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Authors: Le Driant, Franck, and Carlón, Luis

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FRANCK LE DRIANT¹ & LUIS CARLÓN^{2*}

The Saharo-Arabian *Gymnocarpus sclerocephalus* (*Caryophyllaceae*) new to Europe in the semideserts of Almería, Spain

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Abstract: The first European record of *Gymnocarpus sclerocephalus* (*Paronychia sclerocephala*, *Sclerocephalus arabicus*, *Caryophyllaceae*), from the semidesert of Tabernas (Almería, Andalusia, Spain), is presented. After a diagnostic description and ecological interpretation of the species, we provide arguments in favour of its native status in that Spanish region and explore the geographic and historical causes explaining the local occurrence of this and a number of other biogeographically analogous species.

Key words: Almería, Andalucía, Andalusia, *Caryophyllaceae*, dispersal, European flora, *Gymnocarpus*, Mediterranean flora, Saharo-Arabian flora, semideserts, Spain, Spanish flora

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Introduction

On 17 March 2018, during an amateur botanical trip in eastern Andalusia, Spain, organized by the Association Pulsatille, a peculiar member of the *Caryophyllaceae* was found in the semidesert of Tabernas in the province of Almería. The plant could eventually be identified as *Gymnocarpus sclerocephalus* (Decne.) Ahlgren & Thulin (Oxelman & al. 2002; ≡ *Paronychia sclerocephala* Decne.), a strictly deserticolous Saharo-Arabian species not previously recorded in the region of Andalusia (Blanca & al. 2011; Cueto & al. 2018) or, more surprisingly, in any geographically European territory. In the present work, details of this finding and a brief discussion of its biogeographic context and relevance are presented.

The species

Diagnosis and systematic position

The genus *Gymnocarpus* Forssk. is diagnosable against all the other European *Caryophyllaceae* with stipulate leaves (Walters 1993) by its terete, fleshy leaves and, more specifically, by showing: (1) opposite leaves (unlike *Corrigiola* L. and *Telephium* L.); (2) fruit without inflated peduncle (unlike *Pteranthus* Forssk.); (3) gynoecium trimerous, i.e. ovary tricarpellate and style trifid (unlike *Herniaria* L., *Illecebrum* L. and *Paronychia* Mill.); (4) sepals entire (unlike *Loeflingia* L.); (5) flowers apetalous (unlike *Polycarpon* L., *Spergula* L. and *Spergularia* (Pers.) J. Presl & C. Presl); and (6) stipules

1 Association Pulsatille, 1bis route des Demoiselles Coiffées, 05190 Remollon, France (<https://www.pulsatille.com/>).

2 Biosfera Consultoría Medioambiental, C/Candamo 5 Bajo 33012 Oviedo, Spain; *e-mail: luiscarlon@biosfera.es (author for correspondence).

laminar, non-setaceous and fruits indehiscent, 1-seeded (unlike *Ortegia* L.).

Within its genus, *Gymnocarpos sclerocephalus* is unique for its annual habit and for the tightly clustered, partly connate inflorescences and infructescences (Fig. 1). It shares with the shrubby *G. decander* Forssk. the terete leaf-like bracts, so different from the large, scarious, *Paronychia*-like bracts of the rest of the genus.

Owing to its morphological distinctiveness, the species has often been classified in its own genus, *Sclerocephalus* Boiss., under the replacement name *S. arabicus* Boiss. (see, e.g., Chaudhri 1968; Petrusson & Thulin 1996), and as such it is still considered by Marhold (2011). However, molecular phylogenetics has been conclusive in showing that this species is deeply nested within *Gymnocarpos* (Oxelman & al. 2002; Jia & al. 2016).

According to the tribal system of Harbaugh & al. (2010), the most suitable suprageneric category for all these species is the tribe *Paronychieae* (the clade *Gymnocarpos* + *Herniaria* + *Paronychia*).

Ecological interpretation of diagnostic features

The above-mentioned generic and specific distinctive traits can be interpreted as the consequences of the ecological filtering imposed by an increasing aridity on more conventional *Paronychia*-like ancestors (Jia & al. 2016). The narrow, terete leaves and fleshy, green stems are easily cooled by wind to safe levels when stomata are closed under full sun and no transpiration takes place, their circular section also increasing the volume available to store rainwater and to diffuse the heat gained by radiation in the sun-exposed surface. In terms of water savings and survival, these two effects in combination more than compensate for the loss of specific leaf area. Similarly, the characteristic white hairs of the sepals (Fig. 1B, C) are likely to reflect sunlight and reduce thermal stress in the reproductive organs. Moreover, the mucronate apex of the leaves seems a way to facilitate morning dew to form falling droplets that the roots can absorb.

The tightly clustered infructescences and the apically spiny sepals suggest an efficient dispersal by epizoochory (Bittrich 1993: 214), explaining the particularly large geographical range of the species compared to other members of the genus and making still



Fig. 1. *Gymnocarpos sclerocephalus* – A, B: two individuals found in the rambla of Lanujar; note the heterogeneous, stony nature of the soil; C: close-up of the inflorescence; note the tightly clustered flowers, spiny bracts and sepals, and white hairs covering the sepals. – A–C: Spain, Almería, 17 Mar 2018, photographed by F. Le Driant.

more plausible the full autochthony of the Spanish population. In can also be argued that seeds are protected within the spiny, dry heads and released only in response to rain

(when the plant is more likely to complete its short cycle), in which case these unique infructescences can be interpreted as a mechanism of serotiny.

The locality

A colony of two dozen individuals was found in the side slope of the “rambla” (local name for a wadi, or temporary riverbed) of Lanujar near its confluence with the rambla of Tabernas (Fig. 2A). The terrain is topographically even but composed of lithologically and volumetrically heterogeneous materials brought together by erosion and transport during storms (Fig. 2B). This geomorphological activity, combined with the slow growth of vegetation on which it partially depends, maintains a fine-grained mosaic of open, stony soils where annual plants like *Gymnocarpus sclerocephalus* may persist indefinitely without being eventually outcompeted by taller, perennial plants (Cabello & al. 2003: 494).

Within 10 m from the core of the population (Fig. 2B), the following accompanying species were recorded (the code after each species or subspecies summarizes its chorological type: [E] endemic to Spain; [ISA] Ibero-Saharo-Arabian; [IN] Ibero-North African): *Diploaxis harra* (Forssk.) Boiss. [ISA+Sicily] subsp. *lagascana* (DC.) O. Bolòs & Vigo [E], *D. ilorcitana* (Sennen) Aedo & al. [E], *Filago clementei* Willk. [IN], *Forsskaolea tenacissima* L. [ISA], *Genista umbellata* (L’Hér.) Poir. [IN] subsp. *umbellata* [IN], *Lau-naea arborescens* (Batt.) Murb. [IN], *Limonium insigne* (Coss.) Kuntze [E], *Notoceras bicornis* (Aiton) Amo & Mora [ISA], *Pallenis hierichuntica* (Michon) Greuter [ISA], *Pteranthus dichotomus* Forssk. [ISA], *Salsola genistoides* Poir. [IN] and *Salsola oppositifolia* Desf. [ISA+Italy].

Within 100 m, other biogeographically meaningful species like *Cistanche lutea* Desf. [IN], *Cynomorium coccineum* L. (see below) and *Vella bourgaeana* (Coss.) Warwick & Al-Shehbaz [E] were found.

As already stated, the interest of the plant was not fully realized during the first finding in March 2018, and no voucher was collected. A second visit one year later to the exact locality in order to fulfil this requirement was unsuccessful, but eventually the species could be collected in January 2020 in a nearby but different place, some 0.7 km to the southwest in the rambla of Tabernas, where it had already been observed by Julián Manuel Fuentes Carretero in May 2019 and December



Fig. 2. A: orthophotographic view of the location of the populational nuclei presented here for *Gymnocarpus sclerocephalus*; note the aridity of the landscape and the absence of human activities apart from the highway (source of image: Plan Nacional de Ortofotografía Aérea, Instituto Geográfico Nacional, <http://pnoa.ign.es/>). – B: habitat of *G. sclerocephalus* in the rambla of Lanujar (Spain, Almería, 17 Mar 2018, photographed by F. Le Driant).

2020. In the moment of this collection, two nuclei of 28 and 42 individuals were recorded, with 11 more scattered in between, totalling 81 individuals in an area of 2.4 ha. The full collection data of the voucher specimen are as follows:

SPAIN: comunidad autónoma de Andalucía, provincia de Almería, municipio de Rioja, Desierto de Tabernas, rambla de Tabernas, 37°00'00"N, 02°27'50"W, 230 m, therophytic grassland on marly, sand-rich soils, 5 Jan 2020, J. Fuentes & A. Ivorra s.n. [with F. Le Driant, honoris causa] (GDA 65550).

Biogeographic significance

Anything but an outlier

Gymnocarpus sclerocephalus was known to occur in a large area across the North African and Eastern Asian arid regions, from the Cape Verde archipelago to southern



Fig. 3. Map created by combining the fragmentary or imprecise distributional information provided by the Global Biodiversity Information Facility (<https://www.gbif.org/>) and the Catalogue of Life (<https://www.catalogueoflife.org/>) with the general map in Jia & al. (2016). The red dot indicates the Spanish localities presented here.

Iran (Fig. 3), and now must be added to the list of genera and species distributed mainly if not only in the Saharo-Arabian region and with their only European populations in the arid areas of southeastern Spain: *Ammochloa palaestina* Boiss., *Anabasis articulata* (Forssk.) Moq., *Commicarpus plumbagineus* (Cav.) Standl., *Enneapogon persicus* Boiss., *Forsskaolea tenacissima*, *Hammada articulata* (Moq.) O. Bolòs & Vigo, *Ifloga spicata* (Forssk.) Sch. Bip., *Koelpinia linearis* Pallas, *Leysera leyseroides* (Desf.) Maire and *Notoceras bicorne*.

The list grows substantially if mostly Saharo-Arabian xerophytic genera or even species well represented in southeastern Spain but with a few colonies in other European regions, mainly on Mediterranean islands, are taken into account: *Androcymbium* Willd. (with *A. gramineum* (Cav.) J. F. Macbr. in Spain and northwestern Africa and *A. rechingeri* Greuter in Crete and Libya); *Apteranthes europaea* (Guss.) Plowes (SE Spain and Sicily and across North Africa and the Near East); *Cistanche* Hoffmanns. & Link (with *C. phelypaea* (L.) Cout. along western Spanish and Portuguese Atlantic coasts and *C. lutea* (Desf.) Hoffmanns. & Link in southeastern Spain and across Saharo-Arabian areas); *Cynomorium coccineum* (southern Portugal, Ibiza, southern Corsica, Sardinia, Sicily, Basilicata, Malta and across arid regions of North Africa and Asia); *Lasiopogon muscoides* (Desf.) DC. (widespread in the deserts of southern Africa and across the whole arid belt of North Africa and southwestern Asia, from the Canary Islands to the Indus river, it reaches not only southeastern but also central Spain); *Launaea* Cass. (with up to 14 species across arid regions of Africa and the Near East, of which *L. arborescens*, *L. lanifera* Pau and *L. nudicaulis* (L.) Hook. f. occur also in southeastern Spain, *L.*

fragilis (Asso) Pau and *L. pumila* (Cav.) Kuntze are more widespread across eastern Spain, the former occurring also in Sicily, and a 15th species, *L. cervicornis* (Boiss.) Font Quer & Rothm., is endemic to the Balearic Islands); *Periploca angustifolia* Labill. (SE Spain, Sicily, islands south of Crete and across North Africa); *Pteranthus dichotomus* (southeastern Spain, Cyprus, Malta and across North Africa and southwestern Asia); and *Volutaria* Cass. (with ten species: two endemic to Morocco, two endemic to the Canary Islands and six widespread across North Africa, three of which occur also in Europe: *V. crupinoides* (Desf.) Maire in central Portugal, *V. muricata* (L.) Maire in southern Spain and *V. tubuliflora* (Murb.) Sennen in southern Spain and Sicily).

There are still quite a few species which, despite belonging to genera widespread in Europe, also have a wide Saharo-Arabian range and their only European localities in southeastern Spain: *Achillea santolinoides* Lag., *Argyrolobium uniflorum* (Decne.) Jaub. & Spach, *Filago desertorum* Pomel, *Pallenis hierichuntica* (Michon) Greuter, *Plantago notata* Lag., *P. ovata* Forssk. and *Senecio flavus* (Decne.) Sch. Bip.

So what explains the existence of such a contingent of desert flora in this corner of Spain, surrounded by areas with physiognomically and to a great extent also taxonomically standard Mediterranean flora?

Geology, climate and history collude to sculpt a unique landscape

The idiosyncratic summer drought of the Mediterranean belt, imposed by the northward expansion of the Azores High, is enhanced in these areas by the strong rain shadow

of the Baetic mountains, whose highest massif, the Sierra Nevada (up to 3479 m a.s.l.), towers above the western edge of the Tabernas basin. The arrival of any substantial moisture from the Atlantic is hampered throughout the year, and total annual precipitation becomes very modest (around 200 mm on average, but below 100 mm in the drier years), evapotranspiration exceeding it by about fourfold. Precipitation is furthermore very irregular and unpredictable, much coming in short, heavy storms that physically erode the sparsely vegetated soils (Lázaro & al. 2004). Erosion disproportionately aggravates the water stress for plants and back-feeds the aridity of the region by reducing the capacity of soils to store water through the long sunny periods – this area receives the highest mean global daily radiation of continental Spain, above 5.3 kWh m⁻² day⁻¹ (Sancho & al. 2012).

A long history of aridity, dating back to the emersion of the Tabernas basin in the Pliocene (Alonso-Zarza & al. 2002), affects vegetation not only directly but also indirectly, insofar as it has contributed to generate and preserve unleached in the landscape large amounts of soluble evaporites with severe effects on plant development, both physical, as a result of superficial crusts and a too-strong adsorption of soil water, and chemical, because the abundance of certain ions hinders the absorption of essential nutrients and reduces the osmotic potential of soil water, further hampering its absorption by plants (Merlo & al. 2011; Moore & al. 2014; Escudero & al. 2015). In fact, Shmida (1985: 58–64) explored the strong links between desert and coastal flora as a consequence of the common effect of high ionic concentration in the edaphic solution.

However, it is possible that the striking desertic appearance nowadays predominant in this area is partly the result of human influence, and that a virtually continuous shrubland of sclerophyllous woody plants (syntaxonomically referable to the alliance *Asparago albi-Rhamnion oleoidis*) originally covered a substantial part of these slopes (Carrión & al. 2010). But such scrub revealed itself very fragile and was unable to recover fast enough from human destruction by fire and axe, spurred not only by pasturing but by the exploitation of esparto (*Macrarchloa tenacissima* (L.) Kunth) and by the demand for charcoal for smelting the products of ancient mining, all of which led to massive desertification and expanded the suitable habitat for all this strongly xerophytic flora, most likely restricted in the ancestral pre-Neolithic landscape to spots particularly dry for edaphic or topographic reasons (especially gypsum outcrops and saline marls; Mota & al. 2004).

Last but not least, the strong Föhn effect under nearly any wind regime and the low altitude and latitude of these arid regions of southeastern Spain, by almost eliminating frosts and by intensifying evaporation through consistently higher temperatures, strengthen their similarities with North African and Arabian deserts compared to other more northern or higher arid areas of Spain (Ebro, Tajo and Baza-Guadix basins). In these conditions, the

flora of true warm deserts not only survives but thrives at the expense of both Eumediterranean and less thermophilous, xerophytic Irano-Turanian species. Data gathered in the period 1990–2004 at the Experimental Station of “El Cautivo” (Solé-Benet & al. 2008), 1.5 km to the east and some 60 m higher than the site of *Gymnocarpus sclerocephalus*, suffice to establish the exceptionality of this climate: 18.74°C of annual average temperature (45.5°C of absolute maximum, –1.5°C of absolute minimum, 34.5°C of average maximum in July) and average annual precipitation of 243 mm (115 mm in the driest year, and an average of less than 1 mm in July).

According to Shmida’s (1985: 23) definitions, this area qualifies as a semidesert (annual precipitation below 400 mm but above 150 mm, figures conceived for regions with predominant winter rains). Such a label accurately conveys the striking physiognomic and floristic singularity of these southeastern Spanish areas, justifying the straightforward recognition of a distinct phytogeographic province (Murciano-Almeriense province) which, despite its remarkable similarities with Saharo-Arabian territories, is neatly included in the Mediterranean Region and, more precisely, in the West Mediterranean Subregion for its floristic background, for the nature of its connections with bordering provinces and for the fact that the most strongly subarid sectors are local and depend on topographic rather than on macroclimatic causes (Rivas Martínez & al. 2014).

Biogeography of the species: truly new to Europe?

Shmida (1985: 57) listed *Sclerocephalus* as one of the genera endemic to his “Sahara+Arabia” desert region, one out of many biogeographical proposals to reunite the continuous arid belt of Africa and southwestern Asia. Other systems (Rivas Martínez & al. 2017: 20) are less synthetic and distinguish, for instance, a Mediterranean northern Sahara from a tropical one. *Gymnocarpus sclerocephalus* occurs in both, as well as in other African and Asian regions considered to be bioclimatically and biogeographically different. Therefore, we prefer to use the less formal, more general term of “Saharo-Arabian” to summarize the large area occupied by the species.

In strict political terms, the genus and the species are new neither to Spain nor to Europe, since *Gymnocarpus sclerocephalus* is known at least from the Canary Island of Fuerteventura (Scholtz & Palacios 2015: 81, 87, 189), and its close relative *G. decander* from the islands of Fuerteventura, La Gomera, Gran Canaria, Lanzarote and Tenerife. But from a biogeographic perspective, is it clear that the Canary Islands are not part of Europe? It is indeed, because even admitting that the traditional idea of a “Macaronesian region” as opposed to the Mediterranean world is ill-founded, the occurrence of a number of palaeoendemic taxa and the outstanding concentration of taxa connected with eastern Africa as part of the so-called Rand Flora (Pokorný & al. 2015) put the

Canary Islands considerably aside even from the otherwise marginally Mediterranean and by definition African adjacent Moroccan coasts. Therefore, Rivas Martínez & al. (2017), although including the Canary Islands in the Mediterranean Region, recognized them (with Madeira) as a separate subregion, the same rank assigned to the Maghreb Mediterranean, the Mediterranean Desertic Sahara and the West Mediterranean (significantly dubbed “Mediterranean Europe” and to which our population of *G. sclerocephalus*, as explained above, belongs).

As a more informal, pragmatic argument, the Canary Islands were excluded from the main initiatives to compile the floristic knowledge about the continent (*Flora europaea*, *Atlas florae europaeae*) and even about the whole Mediterranean Region (*Med-Checklist*). Only recently were they considered by the more comprehensive Euro+Med PlantBase (Euro+Med 2006+), as well as, most likely for purely normative convenience, by the *European Red List of vascular plants* (Bilz & al. 2011). More conclusively, Brummitt (2001: 37, 109) explicitly considered the Canary Islands as part of Africa.

Native status?

It seems very unlikely that *Gymnocarpos sclerocephalus*, an inconspicuous plant lacking any agricultural, medicinal, material or ornamental value, could have been deliberately introduced by humans. Its habitat is almost by definition unsuitable for human activities, so even an accidental transportation of seeds is hardly conceivable. Moreover, the population (Fig. 2A) lies more than 7 km away from the nearest inhabited, cultivated or in any other way exploited land (with the exception of the highway and a cluster of open-air cinematographic studios). A human introduction in this mostly unspoiled area therefore seems as unlikely as it is likely that the plant has remained unnoticed as a consequence of the opportunistic, ephemeral, unpredictable regeneration niche associated with rains, which as described above made it difficult even to collect a voucher in the very same spot where it was first found. It is true that, as Julián Fuentes Carretero (pers. comm.) tells us, giving voice to the understandable scepticism of some Andalusian botanists, the existence of a theme park with a zoo a few kilometres upstream and the comings and goings of cinematographic crews in this popular scenery make a human introduction plausible. But a second, perhaps stronger line of evidence comes from the accompanying species, all of which are well established as native and associated with natural vegetation (Decocq & al. 2004). No unquestionably alien species, e.g. of American or South African origin, of which there are plenty in the region and which would indicate the recent dumping of exogenous material or a long history of human disturbance, cohabit with *Gymnocarpos sclerocephalus*. On the contrary, as stated above, the accompanying species include many regional or even local endemics.

As suggested above, the best explanation for the local occurrence of *Gymnocarpos sclerocephalus* and all the other plants with a similarly intriguing distribution is the maintenance of larger or smaller patches of suitable habitat throughout the Quaternary climatic transitions, in agreement with the aforementioned abundance of uneroded outcrops of evaporite and with the Iberian endemic races of widespread Saharo-Arabian species (like *Diplotaxis harra* subsp. *lagascana*), whose existence can hardly be reconciled with a recent arrival of all this flora. But even if such arrival was relatively recent, it continues to make perfect sense that *G. sclerocephalus* reached this extreme Spanish outpost as part of the same natural process of range expansion from Asia across the Sahara documented by Jia & al. (2016). A detailed chorological map, given the shortage of sufficiently precise records, is unworkable; but on account of the approximate range presented in Fig. 3, the nearest African populations are at most a few hundred kilometres away, close enough to take a more or less ancient bird-borne dispersal event for granted. In fact, even if a recent colonization could be proven, the process might not only be analogous but also have a direct causal link via epizoochory to that recently documented for the trumpeter finch (*Bucanetes githagineus* Lichtenstein, 1823), a remarkable deserticolous bird having in Tabernas its main European stronghold (Barrientos & al. 2009). Recall that *G. sclerocephalus* occurs, without the least suspicion of being alien, in both the Canarian and the Cape Verde archipelagos, and in the latter case no less than 600 kilometres from continental Africa.

As a final thought on this issue, there is no more reason to question the native status of *Gymnocarpos sclerocephalus* than that of its also epizoochorous Saharo-Arabian relative *Pteranthus dichotomus*, whose full autochthony in southeastern Spain has been unanimously admitted (Amich 1986; Díaz de la Guardia 2011). Along similar lines, the site of *G. sclerocephalus* is very close to those where *Filago desertorum* has finally been confirmed as a European plant, again without the least doubt about its native status (Gutiérrez Larruscain & al. 2017).

Conservation issues

Although more colonies are surely to be found in the same area, the species in continental Spain and Europe is so dependent on the above-described exceptional conditions that it must necessarily be very local. Hopefully, however, this single location is robust, well protected by its harsh environment from the two main agents of land transformation in southeastern Spain: greenhouse agriculture and tourism urbanization. Furthermore, it is expected to benefit rather than suffer from current climatic trends.

In the Canary Islands, the name *Gymnocarpos sal-soioides* Webb ex Christ was once used for a putative

endemic species different from the widespread *G. decander*, and therefore legally protected until 2010. But nowadays no species of the genus enjoys any protection. *Gymnocarpus decander* is listed as vulnerable in the current Spanish Red List (Bañares & al. 2010), whereas *G. sclerocephalus*, despite being much more local and rarer in the archipelago, is omitted.

We would advocate for a reassessment of such a decision. It could be argued that as long as *Gymnocarpus sclerocephalus* is found both in the Canary Islands and, as we now know, in continental Spain, its extinction risk at national level is reduced, and this could recommend against its addition to the Spanish Red List. But given that the concerns about the local conservation of *Forsskaolea tenacissima* presented by Cabello & al. (2003) can be even more justly applied to *G. sclerocephalus*, this latter species should for the same reasons also be included at least in the Andalusian Red List (Cabezudo & al. 2005) and, hopefully, gain legal protection.

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