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Diversity and Evolution of Inflorescences in *Celastrales*

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Abstract: Inflorescences structures in context of their evolution have been conducted for 60 genera and 170 species of *Celastrales* (according to APG (Angiosperm Phylogeny Group) III 2009, almost 60% of genera and 15% of species from this taxon of the world flora). There are two big groups of inflorescences in *Celastrales*-intercalary (more often) and terminal. For many genera of *Celastrales* both types of inflorescences can be observed, although the frequency of their occurrence varies. There is an important difference between two types of inflorescences: character of completion of the main axis (the terminal flower present or absent). Flower opening can be in basipetal (*Celastraceae*, *Brexia*) or acropetal (*Stackhousiaceae*) order. Partial inflorescence types included: simple, compound or umbrellate dichasia, spike, raceme, thyrse. Simple flowers of *Parnassia* are large, nested on long reproductive shoots, emerging from a rosette, with amplexicaule leaf.

Key words: *Celastrales*, *Celastraceae*, *Brexia*, *Parnassia*, *Stackhousiaceae*, inflorescences, structure and development of inflorescences, molecular data.

1. Introduction

In recent times the taxonomic relationship of *Celastrales* was revised in regards to molecular data [1-5]. Together with *Celastraceae* s.str., the genera *Parnassia* and *Brexia* and the family *Stackhousiaceae* were also included in *Celastrales*. Moreover, at the moment these taxa nested in limit of *Celastraceae* s.l.

Many authors paid a lot of attention to features of inflorescence structure in *Celastrales* for species diagnostics and taxonomy (for example [6, 7]). Indeed, many books indicated that small actinomorphic bisexual or unisexual flowers (sometimes dioecious or polygamous) of *Celastrales* were segregated in inflorescences, which were different in structure and located on shoots of the current year in terminal or axillary position. However, the special study of inflorescences diversity and evolution in the *Celastrales* is not conducted.

Following the terminology of Troll [8] and Weberling [9], the inflorescence of *Celastrales* is termed a monotelic synflorescence (rarely polytelic). As per Kuznetsova [10] and according to the typological approach of Troll, under inflorescence (synflorescence) here a system of flowering shoots of Magnoliophyta formed, as a rule, within a single season sylleptically, is accepted. It consists of many structural subunits similar to each other-terminal floral unit (FU) and paracladia (P). Therefore, it appears necessary to conduct the analysis of the full system of flowering branches of the current shoot. Inflorescences are classified after the presence/absence of a terminal flower and the nature of their lateral subunits.

Thus, a study of inflorescence structure in the *Celastrales* encompasses the range of structural variations and rhythmological characters found in the order. This paper is part of a study of structure and development of the taxon. The goal of the study is to determine evolutionary trends in the inflorescence of the order in context of molecular phylogenetic data.

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2. Materials and Methods

Inflorescences and flowers of some studied *Celastrales* were collected from living plants in Main Botanic Garden of Russian Academy of Science (Moscow, Russia), Komarov's Botanical Institute (St.-Petersburg, Russia) and in nature (Center of European Russia; the Crimea; the Caucasus; Russian Far East; the White Sea coast in Karelia, Russia; Baikal Region, Russia; Southeastern Asia). Plant material (vegetative and generative shoots) was fixed and stored in 70% ethanol or was conserved in dry view (as herbarium). For other species of *Celastrales*, herbarium material (from LE, MW, MHA, KW, W, K, E, P) was studied. Inflorescences structure and development research have been conducted for 60 genera and 170 species of the *Celastrales* (according to APG III 2009: almost 60% of genera and 15% of species of this taxon in the world flora) using typological approach by Troll [8] with supplements by Weberling [9], pseudocyclic concept [11] and architectural analysis [12]. According to Kuznetsova [13], these approaches (including physiognomic one) may be considered complementary to each other. The following characters should be taken into consideration:

(1). Structure of lateral flower shoots (branches):

(a). Length of the main axis;

(b). Length of lateral axes;

(c). Presence/absence of a terminal flower;

(d). Order of flowering;

(e). Peculiarities of bract structure.

(2). Position of lateral flower branches on the current shoot;

(3). Size of the current shoot and its role in the construction of the plant's perennial axial system;

(4). Extent, to which the axis of the current shoot dies off after fruiting;

(5). Type of axis termination of the current shoot.

The traditional methods of the morphological studies, with using of the binocular stereomicroscope, were used in the present work. Many graphic Figures were done for all studied species. Photographs were made using digital cameras Sony Cyber-Shot DSC W-1 and Sony Cyber-Shot DSC H-7.

3. Results and Analysis

3.1 Structure and Developmental Rhythms of Shoot Systems

The following types of shoot systems were identified (Fig. 1): (1) Polycarpic polycyclic shoot system with monopodial or acrosympodial growth and intercalary or pseudoterminal inflorescences; in terms of shoot position, here the following types can be distinguished: (a) orthotropous, (b) plagiotropous and (c) mixed shoots; as per the rhythm of development, there were sylleptic and proleptic shoots. (2) Monocarpic mono- and bicyclic, terminal inflorescences (evergreen species of the *Celastrus*). (3) Monocarpic monocyclic-once flowering, with sympodial growth and terminal inflorescences; they may be elongated or shortened (*Tripterygium*, *Mortonia*, some species of *Celastrus*).

3.2 Flower Position and Sequence of Flowering

There are two big groups of inflorescences in the family Celastraceae s.str.-intercalary (more often) and terminal (Fig. 2, 10-12).

For many genera of *Celastraceae*, both types of inflorescences can be observed, although the frequency of their occurrence varies. There is an important difference between two types of inflorescences: character of termination of the main axis (whether the terminal flower is present or absent). For some *Celastraceae* (for example, *Bhesa*), there is also a pseudoterminal flower position. It is intermediate between terminal and axillary (intercalary) flower position. Flowering occurs basipetally. In the genus *Brexia* few-flowered physiognomically dichasial (simple, umbellate, or compound) or reduced thyrsoid bracteous/ebracteous inflorescences are formed, nested in axils of regular green foliage leaves in the upper part of current shoots

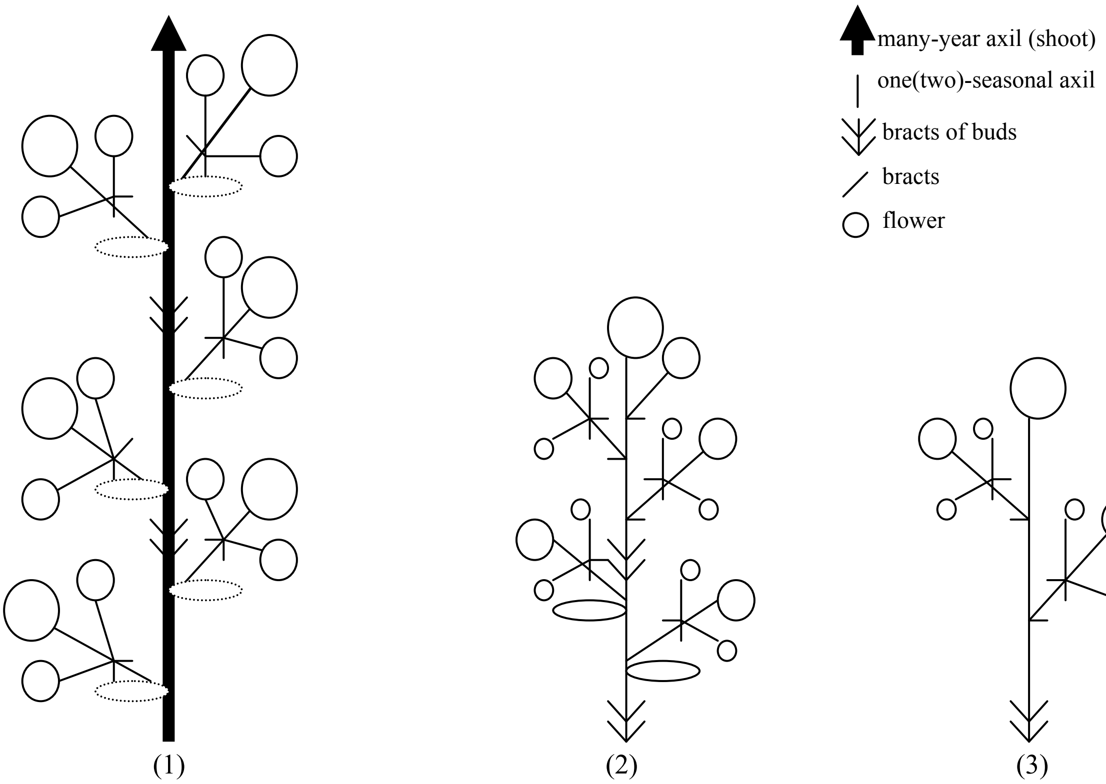

Fig. 1 Structure and rhythm of development of shoot systems in *Celastrales*: 1-polycarpic polycyclic; 2-monocarpic mono- and bicyclic; 3-monocarpic monocyclic.

(Fig. 3). Simple flowers of *Parnassia* are large, nested on long reproductive shoots, emerging from a rosette, with amplexicaule leaf (Fig. 4). Signs of inflorescence reduction are absent, however, this particular way of the plant's reproductive sphere formation is the most likely to occur. In *Lepidobotrys staudtii* Engl. (*Lepidobotryaceae*), inflorescences are specific axillary (intercalary), few-flowered (more often one-flowered), forming on brachyblasts. Each flower has a small bract at the base. Many-flowered inflorescences of *Stackhousia* species are nested on the top of reproductive shoots; there are bracteous racemes or thyrses with gradual transition from usual leafy shoot to bracteous inflorescences. Flowers have long corolla tubes, and sit on very short peduncles (almost sessile). In axils of bracts simple dichasia (*S. viminea*), or solitary flowers (*S. monogina*), with acropetal flowering order, are placed.

3.3 Monopodial or Sympodial Growth of Axes

There are cymose (more often) and racemose types of inflorescences in *Celastrales*. There are also compound inflorescences in *Celastrales*, intermediate between cymose and racemose types. Their lateral axes are branching strongly (for example, closed thyrse with a terminal flower on the main axi-panicle-like thyrse, Fig. 2, 9)

3.4 Types of Partial Inflorescences

Partial inflorescences types included (Fig. 2, 1-9): simple, compound or umbrellate dichasia (Figs. 5a, 5b), spike, raceme, thyrse. Typical and more often meeting of partial inflorescences in *Celastrales* are simple or multi-circled (compound) dichasia. Reduction of inflorescences to single flowers is known in some genera of *Celastraceae* (e.g., *Psammomoya*).

4. Discussion

The most recent studies on the inflorescence of the *Celastrales*/*Celastraceae* are those of Ding Hou [14], Brizicky [15] and Simmons [1]. In these works, it is

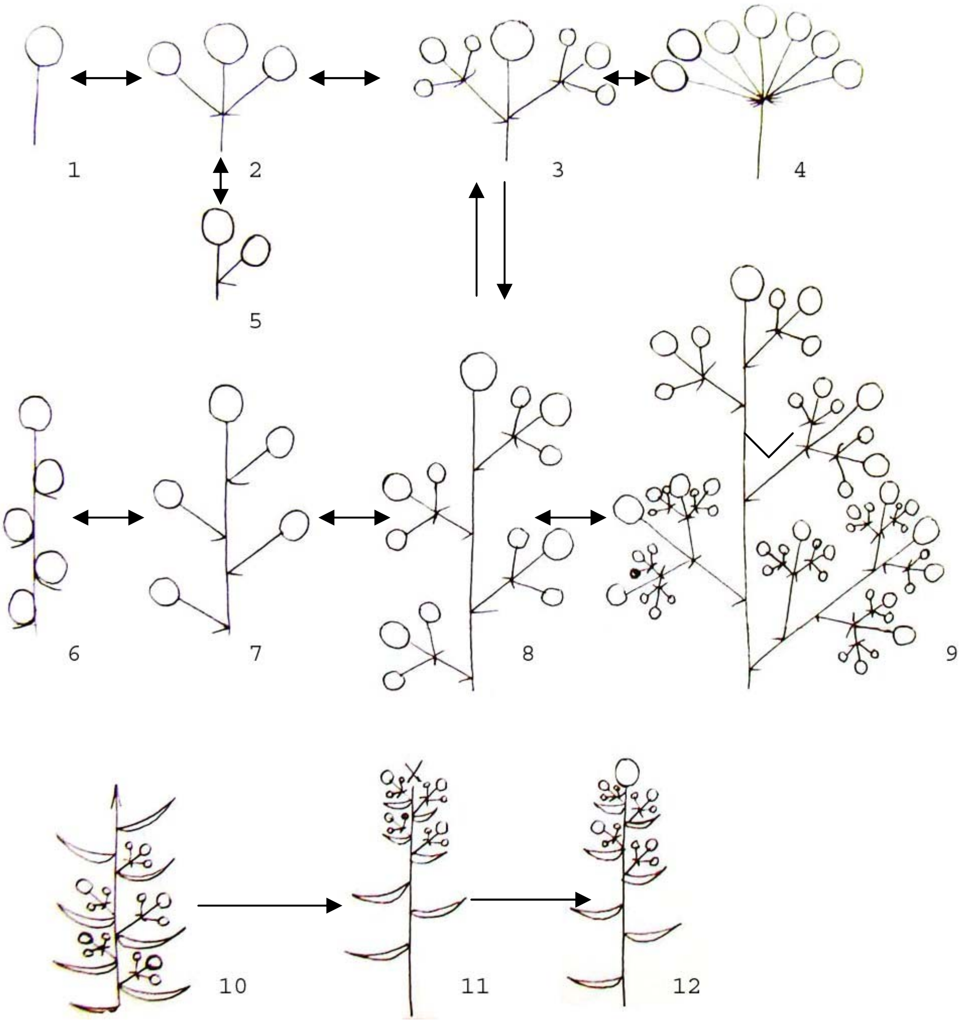

Fig. 2 Main inflorescences types in the *Celastrales* and possible trends of their evolution: 1-single flower; 2-simple dichasia; 3-many-circled (compound) dichasia; 4-umbrellate dichasia; 5-monochasia; 6-spike; 7-raceme; 8-thyrse; 9-panicle-like thyrse; 10-intercalary inflorescence; 11-pseudoterminal inflorescence; 12-terminal inflorescence.

noted that inflorescences of *Celastrales*/*Celastraceae* are usually bracteate, axillary and/or terminal, sometimes extra-axillary, or ramiferous, cymose, thyrsoid, panuculate, racemose, fasciculate, sometimes 1-flowered or in spikes. Most previous work was carried out by investigators who tended to oversimplify in their attempts to supply concise descriptions [6-7]. None of these authors studied the structure or development of the *Celastrales* inflorescences in typological and rhythmological aspects.

As a result, the conducted study indicated that inflorescences in the order *Celastrales*, by their position on current shoots, can be divided into two big group-intercalary and terminal, moreover, in most of studied representatives the first type is common. At the same time, in many genera of *Celastrales* one may observe both types of flower position, although the frequency of their occurrence is different. Such re-occurrence of characters from different species of the genus permits us to construct morphological series, in which extreme variations-terminal and intercalary inflorescences-are connected via intermediate forms. It is a necessary condition for homology identification of plants. In such cases, it is necessary to describe all structural and rhythmological peculiarities of flowering

Fig. 3 Inflorescence and flower of the *Brexia madagascariensis* Thouars ex Ker Gawl. (photo by Ivan Savinov, Greenhouse of Komarov's Botanical Institute, St.-Petersburg, Russia).

Fig. 4 Flowers of the *Parnassia palustris* L. (photo by Ivan Savinov, Baikalsky Biosphere Reserve, Baikal Region, Russia).

and vegetative elements. It is important to underline that there are qualitative differences between species of such genera, the main one of them- the peculiarity of termination of the flowering shoot axis (terminal flower is present or absent). There are terminal flowering shoots in the genera *Celastrus* (Ser. Paniculati), *Tripterygium*, *Bhesa* (*B. paniculata*, *B. ceylanica*) and *Mortonia*. For the majority of studied species, axillary branches appeared to be attached in lower or middle parts of current shoots. As the size of flowering shoots decreases in many representatives (including *Euonymus*), a trend to transfer the zone of axillary branches to the top of the flowering shoot is observed. Flowering shoots of some *Celastrales* were developing during two seasons, having a different degree of specialization, etc..

(a)

(b)

Fig. 5 Flowers of some *Celastraceae:* (a) *Euonymus* × *miniata* Tolm. (Arboretum of Komarov's Botanical Institute, St.-Petersburg, Russia); (b) *E. sieboldiana* Blume (Arboretum of Main Botanical Garden, Moscow, Russia) (photos by Ivan Savinov).

As we know, inflorescence diversity is characterized primarily by different ramification patterns [16]. There are two basic contrasting extreme ramification patterns, namely racemose and cymose (the latter including dichasial and monochasial). Axillary branches for the majority species of *Celastrales* are cymose inflorescences-simple or multi-circled dichasia. The number of flowers in dichasia may be reduced to one. With shortening of internodes in dichasia umbrellate dichasia may be formed, and if at the same time pedicles are shortened, close groupings (clusters) of flowers are formed, which are described as "bunches". Some axiliary flower branches form is presented by closed raceme, thyrse or panicle. Such axillary groupings are formed apparently out of cymes due to the emergence of additional flower branches. Thyrses are combined racemose/cymose inflorescences; between the two extremes, racemose and cymose, there is a third ramification pattern, exhibited by panicles, which are less common than the other patterns [16].

One more important feature in *Celastrales* is serial complexes, formed in vegetative and reproductive spheres. Serial shoots differ not only in their sizes, but structurally and functionally. Not so rarely does it happen, vegetative shoot and axillary flower branch are somewhat more complex, moreover such shoot may be positioned higher or lower on a flower branch. Vegetative shoot can be turned into a thorn very often. Axillary branches may appear on the thorn (many species of *Maytenus*, *Gymnosporia*). Serial complex may consist of two vegetative shoots. Both higher and lower shoots may be bigger and more robust. In the subgenus *Kalonymus* (*Euonymus*) supplement serial flower axes are formed in multi-circled dichasia. Moreover, shoots of serial complex are often different by the rhythm of their development, namely the ones formed sylleptically, others proleptically or cataleptically. So, in *Celastrus* the serial complex is often formed, consisting of vegetative buds, under which an axillary flower branch is developed sylleptically. Sometimes a serial complex of unusual structure (*Catha heyneana*, *Maytenus senegalensis*) can be found: in the axil of a normal leaf developing a robust thorn, above which a bud would be located, and on thorn itself there would be leaves with axillary brachyblasts, carrying inflorescences.

Within *Celastraceae*, two general ways of flowering shoots rebuilding can be distinguished [17]: (1) Axillary cymose groupings can transform into thyrsoids or racemose inflorescences; a reverse transition is possible; (2) Transition from intercalary inflorescences to terminal ones with following termination of the main axis by a terminal flower. Such models of flowering shoots rebuilding was suggested by Parkin [18]. Transitions between opened and closed types of inflorescences can be stipulated by different changes in net of genetic regulation inflorescence development [19] and more than one ontogenetic pathway [20]. Analysis of inflorescence diversity in a molecular phylogenetic context (according to Ref. [21]) suggests that intercalary inflorescences represent a plesiomorphic condition in *Celastrales*. Terminal inflorescences have repeated origins in some lineages of the *Celastrales*.

It is very interesting that within the entire *Celastraceae* family, and also in separate genera and species, the characters listed above are combined independently of combinations of any kind, and quantitative and qualitative parameters of inflorescences are varied significantly (Kuznetsova emphasized their equivalency and a necessity to conduct analysis by a combined method). That has provided the diversity of inflorescence structure. When we are analyzing all material in presence we can notice that the degree of variability is subject to definite regularities, which can be reflected in the form of comparative morphological series. So, in dichasial inflorescences (cymes) the following traits are changed: the number of flowers (solitary flowers, simple, multi-circled (compound) and umbrellate dichasia, monochasia) and the character of axes branching as regards to profils angles, in thyrsoids-degree of branching of lateral axes (the presence of axes of the second, third and higher numbers of branching order: spike ↔ raceme ↔

simple thyrse ↔ paniculate thyrse). Apparently, polymerization and reduction processes in inflorescences are widely distributed among the representatives of *Celastraceae* (Fig. 2, 1-9). Inflorescences in the family have axillary intercalary position on the shoot system, or pseudoterminal, or terminal (moreover, the degree of bracts specialization is varied markedly!). The family *Celastraceae* is characterized by monotelic synflorescences (rarely-polytelic), FU is presented by solitary flower, simple dichasia or thyrse, paracladia are not numerous. An additional aspect of *Celastraceae* inflorescences structural diversity is the sexual differentiation of flowers in an inflorescence (dioecia and gynodioecia in some genera, e.g., *Euonymus*, *Maytenus*) and sexual types of inflorescences themselves (for example, dioecious plants from the genus: *Celastrus* have male individuals with terminal inflorescences, and female ones-with intercalary). One more character of inflorescences diversity in *Celastrales* is presence, absence of bracts. So, inflorescences are typically bracteous (more often: most of *Celastraceae* s.str., *Stackhousiaceae*, *Brexia humbertii*) or almost "ebracteous" (other species of *Brexia*, for example, *B. madagascariensis* has a minute bracteoles at pedicel basis only). There is one very important question—problem of homology between bracts and bracteoles in inflorescences for different taxa of *Celastrales*. Flower-subtending bracts represent key architectural markers in inflorescences [22]. When subtending bracts of lateral flowers are missing (ebracteate inflorescences according to Troll and Weberling), it is normally assumed that they were ancestrally present but then lost in the course of evolution [16].

5. Conclusion

So, main characters of inflorescence architecture for *Celastrales* are the following: (1) inflorescence position on current shoots (intercalary or terminal); (2) presence or absence of the terminal flower; (3) degree of branching of the axis in an inflorescence; (4) type of flower opening (basipetal or acropetal). *Celastrales* order in current understanding (according to molecular data) is demonstrating widely spectrum of variations in inflorescences structure and the rhythms of their development.

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