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ORIGINAL ARTICLE

On the presence of *Xanthium* ser. *Glabrata* in Italy and in the Mediterranean basin

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Abstract

Xanthium ser. *Glabrata* (=*X. chinense*) is native to Central America and southeastern North America, and in recent times it has been introduced in other parts of the world, where in some cases it has become an invasive weed. It has sporadically been observed in Europe and in the Mediterranean area, mostly as a casual introduction and there is almost no evidence of stable populations. In Europe, other two species of *X.* sect. *Xanthium* are present: the native *X. strumarium* and the introduced *X. orientale*. A specimen in the herbarium of the University of Catania resembled morphologically *X. chinense*. It was collected in the Ciane River (southeastern Sicily) and was identified as *X. strumarium.* We used target enrichment of nuclear genes and the reconstruction of complete plastid genomes, along with phylogenetic methods, to ascertain the taxonomic placement of the specimen. The specimen was confirmed to belong to *X. chinense* and represents the first record of the species in the Italian territory. With a brief survey in important European herbaria, we were able to identify other specimens belonging to the species in other Mediterranean countries. Further studies are needed to confirm the presence of *X. chinense* populations in the Mediterranean and evaluate its invasion status.

Keywords Alien species · Asteraceae · Italian alien flora · Neophytes · Sicily

Introduction

Xanthium L. is a genus of the sunflower family (Asteraceae, tribe Heliantheae), peculiar for being one of the few members of the family that are wind pollinated (Tomasello et al. 2019). As with other Asteraceae, the flowers are small and arranged in typical flower heads (capitula). However, in *Xanthium* flowers are unisexual and placed in separate flower heads. Female inflorescences are very distinct structures, that completely enclose

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two female flowers and, later on, the two achenes. These structures (burs) are covered by hooked spines and two apical beaks and can effectively stick to animal fur and human clothing. In this way, *Xanthium* burs can be dispersed over hundreds of kilometres (Liddle and Elgar 1984). The genus has a cosmopolitan distribution, with a diversity centre situated in America, like most of the Heliantheae (Baldwin 2009). One species is native to the Old World including the Mediterranean region, i.e., *X. strumarium* L. (Opravil 1963; Brinkkemper and Kuijper 1993; Manzo and Tomasello 2025). In the past, more taxa were recognised within the latter species, based mostly on morphology. In the Mediterranean region, a form with bigger and more rounded burs was present, recognised as *X. brasilicum* Vell. (Widder 1923) and sometimes referred as *X. strumarium* subsp. *brasilicum* (Vell.) O.Bolòs and Vigo (Greuter 2006+).

However, several members of the genus are weeds of economically important crops. They are extremely competitive in soybean, cotton, and peanut plantations (Bloomberg et al. 1982; Byrd and Coble 1991; Jehlík et al. 2019; Ma et al. 2023). In recent times, lineages that were once confined to restricted geographical areas have become widespread, thanks to bur dispersal favoured by human trade. In the last few centuries, burs of *Xanthium* have been accidentally brought from North- and South America to Europe and Asia, attached to wool, cotton and animal fur (Ihne 1880; Widder 1923; 1972). In these new environments, those were able to form ephemeral populations and/or, in some cases, to start the colonization of vast areas. *Xanthium* grows naturally on beaches and riverbanks, in sandy soils and sunny places (Weawer and Lechowicz 1983). It adapts very well to human-transformed habitats, such as waste places and the margins of roads or cultivated fields (Weawer and Lechowicz 1983). In Italy, *Xanthium* lineages originating from the Americas were found forming stable populations at the beginning of the nineteenth century (Moretti 1822). These populations were described as a new species (*X. italicum* Moretti), nowadays considered a synonym of *X. orientale* (Tomasello 2018) and sometimes treated as *X. orientale* subsp. *italicum* (Moretti) Greuter (Greuter 2003). In the last two centuries, the introduced *Xanthium* has spread all over the Mediterranean basin (and beyond, e.g., Takakura and Fujii 2010) replacing the native species *X. strumarium* (Müller-Kiefer and Tomasello 2022). *Xanthium orientale* subsp. *italicum* can easily be distinguished from *X. strumarium* by the bigger glandular burs covered by several spines, the curved beaks, and the overall bigger size of the plants. *Xanthium strumarium* has smaller (up to 1 cm or slightly more) glabrous burs covered by fewer spines, straight beaks and overall smaller plant size (Tomasello 2018). *Xanthium strumarium* flowers earlier than *X. orientale* and produces ripe fruits when the American congener has started flowering (Miller 1768).

In *X.* sect. *Xanthium* DC. (the *Xanthium* having unarmed branches), there is another lineage: *X.* ser. *Glabrata* Widder (=*X. chinense* Mill. in Tomasello 2018). The latter is the more thermophilic relative of *X. orientale*: it is naturally distributed in Central America (including the Caribbean) and southeastern North America, and along the Mississippi River and its tributaries up to approximately Missouri and southern Illinois. Natural habitats of the it, as for other species in *X.* sect. *Xanthium*, are riverbanks and open coastal environments, but the species can adapt very well to ruderal and disturbed places. Nowadays, it is found as a neophyte in various tropical and subtropical areas of the world, including Africa (Widder 1972), India (McMillan 1972), Japan (Widder 1972; Takakura and Fujii 2010) and Australia (McMillan 1975). The series, as other complexes in the section, is morphologically very variable, and different taxa have been described in the past mostly based on the morphology of the burs (Millspaugh and Sherff 1919; Widder 1923). We will refere to it as *X. chinense* hereafter, altough the series should probably undergo a more comprehensive taxonomic revision. Morphologically, it is to some extent intermediate between *X. strumarium* and *X. orientale* and, because of the relatively small and glabrous burs, can be mistaken with *X. strumarium* by a non-specialized botanist. *Xanthium chinense* has been already observed in Europe. Wallroth (1842) described *X. pungens* Wallr. (= *X. chinense*) based on a plant growing from a bur found attached on remnants of an imported raccoon fur in a waste place in central Germany. In Tomasello (2018), a specimen collected in Austria was genetically identified with the species. However, in both cases (i.e., the type of *X. pungens* and the specimens from Austria) plants were immature and burs were not present. Miller (1768) reported that, even if plants can be cultivated in central and Northern Europe, they do not manage to produce mature burs before the unfavourable season come. In the Euro + Med PlantBase (https://europlusmed.org/), the species is listed as casual alien in France, Germany and Austria, while naturalized in Greece and Egypt. However, for the reasons mentioned above, it is questionable whether introduced individuals can persist and form stable populations in Europe and the Mediterranean. In Italy, the species is not listed in floras or checklists of the alien species (Pignatti et al. 2017-2019; Galasso et al. 2024).

While examining *Xanthium* specimens in various European herbaria, we found a specimen housed in the herbarium of the University of Catania (CAT, acronym according to Thiers 2025) that could resemble morphologically *X. chinense* (CAT020883). The specimen was collected in 1970 in "Fiume Ciane" (southeastern Sicily) and was identified as *X. strumarium* (Fig. 1). It presents slender burs, definitively bigger and different in shape from those of *X. strumarium*, which however, unlike those of *X. orientale*, are glabrous. In the present paper, we aimed at unambiguously identifying the specimen of the Fiume Ciane and discuss on the presence of *X.* ser. *Glabrata* in Italy and the rest of the Mediterranean basin. For the scope, we extracted DNA from the concerned specimen, produced a phylogenomic dataset consisting of hundreds of single copy nuclear genes and complete plastome sequence, and compared it with other accessions belonging to different species of *X.* sect. *Xanthium*.

Materials and methods

Plant material

In order to perform DNA extraction and the subsequent phylogenomic analyses, we sampled the herbarium specimen from the CAT herbarium (X236) and 23 additional herbarium specimens belonging to different taxa of the genus *Xanthium*. We mostly included other specimens belonging to *X.* ser. *Glabrata*, and those belonging to the taxa that could be confused with it: specimens from the *X. orientale* complex from Italy (i.e., *Xanthium orientale* subsp. *italicum*) and other belonging to the native species *X. strumarium* (most of them from Sicily). Moreover, two species belonging to *Xanthium* sect. *Acantoxanthium* DC. (*X. spinosum* L. and *X. catharticum* Kunth) were also included and used as outgroup. In total, 24 specimens from the herbaria B, BOLO, CAT, FI, GOET, M, P, PR, TEX (see Thiers 2025 for herbarium acronyms) were used in the analyses (Table 1). Sequence data for the outgroup samples were already

Herbarium Universitatis Catanensis

Flora Sicula 020883

Nome Xanthium strumarium L.

Località Fiume Ciane (Sr)

Coll. S. Brullo N.

Data 1-10-1970 Det.

Fig. 1 The specimen from the herbarium of the University of Catania (CAT020883) identified by our analyses as *X. chinense*

Table 1 List of specimens used for phylogenomic analyses. Nomenclature follows Tomasello (2018) and Manzo et al. (2024) for species from the section *Acanthocanthium* (i.e., *X. spinosum* and *X. catharticum*). Information is given on the Sample Id (as reported as well in Fig. 2 and Fig. 3), herbarium voucher number, morphotype, collection place and collection date

Sample Id	voucher	species	morphotype	collection place	collec. date
X8	M-0158773	*Xanthium strumarium*	“*japonicum*”	Japan; Nara; Aogakidai	16/9/1996
X10	M-0158774	*Xanthium strumarium*	“*strumarium*”	Germany; Bavaria; Zeilitzheim	15/8/1993
X12	M-0158776	*Xanthium chinense*	“*pungens*”	Botswana; North-West District; Nokaneng	17/3/1965
X20	M-0158783	*Xanthium chinense*	“*pungens*”	USA; Missouri; St. Louis	22/9/1957
X112	GOET060385	*Xanthium orientale*	“*italicum*”	Italy; Sicily; Altavilla Milicia	13/10/2020
X116	GOET061875	*Xanthium orientale*	“*italicum*”	Germany; Bot. Garden Göttingen (from burs collected in Sicily)	20/11/2020
X113	GOET061876	*Xanthium spinosum*		Italy; Sicily; Casteldaccia	21/10/2020
X173	B101094951	*Xanthium orientale*	“*orientale*”	France; Nouvelle-Aquitaine; Agen	1850–1870
X175	B100549529	*Xanthium chinense*	“*chasei*”	USA; Illinois; East Peoria	15/09/1945
X177	B100754514	*Xanthium strumarium*	"*strumarium*"	Germany; North Rhine-Westphalia; Cologne	09/09/1956
X178	B100766855	*Xanthium strumarium*	"*strumarium*"	Italy; Sicily; Caccamo	08/1888
X187	B100528156	*Xanthium chinense*	“*pungens*”	Iraq; Babil Governorate	30/11/1973
X190	B100535623	*Xanthium chinense*	“*pungens*”	USA; Missouri; Lesperance	05/10/1969
X197	B101067808	*Xanthium chinense*	"*occidentale*"	USA; Virgin Islands; St. Thomas	1827–28
X198	PR901932	*Xanthium strumarium*	“*strumarium*”	Czech Republic; Hradec Králové; Hořice	26/08/2018
X209	PR185931	*Xanthium chinense*	“*pungens*”	Germany; Thuringia; Nordhausen	around 1840
X224	BOLO0033408	*Xanthium orientale*	“*italicum*”	Italy; Piedmon; Premosello	11/9/1934
X229	FI064237	*Xanthium orientale*	“*italicum*”	Italy; Tuscany; “alta Lunigiana”	09/1954
X231	FI064239	*Xanthium chinense*	"*occidentale*"	France; Martinique	1870
X236	CAT020883	*Xanthium* sp.		Italy; Sicily; “Fiume Ciane”	1/10/1970
X237	CAT020884	*Xanthium strumarium*	“*brasilicum*”	Italy; Sicily; Mazzara del Vallo	6/9/1973
X305	TEX00407690	*Xanthium orientale*	“*italicum*”	USA; Texas; Greenville	21/9/1995
X328	P02511187	*Xanthium strumarium*	“*sibiricum*”	Vietnam; Central Vietnam (“Annam”)	20/7/1929
X333	P02537131	*Xanthium catharticum*		Colombia; Pasto	1851–1857

published in Manzo et al. (2024), whereas *X. strumarium* samples and X173, X187, X197, and X305 were already used in Manzo and Tomasello (2025).

DNA extraction and library reparation

We utilized up to 10 mg of dry leaf material for DNA extraction, using the Qiagen DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) with a few modifications as in Marinček et al. (2022), or, for the oldest herbarium vouchers, an ancient DNA (aDNA) protocol specific for old plant material (PTB-DTT, Dabney et al. 2013; Gutaker et al. 2017). Library preparation was carried out either with the NEBNext Ultra II FS DNA Library Prep Kit for Illumina or the the NEBNext Ultra II DNA Library Prep Kit for Illumina (New England BioLabs, Ipswich, Massachusetts, USA). The former kit was employed for recent herbarium specimens, whereas the latter was used for old herbarium samples, where enzymatic DNA fragmentation is not required. In both cases, we followed the manufacturer's instructions with the only modification that 1.5 volumes of HighPrep beads (MagBio Genomics, Gaithersburg, Maryland, USA) instead of the default 0.8 volumes were used, when purifying adapter-ligation products of the highly fragmented DNA from old herbarium specimens (see also Marinček et al. 2022). Therefore, sample-specific dual indices (NEBNext Multiplex Oligos for Illumina; New England BioLabs) were added to both ends of the fragments via a few cycles of PCR. The amplified reactions were then purified following the manufacturer's instructions.

Part of the libraries underwent target enrichment using the myBaits COS Compositae 1Kv1 kit (Daicel Arbor Biosciences, Ann Arbor, Michigan, USA), in order to acquire information on hundreds of single (low) copy nuclear genes (Mandel et al. 2014). For the scope, six indexed samples were combined in equal concentrations, then dried in a Concentrator Plus (Eppendorf, Hamburg, Germany), and further diluted in 7 µl of distilled water. Hybridization was carried out at 65 °C for 20 h. The subsequent PCR amplification was done with the P7 and P5 Illumina universal primers and the 2X KAPA HiFi HotStart Ready Mix (Roche, Basel, Switzerland).

Concentrations were measured using the Qubit 3 Fluorometer (Thermo Fisher Scientific, Waltham, Massachusetts, USA) and the Qubit dsDNA HS Assay Kit. Quality control for both enriched and unenriched libraries was performed on a QIAxcel (Qiagen) with the DNA High Resolution Kit 1200, the QX Size Marker 50 bp-800 bp v.2.0, and the QX DNA 15 bp-5 kb Alignment Marker. If adapter-dimer peaks were detected (approximately 125 bp), the libraries were subjected to size selection of 140–600 bp using the BluePippin (Sage Science, Beverly, Massachusetts, USA), and 2% cassettes with the 2% DF Marker V2. The samples were then pooled equimolarly and sequenced (together with samples from other studies) on an Illumina NovaSeq 6000 system (Illumina, San Diego, California, USA) using a SP P300 Xp (2 × 150 bp kit). One lane was used for the "unenriched libraries" (which had not undergone target enrichment), and the other lane for the "targeted" ones. A few samples were sequenced on different runs of an Illumina MiSeq system at either 2 × 250 or the 2 × 150 bp. Sequencing was performed at the NGS Integrative Genomics (NIG) Core Unit of the University of Göttingen.

Sequence data processing

Raw reads were processed in HybPhyloMaker v.1.8.2 (Fér and Schmickl 2018). Adapters and low-quality reads were removed using Trimmomatic v.0.33 (Bolger et al. 2014) with the default settings. Duplicate reads were eliminated using FastUniq v.1.1 (Xu et al. 2012). Surviving reads were mapped using BWA v.0.7.16a (Li and Durbin 2009) with default settings using as reference either the target loci of *Helianthus annuus* L., which were concatenated and separated by batches of 800 Ns (nuclear single copy genes), or with the chloroplast genome sequence of *X. strumarium* (GenBank accession number MH473582.1) for the plastome alignment. Consensus sequences were produced with ConsensusFixer v.0.4 (Töpfer 2018) with "plurality" set to 0.3 and "mincov" set to 5.

The nuclear loci were further processed in HybPhyloMaker and the mapped reads were aligned to the target exons using BLAT v.35 (Kent 2002) to generate PSLX files. The obtained locus-wise *fasta files were aligned using MAFFT v.7.305b (Katoh and Standley 2013) with default settings. Sequences with more than 40% of missing data ("missingpercent" in HybPhyloMaker) were removed from the alignments, and subsequently the alignments including less than 75% of samples ("speciespresence" in HybPhyloMaker) were discarded. Finally, 735 regions were retained and used for the following phylogenetic analyses. The plastome alignment (hereafter cpDNA dataset) was visually checked in AliView v. 1.20 (Larsson 2014), and cases of misaligned positions in gappy regions were eventually corrected.

Phylogenetic analyses

For both the plastome cpDNA and the 735 concatenated nuclear regions (hereafter nrDNA dataset) we inferred Maximum Likelihood (ML) phylogenetic trees in RAXML-NG v. 1.2.0 (Kozlov et al. 2019).

For the cpDNA alignment, which was treated as a single partition consisting of 153,141 bp, we used the GTR+G sequence evolution model and 1,000 bootstrap (bs) replicates. The nrDNA alignment consisted of 234,329 bp. The 735 nuclear regions were treated as different partitions and the best-fitting evolution model for each partition was inferred in MODELTEST-NG v. 1.1.0 (Darriba et al. 2020). Therefore, the RAXML-NG analysis was run using for each partition the respective model found in MODELTEST-NG, and with 1,000 bootstrap replicates.

Results

The ML tree inferred from the cpDNA is relatively well resolved (Fig. 2). *Xanthium* sect. *Xanthium* (all samples except *X. catharticum* and *X. spinosum*) is fully supported (bs:100) and all branches leading to species in the section received full support (i.e., *X. strumarium*, *X. chinense* and *X. orientale*). Within species, the resolution is low and some of the nodes (all the nodes in *X. strumarium*) are not highly supported. The specimen from the herbarium CAT is fully nested in the clade with samples of *X. chinense* and the sister relationship with the type of *X. pungens* Wallr. (=*X. chinense*) is highly supported (bs: 97). Two samples of *X. chinense* (X197 and X231) from the Caribbean (once described as a different taxon, i.e., *X. occidentale* Bertol.) group with samples of *X. orientale*.

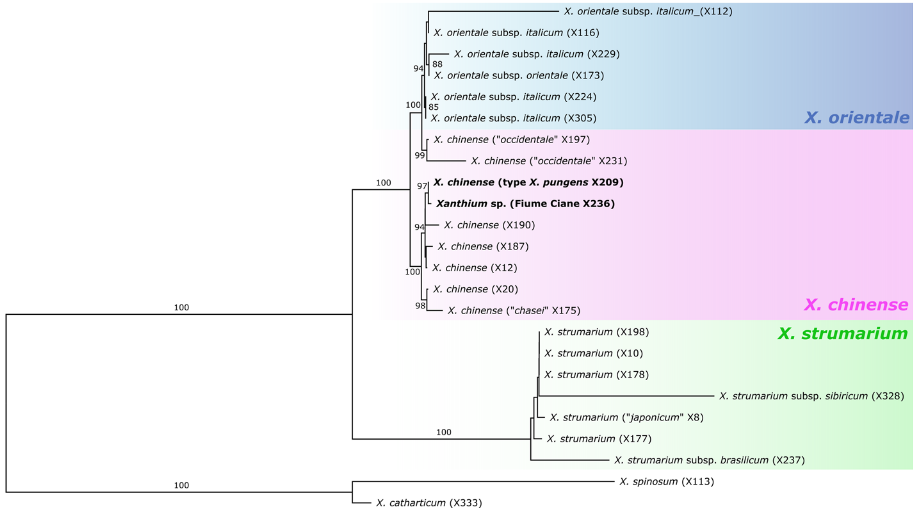

Fig. 2 Maximum Likelihood tree obtained from the analyses based on the plastome alignment. Numbers above branches or beside nodes are bootstrap support values (values below 70 are not reported). Colours refer to species assignment: green for *X. strumarium*, pink for *X. chinense* and blue for *X. orientale*

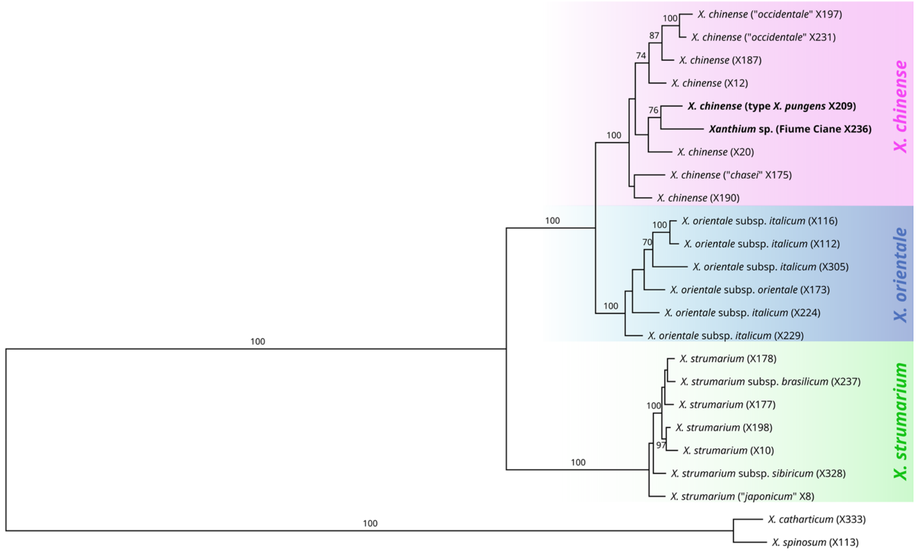

Fig. 3 Maximum Likelihood tree obtained from the analyses based on the single-copy nuclear genes obtained by target enrichment. Numbers above branches or beside nodes are bootstrap support values (values below 70 are not reported). Colours refer to species assignment: green for *X. strumarium*, pink for *X. chinense* and blue for *X. orientale*

A similar situation is observed in the tree inferred from the nrDNA dataset (Fig. 3). The only incongruence is the position of the two above-mentioned samples of *X. chinense* from the Caribbean, that in this case group together with the conspecifics. Otherwise, as for the cpDNA tree, the monophyly of *X.* sect. *Xanthium* in highly supported, as well as the branches leading to species in the section (bs: 100). The sample from the "Fiume Ciane" is again found to be sister to the type of *X. pungens* (bs: 76). Sister to this clade is found sample X20, although this relationship does not receive high support.

Discussion

In the present study we aimed at confirming the taxonomic identification of a herbarium specimen housed in the Herbarium of the University of Catania (CAT020883). The specimen was identified as *Xanthium strumarium*, a species native to the Italian territory but in strong decline in the last decades (Müller-Kiefer and Tomasello 2022). In fact, the species has become extremely rare in Italy and in other parts of its original distribution range, and it is difficult to find recent herbarium vouchers ascribable to the species. Interestingly enough, an image of the specimen concerned (CAT020883) can also be found in the Portal to the Flora of Italy under *X. strumarium* (https://dryades.units.it/floritaly/index.php?procedure=taxon_page&tipo=all&id=8723). However, the morphology of the burs strongly resembles other species of *X.* sect. *Xanthium*, and more specifically *X. chinense*. Our phylogenomic analyses confirmed our hypothesis and placed the concerned specimen together with other samples belonging to *X. chinense*. This is therefore the first confirmed occurrence of the species in the Italian territory and former misidentifications should be corrected.

Xanthium chinense is more thermophilic than other species of the section. It is probably not a coincidence that it was found growing close to the River Ciane. Southeastern Sicily is one of the warmest regions in Italy. In fact, the highest temperature ever registered in Europe was recorded in this area (48.8 °C in Syracuse on the 11/08/2021; The World Meteorological Organization (WMO) 2024; available at: https://wmo.int/news/media-centre/wmo-confirms-verification-of-new-continental-european-temperature-record). There, as in the rest of southern Europe, the recent anthropogenic warming is greater in winter than in other seasons (Twardosz et al. 2021 and citations therein), making these places particularly suitable for subtropical and tropical plant species. The area where the species was found (i.e., the Ciane River) harbours since long time other plants requiring a tropical climate (e.g., *Cyperus papyrus* L.) and it is vulnerable to the invasion of other topical plant species (e.g., *Azolla cristata* Kaulf. and *A. filiculoides* Lam., Rizzo 2021; *Pontederia crassipes* Mart., Cambria et al. 2023).

However, the specimen concerned was collected in 1970, and further studies should be undertaken to confirm its presence nowadays. The specimen has ripe burs, which may indicate a good chance of persistence and production of durable populations. *Xanthium chinense* was already collected in other parts of Europe, where it was introduced and failed to establish stable populations. The collections mentioned in the introduction (i.e., the type of *X. pungens* and a specimens collected in Linz in 1950 and deposited in the herbarium of the Botanical Garden and Botanical Museum Berlin: B 10 0467879), in fact, included plants missing mature burs. The latter specimen was only identified as *X. chinense* thanks to DNA-based analyses (Tomasello and Heubl 2017; Tomasello 2018). It was collected in October, and it is highly unlikely that has been able to produce mature burs before the arrival of the unfavourable Austrian winter.

Recently, *X. chinense* was found in Greece, in the Peloponnese and in Rhodes (Wißkirchen et al. 2013), especially in the latter location forming conspicuous populations. Looking more critically at herbarium collections, other specimens can be found collected in other areas of the Mediterranean basin and identifiable as *X. chinense* based on the bur morphology. For example, the species was already collected in Algeria (P04130810, although probably cultivated; available at: https://science.mnhn.fr/institution/mnhn/collection/p/item/), Morocco (L.2321413; https://bioportal.naturalis.nl/nl/multimedia/L.2321413_506915287), Portugal (L.2321412; https://bioportal.naturalis.nl/nl/multimedia/L.2321412_1012473912), Egypt (L.2321423, https://bioportal.naturalis.nl/nl/multimedia/L.2321423_2014467096; and WAG.1556113, https://bioportal.naturalis.nl/nl/multimedia/WAG.1556113_392589742). All these specimens have mature burs. Most probably, the presence of the species in the Mediterranean basin has been overlooked in the past and *X. chinense* plants have been misidentified as either *X. orientale* or *X. strumarium*.

Conclusions

In the present study we were able to ascertain for the first time the occurrence of *X. chinense* in the Italian territory, using DNA sequencing of nuclear and plastid regions and phylogenetic methods. Furthermore, based on the morphology of the infructescences, we identified other herbarium specimens collected in different regions of the Mediterranean basin as belonging to the species. Further studies are needed to confirm the presence and the persistence of *X. chinense* populations in the Mediterranean and to ascertain the invasion status in the different territories.

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Data availability Raw reads of all samples used in this study are available on the European Nucleotide Archive (ENA) under the accession number PRJEB74768.

Declarations

Disclosure statement No potential conflict of interest was reported by the authors.

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