

# Ecological and evolutionary opportunities of apomixis: insights from *Taraxacum* and *Chondrilla*

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The ecological and evolutionary opportunities of apomixis in the short and the long term are considered, based on two closely related apomictic genera: *Taraxacum* (dandelion) and *Chondrilla* (skeleton weed). In both genera apomicts have a wider geographical distribution than sexuals, illustrating the short-term ecological success of apomixis. Allozymes and DNA markers indicate that apomictic populations are highly polyclonal. In *Taraxacum*, clonal diversity can be generated by rare hybridization between sexuals and apomicts, the latter acting as pollen donors. Less extensive clonal diversity is generated by mutations within clonal lineages. Clonal diversity may be maintained by frequency-dependent selection, caused by biological interactions (e.g. competitors and pathogens). Some clones are geographically widespread and probably represent phenotypically plastic 'general-purpose genotypes'.

The long-term evolutionary success of apomictic clones may be limited by lack of adaptive potential and the accumulation of deleterious mutations. Although apomictic clones may be considered as 'evolutionary dead ends', the genes controlling apomixis can escape from degeneration and extinction via pollen in crosses between sexuals and apomicts. In this way, apomixis genes are transferred to a new genetic background, potentially adaptive and cleansed from linked deleterious mutations. Consequently, apomixis genes can be much older than the clones they are currently contained in. The close phylogenetic relationship between *Taraxacum* and *Chondrilla* and the similarity of their apomixis mechanisms suggest that apomixis in these two genera could be of common ancestry.

**Keywords:** asexual; geographical parthenogenesis; clonal diversity; mutation accumulation; ancient asexuals

## 1. INTRODUCTION

Apomixis is asexual reproduction through seeds. Gametophytic apomixis has been reported in 140 angiosperm genera (Carman 1997), suggesting that this form of apomixis has arisen many times in the history of the angiosperms. It is generally accepted that apomixis can flourish over short time-scales. Theoretically, a dominant apomixis gene would spread to fixation in an outcrossing population of hermaphrodites (Charlesworth 1980; Marshall & Brown 1981).

However, apomixis has not played an important role in the evolution of the angiosperms. It has not led to extensive radiation; it has been estimated that only one in 1000 angiosperm species is apomictic (Mogie 1992). There are no completely apomictic genera in the angiosperms (Stebbins 1950). Phylogenetically, apomixis has a 'twiggy' distribution. Extant apomicts always have closely related sexual taxa, and can often be crossed with these, apomicts acting as pollen donors. Darlington (1939) and Stebbins (1950) argued that apomixis has limited evolutionary potential and that apomicts are doomed to early extinction.

In this article, the short-term and the long-term ecologi-

cal and evolutionary opportunities of apomixis will be illustrated by two closely related genera with apomixis in the Asteraceae family (Compositae), namely *Taraxacum* (dandelion) and *Chondrilla* (skeleton weed). It will be argued that the success of apomicts in the long run depends critically on their ability to cross with sexual relatives and that this enables apomixis to survive much longer time periods than generally thought.

## 2. APOMIXIS IN *TARAXACUM* AND *CHONDRILLA*

The genera *Taraxacum* and *Chondrilla* are species aggregates, variable in breeding system, ploidy level and degree of reproductive isolation. They are perennial hemicryptophytes belonging to the tribe of the Lactuceae. *Taraxacum* is found in disturbed grounds, meadows and woods throughout Europe (Richards & Sell 1976; figure 1). *Chondrilla juncea* occurs in dry open habitats, and has a southern distribution in Europe; northwards into northern France and southern central Russia (Iljin 1930; Sell 1976; figure 2). Both genera also occur in Asia and may have their origin in the Himalayas (Richards 1973). The weedy dandelions have been introduced by humans in all continents, with the exception of Antarctica. *Chondrilla* is introduced in Australia, and North and South America.

The most obvious morphological differences between *Taraxacum* and *Chondrilla* are the shape of the scape and the inflorescence (capitulum). The scape in *Taraxacum* is

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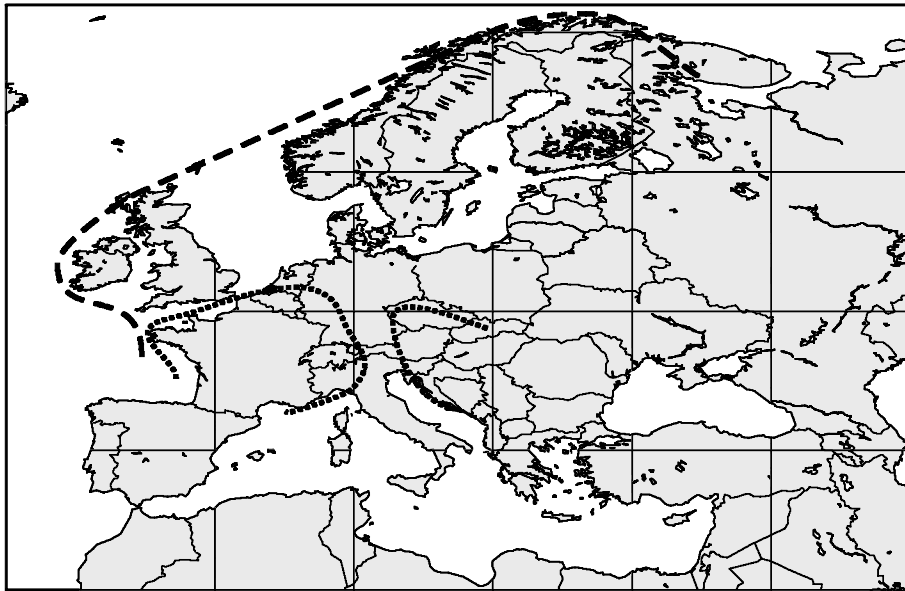


Figure 1. The geographical distribution of sexual and apomictic types in the weedy dandelions (*Taraxacum* section *Ruderalia*) in Europe, based on Menken *et al.* (1995). The dashed line indicates the northern distribution limit of apomictic dandelions, the dotted line that of the sexual dandelions. Note that within the sexual range apomicts also are found. The distributions of sexual and asexual types in the south of Europe are not sufficiently known.

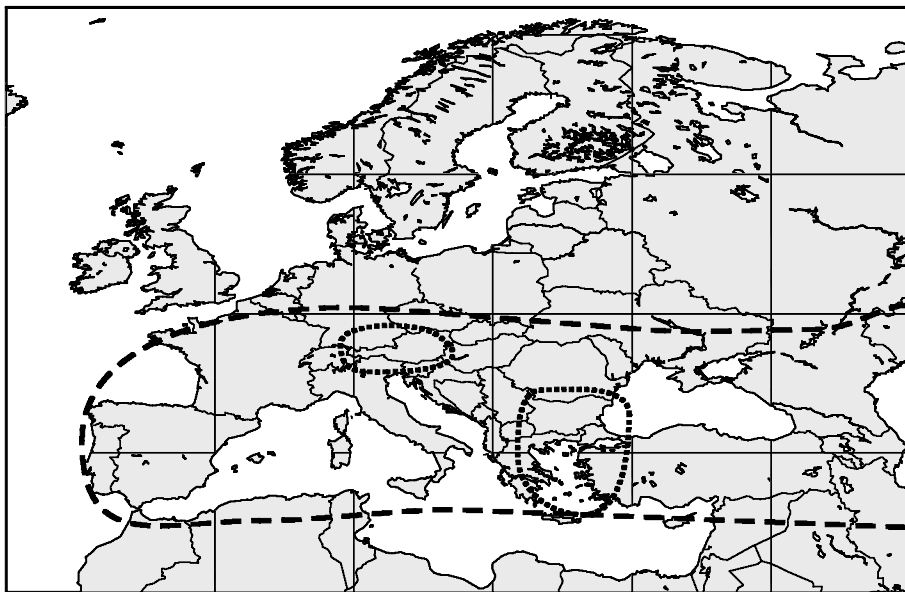


Figure 2. The geographical distribution of sexual and apomictic types in *Chondrilla* in Europe, based on chromosome numbers published in Goldblatt & Johnson (1978–2000), Poddubnaja-Arnoldi (1933), Chaboudez (1994) and Chaboudez & Burdon (1995), assuming that diploids are sexuals and triploids are apomicts. The dashed line indicates the northern distribution limit of apomictic *Chondrilla*, the dotted line the range of the sexual *Chondrilla*. Diploids belong to the species *C. pauciflora* (= *C. urumoffii*) and *C. chondrilloides*.

non-branched, without leaves; that of *Chondrilla* is branched with leaves. The capitulum of *Taraxacum* is large (100–200 florets), solitary and terminal, whereas that of *Chondrilla* is small (9–12 florets) terminal, lateral or axillary, and sometimes produced in groups (Richards & Sell 1976; Sell 1976). The fruits are achenes (single-seeded fruits), with a long rostrum and pappus, providing highly effective dispersal by wind (Sheldon & Burrows 1973). *Taraxacum* and *Chondrilla* are phylogenetically closely related, based on morphology (Bremer 1994) and chloroplast DNA restriction site variation (Whitton *et al.* 1995).

The basic chromosome number in *Chondrilla* is five, in *Taraxacum* eight. Sexuals are always diploid (*Chondrilla*:  $2x=10$ ; *Taraxacum*:  $2x=16$ ) and are generally self-incompatible (Poddubnaja-Arnoldi 1933; Okabe 1956). Apomicts are always polyploids, commonly triploid (*Chondrilla*:  $3x=15$ ; *Taraxacum*:  $3x=24$ ). Apomixis involves meiotic diplospory: a restitution nucleus is produced during meiosis I, followed by a normal meiosis II (Bergman 1950; Nögler 1984). Of the two resulting unreduced megaspores one degenerates and the surviving unreduced megaspore forms an unreduced embryo sac with an unreduced egg cell. This unreduced egg cell then

develops parthenogenetically into an embryo. The endosperm develops without fertilization, directly from the central cell nucleus (autonomous endosperm development). Most *Taraxacum* apomicts are obligate apomicts, but facultative or partial apomixis, with some sexual seed set, has also been reported (Richards 1973).

### 3. THE GEOGRAPHICAL DISTRIBUTION OF SEXUALS AND APOMICTS

Figure 1 shows the geographical distributions of sexual and apomictic weedy dandelions in Europe. Figure 2 shows the same for skeleton weed. The general picture is clear: apomicts have a much wider distribution in both genera. In *Taraxacum*, apomicts dominate the northern regions; in *Chondrilla*, apomicts dominate the western and eastern parts. The distributions, however, are not parapatric; in large parts sexuals and apomicts can be found growing together. Different geographical distributions of sexuals and parthenogens are common in animals and plants (Bell 1982; Bierzychudek 1987); this phenomenon is known as geographical parthenogenesis (Vandel 1928). In Europe, *Taraxacum* shows a more or less classic north–south contrast of geographical parthenogenesis and a similar north–south contrast occurs in *Taraxacum* in Japan (Morita 1976).

Several hypotheses have been put forward to explain the tendency for asexuals to occur farther to the north in the Northern Hemisphere. It has been suggested that asexuals are confined to environments with limited biotic interactions (Levin 1975; Glesener & Tilman 1978; Bell 1982). In these regions apomicts could replace sexuals owing to their intrinsic reproductive advantage; however, in areas with complex communities, sexuals would dominate because they can keep up the coevolutionary arms race with antagonists or because sexuals are better in filling narrow and specialized niches. Another hypothesis assumes that temporally varying environments select more effectively for phenotypically plastic genotypes 'general-purpose genotypes' in apomictic populations than in sexual populations. Apomicts could therefore occupy more extreme and fluctuating, marginal environments (Lynch 1984). Alternatively, Peck *et al.* (1998) pointed out that interbreeding with maladapted immigrants erodes local adaptation in sexual populations, which creates an advantage for asexual reproduction. Therefore asexuals are more likely to replace sexuals when local productivity is low and immigration rates are relatively high, which is the case in the northern regions of the Northern Hemisphere.

Whereas the hypotheses outlined above relate geographical parthenogenesis to environmental heterogeneity, it may also be explained by different historical colonization patterns. Apomictic populations may have expanded more rapidly from the refuges at the end of the Pleistocene than sexual populations (Stebbins 1950), autonomous apomicts, like *Taraxacum* and *Chondrilla*, can start a new population from a single colonist, whereas sexual outcrossers need at least two colonists. The two centres of sexual dandelions in Europe (see figure 1) could reflect expansion from an Iberian and a Balkan Pleistocene refuge at the end of the Pleistocene. The non-classic west–central–east contrasts in *Chondrilla* are difficult to explain by the

environmental hypotheses and may also reflect idiosyncratic historical colonization patterns.

Human introductions of weedy dandelions to North America and of skeleton weed to America and Australia always involve apomicts, suggesting that these indeed are better colonizers than sexuals. *Chondrilla* has become a serious weed of cereal cultivations in Australia and is a target for biological control (Burdon *et al.* 1981).

Because apomixis is intimately associated with polyploidy it is possible that the underlying cause for geographical parthenogenesis is primarily a difference in ploidy level, rather than a difference in breeding system (Bierzychudek 1987). Different geographical distributions between diploids and polyploids are also often observed in strictly sexual plant species (Stebbins 1950; Van Dijk *et al.* 1992).

### 4. CLONAL DIVERSITY

Allozyme, and more recently DNA marker, studies have demonstrated that apomictic *Taraxacum* and *Chondrilla* populations are highly polyclonal within their native range. At the smallest scale, within sites (such as pastures, meadows and roadsides) many clones co-occur. Menken *et al.* (1995) reported between 7 and 16 clones in 11 pasture samples in *Taraxacum* in western and central Europe, in the area where sexuals and apomicts are sympatric (sample size between 14 and 79 plants per population). Because only four polymorphic allozyme loci were used, this is likely to be an underestimation of the number of clones. Van der Hulst *et al.* (2000) applied AFLP markers to estimate clonal diversity in *Taraxacum* in meadows in The Netherlands and Denmark, respectively, 150 and 750 km north of the nearest known sexual population, and between 28 and 34 different AFLP genotypes were found in sample sizes ranging from 61 to 65 plants.

The patterns of clonal diversity found in *Chondrilla* resemble those found in *Taraxacum*. High clonal diversities were found in 16 purely apomictic populations in western Turkey (Chaboudez & Burdon 1995). In small samples of 17 individual plants per site, the number of genotypes ranged from 2 to 11, based on 8 polymorphic loci. In a regional study, sampling 123 apomictic *Chondrilla* populations with 1 plant per population in central Turkey, 6 polymorphic loci distinguished 91 clones (Chaboudez 1994). However, only 3 clones were detected in 23 populations in southeast Australia, where *Chondrilla* was introduced from Europe at the beginning of the twentieth century, indicating a strong founder effect (Chaboudez 1994).

Most genotypes in these studies were confined to a single population, but widespread clones have been found in both genera. One six-locus *Chondrilla* genotype was spread over more than 700 km in eastern Turkey (Chaboudez & Burdon 1995), and Van der Hulst *et al.* (2000) reported two AFLP types occurring in a Dutch and a Danish meadow, separated by 600 km. Widespread clones have also been detected by allozyme studies in non-weedy *Taraxacum* (Van Oostrum *et al.* 1985; Battjes *et al.* 1992). Such widespread clones are probable candidates for general-purpose genotypes, as they will experience a wide range of environments. Their wide distribution must have been achieved over many generations by wind disper-

sal and because of the relatively small sample sizes in studies so far, and the high clonal diversities in populations, it is unclear whether widespread clones are common in *Chondrilla* and *Taraxacum*.

## 5. WHAT CAUSES CLONAL DIVERSITY?

Clonal diversity may be due to: (i) mutations within asexual lineages, generating satellite clones; or (ii) crosses, generating daughter clones. Mutations in asexual lineages may comprise 'normal' mutations (e.g. substitutions, chromosomal rearrangements) and the products of autosegregation (Gustafsson 1947*a*; Richards 1996*a*). Chromosomal rearrangements may cause position effects, such as silencing of genes. Examples of autosegregation are the loss of chromosomes because of incomplete nuclear restitution or because of anaphase bridges, leading to disomics ( $3x - 1$  (Sørensen & Gudjonsson 1946)). Autosegregation may also be due to crossing-over during diplospory, resulting in homozygosity at the chromosomal regions distal to the crossover (Darlington 1939). King & Schaal (1990) reported mutations at ribosomal DNA and alcohol dehydrogenase loci in apomictic progenies of *Taraxacum*. Mes *et al.* (2002) found AFLP, allozyme and microsatellite variation within a widespread North European clone in the *Taraxacum* section *Naevosa*.

In general, the changes caused by mutation will be small. Much larger changes involve the formation of new daughter clones via hybridization, and because *Chondrilla* and *Taraxacum* are hermaphrodites, apomicts can act as pollen donors in crosses with facultative apomicts and with sexuals. A part of the progeny in such crosses is apomictic (Richards 1973; Tas & Van Dijk 1999).

In regions where sexuals and apomicts are sympatric, crosses between sexuals and apomicts can generate new apomictic clones. In purely apomictic regions new apomictic clones can arise locally in crosses between facultative apomicts; however, facultative apomixis in *Taraxacum* is rare and the probability of euploid offspring in a cross between two triploids is very low. Perhaps it is more likely that clones in the purely apomictic regions originated in the regions where sexuals and apomicts are sympatric and have spread since then. The occurrence of widespread clones in *Taraxacum* and *Chondrilla* indicates that clones can disperse over large distances over time. Stebbins (1950) has suggested that if new clones arise via crosses in sympatric ranges, clonal diversity will decrease further away from the sexual regions. In *Taraxacum* high levels of clonal diversity are still found in Denmark, at 750 km north of the nearest known sexual population (Van der Hulst *et al.* 2000). This clonal diversity may represent a dynamic equilibrium between immigration of newly formed clones from the south and local extinction of old clones, due to evolutionary processes discussed below.

## 6. ECOLOGICAL DIFFERENTIATION BETWEEN CLONES

New clones can only establish when they find an empty niche, different from those occupied by the sexuals and the other clones. According to the 'frozen niche variation' model (Vrijenhoek 1984), apomixis fixes only a small part of the sexual gene pool and therefore freezes only a small

part of the niche occupied by the sexuals. Interclonal selection between clones with overlapping niches will result in a partitioning of the ecological space.

Various studies have indicated that coexisting *Taraxacum* clones are ecologically differentiated. As early as 1928, Sukatschew experimentally demonstrated that three dandelion clones that co-occurred in a meadow near St Petersburg reacted differently with respect to density and intraspecific competition (Sukatschew 1928). Similar experiments were conducted by Solbrig & Simpson (1974, 1977) showing that coexisting clones differed in reproductive capacity and response to competition and disturbance. In transplant experiments, Vavrek *et al.* (1996) demonstrated that eight coexisting clones differed in their seasonal development, resulting in differences in competition capacity from other plant species. Over the whole year there were no differences in fitness between these clones, but phenological differentiation promoted clonal coexistence (Vavrek *et al.* 1996, 1998).

In *Taraxacum* little is known about the effect of pathogens on the clonal structure of populations. However, the rust fungus *Puccinia chondrillina* has been used for biological control of *Chondrilla* in Australia (Burdon *et al.* 1981). The introduction of *Puccinia* caused a shift in the frequency of the three *Chondrilla* clones: one sensitive clone decreased but two others increased in frequency. In Turkey, within the native range of apomictic *Chondrilla*, the most frequent clones in populations were over-infected by *Puccinia* (Chaboudez & Burdon 1995). In a detailed study of one Turkish population, Espiau *et al.* (1998) detected eight different resistance phenotypes among 19 *Chondrilla* plants and seven *Puccinia* pathotypes among 15 isolates (Espiau *et al.* 1998). Such biotic interactions have the potential to affect clonal diversity. The distribution of *Taraxacum* and *Chondrilla* clones in populations is typically L-shaped, with a few common and many rare clones (Chaboudez & Burdon 1995; Menken *et al.* 1995). This may be the result of frequency-dependent selection, driven by biotic interactions.

## 7. THE FUTURE OF CLONES

The occurrence of widespread clones in the native range and the successful introduction to other continents illustrate the ecological success of apomictic clones in *Chondrilla* and *Taraxacum*: clearly in the short term apomixis can be successful. In the long term, however, asexual lineages are considered as evolutionary dead ends (Darlington 1939; Maynard Smith 1978; Judson & Normark 1996).

One reason for their early extinction may be that clones cannot adapt well to changing environments, because they lack genetic variation. The rate of adaptation depends on the level of genetic variation. This may be especially important in the coevolutionary arms race with pathogens (the Red Queen hypothesis (Hamilton 1980; Bell 1982)), as illustrated by the *Chondrilla-Puccinia* studies mentioned above.

Another factor that may contribute to the early extinction of clones is degeneration due to an increasing mutation load. Muller's ratchet is the idea that the class with fewest slightly deleterious mutations gets lost by chance in small asexual populations (Muller 1964). This class is then lost forever, because it cannot be recreated

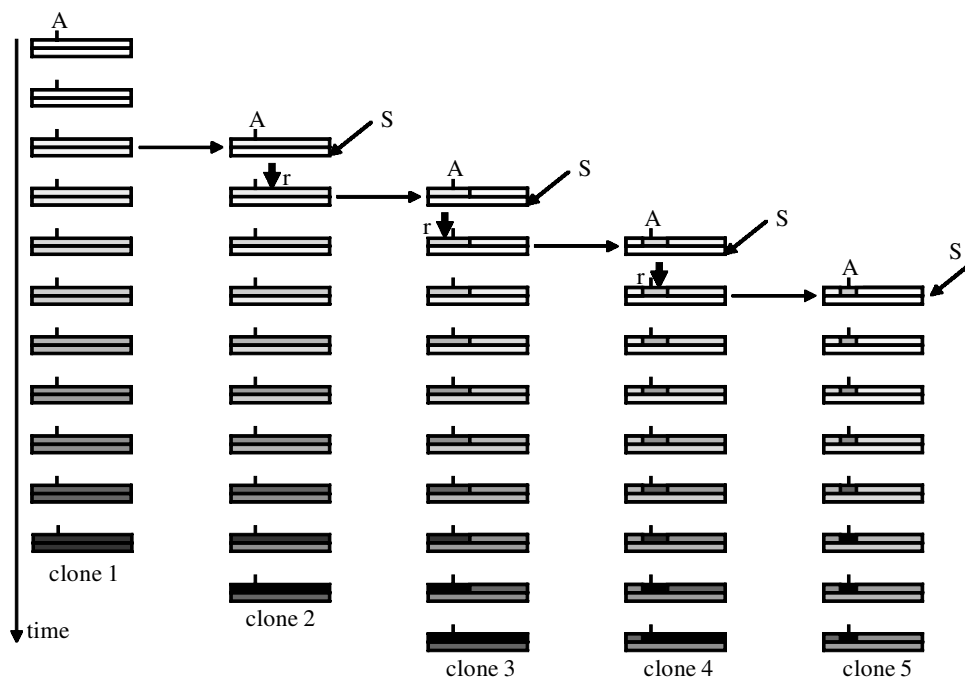


Figure 3. Scheme showing how an apomixis gene (dominant A) can move to a genomic background of a recent sexual history via introgression. For simplicity a diploid with a single chromosome is indicated. The intensity of the shading of the chromosomes indicates the length of the asexual history. New clones arise through crosses between sexuals and apomictic pollen donors. The arrow with S represents a chromosome drawn from the sexual gene pool. The arrow with 'r' indicates a crossover during pollen meiosis in the apomictic clone. Owing to repeated backcrosses and crossing over, the regions closely linked to the apomixis gene (A) will have a longer asexual history than the rest of the genome of the clone and will accumulate deleterious mutations over multiple clonal generations.

by recombination as it can in a sexual population. Repetition of this process leads to a gradual accumulation of slightly deleterious mutations in asexual lineages, which could eventually lead to extinction. When the genomic mutation rate for mildly deleterious mutations is higher than one per generation, mutations will also accumulate deterministically in large asexual populations (Kondrashov 1982). If mildly deleterious mutations interact synergistically, they will not accumulate in sexual populations because these mutations can be effectively purged. The Y sex chromosomes of mammals and plants are the best examples of degeneration in the absence of recombination (Rice 1996; Charlesworth & Charlesworth 2000; Charlesworth 2002). In the long run, a similar degeneration process is expected to occur in apomictic lineages.

The fact that apomicts are polyploids has consequences for mutation accumulation: (i) the mutation rate per individual will be enhanced; and (ii) the effects of deleterious mutations will be better masked by wild-type alleles. This will result in the build-up of a higher mutation load in polyploids than in diploids. Accumulation of deleterious mutations in asexuals is inevitable, but polyploidy will slow down the rate of degeneration.

Unfortunately there are no reliable age estimates of *Taraxacum* clones. Based on their wide and disjunct geographical distribution, Gustafsson (1947b) assumed that certain microspecies in *Taraxacum* could be more than 100 000 years old. Menken *et al.* (1995) found that sexual and apomictic dandelions shared the major allozyme polymorphisms, and that null and private alleles in triploid apomicts were rare. This suggests a recent origin of these clones, at least not older than a few million years.

## 8. ANCIENT APOMIXIS GENES

Apomixis in *Taraxacum* is controlled by two dominant loci: one for unreduced egg cells (diplospory) and one for parthenogenesis (Richards 1973; Van Dijk *et al.* 1999; Van Dijk & Bakx-Schotman 2003). When a new apomictic clone is formed in a cross between a sexual and an apomictic pollen donor, the apomixis genes will move to a new genetic background. This new genetic background can potentially be adaptive and provides new opportunities for the apomixis genes, when the environment is changing (Mogie 1992).

Because the maternal genome of the new apomictic clone is drawn from a sexual gene pool, this genome will be largely freed from deleterious mutations. In a new triploid clone only one of the three genomes will be derived from the sexual genome pool; however, repeated backcrossing over several clonal generations will result in the introgression of the apomixis genes into the sexual genetic background. The apomixis genes become associated with genomes with low genetic loads. Crossing over during pollen meiosis will also remove linked deleterious mutations on the chromosomes on which the apomixis alleles are located. This process is illustrated in figure 3. Meanwhile, the original clones in which the apomixis genes were contained may degenerate owing to accumulation of deleterious mutations and eventually become extinct.

For such a cleansing cycle to work, the frequency of backcrossing should be sufficiently high compared with the rate of deleterious mutation accumulation. Moreover, it will work only in crosses between sexuals and apomicts,

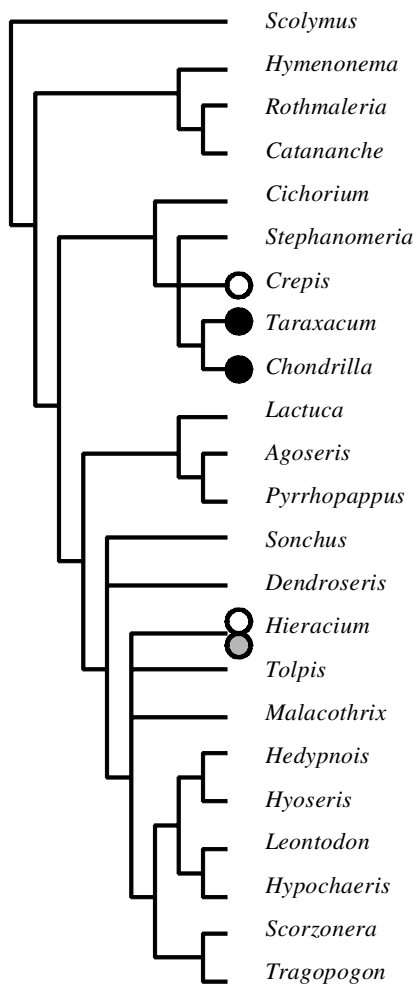


Figure 4. The taxonomic distribution of various types of apomixis in the tribe of Lactuceae (Asteraceae), based on the morphological phylogeny of Bremer (1994). Apomixis was not included in the cladistic analysis. The black circles indicate meiotic diplospory, the grey circle indicates mitotic diplospory and the open circles indicate apospory.

and not in crosses between two facultative apomicts. In the latter case the new apomictic lineage will inherit the mutational loads of the two apomictic parental lineages.

Is there any indication for a high mutation load in *Taraxacum*? In sporophytic polyploid tissue recessive deleterious mutations will be masked by wild-type alleles. However, recessive lethals will become expressed in haploid pollen grains when apomictic triploids are crossed with diploid sexuals. In crosses between diploid sexual and triploid apomictic *Taraxacum* significantly fewer diploid hybrids than triploid hybrids have been reported, suggesting that haploid pollen indeed is less viable than diploid pollen (Morita *et al.* 1990; Tas & Van Dijk 1999).

Nogler (1984) has suggested that apomixis genes are recessively lethal in pollen grains and that therefore apomixis genes can be transmitted only in a heterozygous state in diploid pollen, but not in a homozygous state in haploid pollen. This could explain why diploidy and gametophytic apomixis in general are incompatible. However, apomixis genes in *Taraxacum* are dominant, not recessive (Richards 1973; Van Dijk & Bakx-Schotman 2003). Richards (1996b) has suggested that it is not the apomixis genes themselves but linked recessive lethals that

are responsible for the non-transmission of apomixis genes via haploid pollen grains. This is what is expected to happen according to the introgression scheme in figure 3. As the probability of a crossover between two loci is positively correlated with their physical distance, chromosomal regions close to the apomixis genes have a lower probability of becoming cleansed. Therefore, deleterious mutations are expected to accumulate over clonal generations around apomixis genes. Consistent with this expectation, microsatellite markers that are linked to the diplospory locus in *Taraxacum* show severe segregation distortion in haploid pollen grains, but not in diploid pollen grains (P. J. van Dijk, unpublished results).

## 9. THE FUNCTION OF POLLEN IN *TARAXACUM* AND *CHONDRILLA*

Most apomictic species are pseudogamous, meaning that pollen is necessary for fertilization of the central nucleus in order to develop endosperm. Pollen, however, has no function for seed production in autonomous apomicts like *Taraxacum* and *Chondrilla*. A mutation causing male sterility has no negative effect on seed fertility. On the contrary, if resources no longer needed for pollen production could be allocated to seed production, such a mutation would increase fertility. Functionless characters are expected to degenerate over time. Nevertheless, more than 80% of all British *Taraxacum* microspecies continue to produce pollen (Richards 1986) and in addition they produce functionless yellow petals and most of them nectar. According to Maynard-Smith (1978, p. 41) 'it is difficult to suggest any explanation of these facts, other than that these clones may be relatively recent in origin, and that evolutionary adaptation in asexual populations is slow, so that maladapted features are retained'.

However, pollen production makes sense in the light of new clone formation. Male-sterile clones cannot generate new apomictic daughter clones in crosses with sexuals. Such male-sterile clones may become extinct through insufficient adaptability or an increasing mutation load. Only pollen-fertile apomicts can produce new daughter clones, which will then inherit the pollen function from their apomictic fathers (Mogie 1992). Not only do most apomictic dandelions produce pollen, pollen meiosis is in general also reductional, in contrast to female meiosis, which is restitutional (diplospory). Clones producing only unreduced pollen grains are known in *Taraxacum* (Richards 1973) and in *Chondrilla* (Bergman 1950), but are not common. A reductional male meiosis makes sense in the light of new clone formation: a diploid pollen grain from a triploid apomict produces a new triploid apomict in a cross with a sexual diploid. An unreduced triploid pollen grain, however, would result in a new tetraploid apomict in such a cross. With unreduced pollen meiosis each new clonal generation would have an elevated ploidy level compared with the previous one. Such lineages would 'polyploidize themselves out of existence' (Stebbins 1950, p. 389) and become extinct.

## 10. THE EVOLUTION OF MEIOTIC DIPLOSPORY IN THE ASTERACEAE

The primary evolution of the meiotic diplospory type of apomixis is likely to be a rare event, because at least two

mutations must be combined that individually are deleterious. Diplospory alone generates offspring with increasing ploidy levels, which will polyploidize itself out of existence within a few generations; however, parthenogenesis alone generates haploid offspring with low fitness. Consequently, strong selection is expected against these individual mutations and the chances that these mutations are simultaneously present in a population, and will be combined by intercrossing, are very remote.

However, when apomixis genes can continuously move to new adaptive and clean genetic backgrounds, apomixis genes could thus survive long periods of time and can be ancient. Bergman (1950) stated that 'the restitution mechanism in *Taraxacum* corresponds in all essentials with that of *Chondrilla*'. Could apomixis in these two genera have a common ancestry? Figure 4 shows the occurrence of meiotic diplospory plotted on a morphological phylogeny of the Lactuceae tribe. This shows that meiotic diplospory is clustered within the subtribe of the Crepidineae, to which also *Ixeris*, a third genus with meiotic diplospory, belongs (Nogler 1984; Carman 1997). According to the phylogeny, common ancestry of meiotic diplospory in *Taraxacum*, *Chondrilla* and *Ixeris* is a possibility. Alternatively, meiotic diplospory in these genera evolved independently three times, implying a predisposition for the evolution of meiotic diplospory in the subtribe of the Crepidineae.

Common ancestry of apomixis in *Taraxacum* and *Chondrilla* could be due to hybridization or to a common apomictic ancestor, predating the split between the two genera. Hybridization between *Taraxacum* and *Chondrilla*, however, has never been reported. Given the different chromosome base numbers (five and eight) and the regular ploidy series (10, 15, 20 and 16, 24 and 32), it seems unlikely that common ancestry would be due to hybridization.

Recently, it has been suggested that the divergence between alleles at a locus can be used for the estimation of clonal age (Birky 1996; Judson & Normark 1996). Owing to genetic drift, ASD in a sexual population is restricted, whereas ASD in an asexual organism is, in principle, unlimited (Birky 1996). On the basis of ASD, Lahn & Page (1999) were able to detect four episodes of suppression of recombination on the human X-chromosome. Using ASD, Welch & Meselson (2000) have provided evidence that the bdelloid rotifers have been without sexual recombination for tens of millions of years. Chromosomal regions close to the apomixis genes will have an ancient history of asexual reproduction (figure 3). By contrast, other parts of the clonal genome will have a recent history of asexual reproduction. Therefore, if apomixis genes are indeed ancient and clones recent, a high ASD is to be expected in the vicinity of the apomixis genes and a low ASD is expected in other parts of the clonal genome.

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### Discussion

S. C. H. Barrett (*Department of Botany, University of Toronto, Toronto, Canada*). We have learnt a considerable amount about the evolution of selfing from phylogenetic data, particularly concerning multiple origins and whether selfing lineages persist in evolutionary time. Selfing and apomixis share some similarities but I am unaware of a significant literature on the comparative biology and phy-



logeny of apomixis. Are you familiar with any studies in which apomixis has been mapped onto phylogenies?

P. J. van Dijk. I am not aware of any attempts to conduct this type of study but it would be valuable. (Loren Reisberg pointed out a study that he and a student had published in *American Journal of Botany* in which apomixis was mapped onto a phylogeny.)

R. Vinkenoog (*Department of Biology and Biochemistry, University of Bath, Bath, UK*). An autonomous apomictic 3x dandelion develops a purely maternal endosperm without any paternal contribution. How does it overcome the imprinting problem? One possibility is that in *Taraxacum* (both sexual and apomictic) there is no (strong) imprinting system present. What is known about this?

Have interploidy crosses between sexual 2x and Nx plants been done, and what do they tell us about imprinting in *Taraxacum*?

P. J. van Dijk. Diploid–tetraploid crosses have been made in the 1940s and 1950s by various people, all indicating that 3x plants are easy to obtain in either cross direction. Moreover, Brink and Cooper have shown that early embryo growth is independent of the development of the endosperm. This indeed suggests that there is no (not much) imprinting in *Taraxacum*.

#### GLOSSARY

AFLP: amplified fragment length polymorphism

ASD: allele sequence divergence