

REVIEW

Linnaean sources and concepts of orchids

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• **Background** Linnaeus developed a robust system for naming plants and a useful, if mechanical, system for classifying them. His binomial nomenclature proved the catalyst for the rapid development of our knowledge of orchids, with his work on the family dating back to 1737 in the first edition of his *Genera Plantarum*. His first work devoted to orchids, indeed the first monograph of the family, was published in 1740 and formed the basis for his account in *Species Plantarum*, published in 1753, in which he gave a binomial name to each species. Given the overwhelming number of orchids, he included surprisingly few – only 62 mostly European species – in *Species Plantarum*, his seminal work on the plants of the world. This reflects the European origin of modern botany and the concentration of extra-European exploration on other matters, such as conquest, gold and useful plants. Nevertheless, the scope of Linnaeus' work is broad, including plants from as far afield as India, Japan, China and the Philippines to the east, and eastern Canada, the West Indies and northern South America to the west. In his later publications he described and named a further 45 orchids, mostly from Europe, South Africa and the tropical Americas.

• **Scope** The philosophical basis of Linnaeus' work on orchids is discussed and his contribution to our knowledge of the family assessed. His generic and species concepts are considered in the light of current systematic ideas, but his adoption of binomial nomenclature for all plants is his lasting legacy.

Key words: Classification, Linnaeus, nomenclature, Orchidaceae, orchids.

INTRODUCTION

'If we do not know the names of things, the knowledge of them is lost too' (Linnaeus, 1751).

This simple point, articulated by Carl Linnaeus (Carl von Linné; Fig. 1) over 250 years ago, encapsulates his importance to modern biology. The year 2007 marked the 300th anniversary of his birth on 23 May 1707 in Råshult, southern Sweden, the son of Nils Linnaeus, a pastor. An early interest in natural history, particularly plants, led Carl to begin studying medicine at the University of Lund in 1727, but on advice of the physician and botanist Johan Rothman (1684–1763) he moved to the University of Uppsala in September 1728. There, by 1730 he so impressed the Professors that he was appointed to give demonstrations in botany at the university botanic garden. He also began to prepare the text of several books. In 1732, he visited Lapland, his first botanical expedition, and the resulting *Flora Lapponica* (Linnaeus, 1737b) was his first floristic account. In 1735, he travelled to The Netherlands, a thriving centre of botanical research, where he met the influential botanists Johan Gronovius (1686–1762), Herman Boerhaave (1668–1738) and Johannes Burman (1707–1779). There he was able to publish several of the books he had prepared while in Sweden, including *Systema Naturae* in 1735, *Bibliotheca Botanica* in 1736, *Critica Botanica* in 1737 and *Classes Plantarum* in 1738 (Linnaeus, 1735, 1736, 1737c, 1738b). His *Systema Naturae* (Linnaeus, 1735) was notable for its

innovative classification system of plants. Inspired by ideas on plant sexuality that had been outlined by Camerarius (1694) and Vaillant (1718), Linnaeus created 24 classes based primarily on the number (e.g. *Monandria* with one) and arrangement (e.g. *Gynandria*, where the male organs are attached to, and stand upon, the female organs) of stamens, culminating in *Cryptogamia* (plants without proper flowers). Each class was, in turn, subdivided into orders, usually (but not always) based on the number and arrangement of the female parts of the flower.

In 1736, he made a brief visit to England thanks to his patron George Clifford (1685–1760), an Anglo-Dutch financier and plant lover whose living and preserved plant collections he was cataloguing. During this visit, Linnaeus met Philip Miller, the curator of the Chelsea Physic Garden. Back in The Netherlands, Linnaeus' influential *Genera Plantarum* was published in 1737 and went through five more editions in his lifetime (Linnaeus, 1737a, 1742, 1743, 1753, 1754, 1764). His time with Clifford produced *Hortus Cliffortianus*, published in 1738, often considered a forerunner to *Species Plantarum* (1753).

After his return to Sweden, Linnaeus worked as a physician, but his early, and often overlooked, monograph on orchids, entitled 'Species orchidum et affinium plantarum', appeared in 1740 (Linnaeus, 1740; Fig. 2). Oakes Ames, the eminent American orchid specialist, annotated the copy at Harvard as follows: 'This is the oldest comprehensive treatment on orchids'. Its obscurity can be traced to its use of polynomial names rather than binomials and his later account of orchids in his *Species Plantarum* (1753) in which binomials were used. In his orchid monograph, he described 38 species in

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FIG. 1. Carolus Linnaeus (Carl von Linné) (1707–1778) – a portrait by A. Roslin (1775). With kind permission of the Linnean Society of London.



FIG. 2. The type collection of *Gymnadenia nigra* (L.) Rchb.f. in the Linnaean Herbarium. With kind permission of the Linnean Society of London.

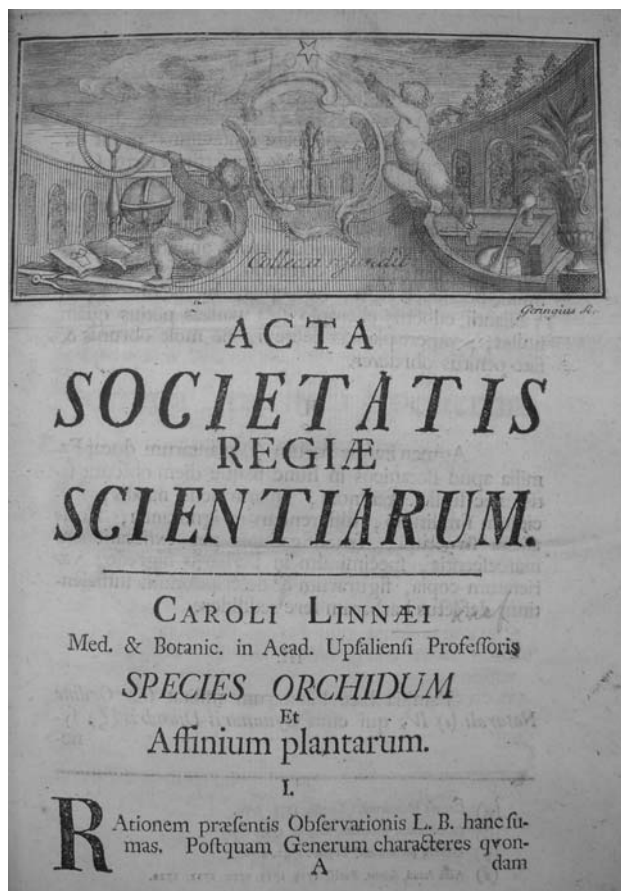


FIG. 3. The title page of Linnaeus' *Species orchidum et affinium plantarum* of 1740. With kind permission of the Natural History Museum, London.

ten genera (the eight he had accepted in *Genera Plantarum*, with the addition of *Arethusa* and *Limodorum*) relating each to names and descriptions used by earlier authors. In all, he referred to over 70 publications (listed by Heller and Stearn, 1959; Jarvis, 2007).

In 1741, Linnaeus was appointed Professor of Medicine and Botany at Uppsala University. His seminal work, *Species Plantarum*, an attempt to catalogue the plants of the world, was begun in 1746 and finally published in 1753. It was notable for its consistent use of binomial names for the first time; these continue to be used today as the basis for botanical nomenclature. *Species Plantarum* gave binomial names to some 5900 plants, and in his later publications, between 1753 and his death in early 1778, he added another 3100, 45 of them orchids (see the Appendix), resulting in a total of more than 9000 names at the ranks of species and variety. Linnaeus captured the first flowering of plant exploration in this book, an occupation that he did much to stimulate through promoting the travels of his adventurous students, including Afzelius, Forsskål, Thunberg and Persoon.

MORPHOLOGICAL CONCEPTS

Linnaeus' study of the plants of the world produced rather few original insights into their morphology, biology or anatomy.

He studied in depth the work of his predecessors, such as Gesner, Cesalpino, Bauhin, Ray, Grew, Camerarius and Tournefort, and he did note that ‘the nectary was not known by name, until we defined it’, illustrating the point by referring to flowers of *Orchis* and *Satyrium*. However, he provided, in *Philosophia Botanica* (Linnaeus, 1751), a critique of earlier authors’ work, applying those ideas with which he agreed and dismissing those he found less useful. Thus, John Ray’s early grasp of the natural affinities of many plants and his resulting classification were rejected by Linnaeus, in favour of his own easier-to-apply (but artificial) system, based on floral and fruiting structures alone.

CLASSIFICATION

We know a great deal about Linnaeus’ methodology and botanical philosophy through his copious publications. His *Philosophia Botanica* summarized thoughts published earlier in his *Critica Botanica* (Linnaeus, 1737c) and also drew on his popular student lectures. His ideas are prescriptive by modern standards and include his aphorism ‘Only genuine botanists have the ability to apply names to plants’ (Linnaeus, 1751; translated by Freer, 2003), going on to define a genuine botanist as one who can identify and name lots of plants.

In this work, Linnaeus outlined in some detail his ideas on classification, starting from the premise that ‘the primary arrangement of the vegetables is to be taken from the fruit body alone’. ‘Any vegetables that agree in the parts of the fruit body should not be separated in a theoretical arrangement; other things being equal’, and ascribed this ‘pre-eminent discovery in the science of botany’ to ‘Gesner, brought forward by Cesalpino, revived by Morison, and supported by Tournefort’.

The species was the basic unit of his classification and nomenclature. He was well aware that defining species on the basis of distribution, flowering time, flower colour, taste, uses, scent, hairiness, etc. was unreliable, stressing floral and vegetative morphology as providing the best characters. He was also well aware of the ability of floral and vegetative abnormalities and effects of selection in cultivation to mislead the botanist, and he emphasized the fruiting body as providing the best characters to define species.

Linnaeus followed the view of Cesalpino that ‘without the concept of a genus, there is no certainty of the species’. He applied the same criteria to the definition of the genus as he had to that of the species, stating that ‘All those genera that do not acknowledge their foundation in the fruit-body alone should be called CONTRIVED GENERA; e.g. A *Limodorum* T[uberosum] with a fibrous root would not be an *Orchis*’ (Freer 2003: 127, Aphorism 164).

Characters of the fruiting body also defined his classes and orders, which he asserted were ‘more arbitrary than the genus’ (Aphorism 205), noting: ‘Tournefort made much of the position of the receptacle in the orders’ (Aphorism 179). Linnaeus also defined what he meant by a character: ‘The character is the definition of the genus, and it exists in three forms; *the factitious, the essential, and the natural*’ (Aphorisms 186–189):

- Factitious: ‘distinguishes the genus from other genera, but only from those of the same artificial order’

- Essential: ‘provides the genus to which it is applied with its most proper and peculiar feature’
- Natural: ‘adduces all possible generic features, and so it comprises the essential and the factitious’.

An habitual character ‘from the habit, which the ancients accepted, has now become intrinsically obsolete in the genera, since the discovery of the fruiting body’. Further, ‘To cling to the habit of the plants, to such an extent that the usually accepted elements of the fruit-body are set aside, is to seek folly instead of wisdom’ (Aphorism 209).

NOMENCLATURE

‘The concept of the species consists of an essential feature by which alone it is distinguished from all others in the same genus’, and ‘A plant is completely named if it is provided with a generic name and a specific one’ (Linnaeus, 1751).

His *Philosophia Botanica* (1751) can be considered to be the forerunner of the Botanical Code in that it is prescriptive of how to name plants, proposing many somewhat arbitrary rules for construction of names. Thus, specific epithets named after places, flowering seasons, people, colour, etc. are all considered undesirable (though it did not prevent Linnaeus from using them himself on occasion, e.g. in *Orchis flava*).

PRE-LINNAEAN ORCHID TAXA

Linnaeus had access to herbals and botanical texts of many earlier authors and drew on their ideas in developing the classification and nomenclature that he was to adopt in his own publications.

Tournefort (1694), in his *Éléments de Botanique*, was the first to consider orchids as a family (‘order’). He defined the orchids as follows: ‘Des herbes à fleur irrégulière composée de plusieurs feuilles, et dont le calice deviant un fruit simple de semences semblables à la sive de bois’. He recognized the genera *Orchis*, *Helleborine*, *Calceolus* (= *Cypripedium*), *Limodorum*, *Ophris* (= *Ophrys*) and *Nidus-avis* (= *Neottia*), most of which were subsequently taken up by Linnaeus.

European orchids had been described and often illustrated by engravings from wood block engravings in many Renaissance herbals, and tropical orchids began to be recognized, illustrated and described in the works of authors such as van Rheede (1678–1693), Plukenet (1691–1694, 1696), Morison (1699), Petiver (1702–1709), Sloane (1707–1725) and Kaempfer (1712) from the late 17th century onwards.

GENERIC CONCEPTS AND ARRANGEMENTS

Linnaeus (1737b) published descriptions of eight orchid species known to him from his Lapland expedition in 1732, but his first summary of the orchids as a whole appeared, also in 1737, in the first edition of *Genera Plantarum* (Linnaeus, 1737a). There he listed and described eight orchid genera: namely *Orchis*, *Satyrium*, *Serapias*, *Herminium*, *Neottia*, *Ophrys*, *Cypripedium* and *Epidendrum*. The inclusion of *Cypripedium* in the orchids is significant because it has two stamens, whereas all the others have only a single anther. However, in the other genera, Linnaeus considered each anther locule to be a stamen, hence

the inclusion of these genera along with *Cypripedium* in his class *Gynandria* (male organs attached to and standing upon the female), order *Diandria* (with two stamens).

Linnaeus' eight genera are still recognized, but each is circumscribed differently today (see the Appendix). Indeed, nowadays, his orchids fall into some 47, rather than eight, genera. His genera were distinguished by their floral features (Linnaeus, 1737a), no mention being made of vegetative characters. Thus, *Cypripedium* is distinguished by its perianth of four 'petals' and a 'nectary' that was calceolate. His generic concepts for *Orchis* and *Ophrys* were particularly broad, encompassing 12 and 11 present-day genera, respectively. All but one species that he included in *Orchis* in *Species Plantarum* (Linnaeus, 1753) are still assigned to genera in subfamily Orchidoideae, tribe Orchideae (*sensu* Pridgeon *et al.*, 2003), the exception being *Limodorum* (subfamily Epidendroideae tribe Neottieae). Only two species, *O. militaris* and *O. mascula*, are still considered to belong to *Orchis*, the former being the type of the genus and family. Five of the 11 genera included in *Ophrys* belong in subfamily Orchidoideae tribe Orchideae, four in subtribe Orchidinae, and one (*Spiranthes*) in subtribe Spiranthininae. The remainder belong in subfamily Epidendroideae: *Neottia* (including *Listera*) in tribe Neottieae, *Corallorhiza* in tribe Calypsoeae and *Hammarbya*, *Malaxis* and *Liparis* in tribe Malaxideae (all tribes *sensu* Chase *et al.*, 2003).

Linnaeus' genus *Satyrium* encompasses six modern genera, four in tribe Orchideae, one (*Goodyera*) in tribe Spirantheae, and one (*Epipogium*) in subfamily Epidendroideae tribe Nervilieae (Epipogieae of most authors). His *Serapias* comprises *Serapias* and the two epidendroid genera *Cephalanthera* and *Epipactis* (tribe Neottieae). His *Arethusa* comprises three modern genera: *Arethusa* is in the epidendroid tribe Arethuseae and *Cleistes* and *Pogonia* which belong in subfamily Vanilloideae, tribe Pogonieae.

Cypripedium sensu stricto belongs in subfamily Cypripedioideae, but *Calypso*, which Linnaeus included in *Cypripedium*, is in the epidendroid tribe Calypsoeae. Linnaeus' *Epidendrum* (Linnaeus, 1753) encompasses ten genera (expanded to 19 in his later works), nine now included in subfamily Epidendroideae: *Epidendrum* is in tribe Epidendreae, *Dendrobium* in tribe Dendrobieae, *Cymbidium* in Cymbidieae and *Arachnis*, *Cleisostoma*, *Phalaenopsis*, *Rhynchostylis* and *Vanda* in Vandaeae. *Brassavola* and *Oncidium* are in Cymbidieae and Epidendreae, respectively, and *Vanilla* is now placed in subfamily Vanilloideae, tribe Vanilleae.

Finally, because *Limodorum* Boehm. (1760) has been conserved against *Limodorum* L. (1753), Linnaeus' concept of this generic name cannot be used, and its generitype, *L. tuberosum* L., is now known as *Calopogon tuberosus* (L.) Britton, Sterns & Poggenb., a species in the epidendroid tribe Arethuseae. The other genus included by him in *Limodorum* is *Eulophia*, now in tribe Cymbidieae.

SPECIES CONCEPTS

The breadth of Linnaeus' generic concepts has inevitably resulted in most of his original species epithets being transferred to other genera (only a handful of his species names remain in their original genera). In addition, his species concepts were

often broader than accepted at present. For example, his concept of *Cypripedium calceolus* L. encompassed *C. calceolus*, both varieties of *C. parviflorum* (β), as well as *C. acaule* (γ) and *C. guttatum* (δ), the last three distinguished by Greek letters signifying varieties that were, however, insufficiently distinct to justify naming them. Similarly, *Orchis latifolia* encompassed *Dactylorhiza incarnata*, *D. majalis* (γ), *D. sambucina* (δ), *D. maculata* (ε) and another unidentified variant (β), all similarly unnamed varieties.

Between 1742 and 1753, when his *Species Plantarum* appeared, Linnaeus increased the number of orchid species recognized from 38 to 62, while reducing the number of genera from ten to eight (*Herminium* and *Neottia* being subsumed within *Ophrys*). The majority of these are temperate orchids from Europe, northern Asia or North America. However, a surprising number originated in tropical countries, including India, Sri Lanka, Java, China, Japan, the Philippines and Jamaica. This publication, with its consistent use of binomial names, now serves as the starting point for botanical nomenclature.

EUROPEAN ORCHIDS

Linnaeus' own travels were confined to northern and western Europe. Clearly, some species would have been known to him from living plants he had seen in the wild, whereas others he would have seen as preserved specimens given to him by or in the collections of friends, correspondents and students. Others would have been known to him either partly, or exclusively, from the writings of other authors. Given Linnaeus' early enthusiasm for botany and his report that by 1729 he already possessed a herbarium containing hundreds of Swedish plants that he had collected himself, it seems likely that by 1732 he would have been familiar with the common orchids found growing in his native Småland, such as *Neottia ovata* L., and in the areas around Lund and Uppsala.

In 1732, Linnaeus made an expedition to Lapland, as a result of which he listed and described eight species of orchids in his published account of the Lapland flora. The preserved specimens that Linnaeus collected here are recognisable, not only because they were mounted on unusually small sheets of paper and annotated with the corresponding number of the relevant species in the published *Flora Lapponica* account, but also because he gave most of them to his great friend Johannes Burman; this separate herbarium collection is now housed at the Institut de France in Paris. It includes specimens of all but one of his Lapland orchids, including *Corallorhiza trifida* Châtel. *Calypso bulbosa* (L.) Oakes is missing because it was not seen by Linnaeus himself, but he included it in his book on the authority of his mentor Olof Rudbeck the Younger, who had seen and described it during his own exploration of Lapland in 1685 (and Linnaeus reproduced the illustration that Rudbeck had published previously). Although Linnaeus' account shows he was aware that these species had already been described by earlier authors, this was the first time he had seen them in the wild. In this and later works, Linnaeus cited books of others where relevant, and his accounts of European species often carry reference to the early descriptions and woodcuts in works such as those by Fuchs (1542) and Dodoens (1616). In 1740, he published his orchid monograph, discussed

earlier, in which he recognized 38 species of orchids ranged over ten genera, his first species-level treatment of the group as a whole.

A year later, Linnaeus was commissioned by the Swedish government to undertake a scientific survey of the Baltic islands of Öland and Gotland, until then almost unstudied. Öland is an almost flat limestone plateau, unlike the Swedish mainland, and as soon as he set foot on the island, Linnaeus realized that it was altogether different in its natural history from the other Swedish provinces with which he was familiar. In his account of the island, Linnaeus described encountering in early June 1741 'the rarest plants, such as have never been heard of in Sweden before, and to see which I travelled in 1738 from Paris to Fontainebleau, where I saw them, thinking I would never see them again', and these included *Ophrys insectifera* L. (Fig. 4), *Orchis militaris* L. and *Neotinea ustulata* (L.) R.M.Bateman, Pridgeon & M.W.Chase. Of *Ophrys insectifera*, he wrote 'Its flowers bear such a resemblance to flies that an uneducated person who sees them might well believe that two or three flies were sitting on the stalk. Nature has made a better imitation than any art could ever perform' (Linnaeus, translated by Åsberg and Stearn, 1973). Öland is now known to be home to 27 species of orchid, at least ten of which were noted by Linnaeus in his journal. Moving on to Gotland, a larger island with a more varied topography, Linnaeus encountered some of the same orchids, but also *Anacamptis morio* (L.) R.M.Bateman, Pridgeon & M.W.Chase, which had not been seen in Sweden until then. This increase in his knowledge allowed him to record a total of 21 orchids in his first Swedish Flora (Linnaeus, 1745).



FIG. 4. The Linnaean Herbarium sheet of *Ophrys insectifera* L. With kind permission of the Linnean Society of London.

The significant herbarium of Joachim Burser in Uppsala, which ran to 23 volumes of mainly central European plants, contains 38 orchids, most of which were determined by Linnaeus and cited indirectly in his publications via Bauhin's *Pinax* (Bauhin, 1623), according to whose system the herbarium was organized. These dried specimens would presumably have been the first examples Linnaeus saw of many species that he would later see in the field (e.g. *Orchis militaris*). European orchids continued to be added after 1753; thus Clas Alströmer collected *Serapias cordigera* L. in Spain, named by Linnaeus in 1763.

ASIAN, AFRICAN AND AMERICAN ORCHIDS

Through contacts established during and after his travels, Linnaeus had managed to expand his library considerably, and a few works within it were of particular value for information about orchids. He relied for information on non-European orchids on the knowledge of earlier and contemporary authors and collectors who had travelled to Asia and the Americas. Several notable explorers collected plants and brought specimens, mostly pressed, back with them and published their findings.

In 1712, Engelbert Kaempfer described his journey to Japan, from where he described and illustrated the species now known as *Dendrobium moniliforme* (L.) Sw. and, en route, *Arachnis flosaeris* (L.) Rchb.f. from Java (Kaempfer, 1712). The impressive volumes of van Rhee's *Hortus Malabaricus* provided engravings and descriptions of a number of southern Indian orchids, including *Cymbidium aloifolium* (L.) Sw. (Fig. 5; van Rhee, 1678–1693), and from the Philippines James Petiver depicted what is now known as *Dendrobium carinatum* (L.) Willd. (Petiver, 1702–1709).

Published information from the New World came not only from Gronovius' *Flora Virginica* (Gronovius, 1739–1743) but also from Mark Catesby's beautifully illustrated book, *The Natural History of Carolina, Florida and the Bahamas* (Catesby, 1731–1747), which described and figured ten orchid species, including *Prosthechea cochleata* (L.)

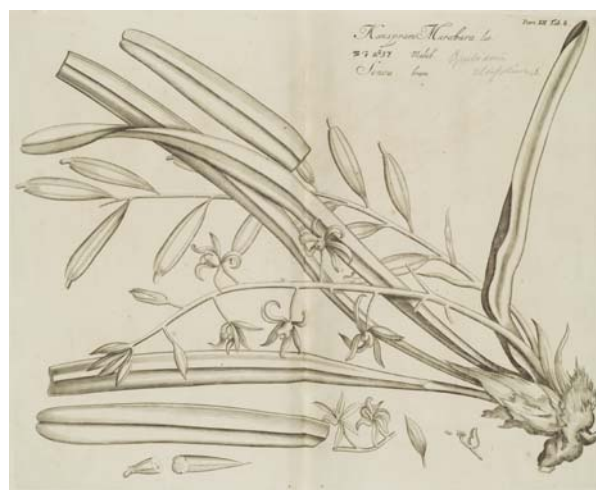


FIG. 5. *Cymbidium aloifolium* (L.) Sw. from H.A. van Rhee's *Hortus Malabaricus* (1678–1693). With kind permission of the Royal Botanic Garden, Kew.

W.E.Higgins and *Epidendrum nocturnum* Jacq. (Fig. 6). In addition, Linnaeus' student, Pehr Kalm, had spent nearly 3 years in eastern North America, returning to Sweden in 1751, and among the new orchids he brought back to his professor were *Pogonia ophioglossoides* (L.) Ker-Gawl. and *Spiranthes cernua* (L.) Rich. A few tropical American orchids were also known, notably those described by Sir Hans Sloane, whose collections formed the nucleus of the British Museum. Sloane contributed descriptions and illustrations of a number of orchids from Jamaica including *Erythrodes plantaginea* (L.) Fawc. & Rendle (Sloane, 1707: t. 147).

By the early 1740s, Linnaeus' fame had spread and, despite never again travelling outside the country, he continued to see more specimens from outside Sweden. For example, in 1744, he was loaned four volumes of specimens (and one of drawings of plants) from Sri Lanka that were collected by Paul Hermann in the 1670s, which included specimens of *Peristylus cubitalis* (L.) Kraenzl. and *Zeuxine strateumatica* (L.) Schltr.

Specimens from various parts of Russia had reached him through Sten Carl Bielke, a Swedish diplomat, as well as from Johann Gmelin, who sent Linnaeus many specimens from Siberia. Along with Georg Steller and Stepan Krascheninnikov, Gmelin was a participant in the Second Kamchatka Expedition (1733–1743). Steller's specimens from the Kamchatka Peninsula were the subject of a dissertation written by Linnaeus in 1750 that included a detailed description of *Neottia camtschatea* (L.) Rchb.f., Steller's specimen of which is now in Linnaeus' herbarium. The descriptions of 22 orchids (eight of them

illustrated) published by Gmelin (1747) in his *Flora Sibirica* were a significant source of information for Linnaeus and are the basis of the names of the species now known as *Neottianthe cucullata* (L.) Schltr., *Platanthera fuscescens* (L.) Kraenzl. and *Epipogium aphyllum* Sw. (Fig. 7). Another of Linnaeus' students, Pehr Osbeck, brought him specimens of *Cymbidium ensifolium* (L.) Sw. from China and *Phalaenopsis amabilis* (L.) Blume from Java (not India as Linnaeus believed) in 1752, the latter now in the Swedish Museum of Natural History in Stockholm.

The orchid account in *Species Plantarum* demonstrated clearly how little information on tropical and Southern hemisphere orchids had reached Europe by 1753, giving Linnaeus and his contemporaries an understandably Euro-centric view of the natural world. His knowledge of European orchids, too, was skewed towards those in central and northern Europe, reflecting the difficulty of travel in southern and south-eastern Europe, the latter largely under the control of the Ottoman Turks. He described 36 Scandinavian orchids (70 % of the currently accepted species), but missed nearly all Mediterranean taxa (*Barlia*, *Comperia*, *Gennaria*, *Neotinea*, most *Ophrys*). Amazingly, however, his orchids include representatives of four of five currently accepted subfamilies (Chase *et al.*, 2003), only Apostasioideae being absent.



FIG. 6. *Epidendrum nocturnum* Jacq. (t. 68) figured for in Mark Catesby's *The Natural History of Carolina, Florida and the Bahamas* (1731–1747). With kind permission of the Royal Botanic Garden, Kew.



FIG. 7. *Epipogium aphyllum* Sw. (right-hand illustration) and *Calypso bulbosa* from J. G. Gmelin's *Flora Sibirica* (1747). With kind permission of the Royal Botanic Garden, Kew.

Following the publication of *Species Plantarum* in 1753, in which 62 species of orchid were recognized, disposed among eight genera, new information and specimens continued to appear. Linnaeus published new names and sometimes descriptions for these new species. For example, through the intervention of Queen Louisa Ulrika, specimens collected by Linnaeus' student Fredrik Hasselquist (who had died near Smyrna in 1752) were sent to Sweden, among them *Anacamptis sancta* (L.) R.M.Bateman, Pridgeon & M.W.Chase. In the seven-volume *Herbarium Amboinense*, Georg Rumphius described plants of the island of Amboina in Indonesia, among them about 40 orchids (Rumphius, 1741–1750), and although Linnaeus was clearly uncertain about many of them and did not cite all of them in his own works, Rumphius' plates are the basis of, among others, *Grammatophyllum scriptum* (L.) Blume.

An important source of information about Antillean orchids came from Linnaeus' great friend Johannes Burman (1707–1779), who was publishing an account of plants depicted by the French monk, Charles Plumier (1646–1704). Plumier collected extensively in Haiti and Martinique during three trips between 1689 and 1697, and Burman's edition contributes the types of a number of names including *Prosthechea cochleata* (L.) W.E.Higgins. His son, Nicolaas Burman (1733–1793), who came to Uppsala to study under Linnaeus in 1760, brought with him a rich collection of herbarium material from the Cape of Good Hope collected by, among others, Henry Oldenland (around 1695). Linnaeus described these specimens in a 1760 dissertation titled *Plantae Rariores Africanae*, which included 11 species of orchids, among which were *Bartholina burmanniana* (L.) Ker-Gawl., *Disa cornuta* (L.) Sw., *Disperis capensis* (L.) Sw., *Pterygodium caffrum* (L.) Sw. and *Schizodium cornutum* (L.) Schltr. (Linnaeus, 1960). These specimens, however, did not reach Linnaeus' herbarium but returned to The Netherlands with Nicolaas Burman and are now in Geneva.

There were other interesting additions in his revised second edition of *Species Plantarum* (Linnaeus, 1763), including some species already named by Nikolaus Jacquin (1760, 1763). Linnaeus now included 102 species of orchids, up from 62 in the first edition in 1753, and an increase over the 74 he had recognized in the tenth edition of his *Systema Naturae* only 4 years earlier in 1759 (Linnaeus, 1759). By the end of his life, he had accepted a total of 113 species and varieties (see the Appendix) and recognized others as distinct (even though not formally named). This is perhaps a surprisingly small number of species given what we now know about orchid diversity.

ORCHIDS IN LINNAEUS' HERBARIUM (LINN) AND TYPIFICATION ISSUES

Linnaeus' own herbarium at the Linnean Society of London contains about 150 orchid specimens arranged under ten generic names, although modern generic concepts would now allocate the specimens to more than 40 genera, and 44 of Linnaeus' orchid binomials have their type specimens in this herbarium. The majority of specimens are of temperate species from Europe, North America and South Africa, whereas few are tropical.

It is difficult to correlate specimens in his herbarium with the early period of collecting in Linnaeus' youth because the sheets

frequently lack any annotation beyond the species epithet. In the case of *Satyrium nigrum* L. [= *Gymnadenia nigra* (L.) Rchb.f.] (Fig. 3), for example, there is also the number of this species' account in the later *Species Plantarum* (i.e. '3'), plus the name 'Jemtia' – now Jämtland – somewhere that Linnaeus never visited, so this must have been collected by someone else (almost certainly his student, J. O. Hagström).

The number of South African orchids present from genera such as *Disa*, *Disperis*, *Eulophia*, *Habenaria*, *Pterygodium* and *Satyrium* is perhaps surprisingly large, but reflects the fact that, although collections made at the Cape by his students Anders Sparrman and Carl Peter Thunberg reached the herbarium, they were received late in Linnaeus' life, and the species names for which they are the basis were generally published after his death, by Linnaeus' son, in *Supplementum Plantarum* (Linnaeus, 1782). Examples include *Arethusa ciliaris* L.f. (1059.4), *Ophrys bracteata* L.f. (1056.27) and *Orchis draconis* L.f. (1054.10).

Of the Asian species, the type of *Cymbidium ensifolium* (Fig. 8) is a fine, probably cultivated, specimen (1062.10) obtained by Osbeck, and well-preserved material of *Phalaenopsis amabilis* also survives.



FIG. 8. The type specimen of *Cymbidium ensifolium* (L.) Sw. in the Linnaean Herbarium. With kind permission of the Linnean Society of London.

As we have seen, there are also types of Linnaeus' names in herbaria that were studied but never owned by Linnaeus, and published illustrations are also important; 44 binomials are typified by them, especially many tropical species that had then not been introduced to Europe and for which the few published descriptions and illustrations were the only information available.

There are, however, a few oddities. The sole basis of *Epidendrum domesticum* L., a name that has been associated with *Vanilla*, is an Engelbert Kaempfer plate, close study of which suggests that it is a composite of an orchid and a member of Iridaceae. Garay (1997) recently designated the iridaceous part of the plate as the lectotype, with the result that *Epidendrum domesticum* no longer applies to an orchid but, in this case happily, falls neatly into synonymy of the species known as *Belamcanda chinensis* (L.) DC.

Herbarium specimens, too, are not without their occasional problems. A Patrick Browne specimen from Jamaica, annotated in Linnaeus' herbarium as *Cactus parasiticus* (a name published by Linnaeus in 1759), is not a member of Cactaceae at all but rather the orchid, *Dendrophylax funalis* (Sw.) Benth. ex Rolfe, for which *Cactus parasiticus* would be an earlier name. This seems to be a case where Linnaeus' name, which is also not in use in Cactaceae, should be rejected.

CONCLUSIONS

Although Linnaeus knew relatively few orchids, their scientific naming and classification, started by him over 250 years ago, laid the ground for the rapid development of our knowledge of the family. Nowadays, orchids are recognized as the largest family of flowering plants, whereas Linnaeus knew of only 113 species and varieties. His relative ignorance of orchid diversity can be firmly placed on the Euro-centric origins of modern botany, the study of which he did so much to stimulate. His work encouraged many of his students to travel abroad and collect, thereby immensely enriching our knowledge of the plant kingdom and orchids, which form such a prominent part of it.

His standardization of botanical binomial nomenclature provides the basis for access to information on orchids today. Access to the internet means that botanical names are used as the key to orchid data of all sorts: synonymy, descriptions, distributions, keys, ecology, biology, DNA sequences, cultivation methods, conservation status, etc. In such a large family, with over 25 000 species currently recognized (Dressler, 2005), rapid access to information is the key to improving our scientific, horticultural and conservation knowledge. That key was first forged by Linnaeus, and for that we should all be immensely grateful.

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LITERATURE CITED

- Åsberg M, Stearn WT. 1973. Linnaeus's Öland and Gotland journey 1741. *Biological Journal of the Linnean Society* 5: 1–220.
- Bauhin C. 1623. *Pinax theatri botanici Caspari Bauhini*. Basel.
- Camerarius J. 1694. *De sexu plantarum epistola*. Tübingen.
- Catesby M. 1731–1747. *The natural history of Carolina, Florida and the Bahama Islands*. London: M. Catesby.
- Chase MA, Cameron KM, Barrett RL, Freudenstein JV. 2003. DNA data and Orchidaceae systematics: a new phylogenetic classification. In: Dixon KW, Kell SP, Barrett RL, Cribb PJ, eds, *Orchid conservation*. Kota Kinabalu: Natural History Publications, 69–89.
- Dodoens R. 1616. *Stirpium historiae pemptades sex*. Antwerp: Plantin.
- Dressler RL. 2005. How many orchid species? *Selbyana* 26: 155–158.
- Freer S. 2003. *Linnaeus's Philosophia botanica*. Oxford: Oxford University Press.
- Fuchs L. 1542. *De historia stirpium commentarii*. Basel: Isingriniana.
- Garay LA. 1997. De nominibus orchidacearum incunabulorum. *Harvard Papers in Botany* 2: 47–54.
- Gmelin JG. 1747. *Flora Sibirica*, Vol. 1. St Petersburg: Academiae Scientiarum.
- Gronovius JF. 1739–1743. *Flora Virginica*. Leiden: C. Haak.
- Heller JL, Stearn WT. 1959. An appendix to the *Species plantarum* of Carl Linnaeus. In: Linnaeus C. *Species plantarum, a facsimile of the first edition, 1753*, Vol. 2. London: Ray Society, 1–148.
- Jacquin N. 1760. *Enumeratio systematica plantarum*. Leiden: T. Haak.
- Jacquin N. 1763. *Selectarum stirpium Americanarum historia*. Vienna: Colophon.
- Jarvis C. 2007. *Order out of chaos: Linnaean plant names and their types*. London: Linnean Society of London and the Natural History Museum.
- Kaempfer E. 1712. *Amoenitatum exoticarum*. Lemgo: H.W. Meyer.
- Linnaeus C. 1735. *Systema naturae*. Leiden: Th. Haak.
- Linnaeus C. 1736. *Bibliotheca botanica*. Amsterdam: S. Schouten.
- Linnaeus C. 1737a. *Genera plantarum*. Leiden: C. Wishoff.
- Linnaeus C. 1737b. *Flora Lapponica*. Amsterdam: S. Schouten.
- Linnaeus C. 1737c. *Critica botanica*. Leiden: C. Wishoff.
- Linnaeus C. 1738a. *Hortus Cliffortianus*. Amsterdam: G. Clifford.
- Linnaeus C. 1738b. *Classes plantarum*. Leiden: C. Wishoff.
- Linnaeus C. 1740. *Species orchidum et affinium plantarum*. *Acta Societatis Regiae Scientiarum Upsaliensis* 1740: 137.
- Linnaeus C. 1745. *Flora Suecica*. Stockholm: L. Salvius.
- Linnaeus C. 1751. *Philosophia botanica*. Stockholm: L. Salvius.
- Linnaeus C. 1753. *Species plantarum*. Stockholm: L. Salvius.
- Linnaeus C. 1759. *Systema naturae*, edn 10, Vol. 2. Stockholm: L. Salvius.
- Linnaeus C. 1760. *Plantae rariores Africanæ*. Stockholm: L. Salvius.
- Linnaeus C. 1763. *Species plantarum*, edn 2, Vol. 2. Stockholm: L. Salvius.
- Linnaeus C. filius. 1782. *Supplementum plantarum*. Brunswick: Orphanotrophus.
- Morison R. 1699. *Plantarum historia universali Oxoniensis. Pars tertia*. Oxford: Sheldonian.
- Petiver J. 1702–1709. *Gazophylacii naturae & arts decades*. London: C. Bateman.
- Plukenet L. 1691–1694. *Phytographia sive Stirpium... icones*. London: L. Plukenet.
- Plukenet L. 1696. *Almagestum botanicum*. London: L. Plukenet.
- Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN, eds. 2003. *Genera orchidacearum*. Vol. 3. *Orchidoideae* (part 2): *Vanilloideae*. Oxford: Oxford University Press.
- van Rheede tot Draakenstein H. 1678–1693. *Hortus Malabaricus*. Amsterdam: van Someren.
- Rumphius GE. 1741–1750. *Herbarium Amboinense... pars prima (–sexta)*. Amsterdam.
- Sloane H. 1707–1725. *A voyage to the islands Madera... and Jamaica, with the natural history of the herbs and trees... &c. of the last of those islands*. 2 Vols. London: H. Sloane.
- Tournefort JP. 1694. *Éléments de botanique*. Paris: Imprimerie Royale.
- Vaillant S. 1718. *Discours sur la structure des fleurs: leurs différences et l'usage de leurs parties*. Leiden: Chez Pierre Vander Aa.

APPENDIX 1

Orchids named by Linnaeus at the ranks of species and variety

Linnaeus' name	Currently accepted name	Origin	Place of publication/sources	Lectotype (numbers refer to specimens in LINN unless otherwise indicated)
<i>Arethusa bulbosa</i>	<i>Arethusa bulbosa</i> L.	USA, Canada	Sp. Pl. 2: 950. 1753. Gronovius, Plukenet	1059-1
<i>Arethusa capensis</i>	<i>Disperis capensis</i> (L.) Sw.	South Africa	Pl. Rar. Afr.: 28. 1760.	Herb. Burman (G)
<i>Arethusa divaricata</i>	<i>Cleistes divaricata</i> (L.) Ames	USA	Sp. Pl. 2: 951. 1753. Gronovius, Catesby	1059-3
<i>Arethusa ophioglossoides</i>	<i>Pogonia ophioglossoides</i> (L.) Ker-Gawl.	USA, Canada	Sp. Pl. 2: 951. 1753. Gronovius, Plukenet, Morison	1059-2
<i>Cactus parasiticus</i>	<i>Dendrophylax funalis</i> (Sw.) Rolfe	West Indies	Syst. Nat., ed. 10, 2: 1054. 1759.	Type not designated
<i>Cypripedium bulbosum</i>	<i>Calypso bulbosa</i> (L.) Oakes	Europe, Asia	Sp. Pl. 2: 950. 1753. Gmelin, Linnaeus, Rudbeck	1061-4 (Bjelke)
<i>Cypripedium calceolus</i>	<i>Cypripedium calceolus</i> L.	Europe, Asia, America	Sp. Pl. 2: 951. 1753. Linnaeus, Gronovius, Gmelin, Bauhin, Dodoens	Dodoens, Stirp. Hist. pempt., ed. 2: 180, left hand fig. (1616)
<i>Cypripedium calceolus</i> β	<i>Cypripedium parviflorum</i> Salisb.	USA, Canada	Sp. Pl. 2: 951. 1753. Plukenet, Morison	
<i>Cypripedium calceolus</i> γ	<i>Cypripedium acaule</i> Aiton	USA, Canada	Sp. Pl. 2: 951. 1753. Cornut, Morison	
<i>Cypripedium calceolus</i> δ	<i>Cypripedium guttatum</i> Sw.	Siberia	Sp. Pl. 2: 951. 1753. Amman, Gmelin	
<i>Epidendrum aloifolium</i>	<i>Cymbidium aloifolium</i> (L.) Sw.	India	Sp. Pl. 2: 953. 1753. Rheede, Rudbeck, Ray	Rheede, Hort. Malab. 12: 17, t. 8 (1693)
<i>Epidendrum amabile</i>	<i>Phalaenopsis amabilis</i> (L.) Blume	'India'	Sp. Pl. 2: 953. 1753. Osbeck	Herb. Linn. Stockholm no. 373-1 (S)
<i>Epidendrum carinatum</i>	<i>Dendrobium carinatum</i> (L.) Willd.	Philippines	Sp. Pl. 2: 953. 1753. Petiver	Petiver, Gazophyl. Nat.: 70, t. 44, f. 10 (1702–9)
<i>Epidendrum caudatum</i>	<i>Brassia caudata</i> (L.) Lindl.	West Indies	Syst. Nat., ed. 10, 2: 1246. 1759.	Plumier in Burman (1758), Pl. Amer.: 172, t. 177 (1758)
<i>Epidendrum ciliare</i>	<i>Epidendrum ciliare</i> L.	Martinique	Syst. Nat., ed. 10, 2: 1246. 1759.	Plumier in Burman, Pl. Amer.: 173, t. 179, f. 2 (1758)
<i>Epidendrum cochleatum</i>	<i>Prosthechea cochleata</i> (L.) W.E.Higgins	Haiti	Sp. Pl., ed. 2, 2: 1351. 1763.	Plumier, Codex Boerhaavianus (Groningen)
<i>Epidendrum cucullatum</i>	<i>Brassavola cucullata</i> (L.) R.Br.	Haiti	Sp. Pl., ed. 2, 2: 1350. 1763.	Plumier in Burman, Pl. Amer.: 173, t. 179, f. 1 (1758)
<i>Epidendrum domesticum</i>	<i>Belamcanda chinensis</i> (L.) A.DC. (Iridaceae)	Java	Sp. Pl. 2: 952. 1753. Kaempfer	Kaempfer, Amoen. Exot. Fasc.: 867, 869 (1712)
<i>Epidendrum ensifolium</i>	<i>Cymbidium ensifolium</i> (L.) Sw.	China	Sp. Pl. 2: 954. 1753. Osbeck	1062-10 (Osbeck)
<i>Epidendrum flos-aeris</i>	<i>Arachnis flos-aeris</i> (L.) Rchb.f.	Java	Sp. Pl. 2: 952. 1753. Kaempfer	Kaempfer, Amoen. Exot. Fasc.: 868, 869 (1712)
<i>Epidendrum furvum</i>	<i>Vanda furva</i> (L.) Lindl.	Ambon	Sp. Pl., ed. 2, 2: 1348. 1763.	Rumphius, Herb. Amboin. 6: 104, t. 46, f. 1 (1750)
<i>Epidendrum graminifolium</i>	<i>Octomeria graminifolia</i> (L.) R.Br.	Martinique	Sp. Pl., ed. 2, 2: 1353. 1763.	Plumier in Burman, Pl. Amer.: 171, t. 176, f. 1 (1758)
<i>Epidendrum guttatum</i>	<i>Trichocentrum guttatum</i> (L.) N.H.Williams & M.W.Chase	Jamaica	Sp. Pl. 2: 953. 1753. Sloane	Sloane, Voy. Jamaica 1: t. 148, f. 2 (1707)
<i>Epidendrum juncifolium</i>	<i>Trichocentrum cebolleta</i> (Jacq.) N.H.Williams & M.W.Chase	Martinique	Sp. Pl., ed. 2, 2: 1351. 1763.	Plumier in Burman, Pl. Amer.: 179, t. 184, f. 2 (1758)
<i>Epidendrum moniliforme</i>	<i>Dendrobium moniliforme</i> (L.) Sw.	Japan	Sp. Pl. 2: 954. 1753.	Kaempfer, Amoen. Exot. Fasc.: 864, 865 (1712)
<i>Epidendrum nodosum</i>	<i>Brassavola nodosa</i> (L.) Lindl.	Jamaica	Sp. Pl. 2: 953. 1753. Hermann, Plukenet, Sloane	Hermann, Parad. Bat.: 207 (1698)
<i>Epidendrum ovatum</i>	<i>Dendrobium ovatum</i> (L.) Kraenzl.	India	Sp. Pl. 2: 952. 1753. Rheede	Rheede, Hort. Malabar. 12: 15, t. 7 (1693)
<i>Epidendrum punctatum</i>	<i>Cyrtopodium punctatum</i> (L.) Lindl.	Tropical Americas	Syst. Nat., ed. 10, 2: 1246. 1759.	Plumier in Burman, Pl. Amer.: 182, t. 187 (1758)
<i>Epidendrum pusillum</i>	<i>Erycina pusilla</i> (L.) N.H.Williams & M.W.Chase	Tropical Americas	Sp. Pl., ed. 2, 2: 1351. 1763.	Herb. Linn. Stockholm no. 373-3 (S)
<i>Epidendrum retusum</i>	<i>Rhynchostylis retusa</i> (L.) Blume	India	Sp. Pl. 2: 953. 1753. Rheede	Rheede, Hort. Malabar. 12: 1, t. 1 (1693)

Continued

Linnaeus' name	Currently accepted name	Origin	Place of publication/sources	Lectotype (numbers refer to specimens in LINN unless otherwise indicated)
<i>Epidendrum scriptum</i>	<i>Grammatophyllum scriptum</i> (L.) Blume	Ambon	Sp. Pl., ed. 2, 2: 1351. 1763.	Rumphius, Herb. Amboin. 6: 95, t. 42 (1750)
<i>Epidendrum spathulatum</i>	<i>Vanda spathulata</i> (L.) Spreng.	India	Sp. Pl. 2: 952. 1753. Rheede	Rheede, Hort. Malabar. 12: 1, t. 1 (1693)
<i>Epidendrum tenuifolium</i>	<i>Cleisostoma tenuifolium</i> (L.) Garay	India	Sp. Pl. 2: 952. 1753. Rheede	Rheede, Hort. Malabar. 12: 11, t. 5 (1693)
<i>Epidendrum terrestre</i>	<i>Phaius terrestris</i> (L.) Ormerod	Ambon	Syst. Nat., ed. 10, 2: 1246. 1759.	Rumphius, Herb. Amboin. 6: 112, t. 52, f. 1 (1750)
<i>Epidendrum tuberosum</i> (nom. illeg.)	<i>Geodorum densiflorum</i> (Lam.) Schltr.	Ambon	Sp. Pl., ed. 2, 2: 1352. 1763.	Rumphius, Herb. Amboin. 6: 112, t. 52, f. 1 (1750)
<i>Epidendrum vanilla</i>	<i>Vanilla mexicana</i> Mill.	Haiti	Sp. Pl. 2: 952. 1753. Royen, Plukenet, Merian, Catesby, Bauhin	Catesby, Nat. Hist. Carolina 2 App.: 7, t. 7 (1747)
<i>Limodorum altum</i>	<i>Eulophia alta</i> (L.) Fawc. & Rendle	Martinique	Syst. Nat., ed. 12, 2: 594. 1767.	1058-2
<i>Limodorum tuberosum</i>	<i>Calopogon tuberosus</i> (L.) Britton, Sterns & Poggenb.	USA	Sp. Pl. 2: 950. 1753. Gronovius, Royen, Plumier	Clayton 76 (BM)
<i>Ophrys alpina</i>	<i>Chamorchis alpina</i> (L.) Rich.	Europe	Sp. Pl. 2: 948. 1753. Bauhin, Haller	1056-23 (middle specimen)
<i>Ophrys anthropophora</i>	<i>Orchis anthropophora</i> (L.) All.	Europe	Sp. Pl. 2: 948. 1753. Linnaeus, Dalibard, Vaillant, Colonna, Bauhin	Vaillant, Bot. Paris.: 147, t. 31, f. 19, 20 (1727)
<i>Ophrys arachnites</i> (L.) L. (nom. inval.) (≡ <i>O. insectifera</i> var. <i>arachnites</i> L.)	<i>Ophrys arachnites</i> (L.) Mill.	Europe	Fl. Anglica: 23. 1754.	
<i>Ophrys atrata</i>	<i>Ceratandra atrata</i> (L.) T.Durand & Schinz	South Africa	Syst. Nat., ed. 12, 2: 593. 1767.	1056-31
<i>Ophrys caffra</i>	<i>Pterygodium caffrum</i> (L.) Sw.	South Africa	Pl. Rar. Afr.: 28. 1760.	1056-39
<i>Ophrys camtschatea</i>	<i>Neottia camtschatea</i> (L.) Rchb.f.	Siberia	Sp. Pl. 2: 948. 1753. Linnaeus, Steller	1056-24 (Steller)
<i>Ophrys catholica</i>	<i>Pterygodium catholicum</i> (L.) Sw.	South Africa	Pl. Rar. Afr.: 27. 1760.	Buxbaum, Pl. Minus Cognit. Cent. 3: 13, t. 21 (1729)
<i>Ophrys cernua</i>	<i>Spiranthes cernua</i> (L.) Rich.	USA, Canada	Sp. Pl. 2: 946. 1753. Linnaeus	1056-9
<i>Ophrys circumflexa</i>	<i>Disperis circumflexa</i> (L.) T.Durand & Schinz	South Africa	Pl. Rar. Afr.: 27. 1760.	Herb. Burman (G)
<i>Ophrys corallorhiza</i>	<i>Corallorhiza trifida</i> Châtel.	Europe	Sp. Pl. 2: 945. 1753. Linnaeus, Rudbeck, Ruppis, Bauhin	1056-5, middle specimen
<i>Ophrys cordata</i>	<i>Neottia cordata</i> (L.) Rich.	Europe	Sp. Pl. 2: 946. 1753. Linnaeus, Gmelin, Bauhin, Mentzel	1056-11
<i>Ophrys insectifera</i>	<i>Ophrys insectifera</i> L.	Europe	Sp. Pl. 2: 948. 1753. Linnaeus	1056-20
<i>Ophrys insectifera</i> var. <i>arachnites</i>	<i>Ophrys apifera</i> Huds.	Europe	Sp. Pl. 2: 948. 1753. Vaillant, Bauhin, Breyn, Tournefort, Lobel, Morison	Plantin, Pl. Stirp. Icon.: 185 (1581)
<i>Ophrys insectifera</i> var. <i>myodes</i>	<i>Ophrys insectifera</i> L.	Europe	Sp. Pl. 2: 948. 1753. Lobel, Vaillant, Bauhin, Breyn, Tournefort	1056-20
<i>Ophrys liliifolia</i>	<i>Liparis liliifolia</i> (L.) Lindl.	USA, Canada	Sp. Pl. 2: 946. 1753. Gronovius, Linnaeus	Clayton 658 (BM)
<i>Ophrys liniifolia</i> [orth. var. of <i>O. liliifolia</i>]	<i>Liparis liliifolia</i> (L.) Lindl.	Europe	Syst. Nat., ed. 12, 2: 592. 1767.	Clayton 658 (BM)
<i>Ophrys loeselii</i>	<i>Liparis loeselii</i> (L.) Rich.	Europe	Sp. Pl. 2: 947. 1753. Loeselius	1056-14
<i>Ophrys monophyllos</i>	<i>Malaxis monophyllos</i> (L.) Sw.	Europe	Sp. Pl. 2: 947. 1753. Loeselius, Mentzel, Clusius	1056-17 (left-hand specimen)
<i>Ophrys monorchis</i>	<i>Herminium monorchis</i> (L.) R. Br.	Europe	Sp. Pl. 2: 947. 1753. Linnaeus, Gmelin, Bauhin, Loeselius, Micheli, Rupp, Bauhin, Mentzel	1056-22 (middle specimen)
<i>Ophrys nidus-avis</i>	<i>Neottia nidus-avis</i> (L.) Rich.	Europe	Sp. Pl. 2: 945. 1753. Linnaeus, Dalibard, Lobel, Bauhin	Plantin, Pl. Stirp. Icon.: 195 (1581)
<i>Ophrys ovata</i>	<i>Neottia ovata</i> (L.) Bluff & Fingerh.	Europe	Sp. Pl. 2: 946. 1753. Linnaeus, Dalibard, Haller, Gmelin, Royen, Fuchs, Bauhin	1056-10
<i>Ophrys paludosa</i>	<i>Hammarbya paludosa</i> (L.) Kuntze	Europe	Sp. Pl. 2: 947. 1753.	1056-16, (middle specimen)
<i>Ophrys spiralis</i>	<i>Spiranthes spiralis</i> (L.) Chevall.	Europe	Sp. Pl. 2: 945. 1753. Linnaeus, Dalibard, Lobel, Brunfels, Bauhin	Brunfels, Herb. Vivae Icones 1: 105 (1530)

<i>Orchis abortiva</i>	<i>Limodorum abortivum</i> (L.) Sw.	Europe	Sp. Pl. 1753. Linnaeus, Dalibard, Clusius, Bauhin, Sauvages	1054-43 (middle specimen)
<i>Orchis bicornis</i>	<i>Satyrium bicornis</i> (L.) Thunb.	South Africa	Pl. Rar. Afr.: 26. 1760.	Herb. Burman (G)
<i>Orchis biflora</i>	<i>Schizodium cornutum</i> (L.) Schltr.	South Africa	Sp. Pl., ed. 2, 2: 1330. 1763.	Herb. Burman (G)
<i>Orchis bifolia</i>	<i>Platanthera bifolia</i> (L.) Rich.	Europe	Sp. Pl. 2: 939. 1753. Linnaeus, Dalibard, Bauhin, Séguier, Camerarius, Vaillant	1054-15
<i>Orchis burmanniana</i>	<i>Bartholina burmanniana</i> (L.) Ker-Gawl.	South Africa	Pl. Rar. Afr.: 26. 1760.	Herb. Burman (G)
<i>Orchis ciliaris</i>	<i>Platanthera ciliaris</i> (L.) Lindl.	USA, Canada	Sp. Pl. 2: 939. 1753. Morison, Ray, Gronovius, Royen	1054-13
<i>Orchis conopsea</i>	<i>Gymnadenia conopsea</i> (L.) R.Br.	Europe	Sp. Pl. 2: 939. 1753. Linnaeus, Dalibard, Vaillant, Fuchs, Bauhin	Fuchs, Hist. Stirp.: 711, 712 (1542)
<i>Orchis coriophora</i>	<i>Anacamptis coriophora</i> (L.) R.M.Bateman, Pridgeon & M.W.Chase	Europe	Sp. Pl. 2: 940. 1753. Linnaeus, Dalibard, Bauhin, Sauvages, Vaillant, Haller, Ray, Lobel	Plantin, Pl. Stirp. Icon.: 177 (1581)
<i>Orchis cornuta</i>	<i>Disa cornuta</i> (L.) Sw.	South Africa	Pl. Rar. Afr.: 27. 1760.	Herb. Burman (G)
<i>Orchis cubitalis</i>	<i>Peristylis cubitalis</i> (L.) Kraenzl.	Sri Lanka	Sp. Pl. 2: 940. 1753. Linnaeus, Hermann	Herb. Hermann 2: 35, No. 320 (BM)
<i>Orchis cucullata</i>	<i>Neottianthe cucullata</i> (L.) Schltr.	Siberia	Sp. Pl. 2: 939. 1753. Gmelin	Gmelin, Fl. Sibir. 1: 16, t. 3, f. 2 (1747)
<i>Orchis flava</i>	<i>Platanthera flava</i> (L.) Lindl.	USA	Sp. Pl. 2: 942. 1753. Gronovius	Clayton 639 (BM)
<i>Orchis flexuosa</i>	<i>Schizodium flexuosum</i> (L.) Lindl.	South Africa	Pl. Rar. Afr.: 26. 1760.	Herb. Burman (G)
<i>Orchis fuscescens</i>	<i>Platanthera fuscescens</i> (L.) Kraenzl.	Siberia	Sp. Pl. 2: 943. 1753. Gmelin	Gmelin, Fl. Sibir. 1: 20, t. 4, f. 2 (1747)
<i>Orchis globosa</i>	<i>Traunsteinera globosa</i> (L.) Rchb.	Europe	Syst. Nat., ed. 10, 2: 1242. 1759.	1054-16
<i>Orchis habenaria</i>	<i>Habenaria quinqueseta</i> var. <i>macroceratitis</i> (Willd.) Luer	Jamaica	Syst. Nat., ed. 10, 2: 1242. 1759.	1054-14
<i>Orchis hyperborea</i>	<i>Platanthera hyperborea</i> (L.) Lindl.	Europe	Syst. Nat., ed. 12, 2: 591. 1767.	1054-42
<i>Orchis incarnata</i>	<i>Dactylorhiza incarnata</i> (L.) Soó	Europe	Fl. Suec., ed. 2: 312. 1755.	1054-33
<i>Orchis latifolia</i>	<i>Dactylorhiza sambucina</i> (L.) Soó	Europe	Sp. Pl. 2: 941. 1753. Linnaeus, Dalibard, Vaillant, Bauhin	1054-32
<i>Orchis latifolia</i> γ	<i>Dactylorhiza majalis</i> (Rchb.) P.F. Hunt & Summerh.	Europe	Sp. Pl. 2: 942. 1753. Bauhin	
<i>Orchis latifolia</i> δ	<i>Dactylorhiza sambucina</i> (L.) Soó	Europe	Sp. Pl. 2: 942. 1753. Bauhin	
<i>Orchis latifolia</i> ε	<i>Dactylorhiza maculata</i> (L.) Soó	Europe	Sp. Pl. 2: 942. 1753. Bauhin	
<i>Orchis maculata</i>	<i>Dactylorhiza maculata</i> (L.) Soó	Europe	Sp. Pl. 2: 942. 1753. Linnaeus, Dalibard, Dodoens, Bauhin	1054-36
<i>Orchis mascula</i> (L.) L. (≡ <i>O. morio</i> var. <i>mascula</i> L.)	<i>Orchis mascula</i> (L.) L.	Europe	Fl. Suec., ed. 2: 310. 1755. Camerarius, Bauhin	Matthioli, Pl. Egit.: 624 (1586)
<i>Orchis militaris</i>	<i>Orchis militaris</i> L.	Europe	Sp. Pl. 2: 941. 1753. Linnaeus, Dalibard, Vaillant, Tournefort, Ray, Fuchs, Bauhin	Fuchs, Hist. Stirp.: 554, 558 (1542)
<i>Orchis morio</i>	<i>Anacamptis morio</i> (L.) R.M.Bateman, Pridgeon & M.W.Chase	Europe	Sp. Pl. 2: 940. 1753. Linnaeus, Dalibard, Haller, Séguier, Royen, Fuchs, Bauhin	Fuchs, Hist. Stirp.: 559, 561 (1542)
<i>Orchis morio</i> var. <i>angustifolia</i>	<i>Anacamptis laxiflora</i> (Lam.) R.M.Bateman, Pridgeon & M.W.Chase	Europe	Sp. Pl. 2: 940. 1753.	Vaillant, Bot. Paris.: 150, t. 31, f. 33, 34 (1727)
<i>Orchis morio</i> var. <i>mascula</i>	<i>Orchis mascula</i> (L.) L.	Europe	Sp. Pl. 2: 941. 1753.	Matthioli, Pl. Egit.: 624 (1586)
<i>Orchis odoratissima</i>	<i>Gymnadenia odoratissima</i> (L.) Rich.	Europe	Syst. Nat., ed. 10, 2: 1243. 1759.	1054-37
<i>Orchis pallens</i>	<i>Orchis pallens</i> L.	Europe	Mant. Pl. Altera: 292. 1771.	Haller, Hist. Stirp. Helv. 2: 143, t. 30 (1768)
<i>Orchis papilionacea</i>	<i>Anacamptis papilionacea</i> (L.) R.M.Bateman, Pridgeon & M.W.Chase	Europe	Syst. Nat., ed. 10, 2: 1242. 1759.	1054-30, right-hand specimen
<i>Orchis pycodes</i>	<i>Platanthera pycodes</i> (L.) Lindl.	Canada	Sp. Pl. 2: 943. 1753. Gronovius, Ray, Kalm	1054-51 (Kalm)
<i>Orchis pyramidalis</i>	<i>Anacamptis pyramidalis</i> (L.) Rich.	Europe	Sp. Pl. 2: 940. 1753. Linnaeus, Dalibard, Haller, Séguier, Ray, Bauhin	1054-17
<i>Orchis pyramidata</i> (orth. var.)	<i>Anacamptis pyramidalis</i> (L.) Rich.	Europe	Amoen. Acad. 4: 492. 1759.	1054-17
<i>Orchis sambucina</i>	<i>Dactylorhiza sambucina</i> (L.) Soó	Europe	Fl. Suec., ed. 2: 312. 1755.	1054-34

Continued

APPENDIX *Continued*

Linnaeus' name	Currently accepted name	Origin	Place of publication/sources	Lectotype (numbers refer to specimens in LINN unless otherwise indicated)
<i>Orchis sancta</i>	<i>Anacamptis sancta</i> (L.) R.M.Bateman, Pridgeon & M.W.Chase	Europe	Syst. Nat., ed. 10, 2: 1242. 1759. Hasselquist.	1054-12
<i>Orchis satyrioides</i> (nom. illeg.)	<i>Schizodium cornutum</i> (L.) Schltr.	South Africa	Amoen. Acad. 6: 109. 1763.	Herb. Burman (G)
<i>Orchis spectabilis</i>	<i>Galearis spectabilis</i> (L.) Raf.	USA	Sp. Pl. 2: 943. 1753. Gronovius, Clayton	1054-44
<i>Orchis strateumatica</i>	<i>Zeuxine strateumatica</i> (L.) Schltr.	Sri Lanka	Sp. Pl. 2: 943. 1753.	Herb. Hermann (BM)
<i>Orchis susannae</i>	<i>Pecteilis susannae</i> (L.) Raf.	Amboina, Maluku	Sp. Pl. 2: 939. 1753.	Hermann, Parad. Bot.: 209 (1698)
<i>Orchis ustulata</i>	<i>Neotinea ustulata</i> (L.) R.M.Bateman, Pridgeon & M.W.Chase	Europe	Sp. Pl. 2: 941. 1753. Linnaeus, Dalibard, Vaillant, Séguier, Clusius, Bauhin	1054-21, left-hand specimen
<i>Satyrium albidum</i>	<i>Leucorchis albida</i> (L.) Á.Löve & D.Löve	Europe	Sp. Pl. 2: 944. 1753. Linnaeus, Haller, Micheli, Chomel	Micheli, Nov. Pl. Gen.: 30, t. 26, f. A-C (1729)
<i>Satyrium capense</i>	<i>Eulophia</i> sp.	South Africa	Pl. Rar. Afr.: 27. 1760.	Not located
<i>Satyrium cornutum</i>	<i>Schizodium cornutum</i> (L.) Schltr.	South Africa	Pl. Rar. Afr.: 27. 1760.	Herb. Burman (G)
<i>Satyrium epipogium</i>	<i>Epipogium aphyllum</i> Sw.	Siberia	Sp. Pl. 2: 945. 1753. Gmelin	Gmelin, Fl. Sibirica 1: 12, t. 2, f. 2 (1747)
<i>Satyrium hircinum</i>	<i>Himantoglossum hircinum</i> (L.) Spreng.	Europe	Sp. Pl. 2: 944. 1753. Linnaeus, Dalibard, Vaillant, Séguier, Morison, Bauhin	Vaillant, Bot. Paris.: 149, t. 30, f. 6 (1727)
<i>Satyrium latifolium</i>	<i>Erythroides hirtella</i> (Sw.) Fawc. & Rendle	Jamaica	Fl. Jam.: 20. 1759.	1055-6
<i>Satyrium nigrum</i>	<i>Gymnadenia nigra</i> (L.) Rchb.f.	Europe	Sp. Pl. 2: 944. 1753. Linnaeus, Royen, Camerarius, Haller, Bauhin	1055-4 (right-hand specimen)
<i>Satyrium plantagineum</i>	<i>Erythroides plantaginea</i> (L.) Fawc. & Rendle	West Indies	Syst. Nat., ed. 10, 2: 109. 1759.	Sloane, Voy. Jam. 1: 250, t. 147, f. 2 (1707)
<i>Satyrium repens</i>	<i>Goodyera repens</i> (L.) R.Br.	Europe	Sp. Pl. 2: 945. 1753.	Camerarius, Hort. Med. Phil.: 111, t. 35 (1588)
<i>Satyrium viride</i>	<i>Dactylorhiza viridis</i> (L.) R.M.Bateman, Pridgeon & M.W.Chase	Europe	Sp. Pl. 2: 944. 1753. Linnaeus, Dalibard, Vaillant, Loeselius, Bauhin	1055-3
<i>Serapias capensis</i>	<i>Acrolophia barbata</i> (Thunb.) Pfitzer	South Africa	Mant. Pl. Altera: 293. 1771.	1057-9
<i>Serapias cordigera</i>	<i>Serapias cordigera</i> L.	Europe	Sp. Pl., ed. 2, 2: 1345. 1763.	1057-8 (Alströmer)
<i>Serapias grandiflora</i> (nom. illeg.)	<i>Cephalanthera longifolia</i> (L.) Fritsch	Europe	Syst. Nat., ed. 12, 2: 594. 1767.	1057-4
<i>Serapias helleborine</i>	<i>Epipactis helleborine</i> (L.) Crantz	Europe	Sp. Pl. 2: 949. 1753. Linnaeus, Dalibard	Herb. Burser X: 40 (UPS)
<i>Serapias helleborine</i> var. <i>latifolia</i>	<i>Epipactis helleborine</i> (L.) Crantz	Europe	Sp. Pl. 2: 949. 1753. Gmelin, Bauhin, Camerarius	Herb. Burser X: 39 (UPS)
<i>Serapias helleborine</i> var. <i>longifolia</i>	<i>Cephalanthera longifolia</i> (L.) Fritsch	Europe	Sp. Pl. 2: 950. 1753. Linnaeus, Vaillant	1057-4
<i>Serapias helleborine</i> var. <i>palustris</i>	<i>Epipactis palustris</i> (L.) Crantz	Europe	Sp. Pl. 2: 950. 1753.	Morison, Pl. Hist. Univ. 3: 487, s. 12, t. 11, f. 7 (1699)
<i>Serapias lingua</i>	<i>Serapias lingua</i> L.	Europe	Sp. Pl. 2: 950. 1753. Linnaeus, Sauvages, Bauhin, Colonna	Colonna, Ekph.: 321, 322 (1606)
<i>Serapias palustris</i> (L.) L. (= <i>S. helleborine</i> var. <i>palustris</i> L.)	<i>Epipactis palustris</i> (L.) Crantz	Europe	Amoen. Acad. 4: 107. 1759.	Morison, Pl. Hist. Univ. 3: 487, s. 12, t. 11, f. 7 (1699)
<i>Serapias rubra</i>	<i>Cephalanthera rubra</i> (L.) Rich.	Europe	Syst. Nat., ed. 12, 2: 594. 1767.	1057-5