

A HISTORICAL PERSPECTIVE ON ORCHID POLLINIUM AND POLLEN CHARACTERS

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ABSTRACT: Pollinium characters have been among the most important in orchid classification since the first systems were proposed at the beginning of the nineteenth century. The first features to be used were texture, composition, and shape. Accessory structures such as stalks were also noted very early. As more orchid species were described in the early nineteenth century, additional variation was recognized and soon pollinium number and arrangement were used as taxonomic characters. Although established early on, most of these characters have been refined since, such that more character states are now known and there is a better basis for decisions on homology. Improved microscopical techniques facilitated the development of additional pollinium characters such as pollen surface structure and number of apertures. Along with the discovery and use of this variation in orchid classifications, a realization of its relevance to the life history of orchids has also grown.

Key words: Orchidaceae, pollinia, pollen, systematics

The study of orchid classification has focused, as with most plant groups, on structural variation in flowers. Particular attention has been paid to the anther and its components, of which pollinia are perhaps the most salient part. While Apostasioideae have powdery pollen like that of most angiosperms and Cypripedioideae tend to have pasty pollen masses, the remainder of the family have pollinia that are coherent to a greater or lesser degree. Today, pollinium variation is of obvious importance in classification, but this was not always the case. Classical writers and Renaissance herbalists recognized the distinctiveness of and similarities among the orchids that they knew; but floral details beyond gross shape, color and arrangement of the perianth were usually not recorded. The small size of pollinia would surely contribute to their being overlooked. It was apparently not until the eighteenth century that pollinia were noted in print. It was also at this time that microscopes were becoming more common, thus facilitating the study of such small structures. Rumphius, in the descriptions of orchids in his *Amboinsche Kruid-boek* (written 1657–1697 but published 1741–1750; Beekman 2003), noted structures in the flower that he described as “grains like a seed” and “yellow kernels,” which undoubtedly were pollinia.

Subsequent authors paid increasing attention to pollinia both as aspects of orchid reproductive biology and as features to distinguish and classify species. Haller (1742), for example, described the physical relation between the pollen masses and the stigma in *Epipactis*, noting also the rostellum. Adanson (1763) described the orchid anther as containing a small yellow “club”

(*massue*), sometimes attached to an elastic stalk, clearly referring to a pollinium. A prominent exception to noting pollinia was Linnaeus (1753), who recognized eight orchid genera but did not refer to pollen characters in distinguishing them or their species. Willdenow (1805) did note differences in pollen shape and cohesion among a few of the genera that he enumerated. He described *Cymbidium* as having “pollen globosum” in contrast to *Arethusa*, with its “pollen pulvereo–granulatum.” Neither he nor Linnaeus grouped the genera they treated in any way.

Swartz (1800a, 1800b) is generally considered to have produced the first orchid classification, because he grouped the 25 genera that he treated in a hierarchic arrangement. The pollinium features that he described for these genera were texture (e.g., pulverulent vs. granulose vs. globular), composition (he noted massulae in *Orchis*), and shape (clavate vs. globose). He also noted a pollinium stalk in orchidoids and *Oncidium*. Robert Brown (1810), in his treatment of the orchid flora of Australia, paid considerable attention to the nature of the pollinia for the taxa that he described and included those features that Swartz had described plus the presence of a stigmatic gland (viscidium). Brown’s familiarity with diverse orchid groups later positioned him well to describe the details of pollinia in orchids broadly (Brown 1833) and to compare orchid pollinia to the similar structures found in Asclepiadaceae (a similarity that also had been noted by Swartz 1800a).

The most significant work of orchid classification in the early nineteenth century was the comprehensive treatment of Lindley (1830–1840), who included over 1800 species. The

broad geographical scope of his treatment meant that a greater degree of variation in pollinium characters was included and valued. Lindley (1830–1840: xvi) stated that, “In classifying this order the most important characters appear to reside in the pollen. . . .” Lindley used the features that Swartz and Brown had described and added to them a number of pollinia and their arrangement (superposed or not). Hence, by the time of Lindley’s work, all of the principal pollinium characters in use today had been established. All subsequent classifications (e.g., Pfitzer 1888–1889; Schlechter 1926; Dressler & Dodson 1960; Dressler 1981, 1993) have depended heavily on these features.

Having briefly reviewed the history of the initial awareness of pollinia and of the introduction of pollinium characters into classification, it is worth focusing in some more detail on individual pollinium characters and how our understanding of them has increased since this early period. It is apparent that there has been some confusion in the meaning of some of these terms.

Pollinium texture was among the first pollen characters to be used in a classification, but when considered across the family, it is clear that it is a continuous character (Dressler 1986). Still, it is usually possible to distinguish those pollinia that are truly coherent from those that are soft enough to be easily crushed when touched. The structural basis for this difference has been elucidated by ultrastructural studies of pollinia (Chardard 1958, 1962, 1963, 1969; Cocucci & Jensen 1969; Schill & Pfeiffer 1977; Wolter & Schill 1986; Yeung 1987b; Hu & Yang 1989; Zavada 1990; Pandolfi et al. 1993). The most important difference is whether or not exine is deposited on internal pollen grains; if not, a more cohesive, calymmate pollinium results, while those that do have exine on all grains are termed acalymmate and are much more friable (van Campo & Guinet 1961). Burns–Balogh and Funk (1986) and Freudenstein and Rasmussen (1999) used pollinium texture in their phylogenetic analyses of the family.

Composition of pollinia, as used here, refers to whether the pollinium is a single homogeneous structure or is further subdivided into smaller units, usually termed *massulae*. The latter pollinia are termed *sectile*. This type of variation was noticed very early on, in part due to the fact that the early authors were European and the majority of northern European orchids have sectile pollinia. Adanson (1763) described orchid pollen masses composed of “somewhat enlarged pyramidal particles, yellow or bluish, which are difficult to detach from one another.” It is clear that he was describing sectile pollinia.

Brown (1810) noted the condition of having pollinia in “numerous angular lobes” in *Habenaria*, again clearly the sectile condition. Richard (1817) proposed a number of names for orchid structures and conditions in an attempt to clarify terminology. He introduced the term *sectile* to refer to such pollinia. He also introduced the term *massula*, but he did not use it to refer to the ultimate units in a sectile pollinium as we do today. Rather, he used it to refer to each of the halves of a bipartite pollinium, such as one often sees in the Orchideae. He used the term *massa pollinica* to refer to the contents of each anther theca, each of which was in turn composed of two massulae. This usage was maintained by some authors through the mid 19th century, such as Reichenbach (1852). However, other authors, at least as early as Hofmeister (1861) began to use *massula* to refer to a single packet of pollen cells in a sectile pollinium, all of which are derived from a single precursor cell. Darwin (1862) called them simply “packets of pollen-grains.” Pfitzer (1888–1889) used *massula* to refer to a sectile packet and the term has been used in this way by most subsequent authors.

Massulae are best known from Orchidoideae, where they characterize Orchideae and Diseae, as well as Goodyerinae in Cranichideae. In these taxa the massulae are typically arranged in a single layer; the massulae are often elongate and attached to an elastoviscin network at one of their ends. However, sectile pollinia are also known from some “basal” epidendroid groups, such as *Epipogium* and *Stereosandra*, *Nervilia* and *Gastrodieae*. In these groups, the massulae are more irregular and often arranged in multiple indistinct layers (Vermeulen 1965; Freudenstein & Rasmussen 1997). Pollinia of *Arethusa* and *Calopogon* are indistinctly sectile and are hollow at maturity (cf. Pace 1909; Freudenstein & Rasmussen 1997). In a most unusual case, the pollinarium of *Thelasis* contains massulae at its base in addition to eight regular pollinia (Rasmussen 1982; Freudenstein & Rasmussen 1997).

With respect to pollinium numbers, the primary ones in orchids are 2, 4, and 8. Other numbers are sometimes reported (e.g., in *Laeliinae*), when additional small masses of pollen that sometimes are found along the caudicles are interpreted as pollinia. Four is the plesiomorphic and most frequent number, and is found in the putatively basal orchid groups, as well as in outgroups (where there are four anther locules). It appears, however, that ontogenetically two may be the earliest state, with other numbers being derived by sterilization of sporogenous tissue producing partitions (Freudenstein & Rasmussen 1996). Freudenstein and Rasmussen (1996) sug-

gested that there may be two ways to produce eight pollinia—by longitudinal or transverse division of embryonic pollen masses.

Variation in arrangement of pollinia in the anther (and after removal) also has been important in orchid classification. The two arrangements currently recognized are *juxtaposed* (Freudenstein & Rasmussen 1996), the plesiomorphic state in which four pollinia are side-by-side in the anther, and *superposed* (Dressler & Dodson 1960), where the pairs of pollinia are stacked on one another. Although Richard (1817) used the Latin term *superposita* to describe the anthers of *Calypso*, *Corallorhiza*, *Liparis* and *Epipogium*, he probably was referring to the incumbent condition of the anthers rather than the arrangement of the pollinia. Lindley (1830–1840) recognized the difference in pollinium arrangement and called the side-by-side state *collateralia* and the superposed state *incumbentia* and illustrated the distinction with small figures in his keys. Benthams (1881) also recognized the variation, but he did not use the term “superposed,” referring rather to “pollinia fore-and-aft in each pair” as opposed to “collateral and parallel.” Superposed pollinia are one feature of the “vandoid” morphology that has at times been used to define a taxonomic group (Dressler 1981) or concluded to have been derived independently in various groups (Dressler 1993). Freudenstein et al. (2002) showed that the superposed pollinium arrangement, early anther incumbency, and cellular pollinium stalk (the key features of the “vandoid” morphology) may be related in a functional way and are due at least in part to a pedomorphic shift in anther development.

In addition to the pollen masses themselves, accessory structures (stalks) associated with pollinia show considerable variation. Some of these are modifications of pollen cells, while others are derived from the rostellum. Pollinium stalks were used in a classification by Swartz (1805), but noted as least as early as Adanson (1763). Richard (1817) applied the name *caudicula* to this structure. Caudicles are pollinium stalks that are composed of pollen and/or pollen-derived substances (Yeung 1987a), as opposed to rostellar tissue (Richard 1817; Mansfeld 1934; Rasmussen 1986). In epidendroid and spiranthoid orchids they are produced apically in the anther, due to the bending of the anther or the apical position of the rostellum, respectively. In Orchideae the caudicles are basal extensions of the pollinia that are held in an erect anther. Fairly early on it was realized that not all pollinium stalks are the same. In fact, Brown (1810) had already distinguished between stalks derived from the anther and from the stigma (rostellum). Wolf (1865–1866) showed the difference in or-

igin between the stalks seen in *Orchis* (caudicula) and *Lycaste* (pedicellus). The same difference was noted by Benthams (1881), who contrasted the caudicle with what he termed a *stipe*, the latter comprising the abaxial surface (top) of the rostellum. Hirmer (1920) examined the rostellum and anther in many orchid groups and noted the origin of pollinium stalks. The distinction between rostellar and anther-derived stalks was recognized by most subsequent authors. Rasmussen (1982) distinguished further between two stipe variants—the *tegula*, a stalk formed from the abaxial surface of the rostellum, and a *hamulus*, the whole apical portion of the rostellum. The tegula may be a multilayered epidermis or may consist solely of the rostellar cuticle, as in *Doritis* (Rasmussen 1986). A distinctive stipe with a “hammer-like” morphology was identified by Rasmussen (1986) in *Sunipia*.

Additional characters from orchid pollen have been used systematically, including the unit of pollen grain cohesion at maturity. While this aspect of orchid pollen is often not obvious in the pollinium-forming orchids, it has been a subject of study since Reichenbach (1852). The variation was described by Schill and Pfeiffer (1977) for a large number of species; others were reported in Newton and Williams (1978), Ackerman and Williams (1980, 1981), and Hesse et al. (1989). Both tetrads and monads are known from orchids, with monads being the plesiomorphic state. Although in most cases it appears that only one state is present, there are some cases in which both states occur, such as some diurids (e.g., *Caladenia*; Ackerman & Williams 1981). Wolter and Schill (1986) suggested that the occurrence of tetrads in orchid pollen may be a pedomorphic transformation in the sense that free monads represent the completion of the developmental program, while tetrads represent a sub-terminal stage present in an adult plant. An additional pollen feature, the arrangement of pollen cells in a tetrad, was studied by Konta and Tsuji (1982) and Konta and Hayakawa (1982). They recognized up to six shapes of pollen tetrads, but found that all species had more than one type of tetrad, with some species having all of the recognized types.

Pollen surface structure has been described by Williams and Broome (1976), Schill and Pfeiffer (1977), Burns-Balogh (1983), Hesse et al. (1989), Zavada (1990), and Schlag and Hesse (1993). The most striking variation is between reticulate and smooth tecta. This difference was in fact known since Reichenbach (1852), who illustrated the variation.

Whether apertures are present on the pollen, and if so, how many, have also been used as systematic characters. The majority of orchid

pollen is inaperturate (Schill & Pfeiffer 1977), but putatively basal groups have colpate/sulcate or porate pollen (Newton & Williams 1978; Hesse et al. 1989). Some of the vanilloids (*Vanilla*, *Epistephium*, *Lecanorchis*) have polyaperturate pollen (Erdtman 1944, 1952; Schill & Pfeiffer 1977; Ackerman & Williams 1980), a feature otherwise unknown among orchids. Schill (1978) and Newton and Williams (1978) described the colpus of *Apostasia* and *Neuwiedia* as "operculate," since it has a marginal rim. Burns-Balogh and Funk (1986) and Freudenstein and Rasmussen (1999) utilized this character in their analyses.

CONCLUDING STATEMENT

The biological implications of all of this variation and specialization in orchid pollinia are significant. Darwin (1862) described many of the implications of this intricate morphology and much has been learned since about the integral part played in orchid life history by the pollinium. Works such as van der Pijl and Dodson (1966), Proctor et al. (1996) and recent reviews by Harder and Johnson (2008) have synthesized the biological role of this variation as we understand it thus far, but much remains to be learned.

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