Chapter 9
Polyploidy in Legumes

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Abstract Legumes are the third largest family of flowering plants, with over 700 genera and more than 19,000 species. Genomic evidence has shown that a whole-genome duplication (WGD) occurred shortly after the origin of the family, in an ancestor that gave rise to the papilionoids, the clade that comprises 65 % of the genera and 71 % of the species, including nearly all of the economically important crop legumes. This polyploidy event may have been associated with the origin of nitrogen-fixing symbiosis (nodulation) in the papilionoids. Nodulation most likely evolved independently in other legumes outside the papilionoids, hence there appears to be no requirement for polyploidy in the evolution of this important symbiosis. More recent polyploidy, as inferred from chromosome counts, occurs in approximately a quarter of all legume genera for which data are available. In most cases, polyploidy is confined to individual genera, species within genera, or cytotypes within species. An exception is the core clade of the genistoid legumes, a major papilionoid group that includes lupines (*Lupinus*). This group is probably fundamentally polyploid and also has a propensity for further polyploidy and aneuploidy in many of its genera. The frequency of polyploidy varies considerably among clades of the family, being most common (outside the genistoids) in the largely temperate, herbaceous Hologalegina (including pea and clover), and low in woody tropical groups such as the caesalpinioids.

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9.1 Introduction

The legumes (Leguminosae or, less preferably, Fabaceae, according to Lewis et al. 2005) are the third largest family of flowering plants, and are tremendously diverse ecologically, morphologically, chemically, and cytologically (Doyle and Luckow 2003; Lewis et al. 2005). Not surprisingly, the family is also cytologically diverse. As in other families, polyploidy is implicated as a major force at all levels of legume evolution, from the early stages of radiation in the family to the origin and recent diversification of modern genera, such as *Glycine* (soybean and allies) and species within genera, such as the *Medicago sativa* complex (alfalfa and allies).

After summarizing progress in understanding the phylogeny of the family, this review will discuss the role of paleopolyploidy during the early stages of the radiation of the entire family and the possible connections with nodulation. The occurrence of polyploidy in each of the major clades of the family will then be reviewed.

9.2 A Brief Overview of Legume Phylogeny

Along with Polygalaceae, Surianaceae, and Quillajaceae, Leguminosae form the order Fabales, one of eight-orders in the Fabidae clade of rosid eudicots (Wang et al. 2009). Bello et al. (2009) suggested that the Fabales are the product of a rapid radiation, with legumes probably sister to Surianaceae plus Quillajaceae.

The Leguminosae has been the focus of considerable phylogenetic study, culminating in solid, chloroplast based, working hypotheses of generic relationships (Fig. 9.1), notably those of Wojciechowski et al. (2004) and Bruneau et al. (2008). The older classification of the family into three subfamilies, Caesalpinioideae, Mimosoideae, and Papilionoideae (sometimes treated as separate families), is not supported by molecular phylogenetic studies, in that although the Mimosoideae (mimosas, acacias) and Papilionoideae (pea, bean, soybean, etc.) are monophyletic, the former is embedded in one clade of a paraphyletic caesalpinioid grade. Relationships at the base of the family are uncertain and differ among the studies of Wojciechowski et al. (2004), which focused most heavily on Papilionoideae, and Bruneau et al. (2008), which emphasized caesalpinioids and included few papilionoids. However, both studies identified caesalpinioids as the earliest-diverging lineages, including such taxa as the tribe Cercideae, which includes *Cercis* (the redbud or Judas tree) and the large genus, *Bauhinia* (orchid tree). Relationships at the bases of the two monophyletic subfamilies are also uncertain.

Fossil evidence places the origin of the family in the Paleocene, around 60 million years ago (MYA; see Lavin et al. 2005 for discussion; see also Bell et al. 2010). Divergence times of all major groups within the family have been estimated from fossil-calibrated molecular data (Lavin et al. 2005; Bruneau et al. 2008) and suggest rapid diversification of many clades, such that within

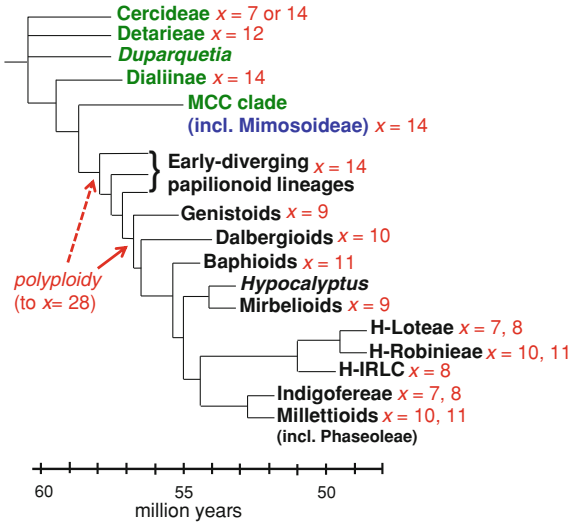

Fig. 9.1 Phylogeny of legumes. Caesalpinioids are shown in *green*, papilionoids in *black*. Relationships among caesalpinoid lineages are shown as unresolved due to conflict among published studies. Papilionoid taxa marked "H" are members of the Hologalegina. Divergence dates for the origins of major clades are from Lavin et al. (2005). Base chromosome numbers are given for groups with published counts. Minimum (*solid arrow*) and maximum (*dashed arrow*) dates for the papilionoid polyploidy event are shown

10 million years of divergence from a common ancestor, all of the major lineages in the family had evolved, including the two monophyletic subfamilies and all of the major clades within the Papilionoideae.

9.3 Polyploidy and the Early Diversification of Legumes

To what degree has polyploidy shaped the radiation of legumes? Given the growing understanding that polyploidy can drive phenotypic diversification (e.g., Freeling et al. 2006) and has played a role in the preservation of lineages during periods of extinction (Fawcett et al. 2009), it might be expected that polyploidy would be an important feature of evolution in a family that is "successful" as judged by its sheer size and ecological dominance in some tropical biomes (e.g., rain forests, woody savannas, and dry forests), and in which a significant adaptive novelty—the symbiotic association with nitrogen-fixing soil bacteria, termed nodulation—has arisen (e.g., Doyle 2011).

9.3.1 Chromosome Number Evidence for Polypoidy in Legumes

Until the advent of genomic data, chromosome number was the prime source of information available for inferring the existence of polyploidy. Goldblatt's (1981) review of the distribution of chromosome numbers in Leguminosae, published in *Advances in Legume Systematics, Part* 2, remains the most comprehensive treatment of chromosomal variation in the family, and includes hypotheses concerning the base numbers and ploidy levels of its constituent subfamilies and tribes. The information from which his summary was drawn was included in the descriptions of genera in *Advances in Legume Systematics, Part* 1 (Polhill and Raven 1981), known to researchers in the family as the legume "bible." The taxonomic treatments provided by this key resource were recently updated in *Legumes of the World* (Lewis et al. 2005), taking into account the rapid progress in legume phylogenetics. The phylogenetic studies that have revolutionized our understanding of relationships within the family also provide a new phylogenetic context for understanding chromosome number evolution that was not available previously, but unfortunately the otherwise excellent *Legumes of the World* does not include any cytological information.

The key contribution of objective phylogenetic data to our understanding of cytological evolution in the family is the confirmation of caesalpinioid legumes as a grade rather than as a natural subfamily. Chromosome numbers for the major clades that comprise the caesalpinioid grade are relatively constant, principally $2n = 24$–28 (Fig. 9.1). Standing out from these higher chromosome numbers are *Chamaecrista* and *Cercis*. The large, mostly, pantropical genus, *Chamaecrista*, is cytologically complex, with $2n = 14$, 16, and 28. Goldblatt (1981) considered its lower numbers to be the products of aneuploid reduction, and this hypothesis has been recently supported (Torres et al. 2011, see below). Phylogenetic studies (Wojciechowski et al. 2004; Bruneau et al. 2008) now nest *Chamaecrista* and other Cassieae s.s. within the Mimosoideae-Caesalpinioideae-Cassieae (MCC) clade ($2n = 28$), supporting this hypothesis.

Cercis is a small genus (10 species) with disjunct worldwide distribution and $2n = 14$. It is a member of the Cercideae, all other members of which are $2n = 28$, including the large pantropical genus, *Bauhinia* s.l. (ca. 250 species). Phylogenetic studies show that *Cercis* is sister to the remaining genera (Bruneau et al. 2008), which may be consistent with Goldblatt's (1981) conclusion that it is diploid and the remainder of the tribe is fundamentally polyploid. This is of some importance given the relatively early divergence of Cercideae in some phylogenies. In the *rbcL* phylogeny of Kajita et al. (2001) the tribe was sister to the remainder of the family, though with relatively weak support, and this topology also appears in the phylogenetic summary of Lewis et al. (2005). The chloroplast *matK* tree of Wojciechowski et al. (2004), which emphasized Papilionoideae, placed Cercideae, and Detarieae (mainly $2n = 24$) together as the first-diverging legume lineage. In these topologies, it is possible that, as Goldblatt (1981) suggested, the legumes are fundamentally $x = n = 7$, with subsequent independent

chromosomal increase both within Cercideae and in the ancestor of all remaining legumes.

In contrast, the concatenated chloroplast *matK/trnK* + *trnL-F* tree of Bruneau et al. (2008) placed Detarieae as the first branch in the legume phylogeny, sister to a trichotomy composed of Cercideae, *Duparquetia*, and the remainder of the family. In this phylogeny, then, the base number for the family would be $x = n = 12$, with $2n = 14$ in *Cercis* representing a reduction. Interestingly, the genome size of *Cercis canadensis* is comparable to measurements from the several species of *Bauhinia* in the Kew C-value database (http://data.kew.org/cvalues/; Leitch and Doyle, unpublished data), supporting this reduction hypothesis.

Even a high base number for early diverging lineages, as suggested by the Bruneau et al. (2008) topology, would not definitively suggest polyploidy at the base of the family, given what is known of chromosome numbers from other Fabales. No information is available for *Quillaja* in the Index of Plant Chromosome Numbers (IPCN; http://www.tropicos.org/Project/IPCN), but Surianaceae is represented by a single species of *Stylobasium,* with a number of $2n = 30$, suggesting that the common ancestor of legumes and Surianaceae could have had a high chromosome number.

Patterns of chromosomal evolution among major groups of legumes are complex even outside of the earliest branching. The bulk of the family belongs to two sister clades: the MCC clade and the Papilionoideae. The two tribes that comprise the MCC clade along with Mimosoideae (Caesalpinieae and Cassieae s.s.) are both diploid based on $x = 14$. Given the presence of taxa with $2n = 28$ in the grade at the base of Papilionoideae, it is likely that the common ancestor of that group and the MCC was diploid based on $x = 14$ as well. The majority of papilionoids, however, have lower base chromosome numbers, ranging from $x = 7$–11, depending on the tribe. These presumably represent reductions in chromosome number, as discussed below; they certainly give no evidence for polyploidy.

9.3.2 Genetic and Genomic Evidence for Polyploidy in the Early Evolution of Legumes

Genomic studies, starting with linkage maps and continuing through studies of expressed sequence tags (ESTs) and genome sequencing, have revolutionized understanding of polyploidy in seed plants. Although it was long known that diploidization can erase chromosomal evidence of polyploidy over time, it is now clear that plant genomes comprise nested sets of WGD. The common ancestor of all seed plants underwent a polyploid duplication, with a later WGD in the ancestor of all angiosperms (Jiao et al. 2011) and numerous lineage-specific duplications in various groups of flowering plants (Soltis et al. 2009).

It has been known for some time that cryptic polyploidy occurs in legume genomes. For example, Shoemaker et al. (1996) used linkage map information to

hypothesize that the soybean genome shows evidence of a more ancient duplication than the one that is responsible for its high chromosome number relative to allied phaseoloid genera (millettioid clade, Fig. 9.1). In 2004, two different groups mined the extensive EST collections of soybean and the diploid model legume, *Medicago truncatula* ($2n = 14$; a member of the Hologalegina IRLC clade), to search for the genomic signature of ancient polyploidy events (Blanc and Wolfe 2004; Schleueter et al. 2004). This signature is produced when all genes in the genome are duplicated by autopolyploidy or when homoeologous loci are brought together by allopolyploidy. It is observed by plotting the frequency distribution of pairwise K_s (synonymous substitutions per synonymous site—a stand-in for time) values for hundreds to thousands of paralogous gene pairs. Simple gene duplication is an ongoing phenomenon in all eukaryotes, but most duplicates are purged from the genome rapidly, producing a characteristic distribution with many recent duplicates with low K_s values and relatively few older pairs with high K_s (Lynch and Conery 2003). Polyploid duplications appear as additional components ("peaks") against this background; the mode of such a K_s peak is taken as an estimate for the age of the polyploid, though it is generally an overestimate of that age (Doyle and Egan 2010).

Both Blanc and Wolfe (2004) and Schleueter et al. (2004) identified two K_s peaks in soybean, as expected (Fig. 9.2); both reported similar K_s modes for these peaks but because they used different substitution rates for plant nuclear genes, this led to different estimates of the age of polyploidy (or homoeologue divergence). The Schleueter et al. (2004) estimates are more in keeping with divergence dates for papilionoid legume taxa (Lavin et al. 2005) and are preferred for that reason (Shoemaker et al. 2006); in addition, the rate used by Schleueter et al. (2004) is much closer to the rate recently estimated for *Arabidopsis* (Ossowski et al. 2010).

Of great interest was the finding, by both groups, of two K_s peaks in the *M. truncatula* EST collection (Fig. 9.2). The younger of the two peaks is recent enough that if due to polyploidy, it would most likely have left chromosomal evidence, and has yet to be explained (Young et al. 2011). The older *Medicago* peak, on the other hand, was estimated by Schleueter et al. (2004) to be around 54.6 MYA, very close to the 54 MY age estimated by Lavin et al. (2005) for the divergence of the soybean (millettioid) and *Medicago* (Hologalegina) lineages, and also similar to the age estimated for the older soybean peak (41.6 MYA). This raised the possibility that the two species shared an ancient WGD.

This hypothesis was tested by Pfeil et al. (2005) using a phylogenomic approach with 39 gene pairs chosen from among those used by Schleueter et al. (2004) to identify the K_s peak in soybean. Topologies of gene trees overwhelmingly favored the hypothesis that their common ancestor was polyploid. Comparisons of linkage relationships between *Medicago* and the other legume model species, *Lotus japonicus* (in the Hologalegina Loteae clade, Fig. 9.1), provided further support for this hypothesis, and also showed that the duplication was not found in poplar. Using the Lavin et al. (2005) date for the divergence of the millettioid (*Glycine*) and Hologalegina (*Lotus, Medicago*) clades, the WGD event had taken place by around 54 MYA. Thus, the common ancestor of the two major

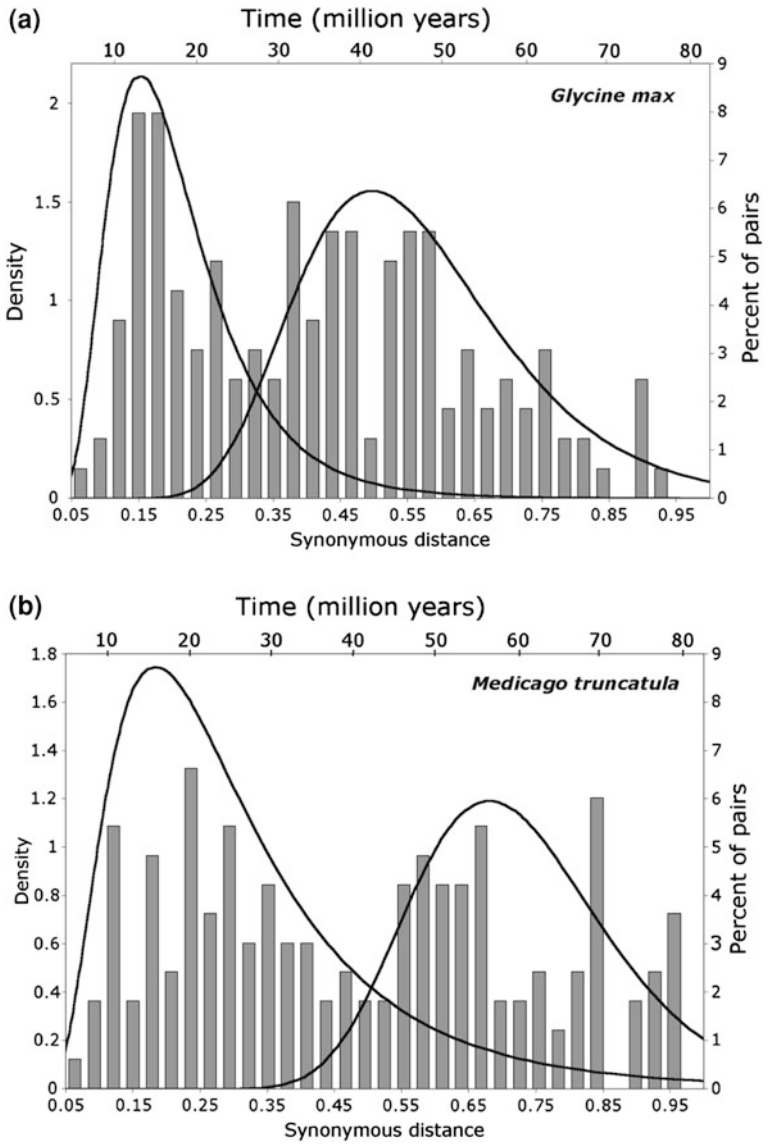

Fig. 9.2 Evidence for polyploidy in the genomes of: **a** *Glycine max* and **b** *Medicago truncatula*. The graphs plot the number of pairs of paralogous sequences ("density" or "percent of pairs") versus binned K_s ("synonymous distances") classes. Pairs with very low divergence (produced by ongoing recent duplications) were not plotted. Curves were fit to the binned divergence data and are interpreted as groups of genes duplicated simultaneously in large-scale genomic events such as polyploidy; modes of peaks provide a maximum age for allopolyploid events (Doyle and Egan 2010). Divergence time was estimated from synonymous distances using standard clock methods; note the different estimated ages (modes of curves) for the older event in the two species. Data are from Schleueter et al. (2004), who used expressed sequence tags (ESTs). Figure courtesy of Jessica Schlueter (UNC-Charlotte)

sister clades that comprise nearly 9,000 species—around 45 % of all legumes and 63 % of papilionoids—was polyploid.

Subsequently, Bertioli et al. (2009) studied *Arachis* (peanut) and showed that its genome also shows evidence of the >54 MYA event, indicating that the large dalbergioid clade is also fundamentally polyploid. Unpublished information reported by McClean (personal communication) at the 2009 International Conference of Legume Genetics and Genomics showed that *Lupinus*, and hence the genistoid clade, also shares this WGD. Thus, all of the lineages of the main radiation of the papilionoids share a polyploid ancestor.

The possibility that all legumes share this polyploidy event remained tenable until transcriptomic data from the caesalpinioid genus, *Chamaecrista*, became available (Singer et al. 2009). Cannon et al. (2010) produced and analyzed over 1,200 gene phylogenies from these data, which overwhelmingly supported the conclusion that the *Chamaecrista* genome shows no evidence of any polyploidy event subsequent to the prerosid triplication, and notably lacks the WGD found in core papilionoids (all but the early diverging lineages in Fig. 9.1). *Chamaecrista* belongs to the MCC clade, which is sister to the papilionoid clade. Therefore, the absence of the WGD in *Chamaecrista* indicates that the common ancestor of the MCC clade and papilionoids was not polyploid, placing the WGD within papilionoids (Fig. 9.1). Whether the WGD took place in the papilionoid common ancestor is still unknown, because the lineages that comprise the paraphyletic grade lacking the putative molecular synapomorphy for the major papilionoid radiation (chloroplast genome 50 kb inversion) remain to be sampled.

Thus, it is possible that this core papilionoid WGD facilitated the radiation of the most species-rich lineage of legumes, comprising 69 % of the species (13,390/19,327) and 59 % (438/741) of the genera of the third largest family of flowering plants. This is the group that is more uniformly characterized by the eponymous legume fruit, by the bilaterally symmetric papilionoid flower, and by the ability to nodulate. The early diverging grade of papilionoids does contain some genera with papilionoid flowers and legume fruits, but many lineages in this part of the tree are characterized by unusual, nonpapilionaceous corollas and drupaceous or samaroid fruits (Pennington et al. 2000); this grade also contains nearly all of the papilionoid genera that do not nodulate (Doyle 2011).

9.3.3 Polyploidy and Nodulation in Legumes

The correspondence between nodulation and polyploidy in the family is interesting. Core papilionoids nearly all nodulate, but this is also true of Mimosoideae, and *Chamaecrista* is among a handful of caesalpinioids known to be able to form a nodulation symbiosis (Sprent 2009). It remains unclear whether there was a single origin of nodulation in the common ancestor of the papilionoid and MCC clades, followed by many losses of nodulation, or whether there were multiple origins of

nodulation in the MCC clade and an independent origin in the ancestor of the core papilionoids (Doyle 2011).

The demonstration that *Chamaecrista* not only lacks the core papilionoid WGD, but also does not show any genomic evidence of other polyploidy events, indicates that polyploidy is not a prerequisite for nodulation in legumes as a whole (Cannon et al. 2010). Thus, in a model of a single origin of nodulation in the family, polyploidy would have played no role (Fig. 9.3). At the other extreme, polyploidy could not have been involved in an origin of nodulation unique to *Chamaecrista*, nor would it have been essential for the origin of nodulation in a model where the symbiosis evolved in a common ancestor of *Chamaecrista* and other members of the MCC clade (e.g., Mimosoideae).

This is not to say, of course, that polyploidy was not important in the origin or evolution of nodulation in core papilionoids or in other nodulating taxa whose genomes have yet to be explored, such as mimosoids. In the case of papilionoids, it is possible that nodulation and the WGD will be found to coincide, either in the ancestor of the main radiation of core papilionoids or at the first papilionoid ancestor, but better phylogenetic resolution is required before this can be tested (Pennington et al. 2001). In either case, refinement of the nodulation symbiosis in taxa such as *Medicago* may well have been facilitated by the availability of homoeologues produced in the core papilionoid WGD (Young et al. 2011).

9.3.4 Harmonizing Chromosomal and Genomic Evolution

Whatever the original basic chromosome number of the family, the earliest radiation from the common ancestor does not seem to have involved polyploidy, despite Goldblatt's (1981, p. 457) conclusion that the "… initial phase of polyploidy is probably very ancient and may have taken place in the late Cretaceous, when major groups of Leguminosae began differentiating and were probably evolving rapidly into new habitats." Evidence against Goldblatt's view of polyploidy in the ancestor of the entire family is the absence of any trace of polyploidy in gene families of *Chamaecrista* other than the prerosid whole-genome triplication (WGT; Jaillon et al. 2007). This indicates that the ancestor of the MCC and older ancestors back to the prerosid WGT did not experience polyploid duplications. The uniformity of base chromosome numbers in the major radiations of the family—Cercideae, detarioids, MCC, and probably papilionoids (see above) suggest that relatively high numbers ($2n = 24$–28) are plesiomorphic in the family.

The most parsimonious hypothesis for papilionoids is that the earliest papilionoid ancestor was also $2n = 28$. Shortly after the divergence of this ancestor from the MCC ancestor, the papilionoids radiated rapidly, and polyploidy occurred nearly simultaneously, no later than the divergence of the first major lineage to diverge in the core clade (genistoids, e.g., *Lupinus*). This WGD did not leave evidence in higher chromosome numbers; to the contrary, polyploidy is associated with chromosome number reduction in core papilionoids (Fig. 9.1). Goldblatt

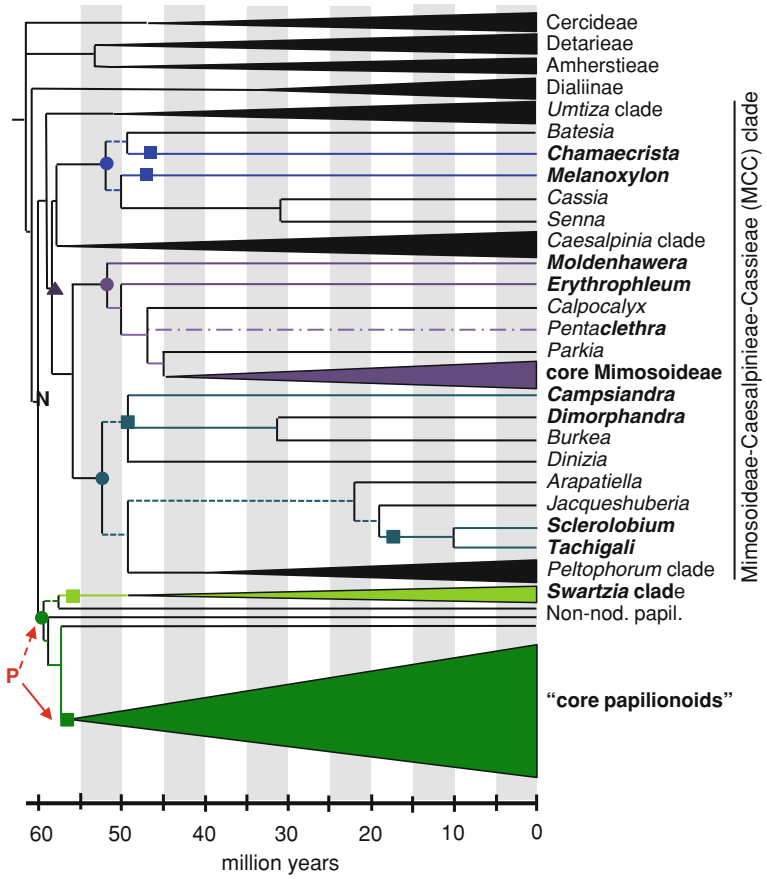

Fig. 9.3 Relationship between polyploidy and nodulation in *Leguminosae*. Genera known to nodulate are shown in bold face; *Pentaclethra* includes both nodulating species and species that apparently cannot nodulate. Possible origins of nodulation are indicated with symbols and colors. A single origin of nodulation for the entire family could have occurred in the common ancestor of the papilionoids and the MCC clade (indicated by "N"); this would have required many independent losses in the course of legume evolution. Independent origins within the MCC clade and Papilionoideae would require fewer losses. In the MCC clade, a single origin could have occurred in the common ancestor of all genera known to nodulate (*triangle*), or once in each major lineage of nodulating taxa (*circles*), or additional times within some clades (*squares*). Similarly, a single origin could be hypothesized for papilionoids (*green circle*), or twice (*squares*). The placement of the papilionoid polyploidy event (*red* "P") is indicated as in Fig. 9.1. Polyploidy is associated with nodulation only in the papilionoids and might not be directly associated there, given the uncertainty about the placement of both the polyploidy event and the origin(s) of nodulation. Figure adapted from Doyle (2011)

(1981, p. 457) notes that "the cytological history of legumes seems to involve some descending aneuploidy in every major evolutionary line but is most pronounced in Papilionoideae, in which most predominantly herbaceous tribes or

genera have achieved relatively low base numbers." The details of this process await elucidation of phylogenetic relationships of the early diverging papilionoid lineages, and sampling of these taxa for the presence of polyploidy. What is clear is that, at some point early in the history of Papilionoideae, chromosome numbers fell from as high as $n = 28$ to $n = 7$–11. This process could have begun in, or prior to, the common ancestor of the core papilionoids (Fig. 9.1). In any case, the initial reduction was rapid, taking place within 10 MY after the polyploid event, and perhaps within only 5 MY of the WGD. Detailed studies of synteny in the various core papilionoid lineages should help elucidate whether initial reorganization occurred in a common ancestor or was completely independent in the long-diverged major clades of the core papilionoids.

9.4 Polyploidy in Tribes and Genera of Legumes

Genomic and phylogenomic information currently is limited to the few genera discussed above. More information can be expected with the advent of new sequencing technologies, notably (at this writing) Illumina and 454. Twenty-five legume genera, representing all three subfamilies, are included in the 1,000 Transcriptomes project (1 kp, see http://www.onekp.com/angiosperms.html), but results from these species have not yet been analyzed (Steven Cannon, personal communication). Chromosome numbers provide a better guide at this level, but clearly should be interpreted with the caveat that high numbers are likely to indicate polyploidy, but low numbers cannot be assumed to be fundamentally diploid, given the potential for cryptic polyploidy, a phenomenon discussed further below.

Three sources of data were used for the following survey of polyploidy in legume clades: Goldblatt (1981); chromosome numbers provided for each genus listed in the tribal treatments in *Advances in Legume Systematics, Part* 1 (Polhill and Raven 1981); and the on-line Index of Plant Chromosome Numbers (IPCN; http://www.tropicos.org/projectwebportal.aspx?pagename=Home&projectid=9). IPCN was searched for all genera in Lewis et al. (2005) for which no data were available in Goldblatt (1981) or Polhill and Raven (1981), and for genera with polyploid counts, to identify infrageneric patterns of polyploidy, particularly when published phylogenies were available. For genera with evidence of polyploidy, BIOSIS was searched using the genus name in conjunction with either <polyploid*> and/or <phylogeny>. For some larger genera, IPCN was also consulted to search for polyploid counts published since 1981. There remain many gaps in our knowledge of legume chromosome numbers. Overall, only around 54 % of legume genera have counts reported (Table 9.1), and the percentage is far lower for tropical woody groups such as the caesalpinioid tribe Detarieae (30 %). This is perhaps not too surprising, given the size of the family, the large number of small genera, and the tropical distributions of many groups. It is also no doubt a commentary on how counting chromosomes has fallen from favor in this age of high-throughput science.

Table 9.1 Polyploidy in legume clades, based on chromosome numbers

Clade	Number of genera (species)[a]	Genera with chromosome counts	Number of genera with polyploidy	Percent genera with polyploidy (%)
Caesalpinioids[b]	171 (2251)	62	4	6
Mimosoideae	82 (3271)	39	10	26
Swartzieae + Sophoreae	40 (415)	15	2	13
Genistoids	83 (2354)	59	24	41
Dalbergioids	53 (1514)	32	11	34
Baphioids	7 (58)	6	1	17
Mirbelioids	32 (763)	22	5	23
Hologalegina: Robinioids + Loteae	34 (414)	23	9	39
Hologalegina: IRLC	54 (4351)	40	15	38
Millettioids: indigofereae	7 (768)	2	1	50
Millettioids: core Millettioids	56 (1104)	22	1	5
Millettioids: phaseoloids	112 (2064)	71	12	17
Total	731	393	95	24

[a] *Source*: Lewis et al. (2005)

[b] Summation of the following monophyletic groups: Cercideae, 12 genera total, 2 of 6 genera with chromosome counts have reports of polyploidy, 33 % (12, 2/6, 33 %); Dialiinae (17, 0/7, 0 %); Detarieae (82, 2/25, 8 %); MCC clade minus mimosoids (59, 0/24, 0 %)

Goldblatt (1981) made a distinction among genera that are exclusively polyploid relative to genera in the same tribe, and genera that include species with both "diploid" and "polyploid" chromosome numbers. In light of our current understanding of polyploidy, this is an artificial distinction, but exclusively polyploid genera are perhaps worth noting, because they represent lineages where polyploids may have replaced their diploid progenitors entirely. Such lineages would constitute evidence of polyploid "success" (e.g., Mayrose et al. 2011) in measures of diversity a million years from now.

The results of this survey show that polyploidy, as inferred solely from chromosome numbers, occurs in nearly a quarter of all legume genera, but varies widely in frequency among different lineages (Table 9.1). As Goldblatt (1981) noted, polyploidy is rare in woody, tropical groups such as caesalpinioids and early diverging papilionoid lineages.

9.4.1 Caesalpinioids and Mimosoideae

9.4.1.1 Clades of the Caesalpinioid Grade, Excluding the MCC Clade

Goldblatt (1981) stated that polyploidy (assuming a basic diploid number of $2n = 28$) is uncommon in caesalpinioid groups. As noted above, unpublished

genome size data do not support the hypothesis that *Bauhinia* (commonly $2n = 28$) is tetraploid relative to *Cercis* ($2n = 14$). However, this is negative evidence, and given the prevalence of genome downsizing (Leitch and Bennett 2004) in polyploids, it remains possible that *Bauhinia* (along with *Adenolobus* and *Griffonia*) is polyploid. More recent polyploidy occurs in the group, with *Tylosema* having $2n = 52$; *Tylosema* is nested within *Bauhinia* s. l. (Sinou et al. 2009). The large Detarieae s.l. clade is overwhelmingly $2n = 24$. The two detarioid genera having higher chromosome numbers (*Hardwickia*, $2n = 34$; *Colophospermum*, $2n = 36$) are strongly supported as sisters within the *Prioria* clade of Bruneau et al. (2008); they could represent independent aneuploid reduction from a polyploid ancestor. Goldblatt (1981) mentioned polyploidy in *Anthonotha* ($2n = 24$, 28, 72), but only $2n = 24$ and 28 are listed by Cowan and Polhill (1981), and no counts are listed in IPCN. All known counts from the Dialiinae clade are $2n = 24$ or 28.

9.4.1.2 The MCC Clade

Chromosome numbers of the caesalpinioid members of the MCC clade range from $2n = 20$–28, with the exception of *Chamaecrista*, in which numbers of $2n = 14$, 16, and 28 occur. Goldblatt (1981) raised the possibility that low chromosome numbers in this genus are not ancestral, but instead represent aneuploid reduction from ancestral $x = 14$ species. This makes good sense given the prevalence of $2n = 28$ counts throughout much of the MCC clade. A recent molecular phylogenetic analysis of *Chamaecrista* (Torres et al. 2011) supported the hypothesis that the $2n = 14$ species of sect. *Xerocalyx* form a monophyletic group nested within species having higher chromosome numbers. *Chamaecrista* is a genus of considerable interest as a potential model for nonpapilionoid legumes (Singer et al. 2009), making it an attractive system for exploring chromosome evolution in the caesalpinioids.

Mimosoideae comprise a monophyletic group embedded in the MCC clade, and the subfamily is dominated by taxa with $n = 13$. Goldblatt (1981) listed only three genera with base numbers higher than $n = 14$: *Schleinitzia* ($2n = 52$, 54), *Leucaena* ($2n = 52$, 56, 104, 112), and *Dichrostachys* ($2n = 50$, 56). These genera are all members of tribe Mimoseae and are relatively closely related within that tribe (Lewis et al. 2005), with the former two being members of the same clade and *Dichrostachys* being part of a sister clade (Luckow et al. 2003). However, *Schleinitzia* and *Leucaena* are not sisters within their clade (Hughes et al. 2003; Luckow et al. 2005), suggesting that polyploidy has originated independently in each case.

Leucaena itself has been fertile ground for systematic investigation. Boff and Schifino-Wittmann (2003) concluded that its species are segmental paleopolyploids. A series of studies has built a strong foundation for understanding the complex history of hybridization and polyploidy in the genus, and the impact of these phenomena on characters such as nrDNA ITS pseudogene evolution, and

their role in domestication (Hughes et al. 2002, 2007; Govindarajulu et al. 2011a, b). Govindarajulu et al. (2011b) concluded that "… a comprehensive picture of the complex evolutionary dynamics of polyploidy in *Leucaena* is emerging. This includes paleotetraploidization, diploidization of the last common ancestor to *Leucaena*, allopatric divergence among diploids, and recent allopolyploid origins for tetraploid species likely associated with human translocation of seed."

Acacia (sens. lat.) is reported to have $2n = 26$, 52, 76, and 104, though the majority of its species are diploid (Gallagher et al. 2011). Polyploidy has not been a focus of recent phylogenetic analyses (e.g., Brown et al. 2010; Murphy et al. 2010). Similarly, phylogenetic studies of *Prosopis* ($2n = 28$, 52, 56) or *Prosopidastrum* ($2n = 28$, 56) do not discuss polyploidy (e.g., Bessega et al. 2006; Catalano et al. 2008). No phylogenetic studies appear to have addressed polyploidy in *Neptunia* ($2n = 28$, 36, 54, 56, 72, 78), though Pandit et al. (2006) note that *N. plena*, an invasive species in Singapore, is a polyploid ($2n = 72$). No studies appear to exist on polyploidy and phylogeny of *Inga* ($2n = 26$, 52; the latter reported by Hanson 1995), *Albizia* ($2n = 26$, c. 78), or *Calliandra* ($2n = 16$, 22, 32, 44).

Mimosa ($2n = 24$, 26, 28, 40, 52) is a genus of around 500 species; a second genus whose species vary in ploidy, *Schrankia* ($2n = 16$, 22, 24, 26, 52), is deeply nested within *Mimosa* (Simon et al. 2011). Dahmer et al. (2011) concluded that the phylogenetic pattern "… suggests that duplication of chromosome numbers evolved several times in the genus and that polyploidy is not restricted to any particular clade within *Mimosa*. On the contrary, it seems that polyploids arose independently from ancestors with lower ploidy levels and are present in divergent lineages in the genus." Seijo and Fernandez (2001) reported chromosome numbers from the southern extreme of the range and discovered polyploidy within *M. balansae*. Chromosomal and morphological studies by Morales et al. (2010) clarified relationships in the *M. debilis-M. nuda* complex, demonstrating that hybridization and polyploidy are responsible for taxonomic complexity in the group.

9.4.2 Papilionoideae

Relatively few papilionoid genera appear to be exclusively polyploid based on chromosome number. As noted above, the early diverging papilionoid lineages have relatively high numbers, like the caesalpinioid and mimosoid groups. *Ateleia* (Swartzieae) is $2n = 40$, presumably representing a second polyploidy event followed by aneuploid reduction. Goldblatt listed *Dipteryx* (Dipterygeae) as being a polyploid genus but with a questionable count of $2n = 32$; this number was not reported in the treatment of the tribe by Polhill (1981a), nor is a count for the genus listed in IPCN.

9.4.2.1 Genistoids

The genistoid clade, which is weakly supported as sister to the remaining core papilionoids (Fig. 9.1), is one of the most complex groups with respect to polyploidy, and detailed discussion is beyond the scope of this review. The frequency of polyploidy in the genistoid clade is the highest for any well-sampled group of legumes (Table 9.1). Cusma-Velari and Feoli-Chiapella (2009) discussed cytology in "so-called 'primitive' genera of Genisteae" in light of molecular phylogenetic data. Genistoids clearly have a base number of $x = 9$ (Goldblatt 1981), with $2n = 18$ being common in most of its tribes.

Sophora s.l. has been divided into several segregates that vary in chromosome number. *Sophora* s.s. is part of the genistoid clade and is $x = 9$. Boatwright and van Wyk (2011) reported on the relationships of several of these based on nrDNA ITS sequences. They focused on the placement of the South African species, *S. ihambanensis*, which is polyploid ($2n = 36$); in their tree it is sister to *S. tomentosa*, a diploid, but they do not discuss origins of the polyploid. A count of $2n = 18$ is common in *Sophora* s.l., and several additional species are polyploids with $2n = 36$ (*S. alopecuroides, S. pachycarpa*, and *S. songarica*); *S. leachiana* is listed by ICPN as having $2n = 36$ and $2n = 54$ cytotypes. The small segregate, *Calia*, has $2n = 18$ and may be sister to the entire genistoid clade. The remainder of *Sophora* s.l. comprises $2n = 28$ species transferred to *Styphnolobium* in the early diverging papilionoid grade.

In Thermopsideae, *Thermopsis* has both diploid and polyploid species ($2n = 18, 36$). In Podalyrieae, two genera are exclusively polyploid: *Virgilia* ($2n = 54$) and *Cyclopia* ($2n = 36$); they are not supported as sisters in Boatwright et al. (2008). Crotalarieae are sister to Genisteae and include the exclusively polyploid *Buchenroedera* ($2n = 28$; Van Wyk and Schutte 1988), as well as polyploids within *Crotalaria* ($2n = 14, 16, 32$) and *Lotononis* ($2n = 18, 28, 36$).

Genisteae are by far the most cytologically complex group in the entire Leguminosae. Even genera with low numbers may be polyploid, such as *Anarthrophyllum* ($2n = 24$; Goldblatt 1981) and *Dichilus* ($2n = 28$). These genera, along with the polyploid *Polhillia* ($2n = 32$) and complex *Melolobium* ($2n = 18, 32$), were once placed in Crotalarieae. It is in the core Genisteae that polyploidy and aneuploidy have run rampant. The group includes *Argyrolobium* ($2n = 24, 26, 30, 32, 48$), *Adenocarpus* ($2n = 26, 46, 48, 52, 54$), *Laburnum* ($2n = 48, 50$), *Cytisophyllum* ($2n = 50, 52$), *Petteria* ($2n = 52$), *Argyrocytisus* ($2n = 50$), *Chamaecytisus* ($2n = 48, 96$), *Cytisus* ($2n = 22, 24, 46, 48, 92, 96$), *Calicotome* ($2n = 24, 48, 50$), *Erinacea* ($2n = 52$), *Spartium* ($2n = 48, 52, 54, 56$), *Retama* ($2n = 48$), *Genista* ($2n = 18, 22, 24, 26, 28, 30, 32, 36, 40, 42, 44, 46, 48, 50, 52, 56, 72, 80, 96$), *Echinospartium* ($2n = 44, 52$), *Stauracanthus* ($2n = 28, 48$, ca. 128), *Ulex* ($2n = 32, 64, 80, 96$), and *Lupinus* ($2n = 24, 30, 32, 34, 36, 38, 40, 42, 48, 50, 52, 96$).

Bisby (1981) considered the plethora of chromosome numbers attributed to individual genera to be partly a real phenomenon, but also due to difficulties in obtaining reliable counts given the small size and high numbers of chromosomes,

combined with the taxonomic complexity of the groups. Some of the taxonomic complexity is being resolved by molecular phylogenetic studies focused on *Cytisus* and *Genista* (Cubas et al. 2002; Pardo et al. 2004), but these studies do not discuss polyploidy per se. For *Lupinus*, three studies have documented the rapid radiation of the genus in its New World center of diversity (Hughes and Eastwood 2006; Drummond 2008; Drummond et al. 2012), and another phylogenetic study focused on the Old World species (Ainouche et al. 2004). Drummond (2008) noted that, "While a complex history of aneuploidy ($2n = 32, 34, 36, 38, 40, 42, 50, 52$) in the Old World and eastern New World … implies that allopolyploidy may have provided an additional mechanism for reproductive isolation and evolutionary divergence, chromosomal numbers in the western New World species ($2n = 48$ with occasional autopolyploids of $2n = 96$) are relatively stable." It is this western group that has radiated explosively, presumably driven by ecology and not due to polyploidy per se (Drummond 2008). Conterato and Schifino-Wittmann (2006) described chromosome numbers and meiotic behavior in diploid and polyploid American lupines, and noted consistencies with phylogenetic relationships in the genus.

The placement of polyploid former Crotalarieae in the same clade with core Genisteae may lend support to the idea that polyploidy arose early in the entire clade, as suggested by Goldblatt (1981), Lavin et al. (2005) dated the common ancestor of Crotalarieae and Genisteae at around 41 MYA. On the other hand, Goldblatt also noted (1981, p. 452) that "basic numbers for these genera (*Genista*, *Ulex*, *Cytisus*) are however in the diploid range and a basic number of $x = 12$ for the group as a whole and for several genera has been suggested …". Genomic data for members of Genisteae should eventually allow the determination of the number and relative timing of polyploid events in the group.

9.4.2.2 Dalbergioids

The dalbergioid s.l. clade is split into two major subclades, Amorpheae and a second clade comprising Adesmieae, Aeschynomeneae, and many members of the polyphyletic Dalbergieae (Lewis et al. 2005). The entire dalbergioid clade is dominated by $2n = 20$ species. Within Amorpheae, polyploidy occurs in genera from each of the major subclades described by McMahon (2005). In the daleoid clade, *Dalea* has $2n = 14$, 16, 28, and 42. Spellenberg (1981) hypothesized that tetraploids and hexaploids of *D. formosa* ($2n = 28$, 42) were autopolyploids derived from the diploid ($2n = 14$) cytotype. In the amorphoid clade, *Amorpha* includes both diploids and polyploids ($2n = 20$, 40), all native to the New World. The widespread *A. fruticosa* is exclusively polyploid and morphologically complex (Wilbur 1975). It has become an invasive weed in Europe (e.g., Hulina 2010), illustrating a common feature of polyploidy (e.g., Pandit et al. 2011; te Beest et al. 2011). Its relationships to other members of the genus appear to be complex, sharing chloroplast haplotypes with different sympatric diploids across its range (Straub and Doyle, unpublished data). Studies of the *A. georgiana* complex

identified mixed populations of diploids and polyploids in what had been assumed to be an exclusively diploid species; these included an apparent allopolyploid between *A. georgiana* and *A. herbacea* (Straub and Doyle 2009). Straub (unpublished data) has identified additional polyploid species in the genus and hypothesized their origins.

The core dalbergioid clade is split into the small *Adesmia* clade (six genera) and the much larger clade comprising the *Dalbergia* and *Pterocarpus* sister clades (Lewis et al. 2005). Polyploidy occurs in all three clades. In the *Adesmia* clade, *Adesmia* includes both diploids and polyploids ($2n = 20, 40$), and *Amicia* is exclusively polyploid ($2n = 38$).

In the *Dalbergia* clade, *Smithia* ($2n = 38$) is exclusively polyploid and is considered closely related to *Kotschya* (Lewis et al. 2005), a genus that includes species with chromosome numbers indicative of polyploidy and aneuploidy ($2n = 28, 30, 36, 40$). These two genera are grouped with *Aeschynomene* species (Lavin et al. 2001), a genus that also includes diploids and polyploids ($2n = 18, 20, 40$). Another dalbergioid-clade genus, *Ormocarpum* ($2n = 24, 26$), was not listed in Goldblatt's discussion of polyploid genera, but could potentially be a cryptic polyploid with aneuploid reduction. Information on chromosome numbers of other members of the *Ormocarpum* group (Thulin and Lavin 2001) would be useful in addressing this issue.

The *Pterocarpus* clade also includes several genera with both diploids (including presumed aneuploids) and polyploids scattered among its subclades: *Platymiscium* ($2n = 16, 18, 20, 32$), *Pterocarpus* ($2n = 22, 24, 44$), *Geoffroea* ($2n = 20, 60$), and *Arachis* ($2n = 20, 40$). *Arachis* includes the tetraploid peanut or groundnut (*A. hypogaea*), as well as three other tetraploid species, one of which (*A. glabrata*) is a tropical forage crop. Peanut is hypothesized to be an allopolyploid derived from A- and B-genome species (e.g., Burow et al. 2009). Seijo et al. (2007) provide a useful summary of hypotheses concerning the origin (or origins) of peanut; controversy exists concerning such issues as the exact progenitor species of both homoeologous genomes, mode and number of origins, and whether there was subsequent introgression from wild species into the cultigen. They identified likely diploid progenitors of *A. hypogaea* using GISH and studied meiotic behavior of two other tetraploids (Ortiz et al. 2011) and a spontaneous autotriploid of *A. pintoi* (Lavia et al. 2011).

9.4.2.3 Baphioids

This small group appears to be interesting from the standpoint of polyploidy. Chromosome numbers are known from six of its seven genera. Of these, four are listed as $2n = 22$, one (*Dalhousiea*) is $2n = 44$, and *Baphia* was reported in Polhill and Raven (1981) to have both numbers, though no reports for any of the 47 species of the genus exists in IPCN.

9.4.2.4 Mirbelioids

Polyploidy in the mirbeliod clade (23 %) is close to the average for the whole family (Table 9.1). *Isotropis* ($2n = 16, 18, 32$) is sister to the large "*Pultenaea* s.l. group" in Orthia et al. (2005), which includes *Oxylobium* ($2n = 16$). Chandler et al. (2001) sank both *Brachysema* ($2n = 16, 32$) and the monotypic *Jansonia* ($2n = 32$) in *Gastrolobium*, previously a genus with only $2n = 16$ species. Chandler et al. (2001) placed the single sampled species of *Jansonia* sister to *Brachysema celsianum* (not listed in IPCN), in a clade that also included *B. praemorsum*; that species is a diploid at $2n = 16$, as is at least one species in the sister clade, *Nemcia coriacea*. Thus, it is likely that polyploidy has arisen more than once just within *Gastrolobium* s.l., and another time in *Isotropis*. Among several "strongly paraphyletic" *Pultenaea* s.l. genera, nearly all of which are $2n = 16$, are two genera with polyploidy: *Pultenaea* s.s. ($2n = 8, 12, 14, 16, 18, 27, 32$) and *Chorizema* ($2n = 16, 32$). Sorting out how the various chromosome numbers in *Pultenaea* s.s. are related will be of considerable interest but will require more complete phylogenies than appear to be available at present. Of the 10 *Chorizema* species (out of 27 in the genus) listed in IPCN, polyploidy is only reported from *C. aciculare*, which has both diploid and tetraploid cytotypes.

Smaller genera in *Pultenaea* s.l. with known polyploidy are *Eutaxia* ($2n = 16, 32$) and *Dillwynia* ($2n = 14, 21, 28$), which are in the same weakly supported clade in Orthia et al. (2005). One of the two *Dillwynia* species (*D. phylicoides*) included in the Orthia et al. (2005) tree has both diploid and tetraploid cytotypes listed in IPCN.

9.4.2.5 Hologalegina

The Hologalegina clade includes robinioids and the Inverted Repeat Loss Clade (IRLC; named for the absence of a prominent feature of the chloroplast genome). Goldblatt (1981) concluded that "Species polyploidy is overwhelmingly concentrated in temperate to cool Eurasia" so it is not surprising that this largest clade of legumes, which includes many temperate genera, has a higher frequency of polyploidy than the family average, nearly 40 % in both of its major subclades (Table 9.1).

The robinioids comprise two clades: one with *Sesbania* plus Loteae (including Coronilleae), the other being Robinieae (s.s.). Diploid chromosome numbers vary considerably within Robinieae s.s., and Goldblatt (1981) suggested several possible base numbers, the most likely being $x = 10$ or 11. There is one apparently exclusively polyploid genus, *Poissonia*, which Goldblatt (1989) counted as ($2n =$ ca. 32). Although only numbers of $2n = 10$ and 11 were given for *Robinia* in Polhill and Sousa (1981), more recent counts of $2n = 30$ for *R. hispida* suggest polyploidy within this small genus.

Even with the limited sampling of Loteae in Wojciechowski et al. (2004), it is clear that numerous problems exist with the genera as circumscribed, notably that

Anthyllis ($2n = 10, 12, 14, 16, 28$) and *Ornithopus* ($2n = 14$) are nested within *Lotus* ($2n = 10, 12, 14, 24, 28$). Other genera with known polyploidy are *Coronilla* ($2n = 12, 20, 24$); *Hippocrepis* ($2n = 14, 28$); *Dorycnium* ($2n = 14, 28$; both cytotypes in *D. axilliflorum*), and *Scorpiurus* (*S. muricatus* has $2n = 14, 16, 28$; other species are $2n = 14$ or 28). Degtjareva et al. (2006) provided phylogenetic hypotheses for *Lotus*, with sampling of other genera, but did not discuss polyploidy. Rosello and Castro (2008) discussed polyploidy in the flora of the Balearic Isles, among which are species of *Anthyllis* and *Coronilla*.

The genus *Lotus* includes the genomic model legume, *L. japonicus* (Sato et al. 2008), which is part of the *L. corniculatus* (birdsfoot trefoil) polyploid complex. Grant and Small (1996) summarized many studies of this complex and concluded that it was a fertile topic for further study, particularly to identify the diploid progenitors of *L. corniculatus* itself, which they considered to be an allopolyploid. Gauthier et al. (1998a, b) discussed evolutionary patterns in the *L. corniculatus*/*L. alpinus* polyploid complex in the Alps of Europe; they described morphological and genetic consequences of autopolyploidy in *L. alpinus* and suggested introgression at the tetraploid level between it and *L. corniculatus*.

The majority of genera and species in the IRLC clade belong to two sister clades in Wojciechowski et al. (2004): one includes the Astragalean clade (*Astragalus* and allies) and Hedysareae, and the second includes the Vicioid clade. The remainder of the IRLC phylogeny, moving successively further from these clades, consists of a clade with *Wisteria* ($2n = 16$) and one species of *Callerya*, followed by a clade with *Glycyrrhiza* ($2n = 16$) and a second species of *Callerya*.

The Astragalean clade has extensive polyploidy. Perhaps most striking is the clade that includes the New Zealand endemic tribe Carmichaelieae plus the Australian *Swainsona* and an additional New Zealand genus, *Montigera*, all of which are polyploid (Wagstaff et al. 1999). The only exclusively polyploid genera that Goldblatt (1981) listed for the IRLC clade belong to this clade: *Swainsona* ($2n = 32$); *Clianthus* ($2n = 32$); *Carmichaelia* ($2n = 32$, ca. 96), *Chordospartium* ($2n = 32$); and *Corallospartium* ($2n = 32$), with the latter two subsumed in *Carmichaelia* in Lewis et al. (2005). Wagstaff et al. (1999) concluded that the New Zealand radiation was recent, involved an already polyploid colonizer, and may have been associated with orogeny and glaciation.

Elsewhere in the Astragalean clade are two large genera with extensive polyploidy and aneuploidy, *Oxytropis* (300–400 species: $2n = 16, 32, 48, 64, 96$) and *Astragalus* (ca. 2500 species: $2n = 16, 22, 24, 26, 28, 32, 44, 48, 64$). In *Astragalus*, polyploidy appears to be more common among Old World than among New World species. Wojciechowski (2005) summarized phylogenetic results for this huge genus, showing that aneuploid species form a clade. According to Gohil and Ashraf (2008), polyploidy occurs in around only 17 % of *Astragalus* species. However, *Astragalus* is one of the largest genera of plants with as many as 2500 species (Lewis et al. 2005), so if this percentage is correct, then there are over 400 polyploid species in the genus. There does not seem to be a comprehensive phylogeny that discusses origins of polyploidy in *Oxytropis*. However, a series of papers describe autopolyploidy, including multiple autopolyploid origins, in

Oxytropis chankaensis (e.g., Artyukova et al. 2011). Jorgensen et al. (2003) suggested "a scenario of multiple formations of polyploids, possibly including hybridization among diverged Alaskan *Oxytropis* populations."

Within the Hedysareae, phylogenetic studies of *Caragana* ($2n = 16, 24, 32, 48$) suggest that polyploidy is confined to a single group of species, and that triploids, tetraploids, and hexaploids may all be autopolyploid in origin (Zhang et al. 2009). Neither *Hedysarum* ($2n = 14, 16, 48$) nor *Onobrychis* ($2n = 14, 16\ 28, 32$) appears to be monophyletic on the basis of nrDNA ITS phylogenies (Ahangarian et al. 2007). Hejazi et al. (2010) discussed karyotypic evolution in diploid and polyploid species but did not provide a phylogenetic context or identify origins of polyploids. Based on IPCN listings, most polyploidy reported for *Hedysarum* in IPCN appears to involve multiple cytotypes within a single species (e.g., *H. arcticum* and *H. hedysaroides*, both $2n = 14, 28$; *H. dasycarpum* and *H. mackenziei*, both $2n = 16, 32$; *H. gmelinii*, $2n = 16, 28, 56$), but some species are exclusively polyploid (e.g., *H. inundatum*, $2n = 28$). Similarly, in *Onobrychis* there is variation within species (e.g., *O. aequidentata*, $2n = 14, 16, 28$; *O. arenaria*, *O. bobrovii*, $2n = 14, 28$; *O. crista-galli*, $2n = 16, 32$), with other species being exclusively polyploid (e.g., *O. biebersteinii*, *O. cyri*, *O. dielsii*, all $2n = 28$). There appear to be no phylogenies or evolutionary studies of polyploidy in *Alhagi* ($2n = 16, 28$; the latter number is not listed in IPCN).

The majority of the vicioid clade forms two sister clades, one with Fabeae (Vicieae) plus *Trifolium*, and a second comprising the remaining Trifolieae genera; polyploidy occurs in both clades. Successive sisters to this clade (*Cicer*, *Galega*, and *Parochetus*) are all $2n = 16$.

Vicia includes both diploids and tetraploids ($2n = 10, 12, 14, 24, 28$), but polyploidy was considered rare in the genus by Kupicha (1981). Indeed, *Vicia* is best known for its extensive non-polyploid variation in genome size (Chooi 1971; Neumann et al. 2006), which shows only weak correlation with ploidy: diploid ($2n = 14$) *V. peregrina* has a genome size of 9.48 pg/1C, double that of tetraploid ($2n = 24$) *V. tenuifolia* (4.73 pg/1C). Endo et al. (2008) did not discuss either issue in their phylogenetic study of New Wold *Vicia*. Travnicek et al. (2010) studied the history of polyploidy in *V. cracca*, determining the ploidy of over 6,500 individuals at more than 250 localities in Europe and mapping the distributions of diploids, triploids, and tetraploids; they noted the rarity of triploids, suggesting strong reproductive barriers between diploids and tetraploids.

Polyploidy is also noted to be rare in *Lathyrus* ($2n = 14, 28, 42$; Kupicha 1981). Gutierrez et al. (1994) hypothesized autopolyploid origins of *L. pratensis* and *L. palustris* from conspecific diploids, but an allopolyploid origin of *L. venosus* from two diploid species (*L. ochroleucus* and *L. palustris*). Only $2n = 14$ counts are listed for the closely related *Pisum* in IPCN, for which Kupicha (1981) listed polyploidy as "rare."

Turini et al. (2010) reconstructed nrDNA ITS and chloroplast phylogenies for 69 of the 86 species of *Ononis* ($2n = 16, 20, 30, 32, 60, 64$) and identified several well-supported clades. They concluded that, "Unfortunately, only limited information is available … on chromosome numbers to test support for these groups".

However, chromosome counts are available for nearly half of the species in their phylogeny in IPCN, and some conclusions can be drawn. For example, the clade that is strongly supported as sister to the remainder of the genus in their nrDNA ITS tree includes only polyploids (*O. tridentata* and *O. fruticosa* are both $2n = 30$; *O. rotundifolia* is $2n = 32$), suggesting that the genus as a whole could be polyploid. Only three species have low, potentially non-polyploid numbers in IPCN. These occur in different clades, and in two cases species with low numbers have higher numbers as well (*O. variegata*, $2n = 16, 30$; *O. ornithopodioides,* $2n = 20, 32$), raising the possibility that they are independent reductions from typical polyploid numbers. The exception, *O. adenotricha*, is only reported as $2n = 16$; its position varies between the nrDNA ITS and *trnL-F* trees of Turini et al. (2010), being sister to the *tridentata* clade in the *trnL-F* tree; however, this entire group is not resolved as sister to the remainder of the genus in that tree. Elsewhere in the genus, *O. spinosa* has multiple cytotypes ($2n = 30, 32, 60$), whereas *O. pendula* is only known at $2n = 64$. Kloda et al. (2008) studied patterns of genetic diversity in several diploid and polyploid species in England and concluded that gene flow was occurring within ploidy levels, but not between diploids and tetraploids.

Medicago includes the genomic model legume, *M. truncatula* (Young et al. 2011). Steele et al. (2010) provided a phylogeny for *Medicago* ($2n = 14, 16, 32, 48$), including multispecies sampling of its sister clade, which comprises the interdigitated species of the two paraphyletic genera *Melilotus* ($2n = 16, 24, 32$; though tetraploids are not reported in IPCN) and *Trigonella* ($2n = 16, 28, 32, 44$). Aneuploid change from $2n = 16$ to $2n = 14$ has occurred several times in *Medicago* (Steele et al. 2010). Polyploidy is concentrated in a clade that comprises most species of sect. *Medicago*, along with *M. arborea* (sect. *Dendrotelis*); an additional polyploid species, *M. scutellata*, occurs in the clade sister to this sect. *Medicago* clade. Rosato et al. (2008) used fluorescence in situ hybridization (FISH) to study relationships between polyploids and diploids in sect. *Dendrotelis*.

Some *Medicago* species are exclusively polyploid whereas others possess multiple cytotypes. The *M. sativa* complex, which includes cultivated autotetraploid alfalfa (*M. sativa* ssp. *sativa*) as well as other diploid ($2n = 16$) and autopolyploid ($2n = 32$) species and their hybrids, has been the focus of several recent studies (Sakiroglu et al. 2010; Havananda et al. 2010, 2011, and unpublished data). Two major autopolyploid pairs in the complex are: (1) *M. s. caerulea* and *M. s. sativa*, both with blue flowers and coiled pods, distinguishable by the larger size of the tetraploid (*M. s. sativa*) for several characters; and (2) *M. s. falcata*, a yellow-flowered taxon with falcate pods whose diploid and polyploid cytotypes are indistinguishable morphologically. Interestingly, although *M. s. sativa* and *M. s. caerulea* are undifferentiated for chloroplast haplotypes, the two cytotypes of *M. s. falcata* possess nearly mutually exclusive sets of haplotypes, with haplotypes in the tetraploid most likely derived by introgression from *M. prostrata*, a species from outside the complex (Havananda et al. 2011). Jenczewski et al. (1999) reported gene flow between wild and cultivated *M. sativa* populations; however, based on chloroplast data, there does not appear to be significant gene flow between blue- and yellow-flowered taxa in the complex either at the diploid or

tetraploid levels, despite the existence of morphologically intermediate hybrid subspecies (Havananda et al. 2011, and unpublished data). Much is known about the genetics of polyploidy in alfalfa, where unreduced gametes have received considerable study as a breeding tool (e.g., Bingham 1972; Veronesi et al. 1986; Tondini et al. 1993; Calderini and Mariani 1997).

Ellison et al. (2006) constructed a phylogeny of *Trifolium* ($2n = 10, 14, 16, 28, 32$) that included 218 of its ca. 255 species, as well as species from 11 genera of the vicioid clade. They showed that the genus is monophyletic; incongruence within the genus between nuclear and chloroplast markers suggests considerable hybridization. They also hypothesized a minimum of 19 shifts to aneuploidy and 22 instances of polyploidy from a base number of $2n = 16$. They identified the progenitors of two important species, both shown to be allopolyploids: the widespread weed, *T. dubium*, and the most commonly cultivated clover species, *T. repens* (Ellison et al. 2006).

9.4.2.6 Indigofereae

Schrire et al. (2009) provided a detailed phylogeny for this tribe, a monophyletic group that is sister to the millettioid clade. Schrire et al. (2009) did not comment on chromosomal variation or polyploidy, but numerous records are readily available in IPCN, and mapping these onto the phylogeny provides some insights into cytological evolution of the group.

The tribe is dominated by the very large genus *Indigofera* (ca. 700 species), which Goldblatt (1981) and Polhill (1981b) listed as having $2n = 14, 16, 32, 48$. The higher numbers thus would be interpreted as representing tetraploids and hexaploids. However, Frahm-Leliveld (1966), summarizing the cytotaxonomy of the tribe, cited two $x = 6$ species, *I. macrocalyx* ($2n = 12$) and *I. emarginella* ($2n = 24$), and concluded that "… the 48-chromosome Himalayan and East-Asiatic shrubby *Indigoferas* may not be hexaploids with base number $x = 8$, but octoploids in an $x = 6$ range." None of the species is listed in IPCN, but Reddy and Revathi (1993) reported $2n = 12$ for *I. anil*, confirming the presence of $x = 6$ in the genus.

The Schrire et al. (2009) phylogeny does not support the Frahm–Leliveld (1966) hypothesis. One of the two $2n = 12$ species, *I. macrocalyx*, is placed in the large Palaeotropical clade of Schrire et al. (2009) and is sister to a group of species that includes *I. pulchra* ($2n = 16$). All three sampled species with $2n = 48$ are in the Palaeotropical clade, but are placed nowhere near *I. macrocalyx*. In the Pantropical clade, *I. rhynchocarpa* ($2n = 16$) is sister to the clade that includes *I. emarginella*, which is on a long branch sister to several other species; the only other species counted from this subclade is also $2n = 16$. Thus, there is no evidence that $2n = 48$ species are derived from $x = 12$ species.

Tetraploids based on $x = 8$ are scattered throughout the phylogeny (Schrire et al. 2009), supporting the observation of Frahm-Leliveld (1966) that $2n = 32$ is common in the genus. In the Palaeotropical clade, *I. atriceps* ($2n = 32$) is in a

subclade that also includes diploids. In another subclade, *I. mysorensis* includes both $2n = 16$ and 32 cytotypes; other two members of its subclade are diploid. *Indigofera microcalyx*, in yet another subclade, is $2n = 32$; no other members of its subclade has been counted, but the only counts from its sister clade are diploid.

In the pantropical clade, a small subclade in Schrire et al. (2009) includes *I. koreana* ($2n = 32$), *I. grandiflora* ($2n = 32, 48$), *I. decora* ($2n = 48$ in Choi and Kim (1997) but not listed in IPCN), as well as *I. venulosa* (no count available) and *I. kirilowii* ($2n = 16$). Topologies differ between Schrire et al. (2009) and Choi and Kim (1997), who focused on this group of mostly Korean endemics. Choi and Kim (1997) listed *I. grandiflora* as $2n = 16$, and given this count their topology could suggest independent derivation of polyploidy in *I. koreana* (from *I. grandiflora*) and *I. decora* (from *I. venulosa* if it is diploid). An alternative explanation is a single derivation of polyploidy within this clade. Elsewhere in the pantropical clade, *I. heterantha* ($2n = 48$) is sister to *I. hebepetala* ($2n = 16$); the clade sister to these two species includes *I. amblyantha* ($2n = 48$) and *I. cassioides* ($2n = 16$). In a different subclade, *I. suffruticosa* is reported to have both $2n = 16$ and 32 cytotypes; the closest reported species to it is diploid. In the Tethyan clade, *I. sessiliflora* ($2n = 32$) is the only member of its subclade with a count in IPCN. *Indigofera hochstetteri* has both $2n = 16$ and 32 counts; its sister species, *I. arabica*, is diploid. *Indigofera angulosa* is $2n = 32$; no other species in its clade has counts in IPCN.

Thus, there appear to be no large clades composed exclusively of polyploids in *Indigofera*. Instead, as in other large legume genera, polyploidy is sporadic.

9.4.2.7 Millettioids

With the recognition that *Wisteria* and *Callerya* are part of the IRLC, and that *Cyclolobium* and *Poecilanthe* belong in the Brongniartieae, chromosome numbers in the Millettieae (Tephrosieae in Polhill and Raven (1981)) are mostly $2n = 20$ or 22, with $2n = 24$ in *Xeroderris*, though many genera have no reported counts in IPCN. Interestingly, *Xeroderris* is placed as sister to the remainder of the entire millettioid clade in Wojciechowski et al. (2004), suggesting that $2n = 20$ or 22 may be synapomorphic for the remainder of the millettioid clade (including phaseoloids; see below). Millettieae comprises the bulk of one of the two major millettioid clades (core millettioids), along with *Abrus* (Abreae), and much of the subtribe Diocleinae of tribe Phaseoleae. Both diploid and tetraploid cytotypes ($2n = 22, 44$) have been reported in three species of the ca. 40 IPCN records for the large (ca. 350 spp.) genus *Tephrosia* (e.g., Srivastav and Raina 1986). The low frequency of polyploidy in the core millettioid clade (5 %) is nearly identical to the frequency in caesalpinioids, both of which are largely woody, tropical groups.

The other large clade (phaseoloids) contains most of the tribe Phaseoleae as well as the tribes Desmodieae and Psoraleeae and is dominated by $2n = 20$ or 22 counts. Polyploidy is more frequent in the phaseoloid clade (17 %), but still less than half as common as in Hologalegina (Table 9.1). Within the phaseoloid clade,

chromosome numbers suggest that several genera are polyploid. The best known of these is *Glycine*, with around 30 species whose lowest chromosome numbers are $2n = 38$ and 40, in contrast to most of its phylogenetic neighbors (e.g., Doyle et al. 2003; Stefanovic et al. 2009) which are typical millettioids with $2n = 20$ or 22. As noted above, genomic data confirm the presence of two cycles of polyploidy in *G. max* (soybean) since the origin of the legumes. The more recent of these has resulted in homoeologous gene pairs that diverged around 10 MYA (Shoemaker et al. 2006; Egan and Doyle 2010), setting a maximum date for the polyploidy event, with the minimum date set by the earliest divergence of the various *Glycine* species around 5 MYA (Innes et al. 2008; Doyle and Egan 2010). Phylogenetic evidence is consistent either with autopolyploidy or with allopolyploidy from extinct species more closely related to one another than to any extant genera outside of *Glycine* (Straub et al. 2006). The presence of two classes of centromeric heterochromatin repeats suggests that *Glycine* could be an allopolyploid, with the two repeat types each derived from one of the diploid progenitor species (Gill et al. 2009). Such a hypothesis is difficult to test due to the extensive rearrangement of homoeologous segments in the soybean genome (Schmutz et al. 2010) and also requires complex patterns of concerted evolution among repeats on different chromosomes.

At least three other phaseoloid genera are likely to be exclusively polyploid based on chromosome number alone (Lackey 1981). In *Erythrina* (coral bean), all sampled species are $2n = 42$. The single count in IPCN for the small genus *Cologania* is $2n = 44$, and the monotypic *Teyleria* is also $2n = 44$ (Kumar and Hymowitz 1989). Goldblatt (1981) considered *Calopogonium*, with counts of $2n = 36$ and ca. 37 in *C. mucunoides*, to be a polyploid, presumably with aneuploid reduction from a base of $x = 10$; however, Gill and Husaini (1986) reported a count of $2n = 24$, which could suggest a more recent derivation of polyploidy within the genus. Similarly, counts of $2n = 28$—considered polyploid in *T. mollis* by Kumari and Bir (1990)—predominate in *Teramnus* species, though *T. labialis* is variously listed as $2n = 20$, 22, and 28. *Strongylodon* is also $2n = 28$.

Polyploidy appears to be rare within Phaseoleae genera. Even relatively large and well-studied genera such as *Rhynchosia* (ca. 230 species), *Phaseolus* (60–65 species), and *Vigna* (ca. 100 species) were reported in Polhill and Raven (1981) as being exclusively diploid, though Sen and Bhattacharya (1988) later reported a count of $2n = 44$ in *V. glabrescens*. Polyploidy has also been reported within species of *Amphicarpaea* and *Neonotonia* by Kumar and Hymowitz (1989; both $2n = 22$, 44). *Apios americana* includes both diploid and triploid cytotypes ($2n = 22$, 33); Joly and Bruneau (2004) reported multiple origins of autotriploidy and high heterozygosity in this species. *Glycine* not only is a relatively recent polyploid at the generic level (see above) but also includes several recently formed allopolyploid species whose genomic relationships to extant diploids have been worked out using molecular phylogenies (reviewed by Doyle et al. 2004), and which are the focus of physiological and transcriptomic studies (Coate and Doyle 2010; Ilut et al. (in press)).

Polyploidy occurs within at least one genus of Desmodieae, *Lespedeza*, which was listed in Polhill and Raven (1981) as $2n = 18, 20, 22, 36$. However, IPCN gives higher numbers, for example *L. bicolor* with both $2n = 22$ and 42 cytotypes, as well as *L. daurica* and *L. potaninii*, both exclusively $2n = 42$. Triploidy occurs in *Campylotropis polyantha* var. *leiocarpa* ($2n = 22, 33$) and possibly in the genus *Pseudarthria*, listed as $2n = 22, 26, 34$. Only diploid counts ($2n = 20, 22$) were reported by Ohashi et al. (1981) from the large (ca. 275 spp.) genus, *Desmodium*. However, additional counts are found in IPCN, both at the diploid ($2n = 24, 26$) and tetraploid levels, the latter in *D. styracifolium* ($2n = 42$) and *D. incanum* ($2n = 22, 44$).

9.5 Searching for Cryptic Polyploidy in the Phaseoloid Legumes

Clearly, all papilionoids are fundamentally polyploid, even those with low chromosome numbers. The tempo and mechanism(s) of chromosomal diploidization are unknown (Doyle et al. 2008; Soltis et al. 2010), and without that information it is difficult to estimate the prevalence of cryptic polyploidy. As noted above, consideration of the divergence times for major lineages suggests that the rate of chromosomal diploidization is rapid—likely 10 MY or less.

On the other hand, "polyploid" chromosome numbers have persisted for at least 5–10 MY in *Glycine* (Fig. 9.2). A cryptic polyploid papilionoid legume is a taxon that has experienced an additional polyploidy event subsequent to the ca. 50 MYA papilionoid WGD but has a low chromosome number typical of its clade. Thus, in the phaseoloid clade, cryptic polyploids would have chromosome numbers of $2n = 20$ or 22. Polyploids on the way to diploidization would have chromosome numbers between these numbers and $2n = 40-44$. As noted above, *Calopogonium* and *Teramnus* are candidates for this class; one perennial *Glycine* species with $2n = 38$ is likely at the first stages of this process.

We know from the paralog K_s profile of *Glycine* (Schleueter et al. 2004) that no additional polyploidy events took place between the two WGD episodes detectable in its genome. Therefore, we can infer that all of the ancestors of *Glycine* experienced only the papilionoid WGD; this includes the ancestors that form the backbone of the phaseoloid clade (Fig. 9.4), as well as the common ancestor of phaseoloids and Indigofereae, and also its common ancestor with the IRLC clade. Given these conditions, candidates for cryptic polyploidy include lineages that are connected to the phaseoloid backbone by branches longer than 5–10 MY. This includes several major groups, such as subtribes Phaseolinae and Cajaninae (Fig. 9.4). Initial sampling of one species of each lineage would provide information on another set of ancestors, and subsequent searches can then be focused on lineages connected to these ancestors by suitably long branches. This has now been done for *Cajanus cajan* (pigeonpea), which Varshney et al. (2011) have shown has no history of recent polyploidy. We are sampling other phaseoloids using 454

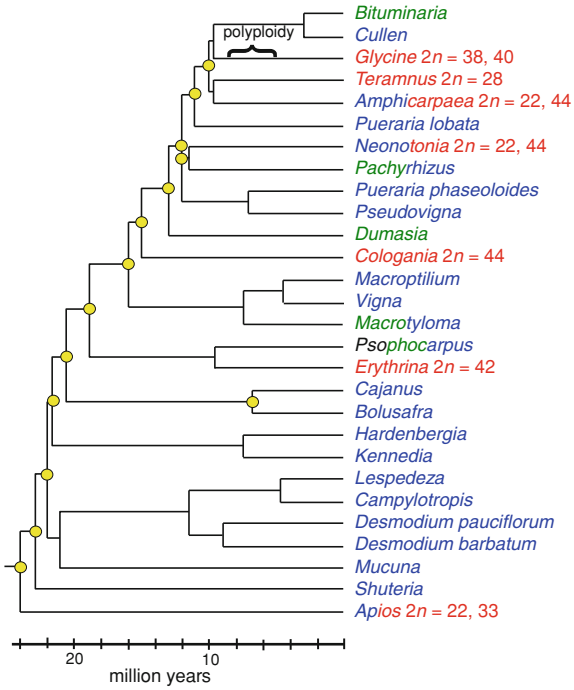

Fig. 9.4 Phylogeny and polyploidy in the phaseoloid clade. Topology and dates of the chronogram are taken from Stefanovic et al. (2009). Chromosome numbers of the species used in that study are color coded as follows: *Green*, $2n = 20$; *blue*, $2n = 22$; *black*, $2n = 18$; *red*, known or possible polyploid numbers, with the numbers shown following the taxon name. Species known to have multiple cytotypes are indicated by multiple colors corresponding to chromosome numbers listed above. The two numbers shown for *Glycine* are from different species, only one of which (*G. max*, $2n = 40$) was used in the Stefanovic et al. (2009) study. The range of dates for the polyploidy event in *Glycine* is indicated. *Yellow dots* indicate ancestral nodes that lacked any polyploidy event subsequent to the papilionoid WGD

transcriptome sequencing, including taxa with both low and high chromosome numbers; for the latter we wish to estimate maximum ages of polyploidy. Thus far we have not found examples of cryptic polyploidy, but have determined that polyploidy in *Erythrina* probably took place on roughly the same time scale as in *Glycine* (<10 MYA; Egan and Doyle, unpublished data).

9.6 Conclusions

Among the most persistent questions concerning polyploidy in plants are how successful the phenomenon is as an evolutionary mechanism. Is polyploidy a ticket to innovation, adaptation, invasiveness, survival in the face of global catastrophes,

or is it an evolutionary dead end … or both? Based on rates of polyploid formation and extinction in the phylogenetic record, Mayrose et al. (2011) conclude that "polyploidy is most often an evolutionary dead end, but the possibility remains that the expanded genomic potential of those polyploids that do persist drives long-term evolutionary success."

Legumes may illustrate both of these points. The most diverse and species-rich clade of this third largest family of flowering plants, the core papilionoids, is ancestrally polyploid. Clearly, the ancestor of this group of around 450 genera and 13,000 species, like the ancestor of seed plants and the ancestor of flowering plants (Jiao et al. 2011), was most emphatically not a "dead end." It remains to be determined whether there is a perfect correlation between the papilionoid polyploidy event and the origin of nodulation in core papilionoids, and it will take much more work to demonstrate that the two are causally related (Doyle 2011; Young et al. 2011). It is also clear that nodulation is not sufficient to explain the explosive radiation of papilionoid legumes, because other nodulating groups both in legumes and elsewhere in the rosids have not proliferated to the same extent as papilionoids (Doyle 2011).

Despite the obvious success of the core papilionoid lineage, the pattern of evolution within the core papilionoids suggests that polyploidy has not been a major feature in establishing new lineages, similar to the conclusion of Mayrose et al. (2011) for angiosperms generally. It is not that polyploidy is rare within the family—indeed, around a quarter of all legumes for which chromosome data are available have one or more species that are polyploid (Table 9.1). However, much of the polyploidy in the family occurs as single polyploid genera embedded within diploids, as scattered species within genera, or as multiple cytotypes within species. Two significant exceptions are the Genisteae, which may be entirely polyploid and within which nearly all genera show a propensity for polyploidy and aneuploidy, and the lineage that includes the IRLC tribe Carmichaelieae. The largest papilionoid genera, including *Astragalus*, are not fundamentally polyploid.

"Success" is a very ambiguous term and can be measured in many ways. Species with short evolutionary histories that have not been involved in subsequent speciation, yet have invaded extensive new territories and had major impact on the environment, certainly could be considered "successful." Many plant polyploids, including genera and species of legumes, fit this description. So does *Homo sapiens*.

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