Structure and development of the coenocarpous gynoecium in angiosperms

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Summary: In modern systems, gynoecium can be of three independent types: apocarpous, paracarpous and syncarpous. These types differ in various features: degree of carpel association, zonate structure of the ovary, structure and position of placentae, structure of sutures and origin of septa. The placentae are located on the sutures of different nature, and they are sutural (central angular placentation in syncarpous gynoecium, parietal placentation in paracarpous gynoecium and simple angular placentation in apocarpous gynoecium) or placentae are formed on carpel lamina (laminal placentation in mainly apocarpous type). The monomerous apocarpous and polymerous apocarpous variants differ in structure. As for the carpels, especially in their lower part, the polymerous apocarpous gynoecium of the synascidiate variation resembles the syncarpous and paracarpous types. Together they form a group of coenocarpous gynoecia. Various variants of a pseudo-monomerous gynoecium could arise in evolution on the basis of the syncarpous and paracarpous types.

The ratio of zones in the gynoecium can be different. The structure of the apocarpous gynoecium, especially of the proximal part, is characterized by some features. In monomerous variants, the ascidiate region (3-zoned peltate carpel) is very early differentiated or this region is absent (2-zoned epeltate, or conduplicate carpel). In polymerous variants with a typical upper ovary, the carpels remain free throughout, and they are likely characterized by the formation of 2-zoned epeltate carpels (plicate variation). In the gynoecium with 3-zoned peltate carpels and an almost upper or semi-lower ovary in its lower part, a synascidiate region (synascidiate variation) is created. The zonate structure is also inherent in the syncarpous gynoecium. In the lower part of the ovary, the synascidiate region is also created, but the ovary is characterized by a symplicate structure over a longer distance. Median septa can be postgenitally created: complete (ovary has a locular structure over a longer distance – typical variation) or incomplete (a cavity forms in the center of the ovary, but the placentation remains central angular – symplicate variation) in the course of rapprochement of the syncarpous sutures in the center. In a number of plants, septa are destroyed in the ovary during morpho- or phylogenesis (the resulting special columnar placentation is a modified central angular – lysicarpous variation).

In the paracarpous gynoecium, the synascidiate and / or symplicate zones may occur in the lower part of the ovary. This gynoecium preliminary demonstrates a hemisymplicate state, while sutures without the middle and apical parts occupy positions near the wall, the placentae are only parietal and the ovules are located near the ovary wall. The structure of the ovary usually does not differ in height (typical or aseptal variation) or it can postgenitally form complete (septal variation) or incomplete (hemiseptal variation) median septa or the destruction and disappearance of such septa during development occur (secondary aseptal variation).

The considered types of gynoecium are characterized by special reproductive strategies. Being a starting point for coenocarpous variants, the apocarpous type itself seems to have been transformed to a minor extent. Evolutionary trends of paracarpous and syncarpous gynoecia were probably independent. In each type, the spatial variants arose as a result of mechanisms for creating extra space in the ovary for the developing ovules.

Keywords: gynoecium, placentation, morphogenesis, structure, types

The central part of the flower is occupied by the gynoecium containing one to many carpels. The principles of typification and the number of distinguished gynoecium types have not yet received an unequivocal interpretation. First of all, the characteristics of gynoecia are often investigated

only at one of the middle stages of flower formation (usually during the development of the embryo sac). Furthermore, due to insufficient knowledge of the gynoecium morphogenesis, the expediency of existence a number of its types is unjustified.

Inferring gynoecium evolution in angiosperms is highly problematic. This was especially intensified after employment of molecular phylogenetic data for analysis. The concepts of primary and secondary traits in development are not used to understand its origin in evolution, but mainly to reflect the original (basal) and derived taxon states. The discussed problem also affected the structure of the gynoecium, with the main trends of its evolution being revised (Doyle & Endress 2000; Rudall et al. 2003; Chen et al. 2004; Nuraliev et al. 2010; Remizowa et al. 2010; Bobrov et al. 2011).

Diversity of gynoecium types. The number of carpels that make up the gynoecium often correlates with the number of elements in the flower cycles. Carpels can be free (apocarpous type: polymerous apocarpous gynoecium consists of many carpels and monomerous apocarpous gynoecium has one carpel) or united in varying degrees (coenocarpous type). In literature, the term 'pistil' is used to characterize both the monomerous (simple pistil) and the polymerous (compound pistil) gynoecium. Each element of the polymerous apocarpous type is also called a pistil. More often (we support this view), the pistil is denoted by gynoecium, morphologically resembling a solitary carpel, but consisting of several carpels. Both the carpel and the pistil are usually organized by three morphologically distinct segments: the ovary (proximal part), stigma (distal part) and the stylodium or style with full intergrowth of stylodia (middle part). Below the ovary, gynophore is sometimes distinguished as an outgrowth or an elongated part of the receptacle, having the form of a cylindrical stalk, on which the gynoecium is located. Together, all these structures provide interaction with pollen and pollen tubes and form the transmitting tract of the carpel or pistil.

In the first classification of pistils, Grisebach (1854) proposed the simplest variant, in which the ovary cavity was formed by one carpel. Such pistil was called apocarpous. In other cases, the ovary cavity is formed by several carpels: their borders are closed, but the ovary remains unilocular – paracarpous pistil; with full unification of the lateral margins, the ovary becomes multilocular – syncarpous pistil. It was noted that either the parietal or the central placentae are formed in the paracarpous pistil. However, many botanists of this time, as indeed most of the modern researchers, do not share Grisebach's view of the three pistil types, reducing all diversity to the apocarpous and syncarpous types of gynoecium (Prantl 1881; Strasburger et al. 1900; Wettstein 1903–1908; Matthews & Endress 2005; Schönenberger 2009).

When describing a gynoecium, the structural unit of which is the carpel (Latin *carpellum*), a substitution historically arisen, when the fruit (Greek *karpos*) was used as the basis for its types (Grisebach 1854). Since then, many researchers have tried to correct this inaccuracy. It was proposed to call the apocarpous gynoecium as choricarpellate (German *das chorikarpellische Gynaeceum*) and syncarpous as syncarpellate (German *das synkarpellische Gynaeceum*) (Juhnke & Winkler 1938). Nevertheless, the concepts of apocarpous, syncarpous, paracarpous and lysicarpous are still preserved for designating types of gynoecium and types of fruits.

Numerous studies on the morphogenesis of gynoecium forced to revert to the ideas of Grisebach (1854). Goebel (1898–1901, 1923, 1933) decided to retain the term 'paracarpous gynoecium', but he implies only the gynoecium with unilocular ovary and axial placenta in the form of a

column as an extension of the flower axis. Troll (1928) returned to the original understanding of paracarpous gynoecium and this interpretation was adopted by some researchers later (Sitte et al. 2007). Based on extensive morphological and anatomical data, Troll (1928) introduced an additional feature for syncarpous gynoecium, the formation of a central angular placenta (German *zentral-winkelständige Plazenta*).

In contrast to Grisebach (1854), Troll (1928) and Sitte et al. (2007), Takhtajan (1942, 1948, 1964) limited the paracarpous type of gynoecium to a unilocular gynoecium with parietal placentation. He identified the unilocular gynoecium with a free central (columnar) placentation as a special type, the lysicarpous one. Its classification includes apocarpous and coenocarpous (syncarpous, paracarpous and lysicarpous) types, which are included in many reports, textbooks and original researches. However, in his last monograph, Takhtajan (2009) used syncarpous gynoecium instead of coenocarpous and singled out the eusyncarpous, paracarpous and lysicarpous types.

In addition to these types, there are: false coenocarpous (Troll 1931) or pseudo-coenocarpous (Troll 1934; Schaeppi 1937) [carpels in the polymerous apocarpous gynoecium grow together with the axis of the flower], fragmocarpous [partitions arise in paracarpous gynoecium during the course of development and a multilocular gynoecium is created (Bobrov et al. 2009)], pseudo-monomerous (Eckardt 1937, 1938; Takhtajan 1948; Eames 1961; Ehrendorfer 1978; Barabe et al. 1987; Shamrov 2009; Gonzalez 2016; Yandovka & Shamrov 2016), which corresponds to secondary apocarpous (Troll 1928) and pseudo-apocarpous (Saunders 1937; Schaeppi 1937; Timonin 2005) [the gynoecium, externally corresponding to one pistil, is a variant of the syncarpous or paracarpous type with only one fertile carpel] and pseudo-syncarpous, or functionally syncarpous [the occurrence of a style or compitum, especially in the polymerous apocarpous gynoecia] (Carr & Carr 1961; Walker 1975; Endress & Bruyns 2000).

During gynoecium studies, it was noted that the paracarpous and syncarpous types are often not 'pure' and include elements of other types. This led a number of authors to doubt the presence of sharp differences between syncarpous and paracarpous types. Investigation of the gynoecium formation in Resedaceae, especially in the genus *Reseda* (Arber 1942), allow to conclude that there are no sharp differences between syncarpous, paracarpous and apocarpous types. These types, according to the author, are a series of transitional forms and can be found even in the same plant. Thus, in *Quercus robur* (Fagaceae), the gynoecium in the lower part is syncarpous, in the middle paracarpous and in the upper part apocarpous (Meyer 1953). In Gesneriaceae, based on the domination of one or another region in the ovary, gynoecium diversity was found – predominantly hemiparacarpous and paracarpous and less often syncarpous and hemilysicarpous (Ivanina 1967). In *Sanango racemosum* (Buddlejaceae), differences in the structure along with the height of the ovary were revealed: in the lower part, there is a full septum and a 2-locular state, in the middle part, the septum is incomplete and the ovary is unilocular and in the uppermost part, there is a septum again. As in most studies, such differences are explained by a change in the structure of the placentae: angular (axile) placentation in the 2-locular region and parietal placentation in the unilocular zone (Dickison 1994). Eames (1961) considered that in some plants the ovary is syncarpous at the base and paracarpous at the top. Troll (1928, 1932, 1949), using the principle of 'varying proportions', believed that any coenocarpous gynoecium includes different areas lying one after the other. It was revealed (Leinfellner 1941, 1950) that vertical segmentation into 4 zones (German *senkrechte Gliederung in vier Zonen*) is inherent in the united

multicarpellate gynoecia. Other researchers (Eckardt 1937; Schaeppi 1971) also drew attention to a certain similarity in the structure of the syncarpous and paracarpous types of gynoecium. They believed that there was an insignificant sterile zone of the syncarpous gynoecium at the base of the paracarpous gynoecium, in which ovules do not form. Baum (1949c) expressed the opinion that the fertile zone of paracarpous gynoecium, which arises congenitally, is homologous to the region of the syncarpous gynoecium, which appears postgenitally on the basis of the original paracarpy. On the basis of this, it was proposed to take into account postgenital fusing during typification of coenocarpous gynoecia (Baum 1949b).

Winkler (1941) and Baum (1949a) believed that syncarpy is created in two ways: due to the congenital association of the tubular bases of the peltate carpels and as a result of postgenital fusing of the wrapping carpel borders in the middle part of the ovary. On this basis, the lower zone was defined as primary syncarpous and the middle zone as secondary syncarpous (Baum 1949a).

Typification principles of the gynoecium. An analysis of the available data suggests that when characterizing types, attention is most often drawn only to the possibility of carpel or carpels to ensure the ovary's closing and to form the locules, in which the ovules are located: gynoecium is multilocular (syncarpous), unilocular and polymerous (paracarpous), unilocular and monomerous (apocarpous type). As our studies have shown, at the base of any gynoecium, including the polymerous apocarpous, multilocular zone can form very early (Shamrov 2012, 2013). Placentation is of secondary importance or the placentae are described as structures, on which ovules develop. According to some authors, the placentation can vary in height of the ovary, and placentae even play a role in the formation of septa in the ovary.

Many authors believe that the placentae of one carpel are characterized by a dual nature and consist of two halves. It is this point of view that turned out to be dominant in literature. As a rule, the placentae clearly differ morphologically (often at the expense of epidermal cells, which are secretory and function as a placental obturator), located on the adaxial surface of the sutures or on ventral edges wrapping inside of the carpel or its plate. The placentae are by their nature individual and each can only expand (the intrusive placenta) in the case of the formation of a large number of ovules, often arranged in rows. Fusion cases of adjacent placentae are possible, but their growth and participation in the formation of septa are unlikely, since septa are most often formed during the closure and subsequent union of sutures of different origin.

There are classifications with 2 groups of placentation: laminal (marginal) or superficial and submarginal (sutural) or marginal, which is more common in angiosperms (Takhtajan 1942, 1948, 1964, 2009; Puri 1952, 1961; Eames 1961). Takhtajan (1942, 1948, 1964) singled out the placenta forms in each group and tried to understand their relevance for the types of gynoecia. Group A (laminal placentation): laminal-lateral, ovules occur on the lateral parts of the adaxial surface of the carpel; median laminal, ovules located along the back of the carpel; lateral-median, ovules form over the entire carpel surface (all types of laminal placentae are found mainly in the apocarpous gynoecium). Group B (sutural): angular, ovules are located along the sutures of the carpel (apocarpous and syncarpous gynoecia); parietal, ovules are located along the 'open' sutures (paracarpous gynoecium); free central or columnar, ovules form around the central column (lysicarpous gynoecium). A similar approach was previously used by Kaussmann (1963), who distinguished the median and lateral placentae in the apocarpous gynoecium proceeding from Troll's ideas (1928, 1932, 1939). There, several placenta types are in the coenocarpous

gynoecium: the central angular in the syncarpous gynoecium and the parietal, central and basal in the paracarpous gynoecium. To date, they allocate the angular, central angular, parietal and central placentae. There are also the apical, basal, lateral and suspended placentae (Eames 1961; Korchagina 1994a, b; Timonin 2005; Matthews & Endress 2011). To characterize the placenta, some authors (e.g. Teryokhin & Nikiticheva 1981) used a whole complex of features: form, degree of differentiation, rumination and intrusiveness.

In modern botanical literature, the concept of 'central angular placentation' is seldomly applied. In describing the morphogenesis of apocarpous and even syncarpous types, the single term 'angular placentation' is widespread. Due to the fact that the structure and position of the angular placentae may turn out to be different in height of the ovary, some authors (e.g. Matthews & Endress 2005) describe them as angular (axile) and lateral in the syncarpous gynoecium of representatives of Celastraceae, if there are a lot of ovules and they are located along the entire length of the ovary, both in the synascidiate and symplicate zones (*Brexia madagascariensis*, *Denhamia viridissima*). Placentae with ovules at the bottom (in each locule more than 2 ovules) are referred to as basal and lateral (*Perrottetia longistylis*, *Pleurostylia opposita*). Placentae are called basal and median, if the ovules are located at the base of the ovary and in each locule per 1 ovule (*Stackhousia monogyna*). Takhtajan used the term 'central angular placentation' in relation to syncarpous gynoecium only in a monograph published in German (Takhtajan 1959). In other studies, starting with the earliest and ending with the last work (Takhtajan 2009), as in most English-language works, he called placentation 'axile'. Some English-Russian dictionaries consider the terms 'axile' and 'axial' as synonyms. The review on placentation (Puri 1952) indicates that the contents of the terms 'axial placentation' and 'axile placentation' are different: the first means that the ovules arise on the axis of the flower (i.e. it is a matter of free central placentation) and the second term indicates that the ovules occupy an angular position and are located at the place of closing ventral edges of the carpels.

Organization principles of the gynoecium. In plant morphology, there are 2 trends of researches explaining the structure of gynoecium. In accordance with the theory of conduplicate carpel, the gynoecium types in many plants, having a similar organization throughout the height of the ovary, can be identified by the characteristics of its middle part. In other plants, the different structure of the ovary is described, based on the ancestral and advanced criteria, while it is believed that the lower part is created due to congenital fusion and it is determined earlier and the upper parts are secondary and are of postgenital origin. According to the theory of the peltate carpel, the gynoecium of any plant is characterized by a zonate structure and represents a series of different 'types' and 'intermediate forms' in longitudinal direction.

The development of the theory of peltate carpel was greatly influenced by the views of scientists who saw similarities in the structure of pitcher-shaped or bag-shaped carpels with the structure of peltate (ascidiate) leaves. On the basis of similarities in the morphogenesis of the peltate leaves and carpels, the theory of bag-shaped carpel (German *Theorie der Schlauchbildung der Karpelle*) (Čelakovsky 1876, 1900) was proposed, which was later called the theory of peltate carpel. According to this theory, a special meristem, the so-called transverse zone, is differentiated very early in the proximal region of the carpel. Due to its activity, the edges of the carpel grow in basipetal direction. Gradually, the edges are almost completely closed in the proximal part, while a narrow ventral fissure (peltate carpel) remains (Troll 1932). In the absence of a transverse zone, the carpels (epeltate) have the shape of a horseshoe in cross section. It should be emphasized

that all ideas about the structure of both peltate and epeltate carpels were developed by Troll (1932, 1939) only for solitary carpels of the apocarpous gynoecium (mainly representatives of the families Alismataceae, Butomaceae, Hydrocharitaceae, Ranunculaceae).

In addition to the peltate and epeltate carpels, intermediate forms were distinguished: latent peltate (Troll 1932) and hemipeltate (Baum-Leinfellner 1953). Baum (1952b) showed in a special study on *Helleborus foetidus* (Ranunculaceae) that each carpel of polymerous apocarpous gynoecium undergoes all stages from the epeltate state to latent peltate and then fully peltate in its development. It was concluded that the epeltate or conduplicate carpels did not differ significantly from the peltate (Baum 1952a, 1953). This conclusion was further confirmed (Kaussmann 1963). It was also revealed that any developing carpel including representatives of Magnoliales (in which it was traditionally regarded as conduplicate) has a peltate structure and a different ontogenetic time for differentiation of the transverse zone (Leinfellner 1966, 1969a, b). The presence of the ascidiate zone in the base of the conduplicate carpel was also found in various dicotyledonous and monocotyledonous plants, among them Crassulaceae, Liliaceae, Ranunculaceae and Rutaceae (Gut 1966; Schaeppi 1975), although earlier (Bailey & Smith 1942; Bailey & Nast 1943; Bailey & Swamy 1949, 1951; Swamy 1949; Periasamy & Swamy 1956; Swamy & Periasamy 1964) and even later (Svoma 1998) this zone was never described and gynoecium was considered only from the point of view of conduplicate carpel theory.

With an apparent deep difference between the theories discussed, the correspondences between them are easily found. One theory arose out of the other and researchers who were right at the source did not oppose them. The structural features of the gynoecium, namely the presence of a complete congenital fusion of the carpel edges below the ventral fissure in the apocarpous gynoecium, was explained by the functioning of the transverse zone meristem (ascidiate region) from the point of view of the theory of peltate origin. In accordance with the theory of peltate carpel, most of the ovary covering the ascidiate area, was called plicate (it corresponds to the entire ovary, according to the theory of conduplicate carpel), and the area of stylodium and stigma is aplicate. According to the theory of peltate carpel, the names of the gynoecium zones in the united multicarpellate variants also correspond to the previously proposed names, based on the concepts of the conduplicate carpel theory: the primary syncarpous zone in the proximal part (Winkler 1941; Baum 1949c) is interpreted as the synascidiate region (due to fusion of the transverse zone meristems in the number of carpels), and the secondary syncarpous zone arising postgenitally on the basis of the original paracarpy in the middle part as a symplicate region. In the distal part of gynoecium there is an asymplicate area (Leinfellner 1950). It should be noted that originally symplicate and asymplicate zones were called synplicate and asynplicate, just as synascidiate was defined (Leinfellner 1950). These names were further transformed on the basis of the rules for the formation of complex words in the German language (Hartl 1956). A similar zoning in the syncarpous type (mainly in the final stages of development) is currently described by many authors: the synascidiate (lower part of the ovary), symplicate (usually middle as well as the upper part of the ovary) and the asymplicate (style and lobes of the stigma) zones (Endress 2001; Matthews & Endress 2005; Remizowa et al. 2008; Schönenberger 2009; Nuraliev et al. 2010; Balthazar von & Schönenberger 2013; Sokoloff et al. 2015; Dyka 2018).

It is important to emphasize that the founders of the peltate theory of the carpel and their followers believed that the true types of gynoecium are only variants that arise congenitally.

However, Leinfellner (1950) who named the symplicate zone realized that it appears postgenitally on the basis of the original paracarpy. In addition, in some early (Winkler 1941; Baum 1949a–c; Hartl 1956; Gut 1966; Rohweder 1967) and modern (Evans & Dickinson 2005; Sokoloff et al. 2007; Remizowa 2011; Rudall et al. 2011; Gonzalez 2016; Tobe et al. 2018) papers, the specifics of the postgenital association of carpels are also taken into account for the characterization of the zones. It should be noted that postgenital fusion is of great interest for explaining the structure's unification mechanisms in the course of development, but its value requires special studies (Endress 2003).

There is a number of mechanisms of fusion and ways to create a closed ovary space as a result of association of the edges of one carpel and at the border of adjacent carpels (Eames 1961; Sattler 1974; Timonin 2005; Sokoloff et al. 2006). Congenital and postgenital (perfect and imperfect) modes of fusion are distinguished. In addition, the formation of closed gynoecium (angiospermy) can occur through a combination of different mechanisms: 1) due to adhesion using secreted substances, 2) due to adhesion and partial postgenital fusion, 3) due to almost complete postgenital fusion and partial adhesion, 4) due to complete postgenital fusion (Endress & Igersheim 1997, 2000) and 5) closure of the edges above the ascidiate zone of the carpel may not fully occur and a unifacial style appears (Endress 2015). Endress (2003) made some adjustments to the interpretation of the second and third modes of angiospermy: 2) mixed, postgenitally fused at the periphery, but with a continuos secretory canal; 3) mixed, postgenitally fused at the periphery, without a continuos secretory canal.

When analyzing the morphogenesis of gynoecium, its zonality is revealed not only in the acropetal direction. In the ovary differences in structure are both interzonal and intrazonal. However, these features are often not taken into account and each zone is described by one term, which does not allow to appreciate the mechanism formation and the final structure of the gynoecium before pollination. The origins of this problem go back to the views expressed by Leinfellner (1950). The diagrams, given by him on the structure of the apocarpous and syncarpous types of gynoecium, reflect only the hypothetical averaged variants, and it remains unclear at which stage of development the gynoecium is seen. According to the author, the zones in syncarpous gynoecium differ in the peculiarities of the association of carpels. At the level of the synascidiate zone, the ovary space is subdivided into a certain number of locules (the holoseptal zone). In the symplicate zone, the carpels are joined in the center, growing together only with abaxial surfaces, and one common locule is formed in the ovary (hemiseptal zone). In the hemisymplicate zone, these are united only at the periphery (aseptal zone). The asymplicate zone corresponds to the stigma lobes or stylodium with stigmae. In the hemisyncarpous type of gynoecium, instead of the synascidiate zone, a hemisynascidiate zone is formed (incomplete fusion of carpels in the center of the ovary). However, the examples of plants given in the article are not so unambiguous in the characteristics of these zones. This is especially true for the symplicate zone. It should be emphasized that the singling out and description of gynoecium zones practically do not use the features of the placentation and the connection of the placenta forms with the types of gynoecium.

Leinfellner (1950) revealed two peculiarities of syncarpous gynoecium: not all of the zones can be represented and the ratio of zones in gynoecium can be different. Based on this suggestion, it was proposed to distinguish several variants of syncarpy. A similar analysis of the gynoecium structure was undertaken later (Volgin & Tikhomirov 1980). However, when justifying the

selected 6 variants, the features of the placentation are not taken into account, and the term 'syncarpous' is used in a broad sense.

Thus, two types of gynoecium (coenocarpous and paracarpous) disappeared in many studies. Instead of the concept of 'coenocarpous gynoecium', the concept of 'syncarpous gynoecium' began to be used. The paracarpous type of gynoecium, characterized by parietal placentation, was included in the syncarpous, and the syncarpous itself was called 'eusyncarpous'. The reduction of the gynoecium types to two (apocarpous and syncarpous) narrows the possibilities of using really essential features of the structure of gynoecium in systematics and phylogeny. With such a presentation of gynoecium, all the advantages of the peltate carpel theory (zonal structure, the ability to explain the mechanisms of zone formation) are depreciated.

Combining all variants with a united multicarpellate gynoecium in one syncarpous type allowed many authors to include automatically all available diversity of placentae, namely angular, parietal and free central in its characteristics. Thus, in the bud of *Lychnis* and *Dianthus* (Caryophyllaceae) the placentation is parietal at the top of the ovary and angular at other levels. Later, the parietal placentation acquires signs of angular, and initial angular (with the exception of the ovary base) and signs of columnar placentae (Bocquet 1959; Eames 1961). In the representatives of Rubiaceae, parietal placentae and intermediate forms were described along with angular forms (Robbrecht 1988). In *Parnassia palustris* (Parnassiaceae), the placentation is angular and lateral in the synascidate zone and parietal in the symplicate zone (Matthews & Endress 2005). In *Cantua coerulea* (Polemoniaceae), the upper ovules are located on the parietal placentae in the symplicate zone, while the lower ovules are formed on the angular placentae in the synascidiate zone (Schönenberger 2009). With this approach, the authors practically return to the ideas of the early researchers (Troll 1928, 1949; Eckardt 1937; Winkler 1941; Baum 1949c; Hartl 1956), who described a paracarpous state above the primary syncarpous zone in the syncarpous gynoecium. Other authors also consider the structure of gynoecium, comparing the symplicate zone with the paracarpous region (Bobrov et al. 2011). However, it is difficult to agree with this point of view, because the structure of the ovary above the primary syncarpous zone only resembles paracarpy (the presence of a cavity, a weak discharge of sutures with placentae from the ovary wall), since the main features of true syncarpy (central angular placentation, syncarpous sutures) are preserved.

On the other hand, the advantages of the conduplicate carpel theory (the same structure of the ovary along its entire height, the characteristic of the gynoecium type according to the features in the middle part of the ovary) are eliminated due to the fact that the zones in gynoecium are also named as independent types of gynoecium. If the description of gynoecium is made from these positions, it will be necessary to recognize that the change of typical characteristics in the coenocarpous gynoecium from the base to the top of the ovary (syncarpous – paracarpous – apocarpous) is accompanied by a change in the forms of the placentae, i.e. in fact, there is a coincidence in understanding the structure of the coenocarpous gynoecium from the standpoint of both existing theories (Table 1).

In our opinion, an objective characteristic of the gynoecium can be given using the postulates of both theories: the principle of discreteness or the zonality according to the theory of peltate carpel and the principle of integrity according to the theory of conduplicate carpel. The zones of polymeric united gynoecium from peltate carpels in fact constitute the conditions of conduplicate

Table 1. Gynoecium structure in the light of theories of conduplicate and peltate carpels.

| Gynoecium structure according to existing theories	Gynoecium types			Gynoecium zones		
	apocarpous	paracarpous	syncarpous	apocarpous	paracarpous	syncarpous
Conduplicate carpel	represented	represented	represented	usually zones are not described	usually zones are not described	usually zones are not described, or they are bottom-up distinguished: primary syncarpous (syncarpous), secondary syncarpous (paracarpous) and apocarpous
Peltate carpel	represented	not represented	represented	bottom-up: ascidiate, plicate, aplicate	not represented	bottom-up: synascidiate (= primary syncarpous), symplicate (= secondary syncarpous), asymplicate

carpels changing in morphogenesis: synascidiate zone = syncarpous state, symplicate zone = intermediate state between syncarpous and paracarpous, hemisymplicate zone = paracarpous state. Both theories suggest changes in the character of the placentation during the transition from one zone to another. But this approach is not correct, since each type of gynoecium corresponds to its own form of placentation. From the formal point of view, the main advantage of the peltate carpel theory is the proposed terminology, which is not associated with the names of gynoecium types. It shows how many zones are present in gynoecium, what are their origins and organization, which allows us to estimate the fundamental differences and similarities between types. Of the two principles of gynoecium typification (the first is the number of locules in the ovary depending on the degree of carpel association, the second is the position of ovules in the ovary depending on the structure of the placentae), in our opinion, the second principle is more significant. Types of gynoecium can be identified precisely by the characteristics of the placenta structure: on the ventral margins of the solitary carpel (simple angular) = apocarpous, on the sutures near the wall of the ovary (parietal) = paracarpous, on the sutures in the center of the ovary (central angular) and at some distance (simple angular) = syncarpous gynoecium, on the wall of the carpel (laminar) = apocarpous and syncarpous. The presence of septa, as in the syncarpous, or their absence, as in paracarpous, does not always indicate the type of gynoecium. Sometimes, the authors do not specify its type, when describing the gynoecium (Hernández-Cruz 2018). They describe the unilocular ovary and parietal placentae with ovules. This allows us to consider such a gynoecium as paracarpous.

Sutures and septa in the gynoecium. Let us consider in more detail the peculiarities of the formation of sutures, septa and their diversity. With reference to gynoecium, septa (Latin *saeptum*) are, first of all, partitions of different origin, which divide the ovary into a certain number of isolated cavities, or locules, corresponding to the number of unified carpels. Sutures (Latin *sutura*) or commissures (Latin *commissura*) are the seams along which the ovules are located. Sutures are common in all types of gynoecium and their degree of development varies. In the apocarpous gynoecium, they are formed congenitally in the ascidiate zone of the peltate carpel or in the plicate zone as a result of postgenital fusion of the ventral edges of the individual carpel (Fig. 1F–G). In the syncarpous gynoecium sutures, which are formed, when the adjacent carpels are joined
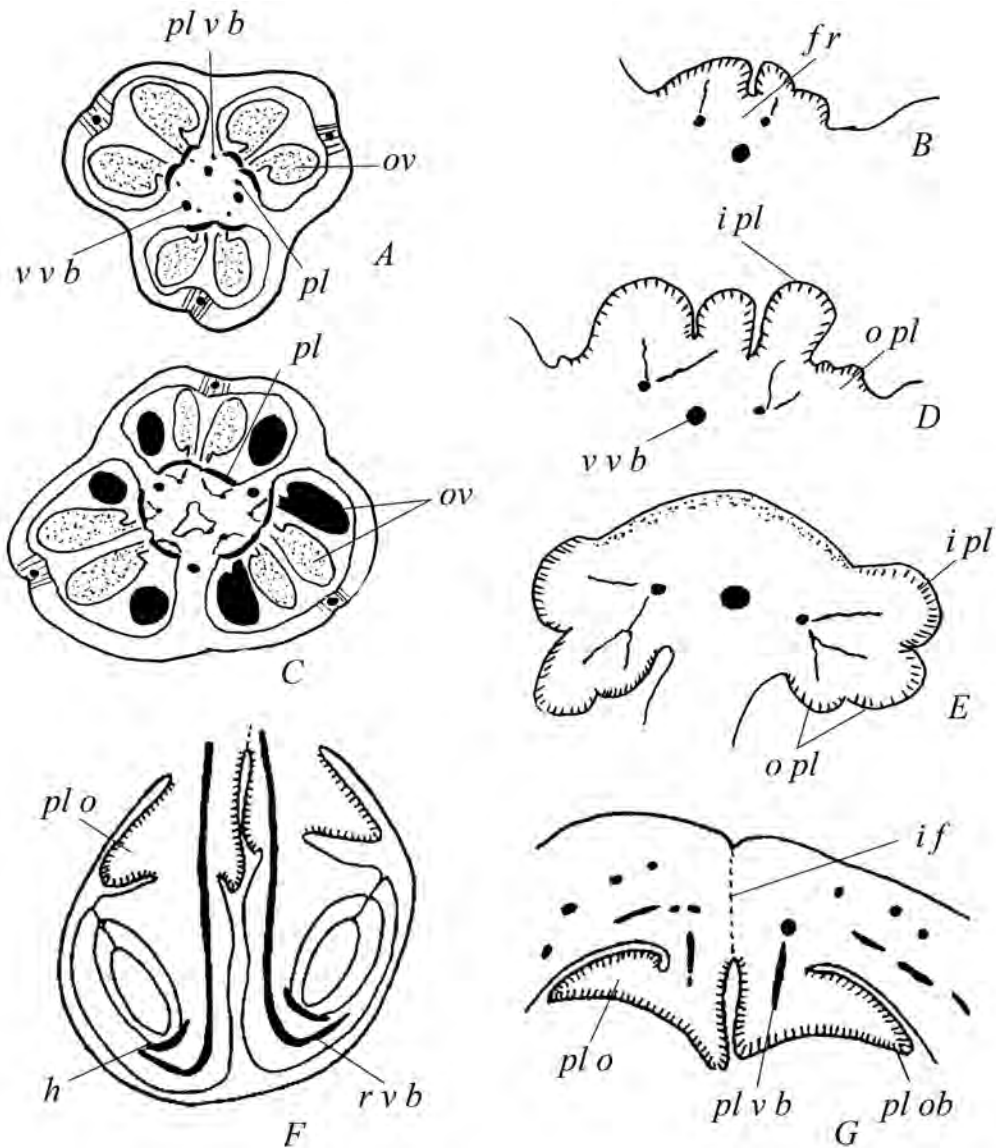
Figure 1. Intrusive placentae and placentary outgrowths. A–E – syncarpous gynoecium of *Juncus filiformis*: A, B – lower part of ovary, ovules are located at inner placentae; C, D – intermediate region between lower and middle parts of the ovary, ovules are at inner and outer placentae; E – intrusive placentae in middle part of the ovary. F–G – polymerous apocarpous gynoecium in *Paeonia lactiflora*. F – ovules are located at placentary outgrowths; G – placentary outgrowths without ovules. *f r* – fusion region, *h* – hypostase, *i f* – imperfect fusion, *i pl* – inner placenta, *ov* – ovule, *o pl* – outer placenta, *pl* – placenta, *pl o* – placentary outgrowth, *pl ob* – placentary obturator, *pl v b* – placentary vascular bundle, *r v b* – raphal vascular bundle, *v v b* – ventral vascular bundle.

by adaxial sides, they usually grow to the center of the ovary and grow there either congenitally (synascidiate zone) (Fig. 2A–B) or postgenitally during rapprochement and subsequent perfect or imperfect fusion (symplicate zone) (Fig. 2C–D), forming partitions. Syncarpous sutures, as a rule, are well differentiated into 3 parts: the basal (part of the ovary wall with full fusion of the edges), the middle (elongated in the shape of a leg; this part creates a different extent of the sutures, as a result of which complete or partial separations occur) and apical (having the form of an arrow, on the sides of the tip of which the placentae are differentiated) (Fig. 2A–B). Sutures in most
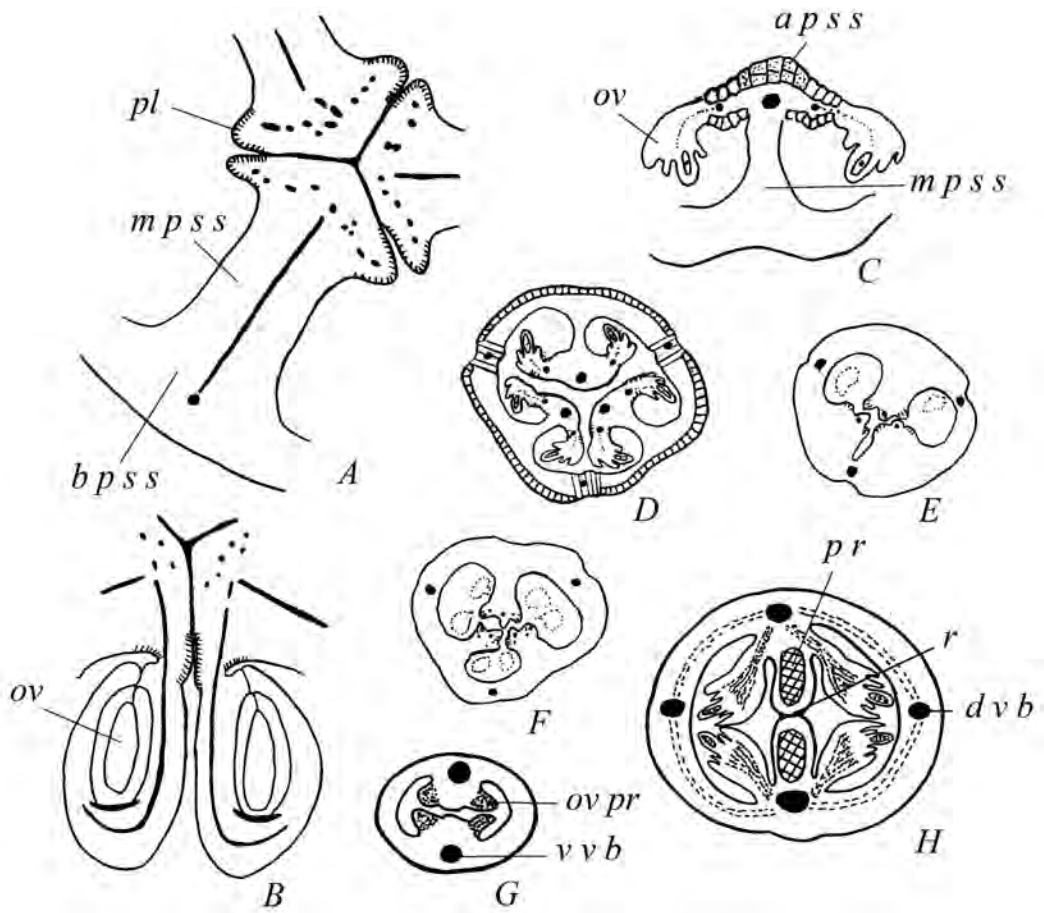
Figure 2. Sutures and septa in the gynoecium. A, B – postgenital closing of syncarpous sutures in the center of symplicate zone in *Tulipa gesneriana*, median septa and central angular placentation. C–F – structure of symplicate zone in *Juncus filiformis* before meiosis: C, D – intrusive placentae with ovules at sutures, periclinal divisions of epidermal cells in apical part of syncarpous suture; E, F – suture closing and postgenital formation of apical septa at upper part of ovary (central angular placentation); G, H – suture closing in paracarpous gynoecium at the stage of ovular primordia in *Capsella bursa-pastoris* (parietal placentation). *a p s s* – apical part of syncarpous suture, *b p s s* – basal part of syncarpous suture, *d v b* – dorsal vascular bundle, *m p s s* – middle part of syncarpous suture, *ov* – ovule, *ov pr* – ovular primordium, *pl* – placenta, *p r* – parenchyma of replum, *r* –replum, *v v b* – ventral vascular bundle.

of the paracapous gynoecium cannot be called septa. The basal part is usually distinguished in them (the placentae differentiate on its lateral sides), the middle part is poorly expressed, and the apical part is not developed, while in the area of the suture a notch is detected in the direction of the ovary wall (Fig. 2G–H).

Two modifications of septa are formed in the course of morphogenesis in the coenocarpous and even the apocarpous (polymerous apocarpous) types characterized by a style: apical (the term suggested by Hartl 1962) and basal. Apical septa are postgenitally formed in the upper part of the ovary due to the rapprochement of the sutures and the reduction of the length of the carpel edges to the size of the style canal; placentae in this part of the ovary are missing or they are sterile (Fig. 2E–F). Basal septa occur congenitally in the lower part of the ovary, mainly in the synascidiate region. At this level, the ovary space is divided into locules, which corresponds to number of carpels (Figs 1A; 2A).

The septa of the third modification (median) can be formed above the synascidiate zone in syncarpous and paracarpous types of the gynoecium. In the symplicate zone of the syncarpous gynoecium, the sutures postgenitally approach in a centripetal direction, not reaching the center (open symplicate zone) (Fig. 2C–D). This leads to the appearance of incomplete septa in this area, but at the same time, the apical and middle parts are well identified in the sutures, and the ovules on the angular placentae are removed from the ovary wall. In other cases, the sutures grow to the center of the ovary, and there they combine postgenitally (closed symplicate zone), forming complete septa (Fig. 1C). The formation of septa is carried out primarily due to the intercalary growth of the middle parts of the sutures, which allows the placenta with ovules to be 'carried out' into the center of the ovary. An important role in this process is played by local periclinal cell divisions of the epidermis in the tip of the apical arrow-shaped part of the suture (*Juncus filiformis*, Juncaceae (Shamrov et al. 2012)) (Fig. 2C). The process of septum formation (also due to the periclinal divisions of epidermal cells at the suture fusion) was described in detail in the gynoecium of *Gratiola officinalis* and *Verbascum thapsiforme*, Scrophulariaceae (Hartl 1956). Postgenital partition formation in paracarpous gynoecum of some plants has been described (fragmocarpous type (Bobrov et al. 2009)). Their formation is explained by the proliferation of placentae toward the center of the gynoecium and subsequent unification (Puri 1952; Hue et al. 2007). However, in the region of the sutures (for example in *Capsella bursa-pastoris*, Brassicaceae (Shamrov & Tsarev 2016)) the cell proliferation is observed (both epidermal and deep-lying cells). There is a special septum or replum without the participation of the placentae.

Special variants of septa formation were found in the gynoecium of the families Boraginaceae, Cucurbitaceae and Lamiaceae. As our research has shown, gynoecium consists of 2 carpels in *Echinocystis lobata* (Cucurbitaceae). In the ovary, the partitions of two types are created. Partitions of the 1st type develop due to the activation of the cell divisions in the apical parts of the paracarpous sutures and their subsequent closure in the center. Partitions of the 2nd type arise in each locule formed by one carpel, possibly as a result of cell divisions of the apocarpous sutures from the ventral edges to the dorsal edge. Due to such partitions, each locule of bicarpellate syncarpous gynoecium is divided into 2 parts in species from the families Lamiaceae and Boraginaceae. As a result, a separate (schizocarpous) fruit-coenobium consisting of 4 erems is formed. It is believed that the partitions of the 2nd type are formed as outgrowths of the ovary wall (Kaden & Zakalukina 1965). Similar subunits of fruit in Heliotropiaceae are called mericarpids (Jeiter et al. 2018). In bicarpellate gynoecium of *E. lobata*, a 4-locular ovary was revealed also (partitions of both types): at the base it is created by the fertile synascidiate region and in the middle part the hemisynascidiate zone takes part in its formation. In the latter one, the central slit is formed by the incomplete fusion of paracapous sutures. Gynoecium has a two-locular state in the upper part of the ovary (partitions of the 2nd type). 4 ovules are placed by one in each locule of 4-locular ovary. All ovules are located near ovary wall, as in paracarpous gynoecium. In some cases, the formation of a fruit from 3 carpels was observed, which is typical of many representatives of the family Cucurbitaceae. However, just 4-locular ovary with 4 seeds arises with the participation of 3 carpels. Only in one carpel, there is a partition of the 2nd type. As for placentation, in *E. lobata* it is parietal even with the basal position of the ovules on the 'bottom' of the ovary. This view is consistent with the findings of several authors (Puri 1954; Matienko 1969). The septa in the Cucurbitaceae ovaries are usually considered as the tissues of placental origin (Matienko 1969), possibly formed by derivatives of placental conducting bundles (Devyatov 2012).
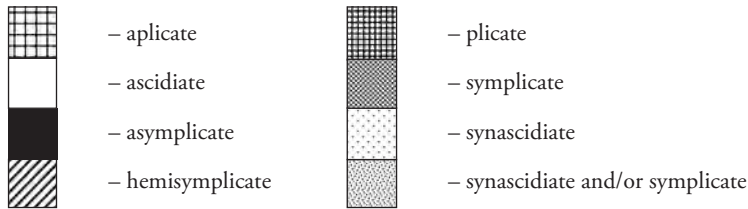
According to our investigation, signs of two types (syncarpous and paracarpous), especially in the character of the placentation, are revealed in *Delosperma tradescantioides*, Aizoaceae). 2 placenta types are formed on sutures in places of fusion of ventral edges of two adjacent carpels: the central angular placentae in the center of the gynoecium (as in syncarpous gynoecium) and parietal placentae at the periphery (as in paracarpous gynoecium). This suggests that gynoecium in this plant is represented by 10 carpels, rather than 5, as it is maintained in literature. Signs of syncarpous gynoecium (the presence of 5 true locules) are revealed throughout the ovary, while features of paracarpous gynoecium are only in the middle extended part of the ovary. 10 locules are found in the lower part of the ovary, with true 5 partitions (syncarpous septa) and 5 other additional partitions arising at postgenital fusion of sterile suture parts: short syncarpous sutures from the center and longer paracarpous sutures from the periphery. All placentae are sterile in the proximal region of the lower part of the ovary and ovules are located on the border to the middle part, where they are accommodated in the central angular and, mainly, parietal placentae. In the middle (extended) part of the ovary, true partitions are retained, while the additional partitions disappear, the central angular placentae become sterile, and the ovules are located on the parietal placentae. It should be noted that the parietal placentae greatly expand and become intrusive. Their branches are sterile and stand out well due to epidermal palisade-like secretory cells functioning as placental obturators. At the transition from the middle to the upper part of the ovary the fertile parietal placentae disappear, additional partitions reappear, and the placentae, both parietal and central angular, become sterile. In the distal region of the upper part of the ovary, first cavities appear in the center, and then the canal and it becomes clear that additional partitions arise postgenitally by an imperfect type. Locules are incomplete, reminding themselves of special pockets in which ovules are located, although their attachment sites are disposed lower in the middle part of the ovary. Such a variant of gynoecium has not been previously described in literature.

The formation of syncarpous-paracarpous gynoecium in *D. tradescantioides* can be explained only on the basis of the notion that not a simple form (as it was indicated by LEINFELLNER 1950, 1951), but a double U-shaped synplacenta is formed at the base of the gynoecium. A similar synplacenta has been described in the lysicarpous gynoecium of *Luzula pedemontana* (Juncaceae) and the paracarpous gynoecium of *Gentiana lutea* (Gentianaceae). Along sutures the branches of one synplacenta extend near the wall of the ovary (parietal placentae), and branches of the other stretch in the center of the ovary (central angular placentae). However, in the mentioned plants, some of the placentae are sterile and then the ovules are located either closer to the wall (in paracarpous gynoecium) or to the center of the ovary (in syncarpous and lysicarpous types (SHAMROV et al. 2012; SHAMROV 2013)). In *D. tradescantioides*, both types of placentae are fertile in the lower and middle parts of the ovary.

Original system of the gynoecium types and variations. In the study of LEINFELLNER (1950), two features of a syncarpous gynoecium were revealed: there may not be all zones in its structure; the ratio of zones in the gynoecium can be different. These ideas can be extended to other types of gynoecium (Figs 3; 4A–M; Table 2). In the proximal region of the monomerous apocarpous gynoecium, the ascidiate region is differentiated very early (peltate carpel) or this area is absent (epeltate or conduplicate carpel). In a 2-zoned epeltate carpel from the bottom up, the conduplicate or plicate (ovary) and aplicate (stylodium and stigma as well) zone arise, whereas in a 3-zoned peltate carpel there are peltate or ascidiate (the lower part of the ovary), plicate
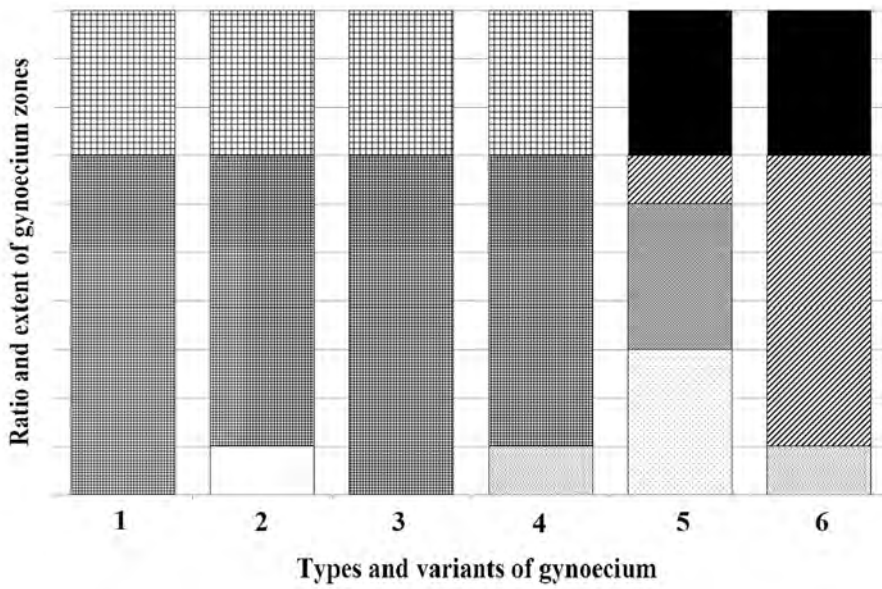
Figure 3. Types, variants and zonate structure of the gynoecium. The abscissa indicates types and variants of gynoecium: monomer apocarpous – epeltate (1) and peltate (2) variants, polymer apocarpous – plicate (3) and synascidiate (4) variants, syncarpous (5), paracarpous (6). The ordinate indicates the ratio and extent of gynoecium zones:
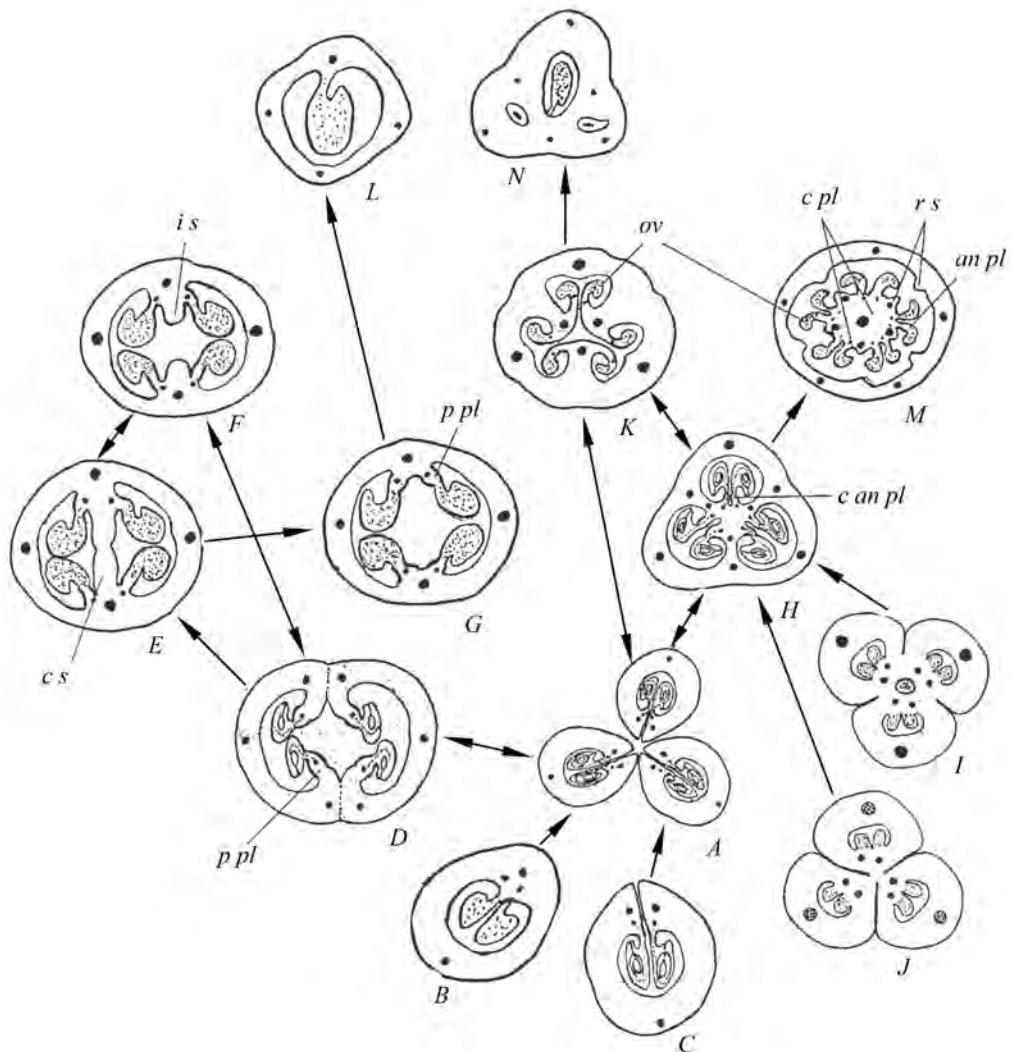
– aplicate   – plicate

– ascidiate   – symplicate

– asymplicate   – synascidiate

– hemisymplicate   – synascidiate and/or symplicate

(middle and upper part of the ovary) and aplicate (stylodium with stigma) zones (Fig. 4B–C). Intermediate structural states of carpels are possible, especially in the lower part of the ovary.

In polymerous apocarpous gynoecium of some plants, the carpels remain free throughout, and they are probably characterized by the organization of a 2-zoned epeltate carpel (plicate variation) (Fig. 4A). These plants seem to include those that are characterized by a typical upper ovary, and the fruits (pseudocarps) contain many nutlets (*Ficaria*, *Ranunculus*, *Thalictrum* and others (Ranunculaceae); *Geum*, *Fragaria*, *Potentilla*, Rosa, *Sanguisorba* and others (Rosaceae)). 3-zoned peltate carpels of other plants with an almost upper or semi-lower ovary have the synascidiate region. This region is created in the lower part due to basal septa. Synascidiate

Table 2. Types and variants of gynoecium in flowering plants

Monomerous apocarpous gynoecium		Polymerous apocarpous gynoecium		Syncarpous gynoecium	Paracarpous gynoecium
Epeltate carpel	Peltate carpel	Epeltate carpels	Peltate carpels		
Gynoecium zones (bottom-up)					
1. plicate 2. aplicate	1. ascidiate 2. plicate 3. aplicate	1. plicate 2. aplicate	1. synascidiate and/or symplicate 2. plicate 3. aplicate	1. synascidiate 2. symplicate 3. hemisymplicate 4. asymplicate	1. synascidiate and/or symplicate 2. hemisymplicate 3. asymplicate

Figure 4. Types, variants and possible evolutionary trends of the gynoecium. A – apocarpous (polymerous) type; B, C – monomerous apocarpous variants: ascidiate (B) and plicate (C); D–G – paracarpous type and its variations: D – typical (aseptal), E – septal, F – hemiseptal, G – secondary aseptal; L – pseudo-monomerous variant on the basis of paracarpous one; syncarpous type and its variations: H – typical, K – symplicate, M – lysicarpous; I, J – synascidiate variation of polymerous apocarpous type; N – pseudo-monomerous variant on the basis of syncarpous one. *an pl* – angular placenta, *c an pl* – central angular placenta, *c pl* – columnar placenta, *c s* – complete septa, *i s* – incomplete septa, *ov* – ovule, *p pl* – parietal placenta, *r s* – remnants of septa.

zone is often sterile in the proximal part and fertile in the distal part. This peculiarity is usually indicated for syncarpous type. The ovary space is divided into locules, which corresponds to the number of carpels. The ovules are located on the central angular placentae. The synascidiate zone has a different origin and arises congenitally by combining the central placentae of each carpel with columella (as a continuation of the central part of the receptacle) at the level of discharge of angular placentae (first variant) or as a result of suture fusion in the center without columella (second variant) (Fig. 4I–J). The first variant corresponds to the pseudo-coenocarpous type described in the families Butomaceae, Hydrocharitaceae, Ranunculaceae (TROLL 1934) and studied in detail in *Nigella* (Ranunculaceae) (ROHWEDER 1967). The second variant was

revealed by us in *Vincetoxicum hirundinaria* (Asclepiadaceae) (Shamrov & Gevorkyan 2010b). A third variant is also possible: carpels grow together with abaxial surfaces to form a common locule above the sterile synascidiate zone, resulting in the formation of a fertile symplicate zone (*Apocynum androsaemifolium*, Apocynaceae (Shamrov & Gevorkyan 2010a)). These structural variants of the lower part of the polymerous apocarpous gynoecium are absent in the scheme of Leinfellner (1950). A large part of the polymerous apocarpous gynoecium is represented by plicate and aplicate zones in each carpel. Based on the structural features of the lower part of the ovary, similar polymerous apocarpous gynoecium can be described as 'synascidiate variation' (Apocynaceae, Asclepiadaceae, Butomaceae, Crassulaceae, Hydrocharitaceae, Paeoniaceae, some Ranunculaceae, etc.).

Syncarpous gynoecium also has a zoned structure with a central angular placentation along almost the entire height of the ovary. The distal part of the gynoecium (stigma) is presented by asymplicate zone. In the lower part of the ovary the synascidiate region is created due to basal septa. Placentae and ovules may be absent (sterile area) or the placentae with ovules are present (fertile area) in this region. Ovary is characterized by a symplicate structure over a long distance. However, full median septa are created postgenitally in the center in the course of rapprochement of the syncarpous sutures (closed symplicate zone – the so-called secondary syncarpy). Ovary on a greater extent has a locular structure (Fig. 4H). A similar course of development of syncarpous gynoecium can be described as 'typical variation' (Buddlejaceae, Cannaceae, Francoaceae, Hemerocallidaceae, Liliaceae, Vochysiaceae and others).

In the symplicate zone of the syncarpous gynoecium, the ventral margins in the middle and apical parts of the sutures may be fused or remain free. Such structure is preserved in the course of further morphogenesis (open symplicate zone) and can lead to the formation of incomplete median septa – symplicate variation (Fig. 4K). At the same time a cavity is created in the center of the ovary, but the placentation remains central angular (Campanulaceae, Cistaceae, Ericaceae, Orchidaceae, Orobanchaceae, Philydraceae, Rapateaceae, most of the Scrophulariaceae and others). A cavity in the ovary can be created postgenitally (for example, in the family Juncaceae) as a result of a change in the ovary form (expansion in the middle part) and divergence of the apical parts of the syncarpous sutures in the almost closed symplicate zone, as well as due to the appearance of the lysigenic cavity in the border of symplicate and synascidiate regions. These changes occur at middle stages of development and, if they did not occur, the gynoecium would become typically syncarpous before pollination with the formation of locules over a longer extent of the ovary (Shamrov et al. 2012). In a number of plants, an additional space in the ovary is created after destruction of septa in the process of morpho- (Amaranthaceae, Caryophyllaceae, Portulacaceae) or phylogenesis (Lentibulariaceae, Primulaceae), i.e. lysicarpous variation (Fig. 4M). The gynoecium begins to develop as typical variation of the syncarpous type, with further preservation of the zone with full septa, especially at the base of the ovary. The special columnar formation with ovules that arises in this case is not a '*sui generis*' or a continuation of flower axis, but a modified form of a central angular placenta (Shamrov & Kotel'nikova 2011; Kotel'nikova & Shamrov 2012).

In the ovary of the syncarpous gynoecium, the transition states can be detected on the border of the symplicate zone. One of them was indicated in a study on the gynoecium in *Brexia madagascariensis* (Celastraceae) (Matthews & Endress 2005). Two other transition states were

proposed by Leinfellner (1950): in the upper part – hemisymplicate (between symplicate and asymplicate) and in the lower part – hemisynascidiate (between symplicate and synascidiate) areas. In the hemisymplicate area, the carpels unite only along the periphery, while the sutures (without the middle and apical parts), and the placentae are devoid of ovules, they are sterile and close to the ovary wall. It was proposed to isolate the hemisynascidiate region for the hemisyncarpous gynoecium, when a glottis is formed in the center as a result of incomplete congenital fusion of the carpels. The presence of a glottis in the center of the ovary above the columella was observed by Shamrov (2010) in *Allium caspium* (Alliaceae). In *Juncus filiformis* (Juncaceae), a similar glottis appears postgenitally also above the columella as a result of cell lysis (Shamrov et al. 2012).

Paracarpous type is not represented in the schema of Leinfellner (1950). However, such a structural variant is described by him on the example of *Gentiana* species, as one of the models of the syncarpous type. In the lower part of the ovary of paracarpous gynoecium, the synascidiate region is also formed due to congenital carpel fusion and subsequent formation of basal septa. In *Gentiana lutea* (Gentianaceae), a short symplicate sterile area occurs instead of the synascidiate zone. Gynoecium of *Allamanda catharica* (Apocynaceae) forms both synascidiate and open symplicate zones. In all cases, the lower area of the ovary is sterile. A large part of paracarpous gynoecium shows a hemisymplicate state, while sutures have not middle and apical parts. Placentae are only parietal, and ovules are located near the wall of the ovary. This allows to make a conclusion about the absence of fertile symplicate zone in paracarpous gynoecium. Hemisymplicate region varies by reproductive ability to form ovules: fertile in the middle part and sterile at the base on the border of lower and middle parts and in the upper part of the ovary close to the apical septa (the latter corresponds to hemisymplicate region of syncarpous gynoecium). The distal part of the gynoecium (individual stigmae) is characterized by an asymplicate structure.

In the paracarpous gynoecium, characterized by parietal placentation and hemisymplicate state of the ovary, there is always free space for the optimal location of developing ovules, therefore the structure of the ovary usually does not differ in height or aseptal variation (Fig. 4D) (Bixaceae, Cactaceae, Moringaceae, Papaveraceae, Philesiaceae). In gynoecium of the representatives of Brassicaceae, Capparaceae, perhaps some Gesneriaceae and Hydrophyllaceae, the median septa may form postgenitally (Fig. 4E) as a result of the apical region's proliferation in the paracarpous sutures (secondarily multilocular paracarpous gynoecium was named fragmocarpous (Bobrov et al. 2009)). It is important to emphasize that the signs of the near-wall position of ovules on parietal placentae are preserved in gynoecium, and the presence of septa allows one to describe such gynoecium as septal variation of the paracarpous type. We have suggested that the partition in the developing gynoecium probably performs the function of a separation platform, on which 'bodies' of campylotropous seeds are subsequently located, and very long funicles are near the wall (Shamrov 2012). In paracarpous gynoecium, an incomplete median septum may postgenitally occur (hemiseptal variation perhaps in some Gesneriaceae) (Fig. 4F) or destruction of such a septum takes place, which arises during the gynoecium morphogenesis and disappears, when the fruit matured (secondarily aseptal variation perhaps in some Araliaceae) (Fig. 4G).

The significance of the placentation form, which should be taken into account as the fundamental feature in identifying of the gynoecium type, can be especially clearly shown when comparing gynoecium in the related families of Scrophulariaceae and Orobanchaceae. In modern literature Scrophulariaceae, including Orobanchaceae, is widely understood. The conclusion about

the similarity between these families (paracarpous gynoecium from two carpels with parietal placentation) was made on the basis of the first stages of formation of the placental structures and main characteristics of gynoecium vascularity (Teryokhin & Nikiticheva 1981). In various representatives of Scrophulariaceae, a syncarpous fragment was described in the ovary, when the ovary is 2-locular over a greater or lesser extent (Tiagi 1962; Teryokhin & Nikiticheva 1981). The presence of the syncarpous zone in the gynoecium was explained by secondary fusion, forming 2 'false' locules. Even when incomplete septa are formed in the ovary, it is clearly seen that syncarpous sutures are formed in it. In this regard, the gynoecium should be characterized as predominantly syncarpous in Scrophulariaceae, with its inherent central angular placentation. This conclusion agrees with the previously stated judgment that in Scrophulariaceae syncarpy is most widespread among fruits, hemilysicarpy is less common and paracarpy and hemiparacarpy are very rare (Kaden & Smirnova 1964). Indeed, in some species of this family (*Clandestina purpurea*, *Lathraea squamaria*, *Melampyrum cristatum*, *M. nemorosum*, *M. pratense* (Hartl 1956), *Lathraea squamaria* (Teryokhin & Nikiticheva 1981)), the gynoecium is paracarpous.

It turned out that most of the representatives of the family Orobanchaceae have the paracarpous gynoecium with its inherent parietal placentation. It is very important that the position of ovules on the parietal placentae remains. However, in some species of this family, the gynoecium is syncarpous. In *Aeginetia indica*, *A. abbreviata*, *A. pedunculata* (Beck-Mannagetta 1930), *Boschniakia rossica* and *Xylanche himalaica* (Teryokhin & Nikiticheva 1981), syncarpous sutures are formed, and ovules are located on the central angular placentae. At the base of paracarpous gynoecium in some representatives from the families Orobanchaceae (*Orobanche caesia*) and Scrophulariaceae (*Lathraea squamaria*), there is only one locule, instead of the usual 2-locular structure. This may indicate a strong reduction of the sterile synascidiate zone, a decrease in the height of the central synplacenta and a lowering of the discharge level of parietal placentae (Teryokhin & Nikiticheva 1981).

Returning to the analysis of gynoecium in the Scrophulariaceae, it should be noted that earlier its structure was studied in a large number of representatives, more than 50 species from different tribes and subtribes of this family. It was found that the gynoecium (called coenocarpous) has a similar structure and consists of syncarpous, paracarpous and apocarpous fragments. In the syncarpous and paracarpous fragments, the sterile zones were revealed on the basis of the placenta presence. The ovary is represented bottom-up by the sterile syncarpous zone at the base and the fertile syncarpous zone in the middle part, by the region in the upper part of the ovary, in which the carpel edges are not closed (paracarpous fertile zone) and the area forming the ovary arch, in which the edges are closed (paracarpous sterile area). The species studied differ in the ratio of zones in the ovary. Based on the dominance of fertile syncarpous or paracarpous zones, the species were divided into 2 groups (Hartl 1956).

We illustrate our findings with examples of some plants, which we studied. The studies included, as a rule, the whole morphogenesis of gynoecium: 1) during the differentiation of placentae (initiation of ovular primordia), 2) during the formation of ovular primordia (occurrence of archesporial cells), 3) during ovule formations (meiosis and the beginning of the embryo sac development) and 4) before pollination (formed ovules with a mature embryo sac).

The study of the gynoecium in representatives of Apocynaceae showed that the topography of the zones, the mechanisms and degree of fusion of the two carpels differ and change during

morphogenesis. In *Apocynum androsaemifolium*, *Tabernaemontana divaricata*, *Trachomitum sarmatiense* and *Vinca minor*, vertical zonality is clearly observed in the gynoecium. Short synascidiate (2-locular structure) and symplicate (unilocular) zones, very long plicate in each carpel, common hemisymplicate (compitum) and short asymplicate (stigma lobes, and in *V. minor* often the upper part of the style) zones can be distinguished (Shamrov & Gevorkyan 2010a, b). The species differ in time and features of the formation of the synascidiate zone and in the structure of the plicate zone and compitum.

In *Apocynum androsaemifolium* and *Trachomitum sarmatiense* (subfamily Apocynoideae, according to Takhtajan 2009), the synascidiate zone is formed earlier than in other species (primordia of ovules). In addition, they have a semi-lower ovary, and the carpel pedicle is lacking. Carpels in the plicated zone are horseshoe-shaped. At first, they closely adjoin together and then fuse postgenitally by lateral surfaces according to imperfect (*A. androsaemifolium*) or perfect (*T. sarmatiense*) types. A closed style is formed, in the center of which transmitting tissue is differentiated. In the ovary wall, there is a number of independent bundles, which probably branch from the ventral bundles.

In *Vinca minor* (subfamily Plumerioideae), a 2-locular structure is created at the base of gynoecium at the beginning of megasporogenesis both congenitally due to the meristem of the transverse zone of both carpels (synascidiate zone) and postgenitally as a result of the transformation of the open symplicate zone into a closed one. A compitum is formed, the lower and middle parts of which are characterized by signs of a semi-solid style (there is a perfect postgenital fusion of the carpel edges), while the upper part often resembles an open style with a canal. This species is characterized by a semi-lower ovary, a perfect postgenital fusion of the ventral edges in the plicate zone of each carpel and the formation of a large number of vascular bundles in the ovary wall along with the dorsal and ventral ones.

Tabernaemontana divaricata (subfamily Tabernaemontanoideae) is characterized by signs of the upper and semi-lower ovary, open ventral edges of each carpel in the plicate zone, very late (after meiosis) occurrence of 2 locules, which takes place mainly as a result of the transformation of the open symplicate zone into an closed one, by open style, except for the gynostegium which is part of it.

In *Vincetoxicum hirundinaria*, belonging to Asclepiadaceae or subfamily Asclepiadoideae of Apocynaceae (according to Takhtajan 1997, 2009), the ovary is almost superior. There is a short sterile synascidiate zone at the base of the gynoecium; a symplicate zone is absent. The plicate structure is inherent in most of the gynoecium, while from the ovary to the gynostegium the carpels are similar to stylodia. Above the gynostegium, features of a semi-solid style are revealed (presence of transmitting tissue and a canal to the border with the stigma lobes). A large number of additional vascular bundles differentiate in the ovary wall near the carpel lamina, where ovules appear (laminal placentation).

In *Paeonia lactiflora* (Paeoniaceae), the polymerous apocarpous gynoecium consists of 3–5 asymmetrical carpels, which are arranged spirally on the receptacle. Carpels at the base grow together with each other and with the surrounding elements of the flower. As a result, a sterile synascidiate zone with the participation of columella and central placentae is congenitally created in the proximal part of the gynoecium. Most of the gynoecium is plicate. In the early stages of development, the ventral margins of each carpel grow together along the common synascidiate
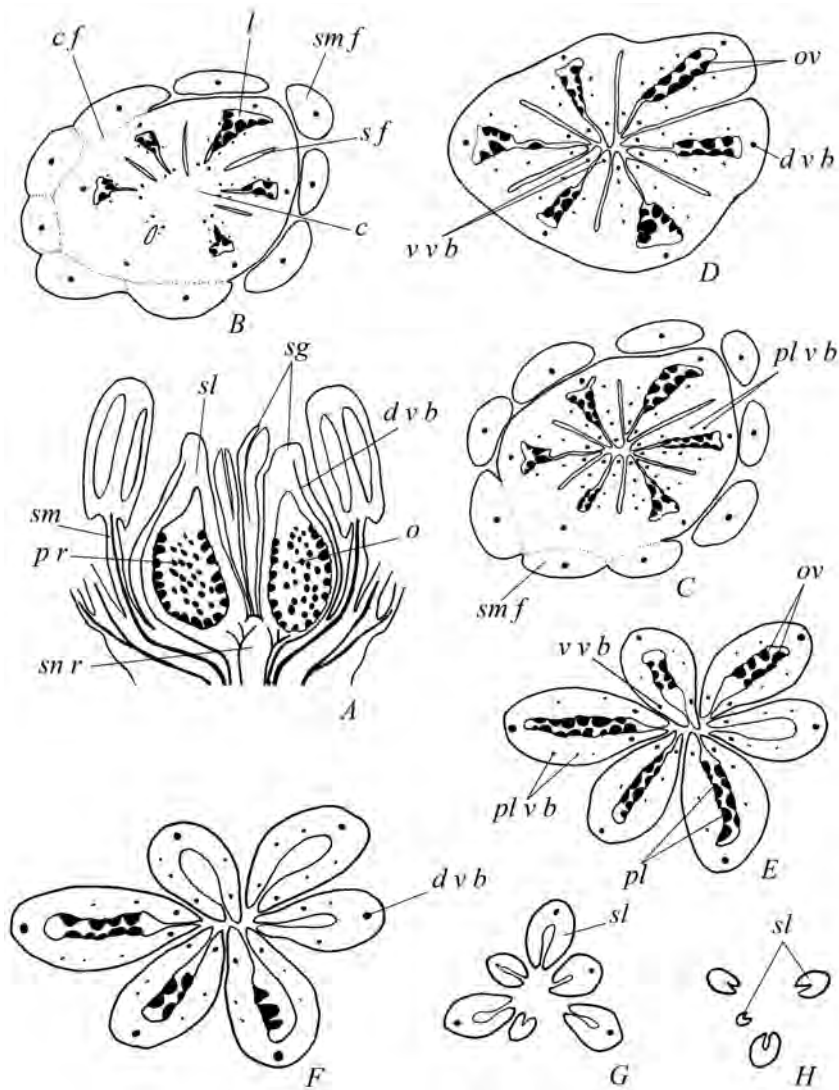
Figure 5. Structure of polymerous apocarpous gynoecium in *Butomus umbellatus* (synascidiate variation). A – longitudinal section of flower; B – synascidiate zone at gynoecium base; C – carpels are united at periphery of gynoecium; D – at boundary with plicate regions, the carpels are closed in the center of gynoecium; E–G – plicate zones in ovary of each carpel; H – aplicate zones of carpels (stigma). *c* – columella, *c f* – congenital fusion, *d v b* – dorsal vascular bundle, *l* – locule, *o* – ovary, *ov* – ovule, *pl* – placenta, *pl v b* – placentary vascular bundle, *p r* – plicate region, *sg* – stigma, *sl* – stylodium, *s f* – septal fissure, *sm* – stamen, *sm f* – stamen filament, *sn r* – synascidiate region, *v v b* – ventral vascular bundle.

zone at the base as imperfect type (short ascidiate zone), whereas above they only merge (extended plicate zone). The distal part of each carpel is represented by a short stylodium, ending in a stigma (aplicate zone). During pollination, an imperfect fusion of ventral margins occurs along the entire length of the ovary, while at its base the fusion of the carpel margins is close to perfect (Fig. 1F–G). The formation of a large number of vascular bundles in the ovary wall is observed along with the dorsal and ventral bundles, as in laminal placentation (Shamrov 2015).

In *Butomus umbellatus* (Butomaceae), the polymerous apocarpous gynoecium consists of 3–6 carpels, which are arranged spirally on the receptacle. At the base of the ovary, they grow together

and with the columella. Ascidiate zones in each carpel are formed due to fusion of ventral margins. Along periphery, the carpels are fused with the formation of septal fissures as well. A short synascidiate zone is created, the proximal part of which is sterile. In the lower part of the ovary above the columella, a cavity is revealed, and the carpels remain interconnected along the periphery, which resembles a symplicate state. At the border with the plicate zones, the central cavity closes due to the tight closure of the carpels in the center of the gynoecium, and the carpels themselves become free. The ovules are located on the laminal-lateral placentae. Plicate zones in the ovary of each carpel become sterile at the top when going into stylodia. Aplicate carpel zones are represented by stigmae (Shamrov 2015) (Fig. 5A–H).

In *Brexia madagascariensis* (Celastraceae), the ovary is cylindrical, extending towards the base. There is a long style, in the center of which a star-shaped canal passes, and a 5-lobed capitate stigma. Short synascidiate region is formed at the base, and most of the ovary has a symplicate structure. It is preserved during the entire development, which leads to the formation of incomplete median septa (open symplicate zone). Probably due to the ovary asymmetry and the location of the locules at different levels in the proximal part of the gynoecium, both fertile and sterile locules are found. Only placentae are in three sterile locules and the ovules are formed in the remaining two fertile locules. The ovules are arranged in 3 rows in each locule on the placentae of different morphological nature. On the outer placentae (closer to the ventral edges of the carpels), they are oriented in the transverse plane and on the inner ones (closer to the septa) longitudinally. The ovary is diminished in size, the locules are shifted closer to the center, and the ovules become 1.5–2 times larger in the upper part of the synascidiate region. This leads to the fact that the number of ovule rows is reduced, the internal placenta ceases to function and ovules arise only on the external placentae in each locule. The placentation is central angular in the synascidiate region (Fig. 6A–D).

The longest region in the ovary of *B. madagascariensis* is symplicate. Its structure varies in length of the ovary. First of all, changes occur at the border with the synascidiate region (diminution of the ovary and ovule size and the appearance of a cavity in the center due to incomplete closure and partial divergence of the sutures). The placentation remains central angular despite the presence in the center of the cavity. The cavity in the middle part of the symplicate region expands, which leads to a slight increase in the ovary size. As in the base of the synascidiate region, the number of ovule rows increases again to 3 in each locule. The ovules are located at the outer and inner placentae. However, all ovules, including those at the inner placentae, are located in the transversal plane (Fig. 6E–G). The ovary size gradually decreases, while the cavity in the center shrinks, sutures come into contact and ovules appear only at the outer placentae from middle to upper part of the symplicate region. At the ovary top, as a result of the closure of the sutures in the center, apical septa are formed. The structure of the gynoecium begins to resemble a hemisymplicate state with a canal in the center, when the ovary passes into the style (Fig. 6H–I). The placentae in *B. madagascariensis* are described as axile and lateral. Our study showed that the number of rows of ovules and the characteristics of the placentae differ depending on the ovary region. At the base of the synascidiate and in the middle part of the symplicate regions, the ovules are formed in 3 rows in each locule, since they develop not only at the outer, but also at the inner branches of the intrusive placentae. In these zones, an increase in the ovary size is observed and either the formation of massive placentae or the cavity formation is in the center. In the remaining regions of the ovary, the ovules appear only at the outer placenta (one row
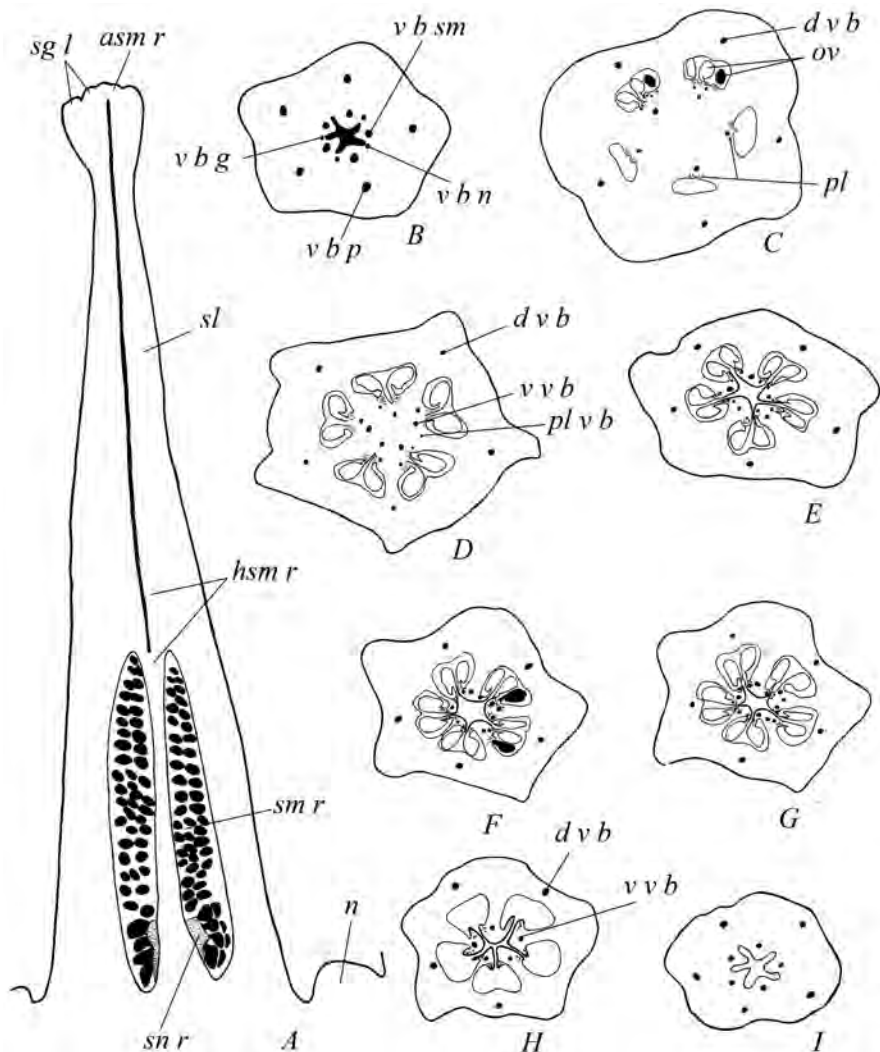
Figure 6. Structure of syncarpous gynoecium in *Brexia madagascariensis* (symplicate variation). A – longitudinal section of gynoecium; B – flower base; C, D – synascidiate zone; E–G – symplicate zone; H, I – asymplicate zone (upper part of ovary and style). *asm r* – asymplicate region, *d v b* – dorsal vascular bundle, *hsm r* – hemisymplicate region, *n* – nectarty, *ov* – ovule, *pl* – placenta, *pl v b* – placentary vascular bundle, *sg l* – stigma lobes, *sl* – style, *sm r* – symplicate region, *sn r* – synascidiate region, *v b g* – vascular bundle of gynoecium, *v b n* – vascular bundle of nectary, *v b p* – vascular bundle of perianth, *v b sm* – vascular bundle of stamen, *v v b* – ventral vascular bundle.

from each ventral margin). These data do not coincide with literary information. Some authors presumed that ovules are located in 2 rows (Matthews & Endress 2005). Others think that number of rows is 3 (Embaturova & Savinov 2006).

In *Kalanchoe laxiflora* and *K. tubiflora* (Crassulaceae) (Anisimova & Shamrov 2018), the gynoecium in the early stages is formed by the synascidiate zone (lower part of the ovary), the plicate (middle and upper part of the ovary) and aplicate (stylodia) zones in each carpel. The boundaries between the united carpels are not visible at the base of the synascidiate zone. The ventral margins of the carpels have grown together. Above the synascidiate zone, the carpels become free. Only the closure of the apical parts of the syncarpous sutures and the formation of a fissure in the center are visible on the border to the middle part of the ovary. A short

symplicate zone is formed, which is characterized by the closing of the lateral surfaces of the adjacent carpels. In the middle and upper parts of the ovary, the carpels are separated and only the heterocarpellate ventral margins are partially closed. Placentation is sutural. At the base of the gynoecium, it is represented by a central synplacenta, which marks the short proximal sterile region of the synascidiate zone. The placentation becomes central angular above at the level of discharge of angular placentae. Angular placentation is preserved over the ovary. Later and due to intercalary growth, the ovary is stretching, especially in the middle and upper parts and in stylodia. The synascidiate zone occupies only half of the lower part of the ovary. At the base of this zone, the boundaries between the united carpels are not visible. In the short symplicate zone the lateral surfaces of the adjacent carpels are free, but the apical parts of the syncarpous sutures grow together. In the symplicate and overlying plicate and aplicate zones of the gynoecium the ventral margins of each of the carpels are closed. Before pollination, the gynoecium is well differentiated into an elongated-oval ovary and long stylodia, ending with stigmae. The length of the sterile synascidiate zone increases. Symplicate zone becomes closed. But over the greater extent of the gynoecium the plicate and aplicate zones remain. Ventral vascular bundles reach the border of the ovary and stylodia.

A small number of species in Apocynaceae has a bicarpellate paracarpous gynoecium. In *Allamanda cathartica*, short sterile synascidiate and symplicate zones form congenitally at the base of gynoecium in early stages of development (SHAMROV & GEVORKYAN 2010b). Most of the gynoecium is plicate. In the course of development, there are some changings in the gynoecium. The hemisymplicate zone appears in the middle part of the ovary, due to the closure and postgenital imperfect fusion of the carpels. A plicate structure is preserved in the upper part of the ovary. The asymplicate zone is represented by 2 independent stigmae. The ovules are located at the parietal placentae in the middle part of the ovary. According to the signs of the structure, the gynoecium of this plant is close to paracarpous gynoecium in species of the Gentianaceae, also consisting of 2 carpels.

In *Allium caspium*, *A. ramosum* (Alliaceae), *Gagea stipitata* (Liliaceae) and *Veratrum lobelianum* (Melanthiaceae), the syncarpous gynoecium consists of 3 carpels and is characterized by vertical zonality created by various mechanisms. In *Allium*, a sterile synascidiate zone arises congenitally in the lower part of the gynoecium (columella is formed in the center of it), but over a longer distance it is formed by plicate zones in each carpel. The gynoecium acquires syncarpous features in the course of postgenital fusion of the edges of adjacent carpels. Septum formation in the upper part of the ovary occurs only due to the closure of the sutures, which grow together with the columella and the base of the stylodia, with the result that the style appears in the center of the ovary between ovary lobes. In *G. stipitata*, the gynoecium is characterized by the presence of a sterile synascidiate zone with the columella, while its majority has signs of a symplicate structure, with the exception of the distal asymplicate zone. The syncarpous organization arises during postgenital fusion, when the sutures between adjacent carpels grow to the center of the gynoecium and coalesce with the columella (fertile region) or tightly close without the participation of columella (upper sterile region). Gynoecium retains the features of the hemisymplicate structure in the style and the asymplicate state in the stigma (Fig. 7A–K). In *V. lobelianum*, a sterile synascidiate zone is found very early at the base of the gynoecium, which is formed congenitally by combining the carpel stalks and the proximal parts of the ovaries. There are also a short fertile symplicate and extended asymplicate regions. Then, due to the closure and postgenital imperfect
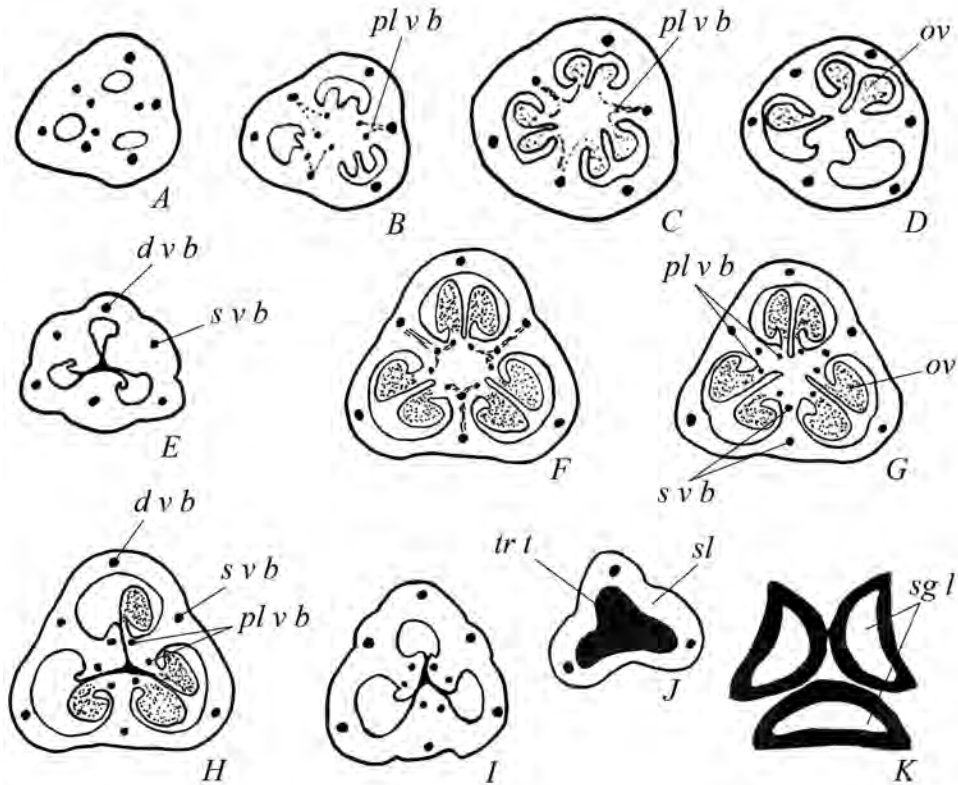
Figure 7. Structure of syncarpous gynoecium in *Gagea stipitata* (typical variation). Before meiosis: A–E – synascidiate zone at lower (A – sterile; B, C – fertile) and middle (D) parts of the ovary; E – closed symplicate zone at upper part of ovary, apical septa; before pollination: F, G – synascidiate zone at lower (F) and middle (G) parts of ovary; H, I – closed symplicate zone (H – fertile, I – sterile); J, K – asymplicate zone (J – style, K – stigma lobes). *d v b* – dorsal vascular bundle, *ov* – ovule, *pl v b* – placentary vascular bundle, *sg l* – stigma lobes, *sl* – style, *s v b* – sutural vascular bundle, *tr t* – transmitting tissue.

fusion of the carpels, the ovary becomes closed symplicate with the formation of median septa in the middle and upper parts. Stylodia retain an asymplicate structure (Shamrov 2010).

The gynoecium of *Hemerocallis citrina* (Hemerocallidaceae) shows syncarpy features in the lower part of the ovary at the earliest stages: synascidiate (sterile at the level of the central synplacenta and fertile at the level of the central angular placentae) and open symplicate (without median septa) zones. A large part of the gynoecium is symplicate, but of different origin. During the formation of ovular primordia, the postgenital fusion is of primary importance, leading to the formation of a closed symplicate zone with median septa in the lower part of the ovary. A symplicate zone of intermediate structure is formed in the middle part of the ovary. Signs of an open symplicate zone appear in the upper part of the ovary, where apical septa arise. Stylodia are combined into style, ending with three lobes of the stigma. The gynoecium becomes syncarpous throughout the ovary during the ovule formation. The open symplicate zone is transformed into a closed one. The apical septa, style with the canal and lobes of the stigma are well defined. Thus, the *H. citrina* gynoecium should be defined as postgenitally syncarpous (Shamrov 2014a).

In *Buddleja davidii* (Buddlejaceae), the gynoecium consisting of 2 carpels, develops as syncarpous. The lower and middle parts of the ovary are represented by the synascidiate zone at the earliest

stages of development. The upper part of the ovary is formed by an open symplicate zone. The distal part of the gynoecium is made up of the lobes of the stigma and a style with features of early specialization. Later, there is a complication in the structure of the symplicate zone, which becomes closed during pollination. The placentae are sterile at the poles of the ovary. The free spaces formed here are filled with ovules of the lower and upper tiers. In the distal region of the synascidiate zone, the placentae become compound median due to the convergence of the individual angular placentae. Placentary obturators are differentiated on the surface of both fertile and sterile placentae throughout the ovary. In the gynoecium structure, there are features of similarities and differences with representatives of Scrophulariaceae, Orobanchaceae and Gesneriaceae belonging to the order Scrophulariales (Shamrov 2014b).

The bicarpellate gynoecium of *Acer ginnala* (Aceraceae) shows the features of a 2-locular syncarpy at the earliest stages only in the lower part of the ovary: the presence of the synascidiate and closed symplicate zones. In the middle part of the ovary, there is a divergence of the adjacent edge carpels, and a fissure is formed in the center of the symplicate zone. The upper part of the gynoecium is represented by an asymplicate zone of different structure. It is formed by plicate areas in which the ventral margins of each carpel are closed together (the upper part of the ovary) or remain open (most of the stylodia). Later, postgenital fusion becomes more important and the gynoecium becomes syncarpous throughout the ovary. In the middle and upper parts, a closed symplicate zone is formed: in the middle part it is characterized by perfect fusion, while in the upper part the ventral margins of each carpel are only closed; the center maintains a fissure, and between the combining carpels there are still signs of imperfect fusion. Placentation is central angular. In each locule of the symplicate zone, there are 2 ovules, developing first as orthotropous and located displaced. Even before fertilization, one of them begins to degenerate, while the remaining ovule continues to develop on a more massive placenta. The fertile ovule, laterally laid on the placenta, is gradually found in the center. Due to the elongation of the funiculus, it begins to bend in the region of the micropyle, showing signs of asymmetry on the side of the bend, as a result, the ovule becomes hemiorthotropous (according to Shamrov 2017). The vascular system of the gynoecium is central-axial and is formed by the ventral and dorsal bundles, which are connected along the entire wall of the ovary (Shamrov 2019).

Based on the analysis of literary and original data, we confirm the point of view about tetracarpellate structure of the gynoecium in the Brassicaceae. In *Capsella bursa-pastoris*, the paracarpous gynoecium carpels are fused congenitally into one structure, with the exception of stigmae, from the earliest developmental stages. In addition to 2 relatively small fertile median carpels of the inner circle, the gynoecium includes 2 large sterile lateral carpels of the outer circle that are embedded between the median carpels. This leads to a change in the ovary shape in the area of the median carpels, making it more convex and causing an increase in the massiveness of sutures. However, the number of placentae does not increase. Lateral carpels create a large (outer) part of the locules and, apparently, do not participate in the construction of the style and stigma. Only the dorsal bundles formed in them, and the ventral bundles are combined with the ventral beams of the median carpels. The emerging fruit is flattened in the bilateral plane that coincides with the dorsal sides of the fertile carpels (Shamrov & Tsarev 2016).

The peculiarities of lysicarpous gynoecium morphogenesis in 4 species (subfamily Silenoideae of Caryophyllaceae) belonging to the tribes Lychnideae (*Viscaria vulgaris*, *Coccyganthe flos-cuculi*) and Diantheae (*Saponaria officinalis*, *Dianthus arenarius*) were studied. It was shown that the

topography of zones, time and mechanisms of lysicarpy differ in species. In early stages, the ovary can be formed by the synascidiate and symplicate zones equally (*Coccyganthe flos-cuculi*), mainly by the synascidiate zone (*Viscaria vulgaris*, *Dianthus arenarius*), or by a lysicarpous zone over a longer distance, with a short synascidiate zone at the gynoecium base (*Saponaria officinalis*). Continuing, the signs of lysicarpy are enhanced and the structure of the ovary acquires similar features in *Coccyganthe flos-cuculi* like in *Saponaria officinalis*. In *Viscaria vulgaris*, the length of the synascidiate zone decreases, and in *Dianthus arenarius* the gynoecium becomes fully lysicarpous. In the center of the ovary, a column is formed, on which intrusive angular placentae are located. Placentation is central angular. The isolation of the columnar structure and the formation of lysicarpy are preceded by an increase of the size of cells in the septa and the accumulation of calcium oxalate druses in them (*Coccyganthe flos-cuculi*, *Saponaria officinalis*, *Viscaria vulgaris*) or apoptosis in the cells (*Dianthus arenarius*). The processes of lysicarpy correlate with changes in the ovary shape, the time of the onset of cell and tissue destruction, the structure of the placentae and the location of the ovules in the lysicarpous zone (Shamrov & Kotel'nikova 2011; Kotel'nikova & Shamrov 2012).

In *Juncus filiformis* and *Luzula pedemontana* (Juncaceae), the gynoecium is formed on a gynophore. The lower region of the synascidiate zone is differentiated with its participation and the bases of the locules. This entire zone is sterile in *L. pedemontana* and ovules are formed in the upper fertile region of the synascidiate zone in *J. filiformis*. In the second species, most of the ovary has a symplicate structure before pollination, characterized by a central angular placentation and by the emergence of space due to the divergence of sutures and by the formation of a lysigenic cavity in the center (Fig. 1A–E). From the earliest stages, the middle and upper parts of the ovary in *L. pedemontana* are predominantly lysicarpous with a columnar placenta, but with signs of a syncarpous type (creating special compartments due to the ribbed structure of the ovary, tight closure of the placentary column with the ovary wall and close contact ovules between each other in the center). However, the main feature of the lysicarpous type (destruction of septa) was not revealed. Nevertheless, some mechanisms for creating additional space in the ovary of *J. filiformis* (the presence of a cavity in the symplicate region) and *L. pedemontana* (the presence of a cavity in the lysicarpous zone) turned out to be common with the mechanisms for the formation of lysicarpy with the involvement of septa: changes in the shape of the ovary, placenta structure and topography of ovules (Shamrov et al. 2012).

Gynoecium in *Canarium pimela* (Burseraceae) consists of 4 carpels, which are spirally arranged on the receptacle and have different sizes. One of the carpels is sterile and embedded between two adjacent carpels. At the earliest stages of development, the synascidiate (lower part of the ovary) and symplicate (middle and upper part of the ovary) zones are congenitally formed. The distal part of the gynoecium is an asymplicate zone (stylodia of different lengths). In the course of development, the postgenital fusion of syncarpous sutures occurs, with the exception of the upper part of the ovary, where apical septa are formed and the sutures are only in contact in the center. Ovary becomes 3-locular over a greater extent. Gynoecium is syncarpous. The wall of the ovary becomes more massive in the area of sterile carpel embedding. The septum doubles, with more powerful septal vascular bundles. In *C. pimela*, a transition from 5 carpels to 3 is possible, and the intermediate stage of this transition is the gynoecium at the stage of 4 carpels, during which the ovary acquires the features of a 3-merous structure. Probably, in this species we observe one of the early stages of the transition of a syncarpous gynoecium to a pseudo-monomerous one
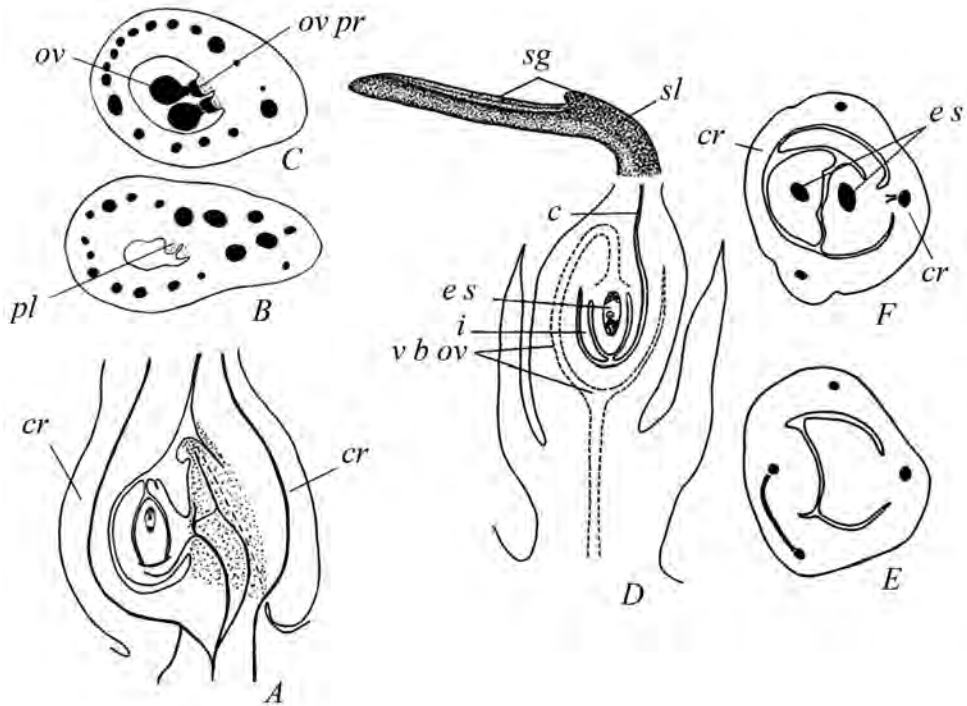
Figure 8. Origin of pseudo-monomerous gynoecium. A–C – from 2 carpels of syncarpous gynoecium in *Cerasus vulgaris*; D–F – from 2 carpels of paracarpous gynoecium. *c* – canal in style, *cr* – carpel, *e s* – embryo sac, *i* – integument, *ov pr* – ovular primordium, *pl* – placenta, *sg* – stigma, *sl* – style, *v b ov* – vascular bundle of ovary and ovule.

(Shamrov 2015). According to Sokoloff (2015), pseudo-monomerous gynoecium has more or less pronounced traces of sterile carpels (or carpel).

When studying the morphogenesis of pseudo-monomerous gynoecium in *Cerasus vulgaris* (Rosaceae), it was found that it is formed on the basis of syncarpy of two carpels, differing in size, structure and reproductive ability. In this case, the single locule turns out to be eccentric, and the wall of the ovary is more massive at the place of carpel fusion. Sometimes, both carpels were fertile and the ovary turned out to be 2-locular (Yandovka & Shamrov 2016) (Fig. 8A–C). Thus, the emerging fruit in *C. vulgaris* is not a drupe, but a pyrenarium. In contrast to *C. vulgaris*, in *Ceratophyllum* species, a pseudo-monomerous gynoecium occurs on the basis of the paracarpous type. The edges of the two carpels are congenitally fused over almost the entire length into one structure. The placentation is primary basal. During gynoecium morphogenesis it becomes secondarily apical. The free edges of the stylodia are closed and postgenitally fused into a style, with the exception of the apical parts, which become asymmetrical stigmae (Shamrov 2009) (Fig. 8D–E). The fruit arising on the basis of two carpels in *Ceratophyllum* cannot be considered a nutlet. It should be attributed to the nut-fruits. In *Polygonum affine* (Polygonaceae), the paracarpous (actually pseudo-monomerous) gynoecium is formed by 3 carpels; the ovary is superior, unilocular and 3-ribbed. Parietal placentation is in a state of extreme reduction. The placenta is differentiated just on one suture. It is fertile only in the lower part of the ovary, where one hemiorthotropous ovule (according to Shamrov 2017) develops, which occupies a lateral position. In the course of development, due to intercalary growth occurring in the lower part of the ovary, the fertile placenta gradually is shifted to the top (Shamrov & Anisimova 2015).
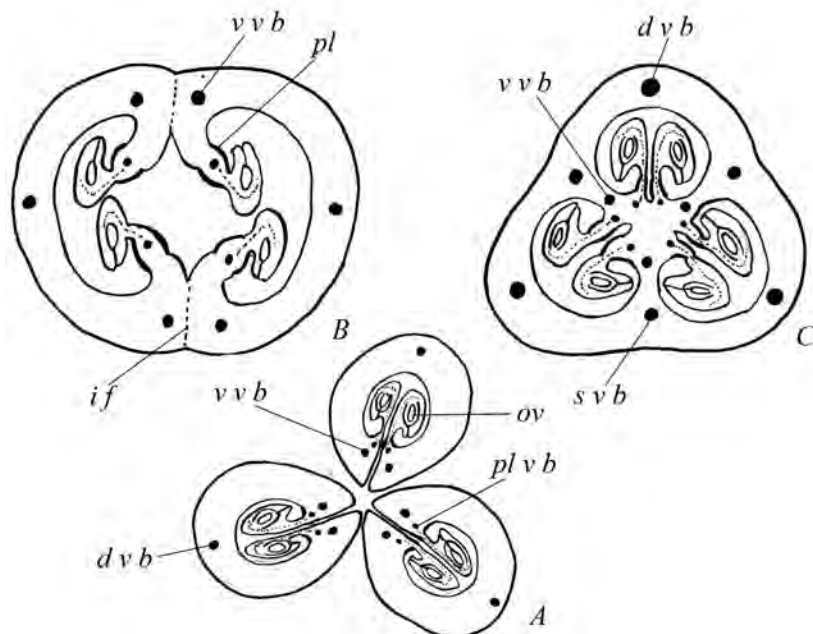
Figure 9. Types of the gynoecium and the ovule position at placentae. A – apocarpous (polymerous) type, angular placentation; B – paracarpous type, parietal placentation; C – syncarpous type, central angular placentation. *d v b* – dorsal vascular bundle, *i f* – imperfect fusion, *ov* – ovule, *pl* – placenta, *pl v b* – placentary vascular bundle, *s v b* – sutural vascular bundle, *v v b* – ventral vascular bundle.

It is possible to attribute those variants to pseudo-monomerous gynoecium, which are transformed after fertilization into single-seeded coenocarpous fruits. In *Corylus avellana* (Betulaceae), the nut-fruit arises on the basis of bicarpellate syncarpous gynoecium, while the ovary is 2-locular at first. After the destruction of the sterile locule it becomes unilocular (Troll 1957). Similarly, a fruit is formed in *Syringodium filiforme* (Cymodoceaceae) on the basis of a syncarpous gynoecium from 2 carpels (Nemirovich-Danchenko 1985). In *Trapa natans* (Trapaceae), the gynoecium is syncarpous and consists of two carpels. The fruit is one-seeded. The single ovule develops in each locule of the bilocular ovary, however, one of them degenerates always after fertilization, irrespectively of the fertilization of the latter (Titova et al. 1997). According to Sinjushin (2018), the septum in the ovary is destroyed in the course of embryo development. Probably, a kind of lysis takes place. The acorn-fruit of the Fagaceae species also arises on the basis of syncarpous gynoecium, often consisting of 3 carpels. 2 carpels are sterile. In the fertile carpel, 2 ovules are formed first, and then only one ovule develops (Korchagina 1991). In Asteraceae, the gynoecium consists of two carpels and its type is discussed in literature: unilocular in *Hyoseris radiata* (Lavialle 1912), syncarpous but unilocular in *Youngia japonica* (Pandey et al. 1978), paracarpous (Takhtajan 1966) and unilocular (Takhtajan 2009). One carpel becomes sterile, and an ovule forms in a fertile carpel, sometimes there are 2 ovules. A study of the flower morphogenesis in *Taraxacum kok-saghyz* (Savchenko 1952) showed that in the early stages the gynoecium is formed by two carpels, which are laid in the form of two rollers. They stretch and touch at the top, forming the ovary and are located above the style and stigma. The ovule occurs laterally. The gynoecium includes an inferior ovary, a style and a 2-separate stigma. After fertilization, the cypselae-fruits appear. In cereals, a paracarpous gynoecium from 3 carpels is

transformed into a corn-fruit. It is also interpreted as pseudo-monomerous on a trimerous basis (Eckardt 1937). Kaden (1959) and Petrova (1965) did not find signs of other carpels in the development of gynoecium (fruit) and attributed it to monomerous apocarpous. Takhtajan (1966) believed that the presence of 3 carpels of paracarpous gynoecium was particularly well expressed in *Streptochaeta*, which is confirmed by a detailed study of the flower and the presence of 3 stigma branches.

Conclusion

On the basis of literature data and original researches, it can be concluded that the modern system of gynoecium types is not represented neither by two (as is customary in most foreign studies) nor by four (as believed by Takhtajan), but only by three types: apocarpous, paracarpous and syncarpous (Fig. 9A–C). The monomerous apocarpous and polymerous apocarpous variants of the apocarpous type differ in structure (Fig. 3; 4A–M; Table 2). As the carpels, especially in the lower part, the polymerous apocarpous gynoecium of the synascidiate variation resembles the syncarpous and paracarpous types. Together they form a group of coenocarpous gynoecia. As already noted, previously all forms of combining single carpels among themselves at the base were attributed to the pseudo-coenocarpous type (Troll 1931, 1934). Comparative analysis of the gynoecium organization in Ranunculaceae (Rohweder 1967; Schaeppi 1972) showed that the family is characterized by a gradual transition from apocarpy to syncarpy. On the basis of the syncarpous and paracarpous types, the various variants of pseudo-monomerous gynoecia could arise in the course of evolution as a result of sterilization of most fertile ovules, reducing the ovary of sterile carpels or merging of the tissue ovary of all carpels into one common unilocular ovary (Fig. 4L, N). At the same time, the fruits become single-seeded after fertilization with a possible preservation of stylodia (style) and independent stigmae. Modern anatomical investigations demonstrated the presence of congenital intercarpellary fusion in the very short basal-most part of gynoecia of some Ranunculaceae, such as some species of *Aconitum*, *Delphinium*, *Staphisagria* and *Aquilegia*. At least, the gynoecium has a very short synascidiate zone in *Aconitum lasiostomum* and *A. lycoctonum*, then a very short unilocular symplicate zone followed by a long asymplicate zone (El et al. 2019).

Paracarpous gynoecium is fundamentally different in structure from syncarpous (eusyncarpous in the narrow sense) and, in our opinion, it cannot be treated with the latter within a single type (Leinfellner 1950; Takhtajan 2009). The combination of all types of united gynoecia in one syncarpous type, adopted in foreign literature, suggests that this type is not homogeneous but aggregative, what is emphasized in studies of placentation characteristics. Among the coenocarpous variants of gynoecia (the processes of carpel combining affect the ovary almost completely), it is advisable to consider two types (syncarpous and paracarpous), each of which has its own special placentation. This allows us to expand the possibilities of using data on the gynoecium morphology for the purposes of systematics and phylogeny. So, in the Annonaceae family, a variety of the gynoecium structure from apocarpy to syncarpy exists (Deroin 2019). Paracarpy is realized in *Isolona* and *Monodora* (Deroin 1997), pseudo-syncarpy is recognized in *Annona*, as suggested by molecular studies (Couvreur et al., 2008).

Takhtajan (1942, 1948, 1964) proposed an original scheme of interrelationships of types and believed that the paracarpous gynoecium could arise both on the basis of an apocarpous and a syncarpous gynoecium as a result of phylogenetic 'opening' of sutures, while the edges

of each carpel move apart, remaining fused with edges of neighboring carpels. In his opinion, the paracarpous gynoecium appeared independently in the most diverse evolutionary lines of flowering plants. At present, many phylogenetic systems have undergone one revision after another. A number of contradictions arose between molecular phylogenetic data and classical ideas about different groups of plants. The problem under discussion has affected many morphological features, including the structure of gynoecium. At the same time, the main trend of gynoecium evolution (as a gradual complication and unification of carpels) from apocarpous to syncarpous and paracarpous types, adopted in most classical morphological studies, has been revised. Its evolution is considered as a multivector system with a possible reversion to its original position. One or another morphological structure receives a new status according to the changed level and position of the taxon on the molecular phylogenetic tree. This led to a simplified interpretation of the history of the emergence and formation of existing variants of gynoecium.

The results, obtained from the characteristics of gynoecium morphogenesis, allow us to agree with the existing point of view on the multivector evolution of gynoecium (Fig. 4A–M) with a possible reversion to its original position (Endress & Matthews 2012). First of all, in all types similar changes are revealed in the structure of the basal and apical parts of the ovary (formation of basal and apical septa) and in stylodia (appearance of a style or compitum). And, if the transformations observed at the base of the ovary reflect the general directions of evolution towards oligomerization of similar organs (including the appearance of pseudo-monomerous variants of gynoecium), then the formation of a style or compitum, when combining the upper part of the ovary and the stylodia, indicates changes in reproductive biology, especially in mechanisms of pollination and fertilization.

Being a starting point for other variants, the apocarpous type itself was probably transformed to a minor extent. In the course of evolution, there was a reduction in the number of carpels and the emergence of a monomerous apocarpous variant based on a polymerous apocarpous one. In addition, some plants show the common signs of coenocarpous gynoecia – the appearance of the synascidiate zone at their base.

The evolutionary directions of paracarpous and syncarpous gynoecia were probably independent. In each type, the spatial variants arose as a result of the condition created in the ovary for the development of all ovules (Shamrov 2018a, b). The initial structure of the carpels, which gave rise to paracarpous or syncarpous gynoecia, is not of less importance. Analysis of the data on the gynoecium morphogenesis suggests that the syncarpous gynoecium occurred on the basis of ancestral carpels, where the elongated horseshoe-shaped form of which was wider at the dorsal side and the edges on the narrow ventral side were close together, which ensured their unification in the center, while preserving the fertile synascidiate and symplicate zones. The formation of the paracarpous gynoecium took place on a different basis – the carpels had the form of an extended arch, and the ventral margins moved apart, which made it possible to form a cavity in the ovary without creating special mechanisms. However, the formation of paracarpy was associated with a reduction in length, subsequent sterilization and reduction not only of the synascidiate, but also of the symplicate zone.

It should be emphasized that the creation of additional space in the ovary of the syncarpous gynoecium (in the center of the open symplicate region, along the ovary wall as a result of the septa destruction) correlates with the formation of intrusive placentae, as a result of which the

number of ovule rows increases. Similar changes in the placentation transformation are inherent in some plants with paracarpous and apocarpous types.

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