

REVIEW

Parasitic angiosperms: How often and how many?

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Abstract Angiosperms that morphologically and physiologically attach to other flowering plants by means of a haustorium have evolved 12 times independently resulting in 292 genera and ca. 4750 species. Although hemiparasites predominate, holoparasitism has evolved in all but two clades, *Cassytha* (Lauraceae) and *Krameria* (Krameriaceae). Santalales contains the largest number of genera (179) and species (2428) among the 12 parasitic plant lineages whereas Orobanchaceae is the largest single family with 102 genera and over 2100 species. This review presents the current state of knowledge on the molecular phylogenetic relationships among all clades of parasitic angiosperms. These methods have been particularly important in revealing the closest non-parasitic relatives of holoparasites, plants that exhibit reduced morphologies, increased substitution rates, and frequent horizontal gene transfers, all of which confound phylogenetics. Although comprehensive molecular phylogenies are still lacking for many of the large genera, nearly complete generic level sampling exists, thus allowing unprecedented understanding of the evolutionary relationships within and among these fascinating plants.

Keywords classification; haustorium; molecular phylogenetics; parasitic plant

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Parasitic flowering plants, defined here as angiosperms that attach to host plants by means of haustoria, continue to attract attention among scientists in myriad disciplines. Interest in parasitic plants has increased over the past three decades as documented by membership in the International Parasitic Plant Society, attendance at their biennial meetings, and number of publications relating to this subject. Discoveries about these plants are increasing at a rapid pace, particularly with Orobanchaceae where physiological, genomic and biochemical work has elucidated the details of host recognition, haustorium formation, and attachment. Only relatively recently have strigolactones been recognized as germination stimulants (Matusova & al., 2005; Wang & Bouwmeester, 2018) and these molecules have since gained increased importance not only in parasitic plants but also non-parasites as they represent a new category of plant growth regulators (Zwanenburg & Blanco-Ania, 2018) and participate in the establishment of arbuscular mycorrhizae (Gough & Bécard, 2016; Luginbuehl & Oldroyd, 2016). The vast majority of the current literature on parasitic plants involves two genera: *Orobanche* L. and *Striga* Lour. (Orobanchaceae) owing to their importance as pathogens of crops (Joel & al., 2013).

Although 292 genera and ca. 4750 species of flowering plants are parasitic, only about 25 genera are considered pathogens owing to their negative impact upon host plants

cultivated by humans (Nickrent & Musselman, 2016). In addition to Orobanchaceae, *Cuscuta* L. (dodder, Convolvulaceae) (Dawson & al., 1994) and *Arceuthobium* M.Bieb. (dwarf mistletoe, Viscaceae) (Hawksworth & Wiens, 1996) impact agriculture and forestry, respectively. Most of the remaining genera comprise species that not only do not damage crops but are in fact keystone components of natural ecosystems (Watson, 2001, 2009). These plant parasites have positive interrelationships with other species in the community by influencing competition, nutrient cycling, and community biodiversity (Press & Phoenix, 2005; Bardgett & al., 2006; Hatcher & al., 2012). Molecular methods have revealed previously unknown phenomena, e.g., floral development in *Rafflesia* R.Br., the largest flower in angiosperms (Nikolov & al., 2013), increased evolutionary rates (Bromham & al., 2013), horizontal gene transfer (Yang & al., 2016), and chloroplast genome (plastome) reduction (Wicke & al., 2013; Su & al., 2019).

In addition to the above areas, molecular phylogenetic methods have been used to address a number of long-standing issues in parasitic plant taxonomy and evolutionary biology. Indeed, it is no exaggeration to say that these methods have revolutionized our understanding of parasitic plant relationships. This is especially true for those clades with members that are holoparasitic (non-photosynthetic) where morphological modifications (especially reductions) provide few clues as to their affinity. As shown below, molecular methods, at all levels of the taxonomic hierarchy, have been effective in



Fig. 1. Representative members of the 12 clades of angiosperm haustorial parasites. Letters A–L correspond to the clades shown in Fig. 2. **A**, *Cassytha filiformis* (South Africa); **B**, *Hydnora africana* (South Africa); **C**, *Cynomorium coccineum* (Spain); **D**, *Krameria ixine* (Puerto Rico); **E**, *Rafflesia pricei* (Malaysia); **F**, *Pilostyles thurberi* (U.S.A.); **G**, *Cytinus ruber* (France); **H**, *Amyema artensis* (Papua New Guinea); **I**, *Mitrastemon yamamotoi* (Japan); **J**, *Pholisma culiacanum* (Mexico); **K**, *Cuscuta rostrata* (U.S.A.); **L**, *Harveya purpurea* (South Africa). — All photos by D.L. Nickrent except G (W. Meijer), I (M. Satou), and K (O. Linares).

resolving relationships, thus providing the basis for developing modern classifications.

■ WHAT IS A PARASITIC PLANT?

Indeed the concept of what exactly constitutes a parasitic angiosperm has in recent years been somewhat confused. This stems from whether one takes a functional or structural perspective. In this paper, two types of heterotrophic angiosperms that derive nutrients from another plant will be recognized: mycoheterotrophs and haustorial parasites. Although phylogenetically distinct, these two types of heterotrophs share a number of physiological, anatomical, developmental, and life history similarities. Some choose to call all of these “parasitic plants” (e.g., https://botany.org/Parasitic_Plants/), and in one sense this is true

because both groups are heterotrophic, deriving their nutrients from another plant. An important distinction, however, is that haustorial parasites feed directly on another plant via modified roots (rarely shoots or leaves) called the haustorium; in contrast mycoheterotrophs obtain their nutrition indirectly from another plant via a mycorrhizal fungus. The mycorrhizal fungus, attached to the roots of a photosynthetic plant, thus acts as a bridge between that plant and the mycoheterotroph, such that nutrients (carbon) flow from plant root, to mycorrhizal fungus and then to the mycoheterotroph. These plants may also be called mycoheterotrophic epiparasites or ectomycorrhizal epiparasites because they are epiparasitic on the fungus. Mycoheterotrophs occur in 10 angiosperm families including monocots and eudicots (Soltis & al., 2018: table 13.3). To avoid confusion, the terms parasite or parasitic plant here refers to haustorial parasites, and examples of all lineages are shown in Fig. 1. Both

parasites and mycoheterotrophs have mixotrophic (combination of autotrophic and heterotrophic feeding) and fully-heterotrophic (non-photosynthetic) representatives. Finally, mycoheterotrophs are sometimes mistakenly called saprophytes (Soltis & al., 2018: table 13.1). There are no true saprophytes in the angiosperms; only fungi can directly utilize dead organic material.

■ HOW OFTEN HAS PARASITISM EVOLVED IN ANGIOSPERMS?

Many publications introduce the subject of parasitic angiosperms by citing figures on the number of different lineages that exist or how many times haustorial parasites have evolved. More often than not, the numbers that are given indicate uncertainty or erroneous/outdated information. Identifying the closest non-parasitic relatives of parasitic plants originated with traditional, pre-molecular classifications (e.g., Takhtajan, 1980, 1997; Cronquist, 1981) which were, in some cases, concordant with what was later confirmed by molecular methods. Examples of this are the inclusion of *Cassytha* Mill. in Lauraceae, *Cuscuta* in (or near) Convolvulaceae, Lennoaceae in (or near) Boraginaceae, and Orobanchaceae with the “rhinanthoid Scrophulariaceae”. In contrast, other groups such as the holoparasites in Hydnoraceae, Rafflesiaceae and Balanophoraceae were problematic as reflected by classifications that varied widely among authors.

To provide the number of times parasitism evolved in angiosperms, one must first recognize that some independent evolutionary lineages of parasites once existed but are now extinct. Considering only extant haustorial parasites, a number can be obtained by placing with confidence all clades with their closest non-parasitic relatives on the global angiosperm phylogeny (Fig. 2). It can be argued that large-scale molecular phylogenetics for flowering plants began in 1993 with the publication of volume 80 number 3 in the *Annals of the Missouri Botanical Garden*, which contained 13 molecular phylogenetic papers that all used the plastome gene *rbcL*. Although ca. 600 sequences were reported in the Appendix, only four hemiparasitic plants were included (*Krameria* Loefl., *Osyris* L., *Phoradendron* Nutt., *Schoepfia* Schreb.). Correct placement of all major parasitic plant lineages did not occur until more than a decade later (suppl. Table S1). The first to assign all groups correctly and to indicate that parasitic angiosperms evolved independently 12 times was Nickrent (2008), but because this work was an encyclopedia contribution, it was not widely seen or cited.

In a much-cited work, Westwood & al. (2010) indicated that parasitism evolved independently “at least 12 or 13 times”. The reason for two estimates was that the affinities of Balanophoraceae were considered uncertain, i.e., whether the family branched off from within Santalales or was sister to it. This uncertainty was reasonable given the topology of

the phylogenetic tree published by Nickrent & al. (2005) where *Dactylanthus* Hook.f., *Hachettea* Baill., and *Mystroptalon* Harv. were sister to three Santalales genera (their fig. 2) or as a clade within Santalales (their fig. 3). Evidence supporting an internal position was provided first in a conference abstract (Su & Hu, 2008) and later published by Su & al. (2012), who used five nuclear and one mitochondrial gene in phylogenetic analyses with several genera in Santalales. The internal positions of Balanophoraceae s.l. (including Mystroptalaceae, see below) were confirmed in the comprehensive analysis of Su & al. (2015). The uncertainty about Balanophoraceae s.l. and Santalales also prevented others (e.g., Barkman & al., 2007; Naumann & al., 2013) from confidently stating the number of origins of parasitism in angiosperms. Bromham & al. (2013) showed that parasitic plants have increased substitution rates in all three subcellular genomes and correctly identified the 12 independent evolutionary origins, including the association of Balanophoraceae (s.l.) with Santalales. In a review of the functional biology of parasitic plants, Těšitel (2016) also recognized the proper 12 haustorial parasite lineages.

From the above discussion, it appeared that by 2016 the scientific community was “on board” with the idea that parasitism evolved 12 times in angiosperms, but unfortunately, misinformation persisted. Despite extensive discussion about the molecular evidence supporting placement of all parasites within the angiosperm phylogeny, Soltis & al. (2018) did not directly address the number of times parasitism evolved. The phylogenetic tree (their fig. 13.2) showing the “major occurrences of parasitism in angiosperm plant families” curiously excluded three lineages (Cynomoriaceae, Cytinaceae, Lennoaceae). Much confusion apparently still surrounds the status of Balanophoraceae s.l. that will be discussed more fully below. In a recent review, Twyford (2018) indicates parasitism evolved “at least 12 times” in angiosperms, deriving this approximation from Christenhusz & al. (2017). Looking at these data more closely (their supplemental table S1), the number of parasitic plant families listed is 14. This list omitted Cynomoriaceae and gives only four families for Santalales (Balanophoraceae, Loranthaceae, Santalaceae, Schoepfiaceae). As discussed below, this estimate is too low, even given differing taxonomic perspectives.

The above examples illustrate that confusion still exists regarding the evolutionary origins of parasitic flowering plants. The purpose of this paper is to rectify this problem by answering the following questions about parasitic angiosperms: (1) how many extant clades exist, (2) what are their closest non-parasitic relatives, (3) what are the phylogenetic relationships within and among the various taxa, and (4) how many taxa (families, genera, species) occur in each of the clades? For the latter, a number of different sources were consulted, including the primary literature and online databases such as IPNI (2019), The Plant List (2019), and the Catalogue of Life 2019 (Hassler, 2019) to arrive at current best estimates. An overview of the current state of knowledge on phylogenetic relationships among all 12 lineages

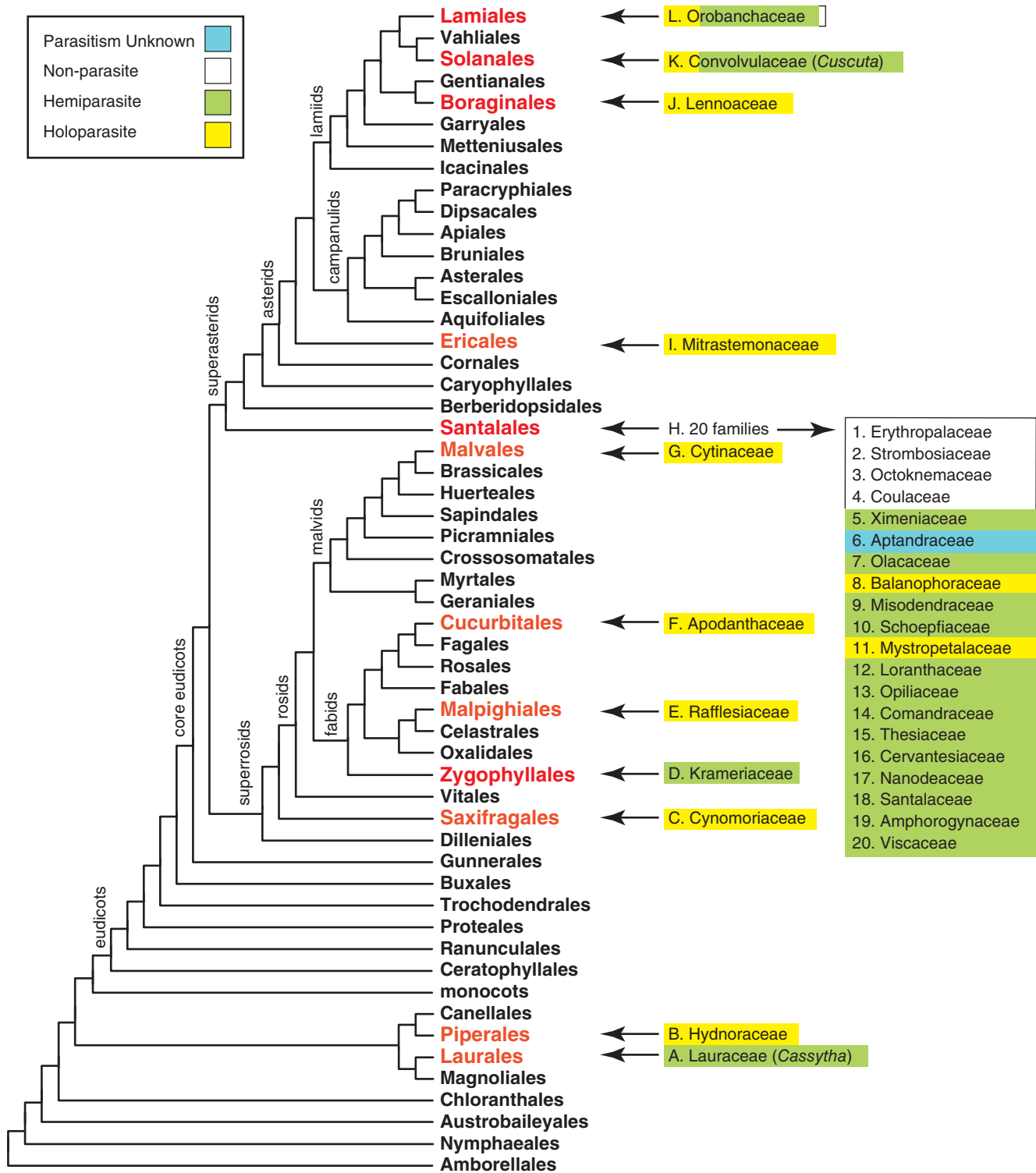


Fig. 2. A simplified phylogenetic tree of angiosperms showing major orders and the 12 independent evolutionary events that gave rise to haustorial parasites. The tree topology is modified from APG IV (2016). See text for literature supporting these relationships.

of haustorial parasitic flowering plants will be discussed in the order of the clades shown in Fig. 2. For some problematic groups, brief discussions will be provided to explain historically the causes of misinterpretation as well as to

demonstrate how concepts have changed with increasing knowledge. This review, although focused mainly on phylogenetics, will also highlight some recent noteworthy publications from other disciplines.

■ PHYLOGENETICS OF HAUSTORIAL PARASITES

Two lineages contain only hemiparasites: *Cassytha* in Lauraceae and *Krameria* in Krameriaceae. The exclusively holoparasitic families are Hydnoraceae, Cynomoriaceae, Rafflesiaceae, Apodanthaceae, Cytinaceae, Balanophoraceae, Mystropetalaceae, Mitrastemonaceae, and Lennoaceae. Both hemiparasites and holoparasites are found in Convolvulaceae, Santalales, and Orobanchaceae. For the latter two groups, non-parasites are known to be sister to the remaining members, thus making these valuable models for studying the evolution of parasitism. Santalales is the only parasitic plant order that contains more than one family.

■ 1. LAURALES

Cassytha is the sole genus in Lauraceae that has evolved the parasitic habit. Because of its resemblance to *Cuscuta* (Convolvulaceae), it represents a remarkable case of parallelism in the angiosperms. Despite the radical departure of its vegetative state from the typical condition in Lauraceae (trees and shrubs), floral morphology in *Cassytha* makes assignment to Lauraceae unequivocal, which was reflected in most classifications of the family (Van der Werff & Richter, 1996; Heo & al., 1998). *Cassytha* contains ca. 20 species (suppl. Table S2), most of which are Australian but one species (*C. filiformis* Mill.) is pantropical. An early molecular phylogenetic study using chloroplast genes (Rohwer, 2000) showed *Cassytha* to be an early-branching member of Lauraceae; however, other analyses (Renner & Chanderbali, 2000; Rohwer & Rudolph, 2005) showed it was nested with woody members of the family.

No macro- or microfossils of *Cassytha* are known (Weber, 1981). Although the order Laurales diverged from Magnoliales ca. 127 mya (Magallón & al., 2015), Lauraceae is more recent (105 mya), and the *Cassytha* stem group age is estimated to be 77 myr (Naumann & al., 2013), but with a wide variance (33 to 118 myr).

■ 2. PIPERALES

The sole parasitic family in this order is Hydnoraceae, which contains two genera: *Prosopanche* de Bary (New World) and *Hydnora* Thunb. (Old World) with a total of 12 species (suppl. Table S2). These holoparasites are unique among angiosperms in that they totally lack leaves of any form (Tennakoon & al., 2007). Two traditional (non-molecular) classifications (e.g., Takhtajan, 1980, 1997; Cronquist, 1981) differed in their concepts of this family. Cronquist placed Hydnoraceae in Rosidae with Rafflesiales whereas Takhtajan put it in Magnoliidae with Rafflesiales. Both were incorrect with regard to a relationship with Rafflesiaceae, however, Takhtajan was “closer to the mark” by placing the

family in Magnoliidae. The first accurate placement using molecular data was by Nickrent & al. (1998), who used 18S rDNA and showed the family to be allied with Aristolochiaceae, Lactoridaceae, and Piperaceae (today classified in Piperales). A multigene study later confirmed this relationship (Nickrent & al., 2002), however, the exact topology of the component families remained uncertain.

The APG III (2009) classification recognized five families in Piperales: Aristolochiaceae, Hydnoraceae, Lactoridaceae, Piperaceae, and Saururaceae. In the APG IV (2016) classification, three families were recognized, Piperaceae and Saururaceae, with Hydnoraceae and Lactoridaceae lumped into Aristolochiaceae. The justification for the lumping derived from the work of Naumann & al. (2013), who used 19 genes, as well as Massoni & al. (2014), who used a 12-gene dataset. Both of these molecular studies detected the same six groups that correspond to the above five families plus a distinct subfamily (Asaroideae) of Aristolochiaceae. It is worth noting that the Naumann and Massoni phylogenetic trees do not have the same topology with regard to the six groups, plus the introduction of Hydnoraceae lowers bootstrap values at key nodes. A reasonable alternative to lumping the shrubby Lactoridaceae (1 sp., *Lactoris fernandeziana* Phil.), the morphologically bizarre holoparasite family Hydnoraceae (12 spp.), and Aristolochiaceae (6 genera, 647 species, modified from Mabberley, 2017), would be to simply elevate Asaroideae Burnett to the rank of family and leave the remaining familial classifications unchanged. This new family (Asaraceae) would contain *Asarum* L. (ca. 80 spp.) and *Saruma* Oliv. (1 sp., *S. henryi* Oliv.). This classification would result in the least amount of disruption to existing classifications and would recognize the morphological distinctions among the members. A similar approach was followed by APG IV with regard to Rafflesiaceae vs. Euphorbiaceae (see below). Following this logic, Hydnoraceae is recognized as a distinct family in Piperales.

No macro- or microfossils of Hydnoraceae are known. The stem/crown age for Piperales is 133/121 myr (Magallón & al., 2015). The molecular dating work conducted by Naumann & al. (2013) suggest *Hydnora* diverged 101 mya (76.5–124.4 mya) whereas a more recent age (58 myr; 29.5–86.9 myr) was determined for *Prosopanche*. The age for *Hydnora* roughly corresponds to a Gondwana breakup model that shows South America and northwest Africa remaining in contact till ca. 110 mya (McLoughlin, 2001; Seton & al., 2012).

■ 3. SAXIFRAGALES

Cynomorium L. is a root holoparasite with one or two species (suppl. Table S2) that occurs in dry areas surrounding the Mediterranean Sea to central Asia. Owing to general similarities in habit and inflorescence morphology, the genus has often been placed within Balanophoraceae s.l. (Cronquist, 1981). Others (Dahlgren, 1983; Thorne,

1992b; Takhtajan, 1997) place the genus in a separate family, Cynomoriaceae, but still allied with Balanophoraceae. The first molecular phylogenetic study of *Cynomorium* used 18S rDNA to show that it was not part of Balanophoraceae but was associated with Saxifragales (Nickrent, 2002). Confirmation of this relationship was obtained following analyses using both nuclear and mitochondrial genes (Nickrent & al., 2005). In that multigene analysis, *Cynomorium* was in a clade with *Peridiscus* Benth. and *Hamamelis* L. (both Saxifragales) with high maximum parsimony and Bayesian inference support values. A relationship with Saxifragales was also reported by Barkman & al. (2007) using *matR*, but a combined *atp1* and *coxI* analysis suggested Sapindales. Similarly, Qiu & al. (2010) discuss how *Cynomorium* was placed in Saxifragales with *matR* and *nad5* but in Sapindales with *atp1* and *rps3*. It is now recognized that *atp1*, *coxI* and *rps3* are susceptible to horizontal gene transfer, thus explaining the conflicting gene trees. Additional conflicting data were presented in an analysis of 561 angiosperms where *Cynomorium* was placed in Santalales (Jian & al., 2008). This phylogenetic position strongly suggests that the authors accidentally used a sample of Balanophoraceae (no voucher exists to verify the identity of the plant sampled). Using the inverted repeat of the plastid genome, Zhang & al. (2009) conducted a phylogenetic study that indicated *Cynomorium songaricum* Rupr. was sister to Rosaceae with 99% BS support, a result later seen by Moore & al. (2011) using the same molecular marker. These results, which differed from the original Nickrent & al. (2005) analyses, were sufficient to cause the authors of the APG III (2009) classification to doubt the placement of *Cynomorium* in Saxifragales. Using several mitochondrial markers, Naumann & al. (2013) recovered the Saxifragales association, however, using chloroplast genes, *Cynomorium* was placed in Rosales. Recently, a phylogenetic analysis using complete mitochondrial genomes placed *Cynomorium* as sister to the superasterids, but with low support (Zervas & al., 2019). Finally, what is here considered the definitive paper on this subject, Bellot & al. (2016) assembled complete plastid and mitochondrial genomes of *Cynomorium* which not only confirmed its location in Saxifragales but also documented several horizontal gene transfers from different hosts. Most recently, Soltis & al. (2018: 325) state, “the phylogenetic relationships of Cynomoriaceae remain uncertain”, erroneously citing that bootstrap values in Nickrent & al. (2005) did not support a relationship with Saxifragales. Despite these reservations, they include Cynomoriaceae in Saxifragales (p. 312).

No macro- or microfossils of Cynomoriaceae are known. An estimate of the Saxifragales crown group age is 113 myr (Magallón & al., 2015). The stem age for *Cynomorium* reported in fig. 5 of Naumann & al. (2013) was ca. 100 myr (note this parasite was not listed in their table 2). The authors suggest that *Cynomorium*, along with Hydnoraceae and Balanophoraceae, is the oldest extant parasitic angiosperm lineage;

however, such estimations should be taken with caution given the effect increased substitution rates have upon molecular dating.

■ 4. ZYGOPHYLLALES

Krameriaceae is a monogeneric New World family with ca. 23 species (suppl. Table S2) of hemiparasitic perennial herbs and shrubs. The plants are recognized by their bilateral, often pink flowers and spinose fruits. Pre-molecular classifications (Cronquist, 1981; Thorne, 1992a; Takhtajan, 1997) allied the family with Polygalales or Vochysiales. *Krameria* was included in an early *rbcL* molecular phylogenetic study (Chase & al., 1993) where a sister relationship with Zygophyllaceae was recovered. The three-gene analysis of Soltis & al. (2000), which included 560 angiosperms, placed *Krameria* with *Guaiaecum* L. (Zygophyllaceae) with strong support. The APG II (2003) classification considered Krameriaceae as an acceptable, monophyletic alternative to Zygophyllaceae and that concept has remained through APG IV (2016). Wang & al. (2009) analyzed two nuclear and ten plastid genes for 117 taxa in the rosid clade and the chloroplast inverted repeat for 59 taxa. Krameriaceae came out with 100% maximum likelihood bootstrap support as sister to Zygophyllaceae.

Neither macro- or microfossils of *Krameria* are known. The stem group age for Zygophyllales was 116.8 myr (Magallón & al., 2015) with the split between Zygophyllaceae and Krameriaceae at 60.9 mya. The latter agrees well with the estimate by Naumann & al. (2013) of 61.8 mya.

■ 5. MALPIGHIALES

Historically, the order Rafflesiales was considered a natural group; however, distinctive floral morphology as well as differences in the ovules and seeds led some workers (e.g., Bouman & Meijer, 1994; Takhtajan, 1997) to recognize four families within: (1) Apodanthaceae, which includes the small-flowered genera *Apodanthes* Poit. and *Pilostyles* Guill., (2) Cytinaceae with *Cytinus* L. and *Bdallophytum* Eichler, which form inflorescences (vs. single flowers), (3) Rafflesiaceae (s.str.) with the large-flowered genera *Rafflesia*, *Rhizanthus* Dumort., and *Sapria* Griff., and (4) Mitrastemonaceae with one genus, *Mitrastemon* Makino, characterized by having a superior ovary. Besides their holoparasitic lifestyle, these endoparasitic genera share features such as unisexual flowers, the presence of a central column, and a tendency toward parietal placentation. Over the course of their evolution, extreme reduction has altered their morphology to such a degree that comparisons with more typical plants was confounded. It is for this reason that major disagreements existed as to where to place these plants in the global angiosperm phylogeny. For example, Cronquist (1981) placed Rafflesiales near Santalales in subclass Rosidae, whereas Takhtajan

(1997) classified the order in subclass Magnoliidae and recognized the above four segregate families. The APG II (2003) classification listed the four Rafflesiales families under “Taxa of Uncertain Position”.

Molecular analyses were conducted on two of the four families by Barkman & al. (2004) using mitochondrial *matR* gene sequences. They found that Rafflesiaceae was allied with Malpighiales whereas Mitrastemonaceae was in a distantly related order Ericales. In the same year, an analysis of all four families was published by Nickrent & al. (2004) using both nuclear 18S rDNA as well as mitochondrial sequence data. The previously determined ordinal relationships of Rafflesiaceae and Mitrastemonaceae were confirmed, and Cytinaceae was confidently placed in Malvales. Placement of the remaining family, Apodanthaceae, was equivocal (Malvales or Cucurbitales) depending upon the gene used. These molecular studies demonstrated that when assessing phylogenetic relationships in these holoparasites, proper model-based methods (e.g., maximum likelihood) are required to account for rate heterogeneity. In addition, the high frequency of horizontal gene transfers, particularly in the mitochondrial genomes, must be accounted for when interpreting species trees. Because the four “Rafflesiales” families were not monophyletic (present in four different orders), their morphological similarities represent amazing examples of convergence, i.e., the independent evolution of phenotypic (not genotypic) similarity in distantly related lineages.

To determine the position of Rafflesiaceae s.str. within the large order Malpighiales, additional molecular work (Davis & al., 2007) showed it was nested within Euphorbiaceae. The APG III (2009) classification recognized the four segregate “Rafflesiales” families and also noted that to maintain a monophyletic Euphorbiaceae, a separate family Peraceae (containing three genera *Clutia* L., *Pera* Mutis & Croizat, and *Pogonophora* Miers ex Benth.) would have to be recognized. This approach was not taken, so at that time, APG considered Rafflesiaceae to be a part of Euphorbiaceae. That position was reversed with the publication of APG IV (2016), where both Peraceae and Rafflesiaceae were accepted.

All three genera in Rafflesiaceae are host specific at the genus level to *Tetrastigma* K.Schum. (Vitaceae); however, multiple host species are utilized (Pelser & al., 2016). The genus *Rafflesia* has been the subject of much scientific research since 2004 when the first molecular phylogenies of the family were published. The work that followed can be categorized as anatomical/developmental, taxonomic, phylogenetic, and molecular evolutionary. The flowers of *Rafflesia* and *Sapria* appear most similar because both have deep perianth tubes topped by diaphragms, whereas *Rhizanthus* lacks a diaphragm. But phylogenetic work showed that *Rafflesia* is sister to *Rhizanthus*, not *Sapria*; thus, the question was raised, “are morphology and phylogeny out of step?” Nikolov & al. (2014) examined organ identity and gene expression using B- and C-class MADS box transcription factors such as PISTILLATA and AGAMOUS. They showed that the perianth tubes in *Rhizanthus* and *Sapria* are derived from ring

derivatives, whereas in *Rafflesia* the ring remains relatively undeveloped and the perianth tube forms from a combination of sepal and petal tissue. Moreover, the diaphragms of *Rafflesia* and *Sapria* are not developmentally equivalent. In *Rafflesia* it derives from petal tissue, but in *Sapria* is from the ring derivative. This work demonstrates how appearances can be deceiving when it comes to assessing homologous organs in highly derived parasitic plants.

Although *Rafflesia* has been known to the western world for over 200 years, new species have continued to be described. In this work, 30 species of *Rafflesia* are recognized (suppl. Table S2); however, several collections named as species are based on incomplete material (e.g., *R. borneensis* Koord., *R. ciliata* Koord., and *R. witkampii* Koord.). Four names have been published for collections from peninsular Malaysia (i.e., *R. parvimaclata* Sofiyanti & al., *R. sharifah-hapsahiae* J.H.Adam & al., *R. su-meiae* M.Wong & al. and *R. tuanku-halimii* J.H.Adam & al.), but these plants appear morphologically similar to *R. cantleyi* Solms, and no molecular data exist to evaluate whether they are genetically distinct. New species have also been discovered and named from the island of Sumatra in Indonesia such as *R. bengkuwuensis* (Susatya & al., 2005), *R. lawangensis* (Mat Salleh & al., 2011), *R. meijeri* (Wiriadinata & Sari, 2010).

Although only four species were validly published in the Philippines before 2002, an explosion of new discoveries has since taken place. With the discovery of *R. speciosa* Barcelona & Fernando on Panay Island (Barcelona & Fernando, 2002), a flurry of activity ensued such that today the archipelago has 13 species, including *R. consueloae* Galindon & al., the “smallest among giants” (Galindon & al., 2016). The taxonomy, population genetics, ecology, and conservation status of all Philippine *Rafflesia* have been discussed (Barcelona & al., 2009, 2011; Pelser & al., 2017, 2018). Molecular phylogenetic and biogeographic work has shown that the Philippine and Sundaic species are each monophyletic (Barkman & al., 2008; Bendiksby & al., 2010) and flower size is not an indicator of phylogenetic affinity.

No macro- or microfossils of Rafflesiaceae are known; thus, the age of this lineage can only be estimated using non-parasites in Malpighiales. Recently generated ultrametric trees (Pelser & al., 2019) indicate that Rafflesiaceae is an old family, diverging from Euphorbiaceae in the Cretaceous with *Rafflesia* diverging from *Rhizanthus* ca. 68 mya, and the crown group age for the genus is ca. 50 myr. These dates are older than previous estimations (Bendiksby & al., 2010) and likely more accurate because a relaxed (instead of strict) molecular clock was utilized. It appears that dispersal between islands has been relatively uncommon and that the high island endemism of *Rafflesia* is a result of limited dispersal between islands, possibly because of ant dispersal of seeds. Two detailed population genetic studies that used microsatellites were recently published (Barkman & al., 2017; Pelser & al., 2017) and reviewed in Twyford (2017) where it was demonstrated that different genetic individuals of *Rafflesia* can inhabit the same *Tetrastigma* host vine and that *R. lagascae*

Blanco may be monoecious instead of dioecious (the more common condition).

Next-generation sequencing has been applied to several species of *Rafflesia* which has revealed a number of surprising features of these genomes. The mitochondrial genomes (chondriomes) of two species of *Rafflesia* have been sequenced (Xi & al., 2013; Molina & al., 2014), and both studies documented massive horizontal gene transfers to the chondriome from host (*Tetrastigma*) and other angiosperm species. The former study also proposed the complete loss of the chloroplast genome (plastome) in *R. lagascae*, although this result has been questioned (Krause, 2015).

■ 6. CUCURBITALES

Apodanthaceae includes two genera, *Apodanthes* and *Pilostyles* (the latter including *Berlinianche* (Harms) Vattimo-Gil), and 10 species (Bellot & Renner, 2014) (suppl. Table S2). *Apodanthes* is restricted to the New World tropics, whereas *Pilostyles* is found in North and South America, Africa, western Asia and Australia. Like Rafflesiaceae, these are endoparasites that emerge from host branches (Salicaceae, Fabaceae) only as flowers. Although Nickrent & al. (2004) suggested either Malvales or Cucurbitales as the ordinal home for this family, further sequencing confirmed the latter which was reported in a publication that has been mostly overlooked (Nickrent, 2008). Later, Filipowicz & Renner (2010) reconfirmed the position of Apodanthaceae in Cucurbitales sampling both mitochondrial and nuclear genes. Within Cucurbitales, these authors suggested Coriariaceae and Corynocarpaceae as the possible photosynthetic relatives of Apodanthaceae. The situation became more complex with the publication of Schaefer & Renner (2011), which showed Apodanthaceae as sister to Oxalidales with nuclear ribosomal genes but sister to (not within) Cucurbitales with mitochondrial *matR* and *nad1*.

No macro- or microfossils of Apodanthaceae are known; thus, fossil data from non-parasitic Cucurbitales must be used for molecular dating. The stem and crown group ages for the order were 109 and 64 myr, respectively, as reported by Magallón & al. (2015). Naumann & al. (2013) arrived at a crown group age of 75 myr for the family based on a relaxed molecular clock estimation using *Pilostyles thurberi* A.Gray.

■ 7. MALVALES

Cytinaceae is composed of *Cytinus* with eight species of southern Africa, Madagascar and the Mediterranean and *Bdallophytum* Eichler with four species from Mexico to northern South America (suppl. Table S2). Among the former “Rafflesiales”, this group is characterized by spicate or racemose inflorescences. The molecular study by Nickrent & al. (2004) showed that *Cytinus* was strongly supported as sister to Malvales using both nuclear and mitochondrial genes.

Indeed, for the 18S rDNA tree, Apodanthaceae was artificially attracted to this long branch. More extensive sampling within Malvales showed that Cytinaceae is most closely related to Muntingiaceae (Nickrent, 2007). The rare *Neotessmannia* Burret from Peru shares some morphological and palynological features with Cytinaceae, hence a possible relationship was postulated. More recently, the range of Cytinaceae in the New World was extended to northern Colombia with the discovery of a plant named *Sanguisuga* Fern.Alonso & H.Cuadros (Fernández-Alonso & Cuadros-Villalobos, 2012). Comparisons (unpub. data) between this taxon and all *Bdallophytum* and *Cytinus* species suggested it would best be accommodated as a member of the former genus. The actual transfer of *Sanguisuga* to *Bdallophytum* was done by Christenhusz & al. (2018), albeit with no accompanying analysis or discussion.

No macro- or microfossils of Cytinaceae are known. A stem group age of 93 and a crown group age of 76 myr were estimated for the order Malvales by (Magallón & al., 2015). Crown group age of 72.1 myr was obtained by Naumann & al. (2013) using *Cytinus ruber* (Fourr.) Kom.

■ 8. SANTALES

The sandalwood order contains the largest number of genera (179) and species (2428) among the 12 parasitic plant lineages (suppl. Table S3). The order also contains the widest array of nutritional modes including autotrophic non-parasites (13 genera/71 species), hemiparasites (149/2312), and holoparasites (17/45), as well as a variety of plant habits such as trees and shrubs, annual and perennial herbs, and aerial parasites (Fig. 3). Here reside many mistletoes, defined as aerial parasites that are classified in the sandalwood order. For these reasons, the term describes both a plant habit and a taxonomic affiliation. That said, all aerial parasites are not monophyletic as they can be found in five clades that represent five independent evolutionary events within Santalales. Two clades (I and T in Fig. 3) are composed exclusively of mistletoes whereas the remaining three clades contain root parasites as well as mistletoes, amphiphagous taxa and dendroparasites (Vidal-Russell & Nickrent, 2008). For reviews of the traditional taxonomic literature on the order, see Kuijt (2015). A history of the molecular phylogenetic work conducted prior to 2010 is given in Nickrent & al. (2010). In brief, the following represent some of the topics that relate to the order: (1) placement of Santalales in the global angiosperm phylogeny, (2) family interrelationships, (3) generic composition of the component families, (4) species relationships in selected genera, and (5) the relationship of Balanophoraceae s.l. to Santalales. For all of these questions, molecular phylogenetic data have been indispensable.

Representatives of Santalales were included in some of the earliest plant molecular phylogenetic studies (suppl. Table S1). Even before the landmark study using *rbcL* (Chase & al., 1993), earlier work was conducted using small-subunit ribosomal RNA that recovered the correct

topology for *Schoepfia*, *Buckleya* Torr., *Dendrophthora* Eichler and *Phoradendron* (Nickrent & Franchina, 1990). This publication is mentioned only because at that time most botanists were focused on *rbcL* and few realized that 18S rDNA had sufficient phylogenetic signal to address questions within angiosperm orders, families, etc. Phylogenetic studies on Santalales from the 1990s to present have increased both taxon and gene sampling such that today nearly all genera in the order are represented by at least some nuclear and chloroplast sequences (Nickrent & al., 2019).

Relationships among the families of the order are shown in Fig. 3 with the data derived from Su & al. (2015) and Nickrent & al. (2019). Previously the early-branching, non-parasitic families included Erythralaceae, Strombosiaceae, and Coulaceae (clades A, B and D), but new data strongly support a relationship between Strombosiaceae and Octoknemaceae (clades B and C). Because no evidence exists that indicates *Octoknema* Pierre is a parasitic plant (Gosline & Malécot, 2011), this new phylogenetic position strongly suggests that it is autotrophic, not parasitic. The next three families (E–G) are Ximeniaceae, Aptandraceae, and Olacaceae, respectively. Previous analyses with less sequence data did not resolve the interrelationships among the families of “Olacaceae s.l.” (clades A–G), even though the support for the individual families was high (e.g., Su & al., 2015). With new data, the E–G clade now has strong support (Nickrent & al., 2019), which introduces some interesting questions regarding the origin of parasitism in the order. For Olacaceae, parasitism has been documented for two of the three genera in the family, *Olax* L. (Pate & al., 1990)

and *Ptychopetalum* Benth. (Anselmino, 1932). Because *Dulacia* Vell. is closely related to *Olax* (and may be nested within it based on molecular data), this genus is likely also parasitic. For Aptandraceae, there are no reports of parasitism for any of the eight genera. No haustoria were mentioned for germinating seedlings of *Ongokea* Pierre (Heckel, 1901). For Ximeniaceae, parasitism has been documented for *Ximenia* L. (DeFilipps, 1969) but not for the Chinese tree *Malania* Chun & S.K.Lee (Lee, 1980) or the South American tree *Curupira* G.A.Black (Rodrigues, 1961; C. Clement, pers. comm.). No information on parasitism exists for the rare Brazilian endemic *Douradoa* Sleumer. For those genera where haustoria have not been found, one cannot infer that these plants are not parasitic because attachment organs can be missed if excavations are not conducted correctly. Given current information, the possibility exists that parasitism is present only in some members of the E–G clade. If this is the case, parasitism in Santalales may have arisen more than once or parasitism existed but was lost in some lineages. A comprehensive examination of living members of the E–G clade is called for to document the presence/absence of haustoria.

The H and I–L clades (Fig. 3) represent the “middle portion” of the Santalales tree (Su & al., 2015) where evolutionary change generated much of the diversity in habit seen today in the order. Here one finds holoparasites (Balanophoraceae, Mystropetalaceae), woody root parasites (Schoepfiaceae, some Loranthaceae), and mistletoes (Misodendraceae, Loranthaceae in part). As discussed previously (Su & al., 2015), Schoepfiaceae is a well-supported family containing *Schoepfia*, *Arjona* Comm. ex Cav. and *Quinchamalium* Molina. The former genus was once considered part of Olacaceae, whereas the latter two genera were traditionally classified in Santalaceae. Strong support for a sister relationship between Schoepfiaceae and the Patagonian mistletoe family Misodendraceae has been obtained ever since the early molecular phylogenetic studies of the order (Nickrent & al., 1998).

One of the reasons for uncertainty in the scientific community about the number of origins of parasitism stemmed from lingering doubts about the situation with Balanophoraceae s.l. The study examining the position of Cynomoriaceae within angiosperms (Nickrent & al., 2005) sampled *Dactylanthus*, *Hachettea* and *Mystropetalon* that were often considered Balanophoraceae s.l. These three genera were chosen because they exhibited lower substitution rates than Balanophoraceae s.str., a feature important in phylogeny estimation because of decreased probability of long-branch attraction artifacts. The clade of these three genera were strongly supported as sister to the three Santalales genera sampled. The later study (Su & al., 2015), which included fast-rate Balanophoraceae s.str., showed that the family was not supported as monophyletic using maximum likelihood and Bayesian methods. The two independent evolutionary events generating holoparasites in Santalales were thus referred to as Balanophoraceae s.str. and Mystropetalaceae. The former was sister to a large clade of “non-Olacaceae” Santalales, whereas the latter was sister to Loranthaceae (Fig. 3).

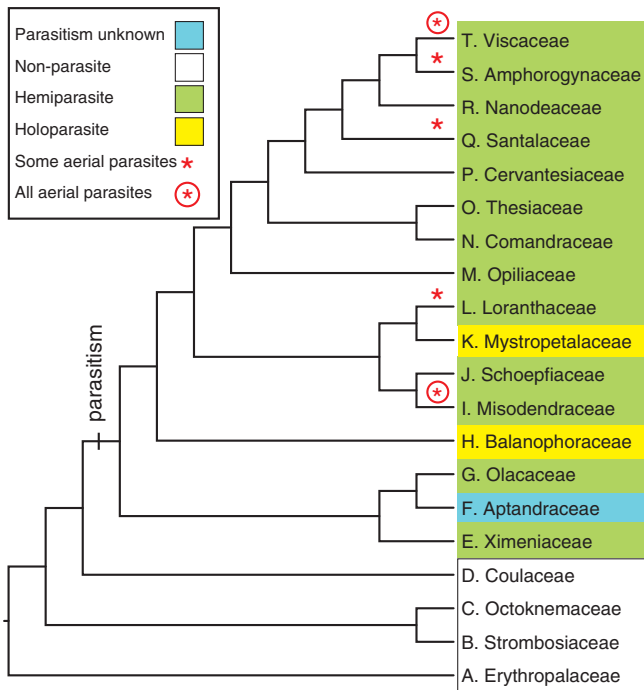


Fig. 3. Interrelationships among the 20 families currently recognized for Santalales. The tree topology derives from Su & al. (2015), Nickrent & al. (2019), and unpublished data on Octoknemaceae.

Despite evidence to the contrary (above), the widely consulted Angiosperm Phylogeny Website (Stevens, 2001–) still lists Balanophoraceae as “unplaced”. A reference to Sun [sic] & al. (2015) is provided with the statement “[*Mystropetalon* [*Dactylanthus* + *Hachettea*]] are sister to a clade containing the rest of the family examined”. This is not accurate because this clade is actually sister to Loranthaceae. APG IV (2016) cites unpublished data by J.W. Byng that suggest Balanophoraceae s.l. is a monophyletic group in “Santalaceae”. Exactly why these unpublished data were being given preference over published data is perplexing. This concept of a relationship to Santalaceae was apparently picked up by Christenhusz & al. (2017), who stated “molecular evidence has confirmed this, placing Balanophoraceae inside Santalaceae, close to *Nanodea* Banks ex C.F.Gaertn.” The reference to the Byng data is also made in the recent treatment of Santalales by Soltis & al. (2018) and such a relationship is shown in their fig. 13.3. The legend for that figure cites Nickrent & al. (2010), yet no holoparasites were included in that work. In that figure, Balanophoraceae were simply grafted onto the Nickrent & al. (2010) tree (in the wrong position, as sister to Santalaceae) and excluded Mystropetalaceae that three years earlier had been shown to have an independent origin within the order (Su & al., 2015).

For clades M–T, eight families were circumscribed by Nickrent & al. (2010), in contrast to traditional classifications that recognized four families: Opiliaceae, Santalaceae, Eremolepidaceae, and Viscaceae (Kuijt, 1969, 2015; Cronquist, 1981, 1988; Takhtajan, 1997). Given the topology of the molecular tree, maintaining the traditional familial classification would require a paraphyletic Santalaceae. Results from early molecular phylogenetic work (Nickrent & al., 1998), that have been supported in all studies since, showed that Eremolepidaceae (composed of the New World mistletoe genera *Antidaphne* Poepp. & Endl., *Eubrachion* Hook.f., and *Lepidoceras* Hook.f.) were embedded within a clade of Santalaceae s.str. The relationship of these mistletoes to Santalaceae had already been proposed based on karyological and morphological evidence (Wiens & Barlow, 1971).

The philosophical rationale for recognizing the families present in clades N–T was given in Nickrent & al. (2010), which consisted of adherence to the primary principle that only monophyletic groups (clades) obtained from molecular phylogenetic analyses be named as families, as well as several secondary principles such as minimizing disruption to existing classifications of groups well established in the literature. Morphological features for each clade were given as well as a key to these families. Overall, a combination approach (Kuntner & Agnarsson, 2006) was adopted where Linnaean (rank-based) and phylogenetic principles were employed.

The APG IV (2016) classification specifically mentioned Santalales as one case where published work was not followed because of “insufficient support for evaluating what possible altered familial circumscriptions might be possible or preferred”. For that reason, the APG III (2009) classification was retained. The decision to lump clades N–T (Fig. 3) into Santalaceae s.l. in the APG IV (2016) classification was likely

influenced by Christenhusz & al. (2015), who reported the opinions of respondents to a questionnaire. Concerning mistletoe families, they said “Some are in Loranthaceae, some in Santalaceae and some have moved about or out (e.g., Misodendraceae), causing great confusion to botanists and other users of classifications. Therefore, the popular stance is to expand Santalaceae.” Indeed, this summary of the issue does reflect great confusion, but apparently on the part of the authors, and it does not accurately reflect the historical changes that took place in mistletoe systematics. Moreover, it is not clear that lumping all these families would help clear up any perceived confusion that may exist about these mistletoes. Recognition of the family Misodendraceae dates to the mid 1800s (Agardh, 1858: 236), and its sole genus *Misodendrum* has resided in this family ever since. Indeed, mistletoes now classified in Loranthaceae, Santalaceae (“Eremolepidaceae”), and Viscaceae were earlier placed in Loranthaceae (Engler & Krause, 1935). Although Danser did not address the New World eremolepidaceous mistletoes, he considered the viscid genera part of Loranthaceae (Danser, 1929, 1931a,b, 1933, 1935). Separate family status for these mistletoes has been accepted even prior to the advent of molecular data (Barlow, 1964; Kuijt, 1968; Barlow & Wiens, 1971; Calder & Bernhardt, 1983). Moreover, the timing and ages for the five independent evolutionary events that gave rise to aerial parasitism in Santalales was given in Vidal-Russell & Nickrent (2008: fig. 2). Thus, the current state of understanding of mistletoe relationships is far from confused.

As shown in Nickrent & al. (2019), many of the relationships among families along the “spine” of the Santalales tree have now been resolved with strong support. It was stated in APG IV (2016) that alterations of APG III must await future resolution; it is here proposed that that time has come for Santalales. For the families present in clades N–T, one change that could be made to reduce the number of families is to lump Comandraceae into Thesiaceae. That clade received strong support in Nickrent & al. (2019), and these two families share a number of morphological synapomorphies. Indeed Linnaeus first classified the North American genus *Comandra* Nutt. as *Thesium umbellatum* L. Whether to lump or split when generating a classification often reduces to personal preference since no specific nomenclatural requirements exist as to where to assign ranks on a cladistic representation of plant evolution. This problem is being played out with pteridophyte phylogeny and generic concepts (Christenhusz & Chase, 2018; Schuettpelz & al., 2018). An analogous question to that controversy would be “are there too many Santalales families?” With regard to Santalaceae, Christenhusz & al. (2017) said “All families of Santalales could instead be placed in a single family.” This extreme position was foreshadowed by the recommendation of Christenhusz & al. (2015), who said “in the future perhaps expand this family to include the majority of Santalales, apart from Balanophoraceae”. This recommendation might only make sense (and maintain monophyly) if (1) Balanophoraceae s.l. were monophyletic and (2) Balanophoraceae s.l. were sister to the remainder of the families in the order. Because neither of these are true,

this uninformed recommendation must be discounted. If the N–T clade is named as Santalaceae s.l. (as is currently the case with the APG system), then subfamilial (e.g., tribal) names would be required to describe the well-supported components of that clade, e.g., Amphorogyneae Stauffer ex Stearn for Amphorogynaceae, Cervantesiae Miers for Cervantesiaceae, Santaleae Dumort for Santalaceae, Thesiae Meisn. for Thesiaceae, and Visceae Horaninow for Viscaceae. It is not clear what real advancement would be achieved by using tribal names instead of family names for the same clades. Finally, there was no justification given by APG IV (2016) for excluding Opiliaceae from an expanded Santalaceae, especially given the strong support for its sister relationship to the N–T clade.

The rationale for circumscribing families given in APG III (2009) was summarized in four helpful guidelines: (1) recognizability, (2) establishment in the literature, (3) size (small groups combined when possible), and (4) minimization of nomenclatural changes. The results from applying the third criterion are reflected in the reduction of the number of family names over the course of the APG series (462 to 416) and by the recent tabulation by Christenhusz & Byng (2016). But have these efforts eliminated or reduced the number of families with few genera and species? Twenty-nine percent (120 families) have a single genus, and 40% have one or two genera, plus there are still 29 monospecific families (suppl. Table S4). Santalales has two monogeneric families, Misodendraceae and Octoknema-ceae, and two with two genera, Comandraceae and Nanodeaceae. As mentioned above, Comandraceae can be merged with Thesiaceae. Nanodeaceae contains only *Mida salicifolia* A.Cunn. of New Zealand and *Nanodea muscosa* C.F.Gaertn. of Patagonian South America, both Gondwanan relictual taxa. The mean number of genera per family for Santalales is 9 and for the families in the N–T clades 7. Thus, the families of Santalales are not unusual in terms of their size.

Santalales are relatively well represented in the fossil record compared to most other parasitic flowering plant lineages. Following the survey of fossil pollen identified as *Anacolosidites Cookson & Pike*, Malécot & Lobreau-Callen (2005) reduced the number of species to 12 that are phenetically related to modern *Anacolosa* Blume (Aptandraceae, Olacaceae s.l.). These fossil pollens and others from Misodendraceae and Loranthaceae (Magallón & al., 2015; Grímsson & al., 2017), have allowed reliable calibration points for divergence time estimations (Vidal-Russell & Nickrent, 2008; Liu & al., 2018; Zhou & al., 2019). Stem and crown estimations of Santalales family divergence times were summarized from various studies that represent 15 of the 20 families (suppl. Table S5). The mean family age varied between 77 and 87 myr depending upon the methodology used (e.g., Bayesian, maximum likelihood, etc.).

■ 9. ERICALES

One of the families to emerge from the former “Rafflesiales” is Mitrastemonaceae. The family is represented by a

single genus, *Mitrastemon* (sometimes erroneously spelled *Mitrastema* or *Mitrastemma*). *Mitrastemon* is a root parasite with bisexual flowers, a superior ovary, and an androecium that is connate into a tube that circumscissally separates from the growing gynoeceum during fruit formation. The genus has a widely disjunct distribution, with *M. yamamotoi* Makino being present from Japan to the Philippines, Indonesia, and New Guinea and *M. matudae* Yamam. known from Central America. This species concept acknowledges the presence of many other named species that are here considered synonyms (suppl. Table S2), which is in agreement with other workers (Hansen, 1973; Meijer & Veldkamp, 1993). Using nuclear and mitochondrial DNA sequence data, Barkman & al. (2004) showed that *Mitrastemon* was sister to *Vaccinium* L., the sole representative of Ericaceae in that study, within the order Ericales, which was confirmed by Nickrent & al. (2004). A supermatrix approach (25 gene loci, 4943 species) was used by Rose & al. (2018) to infer interfamilial relationships in Ericales. *Mitrastemon* was shown to be sister to Lecythydaceae and that clade sister to the entire order Ericales.

No macro- or microfossils of Mitrastemonaceae are known. The stem/crown group ages for Ericales are 112/103 myr (Magallón & al., 2015). A stem group age of 78.3 myr was obtained for *Mitrastemon yamamotoi* (Naumann & al., 2013). The Biogeobears analysis by Rose & al. (2018) gave a 71% probability that the Mitrastemonaceae + Lecythydaceae clade originated in the Neotropics ca. 105 mya.

■ 10. BORAGINALES

Lennoaceae is a small family of fleshy holoparasitic perennial herbs found in the deserts of North and South America (Yatskievych & Mason, 1986). It contains two genera, *Lennoa* Lex and *Pholisma* Nutt. ex Hook. (including *Ammobroma* Torr.), and only four species (suppl. Table S2). Traditional classifications differed as to the sympetalous dicot allies of this family. Cronquist (1981) placed the family near Boraginaceae, and these were classified in Lamiales. Takhtajan (1997) saw a relationship with Boraginaceae, but these families were placed in Boraginales (in Superorder Solananae, not Lamiana). The APG classifications have all considered Lennoaceae a component of Boraginaceae; however, the position of that family within the Euasterids (APG, 1998; APG II, 2003) or Lamiids (APG III, 2009) has been unresolved. The APG IV (2016) classification places Boraginaceae in its own order (Boraginales) within the asterids. Gottschling & al. (2014) showed that *Lennoa* and *Pholisma* were a component of a monophyletic Ehretiaceae, a split-off from Boraginaceae. More recently, Luebert & al. (2016) used additional molecular phylogenetic data as well as morphological features to propose a consensus classification where the order consists of eleven monophyletic families. Here Lennoaceae is well-supported as sister to Ehretiaceae. This classification will be followed here because it maintains nomenclatural stability.

No macro- or microfossils of Lennoaceae are known. The stem/crown ages for Boraginales are 88/61 myr (Magallón & al., 2015). As reported in Naumann & al. (2013), the crown group age for *Lennoa* was 40.8 myr and the stem group age for *Pholisma* was 67.8 myr, both with wide variances.

■ 11. SOLANALES

Cuscuta, the sole parasitic genus in Convolvulaceae, represents one of the three origins of parasitism in the lamiid clade (Fig. 1). Known in English as dodder, *Cuscuta* is easily recognized by its twining non-green stems with reduced, scale-like leaves. There are ca. 200 species of dodder (suppl. Table S2), which occur in many habitats worldwide (Costea & al., 2015). Although cosmopolitan and originating in the Old World, the genus is more diverse in the Americas where all ca. 150 species derive from one long-distance dispersal event (García & al., 2014). Although some species are serious pathogens of crops (e.g., *C. campestris* Yunk.), the vast majority of species do not affect human activities, and indeed some species are rare and worthy of conservation efforts (Costea & Stefanović, 2009). Some traditional classifications (e.g., Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1997) placed *Cuscuta* in its own family, Cuscutaceae, but always allied with Convolvulaceae. Thorne (1992a) included it in Convolvulaceae as have all APG classifications. Possibly the first molecular phylogenetic study to include *Cuscuta*, Soltis & al. (1997) showed that the genus was sister to *Ipomoea* L. Data from nuclear, plastid, and mitochondrial genomes were used by Stefanović & Olmstead (2004) to show that *Cuscuta* was nested within Convolvulaceae, but despite extensive analysis, its exact position in the family could not be determined. Subsequent molecular phylogenetic work has provided a robust framework for the species within the genus (García & Martin, 2007; McNeal & al., 2007b; Stefanović & al., 2007; García & al., 2014).

Van der Kooij & al. (2000) compared six dodder species for chlorophyll content, photosynthetic capacity, and plastid ultrastructure. Some species show intact thylakoids and chlorophyll *a* and *b*, whereas others lack these features entirely. Thus, both hemiparasitic and holoparasitic taxa exist in *Cuscuta*. Complete chloroplast genome (plastome) sequences for seven species of *Cuscuta* currently exist in NCBI Genbank, and they range in size from 85.2 kb (*C. obtusiflora* Kunth) to 125.3 kb (*C. exaltata* Englem.). Two clades appear to have experienced even more plastome gene loss than the above species (Braukmann & al., 2013), e.g., 61 kb plastome was found in *Cuscuta* sect. *Ceratophorae* Costea & Stefanović (Banerjee & Stefanović, 2019). Plastome evolution has apparently proceeded in a stepwise fashion with rapid change followed by periods of relative stasis (McNeal & al., 2007b). Surprisingly, despite high substitution rates in the plastome, photosynthetic genes are under strong constraint (McNeal & al., 2007a), which might suggest a requirement to recycle respiratory CO₂. McNeal & al. (2007b) provided an

alternative explanation involving the role of *rbcL* in lipid biosynthesis in the green ovules that become lipid rich seeds during fruiting. The nuclear genomes of *C. campestris* (Vogel & al., 2018) and *C. australis* R.Br. (Sun & al., 2018) have been sequenced. Both studies show that paralleling the reduction in the plastome, these nuclear genomes have also undergone purifying selection and lost genes involved in photosynthesis, nutrient acquisition, symbiotic relationships (with mycorrhizal fungi), transport processes, and defense. Although dodder haustoria form from aerial shoots, these data suggest that its evolution may be related to expression changes in genes involved in root development.

The only fossil evidence of *Cuscuta* is pollen from 800-year-old peat deposits (Pals & Van Dierendonck, 1988), hence of no value in calibrating molecular phylogenetic trees. The stem/crown ages for Solanales are 85/79 myr, with a stem age for Convolvulaceae of 66 myr (Magallón & al., 2015). A stem group age for *Cuscuta japonica* Choisy of 34.6 myr was given by Naumann & al. (2013).

■ 12. LAMIALES

The third family of parasites within the lamiid clade (Fig. 1) is Orobanchaceae. With 101 genera and over 2100 species (suppl. Table S6), this is the largest parasitic flowering plant family. Although most genera are benign with respect to human activities, *Striga* and *Orobanche* are major plant pathogens on crops, particularly in Africa and the Middle East, respectively. Traditionally, the hemiparasitic members of the family were classified as Scrophulariaceae, whereas most of the holoparasites were placed in Orobanchaceae. Three genera are nonparasitic, 20 include holoparasites, and 32 genera are monospecific (suppl. Table S6). The most recent non-molecular classification of this group was by Fischer (2004), who provides descriptions of most genera. He did not formally segregate any families from the traditional Scrophulariaceae but did arrange the genera according to morphological and molecular data into “Orobanchaceae”. Within this family, he recognized 97 genera in 10 tribes. Ten of these names are now considered synonyms, and 19 names were not known at the time or were considered components (synonyms) of other genera. Three non-parasitic genera have been confirmed by molecular data to be sister to the remaining members: *Lindenbergia* Lehm., *Rehmannia* Libosch. ex Fisch. & C.A.Mey., and *Triaenophora* Soler (Young & al., 1999; Bennett & Mathews, 2006; Albach & al., 2009; Xia & al., 2009; McNeal & al., 2013). Fischer (2004) considered these genera outside of Orobanchaceae, near Plantaginaceae.

Given their economic importance, it is curious that no member of Orobanchaceae (or as Scrophulariaceae) were included in the Chase & al. (1993) or Olmstead & al. (1993) publications that utilized *rbcL*. The first molecular phylogenetic study to examine Orobanchaceae using nuclear 18S rDNA was by Soltis & al. (1997), who showed *Orthocarpus* Nutt. and *Pedicularis* L. as sister within a clade of five

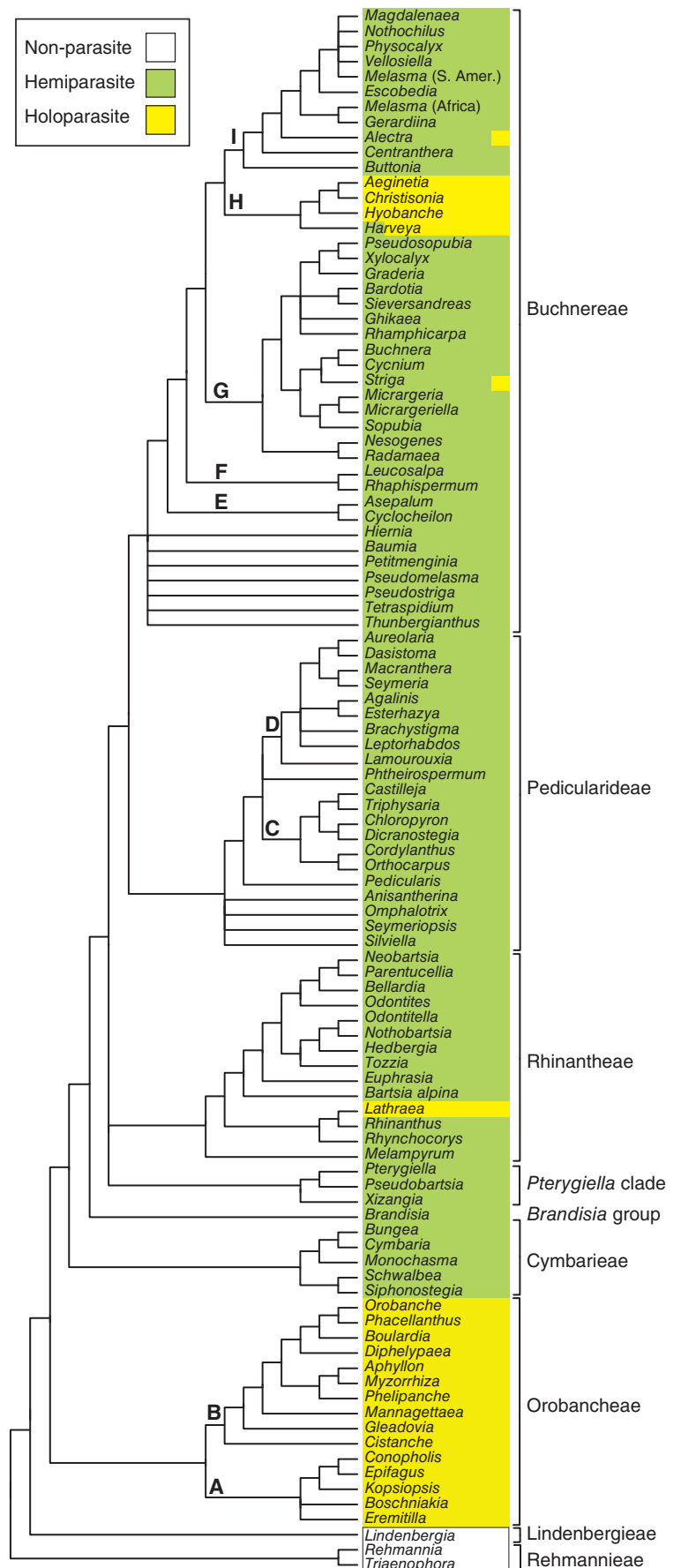


Fig. 4. Supertree showing possible relationships among the 102 genera of Orobanchaceae. The tree topology was derived from Schneeweiss (2013), an unpublished study by C. Randle, and numerous studies from the primary literature (see text). The clade (tribe) names generally follow Yu & al. (2018). See text for discussion of the subclades A–I.

members of Lamiales. In the same year plastid *rps2* was used to generate a phylogeny with 21 genera of Orobanchaceae (dePamphilis & al., 1997). This early study was the first to show that the nonphotosynthetic holoparasites were not monophyletic but originated at least five times. This contrasts with the morphology-based classification of Fischer (2004), which placed most holoparasites in tribe Orobancheae.

Schneeweiss (2013) provided an excellent summary of the state of knowledge on Orobanchaceae phylogeny at that time. In that chapter, the phylogenetic relationships of the various clades in the family were discussed, and five disconnected phylogenetic trees were shown that included lists of unplaced taxa based on their assumed affinity. Although there have been numerous phylogenetic studies since 2013 (e.g., Schneider & al., 2016; Uribe-Convers & Tank, 2016; Fu & al., 2017; Pinto-Carrasco & al., 2017; Gaudeul & al., 2018; Yu & al., 2018; Li & al., 2019), most have been focused on a particular group (tribe) within Orobanchaceae. It appears that there does not exist in the literature an attempt to incorporate all the available phylogenetic information to produce a “super tree” of Orobanchaceae. To remedy this, such a tree was manually constructed (Fig. 4) to help focus future phylogenetic work. This tree should be viewed as a hypothesis for further testing because (1) some taxa remain unsampled, (2) not all relationships are fully resolved, and (3) conflicts exist among studies that differed in taxon sampling or molecular datasets used. For the latter case, relationships were shown as either a polytomy or as a resolved node based upon the most robust data available. Here robust refers to results reported in studies with greater taxon and gene sampling. The clades from Schneeweiss (2013) were used as a starting point and refined by adding the previously unsampled taxa to the trees. The disconnected phylogenetic trees of Schneeweiss (2013) were connected based on studies that sampled more broadly within the family, such as McNeal & al. (2013) and Li & al. (2019). The topology among the major clades of the supertree shown in Fig. 4 follows the recent work by Li & al. (2019), specifically their ten-locus analysis shown in their fig. 2. Uncertainty about the backbone topology emphasizes again that Fig. 4 should be viewed as provisional.

The count of genera in supplemental Table S6 corresponds to the terminal taxa on the super tree. The concepts of species and synonymy in supplemental Table S7 derive from many sources but the Index of Orobanchaceae (Sánchez Pedraja & al., 2005–) was of particular value. For large and problematic genera such as *Euphrasia* L. and *Pedicularis*, an estimate of the number of species was made by consolidating the information in various Floras and databases. Each of the tribes (or groups or clades), as used in Yu & al. (2018), will be discussed in turn below.

Orobancheae. — Perhaps stemming from the agronomic importance of *Orobanche*, this clade has been the subject of more molecular phylogenetic study than other groups in the family. It is also this clade that currently departs the most from the classification in Fischer (2004). In that work, tribe Orobancheae contained not only *Orobanche*, *Cistanche*

Hoffmanns. & Link, *Phacellanthus* Siebold & Zucc., etc. but also *Aeginetia* L., *Christisonia* Gardner, *Harveya* Hook. and *Hyobanche* L., which have been shown, through DNA sequencing, to be members of Buchnereae (below). Moreover, *Conopholis* Wallr., placed in tribe Rhinanthae by Fischer (2004), is sister to *Epifagus* Nutt. in Orobancheae. These relationships were seen in some of the earliest molecular phylogenetic studies conducted on the family (Young & al., 1999; Wolfe & al., 2005; Young & de Pamphilis, 2005). Complete generic sampling in Orobancheae shows that it is composed of two subclades of holoparasites (A and B on Fig. 4). Clade A contains five genera mostly confined to North America, with the exception of *Boschniakia himalaica* Hook.f. & Thomson (synonym *Xylanche himalaica* Beck) from Asia. *Kopsiopsis strobilacea* Beck. and *K. hookeri* (Walp.) Govaerts from western North America were shown to be distinct from *B. rossica* (Cham. & Schltdl.) B.Fedtsch. by Bennett & Mathews (2006), hence they were split from *Boschniakia*. *Eremittilla mexicana* Yatsk. & J.L.Contr. (Yatskievych & Contreras Jiménez, 2009), known only from Guerrero, Mexico, is allied with these genera based on unpublished molecular data (Schneeweiss, 2013). A key using morphological features to the five genera in this subclade was provided by Yatskievych & Contreras Jiménez (2009).

The topology of the ten genera shown in subclade B (Fig. 4) derives mostly from the molecular analyses conducted by Schneider & al. (2016). This generally agrees with the results published by Fu & al. (2017) except that in that study, *Orobanche* was not monophyletic. To maintain monophyly, the genus *Aphyllon* Mitch. (including *Myzorhiza* Phil.) was resurrected for New World taxa and *Boulardia* F.W.Schultz, *Phelipanche* Pomel and *Orobanche* s.str. recognized for Old World taxa (Schneider, 2016).

Cymbarieae. — This clade of five hemiparasitic genera has been recognized based on floral morphological features (Fischer, 2004) and is strongly supported as monophyletic in molecular studies (Bennett & Mathews, 2006; McNeal & al., 2013). Those two studies showed that Cymbarieae was sister to the remaining parasitic members of the family. In contrast, Yu & al. (2018) used nuclear ribosomal ITS sequences to show that this clade diverged later and was sister to the remaining members of the family. This topology places the holoparasitic Orobancheae as sister to the entire family, a result also obtained using low-copy nuclear genes (Li & al., 2019). If this topology is correct, it appears there was a divergence that split the hemiparasites from one clade of holoparasites early in the evolutionary history of the family. This topology also calls into question the simplistic trend from autotroph, to facultative hemiparasite, to obligate hemiparasite, to holoparasite, a progressive morphocline frequently represented on evolutionary trees (e.g., Westwood & al., 2010).

Brandisia and the Pterygiella clade. — The Asian genus *Brandisia* Hook.f. & Thomson was not considered a member of Orobanchaceae by Fischer (2004), and indeed these tomentose shrubs and vines are morphologically quite divergent.

Despite this, molecular phylogenetic studies place the genus in Orobanchaceae (Bennett & Mathews, 2006; McNeal & al., 2013), however, it is not strongly allied with any of the six major parasite clades. Yu & al. (2018) included two species of *Brandisia* and showed moderate support for this clade as sister to tribes Buchnereae, Rhinanthaeae, and Pedicularideae.

Recent work using five- and ten-locus datasets of low-copy nuclear genes (Li & al., 2019) showed different topologies for the *Pterygiella* clade relative to Rhinanthaeae, Buchnereae, and Pedicularidae. This clade, composed of the Asian genera *Pterygiella* Oliv., *Pseudobartsia* D.Y.Hong, and *Xizangia* D.Y.Hong, is therefore shown as arising from a polytomy involving Buchnereae, Rhinanthaeae, and Pedicularidae in Fig. 4. These three genera, as well as *Phtheirospermum tenuisectum* Bureau & Franch., were components of a clade within the *Euphrasia-Rhinanthus* clade in Schneeweiss (2013). But because another species, *Ph. japonicum* (Thunb.) Kanitz, was only distantly related, the genus was rendered polyphyletic. Using both plastid and nuclear genes, Dong & al. (2013) showed that *Ph. tenuisectum* and two other species were part of a clade composed of *Pterygiella*, *Pseudobartsia* and *Xizangia* (*Pterygiella* complex II). A taxonomic solution to the problem of polyphyly in *Phtheirospermum* was made in Pinto-Carrasco & al. (2017), who sunk *Ph. muliense* C.Y.Wu & D.D.Tao, *Ph. parishii* Hook.f., and *Ph. tenuisectum* into *Pterygiella*. *Phtheirospermum japonicum* was retained as it is the generic type species for the genus. The more recent study by Yu & al. (2018) highlighted the same polyphyletic issue as Dong & al. (2013) but did not follow the taxonomy proposed in Pinto-Carrasco & al. (2017) and continued using the generic name *Phtheirospermum* for the *Ph. tenuisectum* complex of species. Moreover, because of poor sampling in the *Pedicularis* clade, they did not obtain an exact placement of *Ph. japonicum*.

Rhinanthaeae. — All 14 genera shown in the Rhinanthaeae clade (Fig. 4) were classified in tribe Rhinanthaeae by Fischer (2004), although that work did not recognize two genera (*Bellardia* All., *Neobartsia* Uribe-Convers & Tank.), and several genera (e.g., *Conopholis*, *Pedicularis*, *Phtheirospermum*, *Pterygiella*) have since been placed in other clades. This clade is mainly a Palearctic group, possibly with a Paratethyan origin (Wolfe & al., 2005), with some widespread genera (*Euphrasia*, *Melampyrum*) present in the Nearctic and even the Neotropics (*Euphrasia*, *Neobartsia*). The genus *Lathraea* L., composed of ca. five Eurasian species, is the sole holoparasitic member of this clade, thus representing the second independent evolution of this trophic mode in the family. Interestingly, the 150 kb plastome of *L. squamaria* L. is the largest among holoparasitic Orobanchaceae (Samigullin & al., 2016) and comparable in size to photosynthetic plants. Despite the plastome size, its genes have experienced relaxed selective constraint, e.g., those in photosystems I and II have become pseudogenes.

The topology for Rhinanthaeae (Fig. 4) for the most part follows Pinto-Carrasco & al. (2017); however, other studies

offered different interpretations of generic boundaries based on different molecular analyses (e.g., Těšitel & al., 2010; Scheunert & al., 2012; Uribe-Convers & Tank, 2016; Gaudeul & al., 2018). *Melampyrum* L. is sister to the rest of the clade, a result seen in all molecular analyses. *Bartsia* L. from Africa were merged with *Hedbergia* Molau (Scheunert & al., 2012), South American species were split and named *Neobartsia*, which is sister to *Parentucellia*, and *B. trixago* L. and *B. viscosa* L. became *Bellardia*. These changes left *Bartsia* monospecific, i.e., *B. alpina* L., which is found in Arctic-alpine Europe and northeastern North America. Pinto-Carrasco & al. (2017) and Gaudeul & al. (2018) agreed on the merger of *Bartsia* Bolliger and *Bornmuellerantha* Rothm. with *Odontites* Ludw. but disagreed as to the circumscription of *Macrosyringion* Rothm. The systematics of the *Odontites* complex is complicated by the presence of hybrid speciation, introgression, and polyploidy (Gaudeul & al., 2018).

The genus *Euphrasia* is second in size only to *Pedicularis*. Estimates of the number of species vary widely: 350 (Fischer, 2004) and 246 (Hassler, 2019); the latter tabulation was used in the present study. This genus is the most widespread in the entire family, occurring in most biogeographic realms. *Euphrasia* is inferred to have a Eurasian origin and its current disjunct bipolar distribution required 17 dispersal events to account for the present distribution (Gussarova & al., 2008). The rapid species-level diversification likely occurred after the late Pliocene and for some species (e.g., in the U.K.) a postglacial origin is assumed.

Pedicularidae. — This clade contains mainly genera classified in tribes Gerardieae and Castillejeae by Fischer (2004). Exceptions include *Omphalotrix* Maxim., *Ptheirospermum* Bunge ex Fisch. & C.A.Mey., and *Pedicularis*, which were placed in Rhinanthaeae, as well as *Leptorhabdos* Schrenk. classified in Micrargerieae. The other three genera in this tribe are scattered in Buchnereae. As of this writing, no molecular data are available for *Anisantherina* Pennell, *Omphalotrix*, *Seymeriopsis* Tzvelev, and *Silvella* Pennell; thus, their association with Pedicularidae is based on morphology (Schneeweiss, 2013). The clade contains 21 genera of mostly Nearctic and Neotropical taxa with four exclusively Palearctic genera (*Leptorhabdos*, *Omphalotrix*, *Ptheirospermum*, *Seymeriopsis*). Early molecular work with *rps2* (Young & al., 1999) placed seven members of this group in a clade, but relationships along the spine of the tree were unresolved. Later work with greater taxon sampling (Wolfe & al., 2005; Tank & al., 2006) revealed the presence of two subclades, basically corresponding to tribes Castillejeae and Gerardieae in Fischer (2004), with *Pedicularis* sister to these. These are indicated in Fig. 4 as C and D, respectively. The *PHYA* gene tree of Bennett & Mathews (2006) reflected a similar topology and added *Phtheirospermum japonicum* in an unresolved position, as it is still reflected in Fig. 4. Relationships in the mostly North American subclade C were greatly clarified by Tank & Olmstead (2008). In addition to subsuming *Clevelandia* Greene

and *Ophiocephalus* Wiggins into *Castilleja* Mutis ex L.f., they split *Chloropyron* Behr and *Dicranostegia* (A.Gray) Pennell from *Cordylanthus* Nutt. ex Benth. In the most complete generic sampling to date, McNeal & al. (2013) included 12 of the 21 genera in this clade, and the tree topologies of their clade IV (equivalent to Pedicularideae) generally conform to those shown in Fig. 4.

Pedicularideae contains two of the largest and most widespread genera in the family: *Castilleja* (ca. 200 species) and *Pedicularis* (ca. 650 species). *Pedicularis* occurs in Europe, Asia, North and South America with the highest diversity seen in China and Himalayan regions. *Castilleja* is most diverse in western North America and Mexico with a handful of Eurasian and South American species. Estimates of the number of *Pedicularis* species ranges widely, from 247 from the Plants of the World Online database (Kew Science) to the highest number given in Mill (2010) who suggested 800, similar to Mabberley (2017) who estimated 750. The number reported here for both genera derives from Catalogue of Life 2019 (Hassler, 2019).

Buchnereae. — With 39 genera Buchnereae is the largest tribe in the family; however, it is currently the least understood phylogenetically. This is partly evidenced by the placement of seven genera in a basal polytomy (Fig. 4) because no DNA sequences have been deposited in Genbank for these taxa. Although most of the genera placed in tribe Buchnereae by Fischer (2004) are present in this clade, it also contains elements from his Buttonieae, Escobedieae, Micrargerieae, and Xylocalyceae as well as a holoparasitic clade that he considered a component of Orobanchaceae. The Buchnereae was recognized from some of the earliest molecular studies where 10 genera (Wolfe & al., 2005) and 13 genera (Bennett & Mathews, 2006) were sampled. This clade, composed mainly of tropical parasites, was found to be monophyletic in the study by Morawetz & al. (2010), where 14 genera were sampled. The treatment in Schneeweiss (2013) reflected the state of knowledge at that time where 21 genera were listed but were not included in the tree for lack of molecular data. Since then, sampling has greatly improved. The relationships in Buchnereae shown in Fig. 4 were derived from unpublished analyses by Dr. Chris Randle whose molecular dataset (ITS plus four plastid genes) included 33 of the 39 genera. Relationships will be discussed in the order of six subclades (E–J) on Fig. 4.

Subclade E contains two genera of northeastern Africa (*Asepalum* Marais, *Cyclocheilon* Oliv.) that were not included in the Fischer (2004) classification. The relationship of these taxa being sister to the remaining members of Buchnereae was first seen in Morawetz & al. (2010). The next two genera, *Leucosalpa* Scott-Elliot. and *Rhaphispermum* Benth., are strongly supported as sister in subclade F. These Malagasy taxa were classified in tribe Buttonieae by Fischer (2004), a tribe whose members are part of Buchnereae but are polyphyletic based on molecular data. With at least 15 genera, subclade G is the largest in the Buchnereae clade. *Xylocalyx*

Balf.f. is clearly a member of this subclade (Morawetz & al., 2010), not the sole member of tribe Xylocalyceae (Fischer, 2004). Three of the four genera placed in tribe Micrargerieae by Fischer (2004) are in Buchnereae but only two (*Micrargeria* Benth., *Micrargeriella* R.E.Fr.) are sister. As mentioned above, *Leptorhabdos* is in Pedicularideae and *Gerardiina* is in Buchnereae, subclade J.

Striga, along with *Buchnera* and *Cycnium*, forms a well-supported clade within subclade G (Young & al., 1999; Morawetz & al., 2010; McNeal & al., 2013), and all three were classified in Buchneriinae by Fischer (2004). *Buchnera* has the fourth-highest number of species in Orobanchaceae (suppl. Tables S6, S7) but has received surprisingly little modern taxonomic attention. Most genera in subclade G have an Afrotropic and Indomalayan distribution. *Buchnera* has Africa as its center of diversity but also has 17 species in the Nearctic and Neotropic biogeographic realms (Philcox, 1965). This genus is monophyletic (Bayat and Randle, unpub. data), and the ten sampled Nearctic/Neotropic taxa form a clade with strong support.

Striga, a genus with 33 species, is perhaps the most intensively studied of all parasitic plants as evidenced by a Google Scholar search that returned nearly 1600 articles since 2018. *Striga hermonthica* on sorghum, *S. asiatica* on maize, and *S. gesnerioides* on cowpea constitute the top three witchweed species, particularly in sub-Saharan Africa. Controlling these crop pathogens, the focus of much research in diverse disciplines, involves chemical control, biocontrol, breeding resistant crops, and integrated agronomic management (Joel & al., 2013; Shayanowako & al., 2017; Belay, 2018; Runo & Kuria, 2018). Some species such as *S. gesnerioides* are holoparasites, thus representing the third independent evolution of this trait in the family.

Clade H represents the fourth independent evolution of holoparasitism in Orobanchaceae. Three of the four genera, *Aeginetia*, *Christisonia*, and *Hyobanche* are holoparasites, whereas in *Harveya* both hemi- and holoparasitic species exist. Although earlier molecular studies all showed monophyly of components of this clade (Young & al., 1999; Wolfe & al., 2005; Young & de Pamphilis, 2005), Morawetz & al. (2010) were the first to provide strong support for a clade that included all four genera, with extensive species sampling within *Harveya*. The taxonomy of *Harveya* used here (suppl. Table S7) lists the 13 species accepted by Randle (2006) but includes 12 others from Catalogue of Life (Hassler, 2019). The holoparasite *Harveya* (*Alectra*) *alba* Hepper, placed in the invalidly published genus “*Paraharveya*” (Fischer, 2004), was returned to *Harveya* by Morawetz & Randle (2010). In a clade with this species is *H. tanzanica* Hepper (non-green) and *H. obtusifolia* Vatke (green and photosynthetic). It was suggested (Morawetz & al., 2010) that this could represent a reversion to hemiparasitism from a holoparasitic ancestor. This hypothesis requires further examination because lack of green color does not necessarily equate with holoparasitism. *Harveya* and *Hyobanche* are exclusively African genera, whereas the closely related *Aeginetia* and

Christisonia are Indomalayan. *Aeginetia indica* can be a pest on sugarcane (Ray & Dasgupta, 2006).

The majority of genera in subclade I were classified in tribe Escobediaceae by Fischer (2004). The exceptions are *Gerardiina* Engl. (tribe Micrargerieae) and two early-branching genera, *Buttonia* Benth. and *Centranthera* R.Br. (tribes Buttonieae and Buchneraeae, respectively). Biogeographically, the presence of *Centranthera* in this subclade is anomalous given its nine species are distributed from China to Australia, whereas most of the other genera are from the Afro- and Neotropics. *Alectra* Thunb. is composed of ca. 35 species distributed mostly throughout tropical Africa and Asia. Most are hemiparasites, however, one species (*A. orobanchoides* Benth.) is holoparasitic (La Harpe & al., 1981; dePamphilis & al., 1997), not a holomycotroph as indicated in Mabberley (2017). This represents the fifth independent evolution of this life form in the family.

The genus *Melasma* P.J.Bergius has been shown to be non-monophyletic in earlier molecular studies (Morawetz & al., 2010), but taxon sampling at that time did not allow confident generic realignment. The more extensive sampling by Randle (unpub.) (Fig. 4) indicates that *M. melampyroides* Pennell might best be classified as *Alectra*. Three African species formed a clade together with *Gerardiina* (also African), separate from the Neotropical species. Six exclusively Neotropical genera, all classified in tribe Escobediaceae (Fischer, 2004), occur in a clade where *Escobedia* Ruiz & Pav. is sister to a polytomy containing the remaining five taxa (*Melasma rhinanthoides* Benth., *Vellosiella* Baill., *Physocalyx* Pohl., *Nothochilus* Radlk., *Magdalenaea* Brade). *Melasma physaloides* (D.Don) Melch. was strongly supported as sister to *Escobedia*, which is surprising given their different floral morphologies (Morawetz & al., 2010). Overall, relationships in subclade I should be considered tentative at this time until further work provides a solid foundation for generic boundaries.

Martínez-Millán (2010) stated that the fossil record for Lamiales is sparse and gave a minimum age dating of 28.4 myr for the order. Although Wolfe & al. (2005) indicated that no macro- or microfossils of Orobanchaceae are known, fossil pollen of *Tricolpites pedicularidus* Wang and two other related types known from the Eocene to the Pliocene of eastern China may be referable to *Pedicularis* (Song & al., 2004). A stem group age of 88.2 myr and a crown group age of 77 myr were estimated for the order Lamiales by (Magallón & al., 2015). That study found a stem group age of 35.9 for Orobanchaceae, which is similar to the 31.5 myr obtained by Naumann & al. (2013) for *Epifagus*.

■ CONCLUSIONS

This review has attempted to provide the background information necessary to address the two questions posed in the title, i.e., how often has haustorial parasitism evolved in angiosperms, and how many parasites exist in the various clades. While some may suggest that tabulating numbers of

species, genera, families, etc. is of limited value, the counter argument is that such data are central to biodiversity studies because those are fundamentally tied to taxonomic lists (Strand & Panova, 2015). Parasitic flowering plants constitute ca. 2.2% of the genera and 1.6% of the species of angiosperms. Molecular phylogenetic methods have been applied to all families and nearly all genera of parasitic flowering plants such that today, all have been placed relative to their non-parasitic ancestors. Although many recent papers express uncertainty about the number of times parasitism evolved, it now seems certain that 12 extant clades exist that contain haustorial parasites. These have evolved independently in 12 orders scattered throughout the angiosperm phylogeny (Fig. 2). Seven of the 12 clades are exclusively holoparasitic and three more (Santalales, *Cuscuta*, Orobanchaceae) contain both hemiparasites and holoparasites. Although hemiparasites (that derive mainly host water and minerals) are common, the frequency across the phylogeny of parasites that achieve higher levels of dependence (i.e., also tapping host photosynthates) suggests strong evolutionary forces driving a trend towards holoparasitism. Studying taxa that are on the cusp of this nutritional shift such as *Arceuthobium* (Nickrent & García, 2009) can provide insight into the selective forces that are altering basic molecular, biochemical, and developmental processes. It seems that nothing is “off the table” as evidenced by the A/T drift phenomenon, first described by Nickrent & al. (1997), that has reached an extreme in the holoparasite *Balanophora* that even has an altered genetic code in its plastome (Su & al., 2019).

It is generally assumed that once parasitism is achieved, it is selectively disadvantageous to revert to the autotrophic condition. A case where this axiom could be tested is Ximeniaceae where parasitism (or lack of it) needs to be confirmed for the three other genera besides *Ximenesia*. Similarly, it is not known whether the evolutionary trajectory from hemiparasite to holoparasite can be reversed. Current evidence suggests that this could be tested using a detailed molecular phylogeny of *Harveya* (Orobanchaceae) and *Cuscuta* (Convolvulaceae) where both hemiparasites and holoparasites are present in one clade. Although parasitism appears to be a successful strategy over evolutionary time, paucispecific genera exist in contrast with extremely speciose ones such as *Pedicularis*, *Euphrasia*, and *Thesium* L. The causes of explosive speciation in some groups but not others have yet to be explained.

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