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Apomixis in the Asteraceae: Diamonds in the Rough

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ABSTRACT

The Asteraceae is commonly listed, along with Poaceae and Rosaceae, as one of the principal families within which asexual reproduction by seed, i.e., apomixis, is prolific. A review of the literature indicates that naturally occurring apomixis is robustly indicated for 22 genera in seven tribes of Asteraceae (Lactuceae, Gnaphalieae, Astereae, Inuleae, Heliantheae, Madieae, and Eupatorieae), all but one of which occurs in the subfamily Asteroideae. Apomixis has been proposed for an additional 46 genera. However, consideration of the evidence indicates that the trait is contra-indicated for 30 of these cases in which developmental abnormalities or components of apomixis are recorded for otherwise sexual taxa. Accumulation and perpetuation of these reports through generations of reviews has inflated the actual number of genera in which apomictic reproduction occurs in the family. Data are strongly indicative or equivocal for effective apomixis for the remaining 16 genera, but thorough documentation is wanting. Our state of knowledge of apomixis in the Asteraceae is generally poor. Interpreting the phylogenetic distribution and evolution of the trait in the family will require systematic effort involving cytological documentation and genetic analysis of reproduction for many candidate genera.

Keywords: apomictic complex, apospory, diplospory, evolution, polyploidy

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INTRODUCTION

Apomixis is arguably one of the most poorly understood and under appreciated traits in flowering plants. Here the term apomixis, which has been variously defined in the past, is used to denote asexual reproduction by seed and is thus synonymous with the term agamospermy (Nogler 1984; Koltunow 1993; Savidan 2000). Because apomixis is a modification of normal sexual reproduction, full comprehension of the trait involves not only detailed understanding of the centrality of the alternation of generations in plant reproduction, but also of how disruption of the sexual pro-

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Invited Review

cesses can yield unreduced spores, unreduced female gametophytes, unreduced eggs, and parthenogenetic embryos that constitute the essence of apomictic reproduction. The objective of this review is to outline the modes of apomictic reproduction and to investigate the state of knowledge regarding the incidence and phylogenetic distribution of apomixis in the largest flowering plant family, the Asteraceae.

Apomixis has been known in flowering plants since the observation that a female *Alchornea* (Euphorbiaceae) produced seed at the Royal Botanic Gardens, Kew in 1841 (Asker and Jerling 1992). Mendel, following his work on *Pisum*, described alternative inheritance patterns in *Hieracium* (Asteraceae) but without knowledge that some of the plants he was working with were apomictic (Nogler 2006). Cytological understanding of apomixis did not occur until the 1890s when improved technical methods in conjunction with understanding of the chromosomal basis of inheritance and of alternation of generations in plants led to the description of most of the major types of apomictic development in plants. Elucidation of apomictic development in the Asteraceae in European *Taraxacum* and *Hieracium* by Juel (1898, 1900) and Rosenberg (1908), respectively, helped establish the foundation of research on apomictic reproduction in flowering plants.

Apomictic reproduction is widespread in flowering plants, having been documented in perhaps 44 different families and representing most major angiosperm clades (Carman 1997; van Dijk and Vijverberg 2005; Carneiro *et al*. 2006). Historically, apomixis has been considered to be merely a short term solution to hybrid sterility and an evolutionary dead-end (Darlington 1939; Stebbins 1950). However, theoretical and empirical considerations, notably the possibility that apomictic reproduction may be much more widespread taxonomically and geographically (Thomas 1997; Plitmann 2002) have allowed apomixis to join outcrossing and selfing as an evolutionarily viable mode of reproduction through seed (Allem 2004; van Dijk and Vijverberg 2005). In addition, our appreciation of apomixis is enhanced because of recent analyses of the intraspecific distributions of apomictic versus sexual populations (geographic parthenogenesis) from a modern ecological-evolutionary perspective (e.g., Hörandl 2006).

Review of literature relating to apomictic development in the Asteraceae notes a proliferation of different sets of terms describing the progression of apomictic development from the period extending from the 1950s to the 1980s, and then, following the seminal review of Nogler (1984), a return to the simplified classification used by Gustafsson (1946-1947). Two main types of apomixis occur in the Asteraceae, apospory and diplospory. Both types are termed gametophytic because each involves the formation of an unreduced female gametophyte (equals embryo sac or megagametophyte) within the ovule. However, the two types differ in the location of the cell that gives rise to the female gametophyte. With apomictic reproduction, the egg of the unreduced gametophyte develops parthenogenetically (without fertilization) into an embryo. In both aposporous and diplosporous apomixis, the end product is a seed that is morphologically identical to that produced by a sexual congener, but offspring are genetic clones of the maternal plant.

In diplospory, the unreduced female gametophyte arises directly from mitotic or modified meiotic divisions of the megaspore mother cell. The precise nature of the division and the fates of the products of that division define three main types of diplospory (Nogler 1984; Koltunow 1993). These have been referred to as the *Taraxacum*-type, the *Ixeris*-type, and the *Antennaria*-type of diplospory. Both the *Taraxacum*- and *Ixeris*-types represent meiotic diplospory because the megaspore mother cell (MMC) enters into meiosis but is restitutional at the end of meiosis I. Realignment and division of chromatids in meiosis II then occur to produce genetically identical dyads. In the *Taraxacum*-type, the micropylar member of the dyad degenerates while the chalazal cell develops mitotically into the unreduced gametophyte. In contrast, with the *Ixeris*-type, restitution of meiosis I and division of chromatids in meiosis II produce a coenospore, i.e., a megaspore consisting of two identical nuclei. The gametophyte enlarges, vacuolization occurs, and mitotic formation of the unreduced gametophyte ensues. The alternative, *Antennaria*-type diplospory, is the direct formation of the female gametophyte by mitotic divisions. In this case, the MMC first undergoes vacuolization, then mitotic divisions produce the unreduced gametophyte without the formation of coenospore and without the degeneration of a dyad member.

Apospory is fundamentally different from diplospory in that the unreduced gametophyte develops by mitotic divisions from a nucellar or chalazal cell of the ovule. The aposporous gametophyte develops in junction with the reduced gametophyte derived from the MMC. However, when apospory is effectively expressed, the unreduced gametophytes replace, either by forcible displacement or because of degeneration, the immature reduced gametophytes. Thus even though all aposporous apomicts are potentially facultative, high penetrance can result in exclusive production of aposporous seed (Bicknell *et al.* 2003; Houliston and Chapman 2004). While it is unlikely that apospory and diplospory are genetically homologous, the question of the homology of different types of diplospory is controversial (van Dijk and Vijverberg 2005).

Adventitious embryony is a third type of apomixis that has been described for flowering plants and occurs, for instance, in *Citrus* and tropical Clusiaceae. With adventitious embryony, an embryo develops directly from a vegetative cell of the ovule without an intervening gametophyte (Naumova 1993). In the Asteraceae, although embryo-like development has been described from vegetative cells of the ovule, for instance, in *Melampodium* (Maheshwari and Pullaiah 1976) and *Carthamus* (Maheshwari and Pullaiah 1977), the phenomenon appears to represent an infrequent developmental abnormality, and, furthermore, has not been demonstrated to lead to viable genetically maternal offspring.

Apomixis in the Asteraceae is frequently autonomous, because fertilization of the polar nuclei for the development of endosperm is generally not required. This is in contrast to apomicts in most other plant families that require fertilization for endosperm and which are therefore pseudogamous. Evidence regarding pseudogamy in the Asteraceae is equivocal. *Parthenium* and *Rudbeckia* (Heliantheae) are commonly considered to be pseudogamous, but whether the pollen contributes to endosperm development and/or merely stimulates parthenogenetic development, as has been proposed for *Soliva* (Anthemideae) (Lovell *et al.* 1986), remains to be clarified. An additional instance of pseudogamy in the Asteraceae may be *Leontopodium*, in which it is reported that the embryo is formed only after endosperm fertilization (Sokolowska-Kulczycka 1959).

Apomicts in the Asteraceae, as in other plant families are almost always restricted to polyploids at triploid and higher levels. The reasons for this may include genetic lethality that prevents the maintenance of apomixis at the diploid level, either affecting developing embryos or preventing haploid gametes from carrying apomixis genes (Nogler 1984). Lethality of this type would mean that apomixis genes (either through egg or sperm cells) could be effectively transferred only through diploid or higher level ploidy gametes. Consequently, novel apomictic genotypes resulting from sexual × apomictic genotypes must always be polyploid. Diploid apomicts can be produced by the parthenogenetic development of reduced eggs produced by an apomictic tetraploid, but this mechanism appears to be rare (de Wet 1968; Nogler 1982). In this case, the resulting diploid apomict would be produced without having gone through the selective haploid stage. Diploid apomicts are occasionally observed in natural populations, most notably in *Boechera* (Brassicaceae) (Schranz *et al.* 2006), but more usually are produced experimentally by destabilized apomictic hybrids (Nogler 1984; Bicknell 1997; Kojima and Nagato 1997). Thus, in general, polyploidy is usually necessary though not sufficient for apomixis in natural populations. In addition, apomicts in nature typically occur in apomict complexes, i.e., taxonomic assemblages within a genus that include both sexual populations and apomictic populations. Sexual populations may occur at the diploid level or higher usually even-ploidal levels, while apomictic plants are normally exclusively polyploid (Grant 1981). Note that while polyploidy in itself has been proposed as a trigger for apomixis (Grimanelli *et al.* 2001) a satisfactory genetic mechanism for this mode has yet to be proposed.

Methods for conclusively documenting apomixis vary depending on the attributes of the species in question (Richards 1997). Most of the early descriptions of the mode of origin of the reduced gametophyte were based on analysis of serial sections of fixed ovules. Visualization of whole cleared ovules using differential interference optics, however, greatly simplifies this procedure (Herr 1971; Nakagawa 1990). The small size of the ovaries and ovules means that apomictic development for most Asteraceae can be scored relatively easily as a quantitative trait (Noyes 2000; Noyes *et al.* 2007). Cytoembryological data by itself may not be sufficient for diagnosis for apomixis in many cases, however. For instance plants may be fundamentally sexual but exhibit divisions in the nucellus or chalaza that are reminiscent of apospory. However, if fully formed female gametophytes of aposporous origin do not function in the reproduction of the species, then apomixis is not indicated. In such cases, apomixis must be demonstrated by showing that progeny include no contribution of a male parent and are genetically maternal. The use of DNA fingerprinting methods for the analysis of progenies produced by apomictic plants is indicated for species in which cytological or manipulative experiments are not conclusive (Nybom 1996; Thompson and Ritland 2006).

Proving that a plant produces seeds in the complete absence of the contribution of a male parent is relatively easy, via isolation of plants from potential pollinators, in dioecious species such as *Antennaria* (Gnaphalieae) (Stebbins 1932) or for normally hermaphroditic taxa in which the anthers are completely aborted as in some *Erigeron* (Astereae) (Noyes and Soltis 1996). Diagnosis of apomixis for functionally hermaphroditic taxa is more complicated (Asker and Jerling 1992; Richards 1997). In some apomicts such as *Crepis* (Babcock and Stebbins 1938), embryos are formed precociously and thus can be observed to develop prior to maturation and release of pollen. Apomictic development in other taxa, however, is not precocious and occurs simultaneously with or after anthesis. For some Asteraceae, the shape and size of the capitulum (as in *Taraxacum*) permits emasculation and removal of stigmas without damaging the ovules and still permitting observation of apomictic development. For other taxa, however, the flowers may be too small and the receptacle too curved to perform this manipulation without damaging the ovaries. In these cases, apomixis must be inferred from cytological and inheritance data. In addition, even when emasculation can be effectively performed, it can only provide evidence for autonomous apomixis. Diagnosis is more complicated for taxa in which pollination is required for endosperm production; pollen must be allowed to germinate, grow, and penetrate the synergids of the female gametophyte, but it must be proved that no sperm nucleus unites with the egg nucleus. A further complication is the possibility that pollen in some cases may act as a development stimulant but make no genetic contribution to either embryo or endosperm (Lovell *et al.* 1986). Auxin induced development of parthenogenetic embryos has been used to estimate apomixis in some pseudogamous taxa (Mazzucato *et al.* 1996; Sherwood 2001). This method has not been applied to the study of pseudogamous Asteraceae, however. Similarly, the method of Matzk *et al.* (2000) for diagnosing apomixis based on the ratio of the ploidal level of embryo versus endosperm is difficult to apply to Asteraceae, which have limited and ephemeral endosperm.

Odd-ploidal level and disrupted microsporogenesis also provide evidence that apomixis may be present, and many apomicts are triploid (Asker and Jerling 1992). In the Asteraceae, however, sexual species frequently consist of diploid and tetraploid cytotypes that hybridize either in nature or experimentally to produce triploid or other odd-ploid hybrids. The fertility of these plants can vary from sterile to partially fertile in both male and female function, but they do not necessarily exhibit apomictic reproduction (e.g., Dunford 1970; Jansen 1985; Lowe and Abbott 2003; Liu 2004). Thus odd-ploidal level can be considered to be an indicator of apomixis, but it is not sufficient evidence in itself.

The Asteraceae is large and diverse, with upper estimates of approximately 1,700 genera and 30,000 species (Funk *et al.* 2005). Among families of flowering plants, only the Orchidaceae is numerically comparable. The Asteraceae is by tradition divided taxonomically into subfamilies and tribes. The definition of tribes and their proposed evolutionary interrelationships, which had been relatively static for over 100 years, has undergone major revisions with the application of molecular systematics. The tumult dates in particular to the discovery of the early diverging subfamily Barnadesioideae (Jansen and Palmer 1987) based on chloroplast restriction site variation. Tremendous volumes of work have led to redefinition of tribal and generic boundaries and repositioned anomalous genera, while emphasizing recognition of monophyletic taxa.

In this work, the phylogenetic tree of Funk *et al.* (2005) is used to evaluate the distribution of apomixis in the Asteraceae (**Fig. 1**). This is a supertree in the sense that it synthesizes topological information from diverse studies but is not the product of a combined analysis. In recognition of monophyletic groups, the work segregates the Heliantheae and Mutisieae into several smaller narrowly defined tribes and recognizes several small isolated lineages at the tribal level. In contrast to the traditional and long held view of the Asteraceae as comprising three subfamilies and about 15 tribes, Funk *et al.* (2005) propose 10 subfamilies and about 40 tribes. This phylogeny is used for the present analysis because the fine divisions permit a closer view of the distribution and evolutionary relationships among apomictic taxa.

It is reasonable to question the importance of a phylogenetic analysis of apomictic taxa. Certainly one rationale is purely to satisfy the human desire to understand diversity in nature. Where does apomixis occur, and how does it relate to patterns of variation in nature? In addition, knowledge of the mode of reproduction for a group of species can impact both decisions regarding conservation and, similarly, assumptions pertaining to the distribution of genetic variation within and among populations. In addition, with robust knowledge of the phylogenetic distribution of apomicts, one can begin to ask meaningful comparative evolutionary questions (van Dijk and Vijverberg 2005): for instance, why does apomixis occur in some groups but not others? Are some taxa predisposed to evolving apomixis? Is there something unique in the development or ecology of the relatives of apomicts that favored evolution of apomixis? Why is apomixis absent from some groups? Lastly, because apomixis in plants can be spread by pollen, a phylogenetic perspective can inform models for the spread of the trait through introgressive hybridization among taxa. Clearly, however, before these types of questions can be addressed, one must have a robust record documenting which taxa are apomictic and which taxa are not. The objective of this work is to determine, through review of the scientific record, those taxa for which apomixis is unequivocal and those for which apomixis has been implicated but in reality are either unlikely to be apomictic or for which the scientific record is incomplete.

METHODS

As a starting point for determining which taxa, at the generic level, are apomictic in the Asteraceae, seven former reviews were evaluated including Gustafsson (1946-1947),

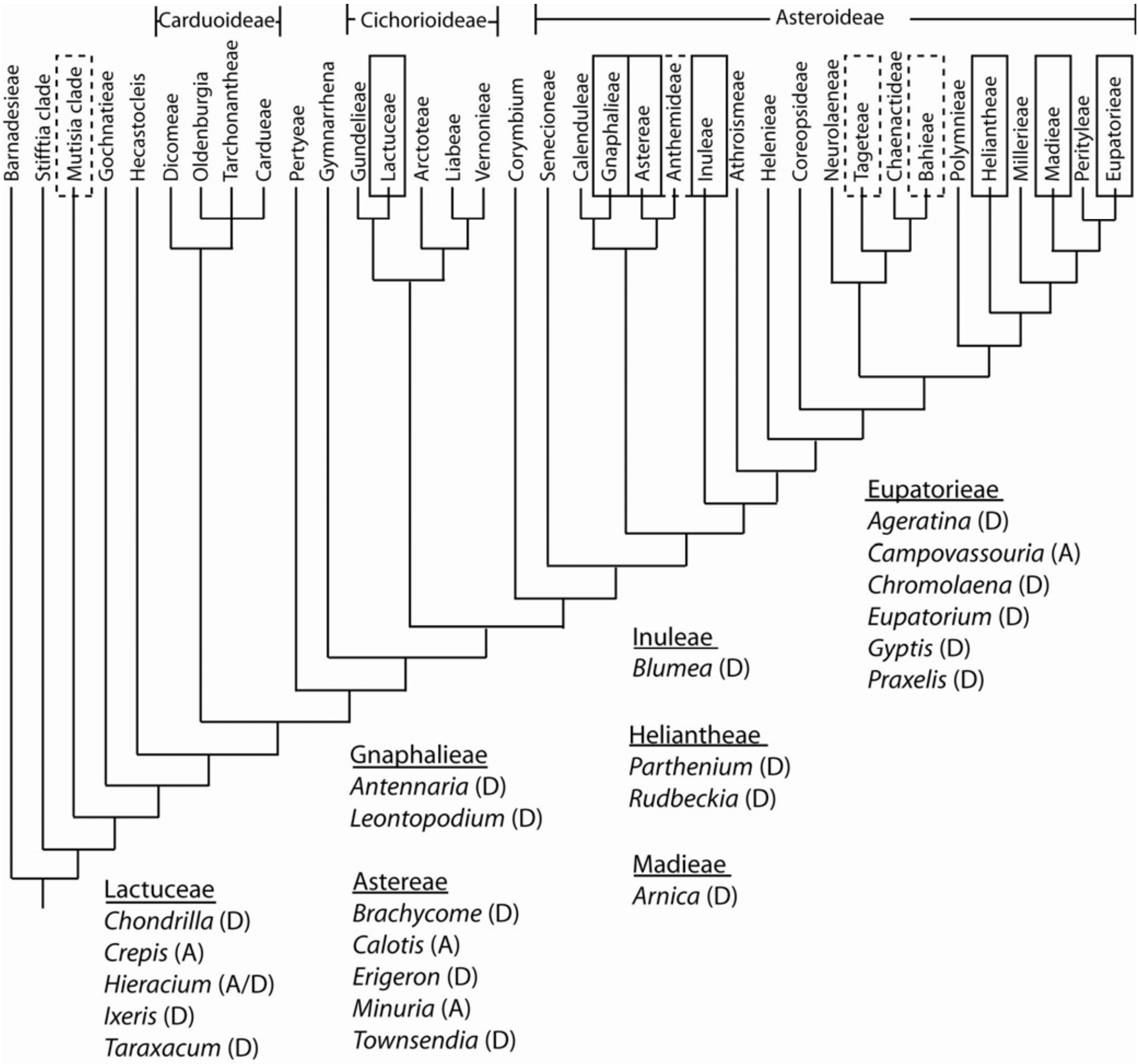

Fig. 1 Phylogenetic distribution of apomixis in the Asteraceae. Subfamilies, tribes, and phylogeny after Funk *et al.* (2005). Seven tribes highlighted with a solid box contain genera, listed below the tree, for which evidence for apomixis is robust. Tribes with a dashed box contain additional genera for which apomixis is likely, but incompletely documented (**Table 2**).

Battaglia (1951), Nygren (1954), Davis (1967), Pullaiah (1984), Czapik (1996), and Carman (1997). Because a substantial number of names cited by these reviews are now synonyms, currently accepted names for all cited taxa were determined using either the recently published Asteraceae volumes for Flora of North America (FNA 2006), volume 4 of Flora Europaea (Moore *et al.* 1976), the taxonomic database TROPICOS of the Missouri Botanical Garden (http://mobot.mobot.org/W3T/Search/vast.html), or published monographs. Nomenclatural standardization permits meaningful tabulation and comparison across reviews.

Whenever possible, original literature cited by these works was consulted to evaluate the evidence for apomictic reproduction for each taxon. Those works, plus original chromosome count literature, were also consulted for supporting evidence for apomixis where deemed appropriate. Apomixis has also been proposed for some genera that do not appear in any of the above review articles. To gather these new examples, the scientific literature was scanned using Google Scholar (http://scholar.google.com) and ISI Web of Science (Thomson Scientific, Philadelphia, PA).

In light of gathered data, determination was made for each genus as to the strength of the evidence for effective apomixis, i.e., reproduction involving apomictic seed production in natural populations. Minimum evidence required for accepted cases of apomixis includes cytological documentation of the mode of origin of the female gametophyte, observation of parthenogenetic embryo formation, observation of seed set in the absence of pollen (or evidence for pseudogamous seed development), observation of morphologically maternal progeny, and documentation of chromosome number. These best cases also often include confirmation of apomixis by independent researchers and, in some cases, geographic, phylogenetic, genetic and ecological analyses.

Implicated but not confirmed cases of apomixis were divided into three categories: (1) genera for which apomixis will likely be fully confirmed but at present the evidence is incomplete, i.e., either chromosome number, cytological, or seed set data are lacking; (2) equivocal cases, including genera for which some of the evidence could be construed to be consistent with apomixis, but for which the scientific record is incomplete and either very brief or speculative; and (3) genera for which apomixis has been attributed but for which apomictic reproduction is contra-indicated. Into this last category fall those plants for which elements of apomixis have been observed, but it is unlikely that full apomictic reproduction is actually achieved. Included in this category are examples for which aposporous-like gametophyte development has been observed but where the species in question is otherwise documented as diploid and sexual, as well as examples in which unreduced female gametophytes in polyploids fail to produce parthenogenetic embryos. In these situations, the plants possess either an element of apomictic reproduction or morphology analogous to apomixis but are not actually apomictic in nature. These separate elements perhaps are indicative of developmental abnormalities or artifact rather than stable intermediate stages in the evolution of apomixis. This inference is based on the likelihood that expression of partial apomixis will be deleterious in regards to reproductive fitness and strongly selected against (van Dijk and Vijverberg 2005).

To evaluate the evolutionary relationship among accepted apomictic genera, their position on the phylogeny of Asteraceae (Funk *et al.* 2005; **Fig. 1**) was plotted at the tribe level. For unaccepted cases, genera were grouped according to tribe and the evidence for or against apomictic reproduction was evaluated for each. The basis and significance of the discrepancy between the number of proposed versus the actual number of apomictic genera were considered. In addition, those genera for which apomixis will likely be proved were added to **Fig. 1** to anticipate the possible complete spectrum of the distribution of apomixis in the Asteraceae.

RESULTS

Apomictic genera of Asteraceae according to the seven reviews are listed in **Table 1**. Changes reflecting current nomenclature are explained in the footnotes of the table. The summary for Gustafsson (1946-1947) includes 17 genera in nine tribes. This includes records for five genera (*Artemisia, Centaurea*, *Coreopsis*, *Leontodon*, and *Picris*) that Gustafsson recorded as possessing evidence for aposporous or diplosporous female gametophyte formation, but not full apomictic development. A tally for Gustafsson that reflects only fully apomictic taxa would also exclude *Youngia*, for which data was incomplete, leaving 11 apomictic genera in six tribes. Diplospory is recorded for ten genera and apospory is recorded for just three genera; both diplospory and apospory are recorded jointly for genera in only two instances. The reports of Battaglia (1951) and Nygren (1954) are similar to Gustafsson (1946-1947) and record apomixis for no additional genera of Asteraceae.

The summary for Davis (1967) shows a dramatic increase in the number of genera for which apomixis was diagnosed (**Table 1**). The addition of four genera (*Brachyscome*, *Calotis*, *Minuria*, *Tridax*) are the result of published observations since Gustafsson (1946-1947), while the addition of ten genera (*Amphiachyris*, *Bellis*, *Bidens*, *Felicia*, *Gerbera*, *Grindelia*, *Helianthus*, *Leucanthemum*, *Solidago*, *Symphyotrichum*), is based on interpretations of apospory from older literature. In total, Davis (1967) diagnoses apomixis for 26 genera in 10 tribes.

The compilation of Pullaiah (1984) reflects considerable accumulation of data in the 17 years since Davis (1967). Apomixis is recorded for 15 new taxa, including apospory for seven genera (*Ageratum*, *Calendula*, *Carthamus*, *Eurybia*, *Hypochaeris*, *Melampodium*, *Tithonia*) and diplospory for eight genera (*Ayapana*, *Blumea*, *Chromolaena*, *Eupatorium*, *Laggera*, *Leontopodium*, *Scorzonera*, *Townsendia*), yielding a total of 39 genera in 12 tribes. Czapik (1996) cites evidence for apomixis in 44 genera in 15 tribes of Asteraceae and includes records for two tribes not previously listed as possessing apomixis (Vernonieae: *Elephantopus*; Senecioneae: *Petasites*) and new generic records for Calenduleae: *Dimorphotheca* and *Castalis*; Anthemidae: *Achillea*; Lactuceae: *Cichorium*; and Cardueae: *Cirsium*. No unique records for apomixis appear in Carman (1997); the 12 tribes and 34 genera reported are a subset of those of Czapik (1996). The compilations of Czapik (1996) and Carman (1997) indicate apomixis for approximately three times the number of genera as Gustafsson (1946-1947), suggesting an accelerated pace of the discovery of apomictic taxa (**Table 1**).

In total, these seven reviews indicate apomixis for 53 genera and 15 tribes of Asteraceae, including Anthemidae, Astereae, Calenduleae, Cardueae, Coreopsideae, Eupatorieae, Gnaphalieae, Heliantheae, Inuleae, Lactuceae, Madieae, Millerieae, Mutisieae, Senecioneae, and Vernonieae. In addition, search in the present study of recent systematic, chromosome, and breeding system literature implicates apomixis for three additional tribes (Bahieae, Neurolaeneae, and Tageteae) and 15 genera that are not included in previous reviews. These include Anthemidae: *Soliva*; Bahieae: *Amauriopsis*; Eupatorieae: *Campovassouria*, *Eitenia*, *Gyptis*, *Praxelis*, *Stevia*; Heliantheae: *Monactis*, *Kingianthus*; Lactuceae: *Krigia*, *Microseris*; Mutisieae: *Leibnitzia*; Neurolaeneae: *Calea*; Tageteae: *Chrysactinia*, *Thymophylla*. The complete tally from the seven reviews plus new candidates indicates apomixis for 68 genera in 18 tribes.

Critical review of the evidence indicates certain occurrence of apomixis for only 22 of the 68 genera (**Table 1**). These occur in seven tribes and closely conform to those presented in the synopsis of Gustafsson (1946-1947). The scientific record for the remaining 46 genera indicates examples that possess elements of apomictic development but not full apomictic reproduction, or the evidence is equivocal, incomplete, or requires independent confirmation. The literature documenting the 22 strong cases for effective apomictic reproduction is briefly summarized below, and the phylogenetic relationships of the tribes in which they occur are plotted in **Fig. 1**. Tribes below are listed in the order that they occur in **Fig. 1**.

Genera (22) of Asteraceae for which apomixis is well documented

Lactuceae (Chondrilla, Crepis, Hieracium, Ixeris, Taraxacum)

Diplosporous apomixis is well documented for *Chondrilla juncea* by (Rosenberg 1912), and further demonstrated by Poddubnaja-Arnoldi (1933), Bergman (1944), and Battaglia (1949). Geographical aspects of apomixis in the species are explored by Chaboudez (1994) and elaborated upon by van Dijk (2003).

Aposporous apomixis was documented for a number of species within the North American *Crepis occidentalis* polyploid complex (Babcock and Stebbins 1938; Stebbins and Jenkins 1939). The geographic and evolutionary aspects of apomixis in *Crepis* are summarized by Gustafsson (1946-1947) and Grant (1981).

Hieracium includes *H.* subg. *Pilosella* (Hill) S.F. Gray, *H.* subg. *Hieracium*, and *H.* subg. *Chionoracium* Dumort. Apospory was demonstrated embryologically for *H.* subg. *Pilosella* by Rosenberg (1908); diplospory was demonstrated for *H.* subg. *Hieracium* by Bergman (1941), among others. Details on early investigations in the genus are provided by Gustafsson (1946-1947). Geographic and evolutionary aspects of apomixis in *Hieracium* are summarized by Fehrer *et al.* (2007a, 2007b). As currently circumscribed, *Hieracium* is the only genus of Asteraceae in which both aposporous and diplosporous apomixis have evolved. This is somewhat of a misleading claim, however, as recent phylogenetic work supports recognition of *Pilosella* and *Hieracium* (s.s.) as separate genera (Fehrer *et al.* 2007a).

Ixeris is a genus of 20-60 species principally of Southeast Asia (Bremer 1994). Diplosporous apomixis was described for *Ixeris dentata* (Thunb.) Nakai by Okabe (1932). Geography and evolution in the *I. chinensis* (Thunb.) Nakai apomictic complex are explored by Pak and Kawano (1990) and Pak *et al.* (1997).

Taraxacum includes about 60 species in North Tempe-

Table 1 Genera of Asteraceae recorded as possessing capacity for apomictic reproduction in seven former reviews. The present analysis accepts apomixis for *Campovassouria*, *Gyptis*, and *Praxelis*, which were not included in previous treatments (see text). Records standardized to currently accepted taxonomy (see text). A = apospory; D = diplospory; M = mode missing, but cited as apomictic.

	Gustafsson[a] **(1946-1947)**	**Battaglia (1951)**	**Nygren (1954)**	**Davis (1967)**	**Pullaiah, (1984)**	**Czapik (1996)**	**Carman (1997)**	**Present**
	9 tribes[b] **17 genera**	**7 tribes** **15 genera**	**5 tribes** **8 genera**	**10 tribes** **26 genera**	**12 tribes** **39 genera**	**15 tribes** **44 genera**	**12 tribes** **34 genera**	**7 tribes** **22 genera**
Mutisieae								
Gerbera				A		A	A	
Cardueae								
Carthamus					A	A[c]	A	
Centaurea	A[d]			A	A[e]	A	A	
Cirsium						A		
Lactuceae								
Chondrilla	D	D	D		D	D	D	D
Cichorium						D	A	
Crepis	A	A		A	A	A	A	A
Hieracium	A,D	A,D	A	D	A,D	A,D[c]	A,D	A,D
Hypochaeris					A[f]			
Ixeris	D	D		D	D[e]	D	D	D
Leontodon	A[d]	A			A,D	A	A	
Picris	A[d]	A			A	A	A	
Scorzonera					D			
Taraxacum	D	D	D	D	D	D	D	D
Youngia	M					M[g]		
Vernonieae								
Elephantopus						M[h]		
Senecioneae								
Petasites						A		
Calenduleae								
Calendula					A[e]	A		
Castalis						A		
Dimorphotheca						A		
Gnaphalieae								
Antennaria	D	D	A,D	A[i],D	A[i],D	A,D	A,D	D
Leontopodium					D	D	D	D
Astereae								
Amphiachyris				A[j]		A[j]	A[j]	
Bellis				A	D[e]	A	A,D	
Brachyscome				D	D	D	D	D
Calotis				A	A	A	A	A
Erigeron	D	D	D	A, D	A,D	D	A,D	D
Eurybia					A[e, k]			
Felicia				A[l]				
Grindelia				A[m]		A[m]	A[m]	
Minuria				A	A	A	A[n]	A
Solidago				A	A[e],D	A	A	
Symphyotrichum				A[o]	A[e,o,p]	A[q]	A[q]	
Townsendia					D	M		D
Anthemidae								
Achillea						M[r]		
Artemisia	A,D[d]	A		A	A	A,D	A,D	
Leucanthemum				A[s]		A[s]	A[s]	
Inuleae								
Blumea					D[t]	D	D	D
Laggera					D			
Coreopsideae								
Bidens				A		A	A	
Coreopsis	A[u,d]	A[u]			A[u]	A	A	
Heliantheae								
Helianthus				A	A[e]	A	A	
Parthenium	A,D	D	D	D	D	A,D	A,D	D
Rudbeckia	D	D	D	D	D	D	D	D
Tithonia					A[v]	A		
Tridax				A	A[e]	A	A	
Millerieae								
Melampodium					A	A	A	
Madieae								
Arnica	D	D	D	D	D	D	D	D
Eupatorieae								
Ageratina	D[w]	D[w]		D[w]	D[w]			D
Ageratum					A			
Ayapana					D[x]			
Campovassouria								A

Table 1 (Cont.)

	Gustafsson[a] **(1946-1947)**	**Battaglia (1951)**	**Nygren (1954)**	**Davis (1967)**	**Pullaiah, (1984)**	**Czapik (1996)**	**Carman (1997)**	**Present**
	9 tribes[b] **17 genera**	**7 tribes** **15 genera**	**5 tribes** **8 genera**	**10 tribes** **26 genera**	**12 tribes** **39 genera**	**15 tribes** **44 genera**	**12 tribes** **34 genera**	**7 tribes** **22 genera**
Eupatorieae (Cont.)								
Chromolaena					D[y]			D
Eupatorium					D	D[z]	A,D[z]	D
Gyptis								D
Praxelis								D

[a] As summarized in Gustafsson (1946-1947), Appendix II, page 309-311

[b] Excluding taxa that are listed as lacking parthenogenetic development in Gustafsson (1946-1947) leaves 11 genera in six tribes that are effectively apomictic

[c] Adventitious embryony also noted

[d] Noted by the author to lack parthenogenetic embryo production and therefore not fully apomictic

[e] Listed in discussion but not in the main table that forms the body of the text

[f] Apospory in *Hypochaeris* is listed as 'rare'

[g] Youngia is listed as 'parthenogenetic' rather than apomictic

[h] Listed as possessing apogamety, i.e., the spontaneous development of an embryo from a gametophytic cell other than the egg cell

[i] Apospory, in addition to diplospory, was observed in *Antennaria*, but the plant studied was sterile

[j] *Gutierrezia* in Davis (1967) refers to *Gutierrezia dracunculoides* (DC.) S.F. Blake = *Amphiachyris dracunculoides* (DC.) Nutt.; *Gutierrezia* in Czapik (1996) and Carman (1997) is likely in reference to this citation

[k] Pullaiah (1984) cites apospory for *Aster sibericus* L. = *Eurybia sibirica* (L.) G.L. Nesom

[l] Davis (1967) cites apospory for *Aster capensis* Less. = *Felicia amelloides* (L.) Voss fide Grau (1973)

[m] *Haploappus* in Davis (1967) refers to *Haplopappus ciliatus* (Nutt.) DC. = *Grindelia ciliata* (Nutt.) Sprengel; *Haplopappus* in Czapik (1996) and Carman (1997) is likely in reference to this citation

[n] as *Eurybiopsis*

[o] Davis (1967) cites apospory for *Aster novae-anglieae* L. = *Symphyotrichum novae-anglieae* (L.) G.L. Nesom, and for *Aster undulatus* L. = *Symphyotrichum undulatum* (L.) G.L. Nesom

[p] Pullaiah (1984) cites apospory for *Aster undulatus* L.= *Symphyotrichum undulatum* (L.) G.L. Nesom

[q] Apospory *for Aster,* cited in Czapik (1996) and Carman (1997), likely reflects Davis (1967) and/or Pullaiah (1984) and may refer to synonyms now in *Eurybia*, *Felicia*, *Symphyotrichum*, or all three. *Symphyotrichum* selected arbitrarily for tabulation purposes

[r] *Achillea* listed as apomeiotic (i.e., either diplospory or apospory) and parthenogenetic without attribution

[s] Apospory is cited by Davis (1967) for *Chrysanthemum leucanthemum* L. = *Leucanthemum vulgare* Lam. *Leucanthemum* in Czapik (1996) and Carman (1997) likely refer to this citation

[t] Pullaiah cites diplospory for both *Blumea* and *Laggera.* Although sometimes united, recent molecular work indicates that these genera are distinct (P. Pornpongrungrueng, University of Aarhus, pers. comm.)

[u] *Coreopsis bicolor* for which apospory was described by Gelin (1934) and cited by Gustafsson (1946-1947), Battaglia (1951), and Pullaiah (1984) is *Coreopsis tinctoria* Nutt., fide Turner (1960)

[v] Pullaiah (1984) notes that apospory in *Tithonia* is "observed in some cases" but that no 'further development of the aposporic embryo sac is noticed', indicating that effective apomixis is not indicated

[w] *Eupatorium glandulosum* H.B.K. cited in Gustafsson (1946-1947) = *Ageratina adenophora* (Sprengel) R. King and H. Robins.

[x] *Eupartorium triplinerve* Vahl cited in Pullaiah (1984) = *Ayapana triplinervis* (Vahl) R. King and H. Robins.

[y] *Eupatorium odoratum* L. cited in Pullaiah (1984) = *Chromolaena odorata* (L.) R. King and H. Robins.

[z] Listing of '*Eupatorium'* in Czapik (1996) and Carman (1997) presumably reflect a mix of segregate genera as cited in Pullaiah (1984)

rate and Temperate South American regions. It is a rich center for the evolution of apomixis, occurring in triploid and tetraploid species in 19 of 26 taxonomic sections (Kirschner and Štěpánek 1996). Diplospory was originally described for the genus by Juel (1904) and Murbeck (1904) and has been verified innumerable times using a variety of anatomical, experimental, and genetic techniques (Richards 1973, 1997; van Baarlen *et al.* 2002). Phylogenetic aspects of apomixis in *Taraxacum* are explored by Wittzell (1999) and Kirschner *et al.* (2003). Geographical aspects are addressed by Menken *et al.* (1995), Kirschner and Štěpánek (1996), van Dijk (2003), and Verduijn *et al.* (2004), among others.

Gnaphalieae (Antennaria, Leontopodium)

Diplosporous apomixis is described for the European taxon *Antennaria alpina* (L.) Gaertn. by Juel (1898, 1900) and for North American species by Stebbins (1932). Geographic and evolutionary aspects of apomixis in *Antennaria* are investigated by Bayer and Stebbins (1983), Bayer (1985, 1987), Bayer *et al.* (1996), and Bayer and Chandler (2007). Curiously, aposporous gametophytes are described by Haberlandt (1921) in *A. dioica* (L.) Gaertn. and in *A. carpatica* (Wahlenb.) Hook. by Bergman (1951). Consequently, *Antennaria* is considered to possess both apospory and diplospory by Nygren (1954), Davis (1967), Pullaiah (1984), Czapik (1996), and Carman (1997). However, Gustafsson (1946-1947), for *A. dioica,* describes the data as indicating only a 'slight tendency' to apospory, while Bergman (1951) notes that the aposporous gametophytes in *A. carpatica* are not functional. In light of these observations, and until the frequency and function of aposporous gametophytes is better understood, *Antennaria* is best described as effectively diplosporous.

Leontopodium includes 41 species and is Eurasian in distribution (Handel-Mazzetti 1927). Diplosporous apomixis is described for polyploid *Leontopodium alpinum* Cass. by Sokolowska-Kulczycka (1959) and Maugini (1962). It is subsequently listed in apomixis reviews of Pullaiah (1984), Czapik (1996), and Carman (1997). This species, the Edelweiss, is an important cultural symbol of the European Alps, but among the 21 apomictic genera, is probably the least well known, and even a relatively recent study of pollination and reproductive behavior for the species fails to acknowledge apomixis (Erhardt 1993).

Astereae (Brachyscome, Calotis, Erigeron, Minuria, Townsendia)

Brachyscome (70 sp.), *Calotis* (26 sp.), and *Minuria* (10 sp.) are principally Australian genera (Bremer 1994). Diplospory and parthenogenetic embryo formation are well detailed for *Brachyscome ciliaris* (Labill.) Less. (Davis 1964b), a tetraploid ($2n=4x=36$) taxon with univalent formation in microsporogenesis (Turner 1970). Aposporous apomixis is documented for tetraploid ($2n=4x=28$) *Calotis lappulacea* Benth. by Davis (1968) and is hypothesized for tetraploid ($2n=4x-2=26$) *C. suffruticosa* Domin and triploid *C. scapigera* Hook. (Stace 1978). Apospory and parthenogenetic embryo development for *Minuria* are definitively detailed for the widespread tetraploid taxon *Minuria integerrima* (DC.) Benth. (Davis 1964a; Watanabe *et al.* 1996).

Diplosporous apomixis has been known for *Erigeron annuus* (L.) Pers. since Tahara (1915) and for *E. strigosus* Muhl. ex Willd. since Holmgren (1919), and is definitively described for four additional species (Noyes 2000). Davis (1967) reports apospory for *E. elatus* (Hook.) Greene and *E. glabellus* Nutt. based on Bergman (1942) and Carano (1921) respectively. In light of the predominance of diplospory in other *Erigeron* taxa, these observations should be confirmed before it is concluded that the genus possesses both types of apomictic development. Curiously, Pullaiah (1984) lists apospory for *E. mucronatus* DC. [= *E. karvinskianus* DC.], but this is apparently due to the imprecise nature of apomixis terminology in use at that time because this species is otherwise documented as diplosporous (Battaglia 1950; Beals 1970).

Diplosporous apomixis is described for several polyploid species in the western North American genus *Townsendia* by Beaman (1957), including *T. incana* Nutt., *T. minima* Eastwood and *T. rothrockii* A. Gray ex Rothr. Geographical patterns and complex mixture of alternate modes of reproduction are recently reported for diploid and tetraploid populations of *T. hookeri* Beaman (Thompson and Ritland 2006; Thompson and Whitton 2006).

Inuleae (Blumea)

Diplospory and parthenogenetic embryo formation is cited by Pullaiah (1984) for triploid genotypes of *Blumea eriantha* DC. and *Blumea oxydonta* DC. based on Chennaveeraiah and Patil (1971). *Blumea* is subsequently cited as apomictic by Pullaiah (1984), Czapik (1996), and Carman (1997). Cennaveeraiah and Patil (1971) further note complete male sterility or abnormal microsporogenesis but high seed set and morphologically uniform progeny of apomictic plants. The authors also describe a type of automictic union of reduced gametophytic nuclei in various triploid and tetraploid genotypes of *B. eriantha*, which possibly represents a novel type of apomictic development in the Asteraceae. The geographic and phylogenetic extent of apomixis in *Blumea* awaits detailed analysis.

Heliantheae (Parthenium, Rudbeckia)

Diplospory for the North American genus *Parthenium* is described for tetraploid *P. argentatum* A. Gray by Esau (1944) and classic studies of the inheritance of apomixis in the genus are presented by Powers (1945). In a detailed study, Esau (1946) further reports that apomixis in the genus is pseudogamous. In addition, while aposporous gametophytes are occasionally encountered in otherwise sexual and diplosporous *Parthenium*, they are rare, often degenerate, and are never observed to produce endosperm. As recommended by Esau (1946, p. 97), *Parthenium* is best described as diplosporous. The characterization of the genus as both diplosporous and aposporous by Czapik (1996) and Carman (1997) is probably unwarranted.

Diplosporous apomixis is known from seven tetraploid *Rudbeckia* taxa based on the works of Battaglia (1946a, 1946b). In addition, Battaglia (1951) reviews several irregular ‘secondary types’ of diplospory, including the occurrence of accessory nuclei during megasporogenesis, irregular structure of the female gametophyte, and ploidal level increase through double meiotic restitution. Further, while Fagerlind (1946) reports that diplospory in *Rudbeckia* is pseudogamous, Battaglia (1946a) describes divisions of the sperm nucleus within unreduced egg cells giving rise to chimeric progeny. Strict pseudogamy in *Rudbeckia* is contested, however, as apomictic development in *Rudbeckia fulgida* Aiton appears to proceed without fertilization of the polar nuclei (Jeff Carmichael, University of North Dakota, pers. comm.).

Madieae (Arnica)

Diplosporous apomixis is documented for *Arnica* (29 sp.) in *A. alpina* (L.) Olin & Landau, *A. chamissonis* Less., and *A. diversifolia* Greene (=*A. ovata* Greene)(Afzelius 1936; Flovik 1940). Polyploidy is rampant in the genus and strongly correlated with apomictic reproduction (Barker 1966). The evolutionary and geographical relationship between sexual cytotypes and polyploids in the genus in North America is explored by Wolf (1980) and more recently for *A. cordifolia* by Kao (2007).

Eupatorieae (Ageratina, Campovassouria, Chromolaena, Eupatorium, Gyptis, Praxelis)

Cytological observations for triploid *Ageratina adenophora* (Spreng.) R. King and H. Robins. indicate diplosporous apomixis (Holmgren 1919; as *Eupatorium glandulosum* H.B.K.). Apomixis is further implicated, but not proven, for additional triploid congeners with poor pollen production including *A. rothrockii* (A. Gray) R. King and H. Robins., *A. bustamenta* (DC.) R. King and H. Robins., *A. pichinchensis* (H.B.K.) R. King and H. Robins., and *A. riparia* (Regel) R. King and H. Robins. (King *et al.* 1976; Jansen and Stuessy 1980; Robinson *et al.* 1989; Watanabe *et al.* 1995). Apomixis is hypothesized to be common and to have played a role in the diversification of the >200 species in the genus (King *et al.* 1976)

Campovassouria is a monotypic genus of southern South America. Apospory and parthenogenetic embryo development are documented for triploid ($2n=3x=30$) *C. cruciata* (Vell.) R. King & H. Robins. by Coleman and Coleman (1984). This taxon is highly variable morphologically (King and Robinson 1987), a facet commonly linked with apomictic reproduction.

Diplosporous apomixis may be common in the large South American genus *Chromolaena* (King and Robinson 1987) and has been documented cytologically for *C. laevigata* (Lam.) R. King and H. Robins (Bertasso-Borges and Coleman 2005), *C. odorata* (L.) R. King and H. Robins (Coleman 1989), *C. callilepis* (Schultz-Bip. ex Baker) R. King and H. Robins (Coleman and Coleman 1984), and *C. squalida* (DC.) R. King and H. Robins (Coleman and Coleman 1988).

Diplosporous apomixis is also common in *Eupatorium*. The trait is described cytologically for triploid *E. pilosum* Walt. and *E. altissimum* L. and, based on irregular pollen, is inferred for several additional species (Sullivan 1976). The geography and evolution of apomixis in *Eupatorium* is explored by Sullivan (1976), Watanabe (1986), and Yahara (1990).

Investigation has documented diplospory, parthenogenetic embryo formation, and abnormal pollen production for triploid *Gytis pinnatifida* Cass. (Rozenblum *et al.* 1988). The systematic analysis of apomixis in the genus awaits further study.

Triploid *Eupatorium pauciflorum* H.B.K. [=*Praxelis pauciflora* (H.B.K.) R. King and H. Robins.] reproduces via diplosporous apomixis (Bertasso-Borges and Coleman 1998). In addition, polyploid *Praxelis kleinioides* (H.B.K.) Schultz-Bip is similarly thought to be apomictic based on the occurrence of univalents in microsporogenesis (Robinson *et al.* 1989).

Genera (46) of Asteraceae for which evidence of effective apomixis is inadequate

The following details 46 genera in 16 tribes for which apomixis has been implicated but for which the evidence either does not indicate apomixis or the evidence is incomplete (**Table 2**). In sum, apomixis appears to be likely but is incompletely documented for seven genera (*Achillea*, *Ayapana*, *Bahia*, *Leibnitzia*, *Soliva*, *Stevia*, *Thymophylla*), contra-indicated for 30 genera, and equivocal for nine genera. Tribes are listed in the order that they appear in **Fig. 1**.

Mutisieae (Gerbera, Leibnitzia)

Gerbera jamesonii Adlam, is one of the progenitors of the widely cultivated gerbera daisy *G.* × *hybrida* and a model organism for floral development. Apospory is cited for *G. jamesonii* by Davis (1967) based on Maheswari Devi (1957), and somatic embryos can be induced from capitula following chemical treatment (e.g., Srivastava and Sharma 2005). However, *Gerbera* is described as consisting of diploid outcrossing perennial herbs and these are used in well developed crossing programs (Teeri *et al.* 2006). While

Table 2 Prospects for confirming apomixis in 46 genera of Asteraceae in addition to those 22 genera for which evidence is robust (Table 1). '+': evidence points to eventual confirmation of apomixis; '-': evidence indicates that effective apomictic reproduction is unlikely. '?': data limited, but apomixis is possible. See text for discussion. Tribes arranged in the order that they appear in **Fig. 1**.

Tribe	Indication for apomixis	Tribe	Indication for apomixis	Tribe	Indication for apomixis
I. Mutisieae		VII. Astereae		XIII. Bahieae	
Gerbera	-	*Amphiachyris*	-	*Amauriopsis*[a]	+
Leibnitzia[a]	+	*Bellis*	-	XIV. Heliantheae	
II. Cardueae		*Eurybia*	-	*Helianthus*	-
Carthamus	-	*Felicia*	-	*Monactis*[a]	?
Centaurea	-	*Grindelia*	-	*Kingianthus*[a]	?
Cirsium	-	*Solidago*	-	*Tithonia*	-
III. Lactuceae		*Symphyotrichum*	-	*Tridax*	-
Cichorium	-	VIII. Anthemidae		XV. Millerieae	
Hypochaeris	-	*Achillea*	+	*Melampodium*	?
Krigia[a]	?	*Artemisia*	-	XVI. Eupatorieae	
Leontodon	-	*Leucanthemum*	-	*Ageratum*	-
Microseris[a]	?	*Soliva*[a]	+	*Ayapana*	+
Picris	-	IX. Inuleae		*Eitenia*[a]	?
Scorzonera	-	*Laggera*	?	*Stevia*[a]	+
Youngia	-	X. Coreopsideae			
IV. Vernonieae		*Bidens*	-		
Elephantopus	-	*Coreopsis*	-		
V. Senecioneae		XI. Neurolaeneae			
Petasites	-	*Calea*[a]	?		
VI. Calenduleae		XII. Tageteae			
Calendula	-	*Chrysactina*[a]	?		
Castalis	-	*Thymophylla*[a]	+		
Dimorphotheca	-				

[a] Twelve genera not included in previous reviews of apomixis in the Asteraceae. Thirty-four other genera implicated in previous reviews (**Table 1**). Three new accepted generic records for apomixis (*Campovassouria*, *Gyptis*, *Praxelis*) occur in **Table 1**.

aposporous gametophytes may be produced on occasion or can be induced, apomixis is unlikely to be a component of the natural breeding system of the species. The diagnosis of *Gerbera* as apomictic in Davis (1967), Czapik (1996), and Carman (1997) is unwarranted.

On the other hand, Nesom (1983) reports that cleistogamous capitula produced by tetraploid (2*n*=34) *Leibnitzia* produce seed apomictically because embryos are observed prior to anthesis. *Leibnitzia* is unusual in that the floral syndrome of chasmogamous flowers suggests descent from a self-pollinating ancestor, a mode of evolution that is considered to be rare (Grant 1981). Cytological documentation of the origin of embryos is necessary to validate apomixis for *Leibnitzia*, and further biogeographic and phylogenetic analysis is warranted to document the evolution of the trait in the genus.

Cardueae (Carthamus, Centaurea, Cirsium)

Carthamus tinctorius L. is cited as aposporous by Pullaiah (1984) based on developmental abnormalities in ovules observed by Maheswari Devi and Pullaiah (1977). Chromosome counts (FNA 2006, 19: 180) indicate that the species is diploid (2*n*=2*x*=24), however, and it thus appears that apomixis is not a regular part of natural reproduction of the species.

Based on reports of apospory for *Centaurea cyanus* L. and *C. scabiosa* L. by Bergman (1935), Poddubnaja-Arnoldi (1976) and Czapik (1954), the genus *Centaurea* is reported as possessing capacity for apomictic reproduction in reviews of Davis (1967), Pullaiah (1984), Czapik (1996), and Carman (1997). However, the original report indicates aposporous female gametophytes but absence of parthenogenesis, as noted by Gustafsson (1946-1947). Furthermore, both species are predominantly diploid with 41 of 44 counts (from TROPICOS) occurring at the diploid level. Therefore, it is likely, barring substantiation of effective apomixis, that reproduction in *Centaurea* is not apomictic.

Cirsium is reported as aposporous by Czapik (1996) without specific attribution. While *Cirsium* species are noted for hybridization and production of complex patterns of morphological variation (e.g., FNA 2006, 19: 95-97), and breeding system for the genus is generally poorly known (Kelch and Baldwin 2003), apomixis is not implicated for any species group, nor is it mentioned in cytological literature for the genus (Moore and Franklin 1969). In sum, the available evidence is consistent with the conclusion that while the Cardueae may exhibit elements of apomictic reproduction, apomictic reproduction is not a regular part of the breeding system of the tribe.

Lactuceae (Cichorium, Hypochaeris, Krigia, Leontodon, Microseris, Picris, Scorzonera, Youngia)

Apospory for chicory (*Cichorium intybus* L.), documented by Longly (1984), is interpreted to be only occasional or induced by Asker and Jerling (1992), and thus is not a regular part of the breeding system of the species. In addition, in nature the species is regularly diploid (FNA 2006, 19: 222) and outcrossing with no evidence for apomixis (Cichan 1983). Therefore the diagnosis of apomictic reproduction for the species in Carman (1997) appears to be unwarranted. The origin of the report of diplosporous apomixis in *Cichorium* by Czapik (1996) is unknown, but it may be an erroneous reference to the original studies cited above. Similarly, Pullaiah (1984) cites the rare occurrence of apospory for *Hypochaeris radicata* L. based on an unpublished thesis and a short meeting abstract. The species is uniformly diploid, however, with 2*n*=8 (FNA 2006, 19: 299). In the absence of additional data it is therefore unlikely that effective apomixis is realized in the species.

Apomixis is suggested for annual species of *Krigia* (Kim and Turner 1992). High seed set despite emasculation is observed for *K. wrightii* (A. Gray) K.L. Chambers ex K.J. Kim, *K. occidentalis* Nutt., and *K. cespitosa* (Raf.) K.L. Chambers. Pollen quality is apparently normal for these taxa, however, and embryo development has not been investigated cytologically.

Apospory is reported for *Leontodon hispidus* L. (Bergman 1935). However, Gustafsson (1946-1947) notes the absence of parthenogenetic development, which indicates that apospory does not lead to seed production in the genus. Furthermore, *L. hispidus* is diploid with 2*n*=2*x*=14. Thus, the reports of apomixis in *Leontodon* perpetuated in reviews of Battaglia (1951), Pullaiah (1984), Czapik (1996) and Carman (1997) are unwarranted.

Apomixis is suggested for tetraploid *Microseris forsteri* Hook. [=*Microseris scapigera* (A. Cunn.) Schultz-Bip.] based on the occurrence in that taxon of irregular and distorted pollen grains that remain clumped together despite prolonged acetolysis (Feuer and Tomb 1977). In the absence of cytological confirmation of embryo production, however, the diagnosis of apomixis is premature.

Apospory is reported for the diploid taxon *Picris hieracioides* L. (Bergman 1935). However Gustafsson (1946-1947), as recorded above for *Leontodon*, notes the absence of parthenogenetic development of aposporous egg cells. Thus the reports of apomixis in *Picris* perpetuated in reviews of Battaglia (1951), Pullaiah (1984), Czapik (1996) and Carman (1997), without further documentation, appear to be unwarranted. Abnormal megagametogenesis in *Scorzonera tausaghyz* Lipsch. & Bosse (Poddubnaja-Arnoldi *et al*. 1935) is interpreted by Pullaiah (1984) to indicate diplosporous apomixis. This observation has apparently not been confirmed.

Youngia is reported as possessing parthenogenetic development (Czapik 1996), possibly in perpetuation of the short report of Stebbins (1941) recorded by Gustafsson (1946-1947). Stebbins (1941) cites apomixis of an unknown nature for *Youngia* sect. *Crepidopsis*, based in part on Babcock and Stebbins (1937). This group of plants is apparently now included in *Crepidiastrum*, a group of 15 species of East Asia (Bremer 1994). There has been phylogenetic and cytological work for some members of this genus, e.g., Ito and Pak (1996), but investigation of apomixis in the genus has not been conducted. Study is warranted to substantiate apomixis in the genus.

Vernonieae (Elephantopus)

Czapik (1996) reports apogamety for *Elephantopus*, i.e., the development of a non-egg cell of a female gametophyte into an embryo (Grant 1981). The original reference for *Elephantopus* is not indicated. Without concomitant expression of apomeiosis, apogamety would likely be lethal, and at most represent the presence of an element, but not full expression, of apomictic reproduction. In addition, chromosome counts for *Elephantopus* indicate uniform diploidy (2*n*=22) for species world wide (FNA 2006, 19: 203; Jones 1979), indicating that effective apomixis is probably not realized in the genus. The paucity of additional reports of apomixis in the Vernonieae indicates that the trait is apparently absent in the tribe.

Senecioneae (Petasites)

Petasites is cited as aposporous (Czapik 1996). Although the original source of this observation is not identified, survey of the systematic literature (Toman 1972; Cherniawsky and Bayer 1998) does not implicate apomixis in the genus. Curiously, vegetative apomixis is cited for unisexual populations of *Petasites hybridus* (L.) P. Gaertn., B. Mey. & Scherb. (Richards 2003). Diagnosis of apomictic reproduction is as yet unwarranted for *Petasites*, and the trait is apparently very rare or absent in the Senecioneae; no other purported cases were uncovered in the scientific literature.

Calenduleae (Calendula, Castalis, Dimorphotheca)

Pullaiah (1984) cites evidence for apospory in *Calendula officinalis* L. based on a brief report, while Czapik (1996) cites evidence for apospory in *Castalis* and *Dimorphotheca* but without original attribution. Sexual reproduction in *C. officinalis* is well documented (e.g., Godineau 1969), and most species in the genus are characterized as selfing (Heyn and Joel 1983). Apomixis does not appear to be a regular part of natural reproduction for any species in the genus. *Castalis* consists of 3 species of southern Africa while *Dimorphotheca* includes seven species of southern and tropical Africa. The South African flora is notable for the paucity of Asteraceae that exhibit apomictic reproduction (Goldblatt 1973), which is at odds with the Czapik (1996) reports. Effective apomixis in Calenduleae would be notable but diagnosis of the trait in the tribe awaits further study.

Astereae (Amphiachyris, Bellis, Eurybia, Felicia, Grindelia, Solidago, Symphyotrichum)

Apospory for *Amphiachyris dracunculoides* (DC.) Nutt. in Davis (1967; as *Gutierrezia dracunculoides* (DC.) S.F. Blake) is based on a brief meeting abstract. This North American species is reported as uniformly diploid (2*n*=10; FNA 2006, 20: 88), however, indicating that the diagnosis of apomixis in this genus as perpetuated in Czapik (1996) and Carman (1997) is unwarranted.

Apospory is reported for *Bellis perennis* L. by Davis (1967) and Pullaiah (1984) based on Carano (1921). However, chromosome counts for this taxon are uniformly diploid (2*n*=18; FNA 2006, 20: 23) indicating that reports of apospory likely record developmental abnormality in the species and that diagnosis of apomixis by these authors and subsequently by Czapik (1996), and Carman (1997) is not warranted.

Apospory is reported for *Eurybia sibirica* (L.) Nesom by Poddubnaja-Arnoldi (1976; as *Aster sibiricus* L.) and reported by Pullaiah (1984). Apospory is unlikely to be effective, however, based on the fact that the taxon is uniformly diploid (2*n*=2*x*=18; FNA 1996, 20: 371).

Apospory is recorded for *Felicia amelloides* (L.) Voss. by Davis (1967) based on anatomical drawings in Dahlgren (1920; as *Aster capensis* Less.). Apospory in this genus is likely inconsequential however because chromosome counts for this species are uniformly diploid (e.g., Nordenstam 1982). Diagnosis of apomictic reproduction in the genus is unwarranted without further study.

Davis (1967) reports apospory for *Grindelia* based on an abstract in which the trait is reported for *Haplopappus ciliata* (Nutt.) DC. [=*Grindelia ciliata* (Nutt.) Sprengel] and *Grindelia lanceolata* Nutt. However, both of these North American species are uniformly diploid (2*n*=12; FNA 2006, 20: 435). If apospory does exist, it appears unlikely that it is part of the normal reproductive cycle in this genus, and the diagnosis of *Grindelia* as apomictic in Davis (1967), Czapik (1996), and Carman (1997) is unwarranted.

Gametophytes of aposporous origin in *Solidago serotina* Aiton [= *S. gigantea* Aiton] are recorded by Davis (1967) based on scrutiny of chalazal regions in the figures of Palm (1914) that otherwise record normal sexual development. Apomixis is not indicated in the species however, despite the occurrence of diploid, tetraploid, and hexaploid cytotypes (FNA 2006, 20: 157; John Semple, University of Waterloo, pers. comm.). Apomixis is also reported for *Solidago purpurea* L. by Pullaiah (1984) based on a short meeting abstract that was later published by Mukherjee and Desai (1990). The actual identity of this taxon is obscure however, the name neither appearing in the Linnean Type Collection nor in taxonomic databases at Kew Botanical Garden (Nicholas Hind, Kew Botanical Garden, pers. comm.). Verification of the identity of the plant studied by these authors is required before the significance of their report can be evaluated. Polyploid series are common in *Solidago* although odd-ploidal levels are rare and apomictic reproduction is not otherwise indictated (John Semple, University of Waterloo, pers. comm.). Apospory, if present in the genus, would appear to represent the presence of only elements of apomixis.

Davis (1967) reports apospory for *Aster novae-angliae* L. [=*Symphyotrichum novae-angliae* (L.) Nesom] based on analysis of microanatomical figures of Chamberlain (1895), Palm (1914), and Carano (1921). *Symphyotrichum novae-angliae* is uniformly diploid (2*n*=10; FNA 2006), however, and it is therefore unlikely that apomixis is a regular part of the breeding system of that species. Similarly, Davis (1967) reports apospory for *Aster undulatus* L. [=*Symphyotrichum* *undulatum* (L.) Nesom] based on figures of Operman (1904). While diploid and polyploid races have been described for this species, odd-ploidal chromosome numbers generally are rare in the genus and apomixis is not otherwise indicated (John Semple, University of Waterloo, pers. comm.).

Anthemideae (Achillea, Artemisia, Leucanthemum, Soliva)

Polyploid complexes are common among the 115 species of *Achillea* (Ehrendorfer 1959). Apomixis via apospory is described for polyploid *A. pannonica* Scheele and suggested as well for *A. collina* J. Becker ex Reich. and also *A. millefolium* L. (Terziiski *et al.* 1995). However, recent biosystematic literature describes *Achillea* as consisting of predominantly even-ploidal outcrossing populations (Guo *et al.* 2004, 2005). Odd-ploidal chromosome numbers appear in the cytological literature but are attributed to rare local hybridization between different even-ploid plants. Pentaploids in North America, furthermore, are described as being ‘almost sterile’ (Gervais 1977) or fertile but sexual (Tyrl 1975). In weighing the evidence, it would appear to be prudent to confirm the results of Terziiski *et al.* (1995) in *Achillea* prior to concluding that apomixis is definitively present in the genus.

Soliva includes annuals native to South America that now occur in many warm regions throughout the world. This genus is distinctive with the peripheral female florets lacking corollas and with a small cluster of central male florets. Analysis of reproduction in *Soliva valdiviana* Phil. and *S. ptermosperma* (Juss.) Less. in New Zealand (Lovell *et al.* 1986) indicates that pollen from the central florets is transferred to the female florets and germinates, but does not penetrate the stigma. However, seed development was only observed in cases where pollen was present on the stigmas, which is consistent with the hypothesis that reproduction in *Soliva* is apomictic but requires pollen as a developmental trigger. This would appear to represent a form of gynogenetic reproduction that has been observed in a diversity of animal lineages (Schlupp 2005) where sperm acts as a developmental trigger but does not otherwise contribute to the genetic make up of offspring. Cytological confirmation of an analogous phenomenon in *Soliva* would be a major contribution to the understanding of apomictic reproduction in flowering plants.

Numerous developmental abnormalities, including the formation of aposporous and diplosporous female gametophytes are reported for *Artemisia nitida* Bertol. (Chiargui 1926). *Artemisia* is subsequently listed with apomictic taxa by Gustafsson (1946-1947), Battaglia (1951), Davis (1967), Pullaiah (1984), Czapik (1996), and Carman (1997). Commentary by Gustafsson (1946-1947), however, notes that while the species shows ‘apomictic tendencies’ (p. 43), the plant is seed sterile and only reproduces vegetatively. Davis (1967) further cites apospory for *Artemisia tridentata* Nutt. presumably based on reexamination of drawings in Howe (1926). The Howe (1926) work does not include drawings of *Artemisia*, however, and the attribution is therefore obscure. Documentation of effective apomixis is thus lacking for *Artemisia*.

Apospory is also listed for *Chrysanthemum leucanthemum* L. [=*Leucanthemum vulgare* Lam.] and *Leucanthemum lacustre* (Brotero) Sampaio by Davis (1967) based on reinterpretation of figures of Goldflus (1898-1899). The genus is subsequently implied to be apomictic by Czapik (1996) and Carman (1997). Polyploidy is rampant in *Leucanthemum* (Villard 1970), but effective apomixis has not been demonstrated in the genus.

Inuleae (Laggera)

Laggera is closely related to the apomictic genus *Blumea*, and apomixis is cited in Pullaiah (1984) for *Laggera alata* (D. Don) Sch.Bip. ex Oliv. and *Laggera aurita* (L. f.) Benth. ex C.B. Clarke based on short meeting abstracts. Chromosome records for *Laggera alata* and *L. aurita* are consistently diploid 2*n*=20, however (e.g., Gupta and Gill 1981; Mathew and Mathew 1988), so the evidence for apomixis appears to be equivocal. The occurrence of apomixis in *Laggera* needs to be verified.

Coreopsideae (Bidens, Coreopsis)

Apospory is reported by Davis (1967) for *Bidens tripartita* L. based on analysis of figures in Dahlgren (1920). *Bidens* is subsequently listed as apomictic in Czapik (1996) and Carman (1997). *Bidens tripartita* possesses a uniform tetraploid chromosome number (2*n*=4*x*=48; FNA 2006, 21: 217) and thus lacks the diversity of chromosome numbers that might be expected were apomixis manifest. Self-compatibility, but not apomixis, is demonstrated for a diversity of *Bidens* species (Mensch and Gillett 1972; Roberts 1983; Grombone-Guaratini *et al.* 2004). However, occurrence of abnormal microsporogenesis is provided as possible evidence for apomixis for the widespread tetraploid species *B. connata* Muhl., *B. frondosa* L., and *B. vulgata* Greene (Crowe and Parker 1981). One must conclude that the evidence overall for effective apomixis in *Bidens* is equivocal until conclusive cytological and genetic investigations have been conducted to substantiate the Dahlgren (1920) and Crowe and Parker (1981) observations.

Apospory is cited for *Coreopsis bicolor* by Gustafsson (1946-1947), Battaglia (1951), and Pullaiah (1984) based on the report of Gelin (1934). According to Turner (1960), this usage refers to *Coreopsis tinctoria* Nutt. Gustafsson (1946-1947) reflects the comments of Gelin (1934) in noting that although the species exhibits apospory, it lacks parthenogenetic embryo formation. This indicates that the aposporous gametophytes are nonfunctional, and therefore the species lacks effective apomixis.

Neurolaeneae (Calea)

Apomixis is reported for *Calea hispida* (DC.) Baker (= *C. triantha* (Velloso) Pruski; Pruski 2005) in Werpachowski *et al.* (2004) based on observation of seed production following emasculation. The species is cytologically poorly known, but apomixis is not reported in the taxonomic literature for this species (Pruski 2005). Further cytoembryological documentation and biosystematic work is warranted before apomixis is conclusively diagnosed.

Tageteae (Chrysactinia, Thymophylla)

Thymophylla tenuiloba (DC.) Small is an annual herb in the southern United States and Mexico. The distribution of chromosome counts for this taxon shows geographically restricted diploid populations and widespread triploids (2*n*=3*x*=24) (Strother 1989). Triploids in this species have very poor pollen but high seed set. Apomixis has also been presumed for triploid *T. acerosa* (DC.) Strother (Carr *et al.* 1999), as well as for the triploid (2*n*=3*x*=45) populations of the related species *Chrysactinia mexicana* A. Gray (Strother 1989). The Tageteae is a well defined group concentrated in the arid New World comprising 22 genera and 225 species (FNA 2006, 21: 222; as subtribe Pectidae). Although Strother (1989) argues that apomixis is widespread in the tribe, and the occurrence of the trait would appear to be highly likely, apomixis has not been documented cytologically.

Bahieae (Amauriopsis)

Amauriopsis dissecta (A. Gray) Rydberg [=*Bahia dissecta* (A. Gray) Rydberg] is a widespread taxon in western North America (FNA 2006, 21: 392). According to Keil *et al.* (1988), high seed set is observed for triploid plants (2*n*=3*x*=36). Anatomical documentation of apomictic development is wanting, however.

Heliantheae (Helianthus, Kingianthus, Monactis, Tithonia, Tridax)

Given its economic importance for seed and oil production, apomixis in the genus *Helianthus* would be extremely noteworthy. Apospory is reported for *Helianthus maximilliani* Schrad. in Davis (1967) because review of anatomical figures of Goldflus (1898-1899) suggested aposporous development. Similarly, apospory in *H. annuus* is cited in Pullaiah (1984) based on Poddubnaja-Arnoldi (1976), and is described as a rare event in cultivated sunflower lines by Ustinova (1976). However, both *H. annuus* and *H. maximilliani* are uniformly diploid (2*n*=34), however, with no reports of polyploidy (Heiser *et al.* 1969). In addition, *H. annuus* is used extensively in breeding programs and in evolutionary genetic studies based on its ability to reproduce sexually. It is apparent that apomixis is not a barrier to these crossing studies, and therefore one must conclude that reports of apospory in *Helianthus* must refer to the rare production of nonfunctional aposporous gametophytes that are of no significant consequence to the natural breeding system of the genus.

Similarly, apospory is recorded for *Tithonia* (Pullaiah 1978). However, Pullaiah (1984) notes that gametophytes of aposporous origin fail to produce embryos. Chromosome numbers for *Tithonia* (FNA 2006, 21: 139) are uniformly diploid indicating that aposporous female gametophyte formation in this genus is likely inconsequential.

Apospory was also observed in the embryo sac of a diploid specimen of the Mexican species *Tridax trilobata* (Cav.) Hemsl. (Hjelmqvist 1951). Subsequently, this taxon appears in lists of apomictic taxa in Pullaiah (1984), Czapik (1996), and Carman (1997). However, Hjelmqvist (1951) notes that mature aposporic gametophytes were never observed, and therefore effective apomictic seed production was apparently never achieved. The related species *T. procumbens* is regularly tetraploid (2*n*=4*x*=36) and is a pantropical weed. But pollen in *T. procumbens* is apparently regular and apomixis has not been implicated for the species (Powell 1965).

The occurrence of apomixis has also been proposed for the South American genera *Kingianthus* (2 spp.) and *Monactis* (20 spp.) (Robinson *et al.* 1981). These taxa are polyploid and exhibit abnormal microsporogenesis and anther development. Apomixis has not been investigated cytologically in these taxa.

Millerieae (Melampodium)

A report of apomixis for *Melampodium divaricatum* (Rich.) DC. appears in the review of Pullaiah (1984). It is based on Maheswari Devi and Pullaiah (1976) who observe, for a strain grown locally in gardens, a high frequency of aposporous female gametophytes (among other developmental disturbances) as well as high pollen sterility. The chromosome number of the plant studied is not reported, however, and while parthenogenetic embryo development is claimed to account for ca. 80% of seed formed, seed viability and variation of progeny is not documented. This is a weedy taxon of South American origin that now occurs in the United States, Central America, and Old World tropical regions (FNA 2006, 21: 35). However, chromosome numbers for this taxon are uniformly diploid (2*n*=24), and taxonomic revision of the genus (Stuessy 1972) does not implicate apomixis for the species. In addition, although complex patterns of polyploidy and interploidal hybridization are inferred for *M. cinereum* DC. and *M. leucanthum* Torr. & A. Gray of western North America, triploids are rare, and apomixis is not otherwise indicated (Stuessy *et al.* 2004). It is possible that *M. divaricatum* represents a rare case of apomixis at the diploid level, but this would have to be confirmed with genetic markers. Until that work is done, the diagnosis of apomictic reproduction in *Melampodium* is not warranted.

Eupatorieae (Ageratum, Ayapana, Eitenia, Stevia)

Ayapana is a genus of 14 species occurring in South America and the West Indies. Diplosporous apomixis was recorded for *Ayapana triplinervis* (Vahl) R. King & H. Robins. (as *Eupatorium triplinerve* Vahl) based on a one page abstract. Chromosome number data is generally wanting for this genus (King *et al.* 1976), and no other indication of apomixis has been published. Similarly, occasional production of aposporous initials is reported for *Ageratum* in Pullaiah (1984) based on Mitra (1947), but effective apomixis is not otherwise indicated for the genus. The occurrence of apomixis has also been proposed, because of irregular microsporogenesis, for *Eitenia* (2 spp.), a taxon related to *Praxelis* that occurs in Brazil (King and Robinson 1987). The trait remains to be documented, however.

Stevia includes approximately 240 species of annuals, perennials, subshrubs, and shrubs in North America and South America. According to Grashoff *et al.* (1972), apomixis is widespread among the perennial herbaceous species. Evidence is based on the widespread occurrence of triploid and tetraploid cytotypes (2*n*=3*x*=33; 2*n*=4*x*=44), microsporogenesis that commonly includes univalent formation, and poor pollen quality. Apomixis is implicated for *Stevia serrata* Cav., *S. elatior* Kunth, *S. viscida* Kunth (Grashoff *et al.* 1972) and also for *S. latifolia* Benth. (Ralston *et al.* 1989). Further, Soejima *et al.* (2001) documents the contrasting distributions of triploid to hexaploid (presumably apomictic) versus diploid (presumably sexual) cytotypes in Mexico for each of *S. nepetifolia* H.B.K., *S. oligophylla* Soejima and Yahara, *S. origanoides* H.B.K., *S. ovata* Willd. and *S. triflora* DC. Confirmation of mode of female gametophyte formation is required to establish with certainty the presence and mode of apomixis in the genus. The geographic and phylogenetic extent of apomixis in the genus may well show that *Stevia* is one of the richer centers of apomixis evolution in the Asteraceae. *Stevia* is also noteworthy because it represents the evolution of the trait at lower latitudes whereas most examples of apomixis in the family occur at higher latitudes.

DISCUSSION

The Asteraceae is commonly cited as one of the three families, along with Poaceae and Rosaceae, as including frequent examples of apomixis. Apomixis is well documented in the family dating to the studies of *Antennaria* and *Hieracium* in the 1890s. Gustafsson (1946-1947) described effective apomixis for 11 genera (*Chondrilla*, *Crepis*, *Hieracium*, *Ixeris*, *Taraxacum*, *Antennaria*, *Erigeron*, *Parthenium*, *Rudbeckia*, *Arnica*, and *Ageratina* (as segregated from *Eupatorium*). These 11 genera have provided important models for the ecology, evolution, and genetics of apomixis, and most have inspired well developed research programs.

A total of 22 genera of Asteraceae are herein considered to be apomictic. This means that since Gustafsson (1946-1947), apomixis has been well documented for only 11 additional genera. Five of these document apomixis in *Eupatorium* (s.l.) segregates, including *Ayapana*, *Chromolaena*, *Gyptis*, *and Praxelis*, as well as *Eupatorium* (s.s.). The other six genera include instances detailed by Davis in the 1960s (*Brachyscome*, *Calotis*, *Minuria*), *Townsendia* and *Leontopodium*, for which apomixis was discovered in the 1950s, and *Blumea* for which apomixis was detailed in 1984. The record thus shows a doubling of known genera with apomixis since Gustafsson (1946-1947), and thus at a rate of about 2 genera per decade. At this rate, and in the absence of a targeted effort to document additional cases of apomixis in the Asteraceae, it may be well past the middle of the present century before apomixis is confirmed for the 16 genera for which the trait is considered likely or plausible (**Table 2**).

The phylogenetic distribution of well documented cases of apomixis in the Asteraceae (**Fig. 1**) indicates that six out of seven of the tribes that show the trait occur in the subfamily Asteroideae. Apomicts of the Lactuceae (Cichorioideae) are unique in lying outside of the Asteroideae. In considering also the seven cases for which apomixis is likely but not fully documented, the overall phylogenetic pattern changes little, with nine of 11 tribes residing within the Asteroideae. In fact, phylogenetic consideration shows the Asteroideae to be a rich center for apomixis evolution, with over half of the 19 Asteroideae tribes recognized by Funk *et al.* (2005) exhibiting the trait. However, there is no apparent phylogenetic clustering of the trait within the subfamily. One interpretation of this pattern is that subsequent to the early divergence of the tribe Senecioneae, which apparently lacks the trait, a developmental or genetic pattern evolved that predisposed the remainder of the subtribe to evolve apomixis. It would be fruitful to conduct comparative analysis of reproductive development of Senecioneae versus other Asteroideae to discern a possible evolutionary transition at that node. Traits of interest might include, for instance, pattern of sexual megagametophyte development that could reflect ectopic or heterochronic shifts related to those observed in apomicts (Carman 1997), or capacity for autonomous endosperm, which might allow a lineage to bypass the restrictive 2:1 maternal to paternal endosperm genome ratio of sexual taxa en route to evolving apomictic reproduction (van Dijk and Vijverberg 2005).

Interestingly, ancient polyploidy is thought to have occurred with the split of the Athroismeae from the Heleniea-Heliantheae-Eupatorieae clade within the Asteroideae (Baldwin *et al.* 2002). Furthermore, ancient polyploidy has been implicated as a factor in the evolution of anomalous gametophyte developmental patterns and apomixis (Carman 1997). However, this ancient polyploidy event does not appear to explain the distribution of the trait in the Asteroideae, as four tribes with confirmed apomixis in the subfamily (Anthemideae, Astereae, Gnaphalieae, Inuleae) reside outside of the polyploid clade (**Fig. 1**)

The occurrence of apomictic reproduction within a taxonomic group can be explained by independent origins, single origin and interspecific spread of the trait through introgressive hybridization, or single origin and inheritance vertically from a common ancestor (van Dijk and Vijverberg 2005). Among tribes of Asteraceae, evolutionary distance would support the argument that apomixis has evolved independently in each. Within tribes, however, the question of number of origins is less certain. In *Erigeron*, for instance, apomixis readily moves between species via introgressive hybridization (Noyes and Rieseberg 2000), and intergeneric spread is well documented in grasses (de Wet and Harlan 1970). In the Lactuceae, it has been proposed that *Taraxacum* and *Chondrilla*, which are closely related but genetically isolated, may share apomixis through common ancestry (van Dijk 2003). The breadth of evolutionary alternatives indicates that robust estimates of number of origins of apomixis may require tests of trait homology at the molecular level.

In the present analysis, diplosporous apomixis in the Asteraceae is represented by 18 genera and aposporous apomixis by five genera. Both modes appear to occur only in *Hieracium*. The predomination of diplospory in the Asteraceae is counter to previous reviews in which apospory was claimed to be more common than diplospory in the family (Davis 1967; Czapik 1996). The conclusion of Czapik (1996) that apospory and diplospory commonly occur together in the same genus is also not supported. Review indicates that cited cases in *Parthenium* and *Antennaria*, for instance, likely reflect rare or nonfunctional apospory in otherwise diplosporous taxa. While additional proposed cases require investigation, for instance in *Erigeron* (see above), for the most part it appears to be rare for both apospory and diplospory to evolve within the same genus.

The apparent absence of apomixis in the tribes Cardueae, Senecioneae and Vernonieae is notable, as these comprise 310 genera and 6800 species and thus a sizeable fraction of the family. The absence of apomixis in these taxa is inexplicable without further genetic and developmental analysis, but it is clear that comparisons of apomictic and non-apomictic tribes within a phylogenetic setting could yield evolutionary insight. The apparent absence of the trait from early diverging tribes of the family is also notable, indicating that capacity for apomictic reproduction likely did not occur with the origin and early diversification of the family, which likely occurred in South America (Funk *et al.* 2005). Documentation of apomixis in *Leibnitzia* (Mutisieae) would greatly expand the phylogenetic breadth of the trait in the family.

Many proposed cases of apomixis cited by Davis (1967) and Pullaiah (1984) are here rejected. Some of the examples, including *Artemisia*, *Centaurea*, *Coreopsis*, *Leontodon*, and *Picris*, are included even though both the original works and Gustafsson (1946-1947) clearly indicate that each lacks the ability to make seed and are therefore not effective apomicts. Ten additional putative cases of aposporous apomixis, in *Amphiachyris*, *Bellis*, *Felicia*, *Grindelia*, *Gerbera*, *Helianthus*, *Leucanthemum*, *Solidago*, *Symphyotrichum*, and *Tridax* are gleaned by Davis (1967) from older descriptions that only hint at aposporous-like gametophyte development. Similarly, of the 15 genera added by Pullaiah (1984) to the tally of apomictic Asteraceae, 10 are herein rejected (*Ageratum*, *Ayapana*, *Calendula*, *Carthamus*, *Eurybia*, *Hypochaeris*, *Laggera*, *Melampodium*, *Scorzonera*, *Tithonia*). In each case the plants are either diploid, and apparently functionally sexual, or the data otherwise are incomplete in their demonstration of apomictic reproduction. Both Davis and Pullaiah are cytoembryological specialists with expertise in female gametogenesis, so it is natural that each emphasizes rare and exceptional phenomena. However, the conclusion one arrives at from reading their reviews is that apomixis is common, only waiting to be discovered through cytological observation of heretofore sexual species. The conservative approach here posits that the burden lies with proving complete apomictic reproduction in each case, not just by demonstrating abnormal ovule development or elements of apomixis. Unfortunately, many of the poorly supported instances of apomixis listed by Davis (1967) and Pullaiah (1984) then appear in the summary reviews of Czapik (1996) and Carman (1997) without critical evaluation of the evidence. These give the false impression of rampant apomixis in the Asteraceae. For Carman (1997), this means that many of the geographic and genetic correlations for the evolution of apomixis and derived gametophyte types in the Asteraceae are either erroneous or obscured. For Czapik (1996), the tally of 44 apomictic genera for Asteraceae in comparison with the total number of Asteraceae genera studied cytologically indicates that many more cases would be discovered if only more surveys of development were conducted. However, apomictic reproduction is not cryptic, in the sense that it is commonly correlated with characteristic chromosomal and taxonomic complexity. Therefore, if one is looking to document apomixis, it doesn't make sense to study any or all Asteraceae with unknown developmental patterns, although this may be interesting in and of itself. Instead, those taxa with extensive polyploidy, especially odd polyploidy, should be targeted as likely candidates for apomictic reproduction.

The significance of aposporous gametophyte formation noted for many diploid taxa in the Asteraceae is a fascinating problem that shouldn't be ignored, however. At an extreme, these observations may be inconsequential, merely developmental aberrations with no bearing on reproduction in natural populations. Certainly in the large genera *Helianthus* and *Symphyotrichum*, for instance, the occurrence of rare aposporous initials does not appear in anyway to be correlated with the manifestation of apomictic reproduction in either genus. On the other hand, thorough documentation using genetic techniques could show that apomixis at the diploid level is much more common than assumed, perhaps serving a role in reproductive assurance. The burden, however, lies with proving that a proportion of the offspring produced by these taxa are diploid genetic clones. Many of the examples rejected herein could provide a springboard for future study of this phenomenon.

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