

Cardueae (Carduoideae)

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HISTORICAL OVERVIEW

The tribe Cardueae is one of the largest in Compositae, with some 2400 species in 73 genera (Susanna and Garcia-Jacas 2007). It is also one of the most complicated because of great morphological diversity and because it comprises some of the largest genera of the family. Cardueae were usually divided into four taxonomic entities, but rank and delimitation of these units has always been problematic, as we shall explain briefly. The earliest classification of the tribe by Cassini (1816) recognized three separate tribes, Echinopseae, Carlineae, and Cardueae, the latter with two subtribes, Carduinae and Centaureinae. Bentham (1873) and Hoffmann (1893), in contrast, suggested a broadly defined Cardueae comprising four subtribes: Echinopsinae, Carlininae, Carduinae, and Centaureinae. This treatment was generally accepted until Wagenitz (1976) segregated Echinopseae as a separate tribe, a proposal that was reintroduced by Petit in 1988. Dittrich (1977) returned to Cassini's views and segregated both Echinopseae and Carlineae. In view of this lack of agreement, Bremer (1994) adopted the more conservative approach and recognized only one tribe. Finally, mainly on the basis of molecular data (Susanna et al. 2006) but also on morphological grounds, Susanna and Garcia-Jacas (2007) adopted the broad concept of a single tribe with four subtribes of Bentham (1873) and Hoffmann (1893) plus one recovered fifth subtribe, Cardopatiinae, which we shall discuss below.

All molecular analyses have concluded that Cardueae are monophyletic, including the most often segregated subtribes Carlininae and Echinopinae. Despite deep dif-

ferences in habit, floral morphology, and achene anatomy, all Cardueae share some characters that are not found elsewhere in Compositae. The key is the style morphology, characterized by a thickened articulation below the branches of the upper region usually provided with a collar of hairs, and internal stigmatic surface. Notwithstanding some claims of deep differences (Duistermaat 1996; H ffner 2000), all the style variants within the tribe can be explained as variations of this basic architecture.

Most of the difficulties for assigning tribal or subtribal rank have originated in subtribes Carlininae and Echinopinae, which are rather different from the core Cardueae (the subtribes Carduinae and Centaureinae). Carlininae show some very archaic features: *Atractylis* L. and part of *Carlina* L. have true ligules (Fig. 20.2A below), which are not found elsewhere in the Cardueae. Most species of *Carlina* share a complicated involucre structure that has been interpreted as a third-order syncephaly (Meusel and Kohler 1960; Meusel and K stner 1994), an interpretation rejected by Petit (1988). Echinopinae are a monotypic subtribe, *Echinops* L., which is characterized by unflowered capitula grouped in second-order heads (Fig. 20.2E, F below). This structure was the main reason for the segregation of Echinopinae as a different tribe by Wagenitz (1976), Dittrich (1977), and Petit (1988, 1997). Homologies of the synflorescence of *Echinops* are extremely difficult to establish, as is usually the case with highly derived syncephalies (Stuessy and Spooner 1988), for example, two genera of troublesome position within Compositae, *Gundelia* L. and *Hecastocleis* A. Gray, are syncephalous. In fact, contradictory results obtained by different authors in cladistic analyses of morphologic data

(compare Karis et al., 1992, versus Petit, 1997) could be partly attributed to different points of view in addressing the problem of homologies of the receptacular structures of *Carlina*, *Echinops*, and related genera.

In addition to the problematic delimitation of Cardueae, the boundaries between the classic four subtribes were also difficult to establish. For example, previous classifications (Bentham 1873; Hoffmann 1893; Dittrich 1977; Bremer 1994) placed *Amphoricarpos* Vis., *Cardopatum* Juss., *Chardinia* Desf., *Cousiniopsis* Nevski, *Siebera* J. Gay, *Stachelina* L., and *Xeranthemum* L. within Carlininae, whereas Petit (1997) moved *Cardopatum* and *Cousiniopsis* to Echinopseae (to which he assigned tribal rank) and the rest of genera to Cardueae–Carduinae. Other genera have been very difficult to classify, such as *Berardia* Vill., included among Cardueae by Bremer (1994), placed in Mutisieae by Dittrich (1996a) and moved back again to Cardueae–Carduinae by Garcia-Jacas et al. (2002).

Finally, there are the problems of generic delimitation posed by some large genera of the tribe: *Carduus* L. (90 spp.), *Cirsium* Mill. (250 spp.), *Centaurea* L. (400 spp. in older classifications), *Cousinia* Cass. (600 spp.), *Jurinea* Cass. (200 spp.), and *Saussurea* DC. (300 spp.). The natural delimitation of *Centaurea* was achieved by Garcia-Jacas et al. (2000, 2001, 2006), some approximations to the limits of *Carduus* and *Cirsium* were made by Häffner and Hellwig (1999), and systematics of the *Arctium* complex has received an important impulse recently (López-Vinyallonga et al. 2009), but the rest of the problems persist. Many small genera from central and west Asia have been described on the basis of splitting *Jurinea*. For example, *Diplazoptilon* Ling, *Hyalochaete* Dittrich & Rech. f., *Jurinea* Jaub. & Spach, *Himalaiella* Raab–Straube, *Modestia* Iljin, and *Outreya* Jaub. & Spach are doubtful segregates merged into the larger genus by Susanna and Garcia-Jacas (2007).

PHYLOGENY

Tribes or subtribes? Molecular evidence

The latest molecular survey (Susanna et al. 2006) (Fig. 20.1), based on three different regions of the genome (*matK*, *trnL-F*, and ITS) and a better outgroup selection, established that the tribe was monophyletic and the subtribal rank was appropriate for the five subtribes

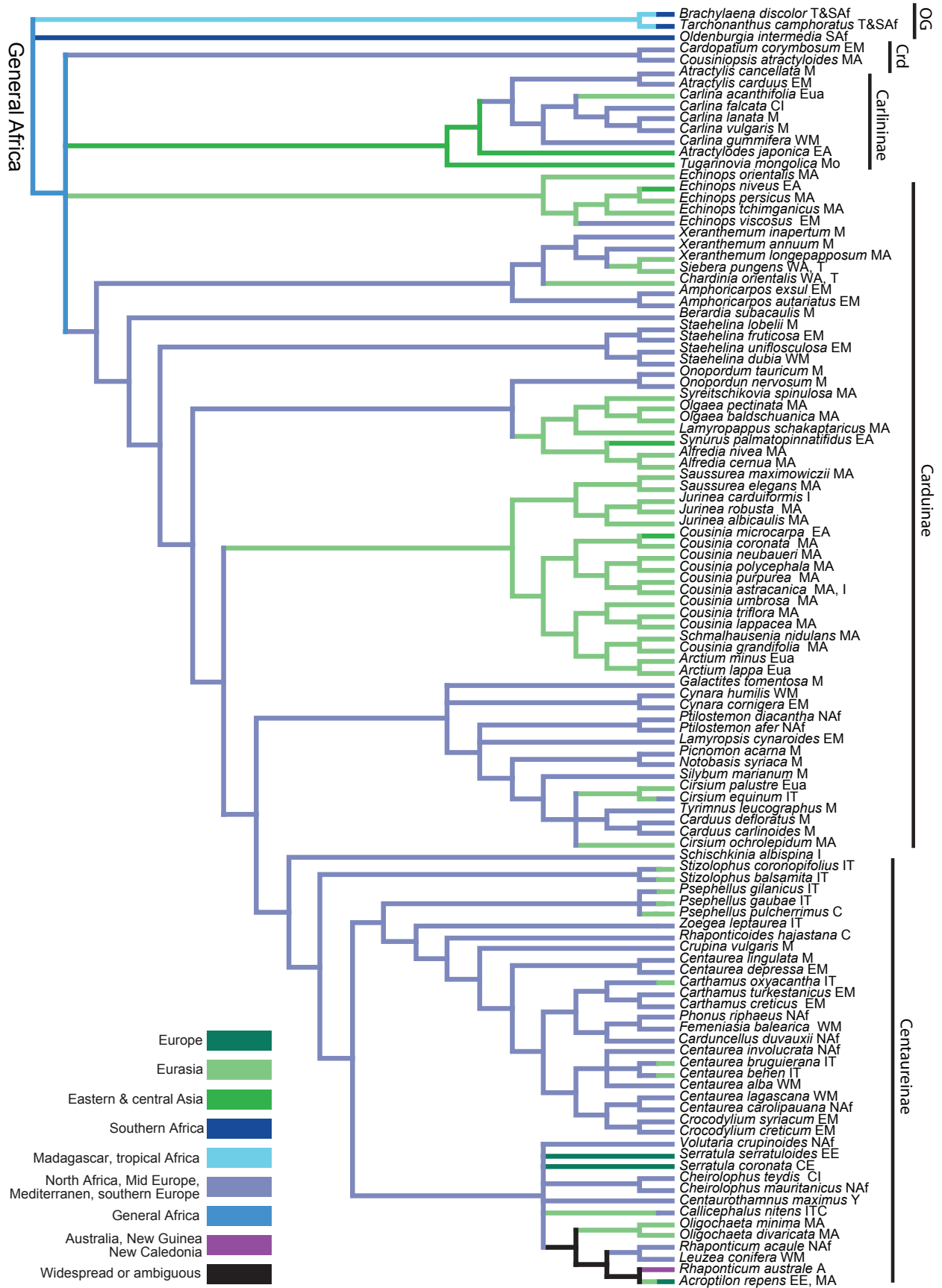
that must be recognized (the classic four, Carlininae, Echinopsinae, Carduinae, and Centaureinae, plus one restored subtribe, Cardopatiinae). Indeed, the three basal subtribes (Carlininae, Cardopatiinae, and Echinopsinae) could be segregated from core Cardueae (Carduinae plus Centaureinae) as independent monophyletic tribes, but we do not favor such a fragmented classification. We must acknowledge that our proposal of classification is not a perfect solution, for two reasons: firstly, sister relationships among basal tribes (Carlininae sister to the rest of the tribe, and Cardopatiinae and Echinopsinae successive sisters to the other subtribes) are weakly supported by parsimony (fig. 2 in Susanna et al. 2006) and unsupported by Bayesian analyses (Fig. 20.1); secondly, Carduinae are a paraphyletic assemblage if we split from this subtribe monophyletic Centaureinae. However, alternative, stricter solutions are impracticable (Susanna and Garcia-Jacas 2007). The broad synthetic approach would group together Centaureinae and Carduinae in a single colossal subtribe encompassing 90% of the 2500 species of Cardueae. A narrow analytical approach would keep Centaureinae as a distinct subtribe at the price of splitting present Carduinae into at least seven new subtribes (many of them presently unsupported): Xerantheminae, Stachelinae, Berardiinae, Onopordiinae, Carduinae, Arctiinae, and Saussureinae (Fig. 20.1). With our present state of knowledge, we do not favor this splitting, even though future studies could finally lead to it. Quoting Jeffrey (1967), the classic, conservative classification adopted here “is purely artificial without doubt, but it has the merit of some convenience”. Chapters 12 and 44 contain overviews of the family and placement of Cardueae.

TAXONOMY

Tribe Cardueae Cass. in J. Phys. Chim. Hist. Nat. Arts 8: 155. 1819 – Type: *Carduus* L., Sp. Pl. 2: 820. 1753

Perennial, biennial, or monocarpic herbs or shrubs, less often annual herbs, very rarely small trees, often spiny. Leaves alternate, frequently forming a rosette, rarely in terminal whorls. Resin-ducts always present in roots, less frequent in aerial parts; laticiferous cells often present but only in aerial parts. Capitula scapose–solitary or diversely corymbose, often aggregate, usually many-flowered, rarely glomerate in secondary capituliform compound

Fig. 20.1. Bayesian inference tree from Susanna et al. (2006) showing the accepted subtribal classification of Cardueae (Crd = Cardopatiinae; OG = outgroup). Branch colors indicate distribution based on color chart using general areas. Abbreviations at the end of taxon names indicate the more specific distribution: C = Caucasus; CE = central Europe; CI = Canary Islands; EA = eastern Asia; EE = eastern Europe; EM = eastern Mediterranean; Eua = Eurasia; I = Iran; M = Mediterranean; MA = middle Asia; Mo = Mongolia; NAf = northern Africa; SAf = southern Africa; T = Turkey; TAf = tropical Africa; WM = western Mediterranean; Y = Yemen.



inflorescences and then one-flowered. Involucral bracts in many rows, spiny or unarmed, foliaceous or membranous, often prolonged into a membranous, variously fimbriate, lacerate or pectinate, spiny or unarmed appendage. Receptacle variously chaffy or more often setose, rarely naked (*Alfredia* Cass. pro parte, *Dolomiaea* DC., *Onopordum* L., *Myopordon* Boiss., *Russowia* C. Winkl., and *Tugarinovia* Iljin). Florets usually tubular, very rarely peripheral florets with true rays (*Atractylis* and *Carlina* [Fig. 20.2A]); all fertile or the peripherals sterile through abortion and radiant sterile peripheral florets often absent (especially in subtribe Carduinae). Corollas usually almost actinomorphic, very rarely zygomorphic, divided into a tube and a campanulate limb, straight or s-shaped. Anthers sagittate, apically extending into a rigid, lignified, lanceolate appendage, basally caudate, often with long divisions; anther filaments glabrous or papillose; in many derived groups (especially in subtribe Centaureinae) the stamens are strongly thigmotropic making up an elaborate mechanism of pollen presentation. Style with a papillose-pilose thickening (functionally a pollen brush) below the branches; stigmatic areas only in the inner surfaces of the branches; nectary present at the base of the style. Achenes very variable, with parenchymatous pericarp (in Carlininae, Cardopatiinae, and Echinopsinae, rarely in Carduinae) or radially lignified (in Carduinae and all Centaureinae), usually hirsute in subtribes Carlininae, Cardopatiinae, and Echinopsinae, glabrous in most of Carduinae and Centaureinae. Insertion areole basal, basal-lateral or lateral. Pappus of scales or bristles, directly attached to the pericarp wall in the subtribes Cardopatiinae, Carlininae, and Echinopsinae, and in the genera *Berardia*, *Stachelina*, and the *Xeranthemum* group of Carduinae, or fixed through a parenchymatous ring to the apical plate in remaining Carduinae and all Centaureinae; pappus usually in two structurally different rows (double pappus) in Centaureinae. Pinnules shorter than width of palea (scabrate), as long as width of palea (pinnulate), or much longer and capillar (plumose). Apical caruncle present in many genera of Carduinae, basal elaiosome in Centaureinae, associated with myrmecochory. Pollen tricolporate, oblate, spherical or more prolate; ektexine formed by two layers of columellae, sometimes caveate (in subtribe Centaureinae), spiny, verrucate, scabrate or almost smooth.

Currently there are 72 accepted genera (73 in Susanna and Garcia-Jacas 2007; *Ochrocephala* Dittrich and *Takeikadzuchia* Kitag. & Kitam. moved to synonymy, *Archiserratula* L. Martins added), ca. 2400 species.

A general description of the morphology, karyology, pollen and distribution of the tribe is a complicated task due to the extreme heterogeneity in every aspect. Annuals, unarmed or spiny perennial herbs, subshrubs, shrubs, tree-lets, trees, alpine meadows or tropical savannahs; there is

no habit or habitat alien to Cardueae, which makes it difficult to discuss overall trends. As a result, apart from the synthetic description and general comments above, each one of the five groups with distinctive characters in which the tribe is hereby divided into is discussed below. The five subtribes will have its own detailed description of morphology, chromosome numbers, biogeography, and diversification.

SUBTRIBAL CLASSIFICATION

Carlininae

Perennial herbs or shrubs, less often annual plants. Leaves usually spiny, deeply pinnatisect, rarely unarmed and entire. Capitula frequently subtended by pectinate leaf-like bracts, homogamous or heterogamous, sometimes with radiate florets (Fig. 20.2A). Inner involucral bracts often showy, radiant, and colored (Fig. 20.2B). Receptacle densely covered with large scales, absent only in *Tugarinovia*. Anther filaments glabrous, appendages long and sericeous. Corolla and style very short. Achenes with parenchymatous pericarp, densely sericeous. Pappus of plumose bristles, often connate into stout scales, persistent or deciduous.

The only genera presently included in Carlininae are *Atractylis*, *Atractylodes*, *Carlina*, *Thevenotia* (maybe not specifically different from *Carlina*), and *Tugarinovia* (Susanna and Garcia-Jacas 2007). No molecular phylogeny is yet available for the subtribe, only a reconstruction by Susanna et al. (2006) on a small sample of all the genera, which finally confirmed that *Tugarinovia* was related to *Carlina* as suggested by Dittrich et al. (1987). The curious and puzzling *Tugarinovia* is the only dioecious genus in the tribe.

Carlininae are mainly an eastern Mediterranean group, extending into Eurasia in the north and into North Africa in the south; some species of *Carlina* are widespread in the Eurosiberian climatic region, from the Pyrenees to the Urals. *Atractylis* is more centered in North Africa. The presence of two isolated genera in Middle and East Asia is very remarkable: *Tugarinovia* in Mongolia and *Atractylodes* in Japan and Korea. A probable new genus is presently being studied (Q. Liu, pers. comm.) from the Qinghai-Tibetan plateau, which could fill the gap between the easternmost range of *Carlina* and the East Asian representatives of the subtribe.

The subtribe appears to have had an African origin because Carlininae are probably the basal lineage of Cardueae (Fig. 20.1), and the other tribes of Cardioideae sister to them, Oldenburgieae and Tarchonantheae, are African. Previous hypotheses on the archaic character of insular endemics of *Carlina* in Crete and Macaronesia must be rejected.

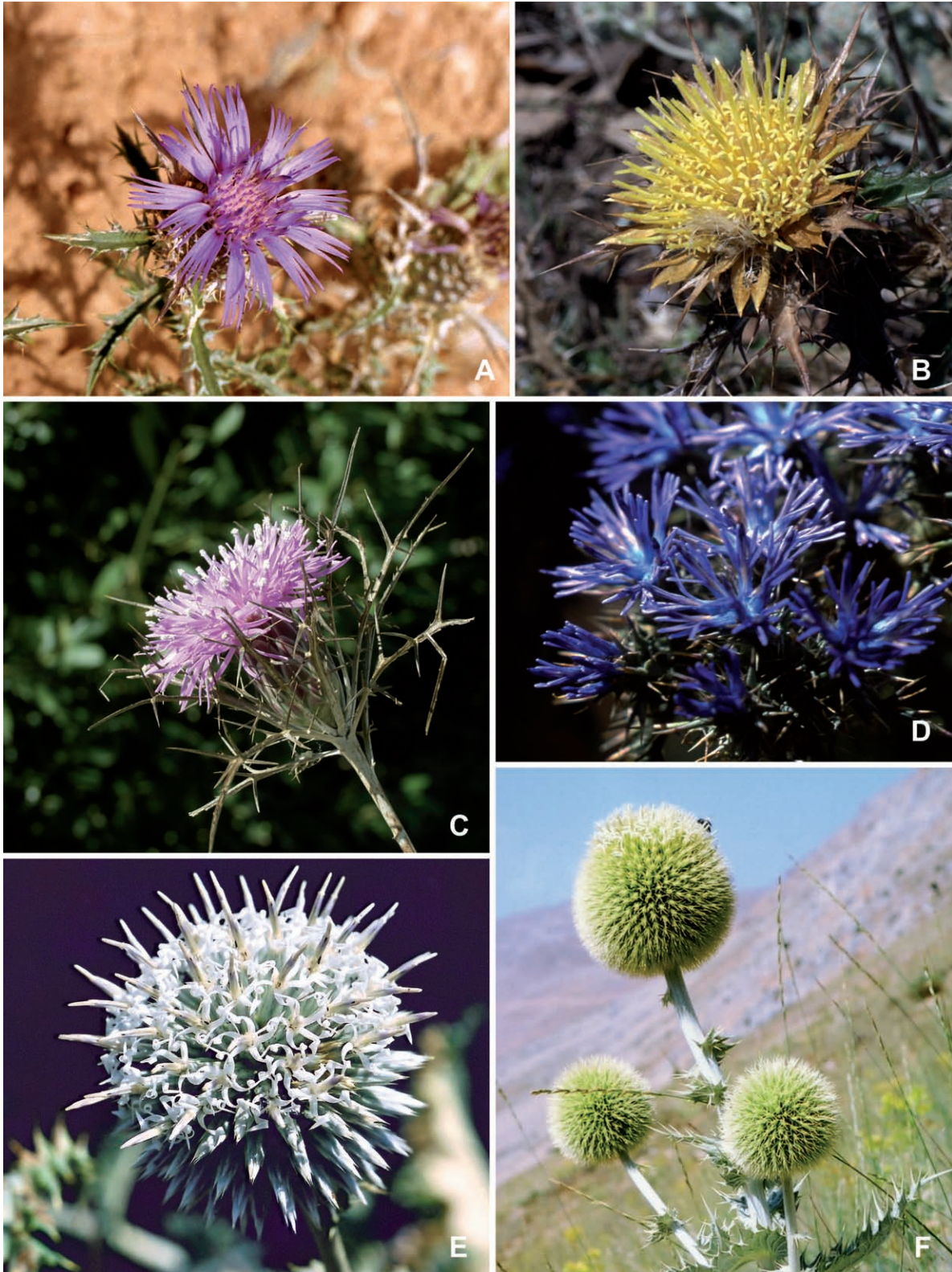


Fig. 20.2. Basal subtribes. Carlininae: **A** *Atractylis carduus* C. Chr. showing true ray florets; **B** *Carlina vulgaris* L.; **C** *Carlina comosa* (Spreng.) Greuter. Cardopatiinae: **D** *Cardopatium corymbosum* Pers. with few-flowered heads grouped in corymbs. Echinopsinae: **E** *Echinops viscosus* Rchb.; **F** *Echinops emiliae* Schwarz ex P.H. Davis and its stunning green-flowered large synflorescences up to 20 cm diameter. [Photographs, authors.]

Cardopatiinae

Spiny perennial or annual herbs. Leaves spiny-dentate or pinnatisect. Capitula either few-flowered and clustered in corymbs, or many-flowered. Involucral bracts with spiny pectinate-fimbriate appendages. Anther filaments glabrous. Florets deep blue, filiform. Style very shortly bilobed. Achenes with parenchymatic pericarp, densely sericeous; pappus double, of two rings of short scales.

Cardopatiinae, as first defined, included only the monotypic genus *Cardopatium*. Later, Nevski (1937) described another monotypic genus, *Cousiniopsis*, closely related to *Cardopatium* (it was first described as *Cardopatium atractylodes* C. Winkler). Classic monographers of Compositae consistently placed both genera among Carlininae, but the only characters that connect these two groups are achenes, which could equally relate *Cardopatium* and *Cousiniopsis* to Echinopsinae. Petit (1997) interpreted the corymbose inflorescence of *Cardopatium*, formed by very small, few-flowered capitula (Fig. 20.2D), as a first step towards the syncephaly of *Echinops* and thus placed *Cardopatium* and *Cousiniopsis* in Echinopsinae. This relationship is unsupported by molecular analyses and we favor interpreting these similarities as convergence, especially since the same trend towards syncephaly appears in all subtribes of Cardueae (Garcia-Jacas et al. 2002). Anyway, Cardopatiinae range among the oldest subtribes, together with Carlininae (Fig. 20.1).

Cardopatiinae show a disjunct distribution. Perennial *Cardopatium corymbosum* grows in central and eastern Mediterranean (from Sicily and North Africa to Greece and Anatolia). In contrast, annual *Cousiniopsis* grows in the deserts of Kara Kum and Kyzyl Kum in Turkmenistan, Kazakhstan, and Uzbekistan.

Echinopsinae

Annual or perennial herbs, spiny or unarmed. Leaves entire or mostly dentate to lobed-pinnatisect, spiny or rarely almost unarmed. Capitula one-flowered, subtended by a tuft of bristles, aggregate in globose secondary heads subtended by small bracts. Involucral bracts in many rows. Outer bracts strongly keeled, winged, apically remotely fimbriate; middle ones more broadly winged, spinose; innermost usually green or green-brown, shiny, linear-lanceolate, often partly or totally connate with only the apical appendages free, not spinose. Length of the bracts varies according to the position of the single-head in the secondary head. Florets violet-blue or greenish. Petals often apically scarious, densely denticulate. Anther filaments glabrous, basal appendages short, laciniate. Achenes with parenchymatous pericarp, oblong, densely sericeous. Pappus of broad, basally connate short scales directly attached to the pericarp.

Our results have demonstrated that Echinopsinae include only *Echinops*s.l. (Fig. 20.2E, F). The only other genus

that was usually recognized in the subtribe, *Acantholepis* Less., is a reduced, unarmed species of *Echinops* (Garnatje et al. 2005) as it was originally described (*Echinops acantholepis* Jaub. & Spach).

The origin of the compound inflorescence of *Echinops* cannot be tracked on molecular grounds because the subtribe does not show affinity to any other group. Cardopatiinae and Carlininae are the best candidates for being sister to subtribe Echinopsinae. The structure of the achenes of Cardopatiinae and Echinopsinae is very similar (Dittrich 1977), but this character is also shared with Carlininae and must be considered a synplesiomorphy.

Geographic distribution of Echinopsinae is centered in the Mediterranean, with some taxa widespread in temperate Eurasia and a secondary centre of speciation in west tropical Africa.

Carduinae

Perennial, biennial or annual spiny herbs or subshrubs, rarely unarmed. Capitula homogamous, very rarely peripheral florets sterile and radiant. Bracts usually spiny, innermost exappendiculate or with rudimentary appendages. Achenes with radially sclerified pericarp (absent in *Stachelina* and the *Saussurea* group), often carunculate with apical caruncle. Insertion areole straight or lateral-abaxial. Apical plate very often inclined adaxially. Pappus inserted on a parenchymatous ring in the apical plate, simple or in many undifferentiated rows, deciduous.

Carduinae are a paraphyletic assemblage if we recognize Centaureinae as a different subtribe (Fig. 20.1). Accepting a widely defined subtribe Carduinae, even paraphyletic, seems the most appropriate solution because Carduinae plus Centaureinae would count for ca. 2200 of the 2500 species of the tribe.

Distribution is mainly Mediterranean and secondarily cosmopolitan as extremely noxious weeds (species of *Carduus*, *Cirsium*, *Onopordum*, *Silybum*, and *Notobasis*). The mountains of Central Asia constitute the eastern boundary, and only a few genera (*Cirsium*, *Saussurea*, and *Synurus* Iljin) extend beyond, and only *Cirsium* and *Saussurea* cross into North America.

There are some informal groups within Carduinae, very well-delineated on the basis of morphology and molecular analyses (Susanna and Garcia-Jacas 2007). The more notable are the following ones.

Xeranthemum group. — Unarmed annual herbs, rarely dwarf shrubs. Leaves always entire, velvety underneath. Capitula heterogamous. Receptacle with large scarious scales. Anther filaments glabrous, anther appendages short, laciniate. Corolla lobes very short. Achenes often dimorphic, with pappus of long-tapering or subulate scales, rarely reduced to a corona in *Chardinia*.

Amphoricarpus, *Chardinia* Desf., *Siebera* (Fig. 20.3B), and *Xeranthemum* (Fig. 20.3A) are variations on a theme; this

is one of the easiest groups to identify because of the very peculiar pappus of the achenes and the papery silver-white phyllaries. Classically placed in Carlininae, the *Xeranthemum* group appears in our latest molecular analyses (Susanna et al. 2006) as part of Carduinae, sister to the rest of the subtribe with low support but indeed in an isolated position. Cassini (1819) granted them even the tribal status (“Xeranthemées”) and if a fractioning of Carduinae should ever be accepted, the *Xeranthemum* group definitely would be one of the best-defined natural subtribes.

Three genera of the group (*Chardinia*, *Siebera*, and *Xeranthemum*) are formed only by annual colonizers of arid and wasteland throughout the Mediterranean and Irano-Turanian regions, especially in the East where, according to genus and species diversity, lies the origin of the group. In contrast, species of the dwarf shrubby genus *Amphoricarpus* are narrow mountain endemics in the eastern Mediterranean (the Balkans, Anatolia, and the Caucasus) and are sister to the rest of the genera.

***Berardia* and *Staelina*.** — *Berardia* is an acaulescent, unarmed perennial herb. Leaves rounded, entire or denticulate, densely woolly, with veins prominent beneath, white above. Capitula solitary, sessile, homogamous. Involucral bracts subulate, scarious, woolly, ending in a slender flat point. Receptacle areolate. Florets yellowish or pinkish. Staminal connective very long, apiculate. Achenes oblong, glabrous, slightly sulcate. Pericarp not sclerified. Pappus of scabrid cylindrical bristles retrorsely twisted, directly attached to the apical plate.

Species of *Staelina* are unarmed dwarf shrubs or subshrubs. Leaves entire or dentate-pinnatifid, linear to obovate, dark green above, white-woolly beneath. Capitula corymbose or rarely solitary, homogamous. Involucral bracts ovate to lanceolate, mucronate, sometimes minutely hirsute. Receptacle with wide, basally connate scales. Florets whitish or pink-purple. Corolla lobes very long. Anther filaments glabrous; basal appendages very long, sericeous. Achenes linear-oblong, glabrous or sericeous, with minute apical coronula. Pappus of bristles basally connate into broader paleae, more or less divided apically into pinnulate fibrillae (into capillary hairs in *Staelina dubia* L. and *S. baetica* DC.), always overtopping involucre, sometimes deciduous in a ring.

Both genera are extreme isolates with no affinities to any other genus of Carduinae, and some molecular analyses suggest without strong support that they could be relatives. *Berardia* was ranked among Mutisieae s.l. on the basis of achenial characters (Dittrich 1977, 1996a) because the pericarp wall is very similar to the type found in tribe Gochnatieae. Curiously, the pericarp of *Staelina* is also “gochnatioid” (Dittrich 1996a), which could support this faint relationship. However, we cannot say whether this similarity is convergence or a very old character conserved in these two strange genera.

Staelina was usually placed among Carlininae (Bentham 1873; Hoffmann 1893; Dittrich 1977; Bremer 1994), but Petit (1997) proposed moving it to Carduinae on the basis of floral morphology, which was later confirmed on molecular grounds (Susanna et al. 2006). For Dittrich (1996b), the two species of *Staelina* with hirsute pericarp (*S. fruticosa* L. and *S. lobelii* DC.) should be classified in a distinct genus, *Hirtellina* Cass. Nevertheless, morphological differences other than achene pilosity are virtually non-existent and we prefer to keep a single genus with *Staelina* and *Hirtellina* recognized with sectional rank (Susanna and Garcia-Jacas 2007).

Berardia is a very narrow endemic of the maritime Alps in southern France, recently migrated from its coastal glacial refuge. *Staelina* grows only in the Mediterranean region, from the Iberian Peninsula, France, and Italy to the southern Balkans, Crete and adjacent Anatolia.

***Onopordum* group.** — There are two lineages. (1) *Onopordum* s.str. (Fig. 20.3F) consists of stout, erect, very spiny biennial herbs with winged stems, rarely acaulescent. Leaves dentate-pinnatisect or pinnatilobed, rarely undivided, spiny. Capitula solitary or rarely corymbose. Receptacle foveolate. Involucral bracts very deeply serrulate, spiny. Florets reddish, purple or pink. Achenes obovoid-oblong, somewhat tetragonal, glabrous, often transversally fringed, sometimes with a short apical rim. Pappus of plumose, barbellate or scabrid bristles. (2) *Ancathia*, *Alfredia*, *Lamyropappus* Knorr & Tamamsch., *Olgaea* Iljin (Fig. 20.3E), *Syreitschikovia* Pavlov, *Synurus*, and *Xanthopappus* C. Winkl.: perennial herbs with entire spiny-toothed leaves, sometimes lobate-pinnatifid. Receptacle usually foveolate. Heads usually solitary or less often corymbose, often nodding at anthesis, with spiny-tipped bracts, the outer ones usually recurved, dark red. Florets cream, yellow, reddish, purple, or pink. Achenes smooth or rugulose.

The usual definition of this group is founded on the absence of receptacular bracts. A pitted, naked receptacle is rare in the tribe. However, not all species of *Alfredia* show epaleate receptacles. In addition to this character, achenes are also peculiar with the pericarp diversely pitted, wrinkled, or rugulose (Susanna and Garcia-Jacas 2007), seldom smooth. The group has negative impact because species of *Onopordum* include some highly noxious weeds widespread in the Mediterranean region, such as *O. acanthium* L. and *O. nervosum* Boiss., giant thistles that can reach up to 3 m high. *Onopordum* is a genus of colonizing biennials, and molecular phylogenies suggest that all the species described in the genus are extremely young and diverged probably in the Pliocene-Pleistocene when the Mediterranean climate first appeared (Suc 1984). In contrast, species of the Central Asian genera of perennial herbs have been dated from the upper Miocene by Wang et al. (2007).

Generic definitions in the group are unclear. All the middle-Asian small genera form a polytomy with a polyphyletic genus *Olgaea*. The inclusion of more species of *Olgaea* and representatives of all the small genera of the group (Garcia-Jacas et al. 2008) has not improved the definition of the genera, besides confirming that *Takeikadzuchia* is a synonym of *Olgaea* as hinted by Dittrich (1977), Bremer (1994) and Susanna and Garcia-Jacas (2007). The only solutions are either lumping all the genera in a single genus *Alfredia*, either redescribing many small segregates from *Olgaea* as distinct genera.

Geographic distribution is very interesting. Species of *Onopordum* are weedy colonizers along the Mediterranean (and other regions with a Mediterranean climate). The remaining genera are narrow endemics in the Tian Shan and Altai mountains, from Mongolia to Tajikistan. Only *Ancathia* has an extended area to Siberia from Tibet.

Cynara group. — Spiny stout perennial herbs. Leaves pinnatisect, very spiny (unarmed in cultivated *C. cardunculus* L.). Capitula large, globose, solitary or clustered in lax corymbs, less often corymbose. Involucral bracts oval or lanceolate, entire, often coriaceous, usually spine-tipped. Receptacle often fleshy, densely setose. Florets pink, purplish or violet. Anther filaments papillose. Achenes glabrous, faintly angular or smooth, globose (*Cynara* and *Ptilostemon*) or linear; apical rim and nectary absent (present only in *Lamyropsis*). Pappus of very long plumose bristles basally connate in a ring.

This group has been recently segregated from the thistles, to which it is closely related (Susanna and Garcia-Jacas 2006). It comprises the genera *Cynara* L. (Fig. 20.3C), *Lamyropsis* (Kharadze) Dittrich, and *Ptilostemon* Cass. They share floral and leaf characters and a peculiar biogeography. Some species of the *Cynara* group are ruderal colonizers with wide areas of distribution like most of the thistles. However, all the genera have undergone intense speciation in the Mediterranean region with narrow endemics in conserved habitats. *Cynara* and *Lamyropsis* show greater species differentiation in the eastern Mediterranean. In contrast, *Ptilostemon* is maybe one of the rare genera of the Carduinae that has most of its endemic taxa in the western Mediterranean (the Iberian Peninsula, southern Italy, and north Africa), even though it ranges from Ukraine to Spain (Greuter 1973).

Carduus-Cirsium group. — Perennial, biennial or annual herbs. Leaves dentate-pinnatisect, spiny, sometimes entire, often semi-amplexicaul. Stems often spiny-winged (especially in *Carduus*). Outer involucral bracts few, spiny; inner bracts without spines, leaf-like, often appendiculate, and colored. Florets red, purple or pink, rarely yellow. Achenes obovoid-oblong, smooth, glabrous, with an apical rim and a small obconical caruncle. Pappus of plumose or barbellate bristles, usually deciduous as a single piece.

This is the large complex of very spiny plants which are usually called “thistles” (Fig. 20.4C, F). All of these have medium or large-sized heads, very spiny leaves, and achenes with apical nectary and a long pappus detachable as a single piece. Our molecular results indicate that at least the largest part (*Carduus* L., *Cirsium* Mill., *Notobasis* Cass., *Picnomon* Adans., *Silybum* Adans., and *Tyrinnus* Cass.) are a natural group (Fig. 20.1). The rest of the genera traditionally placed among thistles (*Cynara*, *Lamyropsis*, and *Ptilostemon*) should rather be positioned in a separate group, the *Cynara* group (see above). *Galactites* Moench probably belongs to the *Carduus-Cirsium* group, but molecular data do not support this. This genus has only two species and shows some intriguing features that are very unusual, not only among thistles, but also in Carduinae: a hygrophanous pericarp and a capitulum with well developed radiant sterile florets very similar to those of Centaureinae, in a fine example of convergence (Fig. 20.3D).

As pointed out by Häffner and Hellwig (1999) and Garcia-Jacas et al. (2002), phylogenetic relationships and generic boundaries within the clade are obscure. One of the reasons for this is the co-existence of annual or biennial species (most of *Carduus*, *Galactites*, *Picnomon* Adans., *Silybum*, and *Tyrinnus*) together with perennials (many species of *Cirsium* and some *Carduus*), which hinders the assessment of the two aspects from a molecular standpoint because of the different mutation rate of annuals and perennials (discussed for annual species of *Cousinia* in López-Vinyallonga et al. 2009; see also references therein). The *Carduus* group, together with the *Jurinea-Saussurea* group, requires a more comprehensive molecular analysis.

Distribution of the group is cosmopolitan. *Cirsium* is mainly Eurasian, with some species native to North America from Canada to Mexico. *Carduus* shows many successful adaptations to the Mediterranean region, where it is ubiquitous. Both *Carduus* and *Cirsium* range among the few genera of Cardueae that have radiated to tropical Africa (Jeffrey 1967). The rest of the genera of the group are mono- or ditypical, constituted by active colonizers in the Mediterranean region s.l. and extremely noxious weeds in other regions of the world with a Mediterranean-type climate.

Arctium-Cousinia group. — Perennial herbs, rarely biennial, exceptionally annuals, spiny or less often unarmed. Receptacle scales are always twisted. Achenes tigrine (with darker wavy stripes), very often winged, without apical nectary. Pappus formed by free deciduous bristles, contrary to most of the thistles in which pappus is usually detached as a single piece.

This is a very well-defined natural group formed by the genera *Arctium* L., *Cousinia* Cass. (Fig. 20.4D, E), *Hypacanthium* Juz., and *Schmalhausenia* C. Winkl. One of them, *Cousinia*, is the largest of the tribe and one of



Fig. 20.3. Carduinae. **A** *Xeranthemum annuum* L. and **B** *Siebera pungens* J. Gay (*Xeranthemum* group) with bright-colored involucre bracts mimicking ray florets; **C** *Cynara humilis* L., a wild relative of artichoke; **D** *Galactites tomentosa* Moench with showy sterile peripheral florets; **E** *Olgaia petri-primi* B.A. Sharipova; **F** *Onopordum nervosum* Boiss. (*Onopordum* group). [Photographs, authors.]

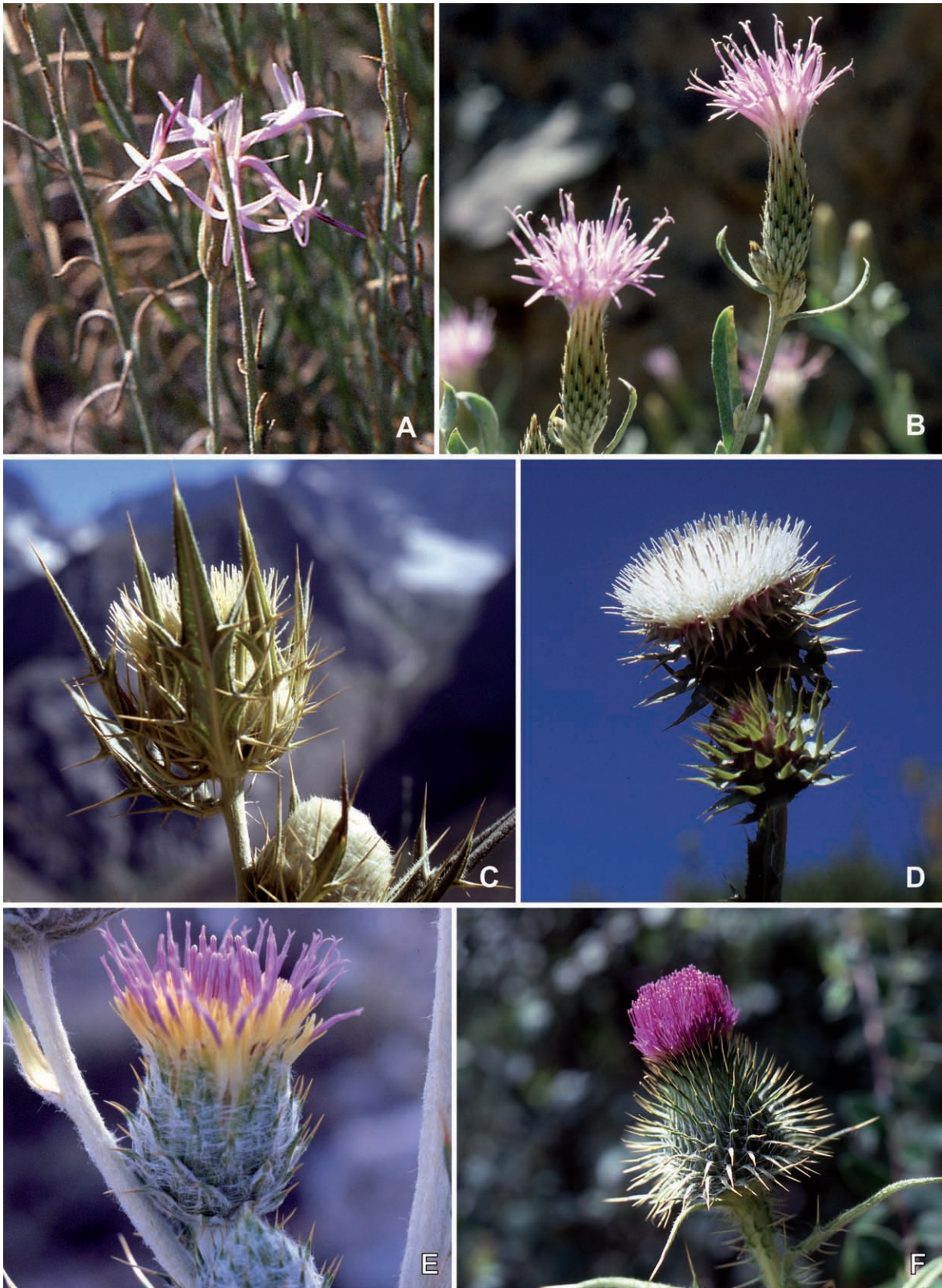


Fig. 20.4. Carduinae. **A** *Jurinea olgae* Regel & Schmal. with florets sharply bent outwards mimicking ligules; **B** *Jurinea* sp.; **C** *Cirsium sairamense* O. Fedtsch. & B. Fedtsch.; **D** *Cousinia ferruginea* Kult.; **E** *Cousinia lanata* C. Winkl.; **F** *Cirsium arvense* (L.) Scop. [Photographs, authors.]

the largest of the whole Compositae with 600 species. New analyses including the ITS and *rpS4-trnT-trnL* region of a very large sample of more than 200 taxa (López-Vinyallonga et al. 2009) have failed in giving a solution to the limits of *Arctium* and *Cousinia*. There are two main lines in the *Arctium* group, the Arctioid clade and the Cousinioid clade, segregated by molecular data, chromosome numbers, and pollen type, but this grouping is not consistent with morphology: two genera of the group, *Schmalhausenia* and *Hypacanthium*, are part of *Arctium* on the basis of pollen, chromosomes, and DNA sequences, but are morphologically much closer to *Cousinia*. In addition to an “Arctioid” group of *Cousinia*, there is also a “Cousinioid” group of *Arctium*. A deep morphological survey is presently ongoing within the Arctioid group to verify whether a natural delineation of genera is possible, but it is highly probable that *Arctium*, *Cousinia* subgenera *Cynaroides* and *Hypacanthodes*, *Hypacanthium*, and *Schmalhausenia* will have to be grouped in *Arctium*.

The distribution of this group shows three patterns. The first one is exemplified by *Arctium*, extended in temperate Eurasia as a colonizer. It has been hypothesized that the biennial habit is a key character for the colonizing success of *Arctium* (López-Vinyallonga et al. 2009) and this is also exemplified in other noxious weeds of Carduinae such as *Onopordum* (García-Jacas et al. 2008) and *Silybum*. The second pattern is the xeric adaptation of *Cousinia* s. str., extended through the Irano-Turanian region in one of the most explosive radiations in the Compositae with ca. 500 species in a limited territory (semideserts and steppes of Afghanistan, Iran, Iraq, and Turkestan). The third pattern appears among the taxa of the Arctioid group with the exclusion of *Arctium* (*Cousinia* sect. *Cynaroides* and *Hypacanthodes*, and the genera *Hypacanthium* and *Schmalhausenia*). Species of this group are very narrow endemics in the mountains of Central Asia, mainly in the Tian Shan.

***Jurinea-Saussurea* group.** — Unarmed perennial herbs or subshrubs; only two annual herbs. Leaves entire or pinnatisect, often silver-white below and glabrous above, sometimes hirsute-scabrid. Capitula cylindrical or globose, often paniculate, homogamous. Anther filaments glabrous. Achenes not lignified, soft. Pappus of very long (longer than involucral bracts), showy, usually pure white plumose bristles, basally connate in a ring; sometimes with a shorter, pinnulate deciduous pappus connate to a globose nectary (*Jurinea*). Three genera, ca. 500 species.

This group was extremely difficult because of the unclear generic boundaries between the larger genera *Jurinea* and *Saussurea* and the high number of small segregates: sixteen genera have been described within the complex. However, this figure should be reduced to three: *Dolomiaea*, *Jurinea*, and *Saussurea*. As hypothesized in the latest survey of the tribe (Susanna and García-Jacas 2007),

the last doubtful segregates *Diplazoptilon*, *Frolovia*, and *Himalaiella* should be placed in *Jurinea* s.l. on the basis of the molecular data contributed by Wang et al. (2007)

Geographic distribution of this group is peculiar. *Jurinea* is mainly Mediterranean, ranging from Iran to the Iberian Peninsula and North Africa, and has a middle-Asian nucleus in the mountains of the Tian Shan, connecting to the area of Sino-Tibetan *Dolomiaea*. *Saussurea* is mainly Eurasian reaching the extreme east Asia (Japan) and is one of the scarce genera of the tribe that is present in North America, with six species. A single rare species of *Saussurea*, *Saussurea lyrata* (often classified as a different genus *Hemistepta*), is one of the only two taxa of the tribe that are native in Australia.

Centaureinae

Perennial, biennial or annual unarmed herbs, shrubs or very rarely treelets, rarely spiny. Capitula often heterogamous with sterile radiant florets, rarely homogamous. Involucral bracts often with a diversely scarious, fimbriate, pectinate, spiny or unarmed appendage; innermost bracts always with a scarious appendage. Achenes with sclerified pericarp. Insertion areole concave, lateral-axial, very rarely (*Crupina*) straight, often with an elaiosome. Apical plate straight. Pappus inserted on a parenchymatous ring in the apical plate, double, formed by two rows of differently pinnulate bristles, rarely single by abortion, deciduous or persistent.

Subtribe Centaureinae has been subject of many studies in every aspect: morphology, chromosome numbers, pollen types and, more recently, comprehensive molecular surveys. As a result, the main problem of the group (the natural delineation of the large genus *Centaurea*) was finally solved (García-Jacas et al. 2000, 2001; Greuter et al. 2001). The evolution of the characters seems also clear and is very illustrative.

Floral morphological evolution. — Evolution of morphological characters in the subtribe is extremely complicated due to the frequent reversals of character states and parallelisms (Wagenitz and Hellwig 1996; Vilatersana et al. 2000a; García-Jacas et al. 2001). The main three trends are: the development of marginal sterile radiant florets (Fig. 20.5C) which, in the most primitive groups, still have staminodes (Fig. 20.5D); the specialization towards myrmecochory by means of a basal elaiosome, combined with the change from a basal hilum of the seed to a lateral hilum; and the trend towards the development of complicated appendages in the phyllaries (Dittrich 1968; Wagenitz and Hellwig 1996; García-Jacas et al. 2001, 2006). Convergence, however, is always present in many of the lines: e.g., peripheral sterile florets has appeared in different lineages of Centaureinae (even in an unrelated genus of the thistles group of Carduinae, *Galactites*, Fig. 20.3D).

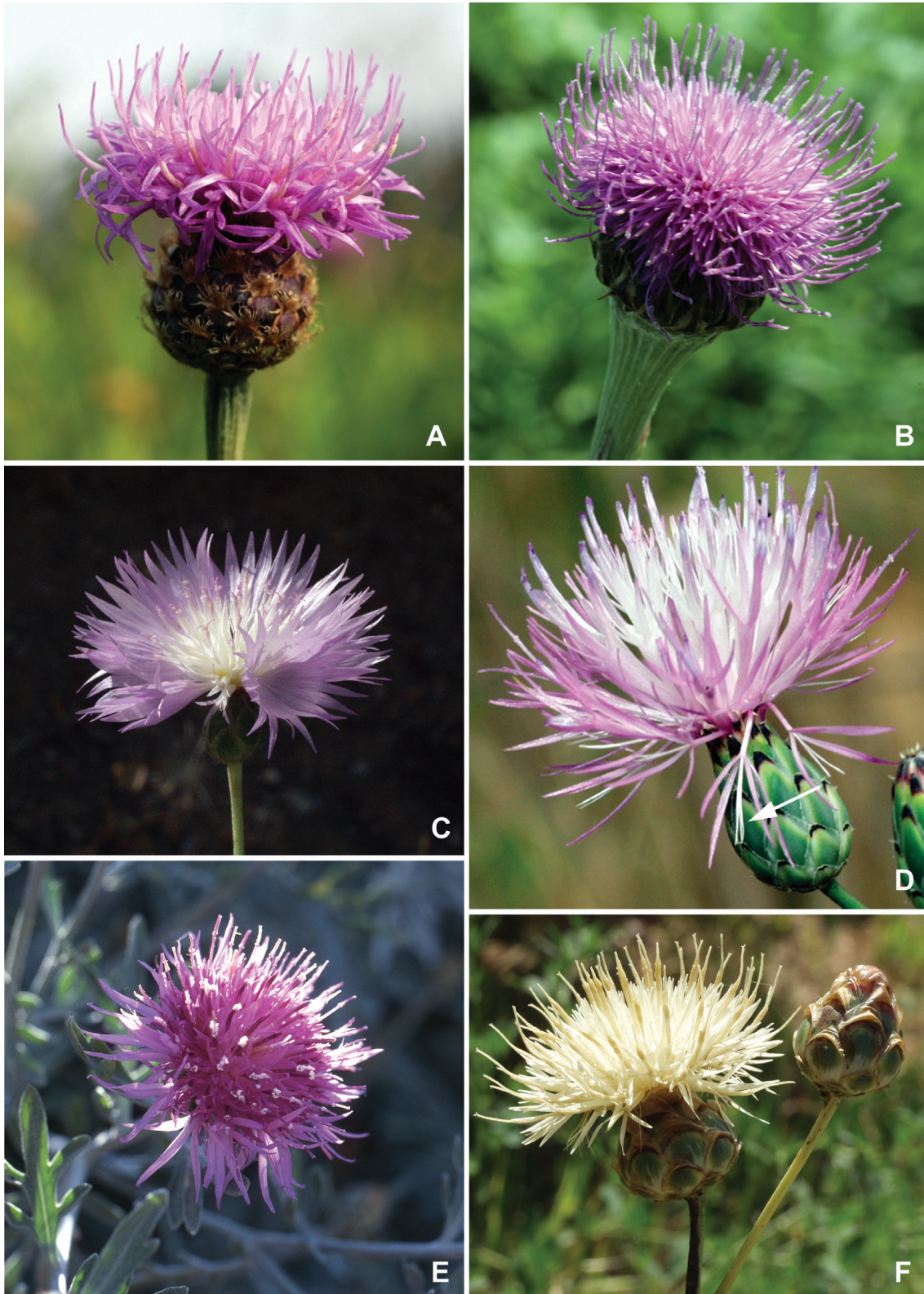


Fig. 20.5. Centaureinae, basal genera. **A** *Cheirolophus junonianus* (Svent.) Holub; **B** *Rhaponticum serratuloides* (Georgi) Bobrov; **C** *Amberboa moschata* (L.) DC.; **D** *Mantisalca salmantica* (L.) Briquet & Cavill. (the arrow indicates the showy staminode in the sterile peripheral florets); **E** *Psephellus* sp., a cultivated ornamental hybrid; **F** *Rhaponticoides africana* (Lam.) M.V. Agab. & Greuter. [Photographs, authors.]

Besides macromorphology, the character that best describes the evolution of Centaureinae is pollen type.

Pollen evolution. — Wagenitz (1955) described eight pollen types in the subtribe Centaureinae. The *Serratula* L. type is found in the basal genera of subtribe Centaureinae and in subtribe Carduinae. The *Crupina* type is restricted to the genus *Crupina* (Pers.) Cass. The *Rhaponticoides* (= *Centaurea centaurium*) pollen type is found in the genera *Rhaponticoides* Vaill. and *Stizolophus* Cass. The *Psephellus* (= *Centaurea dealbata*) type is diagnostic of the genus *Psephellus* Cass. The *Centaurea Cyanus* and *Centaurea Montana* pollen types are limited to *Centaurea* sect. *Cyanus*. The *Acrocentron* (= *Centaurea scabiosa*) type is characteristic of sect. *Acrocentron* in its widest sense (Wagenitz and Hellwig 1996). The *Centaurea Jacea* pollen type occurs most frequently in the genus and is the basis of present, natural circumscription of *Centaurea*.

Wagenitz (1955) gave an evolutionary ranking to the pollen types with *Serratula*, *Crupina*, and *Rhaponticoides* as the most primitive, *Psephellus* (*Centaurea dealbata*), *Centaurea Cyanus*, and *Centaurea Montana* types as intermediate, and *Acrocentron* and *Centaurea Jacea* pollen types as the most advanced. The evolution followed two independent processes, as confirmed on molecular grounds (García-Jacas et al. 2001).

The first trend runs from a spiny pollen type (*Serratula* or similar pollen type) to a smooth pollen type. This evolution is paralleled in the stigma and is caused by the development of a pollen presentation mechanism. As thoroughly described by Briquet (1902), the fertile florets in many species of *Centaurea* are strongly thigmotropic. If an insect touches a floret, the anther papillae react instantly contracting the anther tube and the brush at the base of the stigma drags the pollen from inside the anther tube. Contrary to the usual view, the anther tube is dragged downwards by the contracting anther filaments, not the style tube that extends through the tube. This dragging mechanism is universally present in the tribe (the brush at the base of the stigma is a critical tribal character), but only the most evolved groups exhibit this ability for such a fast reaction (studied in depth by Briquet, 1902). Minimizing the run of the anthers for a fast and repeatable pulling out of the pollen implies a very short stigma, which could not accommodate the long papillae associated with spiny pollen: instead, a sticky gum is secreted and the pollen becomes smooth.

This evolution from spiny to smooth pollen type in correlation with instantaneous pollen presentation has occurred in parallel at least in two different lines in two subtribes: in Centaureinae (García-Jacas et al. 2001) and in the *Arctium* group of Carduinae. In this complex, the species of *Arctium* and related genera have spiny pollen type, long stigmas, and no pollen presentation mechanism. To the contrary, *Cousinia* has smooth pollen, short stigmas,

and reactive pollen presentation (López-Vinyallonga et al. 2009).

The second trend in the evolution of the pollen of Centaureinae runs from an anthemoid exine pattern to the development of a cavea. This is a generalized trend in many groups of Centaureinae, but is poorly studied in Cardueae. The cavea is certainly related to the adaptation of mesophyllous taxa to the hard conditions of the Mediterranean and Irano-Turanian climate and the need to accommodate harmomegathy for extreme oscillations in temperature and humidity. A good example is found in the genera *Myopordon* and *Oligochaeta* K. Koch (studied in depth by Hidalgo et al. 2008). Species of the small genus *Myopordon* evolved from mesophyllous taxa closely related to *Rhaponticum* Vaill. (Hidalgo et al. 2006) with *Serratula* pollen type. Adaptation to extreme high mountain conditions and warmer climate led to the development of caveate pollen types in some species of *Myopordon* in a fine recompilation of the parallel similar evolution in other groups of Centaureinae. An indirect proof of this hypothesis on the origin of caveate pollen are the intermediate types *Carthamus* L. (Vilatersana et al. 2001), *Crupina*, and *Rhaponticoides* (= *Centaurea centaurium* pollen type of Wagenitz, 1955). Exine structure of these three pollen types is intermediate between the *Serratula* exine type, with a dense basal stratum of columellae, and the caveate types where the columellae are strongly reduced. In the three cases, adaptation to extreme conditions is the driving force: the three genera derive certainly from mesophyllous plants that evolved into species adapted even to the Iranian desert, such as *Rhaponticoides lachnopus* or into genera wholly adapted to the most extreme xeric and hot conditions in the Mediterranean and Irano-Turanian region, such as *Carduncellus* Adans., *Carthamus*, and *Crupina*. Figure 20.6 reflects pollen evolution on a phylogeny of Centaureinae, showing the deep correlations between pollen types and overall evolution.

Chromosomal evolution. — The subtribe shows a complex dysploid chromosome series, with base chromosome numbers ranging from $x = 16$ to $x = 7$ (García-Jacas et al. 1996). Correlation between this series and the phylogeny suggested by both pollen type and molecular data is good. The limit between primitive and derived can be placed at $x = 12$ (García-Jacas et al. 1996): base numbers above $x = 12$ are found among the basal grade of the subtribe, whereas numbers of $x = 12$ and lower are found in the most evolved groups (Fig. 20.6). Descending dysploidy was interpreted as an adaptation to arid habitats by favoring shorter life cycle in *Nonea* (Boraginaceae) by Selvi and Bigazzi (2002) and in *Pogonolepis*, *Sondottia*, and *Trichantodium* (Gnaphalieae and Pluccheae) by Watanabe et al. (1999). Thus, we hypothesize that general trend towards descending dysploidy in Centaureinae is correlated with the trend already detected towards the development

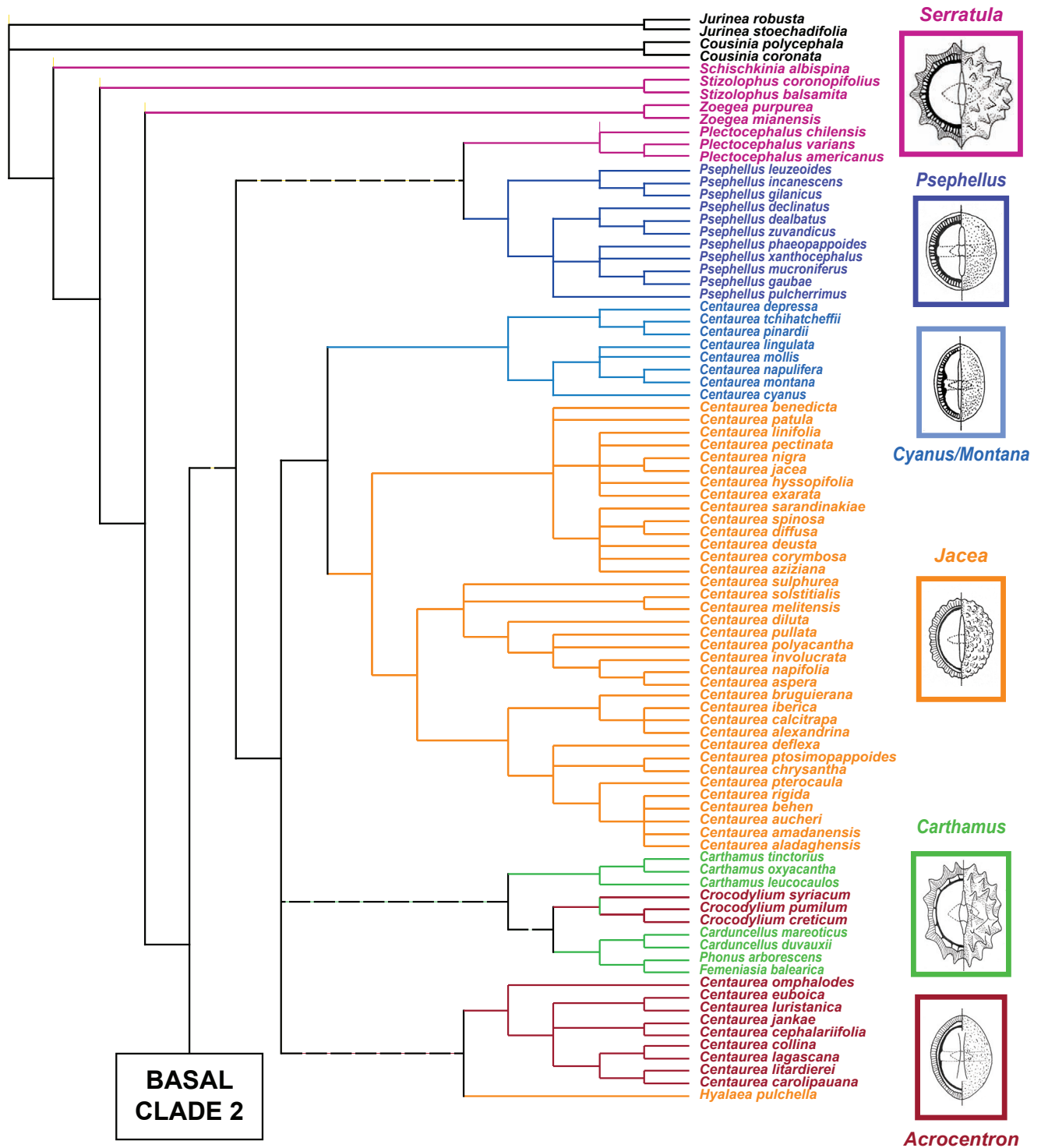
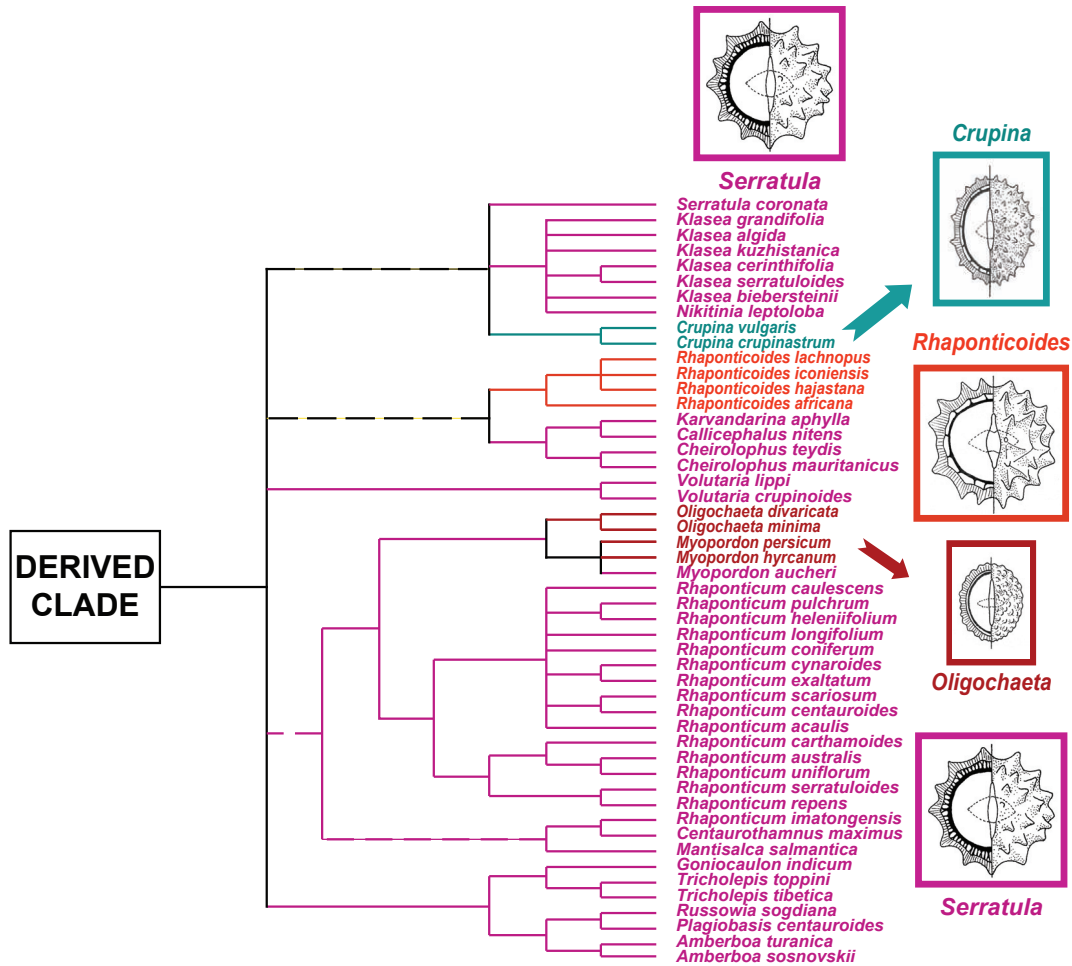


Fig. 20.6. Tentative phylogeny of Centaureinae (basal clade above, derived clade on opposite page) reconstructed on the basis of Garcia-Jacas et al. (2001, 2006) and Hidalgo et al. (2006), showing correlation between pollen types and evolution of the subtribe. Dashed lines indicate unsupported clades.



of caveate pollen. Adaptation of mesophyllous taxa to the xeric conditions of the Mediterranean would be the trigger of changes that, in the case of Centaureinae, are very well correlated with other morphological changes and hence to taxonomy. Other examples in Carduinae could confirm this trend. In the *Xeranthemum* group, perennial and mesophyllous mountain species of *Amphoricarpos* have $x = 14$, whereas annual xerophytes of the genera *Chardinia*, *Siebera*, and *Xeranthemum* show a complex dysploid series from $x = 12$ to $x = 5$ (Garnatje et al. 2001). Within the *Arctium* group, the mesophyllous Arctioid clade has $x = 18$ and the thermophyllous Cousinioid clade $x = 13, 12, 11, 10$, and 9 (López-Vinyallonga et al. 2009).

Polyploidy is also frequent and involves both auto- and allopolyploidy. A classic example of allopolyploidy is *Carthamus* sect. *Atractylis* (Vilatersana et al. 2000b). However, hybrids between taxa with the same number are usually homoploid (García-Jacas and Susanna 1992). Among some monophyletic groups showing dysploidy, hybrids between species with different number are known and even one of them was found to be fertile: e.g., *Centaurea* × *losana* Pau

($2n = 54$) is a naturally occurring fertile cross between *C. lagascana* Boiss. with $2n = 66$ and *C. cephalariifolia* Willk. with $2n = 40$ (cf. Fernández Casas and Susanna 1986).

Major groups in the subtribe Centaureinae. — On the basis of pollen types (Wagenitz 1955), morphology (Wagenitz and Hellwig 1996; Susanna and García-Jacas 2007), DNA sequence analysis (Susanna et al. 1995; García-Jacas et al. 2000, 2001, 2006; Vilatersana et al. 2000a), and karyology (García-Jacas et al. 1997, 1998a, b), some informal groups have been recognized in the subtribe. Some taxa cannot be placed in any group and remain isolated close to the base of the tree (García-Jacas et al. 2001). Besides these unclassified genera, the major informal groups that have been defined are *Carthamus-Carduncellus*, *Centaurea* s. str., *Klasea* Cass., *Rhaponticum*, and *Volutaria* Cass. (Wagenitz and Hellwig 1996; Susanna and García-Jacas 2007).

The unclassifiable rogue annuals. — Three small genera of annuals are placed as successive sister to the rest of Centaureinae, which are mostly perennial herbs: *Schischkinia* Iljin (Iran and Turkestan), *Stizolophus*, and *Zoegea* L. (Iran and Anatolia). Whether this position

reflects true sister relationships or this is an artifact caused by the annual habit, we cannot say. On morphological grounds, the three genera are very isolated. In this case, pollen type is of little help. *Zoegea* has the *Serratula* type, the most primitive. *Stizolophus* shows a pollen type very similar to the *Carthamus* and *Rhaponticoides* types, but certainly this must be the result of convergence. Pollen type of *Schischkinia* is unknown.

Unrelated genera of the basal grade. — The genera *Centaurodendron*, *Cheirolophus* Cass., *Crupina*, *Plectocephalus*, *Psephellus*, *Rhaponticoides*, and *Serratula* are noteworthy isolates. The newly described *Archiserratula* (Martins 2006) probably belongs here, too.

Reconstructing affinities and relationships among these genera is very difficult. In this sense, the problem posed by *Psephellus* (Fig. 20.5E) is intriguing. *Psephellus* is very probably at the origin of the subgenus *Centaurea* subg. *Cyanus* on the basis of geographic distribution (eastern Mediterranean) and pollen type (smooth, not cavate). The achenial characters (hylum lateral and persistent pappus) should place *Psephellus* among the derived group of Centaureinae. However, this is utterly unsupported in all our molecular analyses. A similar close relationship is suspected between *Plectocephalus* and *Psephellus*, also unconfirmed by molecular data.

As could be expected from the oldest stock in the subtribe, many species of the basal genera are relicts. Species of *Cheirolophus* (Fig. 20.5A) grow in the Western Mediterranean and Macaronesia from Malta to Madeira (Susanna et al. 1999). *Plectocephalus* shows one of the most striking disjunctions in the tribe: one species lives in Ethiopia; two more in Siberia (if *Phalacrachena* Iljin is confirmed as a synonym of *Plectocephalus* as was suggested by Susanna and Garcia-Jacas 2007); two species in North America; and two more in South America. Closely related to the South American *Plectocephalus*, the monotypic genus *Centaurodendron* grows in the Juan Fernández archipelago (Bernardello et al. 2006). *Rhaponticoides* (Fig. 20.5F) is a steppe-related genus with many isolated and some widespread taxa ranging from the Tian Shan to the Iberian Peninsula. *Serratula* is Eurosiberian in its widest sense; in the Mediterranean region it grows only in the mountains. *Crupina* is an invader of eastern Mediterranean origin widespread in the Mediterranean and Irano-Turanian region that has become a weed in the western United States.

Klasea, Rhaponticum, and Volutaria groups. — This complex of genera includes most of the “basal grade” of Centaureinae. Relationships of the three groups are obscure but, according to the molecular survey of Hidalgo et al. (2006), *Klasea* is sister to the *Volutaria* plus *Rhaponticum* groups. Recently, Martins (2006) described a new genus in the complex, *Klaseopsis*. The new genus must be included in *Rhaponticum* (Fig. 20.5B), as could be expected

from morphology of the bracts and structure of the pappus, and this has been confirmed by DNA analyses (Hidalgo 2006).

Genus delineation is now clear, but some incongruences persist. Maybe the most vexing is the impossibility of confirming monophyly of the *Volutaria* group with molecular data. The *Volutaria* group is formed by the genera *Amberboa* Less. (Fig. 20.5C) *Goniocaulon* Cass., *Mantiscalca* Cass. (Fig. 20.5D), *Plagiobasis* Schrenk, *Russowia*, *Tricholepis* DC., and *Volutaria*, according to Susanna and Garcia-Jacas (2007). On the basis of morphology (bract appendages, peripheral sterile florets, and achenes), there is little doubt regarding its monophyly. However, all the molecular analyses carried out to date place *Mantiscalca* and *Volutaria* in an unsupported position within other clades (Susanna et al. 2006; Hidalgo et al. 2006).

Species of the *Volutaria* group cover a very broad area in the Mediterranean (*Mantiscalca* and *Volutaria*) and Irano-Turanian regions (*Amberboa*, *Plagiobasis*, and *Russowia*). *Goniocaulon* is an annual colonizer in India that was reported in Sudan and Ethiopia by Jeffrey (1967). *Tricholepis* is the only genus of Centaureinae that has radiated principally in East Asia, from the Himalayas and north India to Myanmar.

The *Rhaponticum* group is better resolved, and its monophyly has been confirmed. It comprises the genus *Rhaponticum* (ca. 25 spp.), which, according to Hidalgo et al. (2006), should also include the genera *Acroptilon* Cass. and *Leuzea* DC. The genus *Ochrocephala* is probably part of *Rhaponticum*. Other smaller genera of the complex are monotypic *Centaurothamnus* Wagenitz & M. Dittrich and *Karvandarina* Rech.f. (placed in the *Volutaria* group by Susanna and Garcia-Jacas 2007), and *Myopordon* (5 spp.) and *Oligochaeta* (4 spp.). Species of the group are characterized by achene characters and by the usually papery silver-white involucre bracts. Nevertheless, habit and morphology are extremely variable.

Distribution of the group is also diverse. Most of the species of *Rhaponticum* (Fig. 20.5B) are mountain endemics in Eurasia, from Siberia to the Iberian Peninsula and north Africa. *Rhaponticum australe* (Gaudich.) Soják is the other only native Australian species of Cardueae, and as was the case with *Saussurea lyrata*, its natural presence in Australia is difficult to explain. *Myopordon* is a small genus of dwarf shrubs from the alpine zone of the mountains of the Middle East (Lebanon, Turkey, and Iran) at heights of 3500–4000 m. *Oligochaeta* comprises only frail annuals from the lowlands of the Irano-Turanian region from the Caucasus to west India. Finally, *Centaurothamnus* is a monotypic endemic from Yemen very closely related to the only species of *Rhaponticum* from Ethiopia (Hidalgo et al. 2006), formerly *Ochrocephala*.

The highly-evolved grade. — This group comprises the most highly nested taxa of the subtribe and they are

defined by a series of characters: the basis of chromosome numbers ($x = 12$ or less), the achenial anatomy (lateral hilum in all the cases), and the presence of well-developed sterile peripheral florets without staminodes (with the exception of the *Carthamus-Carduncellus* complex, which exhibits some unusual archaic features).

***Carthamus-Carduncellus* group.** — This complex is formed by four genera, *Carduncellus* Adanson (Fig. 20.7B), *Carthamus* L., *Femeniasia* Susanna, and *Phonus* Hill. The subtribe position of this complex within Cardueae has been traditionally difficult because most species in the complex have spiny leaves, a frequent characteristic in Carduinae, but highly unusual in Centaureinae. The caducous single pappus found in some species of *Carduncellus* (Cassini 1819; Dittrich 1969) and *Femeniasia* (Susanna 1988) is more representative of the subtribe Carduinae than the tribe Centaureinae. However, the spiny habit could be easily attributed to secondary adaptation against predators; and the reduction from a double to a single pappus occurs frequently in the subtribe Centaureinae, thus it provides minimal systematic value (Dittrich 1968, 1969; Wagenitz and Hellwig 1996). Classification of the complex among Centaureinae is now undisputed, despite primitive traits, such as spiny habit, not cavate pollen, long stigmas, and the absence of peripheral specialized florets (Fig. 20.7B). These characters are in acute contrast with the position of the group within the more advanced groups of the subtribe (García-Jacas et al. 2001; Susanna et al. 2006).

A fifth genus could be part of this group, *Crocodylium* Cass. (Fig. 20.7D), according to Vilatersana et al. (2000a), but without any support. *Crocodylium* (as *Centaurea* sect. *Aegialophila*) was related by Wagenitz and Hellwig (1996) to *Centaurea* subg. *Acrocentron*, from which it was excluded on molecular grounds by Font et al. (2002). In some aspects (pollen type and peripheral sterile florets with sterile “achenoids”), *Crocodylium* could be intermediate between *Carduncellus* and *Centaurea* subg. *Acrocentron*.

Carduncellus centers in the western Mediterranean (the Iberian Peninsula and North Africa, eastward to Greece and Egypt) and grows usually in conserved habitats (garrigues, macchia, and stony places in mid-mountains). In contrast, *Carthamus* centers in the eastern Mediterranean and comprises only colonizers and invaders in waste places. *Crocodylium* grows in the eastern Mediterranean and the Middle East; *Phonus* is endemic to southern Spain and Morocco, and monotypic *Femeniasia* is a very narrow endemic to Menorca (Balearic Islands).

***Centaurea* s.str.** — The natural delineation of *Centaurea* was achieved only on the basis of molecular data (Susanna et al. 1995; García-Jacas et al. 2000, 2001). The group was recognized as unnatural, from Cassini (1819) to Susanna et al. (1995). The main problem was the position of the type of the genus, a species from a small group

of ca. 25 taxa without relationship with the bulk of the genus (ca. 250 species). Nomenclatural consequences of a redefinition of the genus were so dramatic that only the confirmation of the relative position and the boundaries of the natural groups by DNA sequence analyses led to a proposal of a new type for the genus (García-Jacas et al. 2000, 2001; Greuter et al. 2001). As presently circumscribed (Susanna and García-Jacas 2007), it comprises three subgenera: *Centaurea* (formerly the *Jacea* group; Fig. 20.7C, F), with ca. 120 species; *Acrocentron* (Fig. 20.7E) with ca. 100 sp., and *Cyanus* (Fig. 20.7A) with ca. 30. Sister relationships of *Cyanus* and *Centaurea* are firmly established, but the connections of these two subgenera and subgenus *Acrocentron* are unclear.

The distribution of this very large genus is mainly Mediterranean with some taxa widespread in the mountains of temperate Eurasia and many cosmopolitan weeds such as *Centaurea cyanus* L., associated with wheat cultivation since the development of agriculture in the Neolithic (Rösch 1998). According to the well-established origin of subgenera *Acrocentron* (Font et al., in prep.), *Cyanus* (Bořič et al., in prep.) and *Centaurea* (García-Jacas et al. 2006), *Centaurea* has an eastern Mediterranean origin (Anatolia and the Caucasus).

CHEMISTRY

Secondary metabolites include predominantly lipophilic compounds (especially sesquiterpene lactones); hydrophilic compounds are scarcely represented. Only some genera have been investigated in depth (*Centaurea*, cf. Trendafilova et al. 2007 and references therein; *Cirsium*, cf. Chen et al. 2007 and references therein). Subtribes Carduinae and mainly Centaureinae show higher chemical differentiation than the remaining subtribes (Wagner 1977; Böhm and Stuessy 2001). It is interesting that the increased chemical weaponry of Centaureinae is correlated to the loss of the spines so characteristic of thistles. Centaureinae and especially the genus *Centaurea* relies more on chemical than on mechanical deterrents for protection from herbivorous predators.

BIOGEOGRAPHY

The tribe is mainly Mediterranean in its widest sense (including the Irano-Turanian region) with three main centers of diversification: one in Anatolia, the Balkans, and the Caucasus; a second one in the Irano-Turanian area (Afghanistan, Iran, Iraq, and Turkistan) that reaches the mountains of Central Asia; and a western Mediterranean center encompassing the Iberian and Italian peninsulas, the Balearic and Tyrrhenian islands,

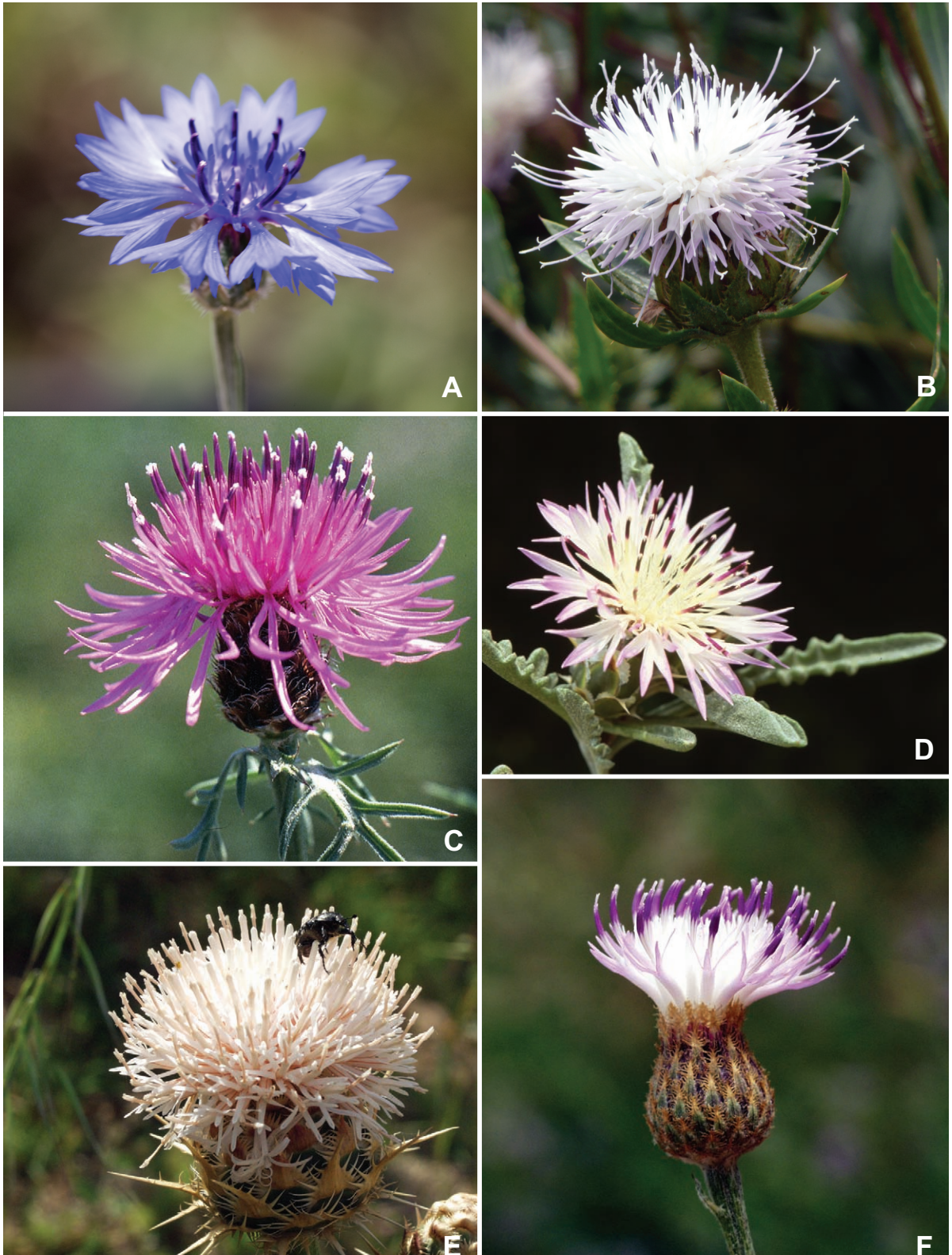


Fig. 20.7. Centaureinae, more highly nested genera. **A** *Centaurea montana* L. from subgenus *Cyanus*; **B** *Carduncellus dianius* Webb with long stigmas (a primitive character!); **C** *Centaurea corymbosa* Pourr. from subgenus *Centaurea*; **D** *Crocodylium pumilio* N. Garcia & Susanna; **E** *Centaurea lydia* Boiss. from subgenus *Acrocentron*; **F** *Centaurea exarata* Boiss. ex Coss., which lacks the sterile peripheral florets by secondary loss. [Photographs, authors.]

and North Africa. The mountains of Central Asia (Tian Shan, Pamir, and the Himalayas) constitute the eastern boundary for most of the genera. The tribe becomes less frequent in central Africa and only a few genera reach equatorial Africa (*Centaurea*, *Carduus*, *Cirsium*, and especially *Echinops*; cf. Jeffrey 1967). Three genera are native to North America (*Cirsium*, *Plectocephalus*, and *Saussurea*), only two to temperate South America (*Centaurodendron* Johow. and *Plectocephalus* D. Don), and two species are doubtfully native to Australia. The tribe contains many subcosmopolitan and noxious weeds. We shall give more details on geographic distribution for each subtribe and group.

ORIGIN AND AGE

According to Panero and Funk (2008), the sister groups of Cardueae are the tropical-African tribes Tarchonantheae and Oldenburgieae (see Chapters 18 and 19). It is generally accepted that the Mediterranean flora contains a tropical mesophyllous component lately adapted to the peculiar climate of the region (Takhtajan 1986). According to the confirmed relationships to African tribes of the subfamily Carduoideae, Cardueae count among this tropical element of African origin of the Mediterranean flora. In fact, as all the studies of the Mediterranean vegetation have pointed out, Cardueae are one of the most characteristic elements in this landscape (Takhtajan 1986).

Regarding the date of differentiation, most of the tribes were already separated by the end of the Oligocene, between 35–22 Ma (Funk et al. 2005). On the basis of ITS divergence, Wang et al. (2007) suggested a date of 29–24 Ma for the separation of the tribe from African Carduoideae. A more precise date of 10 Ma was offered by López-Vinyallonga et al. (2009) for the *Arctium*–*Cousinia* group, based both on molecular data and fossil records. All the dates being largely coincident, Cardueae originated as part of the Tertiary flora and benefited extensively from the new habitats that were open during the deep climate and geological changes during the Miocene (Cox and Moore 2004).

ECONOMIC USES

Economic importance of Cardueae is enormous, but more due to negative reasons than because of their use. Some of the more noxious weeds of Compositae belong to this tribe. The list of invaders in the Mediterranean and temperate regions of the globe is impressive: *Carduus pycnocephalus* L.; *Carthamus lanatus* L.; *Centaurea amara* L., *C. diffusa* Lam., *C. solstitialis* L., and *C. stoebe* L. [“maculosa”]; *Cirsium arvense* (L.) Scop., *C. palustre* (L.) Scop., and *C. vulgare* (Savi) Ten.; *Onopordum acanthium* and *O. nervosum*; *Rhaponticum* [“*Acroptilon*”] *repens* (L.) Hidalgo; *Picnomon acarna* (L.) Cass.; and *Silybum marianum* (L.) Gaertn. (DiTomaso 2000). In contrast, species with medicinal or industrial importance are scarce. Common artichoke (*Cynara scolymus*) and cardoon (*Cynara cardunculus*) are widely cultivated as a vegetable, especially in Italy and Spain and on a smaller scale in California. *Silybum marianum* is also cultivated in Mediterranean countries because of its lactones silybin and silymarin, powerful liver protectors used in the treatment of chronic hepatitis. *Carthamus tinctorius* (safflower) was very popular in olden times as a substitute for the culinary herb saffron, and now it is becoming an important crop as a source of vegetable oil in subtropical climates (Vilatersana et al. 2000a). Finally, some species are (or have been) cultivated as garden plants: *Amberboa moschata*, *Centaurea babylonica* (L.) L., *C. cyanus* [“bachelor’s button”], *C. montana* L., and *Plectocephalus americanus* D. Don [“basket flower”].

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Note added in proof

The enigmatic genus *Dipterocome*, formerly placed in Calenduleae, belongs to Cardueae (see Anderberg et al., *Compositae Newsletter* 45, 2007, and page 528 of this book). More detailed analyses of morphology and molecular data are still lacking, but both floral characters (e.g., the heterogamous heads with outer bilabiate florets) and preliminary analyses of DNA sequences (kindly provided by A. Anderberg) point towards a close relationship with the *Xeranthemum* group.