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Gynoecium Evolution in Angiosperms: Monomery, Pseudomonomery, and Mixomery

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Abstract—The presence of a gynoecium composed of carpels is a key feature of angiosperms. The carpel is often regarded as a homologue of the gymnosperm megasporophyll (that is, an ovule-bearing leaf), but higher complexity of the morphological nature of carpel cannot be ruled out. Angiosperm carpels can fuse to form a syncarpous gynoecium. A syncarpous gynoecium usually includes a well-developed compitum, an area where the pollen tube transmitting tracts of individual carpels unite to enable the transition of pollen tubes from one carpel to another. This phenomenon is a precondition to the emergence of carpel dimorphism manifested as the absence of a functional stigma or fertile ovules in part of the carpels. Pseudomonomery, which is characterized by the presence of a fertile ovule (or ovules) in one carpel only, is a specific case of carpel dimorphism. A pseudomonomerous gynoecium usually has a single plane of symmetry and is likely to share certain features of the regulation of morphogenesis with the monosymmetric perianth and androecium. A genuine monomerous gynoecium consists of a single carpel. Syncarpous gynoecia can be abruptly transformed into monomerous gynoecia in the course of evolution or undergo sterilization and gradual reduction of some carpels. Partial or nearly complete loss of carpel individuality that precludes the assignment of an ovule (or ovules) to an individual carpel is observed in a specific group of gynoecia. We termed this phenomenon mixomery, since it should be distinguished from pseudomonomery.

Keywords: gynoecium, monomery, carpel, pseudomonomery, syncarpy, flower, evolution, review.

The presence of carpels that form a gynoecium is a key feature of angiosperms. Ovules that give rise to seeds are located inside these structures, and, therefore, the term "angiosperm" implies the presence of carpels. Recognition of the carpel as a distinct structure is among the most fortunate generalizations in comparative morphology of plants that facilitates practical work as well. It is rather difficult to formulate a definition of the term "carpel," just as in the case of many other basic scientific terms, and the origin and homologies of the carpel remain among the major puzzling questions of evolutionary botany [1–4]. A solution to the problem of morphological origin of the carpel would make a substantial contribution to the elucidation of the origin and relationships of angiosperms.

The gynoecium is an entity formed by all carpels of a flower. A carpel is usually defined as a structural unit of the gynoecium [5]. This "cyclic" definition does not shed light on the morphological nature of the carpel and the gynoecium, although it is convenient for practical use. The use of this definition is obviously restricted to the cases when the flower under investiga-tion has distinct borders (although difficulties related to the identification of the borders of a flower arise relatively seldom [6–9]). The definition also makes sense only if flowers of all angiosperms are regarded as homologous structures.

The carpels can be free or fused, and the number of carpels in gynoecia varies considerably. Flowers with several free carpels probably represent the ancestral (plesiomorphic) state of the flower in angiosperms [10]. Indeed, all representatives of the basal grade of angiosperms, with the exception of Nymphaeaceae, have free carpels [10, 11]. The presence of several free carpels in the gynoecium is characteristic of Amborellaceae, a putative sister group to other angiosperms [10, 11].

Usually, the gynoecium formed by several fused carpels can be easily distinguished from that formed by a single carpel, although some exceptions have been reported [12–17]. The present review is aimed in the analysis of problematic situations when the task of carpel counting is not trivial. A brief description of the current concepts of the origin of carpel is necessary for a discussion of these problems.

CONCEPT OF A CONDUPLICATE CARPEL AND THE PROBLEM OF THE ORIGIN OF GYNOECIUM

The conduplicate carpel concept was widely recognized in the second half of the 20th century [18−20]. It regards the carpel as an originally leaf-like organ (phyllome) that gives rise to ovules. The ovules are formed on the morphologically upper (adaxial) surface of the carpel, usually near its edges. The carpel is folded upwards along the middle vein. The leaves of many plants are folded in a similar way within the buds, but the folding of the conduplicate carpel is preserved in the definitive state as well. Moreover, right and left edges of the carpel become fused. Fusion of the edges leads to internalization of the adaxial surface and the ovules located thereon and, thus, results in the formation of the ovary cavity. On the one hand, fusion of the edges is regarded as an evolutionary trend, and, on the other hand, it can be observed during the morphogenesis of the conduplicate carpel. Fusion that involves the contact between organ surfaces and can occur during morphogenesis proper is termed postgenital [21]. The capacity for postgenital fusions is believed to have developed during the evolution of higher plants due to the emergence of carpels in angiosperms [22]. The formation of a completely closed ovary cannot occur in the absence of postgenital fusion of the edges [17] if the primary morphological surface remains continuous [23] and the ovule primordia are formed exogenously. The fusion of carpel edges always occurs on the ventral side (that is, on the side facing the center of the flower in the case of a gynoecium with several carpels), and, therefore, the fusion line was termed the ventral slit.

The concept of the conduplicate carpel implies that a fertile leaf (megasporophyll [18, 19]) with ovules developing on the upper side was the evolutionary precursor of the carpel (each ovule incorporated a megasporangium, i.e. nucellus). Evolutionary fixation of the early morphogenetic stage of this sporophyll characterized by longitudinal folding similar to that observed in the bud [19] and the emergence of postgenital fusion of the edges allow to imagine the origin of carpel. Researchers in the field of developmental genetics supported the hypothesis of the phyllomic nature of all elements of a flower [24−27].

The absence of extant or extinct gymnosperm that would carry ovules on the morphologically upper part of the flat phyllomes is a weakness of the concept of the carpel as a megasporophyll. Ovules are indeed located on the upper part of the ovuliferous scales of conifers, but these structures are definitely not phyllomes, since they emerged due to a transformation of entire lateral axes and organs located thereon (the so-called axillary complex). The surface of the structures (termed cupules or capsules) that incorporated the sufficiently internalized ovules in fossil gymnosperms of the orders Caytoniales and Glossopteridales (Arbe-

riales) is considered the adaxial surface [1, 2]. The interpretation of the origin of these structures (that contained several orthotropic unitegmic ovules) implies a fundamental evolutionary transformation of megasporophylls or their parts. These structures (cupules) are currently regarded as putative homologues of the outer integument of the ovule in angiosperms, since this point of view provides an explanation for the origin of both the double integument and the ovule of the anatropous type [2, 3]. The structures that incorporated the ovules in Caytoniales and Glossopteridales cannot be considered as carpel homologues in this case. Thus, the data collected by paleobotanists do not provide a convincing proof for the theory of the carpel as a megasporophyll.

HYPOTHESES THAT CHARACTERIZE THE CARPEL AS A PHYLLOME BUT NOT A MEGASPOROPHYLL

S.V. Meyen [28] and the authors of the Mostly Male Theory of flower origin [29, 30] believe that the carpel is probably homologous to the microsporophyll of the ancestors of flowering plants. The emergence of ovules on the carpel, as well as the disappearance of microsporangia, are assumed to have occurred upon the dramatic homeotic transformations that played an important role in the origin of the carpel. The explanations of the origin of bitegmic ovules of angiosperms used by Meyen and the authors of the Mostly Male Theory [4, 30] do not appear sufficiently convincing and, therefore, represent a weakness of their views. The putative ancestors of flowering plants selected within the abovementioned concepts (Bennettitales and Corystospermaceae) do not allow for a simple representation of a putative mechanism for the emergence of the outer integument from the wall of the structure that incorporated the unitegmic ovules, in contrast to Caytoniales and Glossopteridales. However, researchers in the field of developmental genetics showed that overexpression of *WUSCHEL* in *Arabidopsis* led to the formation of additional integuments, and, therefore, a similar mechanism was assumed to underlie the emergence of bitegmic ovules of angiosperms [31, 32].

Some authors draw parallels between the wall of the angiosperm carpel and the leaves of Glossopteridales that carried the ovule-bearing structures (always on the upper side). One of the viewpoints implies congenital fusion of the axillary shoot that bore the folded megasporophylls to the respective subtending leaf in Glossopteridales. In this case, the subtending leaf may be a homologue of the carpel wall (again, a phyllome, but not a megasporophyll) provided that the megasporophylls themselves are the homologues of the outer integument of flowering plants [1, 2]. The weaknesses of this opinion are the following: (1) a large time gap between Glossopteridales (until the transition from Permian to Triassic) and the most ancient of the reli-

ably identified angiosperms (Cretaceous) [2]; (2) the absence of any structural or developmental proof of the different origin of the placenta and ovary wall in the representatives of the basal grade of flowering plants [11] (with the possible exception of *Illicium*, since some authors assume that the single ovule of this plant is formed on the axis of the flower in the axil of the carpel [33]). Caytoniales, which have many common features with Glossopteridales, coexisted with the first angiosperms, in contrast to Glossopteridales, but the character of the arrangement of capsule-bearing axes on the plant has not been established for Caytoniales because of poor preservation of the material. According to one of the existing hypotheses, the arrangement of capsule-bearing axes in Caytoniales was similar to that in Glossopteridales [1, 2], but there is no direct proof for this idea.

Certain data of developmental genetics support the idea of a carpel as a phyllome but not a megasporophyll. The regulation of ovule morphogenesis shares many features with the regulation of shoot morphogenesis, and there are many similarities between the initiation and development of integuments and leaves [31, 32]. This is indicative of considerable autonomy of ovule morphogenesis relative to carpel morphogenesis. The *AGAMOUS* (*AG*) gene is the key regulator of the development of carpels (in *Arabidopsis*) [32, 34]. Plants with mutations in this gene lack normal carpels. However, the flowers of *Arabidopsis* plants that lack an active *AG* gene can sometimes give rise to ovules that are ectopically located on sepals. Therefore, the regulation of ovule development is apparently partially independent of the regulation of carpel wall development as a whole. Normal development of the carpel in *Arabidopsis* requires the contributions of four genes from the same family: the abovementioned *AG* gene functions in concert with *SEEDSTICK* (*STK*) and *SHATTERPROOF* (*SHP1* and *SHP2*) [32, 34]. *AG* determines the location of the carpels in the center of a flower and defines the sites of expression of *STK* and *SHP* that are "responsible" for ovule development. Characteristically, the *stk shp1 shp2* mutants develop the gynoecium proper but lack normally formed ovules [34].

The facts listed in the previous paragraph cannot be regarded as the components of fundamental argumentation for the carpel being a phyllome but not a megasporophyll, since a similarly autonomous character of ovule morphogenesis must be observed in the true megasporophylls of gymnosperms. The data on the similarity of genetic regulation of the morphogenesis of the entire ovule-bearing placenta to that of the axillary meristem in *Arabidopsis* [32] is of much greater interest. However, the distinction between the processes of placenta and ovule morphogenesis in carpels with a single ovule that predominate in representatives of the basal grade of angiosperms is not completely clear.

ASCIDIATE CARPEL AND THE STRUCTURE OF THE SYNCARPOUS GYNOECIUM

The conduplicate carpel concept does not provide a comprehensive description of the diversity of angiosperm carpels. The ventral slit does not reach the carpel base in many plants. The distal area with the ventral slit is termed the plicate zone in these cases, whereas the proximal area that remains sac-like throughout the development is termed the ascidiate zone [33, 35, 36]. The relative lengths of the two zones in carpels of different angiosperms vary greatly. Ovules can be restricted to one of the zones or located in both zones. If there is only a single ovule per carpel, the ovule is often (although not always) attached to the ventral side in the so-called cross-zone at the border of the ascidiate zone and the plicate zone [35, 36]. The ascidiate carpels of certain angiosperms are completely devoid of a plicate zone. Particularly, this type of structure is characteristic for most members of the basal grade of flowering plants [11], and, therefore, it is identified as the ancestral (plesiomorphic) type upon the reconstruction of the evolution of carpel types according to the maximum parsimony procedure [10]. The ascidiate carpel concept allows for convenient description of the diversity of angiosperm gynoecia, but it does not provide a solution for the problem of the origin and homologies of the carpel formulated above. Indeed, the ovules are located on a morphologically adaxial surface both in the ascidiate carpel and in the conduplicate carpel.

The fusion between carpels in gynoecia, when present, is usually congenital, that is, the fused parts of carpels form a single entity from the earliest stages of development onwards. We will use the terminology of researchers who call a gynoecium syncarpous in the case of congenital fusion between carpels and use the term "apocarpous" for gynoecia that do not exhibit congenital fusion of carpels [35, 36]. Comprehensive comparison of gynoecia of a broad range of flowering plants is the preferred way to confirm the presence of several carpels in a syncarpous gynoecium. A synascidiate zone and a symplicate zone are identified within a syncarpous gynoecium composed of ascidiate carpels [35, 36]. The former zone is formed by congenitally fused ascidiate zones of the carpels, and, therefore, a cross-section of this zone is multilocular from the moment of zone formation, with each locule corresponding to the cavity of an individual carpel. The symplicate zone is formed by congenitally fused plicate zones of the carpels and is unilocular at the moment of formation. The cavity of the symplicate zone is directly connected to the locules of the synascidiate zone. As mentioned above for the free individual carpel, the ventral edges of each carpel (or actually, the walls formed by congenitally fused edges of each pair of neighboring carpels) can undergo postgenital fusion accompanied by the formation of ventral slits in the symplicate zone. The symplicate zone becomes

multilocular if the fusion occurs. The formation of the ventral slit is not a decisive factor in ovule internalization in this case, and, therefore, the formation of ventral slits in the symplicate zone occurs only in some plant species, whereas this zone remains unilocular in many other plants. An asymplicate zone (an analogue of the apocarpous gynoecium) characterized by the absence of congenital fusion of the plicate parts of individual carpels can be located above the symplicate zone [36].

The presence of an originally unilocular area (symplicate zone) in the gynoecium is of great importance for the organization of the growth of pollen tubes. The pollen tubes of most flowering plants grow along the so-called transmitting tissue that is usually derived from the cells of the internal surface of the carpel or from the cell layers located close to the internal surface [5]. The pollen tubes of some other plants grow in the carpel cavity, either along the internal carpel surface or inside the mucilage that fills the carpel cavity [5]. The presence of a symplicate zone allows to form of a special area (compitum) in all these cases. The growth paths of different pollen tubes meet in the compitum, so that the tubes that extend from pollen grains germinated at different stigmas can undergo redistribution between the carpels and compete with each other. These processes are of great biological importance [5, 35, 37, 38]. Complete occlusion of the carpel cavity in the symplicate zone can occur upon the formation of pollen tube transmitting tissue, so that the cavity becomes undetectable on cross-sections. Compitum formation is not unique for typical syncarpous gynoecia, since it can also be observed in apocarpous gynoecia with postgenital carpel fusion [37, 39–41]. Simultaneous internalization of ovules by several carpels is the common feature of these structural variants.

CARPEL DIMORPHISM IN THE SYNCARPOUS GYNOECIUM AND PSEUDOMONOMERY

The presence of a compitum accounts for the possibility of the emergence of structural and functional dimorphism of carpels in the syncarpous gynoecium[1]. A possible and very common situation (1) considered in the following paragraph implies that one carpel (or some of the carpels) is only involved in pollen capture and the organization of initial stages of pollen tube growth but does not bear fertile ovules, whereas the other carpel (or carpels) has both a functional stigma and a fully developed ovary. Redistribution in the compitum area enables the fertilization of ovules (or ovule) of a fertile carpel (or carpels) by pollen tubes from the stigma of a sterile carpel, whereas the presence of several stigmas allows for more reliable pollen capture. However, an increase of the structural complexity of the stigma of a single carpel, such as the division into three (sometimes further branching) branches observed in *Amphibolis* (Cymodoceaceae: Alismatales), can have the same effect [44, 45]. Another kind of carpel dimorphism (2) implies that only a single carpel (or some of the carpels) has a functional stigma, whereas fertile ovules are found in all carpels. This variant is known in Polygalaceae [46]. Finally, the situation (3) can be termed "the full division of labor" between the carpels if one of them (or some of the carpels) bears a functional stigma but does not bear fertile ovules, whereas the other carpel (or carpels) does not bear a fully developed stigma but bears fertile ovules/ovule. *Lagoecia cuminoides* (Umbelliferae: Apiales [47]) can be mentioned as an example of this structural variant. Theoretically, one can imagine a gynoecium (4) that includes three types of carpels: with ovules and a stigma, with ovules and no stigma, and with stigma and no ovules, but no examples of such plants are known to the authors. The functional value of carpel dimorphism in certain gynoecia is unclear. For instance, the sterile carpels of *Triglochin* (Juncaginaceae: Alismatales) do not capture pollen and the gynoecia of these plants are devoid of a symplicate zone with a compitum [44, 48].

The number of sterile and fertile carpels may vary. For instance, *Emmotum* (Icacinaceae) has three fertile carpels and two sterile carpels [49]. The pseudomonomerous gynoecium [5, 17, 33, 36] is a particular case (although the most frequent case) of a gynoecium with dimorphic carpels. All syncarpous gynoecia with a single carpel that carries a fertile ovary can be assigned to this type. A pseudomonomerous gynoecium can also emerge upon postgenital fusion between carpels (as observed in certain palm species) [40, 50]. Considerable reduction of the sterile carpels (or carpel), including the loss of the capacity for pollen capture, can occur in some pseudomonomerous gynoecia [36, 51].

It is very difficult to prove the presence of strongly reduced sterile carpels in a syncarpous gynoecium, since the structure in question is small, probably devoid of specific distinctive features, and congenitally fused to a fertile carpel. Morphological series with an increasing degree of reduction of sterile carpels provide the most convincing proof of the pseudomonomerous nature of these gynoecia [51]. The construction of these morphological series is not always possible, especially if one tries to eliminate all contradictions with the data of molecular phylogenetics that define the relationships between the taxa used for the construction of the series. We believe that the absence of clear morphological series and traces of sterile car-

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[1] The term "carpel polymorphism" has been compromised to a certain extent, since the studies published by E.R. Saunders (for example, [42]) declared the presence of sterile and fertile carpels in an unreasonably large set of flowering plants that almost encompassed the majority of angiosperm groups. The statements made by Saunders are largely due to an insufficiently critical interpretation of data on flower vasculature [43]. However, these statements are still of considerable interest in view of the ideas concerning the putative dual nature of angiosperm carpels as homologues of the reproductive structures of Glossopteridales.

pels unambiguously reflected in structural and morphogenetic data provides sufficient grounds for the classification of the gynoecium in question as monomerous, because this hypothesis is more parsimonious. Let us demonstrate this using an example of a group of families of the order Poales recently re-classified as Restionaceae s.l. [52]. Plants with obviously polymorphic carpels were detected among Restionaceae sensu stricto: for example, *Leptocarpus* has three functional stigmas and an ovary with a single pendent ovule. The location of this ovule relative to one of the stigmas is analogous to the location of an ovule relative to the stigma in each of the ovarian locules of Restionaceae species with three fertile carpels [13, 53]. This structure of the gynoecium can be regarded as pseudomonomerous. The family Anarthriaceae closely related to Restionaceae s.str. includes three genera. The relationships between these genera can be described as *Anarthria* (*Lyginia* + *Hopkinsia*) [54]. A typical trimerous gynoecium composed of similar carpels is characteristic of the first two genera [53, 55], whereas a single fully developed carpel is found in *Hopkinsia* [56]. The occurrence of pseudomonomery in *Leptocarpus* does not provide any arguments against the interpretation of the *Hopkinsia* gynoecium as monomerous, since these are neither sister nor closely related genera within Restionaceae s.l. Different kinds of gynoecium reduction observed in other Restionaceae [57] cannot be used for the elucidation of the nature of *Hopkinsia* gynoecium due to similar reasons.

MONOMEROUS GYNOECIUM

A monomerous gynoecium consists of a single carpel. According to the traditional concepts, the monomerous gynoecium is derived from the apocarpous gynoecium as a result of the gradual reduction of the number of carpels, in contrast to the pseudomonomerous gynoecium [19]. These concepts were developed within the framework of the idea of largely irreversible transition from apocarpy to syncarpy during the evolution of angiosperms. However, analysis of the evolution of the "presence of congenital carpel fusion" trait based on molecular phylogenetic trees of flowering plants pointed at the secondary nature of apocarpy in a large number of groups, including all apocarpous monocotyledons and all apocarpous core eudicots (Pentapetalae) [58]. We believe that the origin of a gynoecium from a polymerous-apocarpous or a polymerous-syncarpous type should not be taken into account during making a decision on its monomerous nature. Individual carpels of the syncarpous gynoecium are very often (although not always) initiated as individual primordia, with the congenitally fused areas emerging at the later stages of morphogenesis. The individuality of carpel primordia suggests that the syncarpous condition can not constrain the variation of the number of primordia, including a decrease of this number to one.

A number of convincing examples of truly monomerous gynoecia that evolved upon a dramatic decrease of the merism of a syncarpous gynoecium in the absence of a gradual series of transition forms (with one fertile carpel and one or several sterile carpels) have been accumulated by now. For example, the syncarpous condition undoubtedly was the ancestral state for the order Caryophyllales, whereas the merism of the gynoecium in this group varied considerably. The monomerous gynoecium of *Trichostigma* (Phytolaccaceae) has an unsealed opening at the base; this opening connects the outer surface of the gynoecium to the ovarian cavity [59]. The opening is similar to the area of the symplicate zone that contains individually open carpels of the syncarpous gynoecia in a number of Caryophyllales species. The preservation of such an opening within the pseudonomomery pathway of gynoecium reduction in this group could have been possible upon a break of the contour of the ovary wall (as seen in a cross-section) only, that is, secondary separation of congenitally fused carpel parts would be required. This explanation appears less parsimonious than the hypothesis on the reduction of entire carpels, i.e., on the monomery of the gynoecium in *Trichostigma*.

Syncarpy and a trimery of the gynoecium were the ancestral states for the group of families of the order Poales that included Cyperaceae, Poaceae, Restionaceae, and Centrolepidaceae. The loss of stability of gynoecium merism occurred in the family Centrolepidaceae (currently regarded as a part of Restionaceae s.l. by some authors). Both monomerous and highly polymerous gynoecia (with up to 45 carpels) are found in the plants of this group [9].

The presence of peculiar features that appeared impossible for a gynoecium formed by a single carpel was often used as an argument in favor of a pseudomonomerous interpretation of gynoecia in representatives of certain taxa. For instance, W.R. Phillipson [60] considered the unilocular gynoecium of *Polyscias (Arthrophyllum) diversifolia* (Araliaceae: Apiales) with a single fertile ovule as pseudomonomerous. This interpretation was argued by the presence of lobes of stigma (regarded as the apices of individual carpels by Phillipson) and the number of vascular bundles in the distal part of the gynoecium being higher than could be expected in one carpel. Phillipson stated that some of these bundles were rudiments of the vasculature of the sterile carpels. Our data show that gynoecium development of this species proceeds through a horseshoe-shaped stage typical to carpel development of many angiosperms, whereas the apical lobes emerge very late. Moreover, the number and shapes of the lobes vary from flower to flower, and, therefore, the lobes could not be the traces of multiple carpels [61]. The numerous small bundles are detected in the top part of the ovary of related species with several fertile carpels. The number of the bundles is several times higher than the number of the carpels. Therefore, the

similar numerous bundles found in the ovary roof of *P. diversifolia* can actually belong to a single carpel. All data taken in combination point at the monomerous character of the gynoecium in *P. diversifolia* [61].

SYMMETRY AND ORIENTATION OF MONOMEROUS AND PSEUDOMONOMEROUS GYNOECIA

As the angiosperm carpels (at least the carpels that have a plicate zone) are monosymmetric, both monomerous and pseudomonomerous gynoecia have a single plane of symmetry. Therefore, one could expect that the generalizations formulated for the monosymmetric flowers would be applicable to flowers with pseudomonomerous and monomerous gynoecia. The groundplan (i.e., the number and relative location of the organs) is in most cases very stable in monosymmetric flowers [62]; this is partially (but probably not fully) related to the role of the genes of the *CYCLOIDEA* family in the regulation of the number of organs in a flower (in addition to the regulation of flower symmetry by these genes) [63]. The orientation of the plane of symmetry is usually stable within a taxon. The plane of symmetry is median in most cases [64], since the bract and the axis of the inflorescence create a morphological gradient that influences the development of a flower [65].

Indeed, most of the convincing examples of gynoecium pseudomonomery are derived from the groups with a stable flower groundplan usually characterized by the presence of a median plane of symmetry. For instance, the large family Umbelliferae (Apiaceae) is characterized by a very stable flower groundplan. The flower of these plants is pentamerous, with the exception of dimerous gynoecium, and the rare deviations from this structure can be regarded as teratological cases [64, 66]. However, pseudomonomery evolved several times in this family, with the stable adaxial position of the sterile carpel in some species (*Lagoecia*) and a stable abaxial position in the others (*Arctopus*) [47]. Legumes constitute the largest group of angiosperms with predominantly monomerous gynoecia. The flowers of these plants are often monosymmetric, the number of organs in a flower is stable, and the carpel is located in the plane of symmetry of the flower [64, 66, 67].

However, contrasting examples that illustrate unstable orientation of monosymmetric gynoecia are known as well. These cases are sometimes related to general instability of flower groundplan in a group. For instance, flower groundplan in Araliaceae (a family related to Umbelliferae) is labile both at the level of the family as a whole and at the level of individual species in some cases [68]. Monomery of the gynoecium evolved independently in several Araliaceae species (all in the genus *Polyscias*), and the character of carpel orientation relative to the median plane of the flower was always unstable within a species and sometimes even within an inflorescence [61]. Importantly, the variation of gynoecium orientation in *Polyscias* is not limited to the cases of monomery [69]. The orientation of the dimerous gynoecium in this group can vary as well, whereas the two carpels of Umbelliferae are always located in the median plane [69].

Instability of carpel orientation was also reported for the pseudomonomerous (monomerous?) gynoecia of Anacardiaceae [14]. Some Anacardiaceae also have a monosymmetric androecium, and the planes of symmetry of the monosymmetric androecium and gynoecium do not necessarily coincide (within the range of infraspecific variation), and even in the case of coincidence the plane of symmetry does not coincide with the median plane of the flower [14]. As in Araliaceae, the flower groundplan varies greatly within Anacardiaceae, although it can be stable within an individual species [14, 64].

The stability of the orientation of the monomerous and pseudomonomerous gynoecium in the groups characterized by stable orientation of this structure is presumably due to the very early occurrence of the key processes defining carpel morphogenesis during the development of the flower. Revealingly enough, the carpel primordium in legumes often becomes apparent earlier than the primordia of the stamens of the inner whorl [67]. However, pre-patterning of carpel positions in flowers with a strictly acropetal appearance of the primordia can occur earlier than the demarcation of stamen positions ("bipolar pre-patterning" of organ positions) [64, 70, 71].

Frequent orientation of the carpel of the monomerous gynoecium of flowering plants in the median plane is indicative of putative direct morphogenetic effects of the flower subtending bract and the axis of the inflorescence. The taxonomically significant diversity of orientation of the carpel of the monomerous gynoecium in Australian Proteaceae-Grevilleoideae [72] is extremely interesting. The authors of the study [72] state that the different variants of carpel orientation in these plants are related to the diversity of shapes of the flower meristem after the initiation of the perianth and androecium. Importantly, the inflorescence of these plants is a double raceme (with the term "raceme" used in a broad sense) with two-flowered second-order axes, which is very compact at the early stages of development. The diversity of gynoecium orientations in Australian Proteaceae may be related to the interaction of morphogenetic signals from the flower subtending bract and the subtending bract of the second-order axis as well.

The instability of gynoecium orientation (including that observed in monomerous gynoecia) similar to that detected in Araliaceae and Anacardiaceae may be due to the absence (or loss?) of the bipolar pre-patterning of organ positions. Furthermore, the establishment of positions of carpels in a flower probably occurs in members of these families at a later morpho-

genetic stage than, for example, in legumes. The character of perianth symmetry can affect carpel orientation. The position of the fertile carpel in Anacardiaceae can be associated with the position of the outermost sepal in the case of imbricate eastivation of the calyx [64]: that is, positional information of the sepals is apparently more important than the morphogenetic effect of the subtending bract and the inflorescence axis in this case.

MIXOMERY: A PHENOMENON RESEMBLING PSEUDOMONOMERY BUT NOT IDENTICAL TO IT

A specific gynoecium type characterized by considerable loss of carpel individuality that prevents the assignment of ovules to individual carpels is sometimes partially confused with pseudomonomery in literature. We propose a novel term mixomery (derived from the Greek words mixis (mixing) and meros (part)) to describe these cases. Preliminary analysis points at the existence of three variants of mixomerous gynoecia characterized by central columnar, basal, or parietal placentation.

The variant characterized by central columnar placentation can be illustrated by an example of Lentibulariaceae. In this case, the wall of a unilocular gynoecium of two carpels (with two stigmas) is formed independently of the central placenta with numerous ovules arranged in a regular pattern; the gynoecium wall is not connected to the placenta [73, 74]. P.K. Endress reported gynoecia with free central placenta in representatives of ten families of eudicots of five different orders and emphasized the initiation of the gynoecium wall in the shape of a continuous ring, with the lobes emerging later; the lobes could be regarded as the apices of individual carpels, although with certain ambiguity [74]. Almost complete loss of carpel individuality was observed in unilocular gynoecia of Primulaceae, where the carpels are fused along the entire length and the numerous ovules are located on the central columnar placenta that emerged as a physical continuation of the flower axis and terminated in the mature gynoecium without reaching the top of the ovary [75, 76]. Endress [74] suggested that the lobes developing on the top of the initially tubular wall of Primulaceae gynoecium at the relatively late stages [75, 76] are only necessary for the closure of the apical opening, and, therefore, they are more likely to be the analogues of the integument lobes that surround the ovule micropile in different angiosperms. The number of teeth formed upon capsule dehiscence may be the only source of information on the number of carpels in this case, but the fruits of Primulaceae do not necessarily dehisce, and, besides, transverse dehiscence that involves the separation of a lid can occur in some plants.

Mixomery is also strongly manifested in gynoecia that have a unilocular ovary with a single basal orthotropous ovule and two or more stigmas (according to the number of carpels that form the gynoecium) developed to the same extent. This gynoecium type is superficially similar to pseudomonomerous gynoecia with a single fertile ovule. However, the equal degree of development of all carpels and the absence of carpel dimorphism is a fundamental distinctive feature of the mixomerous gynoecium. The basal ovule is formed directly at the apex of the floral meristem during morphogenesis and cannot be attributed to any of the carpels, which is also evident from the analysis of flower vasculature. Mixomerous gynoecia with a single central orthotropous ovule are present in several angiosperm groups that could not be regarded as closely related, for instance, in the families Piperaceae (Piperales) [77–79], Polygonaceae [80, 81], and Myricaceae [82]. R. Sattler and his co-authors stated that these gynoecia (as well as most gynoecia described above) should be considered "acarpellate" due to the presumed emergence of ovules on the axis of the flower rather than on the carpels [82, 83]. Thus, we return to the discussion of the possible interpretation of a carpel as a megasporophyll. The point of view of researchers who regard central basal (and columnar) placentation as an evolutionarily derived state of the trait in angiosperms (see, for example, [19, 84]) appears convincing to us. At least, this type of placentation was not observed in any representative of the basal grade of angiosperms [11]. However, there is no reason to doubt the truly terminal location of the ovule in Piperaceae, Polygonaceae, and Myricaceae. This is confirmed by the entire body of data on the structure and morphogenesis of the flower in these plants. The existence of a terminal ovule should not be considered as morphological nonsense (comparable, for example, to a terminal leaf). As mentioned above, the meristem that gives rise to the ovule shares many features with shoot apical meristem.

The emergence of a strictly terminal ovule characterized by radial symmetry can be compared to the emergence of terminal flowers or flower-like structures in racemes, spikes, or thyrses reported for different groups of angiosperms [85]. If similarity to the emergence of terminal structures in the inflorescences is presumed, the terminal ovule can be assumed to have evolved as a result of an abrupt transformation in some cases, and this can explain the absence of clear continuous ranges of transitional forms leading to gynoecia with a terminal ovule (for instance, in Polygonaceae). The similarity between the appearance of terminal ovules in angiosperms and in conifers of the genus *Juniperus* (Cupressaceae) [86] is even more impressive. The ovules of conifers are usually located on the ovuliferous scale that is fused to the bract in Cupressaceae. However, a terminal ovule is located at the end of the main axis of the female cone in certain representatives of the genus *Juniperus*. This ovule can

be the only ovule of the cone and sometimes has three planes of symmetry (associated with trimerous whorls of scales in the cone) [86] rather than two, as in all other conifers [87]. The example of *Juniperus* demonstrates that the instances of terminal ovule emergence are not unique for angiosperms. These instances considered in isolation apparently do not provide any information on the morphological origin of the carpel.

The single terminally initiated ovule of certain plant taxa retains radial symmetry at early developmental stages only and becomes anatropous (in Cyperaceae [88]), anatropous with a funiculus twisted by 180 degrees (in Plumbaginaceae [89]), or bent to varying degrees, often with a twisted funiculus (in Chenopodiaceae [90, 91]) at the later stages. A change in funiculus curvature of a single terminal ovule both before and after pollination was demonstrated in the genus *Polycnemum* closely related to Chenopodiaceae [92]. The direction of ovule curvature could have been used as an argument for the assignment of an ovule to a specific carpel, but the validity of this argument requires proof, preferably presented as a report of the existence of a series of transitional forms. Moreover, information on flower vasculature confirms the terminal position of these ovules (see, for example, [88]).

The multilocular part of the gynoecium (the synascidiate zone or the bases of plicate carpels congenitally fused to the flower axis?) is located below the single terminal ovule in certain groups, such as *Juglans* [93, 94] and *Basella* [83]. This multilocular area appears after the ovule initiation during morphogenesis. The position of the ovule in all these kinds of mixomerous gynoecium is indicative of partial loss of carpel individuality.

Most representatives of the clade that includes the families Chenopodiaceae and Amaranthaceae have a single ovule characterized by terminal initiation, but the formation of numerous ovules on a free columnar central placenta is observed in a small group of these plants [80]. The presence of multiple ovules in this group was hypothesized to represent an evolutionarily derived state [64, 95]; this hypothesis is in good agreement with the data of molecular phylogenetics [96].

Morphological interpretation and origin of the gynoecium of *Peperomia* (Piperaceae) are of considerable interest. This closed tubular structure either has no lobes on the edge or has two poorly developed lobes that emerge at late developmental stages; a single basal orthotropous ovule is located in the center of the gynoecium [97, 98]. Phylogenetic data clearly demonstrate that this gynoecium is derived from a mixomerous gynoecium with a single basal ovule and several stigmas [99]. The reduction of the number of carpels to one is usually believed to have occurred upon the emergence of *Peperomia* gynoecium (which is thus monomerous), but the hypothesis of the origin of this gynoecium upon a complete loss of carpel individuality similar to that observed in Primulaceae is as valid as

the former one (for a review of the hypotheses, see [97]).

The example of Cyperaceae convincingly demonstrates the loss of evolutionary stability of the number and position of carpels upon a partial loss of carpel individuality [88]. Trimerous gynoecia of monocots that do not have bracteoles on the pedicel usually consist of a single median-abaxial carpel and two transversal-adaxial carpels, with extremely rare exceptions [100]. Dimerous gynoecia that can be interpreted as a result of loss of the median carpel occur in many Cyperaceae. In some Cyperaceae taxa, however, two carpels are located in the median plane, that is why their homology with the carpels of original trimerous gynoecium remains obscure [88].

Basal or central columnar placentation is characteristic of all mixomerous gynoecia described above. The possibility of "collectivization" of ovules located in the symplicate zone of a syncarpous gynoecium is of considerable interest. Indeed, it is sometimes difficult to assign a particular (or single) ovule located on the parietal placenta to one of the neighboring carpels in gynoecia with a fertile symplicate zone. These difficulties arise (1) when numerous ovules are arranged in multiple rows on a parietal placenta (for example, in Papaveraceae [101]) and (2) in gynoecia with orthotropous ovules or ovules bent in the vertical plane are arranged in a single row on a parietal placenta. The gynoecium of *Scaphocalyx* (Achariaceae, Malpighiales) is among the most convincing examples challenging the concept of the carpel. This gynoecium contains a tubular ovary and five to seven stigmas. The ovule wall bears orthotropous ovules, with one ovule at the radius of each stigma (this is the lower circle of ovules) and one ovule at each radius between the stigmas (the upper circle of ovules) [102]. Thus, the degree of individuality of the carpels in the symplicate zone of the gynoecium is likely to vary between the different groups of flowering plants, and further research on this issue appears justified.

CONCLUSIONS

The delimitation of pseudomonomerous and monomerous gynoecia has traditionally been a key point in the discussion related to these structures. We believe that the existence of mixomerous gynoecia, along with monomerous and pseudomonomerous gynoecia, should be recognized. A monomerous gynoecium consists of a single carpel. A pseudomonomerous gynoecium is a particular case of a gynoecium characterized by carpel dimorphism (one carpel is fertile, whereas the other(s) are sterile). A mixomerous gynoecium is characterized by partial or nearly complete loss of carpel individuality, so that the assignment of the ovule or ovules to specific carpels is impossible in this case. A pseudomonomerous gynoecium is a monosymmetric structure. If the morphogenesis of a pseudomonomerous gynoecium is stable

in a certain species, a special regulatory mechanism that may show fundamental similarity to the regulation of morphogenesis of flowers with a monosymmetric perianth is expected to exist. The regulatory mechanisms involved in the formation of floral monosymmetry were mostly addressed by studies of the perianth and androecium, and, therefore, the analysis of genetic mechanisms that underlie the development of the pseudomonomerous gynoecium is a promising area of research.

Many questions remain open in the area under investigation, and the identification of gynoecium type in the representatives of specific taxa is one of the most important among these questions. Earlier reports of the existence of pseudomonomery in some taxa cannot be considered correct. The basic conditions for the use of the transitional form criterion to reveal the pseudomonomerous nature of gynoecium must be clarified. An intermediate form is not necessarily a putative transitional form. A form that corresponds to a state fixed within a taxon usually allows for unambiguous interpretation. On the other hand, the use of teratology data is much less likely to lead to reliable conclusions. Let us consider two related species with flowers that contain a single carpel in one species and two carpels in the other species. As the size of sample of material investigated is increased to infinity, the range of intermediate structural types that connect the one- and two-carpel variants will expand towards completion. However, this range will not necessarily be reflective of the scenario of evolutionary transformation of the trait.

Gynoecia that combine the traits of pseudomonomerous and mixomerous structures require further analysis. For instance, two of the three carpel locules in the gynoecium of *Viburnum* are regarded as strongly reduced, whereas the common placenta of these two carpels contains an ovule that extends into the large locule of the third (sterile) carpel [103]. These cases argue against the concept of pseudomonomery and mixomery as two states of the same trait. It is probably more appropriate to consider several individual traits, including "carpel dimorphism" and "connections between the ovules and specific carpels" as long as the analysis of trait evolution is concerned.

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