



ECOMORPHOLOGY AND HISTORY OF A RECURRENT EVOLUTIONARY ADAPTATION TO LONG-DISTANCE BIRD DISPERSAL IN ASTERACEAE

ECOMORFOLOGÍA E HISTORIA DE UNA ADAPTACIÓN EVOLUTIVA RECURRENTE A LA DISPERSIÓN A LARGA DISTANCIA POR AVES EN ASTERACEAE

En homenaje a Ángel Lulio Cabrera

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SUMMARY

Background and aims: Genera of Asteraceae, belonging to different tribes, present a repeated pattern of morphological adaptations to epiorithochory and have unique distributions. This pattern requires the interplay between plant morphology and environmental aspects (ecomorphology), and between morphology and the evolutionary history. *Adenostemma* and *Adenocaulon* are investigated to: 1) establish morphological and histochemical similarity in their diaspores, and associate that similarity to long-distance dispersal by birds, 2) superimpose these similarities in the phylogenetic tree of Asteraceae to determine whether they are homologous or homoplastic.

M&M: Previous work on *Adenostemma* and *Adenocaulon* is reviewed for analyzing morphology, histochemistry, geographic distribution, and mode of dispersion. The phylogenetic tree of Asteraceae is employed as a template to perform evolutionary inferences. The criteria for distinguishing homology from homoplasy, and parallelism from convergence are applied.

Results: *Adenostemma* and *Adenocaulon* are located in the recently radiated crown (tribe Eupatorieae) and in one of the earliest diverging branches (tribe Mutisieae) of the Asteraceae tree, respectively. The set of features shared by both genera in relation to epiorithochory is homoplastic.

Conclusions: A set of diaspore characters optimal for successful external dispersion (compatible with the 'Dispersal Syndrome hypothesis') evolved as homoplasies in several genera of the same family. Similar environmental pressures are expected to elicit similar adaptive morphologies.

KEY WORDS

Adenocaulon, *Adenostemma*, Compositae, epiorithochory, homology, homoplasy.

RESUMEN

Introducción y objetivos: Géneros de Asteraceae de diferentes tribus presentan un patrón repetido de adaptaciones morfológicas a la epioritocoria y tienen distribuciones únicas. Este patrón requiere la interacción entre la morfología de las plantas y el ambiente (ecomorfología), y entre la morfología y la historia evolutiva. *Adenostemma* y *Adenocaulon* se investigan para: 1) establecer similitud morfológica e histoquímica en sus diásporas y asociar esa similitud con la dispersión a larga distancia por aves. 2) superponer estas similitudes en el árbol filogenético de Asteraceae para determinar si son homologías u homoplasias.

M&M: Se revisan trabajos sobre *Adenostemma* y *Adenocaulon* para analizar su morfología, histoquímica distribución geográfica y modo de dispersión. Se emplea un árbol filogenético de Asteraceae como base para realizar inferencias evolutivas. Se aplican criterios para distinguir homología de homoplasia, y paralelismo de convergencia.

Resultados: *Adenostemma* y *Adenocaulon* constituyen un linaje corona que ha experimentado radiación reciente (tribu Eupatorieae) y un linaje tempranamente divergente (tribu Mutisieae) en el árbol de Asteraceae, respectivamente. El conjunto de características que comparten ambos géneros en relación con la epioritocoria es homoplásico.

Conclusiones: Un conjunto de caracteres de las diásporas óptimos para una dispersión externa ('Hipótesis del Síndrome de Dispersión') evolucionó como homoplasias en varios géneros de la misma familia. Presiones ambientales similares provocarían morfologías adaptativas coincidentes.

PALABRAS CLAVE

Adenocaulon, *Adenostemma*, Compositae, epioritocoria, homología, homoplasia.

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INTRODUCTION

Even when most members of the family Asteraceae (= Compositae) are well adapted to wind dispersal facilitated by a feathery parachute-like structure or pappus, the species inhabiting remote islands do not seem to have arrived in this manner by long-distance dispersal. For example, those Asteraceae best fitted for wind-dispersal (e.g., Cardueae, Cichorieae, Senecioneae) are groups notably absent in the Hawaiian Islands (Carlquist, 1967). The main mechanisms of dispersion invoked in these cases are epiornithochory (*i.e.*, the dispersion of diaspores, such as propagules, spores, seeds, and fruits, attached to any part of the birds' body), with the fruits attached to the birds by viscid substances or mechanically by means of barbs, bristles, and awns (Ridley, 1930; Carlquist, 1967; Katinas *et al.*, 2013; Dosil Hiriart *et al.*, 2024, 2025), and less likely endozoochory (*i.e.*, when birds swallow the diaspores) (Ridley, 1930). Sorensen (1986) considers that the diaspores transported through epiornithochory have the potential, over endozoochory, to reach longer distances. Epiornithochory would generate unique geographic distributions since it has the capability of surpassing geographic barriers such as oceans and mountain ranges, even reaching remote islands. Besides, the diaspores are not damaged during the handling and digestion, and they do not have the chance to be eliminated with feces in unsuitable habitats (like sea water) during bird migration (Dosil Hiriart *et al.*, 2025).

Certain genera of Asteraceae, belonging to different tribes, present an interesting phenomenon: a repeated pattern of morphological and histochemical adaptations, compatible with epiornithochory. This pattern, in turn, coincides with the particular geographical distribution of their species (e.g., widely disjunct distributions and/or inhabiting remote islands), which appears to be associated with the distribution or the routes of some migratory birds (Cabrera, 1966; Vasey, 1985; King & Robinson, 1974; Chowdhury *et al.*, 2013). The genera *Adenocaulon* Hook. (5 species; Bittmann, 1990; Funk *et al.*, 2016) (Mutisieae), *Adenostemma* J. R. Forst. & G. Forst. (*ca.* 24 species; Dosil Hiriart & Katinas, 2020) (Eupatorieae), *Lagenophora* Cass. (14

species; Cabrera, 1966; Sancho *et al.*, 2015), *Myriactis* Less. (*ca.* 10 species; Srivastava *et al.*, 2021) (Astereae), and *Lasthenia* Cass. (18 species; Ornduff, 1966; Chan & Ornduff, 2012) (Madieae) are interesting because they share similar adaptations to epiornithochory, such as: sticky structures in the diaspores, a modified, reduced, or absent pappus, in some cases an 'umbrella-like' position of the mature diaspores, and their occurrence in relatively humid habitats.

Other modes of dispersion, such as the adherence to the fur of passing mammals and the close association of some of these genera with water bodies, suggesting hydrochory, are not ruled out. However, these vectors would generate short-distance dispersal events that could contribute to the local establishment and growth of the populations, different from the bird-mediated long-distance dispersal that generates global distribution patterns (Dosil Hiriart *et al.*, 2025).

This form of commensalism between genera of the same family and birds dispersing their fruits, requires the interplay between plants' morphological features and environmental aspects (ecomorphology), and between morphology and the evolutionary history (homology, homoplasy, and phylogeny), that generated this phenomenon. This dichotomy of analysis, ecology-history, could be comparable with the concepts established by Mayr (1961) of proximate and ultimate causes, equivalent to the questions: "how does it work?", and "how did it originate?"

We will focus here on two of the above-mentioned genera of Asteraceae, *Adenostemma* and *Adenocaulon*, to address the recurrent morphological and histochemical traits that seem to have evolved as adaptations to epiornithochory, linked to their unique geographical distributions.

The aims of this study are: 1) to establish some aspects of morphological and histochemical similarity in the genera *Adenostemma* and *Adenocaulon* (Asteraceae) and, applying the concept of ecomorphology, to associate that similarity to the ecological phenomenon of long-distance dispersal by birds, which generates unique geographic distributions. 2) to superimpose these morphological and histochemical similarities in a historical context (phylogenetic tree of Asteraceae), to determine whether they are homologous or homoplastic.

ECOMORPHOLOGY: HOW DOES IT WORK?

Morphology, ecology, and biogeography

Ecomorphology is the integration of form, function, and ecology in the analysis of morphological structures (Betz, 2006). One of the basic aims of ecomorphology is the determination of the adaptiveness of complex morphological features and systems in individual species, followed by comparative analyses of these adaptations in different organisms, be they closely related or not. The studies begin with the morphology (and sometimes also the histochemistry) of the features under question. The first steps are usually detailed morphological descriptions followed by a functional analysis. Then the biological roles of the feature and the environmental demands on the organism are determined (Bock, 1990).

This phenotype-environment correlation has been interpreted as the result of an evolutionary adaptation of the phenotype to a particular environment, which may occur in unrelated organisms (homoplasies) in similar places (Ricklefs & Miles, 1994). In addition, comparative methods link species distribution patterns to functional traits (Ackerly, 2004; Losos, 2011) by testing for correlations between specific trait values and habitat attributes, while accounting for the phylogenetic relationships among species (Forrestel *et al.*, 2015).

Ecomorphological studies were primarily devoted to birds (Bock, 1990), such as the finding of positive correlations between wing length and dispersal distance (Paradis *et al.*, 1998; Skjelseth *et al.*, 2007; Bastidas-Urrutia *et al.*, 2025) or between dispersal distance and habitat choice (Paradis *et al.*, 1998; Sutherland *et al.*, 2000). In plants, the studies have mostly focused on specific morphological traits related to particular niches. For example, some species of *Acaena* Mutis ex L. (Rosaceae) in New Zealand have developed fruits with poorly protected embryos, enveloped in a light-weight hypanthium with barb-tipped spines suitable for attachment to animals, and achieved broad geographic ranges. Other species have fruits with embryos heavily encased in fibrous endocarps and with thick, long, barbless spines, which have limited dispersability. These fruits are typically heavy and have restricted geographic ranges (Lee *et al.*, 2001).

Forrestel *et al.* (2015) performed an ecomorphological study in the genus *Lasthenia* (Asteraceae). *Lasthenia* contains 17 species of western North America and one species that is endemic to Chile. About half of these species are highly associated with, or entirely restricted to, ephemeral wetlands known as vernal pools (Chan & Ornduff, 2012). Forrestel *et al.* (2015) found a link between the leaf morphology (leaf shape and presence of aerenchyma) and the ecohydrological niche, that is, vernal pool and terrestrial species. Likewise, we postulate that *Adenostemma* and *Adenocaulon*, inhabiting relatively humid environments as part of their ecological niche, have morphological and histochemical traits in the capitula linked to epornithochory, which in turn led to the unique geographical distributions of each genus.

Ecomorphology in Adenostemma and Adenocaulon

The pantropical genus *Adenostemma* (Fig. 1A), with *ca.* 24 species (Dosil Hiriart & Katinas, 2020), belongs to the wetland subtribe Adenostemmatiinae (3 genera) of the tribe Eupatorieae. Members of the subtribe inhabit damp areas, on the edges of rivers and swamps, and other watercourses. *Adenostemma* is represented by perennial herbs (Fig. 1B) that produce many tiny fruits per capitulum covered with conspicuous, large, biseriate, and multiseriate glandular trichomes (Fig. 1C). Each fruit has 2-5 sticky, glandular knobs at the apex, which represent a modified pappus (Fig. 1D). The glandular trichomes of the fruits and the glandular pappus have the ability to secrete mucilage with high adhesive power (Dosil Hiriart *et al.*, 2024). When the capitulum is mature, the fruits are arranged in an ‘umbrella-like’ position onto the receptacle (Fig. 1E), exposing the glandular structures in a way that could firmly gum to surfaces (Yapp, 1906). It has been hypothesized that the distribution of *Adenostemma* species, could be generally explained by animal-mediated dispersal (Hildebrandt, 1872; Yapp, 1906), and specifically by birds (Razi, 1950; Carlquist 1967; King & Robinson, 1974; Price & Wagner, 2018). These assumptions were experimentally tested by Dosil Hiriart *et al.* (2025), who demonstrated the ability of the fruits of *Adenostemma brasilianum* (Pers.) Cass. to adhere to birds’ feathers and to remain attached for some time after a disturbance

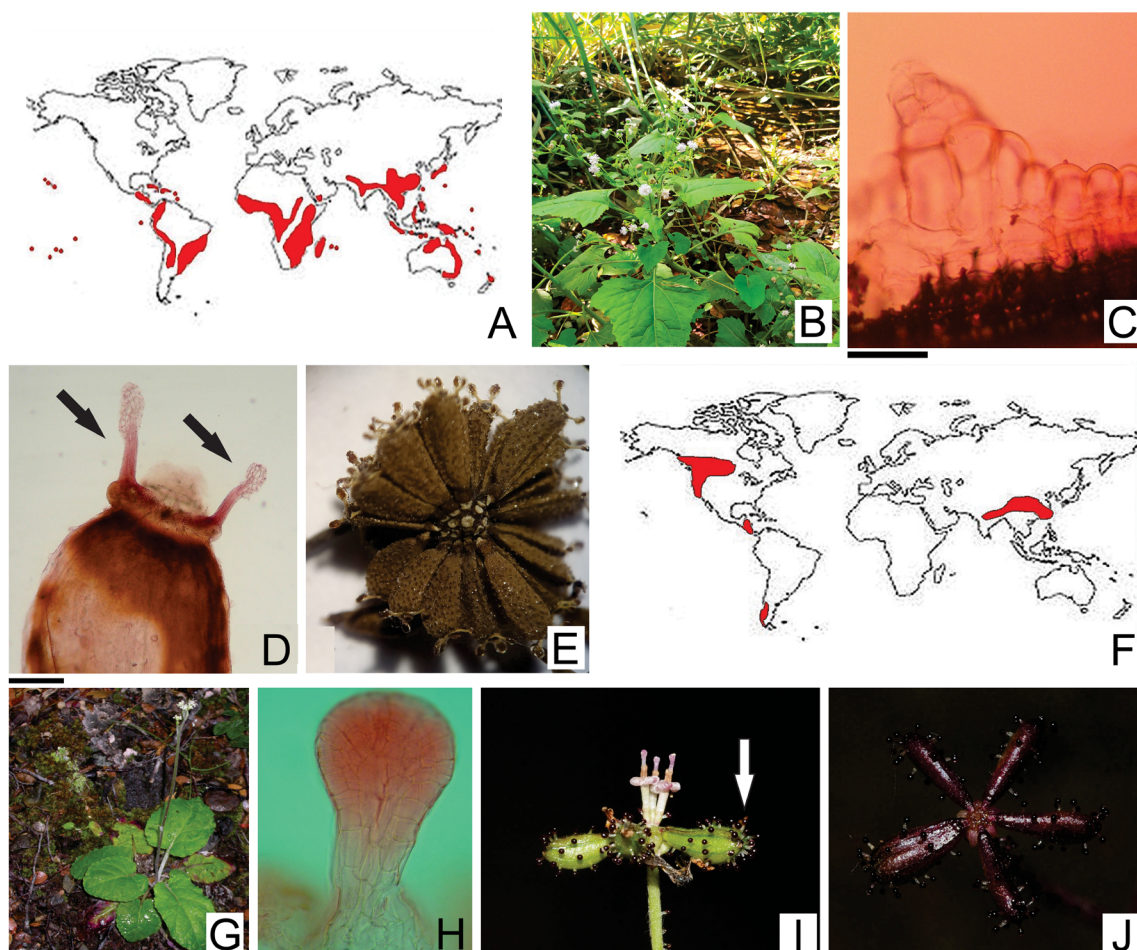


Fig. 1. *Adenostemma* and *Adenocaulon* (Asteraceae). **A-E:** *Adenostemma*. **A:** Geographic distribution. **B:** Habit. **C:** Multiseriate glandular trichome of the fruit. **D:** Glandular pappus (arrows). **E:** 'Umbrella' or horizontal position of the fruits onto the receptacle (upper view). **F-J:** *Adenocaulon*. **F:** Geographic distribution. **G:** Habit. **H:** Multiseriate glandular trichome of the fruit. **I:** Fruit epappose with the glandular trichomes mostly gathered at the apex (arrow) (lateral view). **J:** 'Umbrella' or horizontal position of the fruits onto the receptacle (upper view). Scales = C, H: 40 μ m; D: 0.5 mm. C-E, Dosil Hiriart *et al.* 42 (LP); H, Goodall 271 (LP). Photographs: B by F. Dosil Hiriart; G, I, and J by M. Bonifacino.

event, such as grooming and air currents. These authors reported at least 25 species of birds (e.g., *Ardea alba*, *A. cocoi*, *Ciconia maguari*, and *Pluvialis dominica*) sharing the same habitat with *A. brasilianum*. Among them, ibis, storks, Cocoi Heron, and Great Egret can move daily tens of kilometres to their breeding or roosting sites, functioning as possible vehicles for the dispersal of fruits. In addition, Chowdhury *et al.* (2013)

suggested a transcontinental dispersion Brazil-India of *Adenostemma suffruticosum* Gardner by the migratory Pectoral Sandpiper (*Calidris melanotos*). This capability of adhesion to birds has been proposed as the reason of the colonization of the species of *Adenostemma* of remote islands (Price & Wagner, 2018), for example, Tonga and Samoa (Whistler, 2011), the Mascarenes (Beentje *et al.*, 2005), and Tuamotu, Hawaiian, Micronesia,

Society, and Swains Islands (Whistler, 1983; Smith, 1991; Fosberg & Sachet, 2008).

Adenocaulon has been placed in several tribes across the family, and finally assigned to the tribe Mutisieae (Funk *et al.*, 2016). The genus includes five species of perennial herbs with a distribution occurring in the temperate forests in four widely disjunct areas: 1) Argentina and Chile in South America, 2) Guatemala and México, 3) northern United States and southeastern Canada, and 4) northern India, Nepal, China, Japan, Korea, and the Amur Region and Primorje Province (southern Russia) (Fig. 1F). It grows in the under-stories of moist forests, in the shade of *Nothofagus* Blume, *Pinus* L. and *Quercus* L. (Fig. 1G) (Bittmann, 1990; Katinas, 2000; Funk *et al.*, 2016). The fruits of *Adenocaulon* lack a pappus and are covered by very large, multiseriate glandular trichomes (Fig. 1H) that extrude a sticky, mucilaginous secretion (Karrfalt & Kreitner, 1980). It is interesting to note that the trichomes are mostly gathered at the apex of the fruit (Fig. 1I), probably acting as a ‘functional pappus’. The fruits in the capitula also adopt the typical ‘umbrella-like’ position at maturity (Fig. 1J). The possibility that birds could have a dispersal role in *Adenocaulon* fruits was suggested by Deng *et al.* (2018) to explain the species’ disjunct distributions. Deng *et al.* (2018) proposed that the genus may have originated in Central America and then dispersed to North and South America. According to these authors, long-distance dispersal of species of *Adenocaulon* may have been enhanced by birds due to the prominent, sticky glandular trichomes on the fruits.

Birds could have exerted selective pressures on fruits and pappus, favoring certain traits

such as those mentioned for *Adenostemma* and *Adenocaulon*, which influence their ability to be externally dispersed. This, in turn, resulted in the disjunct geographical distributions and in the presence on remote islands of these taxa.

HISTORY: HOW DID IT ORIGINATE?

Distinguishing homology from homoplasy

To estimate the history of any group of organisms, it is essential to discuss the concept of homology and its complement, homoplasy (Table 1). Homology is the possession by two or more taxa of a character that, with or without modifications, has been inherited from a common ancestor (Fig. 2A).

There are at least three criteria to detect morphological homology (Patterson, 1988; Hall, 1994; Palacio *et al.*, 2020). These criteria are 1) Congruence with the homologies of other characters: it is the congruence with other postulated homologies, as determined by their agreement in supporting the same phylogenetic relationships. For example, the capitulum, the connate and introrse anthers, the pappus, and the bifid, bifacial style in members of the different tribes of Asteraceae are all homologous characters of the family; 2) Morphological, topological, or structural similarity: even when the capitula in members of Asteraceae may present different morphologies (discoid, disciform, radiate) they share all the same topology, structure, and origin, representing a homologous character for the family (Fig. 2B-D) because the capitulum was present in the most recent ancestor of the family; and 3) Non-coexistence: as homology is a relation of ‘sameness’ between two or more traits, either in the same individual organism or

Table 1. Criteria employed to distinguish among homology, parallelism, and convergence. Reversion is not included in the table because it does not involve a comparison between taxa. Modified from Patterson (1988) and Palacio *et al.* (2020).

Relationship	Criteria			
	Congruence	Similarity (structural)	Non-coexistence	Development (ontogeny)
Homology	positive	positive	positive	similar
Parallelism	negative	positive	positive	similar
Convergence	negative	negative	positive	different

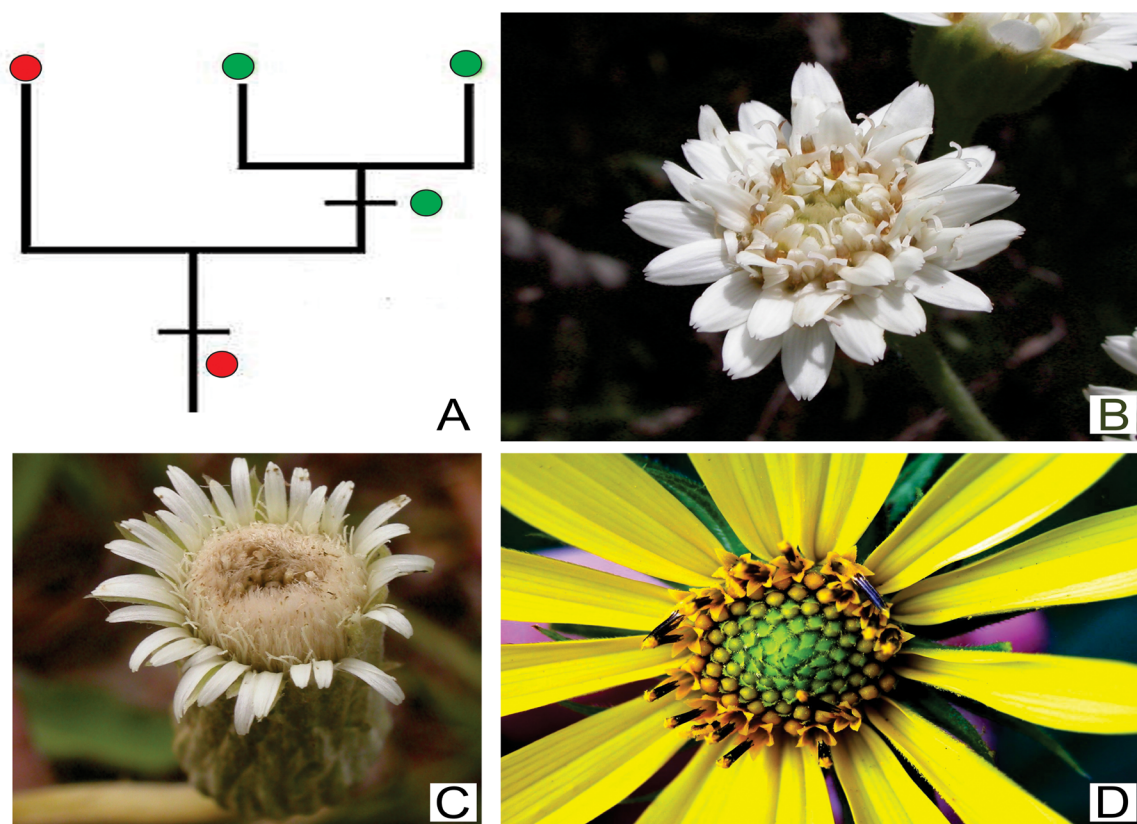


Fig. 2. Homology. **A:** Phylogenetic tree showing two different character states (red and green). The green circles represent homologous character states since they share a recent common ancestor. **B-D:** Example in Asteraceae showing different types of capitula that share all the same topology, structure, and origin, representing a homologous character state for the family. **B:** Discoide capitulum of one species of *Holocheilus* Cass. **C:** Disciform capitulum of one species of *Chaptalia* Vent. **D:** Radiate capitulum of one species of *Silphium* L. Photographs: B and C by M. Bonifacio; D by L. Katinas.

in different individuals of the same or different species, two homologous characters cannot coexist in the same individual. When copies of more than one homologous character coexist in the same individual (*e.g.*, the leaves of the same individual), it is called homonymy.

There is homoplasy when two or more taxa share similar or identical characters, and these do not derive from the common ancestor (*i.e.*, similar characteristics with different evolutionary origins) (Lankester, 1870). The concept of analogy was used by Owen (1843) as opposed to homology. Currently, the term analogy can be synonymized with ‘functional convergence’ (Palacio *et al.*, 2020).

Homoplasy includes parallelisms, convergences, and reversals. Parallelism is the independent evolution in phylogenetically closely related lines of similar or identical characteristics, usually based on the same developmental paths (Fig. 3A). Some species of *Perezia* Lag. and *Leucheria* Lag., two genera of the tribe Nassauvieae (Asteraceae) that do not form a monophyletic group in the phylogenetic tree of the tribe (Katinas *et al.*, 2008; Luebert *et al.*, 2009), inhabiting the same environments, are very similar in their appearance. This is the case of *Perezia prenanthoides* Less. with *Leucheria glacialis* (Poepp. ex Less.) Reiche (Fig. 3B), and *Perezia delicata* Vuilleum. with *Leucheria eriocephala* Speg., all of the *Nothofagus*

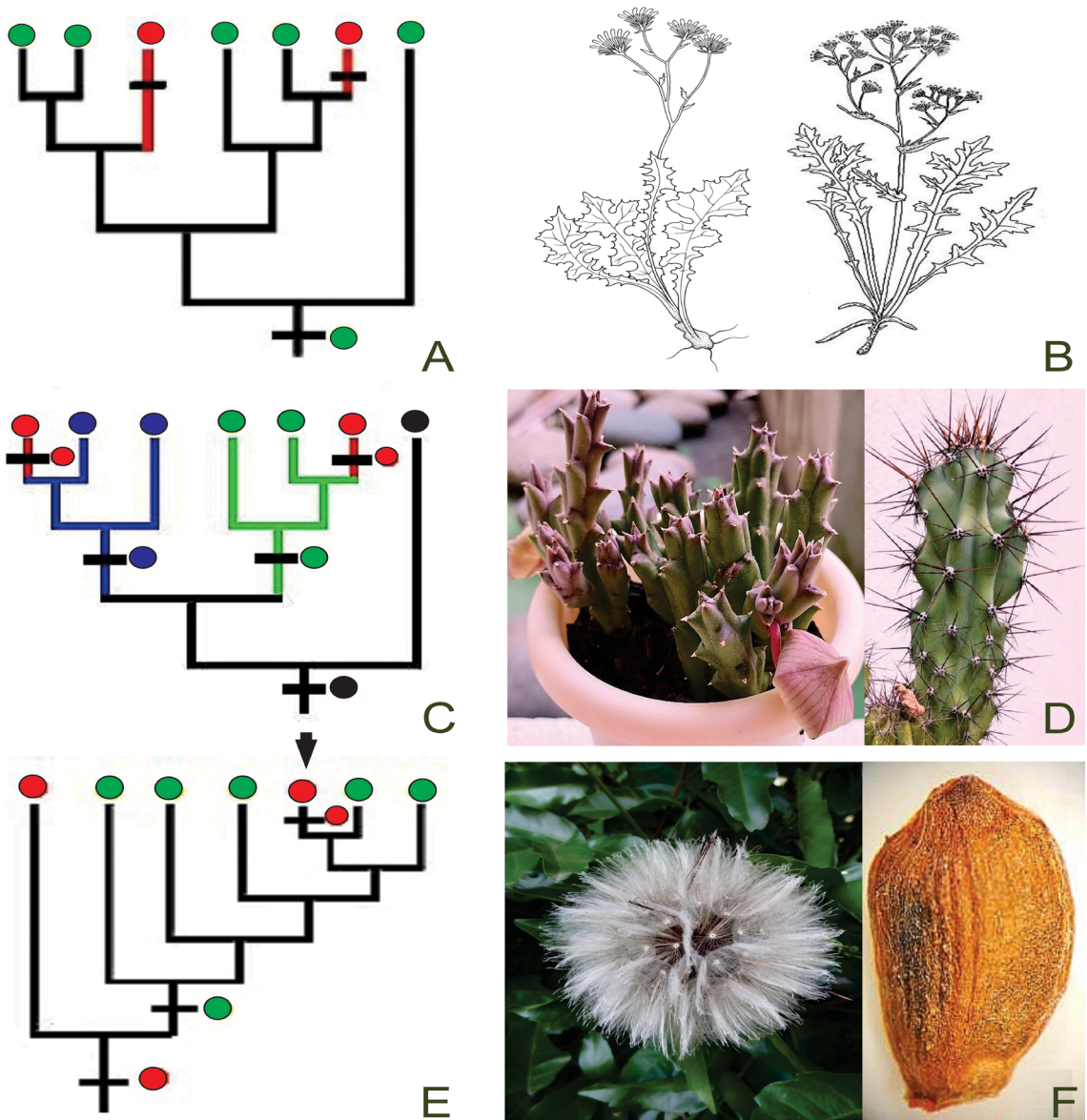


Fig. 3. Homoplasies. **A-B:** Parallelism. **A:** Phylogenetic tree showing two parallel character states (in red). **B:** Example of parallelism in *Perezia prenanthoides* (left) and *Leucheria glacialis* (right) (tribe Nassauvieae), which do not share a recent common ancestor, and are very similar in their habit. **C-D:** Convergence. **C:** Phylogenetic tree showing two convergent character states (in red), the other colors represent different lineages with different character states. **D:** Example of convergence in the similar succulent stems as an adaptation to arid environments of a member of Apocynaceae (left) and a member of Cactaceae (right), families localized in distant branches of the phylogenetic tree of the Angiosperms. **E-F:** Reversion. **E:** Phylogenetic tree showing an ancestral character state at the base of the tree (in red), that evolves to a new character state (in green), and returns in one of the branches of that group to the ancestral character state (in red, arrow). **F:** Capitulum of one species of *Mutisia* L.f. showing fruits with pappus (upper view, left) and fruit of *Smallanthus connatus* (Spreng.) H.Rob. (lateral view, right), lacking a pappus, as a reversion to the ancestral condition of the epappose members of Calyceraceae (sister group of Asteraceae). **F** (right), Hunziker 1545 (GH). Photographs: D, F (right) by L. Katinas. F (left), by F. Dosil Hiriart.

forests. Convergence is the independent evolution of similar characteristics in different evolutionary lines, derived from different ancestral characters and with different developmental paths (ontogenies) (Fig. 3C). An example of convergent evolution is the similar external appearance of the ribbed, succulent stems as an adaptation to arid environments of some cacti (Cactaceae), euphorbias (Euphorbiaceae), and stapeliads (Apocynaceae) belonging to families distantly related in the phylogenetic tree of the Angiosperms (Fig. 3D). Reversion constitutes the return to an ancestral characteristic from a derived character (Fig. 3E). It is assumed that the lack of pappus in some genera of Asteraceae (e.g., *Panphalea* Lag., *Smallanthus* Mack.) (Fig. 3F) is a reversion to the ancestral condition since the members of Calyceraceae (sister group of Asteraceae) have no pappus.

Parallelism can be distinguished from convergence by applying the following criteria (Palacio *et al.*, 2020):

1. If there is structural correspondence, it is a parallelism; otherwise, it is a convergence.
2. If there are similar non-ancestral features in nearby taxa, it is a parallelism; in distant taxa, it is a convergence. It means that parallelism describes the development of features in lineages that more recently diverged from their last common ancestor than those that show convergence (Hall, 2003). It should be noted that there is a continuum in the evolutionary distance of the taxa being compared, making it often difficult to establish a limit between closely related lineages and distantly related lineages. In some cases, finding an objective way to differentiate between parallel and convergent evolution can be challenging (Cerca, 2023).
3. If there are independent characteristics caused by a shared genetic basis and development or an ancestral predisposition, it is a parallelism; otherwise, it is a convergence. Convergence is not based on shared development but reflects different processes producing similar features (Hall, 2007).

Adenostemma and Adenocaulon in a historical context: the phylogeny of Asteraceae

Examining ecomorphological patterns across the phylogeny allows the identification of homoplasies and homologies. The current molecular phylogeny of the family Asteraceae (Zhang *et al.*, 2021) is displayed in Fig. 4. It shows *Adenostemma* and

Adenocaulon located in the recently radiated crown (tribe Eupatorieae) and in one of the earliest diverging branches (tribe Mutisieae) of the tree, respectively. Taking into consideration the position of *Adenostemma* and *Adenocaulon* in the family tree, it is evident that the set of features shared by both genera in relation to epiornithochory has two independent origins. They are homoplastic following Lankaster's (1870) concept, finding two parallelisms, one reversion and one functional convergence. Two features, *i.e.*, the conspicuous multiserial, glandular trichomes that extrude sticky mucilage and the 'umbrella-like' position of the fruits, constitute parallelisms. The two features pass the criteria of parallelism outlined above: there is structural correspondence, and they constitute similar non-ancestral features in phylogenetically nearby taxa (both genera belong to the same family). Furthermore, the trichomes of *Adenostemma* and *Adenocaulon* share similar pathways in the ontogeny (Carlquist, 1958; Ramayya, 1962; Karrfalt & Kreitner, 1980; pers. obs.), with a mother cell dividing through an anticlinal wall and then periclinal cells are formed in acropetal sequence in both cells. Both genera also develop a similar ontogenetic maturation process in which the fruits change their position onto the receptacle from erect to horizontal (Yapp, 1906; Funk *et al.*, 2016; pers. obs.), acquiring an 'umbrella' position.

The lack of pappus in *Adenocaulon* constitutes a reversion to the ancestral condition, which is not the case of *Adenostemma*, with its glandular pappus. The pappus absence, however, constitutes a parallelism with other epiornithochorous genera such as *Lagenophora* and *Myriactis*, and species of *Lasthenia*. The distribution of the glandular trichomes in *Adenocaulon*, mostly gathered at the fruit apex, would constitute a functional convergence with *Adenostemma*. The apical position of the trichomes may constitute a 'functional pappus', being an efficient mechanism that makes the fruits more accessible for dispersion, in the same way that the glandular pappus of *Adenostemma*. It is not a parallelism because there is no structural and developmental correspondence, reflecting different processes that produce a similar function (dispersal).

The effects of the diaspore adhesion power through the trichomes with mucilage and the

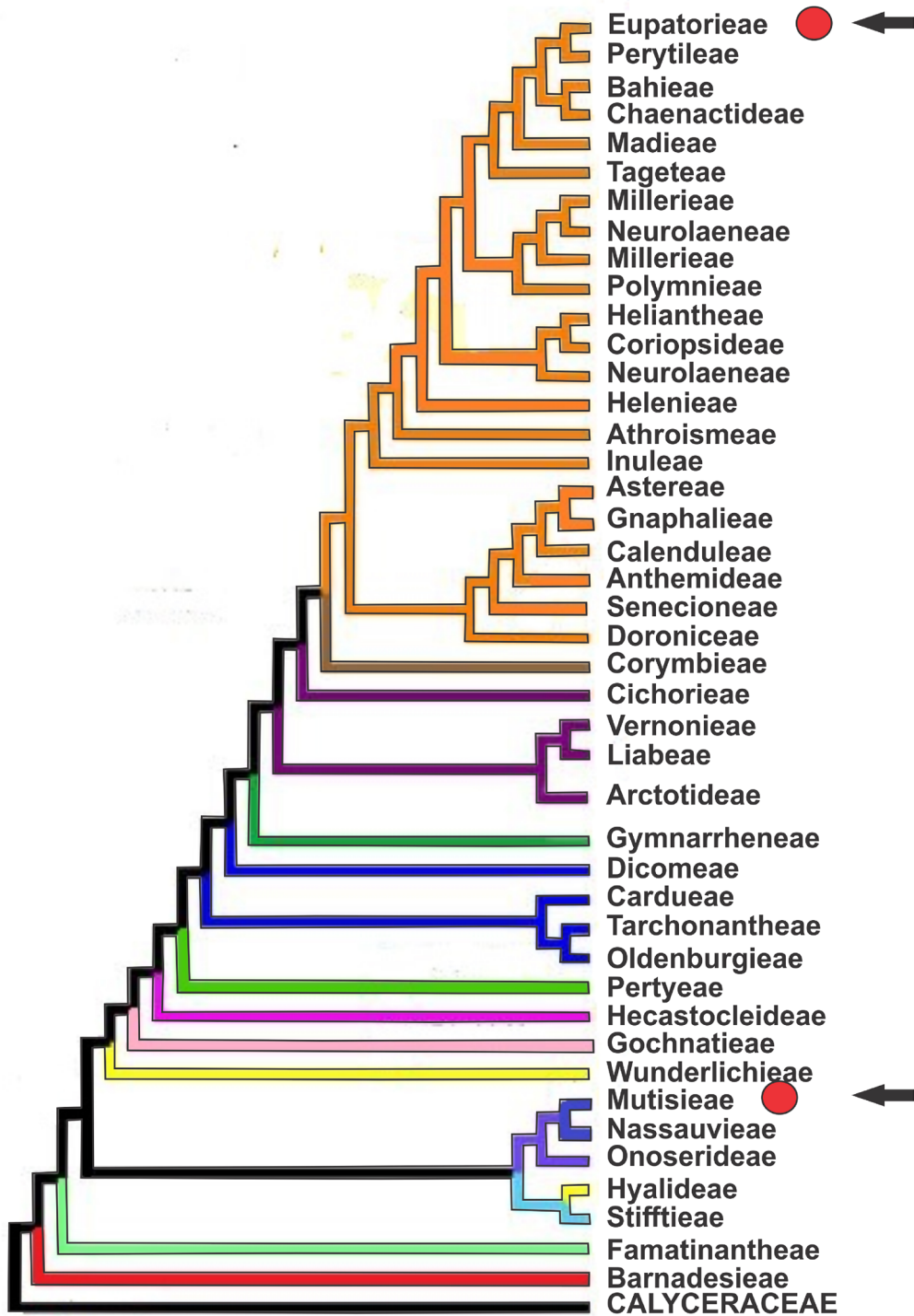


Fig. 4. Molecular phylogenetic tree of the family Asteraceae (modified from Zhang *et al.*, 2021) with the tribes, showing the position (red circles and arrows) of *Adenostemma* in the recently radiated crown (tribe Eupatorieae) and *Adenocaulon* in one of the earliest diverging branches (tribe Mutisieae). The colors in the branches represent different subfamilies.

particular ‘umbrella’ architecture of *Adenostemma* and *Adenocaulon*, could provide a basis for selection of these traits, in the sense of a successful transportation by passing animals. If the animals are birds, their capability of surpassing biogeographic barriers is very probably the cause of the unique distribution of these plants. Sorensen (1986) emphasized that the presence of adhesive fruits in isolated habitats, such as islands, and disjunct distributions of species between widely separated continents provide evidence for long-distance dispersal of adhesive fruits. Adhesive fruits have the potential to travel farther than do fruits carried internally or dispersed by the wind, because they can be carried for a long period of time by the dispersal agent, depending on the grooming activity of the animal. In addition, irritating fruits (*e.g.*, with burrs and hooks) are more likely to be removed by the animal than adhesive fruits.

Carlquist (1976) established that there is evidence that particular characters have shown similar shifts two or more times in Asteraceae and that, probably, no single character within the family is free from parallel evolution. This author says that, for example, all-ligulate heads of flowers have evolved in some members of the current tribe Stiffieae (Katinas & Funk, 2020) as well as in the tribe Cichorieae. The difference between Carlquist’s example and the case presented here is that it is a set of morphological and histochemical characters exhibiting different types of homoplasy, likely in response to similar ecological pressures or selective advantages.

CONCLUSIONS

Correlations between environmental factors, organismal traits, and unique geographical distribution are found widely in plants. In the case analyzed here, a set of diaspore characters, optimal for successful external dispersion, evolved as homoplasies in several genera of the same family. Diaspores may be modified to adhere to animals in several ways. Because this adhesion occurs commonly by chance, the diaspores have specific morphological and histochemical attributes to ensure their transportation. Some authors (*e.g.*, van der Pijl, 1969; Lomáscolo & Schaefer, 2010; Valenta & Nevo, 2020) refer to the set of diaspore traits

hypothesized to evolve under the selective pressure of seed dispersers as the ‘Dispersal Syndrome hypothesis’. This concept is used for endozoochory, where dispersal appears to be non-random, but it could also be applied in our case study, where dispersal occurs accidentally. This means that it is not the result of the birds’ preferences, but rather the morphological traits of the plant.

A major goal in ecomorphology is to find adaptive explanations for specific forms, *i.e.*, to consider the external environment as the main cause of the observed morphology (Betz, 2006). Similar environmental pressures are expected to elicit similar adaptive morphologies, suggesting that phenotypic homoplasy is often a consequence of natural selection (Wake *et al.*, 2011). The phylogenetic history of taxa can be used as a template for explanations concerning the evolutionary origin and diversification of the investigated ecologically relevant structures, and for establishing the homological or homoplastic nature of these structures.

AUTHORS’ CONTRIBUTION

LK conceived the study, LK, FDH and JVC designed the study and wrote the paper.

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