

Flower arrangement in Southeast Asian orchids. Evolution trends and influence of environmental factors

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Abstract – The aim of our research is the comprehension of the organization and the characterization of Southeast Asian orchids. Until now we had not found complete and correct morphological description of flower arrangement in the orchid family. So it was not possible to understand the ways of their adaptation and evolutionary trends. Our research analyzed the flower arrangement and some parts of the androecium structure of more than 150 orchid species, belonging to 54 genera of Southeast Asia. The androecium micromorphology is helpful for the identification of the species and the study of the reproduction efficiency. The orchids of Southeast Asia show several inflorescence types, but often stop at the helicoid cyme stage of the ontogenesis. The inflorescence types can be modified by the environmental conditions in the wild or in cultivation.

Keywords

Environmental conditions, evolution trends, flower, inflorescence, ontogenesis, *Orchidaceae*, phylogeny, Southeast Asia.

INTRODUCTION

The *Orchidaceae* family has more than 25 000 species (Pridgeon *et al.*, 2005). The flower arrangement of East Asian orchids has various types, which are formed either at the shoot top or in a lateral position (in the leaf axils), either with some bracts or without bracts, either by a single flower or by simple or complex inflorescences. The term inflorescence itself is controversial (Rudall and Bateman, 2010), regarding the limits of the flowers and their arrangement. In general, botanists drew attention to the modification of the inflorescence structure in orchids, but they compared the flower arrangement only for adult plants. Consequently, the description of the inflorescence is given with only two types: a raceme or a panicle (Wu *et al.*, 2009). However, racemes and panicles belong to the group of indeterminate inflorescences, and according to our observations, other inflorescence types are formed frequently in the *Orchidaceae* family, like the helicoid

cyme, which is a determinate inflorescence. Another example of a determinate inflorescence is the terminal flower, which is formed not only on the tips, but also in the lateral leaf axis. In different environmental conditions a same species can show both inflorescence types or one of them. This raised doubts about the advisability of opposing a determinate and an indeterminate inflorescence (Parkin, 1914; Ricket, 1944).

In a number of cases, during the morphogenesis of the orchid inflorescence, a single flower, then a simple and a compound monochasium (determinate inflorescences) precede the formation of a raceme (indeterminate inflorescence). The genetic conditionality of the formation of indeterminate and definite inflorescences (Coen, 1991; Coen *et al.*, 1990, 1991; Coen and Meyerowitz, 1991, Coen and Nugent, 1994) could not be obtained. It was also not possible to experimentally change the structure of an indeterminate inflorescence (racemose) to a determinate (cymose). An attempt by

Baumann *et al.* (2015) to change the expression of *TFL1-2* and *tfl1-2* genes, was unsuccessful.

Given this situation, it was necessary to better study the ontogenesis stages, inflorescence morphogenesis and phylogenetic relationships of orchids. We have focused our research on the analysis of the morphological variability in the flower arrangement of Southeast Asian orchids, taking into account the morphogenetic, phylogenetic and geographic data.

MATERIALS AND METHODS

The results of the current study were first obtained from orchid material observed and collected during several expeditions in East Asia from 1998 to 2016 (Telepova-Texier, 2014; Telepova-Texier *et al.*, 2017). Then we have analyzed the transformation of the inflorescence structure during morphogenesis, mainly inside greenhouses of different botanical gardens (Muséum national d'Histoire naturelle, Paris, France; Komarov Botanical Institute, St-Petersburg, Russia; Botanical Garden-Institute, Vladivostok, Russia; Royal Botanical Gardens Kew, London, UK; Munich Botanical Garden, Germany; Botanical Garden of the University of Zurich, Switzerland). So, a comparison of the flower arrangement for both wild and cultivated orchid specimens could have been made.

We have analyzed 150 species belonging to four orchid subfamilies: *Cypripedioideae*, *Epidendroideae*, *Orchidoideae* and *Vanilloideae* (see Annex 1). Additionally to the classical characteristics of the plant morphology, the androecium microstructure has been considered for the taxonomic identification of the studied species (anther caps and pollen dispersion units) (Telepova-Texier, 2017).

The identification of the inflorescence types was carried out on the basis of the classification proposed by Eichler (1875) which, despite the selection of determinate and indeterminate inflorescences, believed that in nature there are no sharp boundaries and one form can pass into another. The identification of complex and composite inflorescences was carried out proceeding from the structure of inflorescences duplicated on lateral axes (Fedorov and Artyushenko, 1979).

It is important to know that, the formation of a terminal flower ceases the growth of the inflorescence terminal axis, but it can continue to produce the lateral axes in space (Figure 1B). Not forgetting that the lateral axis has continued to develop also in the same time (Figure 1 A-B). When analyzing the arrangement of flowers, we have differentiated their location depending on the level of branching of the shoots (Kharchenko, 2012b). The structure of the shoot changes according to the principle of the decreasing proportion proposed by Troll (1969), for whom lateral shoots repeat the structure of the main shoot on a reduced scale.

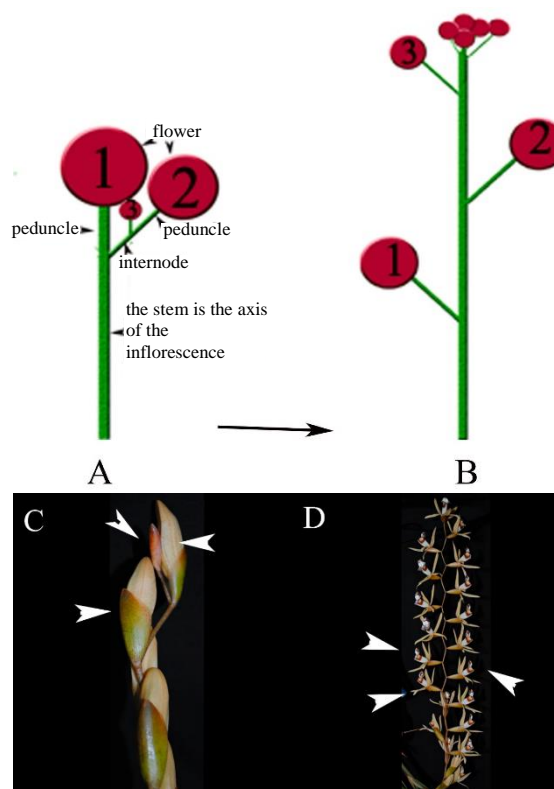


Figure 1. General scheme of formation of the floral axis during the morphogenesis of the inflorescence (1-3: order of flower apparition). Example of *Coelogyne massangeana* (C, D); A, C: formation of a compound monochasium (helicoid cyme); B, D: transformation of the helicoid cyme into a raceme.

For the analysis of the plesiomorphic and apomorphic state of the structure of the orchid inflorescences (Sherbakov and Kharchenko, 2018), cladograms have been constructed on

the nucleotide sequences of nuclear genes taken from the GenBank and constructed with the maximum likelihood method and the selected model of molecular evolution by means of the Mesquite system (Maddison and Maddison, 2018) and Iq-Tree (Nguyen *et al.*, 2014).

RESULTS

We have analyzed the inflorescence morphogenesis of 150 species from 54 genera belonging to four subfamilies of Southeast Asian orchids: *Cypripedioideae*, *Epidendroideae*, *Orchidoideae* and *Vanilloideae* (Annex 1, Table. 1 and Figure 2, Kharchenko, 2013, Telepova-Textier *et al.*, 2018).

Zygomorphic flowers of orchids can be single or several on the inflorescences. They can be formed on the tops of the shoots (*Cypripedium calceolus*, *C. macranthos*) or in the leaf axils (*Bulbophyllum macranthum*, *Dendrobium uniflorum*) (Table 1, Figure 2). Inflorescences can be with bracts or without bracts. Our research has shown that under greenhouse conditions, the number of flowers for each orchid inflorescence is significantly less than in nature (Kharchenko and Telepova-Textier, 2015). This is due to the effect of limiting factors, negatively affecting the productivity of plants (Telepova-Textier *et al.*, 2016, 2018).

Seventy three % of the analyzed orchid species formed simple inflorescence (monochasium, compound monochasium, raceme, spike, head, umbel, spadix); less often (11% of species) they formed compound and complex inflorescences (helicoid cyme from helicoid cymes, helicoid cyme from racemes with terminal flower). Furthermore, single flowers developed in 15% of the species (Table 1, Figure 5). The study of the inflorescence morphogenesis in the four subfamilies of orchids indicates the presence of a general sequence of stages, that was limited in different species at different steps of formation (Table 1, Figure 2).

Some examples are provided here:

1. Representatives of subfam. *Cypripedioideae* have usually one terminal flower (*Cypripedium calceolus*, *C. macranthos*, *Paphiopedilum appletonianum*, *P. callosum*) or two terminal flowers (monochasium). So, their morphogenesis is

composed of two stages (Figure. 2: 1-3, Figure 3: 1-2). In New Guinea, in a warm and humid climate, *Paphiopedilum rothschildianum* has a long flowering period, during which not 2 but 12 flowers are formed, which leads to the formation of a helicoid cyme (Figure 3: 4).

Terminal flower → Monochasium → Helicoid cyme.

2. In the subfam. *Vanilloideae*, in contrast to subfam. *Cypripedioideae*, a raceme is usually formed (*Vanilla annamica*, *V. siamensis*) (Figure 2: 1-4). However, in *Vanilla somae*, distributed to the north of China (with less favorable environmental conditions), usually there are only two flowers. Thus, in this case the morphogenesis ceases at an earlier stage (monochasium). So, the morphogenesis in *Vanilla* is represented by four stages:

Terminal flower → Monochasium → (Helicoid cyme) → Raceme with terminal flower.

3. Among the species of the subfam. *Orchidoideae*, *Epipactis helleborine*, which is a very common species in all European countries, has a raceme. For this reason, it is usually thought that the predominant type of inflorescence for this subfamily is the raceme. However, for the species of *Orchidoideae* studied in the tropics, we can observe other types of inflorescences, corresponding to earlier stages of ontogenesis:

Terminal flower → Monochasium → Helicoid cyme → Raceme with terminal flower.

The maximum duration of morphogenesis was found for *Ludisia discolor*, *Habenaria rhodocheila*, *H. medusa* and *Zeuxine flava*. Unlike most tropical orchids, that develop on trees and have inflorescences hanging down, these species are lithophytic or terrestrial, and their vertical inflorescences are oriented upwards. As the number of flowers increases, the axis of the inflorescence is straightened and the helicoid cyme is transformed into a raceme with a terminal flower (Figure 2:1-4).

4. In the subfam. *Epidendroideae*, a significant polymorphism is observed (especially in the genus *Bulbophyllum*), which is caused by a variability in the degree of axis

development (Figure 2: 1-4, Figure 3: 3, Figure 4: 2-6). The maximum time of morphogenesis course involves also 4 stages, the final one

being the raceme (*Calanthe triplicata*, *C. cardioglossa*, *Pholidota ventricosa*, *Thelasis carinata*, *T. pygmaea*):

Table 1. Characters of the inflorescences and the androecium of the studied genera.

<i>Genus</i>	Terminal flower	Monochasium	Helicoid cyme	Raceme	Spike	Helicoid cyme from helicoid cymes	Head	Umbel	Spadix	Axillary flower	Single flower	Simple inflorescence	Compound inflorescence	Aggregate inflorescence	One group of fertile anthers	PDU: sectile pollinia	PDU: Monads
<i>Acampe</i>	-	-	+	-	-	-	+	-	-	-	-	+	-	+	+	-	-
<i>Acriopsis</i>	-	-	-	-	-	+	-	-	-	-	-	-	+	+	+	-	-
<i>Aerides</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Appendicula</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Arundina</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Ascocentrum</i>	-	-	+	+	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Bletilla</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Bulbophyllum</i>	+	+	+	+	+	-	+	+	+	+	+	+	-	-	+	-	-
<i>Calanthe</i>	-	-	+	+	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Chelonistele</i>	-	-	+	-	-	-	-	-	-	-	+	+	-	-	+	-	-
<i>Chiloschista</i>	-	-	+	+	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Cleisostoma</i>	-	-	+	+	-	+	-	-	-	-	-	+	+	+	+	-	-
<i>Coelogyne</i>	+	+	+	+	-	-	-	-	-	-	+	+	-	-	+	-	-
<i>Cymbidium</i>	+	-	+	+	-	-	-	-	-	-	+	+	-	-	+	-	-
<i>Cypripedium</i>	+	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	+
<i>Dendrobium</i>	+	+	+	-	-	-	-	-	-	+	+	+	-	-	+	-	-
<i>Dipodium</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Doritis</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Eria</i>	+	+	+	-	+	-	-	-	-	-	+	+	-	-	+	-	-
<i>Epipactis</i>	-	-	-	+	-	-	-	-	-	-	-	+	-	-	+	+	-
<i>Flickingeria</i>	+	+	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Gastrochilus</i>	-	-	-	+	-	-	+	-	-	-	-	+	-	-	+	-	-
<i>Geodorum</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Habenaria</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	+
<i>Ludisia</i>	-	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Luisia</i>	+	+	-	-	-	-	+	-	-	-	+	+	-	-	+	-	-
<i>Macropodanthus</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Oberonia</i>	-	-	-	-	-	-	-	-	+	-	+	+	-	-	+	-	-
<i>Paphiopedilum</i>	+	+	+	-	-	-	-	-	-	-	+	+	-	-	+	-	+

Genus	Terminal flower	Monochasium	Helicoid cyme	Raceme	Spike	Helicoid cyme from helicoid cymes	Head	Umbel	Spadix	Axillary flower	Single flower	Simple inflorescence	Compound inflorescence	Aggregate inflorescence	One group of fertile anthers	PDU: sectile pollinia	PDU: Monads
<i>Pelatantheria</i>	+	+	-	-	-	-	+	-	-	-	+	+	-	-	+	-	-
<i>Phalaenopsis</i>	+	+	+	-	-	+	-	-	-	-	+	+	+	-	-	-	-
<i>Pholidota</i>	-	-	+	+	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Pleione</i>	+	-	-	-	-	-	-	-	-	-	+	+	-	-	+	-	-
<i>Polystachya</i>	-	-	+	+	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>Porpax</i>	+	-	-	-	-	-	-	-	-	-	+	+	-	-	+	-	-
<i>Renanthera</i>	-	-	+	-	-	+	-	-	-	-	-	-	+	-	+	-	-
<i>Rhynchostylis</i>	-	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Robiquetia</i>	-	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Seidenfadenia</i>	-	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Schoenorchis</i>	-	-	+	+	-	+	-	-	-	-	+	-	+	-	+	-	-
<i>Smitinandia</i>	-	-	+	+	-	-	-	-	-	-	-	+	-	+	+	-	-
<i>Spathoglottis</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Thelasis</i>	-	-	-	+	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Thrixspermum</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Trias</i>	+	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-
<i>Trichoglottis</i>	+	+	-	-	-	-	-	-	-	+	+	+	-	-	+	-	-
<i>Trichotosia</i>	+	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-
<i>Trudelia</i>	-	+	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Vanda</i>	-	-	+	-	-	-	-	-	-	-	-	+	+	-	+	-	-
<i>Vanilla</i>	-	+	-	+	-	-	-	-	-	-	-	+	-	-	+	-	+
<i>Zeuxine</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	+	+	-

Terminal flower → Monochasium → Helicoid cyme → Raceme with terminal flower.

The structure of the lateral axis of the inflorescence is not straightened. In particular, the structure of the inflorescence is a sympodial branching, and can develop by overturning in the helicoid cyme (*Appendicula hexandra*, *A. reflexa*, *Arundina graminifolia*, *Calanthe sieboldii*, *C. vestita*, *Chelonistele sulphurea*, *Coelogyne flaccida*, *C. pallens*, *C. trinervis*, *C. virescens*, *Dendrobium affine*, *D. glomeratum*, *D. moschatum*, *D. porphyrochilum*, *Dipodium paludosum*, *Eria lasiopetala*, *E. tomentosa*, *E. javanica*, *Pholidota chinensis*, *P. pallida*, *P. imbricata*,

Spathoglottis affinis, *S. pubescens*) (Figure 2: 1-3, Figure 6):

Terminal flower → Monochasium → Helicoid cyme.

In *Coelogyne lawrenceana*, *Flickingeria fimbriata*, *Dendrobium ellipsophyllum*, *D. draconis*, *D. hercoglossum*, *D. glomeratum*, *Eria biflora*, *E. lasiopetala*, *E. tomentosa*, at the base of the solitar terminal flower is formed another flower. As a result, the inflorescence morphogenesis is represented by two stages (Figure 2: 1-2, Figure 8):

Terminal flower → Monochasium.

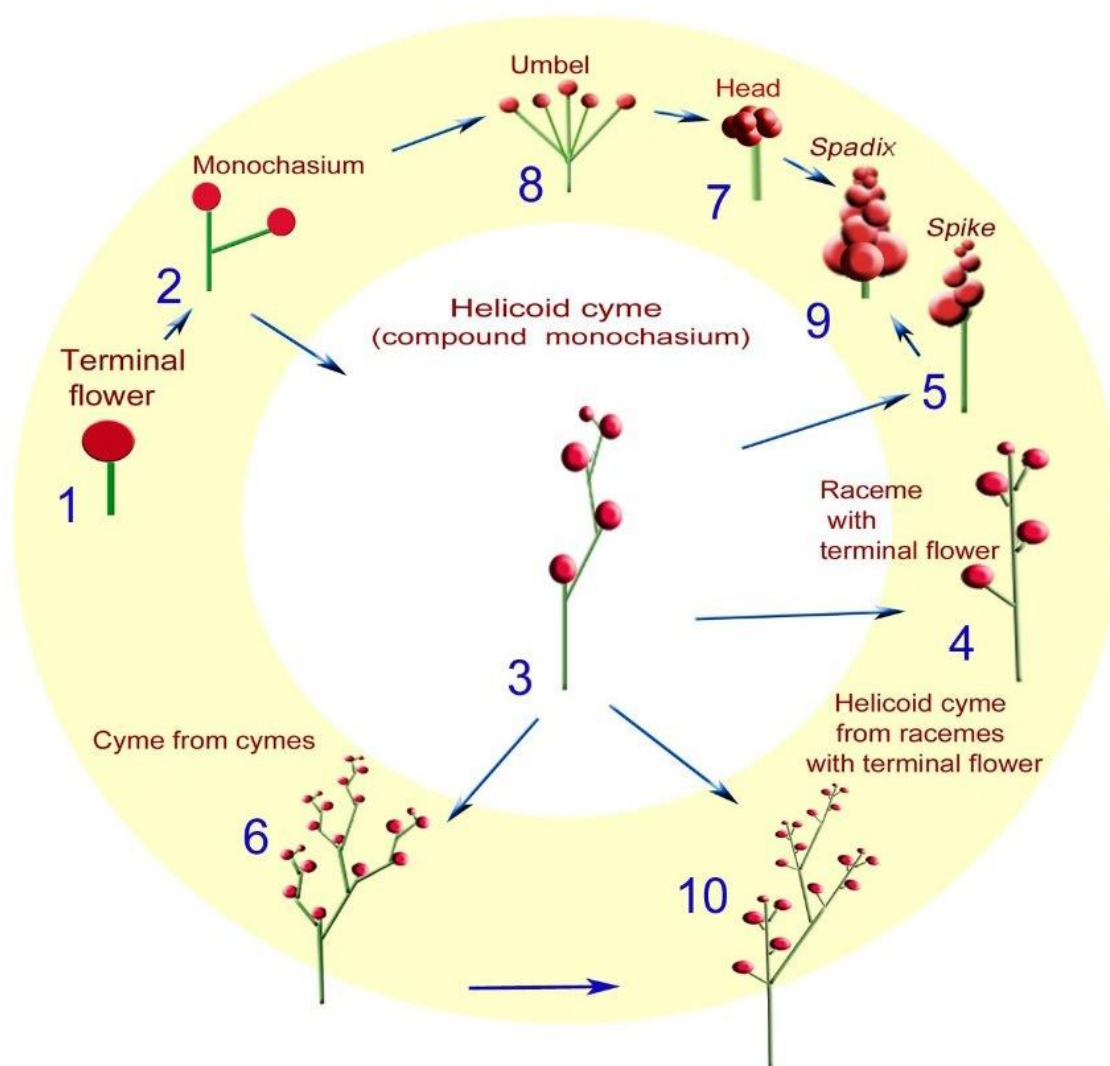


Figure 2. Evolution of the different types of inflorescences in Southeast Asian orchids. 1 - Terminal flower; 2 – Monochasium; 3 - Compound monochasium (helicoid cyme); 4 - Raceme; 5 – Spike; 6 - Compound monochasium from compound monochasium (helicoid cyme from helicoid cymes); 7 - Head; 8 – Umbel; 9 - Spadix; 10 - Aggregate inflorescence: compound monochasium from racemes (helicoid cyme from racemes).

In *Bulbophyllum lobbii*, *Eria lasiopetala*, *E. tomentosa*, *E. (Campanulorchis) thao*, *Pleione formosana*, *Bulbophyllum macranthum*, *Dendrobium uniflorum*, *Flickingeria xantholeuca*, *Porpax elwesii*, *Trias picta* and *Trichotosia velutina*, only one terminal flower is formed (Figure 2: 1, Figure 8):

Terminal flower.

In *Bulbophyllum lepidum* and *B. picturatum*, the internodes remain undeveloped, while the pedicels are well

developed. As a result, an inflorescence of umbrella type (or fan) is formed (Figure 2: 1-2, 8, Figure 4: 2, Figure 5):

Terminal flower → Monochasium → Umbel.

In the case when the pedicels and internodes are poorly developed, as in *Bulbophyllum medusae* and *Eria globulifera*, the morphogenesis takes place in 3 stages, leading to a head inflorescence type (Figure 2: 1-2, 7, Figure 4: 3):

Terminal flower → Monochasium → Head.

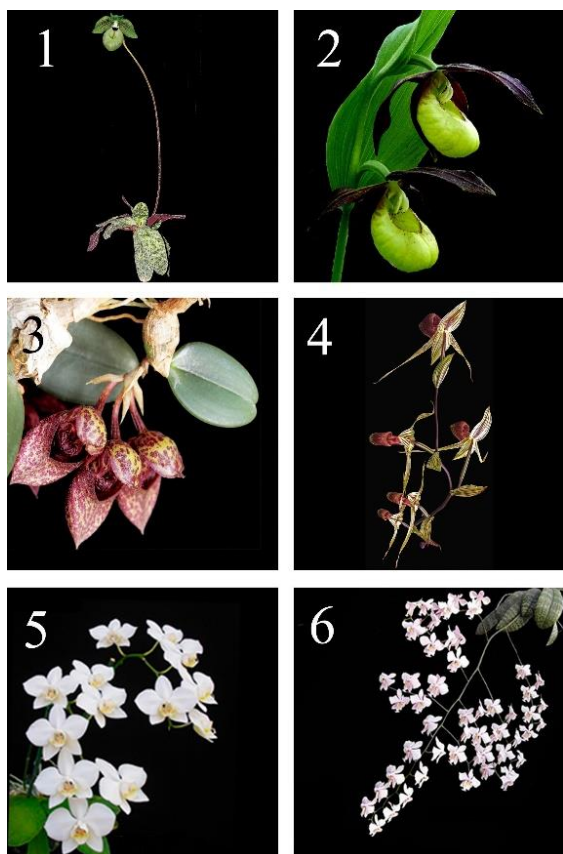


Figure 3. Inflorescence types of Southeast Asian orchids (part. 1). 1: *Paphiopedilum malipoense* - one terminal flower; 2: *Cypripedium calceolus* - monochasium; 3: *Bulbophyllum frostii* - compound monochasium; 4: *Paphiopedilum rothschildianum* - compound monochasium (helicoid cyme); 5: *Phalaenopsis amabilis* var. *aphrodite* - compound monochasium from compound monochasium (helicoid cyme from helicoid cyme); 6: *Phalaenopsis amabilis* var. *aphrodite* - aggregate inflorescence: compound monochasium from racemes (helicoid cyme from racemes).

However, if the axis of the inflorescence grows at the same time, then a cob can be formed as in *Bulbophyllum careyanum*, *Oberonia acaulis* and *Smitinandia micrantha* (Figure 2: 1-2, 9, Figure 4: 5):

Terminal flower → Monochasium → Spadix.

If, in the inflorescence, internodes develop and the flower have no pedicels, then a head or a spike is formed, like in *Bulbophyllum hirtum*, *Eria siamensis* and

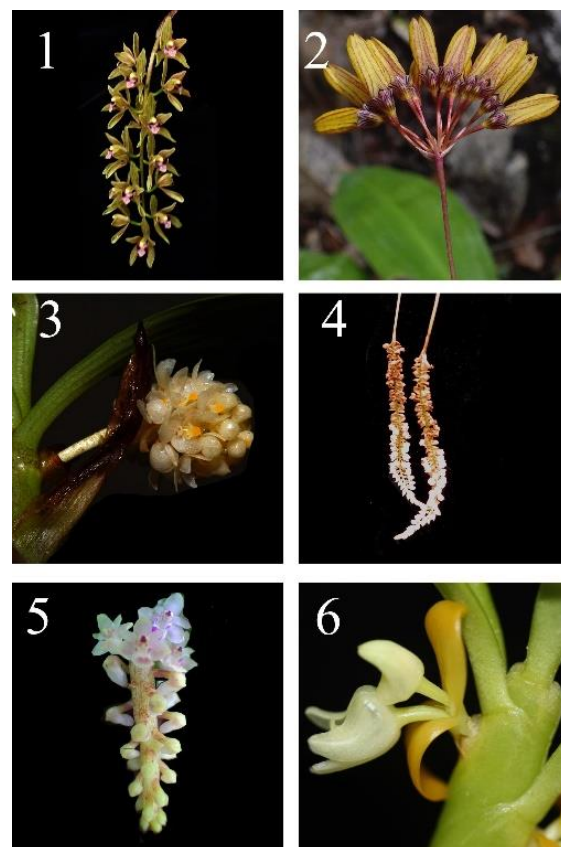


Figure 4. Inflorescence types of Southeast Asian orchids (part. 2). 1: *Cymbidium lowianum* - raceme; 2: *Bulbophyllum picturatum* - umbel; 3: *Eria globulifera* - head; 4: *Pholidota imbricata* - spike; 5: *Smitinandia micrantha* - spadix; 6: *Eria bifolia* - 2 lateral flowers.

Pholidota imbricata (Figure. 2: 1-2, 5, 7, Figure 4: 4):

Terminal flower → Monochasium → Head → Spike.

In *Acropsis javanica*, branching appears on the lateral axis of the inflorescence, with an increase of the flower number. Since the lateral inflorescences develop not in parallel, but in turn, it can be different stages of formation. Therefore, the morphogenesis of such an inflorescence can be represented as follows (Figure 2: 3, 6, 10):

Helicoid cyme → Helicoid cyme from monochasiums → Helicoid cyme from helicoid cymes → Helicoid cyme from racemes.

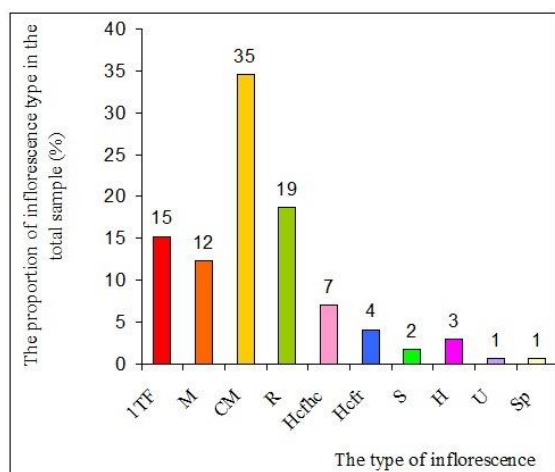


Figure 5. Proportion of inflorescence types (%) for the studied genera (see also Table. 1). One terminal flower (1TF); monochasium (M); compound monochasium (helicoid cyme) (CM); raceme (R); helicoid cyme from helicoid cymes (Hcfhc); helicoid cyme from racemes (Hcfr); spike (S); head (H); umbel (U); spadix (Sp).

Another species, *Acriopsis indica*, is more widespread to the north (India, Thailand, Vietnam) and at an altitude of 900 to 1800 meters. So, the development of its inflorescences ceases at an earlier stage of formation: Helicoid cyme from helicoid cymes (Figure 2: 1-2-3, 6).

5 In the representatives of subfam. *Epidendroideae* tribe *Vandaeae*, the maximum duration of morphogenesis is observed in: *Cleisostoma arietinum*, *C. subulatum*, *Polystachya concreta*, *Schoenorchis gemmata* and *Smitinandia helferi* (Figure 2: 3, 6, 10):

Helicoid cyme → Helicoid cyme from monochasiums → Helicoid cyme from helicoid cymes → Helicoid cyme from racemes.

In plants with large flowers (4-10 cm, for example, in *Phalaenopsis amabilis*), the internodes are usually well pronounced, and thus a leafless inflorescence is formed:

Helicoid cyme or helicoid cyme from helicoid cymes.

In a number of species (*Acampe ochracea*, *Cleisostoma williamsonii*, *C. fuerstenbergianum*, *Renanthera imschootiana*,

R. monachica, *Phalaenopsis amabilis*, *P. cornu-cervi*, *P. equestris*, *P. schilleriana*, *P. stuartiana* and *Vanda tricolor*), the morphogenesis of the inflorescence is limited at the following stage (Figure 2: 6, Figure 3: 5): Helicoid cyme from helicoid cymes.

In *Acampe praemorsa* and *A. rigida*, the internodes on the main axis are well developed, and on the lateral axis of the inflorescence they are short; therefore the structure of the inflorescences corresponds to the morphological definition of a "head". Accordingly, the morphogenesis involves the branching of the main axis of the inflorescence as a helicoid cyme, (Figure 2: 3, 6), and of the lateral axis respectively as a head (Figure 2: 1-2, 7):

Terminal flower → Monochasium → Head;
or:

Helicoid cyme → Helicoid cyme from monochasiums → Helicoid cyme from head.

In those orchids, which form a lot of medium or large flowers (3-10 cm), such as *Aerides crassifolia*, *A. houlletiana*, *A. odorata*, *Cleisostoma simondii*, *Cymbidium atropurpureum*, *C. dayanum*, *C. lowianum*, *C. insigne*, *Doritis pulcherrima*, *Geodorum citrinum*, *Macropodanthus alatus*, *Thrixspermum amplexicaule*, *T. centipeda*, *Vanda lilacina*, *V. coerulea*, *V. brunnea* and *Phalaenopsis violacea*, the flowers are formed consecutively, and are grouped in simple inflorescences, with the following stages of morphogenesis (Figure 2: 1-3):

Terminal flower → Monochasium → Helicoid cyme.

The species *Pelatantheria bicuspidata* is widespread in China, Vietnam and Laos, at an altitude of 800-1400 m; it is distributed in rather harsh conditions and forms only 1-3 flowers, and its morphogenesis is usually limited at the stage of the monochasium (Figure 2: 1-2). The inflorescence morphogenesis is similar for *Trichoglottis pusilla*, *Trudelia alpina* and *T. cristata*:

Terminal flower → Monochasium.

Cymbidium goeringii is distributed in Northeast Asia. A short period of vegetation acts as a factor limiting the development of the

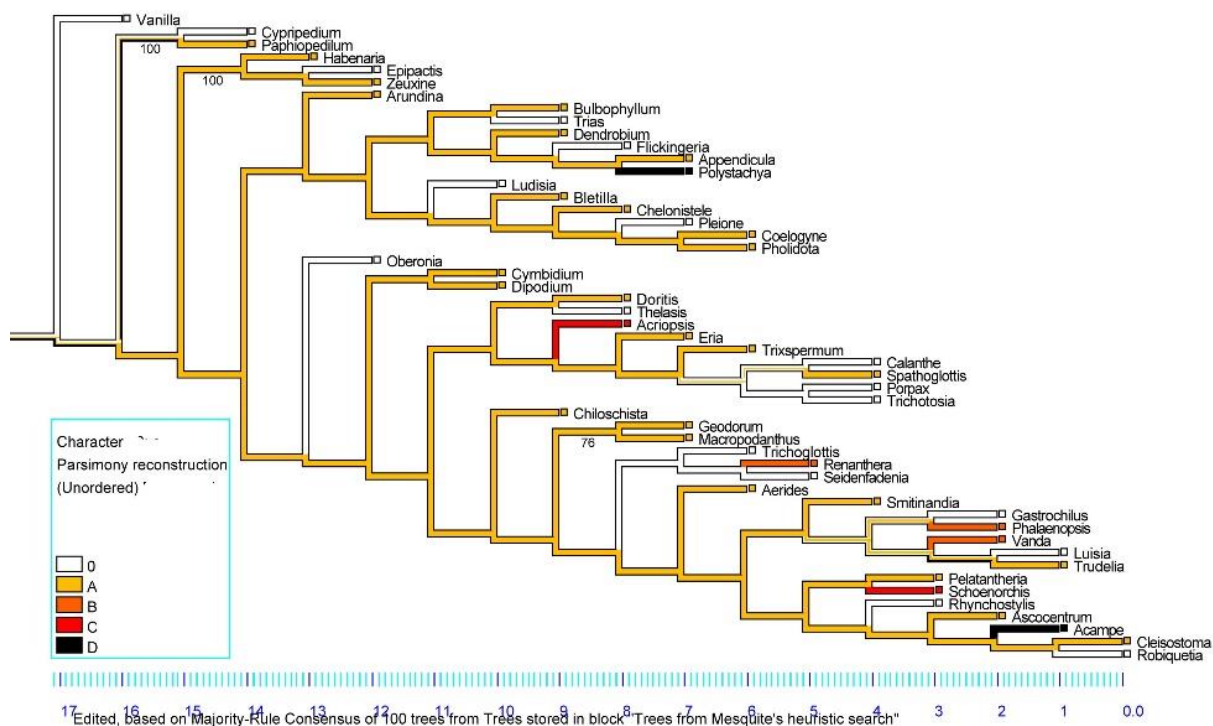


Figure 6. Cladogram showing the monochasium and raceme inflorescence types of the studied orchids. 0 : missing character; A: monochasium; B: monochasium and compound monochasium; C: monochasium, compound monochasium and raceme; D: compound monochasium and raceme.

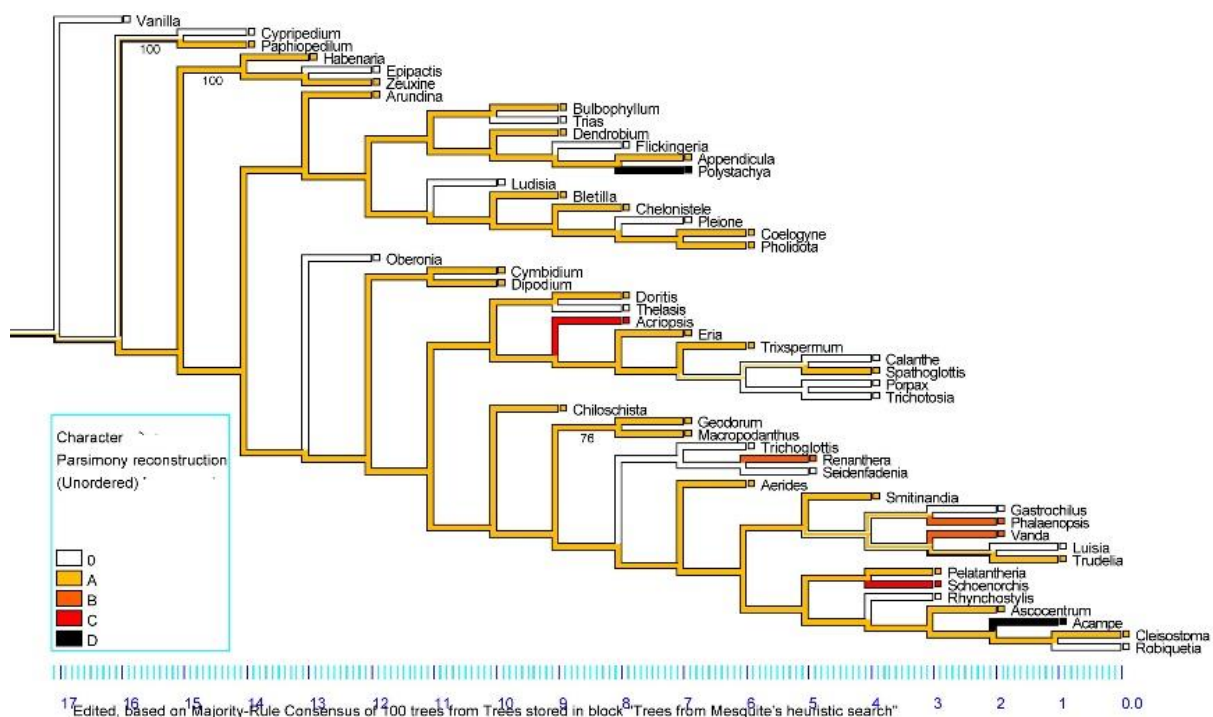


Figure 7. Cladogram showing the compound monochasium inflorescence types of the studied orchids. 0: missing character; A: compound monochasium (helicoid cymes); B: compound monochasium and compound monochasium from compound monochasiums (helicoid cyme from helicoid cymes); C, D: compound monochasium and compound monochasium from racemes (helicoid cyme from racemes).

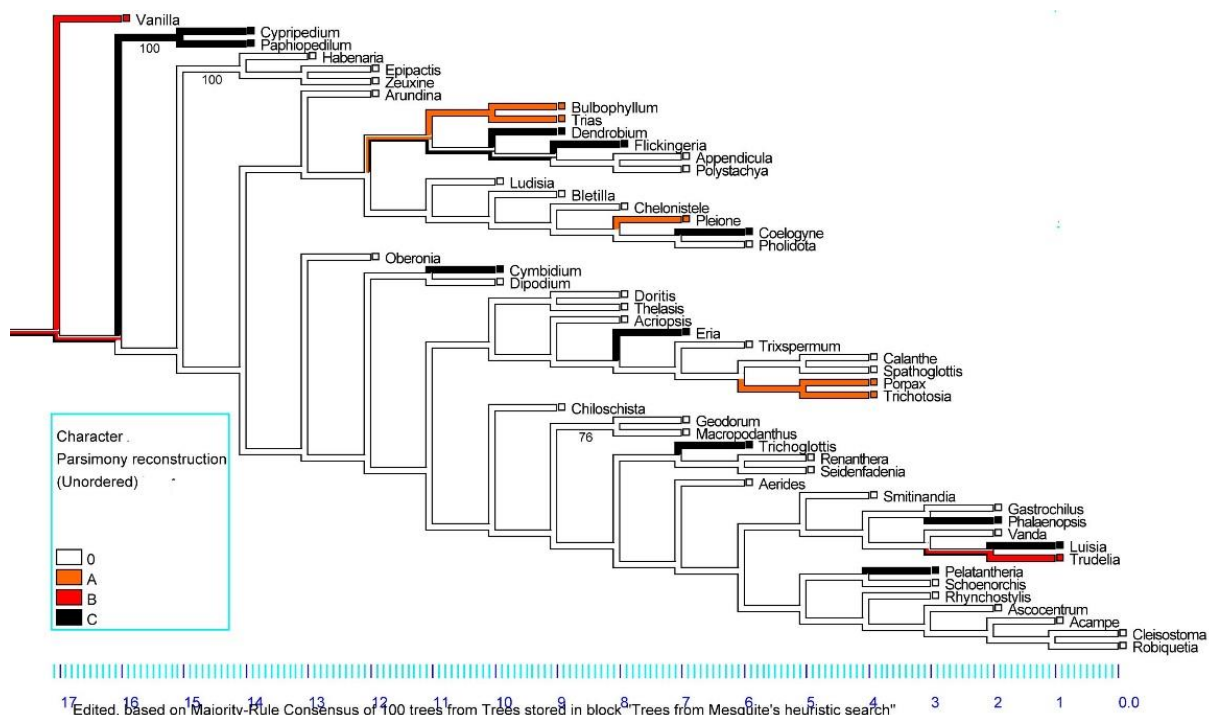


Figure 8. Cladogram showing the terminal flower and monochasium inflorescence types of the studied orchids. 0: missing character; A: terminal flower; B: monochasium; C: terminal flower and monochasium.

structure of the inflorescence for this species. Thus, a single flower is formed, due to the adaptation to harsh environmental conditions (apomorphy). In greenhouse conditions however, this species can form a monochasium.

Trichoglottis atropurpurea has a short vegetation period and forms a single terminal flower in the axils of the leaves.

In *Chiloschista usneoides*, *Cleisostoma discolor*, *Gastrochilus calceolaris*, *Luisia tristis*, *Rhynchostylis gigantea*, *R. retusa*, *Robiquetia minimiflora*, *R. spathulata*, *Schoenorchis fragrans*, *S. micrantha*, *Smitinandia micrantha* and *Seidenfadenia mitrata*, the morphogenesis involves the branching of the main axis of the inflorescence, with respectively, a helicoid cyme on the main axis and on lateral axis – a raceme (Figure 2: 3, 10):

Helicoid cyme → Helicoid cyme from helicoid cyme → Helicoid cyme from raceme.

In particular, *Luisia tristis* forms 3-10 small flowers (up to 2 cm), forming a raceme with terminal flower, but they open simultaneously. In the species *Luisia*

primulina, *Pelatantheria insectifera* and *Gastrochilus obliquus*, the internodes of the inflorescences are poorly developed, therefore during the morphogenesis they can be traced to the following stages:

Terminal flower → Monochasium → Head.

The studies carried out have shown, that the morphogenesis of the inflorescences of Southeast Asian orchids has different durations, and the formation of single terminal flowers in some cases is a plesiomorphic state, in particular in the subfamilies *Cypripedioideae* and also in *Epidendroideae*, and *Orchidoideae*, and apomorphic in *Vanilloideae* and in some species of *Epidendroideae* tribe *Vandae* (ex. *Cymbidium goeringii*). On this basis, *Cypripedioideae* was used as the root group in a cladistic analysis of the morphology of flowers arrangement of Orchids (Figures 6 to 8).

We have noted that usually, in greenhouse conditions, the orchids of Southeast Asia have a terminal flower or its rudiment which dries up and remains underdeveloped at the end of the development of the inflorescence.

Therefore the identification of the inflorescence type depends on the conditions of cultivation, which predetermine the number of flowers and the stage of morphogenesis on which the development of the inflorescence ceases.

The results of our study have shown that the inflorescences of orchids have a general developmental sequence, and their polymorphism is caused by the restriction of the morphogenesis at different stages of formation. In the course of our analysis of orchid inflorescence diversity we can propose the hypothesis of the heterochrony as a source of morphological transformation.

DISCUSSION

Based on the studies carried out, five types of morphogenesis of inflorescences have been identified for Southeast Asian orchids (Figure 2) :

1. Terminal flower → Monochasium → Compound monochasium (helicoid cyme) → Raceme with terminal flower;
2. Terminal flower → Monochasium → Helicoid cyme → Compound monochasium from compound monochasiums (helicoid cyme from helicoid cymes) → Compound monochasium from racemes (helicoid cyme from racemes);
3. Terminal flower → Monochasium → Umbel;
4. Terminal flower → Monochasium → Head → Spike → Spadix;
5. Helicoid cyme → Helicoid cyme from monochasiums → Helicoid cyme from helicoid cymes → Helicoid cyme from racemes.

1. Are determinate and indeterminate inflorescences fundamentally different in the course of their development?

At first, the study of the orchid morphogenesis indicates a gradual transformation of the inflorescence structure. A particular case of this is observed in *Cymbidium lowianum* (Figure 4: 1), where there is a transition from the helicoid cyme (determinate inflorescence) to the raceme (indeterminate inflorescence). Second, the analysis of the orchid phylogenesis have shown that the initial state for a raceme type is the helicoid cyme (Figure 7). Thus, we can observe the coincidence of changes in the

inflorescence structure both in morphogenesis (ontogeny) and phylogenesis, which confirms the biogenetic law.

We want to draw attention to the fact, that changes in the inflorescence structure are quantitative characters. Therefore, determinate and indeterminate inflorescences can not be considered as fundamentally different in the course of their development. This also agrees with the opinion of many morphologists, in particular Parkin (1914) and Ricket (1944). They considered it inappropriate to contrast these types of inflorescences due to the fact that they can both be found on the same shoot and on plants of the same species that have grown up in different environmental conditions. That is, this variability is not inherited.

2. Does the structure of the orchid flower depends on its position in the inflorescence?

All orchids have zygomorphic flowers, which are usually grouped in determinate inflorescences: simple, complex or composite. The flowers have the same structure, regardless of whether if they are formed in the inflorescence with a terminal or a lateral position, on the main shoot or in the leaf axil (Figures 3 and 4). In addition, there are also single terminal flowers.

In the works of Carpenter and Coen (1990), Coen *et al.* (1990, 1991), Coen and Nugent (1994), Prusinkiewicz *et al.* (2007), the program for the development of inflorescence structure is redefined by the balance of the homeotic genes, in such a way that the lateral flowers are zygomorphic and form indefinite inflorescences, and the terminal flowers are actinomorphic, and form definite inflorescences. However, these conclusions are based not on the orchids, but on the *cen* and *cyc* mutants in *Antirrhinum majus* (Plantaginaceae) and the *tfl* mutants in *Arabidopsis thaliana* (Brassicaceae). The assumption that zygomorphic flowers are usually associated with indeterminate inflorescences, whereas actinomorphic flowers occur in determinate inflorescences, was also expressed by Stebbins (1973). The advisability of contrasting determinate and indeterminate inflorescences has been called into question since 1826, and the most famous morphologists participated in the discussion: Wydler (1851), Eichler (1875), Celakovsky (1893), Parkin (1914), Bentman (1918),

Goebel (1931), Ricket (1944) and Müller-Doblies (1977). In our works (Kharchenko, 2012a, Telepova-Texier *et al.*, 2016) the question of the affiliation of the inflorescences to this or that type is posed in connection with their individual or environmental variability in structure. In turn, Takhtajan (1964) paid attention to the fact, that it can be difficult to assign little-flowered inflorescences (2-3 flowers) to any of the types. For example: *Cypripedium calceolus* can form 2-3 flowers, and we are not surprised that both its flowers are zygomorphic; while its inflorescences can be described as two different types (monochasium or compound monochasium).

Moreover, often only an approximate morphological characteristic of the inflorescence or the wrong one is given (Wu *et al.*, 2009), where the inflorescences of orchids are most often characterized as raceme or panicle type (indeterminate inflorescences), although, in some cases, they form determinate inflorescences, in particular: helicoid cyme (*Paphiopedilum rothschildianum*), helicoid cyme from helicoid cymes (*Phalaenopsis amabilis*) and helicoid cyme from racemes (*Acropsis javanica*).

In the light of these results and discussions, we can therefore say that the structure of the flower does not depend on its position in the inflorescence.

3. Homeosis and heterochrony in the regulation of orchid inflorescence structure.

The assumption of Carpenter and Coen (1990) is based on the fact that, the homeosis and the heterochrony are identical in plants, unlike animals, due to the repeated formation of organs during the ontogeny. The meaning of homeostatic mutations consists in the changing of plan for individual development with a possible phylogenetic outlet (Korochkin, 2002), and heterochrony leads to a change in the time of the bookmarking of the organs (or the system of organs) in ontogenesis (Haeckel, 1866). It is difficult to imagine, that quite large-scale genetic changes, that change the plan of the structure of the reproductive system (the types of inflorescences), occurred independently and repeatedly in the evolution of Southeast Asian orchids (Figures 6-8).

Our analysis of the orchid morphogenesis has shown that the single terminal flower and

the indeterminate inflorescences are the preceding stages in the formation of the raceme type; and the differences are not qualitative (depending on homeostatic genes), but quantitative and are a consequence of heterochrony (Kharchenko, 2012a). Heterochrony can develop at different stages of the ontogeny (Severtsov, 1939), and is depending on the stage, where the development stopped. Severtsov distinguished three main modes of variability: the *anabolism* – a change in the final stage of the ontogenesis, the *deviation* – a change in the middle stages, and the *arhallaxis* – a change in the initial stage. For example, in the genus *Acampe*, the neoteny in the deviation stage can lead to underdevelopment of internodes and pedicels (Table 1). The changes in the morphogenesis of the inflorescence can be both positive and negative. Among the negative qualities of heterochrony we can mention the neoteny, suggesting a transition to the reproductive phase before the development of the adult body. In the opinion of Arber (1937) and Takhtajan (1970, 2009) however, the neoteny could be decisive not only in the adaptation of flowering plants, but also in their origin. Unfortunately, the genetic conditioning of neoteny has not been shown previously, despite the fact that Raff and Wray (1989) showed that the *TFL* gene has a heterochronic effect. This *TFL* gene can act as the coordinator of the ontogeny program as a whole, and its mutations lead to the neoteny (Kharchenko and Koksheeva, 2015).

Unlike Carpenter and Coen (1990), we consider it expedient to distinguish the homeosis and the heterochrony in plants as in animals. So, in our hypothesis, the heterochrony is thought to determine evolutionary trends in flower arrangement of Southeast Asian orchids. Within the genus *Cymbidium* for example, three types of inflorescences are observed and their occurrence may be due to the neoteny: single terminal flower, compound monochasium (helicoid cyme) and raceme (Table 1, Figure 2: 1-4, Figure 6). In particular, *Cymbidium lowianum*, which is distributed in Far East India (Figure 9), forms in nature 20-100 inflorescences (helicoid cymes), each composed of 12-40 flowers or more (Figure 4: 1):

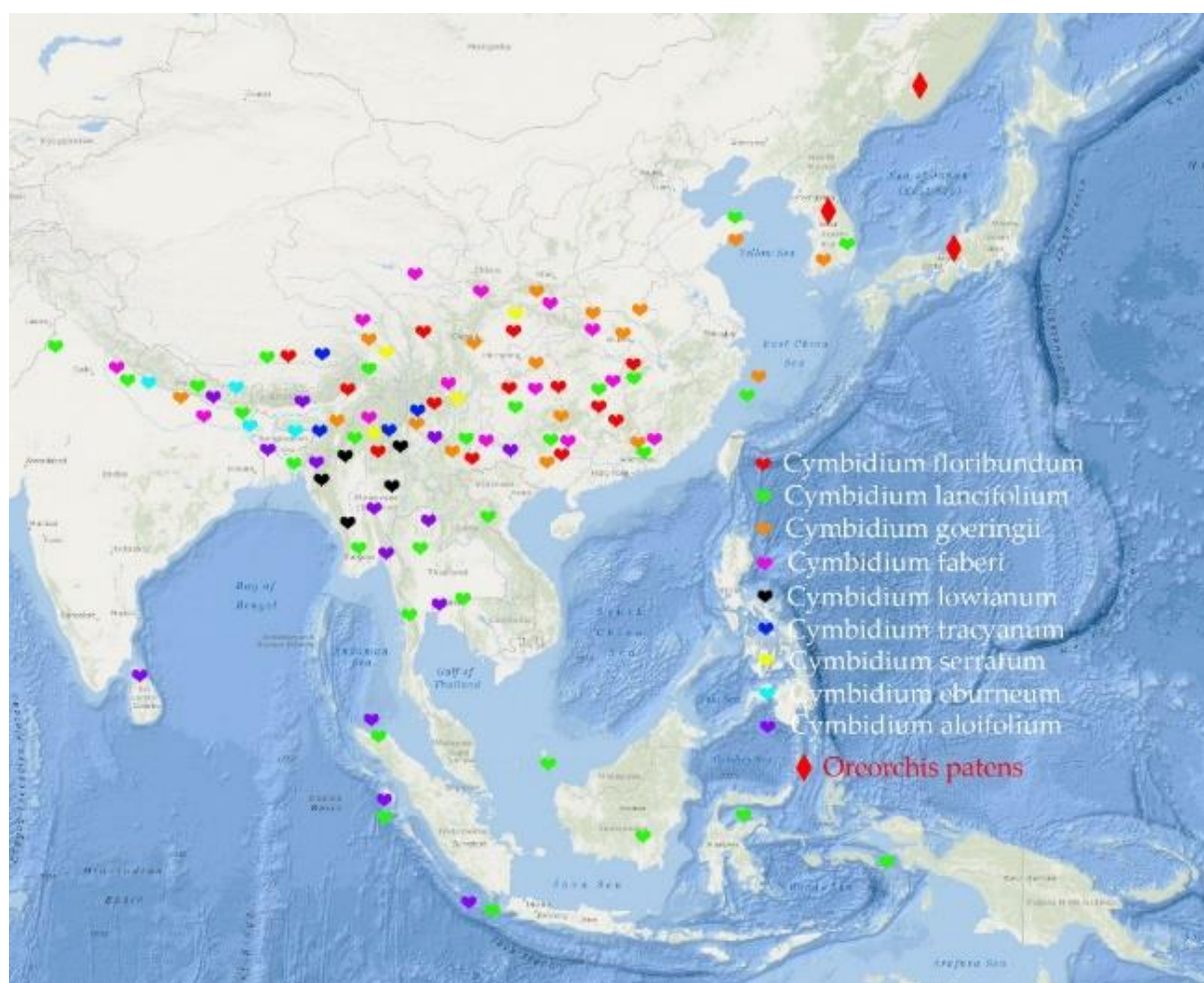


Figure 9. Distribution map of the studied *Cymbidium* and *Oreorchis* species.

Terminal flower → Monochasium → Compound monochasium (helicoid cyme) → Raceme.

Cymbidium goeringii is distributed in East Asia, until Japan, in the most northeastern distribution area of the genus *Cymbidium*, where it usually forms only one terminal flower. The neoteny in the arhallaxis stage can confine itself to the formation of only single flower. A monochasium can however be formed in more favourable environmental conditions (Table 1, Figure 2: 1-2):

Terminal flower → Monochasium.

Cymbidium dayanum, forms 20-30 flowers and grows in East temperate and tropical Asia (Table 1, Figure 2: 1-3), forming:

Terminal flower → Monochasium → Compound monochasium (helicoid cyme).

4. Evolutionary trends of flower arrangement in Southeast Asian orchids.

To determine evolutionary trends, it is important to identify the plesiomorphic and apomorphic state in the arrangement of flowers. Therefore, we have first constructed a cladogram for all the studied species of orchids of Southeast Asia on the basis of the comparison of several nucleotide sequences of nuclear genes (Sherbakov and Kharchenko, 2018). Later on, based on it, a number of cladograms were obtained reflecting the sequence of evolutionary events during the formation of the inflorescences. Three cladograms are presented in this paper (Figures 6-8). The diversity in the flower arrangement is due to the stopping of the morphogenesis at an earlier stage of formation, or, on the contrary, the addition of new stages. This indicates the decisive role of heterochrony in the evolution of flower arrangement.

The monochasium is the plesiomorphic (initial) state for all types of flower arrangement (Figure 6), and the compound monochasium and the raceme are apomorphic in comparison. In this case, the compound monochasium is a plesiomorphic state with respect to the simple inflorescence (raceme) (Figure 6), the compound inflorescence (compound monochasium from compound monochasium or helicoid cyme from helicoid cymes) and the aggregate inflorescence (compound monochasium from racemes) (Figure 7). The presence of a terminal flower is an apomorphic state for orchids of Southeast Asia (Figure 8), despite the fact that its formation is the starting point for any type of inflorescence (Maresquell, 1964, 1970; Maresquell and Sell, 1965). Thus, in the phylogeny of the orchids of Southeast Asia, the structure of the inflorescence is repeatedly transformed like morphogenetic changes (Figures 6-8). The transition of a compound monochasium into racemes is quantitative and may occur in orchids under the influence of the environment, as well as the mutations. According to the opinion of Carpenter and Coen (1990), Coen *et al.*, (1990, 1991), Coen and Nugent (1994), Prusinkiewicz *et al.* (2007), such a transition is a consequence of the action of homeotic genes, which should lead to fundamental changes in the program for the structure development and to the aromorphosis (Severtsov, 2008).

5. Does the geographic and environmental conditions of Southeast Asia affect the flower arrangement of orchids?

In his time, Eimer (1898) had expressed the idea of the source of the inflorescence diversity. In the course of the divergence of the species, he noted the different stages of morphogenesis of the inflorescences, however there was no evidence of regulation of this mechanism.

Our study testify to the similarity of morphogenetic transformations, that lead to a sympodial type of the inflorescence growth in Southeast Asian orchids, where the helicoid cyme is most often formed (Table 1, Figures 5 and 7). In truth, the development of the inflorescence is limited at different stages of formation, but consists only of terminal flowers (Figure 1). Further and further from the species origin center, where the conditions favor the maximum or diversity, the variety of

the forms is reduced, due to the increased influence of limiting factors (Mayr 1970). Therefore, the orchids, distributed at the edge of the range, usually have single flowers or their size is reduced (Figure 9). This is due to the fact that increasing the negative impact of limiting factors reduces their reproductive potential, *via* their productivity reduction, resulting in less flowers or their smaller size, which lowers the formation of pollen. Therefore, in the northern regions of Southeast Asia and in the mountains, the evolution often has progressed along the path of reducing the number of flowers up to one, as in the case of *Cymbidium goeringii* (Figure 5: 1, Figures 8-9), or to the formation of inflorescences with many flowers reduced to the minimum size (less than 1cm), as in the case of *Oreorchis patens* (Figure 9). We can therefore highlight the fundamental influence of the environment and geography on the formation of different types of orchid inflorescences, at least for the region of our study. Different conditions can favor one heterochronous mutation and eliminate others, contributing to the selection and divergence in the course of the speciation.

CONCLUSION

We have used reproductive abmodality in flower arrangements (particularly, the heterochrony in morphogenesis) to identify evolutionary trends and the speciation of Southeast Asian orchids. It appears that the source of species divergence is the stopping of inflorescence development to different stages of the morphogenesis. For better considering the formation of the inflorescence structure, we have relied on the fact that the differences between determinate and indeterminate inflorescences are not qualitative, but quantitative and are a consequence of heterochrony, rather than homeostasis.

The variants of the inflorescences development are as follows:

1. Terminal flower → Monochasium → Compound monochasium (helicoid cyme) → Raceme with terminal flower;

2. Terminal flower → Monochasium → Helicoid cyme → Compound monochasium from compound monochasiums (helicoid cyme from helicoid cymes) → Compound monochasium from racemes (helicoid cyme from racemes);

3. Terminal flower → Monochasium → Umbel;

4. Terminal flower → Monochasium → Head → Spike → Spadix;

5. Helicoid cyme → Helicoid cyme from monochasiums → Helicoid cyme from helicoid cymes → Helicoid cyme from racemes.

We have made a review of the evolutionary history of Southeast Asian orchids, taking into account their molecular data, and coordinating them with morphological structure of inflorescence types and some androecium characters. The results of our study will be useful for reconstructing evolutionary history of orchids in connection with their high morphological flower diversity and the inflorescence arrangements. A larger and more detailed analysis will be presented in our further works.

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Annex 1. List of the 150 studied orchids from Southeast Asia

- Acampe** Lindl. (*A. hulae* Telepova, *A. ochracea* (Lindl.) Hochr., *A. praemorsa* (Roxb.) Blatt. & McCann syn. *A. papillosa*, *A. rigida* (Buch.-Ham. ex Sm.) P.F. Hunt)
- Acriopsis** Blume (*A. indica* C.Wright, *A. liliifolia* Reinwardt ex Blume syn. *A. javanica*)
- Aerides** Lour. (*A. crassifolia* C.S.P. Parish ex Burb., *A. falcata* Lindl. & Paxton, *A. houlletiana* Rchb.f., *A. odorata* Lour.)
- Appendicula** Blume (*A. hexandra* (J.König) J.J.Sm., *A. reflexa* Blume)
- Arundina** Blume (*A. graminifolia* (D.Don) Hochr.)
- Ascocentrum** (J.J.Sm.) Schltr. (*A. ampullaceum* (Roxb.) Schltr., *A. miniatum* Lindl.)
- Bletilla** Rchb. f. (*B. striata* (Thunb.) Rchb.)
- Bulbophyllum** Thouars syn. *Cyrrhopetalum* Thouars (*B. careyanum* (Hook.) Spreng., *B. frostii* Summerh., *B. hirtum* (Sm.) Lindl., *B. lepidum* (Blume) J. J. Sm., *B. lobbii* Lindl., *B. medusae* (Lindl.) Rchb., *B. macranthum* Lindl.)
- Calanthe** R.Br. (*C. cardioglossa* Guill., *C. sieboldii* Regel, *C. succedanea* Guillaum., *C. triplicata* (Willemet) Ames, *C. vestita* Lindl.)
- Chelonistele** Kraenzl. (*C. sulphurea* (Blume) Pfitzer)
- Chiloschista** Lindl., *C. lunifera* Rchb.f. (J.J.Sm.), *C. usneoides* (D.Don) Lindl.)
- Cleisostoma** Blume (*C. arietinum* (Rchb.f.) Garay, *C. birmanicum* (Schltr.) Garay, *C. discolor* Lindl., *C. fuerstenbergianum* Kranzl., *C. racemiferum* (Lindl.) Garay, *C. rostratum* (Rchb.f.) Garay, *C. simondii* (Gagnep.) Seidenf., *C. subulatum* Blume, *C. williamsonii* (Rchb.f.) Garay)
- Coelogyne** Lindl. (*C. flaccida* Lindl., *C. lawrenceana* Rolfe, *C. pallens* Ridl., *C. trinervis* Lindl., *C. virescens* Lindl.)
- Cymbidium** Sw. (*C. aloifolium* (L.) Sw., *C. atropurpureum* (Lindl.) Rolfe, *C. chloranthum* Lindl., *C. dayanum* Rchb.f., *C. eburneum* Lindl., *C. ensifolium* (L.) Sw., *C. faberi* Rolfe, *C. floribundum* Lindl., *C. goeringii* Rchb.f., *C. insigne* Rolfe, *C. lancifolium* Hook., *C. lowianum* Rchb.f., *C. serratum* Schltr., *C. tracyanum* Rolfe)
- Cypripedium** L. (*C. calceolus* L., *C. macranthos* Sw.)
- Dendrobium** Sw. (*D. affine* (Decne.) Steud., *D. draconis* Rchb.f., *D. ellipsophyllum* T.Tang. & F.T.Wang, *D. glomeratum* Rolfe, *D. hercoglossum* Rchb.f., *D. moschatum* (Buch.-Ham.) Sw., *D. porphyrochilum* Lindl., *D. uniflorum* Griff.)
- Dipodium** R.Br. (*D. paludosum* (Griff.) Rchb.f.)
- Doritis** Lindl. (*D. boubetii* Telepova, *D. pulcherrima* Lindl. syn. *Phalaenopsis pulcherrima* Lindl.)
- Epipactis** Zinn, (*E. helleborine* (L.) Crantz)
- Eria** Lindl. (*E. lasiopetala* (Willd.) Ormerod, *E. siamensis* Schltr., *E. tomentosa* (J.Koenig) Hook.f., *E. javanica* (Sw.) Blume, *E. biflora* Griff., *E. thao* Gagnep. syn. *Campanulorchis thao* (Gagnep.) S.C.Chen & J.J.Wood)
- Eulophia** Lindl. (*E. graminea* Lindl.)
- Flickingeria** A.D.Hawkes (*F. fimbriata* (Blume) A.D.Hawkes, *F. xantholeuca* Rchb.f.)
- Gastrochilus** D. Don (*G. obliquus* (Lindl.) Kuntze, *G. calceolaris* (Buch.-Ham. ex Sm.) D.Don);
- Geodorum** Jacks (*G. citrinum* Jacks)
- Habenaria** Willd. (*H. rhodocheila* Hance, *H. medusa* Kraenzl.)
- Ludisia** Rich. (*L. discolor* Ker Gawl. (A.Rich.)
- Luisia** Gaudich. (*L. tristis* (G.Forst.) Hook.f., *L. primulina* C.S.P.Parish & Rchb.f.)
- Macropodanthus** L.O.Will. (*M. alatus* (Holtum) Seidenf. & Garay)
- Oberonia** Lindl. (*O. acaulis* Hook.f., *O. rufilabris* Lindl.)
- Oreorchis** Lindl. (*O. patens* Lindl.)
- Paphiopedilum** Pfitzer. (*P. armeniacum* S.C.Chen & F.Y.Liu, *P. appletonianum* (Gower) Rolfe, *P. callosum* (Rchb.f.) Stein, *P. malipoense* S.C.Chen & Z.H.Tsi, *P. rothschildianum* (Rchb.f.) Stein)
- Pelatantheria** Ridl. (*P. bicuspidata* T.Tang. & F.T.Wang, *P. insectifera* (Rchb.f.) Ridl.)
- Phalaenopsis** Blume (*P. amabilis* (L.) Blume, *P. cornu-cervi* (Breda) Blume & Rchb.f., *P. equestris* (Schauer) Rchb.f., *P. lobbii* Rchb.f., *P. stuartiana* Rchb.f., *P. schilleriana* Rchb.f., *P. violacea* Witte)
- Pholidota** Lindl. (*P. chinensis* Lindl., *P. imbricata* Lindl., *P. pallida* Lindl., *P. ventricosa* Rchb.f.)

Pleione D. Don (*P. formosana* Hayata)
Podochilus Schltr. (*P. microphyllus* Lindl.)
Polystachya Hook. (*P. concreta* (Jacq.) Garay & Sweet)
Porpax Lindl. (*P. elwesii* (Rchb.f.) Rolfe)
Renanthera Lindl. (*R. imschootiana* Rolfe, *R. monachica* Ames)
Rhynchostylis Blume (*R. gigantea* Blume, *R. retusa* (L.) Blume)
Robiquetia Gaudich. (*R. minimiflora* (Hook.f.) Kocyan & Schuit., *R. spathulata* (Blume) J.J.Sm.)
Schoenorchis (Blume) Reinw. (*S. fragrans* (Parish & Rchb. f.) Seidenf. & Smitin., *S. gemmata* (Lindl.) J.J.Sm., *S. micrantha* Reinw.)
Seidenfadenia Garay (*S. mitrata* (Rchb.f.) Garay)
Smitinandia Holttum (*S. helferi* (Hook.f.) Garay, *S. micrantha* (Lindl.) Holttum)
Spathoglottis Blume (*S. affinis* de Vriese, *S. eburnea* Gagnepain, *S. plicata* Blume, *S. pubescens* Lindl.)
Thelasis Blume (*T. carinata* Blume, *T. pygmaea* (Griffith.) Blume)
Thrixspermum Lour. (*T. amplexicaule* (Blume) Rchb.f., *T. centipeda* Lour.)
Trias Lindl. (*T. picta* Parish & Rchb.f.)
Trichoglottis Blume (*T. atropurpurea* Rchb.f., *T. pusilla* Teijsm. & Binn.)
Trichotosia Blume (*T. velutina* (Lodd. ex Lindl.) Kraenzl.)
Trudelia Garay (*T. alpina* (Lindl.) Garay, *T. cristata* Lindl.)
Vanda (R.Br.) Jones (*V. tricolor* Lindl., *V. lilacina* Teijsm. & Binn., *V. coerulescens* Griff., *V. brunnea* Rchb.f.)
Vanilla Mill. (*V. annamica* Gagnepain, *V. siamensis* Rolfe, *V. somae* Hayata)
Zeuxine Lindl. (*Z. flava* (Wall. ex Lindl.) Trimen syn *Z. parvifolia* (Ridl.) Seidenf.)