Chapter 22

Gymnarrheneae (Gymnarrhenoideae)

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INTRODUCTION

Gymnarrhena is an unusual member of Compositae. It is an ephemeral, amphicarpic, dwarf desert annual. Amphicarpic plants have two types of flowers, in this case aerial chasmogamous heads and subterranean cleistogamous ones, and the different flowers produce different fruits. In *Gymnarrhena*, the achenes produced from these two types of inflorescence and the seedlings that germinate from them, differ in size, morphology, physiology and ecology (Koller and Roth 1964; Zamski et al. 1983). The plant is very small and has grass-like leaves, and the aerial heads are clustered together and have functional male and female florets. The familiar parts of the Compositae head have been modified extensively, and most of the usual identifying features are missing or altered (Fig. 22.1). Currently there is one species recognized, *Gymnarrhena micrantha* Desf., but there is some variation across the distribution, and it should be investigated further.

HISTORICAL OVERVIEW

As might be imagined, the history of this taxon reflects its unusual morphology. Bentham (1873), Hoffmann (1890–1894), and Cronquist (1955) put this genus in Inuleae s.l. Hoffmann and Cronquist both mention the similarity to *Geigeria*; Bentham's alternate choice was Astereae. Small (1917–1919) considered Inuleae to be linked to *Centaurea* of Cardueae. Leins (1973), in his examination of the pollen of Inuleae, stated that *Gymnarrhena* did not belong in that tribe and suggested Cynareae-Carlininae. Merxmüller et al. (1977) agreed that *Gymnarrhena* was not in Inuleae and cited Leins (1973). Skvarla et al. (1977) acknowledged a superficial resemblance between *Gymnarrhena* and Cardueae but pointed out that it had Anthemoid type pollen (also found in Senecioneae and other tribes) and did not belong in Inuleae or Astereae. Skvarla et al. further acknowledged that, based on the pollen, the genus was difficult to place. Bremer (1994) listed the genus as belonging to Cichorioideae s.l. but as "unassigned to tribe" along with several other problem genera.

PHYLOGENY

Anderberg et al. (2005), in a study of Inuleae using *ndhF*, determined that *Gymnarrhena* did not belong in Asteroideae but rather was part of the then paraphyletic Cichorioideae s.l. or sister to the entire Asteroideae. In the most recent broad-scale cladograms, *Gymnarrhena* is in a clade by itself and is consistently located below the Cichorioideae s.str.–Corymbieae–Asteroideae clade and above the Cardueae and Pertyeae clades (Panero and Funk 2002, 2008; Chapter 44 of this volume). Its position means that it cannot be placed in any of the other suprageneric taxa and is now recognized as an independent lineage. This position is supported by the fact that *Gymnarrhena* lacks the '9 base pair deletion' in the *ndhF* gene identified by Kim and Jansen (1995) and subsequently used by Bremer (1996) as a molecular characteristic in support of the recognition of the Cichorioideae-Corymbioideae/Asteroideae clade (Chapter 44). In the

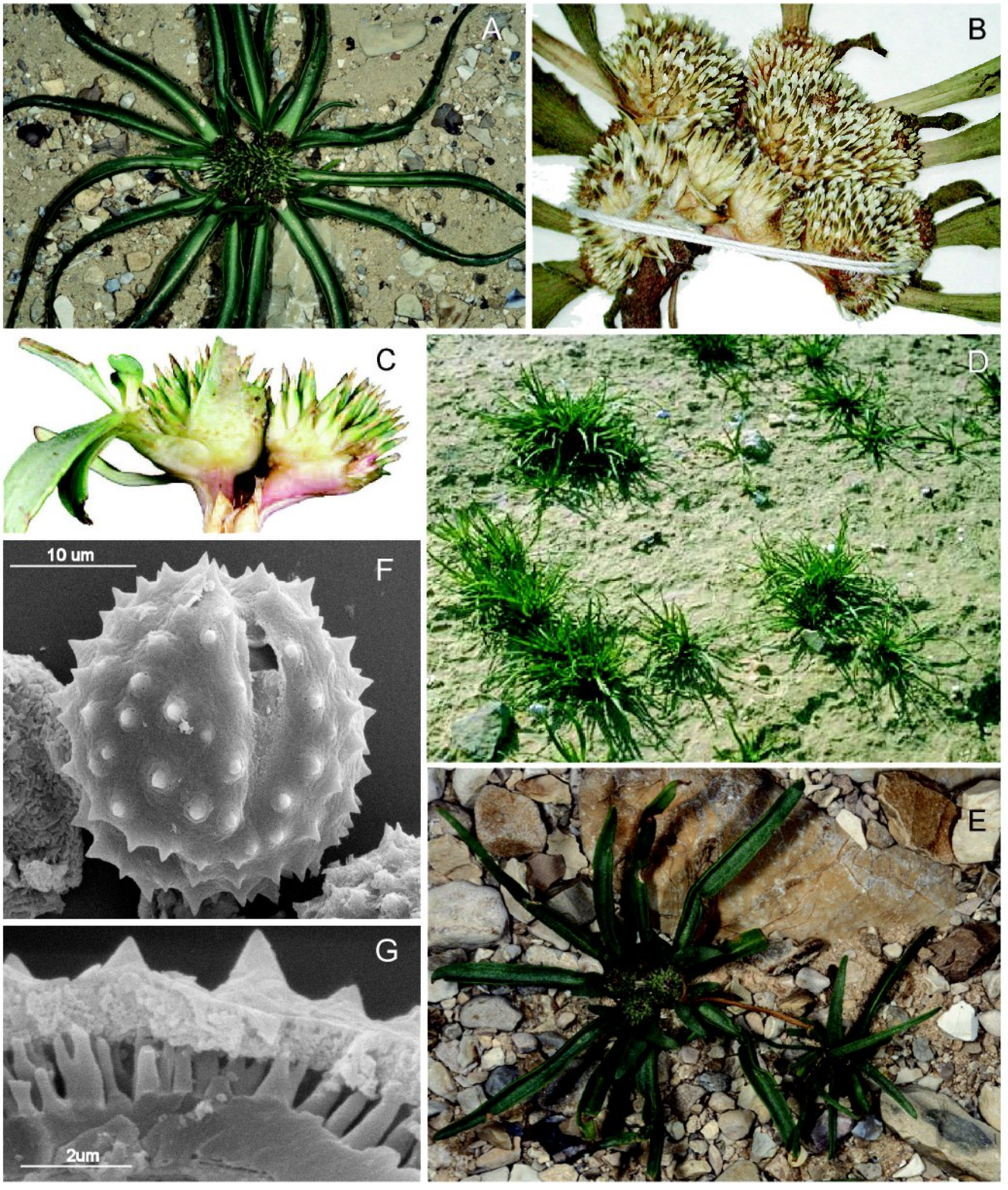

Fig. 22.1. *Gymnarrhena micrantha* Desf. **A, D, E** habit showing rocky substrate and clustered heads; **B** clustered above-ground heads with green (fading to brown) and white bracts; **C** subterranean heads; **D** population showing grass-like growth form; **F, G** pollen showing polar view and a broken grain. [Photographs: A, D, E, O. Fragman-Sapir taken in the Jerusalem Botanical Gardens; B, herbarium specimen, *Mandeville 157*, US; C, underground head, with permission from Brown and Böer (2005); F, G, SEM's, H. Robinson.]

most recent taxonomic overview for the family the tribe *Gymnarrheneae* was accepted by Jeffrey (2007) based on the molecular results reported above.

TAXONOMY

Subfamily Gymnarrhenoideae Panero & V.A. Funk

Tribe Gymnarrheneae Panero & V.A. Funk in Proc. Biol. Soc. Wash. 115: 763–764. 2002 – Type: *Gymnarrhena micrantha* Desf. in Mém. Mus. Hist. Nat. iv.: 1, t. 1. fig. 1. 1818

Annual amphicarpic herbs with a prostrate rosette, no more than a few centimeter high; no reports of milky sap. Leaves simple, forming a dense rosette, sessile, smooth, narrowly lanceolate to narrowly ovate, apex narrowly acute to attenuate, margins denticulate, base truncate, surfaces smooth and glabrous. Subterranean heads homogamous, female, cleistogamous, surrounded by the leaf bases; florets enclosed in involucral bracts, corolla vestigial; achenes relatively large, laterally flattened, blackish, sparsely hairy, remaining below the soil surface on the dead parent plant; pappus absent, vestigial, or of short, basally flattened, somewhat scale-like bristles. Aerial heads congested in the center of the leaf rosette, heterogamous, disciform; involucral bracts imbricate in several series, chartaceous, whitish, acute; receptacle convex, marginally bristly, with a few rows of chartaceous phyllaries. Functionally staminate florets in small groups, loosely connected on very short pedicels, interspersed among the small pistillate florets, corollas small, 3–4-lobed, whitish; stamens 3–4, anthers calcarate, ecaudate, without apical appendage. Pistillate florets solitary, each enclosed in a prominent, stiff, white and green bract; corolla filiform, style arms long, with rounded apices. Achenes of functionally staminate florets vestigial, pappus of a few irregularly lacerate scales or absent; achenes of pistilate florets numerous, tiny, ovoid, ciliate, villous, with long twin hairs, cell walls thin, pappus of long-lanceolate, ciliate, acutely acuminate scales.

A second species *G. balansae* Cross. & Durieu was based on two collections from near the coast in Tunisia and Algeria, and they appear to be somewhat different from the collections from the Middle East and further inland in Algeria. However, a more detailed study will have to be made to determine the validity of this taxon.

Gymnarrhena has been collected from North Africa to the Middle East. It is a winter annual and its flowering depends on the rain but usually takes place in March and April (May). According to Gutterman (1989) the life span of the plants is around 67 days out-of-doors (full sun) where it produces both types of heads, and 140 days in the greenhouse (eight hours of light) where it produces only aerial heads.

MORPHOLOGY

The male florets are not always grouped in the center of the head as previously described, in fact some groups of male florets are found at the outer edge of the receptacle. It seems more likely that the aerial heads are actually groups of heads some of which are few-flowered male heads and others are single-flowered female heads so these could represent dioecious heads grouped on a common receptacle. The subterranean heads flower first, their petals protruding just above the soil surface. Later the aerial inflorescences appear. Likewise the fruits of the two types of heads of *Gymnarrhena* have different developments, the larger subterranean fruits developing first and the aerial fruits being produced later and only in wet years. The aerial fruits are wind-dispersed while the subterranean fruits germinate underground. On the aerial heads, the scales of the pappus as well as the bracts surrounding the achenes are hydrochastic (open when wet), and the achenes are dispersed by wind (Gutterman 2002).

Gymnarrhena exhibits "dimorphic cleistogamy" or "true cleistogamy", in that it has two different flower types: chasmogamous and cleistogamous (Culley and Klooster 2007). While about 228 genera of angiosperms have some type of cleistogamous flowers, only 168 are dimorphic. It is estimated that dimorphic cleistogamy has evolved less than 40 times, and most of the lineages have very few species (Culley and Klooster 2007).

ANATOMY

The only anatomical data found is from Zamski et al. (1983) who examined the taproot of *Gymnarrhena* and found that it starts to contract soon after emergence. Ultimately, this contraction causes retraction of the main shoot apex from the soil surface to a depth of about 10 mm.

POLLEN

Gymnarrhena pollen was examined by Wortley et al. (2007; Fig. 22.1F, G), and they report that it is spheroidal, round in polar and equatorial view, and tricolporate. The colpi are separate with acute ends. The grains are echinate and non-lophate, the spines unevenly distributed, conical-pointed, 1–2 μm long, with bases slightly swollen and with internal cavities. The tectum is microperforate, covering the whole surface of the grain. The infratectum comprises two distinct layers that are not clearly attached to one another; the outer layer is columellate or spongy, the inner supporting layer made up of thick, unbranched,

solid columellae, evenly distributed around the grain. The grains are ecaveate and the endexine is thinner than the foot layer. Despite the sparse spines and lack of a cavea, the ultrastructure of these grains, with unattached layers of evenly distributed columellae, does not fit into Cichorioideae (Anderberg et al. 2005) and is suggestive of the characteristics of Corymbieae, the sister group of Asteroideae (Wortley et al. 2007). This is not as far from the position on the molecular tree as it might seem, since *Gymnarrhena* is the branch just below Cichorioideae, and *Corymbium* is nested one node higher than Cichorioideae. Zhao et al. (2006) commented that *Gymnarrhena* pollen shared the multilevel columellae with Mutisieae s.l., but they noted that this character is found elsewhere in the family including Anthemideae and Cardueae; they concluded that it did not belong in Mutisieae s.l. because of its spinate pollen. Pollen characters, therefore, do not place the genus in any of the existing suprageneric taxa and are, therefore, consistent with recognizing it in its own tribe and subfamily.

CHROMOSOME NUMBERS

There are two different published chromosome counts; Murín and Chaudhri (1970) from Iraq and Kamel (1999) from Egypt; both report $2n = 20$, each from a single plant. Nikulina and Kotseruba (1999) report $2n = 18$.

CHEMISTRY

There is no information on the chemistry of Gymnarrheneae.

ECOLOGY AND REPRODUCTIVE BIOLOGY

Gymnarrhena is an amphicarpic herb (Fig. 22.1B, C) of the Mediterranean biome of North Africa and the Middle East, growing in dry, mostly bare, sandy areas and resembling a grass (Fig. 22.1A, D, E). Research on the reproductive biology of this unusual plant is summarized by Koller and Roth (1964) and in the description above. There are three aspects to its reproductive biology that are most interesting: seed heteromorphism, the presence of aerial as well as subterranean heads, and the presence of both chasmogamous and cleistogamous flowers.

Seed heteromorphism, that is, the production of seeds with variable morphologies and ecological strategies, represents an allocation of different fractions of seed output to different ends, and most examples are found in four flowering plant families, one of which is Compositae (Harper 1977). Seed heteromorphism appears to be largely restricted to relatively short-lived, fugitive species, particularly weeds. Venable and Burquez (1989) say that it might be a form of 'bet hedging' in response to environments that vary spatially or temporally. These morphological heteromorphisms are important because they may be associated with ecological strategies that have evolutionary significance, such as dispersal, dormancy, differential competitive performance, within or among year timing of germination, vulnerability to predators, and seedling growth and survival or fecundity (see many references cited in Chmielewski 1999).

The presence of aerial as well as subterranean heads has several different explanations. Koller and Roth (1964) reported that mean weight of *Gymnarrhena* aerial fruit was only 5%–6% of the weight of a subterranean fruit and that six-day-old subterranean seedlings were six times the weight of aerial seedlings. They reported that the survival was considerably greater for these subterranean seedlings and that plants under dry conditions may fail to produce aerial heads. On the other hand, according to Brown and Böer (2005) the species occurs on firm sometimes rocky, substrates that are generally hostile to plant growth. The above-ground fruits are small and possess a small pappus to aid in their dispersal so they can travel some distance from the parent plant. The one or two large underground fruits (nearly 20 times the weight of the aerial ones) lack a pappus and stay close to the parental plant. It is their opinion that the underground fruits ensure that when the mother plant dies later in the year, the same favorable location is re-colonized. Gutterman (1989) thinks that the underground location protects the seeds from predation. Zeide (1978) described dual strategies for *Gymnarrhena micrantha* in the Negev desert of Israel. He determined that the subterranean fruits were produced according to a "pessimistic strategy", whereby fruit production begins as soon as possible concurrent with continued vegetative growth. The aerial fruits, on the other hand, were produced according to a more "optimistic strategy" (in order to maximize yield, the vegetative stage precedes a last and full switchover to heavy fruiting). Cheplick and Quinn (1982) felt that the pessimistic strategy must therefore arise from other considerations such as unpredictable environments as it is at odds with optimality models of resource allocation in annuals. They summarize by saying that there are three arguments that have been supported for *Gymnarrhena*: *(1)* the seedlings arising from the larger propagules are more tolerant to stress or competition, *(2)* these subterranean seedlings have a higher probability of surviving to produce seed, *(3)* genotypes with an early production of subterranean seed may be the only ones to produce seed under stress (Evenari 1963; Koller and Roth 1964; Zeide 1978). And another has been suggested (Cheplick and Quinn 1982): *(4)* the larger subterranean seed may show

a greater return on energy invested than an aerial seed. Other explanations that have been provided are the protection afforded by burial against catastrophes, and the placement of subterranean seed in the same microhabitat occupied by the parental plant, providing protection from the risks of random dispersal (Evenari 1977; Koller and Roth 1964). Cheplick and Quinn (1982) concluded that the early production of few larger seeds followed by the later production of many small seeds was presumably the result of the variable and unpredictable length of their growing periods and to their role as a fugitive species.

There are about 50 amphicarpic species worldwide, approximately one in every 5000 species of flowering plants; most of them occur in either frequently disturbed and/or stressful habitats. Eight of these are found in Israel, which has only 2500 species in its known flora, i.e., 1 in ca. 310 species, a very high ratio compared to flowering plants in general (Kaul et al. 2000; Lev-Yadun 2000). Given the suggested reasons above, Lev-Yadun (2000) adds that many of the amphicarpic annuals are found in disturbed areas that are the result of drought, fire and grazing. He thinks this indicates a long history of disturbances in the eastern Mediterranean region that pre-dates human impact.

The cleistogamous aspect of the subterranean florets is more easily explained in that such flowers are invariably cleistogamous (Kaul et al. 2000).

Additional information can be found in the recent book by Gutterman (2002).

APPLIED ASPECTS

Gymnarrhena is listed on the web in the "Global Compendium of Weeds" as being on a list of weeds from Egypt (www.hear.org/gcw/species/gymnarrhena_micrantha/), however, an examination of the book (Boulos and el-Hadidi 1984) yielded no mention of the species.

In a study of the areas of Kuwait that were damaged by oil towards the end of the Gulf War in 1991, the area covered by oil or by tar tracks is largely sterile. However, *Gymnarrhena* was one of the taxa found in this area growing in the control sites and in areas where the sand has blown out from under the tar tracks indicating that it has the ability to move into disturbed habitats (Brown and Porembski 2000). But perhaps the most interesting study involving pollution and *Gymnarrhena* concerns the copper mining and smelting activities of the Nabatean, Roman and Byzantine periods in the southern Jordanian desert that has, for 2000 years, continued to exert an influence on the plants and animals, and no doubt the people, of the area (Pyatt et al. 2000). Khirbet Faynan (believed to be the Roman city of Phaino) was a major center of metal-working in the ancient world and left huge deposits of slag containing copper and lead. Testing of recent soil, plants, and animals show enhanced concentrations of this lead and copper: one of the two plants with the highest concentrations was *Gymnarrhena*, which is one of the favorite plants for the grazing goats in the area. The goats, in turn, also showed elevated levels of lead and copper (Pyatt et al. 2000). Past levels were certainly much higher and possibly impacted the plants, animals and humans for 2000 years. Anthropologists have a wonderful ability to meld interesting science with drama, and so the final words of Pyatt et al. (2007) are worth repeating:

> The copper and lead rich wadis of southern Jordan … saw industrial pollution on a scale which would have been familiar to the inhabitants of Victorian Sheffield …. Small wonder then that in Romano-Byzantine times the mines of Phaino were seen as a place to send recalcitrant criminals. Eusebius of Caesarea in his "Martyrs of Palestine" describes such a scene; "they demanded that he should be sent away to the mines, and not just any mines but to that of Phaino where even a condemned murderer is hardly able to live a few days."

Nothing else has been found on either this topic or any other applied aspects of this species.

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