

Evolution of the Species of *Narcissus*: A Review

Dr. John David

Introduction

Abílio Fernandes published a paper in 1975 in which he laid out his ideas about the evolution of species in the genus *Narcissus*. It was, to some extent, the summation of his many years of research on the genus and one that relied heavily on chromosome data. The paper, of course, predates the application of molecular analysis to problems of evolution and systematics that took place from the 1990s onwards. What is perhaps remarkable is how much of the system put forward by Fernandes remains valid today. Remarkable because observations made by Fernandes in that paper seem to foreshadow the complexities of the evolution of daffodils that molecular data have revealed.

Any discussion about the evolution of species has to begin with the age-old problem of “splitters” and “lumpers”: a problem that has had its consequences for *Narcissus* and as a result caused much confusion among those who are not taxonomists, but like to study the genus in the wild or want to use the correct names. It should be self-evident that there is no hard and fast rule on whether someone’s new species is acceptable or not; nor is there a supreme authority sitting in judgement on any new species that are proposed. The only tests are the strength of the supporting evidence and acceptance by those who work with the genus. Splitters tend to give greater weight to minor variations which lumpers will tend to regard as part of a continuous range of variation that can be encompassed within a species. For instance, depending upon your approach, the genus has between 30 and 80 species. Fernandes (1968) recognised 62; Blanchard (1990)

included 64 and Mathew (2002) listed 86 species. These are the three most 'recent' comprehensive surveys of *Narcissus*. Webb (1980) in his account for Flora Europaea only accepted 26 species and in Aedo's recent treatment in Flora Iberica (Aedo, 2013), has 25 species occurring in Spain. This is a world apart from the kaleidoscopic rearrangements of the genus published by Fernández Casas over the last twenty years with new species being published almost every year. In some cases, molecular data have been used to examine where segregate species have been recognised based on morphology. A good example is in the *N. nevadensis* group, where both Jiménez *et al.* (2009) and Medrano *et al.* (2014) found that *N. segurensis*, *N. alcaracensis* and *N. yepesii*, described as new species by Ríos *et al.* (1999), were indistinguishable from *N. nevadensis*.

For *Narcissus*, a further problem is the readiness with which species, even quite distantly related species, hybridise. A large number of interspecific hybrids have been named; a situation complicated by whether the parent species are narrowly defined (species splits) or broadly circumscribed, so that the name used depends upon which species concepts are accepted. Aedo (2013) helpfully lists the hybrid names according to the species he recognises, together with their synonymous hybrids. Because many of these hybrids occur in the wild and back-cross just as readily with either parent, a range of variation between the parents and the hybrids arises which not only can confuse the taxonomy of the parents, but also give rise to further species or varieties being described when the hybrid nature of the plants is not realised. This process is known as introgression and has been revealed by DNA sequencing where one species will be found to have small amounts of genetic material from another, although there is no outward expression of the presence of that genetic material. These can arise where hybridisation has taken place in the past but is no longer happening.

Although it has been long recognised that *Narcissus* was in need of a comprehensive and thorough revision, for various reasons in addition to those discussed above, there had been no move to undertake such work.

The advent of molecular methods to gain a better understanding of the evolution of the genus and the relationships of the species has provided a basis for attempting a new revision. Work is ongoing at the moment in Spain and in the UK to study each of the sections in turn, and when this is complete, bring all the results together to produce a monograph. The first phylogenetic study of *Narcissus* was that by Graham and Barrett (2004), who sampled over 30 different species, and it is in this paper we see the first indications of the complexities in the origin of the species groups (sections) and some of the species. In this article I will discuss the main species groups and their relationships as revealed principally by the work of Graham and Barrett (2004), Santos-Gally *et al.* (2012) and an unpublished chapter from Isabel Marques's doctoral dissertation (Marques, 2010).

Impact of molecular methods

Before doing this, it might be useful to say something about the origin of *Narcissus* based on molecular data. Meerow *et al.* (2000) showed that broadly the main lineages in the *Amaryllidaceae* evolved on separate continents, which he referred to as the American clade and the Eurasian clade, while the African and Australasian amaryllids are divided into four separate clades. In a later paper Meerow *et al.* (2006) provided a more detailed analysis of the Eurasian clade. The results indicated that the Mediterranean genera belonged in two groups, recognised as the tribes *Galantheae* and *Narcisseae* (Figure 1). The latter contains two genera: *Sternbergia* and *Narcissus*. These are the only two to have carotenoid pigments in their flowers, in that both have yellow flowers, among the Mediterranean amaryllids. Meerow *et al.* (2006) suggested that the Mediterranean amaryllids originated in North Africa and the Iberian Peninsula. This is where the greatest diversity of *Narcissus* species occurs.

Pancratium is a sister genus to *Narcissus* and *Sternbergia*, although this relationship is not well supported in the molecular analysis. This may appear surprising given that *Pancratium* has a conspicuous corona and

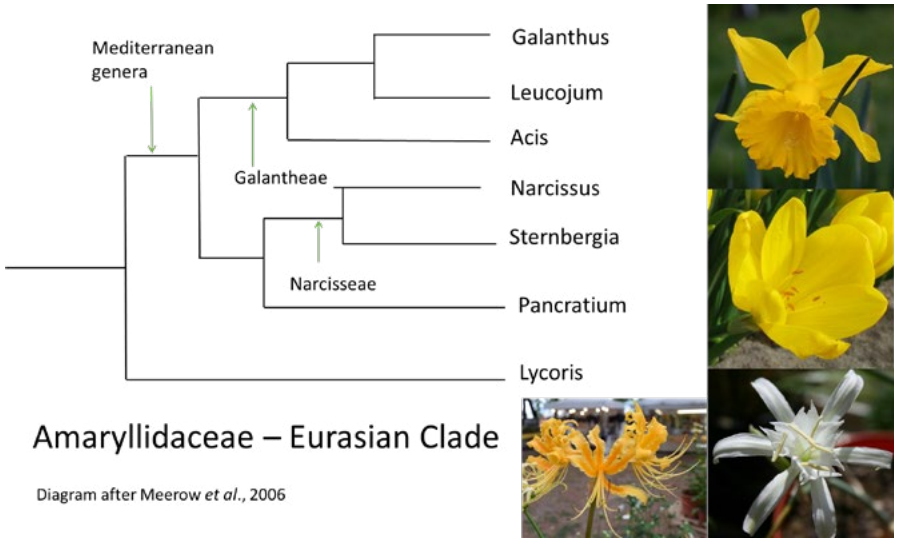


Diagram after Meerow *et al.*, 2006

Figure 1. Diagram of the phylogenetic relationships between the major genera of Eurasian Amaryllidaceae, after Meerow *et al.*, 2006.

Sternbergia does not. However, the corona in *Pancratium* has a different origin to that in *Narcissus*. In the former genus the corona is derived from the staminal filaments and appears to be an adaptation to pollination by sphingid moths (Meerow *et al.*, 2006). The origin of the corona in *Narcissus* seems to be unique, in that it is a late development from the tissues between the perianth (tepals) and the stamens (Waters *et al.*, 2013). It is not homologous with the corona in *Pancratium* and seems to have been independently developed. The corona is significant in that it is a defining characteristic of the genus and once evolved has undergone various alterations to give rise to the diversity of forms we see among the species today. What is also possibly of interest is that the corona in *Narcissus* initiates as six separate groups of cells. This may be why it has proved possible to breed the split-corona cultivars.

What has proved surprising in the phylogenetic trees derived from the analysis of DNA sequences in Graham and Barrett (2004), and has been confirmed by subsequent analyses including more species and a greater number of samples (Santos-Gally *et al.*, 2012; Marques 2010), is the appear-

ance of groups of species that are classified on morphological grounds in one section, in parts of the tree well away from the rest of their section. This occurs in a number of sections: *Tazettae*, *Jonquillae*, *Bulbocodii* and *Pseudonarcissi*. These anomalies, or incongruences, in Marques (2010) seem to be linked to ancient hybridisation events. The evidence for this is found by sequencing different types of DNA. In a plant cell there are three main types of DNA associated with the three main organelles: the nucleus, the mitochondrion and the chloroplast. The nuclear DNA will contain a combination of maternal and paternal DNA, but as the chloroplasts are always inherited from the maternal parent the DNA will reflect the contribution of the seed parent. Phylogenetic trees derived from chloroplast DNA will place most hybrids with their maternal parent, whereas those using nuclear DNA can end up with either the pollen parent or the seed parent. This gives rise to mismatches between the trees that are usually explained by hybridisation. There are other explanations, such as horizontal gene transfer, but as hybridisation is so common in plants this is the most likely cause of such anomalies.

A relatively recent development in molecular methods is using estimated rates of change in DNA to arrive at approximate dates when lineages diverged. This is sometimes referred to as the molecular clock. Using this approach, Santos-Gally *et al.* (2012) provided estimated dates for the divergence of *Narcissus* and *Sternbergia* (23.6 Mya¹); the divergence of two main groups in *Narcissus*, subgenus *Hermione* and subgenus *Narcissus* (21.4 Mya), and the appearance of the sections and the species within them. These dates can be linked to major geological events in the evolution of Europe and the Mediterranean. Santos-Gally *et al.* (2012) propose that divergence of *Narcissus* and *Sternbergia* happened about the time when the African plate collided with the SW European microplate, causing a break-up of what had once been a contiguous mountain system comprising the Iberian Peninsula, the Rif and Kabylies ranges in North Africa, Corsica and Sardinia as

¹ In this paper Mya stands for million years ago.

well as southern Italy. The origin of some sections or groups of species and diversification of some species takes place some 5-6 Mya. Santos-Gally *et al.* (2012) correlate this with the period of the Messinian salinity crisis when the western Mediterranean almost dried out. This would have led to a major change in the climate of the region, bringing species back into contact that had already diverged and stimulating the evolution of new species to cope with the changed environment. This period was brought to an end by the opening of the Straits of Gibraltar about 5 Mya. The most recent major geological event has been the succession of glacials and interglacials over the last 2.6 million years during which, at the maximum extent of glaciation, sea levels fell by up to 120m and the climate of the Mediterranean would have changed, becoming cooler and wetter.

Survey of Narcissus

As indicated above, the molecular data confirm that the genus is divided into two major lineages² that correspond to the subgenera *Hermione* and *Narcissus* recognised by Fernandes (1968, 1975). While there is no neat morphological character by which the two subgenera can be separated, as Fernandes pointed out, the two lineages have different base chromosome numbers. Subgenus *Hermione* has a base number of $x=5$ ($2n=10$)³ and subgenus *Narcissus* is $x=7$ ($2n=14$). Variations of these exist arising from hybridisation and polyploidy. There is no support for the recognition of subgenus *Corbularia* for *N. bulbocodium* and related species as proposed by Mathew (2002).

² In papers on phylogeny the term clade is used for any group of taxa (such as species) that share a common ancestor. As the word 'lineage' seems more accessible, that is the term used in this article except where quoting from another paper.

³ It is interesting to note that in *Sternbergia* the base chromosome number is either $x=10$ or $x=11$ (although *S. sicula* is said to be $x=9$). Fernandes (1975) speculated that the ancestral state in *Narcissus* was $x=6$, giving rise to the base numbers for the two subgenera either by loss or gain of a single chromosome. In *Pancretium* it is $x=11$.

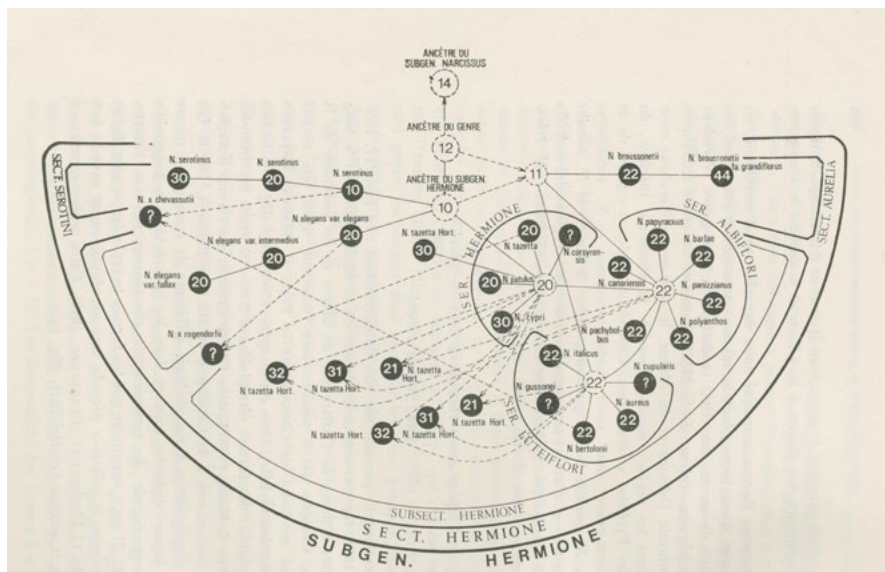


Figure 2. Diagram of evolutionary relationships for Subgenus *Hermione* as conceived by Abilio Fernandes (1975).

Subgenus *Hermione* is generally regarded as comprising three sections (Fernandes, 1975; Blanchard, 1990), although Mathew (2002) includes the *Serotini* in his Section *Hermione* (Figure 2). Section *Aurelia*, with one species⁴ (*N. broussonetii*) (Figure 3), and Section *Serotini*, with two species, are autumn-flowering. The third section is the largest, Section *Tazettae*, where in the past many species have been recognised, although much of the diversity may well be due to hybridisation arising during domestication by Man. It is evident that species in this section attracted humans from early on, and this is reflected by their current distribution well outside the Mediterranean region, as they are now naturalised in China and Japan where they have been given the name *N. orientalis*.

Narcissus broussonetii is distinguished by the almost complete absence of a corona, which is reduced to a tiny rim around the mouth of the

⁴ Fernández Casas and Lloret i Sabaté (2012) have described a second species, *N. antiatlanticus*, from the southernmost range of the distribution of *N. broussonetii*, but the new species is doubtfully distinct.



Left: Figure 3. Aurelia: *Narcissus broussonetii*.

Right: Figure 4. Tazettae: *Narcissus papyraceus*.

perianth tube. It has in the past been thought sufficiently distinct to be treated as a separate genus (Gay, 1858). However, the molecular data consistently show this species to belong with the tazettas, associated with the other white-flowered species, *N. papyraceus* (Figure 4) and *N. pachybolbus*. Indeed Zonneveld (2008) included *N. broussonetii* in Section *Tazettae*. The reduction of the corona can be postulated as the result of an ancient hybridisation between *N. papyraceus* and a member of the *Apodanthe*, as suggested by Marques (2010) on the basis of similarities in the chromosomes, or as a result of hybridisation with *N. serotinus* (Figure 5), which also has similar chromosomes and a reduced corona. It is interesting that the published phylogenetic trees show *N. papyraceus* as the earliest diverging species in the subgenus. This might be thought to mean that the species has the ancestral characters of the genus, but this is not necessarily the case since, despite diverging early on, a species continues to evolve and adapt and can develop features quite different to the ancestral condition. Based on the observations of Meerow *et al.* (2006) it is likely that the ancestral *Narcissus* had yellow flowers⁵ and that white flowers have arisen repeatedly in *Narcissus*

⁵ This suggestion was also made by Fernandes (1975) where at the end of his paper he lists those characters he considered "primitive" and those he thought "derived."



Left: Figure 5. Serotini: *Narcissus serotinus*.

Right: Figure 6. Hybrid Tazettae: *Narcissus tortifolius*. Photo by Kálmán Könyves.

as flower colour is a simple genetic switch. Within Section *Tazettae* are two anomalous species, *N. dubius* and *N. tortifolius*. Fernandes (1937), based on studies of the chromosomes, concluded that the former represented a hybrid between *N. papyraceus* and *N. assoanus* (as *N. requienii*) that has stabilised and become fully fertile and so functions as a species. Likewise, *N. tortifolius* (Figure 6) is considered to be a hybrid of *N. papyraceus* and possibly *N. gaditanus* (Fernández Casas, 1977). The molecular data are not consistent with *N. assoanus* as a parent of *N. dubius*, as both *N. dubius* and *N. tortifolius* cluster with Section *Jonquillae* (with plastid DNA) rather than with *N. assoanus*, which is in a separate lineage (*Juncifolii*). Using the nuclear DNA, both species sit within Section *Tazettae* as expected. Based on total DNA content, Zonneveld (2008) asserted that the parents of both *N. dubius* and *N. tortifolius* are *N. papyraceus* subsp. *panizzianus* and *N. assoanus*; and while *N. tortifolius* is either triploid or tetraploid, *N. dubius* he found to be hexaploid or nonoploid.

Santos-Gally *et al.* (2012) concentrated on the Sections *Tazettae* and *Apodanthe*, contrasting evolution in the lowland *Tazettae* with the montane *Apodanthe*. Their phylogenetic tree seems to confirm the broad classification of species based on perianth colour which was suggested by Fernandes



Left: Figure 7a. Jonquillae: *Narcissus fernandesii*.

Right: Figure 7b. Jonquillae: *Narcissus viridiflorus*.

(1975) (Figure 2). However, more sampling of a greater range of named species would be helpful to resolve species delimitation in this group more firmly. Likewise, in Santos-Gally *et al.* (2012) the two species in Section *Serotini* are mixed up within the Section *Tazettae* lineage, whereas in Marques (2010) Section *Serotini* is a separate lineage, although it includes *N. elegans*, traditionally considered to be a member of Section *Tazettae*. This is almost certainly the result of the origin of *N. obsoletus*⁶ as an ancient hybrid between *N. serotinus* and *N. elegans* (Marques, Feliner, Draper Munt, Martins-Loução, & Aguilar).

Within subgenus *Narcissus* there are traditionally seven sections: the rush-leaved daffodils (*Jonquillae*), the keel-leaved daffodils (*Apodanthi*), the hoop-petticoat daffodils (*Bulbocodii*), the trumpet daffodils (*Pseudonarcissi*⁷), the poets daffodils (*Narcissus*), the bell-flowered

⁶ The name *N. obsoletus* (Haw.) Steud. is used here for the species that has also been named as *N. miniatus* (Donnison Morgan *et al.*, 2005). The choice of name depends upon the interpretation of the typification of *N. obsoletus* by Díaz Lifante and Camacho (2007) which was resolved by the designation of an epitype for the species by Aedo (2010).

⁷ Traditionally this section has been given as *Pseudonarcissus*, but it was originally published as *Pseudonarcissi* by De Candolle in Redouté, *Les Liliacées* 8, t.486 (1816) which, being orthographically correct, is adopted in this paper.



Figure 8. *Apodanthi*: *Narcissus rupicola*, *N. cuatrecasasii* and *N. watieri*.

daffodils (*Ganymedes*) and section *Braxireon* (formerly *Tapeinanthus*). Molecular analyses show that two of these sections, *Jonquillae* and *Bulbocodii*, have species in different places, while *Pseudonarcissi* splits into two distinct lineages. In the published phylogenetic trees (Graham & Barrett, 2004; Santos-Gally *et al.*, 2012), it is part of Section *Jonquillae* which is the earliest diverging group in the subgenus. This section comprises *N. jonquilla*, *N. fernandesii* (Figure 7a) and *N. viridiflorus* (Figure 7b). Grouping with these species are *N. dubius* and *N. tortifolius* as discussed previously. However, the trees in Marques (2010) show the *Apodanthi* as the earliest diverging group.

The *Apodanthi* in all the phylogenetic trees are a distinct lineage that appears not to have been affected by ancient hybridisation. Species in this group were treated for many years as Section *Jonquillae*, which in floral form they resemble, but they are often single-flowered and have leaves with keels on the outer side as well as seeds with a strophiole. As a group they are restricted to the Iberian Peninsula and Morocco and occur in upland areas, usually in dry rocky sites. There appears to be two main groups within the section: *N. scaberulus* and *N. calcicola* in one, the remainder in the other. Aedo (2013) treats *N. calcicola* as a subspecies of *N. scaberulus*. *N. cuatrecasasii* seems to be a good species, and clusters



Bulbocodii: Clockwise from Left:
Figure 9a. *Bulbocodii*: *Narcissus*
hedraeanthus; Figure 9b. *Narcissus*
bulbocodium; and Figure 9c.
Narcissus cantabricus.

with *N. albimarginatus* from northern Morocco, while *N. rupicola* is grouped with *N. marvieri* and *N. watieri*, both of which have been treated as subspecies of *N. rupicola* (Maire, 1959; Mathew, 2002) (Figure 8). *Narcissus atlanticus* clusters with *N. rupicola* or with *N. cuatrecasasii*, but how this should be interpreted is not clear.



Section *Bulbocodii* is, for such a morphologically distinct group, the most puzzling in how it clusters in the phylogenetic trees. The position of the various lineages is not consistent, and it provides the only case where a single species, *N. bulbocodium*, crops up in different lineages. For instance, in the trees in Santos-Gally *et al.* (2012), *N. bulbocodium* appears in the *Jonquillae* lineage as well as in a lineage with *N. cantabricus* and *N. hedraeanthus*. Marques (2010) sampled extensively in this section but



Left: Figure 10a. Jonquillae II: *Narcissus assoanus*.

Right: Figure 10b. Jonquillae II: *Narcissus gaditanus*. Photo by Sally Kington.

her trees show poor resolution of the species. Broadly, all that can be drawn from these trees is that *N. hedraeanthus*, *N. romieuxii* and *N. cantabricus* cluster together (Figures 9a, b, c), while the other grouping comprises the rest of *N. bulbocodium*, including *N. tingitanus*, *N. jeanmonodii* and *N. jacquemoudii* (Marques, 2010). It may be of relevance that Fernandes (1975) pointed out the wide range of chromosome numbers in this group, from the diploid $2n=14$, up to $2n=42$, 49 & 56 (octoploid) in *N. bulbocodium* var. *serotinus*; and Marques (2010) reports a chromosome number of $2n=72$ in one case. Fernandes also drew attention to the curious chromosome numbers in *N. obesus* in Portugal where both $2n=26$ and $2n=39$ (triploid) are found, suggesting a base chromosome number of $x=13$. Further molecular analysis of Section *Bulbocodii* by Könyves (2014) and Fonseca *et al.* (2015) confirmed the two different lineages in the section, with one lineage associated with Section *Jonquillae*, the other in the cluster with Sections *Pseudonarcissi*, *Ganymedes* and *Narcissus*. The lineages do not, though, show a clear morphological pattern, but there are indications that the lineages have a geographical basis, with the more southerly distributed species (*N. hedraeanthus*, *N. cantabricus* and *N. romieuxii*) being associated with the *Jonquillae* lineage and *N. bulbocodium*, in its various forms, occupy-



Left: Figure 11a. Pseudonarcissi: *Narcissus longispathus*.

Right: Figure 11b. Pseudonarcissi: *Narcisus bujei*.

ing a more northerly and westerly range. Both Könyves (2014) and Fonseca *et al.* (2015) found that *N. obesus* was genetically distinct enough to be recognised at species level (Haplotype group 3 in Könyves, 2014). Further, Könyves suggested that *N. cantabricus* subsp. *luteolentus*, transferred to *N. hedraeanthus* by Aedo (2013), is likely to be of hybrid origin, with *N. cantabricus* and *N. hedraeanthus* as parents.

Moving up the phylogenetic tree we come to a cluster of *Narcissus* sections that are linked to the other half of Section *Jonquillae*. This part of the *Jonquillae* includes *N. assoanus* (*N. requienii*) (Figure 10a) which is widely distributed across the Iberian Peninsula. Fernandes (1975) distinguished this group of species based on the chromosome pattern as Subsect. *Juncifolii* which Zonneveld (2008) has raised to a Section on account of the overall nuclear DNA content. Zonneveld (2008) notes that the amount of DNA in the *Juncifolii*, “is otherwise only found in the unrelated *N. triandrus*” (p. 122). Also included in this group is *N. gaditanus* (= *N. pusillus* of Fernandes, 1975) (Figure 10b). In the published trees (Graham & Barrett, 2004; Santos-Gally *et al.*, 2012), these two jonquils are linked to a group of trumpet daffodils comprising *N. nevadensis* and



Left: Figure 12a. Ganymedes: *Narcissus triandrus*.

Right: Figure 12b. Ganymedes: *Narcissus triandrus* (bicolor form).

N. longispathus. This group was separated by Zonneveld (2008) as Section *Nevadenses*. These species are distinctive in often having more than one flower on the scape and this may indicate the influence of the jonquils in their parentage. An intriguing species is *N. bujei*, previously treated as a subspecies both of *N. longispathus* and *N. hispanicus*. This may represent a backcross of a species in the *N. nevadensis* group on a trumpet daffodil (possibly *N. hispanicus*) (Zonneveld, 2008 & 2010) (Figures 11a, b). However, in the trees of Marques (2010), although the *N. nevadensis* group formed a distinct lineage which she refers to as “Pseudonarcissus 2” (p. 135 *et seq.*), she did not endorse the recognition of the group of species as a separate section.

Into this cluster comes the small but quite variable Section *Ganymedes* for *Narcissus triandrus* (Figure 12a, b). Species delimitation in this group has been a problem, with some preferring to recognise species (Pérez-Barrales *et al.*, 2006; Zonneveld, 2008) where others only subspecies or varieties (Webb, 1980). In the phylogenetic trees, *N. triandrus* comes out as a distinct lineage linked either to the *Juncifolii* or to *Pseudonarcissi*. This is interpreted by Marques (2010) as an indication of ancient hybrid origin of the section, as a cross between a species from both sections, a suggestion which seems to fit with the floral morphology of *N. triandrus*, and with

the observation by Zonneveld (2008) noted previously. What is interesting is that *N. triandrus* has become widespread in the Iberian Peninsula and readily crosses with a wide range of other *Narcissus* species. The other distinctive feature of *N. triandrus* is its heterostyly, which only otherwise occurs in the genus in *N. albimarginatus* (*Apodanthi*) (Graham & Barrett, 2004; Pérez-Barrales *et al.*, 2006). This is a feature that has evolved independently and must have arisen after the initial hybridisation event that created the *N. triandrus* lineage. A detailed study of populations of the *N. triandrus* in the Iberian Peninsula (Hodgins & Barrett, 2007; Hodgins & Barrett, 2008) indicates that the diversification of this group occurred during the ice ages when the species would have been confined to isolated refugia in NW Spain, south-central Spain and central Portugal. These seem to correlate with var. *triandrus* (white-flowered), var. *cernuus* (pale yellow-flowered) and var. *concolor* (deep yellow-flowered), which when treated as species become *N. pallidulus* and *N. lusitanicus* respectively. After the end of the last glaciation it is apparent that when these taxa came into contact again, hybridisation occurred, giving rise to intermediates that blur the definition of these varieties.

The final element of this cluster of sections is also a single species, the autumn-flowering *N. cavanillesii*, so different in floral morphology as to have been regarded for a long time as a separate genus; *Tapeinanthus* (1837), *Braxireon* (1838) and *Carregnoa* (1842) were all described for it. It was only transferred to *Narcissus* in 1969⁸ (Traub, 1969), and Fernandes (1975) recognised it as a member of subgenus *Narcissus* where he noted that the rudimentary corona, the short perianth tube and the yellow flowers suggest that it is a primitive member of the genus. However, Fernandes (1975)

⁸ *Tapeinanthus humilis* was transferred by Traub to *Narcissus* as *N. humilis*, which was an illegitimate name as there already was an *N. humilis* Heynh. (1841). It was given a new name, *N. cavanillesii* by Barra and López (1984). Likewise Traub used the genus name *Tapeinanthus* Herb. as the basis of Sect. *Tapeinanthus* in *Narcissus*, but the genus name is also illegitimate and hence the next available genus name, *Braxireon* Raf., was adopted for the section for *N. cavanillesii* by Valdés, *Lagascalia* 12: 274-5 (1984).



Figure 13. Braxireon: *Narcissus cavanillesii*.

also notes the strong resemblance in chromosome pattern to *N. gaditanus* (as *N. pusillus*), an observation also supported by Zonneveld (2008) on the basis of total nuclear DNA content. In all the trees *N. cavanillesii* (Figure 13) consistently comes out associated with *N. assoanus* and *N. gaditanus*. On floral morphology alone it is hard to see how *N. cavanillesii* could be derived from a jonquil, but Marques *et al.* (2010) make some interesting

suggestions about the past distribution of *N. cavanillesii* and the impact of hybridisation on the survival of species.

The last sections in subgenus *Narcissus* are Sections *Narcissus*, for *N. poeticus*, and *Pseudonarcissi* for a large array of trumpet daffodils. One part of the latter has already been discussed as the *N. nevadensis* group but the remainder will be dealt with here. Based on the rather limited sampling in the published phylogenetic trees, a pattern seems to emerge among the trumpet daffodils of three groups: one with *N. pseudonarcissus* and *N. bicolor*; another with *N. hispanicus* and *N. alpestris* and a third with *N. cyclamineus* and *N. asturiensis* (Figures 14a, b) (Santos-Gally *et al.*, 2012). This largely repeats the results of Graham and Barrett (2004), although they also found *N. jacetanus* to cluster with *N. asturiensis* and *N. cyclamineus*. This pattern is not, however, well supported by the trees in Marques (2010) which include a much greater number of species and multiple samples within species. In one of her trees, the *N. asturiensis* group of species is clustered with *N. nobilis* (Figure 15), *N. pallidiflorus* and *N. pseudonarcissus* subsp. *eugeniae* (Figure 16). A second cluster brings together the *N. bicolor*/*N. pseudonarcissus* group with *N. hispanicus* (Figure 17a), *N. alpestris*, *N. abscissus* (Figure 17b) and *N. portensis*. There



***Pseudonarcissi*, Clockwise from Top Left:** Figure 14a. *Narcissus cyclamineus*. Photo Philippa Gibson; Figure 14b. *Narcissus asturiensis*; Figure 15. *Narcissus nobilis*; Figure 16. *Narcissus pseudonarcissus*.



Left: Figure 17a. *Pseudonarcissi*: *Narcissus hispanicus*.

Right: Figure 17b. *Pseudonarcissi*: *Narcissus abscissus*.

is no clear morphological pattern to link to these clusters of species and even Fernandes (1975) does not suggest any chromosomal basis for this pattern. It is also unfortunate that the treatment of Section *Pseudonarcissi* by Aedo (2013) does not correspond with the molecular data, most notably in his concept of *N. pseudonarcissus* that contains representatives of all three lineages within the Section. There is scope here for much further research, and one group of the *Pseudonarcissi* (the *N. asturiensis* group) is now being tackled as a PhD project at the University of Reading.

Last but not least, the type species of the genus *N. poeticus* is the sole species in Section *Narcissus*. As with Section *Ganymedes* it has been treated either as a single species or a small number of species. Mathew (2002) accepts *N. radiiflorus* as distinct from *N. poeticus*. The molecular data show *N. poeticus* to be embedded within *Pseudonarcissi*, which is surprising given its distinctive floral morphology. However, it hybridises readily with species in *Pseudonarcissi* in the wild and has given rise to a great diversity of man-made cultivars as a result. There is no obvious explanation for its position in the phylogenetic trees, although, given how frequently hybridisation has given rise to new lineages in *Narcissus*, it is not inconceivable

that Section *Narcissus* is also the product of an ancient hybridisation event.

That completes the survey from which can be seen that we now have a broad understanding of how the major groups within the genus have evolved. There is strong evidence for the role of hybridisation in the origin of some of the major groups, indeed, in some species and this inevitably gives rise to difficulties when it comes to classification. With that proviso, the subgenera and most of the sections recognised by Fernandes (1975) seem to hold good. There is much more work to be done on the species, particularly in Section *Pseudonarcissi* where current understanding of species is poor, but in other sections as well, such as *Jonquillae* and *Tazettae*. This will be necessary before the planned monograph can be completed.

References

- Aedo, C. (2010). Typifications of the names of Iberian accepted species of *Narcissus* L. (Amaryllidaceae). *Acta Botanica Malacitana* 35, 113-122.
- Aedo, C. (2013). *Narcissus*. In: Rico, Crespo, Quintanar, Herrero and Aedo (eds), *Flora iberica* 20, 340-397. Real Jardín Botánico, Madrid.
- Barra, A. & López, G. (1984). Notas sobre el género *Narcissus* L. *Anales Jardín Botánico de Madrid* 41(1), 202.
- Blanchard, J. W. (1990). *Narcissus. A guide to wild daffodils*. Woking, UK: Alpine Garden Society.
- Díaz Lifante, Z. & Camacho, C. A. (2007). Morphological variation of *Narcissus serotinus* L. s.l. (Amaryllidaceae) in the Iberian Peninsula. *Botanical Journal of the Linnean Society* 154, 237-257.
- Díaz Lifante, Z., Camacho, A. C., Viruel, J. & Caballero, A. C. (2009). The allopolyploid origin of *Narcissus obsoletus* (Alliaceae): identification of parental genomes by karyotype characterisation and genomic in situ hybridization. *Botanical Journal of the Linnean Society* 159, 477-498.
- Donnison-Morgan, D., Koopowitz, H., Zonneveld, B. & Howe, M. (2005). *Narcissus miniatus* Donnison-Morgan, Koopowitz & Zonneveld sp. nov., a new species from southern Spain. *Daffodil, Snowdrop and Tulip Yearbook 2005-6*, 19-25.
- Fernandes, A. (1937). Sur l'origine du *Narcissus dubius* Gouan. *Boletim da Sociedade Broteriana*, Ser. 2, 12, 93-118.

- Fernandes, A. (1968). Keys to the identification of native and naturalized taxa of the genus *Narcissus* L. *RHS Daffodil and Tulip Yearbook* 1968, 37-66.
- Fernandes, A. (1975). L'évolution chez le genre *Narcissus* L. *Anales del Instituto Botánico Antonio José Cavanilles* 32(2), 843-872.
- Fernández Casas, J. (1977). Recuentos cromosomicos en plantas vasculares espanoles. *Saussurea* 8, 33-55.
- Fernández Casas, J. & Lloret i Sabaté, F J (2012). *Narcissorum* Notulae, XXXIII. *Fontqueria* 56 (28), 253-254.
- Fonseca, J. P., Levy, A., Henriques, R., Costa, J. C., Neto, C. & Robalo, J. (2015). Phylogenetic approach of the section *Bulbocodii* D.C. of *Narcissus* based on cpDNA. A case of taxonomic inflation? *Plant Biosystems*. doi: 10.1080/12263504.2014.1001460.
- Gay, J. (1858). Recherches sur la famille des Amaryllidacées. Premier mémoire: Esquisse monographique des Narcisées a couronne rudimentaire. *Annales des sciences naturelles, Botanique, Ser. 4*, 10, 75-109.
- Graham, S. W. & Barrett, S. C. H. (2004). Phylogenetic reconstruction of the evolution of stylar polymorphisms in *Narcissus* (*Amaryllidaceae*). *American Journal of Botany* 91, 1007-1021.
- Hodgins, K. A. & Barrett, S. C. H. (2007). Population structure and genetic diversity in tristylous *Narcissus triandrus*: insights from microsatellite and chloroplast DNA variation. *Molecular Ecology* 16, 2317-2332.
- Hodgins, K. A. & Barrett, S. C. H. (2008). Geographic variation in floral morphology and style-morph ratios in a sexually polymorphic daffodil. *American Journal of Botany* 95, 185-195.
- Jiménez, J. F., Sánchez-Gomez, P., Guerra, J., Molins, A. & Rosselló, J. A. (2009). Regional speciation or taxonomic inflation? The status of several narrowly distributed and endangered species on *Narcissus* using ISSR and nuclear ribosomal ITS markers. *Folia Geobotanica* 44, 145-158.
- Könyves, K. (2014). *Taxonomy to underpin cultivar identification in hoop-petticoat daffodils*. (Doctoral dissertation). Centre of Plant Diversity and Systematics, School of Biological Sciences, University of Reading.
- Marques, I. (2010). *Evolutionary outcomes of natural hybridization in Narcissus (Amaryllidaceae): the case of N. xperezlarae s.l.* (Doctoral dissertation). Universidade de Lisboa, Faculdade de Ciências, Departamento de Biologia Vegetal.
- Marques, I., Feliner, G. N., Draper Munt, D., Martins-Loução, M. and Aguilar, J. F. (2010). Unraveling cryptic reticulate relationships and the origin of orphan hybrid disjunct populations in *Narcissus*. *Evolution* 64, 2353-2368.

- Mathew, B. (2002). Classification of *Narcissus*. In: Hanks (ed), *Narcissus and Daffodil*. 31-52. New York: Taylor & Francis.
- Medrano, M., López-Perea, E. & Herrera, C. (2014). Population genetics methods applied to a species delimitation problem: endemic trumpet daffodils (*Narcissus* section *Pseudonarcissi*) from southern Iberia. *International Journal of Plant Science* 175, 501-517.
- Meerow, A. W., Fay, M. F., Chase, M. W., Guy, C. L., Li, Q-B., Snijman, D. & Yang, S-L. (2000). Phylogeny of Amaryllidaceae: molecules and morphology. In: Wilson, K. & Morrison D. (Eds.), *Monocots: Systematics and Evolution*, 372-386.
- Meerow, A. W., Francisco-Ortega, J., Kuhn, D. N. & Schnell, R. J. (2006). Phylogenetic relationships and biogeography within the Eurasian Clade of Amaryllidaceae based on plastid *ndhF* and nrDNA ITS sequences: Lineage sorting in a reticulate area? *Systematic Botany* 31, 42-60.
- Pérez-Barrales, R., Vargas, P. & Arroyo, J. (2006). New evidence for the Darwinian hypothesis of heterostyly: breeding systems and pollinators in *Narcissus* sect. *Apodanthi*. *New Phytologist* 171, 553-567.
- Ríos, S., Rivera, D., Alcaraz, F. & Obón, C. (1999). Three new species of *Narcissus* L. subgenus *Ajax* Spach (Amaryllidaceae), restricted to the meadows and forests of south-eastern Spain. *Botanical Journal of the Linnean Society* 131, 153-165.
- Santos-Gally, R., Vargas, P. & Arroyo, J. (2012). Insights into Neogene Mediterranean biogeography based on phylogenetic relationships of mountain and lowland lineages of *Narcissus* (Amaryllidaceae). *Journal of Biogeography* 39, 782-798.
- Traub, H. P. (1969). Amaryllid Notes 1969. *Plant Life (Herbertia)* 25, 46-50.
- Waters, M. T., Tiley, A. M. M., Kramer, E. M., Meerow, A. W., Langdale, J. A. & Scotland, R. W. (2013). The corona of the daffodil *Narcissus bulbocodium* shares stamen-like identity and is distinct from the orthodox floral whorls. *The Plant Journal* 74, 615-625.
- Webb, D. (1980). *Narcissus*. In: Tutin, Heywood, Burges, Moore, Valentine & Webb (Eds.). *Flora Europaea* 5, 78-84. Cambridge, UK: Cambridge University Press.
- Zonneveld, B. J. M. (2008). The systematic value of nuclear DNA content for all species of *Narcissus* L. (Amaryllidaceae). *Plant Systematics and Evolution* 275, 109-132.
- Zonneveld, B. J. M. (2010). The involvement of *Narcissus hispanicus* Gouan in the origin of *Narcissus bujei* and of cultivated trumpet daffodils (Amaryllidaceae). *Anales del Jardín Botánico de Madrid* 67, 29-39.