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Confirmation and origin of the paracarp in Annonaceae, with comments on some methodological aspects

THIERRY DEROIN

ABSTRACT

DEROIN, T. (1997). Confirmation and origin of the paracarp in Annonaceae, with comments on some methodological aspects. *Candollea* 52: 45-58. In English, English and French abstracts.

Some anatomical features of the annonaceous gynoecium are reviewed in the scope of the origin of paracarp in Magnoliales. The ovary in Annonaceae-Monodoroideae is characterized by more or less trimerous carpel whorls, whose inner one builds the stigmatic plate. Carpel vasculature study shows no evidence of a placentation change, as suggested by some authors. It demonstrates even an appearance of syncarpy among apocarpous gynoecia made up of carpels showing a derived condition in their vascular pattern, as in e.g. *Cananga*, an extant genus where an experimental check is proposed. Recent contradictory hypotheses, claiming for a monodoroidean monocarpelly, are discussed and may be rejected. They were based on a misinterpretation of the ontogenetical features.

RÉSUMÉ

DEROIN, T. (1997). Confirmation et origine de la paracarpie chez les Annonacées avec des commentaires sur certains aspects méthodologiques. *Candollea* 52: 45-58. En anglais, résumés anglais et français.

Quelques particularités anatomiques du gynécée des Annonacées sont revues, dans la perspective de l'origine de la paracarpie des Magnoliales. L'ovaire des Annonacées-Monodoroidées est caractérisé par des verticilles de carpelles, plus ou moins trimères, dont l'interne seul forme le plateau stigmatique. L'étude de la vascularisation carpellaire ne montre aucune preuve d'un changement fondamental de placentation, et indique même une ébauche de syncarpie parmi les gynécées apocarpes à vascularisation évoluée, notamment dans le genre *Cananga*, où une expérimentation est envisagée. Les hypothèses récentes soutenant la monocarpellie sont discutées et peuvent être rejetées. Indifférentes aux données anatomiques, elles conduisent à une mauvaise interprétation des observations ontogéniques.

KEY-WORDS: *ANNONACEAE* – Magnoliales – Syncarpy – Compitum – Carpel vasculature.

Introduction

The Annonaceae family is remarkable in Magnoliales in consideration of the species number (ca. 2000, at least two thirds of the order) and the structural and ecological diversity (CRONQUIST, 1981; TAKHTAJAN, 1980).

Though carpel number is exceedingly variable (1 to 250, or more), all the annonaceous gynoecia may be referred to three main patterns (FRIES, 1958; LE THOMAS, 1969, 1988):

- the apocarpous pattern, where carpels are wholly separate at the flower and fruit stages;
- the pseudosyncarpous one, where previously distinct carpels fuse during fruit development, simulating then a multilocular syncarpous fruit;
- the syncarpous pattern, where carpels are ontogenetically fused in an unilocular ovary.

This last pattern, otherwise very unusual in the Magnoliales, is known in the only two annonaceous genera *Monodora* and *Isolona*. Its existence has been recently questioned by LEINS & ERBAR (1979, 1982), and VAN SETTEN (1990). In fact, during the last century LINDLEY (1853, repeated by MABBERLEY, 1987) already considered *Monodora* ovary as a unique carpel, without any precise study. In spite of morphological statements (GUÉDÈS & LE THOMAS, 1981; DEROIN, 1985, 1991b) in answer to these criticisms, no consideration of them appeared in recent reviews on floral morphology of Annonaceae (KOEK-NOORMAN & al., 1990; VAN HEUSDEN, 1992). This is rather surprising from authors preparing extensive cladistic studies on the family.

It is therefore useful to provide a concise review of this syncarpy problem, in the context of the whole family. I hope that some evolutive trends in Magnoliales will be here enlightened.

Material and methods

From the Herbarium of Paris (P), eleven annonaceous species have been retained for this study: *Ambavia gerrardii* (Baillon) Le Thomas (*Le Thomas s.n.*, Madagascar); *Anaxagorea luzonensis* A. Gray (*Poilane 10755*, Vietnam); *Annona muricata* L. (*Deroin s.n.*, Ivory Coast); *A. senegalensis* Pers. (*Deroin s.n.*, Ivory Coast); *A. squamosa* (*Deroin s.n.*, Ivory Coast); *Cananga odorata* (Lam.) Hook. & Thomson (*Deroin s.n.*, Ivory Coast); *Isolona campanulata* Engl. & Diels (*Aké-Assi s.n.*, Ivory Coast); *Meiocarpidium lepidotum* (Oliver) Engl. & Diels (*Villiers 633*, Cameroon); *Monodora brevipes* Benth. (*Aké-Assi s.n.*, Ivory Coast); *Piptostigma fasciculatum* (De Wild.) Boutique (*Letouzey 12345*, Cameroon); *Rollinia exsucca* A. DC. (*Raynal 18358*, French Guyana).

After rehydration and postfixation by F. A. A., the opened flowers were included in paraffin 60°, cut at 8-12 mm and stained by the combination: Safranin – Crystal violet – Light green (GERLACH, 1984), then mounted in Euparal or Eukitt. Clearings of flower halves have been attempted, but they fail to demonstrate phloem and thin vascular bundles.

Gynoecial anatomy

Vascular supply of ovules in apocarpous and pseudosyncarpous gynoecia (Fig. 1-3).

Concerning the carpel vasculature, we can distinguish two systems in cross section: 1) a network of loose anastomoses (dashes in Fig. 1); 2) more distinct bundles supplying the ovules (solid lines in Fig. 1), whose origin is especially important to consider.

Thus in the Gondwanian genus *Anaxagorea* (Fig. 1, 1), lateral bundles provide straight the two ovules in accordance with the usual pattern in angiosperms (GUÉDÈS, 1979). Nevertheless ovular irrigation by the median bundle, as in e.g. *Meiocarpidium* (DEROIN, 1987, Fig. 1, 3) seems to be the rule in Annonaceae. An intermediate pattern has been recognized in the Malagasy genus *Ambavia* (DEROIN & LE THOMAS, 1989, Fig. 1, 2), in which mediolateral bundles supply the two superposed ovules. Such an arrangement is remarkably similar to the winteraceous one (GUÉDÈS, 1979).

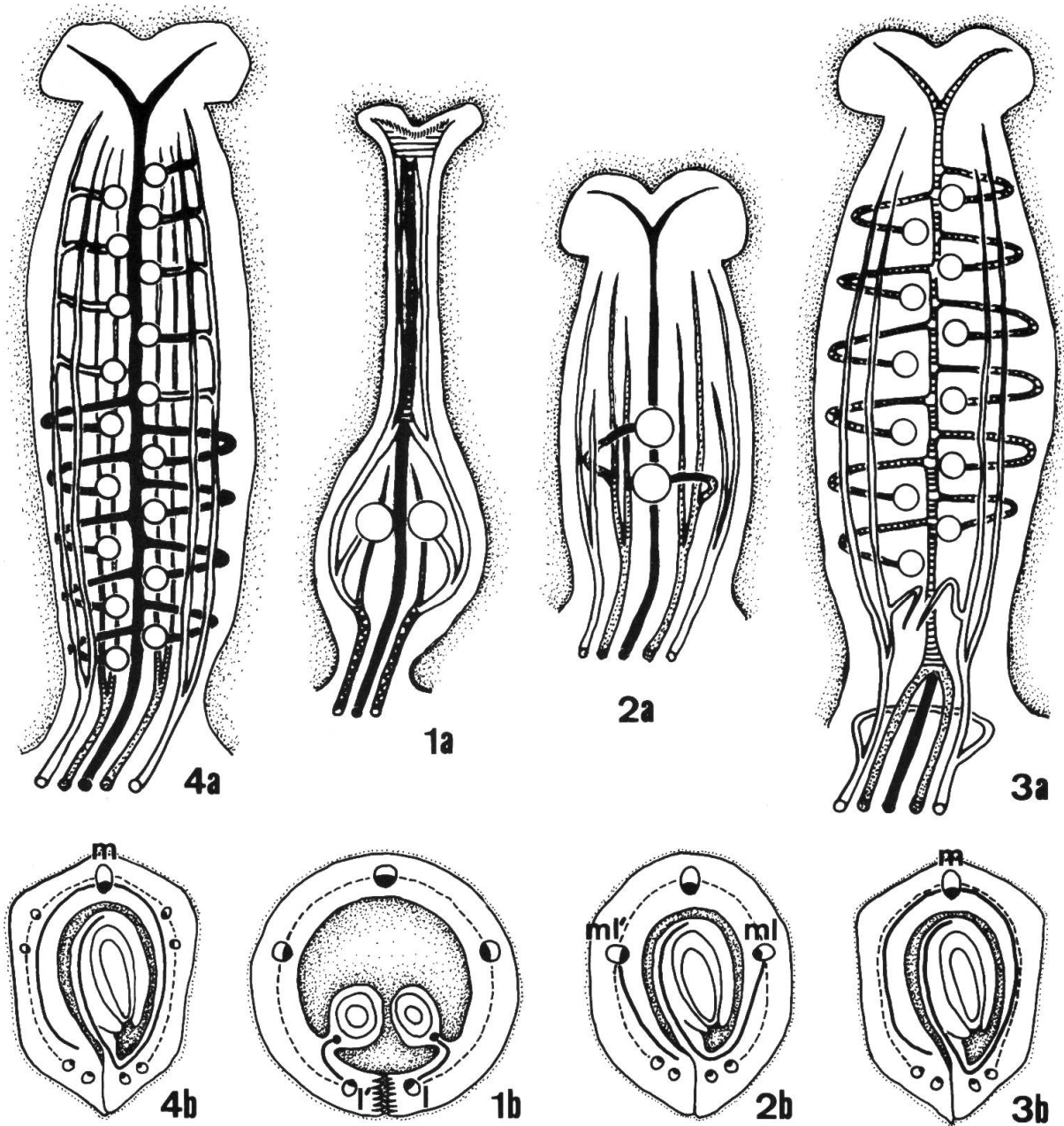


Fig. 1. – Main vascular patterns in annonaceous carpels.

1. *Anaxagorea luzonensis*; 2. *Ambavia gerrardii*; 3. *Meiocarpidium lepidotum*; 4. *Piptostigma fasciculatum*; a. Vascular sketch (lateral, mediolateral, and median bundles respectively in white, stippled, and black); b. Ovary in cross-section (l, ml, m: lateral, mediolateral and median strands).

Some other features of ovule vasculature are worth noting:

- 1) Ovules are always served by vascular strands reaching the stigma, and in many annonaceous genera only the median bundle serves this region. This rule shows perhaps a physiological constraint (DEROIN, 1991a). A constant link may be necessary to coordinate pollination and fertilization stages (DEROIN, 1988a).
- 2) Consequently, ovule supply cannot give any indication on placentation pattern: for example irrigation by the median bundle is certainly not a proof of a laminal placentation. In e.g. *Piptostigma fasciculatum*, upper ovules are supplied by lateral bundles, but lower ones by the median bundle (DEROIN, 1988b, Fig. 1, 4a, and Fig. 2, 3): there is however no clue of a corresponding change in placentation. In the genus *Annona* itself (Fig. 3), the single ovule may be irrigated either by a lateral bundle (e.g. *A. senegalensis*), or by the median bundle (e.g. *A. squamosa*). It seems indeed very unlikely that marginal and laminal placentations may coexist in the same genus. Laminal placentation is more probably related to a multiplication of the ovule number, as seen in Papaveraceae, Nymphaeaceae, and Butomaceae (GUÉDÈS, 1979).

Thus, placentation in apocarpous and pseudosyncarpous Annonaceae is to be described as truly marginal despite the frequent ovule irrigation by the median bundle, resulting from probable functional constraints.

Placentation in the Monodoroideae (Fig. 4 and 5).

Contrasting with the previous genera, *Monodora* and *Isolona* exhibit a very astonishing gynoecium (Fig. 5): it consists of a seemingly simple unilocular ovary, whose internal surface bears numerous ovules.

Already in his diagnosis of *Monodora*, DUNAL (1817) emphasized the pluricarpellous nature of the ovary in order to explain the unusual arrangement of the ovules: these are distinctly disposed in double rows, in whose they face each other by their raphes (Fig. 4). This feature was later recognized in *Isolona (Monodora) madagascariensis* by BAILLON (1869), admitted by LEINFELLNER (1969), and confirmed by GUÉDÈS & LE THOMAS (1980).

A classical analysis of the gynoecial vasculature is wholly consistent with a pluricarpellate pattern for the two genera (DEROIN, 1985). Localization of median carpel bundles by Guédès & Le Thomas has afforded to recognize the expected lateral bundles, at the level of the double ovule rows. In the case of *Monodora brevipes* (Fig. 5, 1b), these small bundles (l) are of phloemian nature, and thus easily visible on paraffin thin (10-15 µm) sections only. Lateral bundles are sometimes fused (sl). The same pattern of syncarpy occurs in *Isolona campanulata* (Fig. 5): only fused lateral strands (sl) occur, and sometimes even lack by reduction.

Thus the hypothesis of pluricarpelly leads to a clear understanding of the structural features. It is noticeable that vasculature in each carpel unit (Fig. 4) is like the usual pattern previously described for apocarpous and pseudosyncarpous gynoecia, even by the occurrence of loose connections between lateral and median bundles. Ovules are normally disposed for a parietal placentation. In fact, in the entire family, ovules are fundamentally marginal.

Although *Monodora* and *Isolona* show true syncarpous (paracarpous) gynoecia, they differ anatomically: median bundles are amphiphloic in *Monodora*, collateral in *Isolona* (at least *I. campanulata*); nature and relative position of lateral bundles differ, and possibly also range in carpel number. These two genera have reached a comparable evolutive level, but are not necessarily very closely related, as maybe shown by the contrasting corolla patterns (LE THOMAS, 1969).

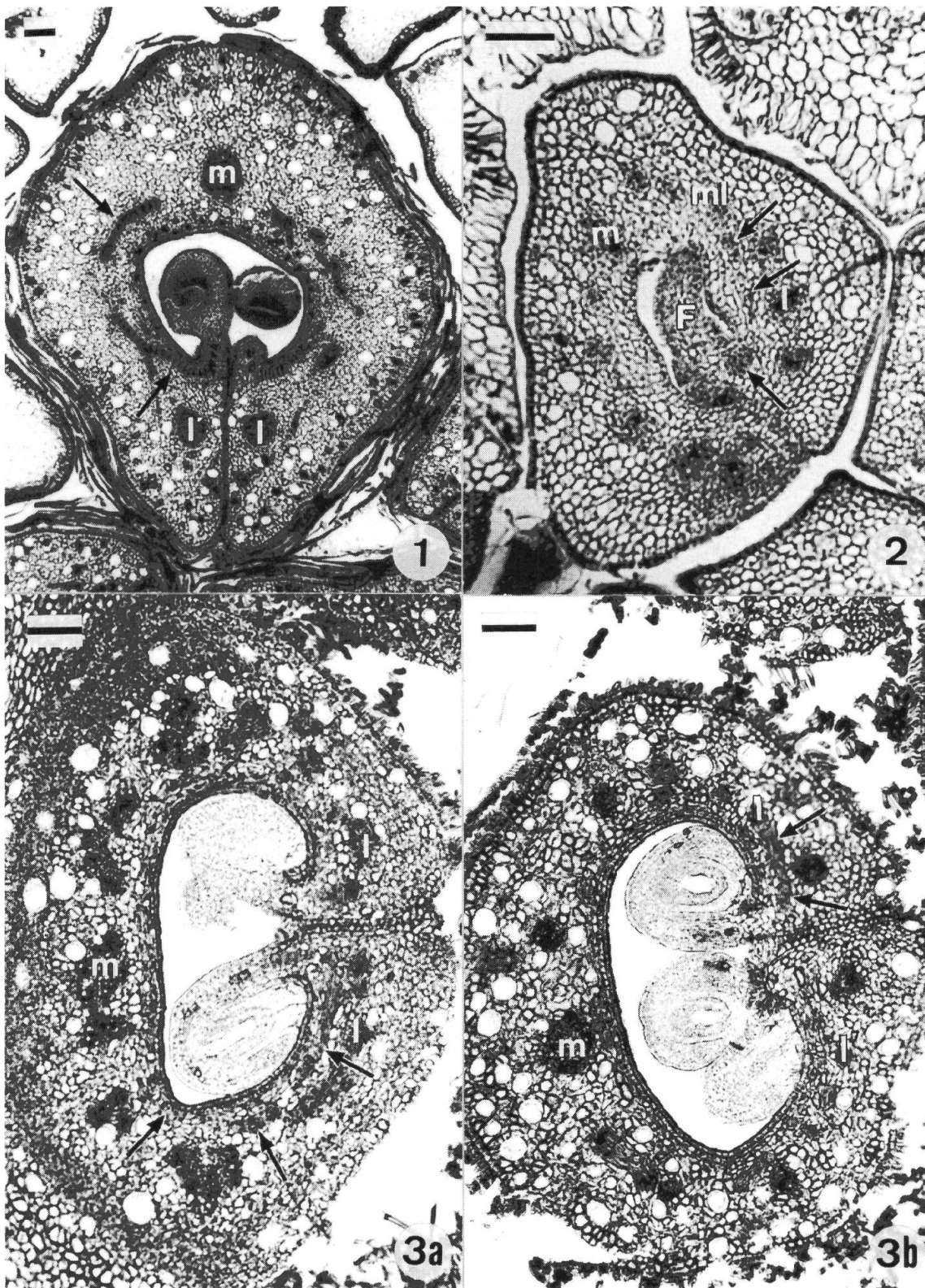


Fig. 2. – Ovular supply in some annonaceous ovaries.

1. *Meiocarpidium lepidotum*; 2. *Ambavia gerrardii*; 3. *Piptostigma fasciculatum* (a. At the ovary basis; b. At the top). F, funicle; arrows show the path of the ovular supply. Bar scale = 100 μ m.

Unicarpelly hypotheses

Several authors have recently disputed these conclusions, mainly drawn from an anatomical approach, and claimed for unicarpelly of Monodoroideae. Their arguments need a careful discussion.

Gynoecial ontogeny

Ontogenetical features were put forward by LEINS & ERBAR (1979, 1982). They described the development of the *Monodora* gynoecium as a morphogenetical unit, but concluded it to be unicarpellate by a comparison with an other assumed equivalent pattern, i.e. the *Mezzettia* carpel. However, this carpel does not show neither a regular alternance of small and large ovarian bundles – but an usual prominent median strand – and any trend toward a laminal placentation, e.g. by an ovule multiplication on the placental ridges. Obviously, the first analytical step should be a thorough knowledge of the morphological gynoecial features at anthesis. Ontogeny – as established by VAN TIEGHEM as early as 1875 – shows how the structures develop from primordia, and in no way their morphological nature. The unicarpelly hypothesis has led the authors to propose a laminal placentation of the ovules in accordance with a new – not yet described – pattern. Ovary vasculature and ovular arrangement conflict obviously this proposal. They may be better explained by a syncarpy, affecting carpels showing an usual and rather advanced “annonaceous” organization.

Fruit structure and ovular supply

In 1990, VAN SETTEN has described a transformation series in the seed arrangement – of about 75 annonaceous genera – from one or two rows to a seemingly laminal disposition. She concluded then the unicarpelly of Monodoroideae. Such data, significant for the fruit ecology, cannot be used in the interpretation of gynoecial morphology. Placentation indeed is defined by ovule – not seed – disposition. During fruit set, deep histological alterations occur, seed shifting and abortion may be expected, obscuring the original arrangement (GUÉDÈS, 1979).

Moreover, Van Setten claimed that an ovular supply by the median bundle indicates a laminal placentation. In fact, such a vasculature results from a peculiar evolutive trend, as all intermediate stages occur in the family (Fig. 1).

Other arguments

In her recent synthetical work on the annonaceous flowers, VAN HEUSDEN (1992) repeated uncritically the previous considerations, but also added new unexpected ones, only drawn from external studies. For example (p. 27) she did not find the longitudinal sutures which, after her, would prove the composed origin of the ovary. In fact, these sutures are the fused carpel margins in the apocarpous gynoecia (SINCLAIR, 1955), and they cannot be expected in paracarpous ones, because of the congenital fusion of carpels.

At the end of the same work (p. 199-200) another hypothesis is proposed, with the collaboration of Van Setten: the ovule number per inflorescence would be more or less constant for all genera. As *Isolona* and *Monodora* have 1-2 flowered inflorescences, and – in her scope – only one carpel per flower, there would be a constraint for “packing” all ovules in the same carpel, modifying then the 2-seriate placentation. It is indeed unfortunate that such an extraordinary idea has not been properly developed in the course of her book, and supported by some statistical data.

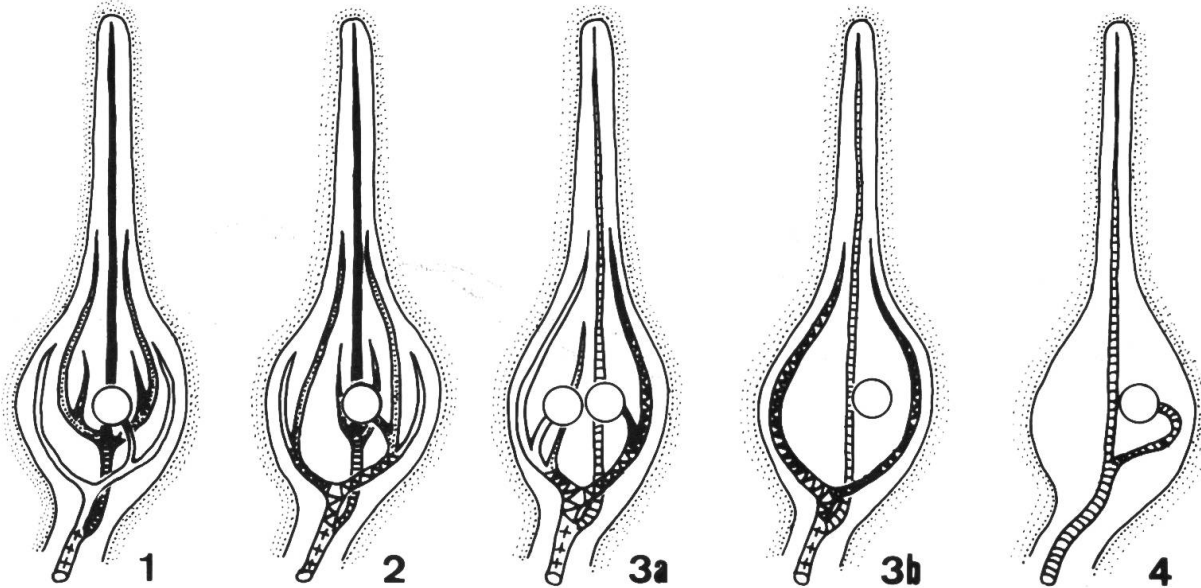


Fig. 3. – Vascular sketches of *Rollinia* and *Annona* carpels.

1. *Rollinia exsuka*; 2. *Annona senegalensis*; 3. *A. muricata* (a. Bioovulate central carpel; b. Uniovulate carpel); 4. *A. squamosa*.

After my own observations, such a claim is untenable: there are about 40-85 ovules per inflorescence in *Isolona campanulata*, 75-150 in *Monodora brevipes*, 250-300 in *Hexalobus crispiflorus* A. Rich., and 800-1000 in *Cananga odorata*. Even in the genus *Annona*, there is a large range of ovule numbers: about 75-250 in *A. senegalensis*, 100-300 in *A. squamosa*, and 250-750 in *A. muricata*.

An attempt for solving the dilemma

A preliminary consensual hypothesis had been cleverly proposed by ENDRESS (1981, 1990) for explaining both the solitary gynoecial primordium, and the obvious pluricarpelly at anthesis. For him however, morphogenetical analysis would indicate the primitive structure, and would be thus more significant than vascular anatomy. Monodoroideae, in this scope, would have a multicarpellate gynoecium that develops ontogenetically from a single carpel primordium.

First, he quoted the extensive fusion of carpels in syncarpous Magnoliales, encompassing the stigmatic region, and resulting in an internal compitum (ENDRESS, 1982). But in vascular anatomical terms, this is not so simple at the ovary level: as we have seen, carpel lateral bundles are fused or not (*Monodora*), and even synlateral ones may disappear (*Isolona*). In *Pleodendron* (Canellaceae), studied by LEINFELLNER (1967), mediolateral bundles of adjacent carpels are fused, but lateral ones are free. These examples show that syncarpy is not always at the same advanced stage, carpel units keeping often an autonomous vasculature. It is then very noticeable that annonaceous syncarps exhibit an obvious whorled trimerous phyllotaxis (Fig. 4), this pattern being precisely related by ENDRESS (1990) to the emergence of a “syncarpy by congenital fusion of several originally free carpels”.

Second, Endress maintained that the closest relatives of syncarpous genera possess unicarpellate gynoecia. He assumed a multiplication of the primary carpel meristem in many derived carpels, in an analogous pattern as in *Nolana paradoxa* Lindl. (HUBER, 1980). But in this case, the additional carpels are randomly arranged, not at all whorled.

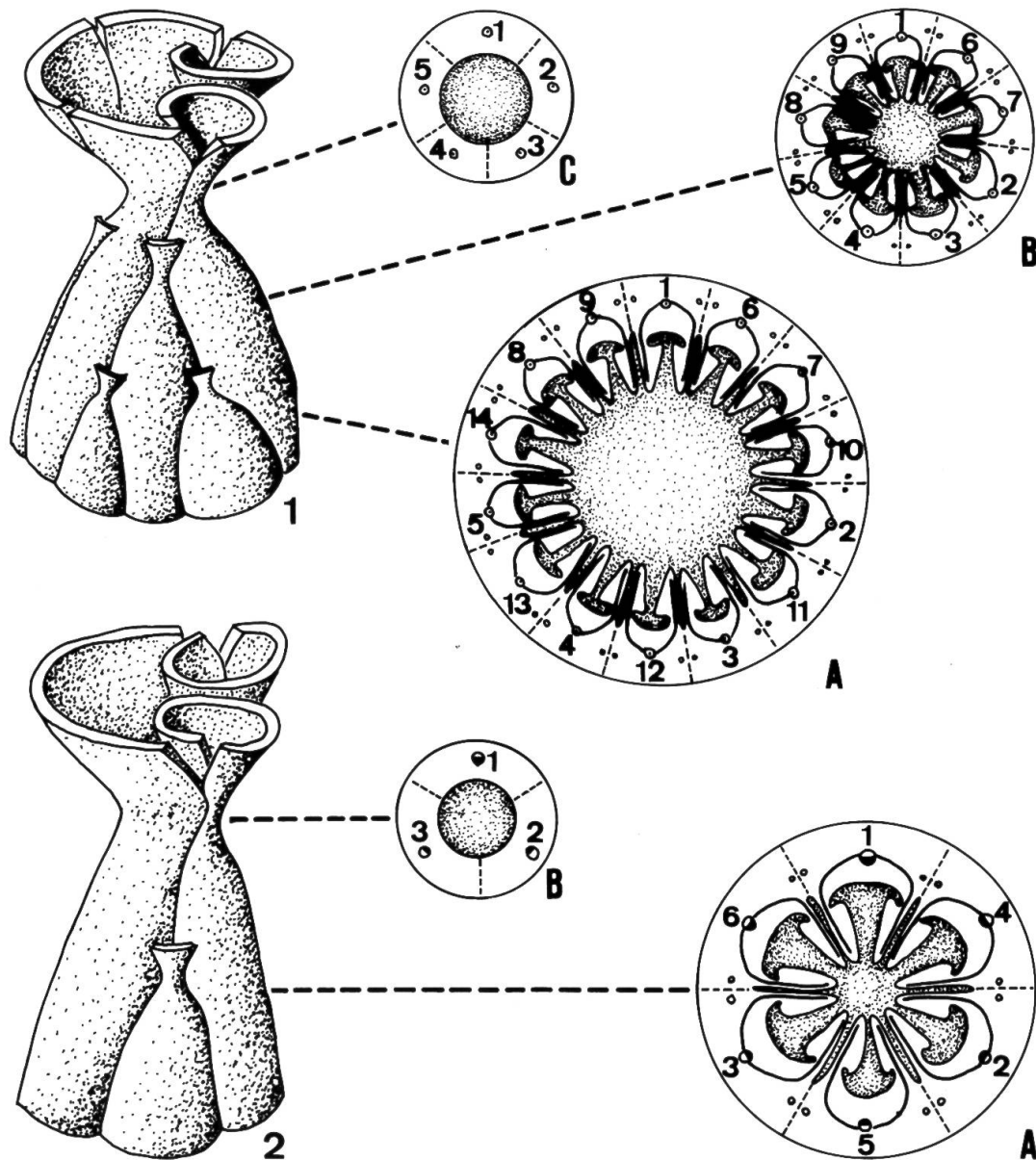


Fig. 4. – Interpretative diagrams of monodoroidean gynoecia.

1. *Monodora brevipes*; 2. *Isolona campanulata*. A, B, C: cross-sections showing the carpel whorls (numbered from top to bottom) at different levels.

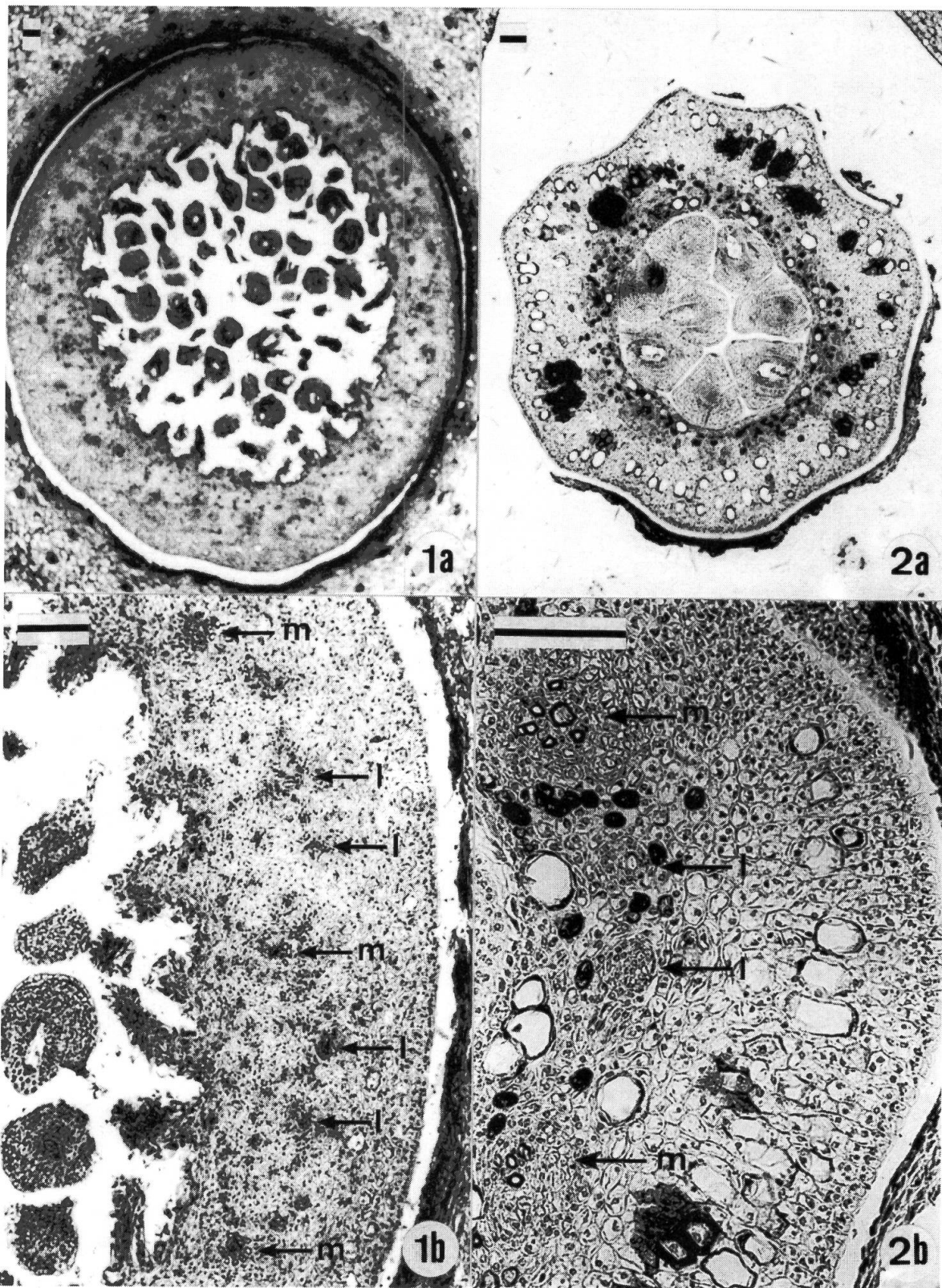


Fig. 5. – Vasculature in the ovary wall of Monodoroideae.

1. *Monodora brevipes*; 2. *Isolona campanulata*. a. Ovary in whole; b. Detail. Bar scale = 100 μ m.

In Annonaceae, such a proposal is wholly untenable (DEROIN, 1991b): the primitive – probably 3-carpellate, as in e.g. *Meiocarpidium* – gynoecium has likely evolved along three main lines:

- a moderate increase in carpel number (towards “*Hexalobus* pattern”, with true syncarpy sporadically occurring in Monodoroideae),
- a great increase in carpel number, with a correlated trend to uniovuly and pseudosyncarpy (towards “*Annona* pattern”), and finally,
- a genetical fixation of the unicarpelly, an otherwise very common feature in few-carpelled gynoecia (e.g. *Asimina triloba* Dunal, with 1-5 carpels). Among the extant Annonaceae, an unicarpellate gynoecium sets apart only four monospecific genera: *Dasoclema*, *Dielsiothamnus*, *Kingstonia*, *Monocarpia*, and the genus *Mezzettia* (at least 6 species), but some unicarpellate species are reported in nine other genera, including large ones such as *Uvaria* and *Xylopia* (FRIES, 1958). If we recognize about 150 annonaceous genera, then ca. 10% are concerned in the unicarpelly trend, a rather low frequency. Endress supposed nevertheless that “a first evolutionary trend to a single carpel was easier morphogenetically than to produce a syncarpous gynoecium”. In FRIIS & ENDRESS (1990), and more recently in ENDRESS (1994), the derivation of syncarpy from unicarpelly is expressed again. But, upon cladistic studies, DOYLE & LE THOMAS (1994) have confirmed a close affinity between Monodoroideae and the African genus *Hexalobus*, whose gynoecium shows 3-12 carpels – i.e. the expected number range – and a connected stigmatic head pattern (DEROIN, 1991b).

Moreover, the pluricarpelly hypothesis is consistent with the evolutionary trends revealed by pollen morphology (LE THOMAS, 1980-1981), and anatomy of receptacle and stamen (DEROIN, 1988a). We shall see, in the next section, that a “classical” comparative morphological approach may, in this case, lead to a more fruitful working hypothesis.

A probable origin of the annonaceous paracarpy

The previous unicarpelly hypotheses are distinguished by a more or less admitted rejection of the classical – i.e. anatomical – definition of carpel (VAN TIEGHEM, 1875), intuitively yet recognized at first in Annonaceae (DUNAL, 1817; STEARN, 1992). Surprisingly none of their authors has been aware that a monodoroidean unicarpelly would mean an alteration in carpel concept, and would be then not very parsimonious. This results in many additional, and rather ill-founded hypotheses, such as unexpected appearance of a new placentation pattern, by an unanalyzed morphogenetical process (Leins & Erbar), or a “packaging” of ovules in an assumed constant number (Van Heusden). These hazy reflections fail to compare with the numerous other Annonaceae. Thus, the monodoroidean ovary appears so peculiar, that no clear explanation may be brought to the fore concerning its origin.

We have seen, in section 1.2, that *Isolona* and *Monodora* gynoecia are anatomically paracarpous, each carpel unit showing the usual vasculature. They seem however characterized by a complete compitum, that is a hollow styler zone, common to all carpels (ENDRESS, 1982; DEROIN, 1991b) but, in these taxa, built only by one gynoecial whorl, the most inner one (Fig. 4; GUÉDÈS & LE THOMAS, 1981; DEROIN, 1985).

This original stigmatic architecture, obviously related to syncarpy, is recognized in the apocarpous genus *Cananga* (Fig. 6), whose two central carpels fuse their styler zones. In the developing fruit the peripheral fruitlets abort (DEROIN, 1988a), emphasizing the functional significance of the compitum for improving the fertilization (CARR & CARR, 1961). During the gynoecial morphogenesis, the central carpels opened and fused at this level in a compitum, then paracarpy might merely evolve from the extension of this scheme until the completion of the ovarian development. In Fig. 7, this hypothesis is sketched.

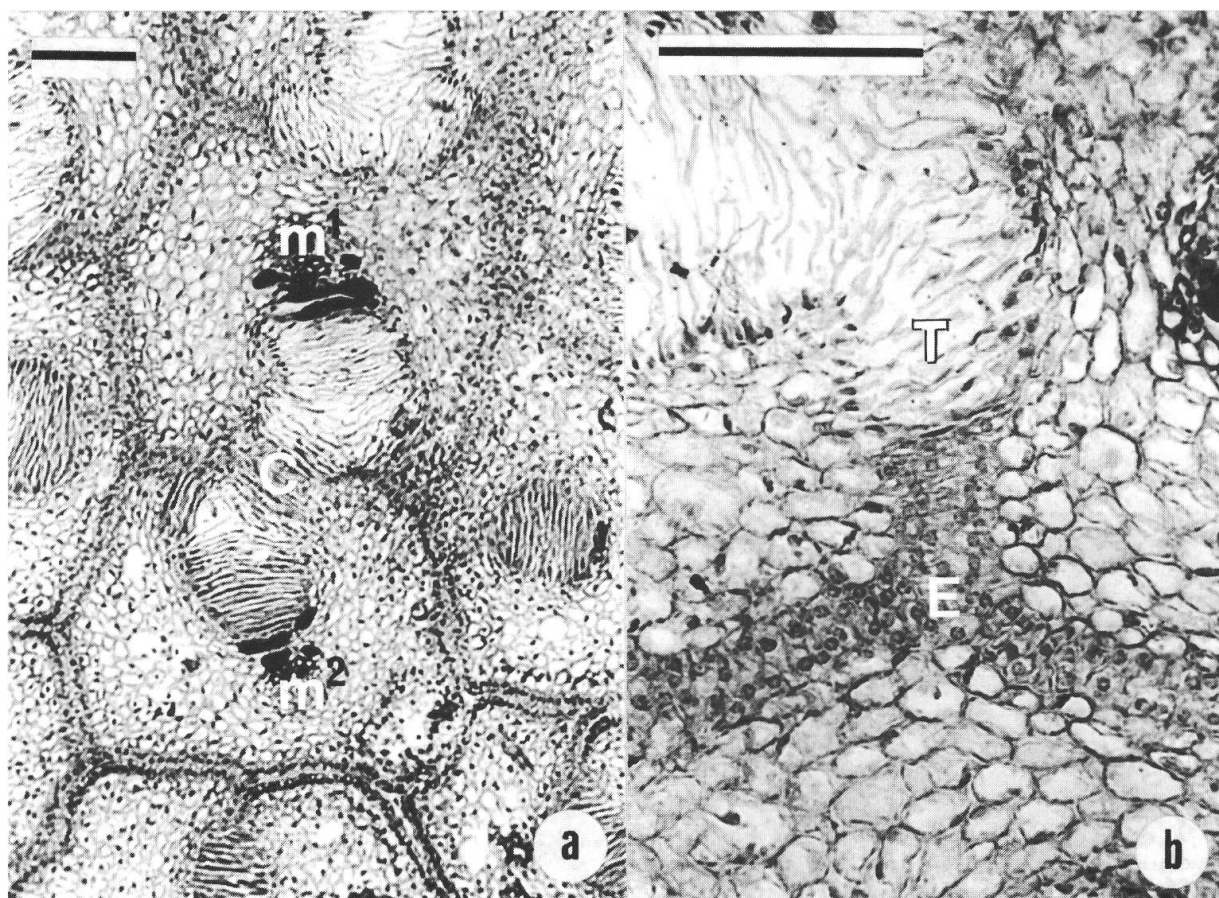


Fig. 6. – Details of stigmatic plate in *Cananga odorata*.

a. The two central carpels building a compitum (C); **b.** Transition between meshed epidermises (E) and stigmatic trichomes (T). Bar scale = 100 μ m.

At first we have an apocarpous gynoecium, all carpels are equal and separate (e.g. *Piptostigma*, Fig. 7, 1). Then a partial compitum (C) is built by the inner carpel whorl, the outer one(s) is (are) smaller, because of a stigma reduction. As separation is maintained at the ovarian level, outer carpels sometimes do not develop into fruitlets (e.g. *Cananga*, Fig. 7, 2). The most difficult process to be explained is the later stigmatic loss in outer carpels, combined with their opening towards the solitary locule (Fig. 7, 3), the compital zone being extended to the ovarian level. The *Isolona gynoecium* differs only in the disappearance of sutures, by congenital fusion (Fig. 7, 4). The decisive transition is consequently between stages 2 and 3.

Thus, no sharp distinction occurs between Monodoroideae and other Annonaceae: paracarpous evolves from usual trends of the family. Furthermore, this paracarpous pattern is very similar to that recognized in Canellaceae (WILSON, 1966; LEINFELLNER, 1967), and the winteraceous Malagasy genus *Takhtajania* (LEROY, 1977, 1978, 1980, 1993; VINK, 1978). In brief, magnolialean syncarpy may be defined as a peculiar paracarpous, in which ovules are never supplied by lateral carpel bundles, and placental ridges are lacking (DEROIN & LEROY, 1993).

Conclusions

Interpreting monodoroidean ovaries does not require an entire overhaul of floral morphology. It is just needed to refer to other annonaceous and magnolialean gynoecia, by using the clas-

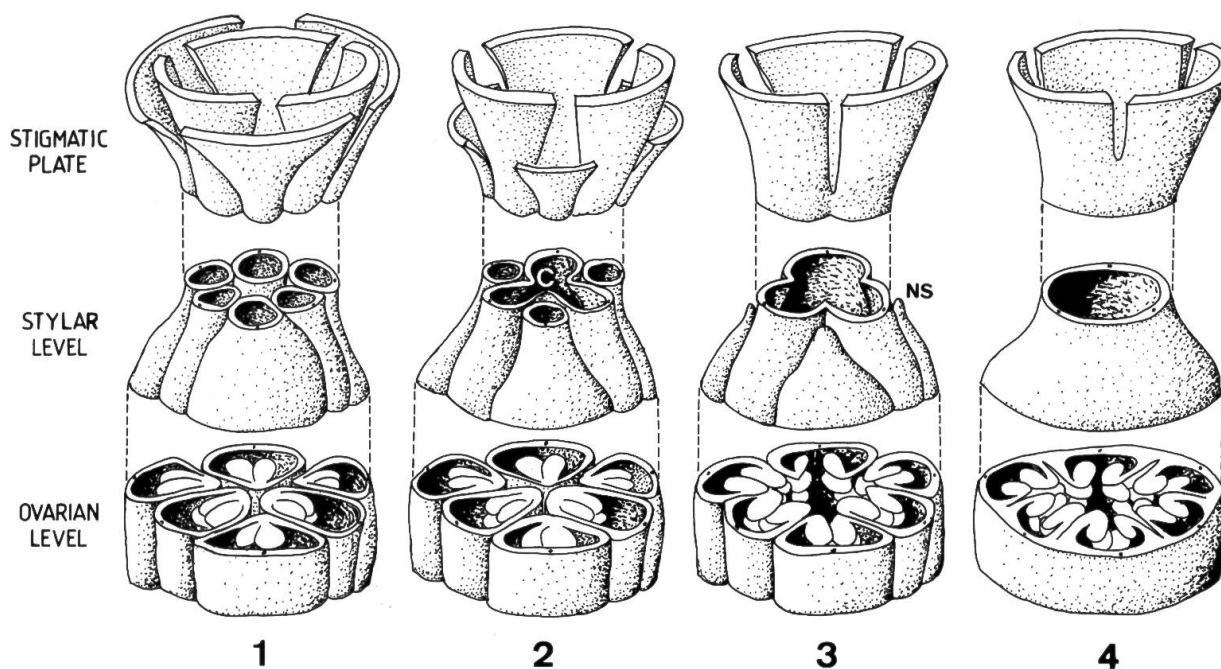


Fig. 7. – Hypothetical origin of annonaceous paracarpary from apocarpy (cutaway drawings).

1. Apocarpous gynoecium (*Piptostigma* pattern); 2. Building of a compitum by central carpels, stigma reduction in outer ones (*Cananga* pattern); 3. Stigma loss and opening of locules in outer carpels, compitum extending to the ovarian base, leading to a solitary locule (hypothetical stage); 4. Disappearance of external sutures by congenital fusion (*Isolona* pattern). C: compitum; NS: not-stigmated carpel.

sical carpel definition. The morphological homogeneity of Annonaceae is thus very obvious, and refutes any sudden alteration in placentation.

Furthermore, at least one apocarpous genus (*Cananga*) exhibits a beginning paracarpary. Perhaps in this favourable case, it would be conceivable to achieve a true, but teratological, paracarpous gynoecium by an hormonal effect, at a suitable ontogenetical stage of the floral bud. Such an experiment would allow to elucidate the crucial events of stigma loss in outer carpels, and the simultaneous withdrawing of carpel margins (Fig. 7, 3).

On the other hand, the biological value of vasculature is not to be overlooked: it plays a prominent rôle in floral physiology, because of the nutritive and hormonal translocations occurring during pollination, fertilization and fruit stages (see, for whole flower, DEROIN, 1991a). Carpel is both a morphological and a functional unit, but not always a morphogenetical one, especially when it is implied in a congenital fusion. The compound nature of the primordium is then revealed only by the vascular organization at anthesis.

Logically morphology precedes (or should precede) ontogeny, and the second cannot be substituted by the first, simply because their aims are different. Unlike the assumptions of CRESENS & SMETS (1992, p. 385), it seems sometimes unsatisfactory, or at least difficult "...to use basic developmental patterns of pistils as elements to determine homologies".

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