex dome in *Gnetum* and the pistillary primordia developing on a concave support in *Magnoliophytina*) is further exemplified

¹From the Latin "pario" which means "I bring forth"; the term "biparous" can thus be explained as "bearing two" (JACKSON, 1965).

²We distinguish pistil primordia or carpel primordia (i.e. the carpel primordia in conventional descriptions) from pistillary primordia. The latter are growth centres (primordia) which are part of a pistil primordium.

by the fact that the phyllomatic primordia of *Gnetum* (TAKASO & BOUMAN, 1986) as well as the pistillary primordia may realize intraprimordial continuity (see CRESENS & SMETS, 1989: Fig. 2, p. 387). The link becomes even more pronounced when *Myricaceae* are brought into the debate. The ovule of *Myrica* will develop from the initially flat bottom of the pistillary locule (Fig. 3b + 3c) as can be deduced from the pictures in MACDONALD & SATTTLER (1973). The initial pistillary locule is nothing more than the cavity of a circumplastic pistil primordium on which two or three pistillary primordia are initiated. MACDONALD & SATTTLER (1973: p. 1966) describe the structure that we call the circumplastic pistil primordium as "a gynoeceal primordium girdling the (flattened) floral apex" (see also their Figures 9-14 and 19-20).

From the above we learned that the major difference between the female reproductive units of *Gnetum* and *Magnoliophytina* is the absence and the presence, respectively, of carpel primordia on which the pistillary primordia are initiated. In other words, the appearance of a carpel primordium which gives rise to the monocarpellate pistil must be seen as an innovation. *Myrica* can be interpreted as an intermediate form, opposing most other primitive taxa where (1) ovuliferous potentiality is associated with the pistillary primordia and (2) the pistillary primordia develop unequal or asymmetrical (cf. the terminological distinction between abaxial and adaxial pistillary primordia which is also used for terminal monocarpellate pistils; CRESENS & SMETS, 1989). In most monocarpellate pistils ovuliferous potentiality is associated with either the adaxial (Fig. 3d + 3e) or the abaxial pistillary primordium (Fig. 3f). The adaxial primordium might even be completely used up in the formation of a single ovule.

According to our hypothesis the development of a whole which is designated as a circumplastic monocarpellary carpel primordium, on which the pistillary primordia are initiated, and the transference of ovuliferous potentiality to the pistillary primordia must be seen as basic events in every semophyletic reasoning about carpels. Another major organizational level is the lateral initiation of monocarpellate pistils — as opposed to the terminal inception — and the possibilities which lateralization create for increasing the number of pistils in one flower. As illustrated by the SEM-observations of *Myosurus minimus* (CRESENS & SMETS, 1989), lateral inception does not necessarily affect the circumplastic-biparous development of the monocarpellate pistils¹.

Lateral inception and the increase of the number of ovuliferous units in each gynoeceum introduced new possibilities for realizing diversification, namely by means of the formation of gynoeceum primordia. The term "*gynoeceum primordium*" is used in our framework to refer to a set of pistil primordia which are initiated not completely free from each other, their upper sides being confluent with the floral center so that the earliest ontogenetic phase of the gynoeceum appears as a preshaped dome flattened on its upper-side (Fig. 3g; see also van Heel, 1981: photographs 38 + 39). Gynoeceum primordia in which the constituting parts still pass a circumplastic developmental phase occur for instance in *Nigella damascena*, *Ranunculaceae* (Fig. 5) and in *Portulacaceae*, *Phytolaccaceae* and so on (pers. observ., VANVINCKENROYE & al., in press).

Besides the circumplastic-biparous developmental pattern, other early developmental schemes stand in relation to circumplasty and the appearance of gynoeceum primordia (e.g. the circumplastic-monoparous development which is marked by the absence of adaxial pistillary primordia; the fertile plicate zone is generated by the abaxial primordium as in Fig. 3f²). Accordingly, the whole of these interconnected early developmental phenomena is referred to as the *leptate carpel-form*. It should be clear that the leptate carpel-form character-state brings pistils into relation with each other which might have little in common at their anthetic stage. On the basis of the concept carpel-form it is for example no mystery at all that — speaking in descriptive terms — both carpellate and acarpellate gynoecea as well as so-called phyllosporous and stachyosporous pistils stand in close morphogenetic relation to each other (CRESENS & SMETS, 1989).

¹With regard to the earliest development we postulate that some plesiomorphous unicarpellate gynoecea are more primitive than e.g. the polymerous *Magnolia* gynoeceum which is traditionally viewed as one of the most primitive angiospermous gynoecea. However, this statement does not rule out that unicarpellate gynoecea have arisen within several taxa by transitions from polymerous to monomerous, i.e. apomorphous unicarpellate, gynoecea (e.g. in *Rosales* and *Fabales* which are both characterized by the pseudoleptate carpel-form).

²These and other developmental patterns will be presented in detail elsewhere.

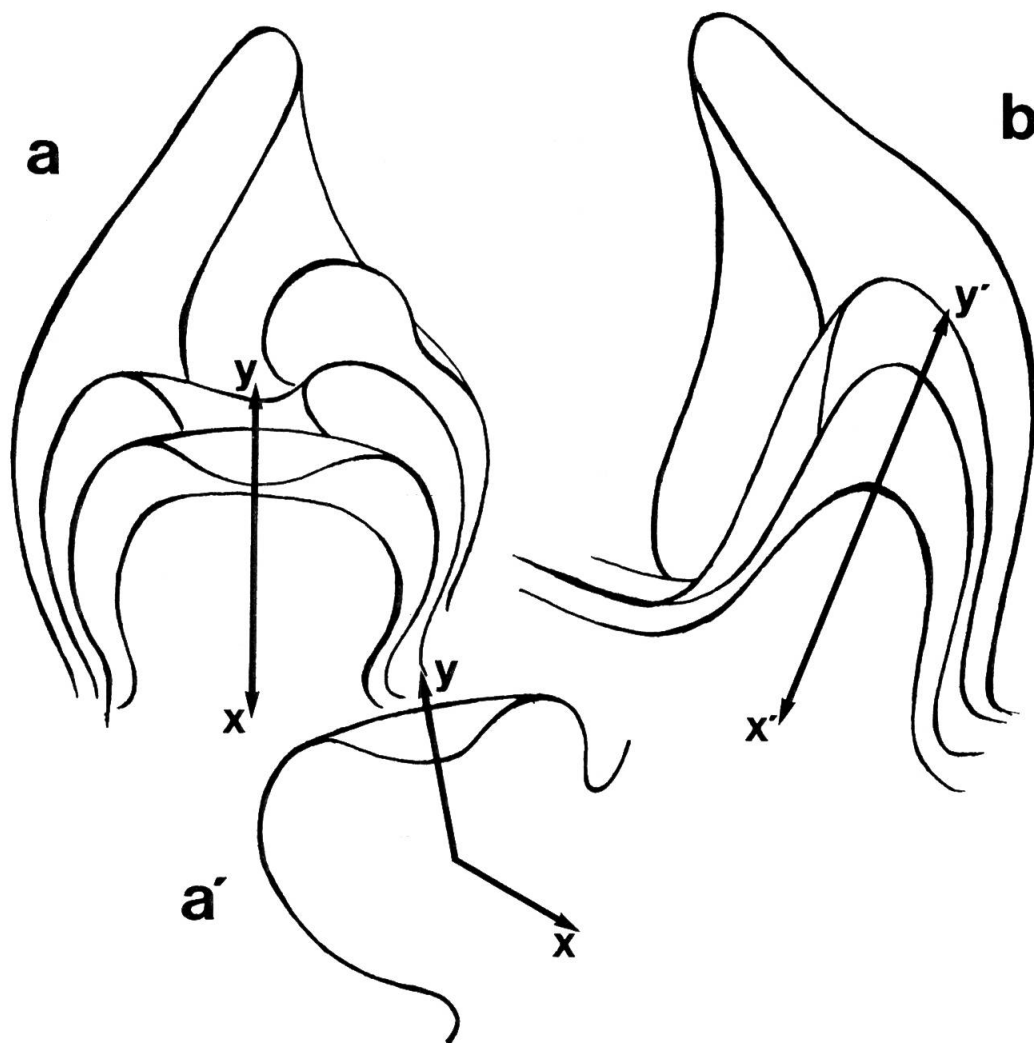


Fig. 4. — Developmental stages of monocarpellate pistils in relation to circumplasty (a and a') and pleuroplasty (b); x-y and x'-y' are imaginary axes revealing, respectively, radial symmetry and dorsiventral symmetry in the earliest developmental stages; see text for further explanation.

In case of unilocarpellous gynoecia in which the initial primordium occupies a terminal position, the imaginary axis, which reveals radial symmetry, matches exactly the perpendicular through the floral axis. Hence the distal part of the primordial cavity is in line with the primordial support (Fig. 4a). However, in case of lateral inception of the carpellate primordia on the receptacle, the body of the primordium becomes half-inverted so that the upper-side (the distal part in comparative morphological sense) is overtopped by the structurally most distal part, and the primordial cavity is at a sloped angle with the primordial support. In order to reveal all elements of radial symmetry one must construct an angular axis as depicted in Figure 4a'. Unlike the initial radial symmetric elements, the inception of an abaxial pistillary primordium and abaxial intercalary growth causes the dorsiventral shape of the mature pistil.

The *pseudoleptate carpel-form* refers to a similar but distinct set of interconnected early developmental patterns. The developmental schemes characterizing the pseudoleptate character-state coincide with *pleuroplasty*. The development of *Geum urbanum* (VAN HEEL, 1983: photographs 78-82, 1984: photographs 10-16) may serve as a typical example of monocarpellate pistils which pass through a pleuroplastic developmental phase. This means, that the dorsal-median portion of the more mature pistil is already recognizable in an early developmental stage (Fig. 4b).

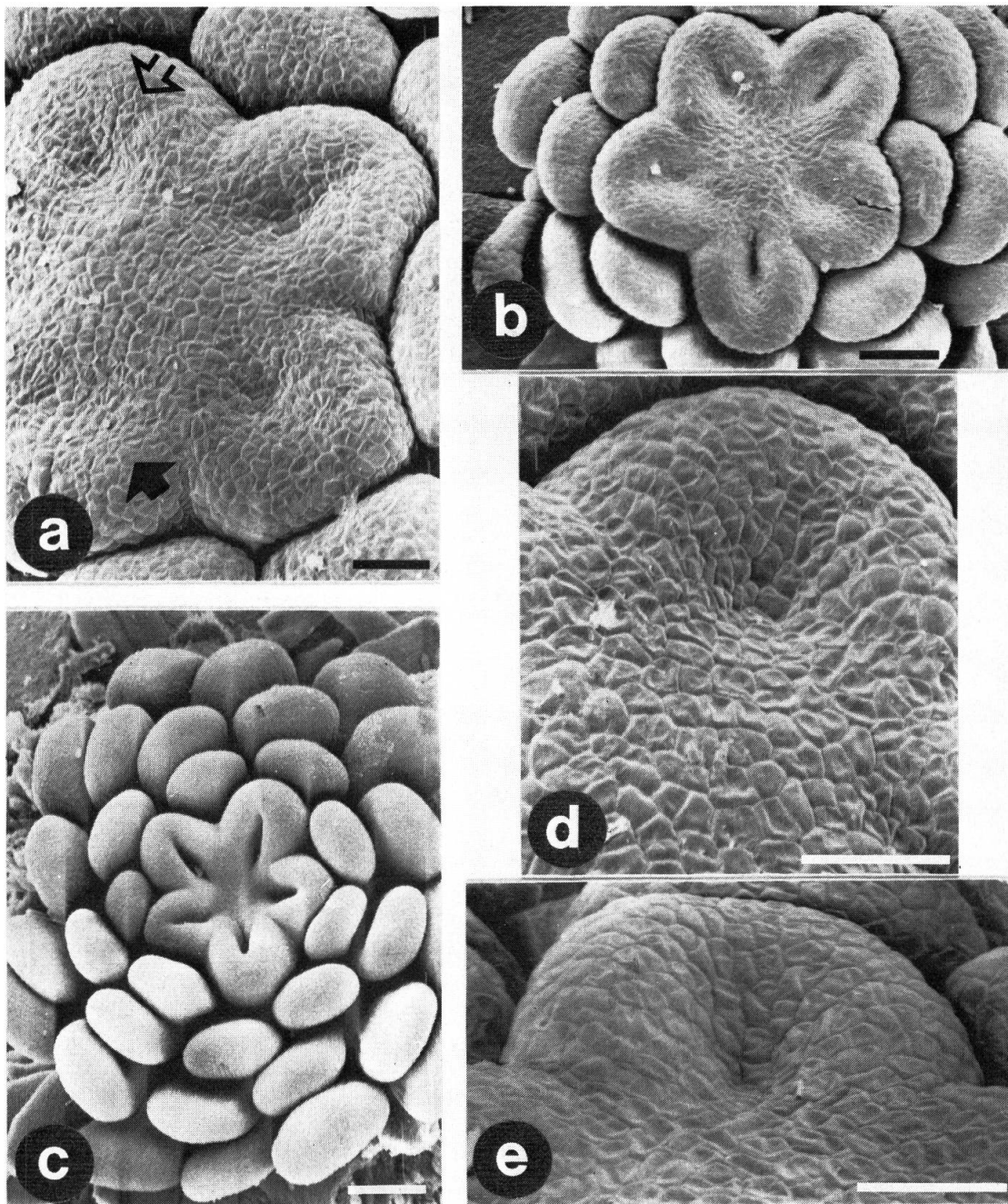


Fig. 5. — Circumplastic-monoparous gynoecial development of *Nigella damascena* L. (*Ranunculaceae*): **a**: the individual carpellary units are initiated in close vicinity to each other. Not all units are in the same developmental stage; the oldest primordium (open arrow) has already attained a circumplastic stage, the youngest (solid arrow) is still in a pre-circumplastic stage. For this reason, the early gynoecium appears as being built up out of laterally fused horseshoe-shaped carpel primordia (which is the classical interpretation); **b**: the youngest primordia exhibit circumplasty, while the oldest have already passed this stage and started the monoparous developmental phase; **c**: although the early gynoecial development is sequential in later stages, all carpellary units develop synchronised; **d**: detail of a circumplastic developmental phase; **e**: detail of a monoparous developmental phase (scale bar = 50 μ m in Figures a, d and e, 100 μ m in Figure b and 200 μ m in Figure c).

The pleuroplastic pistil primordia have an intrinsic dorsiventral appearance and the abaxial pistillary primordia are initiated as lateral appendages (Fig. 3h). The ventral portion of the compact primordium interflows with the receptacle. We call this dorsiventrality primary, opposing the secondary dorsiventrality inherent to the later developmental phases of circumplastic pistils (cf. HAGEMANN's, 1970, morphogenetic foundation of primary and secondary dorsiventrality). The only perpendicular through the primordium worth to consider is the proximal-distal axis, i.e. the one revealing primary dorsiventrality (Fig. 4b).

Till now we saw two major phenomena, circumplasty and pleuroplasty. Given some particular specialization tendencies which provide a basis for the thorough association of the gynoeceum with the parts of the receptacle, we consider a third carpel-form character-state, namely the *coenoleptate carpel-form*. The coenoleptate carpel-form must also be seen as a set of related developmental patterns. The early developmental schemes are here related to the phenomenon "*gynoreceptacularity*". Gynoreceptacularity refers to the presence of a gynoreceptacular zone, that is the terminal and centrally situated zone of a primordial flower apex with an annular meristem which evolved in a concentric way from the initial apical floral meristem (see for instance MAGIN, 1977). The meristematic activity at the inner border of the annular meristem is of carpellate origin. Indeed, often the primordia develop on the border of a more or less central depression (Fig. 3i). In our opinion these primordia must be seen as abaxial pistillary primordia. Whereas the abaxial pistillary primordia of pseudoleptate pistils arise on a lateral appendage, the pistil primordium (Fig. 3h: black part), the support of the abaxial primordia in coenoleptate pistils is represented by the gynoreceptacular

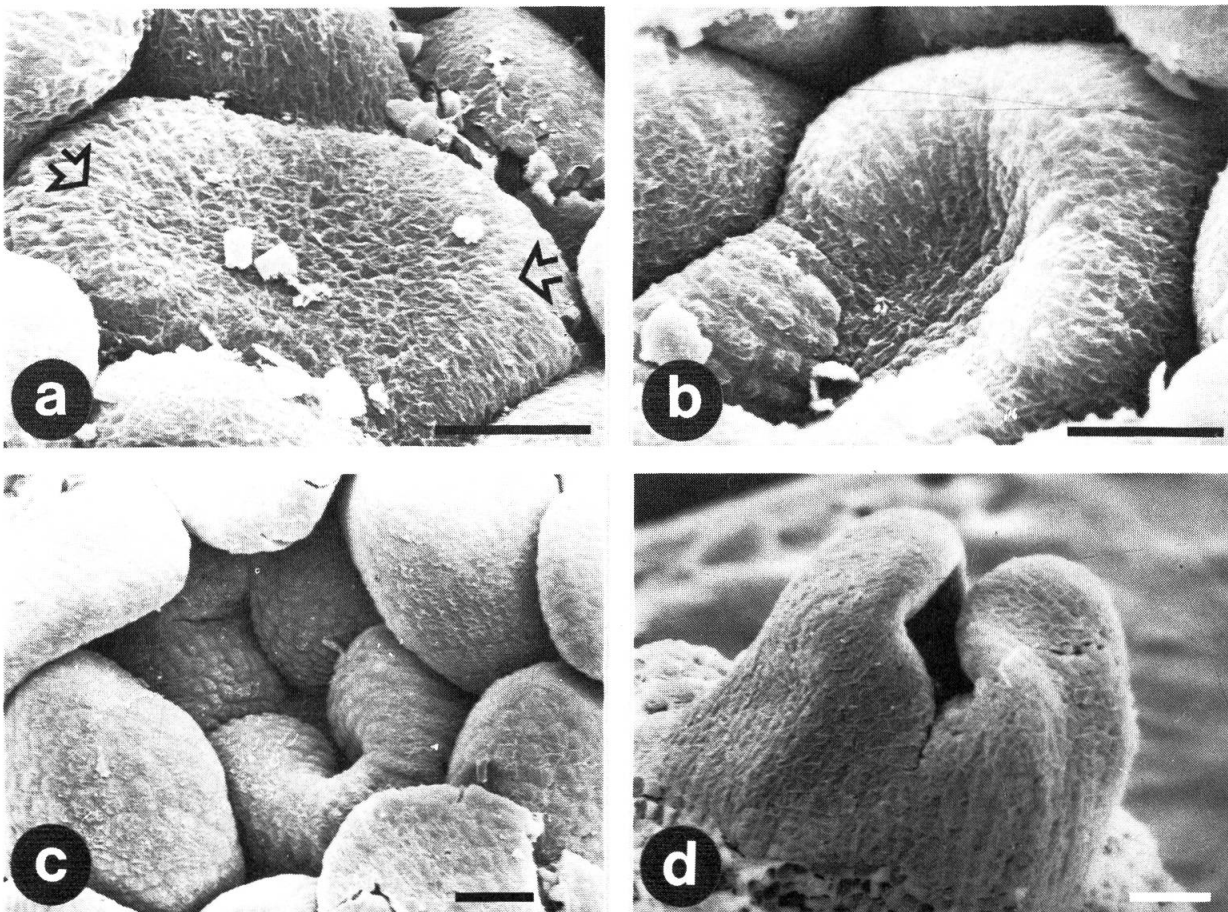


Fig. 6. — Gynoecial development of *Aeginetia indica* L. (*Orobanchaceae*) characterized by the coenoleptate carpel-form: **a**: initiation of two abaxial pistillary primordia (arrows) on a gynoreceptacular zone; **b**: the primordia realized continuity. The abaxial growth of one of the primordia is visualized; **c**: later stage showing the two abaxial growth centres; **d**: intercalary growth results in the formation of the ovarian wall (scale bar = 50µm).

zone (Fig. 3i: black part). The SEM-observations of *Aeginetia indica*, *Orobanchaceae* (Fig. 6) illustrate a developmental scheme that belongs to the coenoleptate carpel-form.

3.2. Some comments on the new concepts

We might have given the misleading impression that "circumplasty" versus "leptate carpel-form", "pleuroplasty" versus "pseudoleptate carpel-form" and "gynoreceptacularity" versus "coenoleptate carpel-form" are interchangeable concepts. However, opposing the carpel-form character-states, the concepts circumplasty, pleuroplasty and gynoreceptacularity refer to specific observable events taking place during the earliest ontogeny of pistils. Just as gynoreceptacularity alludes to the inception of a primordial support, which is designated as the gynoreceptacular region, circumplasty and pleuroplasty refer to the circumplastic and pleuroplastic inception of the ontogenetic supports on which the pistillary primordia become initiated¹.

One could approach circumplasty, pleuroplasty and gynoreceptacularity as low-level characters (CRESENS & SMETS, 1989). Subsequently one can delineate low-level character-states (e.g. a character circumplasty with two states, viz. latent and manifest circumplasty) and eventually determine their occurrence. On the one hand, such a characterization would be well-suited for getting a deeper insight into the homologization of the primordial supports on which abaxial and/or adaxial pistillary primordia arise. On the other hand, such low-level types would contribute little to further understanding of, e.g., the placentation-issue and other major problems with regard to the characterization of magnoliophytinean pistils (CRESENS & SMETS, 1989). These aims asks for homologizations in a wider sense (see SATTLER, 1984); indeed, instead of mature structures or structures at a particular developmental stage it is more appropriate to use basic developmental patterns of pistils as elements to determine homologies (compare our scheme in Figure 3 with LAWRENCE, 1951: p. 74-76 or STEBBINS, 1974: p. 297). In a broad sense, the lineages (series visualizing ontogenetic transformations) of our scheme may be called "ontoclines" to make a clear distinction with the "morphoclines" depicted in the schemes of LAWRENCE (1951) and STEBBINS (1974). Accordingly, the whole set of ontoclines related to the phenomenon "circumplasty" is designated as the leptate carpel-form. In addition, the taxa that are marked by the occurrence of an element of this set belong to the leptate carpel-form complex. The same can be applied to the pseudoleptate and the coenoleptate carpel-form, respectively the pseudoleptate and coenoleptate carpel-form complex. With regard to, e.g., the leptate carpel-form we already discovered some ontoclines, viz. the (manifest) circumplastic biparous-development (Fig. 3e), the (manifest) circumplastic monoparous-development (Fig. 3f), the extreme biparous-development.

In order to tackle some polemics about the validity of our carpel-form approach we want to focus the readers attention also to the fact that, e.g., the presence of the low-level character circumplasty is not exclusively correlated with the occurrence of a low circular rim on the earliest carpel primordium (the character-state "manifest circumplasty"). Indeed, we call some taxa leptate although their carpel primordia do not exhibit an apparent circumferential rim; the way in which the primordial supports become visible can be characterized by another character-state, e.g. "latent circumplasty". As already pointed out in CRESENS & SMETS (1989: Fig. 5) the distribution of a low-level type (character or character-state) does not necessarily has to match that of a high-level character-state. Hence, the low-level character circumplasty might not be diagnostic for the leptate carpel-form complex as a whole. However, till now we have formulated our approach of the character carpel-form (see the semophyletic scheme in Fig. 3) from the perspective that the distribution of the low-level character circumplasty matches exactly with that of the high-level character-state leptate carpel-form. More detailed interpretations of existing and new ontogenetic data will be essential to make the leap to the ultimate goal, namely a dynamic representation of gynoecial ontogeny and semophylysis in which all predictive relations among all recognizable hierarchical types are embodied.

¹The theoretical underpinning is that we, implicitly, use low-level types (among which circumplasty, pleuroplasty, gynoreceptacularity) for delineating high-level types, viz. the character-states leptate, pseudoleptate and coenoleptate carpel-form (see CRESENS & SMETS, 1989).

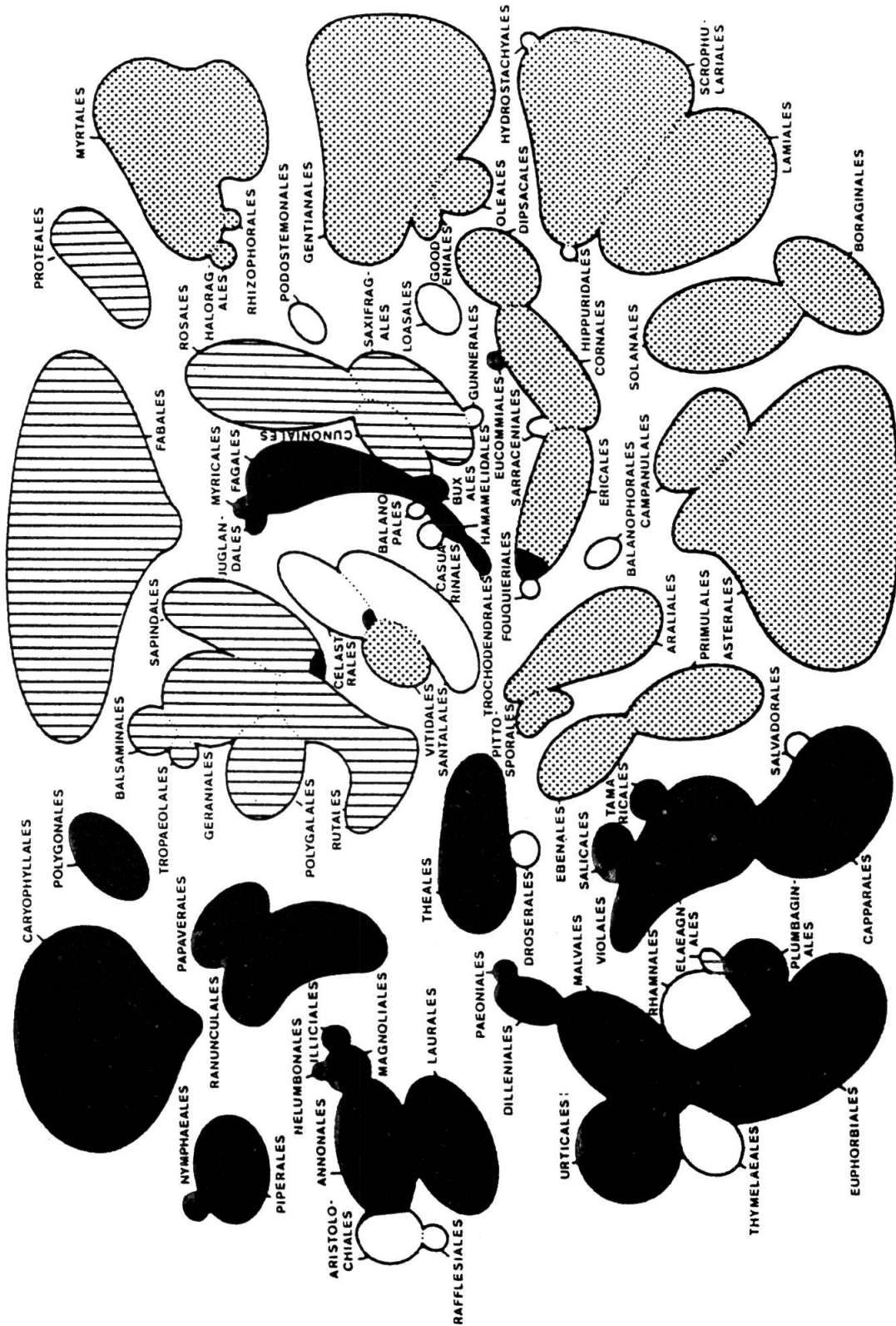


Fig. 7. — Dahlgrenogram of the *Magnoliatae* illustrating the presumable distribution of the leptate (black areas), the pseudoleptate (vertical hatching) and the coenoleptate (dots) carpel-form character-states.

3.3. *Distribution of the carpel-form types*

In order to give a tentative representation of the presupposed distribution of the three carpel-form character-states we compiled a shaded Dahlgrenogram of the *Magnoliatae* (Fig. 7), mainly on the basis of ontogenetic data available from literature. Although a new classification diagram has been prepared (DAHLGREN, 1989) we plotted the available information on Dahlgren's 1980 diagram. This permits to compare the diagrams (see also above) easier with former published shaded diagrams.

Unfortunately, a general inevitability of compiling diagrams and tables is that one has to infer the presence, or absence, of a characteristic within a family often from only a few published observations. In our opinion, this imperfection cannot be taken as an element to challenge the intrinsic value of the methodology of character-research. Actually, one encounters the same problems when constructing systems of classification.

3.4. *Some comments on the proposed scheme*

It should be clear that the scheme in Figure 3 rather claims to reflect our working-hypothesis than being a final conclusion on the semophytesis of the female reproductive structures of the angiosperms. It is marked by two major characteristics. Firstly, Figure 3 comprises discrete morphogenetic phenomena (e.g. circumplasty, pleuroplasty, gynoreceptacularity, etc.) and morphogenetic ontoclines (e.g. circumplastic-biparous development, circumplastic-monoparous development, etc.) which are put into mutual relation by using (mental) organizational levels and processes (e.g. plesiomorphous unilocarpellate gynoecia, lateralization, transference of ovuliferous potentiality, etc.). Secondly, the scheme is dynamic and flexible. Since it comprises elements which either should get a place in botanical observational language, or which belong to the realm of comparative morphogenetic language, ideas about semophytesis may be easily adapted to new insights without causing the necessity to blur the whole scheme or the concepts such as circumplasty, circumplastic-biparous development and so on. The scheme in Figure 3 will be illustrated and treated in more detail in later communications.

One additional element is worthwhile mentioning here. It seems necessary to reinterpret the primordial monocarpellate pistil as a compound arrangement of phyllomes (i.e. pistillary primordia) on a primordial support (the circumplastic pistil primordium). This condition is regarded as a plesiomorphous feature in the angiosperms. Since we use the term "phyllome" to designate all kinds of flattened appendages, irrespective of their morphological nature (CRESENS & SMETS, 1989), the pistillary primordia can also be interpreted as phyllomes while — in accordance with our views on the gynoecium — the developing monocarpellate pistil can be denoted as ovuliferous phyllome.

4. Conclusion

It is important to understand that our characterization of the character carpel-form, with its accompanying semophyletic scheme, does not aspire to be an alternative for peltate carpel theory. The concept "carpel-form" must be interpreted as being complementary to Leinfellner's "typification".

The aim of character-research is to discover types, viz. characters and character-states, and to augment the predictivity of the magnoliophytinean classification system. It should be clear that features such as the various peltate carpel types, which in our conceptualization are labelled as "nontypes", can be useful for describing observations. However, these nontypes do not possess predictive value with regard to the whole of the angiosperm system. Concerning the discussion about "types" versus "nontypes" it is interesting to compare the additional usefulness of the concepts "gynoecial nectary" and "receptacular nectary" with the nontype "nectarial discus" (see SMETS, 1986, 1988; SMETS & CRESENS, 1988).

We are convinced that characteristics such as the leptate, the pseudoleptate and the coenoleptate carpel-form can be considered as types. On the other hand, the schematic outline of the trends

in the development of the pistil of the *Magnoliatae* needs further refinement, so that future characterizations of the gynoecium will become more natural and the usefulness of gynoecial characteristics for systematics purposes will be revitalized.

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