



CHAPTER 1  
INTRODUCTION

## 1.1. INTRODUCTION

Orchids have been very closely associated with human beings since ancient times. The ancient Greeks were the first to take note of these strange plants. The word ‘Orchid’ has been originated from the Greek word ‘*Orchis*’ meaning testicles (Bedford, 1969; George, 1999; Rittershausen et al., 2002). The Greek Philosopher Theophrastus (370 – 285 B.C.) gave the name to a group of bizarre plants having paired, underground testiculate tubers in his book ‘Enquiry into Plants’ (Hort, 1990; Singh et al., 2001). In the Indian Vedic scripture there is a group of plants mentioned under the name Vanda, which has been adapted as a generic name for one of the most beautiful orchid group (Jalal et al., 2008).

Orchids are considered to be the highly evolved of all flowering plants (Waller, 2016). Technically, orchids are the set of flowering plant that exhibits a unique reproductive strategy *i.e.* ‘column’ in which both the male and female reproductive structures fused into a single structure (Arditti et al., 1968; Meisel et al., 2014). Some special floral characteristics comprised of a highly modified petal called ‘labellum’, a landing pad for pollinators. These structures are easy to observe in orchids; but in some orchid flowers due to their miniature size it is difficult to observe the characteristic features; in that case, expert’s assistance is necessary (MacKinnon, 1996; Tibbs, 2008). They are universally admired for their beautiful flowers of myriad shapes, sizes and colors.

The Orchidaceae is one of the largest families of plant kingdom and biologically it is one of the most complex groups of plants. The family comprises about 28,484 species representing 736 genera showing pantropic distribution (Christenhusz and Byng, 2016; Govaerts et al., 2018). Orchids are inhabitant of tropical countries explicating its greatest diversity, which includes tropical forest of South and Central America, Mexico, India, Ceylon, Burma, South China, Thailand, Malaysia, Philippines, New Guinea and Australia (Irawati, 2013). The largest genera among the family are *Bulbophyllum* Thouars (2000 species), *Epidendrum* L. (1500 species), *Dendrobium* Sw. (1400 species) and *Pleurothallis* R. Br. (1000 species) (Whitten et al., 2007).

Hybridization is a most common mechanism of new species formation within the Orchidaceae (Hollick et al., 2005) and newly emerged species were maintained by

explicit pollinator as orchids have an exclusive relationship with their pollinators (Christenson, 2003). More than 1,20,000 natural and manmade hybrids are created and these include several multi-generic hybrids. The natural diversity within and among orchids has often confused taxonomists, resulting in trouble in describing natural groups with the explanation that the family is still actively evolving (Garay, 1960). This is one of the reasons for increasing number of new species of orchids and simultaneously many orchid species are becoming extinct day by day.

## **1.2. ORIGIN OF ORCHIDACEAE**

The family Orchidaceae is considered to have originated between 26 to 110 million years ago (Bremer, 2000; Wikstrom et al., 2001; Janssen and Bremer, 2004; Ramírez et al., 2007). Various taxonomists have proposed conflicting remarks regarding the origin of this family. According to Bentham and Hooker (1883) and Engler and Prantl (1897), it is derived from Burmaniaceae. Hallier (1912) proposed its origin from Scitamineae whereas as per Lawrence (1951) and Cronquist (1988) it arose from Amaryllidaceae. Hutchinson (1969) affirmed Apostasiaceae as the precursor of Orchidaceae. According to Vermeulen (1966) the family was derived from Commelinaceae. Takhtadzhian (1969) found its origin from the genus *Curculigo* of family Hypoxidaceae. Garay (1960, 1972) predicted a polyphyletic origin for this family. Rasmussen (1985) included Apostasiaceae, Cyripediaceae and Orchidaceae together in Orchidales as a monophyletic group, distinct from all other orders in the reduction of the number of stamens and possession of microscopic, non-endospermic seeds.

## **1.3. FAMILY ORCHIDACEAE**

### **1.3.1. General Morphology**

Orchids are annual or perennial herbs that lack any permanent woody structure (Randhawa and Mukhopadhyay, 1986). Depending on the mode of habit they can be terrestrial (growing on the ground) epiphytic (growing on trees), lithophytic (growing on rocks) or mycoheterotrophic (growing on the dead and decaying matter).

**Terrestrial orchids** generally grow under the dense shade of forest floor e.g. *Habenaria* Willd., *Peristylus* Blume (Plate 1.1). The **epiphytic orchids** usually grow on tree trunks and do not harm the host plant, being dependent upon them for support and forms commensalism type of symbiotic relationship with the host e.g. *Rhynchostylis*

Blume, *Vanda* R.Br. (Plate 1.1). **Lithophytic orchids** grow on rocks and absorb nutrients from rain water and nearby decaying plants material e.g. some species of genus *Paphiopedilum* Pfitzer. **Mycoheterotrophic orchids** grows in association with mycorrhizal fungi e.g. *Didymoplexis pallens* Griff., *Aphyllorchis montana* Rchb.f. No mycoheterotrophic orchids have yet been recorded from Gujarat.

The vegetative features in orchids are very diverse, but in general, their common components are root, stem, leaf, flower and fruit.



**Plate 1.1:** Habit of Orchids found in Gujarat (a) Epiphyte; (b) Terrestrial

### 1.3.2. Root

The roots are adventitious in family Orchidaceae. Terrestrial orchids possess underground tubers, bulbs and corms. The epiphytic and lithophytic orchids possess similar root systems which are highly evolved. The utmost adaptation of the epiphytic orchid to its aerial existence is the development of exclusive tissue in the roots called as 'Velamen'. The roots of epiphytes serve the double purpose *i.e.* anchoring and absorption. The velamen tissue reaches its maximum development in epiphytic orchid producing multi layers of cells to prevent collapse. These tissues have cells filled with air in the dry condition, which gives characteristic grey color (Groom, 1893; Engard, 1944; Dycus and Knudson, 1957; Zotz and Winkler, 2013). Mycoheterotrophic orchids possess bunch of coralloid roots and they derive nutrition from the dead and decaying organic materials with the mycorrhizal association with fungus.

### 1.3.3. Stem

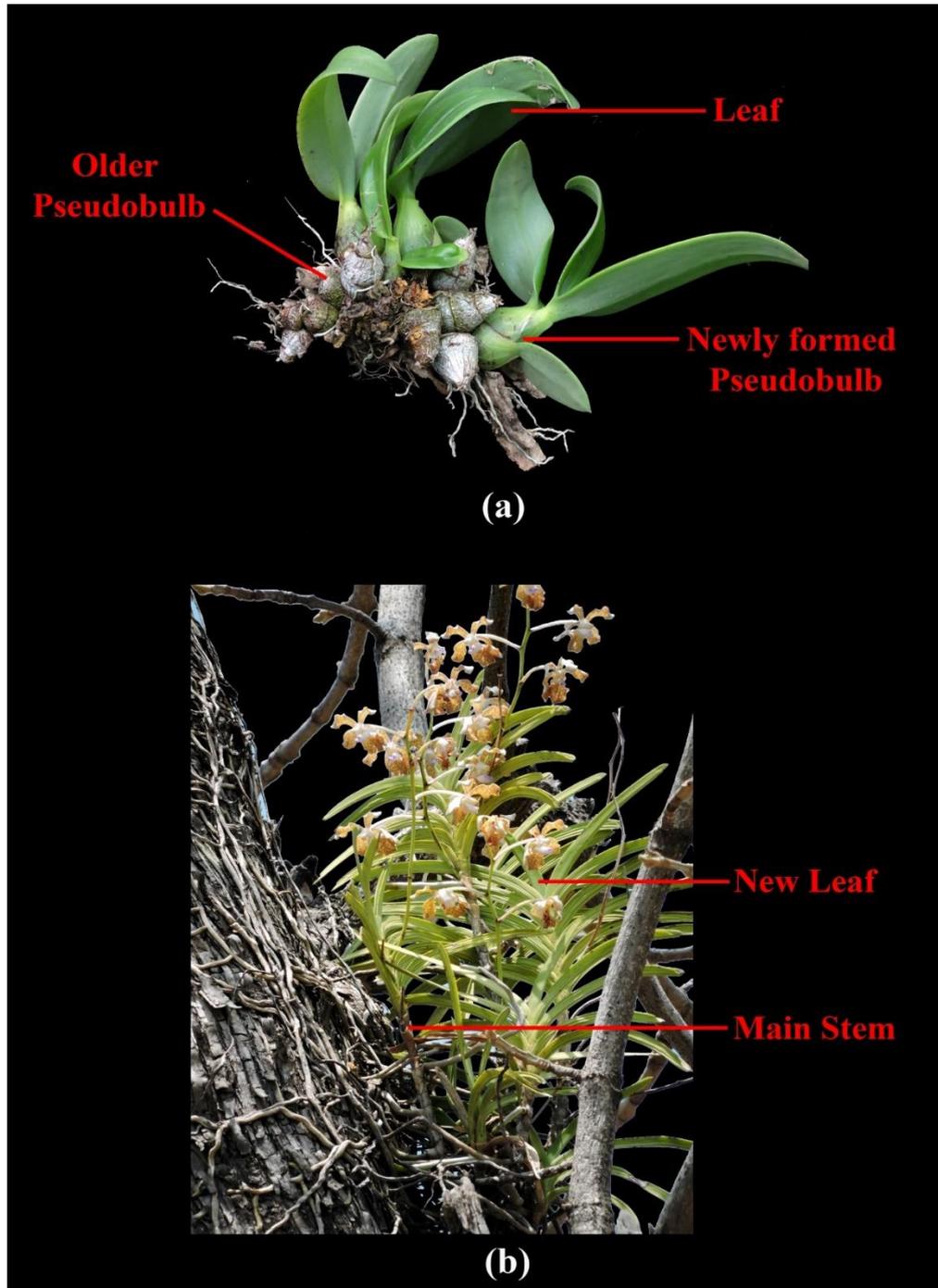
The orchid stems are quite as variable as roots. They may be thin, wiry, tough and rigid to soft and succulent. The foliage shoot often has a main stem with a uniform axis and a single growing point. The aerial shoot emerges from underground modified stem in terrestrial orchids. The underground stem lies in the dormant stage and under favourable condition, they give rise aerial shoots annually. These types of stems have a heavy deposit of reserve food. The modified underground stem often is in the form of a corm e.g. *Eulophia* R.Br. and *Geodorum* Andrews. Genera like *Liparis* Rich. and *Crepidium* Blume has pseudobulb. Pseudobulb stores water and food. More the amount of food and water stored leads to enlargement of pseudobulb as well as an increase in its fleshy content.

The stem morphology of epiphytic orchids is more variable than terrestrial orchids. Based on the morphology of stem, epiphytic orchids are divided into two groups either sympodial or monopodial (Fitch, 2004; Hew and Yong, 2004; Squire, 2005).

- **Sympodial** (many footed) have stems with determinate growth. The creeping rhizome produces pseudobulb each year, it grows to a certain size, bloom, then stop growing and replaced by the new pseudobulb from the sides of the older one next year. e.g. *Dendrobium* Sw. (Plate 1.2).

- **Monopodial** (one footed): have stem with indeterminate growth and new shoots grow upwards from a single stem which originates at the end of the old shoots. It then produces leaves and flowers along the stem. The stem of these orchids can reach a length of several meters as in the genera *Vanda* R.Br., *Rhynchostylis* Blume (Plate 1.2).

In case of mycoheterotrophic orchids stems are slender and colorless (Leake, 1994).



**Plate 1.2:** Growth forms of Epiphytic Orchids (a) Sympodial; (b) Monopodial

#### 1.3.4. Leaves

The leaves are usually same as that of other monocotyledons, although some Vanilloideae have a reticulate venation. Leaves are alternate, rarely opposite or whorled, simple, often distichous and sometimes closely imbricate, occasionally reduced to scales, membranous, coriaceous or succulent, sheathing basally with the sheath generally closed and enveloping the stem (Jakubská-Busse et al., 2017).

In terrestrial species, leaves are long and plicate or short, elliptic, oblong or linear, ovate, but always with sheathing bases. As an exception, leaves are orbicular in *Nervilia* Comm. ex Gaudich. (Jalal et al., 2009). Some orchid species possess velvety leaves with silver golden veins providing beautiful ornamentation (e.g. *Anoectochilus* Blume, *Haemaria* Lindl.) (McDonald, 1999; Singh, 2015).

In epiphytic and lithophytic species, leaves are thick and coriaceous to reduce the transpiration rate. In many species they perform the function of storage as in terete leaves of *Vanda* Jones ex R. Br., *Rhynchostylis* Blume, *Aerides* Lour., *Acampe* Lindl., etc (Baruah, 1978; Averyanov et al., 2014). In some species leaves are long, linear and ensiform, often reaching up to a length of half meter e.g. *Cymbidium* Sw. (Loudon, 1829). The leaves of *Oberonia* Lindl. are laterally compressed and succulent (Teoh, 2016). In some species, leaves are much reduced and deciduous and the stem is also much reduced with spreading succulent leaves which perform the function of photosynthesis (*Chiloschista* Lindl. and *Taeniophyllum* Blume.) (Stern et al., 2014; Gray, 2015).

In mycoheterotrophic orchids leaves are reduced to widely spaced achlorophyllous scales on the inflorescence axis. In spite of preparing food from photosynthesis, they get nourished from a mutual relationship between fungi and plants root (Leake, 1994).

#### 1.3.5. Inflorescence

Inflorescences are usually terminal or lateral raceme, varies from one to many flowered in almost all the habits of orchids. Usually, the inflorescences are produced from a leafy shoot but in few genera like *Bulbophyllum* Thouars, *Dendrobium* Sw. leaves are shed before flowering (Pellegrino et al., 2010; Ferry, 2013).

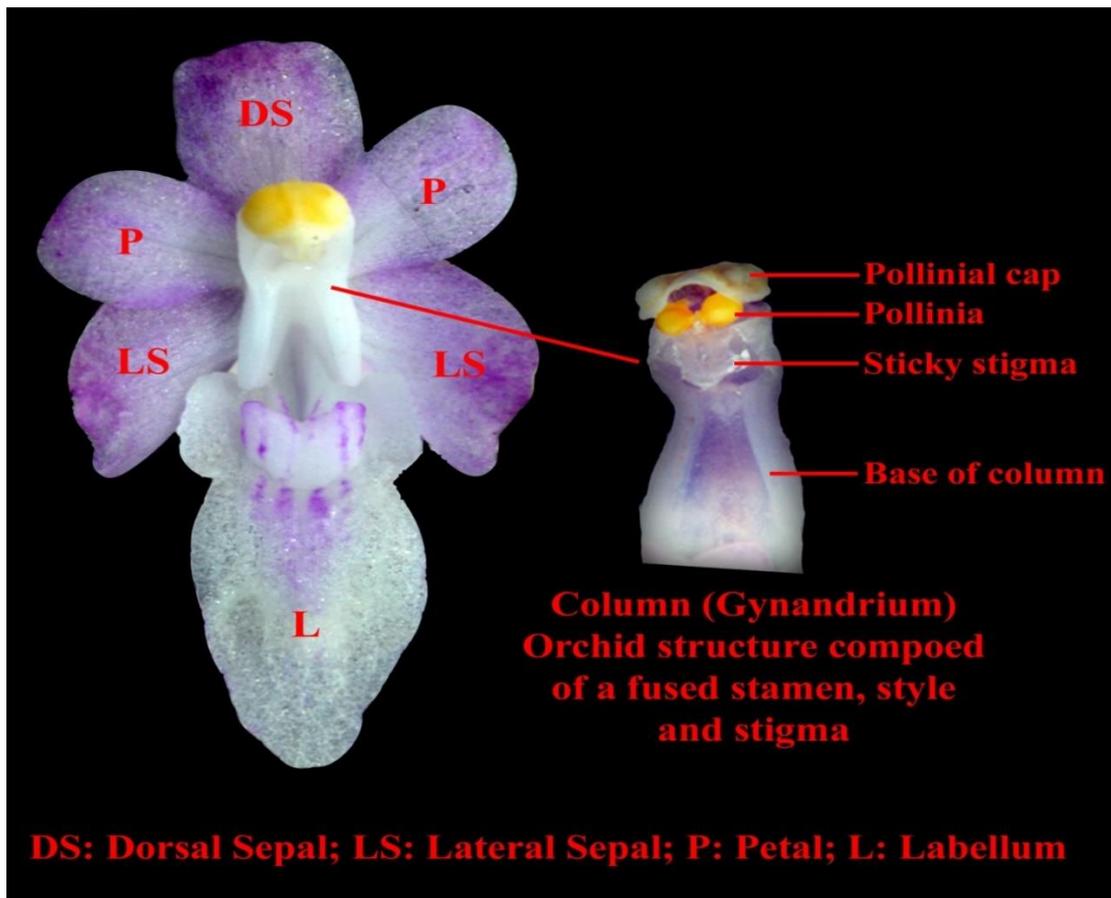
### 1.3.6. Flower

Orchid flowers exhibit a wide range of variations. There is an immense disparity in size of orchid flowers, which ranges from the minute flowers of *Platystele cornejoi* Luer, Central America, which are no more than 2 mm across, to the large ones in *Grammatophyllum speciosum* Blume, New Guinea, which may be greater than 25 cm across. The most unusual is an Australian genus *Rhizanthella* R. S. Rogers (3 species), which lives and flowers completely underground (George, 1981).

Resupination is the typical phenomenon observed in most of the orchid flowers. In the majority of the species labellum is on the upper side in flower buds but it becomes lowermost when the bud blooms. This reversion in the position of labellum takes place as a result of a phenomenon called resupination (Hill, 1939; Arditti, 2003). In most species, the buds turn at 180° to place the labellum lowermost. Non resupinate flowers with labellum on the uppermost position either do not undergo for resupination at all (e.g. *Calopogon* R.Br.) (Ames, 2005; Fowler, 2005) or twist at 360° ending up as they started (e.g. *Crepidium* Blume) (Kull and Arditti, 2013). In all cases labellum plays a key role in pollination process and serves as a landing pad for pollinators.

Flowers are usually bisexual and/or rarely unisexual e.g. *Catasetum* Rich. ex Kunth (Oliveira et al., 2010; Franken et al., 2016), *Cynoches* Lindl. (Cullina, 2004; Meisel et al., 2014), *Mormodes* Lindl. (Stern and Judd, 2001; Salazar et al., 2016), zygomorphic, bracteate, sessile or pedicelled, bilateral, mostly resupinated; **Perianth** encompass six segments in two series exhibiting trimerous pattern. The outer series comprises three **sepals**, two lateral sepals slightly differ from the dorsal one and sometimes connate in a short or long sac or spur like base (mentum). The inner series comprises three **petals**, among them two lateral petals resemble the dorsal sepal and the dorsal petal is usually larger and extraordinarily different, called as **labellum** (or **lip**). The labellum is greatly modified with or without spur. The major evolutionary trait in orchids is fusion of male and female organs called as **column** or **Gynostemium**. At the top of column is anther which contains discrete mass of pollen called **pollinia** (single pollinium), which are covered by a pollinial cap. The pollinia are attached to a sticky mass called a **viscidium**. They are attached to viscidium either directly or by a stalk called **stipe** in epiphytic orchids and **caudicle** in terrestrial ones. **Ovary** tricarpeal, syncarpous, inferior, usually unilocular with parietal placentation rarely trilobular with

axile placentation e.g. *Neuwiedia* Blume, *Selenipedium* Rchb.f., *Apostasia* Blume; ovules many, minute. Just beneath the anther is **Rostellum** which is a result of modification of one of the stigma. It separates the anther from functional stigma and commonly prevents self-fertilization (Woltering and Harren, 1989; Darwin, 1899). Beneath the rostellum is a hollow cavity which is the functional stigma of the flower. It is covered by the sticky substance which helps to hold the pollinia during the process of pollination (Plate 1.3) (Johnson and Edwards, 2000; Rudall and Bateman, 2002; Simpson, 2006).



**Plate 1.3:** Details of an Orchid Flower

### 1.3.7. Fruit

In almost all the forms of orchid habits fruits are dehiscent capsule. In some basal groups, the fruits are fleshy berries (e.g. *Cyrtosia* Blume, *Neuwiedia* Blume, *Palmorchis* Barb. Rodr., *Vanilla* Plum. ex Mill.). Capsule dehisces by 3 – 6 hygroscopically sensitive valves which remain connate apically (Ackerman and Montalvo, 1990; Rasmussen and Johansen, 2006; Ariyaratne, 2014).

### **1.3.8. Seed**

Orchid capsule typically possesses millions of dusts like, minute, wind dispersed seeds. The seed size varies from 0.1 – 6.0 mm. The fresh orchid seeds are white, brown or dark brown in color but can also be beige, yellow, reddish, orange, greenish, yellowish brown or black. The seeds are characterized by a thin balloon-like seed coat and lack of endosperm (Barthlott et al., 2014). Orchid seeds when comes in contact with fungal host then only it will germinate (Cribb and Bailes, 1989; Backhouse and Jeanes, 1995).

### **1.4. DISTINGUISHING FEATURES OF ORCHIDACEAE**

- The presence of an odd petal called labellum with spur without spur.
- The presence of a column called as Gynostemium.
- Pollens are packed together into the pollinia or pollinium, a mass of waxy pollen.
- The seeds are minute, dust like and numerous.
- The seeds can only germinate in symbiosis with specialized fungi called as mycorrhizae under natural circumstances.

### **1.5. SYSTEMATIC OF ORCHIDACEAE**

The systematic of Orchidaceae began with the classification by Linnaeus (1753), who recognized eight genera and placed them in “Classis XX Gynandria Diandria”. Swartz (1805) provided the identification key for 25 genera and classified them on the basis of the number of anthers, which formed the basis for sub-familial classification. On the basis of Swartz’s classification, Lindley (1840), the father of orchid taxonomy, classified 3000 species of orchids in seven tribes on the basis of the number of fertile anthers and pollen structure. He was the first to classify the family into tribes. However, Bentham (1881) reframed Lindley’s classification recognizing five tribes *viz.* Epidendreae, Vandae, Neottieae, Ophrydeae and Cyripedieae which were further divided into 27 subtribes. Pfitzer (1887) criticized the classification of Bentham and laid more emphasis on vegetative characters by recognizing 32 tribes and a number of subtribes. Based on Pfitzer’s (1887) classification, Schlechter (1926) proposed the classification considering both vegetative as well as floral characters. He recognized four tribes and the remaining tribes and subtribes of Pfitzer’s classification were treated as subtribes. The Schlechter’s system of classification was conflicting with the nomenclature rules proposed at that time, therefore, Dressler and Dodson (1960) slightly

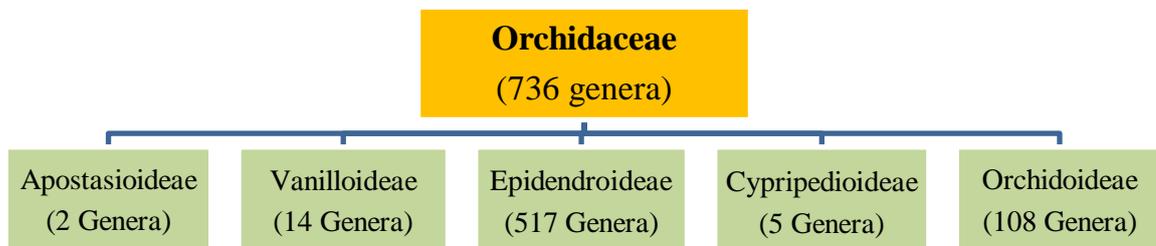
changed the classification to bring it into compliance with the ICBN. They recognized 40 subtribes in two subfamilies *i.e.* Cyripedioideae (including *Apostasia* and *Neuwiedia*) and Orchidoideae. Garay (1972) considered the additional characters *i.e.* vasculature of flower, embryology, seeds etc. and divided the family into five subfamilies, *viz.* Apostasioideae, Cyripedioideae, Orchidoideae, Neottioideae and Epidendroideae. Dressler (1974) revised the classification of Orchidaceae formerly projected by him along with Dodson (1960), by addition of the subfamily Apostasioideae, as proposed by Garay (1972). Dressler (1981) again revised his earlier proposed classification by recognizing six sub-families. The three newly added sub-families were Epidendroideae, Spiranthoideae and Vandoideae by considering additional characters *i.e.* column structure and subsidiary cell development.

The most accepted classification system of the family Orchidaceae was proposed by Dressler (1993) based on the anther morphology. According to this classification, Orchidaceae comprises 20,000 species under 850 genera, arranged in 70 sub-tribes, 22 tribes and five sub-families. The five sub-families were Apostasioideae, Cyripedioideae, Orchidoideae, Spiranthoideae and Epidendroideae, the last being the largest. The main drawback of Dressler's classification (1993) was a narrow treatment of Neottiid orchids, as they were kept within sub-family Epidendroideae (Dressler, 1993; Chase, 2005). The other controversial group was Vanilloids, in which the columns are like those of the Epidendroids, but vegetatively they are highly divergent (Cameron and Dickison, 1998; Stern and Judd, 2001; Chase, 2005).

The classification of orchids based on the morphology of flower could never be accurate as they are greatly susceptible to morphological plasticity due to pollinator selection pressure, yet floral characters were used traditionally to classify the family (Dressler and Dodson, 1960; Dressler, 1974, 1981, 1993). With the increasing availability of DNA data and molecular phylogenetic studies, slight different relationships among sub-families, tribes and sub-tribes have been revealed. The pioneering DNA based studies of Cameron et al. (1999) and Chase (2005) had pointed out different patterns of relationships within Orchidaceae as compared to the morphological cladistics of Dressler (1993). Subsequent to these two initial reports, numerous DNA based phylogenetic analysis have been published, at the level of family (Cameron, 2004; Freudenstein et al., 2004), sub-families (Neyland and Urbatsch, 1995,

1996; Cox et al., 1997; Freudenstein and Chase, 2001), tribes (Douzery et al., 1999; Goldman et al., 2001; Kores et al., 2001) and sub-tribes (Yukawa et al., 1996; Cozzolino et al., 1998; Pridgeon et al., 2001; Clements, 2003; Berg et al., 2005). Based on these relationship patterns, as revealed by different DNA regions, a new classification of Orchidaceae was proposed by Chase et al. (2003). The new classification based on both morphological and molecular data divided the family Orchidaceae into five subfamilies – Apostasioideae, Vanilloideae, Cyripedioideae, Epidendroideae and Orchidoideae. In this classification, the members of the Neottioideae, were distributed in Epidendroideae and Orchidoideae (Garay, 1972). The fifth family named as Vanilloideae was created by assembling some members, which were earlier included in Epidendroideae and which have distinct morphological characters, such as, reticulate venation and crustose seeds (Chase et al., 2003). After the last classification of Chase et al., in 2003, he again revised the classification by including a list of 736 newly recognized genera. The major changes have occurred in subfamily Epidendroideae and Orchidoideae (Chase et al., 2015).

Recently, the APG IV system (Angiosperm Phylogeny Group III system) has been published according to which Orchidaceae belongs to group Asparagales, and is further divided into 5 subfamilies - Apostasioideae, Vanilloideae, Cyripedioideae, Orchidoideae and Epidendroideae (APG IV, 2016) (Figure 1.1).



**Figure 1.1:** Sub familial Classification of Orchidaceae (Chase et al., 2016)

## 1.6. THREATS TO ORCHIDS

Orchids are very sensitive toward habitat change which leads to a restricted distribution of certain species. Orchid habitats are under risk globally due to fast urbanization and industrialization. Many species are becoming threatened due to habitat change, degradation, fragmentation and destruction. Various anthropogenic activities such as land development activities, the building of dams, constructions of roads, mining, hydroelectric power projects, wind mills and large scale agricultural expansion play a chief role in the reduction of habitats (Kumar et al., 2006, 2007). Furthermore, the

monoculture plantations, collection of the orchid bulbs for livelihood and medicinal purposes, mass over-collection due to fascination, leads to exploitation of orchids.

The change in Global climatic conditions affects the local climate of the region e.g. rainfall patterns. With commencing of rainy season number of terrestrial orchids start their lifecycle *i.e.* *Habenaria* Willd., *Peristylus* Blume and *Nervilia* Comm. ex Gaudich. and the change in rainfall pattern affects their life cycle. Impacts of invasive species also pose threats to ground orchids. Many species of orchids were extinct which were commonly available earlier in India. For instance, *Paphiopedilum druryi* Bedd. Stein., once found abundantly in Agastyamalai Hills (Jalal and Jayanthi, 2012) in Southern India is now difficult to locate. *In-situ* and *ex-situ* conservation efforts are necessary to provide sound conservation plans for threatened species in the wild (Cribb et al., 2003).

Plenty of orchid species were reported from all over India but still, there is no detailed scientific documentation carried out in Gujarat. There is sporadic information available on orchids of Gujarat state. No significant efforts have been made to study the detailed taxonomic and distributional status of orchids in Gujarat. There is all probability that there are more members of orchids in various parts of Gujarat. However, in-depth study will reveal the status of the orchids. It is a forwarding step for surveying and documenting the orchid wealth of the state for conserving the threatened and endangered species of orchids and to make people aware about the importance of the orchids aesthetically as well as medicinally that can reduce over exploitation of indicator species of an ecosystem and endemic and threatened orchid taxa from the wild habitat.

### 1.7. OBJECTIVES

The present study was planned to explore and document the orchid diversity in Gujarat with following objectives:

1. Survey of orchids within the state.
2. Detailed taxonomic identification
3. *Ex-situ* conservation.
4. DNA barcoding for identification of orchids.
5. Leaf anatomy of orchids.
6. Phytochemical analysis of some ethnobotanically important orchid species.

**1.8. REFERENCES**

- Ackerman, J.D., Montalvo, A.M., 1990. Short- and Long-Term Limitations to Fruit Production in a Tropical Orchid. *Ecology* 71, 263 – 272.  
<https://doi.org/10.2307/1940265>
- Ames, D.E., 2005. Orchids of Manitoba: A Field Guide. Native Orchid Conservation, Incorporated Press, 1 – 158.
- APG IV, 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181, 1 – 20.  
<https://doi.org/10.1046/j.1095-8339.2003.t01-1-00158.x>
- Arditti, J., 2003. Resupination. *Lankesteriana* 7, 95 – 96.
- Arditti, J., Vander Pijl, L., Dodson, C.H., 1968. Orchid Flowers: Their Pollination and Evolution. *Bioscience* 18, 452 – 453.
- Ariyaratne, A.M.W., 2014. Fruits of Orchids : Have You Ever Noticed ? *Young Res. Forum-PGIS* 1, 10 – 12. <https://doi.org/10.13140/RG.2.2.18851.66083>
- Averyanov, L., Loc, P., Canh, C., 2014. *Aerides phongii* (Orchidaceae), a new species from Southern Vietnam. *Turczaninowia* 17, 6 – 9.  
<https://doi.org/10.14258/turczaninowia.17.1.2>
- Backhouse, G., Jeanes, J., 1995. The orchids of Victoria. Miegunyah Press, 1 – 388.
- Barthlott, W., Große-Veldmann, B., Korotkova, N., 2014. Orchid seed diversity: A scanning electron microscopy survey. Berlin: Botanical Garden and Botanical Museum Berlin-Dahlem, 1 – 245.
- Baruah, B., 1978. Studies on systematics of orchids in the Brahmaputra valley Assam. Gauwhati University, Ph.D. Thesis.
- Bedford, R.B., 1969. A guide to native Australian orchids. Angus and Robertson Press, 1 – 134.
- Bentham, G., 1881. Notes on Orchidaceae. *Bot. J. Linn. Soc.* 18, 281 – 360.

- Bentham, G., Hooker, J.D., 1883. *Genera Plantarum ad exemplaria imprimis in herbariis Kewensibus servata definita*, 1 – 317. <https://doi.org/10.1038/028485a0>
- Berg, C., Goldman, D.H., Freudenstein, J.V., Pridgeon, A.M., Cameron, K.M., Chase, M.W., 2005. An overview of the phylogenetic relationships within Epidendroideae inferred from multiple DNA regions and recircumscription of Epidendreae and Arethuseae (Orchidaceae). *Am. J. Bot.* 92, 613 – 624. <https://doi.org/10.3732/ajb.92.4.613>
- Bremer, K., 2000. Early Cretaceous Lineages of Monocot Flowering Plants. *Proc. Natl. Acad. Sci.* 97, 4707 – 4711. <https://doi.org/10.1073/pnas.080421597>
- Cameron, K.M., 2004. Utility of plastid *psaB* gene sequences for investigating intrafamilial relationships within Orchidaceae. *Mol. Phylogenet. Evol.* 31, 1157 – 1180. <https://doi.org/10.1016/j.ympev.2003.10.010>
- Cameron, K.M., Chase, M.W., Whitten, W.M., Kores, P.J., Jarrell, D.C., Albert, V.A., Yukawa, T., Hills, H.G., Goldman, D.H., 1999. A phylogenetic analysis of the Orchidaceae: Evidence from *rbcL* nucleotide sequences. *Am. J. Bot.* 86, 208 – 224. <https://doi.org/10.2307/2656938>
- Cameron, K.M., Dickison, W.C., 1998. Foliar architecture of vanilloid orchids: next term insights into the evolution of reticulate leaf venation in monocotyledons. *Bot. J. Linn. Soc.* 128, 45 – 70. <https://doi.org/10.1111/j.1095-8339.1998.tb02106.x>
- Chase, M., Cameron, K., Barrett, R., Freudenstein, J.V., 2003. DNA data and Orchidaceae systematics: a new phylogenetic classification. *Orchid Conserv.* 69 – 89.
- Chase, M.W., 2005. Classification of Orchidaceae in the age of DNA data. *Curtis's Bot. Mag.* 22, 2 – 7. <https://doi.org/doi:10.1111/j.1355-4905.2005.00466.x>
- Chase, M.W., Cameron, K.M., Freudenstein, J. V., Pridgeon, A.M., Salazar, G., Berg, C., Schuiteman, A., 2015. An updated classification of Orchidaceae. *Bot. J. Linn. Soc.* 177, 151 – 174. <https://doi.org/10.1111/boj.12234>
- Christenhusz, M.J.M., Byng, J.W., 2016. The number of known plants species in the world and its annual increase. *Phytotaxa* 261, 201 – 217.

<https://doi.org/10.11646/phytotaxa.261.3.1>

- Christenson, E.A., 2003. Machu Picchu Orchids: A Manual to the Orchids of the Machu Picchu Historical Sanctuary. Fondo Nacional para Areas Naturales Protegidas por el Estado, 1 – 202.
- Clements, M.A., 2003. Molecular phylogenetic systematics in the Dendrobiinae (Orchidaceae), with emphasis on *Dendrobium* section Pedilonum. Telopea 10, 247 – 298.
- Cox, A.V, Pridgeon, A.M., Albert, V.A., Chase, M.W., 1997. Phylogenetics of the slipper orchids (Cypripedioideae, Orchidaceae): nuclear rDNA ITS sequences. Plant Syst. Evol. 208, 197 – 223.
- Cozzolino, S., Aceto, S., Caputo, P., Gaudio, L., Nazzaro, R., 1998. Phylogenetic relationships in *Orchis* and some related genera: An approach using chloroplast DNA. Nord. J. Bot. 18, 79 – 87.
- Cribb, P., Bailes, C., 1989. Hardy orchids: Orchids for the Garden and frost-free glasshouse. Timber Press, North America, 1 – 176.
- Cribb, P.J., Kell, S.P., Dixon, K.W., Barrett, R.L., 2003. Orchid Conservation: A global Perspective. Orchid Conserv. 1 – 24.
- Cronquist, A., 1988. The evolution and classification of flowering plants. New York Botanical Garden, 1 – 503.
- Cullina, W., 2004. Understanding Orchids: An Uncomplicated Guide to Growing the World's Most Exotic Plants. Houghton Mifflin, 1 – 260.
- Darwin, C., 1899. The various contrivances by which Orchids are fertilised by insects. John Murray, London, New York, 1 – 273.
- Douzery, E.J.P., Pridgeon, A.M., Kores, P., Linder, H.P., Douzery, E.J.P., Pridgeon, A.M., Kores, P., Linder, H.P., Kurzweil, H., Chase, M.W., 1999. Molecular Phylogenetics of *Dendrobium* (Orchidaceae): A Contribution from Nuclear Ribosomal ITS Sequences. Am. J. Bot. 86, 887 – 899.

- Dressler, R., 1974. Classification of the orchid family, in: Proc. 7<sup>th</sup> World Orchid Conf., Medellin. World Orchid Conference Trust, Medellin, Redout, South Africa, 259 – 279.
- Dressler, R.L., 1981. The orchids: natural history and classification. Harvard University Press, 1 – 332.
- Dressler, R.L., 1993. Phylogeny and Classification of the Orchid Family. Cambridge University Press, 1 – 314.
- Dressler, R.L., Dodson, C.H., 1960. Classification and Phylogeny in the Orchidaceae. Ann. Missouri Bot. Gard. 47, 25 – 68.
- Dycus, A.M., Knudson, L., 1957. The Role of the Velamen of the Aerial Roots of Orchids. Bot. Gaz. 119, 78 – 87. <https://doi.org/10.1086/335966>
- Engard, C.J., 1944. Morphological Identity of the Velamen and Exodermis in Orchids. Bot. Gaz. 105, 457 – 462. <https://doi.org/10.1086/335255>
- Engler, A., 1897. Die Natürlichen Pflanzenfamilien, 1 – 474. <https://doi.org/10.1017/CBO9781107415324.004>
- Ferry, R.J., 2013. Inflorescence types. MIOS J. 14, 2 – 8.
- Fitch, C.M., 2004. The Gardener's Guide to Growing Orchids, Brooklyn Botanic Garden, 1 – 128.
- Fowler, J.A., 2005. Wild Orchids of South Carolina: A Popular Natural History. University of South Carolina Press, 1 – 242.
- Franken, E.P., Pansarin, L.M., Pansarin, E.R., 2016. Osmophore diversity in the *Catasetum cristatum* alliance (Orchidaceae: Catasetinae). Lankesteriana 16, 317 – 327. <https://doi.org/10.15517/lank.v16i3.26649>
- Freudenstein, J.V., Berg, C., Goldman, D.H., Kores, P.J., Molvray, M., Chase, M.W., 2004. An expanded plastid DNA phylogeny of Orchidaceae and analysis of jackknife branch support strategy. Am. J. Bot. 91, 149 – 157. <https://doi.org/10.3732/ajb.91.1.149>

- Freudenstein, J.V., Chase, M.W., 2001. Analysis of Mitochondrial nad1b-c Intron Sequences in Orchidaceae : Utility and Coding of Length-Change Characters. *Syst. Bot.* 26, 643 – 657.
- Garay, L.A., 1960. On the origin of the Orchidaceae. *Bot. Museum Leafl.* 19, 57 – 96.
- Garay, L.A., 1972. On the origin of the Orchidaceae II. *J. Arnold Arbor.* 53, 202 – 215.
- George, A.S., 1981. *Rhizanthella*-The Underground Orchid of Western Australia. *Proc. Orchid Symp. 13th Int. Bot. Congr.* 77 – 78.
- George, I., 1999. *The Nature Guide to New Zealand Native Orchids.* Random House Press, New Zealand, 1 – 176.
- Goldman, D.H., Freudenstein, J. V, Kores, P.J., Molvray, M., Jarrell, D.C., Whitten, W.M., Cameron, K.M., Jansen, R.K., Chase, M.W., 2001. Phylogenetics of Arethuseae (Orchidaceae) based on Plastid matK and rbcL Sequences. *Syst. Bot.* 26, 670 – 695. <https://doi.org/10.1043/0363-6445-26.3.670>
- Govaerts, R., Bernet, P., Kratochvil, K., Gerlach, G., Carr, G., Alrich, P., Pridgeon, A.M., Pfahl, P., Campacci, M.A., Baptista, D.H., Tigges, H., Shaw, J., Cribb, P., George, A., Kreuz, K., Wood, J., 2018. World Checklist of Orchidaceae. URL <http://wmsp.science.kew.org>
- Gray, B., 2015. Three new species of *Taeniophyllum* Blume (Orchidaceae) from northern Queensland. *Austrobaileya* 9, 382 – 392.
- Groom, P., 1893. Botanical Notes, No. 4. On the Velamen of Orchids. *Ann. Bot.* 7, 143 – 151.
- Hallier, H., 1912. L'origine et le système phylétique der Angiospermes exposés à l'aide de leur arbre généalogique. *Arch. Néerl. Sci.* 1, 146 – 234.
- Hew, C.S., Yong, J.W.H., 2004. *The Physiology of Tropical Orchids in Relation to the Industry.* World Scientific Press, 1 – 370.
- Hill, A.W., 1939. Resupination Studies of Flowers and Leaves. *Ann. Bot.* 3, 871 – 887.

- Hollick, P.S., Taylor, R.J., McComb, J.A., Kingsley W. Dixon, 2005. If Orchid Mycorrhizal Fungi Are So Specific , How Do Natural Hybrids Cope? *Selbyana* 26, 159 – 170.
- Hort, A., 1990. *Theophrastus Enquiry into plants*, Loeb classical library. W. Heinemann, 1 – 516.
- Hutchinson, J., 1969. *Evolution and Phylogeny of Flowering Plants: Dicotyledons Facts and Theory*. Blackwell Science Academic Press, 1 – 717.
- Irawati, 2013. Conservation of Orchids the Gems of the Tropics, in: Normah, M.N., Chin, H.F., Reed, B.M. (Eds.), *Conservation of Tropical Plant Species*. Springer New York, 171 – 187. [https://doi.org/10.1007/978-1-4614-3776-5\\_9](https://doi.org/10.1007/978-1-4614-3776-5_9)
- Jakubská-Busse, A., Żołubak, E., Łobas, Z., Gola, E.M., 2017. Leaf arrangements are invalid in the taxonomy of orchid species. *PeerJ*. 5, e3609. <https://doi.org/10.7717/peerj.3609>
- Jalal, J., Jayanthi, J., 2012. Endemic orchids of peninsular India: a review. *J. Threat. Taxa* 4, 3415 – 3425.
- Jalal, J.S., Kumar, P., Pangtey, Y.P.S., 2008. Ethnomedicinal Orchids of Uttarakhand, Western Himalaya. *Ethnobot. Leaflet*. 12, 1227 – 1230.
- Jalal, J.S., Tewari, L.M., Pangtey, Y., 2009. *Nervilia gammieana*. *J. Am. Sci.* 5, 91 – 94.
- Janssen, T., Bremer, K., 2004. The age of major monocot groups inferred from 800+ rbcL sequences. *Bot. J. Linn. Soc.* 146, 385 – 398. <https://doi.org/10.1111/j.1095-8339.2004.00345.x>
- Johnson, S.D., Edwards, T.J., 2000. The structure and function of orchid pollinaria. *Plant Syst. Evol.* 222, 243 – 269. <https://doi.org/10.1007/BF00984105>
- Kores, P.J., Molvray, M., Weston, P.H., Hopper, S.D., Brown, A.P., Cameron, K.M., Chase, M.W., 2001. A phylogenetic analysis of Diurideae (Orchidaceae) based on plastid DNA sequence data. *Am. J. Bot.* 88, 1903 – 1914. <https://doi.org/10.2307/3558366>

- Kull, T., Arditti, J., 2013. *Orchid Biology VIII: Reviews and Perspectives*. Springer Netherlands, 1 – 81.
- Kumar, P., Jalal, J.S., Rawat, G.S., 2007. *Orchidaceae, Chotanagpur, state of Jharkhand, India.*, in: *Check List*. 297 – 304.
- Kumar, P., Pandey, A.K., Rawat, G.S., Jalal, J.S., 2006. Diversity and conservation of orchids in state of Jharkhand, in: *Plant Taxonomy: Advances & Relevance*. CBS Publishers and Distributors, 345 – 353.
- Lawrence, G., 1951. *Taxonomy of Vascular Plants*. New York: The Macmillan Company Press, 823. <https://doi.org/10.1126>
- Leake, J.R., 1994. The biology of myco-heterotrophic ('saprophytic') plants. *New Phytol.* 127, 171– 216.
- Lindley, J., 1840. *The Genera and Species of Orchidaceous Plants*. Ridgways, Piccadilly, 1 – 553.
- Linnaeus, C., 1753. *Species plantarum*. Impensis G. C. Nauk, 1 – 560.
- Loudon, J.C., 1829. *An Encyclopaedia of Plants*. Longman, 1 – 1161.
- MacKinnon, K., 1996. *The Ecology of Kalimantan, Ecology of Indonesia series*. Periplus Editions, 1 – 870.
- McDonald, E., 1999. *Ortho's All about Orchids*. Meredith Books, 1 – 96.
- Meisel, J.E., Kaufmann, R.S., Pupulin, F., Cribb, P.J., 2014. *Orchids of Tropical America: An Introduction and Guide*. Cornell University Press, 1– 272.
- Neyland, R., Urbatsch, L.E., 1995. A terrestrial origin for the Orchidaceae is suggested by a phylogeny inferred from *ndhF* chloroplast gene sequences. *Lindleyana* 10, 244 – 251.
- Neyland, R., Urbatsch, L.E., 1996. Phylogeny of Subfamily Epidendroideae (Orchidaceae) Inferred from *ndhF* Chloroplast Gene Sequences. *Am. J. Bot.* 83, 1195 – 1206.

- Oliveira, L.V.R., Faria, R.T., Fátima Ruas, C., Ruas, P.M., Oliveira Santos, M., Carvalho, V.P., 2010. Genetic analysis of species in the genus *Catasetum* (Orchidaceae) using RAPD markers. *Brazilian Arch. Biol. Technol.* 53, 375 – 387. <https://doi.org/10.1590/S1516-89132010000200017>
- Pellegrino, G., Bellusci, F., Musacchio, A., 2010. The effects of inflorescence size and flower position on female reproductive success in three deceptive orchids. *Bot. Stud.* 51, 351 – 356.
- Pfitzer, E.H.H., 1887. Entwurf einer Natürlichen Anordnung der Orchideen. C. Winter's Universitätsbuchhandlung, 1 – 108.
- Pridgeon, A.M., Cribb, P.J., Chase, M.W., Rasmussen, F., 2001. *Genera Orchidacearum: Volume 2. Orchidoideae, Genera Orchidacearum.* OUP Oxford Press, 1 – 438.
- Ramírez, S.R., Gravendeel, B., Singer, R.B., Marshall, C.R., Pierce, N.E., 2007. Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. *Nature* 448, 1042 – 1045. <https://doi.org/10.1038/nature06039>
- Randhawa, G.S., Mukhopadhyay, A., 1986. *Floriculture in India.* Allied Publishers, 1–660.
- Rasmussen, F.N., 1985. Superorder Liliiflorae, in: *The Families of the Monocotyledons.* 107 – 274.
- Rasmussen, F.N., Johansen, B., 2006. Carpology of Orchids. *Selbyana* 27, 44 – 53. <https://doi.org/10.2307/41760259>
- Rittershausen, B., Cranch, D., Rittershausen, W., 2002. *The Practical Encyclopedia of Orchids: A Complete Guide to Orchids and Their Cultivation.* Anness Publishing Press, 1 – 256.
- Rudall, P.J., Bateman, R.M., 2002. Roles of synorganisation, zygomorphy and heterotopy in floral evolution: The gynostemium and labellum of orchids and other lilioid monocots. *Biol. Rev.* 77, 403 – 441. <https://doi.org/10.1017/S1464793102005936>

- Salazar, G.A., Cabrera, L.I., Gerlach, G., Hágsater, E., Chase, M.W., 2016. Phylogenetic relationships in *Mormodes* (Orchidaceae, Cymbidieae, Catasetinae) inferred from nuclear and plastid DNA sequences and morphology. *Phytotaxa* 263, 18 – 30. <https://doi.org/10.11646/phytotaxa.263.1.2>
- Schlechter, R., 1926. Das System der Orchidaceen. *Notizblatt des Königl. Bot. Gartens und Museums zu Berli* 9, 563 – 591.
- Simpson, M.G., 2006. *Plant Systematics*. Elsevier/Academic Press, 1 – 608.
- Singh, B., 2015. Extended distribution of rare *Anoectochilus papilosus* L.V. Averyanov (Orchidaceae) to the Indian Himalaya in Asia. *Pleione* 9, 217 – 221.
- Singh, K.P., Phukan, S., Bujarbarua, P., 2001. Orchidaceae, in: *Floristic Diversity and Conservation Strategies in India. Volume IV* (N.P. Singh, D.K. Singh & K.P. Singh Ed.). Botanical Survey of India, Howrah, Calcutta, India, 1735 – 1846.
- Squire, D., 2005. *The Orchid Specialist, Specialist Series*. New Holland Press, 1 – 80.
- Stern, W.L., Gregory, M., Cutler, D.F., 2014. *Anatomy of the Monocotyledons Volume X: Orchidaceae*. OUP Oxford Press, 1 – 288.
- Stern, W.L., Judd, W.S., 2001. Comparative anatomy and systematics of Catasetinae (Orchidaceae). *Bot. J. Linn. Soc.* 136, 153 – 178. <https://doi.org/10.1006/bojl.2000.0439>
- Swartz, O., 1805. *Genera et species orchidearum systematice coordinatarum ab Olao Swartz*, 1 – 108.
- Takhtadzhian, A.L., 1969. *Flowering plants: origin and dispersal*. Smithsonian Institution Press, 1 – 310.
- Teoh, E.S., 2016. *Medicinal Orchids of Asia*. Springer International Publishing Press, 1 – 733. <https://doi.org/10.1007/978-3-319-24274-3>
- Tibbs, M., 2008. *Orchids*. New Holland Press, 1 – 159.
- Vermeulen, P., 1966. The system of the Orchidales. *Acta Bot. Neerl.* 15, 224 – 253.

<https://doi.org/10.1111/j.1438-8677.1966.tb00228.x>

Waller, S.B., 2016. *The Forbidden Orchid*. Penguin Young Readers Group Press, 1 – 416.

Whitten, W.M., Blanco, M.A., Williams, N.H., Koehler, S., Carnevali, G., Singer, R.B., Endara, L., Neubig, K.M., 2007. Molecular phylogenetics of *Maxillaria* and related genera (Orchidaceae: Cymbidieae) based on combined molecular data sets. *Am. J. Bot.* 94, 1860 – 1889. <https://doi.org/10.3732/ajb.94.11.1860>

Wikstrom, N., Savolainen, V., Chase, M.W., 2001. Evolution of the angiosperms: calibrating the family tree. *Proc. R. Soc. B Biol. Sci.* 268, 2211 – 2220. <https://doi.org/10.1098/rspb.2001.1782>

Woltering, E.J., Harren, F., 1989. Role of Rostellum Desiccation in Emasculation-Induced Phenomena in Orchid Flowers. *J. Exp. Bot.* 40, 907 – 912. <https://doi.org/10.1093/jxb/40.8.907>

Yukawa, T., Ohba, H., Cameron, K.M., Chase, M.W., 1996. Chloroplast DNA phylogeny of subtribe *Dendrobiinae* (Orchidaceae): Insights from a combined analysis based on *rbcL* sequences and restriction site variation. *J. Plant Res.* 109, 169 – 176. <https://doi.org/10.1007/BF02344542>

Zotz, G., Winkler, U., 2013. Aerial roots of epiphytic orchids: The velamen radicum and its role in water and nutrient uptake. *Oecologia* 171, 733 – 741. <https://doi.org/10.1007/s00442-012-2575-6>