Evolutionary History of the Leguminous Flower

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Received June 11, 2020; revised June 11, 2020; accepted June 11, 2020

Abstract—The contemporary evolutionary developmental biology includes molecular phylogeny, studies on morphology and morphogenesis, genetics, and genomics. The most reliable conclusions about main trends of floral evolution can result from investigations of highly polymorphic group, which is precisely characterized from the positions of both modern systematics and molecular developmental biology. The legume family, Leguminosae, is a group of such kind. It demonstrates an outstanding variation in flower structure. The ancestral floral structure in this family includes monosymmetry, pentacycly, pentamerous perianth and androecium, and a monomerous gynoecium. However, distinct evolutionary lineages resulted in origin of polysymmetric perianth, different patterns of staminal reduction or polymerization, as well as multicarpellate gynoecium. A strikingly high level of homoplasy is found in Leguminosae. Besides the existing evolutionary tendency to stabilize floral structure, the exact "instability syndrome" evolved repeatedly, associated with a polysymmetry and characterized with a highly variable number and position of floral organs.

Keywords: actinomorphy, floral merism, homoplasy, polymerization, reduction, symmetry, zygomorphy
DOI: 10.1134/S2079086421040083

INTRODUCTION

The pronounced evolutionary success of angiosperms strongly correlates with a diversity of structure unique for this taxon, i.e., flower adapted to different types of pollination. Since the second half of 20th century, the fruitful synthesis of modern systematics, classical morphology and developmental genetics has emerged. The resulting research strategy is called evolutionary developmental biology (evo-devo). Researches in this field led to a deeper understanding of mechanisms underlying evolutionary events. Obscure statements such as "reduction occurred" were substituted with perfect knowledge, which genes are responsible for certain morphological changes and when they occurred (or, better to say, possibilities to get such knowledge appeared).

The foundation in understanding floral evolution has been laid in studies of model plant species, especially *Arabidopsis thaliana* (Brassicaceae) and *Antirrhinum majus* (Plantaginaceae). The obtained results provided a possibility to identify genes governing flower development in representatives of other taxa. Among them, one may list the third largest angiosperm family, Leguminosae, with its highly diverse flowers.

Legumes hold the top position with respect to a number of cultivated representatives (Harlan, 1992). This family includes the oldest model object of genetics, a garden pea (*Pisum sativum*). Moreover, Leguminosae now have the largest number of whole-genome sequences (Bauchet et al., 2019). Taken together, this context provides a possibility to study genetic regulation of floral ontogeny in legumes.

Numerous papers are dedicated to floral development in legumes. Among pioneers in this field, it is meaningful to mention Shirley Tucker, who devoted a series of publications to flower ontogeny in Leguminosae since mid-1980s till the beginning of 2000s (Tucker, 1984, 1989a, 1989b; etc.). These works found their response in the ongoing revision of legume phylogeny. A number of significant aspects of floral morphology and evolution in legumes were elucidated in these studies.

During recent decades, a phylogeny of Leguminosae was under a detailed investigation with application of the most contemporary molecular genetic approaches. One of the most impactful results is a revised system of family, now including six subfamilies instead of former three (LPWG, 2017): Caesalpinioideae (148 genera), Cercidoideae (12 genera), Detarioideae (84 genera), Dialioideae (17 genera), Duparquetioideae (one genus), and Papilionoideae (503 genera). We will follow this classification throughout this review. As compared with a traditional system of legumes (e.g., Yakovlev, 1991), Caesalpinioideae split into several smaller subfamilies, but Caesalpinioideae s.s. included a former subfamily Mimosoideae.

The contemporary methods of analysis of genome and transcriptome enable to diverge from a concept of model object. For example, active studies in phyloge-

nomics of subfamily Detarioideae, exotic trees relatively unknown among European morphologists, rapidly led to possibilities to use this group as a "model clade" in evolutionary morphology of legumes (Ojeda et al., 2019).

When reviewing the available literature on leguminous flowers, one comes across the fact that different aspects are covered in unequal degree. Floral morphology of most representatives is described precisely enough to make comparisons (at least in specific and generic diagnoses). Contrarily, ontogenetic series are available for fewer genera, which however include most of key taxa insightful to understand a degree of variation in main clades. Genetic and physiological regulation of development is discovered only in some points and mostly in a narrow group of model species.

For conciseness, we will avoid citing papers describing floral morphology in a further review, referencing only publications dedicated to ontogeny and its regulation.

When discussing floral evolution, we are realistic about impossibility to review all apomorphies of taxa of low grade, such as tribes or genera, while origin of such apomorphies meets the definition of evolutionary history. Hence the emergence of different style morphology or calyx pubescence will remain beyond a scope of a given review. Rather, we will focus on cases when symplesiomorphies of the intuitively understood "typical" leguminous flower are disturbed. They include monosymmetry, whorled arrangement of organs, pentamerous perianth, pentamerous androecium in two whorls, monomerous gynoecium. Otherwise stated, the review focuses mostly on processes of initiation of floral structures in Leguminosae rather than their differentiation.

CALYX

In all legumes, the calyx whorl is initiated first and seemingly dictates the overall floral geometry, as organs of different whorls properly alternate with each other, except for cases interpreted as reduction of a single or several whorl(s), e.g., *Ceratonia*—Caesalpinioideae. This statement refers to flowers with whorled arrangement of organs, the gynoecium almost always being an exception.

One of the most important events in the ontogeny of leguminous flower is patterning of a median sepal, i.e., the one on abaxial-adaxial symmetry axis. In most known cases, a median sepal is abaxial, thus defining the adaxial position of a median petal. This petal possesses certain "special properties." In monosymmetric flowers, it is distinguishable from other petals and typically persists even in cases of a partial corolla reduction (see below).

However, several exceptions exist. It is well known that a median sepal often, although not always, initiates in adaxial position in members of the former sub-family Mimosoideae. This can be stated with certainty only with respect to "mimosoids" with a pentamerous calyx, although even in the latter case a median sepal can initiate variably. For example, in *Inga* this pattern is unstable on both between- and within-species level (Paulino et al., 2017). It is more precisely to state than adaxial position of a median sepal is possible in this group. Similar, and equally variable, calyx ontogeny is described in *Gleditsia* (Tucker, 1991), *Ceratonia*, and *Erythrophleum* (Tucker, 1992). Comparison of morphological and phylogenetic data evidences that similar position of a median sepal is inherent to a certain caesalpinioid clade with polysymmetric flower, in which a former subfamily Mimosoideae is nested (De Barros et al., 2017). It is of special interest that high plasticity of floral development in this group is connected not only with a position of a median sepal, but also merism, organ sizes, sexual expression, and even orientation of a carpel cleft (Tucker, 1992).

When considering a special significance of the adaxial petal in monosymmetric corolla, it becomes evident that the adaxial position of a median sepal is incompatible with monosymmetry in Leguminosae. Such association, common in families like Violaceae or Geraniaceae, is unknown in legumes. It is unclear which event was initial, either atypical patterning of a median sepal or acquisition of a polysymmetry. However, listed features comprise a syndrome in Leguminosae, including some other features of instability, such as variable merism and unstable position of a carpel cleft (Tucker, 1991, 1992).

Comparison of data on perianth morphology and phylogeny of angiosperms evidences that the ancestral state of pentamerous flower included the adaxial position of a median sepal. Changes in geometry occurred in evolution for ca. 30 times independently (Bukhari et al., 2017). The abaxial position of a median sepal is a synapomorphy of Leguminosae untypical for other families of order Fabales (Bello et al., 2012). Seemingly the reversion to ancestral condition took place in Caesalpinioideae, or even two such reversions, as group of genera including *Ceratonia* and *Gleditsia* is the earliest diverging from other caesalpinioids, while former Mimosoideae is a comparatively derived caesalpinioid group.

In some of basal Papilionoideae (*Swartzia*, *Bocoa*, *Candolleodendron*, *Cordyla*), calyx of mature flower comprises a completely closed sheath with individual sepals undiscernible, which splits irregularly at anthesis. Initiation of such calyx begins from three (or more) lobes, sometimes interpreted as separate sepal primordia (Tucker, 2003a). However, in some species of *Swartzia* more common initiation of five primordia was described (Tucker, 2003a), hypothetically corresponding to sepals. Sometimes calyx grows as a joint ring without lobes, and different patterns may coexist in the same species or even the same inflorescence (Sinjushin, 2018). These observations give an impres-

sion that three lobes visible at calyx initiation in these species are not sepal primordia, but folds of a single annular meristem. This interpretation relieves from entanglement concerning trimerous calyx in group containing numerous species with a pentamerous flower.

In many representatives of Detarioideae, two adaxial sepals emerge as separate primordia but fuse on early stages, thus giving the impression of tetramerous calyx in mature flower. Other floral whorls remain pentamerous. Genera with five sepals are also known in this subfamily (Tucker, 2002a, 2003b). In some genera of tribe Loteae (Papilionoideae), the same sepals initiate as a single primordium, later splitting into two parts (Sokoloff et al., 2007). Two adaxial sepals, even if emerge independently, may fuse giving rise to a bilabiate calyx (e.g., *Aeschynomene*—Papilionoideae).

COROLLA

Corolla, the most remarkable part of flower, contributes most fully to the subjective estimate, whether the exact leguminous flower is "typical."

There are many representatives of Leguminosae having radially symmetric (polysymmetric or actinomorphic) corolla. In historical perspective, cases of polysymmetry were given a significant importance in phylogenetic reconstructions. After application of molecular methods in systematics, many taxa described in accordance with symmetry of their flowers were reinterpreted in new status. For example, tribes Swartzieae and Sophoreae were deeply reorganized. A generic status of some morphologically distinct taxa was found unjustified. For instance, *Etaballia* was found as one of species within *Pterocarpus* (Klitgård et al., 2013). Numerous cases were recorded, when a group with high support from molecular phylogeny is highly diverse morphologically (Povydysh et al., 2014; Cardoso et al., 2012a, 2012b). Such observations in legumes, a group with highly variable floral morphology, point at a high value of molecular methods in phylogeny and, at the same time, at possibility of strikingly high level of homoplasy (Pennington et al., 2000; Fougère-Danezan et al., 2010).

Genetic regulation of corolla monosymmetry has been dissected precisely in studies of model species, such as *Antirrhinum* (Plantaginaceae), *Lotus*, *Pisum* (Papilionoideae). The key role in symmetry patterning is attributed to genes of TCP family. They encode proteins with a basic helix-loop-helix motif (bHLH), responsible for interactions with DNA and other proteins (Martín-Trillo and Cubas, 2010). Morphogenetic role of these proteins is associated with inhibition of cell proliferation via promotion of their differentiation. Genes *CYCLOIDEA* (*CYC*) and *DICHOTOMA* (*DICH*) of a snapdragon belong to this family (Luo et al., 1999). Both genes express in the adaxial domain of floral primordium. In mutant *cyc*, the developmental program of abaxial petals expands to lateral petals ("ventralization"). In double mutants *cyc dich*, this process reaches its maximum: all petals (usually six instead of five) become abaxial-like, and fertile stamen develops instead of adaxial staminodium (Luo et al., 1999).

Since identification of genes *CYC* and *DICH*, it has been discovered that homologous genes, typically expressed in the adaxial domain, define monosymmetry in many other angiosperm taxa (Preston and Hileman, 2008). Genomes of legumes contain several orthologs of *CYC* resulting from at least one ancient duplication (Citerne et al., 2003). Role of these genes has been studied in details in *Pisum* and *Lotus* (Wang et al., 2008; Xu et al., 2013; He et al., 2020). There are several recessive mutations in pea which affect corolla symmetry. Mutants *keel wings* (gene *K* corresponds to *PsCYC3*) have wing petals differentiated like keel elements. Flag in flowers of mutants *lobed standard 1* (gene *LST1* corresponds to *PsCYC2*) bears symmetric marginal incisions. In mutants *symmetric petals 1* (gene *SYP1* encodes transcription factor unrelated to bHLH proteins), all petals become symmetric with respect to their midvein. Thus, *CYC*-like genes participate in regulation of floral symmetry in legumes. Their role in evolution was exemplified by *Cadia* (Papilionoideae). Taxonomic position of this genus has been problematic for long, as derived features associate with a polysymmetric flower in *Cadia*. According to molecular data, *Cadia* is nested within a comparatively derived clade of "core genistoids," having closest affinity to *Calpurnia* with a typically papilionate corolla (Cardoso et al., 2012b). The corolla polysymmetry in *Cadia* was found related with ectopic expression of one of *CYC* orthologs in primordia of all petals rather than only in adaxial domain (Citerne et al., 2006). That means, that recent homeotic mutation provokes flag-like differentiation of all petals, causing floral monosymmetry. The anomalous forms with all petals dorsalized are known in some other species of Leguminosae (Sinjushin et al., 2015).

The entirely different case is described in *Etaballia* with a polysymmetric flower, a monotypic genus (or species of *Pterocarpus*: Klitgård et al., 2013) nested within a clade having typically papilionate corolla. Narrow, symmetric and undivided into limb and claw petals of *Etaballia* are diverse from unguiculate petals of other *Pterocarpus* and hence cannot result from a homeosis. Petal epiderm in *Etaballia* is composed of small cells arranged in long proximodistal files (Sinjushin, 2019). Most probably, mutation preventing cell divisions and/or expansion towards petal margins occurred in this genus, resulting in narrow identical petals in all positions. Phenotypically similar mutants were described in *Rhododendron* (Ericaceae; Tasaki et al., 2012). A homeosis cannot be fully rejected as a cause of floral polysymmetry in some other genera of the "*Pterocarpus* clade" (Sinjushin, 2019).

The listed examples together with analysis of phylogeny of Leguminosae (LPWG, 2017) give impression, that monosymmetry comprises a symplesiomorphy of the whole family. Most likely, it established once, but there are numerous ways to disturb it, which realized repeatedly in different subfamilies providing taxonomic curiosities. In perspectives, studies on floral ontogeny and its regulation may discover new mechanisms of shifts between mono- and polysymmetry. The number of such possibilities may be very high. For example, 462 genes were discovered in *Vicia sativa*, which specifically express in the adaxial petal and are putatively governed by two orhologs of *CYC* (Liu et al., 2013).

Typical "flag blossom" of many Papilionoideae is composed of three petal types. A shared feature of the whole order Fabales is free petals (Bello et al., 2012), but in many papilionoids the abaxial petals postgenitally fuse into a carina, the latter conjoined with lateral (wing) petals in some way or other. In some cases, lateral and abaxial petals have almost identical structure. There is a temptation to reconstruct evolution of the monosymmetry in Papilionoideae as an increase of complexity towards truly papilionate morphology. However, the aforementioned example of *keeled wings* mutant in pea illustrates, that lateral petals can ventralize very easily. In tribe Amorpheae, a secondary simplification of corolla structure is postulated, resulting in complete reduction of lateral and abaxial petals in some genera (McMahon and Hufford, 2005). In some species of *Lotus*, a developmental program of lateral petals expands to adaxial and abaxial petals, thus leading to an unusual morphology of corolla adapted for ornithophily (Ojeda et al., 2017). A "hooded" flag of many ornamental forms of *Lathyrus odoratus* (Papilionoideae) results from shift of expression of wing-specific genes to the flag, caused by mutation in a *CYC*-like gene (Woollacott and Cronk, 2018).

These examples confirm that corolla symmetry and differentiation pattern of petal types are very variable. Even within a single subfamily, transitions between corolla with two petal types, three petal types or completely polysymmetric perianth occurred repeatedly (Ojeda et al., 2019). The taxonomy of legumes (LPWG, 2017) points that the most probable ancestral state is monosymmetry, secondarily lost in certain genera in almost every subfamily. Polysymmetric flowers are inherent to most Caesalpinioideae in their contemporary volume. The papilionate (or similar) corolla is absent only from Detarioideae and Duparquetioideae (LPWG, 2017). Tucker (2002b) suggested, that similar morphology of corolla in *Cercis* (Cercidoideae) and Papilionoideae result from convergence.

Some of petals may fully reduce. In many cases, only adaxial petal remains: *Amburana*, *Bocoa*, *Swartzia* p.p. (basal Papilionoideae), *Amorpha* (derived Papilionoideae), *Aphanocalyx*, *Monopetalanthus* (Detarioideae). Two abaxial petals are sometimes strongly underdeveloped, as compared with other ones: *Hymenaea*, *Neochevalierodendron* (Detarioideae). The apetalous flowers are not rare: *Swartzia* p.p., *Cordyla* (basal Papilionoideae), *Ceratonia* (Caesalpinioideae), *Colophospermum*, *Crudia*, *Saraca* (Detarioideae), *Dialium* (Dialioideae).

Detailed analysis of ontogenetic series indicates, that similar final condition (e.g., absence of petals) is conditioned by unequal degree of reduction. While there are no signs of corolla initiation in *Cordyla*, apetalous *Swartzia*, and *Dialium* (Tucker, 2003a; Zimmerman et al., 2013; Sinjushin, 2018), the primordia of four or five petals emerge but have no further development in *Crudia* and *Amburana* (Tucker, 2001; Leite et al., 2015). Sometimes rudimentary petals persist (*Copaifera*—Detarioideae) or rarely unfold (*Ceratonia*) (Tucker, 1992; Pedersoli et al., 2010).

In literature on plant morphology, two degrees of organ reduction are traditionally recognized, viz., abort and ablast (for terms, see: Schmitz, 1872; Choob, 2010). In a former case, development begins, but organ fails to reach its "typical" size and structure. The benchmarks for "typical" morphology are either other organs of the same series (e.g., other petals) or similar organs in related taxa. The "ablast" suggests that there are no signs of initiation and development, but structure is present in the same position in related taxa. The hypothesis on ablast is required to explain the specificity of the whole system, such as opposition of floral organs versus alternation in related species. The aborted organ may reach significant sizes. For example, we define formation of staminodia instead of stamens as abort. Hence, both abort and ablast are possible in corolla, often resulting in similar structure of mature flower, but via different mechanisms.

ANDROECIUM

The androecium is the most variable floral part in legumes, in both evolutionary and ontogenetic sense (Prenner, 2013; Sinjushin and Karasyova, 2017). Ten stamens in two whorls are a symplesiomorphy of Leguminosae (Bello et al., 2012), but this bauplan is often transformed.

Reduction of part of stamens is frequent. Although degree of this reduction is unequal in different groups of Leguminosae, there are two principal patterns, connected with the position of reduced stamens (Fig. 1).

1. Reduction of stamens of one or both whorls in the adaxial floral domain. There are no signs of initiation of inner whorl stamen opposed to flag (vexillary stamen) in *Abrus* (Papilionoideae; Prenner, 2013). In *Castanospermum* (basal Papilionoideae), *Amherstia*, and *Brownea* (Detarioideae) the same stamen remains underdeveloped. In *Arachis* (Papilionoideae), the vexillary stamen and one or two adjacent stamens of outer
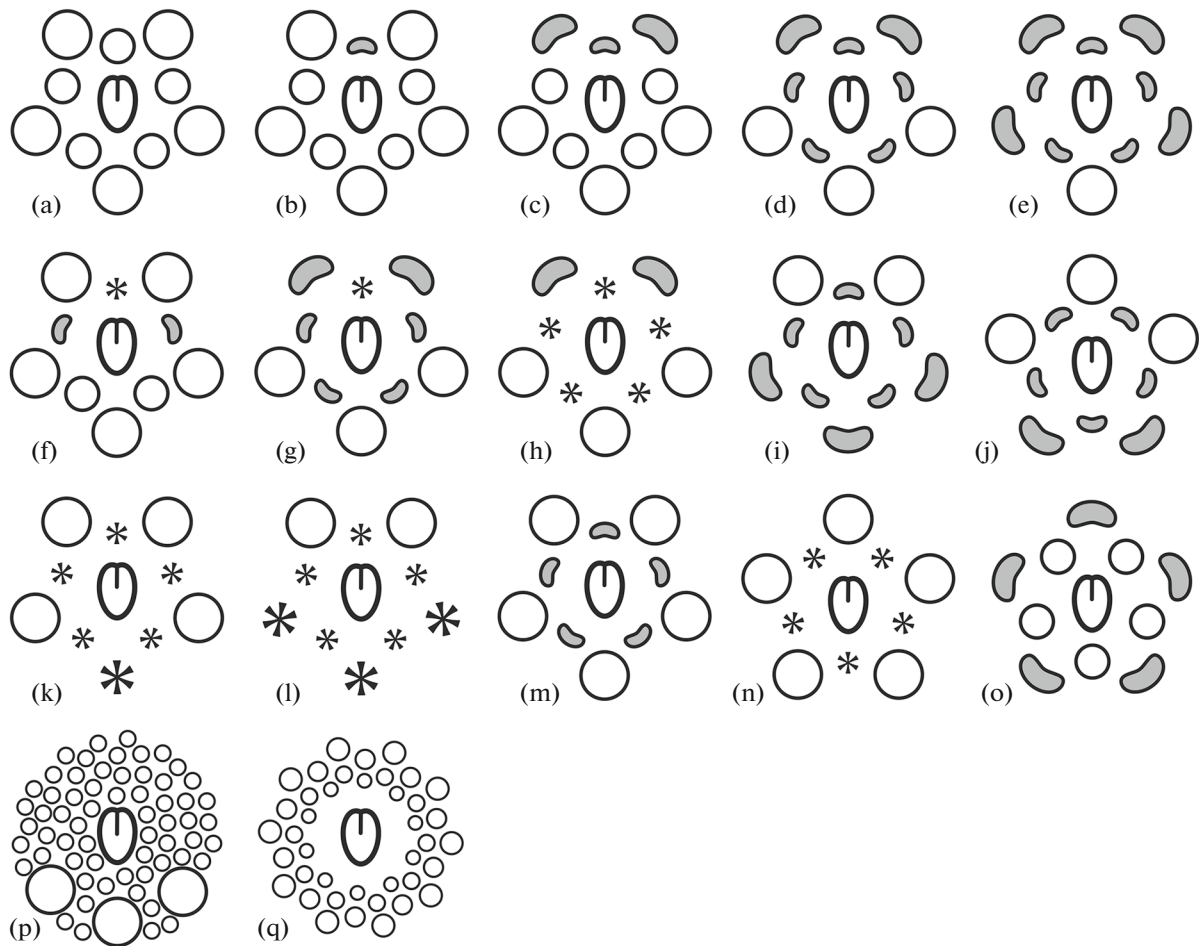
Fig. 1. Examples of transformation of androecium in Leguminosae. Perianth and staminal fusion are not depicted. (a) Initial morphology of androecium in family; (b) *Amherstia*, *Bauhinia petiolata*, *Brownea*, *Castanospermum*; (c) *Arachis*, *Senna* p.p.; (d) *Gilbertiodendron*, *Phanera*; (e) *Bauhinia monandra*; (f) *Afzelia*; (g) *Tamarindus*; (h) *Petalostylis*; (i) *Sindora*; (j) *Neptunia* (male flower); (k) *Duparquetia*; (l) *Dialium* p.p., *Distemonanthus*; (m) *Astragalus* p.p., *Bauhinia variegata*, *Staminodianthus*; (n) *Cerationia*; (o) *Dimorphandra*; (p) *Swartzia* p.p.; (q) *Cordyla*. Stamens are shown as circles, staminodia as grey figures, ablasted organs as asterisks. Larger figures correspond to the outer whorl.

whorls are sterile, i.e., converted into staminodia. Possibly the conversion of the same three adaxial stamens into petaloid staminodia in *Senna* (Caesalpinioideae) falls in the same category. Marazzi et al. (2007) suggest that these staminodia are synapomorphic for *Senna*, and the secondary fertilization of adaxial stamens is hypothesized in one of clades of this genus. Analysis of transcriptome in stamens with different position in *S. bicapsularis* demonstrates that several hundreds of unique genes are active in different stamens, as well as in staminodia (Luo et al., 2016). Luo et al. (2016) hypothesize that formation of staminodia is connected with reduced level of expression of genes, putatively encoding proteins with bHLH motif, as well as with peculiarities of hormone regulation.

The androecium of *Bauhinia* s.l. (Cercidoideae; Taubert, 1894) exhibits a strikingly wide range of reductions; the vexillar stamen in underdeveloped in *B. petiolata*. Transformations of the abaxial stamens

are rarely found, such as ablast of median abaxial stamen in *Duparquetia* (Duparquetioideae; Prenner, Klitgaard, 2008) or staminodial conversion of the abaxial stamens of both whorls in *Neptunia* ("mimosoid" Caesalpinioideae; Tucker, 1988). In some species of *Senna*, groups of three stamens from both abaxial and adaxial sides are staminodial (Marazzi et al., 2007).

When considering the whole variation of angiosperms, one may notice that reduction of the adaxial stamen(s) often accompanies monosymmetry. This is the case of representatives of orders Lamiales (many Acanthaceae, Gesneriaceae, Lamiaceae, Plantaginaceae, Scrophulariaceae, etc.); Sapindales (*Aesculus*, Sapindaceae; *Galipea*, Rutaceae); Myrtales (*Cuphea*, Lythraceae); Zingiberales (Musaceae, Strelitziaceae, Lowiaceae, and Heliconiaceae).

The reduction of adaxial stamens is directly connected with expression of *CYC*-like genes. In mutants

cyc dich of a snapdragon, all five stamens are fertile (Luo et al., 1999). In *Saintpaulia* (Gesneriaceae), there are ornamental cultivated forms with either "dorsalized" (all stamens are adaxial-like) or "ventralized" (all stamens are abaxial-like) corolla. Both anomalies are associated with shift in expression level and/or pattern of two *CYC*-orthologs (Hsu et al., 2018). Normally, three adaxial stamens are underdeveloped and staminodial. In "ventralized" flowers, all stamens develop fully (although the adaxial one is slightly smaller), while in "dorsalized" flowers all stamens are replaced with staminodia. Hence, the adaxial developmental program of perianth (usually *CYC*-mediated) defines the degree of developmental fullness,[1] as well as other "special properties" of the adaxial stamen(s), such as fusion with the adjacent stamens, see below.

2. The complete or partial reduction of one staminal whorl. The androecium composed of two pentamerous whorls is symplesiomorphic for the whole order Fabales. Different groups of legumes exhibit underdevelopment of one staminal whorl or its complete absence. Typically, the inner whorl undergoes changes, e.g., transforms into staminodia in such unrelated genera as *Astragalus* (*A. epiglottis* and *A. pelecinus*), *Staminodianthus* (Papilionoideae), *Tetrapterocarpon*, *Pentaclethra* (Caesalpinoideae). In the caesalpinioid genus *Dimorphandra*, staminodia originate from stamens of the outer whorl, which is rather less common case (De Barros et al., 2017). The inner staminal whorl becomes staminodial in some representatives of family Surianaceae (*Cadellia*, *Suriana*), also included into the order Fabales.

In different subfamilies there are genera with the inner whorl of stamens ablasted, if judged by the fact that only antesepalous stamens persist. In some species of *Bauhinia* (*B. variegata*—Cercidoideae), a single (outer) androecial whorl is associated with a double perianth. Tucker (2000) suggested, that in flowers of *Saraca* (Detarioideae) petals convert into stamens, while attractive anthocyanin-colored sepals are petal-like. Stamens do not develop in the adaxial flower domain. In accordance with this hypothesis, flowers of *S. declinata* have no stamens in the same positions as in other leguminous flowers.

The petaloid morphology of sepals is infrequent in legumes, occurring in different evolutionary lineages and not always associated with loss of other floral organs. The inner surface of sepals is pigmented in the same way as petals in *Delonix* (Caesalpinioideae), although this plant has a full set of floral organs. The petaloid sepals associate with small petals in *Duparquetia* (Duparquetioideae).

The simultaneous loss of petals and part of stamens (often antepetalous) is found in different angiosperm families. Among legumes, genera *Ceratonia*, *Saraca* and possibly some others may serve as an example, but the aforementioned cases evidence that reduction of stamens may occur independently from petals, i.e., these two reduction patterns are separable. Similarly, petals and the outer whorl stamens are absent in flowers of *Seetzenia* (Zygophyllaceae), although in this family stamens may be reduced in flowers with a double perianth (*Tribulopsis*, *Kallstroemia*). The example of *Lepidium* (Brassicaceae) is well-known, demonstrating a wide homoplastic range of reduction processes in corolla and/or androecium (Bowman et al., 1999). Genetic control of development of stamens and petals shares many similar features, and experimentally they may be both suppressed simultaneously (e.g., Yun et al., 2002).

Some of Leguminosae (primarily subfamilies Caesalpinoideae and Cercidoideae) associate the two listed patterns of the androecial reduction. This may explain number and position of stamens in flowers of these exotic plants. Only three abaxial stamens of outer whorl develop fully in many species of *Cheniella* (=*Phanera* s.l.—Cercidoideae), while other seven give rise to staminodia. Five of them produce the adaxial fleshy colored disk, hypothetically serving to attract insect pollinators (Clark et al., 2017). Only the median abaxial stamen of the outer whorl develops in *Bauhinia monandra* (Cercidoideae), the other nine being staminodial. The whole genus *Bauhinia* s.l. exhibits almost all possible ways of the androecial reduction.

In the unusual flowers of plants of subfamily Dialioideae, the ablast of inner staminal whorl (found not in all genera) is associated with the underdevelopment (abort) of outer whorl stamens, either from adaxial (*Petalostylis*) or, rarely, from abaxial side (*Dialium*). Similarly, all stamens of the inner whorl and the median abaxial stamen of the outer whorl are ablasted in *Duparquetia* (Duparquetioideae; Prenner and Klitgaard, 2008). Only two adaxial stamens are fully developed in *Sindora* (Detarioideae).

The complete ablast of all stamens seemingly does not exist in legumes. In functionally female flowers (e.g., *Ceratonia*), stamens are always initiated, but their further development is arrested. All stamens are converted into petaloid staminodia in the sterile flowers of *Neptunia* (Tucker, 1988).

Hence, the most common reduction pattern is suppression or retardation of development of the adaxial stamens, which we connect with the activity of *CYC*-like genes. The exceptions, when the abaxial stamens are transformed, are rare. Generally, the observed variation is connected with certain terminological ambiguity. Both "underdevelopment" and "transformation" can be interpreted widely, thus suggesting variable mechanisms underlying such phenomena. The reduction processes in the leguminous androecium exhibit a high level of homoplasy.

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[1] Interestingly, the adaxial stamen of inner whorl is reduced most often in Leguminosae, while the opposed adaxial petal is reduced least often.

Flowers of some legumes are remarkable with their polyandry. In this respect, some of genera of Caesalpinioideae are best known, formerly placed in a separate subfamily Mimosoideae (*Acacia*, *Inga*), as well as members of Detarioideae (*Colophospermum*, *Maniltoa*, *Polystemonanthus*) and Papilionoideae (*Swartzia*, *Bocoa*, *Cordyla*). Not all of these plants are fully characterized with a special reference to their ontogeny, but the available data suggest the existence of different mechanisms of the androecial polymerization in legumes. In *Acacia*, the so-called complex acropetal polyandry takes place, see (Remizowa, 2019) for terms. The whole androecium originates from a ring meristem, and the first discernible primordia of individual stamens are opposed to sepals (Gómez-Acevedo et al., 2007; Prenner, 2011). In the course of acropetal formation of staminal primordia, any visible regularity in their arrangement is lost. Probably, the regular alternation of sepals and first stamens is connected with a geometry of ring meristem, as it acquires tetra- or pentagonal shape due to a physical pressure from primordia of petals.

The initiation of androecium from a ring meristem was described in *Swartzia* (Tucker, 2003a). However, in the monosymmetric flowers of this genus stamens are typically dimorphic, rarely monomorphic (*S. auriculata*) or even trimorphic (*S. trimorphica*). In the abaxial part of ring meristem, the primordia of several large stamens become visible early. The rest of ring meristem gives rise to primordia of smaller stamens, and this process begins from the abaxial side and spreads basipetally (Tucker, 2003a).

Cordyla, which was formerly supposed to be related to *Swartzia* (see (Cardoso et al., 2015) for discussion of its contemporary taxonomic placement), exhibits a distinct developmental pattern in the polymerous androecium. Staminal primordia emerge in acropetal order (i.e., morphologically downwards) on growing hypanthium, which is absent in *Swartzia*. They have unequal sizes and seem regularly alternating, at least on early stages (Sinjushin, 2018). While all small stamens in *Swartzia* are identical even on primordial stages, the inner stamens in *Cordyla* often lack anthers. It served as reason to separate Malagasy species of *Cordyla* in genus *Dupuya* (Kirkbride, 2005), although presence of staminodia is not unique for the Malagasy forms.

Development of the polymerous androecium was also described in *Colophospermum* from subfamily Detarioideae (Krüger et al., 1999). Stamens seem to initiate on the ring meristem in acropetal order. All primordia are of equal sizes and have no clear regularity in their arrangement.

The existing observations suggest that polyandry emerged in distinct lineages of Leguminosae independently and via different mechanisms. None of studied leguminous species exhibited the inception of the polymerous androecium as several common primordia, regularly alternating with perianth members, as it takes place in many other families (Ronse Decraene and Smets, 1993).

Fusion of stamens is characteristic for genera in several subfamilies of Leguminosae. The review of available literature evidences, that different authors interpreted dissimilar phenomena as fusion and described them not uniformly. Sometimes the existence and type of staminal fusion may be debatable (e.g., Sokoloff, 1995). Patterns of androecial fusion are very variable even within comparatively small groups. Genera of the highly specialized Inverted-Repeat Lacking Clade (IRLC, Papilionoideae) are generally characterized with diadelphous androecium with a free vexillary stamen. However, all stamens are reported to fuse in *Ononis* (tribe Trifolieae), several species of *Astragalus* from different sections (*A. donianus*, *A. himalayanus*, *A. monadelphus*, *A. oxyodon*), and *Galega* (tribe Galegeae s.l.). In addition, some genera of this clade have the so-called pseudomonadelphous androecium, in which the vexillary stamen postgenitally fuses or tightly adjoins the neighboring ones (Tucker, 1989a). Typically, there are fenestrae at the base of this stamen, providing access to nectaries. Such androecium was recorded in different groups and probably evolved independently from the diadelphous type.

On regulatory level, the "special properties" of the vexillary stamen are connected with expression of *CYC*-like genes in the adaxial floral domain. Such expression was found in primordia of adaxial petal and vexillary stamen in *Lotus* (Feng et al., 2006). If mutation or ectopic expression of *CYC*-like genes leads to flag-like differentiation of all petals, stamens become unfused, as it is in *Cadia* or cultivated form of *Clitoria* (Sinjushin et al., 2015). It has been concluded, that the papilionate corolla may associate with all possible forms of staminal fusion, but monosymmetric perianth (at least in Papilionoideae) almost never accompanies somehow fused stamens (Sinjushin et al., 2015). *Etaballia* from tribe Dalbergieae comprises the exception, possibly unique, with its polysymmetric corolla and monadelphous androecium; see above the discussion on possible nature of actinomorphy in this enigmatic genus. Such association is rarely found beyond Papilionoideae, in such genera as *Brownea* and some other members of the "*Brownea* clade" (Detarioideae), as well as in *Inga* ("mimosoid" Caesalpinioideae).

The peculiarities of staminal fusion are connected with pollination strategy and, among other things, with presence and structure of floral nectaries. Representatives of Papilionoideae are described most precisely in this respect. Normally nectaries are found in flowers with free stamens, diadelphous or pseudomonadelphous (if fenestrae are present at the base of vexillary stamen) androecia. In contrast, flowers with monadelphous androecia usually attract pollinators

with pollen and rarely (e.g., *Galega orientalis*) secrete nectar (Bernardello, 2007). Exceptions are known in both cases. Although a basic structural plan of the leguminous floral nectaries is similar, they are quite diverse. Their morphology and position may coordinate with floral symmetry; for example, they are localized in the abaxial part of receptacle in *Pisum* and *Vicia*.

If pollen serves the main attractant, stamens may differentiate, some of them producing pollen for feeding and some for pollination. Differences may be found not only in size of stamens, but also in ultrastructure and physiological features of produced pollen grains (Paulino et al., 2016). In *Lupinus* (Papilionoideae), feeding function is directed to stamens of the inner whorl, while in *Cytisus* (Papilionoideae) the adaxial stamens of both whorls produce pollen for attraction. The diversification of stamens in *Senna* is attributed to the special pollination mode, buzz-pollination (Marazzi et al., 2007).

The stamens may fuse with perianth members. Such morphology is known in different tribes and seemingly arose through different mechanisms. The examples of *Gymnocladus* (Caesalpinioideae), *Trifolium*, *Psoralea*, and *Inocarpus* (Papilionoideae) are well known. The ontogeny of such flowers was precisely dissected in tribe Amorpheae (McMahon and Hufford, 2002). Zonal growth of staminal bases results in production of the so-called stemozone, which unites bases of filaments and petals; this fusion is most probably congenital. In flowers of *Dalea*, this stemozone together with ablast of inner stamens creates an illusion of staminal tube, in which five stamens fuse and alternate with petals. This phenomenon impressed some of morphologists very much, provoking the discussion on homologies between floral parts in *Dalea* and other papilionoids. As a result, it was hypothesized, that monosymmetric flowers of Amorpheae evolved independently from other members of Papilionoideae as a convergence; see (McMahon and Hufford, 2002) for details. Ontogenetic surveys relaxed this problem.

GYNOECIUM

The monomerous gynoecium is considered synapomorphic for Leguminosae among other families of Fabales (Bello et al., 2012). Some of Polygalaceae (*Monnina*, *Pteromonnina*) produce pseudomonomerous gynoecia. In Surianaceae (*Guilfoylia*, *Stylobasium*), the gynoecium is probably truly monomerous, although Endress (2012) suggests that it resulted from reduction.

In several evolutionary lineages of Leguminosae, the polymerous gynoecium was recorded. Cases, when two or more floral meristems fuse producing aberrant multicarpellate structure, have no taxonomic significance and possibly may arise in every group.

Several carpels regularly develop in most of flowers in *Inga* p.p., *Archidendron*, *Acacia celastrifolia* ("mimosoid" Caesalpinioideae), *Swartzia* p.p., *Aldina diplogyne* (basal Papilionoideae), *Thermopsis turcica* (derived Papilionoideae). Flowers with polymerous gynoecium occasionally emerge in *Ceratonia* (Caesalpinioideae), *Cordyla pinnata* (basal Papilionoideae) and some other legumes.

The phylogenetic interpretation of these phenomena has been under discussion for long. For example, Yakovlev (1991, p. 35) suggested, that polymerous gynoecia in legumes comprised "morphological relicts persisting due to heterobatmy in groups having different taxonomic position and evolutionary unequally advanced." The later works agree that the monomerous gynoecium is plesiomorphic in legumes, while the multicarpellate habit arose independently in several evolutionary lineages. For example, Paulino et al. (2014) listed seven events of the gynoecium polymerization. Studies of mutants of model legume species indicate, that superfluous carpels may appear as a result of homeotic transformation of stamens, fusion of several floral meristems or enlargement (fasciation) of a single floral meristem (Sinjushin, 2014; Sinjushin et al., 2019). The latter scenario is the most probable cause of the gynoecium polymerization in Leguminosae. Notably, in most cases the multicarpellate gynoecium develops in polysymmetric flower with unstable merism.

In *Thermopsis turcica*, the trimerous gynoecium associates with typical papilionate corolla. The carpels initiate not simultaneously in this unusual flowers. It is connected with longer proliferation of floral meristem, providing additional space for initiation of carpels, rather than with increase of floral meristem size, as such increase would cause destabilization of flower (Sinjushin et al., 2018). The association of monosymmetry with polymerous gynoecium is characteristic for some species of *Swartzia*. In flowers of *S. dipetala*, two carpels are commonly present, both oriented with their clefts to the adaxial side, where two adaxial petals develop. Such morphology may result from fasciation, i.e., early fusion or incomplete separation of two floral meristems. The most possible explanation is production of a single oblong meristem (Paulino et al., 2013) with sizes allowing to initiate paired organs in every floral node instead of solitary ones.

One may agree with statement, that the polymerous gynoecium is hardly compatible with papilionate corolla ("flag blossom"; Paulino et al., 2014), as instability in organ number and position impairs the orchestration between floral parts, what is especially significant for corolla. That is why the polymerous gynoecium in Leguminosae often comprises a feature of the "instability syndrome" or, in the other words, a comparatively harmless consequence rather than adaptive advantage. Although possessing the trimerous gynoecium, *T. turcica* does not produce more

seeds that other species of the same genus with mono-carpellate flowers (Sinjushin et al., 2018). Only ca. 10% of all flowers produce dimerous fruits in *S. dipetala* (Paulino et al., 2013). The dimerous fruits were never recorded in *Cordyla*, while this plant regularly develops the dimerous gynoecia (Sinjushin, 2018).

Most likely, all cases of gynoecium polymerization in Leguminosae comprise the results of evolutionary recent mutations, which destabilize size of floral meristem and/or prolong its proliferation. Numerous mutations with such effect are known in *Arabidopsis* (Choob and Sinyushin, 2012). It should be noted, that there are no leguminous genera (at least, not monotypic), in which all species possess the polymerous gynoecium.

The discussion of position (terminal or lateral) of a single carpel in Leguminosae is a subject with deep history, see (Derstine and Tucker, 1991) for review. The prevailing opinion is that this carpel is true terminal derivative of floral meristem. Hence, the emergence of the polymerous gynoecium is interpreted as a transition from "closed" to "open" system, i.e., very significant transformation of floral meristem (Paulino et al., 2014).

In our opinion, a single carpel is a lateral structure with respect to floral apex. The structure having abaxial and adaxial surfaces cannot emerge in terminal position, while there are legumes with truly terminal bisexual flower in racemose (*Gleditsia*, *Gymnocladus*) and probably cymose (*Apuleia*—Dialioideae[2]) inflorescences. Changes in merism of gynoecium can be explained from the positions of floral organotaxis, i.e., anthotaxis (Sinjushin, 2015). There are two partially independent parameters, size of floral meristem and longevity of its proliferation. Increase of meristem size lets initiation of additional carpels in the same node as the first one (possibly the case of *Swartzia*), or even produce a whorl of carpels (*Inga*). Longer proliferation allows to initiate additional carpels in different nodes, i.e., in a sequential pattern (*Thermopsis turcica*). Combination of both alterations causes production of more than one carpel whorl (*Inga*, *Acacia celastrifolia*). In fasciated mutants of legumes (see above) and *Arabidopsis* (Clark et al., 1995), all listed variants can be observed. It means that switches between mono- and polymerous gynoecium comprise quantitative variations and can occur easily from regulatory point of view, as well as all meristic changes.

Solitary (or first in polymerous gynoecium with nonsimultaneous initiation of elements) carpel is oriented with its cleft to adaxial side in most cases. All known exceptions are connected with polysymmetric flowers (*Ceratonia*, *Gleditsia*, *Acacia*). Possibly, the abaxial-adaxial polarity of floral meristem defines the orientation of carpel, and even accessory carpels are partly turned to flag with their clefts in monosymmetric flowers of *Thermopsis turcica* (Sinjushin et al., 2018). However, carpel is "properly" oriented in majority of polysymmetric flowers in *Gleditsia* (Tucker, 1991). Nature of mechanisms determining carpel orientation in monomerous gynoecium is of interest on a scale of angiosperms, and possibly there is no universal solution. For example, a single carpel is oriented uniformly in polysymmetric "chaotic" flowers of *Achlys* (Berberidaceae; Endress, 1989), while in monosymmetric flowers of *Consolida* (Ranunculaceae) a single carpel has a variable orientation (original unpublished data). In *Posidonia* (Posidoniaceae), a single carpel is regularly turned with its cleft to abaxial side (Remizowa et al., 2012).

OTHER PECULIARITIES OF FLOWERS IN LEGUMINOSAE

Two parameters were suggested to describe flowers with whorled arrangement of organs, viz., merism (number of organs per whorl) and completeness (number of whorls) (Choob, 2010). This concept can be applied to the leguminous flowers, although with some limitations, primarily connected with a mono-symmetry.

Although the ancestral leguminous flower is pentamerous, some groups exhibit changes in floral merism. Such shifts characterize clades with polysymmetric flowers regardless of their taxonomic position. The trimerous flowers were recorded in some "mimosoid" Caesalpinioideae (*Mimosa ceratonia* and some other species of *Mimosa*, *Sanjappa*) and Dialioideae (*Apuleia*). The tetramerous flowers are common in *M. pudica* ("mimosoid" Caesalpinioideae), *Tetrapterocarpon* (Caesalpinioideae). Floral merism has a certain taxonomic significance in *Mimosa* (Simon et al., 2011). Flowers of some *Mimosa* can be listed among the "minimum" ones in legumes, as low merism associates with reduction of one staminal whorl. Oppositely, the atypically high merism is also possible. For example, corolla in *Aldina diplogyne* (basal Papilionoideae) and both perianth whorls in *Englerodendron usambarense* (Detarioideae) are hexamerous.

In addition to a wider range of merism, polysymmetric leguminous flowers are remarkable with lower stability, as compared with monosymmetric ones. Floral merism is variable in *Inga* ("mimosoid" Caesalpinioideae; Paulino et al., 2017), *Gleditsia* (Tucker, 1991), *Ceratonia* (Tucker, 1992). The comparative survey of floral stability in Leguminosae with different flower structures led to conclusion, that polysymmetric flowers are more variable than monosymmetric (Sinjushin and Karasyova, 2017). Fluctuations in number of floral organs are found between individual organisms of the same species or even within a single

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[2] The inflorescences of *Apuleia* are interpreted as cymose (Falcão et al., 2020), but their terminal flowers have clearly zygomorphic position of stamens, thus casting doubts on the existing interpretation. Terminal flowers in *Ceratonia* most probably emerge via fusion of several meristems of uppermost lateral flowers (Tucker, 1992).

organism, hence reflecting an overall morphogenetic stability rather than genetic variation.

The adaxial parts of perianth are the least prone to spontaneous fluctuations (Sinjushin and Karasyova, 2017; Sinjushin et al., 2019). It is in fine agreement with fact, that symmetry-defining *CYC*-like genes promote differentiation and hence suppress cell proliferation. These genes inhibit expression of some factors responsible for cell cycle, such as cyclins (Martín-Trillo and Cubas, 2010). Notably, mutations in *CYC*-like genes lead to increased floral merism (Luo et al., 1999; Hsu et al., 2015). Superfluous organs initiate in flowers of *cyc*-like mutants of pea (Wang et al., 2008).

As a result of studies on *Arabidopsis*, a complicated system of negative regulation of floral and apical meristem sizes was dissected, see (Choob and Sinyushin, 2012) for review. A set of genes, with groups *CLAVATA* and *FASCIATA* being the best known, inhibit proliferation of meristematic cells. Mutations in these and some other genes despair this inhibition, thus causing fasciation, i.e., anomalous meristem enlargement. In flower it leads to initiation of supernumerary organs and inevitable loss of stability. However, in most of known legumes sizes of apical and floral meristems are controlled independently, so flowers of fasciated legume mutants are normal (Sinjushin, 2016). One of known exceptions is *Lupinus angustifolius*. Fasciated mutants of lupine produce flowers with increased number of organs in all whorls, but the adaxial part of corolla, the presumable site of expression of *CYC*-like genes, is more stable than the others (Sinjushin et al., 2019). It means that Leguminosae, as possibly many taxa with monosymmetric flower, possess two independent systems of regulation of floral meristem sizes, as monosymmetry assumes floral development more resistant to fluctuations.

Many ontogenetic phenomena in the leguminous flowers can be explained in the light of concept of blastozones. Initially this term was introduced to define stem regions competent to organogenesis (Hagemann and Gleissberg, 1996). As an additional meaning, blastozone describes meristem, which is patterned as unity but capable of secondary morphogenesis (Choob and Sinyushin, 2012). In a given sense, common petal-stamen primordia in *Pisum* (see below; Tucker, 1989b) can be interpreted as blastozones.

If meristem of monosymmetric flower enlarges, some of blastozones may expand correspondingly, allowing to initiate more organs within them. As a result, regular alternation of organs in whorls is lost. In fasciated flowers of *Lupinus*, paired stamens may emerge instead of solitary ones, and these pairs in one whorl alternate with single or twin stamens of the other whorl (Sinjushin et al., 2019). Similar morphology, although untypical for legumes, is found in very unstable flowers of *Mendoravia* (Dialioideae) (Zimmerman et al., 2013). Two adaxial petals in *Swartzia dipetala*

seemingly emerge from a joint blastozone, as well as two carpels in flowers of the same species.

The idea of changes in floral "completeness" was based mostly on material of polysymmetric flowers (Choob, 2010) and can be applied to polysymmetric flowers of Leguminosae. The most expressed "depletion" of flower results from reduction of petals and one staminal whorl (*Ceratonia*). It is the case of ablast rather than of "deletion" of whorls, see (Choob, 2010) for definitions. Otherwise, stamens of the single whorl in flower of *Ceratonia* would regularly alternate with sepals, which is not recorded. In case of stochastic fluctuations in structure of leguminous flowers, merism of opposed whorls (such as corolla and outer stamens) often correlates more strongly, than one of alternating, even adjacent, whorls (Sinjushin and Karasyova, 2017). In some of specialized Papilionoideae (e.g., *Astragalus*), each petal and opposed stamen emerge from a common primordium (Movafeghi et al., 2011).

A certain importance is attributed to the order of initiation of floral organs in Leguminosae. Generally, leguminous flowers are characterized with acropetal development. The abaxial structures typically initiate first and develop with some acceleration, while opposite cases are uncommon (Tucker, 2003b). Sepals and, rarely, petals may initiate in a spiral order, which is interpreted as primitive feature (Tucker, 1984). Whorled initiation of organs with slight delay in the adaxial domain is supposed as advanced character. A general tendency towards acceleration of development is hypothesized, when organs of different whorls emerge synchronously, e.g., carpel appears together with the outer stamens and even petals (Tucker, 1984; Prenner and Klitgaard, 2008). This trend finds its logical conclusion in *Pisum* and some other members of the IRLC having the so-called common floral primordia (Tucker, 1989b). After initiation of sepals, carpel emerges together with four common primordia, each giving rise to corolla and stamens.

Although different patterns of floral organ initiation in Leguminosae may be classified as archaic or derived, natural selection affects primarily the resulting morphology of mature flower. On this level, one may postulate the equifinality, as similar floral structure is achieved regardless of the order of floral primordia emergence. The contemporary ideas about evolution of initiation order of floral primordia agree, that switch between distinct patterns occurred easily and resulted in high level of homoplasy (Remizowa, 2019). There are observations that this order may be irregular even within a single organism. It is not only the case of taxa with "chaotic" floral morphogenesis, such as *Gleditsia* and *Ceratonia* (Tucker, 1991, 1992), but also of "orthodox" flowers of *Astragalus* (Naghiloo et al., 2012). Variation in the order of calyx initiation in *A. compactus* is presumably mediated by physical pressure from subtending leaf of the inflores-

cence. Hence, the spatiotemporal pattern of primordia initiation is not definitive for structure and function of mature flower.

CONCLUSIONS

Studies of floral ontogeny in Leguminosae possibly comprises one the most convincing successes of plant evo-devo. Progress in systematics of family associates with detailed investigations of morphology and morphogenesis. On the one hand, the most informative "key taxa" are in scope; on the other hand, studies on model species bring results in developmental genetics. This approach enables to conclude unambiguously, whether a certain state is ancestral or derived. In many cases, one may confidently postulate the molecular mechanisms of transformations.

Legumes exemplify a kind of "inversion" in methodology of evolutionary biology. For centuries, morphology has been underlaying for systematics. At the same time, the impossibility to range morphological features with respect to their significance remained the persisting problem. Homoplasy has been interfering with evolutionary reconstructions, and only recent decades uncovered how pronounced it may be. Phylogenetics together with phylogenomics provide tools to definitively reconstruct the course of taxon evolution and distinguish ancestral characters from derived. One of the most striking examples of such "inversion" is connected with investigations of subfamily Dialioideae. Very significant, achieved through contemporary genomics and fitting in the single paper (Ojeda et al., 2019) breakthrough in systematics of this unusual group provided possibilities to reconstruct its floral evolution and suggested it as a model taxon in evolutionary biology of legumes.

In recent decades, the high degree of equifinality of floral ontogeny of Leguminosae became evident, contrasting with variability of intermediate stages. Typical papilionoid corolla, the object and the result of natural selection, can be produced through different sequences of organ initiation.

Studies on leguminous flowers uncovered a strikingly high level of homoplasy, which has been interfering with construction of the uncontroversial system of the family for long. For example, the contemporary level of development of leguministics gives no support to idea that polysymmetric flower is uniform phenomenon across the whole family and can be interpreted as either undoubtedly ancestral or undoubtedly derived state. The convergent evolution resulted in repeated emergence of such features, as polysymmetry, joint calyx without separate sepals, polymerous or reduced androecium, polymerous gynoecium.

The monosymmetric pentamerous and pentacyclic flower are clearly symplesiomorphic features for Leguminosae. The monosymmetry is possibly governed by the same mechanism in the whole family and associates with additional stabilization of floral structure. However, in distinct groups different regulatory shifts produce polysymmetry, and a similar set of apomorphies often emerges, including variable pattern of organ initiation, unstable position of median sepal and carpel cleft, irregular merism in different whorls, polymerous androecium and gynoecium. These features in legumes compose a certain "instability syndrome," which is not less fitted than initial monosymmetric and stabilized floral structure.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The author declares that he has no conflict of interests.

Statement on the welfare of humans or animals. This article does not contain any studies involving animals performed by the author.

ADDITIONAL INFORMATION

The article is translated by the author.

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