

# The monophyly of island radiations: an evaluation of niche pre-emption and some alternative explanations

JONATHAN SILVERTOWN\*†, JAVIER FRANCISCO-ORTEGA‡ and  
MARK CARINE§

†Ecology and Evolution Research Group, Department of Biological Sciences, Open University, Walton Hall, Milton Keynes, MK7 6AA, UK, ‡Department of Biological Sciences, Florida International University, University Park, Miami FL 33199, USA and Center for Tropical Plant Conservation, Fairchild Tropical Botanic Garden, 11935 Old Cutler Road, Coral Gables (Miami), FL 33156, USA, and §Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

## Summary

**1** It has been argued that niche pre-emption is not the only possible explanation for monophyly among Macaronesian endemic plants because (i) interspecific competition is diffuse, not species-specific, (ii) the radiations in question may not in fact be monophyletic, and (iii) later colonists may have hybridized with earlier ones, making a small and undetected contribution to the gene pool of lineages that appear to be monophyletic.

**2** The niche pre-emption mechanism does not, however, require species-specific competitive interactions. It merely proposes that the clade created by adaptive radiation will occupy more niche space than the original colonist could on its own. Members of the clade will then collectively inhibit establishment by new colonists more effectively than can a colonist that has not radiated.

**3** The monophyly of many larger radiations in the Macaronesian flora is well established and new studies tend to confirm this pattern.

**4** A few later-arriving colonists may have undetectably hybridized with earlier arrivals, but this is only a genetic interpretation of the essential idea behind pre-emption, i.e. that early arrivals so outnumber later colonists that the latter cannot establish.

**5** We do not therefore believe that hybridization provides an alternative explanation of why groups with multiple colonization failed to radiate in Macaronesia.

*Keywords:* Macaronesia, phylogeny, adaptive radiation, niche pre-emption

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## Introduction

Silvertown (2004) showed that 20 genera that are each represented in Macaronesia by unique colonization events had between them given rise to 269 endemic species, whilst 20 repeated colonization events (i.e. where two or more lineages within a genus colonized independently) gave rise to only 38 species. Silvertown (2004) then sought to answer the central question of why genera that have managed to establish themselves only once in Macaronesia should have radiated so profusely, while those that have established more than once failed to do so. He advanced the hypothesis that niche

pre-emption could provide the answer: colonists that radiated, created a clade that occupied more niche space than colonists that did not radiate. Thus, by filling niche space, adaptive radiation created a barrier that prevented later, closely related (i.e. congeneric) arrivals from establishing. A similar argument was also proposed by Carine *et al.* (2004). Here, we consider some alternatives and objections to the niche pre-emption hypothesis that have been raised by Herben *et al.* (2005) (HSM) and Saunders & Gibson 2005 (SG).

HSM argue three main points: (1) interspecific competition does not operate in a sufficiently precise manner to permit early colonists to prevent the establishment of later arrivals belonging to the same group, (2) the radiations in question may not in fact be monophyletic, and (3) later colonists may have hybridized

with earlier ones, making a small and undetected contribution to the gene pool of lineages that appear to be monophyletic. SG agree with HSM's three points and offer some additional ideas on island radiations. They also suggest that Silvertown (2004) 'used the tips of the phylogenetic trees' to illustrate the differences in radiation patterns between unique and multiple congeneric colonizations and that this is inconsistent with Silvertown's own advocacy of phylogenetic correction in comparative studies. However, each data point in Silvertown's (2004; Table 1) analysis is a separate colonization event and the radiations arising from them are independent of each other. There is therefore no pseudo-replication, which is the problem that Silvertown & Dodd (1997), among others, warned against.

We shall address points 1–3 in turn and then briefly consider SG's other ideas.

### Competition and niche pre-emption

HSM argue that niche pre-emption requires species-specific competitive interactions and that the evidence for the existence of these in plants is poor. Actually, the niche pre-emption mechanism does not require species-specific competitive interactions. It merely proposes that the clade created by adaptive radiation will occupy more niche space than the original colonist could on its own. Members of the clade will then collectively inhibit establishment by new colonists more effectively than can a colonist that has not radiated.

HSM are quite right to emphasize the importance of plant size in the outcome of competition between adjacent plants, but they completely reverse its true effect on niche pre-emption because they base their arguments on a scenario where there are no niche differences between species. Hence, they argue that size-related competitive success prevents niche pre-emption when, to the contrary, it is part of the mechanism by which it operates. When species segregate along a niche axis, new colonists will compete with members of the same species that have already become established. Because new colonists arrive as seed and must establish as seedlings, they are at a considerable disadvantage against earlier arrivals that are already full grown. So strong can this priority effect be, that even germination differences of a day or two between cohorts can be sufficient for earlier-germinating seedlings to suppress later arrivals (Silvertown & Charlesworth 2001).

HSM are incorrect to claim that niche pre-emption is 'difficult to reconcile with the patterns of inter-island colonization of Macaronesian plants'. In the radiation of *Argyranthemum*, for example, new species appear to have evolved by allopatric speciation (Francisco-Ortega *et al.* 1996), with inter-island colonization among similar habitats as the rule and not the exception. *Argyranthemum* island-hopped between equivalent habitats, invaded from high-elevation deserts into low-elevation deserts by leaping over the mesic habitats that separate them, or (more rarely) invaded across the boundaries

of adjacent habitats into a different type to that occupied by their ancestors. Morphological data based mostly on growth-form patterns support colonization among similar habitats as a main avenue for speciation in other taxa such as *Taeckholmia* (Asteraceae), *Limonium* sect. *Nobile* (Plumbaginaceae), the *Gonospermum* alliance (Asteraceae), *Bystropogon* (Lamiaceae), *Crambe* (Brassicaceae), *Echium* (Boraginaceae) and *Cheirolophus* (Asteraceae) (Sventenius 1960; Boulos 1967; Bramwell 1969; Bramwell 1975; La-Serna-Ramos 1984; Marrero-Rodríguez 1992; Francisco-Ortega *et al.* 2001). For most of the species in these taxa this speciation mode is supported by the available molecular phylogenies (Kim *et al.* 1996; Francisco-Ortega *et al.* 2001, 2002; Trusty *et al.* 2005).

We do not claim that this proves that niche pre-emption occurred, but it is certainly completely consistent with it playing a role in speciation and monophyly. Where members of the same radiations do co-occur within habitats, they are often of different growth form. The best examples can be found in genera/species of the *Dendrosonchus* alliance and the *Aeonium* alliance (Boulos 1974; Liu 1989).

### The monophyly of island radiations

HSM argue that the sampling of both taxa and characters in some molecular phylogenetic analyses is inadequate to test the monophyly of endemic Macaronesian plant groups robustly. They cite *Asteriscus* as an example in which character sampling has impacted on the number of hypothesized colonizations. We disagree both with HSM's interpretation of the impact of character sampling on the number of Macaronesian colonization events in *Asteriscus* and with their implicit suggestion that the monophyly of many Macaronesian groups may be an artefact of sampling.

*Asteriscus* is represented in Macaronesia by five endemic taxa and a further species that is distributed in both the Canary Islands and southern Morocco. A minimum of between one (single colonization + radiation) and six (six colonizations + no radiation) colonization events are therefore necessary to explain the occurrence of these species in Macaronesia. The ITS analysis of Francisco-Ortega *et al.* (1999b) lacked resolution and support for many nodes within *Asteriscus* but did indicate that *at least* two independent colonizations of Macaronesia had occurred. A more precise estimate was not possible given the limited resolution. The results of Goertzen *et al.*'s (2002) analysis, based on ITS, ETS and *ndhF*, provided more resolution and support and indicated that at least four events were necessary to explain the origins of Macaronesian *Asteriscus*. The results of these analyses were, however, entirely consistent and improved sampling simply provided greater precision in the number of colonization events inferred rather than contradicting the earlier result.

Silvertown (2004; Table 1) incorrectly counted *Asteriscus* as a case of monophyly, but as such it appeared

to be an exception to the rule that most smaller Macaronesian genera colonized more than once. When correctly scored as a case of multiple colonization, *Asteriscus* now reinforces rather than contradicts the rule. Repeating Fisher's exact test on the frequency of monophyly for groups with greater than 5 species vs. those with 5 or fewer, the probability of obtaining the observed pattern by chance decreases from  $P = 0.0178$  calculated by Silvertown (2004) to  $P = 0.0078$ .

We accept that the relationships of some Macaronesian endemic groups remain equivocal. Nevertheless, the relationships of many other groups are well supported by molecular data, with bootstrap percentages for relevant nodes typically greater than 75%. These groups include *Crambe*, *Pericallis*, the *Bencomia* alliance, *Echium*, *Sedum*, *Solanum*, *Sideritis* and *Cheirolophus* (Van Ham & 'T Hart 1998; Francisco-Ortega *et al.* 1999a; Panero *et al.* 1999; Susanna *et al.* 1999; Helfgott *et al.* 2000; Böhs & Olmstead 2001; Barber *et al.* 2002; Pelsner *et al.* 2002; Swenson & Manns 2003). All of these molecular phylogenetic studies have very extensive taxonomic sampling both on the islands and on the continent and have included all the putative continental relatives of the insular groups; they also have a broad taxonomic selection of other continental species. Increased character sampling undeniably provides a more rigorous test of group monophyly and may overturn weakly supported relationships. However, there has been no example to date in which the monophyly of a well-supported Macaronesian group has been refuted by additional character sampling. We therefore suggest that in cases where monophyly is strongly supported, such hypotheses are robust and are only likely to be further corroborated by additional data. Overall, the data support the monophyly of the larger Macaronesian endemic groups. Any alternatives to niche pre-emption as an explanation of the pattern reported by Silvertown (2004) must therefore be consistent with monophyly.

### Hybridization

Silvertown (2004) acknowledged that some hybridization among the first arrivals might have occurred. Indeed, Francisco-Ortega *et al.* (2000) suggested that such hybridization might explain why populations of Canarian endemics typically have higher genetic diversity than endemic populations in more isolated archipelagos. Hybridization between related Canarian endemics is frequent, but HSM's arguments require hybridization between endemics and their continental progenitors. We find three problems with HSM's arguments concerning hybridization. (1) There are very few examples of natural hybrids between the Macaronesian endemics and their continental counterparts; (2) were it to have occurred in the past, it would strengthen rather than invalidate niche pre-emption; and (3) hybridization cannot explain why multiple colonizations have so rarely, if ever, produced large radiations. We shall deal with each of these points in turn.

There have been few crossing studies involving Macaronesian endemics and their continental relatives. We are aware of studies only for the *Asteriscus* alliance, *Senecio*, *Scrophularia*, *Solanum*, *Avena*, *Argyranthemum* and *Lolium* (J. Francisco-Ortega *et al.*, unpubl. data; Thomas & Leggett 1974; Dalgaard 1979; Daunay *et al.* 1979; Borgen 1984; Halvorsen & Borgen 1986; Charmet *et al.* 1996). Studies for *Avena*, *Solanum*, and *Lolium* have a limited sampling in the continent and therefore conclusions for these genera should be interpreted with caution. Strong reproductive barriers have been clearly found between *Argyranthemum* and the rest of the genera of the tribe Chrysantheminae, and also between the endemic *Avena canariensis* and *A. sativa* and *A. prostrata* (Thomas & Leggett 1974; J. Francisco-Ortega *et al.*, unpubl. data). The Canarian endemic *Lolium canariense* crosses with *L. temulentum* and *Festuca pratensis*, however, hybrids were obtained by means of *in vitro* embryo rescue techniques (Charmet *et al.* 1996). Artificial hybrids between *Solanum lidii* and its sister species *S. melongena* yield a F1 with very limited fertility. Among the 16 taxa of the *Asteriscus* alliance only one continental taxon, *Asteriscus graveolens* ssp. *odorus*, produces F1 fertile hybrids when crossed with four of the six taxa endemic to Macaronesia (Borgen 1984; Halvorsen & Borgen 1986). This taxon does not occur in Macaronesia. Similar results have been reported for *Scrophularia*, as the nonendemic *S. scordonia* yields fertile hybrids with most of the Macaronesian endemics. *Scrophularia scordonia* occurs in Madeira, and natural hybrids between this taxon and the endemics *S. hirta* and *S. racemosa* have been reported (Press & Short 1994). Crossing studies for *Senecio* show that approximately 50% of the artificial crosses between the Canarian endemic *S. teneriffae* and the introduced weed *S. vulgaris* yielded fertile hybrids (Gilmer & Kadereit 1989).

Besides these few studies, the only other evidence we have for the occurrence of hybrids between endemic and nonendemic species comes from floristic studies within the region itself. The four cases of hybridization mentioned by HSM for *Arbutus*, *Phoenix*, *Senecio* and *Teline* are between Macaronesian endemics and invasive aliens, and concern a very small fraction of the Macaronesian flora. There are no reports of natural hybrids between endemic and nonendemic elements of the flora for any of the major species-rich groups such as the woody-*Sonchus* alliance, *Tolpis*, *Echium*, *Silene*, *Convolvulus*, *Euphorbia*, *Lotus*, *Plantago* and *Limonium* (Hansen & Sunding 1993). Besides the previously mentioned examples the only other case we are aware of involving the occurrence of natural hybrids between endemic and nonendemic plant species concerns the endemic genus *Bencomia*. Santos-Guerra (1983) reported the finding of a single plant of what appears to be a hybrid between *Bencomia caudata* and *Sanguisorba minor* in the pine forest of La Palma. In general, there is little evidence of natural hybridization between Macaronesian endemics and their continental relatives and

the few studies based on artificial crosses are inconclusive about what proportion of the endemic flora hybridizes easily with its continental relatives.

There may have been hybridization between new arrivals and established populations in the past, as HSM suggest, but such a scenario can comfortably be accommodated within Silvertown's original hypothesis no. 2 that early colonists prevent the establishment of later ones by occupying available niche space. We readily accept the point that, if any later-arriving colonists did become established in small numbers, they may have hybridized with earlier arrivals, but the genetic consequences of this would not be detected because the early arrivals would be far more numerous. This seems to us to be only a genetic interpretation of the essential idea that early arrivals so outnumber later colonists that the latter cannot establish. It amplifies the role of pre-emption rather than nullifying it, and cannot be considered an alternative explanation of monophyly.

Finally, the weakest part of the hybridization argument is that it simply does not provide an alternative explanation of why groups with multiple colonization failed to radiate in Macaronesia. Not only is there no 'ghost of hybridization past', but if there were, it would not explain the pattern which can be readily explained by niche pre-emption.

### Other hypotheses

SG find both hybridization and niche pre-emption to be plausible explanations of the patterns identified by Silvertown (2004), and list some other hypotheses that they regard as 'equally probable'. Unfortunately, no data are presented to justify this conclusion in the context of island radiations; experiments with *Pseudomonas* (Kassen *et al.* 2004) are doubtfully relevant. SG also raise the question of why some genera radiated and others did not, an issue that neither Silvertown (2004) nor HSM addressed. SG suggest that hybrid swarms (Seehausen 2004) might stimulate radiation and offer the example of the Hawaiian silversword alliance, although the hybrid event in the history of this group occurred before its solitary colonization of Hawai'i.

As Silvertown (2004) acknowledged, the geological history of Macaronesia is more complicated than the simple scenarios outlined in that paper. There are phylogenetic and biogeographical patterns that can only be explained by details of geological history that we have not considered, but the pattern of monophyly and its relation to the size of radiations is so strong and covers so many taxa that only a general explanation is likely to suffice. Niche pre-emption is such an explanation, while hybridization is not. HSM and SG fail to explain how hybridization could produce the striking pattern that monophyletic taxa are larger than non-monophyletic ones, and so do not offer a viable alternative to the niche pre-emption hypothesis that is consistent with the data.

### References

- Barber, J.C., Francisco-Ortega, J., Santos-Guerra, A., Turner, K.G. & Jansen, R.K. (2002) Origin of Macaronesian *Sideritis* L. (Lamioideae: Lamiaceae) inferred from nuclear and chloroplast sequence datasets. *Molecular Phylogenetics and Evolution*, **23**, 293–306.
- Böhs, L. & Olmstead, R.G. (2001) A reassessment of *Normania* and *Triguera* (Solanaceae). *Plant Systematics and Evolution*, **228**, 33–48.
- Borgen, L. (1984) Biosystematics and Macaronesian Flowering Plants. In: *Plant Biosystematics* (ed. W.F. Grant), pp. 477–496. Academic Press, Toronto, Canada.
- Boulos, L. (1967) *Taeckholmia*, a new genus of Compositae from Canary Islands. *Botaniska Notiser*, **120**, 95–108.
- Boulos, L. (1974) Revision systematique du genre *Sonchus* L. *S.I. V. Sous-Genre 2. Dendrosonchus*. *Botaniska Notiser*, **127**, 7–37.
- Bramwell, D. (1969) The genus *Crambe* (Cruciferae) in the Canary Islands Flora. *Cuadernos de Botánica Canaria*, **6**, 5–12.
- Bramwell, D. (1975) Some morphological aspects of the adaptive radiation of Canary Islands *Echium* species. *Anales del Instituto de Botánica Antonio Jose Cavanilles*, **32**, 241–254.
- Carine, M.A., Russell, S.J., Santos-Guerra, A. & Francisco-Ortega, J. (2004) Relationships of the Macaronesian and Mediterranean floras: Molecular evidence for multiple colonizations into Macaronesia and back-colonization of the continent in *Convolvulus* (Convolvulaceae). *American Journal of Botany*, **91**, 1070–1085.
- Charmet, G., Balfourier, F. & Chatard, V. (1996) Taxonomic relationships and interspecific hybridization in the genus *Lolium* (grasses). *Genetic Resources and Crop Evolution*, **43**, 319–327.
- Dalgaard, V. (1979) Biosystematics of the Macaronesian species of *Scrophularia*. *Opera Botanica*, **51**, 1–63.
- Daunay, M.-C., Lester, R.N. & Laterrot, H. (1979) The use of wild species for the genetic improvement of brinjal egg-plant (*Solanum melongena*) and tomato (*Lycopersicon esculentum*). In: *Solanaceae III: Taxonomy, Chemistry, Evolution* (eds J.G. Hawkes, R.N. Lester, M. Nee & N. Estrada), pp. 389–412. Royal Botanic Gardens, Kew and Linnean Society of London, London, England.
- Francisco-Ortega, J., Barber, J.C., Santos-Guerra, A., Febles-Hernández, R. & Jansen, R.K. (2001) Origin and evolution of the endemic genera of Gonosperminae (Asteraceae: Anthemideae) from the Canary Islands: Evidence from nucleotide sequences of the Internal Transcribed Spacers of the nuclear ribosomal DNA. *American Journal of Botany*, **88**, 161–169.
- Francisco-Ortega, J., Fuertes-Aguilar, J., Gómez-Campo, C., Santos-Guerra, A. & Jansen, R.K. (1999a) Internal transcribed spacer sequence phylogeny of *Crambe* L. (Brassicaceae): molecular data reveal two old world disjunctions. *Molecular Phylogenetics and Evolution*, **11**, 361–380.
- Francisco-Ortega, J., Fuertes-Aguilar, J., Kim, S.C., Santos-Guerra, A., Crawford, D.J. & Jansen, R.K. (2002) Phylogeny of the Macaronesian endemic *Crambe* section *Dendrocrambe* (Brassicaceae) based on internal transcribed spacer sequences of nuclear ribosomal DNA. *American Journal of Botany*, **89**, 1984–1990.
- Francisco-Ortega, J., Goertzen, L.R., Santos-Guerra, A., Benabid, A. & Jansen, R.K. (1999b) Molecular systematics of the *Asteriscus* alliance (Asteraceae: Inuleae) I: Evidence from the internal transcribed spacers of nuclear ribosomal DNA. *Systematic Botany*, **24**, 249–266.
- Francisco-Ortega, J., Jansen, R.K. & Santos-Guerra, A. (1996) Chloroplast DNA evidence of colonization,

- adaptive radiation, and hybridization in the evolution of the Macaronesian flora. *Proceedings of the National Academy of Sciences of the United States of America*, **93**, 4085–4090.
- Francisco-Ortega, J., Santos-Guerra, A., Kim, S.C. & Crawford, D.J. (2000) Plant genetic diversity in the Canary Islands: a conservation perspective. *American Journal of Botany*, **87**, 909–919.
- Gilmer, K. & Kadereit, J.W. (1989) The biology and affinities of *Senecio teneriffae* Schultz Bip. and annual endemic from the Canary Islands. *Botanische Jahrbücher für Systematik*, **111**, 263–273.
- Goertzen, L.R., Francisco-Ortega, J., Santos-Guerra, A., Mower, J.P., Linder, C.R. & Jansen, R.K. (2002) Molecular systematics of the *Asteriscus* alliance (Asteraceae: Inuleae) II: Combined nuclear and chloroplast data. *Systematic Botany*, **27**, 815–823.
- Halvorsen, T. & Borgen, L. (1986) The perennial Macaronesian species of *Bubonium* (Compositae – Inuleae). *Sommerfeltia*, **3**, 1–103.
- Hansen, A. & Sunding, P. (1993) Flora of Macaronesia. Checklist of vascular plants. 4th revised edition. *Sommerfeltia*, **17**, 1–295.
- Helfgott, D.M., Francisco-Ortega, J., Santos-Guerra, A., Jansen, R.K. & Simpson, B.B. (2000) Biogeography and breeding system evolution of the woody *Bencomia* alliance (Rosaceae) in Macaronesia based on ITS sequence data. *Systematic Botany*, **25**, 82–97.
- Herben, T., Suda, J. & Munclinger, P. (2005) The ghost of hybridization past: Niche pre-emption is not the only explanation of apparent monophyly in island endemics. *Journal of Ecology*, **93**, 572–575.
- Kassen, R., Llewellyn, M. & Rainey, P.B. (2004) Ecological constraints on diversification in a model adaptive radiation. *Nature*, **431**, 984–988.
- Kim, S.-C., Crawford, D.J., Francisco-Ortega, J. & Santos-Guerra, A. (1996) A common origin for woody *Sonchus* and five related genera in the Macaronesian islands: Molecular evidence for extensive radiation. *Proceedings of the National Academy of Sciences, U.S.A.*, **93**, 7743–7748.
- La-Serna-Ramos, I.E. (1984) Revisión del género *Bystropogon* L'Her., nom. cons. (Lamiaceae-Stachyoideae): endemismo de la region macaronésica. *Phenerogamarum Monographiae*, **18**, 1–380.
- Liu, H.-Y. (1989) Systematics of *Aeonium* (Crassulaceae). *National Museum of Natural Science, Taichung, Taiwan Special Publication*, **3**, 1–102.
- Marrero-Rodríguez, A. (1992) Evolución de la flora canaria. In: *Flora Y Vegetación Del Archipiélago Canario*, 1 (ed. G. Kunkel), pp. 55–95. Edirca, Las Palmas de Gran Canaria, Canary Islands, Spain.
- Panero, J.J., Francisco-Ortega, J., Jansen, R.K. & Santos-Guerra, A. (1999) Molecular evidence for multiple origins of woodiness and a New World biogeographic connection of the Macaronesian island endemic *Pericallis* (Asteraceae: Senecioneae). *Proceedings of the National Academy of Sciences, U.S.A.*, **96**, 13886–13891.
- Pelser, P.B., Graveland, B. & van der Meijden, R. (2002) Tackling speciose genera: species composition and phylogenetic position of *Senecio* sect. *Jacobea* (Asteraceae) based on plastid and nrDNA sequences. *American Journal of Botany*, **89**, 929–939.
- Press, J.R. & Short, M.J. (1994) *Flora of Madeira*. Intercept, Andover, England.
- Santos-Guerra, A. (1983) *Vegetación y flora de La Palma*. Editorial Interinsular Canaria, Santa Cruz de Tenerife, Canary Islands, Spain.
- Saunders, N.E. & Gibson, D.J. (2005) Breeding system, branching processes, hybrid swarm theory, and the hump-back diversity relationship as additional explanations for apparent monophyly in the Macaronesian island flora. *Journal of Ecology*, **93**(4), doi: 10.1111/j.1365-2745.2005.01024.x.
- Seehausen, O. (2004) Hybridization and adaptive radiation. *Trends in Ecology and Evolution*, **19**, 198–207.
- Silvertown, J. (2004) The ghost of competition past in the phylogeny of island endemic plants. *Journal of Ecology*, **92**, 168–173.
- Silvertown, J. & Charlesworth, D. (2001) *Introduction to Plant Population Biology*, 4th edn. Blackwell Science, Oxford.
- Silvertown, J. & Dodd, M. (1997) Comparing plants and connecting traits. In: *Plant Life Histories: Ecology, Phylogeny and Evolution* (eds J. Silvertown, M. Franco & J.L. Harper), pp. 3–16. Cambridge University Press, Cambridge.
- Susanna, A., Garnatje, T. & García-Jacas, N. (1999) Molecular phylogeny of *Cheirolophus* (Asteraceae – Centaureinae) based on ITS sequences of nuclear ribosomal DNA. *Plant Systematics and Evolution*, **214**, 147–160.
- Sventenius, E.R. (1960) Las centaureas de la sección *Cheirolophus* en las Islas Macaronésicas. *Anuario de Estudios Atlánticos*, **6**, 219–236.
- Swenson, U. & Manns, U. (2003) Phylogeny of *Pericallis* (Asteraceae): a total evidence approach reappraising the double origin of woodiness. *Taxon*, **52**, 533–546.
- Thomas, H. & Leggett, J.M. (1974) Chromosome relationships between *Avena sativa* and the two diploid species *A. Canariensis* and *A. Prostrata*. *Canadian Journal of Genetics and Cytology*, **16**, 889–894.
- Trusty, J.L., Olmstead, R.G., Santos-Guerra, A., Sa-Fontinha, S. & Francisco-Ortega, J. (2005) Molecular phylogenetics of the Macaronesian endemic genus *Bystropogon* (Lamiaceae): palaeo-islands, ecological shifts and interisland colonizations. *Molecular Ecology*, **14**, 1177–1189.
- Van Ham, R.C.H.J., 'T. Hart, H. (1998) Phylogenetic relationships in the Crassulaceae inferred from chloroplast DNA restriction-site variation. *American Journal of Botany*, **85**, 123–134.

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