Integrating palaeo- and archaeobotanical data for a synthesis of the Italian fossil record of Lycopus (Lamiaceae, Mentheae)

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Digging up the roots of the Italian flora: fossil record of *Lycopus* (Lamiaceae Mentheae)

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Abstract

We present the results of an "ad hoc" research team whose task was to revise and summarize the fossil record of a specific taxon which is currently part of the Italian Flora. The authors' team has been assembled from a group of researchers working on past records (mainly the BRAIN network), who invited experts of modern floristics to discuss the palaeobotanical data at the light of knowledge on the modern flora. Such analysis, focused on a national scale, did not preclude an expansion to a Eurasian and global scale for the analysis of evolutionary and historical biogeography issues, for which a country-scaled analysis may not be meaningful. The small genus *Lycopus*, frequently found in European archaeological contexts, provided a suitable study case for our "ad hoc" team. The fossil record is composed by nutlets, easily preserved in sedimentary deposits. In a worldwide context, the oldest ones date from the Early Oligocene (c. 30 Ma) and are limited to West Siberia, followed by more common Miocene (23-5 Ma) records, ranging from West Siberia to central Europe. In the literature, the Oligocene and Miocene records (plus a few Pliocene ones) were assigned to fossil-species, whereas the abundant Pliocene and Pleistocene records (5-0.01 Ma) of Europe were mainly assigned to the modern species *L. europaeus*. This synthesis reports on c. 6000 *Lycopus* nutlets from 61 sites located in 9 regions of northern and central Italy. On the basis of the available information on nutlets of modern species, we detected 8 morphological types of nutlets than can be used also for the characterisation of fossils. This analysis suggests that from 4 Ma to 2 Ma a single taxon bearing the *L. americanus*-type of nutlets occurred in Italy. The abundant records of the last 0.2 Ma, including finds from archaeological sites, are only referred to *L. europaeus*. Past occurrence of other exotic (extirpated) or extinct species of *Lycopus* does not emerge from the fossil record.

Key words: fruits, palaeontological collections, Cenozoic, Quaternary, Holocene, archaeobotany

Introduction

Research in the fields of neo- and palaeobotany uses to develop in parallel, sometimes with poor interchanges (Rull 2015; Marignani et al. 2016). Jimenez-Mejias et al. (2016) noted that, for the study of the genus *Carex*, many “neobotanists” tended to neglect the existing knowledge about the fossil record, almost ignoring the wealth of information potentially available in several palaeobotanical collections (e.g., Dorofeev 1963; Negru 1986; Palamarev 1994; Van der Burgh & Zetter 1998; Mai 2000; Czaja 2003; Velichkevich & Zastawniak 2003; Nikitin 2006; Martinetto 2015). In other cases, especially in molecular phylogenetic studies, palaeobotanical data have been randomly picked up, in an unwillingly selected way (Drew & Systma 2012). Actually, many experts in systematics do not integrate fossil-species into their considerations of character evolution, also because at least part of the necessary information is published in obscure papers without English/Latin descriptions (e.g., Nikitin 1948, Dorofeev 1963, Velichkievich 1973).

This problem might be mitigated by the ongoing progress of the International Fossil Plant Name Index (IFPNI) database (Barkworth et al. 2016), but also by synthetic reports summarizing the fossil record of specific taxa of the modern flora (e.g., Jimenez-Mejias et al. 2016), which indeed contribute to overcome this disconnection between botanists and palaeobotanists.

In the Italian context, the availability of the BRAIN research network (Botanical Records Archaeobotany Italian Network; http://brainplants.successoterra.net/) allows to quickly summarize the late Quaternary fossil record of specific living taxa. Additionally, the plant fossil record of Italy is less discontinuous over the last 6 million years than in other European countries, and recently summarized according to the different chronologies and plant parts by Bertini (2010), Kustatscher et al. (2014), Mercuri et al. (2015), Combourieu-Nebout et al. (2015) and Martinetto (2015). On this basis, it did not seem difficult to establish an "ad hoc" team able to revise and summarize the whole fossil record of a specific living taxon, with a focus on Italy. Such "ad hoc" team started from a group of Italian researchers working on past records (mainly the BRAIN network) who invited experts of modern floristics to discuss the palaeobotanical data at the light of the current knowledge on the modern flora. The analysis was extended to a Eurasian and global scale, when needed, as for example in the examination of taxonomic and phylogenetic issues, for which a country-scale analysis would not have been meaningful and the contribution of non-Italian fossils cannot be ruled out.

A specific interest in disentangling the taxonomy of fossils of the genus *Lycopus* Linnaeus (1753: 21), frequently found in European archaeological contexts, provided a suitable study case to engage our "ad hoc" research team. The phylogenetic placement of this genus is well-assessed and its divergence from the most closely related genera is attributed to relatively deep times (Drew & Systma 2012). The fossil record of *Lycopus* is mainly represented by nutlets, whose preservation is linked to sedimentary deposits where a scarce to moderate decay of the organic matter occurs, especially in waterlogged continental palaeoenvironments. The nutlet morphology is considered to provide diagnostic characters for the distinction of the living species (Moon & Hong 2006), whereas pollen grains, probably present in fossil assemblages, are not easily identifiable at the light microscope, thus they are commonly included in the *Mentha*-type or in the hexacolpate Lamiaceae undifferentiated grains (Beug 2004).

In contrast to the purported “lack of a strong fossil record” (Drew & Systma 2012), several authors (e.g., Reid 1920, Nikitin 1948, Dorofeev 1963, Velichkievich 1973, Mai & Walther 1988, Łańcucka-Środoniowa 1979, Martinetto 1994a; Mai 2000, 2001) reported fossil fruit records of *Lycopus* in Europe and West Asia: from the oldest ones of the Early and Late Oligocene (c. 30 Ma), limited to West Siberia (Nikitin 2006), through more common Miocene (23-5 Ma) records, ranging from West Siberia to central Europe, to the abundant Pliocene and Pleistocene records (5-0.01 Ma). Most of the Pliocene and Pleistocene records of Western Eurasia (see also O'Brien & Jones 2003, Velichkevich & Zastawniak 2003, Maul et al. 2013, Alçiçek et al. 2016) were assigned to the modern species *Lycopus europaeus* Linnaeus (1753: 21), whereas the Oligocene and Miocene records (plus a few Pliocene ones) were assigned to the fossil-species *L. antiquus* Reid (1920: 67). Additionally, Nikitin (2006: 42) suggested the presence of up to five not described species in the Oligocene and Miocene of West Siberia, and two species with characteristic morphology occur in the Pliocene of Eastern Europe: *L. cholmechensis* Velichkievich & Zastawniak (2003: 200) and *L. pliocenicus* Dorofeev (1987: 69).

This paper presents the inventory of fossil remains of *Lycopus* recorded from deposits dated to the last 5 million years (Ma), from Pliocene to Late Holocene, in Italy (Fig. 1). Since the reliable fossil record of *Lycopus* is only represented by fruits, a review of fruit morphology was undertaken in order to verify the accuracy and level of identification. The morphology of the nutlets is one of the best characters on which the species identification may be based, even in living plants (Henderson 1962, Moon & Hong 2006), but not all of the characters can be detected also in fossil specimens. Therefore, an identification key of new morphological types (also including some specific nomenclature) applicable to fossil remains is proposed.

***Botanical and taxonomical features of* Lycopus:**—The divergence of *Lycopus* from the most closely related genera is attributed, on a molecular basis (Drew & Systma 2012), to relatively deep times (c. 35 Ma). However, the biogeographic and temporal radiation of Mentheae should be better assessed, since it was based on calibrations of only two fossils. Although several fruit fossils reported from Europe have not been considered in the phylogenetic analysis (Drew & Systma 2012), the Oligocene date of a fossil, reported by

Mai (1985), was cited in support to the long phylogenetic stem of *Lycopus*. The Plant List (2013) reports 19 accepted species names for *Lycopus* (excluding hybrids and unresolved names), whereas Moon & Hong (2006) considered that *Lycopus* "consists of approximately 16 species". The geographic distribution of the genus covers most of the northern Hemisphere, and one species (*L. australis* Brown 1810: 500) occurs in Australia (Henderson 1962, Cantino 2004, Moon & Hong 2006, Morales 2010, Moon *et al.* 2013). In Europe, three species are known (Euro+Med 2006–2015, Ardenghi *et al*. 2014; Bartolucci et al., 2018; Galasso et al., 2018): *L. europaeus* Linnaeus (1753: 21), *L. exaltatus* Linnaeus f. (1781: 87), and *L. lucidus* Turczaninow ex Bentham in Candolle (1848: 179), the latter introduced at the beginning of the 21st century from eastern Asia. Historically, Briquet (1896) recognized two sections within *Lycopus*, sect. *Stoloniferi* Briquet (1896: 316) and sect. *Astolonosi* Briquet (1896: 317) [the latter consisting of only one species, *L. americanus* Muhlenberg ex Barton (1815: 15)]. The sections were mainly distinguished by the presence/absence of long runners from the lower nodes of the stem. Briquet's infrageneric classification was not followed by Henderson (1962) nor by Moon & Hong (2006), who identified four groups of species on the basis of nutlet morphology and anatomy.

According to Drew & Systma (2012) the presence of only two stamens, a unique pericarp structure (Ryding 2010), and a very long branch in both cpDNA and nrDNA support subtribal status for *Lycopus* [Lycopinae Drew & Systma (2012: 945)]. As said above, fruits of Lycopinae/*Lycopus* are diagnostic, being tuberculate with thickened pericarp and showing an abscission scar without an expanded area.

Materials and methods

Age estimation:—The age of each site has been mostly taken from the literature (Martinetto 2015; Mercuri et al. 2014). New 14C analyses have been carried out, in the Heidelberg 14C laboratory, only for two sites: Cave Germaire and Colombari. The Cave Germaire sample was a peat block extracted by a suction pipe at the bottom of an artificial lake, where peat deposits have been observed underwater. The three Colombari samples were small compressed woody axes with preserved tree rings collected in situ from a short outcropping peat-bearing section along the Chiusella river. The Cave Germaire and Colombari samples were pre-treated by the ABA sequence and bleached by NaClO2. 14C ages were calibrated using OxCal 4.3 and IntCal13.

Nutlet morphology of extant species:—The morphological analysis of the Italian fossil nutlets has been carried out for helping the species identification in comparison to modern and fossil reference material. The analyses pointed to the detection of diagnostic combinations of morphological characters which could characterize definite nutlet types both in fossil and modern samples. This required a comparative analysis of modern species, which was not restricted to those occurring today in Europe. In fact, there is no reason to assume a priori that only the two European living species should occur in the European fossil record. Rather, in other plant genera, the past occurrence in Europe of species now lacking in this territory was firmly demonstrated (e.g., Mai & Walther 1988; Velichkievich & Zastawniak 2003; Martinetto 2015). The possibly diagnostic characters of the nutlets of modern species (Tab. 3), in part newly detected by us, have been listed on the basis of the images provided, first of all, by Moon & Hong (2006), and secondarily by Henderson (1962), Crow & Helmquist (2000) and Son et al. (2016). For *L. americanus* we also used two images from reliable websites (http://castle.eiu.edu; https://plants.sc.egov.usda.gov; see Tab. 4). The selection of characters was biased towards those easily preserved in the fossils, and therefore did not correspond to the selection operated by Moon & Hong (2006), which included several non-fossilizable characters (thickness of anatomical details, trichomes, epidermal cell shape). Those species showing very similar characters were assigned to a same, precisely named morphological type (Tab. 4), which was also used to characterize fossil nutlet assemblages.

More detailed direct observations, in order to assess the degree of variability of several characters (Tab. 4), were carried out on a rich sample (US2814056) of *L. americanus* and two samples of *L. europaeus* (MCC0708, MCC2547) and *L. exaltatus* (MCC1335, MCC2548). The material of *L. europaeus* and *L. exaltatus* originated from different plants and localities (Tab. 3) and was stored in the Modern Carpological Collection of the Turin University (MCC, see Martinetto et al. 2014).

Fossil species:**—**The comparison with modern reference material cannot be regarded as exhaustive for the Italian pre-Quaternary fossil samples, because Dorofeev (1987) and Velichkievich & Zastawniak (2003) reported the occurrence of fossil-species already during Pliocene in other areas. Therefore, we pointed to compare the Italian fossils with previously described fossil-species of *Lycopus*. The aim was to evaluate the possible morphological correspondence with one or more putatively extinct species. To our knowledge, three fossil-species were described for the Cenozoic of this area (see Introduction) by Reid (1920), Dorofeev (1987) and Velichkievich & Zastawniak (2003). Concerning the earliest described species (Reid 1920), *L. antiquus*, the first author was able to use for this work the notes taken in the 1990s, when he studied the type material at the British Museum of Natural History of London. In order to locate material of *L. pliocenicus*, we analyzed all of the available fossil samples of *Lycopus* at Komarov Botanical Institute (label KBI), but we were unsuccessful. Therefore, the information about this species was based on the literature, as it was for *L. cholmechensis*. On the other hand, we located in the same repository some samples of five putatively distinct fossil-species from West Siberia, which were mentioned, but not described by Nikitin (2006). Actually, Nikitin named three of these species (that are obviously not validly published) in his digital database, available to one of us (A.V.H.) as a catalogue of his collection, presently stored at Komarov Botanical Institute (label KBI-H). Even if a revision of *Lycopus* fossils in this collection was beyond the scope of the present paper, we analysed selected material (KBI-H2514, KBI-H4313, KBI-392_5, 392_6, 392_7) of Nikitin's putative fossil-species in order to evaluate the affinities to the Italian fossil samples. Additionally, because of the relevance for our study, we analyzed the following fossil samples of *Lycopus* at Komarov Botanical Institute: KBI-K20, KBI-K320, KBI-K432, KBI-K453, KBI-K517, KBI-K519, KBI-K520, KBI-K523, KBI-K543, KBI-K547. The low number of well-preserved specimens (1-3) available for each sample was not suitable for a sound analysis of degree of variability of several characters.

Italian fossil samples:—A total of c. 6000 fossil nutlets of *Lycopus* have been isolated thanks to the cooperative work of the authors who have collected independent analyses from 23 pre-Holocene sedimentary records (Tab. 1), and 38 Holocene sedimentary records or archaeological sites (Tab. 2). The sites are located in 9 regions of northern (Piemonte, Emilia-Romagna, Liguria, Lombardia, Trentino-Alto Adige, Friuli-Venezia Giulia, Veneto) and central Italy (Toscana, Umbria) (Mercuri *et al.* 2014). The more recent sites are actually archaeological contexts whose results have been shared by the BRAIN members.

Results

New 14C dates:—The Cave Germaire (Hd-24603) sample dated beyond the 14C range (>50.000 cal BP), whereas the results of 14C analyses of the tree ring samples from Colombari provided very similar ages, and only sample Hd-23867 proved to be c. 300 years younger than the other two (Fig. 2). Due to the14C result we are forced to keep the generic middle-late Pleistocene age indicated by Tropeano and Cerchio (1987) for the sediments of the Cave Germaire peat sample (Hd-24603). Conversely, we obtained a sound date for the Colombari succession, deposited between 13200 and 13600 years cal BP.

Diagnostic nutlet characters of extant species:—The morphological variability of the nutlets, observed in c. 40-100 specimens (Tab. 4) from single plants, was rather high in *L. europaeus* and more limited in *L. americanus* and *L. exaltatus*. Also, the mismatch of characters between two samples of *L. europaeus* from different localities (Tabs. 3, 4) was consistent, and a further mismatch was noticed in the nutlet dimensions provided by Moon & Hong (2006) for this species, which were definitely larger than those measured by us (Tab. 3). In general, we observed that the occurrence of a contrasting character (e.g., open collar in a sample of nutlets with prevailing closed collar) in single nutlet may occur in several samples, therefore we suggest to evaluate the frequency (Tab. 4) of the relevant characters in an assemblage of nutlets. Unfortunately, analogous observations on the nutlet variability were not possible for other non-European species, and we had to rely on the information provided by the literature (summarized in Tab. 3). On the basis of the characters commonly preserved in fossils (Tabs. 3, 4), the characterization of single modern species was possible in a few cases, but in other cases a group of species shared the same morphological type of nutlets.

More in detail, five diagnostic combinations of characters were useful for the definition of morphological types that only occur in a single living species (Tab. 3): *L. asper* Greene (1898: 339), *L. australis*, *L. charkeviczii* Probatova (1995: 351), *L. laurentianus* Rolland-Germain (1945: 177), *L. lucidus*. Conversely, other six species [*L. amplectens* Rafinesque (1840: 115), *L. angustifolius* Elliott (1816: 26), *L. cokeri* Ahles ex Sorrie (1997: 124), *L. rubellus* Moench (1802: 146), *L. uniflorus* Michaux (1803: 14), *L. virginicus* Linnaeus (1753: 21)] seemed to share a stereotyped type of nutlets, that we called *L. virginicus*-type. To be noticed that a nutlet figured by Moon & Hong (2006), and assigned to *L. parviflorus* Maximowicz (1859: 216) (probably a synonym of *L. uniflorus*, see The Plant List 2013), approaches to the *L. charkeviczii*-type because of its apparent scutum, even if the dimensions are definitely smaller.

The easily distinguishable *L. americanus*-type was shared by three species, for which we noticed putative differential characters that should be better evaluated in larger samples of nutlets: *L. americanus* has regularly round apical outline and length mostly < 1.3 mm; *L. coreanus* Léveillé (1910: 423) has an apex mostly subtruncate; *L. exaltatus* has a length mostly > 1.3 mm, irregularly round apical outline and collar definitely thicker in the apical part than in the lateral one.

Finally, the *L. europaeus*-type was detected in *L. europaeus* and *L. maackianus* Makino (1897: 382). However, the nutlets of this last species have often characters which were rarely observed in the first one: very thick collar and asymmetrical outline.

The most diagnostic characters (see Fig. 3 for explanation) of these eight morphological types, that can be detected also in fossil assemblages, are listed in the following key:

1 Asymmetrical nutlets	2
1 Symmetrical nutlets, non-tuberculated corky crest	5
2 tuberculated corky crest	3
2 non-tuberculated crest, poorly apparent scutum	4

3 apparent scutum, L > 2 mm = *L. charkeviczii*-type;

3 scutum poorly apparent, L < 2 mm = *L. virginicus*-type

4 truncate apex, crest indefinite, mean L:W ratio 1.1 = *L. asper*-type;

4 subtruncate apex, crest very thin, mean L:W ratio 1.5 = *L. laurentianus*-type.

5 scutum poorly apparent, collar mostly closed = *L. lucidus*-type

5 apparent scutum ... 6

6 collar broader than 1/4 of the nutlet's width = *L. australis*-type

6 collar narrower than 1/4 of the nutlet's width ... 7

7 round apex common, wb frequently < 2/3 wa = *L. americanus*-type

7 round apex absent, wb frequently > 2/3 wa = *L. europaeus*-type

Morphological characterisation of fossil-species:— We obtained a re-evaluation of validly published fossil-species based on nutlet morphology. As for *L. antiquus*, the thick, robust and shining wall of the type specimens (Reid, 1920: pl. 4, figs. 15, 16) indicate that these remains do not represent any type of *Lycopus* nutlets, but fragments of fruits of the lythraceous genus *Decodon*. Consequently, this name cannot be applied to fossil specimens of *Lycopus* as in Dorofeev (1963), Mai & Walther (1988) and Nikitin (2006). Certainly belonging to *Lycopus* are the nutlets of *L. pliocenicus* (Dorofeev 1987) from the East European Pliocene. They conform the *L. americanus*–type, and differ from the modern American species *L. americanus* only for the tendency of nutlets to have a broader base and larger dimensions. Indeed, the distinction of the two formerly cited species needs to be accurately re-assessed. The characters indicated by Velichkievich & Zastawniak (2003) for the other fossil-species described from the Pliocene of Eastern Europe, *L. cholmechensis*, indicate that it approaches the *L. europaeus*–type, but may represent an extinct relative of *L. europaeus*, being morphologically distinct for the slightly concave crest, sometimes bearing small auricles.

Main characteristics of Russian fossils:—Most of the fossil samples from West Siberia and European Russia analysed by us, dating from Oligocene to Pleistocene and including the five putatively distinct fossil-species suggested by Nikitin (2006), approach either the *L. americanus* or the *L. europaeus*-type, but have very different size and do not agree in the combination of characters with any living species. However, at least one sample of nutlets from the Early Oligocene of West Siberia (KBI-H4313) can be assigned to the *L. americanus*-type. Furthermore, individual nutlets of the *L. europaeus*-type (e.g. wb frequently > 2/3 wa and subtruncate crest) occur in a Miocene sample (KBI-K517) from Russia, mixed with nutlets showing at least one contrasting character (e.g. wb frequently < 2/3 wa). Only among Pliocene and Pleistocene materials we detected whole nutlet assemblages (KBI-K453, less so KBI-K20) which are morphologically identical to the modern ones of *L. europaeus*. A third nutlet type detected in an Oligocene or Miocene West Siberian sample (KBI392_6) is the *L. charkeviczii*-type. At the present state of the art, the Russian fossils can only confirm with the existence of a reliable record for the genus *Lycopus* since Early Oligocene and an early diversification, before the end of the Miocene, of at least three groups bearing different nutlet types. Some of these groups actually represent distinct fossil-species, but more accurate analyses are needed for their characterisation.

Revised taxonomy of Italian fossil samples:—All of the studied fossil assemblages with good preservation of the diagnostic characters (Tables 2, 3) could be assigned either to the *L. europaeus*-type or to the *L. americanus*-type, and only in one case (Sample NVE58, Tab. 2) one nutlet of the *L. americanus*-type was mixed up with a majority of nutlets of the *L. europaeus*-type (Fig. 4). Based on what we observed in modern samples, this case was parsimoniously interpreted as a product of intraspecific variation. The results obtained from the analysis of modern and fossil comparative materials led us to propose the following taxonomic framing, that will be discussed in detail below.

Order **Lamiales**

Family **Lamiaceae**

Genus ***Lycopus***

Lycopus cf. ***americanus*** Muhlenberg ex Barton (1815: 15) (Fig. 5)

Specimens:— NPI-CV3 CCN2406; NPI-RDB1 CCN2413; NPI-RDB6 CCN2414; NPI-STU CCN2417; NPI-GA21 CCN2407; NPI-GA5 CCN2408, CCN2409, CCN2410.

Lycopus europeaus Linnaeus (1753: 21) (Fig. 4)

Specimens:— CTO-BUT1 CCN 5967; CTO-BCN1 CCN 6043; CTO-BCN1 CCN 6110; NPI-CLB1 CCN 6381.

Lycopus cf. ***europeaus*** Linnaeus (1753: 21)

Specimens:— CTO-CLV1 CCN 6122; NPI-CGE1 CCN 6307.

Lycopus sp.

Specimens:— NPI-BG4 CCN2415; NPI-BG3 CCN2416; NPI-DU23 CCN2396; NPI-BA2 CCN2399; NPI-CE1 CCN2403; NPI-GA8 CCN2411; NPI-LC2 CCN2412; NPI-BU21 CCN2400; NLO-CG2 CCN2405; NLO-VGT2 CCN2398; CUM-PF2 CCN2418; NVE-STG2 CCN7998; NLO-BVC3 CCN 5817.

Discussion

Intraspecific variation:—Our observations on many specimens of a single sample indicate that the fruit characters in *Lycopus* are more variable than described by Moon & Hong (2006), so that a rigorous assignment of a single fossil nutlet (even perfectly preserved) to a precise species seems to be hazardous. For example, within a nutlet assemblages collected from a single plant of *L. europaeus* (MCC2547), where the dominant condition was L:W ratio c. 1.2 and closed collar, we detected a few nutlets with L:W ratio c. 1.5 and open collar, as more typical for *L. exaltatus*. Conversely, in the modern samples of *L. exaltatus* the morphological variation of the nutlets was definitely scarce, and we did not observe nutlet morphologies approaching those of *L. europaeus*. The observations on *L. europaeus* and *L. exaltatus* suggest that the analysis of dominant and more stable characters in nutlet assemblages (Tab. 4) would permit the distinction of the two species, also in fossil assemblages.

Identification of Italian fossil samples:—Most of the studied Italian fossil assemblages (Tables 2, 3) can be assigned either to the *L. europaeus*-type or to the *L. americanus*-type. The Italian fossil samples with the exclusive presence or prevalence of *L. europaeus*-type do not correspond to any of Nikitin's purported fossil-species. So, they could be hypothetically assigned only to the fossil-species *L. cholmechensis* or to the living species *L. europaeus* or *L. maackianus*. However, the nutlets of *L. cholmechensis* are characterized by a concave crest, often with auriculae, not observed in the Italian fossils. Likewise, nutlets of *L. maackianus* have very thick collar and slightly asymmetrical outline. By further considering the East Asian distribution of *L. maackianus*, we confidently assigned to *L. europaeus* all the Italian samples showing a prevalence of *L. europaeus*-type. This concerns all Holocene and a few Pleistocene assemblages, dating back to no more than 0.1-0.2 Ma (CTO-BCN1: Tab. 1).

The exclusive occurrence of the *L. americanus*-type was detected in two fossil populations from the oldest localities, CV3 (4.0-3.5 Ma: Fig. 5) and STU (c. 3.1 Ma). These fossil populations, for the pattern of apical and basal collar thickness and the regularly round outline of the apex, are morphologically closer to *L. americanus* than to the living species *L. coreanus* and *L. exaltatus*. In particular, these European fossils do not seem to represent a past occurrence of the European species *L. exaltatus*, because of the regularly rather than irregularly round apical outline and narrower collar in the apical part. Very similar to the Italian Pliocene fossils are the East European nutlets of the fossil-species *L. pliocenicus*, also from the Pliocene, whose distinction from *L. americanus* needs to be accurately re-evaluated. Another sample of nutlets from the Oligocene of West Siberia (H4313), putatively assigned in Nikitin's collection to a separate fossil-species (not validly published), only differs for a slightly more toothed crest. At the light of the present evidence we cannot decide between these 2 possibilities: a) the Italian fossils from the Ca' Viettone and Stura di Lanzo sites may actually indicate the past occurrence of *L. americanus* in Europe; b) they may represent a European fossil-species that can be distinguished from *L. americanus* only on the basis of the slightly larger nutlet dimensions (length 1.35-1.70 versus 1.00−1.40 mm). Waiting for further evidence, the Italian fossils from the Ca' Viettone and Stura sites can be better treated with the open nomenclature *L.* cf. *americanus*.

Other Italian localities in the range 4−2.6 Ma provided scarce or incomplete nutlets, which however agree in all the detectable characters with the samples from the Ca' Viettone and Stura di Lanzo sites, and are also assigned to *L.* cf. *americanus.* The Early Pleistocene fossils are problematic, mainly because of the scarcity of remains, which do not allow to study the variation. However, 5 nutlets from the poorly dated Castelletto Cervo II site (supposed Gelasian, 2.6-2.0 Ma: Martinetto 2015) still show a combination of characters pointing to *L.* cf. *americanus*. From 1.8 to 0.2 million years ago, the fossil record is only represented by scarce, ambiguous remains and also a fossil from Pietrafitta (Martinetto et al. 2014), which was doubtfully attributed to *L. exaltatus*, does not show convincing diagnostic characters for that species, so that here is revised as *Lycopus* sp.. The abundant samples from sediments younger than 0.2 Ma (Fig. 4) showed a combination of characters typical of the *L. europaeus*-type, and can be confidently assigned to *L. europaeus*. Only in one site (NVE58, Altino) a few nutlets with all the typical characters of *L. exaltatus* were found (Fig. 4). Since these are associated to a large quantity of nutlets with typical characters of *L. europaeus*, we cannot rule out that their morphology could result from intraspecific variation, so that we regard the occurrence of *L. exaltatus* in this site as uncertain.

Ecology and distribution in Italy:—The habitat of *Lycopus* species is mostly linked to wetlands and river margins (Henderson 1962, Moon & Hong 2006, Euro+Med 2006–2015). For example, *L. americanus* is considered an obligate wetland plant as it is common in marshes, wet meadows, shores, streambanks, ditches, calcareous fens, and wetland margins (Chadde 2002). Also *L. europaeus* grows in wetlands, typically marshy grassland, tall-herb fen, margins of ponds and rivers, and shaded streams (Akhani 2014). Today in Italy these kinds of habitat are definitely more common in the northern and central part of the country and, interestingly, most of the palaeobotanical record of *Lycopus* comes from the northern Italy regions. Only a few traces are available from the two northern regions of central Italy, whereas no records are available from the southern regions, Sicily and Sardinia. We can certainly invoke preservation issues, but also the uneven intensity of palaeobotanical investigations, among the causes of such missing evidence.

However, ecological and phytogeographical, besides taphonomical and scholarly reasons, can explain why the records are concentrated in the northern districts of the country.

Conclusions

Taxonomical and chronological overview of the Italian fossils:—The overview of the collections and field study reports points to a significant presence of *Lycopus* records since 4 million years ago in Italy. The nutlet morphology is considered useful to detect several morphological types, that include a few modern species. All of those Italian fossil assemblages which showed a good preservation of the diagnostic characters could be assigned either to the *L. europaeus*-type or to the *L. americanus*-type. The fossil record of *Lycopus* in Italy starts with a rich population of *L.* cf. *americanus* dated to the late Zanclean (late Early Pliocene). This taxon also occurs in the Piacenzian (late Pliocene), and most probably in the Gelasian (Early Pleistocene). During the Calabrian (Early Pleistocene), from 1.8 to 0.8 Ma, the presence of the genus *Lycopus* in northern-central Italy is well documented by fossils, but the remains are not sufficiently abundant and well-preserved to obtain a definite species or morphotype identification. A previous doubtful record of *L.* cf. *exaltatus* (Martinetto et al. 2014) is here revised as *Lycopus* sp. This open nomenclature is suggested for all the scarce or incomplete remains recovered from deposits dated from 1.8 to 0.2 Ma, until new data on the morphological variation of nutlets will be available for this time interval. The abundant samples from sediments younger than 0.2 Ma showed a combination of characters typical of the *L. europaeus*-type, and can be confidently assigned to *L. europaeus*. The oldest population assigned to this species dates back to the 0.2-0.1 Ma interval (Cava Campitello: Tab. 1), whereas the Holocene record is extensive and also includes many archaeological sites.

Phylogenetic hints:—The possible phylogenetic relationships of the Pliocene *L.* cf. *americanus* from Italy with the modern European species *L. europaeus* and *L. exaltatus*, but also with the morphologically similar non-European species *L. americanus, L. maackianus* and *L. coreanus*, remain unclear. However, on the basis of our detection of a plant with a *L. americanus*-type of nutlets in the Neogene of Europe, and back to the Early Oligocene in west Siberia, it should be investigated whether these five living species, sharing very similar fruit morphology, may have diverged from a common ancestor with nutlet characters very similar to those of the modern *L. americanus*. Of course, the remains of this putative ancestor could be represented by the fossil nutlets reported from West Siberia (Dorofeev 1963, Nikitin 2006), where a lineage bearing the *L. americanus*-type started during Early Oligocene, later expanding its range down to southern Europe, where it is represented today by *L. exaltatus*. At the light of the present evidence it seems that *L. americanus* could be the descendant of this Eurasian lineage, through expansion of its range to North America. The evolution of *Lycopus europaeus* may well have taken place in Eurasia, where its nutlet type is documented at least since the Miocene (west Siberia), and some nutlet assemblages which are morphologically identical to the modern ones occur since the Pliocene.

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FIGURE 1. Map of Italian fossil sites where *Lycopus* nutlets have been detected. Site numbers are referred to those listed in Tab. 1 and Tab. 2.

FIGURE 2. 14C dates and ranges of the Colombari (“Ivrea”) samples, calibrated using OxCal 4.3 (above) and IntCal13 (below).

FIGURE 3. Diagnostic characters detected in nutlets of *Lycopus*, largely modified from Moon & Hong (2006).
a scutum apparent; **c** collar closed; **l4** mean collar thickness larger than 1/4 nutlet's width; **n** nutlet's apical end not-tuberculated; **n4** mean collar thickness narrower than 1/4 nutlet's width; **o** collar open; **p** scutum poorly defined; **r** apical outline round, **st** apical outline subtruncate, **u** collar open but unclear border of collar margin. These characters are scored for each species of *Lycopus* in Tab. 3.

FIGURE 4. Examples of fossil fruits of *Lycopus* in dorsal view, from the Early Pliocene Ca' Viettone site, northern Italy.

FIGURE 5. Examples of fossil fruits of *Lycopus* in dorsal view, from the Holocene Altino site, northern Italy.

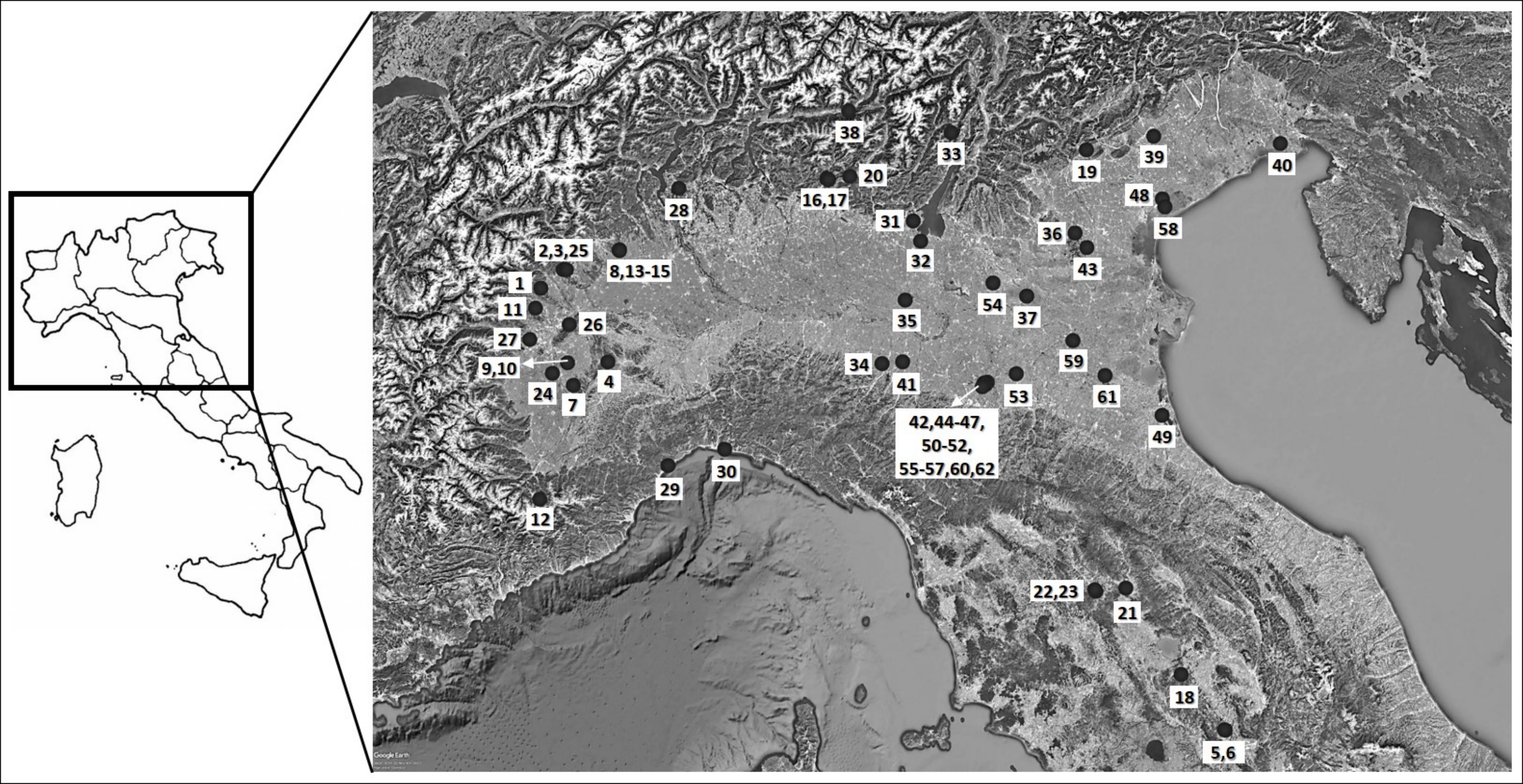
TABLE 1. List of Plio-Pleistocene samples of *Lycopus* nutlets with data on the geographical location of the sites, age, material, etc. Chronology is reported as million years ago (Ma) or as calendar years before present (cal BP). **Elev.** = elevation; **Nr. rem.** = number of remains (fruits); **Con.** = concentration.

TABLE 2. List of Holocene samples of *Lycopus* nutlets with data on the geographical location of the sites, age, material, etc. Chronology is reported as century of calibrated ages BC/AD. All the remains are uncharred. **Elev.** = elevation; **Nr. rem.** = number of remains (fruits); **Con.** = concentration. The tentative determinations also consider site-specific data, age and floral history.

TABLE 3. Nutlet characteristics in *Lycopus*, largely modified from Moon & Hong (2006), and integrated with data from Henderson (1962) and Crow & Helmquist (2000). Data on nutlet morphology of *L. amplectens* and *L. rubellus* are only based on Henderson (1962) and Crow & Helmquist (2000), because the nutlets of these species figured in Moon & Hong (2006) showed a

too strong morphological disagreement. See Fig. 3 for explanation of how the parameters L, W, wa, wb have been measured. **NA** nutlet's apical end (**n** not-tuberculate, **t** tuberculate corky crest); **AO** apical outline of nutlets (**r** round, **st** subtruncate, **t** truncate); **CS** collar base shape on the dorsal side (**o** open, **u** open but unclear border of collar margin, **c** mainly closed); **SY** nutlets symmetry in dorsal or ventral view (**a** asymmetrical, **s** symmetrical); **CT** mean collar thickness (**l4** larger than 1/4 nutlet's width, **n4** narrower than 1/4 nutlet's width, **n5** narrower than 1/5 nutlet's width); **SC** scutum (**a** apparent, **p** poorly defined); the morphological types defined in this work are listed next to those of Moon & Hong (2006), which are inconvenient for the characterization of fossils, being based on several characters which are not preserved. The label CCN designates samples of the CENOFITA Collection of fossils (Martinetto 2015), whereas acronym MCC indicates materials examined in the Modern Carpological Collection (Martinetto et al. 2014), and US is the conventional herbarium acronym.

TABLE 4. Comparison of the nutlet characteristics of modern populations of *L. europaeus*, *L. exaltatus*, *L. americanus* and their frequency in several fossil assemblages: A = absent; F = frequent; P = present. See Fig. 3 for explanation of how the parameters L, W, wa and wb have been measured. See Tabs 1-3 for explanation of site and sample labels.**NN**: number of nutlets analysed; **Small L:W**: nutlet's L:W ratio c. 1.1-1.2; **Large L:W**: nutlet's L:W ratio c. 1.5; **ASC**: almost straight crest; **CR**: crest round; **OT**: crest bearing obtuse teeth; **CC**: collar closed; **CO**: collar open; **SC**: subequal collar (collar as thick in the apical part as in the lateral one); **UC**: unequal collar (collar thicker in the apical part than in the lateral one); **wa≈wb**: wa similar to wb; **wb<2/3 wa**: wb smaller than 2/3 wa; **wb<1/2 wa**: wb smaller than 1/2 wa.



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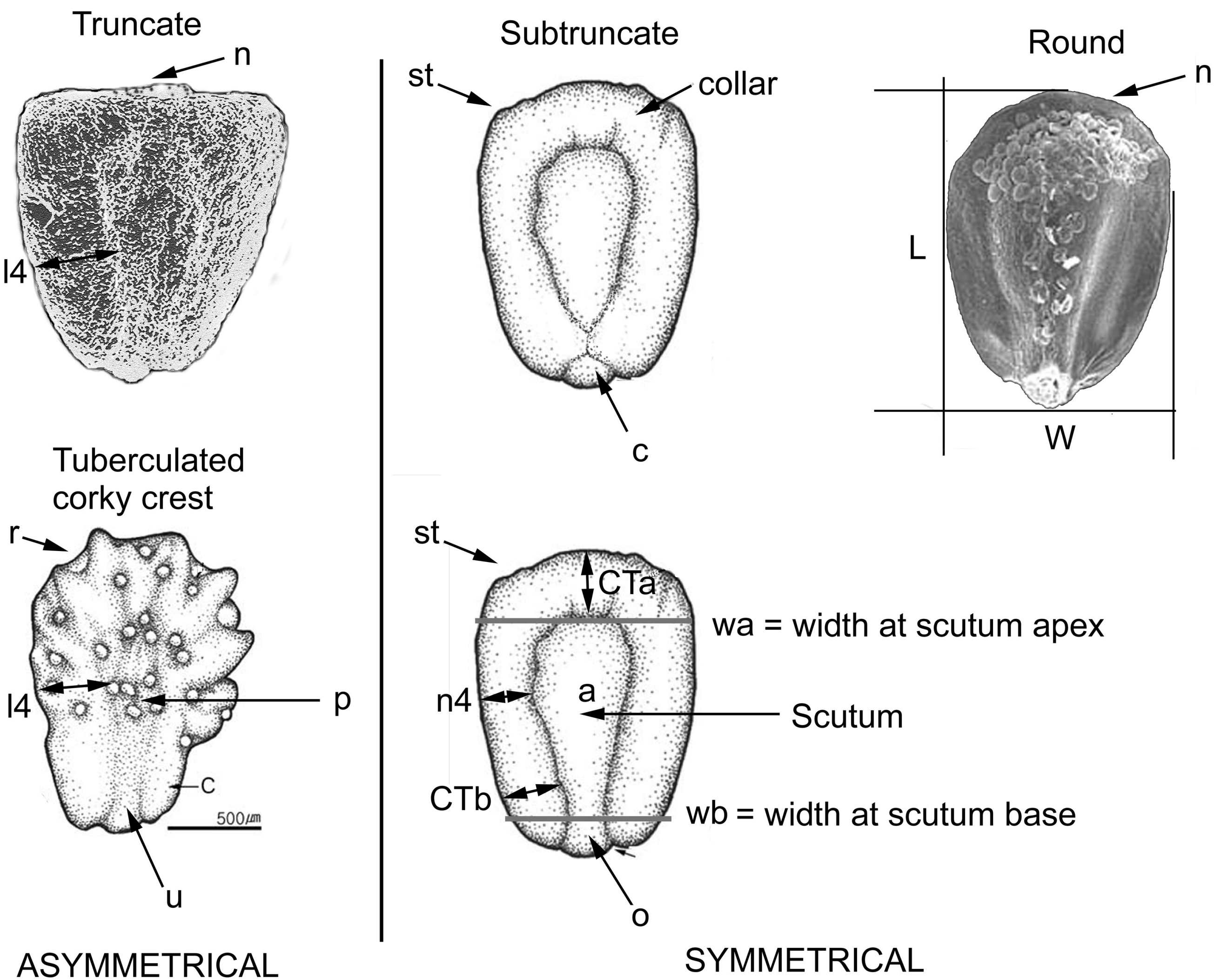
Name	^{14}C	±	cal BP 1σ	cal BP 2σ
Hd-23867 Ivrea 110 Ring 63-72	11505	26	13388-13308	13425-13279
Hd-23868 Ivrea 109 Ring 21-30	11681	31	13547-13472	13571-13445
Hd-23893 Ivrea 106 Ring 66-75	11665	28	13545-13454	13566-13437



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CTa
wa = width at scutum apex
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Scutum
CTb
wb = width at scutum base
o
Round
n
L
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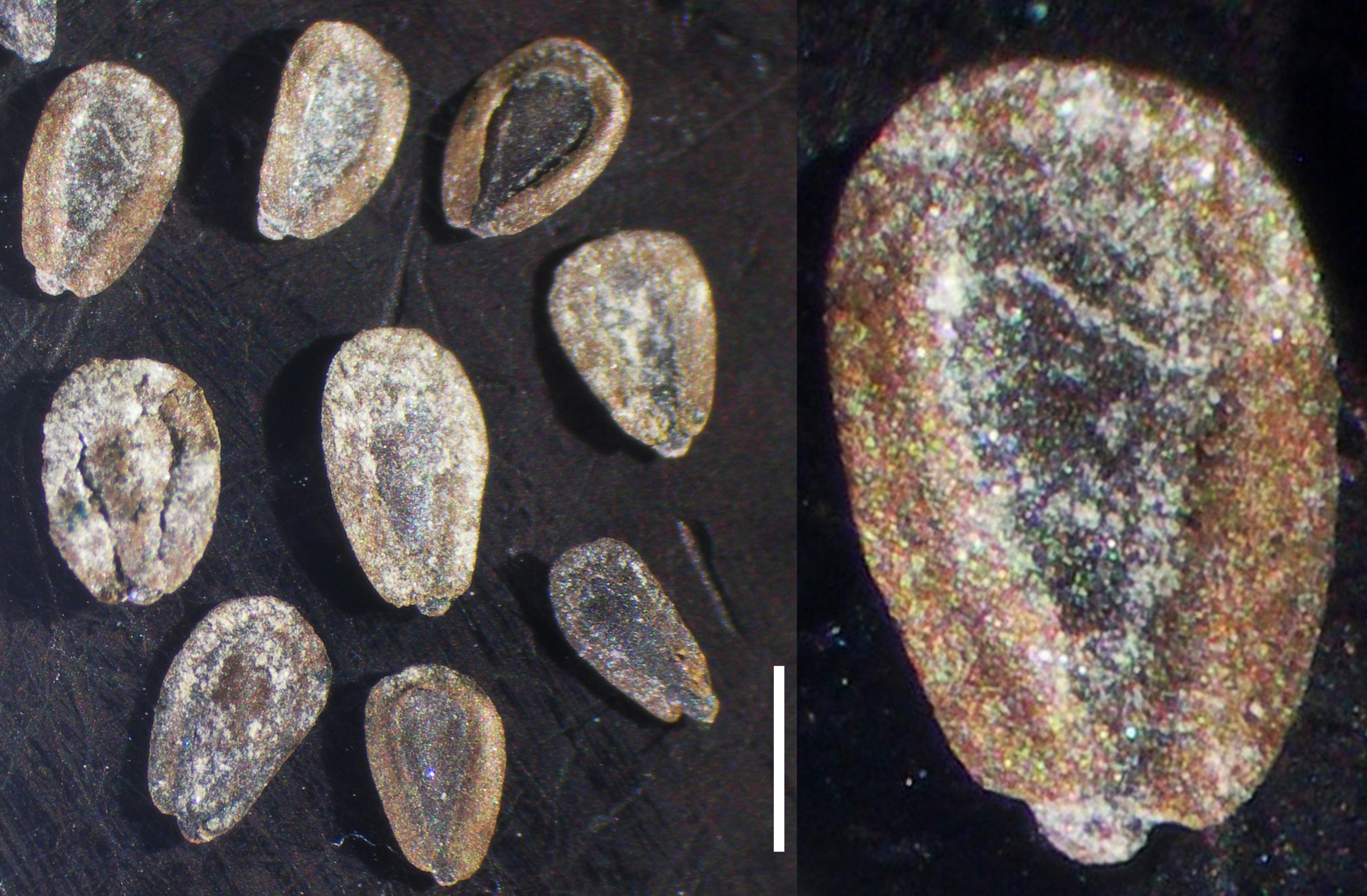
SYMMETRICAL


0,5 mm
500 µm



Site Nr.	Site ID	Site name	Region	Northing	Easting	Elev. (m a.s.l.)	Site type	Age	Stage	Nr. rem.	Con.	CENOFITA samples	Nutlet type	Tentative determination	Publication/report
1	NPI-CV3	**Ca' Viettone**	Piemonte	45°19'24"	7°36'37"	350	wetland	range 4.0 to 3.6 Ma	Zanclean	15	/	CCN2406	*L. americanus* -type	L. cf. americanus	Martinetto 1995
2	NPI-BG4	**Sento-S8-Parella**	Piemonte	45°25'01"	7°47'27"	340	sea-coast wetland	uncertain: 4.0 to 3.6 Ma	Zanclean	1	/	CCN2415	indeterminable (no collar)	*Lycopus* sp.	Basilici et al. 1997
3	NPI-BG3	**Sento-S9-Parella**	Piemonte	45°25'01"	7°47'27"	345	sea-coast wetland	uncertain: 4.0 to 3.6 Ma	Zanclean	2	/	CCN2416	indeterminable (no collar)	*Lycopus* sp.	Basilici et al. 1997
4	NPI-BA2	**Baldichieri d'Asti-Fornace**	Piemonte	44°54'27"	8°6'02"	160	shallow sea	uncertain: 4.0 to 3.0 Ma	late Zan. or early Pia.	3	/	CCN2399	indeterminable (no collar)	*Lycopus* sp.	Martinetto 1995
5	NPI-DU23	**Dunarobba-CN**	Umbria	42°40'00"	12°27'25"	400	lake delta	uncertain: 3.6 to 2.6 Ma	Piacenzian?	1	/	CCN2396	indeterminable (no collar)	*Lycopus* sp.	Martinetto et al. 2014
6	NPI-DU10	**Dunarobba-FF**	Umbria	42°39'46"	12°27'47"	395	wetland	uncertain: 3.6 to 2.6 Ma	Piacenzian?	1	/	CCN2397	cf. *Melissa*	cf. *Melissa*	Martinetto 1994b
7	NPI-CE1	**Ceresole d'Alba**	Piemonte	44°47'31"	7°49'36"	282	wetland	3.6 to 2.6 Ma	Piacenzian	1	/	CCN2403	indeterminable. (no variation)	*Lycopus* sp.	Ciangherotti et al. 2007
8	NPI-GA8	**Castelletto Cervo I**	Piemonte	45°30'20"	8°13'59"	185	river channel	uncertain: 3.6 to 2.6 Ma	Piacenzian	1	/	CCN2411	indeterminable. (no variation)	*Lycopus* sp.	unpubl.
9	NPI-RDB1	**Villafranca d'Asti-RDB Quarry**	Piemonte	44°54'54"	7°47'27"	200	wetland	ca. 3.2 Ma	Piacenzian	3	/	CCN2413	*L. americanus* -type	*L.* cf. *americanus*	Martinetto 1995
9	NPI-RDB6	**Villafranca d'Asti-RDB Quarry**	Piemonte	44°54'54"	7°47'27"	200	wetland	ca. 3.2 Ma	Piacenzian	1	/	CCN2414	*L. americanus* -type	*L.* cf. *americanus*	Martinetto 1995
10	NPI-STU	**Stura di Lanzo-Nole Canavese**	Piemonte	45°13'03"	7°33'45"	333	wetland	ca. 3.1 Ma	Piacenzian	30	/	CCN2417	*L. americanus* -type	*L.* cf. *americanus*	Martinetto 1994a
11	NPI-LC2	**La Cassa**	Piemonte	44°11'18"	7°31'36"	320	wetland	ca. 3.1 Ma	Piacenzian	1	/	CCN2412	indeterminable. (no variation)	*Lycopus* sp.	Martinetto 1995
12	NPI-BU21	**Buronzo**	Piemonte	45°30'06"	8°13'58"	180	river channel	uncertain: 2.6 to 1.8 Ma	Gelasian	1	/	CCN2400	indeterminable. (no variation)	*Lycopus* sp.	Martinetto & Festa 2013
13	NPI-GA21	**Castelletto Cervo II**	Piemonte	45°30'19"	8°13'53"	185	river channel	uncertain: 2.6 to 2.0 Ma	Gelasian	3	/	CCN2407	*L. americanus* -type	*L.* cf. *americanus*	Cavallo & Martinetto 2001
13	NPI-GA5	**Castelletto Cervo II**	Piemonte	45°30'20"	8°13'59"	185	river channel	uncertain: 2.6 to 2.0 Ma	Gelasian	2	/	CCN2408	*L. americanus* -type	*L.* cf. *americanus*	Cavallo & Martinetto 2001
13	NPI-GA5	**Castelletto Cervo II**	Piemonte	45°30'20"	8°13'59"	185	river channel	uncertain: 2.6 to 2.0 Ma	Gelasian	1	/	CCN2409	*L. americanus* -type	*L.* cf. *americanus*	Cavallo & Martinetto 2001
13	NPI-GA5	**Castelletto Cervo II**	Piemonte	45°30'20"	8°13'59"	185	river channel	uncertain: 2.6 to 2.0 Ma	Gelasian	1	/	CCN2410	*L. americanus* -type	*L.* cf. *americanus*	Cavallo & Martinetto 2001
14	NLO-CG2	**Casnigo**	Lombardia	45°48'41"	9°51'40"	405	wetland	2.0 to 1.8 Ma	Gelasian	1	/	CCN2405	indeterminable. (no variation)	*Lycopus* sp.	unpubl.
15	NLO-VGT2	**Villa Giuseppina-Leffe**	Lombardia	45°48'23"	9°52'19"	440	lake margin	1.7 to 1.4 Ma	Calabrian	1	/	CCN2398	indeterminable (no collar)	*Lycopus* sp.	unpubl.
16	CUM-PF2	**Pietrafitta**	Umbria	42°59'31"	12°10'44"	230	lake	1.7 to 1.4 Ma	Calabrian	1	/	CCN2418	indeterminable (no variation)	*Lycopus* sp.	Martinetto et al. 2014
17	NVE-STG2	**Steggio**	Veneto	45°50'45"	11°52'00"	325	lake and river channel	1.8 to 0.8 Ma	Calabrian	3	/	CCN7998	indeterminable (no variation)	*Lycopus* sp.	Ghiotto 2010
18	NLO-BVC3	**Pianico Sellere**	Lombardia	45°48'52"	10°02'16"	300	lake	c. 0.8 Ma	Middle Pleistocene	3	3.7	CCN 5817	indeterminable (no variation)	*Lycopus* sp.	Martinetto 2009; Vassio 2012
19	CTO-BUT1	**Cava Butteri-Arezzo**	Toscana	43°29'13"	11°50'01"	230	river	ca 0.1-0.2 Ma	interstadial/interglacial period before MIS 6 or interglacial 5	9	1.1	CCN 5967	*L. europaeus* -type	*L. europaeus*	Vassio 2012
20	CTO-BCN1	**Cava Campitello-Bucine**	Toscana	43°29'12"	11°36'36"	235	river	c. 0.1-0.2 Ma	interstadial period before MIS 6	18	6.0	CCN 6043	*L. europaeus* -type	*L. europaeus*	Vassio 2012
20	CTO-BCN1	**Cava Campitello-Bucine**	Toscana	43°29'12"	11°36'36"	235	river	c. 0.1-0.2 Ma	interstadial period before MIS 6	31	15.5	CCN 6110	*L. europaeus* -type	*L. europaeus*	Vassio 2012
21	CTO-CLV1	**Cava Le Vigne-Bucine**	Toscana	43°29'43"	11°36'13"	187	river	c. 0.1-0.2 Ma	interstadial period before MIS 6	2	6.7	CCN 6122	indeterminable (no collar)	*L.* cf. *europaeus* (nutlet outline)	Vassio 2012
22	NPI-CGE1	**Cave Germaire-Carmagnola**	Piemonte	44°51'44"	7°40'14"	210	peat bog	0.05-0.13 Ma	a cold period within the Late Pleistocene	2	4.0	CCN 6307	indeterminable (no collar)	*L.* cf. *europaeus* (nutlet outline)	Vassio 2012
23	NPI-CLB1	**Colombari-Parella**	Piemonte	45°24'56"	7°48'53"	240	peat bog	c. 13400 cal. BP	Late Pleistocene	21	7.0	CCN 6381	*L. europaeus* -type	*L. europaeus*	Vassio 2012

Site Nr.	Site ID	Site name	Region	Northing	Easting	Elev. (m a.s.l.)	Site type	Stage or period-culture	Age (century)	Nr. rem.	Con.	Nutlet type	Tentative determination	Lab. Code	Publication/report
24	NPI-CAT1	**Castiglione Torinese**	Piemonte	45°07'11"	7°49'05"	200	river	Holocene	Holocene, not dated	3	<1	*L. europaeus* -type	*L. europaeus*	DST-TO	Vassio 2012
25	NPI-RV1	**Garosso di Rivalta**	Piemonte	45°03'00"	7°30'27"	350	foot of a hill slope	recent warm phase of the Holocene	Holocene, not dated	26	13	*L. europaeus* -type	*L. europaeus*	DST-TO	Vassio 2012
26	NLO61	**Isolino di Varese**	Lombardia	45°49'00"	8°43'00"	238	pile dwelling	Early Neolithic	ca 50 BC	2	4	not suitable for revision: no collar	*L. cf. europaeus*	LA-MC-CO	Castiglioni & Rottoli 2000; Banchieri & Rottoli 2009
27	NLI49	**Albisola Marina**	Liguria	44°20'06"	08°30'44"	6	wetland	Early-Middle Neolithic	VI millenium BC cal.	3	nn	*L. europaeus* -type	*L. europaeus*	MAF-SV, UniTO-TO	Arobba et al. 2016 (in c.d.s.)
28	NLI46	**Genova - Piazza della Vittoria**	Liguria	44°24'12"	08°56'47"	14	wetland	Middle Neolithic	VI-V millenium BC cal.	39	nn	*L. europaeus* -type	*L. europaeus*	MAF-SV	Arobba et al. 2001
29	NLO21	**Polpenazze del Garda - Lucone D**	Lombardia	45°32'53"	10°29'40"	249	pile-dwelling	Early Bronze Age	21-18 BC	354	4	*L. europaeus* -type	*L. europaeus*	IPNA-CH, LPP-CNR-IDPA-MI	Perego 2015
30	NLO28	**Lavagnone**	Lombardia	45°26'13"	10°32'17"	101	pile-dwelling	Early Bronze Age	21-16 BC	274	12	*L. europaeus* -type	*L. europaeus*	IPNA-CH, LPP-CNR-IDPA-MI	Perego 2015
30	NLO28	**Lavagnone**	Lombardia	45°26'13"	10°32'17"	101	pile-dwelling	Middle Bronze Age	16-14 BC	103	2	*L. europaeus* -type	*L. europaeus*	IPNA-CH, LPP-CNR-IDPA-MI	Perego 2015
31	NTR35	**Fiavé**	Trentino Alto Adige	46°00'16"	10°50'32"	660	pile dwelling	Middle Bronze Age	17-14 BC	?	nn	not suitable for revision: no collar	*L. cf. europaeus*	LA-MC-CO	Rottoli unpublished; Schweingruber 1984
32	NER79	**Noceto - Vasca votiva**	Emilia Romagna	44°48'03"	10°10'19"	81	settlement	Middle Bronze Age	15-14 BC	4	1	not suitable for revision: no collar	*L. cf. europaeus*	LA-MC-CO	Aceti et al. 2009; Castiglioni et al. 2009; Rottoli & Castiglioni 2009
33	NLO42	**Castellaro del Vhò di Piadena**	Lombardia	45°07'46"	10°23'05"	21	pile dwelling	Middle Bronze Age/Late Bronze Age	15-13 BC	?	nn	not suitable for revision: no collar	*L. cf. europaeus*	LA-MC-CO, LPP-CNR-IDPA-MI	Rottoli 1997, 2001; Ravazzi & Valsecchi 2001
34	NVE9	**Padova - Palazzo Roccabonella**	Veneto	45° 24' 22"	11° 42' 54"	22	urban settlement	Bronze age/Iron Age	10-9 BC	5	2	not suitable for revision: no collar	L. cf. europaeus	UniPD-PD	Maritan 2012
35	NVE47	**Fondo Paviani - Vangadizza**	Veneto	45°05'40"	11°18'11"	?	pile dwelling	Late Bronze Age	13-12 BC	3	30	not suitable for revision: no collar	*L. cf. europaeus*	LA-MC-CO	Berto 2013
36	NLO67	**Teglio - Meden**	Lombardia	46°10'00"	10°04'00"	840	peat bog	Late Bronze Age/Iron Age	11-9 BC	?	nn	not suitable for revision: no collar	*L. cf. europaeus*	LA-MC-CO	Castiglioni & Rottoli 2015
37	NVE57	**Altino - Canale CNS-1bis**	Veneto	45° 52' 60"	12° 23' 41"	1	urban settlement	Bronze Age/Iron age/Roman Age	10-3 BC	79	11	*L. europaeus* -type + *L. americanus* -type (rare)	*L. europaeus*	UniPD-PD	Maritan, unpublished data
38	NFV20	**Aquileia - Ex Essiccatoio**	Friuli Venezia Giulia	45°46'19"	13°21'58"	1	settlement	Iron Age/Roman Age	8-7 BC and 1BC	11	<1	not suitable for revision: no collar	*L. cf. europaeus*	LA-MC-CO	Maselli Scotti & Rottoli 2007
39	NER80	**Parma - piazza Garibaldi**	Emilia Romagna	44°48'05"	10°19'41"	55	rural settlement	Republica Age	3-2 BC	7	4	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2011
40	NER57	**Modena - ex Cinema Capitol1**	Emilia Romagna	44°38'41"	10°55'41"	34	urban *domus*	Republica Age	3-2 BC	278	1	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2015
40	NER57	**Modena - ex Cinema Capitol2**	Emilia Romagna	44°38'41"	10°55'41"	34	urban *domus*	Republica Age	2-1 BC	77	<1	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2015
41	NVE10	**Montegrotto - via Neroniana**	Veneto	45°19'23"	11°47'34"	11	villa foundations	Republican/Imperial Age	1 BC - 1 AD	37	231	not suitable for revision: no collar	*L. cf. europaeus*	UniPD-PD	Maritan 2012
42	NER53	**Modena - area Novi Sad 1**	Emilia Romagna	44°39'03"	10°55'23"	32	sub-urban settlement	Republican/Imperial Age	1 BC - 1 AD	338	8	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2015
42	NER53	**Modena - area Novi Sad 3**	Emilia Romagna	44°39'03"	10°55'23"	32	sub-urban settlement	Republican/Imperial Age	1 BC - 1 AD	1191	92	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2017
43	NER56	**Modena - ex Cassa Risparmio**	Emilia Romagna	44°38'44"	10°55'30"	34	urban settlement	Imperial Age	15-40 AD	57	<1	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2017
42	NER53	**Modena - area Novi Sad 2**	Emilia Romagna	44°39'03"	10°55'23"	32	sub-urban settlement	Imperial Age	1-2 AD	164	4	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2015
42	NER53	**Modena - area Novi Sad 4**	Emilia Romagna	44°39'03"	10°55'23"	32	sub-urban settlement	Imperial Age	1-2 AD	32	9	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2017
40	NER57	**Modena - ex Cinema Capitol3**	Emilia Romagna	44°38'41"	10°55'41"	34	urban *domus*	Imperial Age	1-2 AD	13	<1	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2015
44	NER61	**Modena - viale Amendola1**	Emilia Romagna	44°38'00"	10°54'27"	34	aqueduct	Imperial Age	1-2 AD	637	28	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2015
45	NER107	**Modena - ex Manifattura Tabacchi1**	Emilia Romagna	44°39'09"	10°55'45"	31	rural settlement	Imperial Age	1-2 AD	4	<1	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2015
40	NER57	**Modena - ex Cinema Capitol4**	Emilia Romagna	44°38'41"	10°55'41"	34	urban *domus*	Imperial Age	2-3 AD	5	<1	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2015
46	NVE58	**Altino - Canale VR-11**	Veneto	45° 32' 33"	12°24'27"	1	harbour area	Roman/Late Roman	1 BC - 4 AD	11	5	*L. europaeus* -type	*L. europaeus*	UniPD-PD	Maritan, unpublished data
47	NER109	**Classe - condotto idrico**	Emilia Romagna	44°23'21"	12°13'48"	5	harbour	Imperial Age/Late Roman	2-7 AD	4	<1	*L. europaeus* -type	*L. europaeus*	LPP-MO	Triolo 2013/2014
44	NER61	**Modena - viale Amendola2**	Emilia Romagna	44°38'00"	10°54'27"	34	aqueduct	Late Roman	4-5 AD	89	3	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2015
45	NER107	**Modena - ex Manifattura Tabacchi2**	Emilia Romagna	44°39'09"	10°55'45"	31	rural settlement	Late Roman	4-5 AD	85	3	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2015
48	NER59	**Modena - Palazzo Vaccari**	Emilia Romagna	44°38'36"	10°55'58"	34	urban *domus*	Late Roman	5-6 AD	367	46	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2018
49	NER108	**Modena - via Nonatolana (Abitcoop)**	Emilia Romagna	44°39'18"	10°56'52"	30	rural settlement	Late Roman	6 AD	1	<1	*L. europaeus* -type	*L. europaeus*	LPP-MO	Bosi et al. 2017
50	NER102	**Modena - Corso Duomo1**	Emilia Romagna	44°38'49"	10°55'31"	31	urban settlement	Early Medieval	end 7-9 AD	283	1	*L. europaeus* -type	*L. europaeus*	LPP-MO	Marra 2014/2015
51	NER3	**S. Agata - Nuova Geovis**	Emilia Romagna	44°41'10"	11°10'12"	13	rural settlement	Early Medieval/Medieval	7-12 AD	40	1	*L. europaeus* -type	*L. europaeus*	LPP-MO, LPA-SGP-BO	Bosi et al. 2014

52	NVE50	**Nogara - Mulino di sotto**	Veneto	45°10'50"	11°03'28"	18	settlement	Medieval	9-10 AD	6	nn	not suitable for revision: no collar	*L. cf. europaeus*	LA-MC-CO	Castiglioni & Rottoli 2011; Marchesini et al. 2011
53	NER103	**Modena - via Castellaro**	Emilia Romagna	44°38'44"	10°55'35"	31	urban settlement	Medieval	9-11 AD	3	<1	*L. europaeus* - type	*L. europaeus*	LPP-MO	Osti 2012/2013
54	NER104	**Modena - Palazzo Solmi**	Emilia Romagna	44°38'52"	10°55'22"	48	urban settlement	Medieval	10-11 AD	1	<1	*L. europaeus* - type	*L. europaeus*	LPP-MO	Osti 2012/2013
55	NER58	**Modena - Largo S. Francesco**	Emilia Romagna	44°38'37"	10°55'18"	31	urban walls	Medieval	10-11 AD	954	4	*L. europaeus* - type	*L. europaeus*	LPP-MO	Osti 2012/2013
56	NVE59	**Torcello - area N Basilica S. Maria Assunta**	Veneto	45°29'55"	12°25'13"	0	urban settlement	Medieval	10-11 AD	1	3	not suitable for revision: no collar	*L. cf. europaeus*	UniPD-PD	Miola, unpublished data
42	NER53	**Modena - area Novi Sad5**	Emilia Romagna	44°39'03"	10°55'23"	32	woodland	Medieval	11-12 AD	548	11	*L. europaeus* - type	*L. europaeus*	LPP-MO	Montecchi et al. 2017
57	NER34	**Ferrara - corso Porta Reno/via Vaspergolo1**	Emilia Romagna	44°50'03"	11°37'06"	9	vegetable garden (sub-urban)	Medieval	second half 10 - first half 11	11	<1	*L. europaeus* - type	*L. europaeus*	LPP-MO	Cuoghi 2006/2007
57	NER34	**Ferrara - corso Porta Reno/via Vaspergolo2**	Emilia Romagna	44°50'03"	11°37'06"	9	urban settlement	Medieval	second half 11 - first half 12	4	1	*L. europaeus* - type	*L. europaeus*	LPP-MO	Bosi 2000
58	NER54	**Modena - Vescovado**	Emilia Romagna	44°38'47"	10°55'29"	31	bishop palace	Medieval	12-13 AD	2719	45	*L. europaeus* - type	*L. europaeus*	LPP-MO	Benatti et al. 2011
59	NER41	**Argenta - via Vinarola/via Aleotti**	Emilia Romagna	44°37'55"	11°50'01"	5	urban settlement	Late Medieval	13-14 AD	188	4	*L. europaeus* - type	*L. europaeus*	LPP-MO	Bandini Mazzanti et al. 1999
57	NER34	**Ferrara - corso Porta Reno/via Vaspergolo3**	Emilia Romagna	44°50'03"	11°37'06"	9	urban gardens	Late Medieval/Renaissance	13 - beginning 15	10	2	*L. europaeus* - type	*L. europaeus*	LPP-MO	Bosi 2000
60	NER105	**Modena - via Rismondo**	Emilia Romagna	44°38'53"	10°55'35"	31	urban settlement	Renaissance/Modern	16-17 AD	2	10	*L. europaeus* - type	*L. europaeus*	LPP-MO	Osti 2012/2013
61	NPI-SBC	**San Benigno Canavese-OC1**	Piemonte	45°13'25"	7°48'46"	200	pond in abandoned river channel	Modern	20th century, Holocene	36	24	*L. europaeus* - type	*L. europaeus*	DST-TO	Vassio 2012

Species	L. mm [min (mean) max]	W. mm [min (mean) max]	L:W [mean]	NA	AO	CS	SY	CT	SC	wa/wb	Morph. type	Moon-Hong type	Data from:
L. coreanus	1.10 (1.20) 1.50	0.80 (0.93) 1.20	1.3	n	st	o	s	n4	a	1.8	americanus	4	Moon & Hong (2006) + Son et al. (2016b)
L. americanus	0.9 (1.1) 1.4	0.7 (0.8) 1.0	1.4	n	r/st	o	s	n4	a	1.5-1.8	americanus	4	US2814056—USA. Michigan, October 1963.
L. americanus	1.00 (1.14) 1.40	0.70 (0.78) 0.95	1.4	n	r	o	s	n4/n5	a	1.5	americanus	4	Moon & Hong (2006)
L. exaltatus	1.3 (1.5) 1.8	0.9 (1.0) 1.2	1.5	n	t/r	o	s	n4/n5	a	1.5-2.0	americanus	4	Moon & Hong (2006)
L. exaltatus	1.2 (1.5) 1.9	0.9 (1.0) 1.2	1.5	n	t/r	o	s	n4/n5	a	1.5-1.9	americanus	4	MCC1335—NORTHWEST ITALY. Botanical Garden of Torino, cultivated, June 1990
L. exaltatus	1.3 (1.5) 1.8	0.9 (1.0) 1.2	1.5	n	t/r	o	s	n4/n5	a	1.5-2.0	americanus	4	MCC2548—CENTRAL ITALY. Pisa, Tuscany, right bank of the Arno river, spontaneous, October 1983
Fossil NPI-CV3	1.3 (1.5) 1.7	0.6 (0.8) 1.1	1.4	n	r	o	s	n4	a	1.5-2.0	americanus	4	Ca' Viettone, sample CCN2406
L. asper	1.80 (1.97) 2.30	1.40 (1.51) 1.90	1.1	n	t	o	a	l4	p	1.6-1.7	asper	4	Moon & Hong (2006)
L. australis	1.60 (1.93) 2.20	1.00 (1.25) 1.50	1.5	n	r	o	s	l4	a	1.2	australis	4	Moon & Hong (2006)
L. europaeus	1.5 (1.5) 1.8	1.1 (1.1) 1.4	1.2	n	t	c/o	s	n4	a	1.0-1.5	europaeus	2	Moon & Hong (2006)
L. europaeus	0.9 (1.1) 1.3	0.7 (0.9) 1.0	1.2	n	st	c (o)	s	n4	a	1.2-1.8	europaeus	2	MCC2547—NORTHWEST ITALY. Ternavasso, Poirino, province of Torino, spontaneous in a fish pond, October 2013
L. europaeus	0.9 (1.0) 1.1	0.6 (0.8) 0.9	1.2	n	st/t	o	s	l4/n4	a	1.2-1.5	europaeus	2	MCC0708—EAST FRANCE. Sessenheim, Alsace, spontaneous, July 1990
L. maackianus	0.9 (1.3) 1.5	0.7 (0.9) 1.1	1.2	n	st/t	o/c	s/a	l4	a	1.5	europaeus	4	Moon & Hong (2006) + http://www.seedbank.re.kr/detail.php?seed=2627
Fossil NVE58	1.0 (1.1) 1.3	0.6 (0.8) 1.0	1.4	n	t	c/o	s	n4	a	1.3-1.8	europaeus	2	Altino-Canale VR-11
L. laurentianus	1.10 (1.22) 1.35	0.85 (0.92) 1.05	1.5	n	st	o	a	n5	p	1.7	laurentianus	4	Moon & Hong (2006)
L. lucidus	2.00 (2.12) 2.85	1.20 (1.25) 1.80	1.7	n	r	c	s	n4	p	1.2-1.4	lucidus	2	Moon & Hong (2006)
L. charkeviczii	2.3-3.0	1.0-1.5	2.0	t	/	/	a/s	n4	a	/	charkeviczii	/	Son et al. 2016
L. "parviflorus" (= *L. uniflorus* ?)	1.60 (1.64) 1.85	1.20 (1.25) 1.50	1.3	t	r	o	a	l4	a	2.2	charkeviczii/virginicus	1	Moon & Hong (2006)
L. uniflorus	1.35 (1.45) 1.75	1.00 (1.12) 1.55	1.3	t	t	u	a	/	p	2.1	virginicus	3	Moon & Hong (2006)
L. angustifolius	1.00 (1.05) 1.40	0.80 (0.89) 1.10	1.1	t	t	u	a	l4	p	1.6	virginicus	1	Moon & Hong (2006)
L. virginicus	1.20 (1.38) 1.50	1.05 (1.06) 1.20	1.4	t	t	o	a	l4	p	1.8	virginicus	1	Moon & Hong (2006)
L. cokeri	1.40 (1.49) 1.70	0.80 (0.93) 1.10	1.6	t	t	o	a	l4	p	1.6-1.8	virginicus	3	Moon & Hong (2006)
L. amplectens	?	?	1.2	t	t	o	a	l4/n4	p	1.9	virginicus	rev. needed	Henderson (1962)
L. rubellus	?	?	1.2	t	r	?	a	n4	p	2	virginicus	rev. needed	Henderson (1962)
L. alissoriae	characters unknown. NE Asian microendemic species												The Plant List (2013)
L. cavalerei	characters unknown. possibly synonym of L. coreanus												Son et al. 2016b
L. kurilensis	characters unknown. NE Asian microendemic species												The Plant List (2013)
L. sichotensis	characters unknown. NE Asian microendemic species												The Plant List (2013)

Sample or Site ID	**Locality**	**Age BP**	**NN**	**Small L:W**	**Large L:W**	**ASC**	**CR**	**OT**	**CC**	**CO**	**SC**	**UC**	**wa≈wb**	**wb < 2/3 wa**	**wb < 1/2 wa**	**Determination**
MCC2547	Ternavasso, Italy	0	100	F	A	F	P	P	F	P	F	A	F	P	A	*L. europaeus*
MCC0708	Sessenheim, France	0	100	F	A	F	P	P	A	F	F	A	F	P	A	*L. europaeus*
MCC1335	Torino, Italy	0	50	P	F	P	F	A	A	F	A	F	A	F	P	*L. exaltatus*
MCC2548	Pisa, Italy	0	100	A	F	P	F	P	A	F	A	F	A	F	P	*L. exaltatus*
US2814056	Michigan, USA	0	40	A	F	P	F	A	P	F	F	A	A	F	P	*L. americanus*
image from USDA plants database	Idaho, USA	0	6	A	F	P	F	A	P	F	F	A	A	F	P	*L. americanus*
image from Illinois Nat. Hist. Surv.	Illinois, USA	0	9	A	F	P	F	A	P	F	F	A	A	F	P	*L. americanus*
NPI-CV3	Ca' Viettone	4.0-3.5 Ma	8	P	F	P	F	A	P	F	F	A	P	F	P	*L.* cf. *americanus*
NPI-STU	Stura di Lanzo	3.1 Ma	47	P	F	P	F	A	P	F	F	A	P	F	P	*L.* cf. *americanus*
NPI-GA5,21	Castelletto Cervo II	2.6-2.0 Ma	5	F	P	P	F	A	A	F	F	A	A	P	A	*L.* cf. *americanus*
NVE-STG2	Steggio	1.8-0.8 Ma	2	/	P	P	P	/	/	P	P	/	/	P	/	*L.* sp.
CUM-PF2	Pietrafitta	ca. 1.5-1.3 Ma	1	P	/	P	/	P	/	P	P	/	/	P	/	*L.* sp.
CTO-BCN1	Cava Campitello	100-200 ka	22	F	A	F	P	P	F	P	F	A	F	P	A (1!)	*L. europaeus*
CTO-BUT	Cava Butteri	100-200 ka	5	F	A	F	P	P	F	P	F	A	F	P	A	*L. europaeus*
NPI-CLB1	Colombari	11 ka	18	F	A	F	P	P	F	P	F	A	F	P	A	*L. europaeus*
NPI-RV1	Garosso di Rivalta	10-1 ka	14	F	A	F	P	P	F	P	F	A	F	P	A	*L. europaeus*
NPI-CAT1	Castiglione Torinese	10-1 ka	3	F	A	F	P	P	F	P	F	A	F	P	A	*L. europaeus*
NVE57	Altino	3.0-2.2 ka	7	F	A	F	P	P	P	F	F	A	F	P	A	*L. europaeus*
NPI-SBC	San Benigno Canavese, Italy	0	36	F	A	F	P	P	F	P	F	A	F	P	A	*L. europaeus*