Diversity and Evolution of Inflorescences in Celastrales

Ivan A. Savinov

Department of Microbiology, virology and genetic engineering, Moscow State University of Food Production, Moscow 109316, Russia

Received: October 28, 2012 / Accepted: December 21, 2012 / Published: February 28, 2013.

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.
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 acrosymphodial growth and intercalary or pseudoterminal inflorescences; in terms of shoot position, here the following types can be distinguished: (a) orthotropic, (b) plagiotropic 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.
Diversity and Evolution of Inflorescences in Celastrales

(1)                               (2)                            (3)

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 bracteious 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 thyrs with a terminal flower on the main axi-panicle-like thyrs, 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, thyrs. 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
noted that inflorescences of Celastrales/Celastraceae are usually bracteate, axillary and/or terminal, sometimes extra-axillary, or ramiferous, cymose, thyrsoid, paniculate, 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. 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.
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..

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.
Diversity and Evolution of Inflorescences in Celastrales

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 axillary 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 brachylasts, 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, Brixia humbertii) or almost “ebracteous” (other species of Brixia, 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.

Acknowledgments

The author wishes to thank Dr. Anton S. Beer, Prof. Dmitry D. Sokoloff (Moscow State University, Moscow, Russia), Prof. Marina V. Kostina (Main Botanic Garden RAS, Moscow, Russia), Dr. Regine Claßen-Bockhoff (Institut für Spezielle Botanik, Johannes Gutenberg-University Mainz, Germany) and Dr. Bruce Kirchoff (University of North Carolina at Greensboro, USA) for useful discussions. Thanks also to Dr. Elena Y. Yembaturova (Timiriazev’s Agricultural Academy, Moscow, Russia) for advices, and anonymous reviews for valuable suggestions on the manuscript. This material is based on work supported by the Russian Foundation for Basic Research under grant 12-04-31407.

References

[1] M.P. Simmons, Celastraceae, in: K. Kubitzki (Ed.), The families and genera of flowering plants, Vol. VI, Flowering plants, Dicotyledons, Celastrales, Oxalidales, Rosales, Cornales, Ericales, Berlin, 2004, pp. 29-64.
[2] M.P. Simmons, Parnassiaceae, in: K. Kubitzki (Ed.), The families and genera of flowering plants, Vol. VI, Flowering plants, Dicotyledons, Celastrales, Oxalidales, Rosales, Cornales, Ericales, Berlin, 2004, pp. 291-296.
[3] Z.L. Bing, M.P. Simmons, Phylogeny and delimitation of the Celastrales inferred from nuclear and plastid genes, Syst. Bot. 31 (1) (2006) 122-137.
[4] A. Takhtajan, Diversity and Classification of Flowering Plants, 2nd, Springer, Berlin, 2009.
[5] Angiosperm Phylogeny Group (APG), An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III, Bot. J. Linn. Soc 161 (2009) 105-121.
[6] Th. Loesener, Celastraceae, in: A. Engler, K. Prantl (Eds.), Die Naturlishen Pflanzenfamilien, Leipzig, Berlin, 1942, PP. 87-197.
[7] Th. Loesener, Hippocrateaceae, in: A. Engler, K. Prantl
Diversity and Evolution of Inflorescences in Celastrales

(Eds.), Die Naturlischen Pflanzenfamilien, Leipzig, Berlin, 1942, pp. 198-231.

[8] W. Troll, Die Infloreszenzen, Jena: VEB Gustav Fischer Verlag, 1964, 1969, Bd. I-II.

[9] F. Weberling, Morphology of Flowers and Inflorescences, Cambridge, 1989.

[10] T.V. Kuznetsova, Reduction in inflorescence, its essence and role in the evolution of module organisms, Journal of General Biology 59 (1) (1998) 74-103. (in Russian)

[11] H.J. Maresquelle, Y. Sell, Les problèmes physiologiques de la floraison descendante, Bull. Soc. Fr. Physiologie végétale 11 (1) (1965) 94-98. (in French)

[12] F. Halle, R. Oldeman, P.B. Tomlinson, Tropical Trees and Forests, An Architectural Analysis, Berlin etc., Springer, 1978.

[13] T.V. Kuznetsova, Inflorescences morphology: Modern condition, Results of science and technology, Ser. Botany 12 (1991) 51-174. (in Russian)

[14] H. Ding, Celastraceae I, in: C.G.G.J. van Steenis (Ed.), Flora Malesiana. Ser. I, Leyden: Flora Malesiana Foundation, 1962, pp. 227-291.

[15] G.K. Brizicky, The genera of Celastrales in the southeastern United States, J. Arn. Arbor 45 (2) (1964) 206-234.

[16] P.K. Endress, Disentangling confusions in inflorescence morphology: Patterns and diversity of reproductive shoot ramification in angiosperms, Journal of Systematics Evolution 48 (4) (2010) 225-239.

[17] M.V. Kostina, I.A. Savinov, Structure and seasonal rhythm of fertile shoots in the genus Celastrus (Celastraceae R.Br.), Byull. Glavn. Bot. Sada (Moscow) 183 (2002) 31-40. (in Russian)

[18] J. Parkin, The evolution of the inflorescence, J. Linn. Soc. Botany 42 (287) (1914) 511-563.

[19] P. Prusinkiewicz, Y. Erasmus, B. Lane, L.D. Harder, E. Coen, Evolution and development of inflorescence architectures, Science 316 (5830) (2007) 1452-1456.

[20] K. Bull-Hereñu, R. Claßen-Bockhoff, Open and closed inflorescences: More than simple opposites, Journal of Experimental Botany 62 (2011) 79-88.

[21] M.P. Simmons, V. Savolainen, C.C. Clevinger, R.H. Archer, J.I. Davis, Phylogeny of the Celastraceae inferred from 26S nuclear ribosomal DNA, phytochrome B, rbcL, atpB and morphology, Molec. Phylog. Evol. 193 (2001) 353-366.

[22] G. Prenner, F. Vergara-Silva, P.J. Rudall, The key role of morphology in modelling inflorescence architecture, Trends in Plant Science 14 (2009) 302-309.