Appendix S2: Definition and explanation of floral characters

This appendix is based the online Supplementary Information for Sauquet et al. (2017) but has been complemented with definitions and explanations for six additional androecial and gynoecial characters plus two pollen characters.

This section provides the criteria for how we defined and treated each floral character analysed in this study and partially also in Sauquet et al. (2017, 2018). All floral characters were recorded in the PROTEUS database (Sauquet, 2019). In total, our analyses are based on 29 characters. As in Sauquet et al. (2017), all characters, as they are scored in PROTEUS (primary characters), were transformed into secondary characters for analysis by converting continuous characters into discrete characters and by reducing the number of character states of discrete characters. For one of the 29 primary characters, "number of perianth parts", we analyse two secondary characters "absence/presence of a perianth" and "number of perianth parts when present", as they capture essentially different information. Accordingly, the morphological matrix used for the molecular backbone analyses in this paper contains a total of 30 secondary characters. The complete list of data records, each of them linked to an explicit reference, and the final matrix used in all analyses are provided in Appendix S1.

Primary characters, either qualitative/discrete (D1) or quantitative/ordinal/continuous (C1), represent characters as recorded from primary literature sources. *Secondary characters* used in the analyses are all discrete (D2) and were derived by reduction of states from discrete primary characters (D2d), or from modification of continuous primary characters into discrete classes of variation (D2c). We acknowledge that some quantitative characters, such as number of organs, may be discrete in their variation rather than continuous, but refer to them as continuous for the sake of convenience. Each character was assigned a number within a range that refers to organ type: 100-199 for general floral characters, 200-299 for perianth characters, 300-399 for androecial characters, 400-499 for gynoecial characters, and 5000-5099 for pollen characters. Primary characters have a number only (e.g., 100), while secondary characters share the number of the primary character from which they are derived and, in addition, are provided with a letter suffix referring to different versions of secondary characters (e.g., 100_A). As outlined above, for one character ("number of perianth parts", we have used two secondary characters that are based on the same primary character (201_A, 201_B). In our original study (Sauquet et al., 2017), this strategy had also allowed us to address different questions as well as to test the effect of many vs. two or three character states on the results from model selection analyses, parameter estimations, and ancestral state reconstructions.

Scoring philosophy

There is no general consensus on the optimal way to score phenotypic data, especially with respect to discrete characters. In particular, the appropriate number of character states may depend on the type of analysis and/or the type of questions being asked. Thus, we have developed the two-step approach to character scoring outlined above, whereby we separate primary characters for scoring the observed data without too many assumptions, from secondary characters used in a given analysis. This approach also provides the option for future users to query the primary scorings and derive scoring schemes that fit their own needs.

Rationale for reducing the number of character states. In our original study (Sauquet et al., 2017), we aimed to reduce the number of character states of discrete secondary characters (D2) as much as possible. While a large number of character states is not necessarily a problem with parsimony optimization (at least as long as the sample size is large), this becomes a serious problem with maximum likelihood or Bayesian analyses based on probabilistic models. The latter types of analyses require much greater computational power as the number of transition rate parameters for the general Markov model with all rates different increases very fast. The number of such parameters for a k-state character is equal to k (k – 1) meaning that a 3-state character has six transition rates, whereas a 6-state character has already 30. Even with a large data set such as ours, we may not have enough data to accurately estimate these transition rates, particularly for rare character states. Model selection can partly correct for this problem by constraining two or more parameters to be equal or zero, and by the use of metrics such as the Akaike Information Criterion (AIC) to choose the best-fit model for a given analysis (Posada and Buckley, 2004). In spite of these aids, the size of model space increases even more drastically with additional character states. For instance, a 3-state character has 876 distinct Markov models, while a 4-state character has 27,644,436 distinct models. Even Bayesian strategies developed to explore model space, such as reversible-jump Markov Chain Monte Carlo (Pagel and Meade, 2006), may not have enough power to explore the entire model space within a reasonable computational time frame. For these reasons, we have strived to keep the number of character states low in discrete secondary characters (used in analyses) and have occasionally excluded (i.e., treated as missing data) rare or exceptional character states (e.g., hexamery). In this study, we did not use probabilistic methods to reconstruct the phylogenetic position of fossils. However, it is our aim to do so in the future, hence the principles above were maintained to build our new set of secondary characters, most of which overlap with those in our previous paper (Sauquet et al., 2017).

Inapplicable and missing data. None of the currently available methods for character analysis and ancestral state reconstruction can distinguish inapplicable data from missing data. Scoring inapplicable data as a separate character state has several disadvantages: (1) it adds an extra state to the model (see above); (2) it adds redundancy to the data set (e.g., adding a "perianth absent" state each to the characters perianth phyllotaxis, merism, and differentiation); and (3) it transforms the question asked by the analysis. For instance, it is not the same to ask how spiral and whorled flowers evolved from each other in a 2-state character analysis as to ask how flowers with no perianth, a spiral perianth, or a whorled perianth evolved from each other in a 3-state character analysis. For these reasons, all inapplicable data were treated as missing data for this project.

Polymorphic data. Whenever two or more states co-exist in any given species (either due to intraspecific variation, actual co-existence in the same individual, or intermediate states), we scored them as polymorphic data, which is unproblematic for the type of analysis that we use in this paper. Not all methods for ancestral state reconstruction can take polymorphic data into account. However, all methods we used in this and our previous papers allowed polymorphic data (incl. parsimony, maximum likelihood as implemented in the R package corHMM (Beaulieu et al., 2013) and Bayesian analysis as implemented in BayesTraits (Pagel and Meade, 2013)).

Sexual dimorphism. It is not uncommon that unisexual flowers differ in specific aspects of their morphology. For instance, in the genus *Buxus*, male flowers have a whorled perianth whereas female flowers have a spiral perianth (von Balthazar and Endress, 2002). Accounting properly for such differences would be interesting in lower-level studies focusing on a particular

unisexual clade, for instance by using separate characters for male and female flowers or by adding special characters to record sexual dimorphism. However, for this large-scale project, such an approach is neither suitable nor relevant. Therefore, we scored all cases of sexual dimorphism of nonsexual characters as polymorphic data. For instance, in *Buxus*, we scored perianth phyllotaxis as both whorled and spiral. For sexual characters (androecium and gynoecium), sexual dimorphism is usually directly linked to unisexuality. Thus, we scored androecial characters (e.g., number of stamens) of unisexual species based on their male flowers, and gynoecial characters (e.g., number of carpels) of unisexual species based on their female flowers.

Continuous characters. For continuous (quantitative) characters (C1), we scored either a value or a range of values (as minimum and maximum), depending on intraspecific variation and accuracy of measurement. For instance, a flower with perianth parts fused more or less along 50% of their length may be scored with a value range from 0.4 to 0.6. When compiling discrete secondary characters from such a continuous character (D2c), the entire range of values scored in each species is taken into account.

Use of terminology describing organ fusion. The taxonomic and morphological literature uses various terms to describe the fusion of organs of the same type (often called "connation" or "union") vs. the fusion of organs of different types (often called "adnation" or "fusion"). However, the use of these terms is not consistent in the literature and in order to avoid confusion, we decided to only use the term "fusion" and to always explicitly mention the organs involved.

Congenital vs. postgenital fusion. In theory, it would be interesting and important to distinguish between congenital and postgenital fusion (von Balthazar and Endress, 2002). In practice, this is mostly impossible unless adequate developmental data are available, which was the case only for a fraction of the species in our sample. Therefore, all of the fusion characters in this paper include both congenital and postgenital fusion.

Developmental evidence. Detailed observations of floral organs throughout floral development may inform us on their homology and the processes that lead to their final shape and architecture at anthesis. However, such data are available only in a small number of angiosperm species. In addition, some characters may change during ontogeny. For instance, perianth parts may be initiated spirally but be arranged in whorls at anthesis (Erbar and Leins, 1994; Schönenberger and Grenhagen, 2005). For this project, we were careful to only record characters at anthesis so that all of our characters could be comparable and scorable across our entire sample. This does not mean that we ignored solid, morphological studies including developmental observations, but we made sure to score only data as observed in the later (near-anthetic) stages of the floral developmental sequence (for additional discussion, see also Sauquet et al., 2018; Sokoloff et al., 2018). This decision was all the more important in the context of the present study as developmental data is generally lacking for fossil flowers.

General floral characters

100. Structural sex of flowers (D1). Flowers can be either bisexual (hermaphrodite) or unisexual. In our original study (Sauquet et al., 2017), we used a single character to distinguish among the many possible ways to be unisexual, depending on whether sterile organs of the opposite sex (staminodes or carpellodes) are found in flowers of a given sex, whether male and female flowers are found on the same plant (monoecy) or separate plants (dioecy), as well as the various intermediate combinations that exist (e.g., androdioecy, gynomonoecy). We have

now simplified and divided this character into two and here capture only floral sex, distinguishing among three states: bisexual, incompletely unisexual (i.e., with pistillode in male flowers and/or staminodes in female flowers), and unisexual. All data from our previous dataset have now been rescored permanently into one of these three states. A second new character, *Plant sexual system*, resulting from the simplification outlined above, is excluded here because fossil flowers are usually found as individual, dispersed specimens, making it impossible to distinguish among different sexual systems such as monoecy and dioecy.

100_B. Structural sex of flowers (D2d). In this binary version of the character above, we treat incompletely unisexual flowers as structurally bisexual, and distinguish these from strictly unisexual flowers, as in our previous study using this secondary character (Sauquet et al. 2017). Co-occurrence of structurally unisexual and bisexual flowers is polymorphic and treated as missing data here. For instance, *Amborella trichopoda*, with structurally male and bisexual flowers but acting functionally unisexual dioecious (i.e., the bisexual flowers are functionally female flowers), is polymorphic for this character.

102. Ovary position (D1). The ovary is the part of the gynoecium where the ovules are produced. The ovary may be located on the receptacle and thus be positioned above the insertion level of the remaining floral organs (i.e., the ovary is superior and the flower is hypogynous). Alternatively, the ovary may be embedded in the receptacle and therefore be located below the insertion level of the remaining floral organs (i.e., the ovary is inferior and the flower is epigynous). Flowers with a hypanthium may either have a superior ovary (perigyny; e.g., many Rosaceae) or an inferior ovary (epiperigyny) (Simpson, 2010). It is also possible that the ovary is inferior to a certain degree only, such as half-inferior, if the receptacle is surrounding the ovary to its mid-level. Here we recorded the ovary position either as superior, inferior, or one of the following intermediate states: ¼ inferior or less, half-inferior, ¾ inferior or more.

102_B. Ovary position (binary) (D2d). Here we treat ovary position as a binary character, distinguishing only superior and inferior ovaries, and conservatively including all intermediate inferior states (i.e., ¼ inferior or less, half-inferior, ¾ inferior or more) in the character state inferior.

Perianth

There is considerable variation in the number and morphology of sterile organs surrounding the fertile organs across angiosperms. Some species do not have a perianth at all (e.g., *Chloranthus*), while others have a simple perianth of morphologically similar organs arranged either in a single whorl (e.g., *Myristica*), in two whorls (e.g., *Lilium*), or in a continuous spiral (e.g., *Amborella*), and the majority of species have a differentiated perianth commonly comprising an outer whorl of sepals and an inner whorl of petals (e.g., *Geranium*). In addition to this structural variation, it is generally acknowledged that perianth organs have different evolutionary origins, depending on the lineage considered (von Balthazar and Endress, 2002). Thus, petals may have evolved multiple times across angiosperms across angiosperms as a whole, which is why we decided not to use distinct characters for sepals and petals for this angiosperm-wide study. Instead, we only use broadly defined perianth characters to compare the evolutionary history of the perianth at the functional level. We acknowledge that at the developmental or genetic level the perianth as such may not have a single evolutionary origin in the angiosperms, but current knowledge on perianth organ evolution is too fragmentary to use it as a basis for defining perianth characters across all angiosperms.

Perianth vs. staminodes. Here, we define the perianth at the functional level as the collection of all sterile organs surrounding the reproductive floral organs. In some species, sterile organs resembling fertile stamens are present in addition to the fertile stamens. These organs are generally referred to as staminodes and may be outer staminodes, that is, inserted outside the fertile stamens (e.g., *Galbulimima*), inner staminodes, inserted between the fertile stamens and the gynoecium (e.g., *Degeneria*), or staminodes intermixed with fertile stamens of the same whorl or series (e.g., *Penstemon*) (Endress, 1984, 1990, 1994; Walker-Larsen and Harder, 2000). In many cases, such organs are morphologically more similar to fertile stamens than to typical perianth organs; hence, there is a general consensus that they should be considered as part of the androecium. However, some taxa challenge the traditional boundary between the perianth and the androecium (Ronse De Craene and Smets, 2001). For instance, stamens or staminodes may be petaloid and take over or at least add to the attractive function of the perianth (e.g., *Bonellia, Canna*). Or there may exist unique floral organs between the perianth and the androecium that resemble neither typical perianth organs nor fertile stamens (e.g., funnel-shaped nectar leaves of *Helleborus*). Or in exceptional cases, fertile stamens and peripheral sterile organs may both be petaloid and be morphologically nearly identical except for the presence of the pollen sacs (e.g., *Galbulimima*). In such cases, we decided to treat as members of the perianth only sterile organs that are morphologically clearly distinct from the fertile stamens. Thus, we treat the "petals" of *Nuphar* as part of the perianth, the staminodes of *Canna* as part of the androecium, the nectar leaves of *Helleborus* (not sampled in this data set) as part of the perianth (together with the sepaloid tepals), and the peripheral organs of *Galbulimima* as part of the androecium (Endress, 1984).

Perianth vs. bracts. In addition, the boundary between outer perianth organs and extrafloral organs such as bracts and prophylls is problematic in some taxa and there is no unique criterion that allows delimiting the flower from preceding organs. Here we follow published hypotheses on a case-by-case basis. For example, we treat the epicalyx of Malvaceae and the calyptra of *Eupomatia* as bracts (Endress, 2003; Kim et al., 2005), but the pair of deciduous organs enclosing the bud in *Papaver* as outer perianth organs (Endress, 1995; Rasmussen et al., 2009).
Interpretation of hypanthia and inferior ovaries. Floral cups, or hypanthia, are common in angiosperms. In most cases, these correspond to concave structures of undifferentiated tissue, on the margins of which both the perianth and the androecium are inserted, and at the base of which the gynoecium is inserted. Usually, hypanthia are interpreted to be expanded receptacles (Ronse De Craene, 2010). Here we follow this interpretation and consider perianth parts and stamens to begin on the rim of the hypanthium, not at its base, and therefore not necessarily all fused at the base. Similarly, when ovaries are inferior, we consider both the perianth and the androecium to start above the ovary, not at its base, and therefore not necessarily all fused along the length of the ovary.

Double positions. Organ doubling often happens when there is a change from broader to narrower organs, or when the meristem is elongated (Endress, 1994; Endress and Doyle, 2015). This process appears to be restricted to whorled organs and will cause a change in merism: typically, the number of parts in a given whorl is doubled. This is the common interpretation, for instance, to explain the octamerous inner perianth whorls of *Nymphaea* or the hexamerous androecium of *Alisma, Aristolochia*, and *Cabomba*. It has also been proposed as an explanation for the peculiar androecium of Fumarioideae (Murbeck, 1912) and the inner (tetramerous) stamen whorl of Brassicaceae (Endress, 1992). However, no consensus exists for these interpretations. Therefore, we opted for an agnostic approach when scoring perianth or androecium merism in such taxa and simply counted the number of organs in each distinct whorl.

Special cases. We treat the pappus of Asteraceae as a highly specialized calyx (Harris, 1995) and thus scored two perianth whorls and marked perianth differentiation in all species of Asteraceae. However, because it is not possible to count the number of original sepals in a pappus, we scored the number of perianth parts as five (based on the corolla only) in members of this family. We treat the lodicules of Poaceae as perianth parts, but only when they are clearly visible at anthesis (Whipple et al., 2007; Yoshida, 2012). The calyx of Apiaceae is, in many cases, small and only present as a toothed or non-toothed, truncate rim on top of the ovary; in a few taxa the calyx has been lost entirely. We treat the perianth in Apiaceae as two-whorled if a calyx rim of any form is present. In a non-toothed, truncate calyx rim we interpret the sepals as entirely fused and at the same time it is not possible to determine the number of sepals and as a consequence the character 201 'Number of perianth parts' is inapplicable. The cyathium of Euphorbiaceae is interpreted as an inflorescence of perianthless unisexual flowers rather than a flower (Prenner and Rudall, 2007). Pseudanthia, in general, are treated as inflorescences, not flowers. Reproductive structures of Hydatellaceae represent a special challenge to interpretation and have been termed by some authors as 'nonflowers' (Rudall et al., 2007). Here we do not opt for their interpretation either as inflorescences of unisexual flowers or very peculiar flowers with an inversion of the androecium and the gynoecium. Instead, we chose to not score (i.e., leave as missing data) characters that depend on the interpretation of the reproductive structures of Hydatellaceae. Flowers of Proteaceae have been interpreted as either tetramerous or dimerous. The latter is supported in part by the fact that the four stamens are always opposite the four tepals. However, this situation could equally be interpreted as loss of a perianth or androecial whorl. Although there is some indication that the four tepals develop as two decussate pairs in some species (Douglas and Tucker, 1996), this does not appear to be the case of stamens, and the perianth of all flowers of Proteaceae clearly appear as a single whorl of four tepals at anthesis (Weston, 2006). Thus, we treat the perianth and androecium of Proteaceae as tetramerous.

201. Number of perianth parts (C1). In this character, we scored the total number of perianth parts, including sepals, petals, or any form of tepal. A value of zero was scored when the perianth is absent. In flowers with perianth whorls fused along their complete length (e.g., *Convolvulus*), counting the number of perianth organs may be difficult or challenging. This is traditionally done based on merism (e.g., if a calyx has 5 distinct sepals and the corolla is entirely fused, then the corolla is often interpreted to consist of five fused petals), anatomy (e.g., number of vascular traces), development (e.g., number of primordia), or comparison with closely related taxa. This character is linked with several other aspects of perianth structure, in particular phyllotaxis, merism, and number of whorls, each of which was also recorded as a separate character and analysed on its own (see below). Our main goal with this character was to account for the number of perianth parts in key nodes of the angiosperm tree taking into account these combined characters and, in whorled clades, contrast it to inferences based on merism and number of whorls. The total number of perianth parts also has the advantage of being applicable to all angiosperms, including those with spiral phyllotaxis.

201_A. Perianth presence (D2c). Simplest discretization of the number of perianth parts to account for the evolution of perianth absence (0 parts) vs. presence (1 or more parts).

201_B. Number of perianth parts (3-state) (D2c). Here we discretized the number of perianth parts into three character states. Flowers with a perianth consisting of a single or two parts are extremely rare in the angiosperms and were treated here as the same state as perianths consisting of three, four, or five parts, which includes all single whorls of merism up to five. Perianths of six to 10 parts were pooled together in a state that includes all double whorls of merism between

three and five. Last, all numbers above 10 were treated together (usually corresponding to spiral perianths or rare perianths of four or more whorls).

230. Perianth phyllotaxis (D1). Perianth parts may be organized in one or more whorls or along a continuous spiral, usually with wide divergence angles more or less equal to 137.5° (Endress, 1987a, 2011; Endress and Doyle, 2007; Kuhlemeier, 2007). Less frequently, perianth phyllotaxis may be irregular (Zhao et al., 2012). Perianth phyllotaxis at anthesis may differ from phyllotaxis of perianth part primordia at their inception and it is not uncommon that spirally initiated perianths become whorled later through development (Erbar and Leins, 1994; Schönenberger and Grenhagen, 2005; Endress, 2010, 2011; Zhang and Schönenberger, 2014; Löfstrand et al., 2016). Here we score perianth phyllotaxis only at anthesis because developmental data are lacking for most species in our data set (for a detailed discussion of this important point, see Sauquet et al., 2018; Sokoloff et al., 2018).

Perianth phyllotaxis at anthesis is not always easy to recognize. The first criterion, when perianth parts are in sufficient number, is the pattern of parastichies and presence or absence of orthostichies (Endress and Doyle, 2007; Endress, 2010). However, this criterion cannot be used when perianth parts are few (e.g., five) and the insertion of parts along a circle at anthesis does not inform us on whether phyllotaxis is whorled or spiral or irregular. A more universal criterion lies in the divergence angles between successively initiated parts, which usually approximates 137.5° (golden angle) in Fibonacci spiral flowers (Staedler and Endress, 2009). However, it may be difficult or impossible to recognize successively initiated perianth parts in an anthetic flower. If we define a series as a set of more or less similar parts occupying the space of and arranged more or less in a circle, we may then use the number of distinct distances between two adjacent parts in a series as a criterion to identify phyllotaxis. Whorled series only have one identical distance between parts, whereas spiral series are typically expected to show two distinct distances: a short distance and a longer distance (Hirmer, 1931). In addition, most spiral series are characterized by a Fibonacci number of parts (e.g., 3, 5, 8) although individual variations are common so that this number is rarely completely fixed in spiral flowers. Thus, series with a consistent number of parts of 4 or 6 are less likely to be spiral. Furthermore, developmental data, when available, may still inform us on phyllotaxis at anthesis because spiral phyllotaxis never appears to result from simultaneous, whorled initiation (but note that the contrary is not true). Last, a potentially very confusing situation may arise when a perianth has two or more distinct, well differentiated series of identical number of parts. In such cases, whorled perianths are generally expected to show perfect alternation of successive whorls in addition to equal angles and distances within each whorl, whereas spiral perianths are expected to display less exact and less regular alternation of successive series and are expected to show the above pattern of two distances within each series caused by the golden angle. Such is the case of *Ranunculus acris* (Ranunculaceae), a species commonly assumed to have a whorled perianth, but which in fact has a spiral perianth (Schöffel, 1932). Although these rules can help us clarify difficult situations, one should note that they are not universal: zygomorphy and double positions may superpose on all types of phyllotaxis and create more complex patterns. In particular, unequal distances and divergence angles are expected at anthesis in whorled flowers that are also zygomorphic or characterized by double positions.

Scoring perianth phyllotaxis is further complicated by the fact that many eudicots appear to have a more or less spiral calyx and a whorled corolla (Ronse De Craene, 2010). However, this has not been thoroughly documented yet across the clade and most descriptions and illustrations of these taxa do not allow us to distinguish easily between a spiral and a whorled calyx, even

with the rules outlined above. Therefore, in this study, we have scored perianth phyllotaxis of most eudicots based on phyllotaxis of the inner perianth series (i.e., the corolla).

230_A. Perianth phyllotaxis (binary) (D2d). Perianth phyllotaxis treated as a binary character: spiral vs. whorled (rare cases of irregular phyllotaxis treated as missing data).

231. Number of perianth whorls (C1). The number of perianth whorls was recorded as a continuous character (with integer values of 1 and above). Not applicable when perianth phyllotaxis is spiral or irregular or when the perianth is absent.

231_A. Number of perianth whorls (D2c). Simple discretization of the number of perianth whorls as a three-state character: one, two, or more than two whorls.

232. Perianth merism (C1). Here we define perianth merism as the number of perianth parts in each whorl, recorded as a continuous character (with integer values of 1 and above). Not applicable when perianth phyllotaxis is spiral or irregular or when the perianth is absent.

232_A. Perianth merism (4-state) (D2c). Discretization of perianth merism as a four-state character, distinguishing dimerous, trimerous, tetramerous, and pentamerous perianths. We ignore (treat as missing data) other merisms (e.g., hexamery, octomery) because these states are comparatively very rare and caused reconstruction artefacts (due to low statistical power) in early analyses of this data set.

234. Perianth differentiation (D1). There are many ways in which perianth organs may look different from each other in a given flower. Typically, outer perianth parts are sepaloid and protect the other floral organs during floral development, while inner organs are often petaloid and play a role in pollinator attraction (Endress, 1994). However, it is also possible that all parts are either sepaloid or petaloid but remain differentiated in shape, size, and/or texture. In case of spiral perianths, differentiation may be continuous (i.e., gradual), whereby two successively initiated organs are very similar or only slightly different, while the outermost and innermost organs at both ends of the spiral are very different from each other (e.g., *Chimonanthus*). Here, we broadly define differentiation as any form of such differences, but record these various situations as separate character states. In contrast, we score all undifferentiated perianths (i.e., with all organs alike) in the same character state, regardless of phyllotaxis and number of whorls. In the special case of perianths consisting of a single whorl, we have decided to score them as undifferentiated rather than treat them as inapplicable because we aimed at a broadly comparable character describing the expression of general differentiation among perianth organs, rather than only the differentiation among multiple whorls. Thus, our perianth differentiation character may be seen as both functional (the parting vs. sharing of functions among perianth parts) and developmental (the expression of a genetic program for different forms of perianth parts vs. a single program for a single type of perianth part morphology). Within-whorl differentiation, whereby organs of the same whorl take different forms, is common in zygomorphic flowers (e.g., Balsaminaceae, Fabaceae, Orchidaceae) but is not taken into account here. This character is not applicable when the perianth is absent.

234_B. Perianth differentiation (binary) (D2d). Simplification of the character above as a binary character, distinguishing undifferentiated from differentiated perianths. Here we treated all forms of differentiation, including continuous and weak differentiation as differentiated. This is an alternative way to analyse this character to the one (234_A) used in our original study (Sauquet et al., 2017).

204. Fusion of perianth (C1). Fusion of perianth organs (congenital or postgenital) at anthesis, recorded on a continuous scale, from 0 (free parts) to 1 (parts fused along their entire length). Partial fusion was recorded using an approximate number between these two extremes (e.g., 0.1 corresponds to basal fusion, 0.5 to fusion along half of the length of perianth parts). In case of multiple whorls, we recorded within-whorl fusion in this character. For example, if organs within each whorl are fused along their entire length, we have recorded a value of 1 here. In cases where organs of two whorls are fused into a common tubular structure, such as frequently observed in monocots (e.g., *Polygonatum*), we have also recorded this as fusion in this character. If the two (or more) whorls differed in their extent of fusion, we have recorded this character as a range of values. For example, if the calyx is only basally fused, up to 10% of its length, but the corolla is entirely fused, we have recorded a range of 0.1 to 1 here. Our rationale for this was to provide a general character that allows comparison of fusion among all angiosperms, regardless of perianth architecture. Finally, we acknowledge that perianth parts may be fused very early in their development but then appear to be free at anthesis (i.e., early sympetaly as in Apiaceae for instance (Erbar and Leins, 1996)). Given that developmental studies are lacking for most extant species as well as for all fossils in our data set, we treat such flowers as having free perianth parts in order to treat all species in a comparable way (i.e., at anthesis).

204_A. Fusion of perianth (D2c). Here we discretized fusion of the perianth as a binary character (free vs. fused) with a threshold at 5%. For example, a perianth with parts fused up to 4% of their length will be treated as free, whereas a perianth with parts fused along 10% of their length will be treated as fused (both cases would traditionally be referred to as basal fusion). The rationale for the 5% threshold is that organs of the same whorl or even of two successive whorls often appear to have a short common base (which may be interpreted as part of the receptacle) and accordingly are often described as “basally connate” or “basally adhering” without being clearly fused. In addition, it appears reasonable to treat perianths fused for only less than 5% of their length in the same way as secondarily free perianths (early sympetaly) mentioned above.

207. Symmetry of perianth (D1). There are many ways in which flowers can be zygomorphic (monosymmetric, with a single plane of bilateral symmetry). Here we record perianth symmetry, regardless of androecium or gynoecium symmetry; thus the character is not applicable when the perianth is absent. We distinguish strict actinomorphy (i.e., polysymmetry, with three or more planes of bilateral symmetry) from spiral actinomorphy. In addition, disymmetry (two orthogonal planes of bilateral symmetry; e.g., Papaveraceae) and asymmetry are treated here as separate character states. As for the fusion of the perianth, this character is applied to the perianth as a whole. In case of flowers with two or more perianth whorls, species were scored as actinomorphic if all whorls are actinomorphic and as zygomorphic if one or more whorls are zygomorphic.

207_A. Symmetry of perianth (binary) (D2d). Here we treat perianth symmetry as a binary character, merging strict and spiral actinomorphy, and ignoring disymmetry (which may be considered intermediate between actinomorphy and zygomorphy, see Sauquet et al., 2015) and asymmetry. Accordingly, the two latter states are treated as missing data.

Androecium

The androecium encompasses the male reproductive organs of the flower and is sometimes composed of both fertile and sterile stamens (i.e., staminodes). Staminodes are widely distributed taxonomically and occur in at least one species in 32.5% of the angiosperm families

(Walker-Larsen and Harder, 2000). Although we are not analyzing the morphological diversity of staminodes, the presence of staminodes is taken into account for characters that are related to the overall androecial organization. Thus, they are included when recording the number of androecium whorls, androecium phyllotaxis as well as androecial merism and fusion of filaments, but not when recording number of fertile stamens, filament shape, and the various anther characters. The presence of outer petaloid staminodes is also discussed in the section on the definition of the perianth (see above).

Stamen shape is highly variable in angiosperms, including the shape of both the anther and the filament. In order to compare these variable structures across angiosperms, we work with the following simple definition of stamen morphology: the part of a stamen where pollen sacs are positioned is referred to as the anther (see also Hufford, 1996). The part proximal to the anther corresponds to the filament and the area distal to the anther is defined as the connective extension.

301. Number of fertile stamens (C1). Number of fertile (functional) stamens in bisexual or male flowers. Staminodes (co-occurring with fertile stamens) are not counted and female flowers are ignored for this character. Stamen number is highly variable within angiosperms and ranges from one (e.g., Chloranthaceae, Endress, 1987b) to several thousands (e.g., Cactaceae, Barthlott and Hunt, 1993). We record the number of fertile stamens in whorled or spiral flowers as a continuous character (with integer values of 1 and above). In cases of fusion among stamen whorls, the number of stamens may be difficult to determine. In such cases, additional information based on merism, anatomy, development, or comparison with closely related taxa may be taken into account. In synandria of Myristicaceae, for example, the number of fertile stamens can be deduced from the number of thecae present (Sauquet, 2003). In cases where stamen or anther morphology is not fully understood, we recorded the number of fertile stamens only when unequivocally clarified in the literature (e.g., Malvaceae, von Balthazar et al., 2004). Equivocal cases were left as missing data.

301_B. Number of fertile stamens (3-state) (D2c). Here we distinguish among androecia with 1-5 stamens, 6-10 stamens, and more than 10 stamens. These character states allow us to analyse stamen number in relation to various perianth characters irrespective of the number of stamens in one whorl. Thus, in clades with a whorled perianth and androecium, they inform us about transitions between haplostemonous and diplostemonous flowers regardless of whether the transition is from a trimerous or pentamerous stamen whorl to two such whorls or vice versa. Polystemony is the presence of an increased number of stamens, which can be achieved by the insertion of stamens pairs (e.g., Fouquieriaceae, Schönenberger and Grenhagen, 2005), the formation of stamen fascicles (e.g., Clusiaceae, Perrier de la Bâthie, 1951), the development of multiple stamens on a ring-primordium (e.g., Lecythidaceae, Tsou and Mori, 2007; Actinidiaceae, Löfstrand et al., 2016) or the multiplication of stamens whorls (e.g., Ranunculaceae, Ren et al., 2009, 2011).

330. Androecium structural phyllotaxis (D1). Androecium phyllotaxis may be spiral, whorled or irregular (Endress, 1987a). We call this character structural because both fertile stamens and staminodes were considered here. Furthermore, in cases of stamen fascicles, it is the phyllotaxis of fascicles, not individual stamens that we record here. Stamen arrangement is most often either spiral or whorled and in the latter case stamens may be arranged in one or more whorls. Irregular stamen arrangements occur less commonly and are often associated with polystemony (e.g., *Medusagyne*, Matthews et al., 2012). Androecium phyllotaxis is not always easy to determine, especially when there are many stamens (for guidelines, see notes under character

230. Perianth phyllotaxis). Particular caution should be exerted when scoring this character based on taxonomic literature, where irregular phyllotaxis is commonly mistaken for spiral phyllotaxis (e.g., Annonaceae, Xu and Ronse De Craene, 2010; Endress and Armstrong, 2011). This character is not applicable when there is a single structural stamen (i.e., one stamen, no staminodes; e.g., *Chloranthus*, Chloranthaceae).

330_A. Androecium structural phyllotaxis (binary) (D2d). Androecium phyllotaxis treated as a binary character (spiral vs. whorled; irregular phyllotaxis treated as missing data).

331. Number of androecium structural whorls (C1). The number of whorls was recorded as a continuous character (with integer values of 1 and above). We call this character structural because both fertile stamens and staminodes were considered. Furthermore, in cases of stamen fascicles, it is the whorls of fascicles that we record here. This character is not applicable for spiral or irregular stamen arrangements, or when there is a single structural stamen (i.e., one stamen, no staminodes; e.g., *Chloranthus*, Chloranthaceae). In the case of stamen fusion, the organization of the androecium may be difficult to evaluate and in such cases additional information from developmental or anatomical studies was considered if available. Equivocal cases were left as missing data.

331_A. Number of androecium structural whorls (3-state) (D2c). Here we discretized the number of androecium whorls into three character states: androecia consisting of a single whorl, androecia with two whorls, or androecia with more than two whorls (spiral or irregular androecia not scored).

332. Androecium structural merism (C1). Androecium merism is defined as the number of stamens or stamen bundles (fascicles) in one whorl and was recorded as a continuous character (with integer values of 1 and above). We call this character structural because both fertile stamens and staminodes were considered. This character is not applicable for spiral or irregular stamen arrangements, nor when there is a single structural stamen (i.e., one stamen, no staminodes; e.g., *Chloranthus*, Chloranthaceae).

332_A. Androecium structural merism (4-state) (D2c). Discretization of androecium merism as a four-state character, distinguishing dimerous, trimerous, tetramerous, and pentamerous androecia. We ignore (treat as missing data) other merisms (e.g., hexamery, octomery) because these states are comparatively rare and caused reconstruction artefacts due to low statistical power in early analyses of this data set.

305. Filament (D1). Here we here record absence or presence of the filament, and in the latter case, the shape of the filament. Shape is considered in terms of length and width and is defined in relation to anther length/width. The width of the filament may thus either be broad as in laminar (e.g., Eupomatiaceae) or bulky stamens (e.g., Chloranthaceae), or narrow (filamentous) as found in many core eudicots groups (e.g., Rosaceae). This character was considered inapplicable when filaments were entirely fused with each other or to the perianth.

305_A. Filament (binary) (D2d). The length of the filament is not taken into account here and two forms of filament differentiation are compared: laminar (wide filament as in, e.g., Eupomatiaceae or Chloranthaceae) vs. narrow (filamentous as in many core eudicots).

306. Fusion of filaments (C1). Fusion of stamen (and staminode) filaments among each other at anthesis (congenitally or postgenitally) is recorded on a continuous scale, from 0 (free

filaments) to 1 (filaments fused along their entire length). Partial fusion is recorded using an approximate number between these two extremes (e.g., 0.1 corresponds to basal fusion, 0.5 to fusion along half of the length of filaments). In cases of distal (postgenital) fusion of filaments (e.g., *Impatiens*, von Balthazar and Schönenberger, 2013), the length of the fused section is measured against total filament length. In cases where the filaments are proximally fused with the corolla (i.e., flowers with a stamen-corolla tube as present in most asterids), only the distal part of the filaments that are free from the corolla are considered. In cases of multiple stamens whorls, we record within-whorl fusion in this character. For example, if organs within each whorl are fused along their entire length, we record a value of 1 here. In cases where organs of two or more whorls are fused into a common tubular structure, (e.g., Malvaceae, Lecythidaceae), we also record this as fusion in this character. If two (or more) whorls differ in their extent of filament fusion (e.g., *Napoleonaea*), we record this character as a range of values. For example, if an outermost stamen whorl is only basally fused, up to 10% of its length, but an inner whorl is entirely fused, we record a range of 0.1 to 1 here. Our rationale for this is to provide a general character that allows comparison of fusion among all angiosperms. This character is not applicable when there is a single structural stamen (i.e., one stamen, no staminodes; e.g., *Chloranthus*, Chloranthaceae).

306_A. Fusion of filaments (D2c). Here we discretized fusion of the filaments as a binary character (free vs. fused) with a threshold at 5%. For example, an androecium with filaments fused up to 4% of their length will be treated as free, whereas an androecium with parts fused along 10% of their length will be treated as fused (both cases would traditionally be referred to as basal fusion; see *204_A. Fusion of perianth* for a justification of threshold selection).

308. Fusion of filament to inner perianth series (C1). Here we record the fusion of filaments with the innermost perianth organs at anthesis on a continuous scale, from 0 (filaments completely free from perianth) to 1 (filaments fused along their entire length with the perianth; the "entire length" of the filament is defined as the distance between the floral base and the joint between filament and anther). Partial fusion is recorded using an approximate number between these two extremes (e.g., 0.1 corresponds to basal fusion, 0.5 to fusion along half of the length of perianth parts). If two (or more) stamen whorls (including staminodial whorls) differ in their extent of filament fusion with the perianth, we record this character as a range of values. For example, if the filaments of an outermost stamen whorl are fused, up to 90% of their length, but an inner whorl only up to 50%, we record a range of 0.5 to 0.9 here. Our rationale for this is to provide a general character that allows comparison of fusion among all angiosperms.

308_A. Fusion of filament to inner perianth series (D2c). Here we discretized fusion of the filaments to the perianth as a binary character (free vs. fused) with a threshold at 5%. For example, fusion to the perianth of up to 4% of the entire filament length will be treated as free, whereas a filament that is fused along 10% of its length to the perianth will be treated as fused (both cases would traditionally be referred to as basal fusion; see *204_A. Fusion of perianth* for a justification of threshold selection).

311. Anther orientation (D1). Anthers of angiosperms are rather uniform in their basic structure. They normally have four microsporangia (pollen sacs) that are arranged pair-wise in two thecae. The two microsporangia of a theca usually release their pollen grains through a common opening (stomium). At anthesis, the stomium of these thecae may face the floral centre (i.e., anther orientation is introrse) or the floral periphery (i.e., anther orientation is extrorse). A third possibility is latrorse anther orientation, where pollen is released toward the side (i.e., toward

neighbouring anthers). Often, it is difficult to establish anther orientation clearly in a flower as this is a gradual feature with many intermediate stages. In addition, a given flower may also be polymorphic for this feature. Lastly, thecae may be positioned in a transverse position at the tip of the connective and thus dehisce upward in the flower (e.g., *Sinofranchetia*, Endress and Hufford, 1989). We use "apical" to describe this latter character state.

311_A. Anther orientation (D2d). Here we treat anther orientation as a three-state character (introrse, extrorse, latrorse), ignoring the rare apical state.

312. Anther attachment (D1). Anther attachment refers to the area of insertion of the filament on the anther connective (i.e. the tissue connecting the two thecae of an anther). Anthers may be basifixed, with the filament attached to the base of the connective; dorsifixed, with the filament attached to the dorsal side of the anther, or ventrifixed, with the filament attached to the ventral side of the anther. With our definition of the filament as encompassing the region below the pollen sacs (see Character 305), we score laminar stamens as basifixed. Anther versatility is not scored here as it is not directly linked to any of the three types of anther attachment, for example the basifixed stamens of *Tulipa* or the dorsifixed stamens of *Lilium* may be versatile.

312_A. Anther attachment (binary) (D2d). Here we treat anther attachment as a binary character, treating the rare ventrifixed state as missing data.

313. Anther dehiscence (D1). Anther dehiscence refers to the type of opening of the anther when releasing its pollen through the stomia. The most common mode of dehiscence is by longitudinal slits that extend along the entire length of each theca. The stomium may bifurcate at its distal and/or proximal end and thus a valve is formed (e.g., *Eupomatia*, Endress and Hufford, 1989; Endress, 1994). Such dehiscence is commonly referred to as H-valvate. Specialized valves in the form of flaps for each pollen sac occur in some Laurales and basal eudicots (Endress and Hufford, 1989). We refer to them here as flap-valvate. Dehiscence of longitudinal slits may be incomplete and only occur over a short extent in the distal, proximal or central part of these slits and may thus be pore-like (e.g., *Bixa*, Venkatesh, 1956). In several taxa, however, specialized pores are observed (e.g., *Erica*, Hermann and Palser, 2000). In addition, there are several rarer modes of dehiscence such as circular dehiscence of one anther (e.g., *Hennecartia*) or several anthers (*Stephania*, Meng et al., 2012). Longitudinal slits may also be confluent distally (e.g., *Cocculus*, Endress and Hufford, 1989; Triuridaceae, Rudall, 2003).

313_A. Anther dehiscence (3-state) (D2d). Here we categorize anther dehiscence into three states, focussing on variation in angiosperms outside monocots and core eudicots: longitudinal, H-valvate, and flap-valvate. Pores and short apical slits are morphologically derived from longitudinal slits and are treated here as such.

314. Connective extension (apical) (D1). We define apical (distal) connective extensions (also called "distal connective protrusions", e.g., Hufford and Endress, 1989) as sterile anther structures that distally extend beyond the level of the thecae (i.e., the two lateral pairs of pollen sacs of a tetrasporangiate anther). Here we record absence or presence of anther connective extensions and we also record the shape of these extensions in terms of length in relation to the length of the thecae. We refer to connective extensions as short if they are shorter than a third of the length of the thecae. Such short extensions are found in many angiosperm lineages (e.g., *Daphniphyllum*, Hufford and Endress, 1989; *Thunbergia*, Schönenberger, 1999). Connective

extensions that are longer than a third of, but not longer than the thecal length are here referred to as long (e.g., *Loropetalum*, Hufford and Endress, 1989), while we reserve the state 'very long extension' for those that are longer than the thecae (e.g., *Asarum*, Endress and Hufford, 1989; *Chloranthus*, Endress, 1987b).

314_A. Connective extension (apical) (D2d). Here we distinguish only between absence and presence of connective extensions but do not take into account their relative length.

Gynoecium

401. Number of structural carpels (C1). Number of fertile or sterile carpels in bisexual or female flowers, recorded as a continuous character (with integer values of 1 and above). Contrary to the number of stamens (character 301), the number of co-occurring carpellodes (sterile carpels) is counted here because this number is often more easily obtained from the literature than the actual number of fertile carpels. However, consistently with our treatment of sexual dimorphism, the number of carpellodes in male flowers is ignored for this character. In multicarpellate, unilocular gynoecia with complete carpel fusion up to the stigma (e.g., *Primula*), it may be difficult to assess the number of carpels unequivocally. In such cases, we have scored the number of carpels only if it is well established based on anatomical or developmental investigations. Similarly, in gynoecia where one or more carpels are reduced (e. g., in the pseudomonomerous gynoecia of some Arecaceae, Stauffer et al., 2002), the total number of structural carpels was only scored when unequivocally determined in the literature. Contrary to the perianth and the androecium, we do not have a separate character for gynoecium merism here. This is because gynoecia with two or more whorls are rare in angiosperms and gynoecium merism therefore usually equals the number of carpels per flower.

401_B. Number of structural carpels (5-state) (D2c). About 10% of angiosperms are unicarpellate, but in the majority of angiosperms carpel number is either three (most monocots) or between two and five (most core eudicots; Endress, 2011). Compared to two and five, presence of four carpels is relatively rare and here we treat it in the same state as five carpels. In addition, we lump all multicarpellate gynoecia (i.e., with more than five carpels, Endress, 2014) in a single category.

400. Gynoecium phyllotaxis (D1). Gynoecium phyllotaxis may be spiral or whorled (Endress, 2014). In rare cases, carpels may also be arranged in an irregular fashion, but such cases are not represented in our data set. Gynoecia with two or more whorls of carpels are rare in angiosperms (Staedler and Endress, 2009). Therefore, contrary to what was done in scoring the perianth and the androecium, we do not have a separate character for the number of gynoecium whorls. Instead, we distinguish between single whorls and multiple whorls in this character. This character is not applicable to unicarpellate flowers.

400_A. Gynoecium phyllotaxis (D2d). Here we distinguish only between spiral and whorled carpel arrangement, irrespective of the number of whorls.

403. Fusion of ovaries (C1). Degree of ovary fusion expressed as a fraction of the total length of the ovary (from the floral base to the apex of the ovary). Fusion of styles and stigmas is not taken into account here. Not applicable when there is a single carpel.

403_A. Fusion of ovaries (binary) (D2c). Here we basically distinguish between apocarpous (free) and syncarpous (fused) gynoecia. Ovaries with less than 5% of their total length fused are treated here as apocarpous. The reason for this is that floral organs of the same whorl or

even of two successive whorls often appear to have a short common base and accordingly are often described as “basally connate” or “basally adhering” without being clearly fused.

404. Style differentiation (D1). Here we record absence or presence of a style. The absence of a style equals a sessile stigma (e.g., some Clusiaceae). When present, we also record the shape of the style in terms of length and width in relation to ovary length and width. We do not distinguish between fused or free styles (see character 406).

404_B. Style differentiation (D2d). Here we distinguish only between absence and presence of a style but do not take into account relative lengths and widths.

406. Fusion of styles (C1). Here we record the degree of fusion of styles at anthesis, recorded on a continuous scale, from 0 (free styles) to 1 (styles fused along their entire length, but excluding the stigmatic region). Partial fusion is recorded using an approximate number between these two extremes (e.g., 0.1 corresponds to basal fusion, 0.5 to fusion along half of the total length of the styles). This character is not applicable in unicarpellate flowers.

406_A. Fusion of styles (D2c). Here we only distinguish between free and fused styles, irrespective of the degree of fusion in the latter case. Styles with less than 5% of their total length fused are treated here as free. The reason for this is that styles of completely syncarpous ovaries often appear to have a short common base and accordingly are often described as “basally connate” or “basally adhering” without being clearly fused.

411. Number of ovules per functional carpel (C1). Number of ovules per carpel recorded as a continuous character (with integer values of 1 and above). Reduced (sterile) carpels are not taken into account here.

411_A. Number of ovules per functional carpel (3-state) (D2c). Here we discretize the number of ovules per carpel as a three-state character, distinguishing among one, two, and three or more ovules per carpel.

412. Placentation (D1). Here we record the different types of placentation in apocarpous/unicarpellate and in syncarpous gynoecia. In apocarpous and unicarpellate gynoecia, placentation is often described as marginal as the ovules are usually attached along the ventral slit (i.e., the zone where the carpel margins become postgenitally closed during carpel development). In syncarpous gynoecia there are three main types of placentation (e.g., Endress, 1994): 1) axile placentation refers to ovaries where the ovules are placed in the angle between carpel flanks in the center of the ovary; 2) in ovaries with parietal placentation the ovules attach to the ovary wall where two carpels meet; 3) in ovaries with free-central placentation the ovules are attached to a central column that emerges from the base of the ovary and protrudes into the non-septate ovary. It is not unusual that syncarpous gynoecia show a transition from proximally axile to a distally parietal placentation (e.g., Polemoniaceae, Schönenberger, 2009). Basal and apical placentation may occur both in apocarpous/unicarpellate and in syncarpous gynoecia. Usually there is one longitudinal series of ovules attached to each carpel margin. However, both in apocarpous/unicarpellate and in syncarpous gynoecia there may be more than one series of ovules at the flanks of a carpel. These latter cases are referred to as laminar (or laminar-diffuse) placentation (e.g., in some Nymphaeaceae). A placenta that is protruding from its surroundings and has more than two series of ovules (either axile or parietal) is called protruding-diffuse.

412_A. Placentation (D2d). Here we categorize placentation into four states, focusing on the main types found in syncarpous gynoecia: axile, parietal, free-central, and laminar. Here, we treat apical and basal placentation as missing data because these could be interpreted as either axile or parietal (or laminar); we also exclude marginal placentation, which is restricted to single or free carpels, and is considered inapplicable here.

Pollen

5000. Number of apertures (C1). A pollen aperture is a structurally delimited region of the pollen grain wall through which the pollen tube emerges during pollen germination and which plays a role in harmomegathy (Halbritter et al., 2018). Here we report the number of apertures per pollen grain as a continuous character. A value of zero is scored when pollen is inaperturate (i.e. when there is no distinct aperture). Aperturate pollen is scored with integer values of 1 and above.

5000_A. Number of apertures (5-state) (D2c). Here we discretize the number of apertures per pollen grain as a five-state character, distinguishing among pollen grains with zero, one, two, three, and four or more apertures.

5002. Aperture shape (D1). Pollen grains are often described according to the shape, structure, and position of their apertures. Here we score the main shape of the many described aperture types. Aperture terminology is partly determined by the position of the aperture on the pollen grain (either at the pole or at the equator) and pollen grain polarity, in turn, is determined by the spatial orientation of the microspore in the meiotic tetrad. Porate apertures are round and pore-like and may be situated globally or equatorially (a pore-like aperture is referred to as ulcus if positioned at the pole). Colpate apertures are elongate and grooved (referred to as sulcate if positioned at the pole). Colporate apertures combine the groove of colpate and the pore of porate apertures. In addition, there are some rare shapes including, for instance, spiraperturate apertures (a pollen grain with one or more spiral apertures). Number (see character 5000. Number of apertures) and shape of apertures are usually expressed in combined terminology (e.g., monocolpate, tricolporate; see Halbritter et al., 2018 for detailed explanation and examples).

5002_A. Aperture shape (D2d). Here we categorize aperture shape into three states: elongate apertures (e.g., colpi, sulci), pore-like (incl. ulci), and colporate. Inaperturate and spiraperturate pollen grains are here treated as missing data.

LITERATURE CITED

Barthlott, W., and D.R. Hunt. 1993. Cactaceae. *In* K. Kubitzki, J. Rohwer, and V. Bittrich [eds.], The Families and Genera of Vascular Plants. Vol. II. Flowering Plants: Dicotyledons, The Families and Genera of Vascular Plants, 161–197. Springer Berlin Heidelberg. Available at: http://dx.doi.org/10.1007/978-3-662-02899-5_17.

Beaulieu, J.M., B.C. O'Meara, and M.J. Donoghue. 2013. Identifying hidden rate changes in the evolution of a binary morphological character: the evolution of plant habit in campanulid angiosperms. *Systematic Biology* 62: 725–737. Available at: http://sysbio.oxfordjournals.org/content/62/5/725.abstract.

Douglas, A.W., and S.C. Tucker. 1996. Inflorescence ontogeny and floral organogenesis in Grevilleoideae (Proteaceae), with emphasis on the nature of the flower pairs. *International Journal of Plant Sciences* 157: 341–372.

Endress, P.K. 1994. Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge.
Endress, P.K. 2003. Early floral development and nature of the calyptra in Eupomatiaceae (Magnoliales). *International Journal of Plant Sciences* 164: 489–503.
Endress, P.K. 1992. Evolution and floral diversity: the phylogenetic surroundings of Arabidopsis and Antirrhinum. *International Journal of Plant Sciences* 153: S106–S122.
Endress, P.K. 2011. Evolutionary diversification of the flowers in angiosperms. *American Journal of Botany* 98: 370–396. Available at: http://www.amjbot.org/cgi/content/abstract/98/3/370.
Endress, P.K. 1987a. Floral phyllotaxis and floral evolution. *Botanische Jahrbücher für Systematik* 108: 417–438.
Endress, P.K. 1995. Floral structure and evolution in Ranunculanae. *Plant Systematics and Evolution* Suppl.: 47–61.
Endress, P.K. 2010. Flower structure and trends of evolution in eudicots and their major subclades. *Annals of the Missouri Botanical Garden* 97: 541–583. Available at: http://dx.doi.org/10.3417/2009139.
Endress, P.K. 2014. Multicarpellate gynoecia in angiosperms: occurrence, development, organization and architectural constraints. *Botanical Journal of the Linnean Society* 174: 1–43. Available at: http://dx.doi.org/10.1111/boj.12099.
Endress, P.K. 1990. Patterns of floral construction in ontogeny and phylogeny. *Biological Journal of the Linnean Society* 39: 153–175.
Endress, P.K. 1987b. The Chloranthaceae: reproductive structures and phylogenetic position. *Botanische Jahrbücher für Systematik* 109: 153–226.
Endress, P.K. 1984. The role of inner staminodes in the floral display of some relic Magnoliales. *Plant Systematics and Evolution* 146: 269–282.
Endress, P.K., and J.E. Armstrong. 2011. Floral development and floral phyllotaxis in *Anaxagorea* (Annonaceae). *Annals of Botany* 108: 835–845. Available at: http://aob.oxfordjournals.org/content/108/5/835.abstract.
Endress, P.K., and J.A. Doyle. 2015. Ancestral traits and specializations in the flowers of the basal grade of living angiosperms. *Taxon* 64: 1093–1116.
Endress, P.K., and J.A. Doyle. 2007. Floral phyllotaxis in basal angiosperms: development and evolution. *Current Opinion in Plant Biology* 10: 52–57. Available at: http://www.sciencedirect.com/science/article/B6VS4-4MG1PCG-2/2/852868f449ba692661027a5383ad3252.
Endress, P.K., and L.D. Hufford. 1989. The diversity of stamen structures and dehiscence patterns among Magnoliidae. *Botanical Journal of the Linnean Society* 100: 45–85.
Erbar, C., and P. Leins. 1996. Distribution of the character states “early sympetaly” and “late sympetaly” within the “Sympetalae Tetracyclicae” and presumably allied groups. *Botanica Acta* 109: 427–440. Available at: http://dx.doi.org/10.1111/j.1438-8677.1996.tb00593.x.
Erbar, C., and P. Leins. 1994. Flowers in Magnoliidae and the origin of flowers in other subclasses of the angiosperms. I. The relationships between flowers of Magnoliidae and Alismatidae. *Plant Systematics and Evolution* Suppl. 8: 193–208.
Halbritter, H., S. Ulrich, F. Grimsson, M. Weber, R. Zetter, M. Hesse, R. Buchner, M. Svojtka, and A. Frosch-Radivo. 2018. Illustrated pollen terminology. Springer.
Harris, E. 1995. Inflorescence and floral ontogeny in asteraceae: A synthesis of historical and current concepts. *The Botanical Review* 61: 93–278. Available at: http://dx.doi.org/10.1007/BF02887192.
Hermann, P.M., and B.F. Palser. 2000. Stamen development in the Ericaceae. I. Anther wall, microsporogenesis, inversion, and appendages. *American Journal of Botany* 87: 934–

957. Available at: http://www.amjbot.org/content/87/7/934.abstract.
Hirmer, M. 1931. Zur Kenntnis der Schraubenstellungen im Pflanzenreich [Title translation: On spiral phyllotaxis in the plant kingdom]. *Planta* 14: 132–206.
Hufford, L. 1996. The origin and early evolution of angiosperm stamens. *In* W. G. D'Arcy, and R. C. Keating [eds.], The Anther: Form, Function, and Phylogeny, 58–91. Cambridge University Press.
Hufford, L.D., and P.K. Endress. 1989. The diversity of anther structures and dehiscence patterns among Hamamelididae. *Botanical Journal of the Linnean Society* 99: 301–346.
Kim, S., J. Koh, H. Ma, Y. Hu, P.K. Endress, B.A. Hauser, M. Buzgo, et al. 2005. Sequence and expression studies of A-, B-, and E-class MADS-box homologues in *Eupomatia* (Eupomatiaceae): Support for the bracteate origin of the calyptra. *International Journal of Plant Sciences* 166: 185–198.
Kuhlemeier, C. 2007. Phyllotaxis. *Trends in Plant Science* 12: 143–150. Available at: http://www.cell.com/trends/plant-science/abstract/S1360-1385(07)00058-1.
Löfstrand, S.D., M. von Balthazar, and J. Schönenberger. 2016. Early floral development and androecium organization in the sarracenioid clade (Actinidiaceae, Roridulaceae and Sarraceniaceae) of Ericales. *Botanical Journal of the Linnean Society* 180: 295–318. Available at: http://dx.doi.org/10.1111/boj.12382.
Matthews, M.L., M.D.C.E. Amaral, and P.K. Endress. 2012. Comparative floral structure and systematics in Ochnaceae s.l. (Ochnaceae, Quiinaceae and Medusagynaceae; Malpighiales). *Botanical Journal of the Linnean Society* 170: 299–392. Available at: http://dx.doi.org/10.1111/j.1095-8339.2012.01299.x.
Meng, A., Z. Zhang, J. Li, Craene Louis Ronse De, and H. Wang. 2012. Floral development of *Stephania* (Menispermaceae): Impact of organ reduction on symmetry. *International Journal of Plant Sciences* 173: 861–874. Available at: http://www.jstor.org/stable/10.1086/667235.
Murbeck, S. 1912. Untersuchungen über den Blütenbau der Papaveraceen. *Kungl. Svenska Vetenskapakademiens Handlingar* 50: 1–168.
Pagel, M., and A. Meade. 2006. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *American Naturalist* 167: 808–825. Available at: http://www.journals.uchicago.edu/doi/abs/10.1086/503444.
Pagel, M., and A. Meade. 2013. BayesTraits V2. Available at: http://www.evolution.rdg.ac.uk/BayesTraitsV2.html.
Perrier de la Bâthie, H. 1951. Guttifères. *Flore de Madagascar et des Comores* 136: 1–96.
Posada, D., and T.R. Buckley. 2004. Model selection and model averaging in phylogenetics: advantages of Akaike Information Criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology* 53: 793–808. Available at: http://sysbio.oxfordjournals.org/content/53/5/793.abstract.
Prenner, G., and P.J. Rudall. 2007. Comparative ontogeny of the cyathium in Euphorbia (Euphorbiaceae) and its allies: exploring the organ flower inflorescence boundary. *American Journal of Botany* 94: 1612–1629. Available at: http://www.amjbot.org/cgi/content/abstract/94/10/1612.
Rasmussen, D.A., E.M. Kramer, and E.A. Zimmer. 2009. One size fits all? Molecular evidence for a commonly inherited petal identity program in Ranunculales. *American Journal of Botany* 96: 96–109. Available at: http://www.amjbot.org/cgi/content/abstract/96/1/96.
Ren, Y., H.-L. Chang, X.-H. Tian, P. Song, and P. Endress. 2009. Floral development in Adonideae (Ranunculaceae). *Flora* 204: 506–517.
Ren, Y., T. Gu, and H. Chang. 2011. Floral development of Dichocarpum, Thalictrum, and *Aquilegia* (Thalictroideae, Ranunculaceae). *Plant Systematics and Evolution* 292: 203–213. Available at: http://dx.doi.org/10.1007/s00606-010-0399-6.

Ronse De Craene, L.P. 2010. Floral Diagrams: An Aid to Understanding Flower Morphology and Evolution. Cambridge University Press, Cambridge.

Ronse De Craene, L.P., and E.F. Smets. 2001. Staminodes: Their morphological and evolutionary significance. *The Botanical Review* 67: 351–402. Available at: http://dx.doi.org/10.1007/BF02858099.

Rudall, P.J. 2003. Monocot pseudanthia revisited: Floral structure of the mycoheterotrophic family Triuridaceae. *International Journal of Plant Sciences* 164: S307–S320. Available at: http://www.jstor.org/stable/10.1086/376879.

Rudall, P.J., D.D. Sokoloff, M. V Remizowa, J.G. Conran, J.I. Davis, T.D. Macfarlane, and D.W. Stevenson. 2007. Morphology of Hydatellaceae, an anomalous aquatic family recently recognized as an early-divergent angiosperm lineage. *American Journal of Botany* 94: 1073–1092. Available at: http://www.amjbot.org/cgi/content/abstract/94/7/1073.

Sauquet, H. 2003. Androecium diversity and evolution in Myristicaceae (Magnoliales), with a description of a new Malagasy genus, *Doyleanthus* gen. nov. *American Journal of Botany* 90: 1293–1305.

Sauquet, H. 2019. PROTEUS: A database for recording morphological data and fossil calibrations. Version 1.27. http://eflower.myspecies.info/proteus.

Sauquet, H., M. von Balthazar, J.A. Doyle, P.K. Endress, S. Magallón, Y. Staedler, and J. Schönenberger. 2018. Challenges and questions in reconstructing the ancestral flower of angiosperms: A reply to Sokoloff et al. *American Journal of Botany* 105: 127–135. Available at: http://dx.doi.org/10.1002/ajb2.1023.

Sauquet, H., M. von Balthazar, S. Magallón, J.A. Doyle, P.K. Endress, E.J. Bailes, E. Barroso de Morais, et al. 2017. The ancestral flower of angiosperms and its early diversification. *Nature Communications* 8: 16047. Available at: http://www.nature.com/doifinder/10.1038/ncomms16047.

Sauquet, H., L. Carrive, N. Poullain, J. Sannier, C. Damerval, and S. Nadot. 2015. Zygomorphy evolved from disymmetry in Fumarioideae (Papaveraceae, Ranunculales): new evidence from an expanded molecular phylogenetic framework. *Annals of Botany* 115: 895–914. Available at: http://aob.oxfordjournals.org/content/115/6/895.abstract.

Schöffel, K. 1932. Untersuchungen über den Blütenbau der Ranunculaceen. *Planta* 17: 315–371.

Schönenberger, J. 2009. Comparative floral structure and systematics of Fouquieriaceae and Polemoniaceae (Ericales). *International Journal of Plant Sciences* 170: 1132–1167. Available at: http://www.journals.uchicago.edu/doi/abs/10.1086/605875.

Schönenberger, J. 1999. Floral structure, development and diversity in *Thunbergia* (Acanthaceae). *Botanical Journal of the Linnean Society* 130: 1–36.

Schönenberger, J., and A. Grenhagen. 2005. Early floral development and androecium organization in Fouquieriaceae (Ericales). *Plant Systematics and Evolution* 254: 233–249.

Simpson, M.G. 2010. Plant Systematics, 2nd edition. 2nd ed. Academic Press.

Sokoloff, D.D., M. V. Remizowa, R.M. Bateman, and P.J. Rudall. 2018. Was the ancestral angiosperm flower whorled throughout? *American Journal of Botany* 105: 5-15. Available at: http://doi.wiley.com/10.1002/ajb2.1003.

Staedler, Y.M., and P.K. Endress. 2009. Diversity and lability of floral phyllotaxis in the pluricarpellate families of core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, Monimiaceae). *International Journal of Plant Sciences* 170: 522–550. Available at: http://www.journals.uchicago.edu/doi/abs/10.1086/597272.

Stauffer, F.W., R. Rutishauser, and P.K. Endress. 2002. Morphology and development of the female flowers in *Geonoma interrupta* (Arecaceae). *American Journal of Botany* 89:

220–229. Available at: http://www.amjbot.org/content/89/2/220.abstract.
Tsou, C.-H., and S.A. Mori. 2007. Floral organogenesis and floral evolution of the Lecythidoideae (Lecythidaceae). *American Journal of Botany* 94: 716–736. Available at: http://www.amjbot.org/content/94/5/716.abstract.
Venkatesh, C.S. 1956. The curious anther of Bixa--its structure and dehiscence. *American Midland Naturalist* 55: 473–476. Available at: http://www.jstor.org/stable/2422607.
von Balthazar, M., W.S. Alverson, J. Schönenberger, and D.A. Baum. 2004. Comparative floral development and androecium structure in Malvoideae (Malvaceae s.l.). *International Journal of Plant Sciences* 165: 445–473. Available at: http://www.journals.uchicago.edu/doi/abs/10.1086/386561.
von Balthazar, M., and P.K. Endress. 2002. Reproductive structures and systematics of Buxaceae. *Botanical Journal of the Linnean Society* 140: 193–228.
von Balthazar, M., and J. Schönenberger. 2013. Comparative floral structure and systematics in the balsaminoid clade including Balsaminaceae, Marcgraviaceae and Tetrameristaceae (Ericales). *Botanical Journal of the Linnean Society* 173: 325–386. Available at: http://dx.doi.org/10.1111/boj.12097.
Walker-Larsen, J., and L.D. Harder. 2000. The evolution of staminodes in angiosperms: patterns of stamen reduction, loss, and functional re-invention. *American Journal of Botany* 87: 1367–1384. Available at: http://www.amjbot.org/content/87/10/1367.abstract.
Weston, P.H. 2006. Proteaceae. *In* K. Kubitzki [ed.], The Families and Genera of Vascular Plants. Volume IX, 364–404. Springer-Verlag, Berlin.
Whipple, C.J., M.J. Zanis, E.A. Kellogg, and R.J. Schmidt. 2007. Conservation of B class gene expression in the second whorl of a basal grass and outgroups links the origin of lodicules and petals. *Proceedings of the National Academy of Sciences* 104: 1081–1086. Available at: http://www.pnas.org/content/104/3/1081.abstract.
Xu, F., and L. Ronse De Craene. 2010. Floral ontogeny of Annonaceae: evidence for high variability in floral form. *Annals of Botany* 106: 591–605. Available at: http://aob.oxfordjournals.org/content/early/2010/09/01/aob.mcq158.abstract.
Yoshida, H. 2012. Is the lodicule a petal: molecular evidence? *Plant Science* 184: 121–128.
Zhang, R.-J., and J. Schönenberger. 2014. Early floral development of Pentaphylacaceae (Ericales) and its systematic implications. *Plant Systematics and Evolution* 300: 1547–1560. Available at: http://dx.doi.org/10.1007/s00606-014-0981-4.
Zhao, L., J. Bachelier, H. Chang, X. Tian, and Y. Ren. 2012. Inflorescence and floral development in Ranunculus and three allied genera in Ranunculeae (Ranunculoideae, Ranunculaceae). *Plant Systematics and Evolution* 298: 1057–1071. Available at: http://dx.doi.org/10.1007/s00606-012-0616-6.