On the identity of plants belonging to the *Opuntia humifusa* complex (Cactaceae) naturalized in northeastern Iberian Peninsula

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Abstract

Recent studies on the *Opuntia humifusa* complex allow us to review the identity of plants called *O. humifusa* (Raf.) Raf. in Catalonia. All the studied plants of the *O. humifusa* complex from this area exhibit the same morphological characteristics (mainly the thickness of the spines, the number of areoles and the seed form) as *O. mesacantha* Raf. subsp. *mesacantha*.

Keywords: Catalonia; *Opuntia;* non-native plants

Resum. *Sobre la identitat de les plantes del complex* Opuntia humifusa *(Cactaceae) naturalitzades al nord-est de la península Ibèrica*

Els nous estudis del complex *Opuntia humifusa* ens permeten revisar la identitat de les plantes anomenades *O. humifusa* (Raf.) Raf. a Catalunya. Totes les plantes estudiades d'aquest complex en l'àrea citada presenten els mateixos trets morfològics (principalment el gruix de les espines, el nombre d'arèoles i la forma de les llavors) que *O. mesacantha* Raf. subsp. *mesacantha*.

Paraules clau: Catalunya; *Opuntia*; plantes al·lòctones

Introduction

The genus *Opuntia* Mill. (Cactaceae) includes ca. 200 species native to the Americas (Anderson, 2001; Hunt, 2016; Majure et al., 2017), with the main diversity center in Mexico, the South of United States and the Caribbean Islands (Illoldi-

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Rangel et al., 2012). This genus contains the majority of the widely introduced, cultivated and invasive species in the family (Novoa et al., 2015). According to Majure et al. (2017), the species of the *O. humifusa* complex have been introduced in Europe, South Africa and eastern Asia. Moreover, Essl (2008) consider the most widespread species in Europe is *O. humifusa* (six countries) followed by *O. ficus-indica* (L.) Mill. Until recently, between 16 and 19 species of the genus *Opuntia* had been reported from Catalonia (northeastern Iberian Peninsula) (Aymerich, 2015, 2016; Guàrdia Valle, 2016; Pino & Álvarez, 2016). The first reference of *O. humifusa* in our area dates back to 1990, when Berthet (1990: 69, lam. 16) reported it from Vic (Barcelona Province) under *O. vulgaris* Mill. Subsequently, new populations of this species have been discovered in our area (Batriu et al., 2012; Aymerich, 2015, 2016).

The recent publication of a taxonomic revision by Majure et al. (2017) has allowed a better understanding of the relationships and boundaries among the members of the *O. humifusa* complex. Based on this premise, plants that have been referred to as *O. humifusa* from Catalonia may not correspond to this species, but to another closely related: *O. mesacantha* Raf., for which two subspecies are currently recognized. In this context, we proceed to review the identity of the plants of the *O. humifusa* complex naturalized in Catalonia.

The *Humifusa* clade consists of about 10 species widely distributed in North America from northern Mexico, north to Ontario, Canada, and south to the Florida Keys. This clade likely originated in northern Mexico and the southwestern United States, and from there it later spread to the southeastern United States and ultimately produced a small radiation in the eastern United States (Majure et al., 2017). This clade is subdivided in two groups in the south of the United States: the southwestern (SW) subclade, characterized by diploid procumbent species with non-retrorsely barbed spines and yellow and red flowers; and the southeastern (SE) subclade (treated by the latter authors as *O. humifusa* complex) with diploid species and polyploid derivatives, procumbent to erect, with retrorsely barbed spines and entirely yellow flowers. Several of those taxa originated from hybridization between the SE and SW subclades and display characters of both subclades (Majure et al., 2012, 2017). In this sense, *O. humifusa* and *O. mesacantha* are considered two taxa of the O. *humifusa* complex.

Costa & Morla (1986) reported *O. humifusa* var. *humifusa* from northern Iberian Peninsula. Later, the same taxon was reported for Catalonia as *O. vulgaris* Mill. by Berthet (1990) and Quadrada (1997). *Opuntia vulgaris* is currently regarded synonym of *O. ficus-indica* (Leuemberger, 1993; Pinkava, 2004), an erect phanerophyte noticeably different from the prostrate cactus *O. humifusa*. As a consequence, these issues led to some misidentifications in afterward publications. Moreover, Batriu et al. (2012) used the name *O. humifusa* for the first time to refer to this plant for Catalonia, and the following issues have used this name so far (see Annex). This plant has also been reported in the Iberian Peninsula for the autonomous communities of Aragon (Fabregat et al., 1995, sub *O. vulgaris*; Atlas of the Flora of the Pyrenees, 2017), Castile and Leon (Bariego & Rico,

2003, sub *O. vulgaris*; Acedo & Llamas, 2006), Galicia (Costa & Morla, 1986; Berthet, 1990, sub *O. vulgaris*) and Valencia (Guillot, 2003).

Materials and methods

In order to identify positively the plants of the *O. humifusa* complex naturalized in Catalonia, we visited in the field 10 populations (new or previously attributed to this species) for the purpose of examining living plants. Herbarium specimens deposited in the BC and BCN herbaria were also studied. Nomenclature of taxa follows Majure et al. (2017). Coordinates and elevation of localities were obtained from the internet map application VISSIR v.3.26 in <www.icc.cat/vissir/>. For the geographic reference of the records we used the 1 × 1 km UTM square grid (31T zone), ETRS89 datum.

Results and discussion

Plants found in the visited sites showed similar morphological characteristics: low-spreading shrubs in small groups (even isolated plants) or large colonies, in some cases more than 40-80 individuals (Vallès Oriental and Osona, Barcelona Province). Plants form rows up to 4, 5 and uncommonly 6(7) joined cladodes (Fig. 1C), which are more or less easily disarticulating. Cladodes 3.0-13.5 × 3.0-8.2 cm, 8.5-12.2 mm thick, with 3-4 areoles per diagonal row at midstem, obovate, elliptical or rounded in outline, margins smooth, disposed with the flat side on soil surface, turgid and dark green, but cross-wrinkling during the winter (or under desfavourable weather periods), reddish green the adaxial surface, light green to yellowish green the underside. Cladodes are spineless or bear from 1 up to 7(8) spines. Spines conspicuous, white to slightly grey when mature, 0.8-3.5 cm long, 0.85-1.10 mm in diameter, 0-2 per areole, usually restricted to the mid-upper part and especially along the margins of mature segments. Glochids scarcely exserted or included within the areole (Fig. 1B). Outer tepals green. Inner tepals 8, 2.5–3.6 cm long, entirely yellow. Stamen filaments yellow. Stigma whitish. Fruits 20-35 × 13-19.5 mm, red to reddish-purple, clavate to barrel-shaped. Seeds 4-5.4 mm in diameter, with bumpy funicular girdle, and cotyledons and hypocotyl noticeably protruding (Fig. 2E).

According to Majure (2015) and Majure et al. (2017), there are three taxa included within *O. humifusa* complex that bear a close ressemblance: *O. humifusa*, *O. mesacantha* subsp. *mesacantha* and *O. mesacantha* subsp. *lata* (Small) Majure. *Opuntia humifusa* is an allopolyploid (tetraploid, 2n = 44) derived from a SE subclade maternal lineage (probably *O. mesacantha* subsp. *mesacantha*) and from a SW subclade paternal lineage. The subspecies *mesacantha* is tetraploid (2n = 44) whereas subsp. *lata* is diploid (2n = 22), both apparently derived from the SE clade.

According to Majure et al. (2017) *Opuntia humifusa* has spineless cladodes, not easily disarticulating, generally 4(5) areoles per diagonal row at the widest point of the cladode. In contrast, *O. mesacantha* has cladodes more or less easily

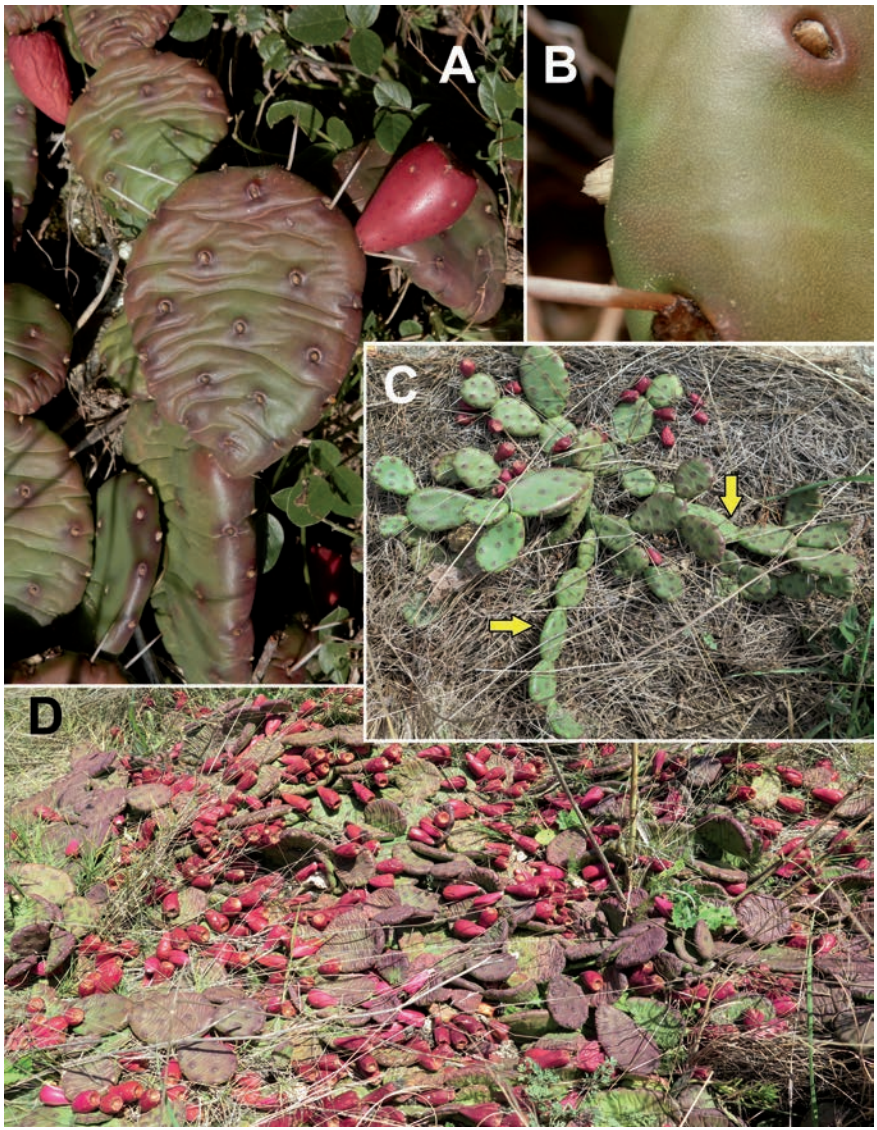

Figure 1. *Opuntia mesacantha* subsp. *mesacantha*. A: General aspect of the plant; B: Glochids scarcely exserted or included within the areole (A, B: Sant Feliu de Codines, Barcelona); C: Up to 6 (7) cladodes joined in a row (La Roca del Vallès, Barcelona); D: Significant fruit production (Súria, Barcelona).

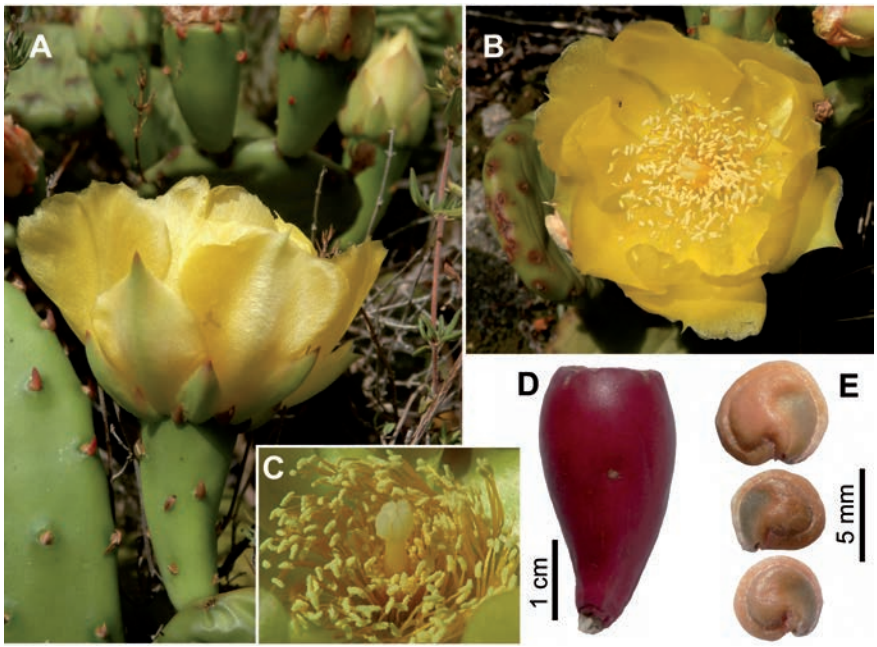

Figure 2. *Opuntia mesacantha* subsp. *mesacantha.* A-B: Flower; C: Stigma and stamens; D: Fruit; E: seeds (A, B, D, E: Sant Feliu de Codines, Barcelona).

disarticulating, that generally bear spines, at least the uppermost areoles, 3(4) areoles per diagonal row at midstem. Seeds of *O. mesacantha* subsp. *lata,* have smooth funicular envelope, moderate or without protrusion of the cotyledons and hypocotyl, spines delicate, 0.7–0.9 mm in diameter, whereas in subsp. *mesacantha*, seeds bear bumpy funicular envelope, cotyledons and hypocotyl noticeably protruding, robust spines, 0.95–1.3 mm in diameter.

Glochids in *O. mesacantha* are described by Majure et al. (2017) as "conspicuous, exserted or inconspicuous, included within the areole", but afterwards no specific differences for the two subspecies were provided. Nevertheless, these authors provide pictures of both subspecies that reveal differences between them: glochids in subspecies *lata* are conspicuous while in *mesacantha* are inconspicuous (similar to those presented by *O. humifusa*).

Some of the characters described above could make us think that our studied plants are more or less intermediate forms between both subspecies, especially due to the slightly minor size of the seeds and the thickness of the spines. This could perhaps be related to plant phenotypic plasticity in response to environmental factors. Most probably, this short-term adaptation also seems to be accompanied by others such as a significant fruit production (Fig. 1D). However, for most morphological characters (Table 1), the plants studied would be referable to *O. mesacantha* subsp. *mesacantha*.

Table 1. Comparative table with discriminant characters between *Opuntia humifusa, O. mesacantha* and plants belonging to *O. humifusa* complex from Catalonia, based on Majure et al. (2017) and measurements from our samples

Character	*O. humifusa*	*O. mesacantha*		Plants in our study
		subsp. *mesacantha*	subsp. *lata*	
Spines per areole	0	0–3	0–5	0–2
Spines measurements	absent	robust, 0.95–1.3 mm diameter	delicate, 0.7–0.9 mm diameter	0.85–1.10 mm diameter
Spines arrangement	absent	restricted to upper areoles	restricted to upper areoles or over the cladode surface	restricted to mid-upper areoles, mainly along the margins
Areoles per diagonal	(3)4–5 (mostly 4)	3(4)	3(4)	3–4
Glochids in areole	mostly included within the areole	slightly exserted or included within the areole	exserted	scarcely exserted or included within the areole
Cladode margins	smooth	smooth	scalloped	smooth
Cladodes long × wide, thick	9–15 × 5.7–8.3 cm, 9.6–15.7 mm thick	3.1–17.7 × 2–9 mm, 3.6–19.9 mm thick		3.0–13.5 × 3.0–8.2 cm, 8.5–15.5 mm thick
Cladodes disarticulation	cladodes not easily disarticulating	cladodes easily disarticulating in summer months		cladodes more or less easily disarticulating
Outer tepals	dark green to gray-green	Green		green
Inner tepals number, length	8-9, 3.7-4.0 cm long, entirely yellow	8, 2.3-3 cm long, entirely yellow	8, 3.4-4.3 cm long, entirely yellow	8, 2.5–3.6 cm long, entirely yellow
Berries	4.2–4.8 cm long	2.1–4.9 cm long		2–3.5 cm long
Seeds length	3–3.5 mm [4–4.6 mm (Majure, 2015)]	5.0–5.9 mm	4.7–5.3 mm	4–5.4 mm
Funicular girdle wide	0.4–0.7 mm wide, bumpy or irregular	0.7–1.3 mm, often bumpy or irregular	0.6–1.1 mm, regular, generally not bumpy	up to 1 mm, bumpy
Funicular envelope	bumpy	bumby, cotyledons and hypocotyl noticeably protruding	smooth, if any, protrusion of the cotyledons and hypocotyl	bumby, cotyledons and hypocotyl noticeably protruding

In conclusion, the available data suggest that the studied plants reported as *O. humifusa* from Catalonia are referable to *O. mesacantha*, mainly because of the presence of spines, fewer areoles per row and larger size of seeds. Moreover, diameter of spines, glochids appearance and form of seeds allow us to consider these plants as subsp. *mesacantha*. In absence of sound evidence of the presence of *O. humifusa* in the studied area, it is likely that all reports of this species in Catalonia are referable to *O. mesacantha* subsp. *mesacantha*.

We found *O. mesacantha* subsp. *mesacantha* growing in open sunny and dry environments in well-drained soils such as on rocky places, frequently open granitic (granodiorite) outcrops, and also on limestone or sandy soils. In all locations visited, this newcomer grew in ruderal and semi-natural communities. Thus, *O. mesacantha* can be considered an epoecophyta and hemiagriophyta sensu Kornás (1990).

We observed different dispersal mechanisms featured by this cactus, being the most prevalent the vegetative dissemination by fragmentation of the cladodes and subsequent falling down slope. This mechanism is similar to the process of fruit dissemination, due to its cylindrical shape they can roll down relatively long distances as well. Furthermore, seeds and fruits can be dispersed by animals. We noticed that some fruits seemed to be eaten by rodents or other small-sized mammals, but in other cases the numerous tracks around the plants indicate wild boars feeding activity. Also, it has been reported that their cladodes can occasionally be carried away by water courses during times of flooding or heavy rains. Latter aspect has not been verified in our study, but it is very likely to occur, especially in spring and autumn rainy periods.

The native area of *Opuntia mesacantha* subsp. *mesacantha* comprises the main part of the SE United States, from Maryland, probably from New Jersey, to Mississippi and Louisiana. However, is not present in the Florida Peninsula (Majure, 2015; Majure et al., 2017).

Three new localities of *Opuntia mesacantha* subsp. *mesacantha* are provided in this study for Vallès Oriental County, in Barcelona Province (Catalonia): Sant Feliu de Codines, between el Serrat de les Moles and l'Era Nova, 31TDG3016, 520-530 m, open rocky places on limestone substrate, 19 Feb 2017 and 5 June 2017 (photo), L. Sáez; Sant Feliu de Codines, Roques d'en Pere Pericó, 31TDG2916, 572 m, open rocky places on siliceous soil, 5 June 2017, L. Sáez (photo); La Roca del Vallès, near Pirineu street, 31TDG4404, 149 m, 22 March 2016, H. Álvarez & C. Gómez-Bellver (BC 951241, BCN 130203), numerous dense and decumbent groups on siliceous soil, occupying an area of approximately 60-70 m^2, with fruits.

In addition, because of the many populations found throughout the territory, the variety of seed and fruit dispersal agents (mainly gravity, dragging floods, animals and human action), and the reported invasive capacity of *O. mesacantha*, we consider that a further spreading of this species in Catalonia is very likely.

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Annex

New records, confirmed localities and putative reports for *Opuntia mesacantha* subsp. *mesacantha* in Catalonia. Reports under *Opuntia vulgaris* are not included.

Opuntia mesacantha subsp. *mesacantha*: populations and herbarium specimens studied

Barcelona Province: L'Anoia, el Forn, between can Aguilera and the font de la Teula. 31TCG9403, 600 m, schistose and rocky soils, on roadsides and spare thickets, 10 March 1996, *R.V. Quadrada Llovera* (BC 35122, sub *Opuntia vulgaris* Mill.); Vallès Oriental, La Roca del Vallès, near Pirineu street, 31TDG4404, 149 m, numerous dense and decumbent groups on siliceous soil, occupying an area of approximately 60-70 m^2, with fruits, 22 March 2016, *H. Álvarez & C. Gómez-Bellver* (BC 951241, BCN 130203); Vallès Oriental, Sant Feliu de Codines, between el Serrat de les Moles and l'Era Nova, 31TDG3016, 520-530 m, sunny rocky places, open calcicolous scrubs with false brome, 19 Feb 2017 and 5 June 2017, *L. Sáez* (photo); Sant Feliu de Codines, Roques d'en Pere Pericó, 31TDG2916, 572 m, open rocky places on siliceous soil, 5 June 2017, *L. Sáez* (photo); Bages, Súria's old town, 31TCG9632, 310 m, hillside covered by Mediterranean dry grassland with ruderal plants [revisited locality from Aymerich (2016, sub *Opuntia humifusa* (Raf.) Raf.]; Bages, Balsareny, at the foot of the castle chapel, 31TDG0735, 400 m [revisited locality from Aymerich (2015, sub *Opuntia humifusa* (Raf.) Raf.)]; Barcelona, Osona, Roda de Ter, between the Mo-

ros mountain and Sant Pere de Casserres, 31TDG4649, 545 m [revisited locality from A. Mercadé pers. comm.]; Osona, Vilanova de Sau, road from Vilanova to Folgueroles, near km. 14, 31TDG4843, 615 m [revisited locality from A. Mercadé pers. comm.]; Barcelona, Osona, Vilanova de Sau, at the bottom of the Mina hill, Collsameda, 31TDG4642, 735 m, stony ground [revisited locality from E. Batriu pers. comm.]; Barcelona, Osona, Vilanova de Sau, at the bottom of the Munts, 31TDG4742, 775 m, dry grassland on stony ground [revisited locality from E. Batriu pers. comm.]

Putative records of *O. mesacantha* subsp. *mesacantha* under *O. humifusa*

Barcelona Province: Osona, St. Sadurní d'Osormort, la Pedrija, 31TDG4537, 760 m, stony ground, (E. Batriu, pers. comm.); Osona, Tavertet, near el Llobet, Collformic, 31TDG4649, 520-550 m, sandy soils and stony ground (E. Batriu, pers. comm.); Osona, Sant Sadurní d'Osormort, els Terressos Roigs, between Bojons i la Verneda de Sant Feliu, 31TDG4841, 600 m, sandstone (E. Batriu, pers. comm.); Osona, Sant Sadurní d'Osormort, near the Verneda de Sant Feliu, els Terressos Roigs, 31TDG4841, 630 m, sandy soils, (E. Batriu, pers. comm.); Osona, Sant Sadurní d'Osormort, els Terressos Roigs, between Bojons i la Verneda de Sant Feliu, 31TDG4941, 600 m, sandstone (A. Mercadé, pers. comm.); Osona, Sant Sadurní d'Osormort, Can Puig, 31TDG4942, 610 m, stony ground (E. Batriu, pers. comm.); Osona, Vilanova de Sau, c. les Fagedes, els Terressos Roigs, 31TDG4942, 610 m, sandy soils (A. Mercadé, pers. comm.); Osona, Vilanova de Sau, c. la Pendissa Barcelona, 31TDG4944, 500-525 m, sandy soils and stony ground (A. Mercadé, pers. comm.); Osona, Vilanova de Sau, font del Martí, 31TDG5042, 475-575 m, dry slope between fields (Batriu et al., 2012); Osona, Vilanova de Sau, prop can Burjada, 31TDG5044, 560 m, dry grassland (Batriu et al., 2012); Osona, Vilanova de Sau, Bancells, 31TDG5244, 745 m (E. Batriu, pers. comm.); Osona, Vilanova de Sau, join of the river Ter with the Major river mouth, 31TDG5246, 350 m, sunny dry grassland (on schists) (Batriu et al., 2012); Osona, Vilanova de Sau, l'Albereda, 31TDG5247 510 m, dry meadows (Batriu et al., 2012) [the UTM coordinate has been rectified regarding an error in the original publication]; Barcelona, Osona, Vic [31TDG34] (MA 349174) (Berthet, 1990 sub *O. vulgaris*); Girona Province: Selva, Susqueda, el Llomà or la Rierica, near of la Grevolosa, 31TDG5949, 380 m, meadows (Batriu et al., 2012); Lleida Province: Pallars Jussà, Basturs, 31TCG3568, 630 m (Aymerich, 2015); Solà de Noves, Noves de Segre, 31TCG6483, 620 m, abandoned fields (Guardiola et al., 2016); Alt Urgell, Josa i Tuixén, bajo Cal Ramonillo, 31TCG7977, 1060 m (Aymerich, 2015); Cerdanya, Montellà i Martinet, outskirts of Martinet, 31TCG9290, 965 m, grassy slope between the road and houses (Aymerich, 2016).