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Hairy Anthers & Mountain Stars:

the speciation of Andean Asteraceae in response to geological and climate change

Alison M. R. DAVIES*

■ Evolution in action

These words conjure up an occasion of momentous importance, something that one would be privileged to witness. Ask a natural scientist for a list of the most well known examples of evolution in action, i.e. species evolving through the process of natural selection, and the list will undoubtedly include examples of vertebrates, invertebrates, and even bacteria. But, although biologists document an estimated 2000 new flowering plant species a year (after Chapham 2009), popular science literature seldom reports the dynamic revolutions taking place amongst flowers.

Plant taxonomy (definition & description of plants) and systematics (plant diversification & relationships) is one of the most exciting arenas in natural sciences. The detective work of a taxonomist requires the ability to consider the collections and associations of plants, identify them and their relationships with each other, untangle their historical and evolutionary origins and then disseminate the information. Thus, the taxonomist is best placed to understand how particular plants react to change and consider the implications of such responses, be it about conservation strategies or deeper understanding about life itself (after Knapp 2010).

"Hairy anthers" and "Mountain Stars" are the literal translations of the latinized Greek names of two related genera described around the beginning of the 19th Century, *Chaetanthera* and *Oriastrum*. "**Chaeta**" (= hair) and "**anthera**" (= anthers) refers to the anthers having ciliate tails, while "**ori**" (= mountain) and "**astro**" (= star) refers to the species' typical Andean habitat. Character variation, the function of the characters and the plants' habitat can provide clues to adaptive strategies while parallels in related species can be indicators of evolutionary processes. Plant responses to past change, e.g. climatic changes on geological timescales, can be relevant to modern scenarios. However, species are dynamic and polymorphic species can be particularly hard to define. Looking at variation in polymorphic species can reveal current speciation events and the driving forces behind them – evolution in action.

This paper is based on the inaugural talk given at the award of the Augustin-Pyramus De Candolle Prize 2012 for the authors' monograph, which was published as Davies 2010¹.

■ Setting the scene

The Asteraceae, popularly known as the Sunflower family, are a species-rich, cosmopolitan family of flowering plants, represented by ca 23 000 species (Stevens 2001). Characterized by their compound head of specialized flowers surrounded by a whorl of involucral bracts they are universally recognized, but

technically often challenging to identify. The family is so large it is segregated into 12 monophyletic subfamilies, each of which is further organized into tribes. The Tribe Mutisieae are, phylogenetically speaking, considered to be a basal lineage and are characteristically rather diverse and highly anomalous (Panero & Funk 2008). The ca 750 species of Mutisieae are united by several characters (Katinas et al. 2009), one of which is having imbricate involucral bracts surrounding the capitulum. Commonly, the leaves and involucral bracts are not alike in their shape or size (Fig. 1A). However, there are two genera of Andean

¹ Many of the figures used here were first published in the Davies 2010 monograph (Südwestdeutscher Verlag) albeit appear here in a modified form.

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Fig. 1. Imbricate involucral bracts of Mutisieae. A. *Mutisia decurrens*. B. *Chaetanthera frayjorgensis*.

Asteraceae – *Chaetanthera* and *Oriastrum* – whose involucral bracts undergo a continuous morphological progression from leaf to simple bract, giving the illusion of a capitulum surrounded by a dwindling rosette (Fig. 1B).

■ Chile, a natural biogeographic island

Subercaseux (1940) poetically described Chile as a “una loca geografía” (a geographic extravaganza), bound as it is to the North by the driest desert (Atacama), to the East by the highest mountains (Andes), to the South by the permanent ice of Patagonia and to the West by the deepest ocean (Pacific). The most dramatic elevation changes (0 to over 5000 m.a.s.l.) occur over just a few hundred km west to east, and the climate zones from north to south occur over 4300 km. The *Atlas Geográfico de Chile* (1998) recognizes 27 vegetation types in Chile, a number that reflects the meteorological and geographical diversity of this continental, biogeographical island.

In Chile, related species are often biogeographically linked across climate zones (GRAU 1995). Species radiations can be evidence of past dynamic change in a genus and are interesting from both a biological and an evolutionary perspective. By collating hotspots of species – that is the number of species coexisting in

the same area (ecological or geographical) – one can consider the environmental influences driving the sympatric aggregation of related taxa. *Chaetanthera* is mostly endemic to Chile (20 of 30 species) with the remaining nine species also occurring in neighbouring tracts of Argentina, Bolivia, and Peru and one Peruvian endemic. *Oriastrum* (with 18 species) is endemic in the Andes. *Chaetanthera* and *Oriastrum* share their diversity hotspots in the Chilean Regions of Coquimbo (ca 29–30°S) and Santiago (ca 33–34°S).

■ Form, Function & Habitat: evolution of adaptive strategies

The Asteraceae are well known for their adaptive success (Funk et al. 2005). This is evident in the huge variety and number of species in the family. But what is it that drives evolution in a particular group, causing speciation and extinctions? How do plants adapt to change? The variation in a character (e.g. leaf succulence = form) with a functional significance (i.e. water storage = function) is an environmental indicator of adaptation to a water-stressed habitat. Species (or groups of species) united by shared characters are more useful in a predictive sense, morphologically and phylogenetically, than a group of taxa circumscribed on the basis of their exclusion from another group. Among *Chaetanthera* and *Oriastrum* there is plenty

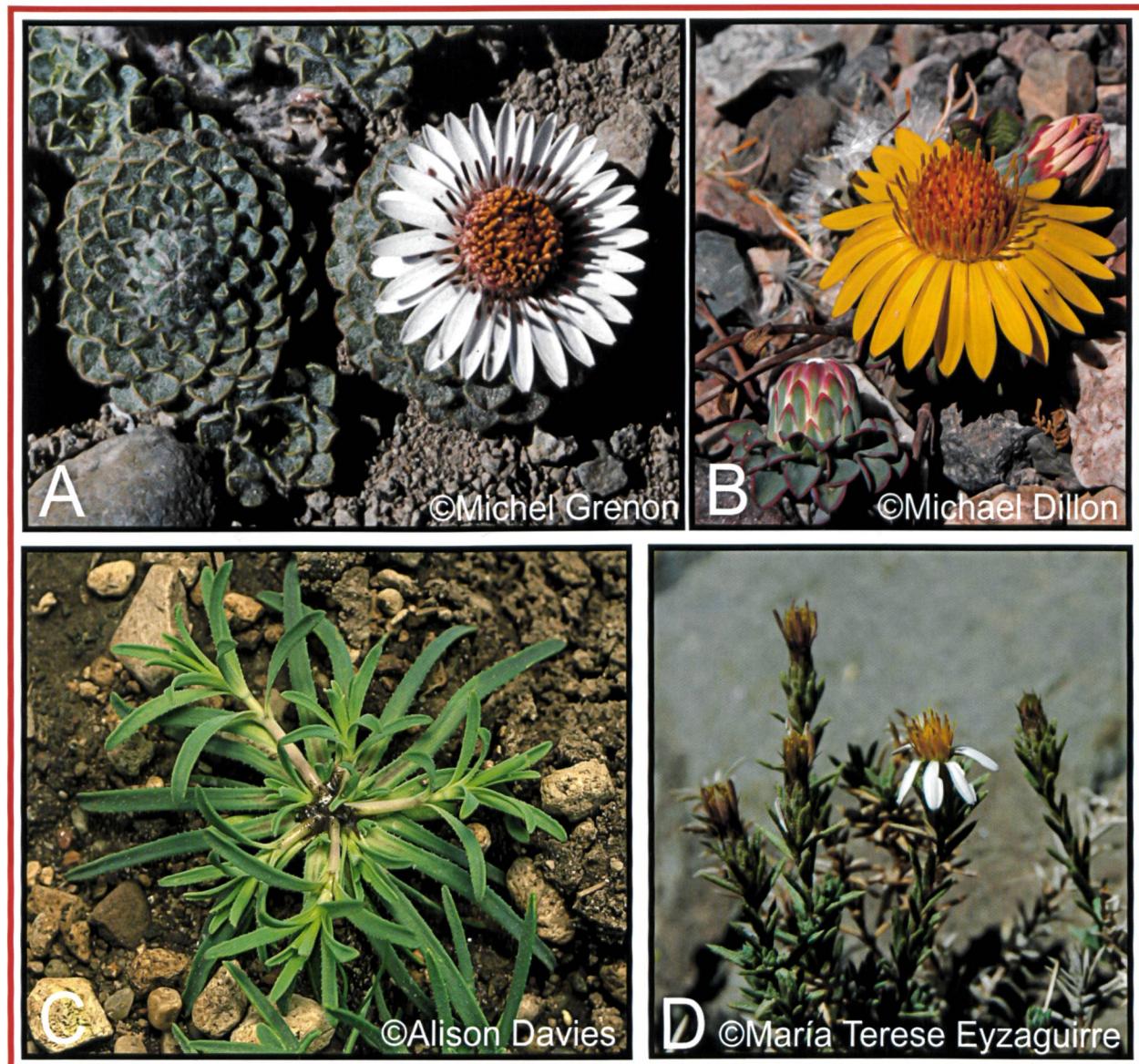


Fig. 2. Adaptive strategies to cold and aridity in *Chaetanthera*. A. Rosettes, also in involucral bracts, high elevation (ca 3000 m.a.s.l.) C. *philippii*. B. Succulent involucral bracts in lowland (ca 500 m) C. *glabrata*. C. Juvenile ephemeral rosette formation in low-mid elevation annual C. *linearis*. D. Mid-elevation sclerophyllous subshrub C. *glandulosa*.

of variation in the habit, leaves, capitula, hairs, floret colour etc. that is useful for circumscribing species. Many of the species in both genera are morphologically well-defined, typically forming suites of related taxa, i.e. similar habit and leaf type indicates a close phylogenetic relationship.

Rosettes, succulence and sclerophyllly in *Chaetanthera*

All *Chaetanthera* species have rosette stem architecture (Fig. 2A). Rosettes have several different functions in plants. Martorell and Ezcurra (2002) write that in cold habitats, a rosette arrangement of leaves may provide protection for the meristem, while in arid

habitats they allow for efficient water capture (Fig. 2C). The leaves of a number of *Chaetanthera* species are succulent (Fig. 2B), a feature that enables the plant to store water and thus advantageous in water stressed environments. One or two taxa even have sclerophyllous leaves (Fig. 2D), a typical adaptation seen in plants growing in xeric habitats with periodic drought (Balsamo et al. 2003).

Cushions, stem buds and scleroid bracts in *Orisatum*

Oriastrum species form loose or dense cushions (Fig. 3A, D). The rosette-like foliaceous outer involucral bracts are not homologous with the rosette

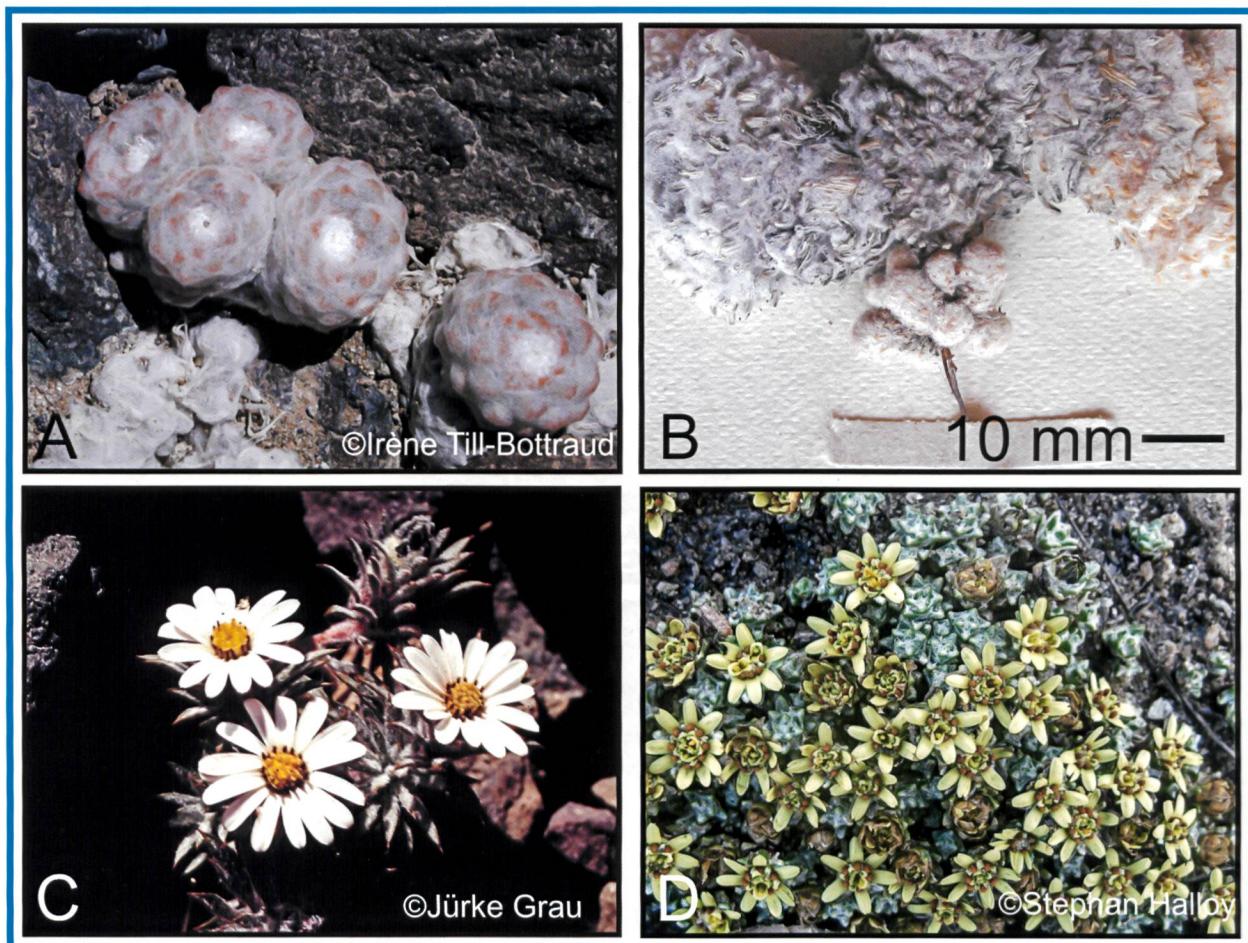


Fig. 3. Adaptive strategies to high elevation Andean habitats in *Oriastrum*. A. *O. polymallum*. B. Perennating stem buds of *O. polymallum* (Werderman 250, M). C. Closed involucrum showing black-coloured scleroid bract apices of *O. apiculatum*. D. Cushion habit of *O. abbreviatum*.

development in *Chaetanthera*. The cushion habit is one of the growth forms best adapted to the alpine habitat. Because of their low stature and compact form, cushions attenuate the effect of extreme environmental conditions by being efficient heat traps (after Arroyo et al. 2003). The perennial species in *Oriastrum* subgenus *Egania* have perennating stem buds (Fig. 3B), which are an adaptation to cold tolerance (Körner 1999). Anatomically, the inner involucral bract apices of *Oriastrum* species are distinctively packed with scleroid (woody) cells (Fig. 3C, see Davies 2010 for detailed illustrations). It is possible that the apices play an important protective role for the capitula, not only in terms of insulation, but also against damage from sudden storms – typical at higher elevations during summer.

■ Fragile pappus and indehiscent achenes²

An achene represents the next generation and as such its dispersal is paramount to a species' success. An illustration of a typical achene, located below the floret and crowned with a ring of barbed pappus bristles is given in Fig. 4A. Pappus bristles and their barbs are considered to have a functional role in defence against seed predation and in dispersal (Stuessey & Garver 1996), especially anemochory – a strategy typical of pioneer vegetation (Prach & Pyšek 1999) in alpine environments. Indehiscent pappus and plumose pappus setae are considered adaptations promoting long-distance dispersal.

The pappus of *Chaetanthera* is densely barbed (Fig. 4B) and firmly attached to the top of the achene (Fig. 4D) indicating a functional advantage for dispersal away from the parent. *Oriastrum* pappus is typically sparsely barbed (Fig. 4C) and only loosely attached to the achene, dehiscing easily when touched (Fig. 4D). This indicates a strategy that disperses the ach-

² Images from Fig. 4B-G and Fig. 5C, D were taken using LEO 483VP Scanning Electron Microscope. Figure 5A and 5B are polarized Light Microscope images. Figs 5E and 5F are drawings made from mounted freeze microtome slices, observed using a LM.

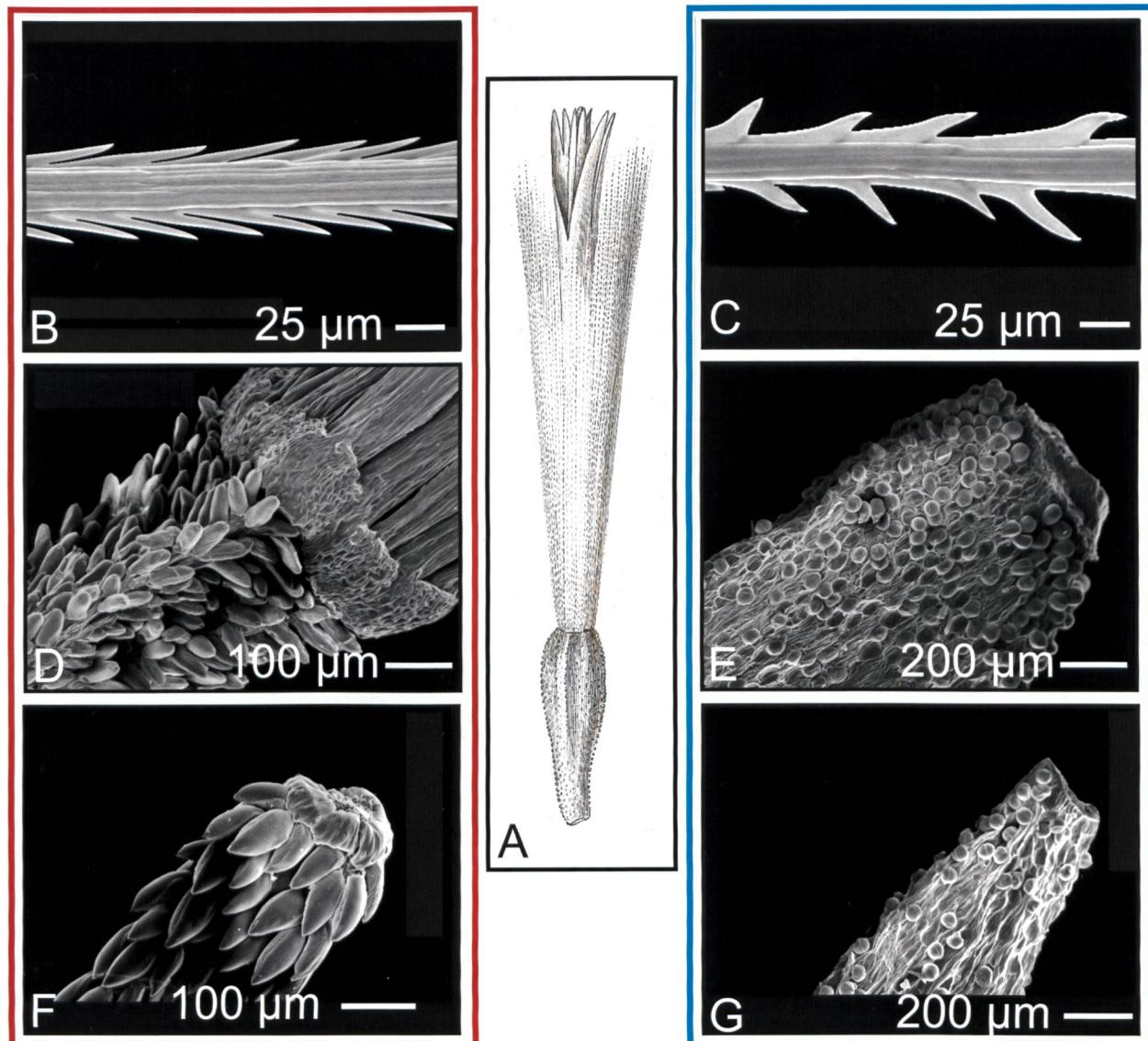


Fig. 4. Fragile pappus and indehiscent achenes. A. Part of an illustration from Delessert's *Icônes Plantarum*, showing the disc floret of *C. euphrasiooides* with pappus and achene. B. Typical *Chaetanthera* densely barbed pappus bristle. C. Typical *Oriastrum* loosely barbed pappus bristle. D. Apical region of *Chaetanthera* achene showing pappus firmly attached to achene. E. Apical region of *Oriastrum* achene showing naked dehiscence zone at region of pappus insertion. F. Base of *Chaetanthera* achene showing distinct carpopodial ring. G. Base of *Oriastrum* achene, illustrating lack of specialized disarticulation cells.

enes close to the parent, so-called secondary barochory, which is typical in the *Oriastrum* species, all of which are mid-high elevation inhabitants.

Mukherjee and Nordenstam (2004) write that a carpodium (a specialised ring of cells enabling the disarticulation of the fruit from the parent plant) is an apomorphic derived feature that promotes dispersal while the absence of a carpodium is a plesiomorphic character. All annual *Chaetanthera* species possess carpodia (Fig. 4F), whilst only a few perennial species have them. Neither annual nor perennial species of *Oriastrum* have well-defined carpodia (Fig. 4G).

■ Xeromorphic adaptations in pollen and achenes

The adaptive significance of *Chaetanthera* (including *Oriastrum*) pollen types and other features was discussed by Tellería and Katinas (2004). They suggest that the structure of the pollen grain wall with its thick exine and a well developed columellate internal tectum promote mechanical endurance of the pollen grain under hydration stress. Figure 5A – B show the structural contrast between typically thick walled (=exine), dumb-bell shaped pollen grains of *Chaetanthera* (Fig. 5A), and the thinner walled, elliptical *Oriastrum* pollen grains (Fig. 5B).

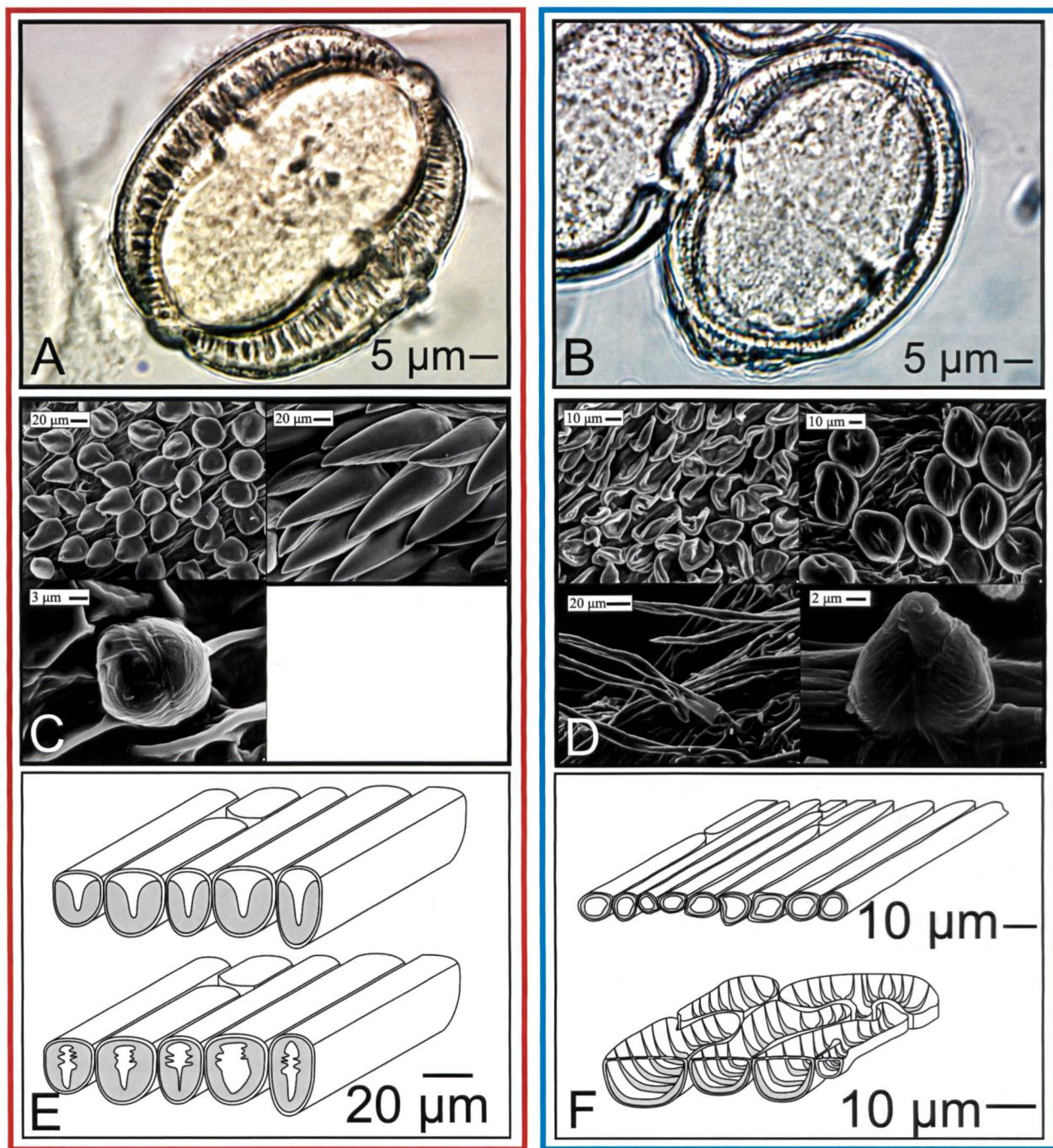


Fig. 5. Xeromorphic adaptations in pollen and achenes. A. Pollen grain of *C. splendens*. Note thick columellate exine and dumb-bell shaped nexine. B. Pollen grain of *O. cochlearifolium*. Note thin columellate exine and elliptical nexine. C. Diversity of *Chaetanthera* achene hairs on pericarp surface (top left: *C. flabellata*, top right *C. incana*, bottom left: *C. spathulifolia*). D. Diversity of *Oriastrum* achene hairs on pericarp surface (clockwise from top left: oblate flattened hairs of *O. revolutum*, inflated twin hairs of *O. pusillum*, minute inflated twin hairs of *O. gnaphaloides*, long filamentous hairs of *O. acerosum*). E. Testa epidermis (transverse section) of *Chaetanthera* showing U-shaped (above) and O-shaped (below) thickenings. F. Testa epidermis (transverse section) of *O. subgenus Egania* (above) and *O. subgenus Oriastrum* (below).

The pericarp (outer surface) of the achenes is a major line of defence against predation and desiccation. All *Chaetanthera* species bear myxogenic "Zwillingshaare" on their achene pericarps (Fig. 5C). The hairs (20-120 μm long) typically densely coat the achenes (Davies and Facher 2001). The myxogenic

property is typical of desert plants (Gutterman 2002) and is a functional adaptation for anchorage and rapid germination in the presence of an ephemeral water supply. Some *Oriastrum* species also have myxogenic "Zwillingshaare" while other *Oriastrum* species have single-celled papillae or filamentous

hairs or are glabrous (Fig. 5D). Expanding on the studies of Freire and Katinas (1995) in the Nassauviinae, and Hansen (1991) in the Mutisieae, there are three lines of development here: *Chaetanthera* with apomorphic myxogenic twin hairs, *Oriastrum* subgenus *Oriastrum* with apomorphic myxogenic twin hairs, and *Oriastrum* subgenus *Egania* with ancestral features and no myxogenic capabilities.

The testa epidermis cell thickenings is also a form of embryo protection (Grau 1980), protecting the seed from hydration injury (Duke et al. 1986). The prevalent *Mutisia-Gochnatia* type scleroid thickenings seen in *Chaetanthera* (Fig. 5E) represents a mechanically and hydrologically stable apomorphic trait. The plesiomorphic thin-walled testa epidermis found in *Oriastrum* subgenus *Egania* confers less protection against hydration fluctuations, while the presence of scleroid ribbed thickenings in the testa epidermis from *Oriastrum* subgenus *Oriastrum* points to the secondary development of xeromorphic adaptation (Fig. 5F).

■ Genetic information and palaeoclimate change

Hershkovitz et al. (2006) analysed Internal Transcribed Sequences of nuclear ribosomal DNA from *Chaetanthera* [and *Oriastrum*] species. The reconstructed phylogeny clearly supports the two recognized morphological genera. They then scaled the maximum parsimony bootstrap consensus tree using a penalized likelihood estimate of divergence and diversification dates of *Chaetanthera* [and *Oriastrum*]. The data were interpreted in the context of aridity development in lowland habitats in Chile during the Miocene and Pliocene epochs, coming to the conclusion that the modern Andes ("geologically young high elevation habitats") have served as both a cradle and a museum for *Chaetanthera* [and *Oriastrum*]. The divergence of the two genera was dated by Hershkovitz et al. (2006) to ca 16.5 Mya, around the time of the start of the Andean uplift (Hartley and Chong 2002). *Oriastrum* subgenus *Egania* and *O.* subgenus *Oriastrum* diverged (and the latter also radiated) during the Miocene, about 13.5 Mya, when the Pre-Andes had been raised to half their current height and marking the start of the semi-arid climate in northern Chile (Gregory-Wodzicki 2000). The *Chaetanthera* s.str. clade, particularly among the lowland species, underwent a number of radiations during the Pliocene as did the apparently ancestorless, high elevation *Oriastrum* subgenus *Egania*. During the Pliocene (ca 5 to 2.3 Mya) the Andes reached their current elevations, and are in part responsible for the development of the

hyperarid climate in their rain shadow (for complex interactions influencing Quaternary palaeoclimate, see Latorre et al. 2007). The recent Pleistocene and Holocene epochs are characterized in Chile by (geologically) rapid cycling of extreme cool wet glacial and extreme arid interglacial climates, shifting vegetation belts up to 5° in latitude, and nearly 2000 m in elevation (Stuessy and Taylor 1995).

■ Drawing the threads together: plant responses to geological and climate change

Chaetanthera and *Oriastrum* vary across a wide range of size scales, in their distribution and habitat preferences, from habit to achene features, their pollen and also genetically. The function of the shared morphological features can be very informative, indicating the kinds of habitat regimes the plants might have lived in during the past. Analysis of form (character variation), function (adaptive strategy) and habitat (source of environmental stress), together with phylogenetic lineages and biogeographic analysis in the context of palaeoclimate changes shows there are several contrasting modes of evolutionary development in *Chaetanthera* and *Oriastrum*.

Chaetanthera has adaptations to cold and secondary adaptations to aridity, especially in the lowland annual species. The cold adaptations are found in the rosette stem architecture, duplicated by the rosette-like arrangement of the foliaceous involucral bracts. The species are secondarily adapted to arid conditions. The leaves may be succulent or sclerophyllous, the pollen is hydrologically robust, the pericarp is coated with myxogenic twin hairs and the testa epidermis is strengthened. Stem morphoclines indicate an apomorphic group of mid-elevation to lowland perennial species, while the relict stem rosette in the lowland annuals indicates they are also a more derived group. This corroborates the biogeographic scenario suggested by Hershkovitz et al. (2006) of migration and recolonisation from cooler, wetter, higher (but geologically younger) elevations in the western Andes to more arid (geologically older) lowland habitats in Chile.

The perennial high elevation dwarf *Oriastrum* species are cold-adapted but not adapted to water-stressed habitats. This is evidenced by the perennating stem buds, the cushion-form stem architecture, hairy leaves, and protective scleroid bracts. There are no obvious adaptations to arid conditions; the testa epidermis is not strengthened and the achene hairs are plesiomorphic. The group shows features of an Insular Syndrome (after Carlquist 1974), includ-

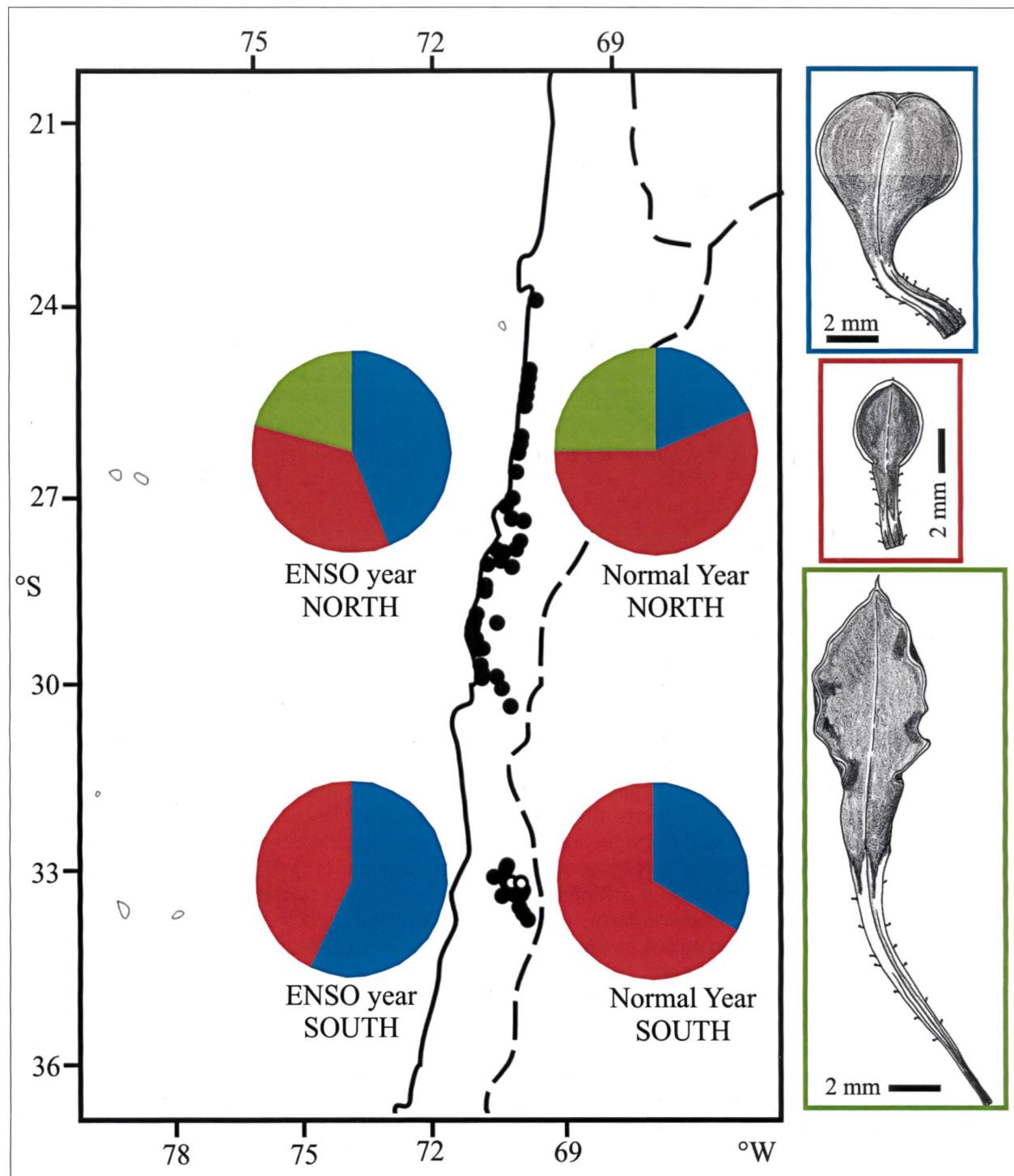


Fig. 6. The distribution of *C. glabrata* along the coast of Chile from 24°S to 31°S, and disjunctly around Santiago (33°S). The proportion of the 3 different leaf types colour-coded blue, red and green in ENSO and Normal years is given in the pie diagrams.

ing dwarfism, gynodioecy, genetic and morphological polymorphism and secondary barochory. *Oriastrum* subgenus *Egania*, is a phylogenetically young group of dynamic taxa very well adapted to, but also islanded in, the Piso Andino/ Altoandino/ Andino Superior of the modern southern Andes.

The *Oriastrum* annuals occur as mid-elevation dwarfs and, with their cushion architecture, hairy leaves and scleroid protective involucral bracts, as well as their small myxogenic twin hairs on the achenes and ribbed testa epidermis, are weakly adapted to both arid and cold conditions. Phylogenetically, it

is a relict group of mid-elevation annuals that is adapted to both dry and cold conditions of the modern mid-elevation Andes.

■ Plant responses to current dynamic change

Clearly defined species that share traits whose functional properties confer an evolutionary advantage are good subjects on which to base studies regarding speciation patterns and evolutionary processes. Corroboration of trait variation from different sources, e.g. morphological, anatomical and genetic characters, serves to make the conclusions more scientifically robust. But what can be learnt from those taxa that are so variable that even applying an appropriate name can be difficult? Stuessey et al. (2003) wrote that systematics and biogeography can be brought together to investigate patterns of isolation and speciation, especially where the patterns are not supported by the existing taxonomy. Some taxa within *Chaetanthera* are highly polymorphic, and thus taxonomically anomalous. These taxa were subjected to more intense study, and revealed some very interesting results. From an evolutionary biology perspective, areas where species boundaries break down or are incomplete are just as interesting as those areas where there is distributional congruence amongst different endemic taxa.

■ *Chaetanthera glabrata*: incipient speciation or a vegetative response to El Niño?

First described by A.P. De Candolle (1838), *C. glabrata* is a highly polymorphic annual species distributed along the Pacific coast of Chile from Taltal ($23^{\circ}30' S$) to Ovalle ($30^{\circ}30' S$) and disjunctly, around the Santiago Basin (ca $33^{\circ}S$); see the distribution map in Fig. 6. The herbarium collections are extensive both historically and geographically and yet the phenotypic plasticity of the plants was challenging. Cabrera (1937) wrote of *C. glabrata* in his revision of *Chaetanthera* "El tamaño y la forma de las hojas son muy variables... A la vista de material abundante es imposible delimitar estas formas".

But why the curious discontinuity of the *C. glabrata* populations? And why should they be morphologically closer to those from around Antofagasta, at the northern limit of the range?

The climatic phenomenon of El Niño is a key issue for the Chilean flora, especially along the northern parts of Chile's Pacific coastline. The Southern Oscillation Index (SOI) is an index directly related to El Niño

Southern Oscillation events (ENSO), with a continuous data record from 1915 onwards. *C. glabrata* leaves were assigned into one of three shape/size groups as shown on the right of Fig. 6: Large cordate (red), Small ovate (blue), and Elongated with undulate margins (green). Their frequency was plotted against the SOI, and the proportional occurrence of the different leaf types is given for the northern and southern populations for ENSO years and normal (non-ENSO) years. Even taking seasonal shift across latitudes and elevation into account, proportionally twice as many of the collections had large leaves in El Niño years, both in the north and south of the distribution, indicating that the leaf variation of this species is a vegetative response to El Niño events.

Plant responses to this quasi-periodic phenomenon have been studied (Squeo et al. 2006, Lopez et al. 2006) although at the time of completion of this research (2008) there were few documented examples of phenotypic plasticity being directly attributable to El Niño events. In the instance of El Niño-driven polymorphism, it is important to realise that the hydration stress typically experienced by the plants occupying arid/semi-arid regions is alleviated, not that the El Niño event itself is a cause of stress (after Holmgren et al. 2006). Thus, in the case of *C. glabrata* the leaf polymorphism (= increased vegetative productivity) is a result of absence of hydration stress.

■ *Chaetanthera linearis* & *C. albiflora*: a porous genome?

Chaetanthera linearis is a yellow-flowered glabrous annual with bright green leaves from the Andean foothills north of Santiago (Fig. 7, dark grey area). *C. albiflora* is white-rayed (with dorsal stripes on rays) lightly pubescent species with glaucous, semi-succulent, leaves, distributed along the coast from Taltal to Río Aconcagua (Fig. 7, light grey area). Both species have different habitat preferences and different flowering times but they are sympatric between La Serena ($31^{\circ}45' S$) and Petorca ($32^{\circ}45' S$), even in the foothills (Fig. 7, black localities). The plants collected between these two locations show many intermediate features in various morphological characters. Figure 7 shows images of the two species and some typical intermediates where the colour coded frames match coloured regions on map. The sympatric occurrence of morphological intermediates can be an indicator of active hybridisation events. Therefore, using 48 herbarium collections, the variable characters (e.g. ray floret colour and markings, leaf colour, succulence and hairiness) were quantified and analysed to generate hybrid indices (Anderson 1949).

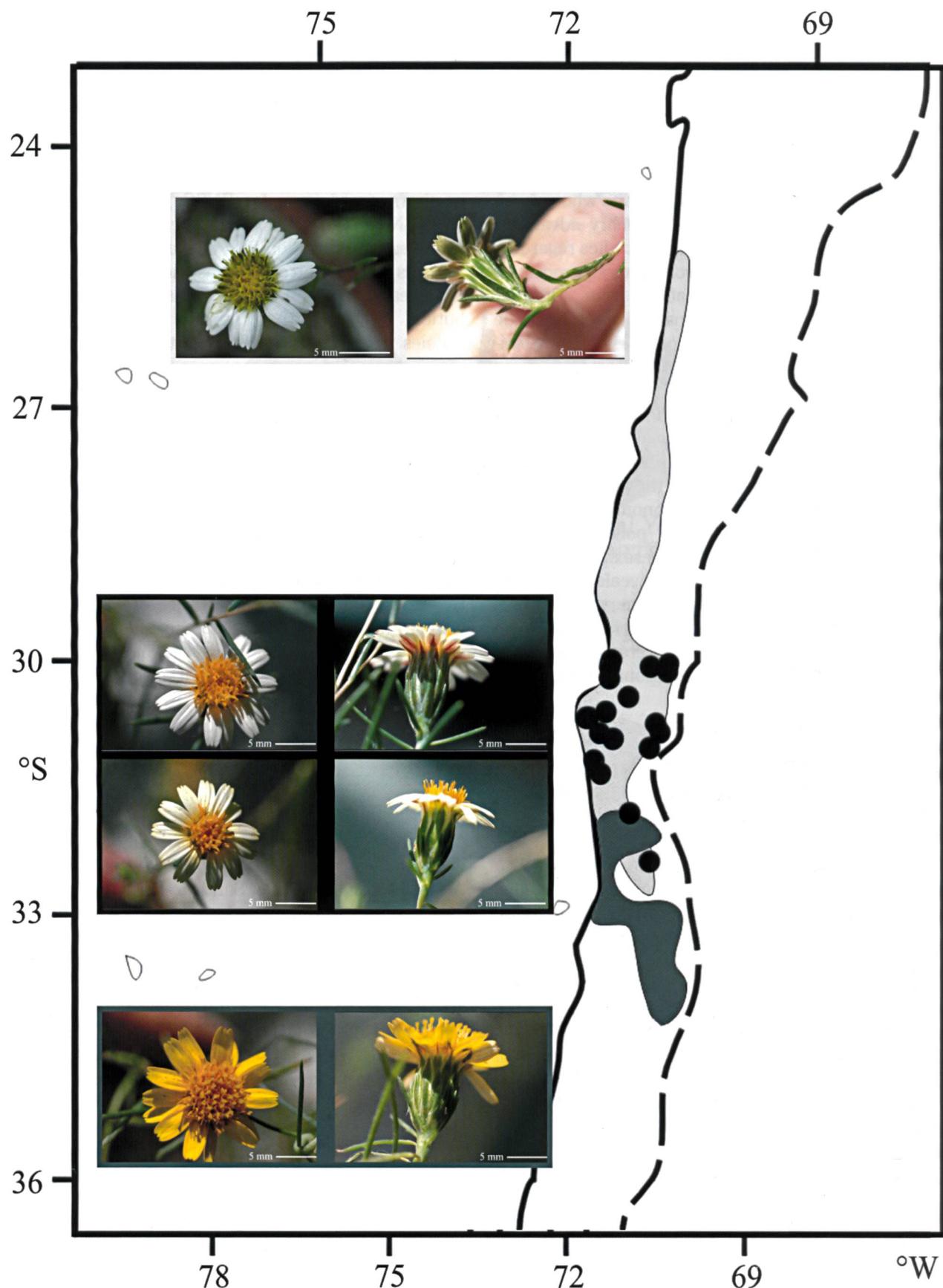


Fig. 7. The distributions of *C. linearis* (dark grey), *C. albiflora* (light grey) and morphological intermediates (black) are marked on the map, together with images illustrating the variation in some characters for each taxon placed adjacent to the distributions.

The results indicated the presence of a large scale shallow cline over several hundred kilometres with genetic drift towards the north (see Davies 2010). Geographically, the intermediate plants are always found together with one parent. The apparent introgression of the upland southern species into the lowland (coastal) northern species, to the exclusion of the southern parent in northern upland areas, indicates that natural selection favours the hybrid genotype in that environment. The hybrid forms are more numerous than either parent in the sympatric areas, indicating greater fitness of the hybrid in the transition zone than the parent. Hybridisation across eco-zones is probably driven by the change from one eco-zone to the other.

■ **Perennial *Chaetanthera*: 1 species or 13?**

A group of perennial scapose *Chaetanthera* (Fig. 8) form a complex association of montane mid-elevation taxa. They are distributed in mid to upper elevations of the Andean foothills from Santiago in Central Chile southwards towards Temuco, associated with relict native Chilean woodland floras such as those characterised by *Nothofagus* (El Roble) *Acacia caven* (Matorral), and *Araucaria* (Pehuén). Phylogenetically conspicuous due to the lack of resolution in the upper regions of the nrDNA tree generated by Herskovitz et al. (2006), these perennial taxa are morphologically very polymorphic in many features including habit, leaves and capitula characters. Historically, this polymorphism has caused much taxonomic confusion and resulted in the publication of many synonyms. Fig. 8 (right hand side) has a panel of images examples of these taxa from different montane and coastal localities.

Three statistical approaches were applied to the data set of characters recorded from over 200 herbarium specimens. Initially, a straightforward analysis of the traditional characters revealed that the popularly used leaf margin characters, habit and pubescence were insufficient for constructing a taxonomic relationship, especially as there appeared to be clinal variation in the indumentum features. A factor analysis was then carried out on a reduced subset of the data but merely confirmed that, without weighting the characters in any way, the characters were of little taxonomic value unless correlated into suites because the individual ranges of variation were so large. Finally, the morphological variation was screened using HYWIN (Estabrook et al. 1996) and possible hybrid scenarios were generated; one with equal weighting and one weighted for a possible introgression scenario. This latter was the scenario that seemed most likely when compared with the biogeographic data for the collections.

Two parents Y and Z were identified, with a couple of outliers, together with a swarm of hybrid material. This scenario, when plotted biogeographically (Fig. 8, left hand side), was interpreted as follows: there are montane parents "Z" and "Y" associated with the volcanic formations (with lakes) down the spine of the southern Andes and on the disjunct Nahuelbuta massif. Interestingly (although not shown here), Parents Z_{22} and Z_{37} came out as isolated in the Principle Components Analysis plot, and are geographically close (around Laguna del Teno) – possibly a further microspecies? The outlier Y_{80} from Chillán is possibly an example of heterosis. The hybrids are scattered across the Central Valley. The variation seen in the statistically designated hybrids supports a scenario of reticulate hybridisation and introgression within the sampled material.

Taxononomically, this translates into one polymorphic widespread species ($Z = C. chilensis$) with a porous genome, incompletely isolated from *C. elegans* (= Y, a montane microspecies). Combined, they form a stable hybrid with its own habitat preferences and characterized by having vegetative stolons (*C. x serrata*), adapted to a different ecozone than either of the parents.

■ **Hybridisation as an adaptive strategy across ecozones**

Hybrids often occur at ecotones or boundaries between different habitats (Harrison 1993). Phenotypic variation as a result of active hybridisation between two (or more) species is recorded in the literature concerning native Chilean species, although it has not been considered in terms of ecological boundaries found in Chile. For example, a number of hybrids within the Chilean *Calceolaria* (Scrophulariaceae) are said to be ephemeral or exist as stable swarms (Ehrhart 2005) where the parents coexist sympatrically. Similarly, the species-rich genus *Haplopappus* (Astereae) forms hybrids where the species distributions are sympatric (Klingenberg 2007) but little is recorded about the ecological significance of the sympatric zone. *Chaetanthera* has two instances of species instability across boundary zones. The significance of hybridisation events over the arid – semi-arid boundary in Coquimbo seems to be largely undocumented, although the high number of species, especially endemics, characterising this region is well known. The hybrid swarm between the annuals *C. linearis* and *C. albiflora* seems stable (not ephemeral) and selection appears to favour the hybrid genotype in ecozones where the parent species are less fit. The north-south climatic/hydrological boundary zone between Laguna del Maule and Nevados de Chillán

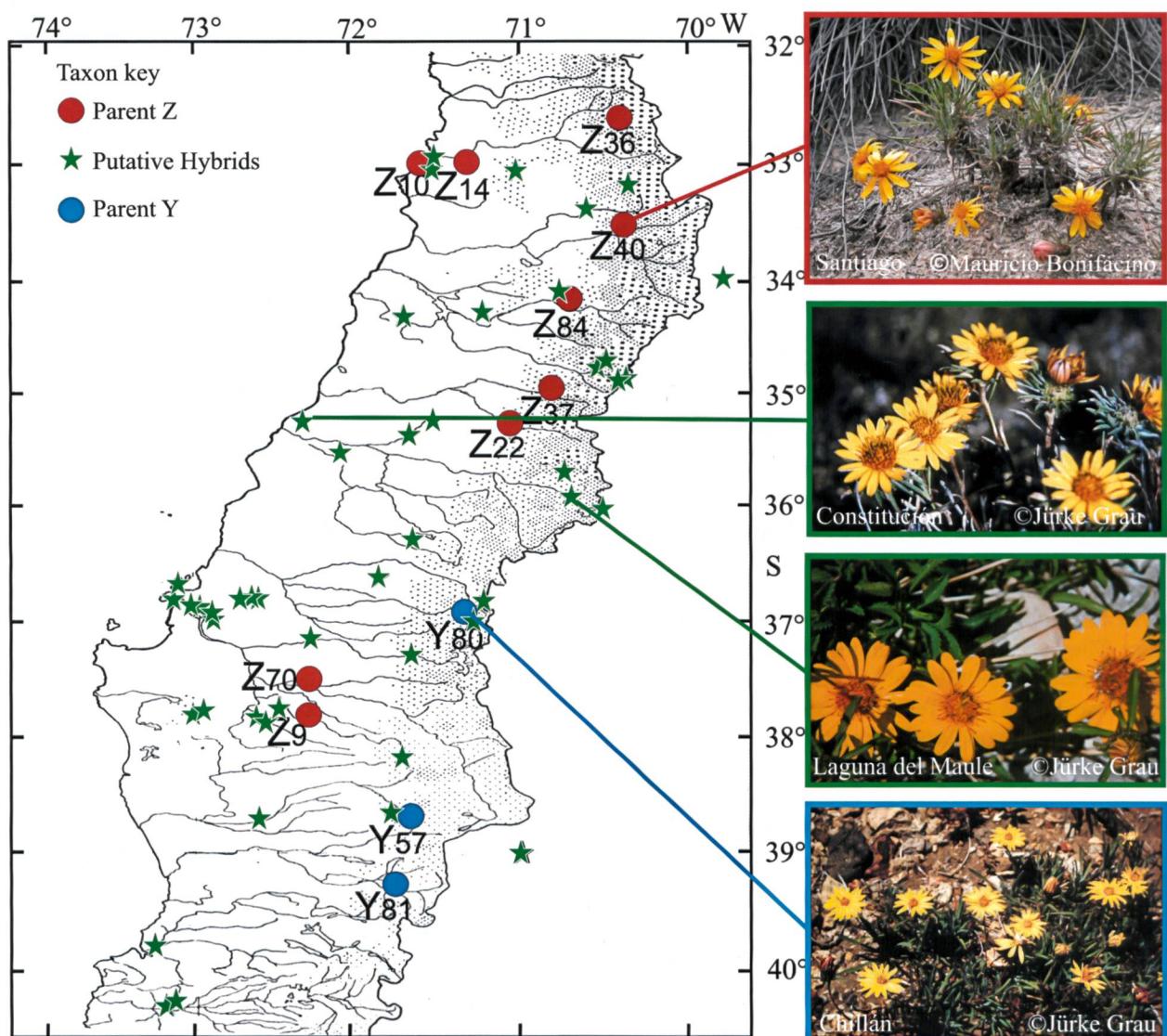


Fig. 8. Perennial scapose *Chaetanthera*. Images (right hand side) depicting plants from Santiago, Laguna del Maule, Constitución (on the coast) and Chillán. The lines linking the photos to the map indicate their approximate locality. The map (left hand side) shows the geographical location of the collections designated as Parent Y, Parent Z or a putative hybrid according to the introgression scenario calculated using HYWIN.

seems to be a locus of change in the caespitose *C. chilensis*/ *C. elegans* species. The hybrid-rich genus *Baccharis* L. (Astereae; Hellwig 1990), two species of *Nothofagus* (Donoso and Landrum 1979) and the dwarf hybrid shrub *Haplopappus glutinosus* x *pau-cidentatus* (Klingenberg 2007) all form hybrids local to the Chillán area. Although a comprehensive vegetation survey of the Nevados de Chillán was published in 2008 (Pfanzelt Grau and Rodríguez) the emphasis was on conservation of biodiversity and did not address the occurrence of hybrids.

On geological timescales, the biogeographical island of Chile has undergone many rapid swings in climate, so it follows that the ability to adapt is advantageous to plants in the region. Hybridisation generates polymorphism at many levels and is one strategy for cop-

ing with change (literally keeping options open). As the reality of climate change percolates through to all levels of society, studying the remarkable diversity of ecozones throughout Chile and the potentially large number of hybridisation events occurring across these zones as species compete for resources at the limits of their endurance will certainly take on a new significance and would be a fascinating project for the future.

■ Closing remarks

Chaetanthera and *Oriastrum* are two discrete but closely related South American Mutisiod genera distinguished from each other by morphological, anatomical and genetic variation. The array of novel

characters observed is particularly rich for a study of the Asteraceae. Together with the reassessment of traditional features the identification of novel characters has enabled the re-defining of the generic boundary of a primarily Chilean *Chaetanthera*, and resulted in the reinstatement of *Oriastrum*, endemic to the Andes.

Endemism and polymorphism can be valuable indicators of historical and current dynamism in a genus. Species diversity hotspots in the endemic Chilean genus *Chaetanthera* demonstrate historical dynamic change. These radiation events have stabilised into well-defined suites of taxa with shared leaf morphologies and are robustly supported by several other shared features, including genetic variation. Geological changes resulting in landscape, ecozones and climate changes have played a significant role in the evolution of *Chaetanthera* and *Oriastrum*. Character variation analysed in the context of adaptive strategy and biogeographic and palaeoclimatic information has revealed several evolutionary processes that have taken place: some species are relicts, some are very well adapted to their current environment, but are islanded there, while other species are actively radiating, or have in the recent past, occupying novel and ancient habitats according to opportunity.

Climate change, either meteorological or across eco-zones, also drives speciation. Polymorphic species may be regarded as indicators of dynamic events. In *Chaetanthera* polymorphism has been shown to be driven by two different mechanisms: 1) phenotypic flexibility as a response to periodic changes in water stress and 2) the polymorphism is a result of weak species boundaries or porous genomes, resulting in hybridisation events and microspeciation.

Ortiz et al. (2009) wrote that understanding the Mutisieae is key to understanding the systematics, early evolution, and biogeography of Compositae (=Asteraceae). "Hairy anthers" and "Mountain stars" together represent nearly 7% of the Mutisieae. Understanding the diversity of characters and speciation mechanisms in these two genera certainly contributes towards the better understanding of the Mutisieae, but also in wider issues such as dynamic change of species across ecozones.

The word "taxonomy" was coined by De Candolle in 1813. He also taught that plants should be grouped on the basis of shared characteristics, as well as the importance of linking character form to function (after Smith 2005), which remain central tenets of modern taxonomy. This current research was based principally on herbarium material and laboratory studies. Herbarium collections form an enormously valuable repository of information. However, the seeds of understanding about these plants in this study – their relationships to each other and their interactions with their environment – germinated as a result of fieldwork done in Chile, pouring over field notes of my own and others, and by studying images taken of the living plants in situ. In the reflective closing passages of his "Journal of Researches" (1845) Charles Darwin wrote "... a traveller should be a botanist, for in all views plants form the chief embellishment." This is equally applicable in the 21st Century, although undoubtedly the converse is also true: a botanist ought to be a traveller too, if they aspire to understand the marvel of plant diversity.

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