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

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Abstract

Lycopus is a widespread herbaceous plant, currently part of European flora. Fossil remains of fruits (nutlets or mericarps) attributed to this genus are frequently found in European archaeological and palaeontological sites, being easily preserved in sedimentary deposits. In a worldwide context, the oldest fossils are from the early Oligocene (ca. 30 Ma) of West Siberia, but they become more common in Miocene (23.0–5.3 Ma) records, ranging from West Siberia to Central Europe. In the literature, the Oligocene and Miocene remains (plus a few Pliocene ones) were assigned to fossil-species, whereas the abundant Pliocene and Pleistocene occurrences (5–0.01 Ma) in Europe were mainly assigned to the extant species *L. europaeus*. The present work is conceived as the result of an *ad hoc* research team whose task was to revise and summarize the Italian fossil record of *Lycopus*, assembling palaeobotanical and archaeobotanical data. We herein report ca. 6000 *Lycopus* nutlets from 61 sites located in nine regions of Northern and Central Italy. Based on the available information on extant species, we detected nine morphological types of nutlets that can be used for the characterisation of fossils. Our analysis suggests that from 4 to 2.6 Ma a single taxon (*L.* cf. *pliocenicus*) with *L. americanus*-type of nutlets occurred in Italy. The first occurrence of the latter morphological type is from the early Oligocene of West Siberia. The available fossils mildly suggest that extant *L. americanus* could be the descendant of ancient Eurasian plants characterised by the *L. americanus*-type of nutlets, through

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expansion of their range to North America. Conversely, the abundant Italian records of the last 0.2 Ma, including remains from archaeological sites, are only referable to the Eurasian species *L. europaeus.*

Keywords: Cenozoic, fruits, Holocene, morphology, palaeontological collections, Quaternary

Introduction

Research in the fields of botany and palaeobotany, besides phytogeography, used to develop in parallel during the last 30 years, sometimes with poor interchanges (Rull 2014, Marignani *et al.* 2017). Jiménez-Mejías *et al.* (2016) noted that, for the study of the genus *Carex*, many botanists tended to neglect the existing knowledge about the fossil record, almost ignoring the huge information potentially available in several palaeobotanical collections (e.g., Dorofeev 1963a, 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 & Sytsma 2012). Part of the problem of incommunicability rises from the difficulty in extrapolating the necessary information about fossils, as material is often published in papers without English descriptions (e.g., Nikitin 1948, Dorofeev 1963a, Velichkevich 1973, Nikitin 2006). 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 summarising the fossil record of specific taxa of the extant flora (e.g., Jiménez-Mejías *et al.* 2016), which indeed contribute to overcome this disconnection between botanists and palaeobotanists. Late Quaternary fossil records are also crucial in this sense, and in Italy the Botanical Records Archaeobotany Italian Network (BRAIN; http://brainplants.successoterra.net/) can quickly provide data on specific extant taxa to be integrated with palaeobotanical data from deeper time. Until now, in Italy, archaeo- and palaeobotanical data have been rarely summed up together and the record of the evolutionary history of the Italian flora resulted in this way fragmented within different works. This is far more inconvenient because the plant fossil record of the last 6 million years is less discontinuous in Italy than in other European countries, as recently shown for different chronologies and plant parts by Bertini (2010), Kustatscher *et al.* (2014), Mercuri *et al.* (2015), Combourieu-Nebout *et al.* (2015) and Martinetto (2015). This work is conceived as a first step in combining palaeobotanical and archaeobotanical data of the Italian fossil record, starting from a selected, still extant, plant taxon. The analysis was extended to Eurasian and global scales, when needed, as for example in the examination of taxonomic and phylogenetic issues, for which a country-scale analysis is not meaningful, and the contribution of non-Italian fossils cannot be ruled out.

Disentangling the taxonomy of fossils of the genus *Lycopus* Linnaeus (1753: 21), provides a suitable study case to engage our combined approach. The phylogenetic placement of this genus is well-assessed and its divergence from the most closely related genera is attributed, on a molecular basis, to relatively deep times (ca. 35 million years ago = Ma; Drew & Sytsma 2012). Several fossil fruits reported from Europe have not been included in the phylogenetic analysis of Drew & Sytsma (2012), but the Oligocene date of a fossil, reported by Mai (1985), was cited in support to the long phylogenetic stem of *Lycopus*. Both Govaerts (2020) and The Plant List Ver.1.1 (2013; http://www.theplantlist.org) reported 19 accepted species names for *Lycopus* (excluding hybrids and unresolved names), whereas Moon & Hong (2006) considered *Lycopus* as consisting of "approximately 16 species". The geographic distribution of this genus covers most of the Northern Hemisphere, and only 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 reported (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 last species was introduced at the beginning of the 21st century from eastern Asia. Historically, Briquet (1896) recognised two sections within *Lycopus*, sect. *Stoloniferi* Briquet (1896: 316) and sect. *Astolonosi* Briquet (1896: 317), the latter with only one species, *L. americanus* Muhlenberg ex Barton (1815: 15). The two sections are distinguishable mainly by the presence/absence of long runners from the lower nodes of the stem. Briquet's infrageneric classification, however, was not followed by Henderson (1962) nor by Moon & Hong (2006), who identified four groups of species, without systematic implications, based on nutlet (= mericarp) morphology and anatomy. According to Drew & Sytsma (2012), the presence of only two stamens, a unique pericarp structure (Ryding 2010), and a very long branch in both cpDNA and nrDNA support a subtribal status for *Lycopus* [Lycopinae Drew & Sytsma (2012: 945)].

The fossil record of *Lycopus* is mainly represented by nutlets, whose preservation is possible in those sedimentary deposits in which scarce to moderate decay of the organic matter occurs, especially in waterlogged palaeoenvironments. On the contrary, pollen grains in the sediments cannot be easily discriminated under the light microscope, thus they are commonly included in the *Mentha*-type or in undifferentiated hexacolpate grains of Lamiaceae (Beug 2004, Martinetto & Macaluso 2018).

Several authors (e.g., Reid 1920, Nikitin 1948, Dorofeev 1963, Velichkevich 1973, Mai & Walther 1988, Łańcucka-Środoniowa 1979, Martinetto 1994a, Mai 2000, 2001, Nikitin 2006) reported fossil fruits attributed to *Lycopus* in Europe and West Asia: from the oldest, early Oligocene (ca. 30 Ma) nutlets of West Siberia (Nikitin 2006), through more common Miocene (23.0–5.3 Ma) records, ranging from West Siberia and Northern Kazakhstan to Central Europe, and to the abundant Pliocene and Pleistocene occurrences (5.33–0.01 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 extant species *L. europaeus,* whereas Oligocene and Miocene records (plus a few Pliocene ones) were assigned to the fossil-species *L. antiquus* E.M. Reid (1920: 76). Additionally, Nikitin (2006: 42) suggested the presence of up to five undescribed fossil-species in the Oligocene and Miocene of West Siberia, and three fossil-species with characteristic morphology were described in the late Cenozoic of Eastern Europe: *L. cholmechensis* Wieliczkiewicz & Zastawniak (2003: 200), *L. europleistocenicus* Doweld (2018: 82) and *L. pliocenicus* Dorofeev (1987: 69).

This paper presents the inventory of fossil remains of *Lycopus* recorded in Italy (Fig. 1) from deposits dated to the last 5 million years (Tab. 1, Tab. 2), i.e. from early Pliocene to late Holocene. Fossil nutlets of this genus are herein selected for a combined palaeo- and archaeobotanical approach, because the morphology of the nutlets is well-studied, being one of the most diagnostic characters for the identification of the species, even in extant plants (Henderson 1962). The morphological analysis of the Italian fossil nutlets was carried out to help the species identification in comparison to extant and fossil reference materials. Nevertheless, only some of the characters used for identification of extant nutlets can be detected in fossil specimens. For this reason, a review of fruit morphology was undertaken to verify the accuracy and level of identification.

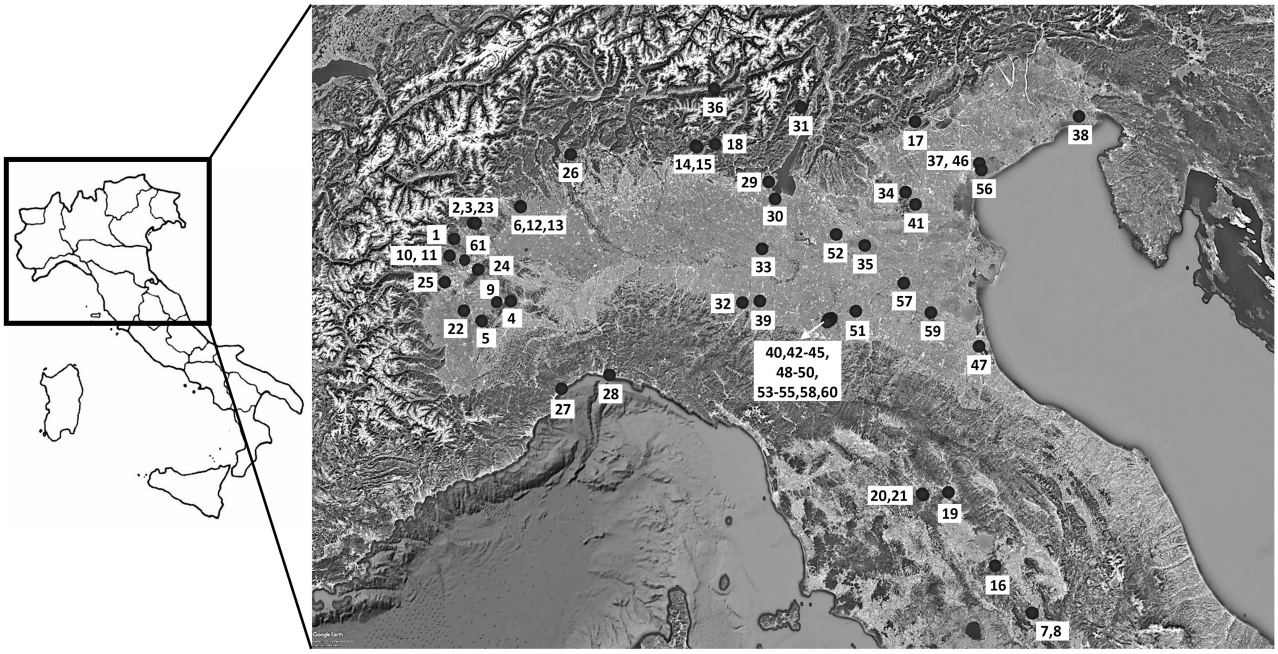

FIGURE 1. Map of Italian fossil localities where *Lycopus* nutlets have been detected. Site numbers are referred to those listed in Tab. 1 and Tab. 2.

TABLE 1. List of Plio-Pleistocene samples of *Lycopus* nutlets with data about localities, 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. The abbreviation "indet." stands for "indeterminabilis", see Sigovini 2016.

Site Nr.	Site ID	Site name	Region	Northing	Easting	Elev. (m a.s.l.)	Site type	Age	Stage	Nr. rem.	Con.	Collection code	Nutlet type	Tentative determination	**Publication/report**
1	NPI-CV3	Ca' Viettone	Piemonte	45°9'24"	7°6'37"	350	wetland	range 4.0 to 3.6 Ma	Zanclean	15	/	CCN2406	*L. americanus*-type	*L.* cf. *pliocenicus*	Martinetto *et al.* 2018
2	NPI-BG4	**Sento-S8-Parella**	Piemonte	45°5'01"	7°7'27"	340	sea-coast wetland	uncertain: 4.0 to 3.6 Ma	Zanclean	1	/	CCN2415	indeterminable (no collar)	*Lycopus* sp. indet.	Basilici *et al.* 1997
3	NPI-BG3	**Sento-S9-Parella**	Piemonte	45°5'01"	7°7'27"	345	sea-coast wetland	uncertain: 4.0 to 3.6 Ma	Zanclean	2	/	CCN2416	indeterminable (no collar)	*Lycopus* sp. indet.	Basilici *et al.* 1997
4	NPI-BA2	**Baldichieri d'Asti-Fornace**	Piemonte	44°4'27"	8°'02"	160	shallow sea	uncertain: 4.0 to 3.0 Ma	late Zan. or early Pia.	3	/	CCN2399	indeterminable (no collar)	*Lycopus* sp. indet.	Martinetto 1995
5	NPI-CE1	**Ceresole d'Alba**	Piemonte	44°7'31"	7°9'36"	282	wetland	3.6 to 2.6 Ma	Piacenzian	1	/	CCN2403	indeterminable (no variation)	*Lycopus* sp. indet.	Ciangherotti *et al.* 2007
6	NPI-GA8	**Castelletto Cervo I**	Piemonte	45°0'20"	8°3'59"	185	river channel	uncertain: 3.6 to 2.6 Ma	Piacenzian	1	/	CCN2411	indeterminable (no variation)	*Lycopus* sp. indet.	unpubl.
7	NPI-DU23	**Dunarobba-CN**	Umbria	42°0'00"	12°7'25"	400	lake delta	uncertain: 3.6 to 2.6 Ma	Piacenzian?	1	/	CCN2396	indeterminable (no collar)	*Lycopus* sp. indet.	Martinetto *et al.* 2014
8	NPI-DU10	**Dunarobba-FF**	Umbria	42°9'46"	12°7'47"	395	wetland	uncertain: 3.6 to 2.6 Ma	Piacenzian?	1	/	CCN2397	not applicable	cf. *Melissa*	Martinetto 1994b (wrong identification as *Lycopus* sp.)
9	NPI-RDB1	**Villafranca d'Asti-RDB Quarry**	Piemonte	44°4'54"	8°01'29"	200	wetland	ca. 3.2 Ma	Piacenzian	3	/	CCN2413	*L. americanus*-type	*L.* cf. *pliocenicus*	Martinetto 1995
9	NPI-RDB6	**Villafranca d'Asti-RDB Quarry**	Piemonte	44°4'54"	8°01'29"	200	wetland	ca. 3.2 Ma	Piacenzian	1	/	CCN2414	*L. americanus*-type	*L.* cf. *pliocenicus*	Martinetto 1995
10	NPI-STU	**Stura di Lanzo-Nole Canavese**	Piemonte	45°3'03"	7°3'45"	333	wetland	ca. 3.1 Ma	Piacenzian	30	/	CCN2417	*L. americanus*-type	*L.* cf. *pliocenicus*	Martinetto 1994a
11	NPI-LC2	**La Cassa**	Piemonte	45°11'18"	7°31'35"	320	wetland	ca. 3.1 Ma	Piacenzian	1	/	CCN2412	indeterminable (no variation)	*Lycopus* sp. indet.	Martinetto 1995
12	NPI-BU21	**Buronzo**	Piemonte	45°0'06"	8°3'58"	180	river channel	uncertain: 2.6 to 1.8 Ma	Gelasian	1	/	CCN2400	indeterminable (no variation)	*Lycopus* sp. indet.	Martinetto & Festa 2013
13	NPI-GA21	**Castelletto Cervo II**	Piemonte	45°0'19"	8°3'53"	185	river channel	uncertain: 2.6 to 2.0 Ma	Gelasian	3	/	CCN2407	possible *L. americanus*-type	*Lycopus* sp. indet.	Cavallo & Martinetto 2001

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TABLE 1. (Continued)

Site Nr.	Site ID	Site name	Region	Northing	Easting	Elev. (m a.s.l.)	Site type	Age	Stage	Nr. rem.	Con.	Collection code	Nutlet type	Tentative determination	**Publication/ report**
13	NPI-GA5	**Castelletto Cervo II**	Piemonte	45°0'20"	8°3'59"	185	river channel	uncertain: 2.6 to 2.0 Ma	Gelasian	2	/	CCN2408	possible *L. americanus*-type	*Lycopus* sp. indet.	Cavallo & Martinetto 2001
13	NPI-GA5	**Castelletto Cervo II**	Piemonte	45°0'20"	8°3'59"	185	river channel	uncertain: 2.6 to 2.0 Ma	Gelasian	1	/	CCN2409	possible *L. americanus*-type	*Lycopus* sp. indet.	Cavallo & Martinetto 2001
13	NPI-GA5	**Castelletto Cervo II**	Piemonte	45°0'20"	8°3'59"	185	river channel	uncertain: 2.6 to 2.0 Ma	Gelasian	1	/	CCN2410	possible *L. americanus*-type	*Lycopus* sp. indet.	Cavallo & Martinetto 2001
14	NLO-CG2	**Casnigo**	Lombardia	45°8'41"	9°1'40"	405	wetland	2.0 to 1.8 Ma	Gelasian	1	/	CCN2405	indeterminable (no variation)	*Lycopus* sp. indet.	unpubl.
15	NLO-VGT2	**Villa Giuseppina-Leffe**	Lombardia	45°8'23"	9°2'19"	440	lake margin	1.7 to 1.4 Ma	Calabrian	1	/	CCN2398	indeterminable (no collar)	*Lycopus* sp. indet.	unpubl.
16	CUM-PF2	**Pietrafitta**	Umbria	42°9'31"	12°0'44"	230	lake	1.7 to 1.4 Ma	Calabrian	1	/	CCN2418	indeterminable (no variation)	*Lycopus* sp. indet.	Martinetto et al. 2014
17	NVE-STG2	**Steggio**	Veneto	45°0'45"	11°2'00"	325	lake and river channel	1.8 to 0.8 Ma	Calabrian	3	/	CCN7998	indeterminable (no variation)	*Lycopus* sp. indet.	Ghiotto 2010
18	NLO-BVC3	**Pianico Sellere**	Lombardia	45°8'52"	10°2'16"	300	lake	c. 0.8 Ma	Middle Pleistocene	3	3.7	CCN5817	indeterminable (no variation)	*Lycopus* sp. indet.	Martinetto 2009; Vassio 2012
19	CTO-BUT1	**Cava Butteri-Arezzo**	Toscana	43°9'13"	11°0'01"	230	river	ca 0.1-0.2 Ma	interstadial/ interglacial period before MIS 6 or interglacial MIS 5	9	1.1	CCN5967	*L. europaeus*-type	*L. europaeus*	Vassio 2012
20	CTO-BCN1	**Cava Campitello-Bucine**	Toscana	43°9'12"	11°6'36"	235	river	c. 0.1-0.2 Ma	interstadial period before MIS 6	18	6.0	CCN6043	*L. europaeus*-type	*L. europaeus*	Vassio 2012
20	CTO-BCN1	**Cava Campitello-Bucine**	Toscana	43°9'12"	11°6'36"	235	river	c. 0.1-0.2 Ma	interstadial period before MIS 6	31	15.5	CCN6110	*L. europaeus*-type	*L. europaeus*	Vassio 2012
21	CTO-CLV1	**Cava Le Vigne-Bucine**	Toscana	43°9'43"	11°6'13"	187	river	c. 0.1-0.2 Ma	interstadial period before MIS 6	2	6.7	CCN6122	indeterminable (no collar)	*Lycopus* sp. indet.	Vassio 2012
22	NPI-CGE1	**Cave Germaire-Carmagnola**	Piemonte	44°1'44"	7°0'14"	210	peat bog	0.05-0.13 Ma	a cold period within the Late Pleistocene	2	4.0	CCN6307	indeterminable (no collar)	*Lycopus* sp. indet.	Vassio 2012
23	NPI-CLB1	**Colombari-Parella**	Piemonte	45°4'56"	7°8'53"	240	peat bog	13600-13200 years cal BP	Late Pleistocene	21	7.0	CCN6381	*L. europaeus*-type	*L. europaeus*	Vassio 2012

TABLE 2. List of Holocene samples of *Lycopus* nutlets with data about localities, 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. Tentative determinations are provided by considering also site-specific data, age and floristic history. Explanation of laboratory codes (**Lab. code**) and repositories of the material: **CCN,** Collezione CENOFITA, Università di Torino; **LA-MC-CO** Laboratorio di Archeobiologia, Musei Civici di Como; **LPA-SGP-BO** Laboratorio di Palinologia e Archeobotanica, C.A.A. Giorgio Nicoli, San Giovanni in Persiceto (Bologna); **LPP -CNR-IDPA-MI** Consiglio Nazionale delle Ricerche, I.D.P.A., c/o DISAT, Università Milano Bicocca; **LPP-MO** Laboratorio di Palinologia e Paleobotanica, Dipartimento di Scienze della Vita, Università di Modena e Reggio Emilia; **MAF-SV** Museo Archeologico del Finalese, Finale Ligure (Savona); **UniPD-PD** Dipartimento di Biologia, Università di Padova; **UniTO-TO** Laboratorio di Palinologia, Dipartimento di Biologia Vegetale, Università di Torino.

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°7’11”	7°9’05”	200	river	Holocene	Holocene, not dated	3	<1	*L. europaeus*-type	*L. europaeus*	CCN	Vassio 2012
25	NPI-RV1	**Garosso di Rivalta**	Piemonte	45°3’00”	7°0’27”	350	foot of a hill slope	recent warm phase of the Holocene	Holocene, not dated	26	13	*L. europaeus*-type	*L. europaeus*	CCN	Vassio 2012
26	NLO61	**Isolino di Varese**	Lombardia	45°9’00”	8°3’00”	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°0’06”	08°0’44”	6	wetland	Early-Middle Neolithic	VI millenium BC cal.	3	nn	*L. europaeus*-type	*L. europaeus*	MAF-SV, UniTO-TO	Arobba et al. 2016
28	NLI46	**Genova - Piazza della Vittoria**	Liguria	44°4’12”	08°6’47”	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°2’53”	10°9’40”	249	pile-dwelling	Early Bronze Age	21-18 BC	354	4	*L. europaeus*-type	*L. europaeus*	LPP-CNR-IDPA-MI	Perego 2015
30	NLO28	**Lavagnone**	Lombardia	45°6’13”	10°2’17”	101	pile-dwelling	Early Bronze Age	21-16 BC	274	12	*L. europaeus*-type	*L. europaeus*	LPP-CNR-IDPA-MI	Perego 2015
30	NLO28	**Lavagnone**	Lombardia	45°6’13”	10°2’17”	101	pile-dwelling	Middle Bronze Age	16-14 BC	103	2	*L. europaeus*-type	*L. europaeus*	LPP-CNR-IDPA-MI	Perego 2015
31	NTR35	**Fiavé**	Trentino Alto Adige	46°0’16”	10°0’32”	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

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TABLE 2. (Continued)

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**
32	NER79	**Noceto - Vasca votiva**	Emilia Romagna	44°8'03"	10°0'19"	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 Vhòdi Piadena**	Lombardia	45°7'46"	10°3'05"	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°5'40"	11°8'11"	?	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°0'00"	10°4'00''	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° 33'00"	12°23' 41"	1	urban settlement	Bronze Age/Iron age/Roman Age	10-3 BC	79	11	*L. europaeus* + *L. americanus*-types	*L. europaeus*	UniPD-PD	Maritan, unpublished data
38	NFV20	**Aquileia - Ex Essiccatoio**	Friuli Venezia Giulia	45°6'19"	13°1'58"	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°9'41"	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°5'41"	34	urban *domus*	Republica Age	3-2 BC	278	1	*L. europaeus*-type	*L. europaeus*	LPP-MO	Bosi et al. 2015

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TABLE 2. (Continued)

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**
40	NER57	**Modena - ex Cinema Capitol2**	Emilia Romagna	44°38'41"	10°5'41"	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°9'23"	11°7'34"	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°9'03"	10°5'23"	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°9'03"	10°5'23"	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°5'30"	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°9'03"	10°5'23"	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°9'03"	10°5'23"	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°5'41"	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°4'27"	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°5'45"	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°5'41"	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°4'27"	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°3'48"	5	harbour	Imperial Age/ Late Roman	2-7 AD	4	<1	*L. europaeus*-type	*L. europaeus*	LPP-MO	Triolo 2013/2014

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TABLE 2. (Continued)

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**
44	NER61	**Modena - viale Amendola2**	Emilia Romagna	44°38'00"	10°4'27"	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°5'45"	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°5'58"	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°6'52"	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°8'49"	10°5'31"	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°1'10"	11°0'12"	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°0'50"	11°3'28"	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°8'44"	10°5'35"	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°8'52"	10°5'22"	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°8'37"	10°5'18"	31	urban walls	Medieval	10-11 AD	954	4	*L. europaeus*-type	*L. europaeus*	LPP-MO	Osti 2012/2013

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TABLE 2. (Continued)

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**
56	NVE59	**Torcello - area N Basilica S. Maria Assunta**	Veneto	45°9'55"	12°5'13"	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°9'03"	10°5'23"	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°0'03"	11°7'06"	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°0'03"	11°7'06"	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°8'47"	10°5'29"	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°7'55"	11°0'01"	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°0'03"	11°7'06"	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°8'53"	10°5'35"	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°3'25"	7°8'46"	200	pond in abandoned river channel	20th century, Holocene	20 AD	36	24	*L. europaeus*-type	*L. europaeus*	CCN	Vassio 2012

Materials and methods

Nutlet morphology of extant species:—The comparative analysis of extant species was not restricted to those occurring today in Europe, and an attempt was made to gather information about all the extant species. In fact, there is no reason to assume *a priori* that only the two European extant 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, Velichkevich & Zastawniak 2003, Martinetto 2015). The analyses of extant nutlets pointed to the detection of diagnostic combinations of morphological characters which could characterise particular nutlet types of taxonomical relevance, also recognizable in fossil assemblages. We pointed to construct a key (see below) useful to assign each extant or fossil nutlet to a definite morphological type. The possible diagnostic characters of the nutlets of extant 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 (Eastern Illinois University: http://castle.eiu.edu; United States Department of Agriculture: https://plants.sc.egov.usda.gov; see Tab. 4). Direct observations at the stereomicroscope of six specimen-rich extant samples (more than 40 nutlets: Tab. 4) were particularly relevant to assess the degree of intraspecific variability in *L. americanus* (US2814056), *L. europaeus* and *L. exaltatus*. The material of *L. europaeus* (MCC0708, MCC2540, MCC2547) and *L. exaltatus* (MCC1335, MCC2548) originated from different individual plants and localities (Tab. 4), and was stored in the Modern Carpological Collection of the Turin University (MCC, see Martinetto et al. 2014).

The selection of characters was biased towards those easily retained in the fossils, and therefore it did not correspond to the selection operated by Moon & Hong (2006), which included several characters not preserved in fossils (thickness of anatomical details, trichomes, epidermal cell shape). Based on the previous morphological studies, the characters useful for identification were observed from the dorsal view, because the ventral view does not show the diagnostic traits of the collar (open/closed and subequal/unequal collar, see explanation of Fig. 2). Beyond the collar and its variable thickness, the dorsal view showed different states of the central area, which we called "scutum" (Fig. 2) and may be neatly delimited by the collar (apparent) or not (poorly apparent). Nevertheless, the states of a few other characters, considered to be relevant, are detectable in both dorsal and ventral view, such as the truncate, subtruncate, or round apical outline and the tuberculated or non-tuberculated corky crest (the crest is the apical portion of the collar: Fig. 2). Of course, also the L:W ratio and the width at scutum apex/base could be measured regardless of the dorsal or ventral view.

Fossil-species:—The comparison with extant reference material cannot be sufficient for the Italian pre-Quaternary fossil samples, because the occurrence of a few fossil-species was reported from the late Cenozoic of other European localities. Therefore, we pointed to compare the Italian fossils with previously described fossil-species of *Lycopus*, focusing on the nutlet's dorsal view. To our knowledge, four fossil-species were described for the Cenozoic of this area (see Introduction) by Reid (1920), Dorofeev (1963, 1987) and Velichkevich & Zastawniak (2003). Concerning the earliest described species, *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 analysed all the available fossil samples of *Lycopus* in the palaeobotanical collections of the Komarov Botanical Institute (label BIN-PB), but we were unsuccessful, since palaeocarpological collections from Belarus are no longer stored there. Therefore, the information about this species was based on the literature, as it was also for *L. cholmechensis*. On the other hand, we located in the same repository some samples of several putative fossil-species from Siberia, which were mentioned, but not described by Nikitin (2006). Even if a revision of *Lycopus* fossils in this collection was beyond the scope of the present paper, we analysed selected material (BIN-PB-H2514, H2023, H2926, H3404, H3616, H4313) of Nikitin's putative fossil-species with the aim to evaluate the affinities with the Italian fossil samples. Additionally, in order to include a wider assortment of nutlets from East Europe and West Siberia, selected fossil samples of *Lycopus* in the general collection of the Komarov Botanical Institute were also analysed: BIN-PB-K20, K320, K432, K453, K457, K517, K519, K520, and K523. The low number of well-preserved specimens (1-3) available for each sample of this last set was not suitable for a sound analysis of the degree of variability for several characters.

Italian fossil samples:—A total of ca. 6000 fossil nutlets of *Lycopus* have been collected from 23 pre-Holocene sedimentary records (Tab. 1), and 38 Holocene sedimentary records or archaeological sites (Tab. 2). The sites are located in nine regions of Northern (Piemonte, Emilia-Romagna, Liguria, Lombardia, Trentino-Alto Adige, Friuli-Venezia Giulia, Veneto) and Central Italy (Toscana, Umbria) (Mercuri *et al.* 2015). The pre-Holocene materials are

stored at the CENOFITA collection of the Turin University (CCN, see Martinetto 2015), whereas Holocene materials are stored at various laboratories indicated in Tab. 2.

Age estimation:—The age of each site bearing *Lycopus* fossil nutlets has been mostly taken from the literature (Martinetto 2015, Mercuri *et al.* 2015). New ^{14}C dating has been carried out, in the Heidelberg ^{14}C laboratory, only for two sites: Cave Germaire and Colombari. The Cave Germaire sediment sample used for ^{14}C dating 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 $NaClO_2$. ^{14}C ages were calibrated using OxCal 4.3 and IntCal13.

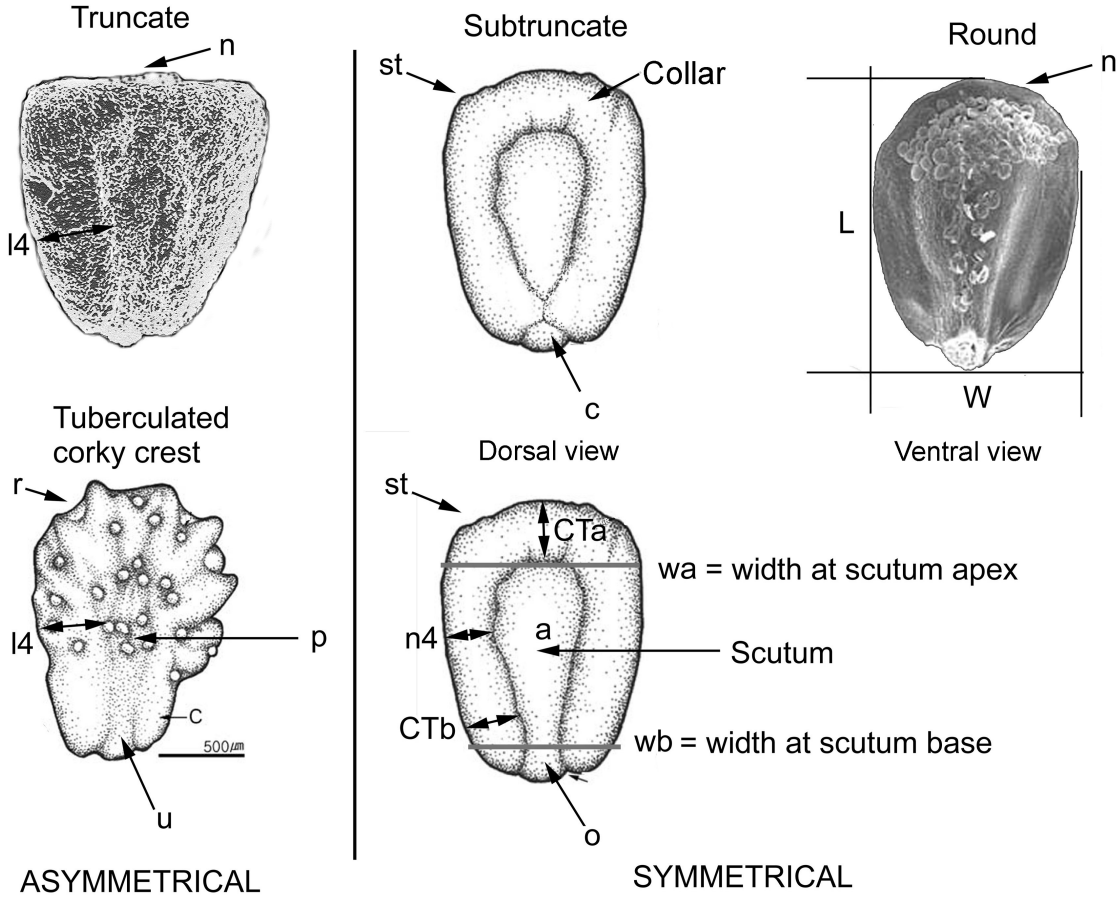

FIGURE 2. Diagnostic characters suggested for *Lycopus* nutlets, modified from Moon & Hong (2006).
a scutum apparent; **c** collar base closed; **CTa** collar thickness at the apex; **CTb** collar thickness at the base (the collar is defined as "subequal" when CTa≃CTb and as "unequal" when CTa>CTb); **l4** mean collar thickness larger than 1/4 nutlet's width; **n** nutlet's apical end non-tuberculated; **n4** mean collar thickness narrower than 1/4 nutlet's width; **o** collar base open; **p** scutum poorly defined; **r** apical outline round, **st** apical outline subtruncate; **u** collar base open but border of collar margin unclear. These characters are scored for each species of *Lycopus* in Tab. 3.

Results

New ^{14}C dates:—The analysis of the Cave Germaire sediment sample (Hd-24603) provided a result beyond the ^{14}C range (>50000 calendar years before present = cal BP), whereas the three wood samples from Colombari provided very similar ages, and only sample Hd-23867 proved to be ca. 300 years younger than the other two (Fig. 3). Due to the ^{14}C 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 robust latest Pleistocene date for the Colombari succession, deposited between 13600 and 13200 years cal BP.

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 too strong a morphological disagreement. See Fig. 2 for explanation of parameters L, W, wa and wb. Apical end of nutlets: **n** not-tuberculated, **t** tuberculated corky crest; Apical outline of nutlets: **r** round, **st** subtruncate, **t** truncate; Collar base shape (on the dorsal side): **o** open, **u** open but unclear border of collar margin, **c** closed; Symmetricity (in dorsal or ventral view): **a** asymmetrical, **s** symmetrical; 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; Collar uniformity: **i** indeterminable, **s** subequal, **u** unequal; 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 characterisation of fossils, being based on several characters which are not preserved.

Species	L [min (mean) max] mm	W [min (mean) max] mm	Mean L:W	Apical end	Apical outline	Collar base shape	Symmetry	**Mean collar thickness**	Collar uniformity	Scutum	**wa/wb**	Morphological type	Moon-Hong type	Collection code or data source reference
L. coreanus	1.10 (1.20) 1.50	0.80 (0.93) 1.20	1.3	n	st	o	s	n4	?	a	1.8	*L. 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	s	a	1.5-1.8	*L. americanus*	4	US2814056—SA. 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	s	a	1.5	*L. americanus*	4	Moon & Hong (2006)
Fossil NPI-CV3	1.3 (1.5) 1.7	0.6 (0.8) 1.1	1.4	n	r	o	s	n4	s	a	1.5-2.0	*L. americanus*	4	Ca' Viettone, sample CCN2406
L. exaltatus	1.3 (1.5) 1.8	0.9 (1.0) 1.2	1.5	n	t/r	o	s	n4/n5	u	a	1.5-2.0	*L. exaltatus*	4	Moon & Hong (2006) + Tab. 3
L. exaltatus	1.2 (1.5) 1.9	0.9 (1.0) 1.2	1.5	n	t/r	o	s	n4/n5	u	a	1.5-1.9	*L. exaltatus*	4	MCC1335—ORTHWEST 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	u	a	1.5-2.0	*L. exaltatus* (+*L. europaeus*)	4 (2)	MCC2548—ENTRAL ITALY. Pisa, Tuscany, right bank of the Arno river, spontaneous, October 1983
L. asper	1.80 (1.97) 2.30	1.40 (1.51) 1.90	1.1	n	t	o	a	l4	i	p	1.6-1.7	*L. 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	s	a	1.2	*L. 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	s	a	1.0-1.5	*L. europaeus*	2	Moon & Hong (2006)

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TABLE 3. (Continued)

Species	L [min (mean) max] mm	W [min (mean) max] mm	Mean L:W	Apical end	Apical outline	Collar base shape	Symmetry	**Mean collar thickness**	Collar uniformity	Scutum	**wa/wb**	Morphological type	Moon-Hong type	Collection code or data source reference
L. europaeus	0.9 (1.1) 1.3	0.7 (0.9) 1.0	1.2	n	st	c (o)	s	n4	s(u)	a	1.2-1.8	*L. europaeus* (+*L. exaltatus*)	2 (4)	MCC2547—ORTHWEST ITALY. Ternavasso, Poirino, province of Torino, single plant 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	s(u)	a	1.2-1.5	*L. europaeus* (+*L. exaltatus*)	2 (4)	MCC0708—AST FRANCE. Sessenheim, Alsace, spontaneous, July 1990
L. europaeus	0.9 (1.0) 1.2	0.6 (0.8) 1.0	1.2	n	st/t	o	s	l4/n4	s	a	1.2-1.6	*L. europaeus*	2	MCC2540—ORTHWEST ITALY. San Carlo Canavese, province of Torino, single plant spontaneous along a ditch, November 2020
L. maackianus	0.9 (1.3) 1.5	0.7 (0.9) 1.1	1.2	n	st/t	o/c	s/a	l4	s	a	1.5	*L. 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	s	a	1.3-1.8	*L. europaeus* (+*L. exaltatus*)	2 (4)	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	i	p	1.7	*L. 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	i	p	1.2-1.4	*L. lucidus*	2	Moon & Hong (2006)
L. charkeviczii	2.3-3.0	1.0-1.5	2.0	t	/	/	a/s	n4	?	a	/	*L. charkeviczii*	/	Son et al. 2016

...continued on the next page

TABLE 3. (Continued)

Species	L [min (mean) max] mm	W [min (mean) max] mm	Mean L:W	Apical end	Apical outline	Collar base shape	Symmetry	**Mean collar thickness**	Collar uniformity	Scutum	**wa/wb**	Morphological type	Moon-Hong type	Collection code or data source reference
L. "parviflorus" (= *L. uniflorus*?)	1.60 (1.64) 1.85	1.20 (1.25) 1.50	1.3	t	r	o	a	l4	u	a	2.2	*L. charkeviczii* or *L. 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	/	u	p	2.1	*L. 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	i	p	1.6	*L. 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	i	p	1.8	*L. 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	i	p	1.6-1.8	*L. virginicus*	3	Moon & Hong (2006)
L. amplectens	/	/	1.2	t	t	o	a	l4/n4	s	p	1.9	*L. virginicus*	rev. needed	Henderson (1962)
L. rubellus	/	/	1.2	t	r	/	a	n4	s	p	2	*L. 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)

Diagnostic nutlet characters of extant species:—Observations on the intraspecific variability of nutlets in specimen-rich samples were fundamental for the selection of those morphological characters seeming to have major taxonomical relevance. The morphological variability observed in ca. 40–100 specimens (Tab. 4) from single samples was rather high in *L. europaeus* and more limited in *L. americanus* and *L. exaltatus*. Also, the mismatch of characters between three 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 larger than those measured by us (Tab. 3). We observed that the occurrence of a single nutlet with a contrasting character (e.g., open collar base in a sample of nutlets with prevailing closed collar base) may often occur in individual extant specimen-rich samples, therefore we considered more important the frequency (Tab. 4: absent, rare, frequent) of the relevant characters in an assemblage of nutlets. For example, an unequal collar was rarely detected in *L. europaeus*, but a very high frequency of nutlets with unequal collar was only observed in the two extant samples of *L. exaltatus*, so that this character was considered diagnostic for an own morphological type. Likewise, a few characters (e.g., spongy tissue at the apex of ventral ridge: Tab. 4) were regarded as scarcely diagnostic because they occurred rarely in different species, and in none of these were frequent.

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

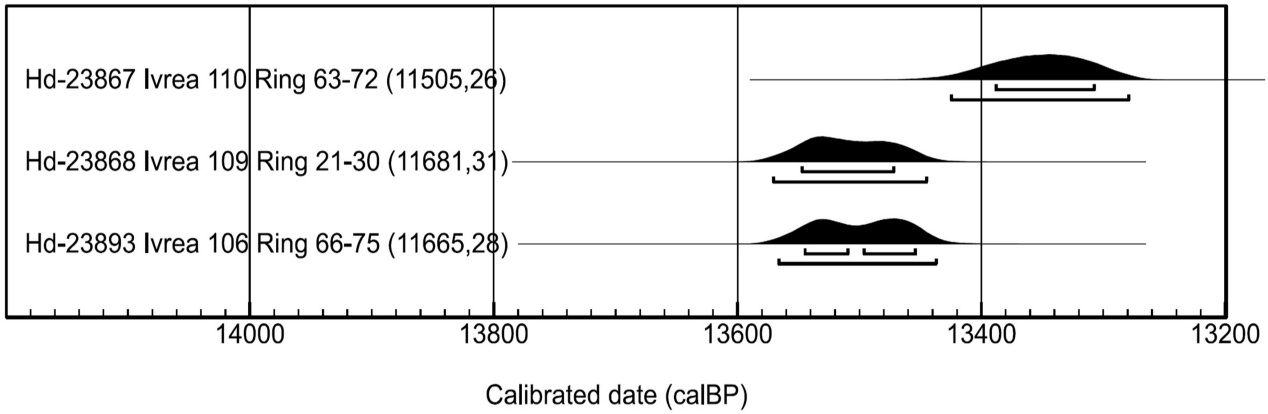

FIGURE 3. ^{14}C dates and ranges of the Colombari ("Ivrea") samples, calibrated using OxCal 4.3 (above) and IntCal13 (below).

The definition of nine morphological types (see the key below) was based on the following characters, considered to be more constant: symmetricity, crest features, apparentness of the scutum, mean L:W ratio, collar base type and breadth at different positions, apical outline. Six of these morphological types were recognised thanks to images provided by the literature (summarised in Tab. 3), without information on the variability.

Six extant species showed distinct and diagnostic combinations of characters (Tab. 3), corresponding to morphological types named after each species: *L. asper* Greene (1898: 339), *L. australis*, *L. charkeviczii* Probatova (1995: 351), *L. exaltatus*, *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 stereotype of nutlets, that we called *L. virginicus*-type. Some doubts about the type of nutlets of *L. uniflorus* arose from the observation of a specimen figured by Moon & Hong (2006) and assigned to *L. parviflorus* Maximowicz (1859: 216) (probably a synonym of *L. uniflorus*, see The Plant List 2013). In fact, its morphology conforms to the *L. charkeviczii*-type (and not to the *L. virginicus*-type) because of its apparent, smooth central area (here newly named "scutum": Fig. 2), even if the dimensions are smaller than those of the nutlets of *L. charkeviczii* (Tab. 3).

The easily distinguishable *L. americanus*-type of nutlets was shared by two 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; *L. coreanus* Léveillé (1910: 423) mostly shows a subtruncate apex.

Finally, the *L. europaeus*-type was detected in *L. europaeus* and *L. maackianus* Makino (1897: 382). However, the nutlets of the latter species often have characters which were rarely observed in the first one: very thick collar and asymmetrical outline. The occurrence of one nutlet of the *L. exaltatus*-type (unequal collar thickness) in a sample (MCC2547) originating from a single plant of *L. europaeus* was also remarkable to point out that single fossil nutlets, with morphology diverging from the bulk of the others (of the *L. europaeus*-type), may lead to wrong determinations.

Individual extant or fossil nutlets can be assigned to one of the nine above-mentioned morphological types according to the diagnostic characters listed in the following key (without phylogenetic implications).

Identification key for the morphological types of *Lycopus* nutlets (mericarps)

See Fig. 2, Tab. 3 and Tab. 4 for explanation of characters and terminology

1. Asymmetrical nutlet 2
- Symmetrical nutlet, non-tuberculated corky crest 5

2. Tuberculated corky crest 3
- Non-tuberculated crest, poorly apparent scutum 4

3. Apparent scutum, L > 2 mm = *L. charkeviczii*-type;
- Poorly apparent scutum, L < 2 mm = *L. virginicus*-type

4. Truncate apex, crest indefinite, mean L:W ratio 1.1 = *L. asper*-type;
- Subtruncate apex, crest very thin, mean L:W ratio 1.5 = *L. laurentianus*-type.

5. Poorly apparent scutum, collar base mostly closed = *L. lucidus*-type
- Apparent scutum 6

6. Collar broader than 1/4 of the nutlet's width = *L. australis*-type
- Collar narrower than 1/4 of the nutlet's width 7

7. Apical outline truncate or subtruncate, wb frequently > 2/3 wa = *L. europaeus*-type
- Apical outline commonly round, wb frequently < 2/3 wa 8

8. Collar subequal = *L. americanus*-type
- Collar unequal = *L. exaltatus*-type

Morphological characterisation of validly published fossil-species:—After our analysis, a re-evaluation of validly published fossil-species was possible based on nutlet morphology. The earliest described fossil-species of *L.* in the Cenozoic of Eurasia is *L. antiquus*, represented by a single specimen (the holotype) from the late Miocene French site of Pont-de-Gail (Reid 1920). Other four fragmentary specimens, dubitatively assigned to *L. antiquus* by Reid (1920, pl. 4, figs. 15, 16), have such a thick, robust, and shiny structure (unknown in extant *L.*) that their interpretation as *L.* nutlets must be rejected. Rather, they seem to represent fragments of seeds of the lythraceous genus *Decodon,* which is common in the same fossil assemblage. Conversely, the available images of the holotype (Reid 1920, pl. 4, figs. 12a, b) indicate that it may actually represent a nutlet of *L.* (even if a more accurate analysis would be desirable) of the *L. virginicus*-type, because of the tuberculated corky crest, poorly apparent scutum and L < 2 mm (= 1.3 mm). It should be noted that Dorofeev (1963), Mai & Walther (1988) and Nikitin (2006) assigned to *L. antiquus* several fossil specimens with contrasting characters (non-tuberculated corky crest, apparent scutum), whose identification should be revised.

A second fossil-species was described by Dorofeev (1963b) on the basis of Pleistocene nutlets from Belarus which, according to him, seemed to "differ from modern *L. europaeus* L. by a characteristic excrescence of a spongy tissue at the apex of the ventral side, not connected to the collar, and by a completely closed up gap at the base of the dorsum" (closed collar in this paper). This fossil-species was named *L. intermedius* Dorofeev (1963b: 168), but was not validly published (missed holotype designation) until Doweld (2018) validated it and renamed it *L. europleistocenicus*.

The third fossil-species described from the Cenozoic of Eurasia, *L. pliocenicus*, is based on material from locality Dvorets (Belarus, East Europe). The types were illustrated by Dorofeev (1987) in six drawings of nutlets only shown in ventral view. These fossil specimens are presently unavailable, but the characters shown by the drawings are sufficient to assess that they belonged to *Lycopus*. A single photograph of a nutlet (ventral view) of *L. pliocenicus* from Dvorets seems having been published so far (Velichkevich & Zastawniak 2007, pl. 3, fig. 5). Even if the dorsal side of the fossil nutlets from Dvorets was not illustrated, the characters seen in ventral view conform to the *L. americanus*–type and only the generally broader base and larger size distinguish the fossil nutlets from those of the extant American species *L. americanus*. Indeed, *L. pliocenicus* should be better characterised and the distinction of the fossil-species from the extant species *L. americanus* would need to be accurately re-assessed.

The most recently described fossil-species is *L. cholmechensis* from the Eastern European locality Kholmech (Belarus) (Velichkevich & Zastawniak 2003). Its nutlets with non-tuberculated corky crest, apparent scutum and truncate or subtruncate apical outline, can be assigned to the *L. europaeus*–type, but they differ from the nutlets of the extant species (*L. europaeus, L. maakianus*) because of the slightly concave crest that sometimes bears small lateral extensions, named "auricles".

Main characteristics of Russian fossils:—Most of the Oligocene to Miocene fossil samples from Siberia and European Russia analysed by us contain assortments of nutlets that, for size and combination of characters, do not agree with any extant species. Indeed, these nutlets approach either the *L. americanus* or the *L. europaeus*-type but often they cannot be assigned to either. However, at least two samples of nutlets in the Nikitin collections can be assigned (according to the key above) to the *L. americanus*-type: one from the early Oligocene of West Siberia (BIN-PB-H4313) and a second one from the early Miocene of the Russian Far East (BIN-PB-H3616). Fossils of this type were labelled by Nikitin (2006, 202) as "*Lycopus parvulus*", which is, however, a *nomen nudum*. Furthermore, individual nutlets with characters pointing to the *L. europaeus*-type (e.g., wb frequently > 2/3 wa and subtruncate crest) occur in an early Miocene sample (BIN-PB-K517) from West Siberia, mixed with nutlets showing at least one contrasting character (e.g. wb frequently < 2/3 wa). A third nutlet type, detected in a single early Miocene West Siberian sample (BIN-PB-H3404), is the *L. charkeviczii*-type.

Only among Pliocene materials we detected whole nutlet assortments (BIN-PB-K453, less so BIN-PB-K20) which not only agree with the *L. europaeus*-type, but also show the same morphological variation as the extant ones of *L. europaeus* (Tab. 3, 4: MCC2547). At the present state of the art, the Russian fossils can only confirm the existence of a reliable record for the genus *Lycopus* since early Oligocene and an early morphological diversification before the end of the Miocene (as proved by the occurrence of three different nutlet types within the Miocene). Indeed, the abundant and well-preserved material of the BIN-PB collections deserves a thorough revision.

Revised taxonomy of Italian fossil samples:—All 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 two cases (samples CTO-BCN1 and NVE58, Tab. 1 and Tab. 2) one nutlet of the *L. exaltatus*-type was mixed up with a majority of nutlets of the *L. europaeus*-type (Fig. 4). Based on the same situation observed in the extant samples MCC0708 and MCC2547 (see above), this latter case was parsimoniously interpreted as a product of intraspecific variation. The results obtained from the comparative analysis of extant and fossil materials led us to propose the taxonomic framing presented below.

FIGURE 4. Broad morphological variation of nutlets in dorsal view from the Holocene of Altino (NVE58, Department of Biology of the Padova University), Northern Italy. Seven specimens conform to the *L. europaeus*-type, and only the specimen in the bottom right corner is of the *L. exaltatus*-type.

TABLE 4. Comparison of the nutlet characteristics of extant samples of *L. europaeus*, *L. exaltatus*, *L. americanus* and their frequency in fossil assemblages: A = absent; F = frequent; R = rare. See Fig. 2 for explanation of parameters L, W, wa and wb.

The label CCN designates samples of the CENOFITA Collection (Martinetto 2015) and MCC those of the Modern Carpological Collection of the Turin University (see Martinetto et al. 2014); **Small L:W**: nutlet's L:W ratio ca. 1.1–1.2; **Large L:W**: nutlet's L:W ratio ca. 1.5; **Subequal collar**: collar as thick in the apical part as in the lateral one; **Unequal collar**: collar thicker in the apical part than in the lateral one (Fig. 2). Grey cells highlight the most diagnostic features.

Sample or Site ID	Locality	Age BP	Number of nutlets in the sample	Small L:W	Large L:W	Almost straight crest	Round crest	Crest with obtuse teeth	Spongy tissue, apex of ventral ridge	Closed collar	Open collar	Subequal collar	Unequal collar	wa≈b	wb < 2/3 wa	wb < 1/2 wa	**Attribution**
MCC2547	Ternavasso, Italy	0	100	F	A	F	R	R	R	F	R	F	R	F	R	A	*L. europaeus*
MCC2540	San Carlo Canavese, Italy	0	100	F	A	F	R	R	R	F	R	F	A	F	R	A	*L. europaeus*
MCC0708	Sessenheim, France	0	100	F	A	F	R	R	A	A	F	F	R	F	R	A	*L. europaeus*
MCC1335	Torino, Italy	0	50	R	F	R	F	A	R	A	F	R	F	A	F	R	*L. exaltatus*
MCC2548 (ex Herb. Soldano 5518)	Pisa, Italy	0	100	A	F	R	F	R	R	A	F	R	F	A	F	R	*L. exaltatus*
US2814056	Michigan, USA	0	40	A	F	R	F	A	R	R	F	F	A	A	F	R	*L. americanus*
image from USDA plants database	Idaho, USA	0	6	A	F	R	F	A	A	R	F	F	A	A	F	R	*L. americanus*
image from Illinois Nat. Hist. Surv.	Illinois, USA	0	9	A	F	R	F	A	R	R	F	F	A	A	F	R	*L. americanus*
NPI-CV3	Ca' Viettone	4.0-3.5 Ma	8	R	F	R	F	A	A	R	F	F	A	R	F	R	*L.* cf. *pliocenicus*
NPI-STU	Stura di Lanzo	3.1 Ma	47	R	F	R	F	A	A	R	F	F	A	R	F	R	*L.* cf. *pliocenicus*

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TABLE 4. (Continued)

Sample or Site ID	Locality	Age BP	Number of nutlets in the sample	Small L:W	Large L:W	Almost straight crest	Round crest	Crest with obtuse teeth	Spongy tissue, apex of ventral ridge	Closed collar	Open collar	Subequal collar	Unequal collar	wa≈b	wb < 2/3 wa	wb < 1/2 wa	**Attribution**
NPI-GA5,21	Castelletto Cervo II	2.6-2.0 Ma	5	F	R	R	F	A	A	A	F	F	A	A	R	A	L. sp. indet.
NVE-STG2	Steggio	1.8-0.8 Ma	2	/	R	R	R	/	A	/	R	R	/	/	R	/	L. sp. indet.
CUM-PF2	Pietrafitta	ca. 1.5-1.3 Ma	1	R	/	R	/	R	A	/	R	R	/	/	R	/	L. sp. indet.
CTO-BCN1	Cava Campitello	100-200 ka	22	F	A	F	R	R	R	F	R	F	R	F	R	A (1!)	*L. europaeus*
CTO-BUT	Cava Butteri	100-200 ka	5	F	A	F	R	R	R	F	R	F	A	F	R	A	*L. europaeus*
NPI-CLB1	Colombari	11 ka	18	F	A	F	R	R	R	F	R	F	A	F	R	A	*L. europaeus*
NPI-RV1	Garosso di Rivalta	10-1 ka	14	F	A	F	R	R	A	F	R	F	A	F	R	A	*L. europaeus*
NPI-CAT1	Castiglione Torinese	10-1 ka	3	F	A	F	R	R	A	F	R	F	A	F	R	A	*L. europaeus*
NVE58	Altino	3.0-2.2 ka	7	F	A	F	R	R	A	R	F	F	R	F	R	A	*L. europaeus*
NPI-SBC	San Benigno Canavese, Italy	0	36	F	A	F	R	R	R	F	R	F	A	F	R	A	*L. europaeus*

Order **Lamiales** Bromhead (1838: 210)
Family **Lamiaceae** Martinov (1820: 355)
Genus ***Lycopus*** Linnaeus (1753: 21)

Lycopus cf. ***pliocenicus*** Dorofeev (1987: 69) (Fig. 5)
Specimens:—See Tab. 1.

Lycopus europaeus Linnaeus (1753: 21) (Fig. 4)
Specimens:—See Tab. 1, Tab. 2.

Lycopus cf. ***europeaus*** Linnaeus (1753: 21)
Specimens:—See Tab. 2.

Lycopus sp. or spp. indet.
Specimens:—See Tab. 1.

Discussion

Intraspecific variation:—Our observations on many specimens of single extant species 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 extant species or fossil-species seems to be hazardous. For example, within a nutlet assemblage collected from a single plant of *L. europaeus* (MCC2547), where the dominant condition was L:W ratio ca. 1.2 and closed collar base, we detected a few nutlets with L:W ratio ca. 1.5 and open collar base, characters that are more typical for *L. exaltatus*. In extant samples of *L. exaltatus* the morphological variation of the nutlets was scarce, nevertheless we did observe nutlet morphologies approaching those of *L. europaeus* in a few specimens of sample MCC2548. Hence, individual fossil nutlets assignable to a definite morphological type (e.g., the *L. europaeus*-type) do not necessarily testify for the occurrence of the species in which that type is dominant (e.g., *L. europaeus*). However, the observations on specimen-rich extant samples of *L. americanus, L. europaeus* and *L. exaltatus* suggest that the dominant, more stable characters (Tab. 4) permit the identification of the species. Such characters are often preserved also in fossil assemblages, and can be exploited to assign a homogeneous assortment of fossil nutlets to a dominant and definite morphological type, by following the key provided above. The possibility of a next step, i.e. assignment to an extant species or fossil-species (Turland et al. 2018, article 1.2), depends on the evaluation of the context (i.e. location and age of the fossil-bearing deposit, degree of knowledge of the fossil flora in that area).

Identification of Italian fossil samples:—Most of the studied Italian fossil assemblages (Tables 1, 2) can be assigned either to the *L. europaeus*-type or to the *L. americanus*-type. All Holocene and a few Pleistocene assemblages, dating back to no more than 0.1-0.2 Ma (CTO-BCN1: Tab. 1), are characterised by the exclusive presence or prevalence of *L. europaeus*-type. This type of nutlets occurs in the fossil-species *L. cholmechensis* and *L. europleistocenicus* as well as in the extant species *L. europaeus* and *L. maackianus*. However, the nutlets of *L. cholmechensis* are characterised by a concave crest, often with auriculae, which was not observed in the Italian fossils. The purported diagnostic characters of *L. europleistocenicus* (spongy tissue at the apex of the ventral side, closed collar) have been observed in extant samples of *L. europaeus* (Tab. 4), suggesting that it is not a separate taxon. Nutlets of the extant *L. maackianus* differ from the Italian fossils for the very thick collar and slightly asymmetrical outline. Only the extant samples of *L. europaeus* showed a total match to the fossils, therefore we confidently assigned to *L. europaeus* all the Italian samples showing a prevalence of *L. europaeus*-type.

The exclusive occurrence of the *L. americanus*-type (Fig. 5) was detected in two fossil assemblages from the oldest, Pliocene localities: Ca' Viettone (4.0-3.5 Ma: Martinetto et al. 2018) and Stura di Lanzo-Nole Canavese (ca. 3.1 Ma: Martinetto et al. 2007). Fossils from these assemblages, due to the subequal collar (Fig. 2) and the frequently round outline of the apex, are morphologically closer to *L. americanus* than to *L. coreanus, L. europaeus* and *L. exaltatus* (Tab. 4). In particular, despite the consistent morphological similarity of these European fossils with the nutlets of the extant European *L. exaltatus*, they do not seem to indicate past occurrence of such species, because of the regularly rather than irregularly round apical outline and narrower collar in the apical part. The Italian Pliocene

fossils are very similar to the late Cenozoic East European nutlets of the fossil-species *L. pliocenicus* and to a sample of nutlets from the early Oligocene of West Siberia (BIN-PB-H4313), putatively assigned in Nikitin's collection to a separate fossil-species ("*L. parvulus*", not validly published), which only differs for a slightly more toothed crest.

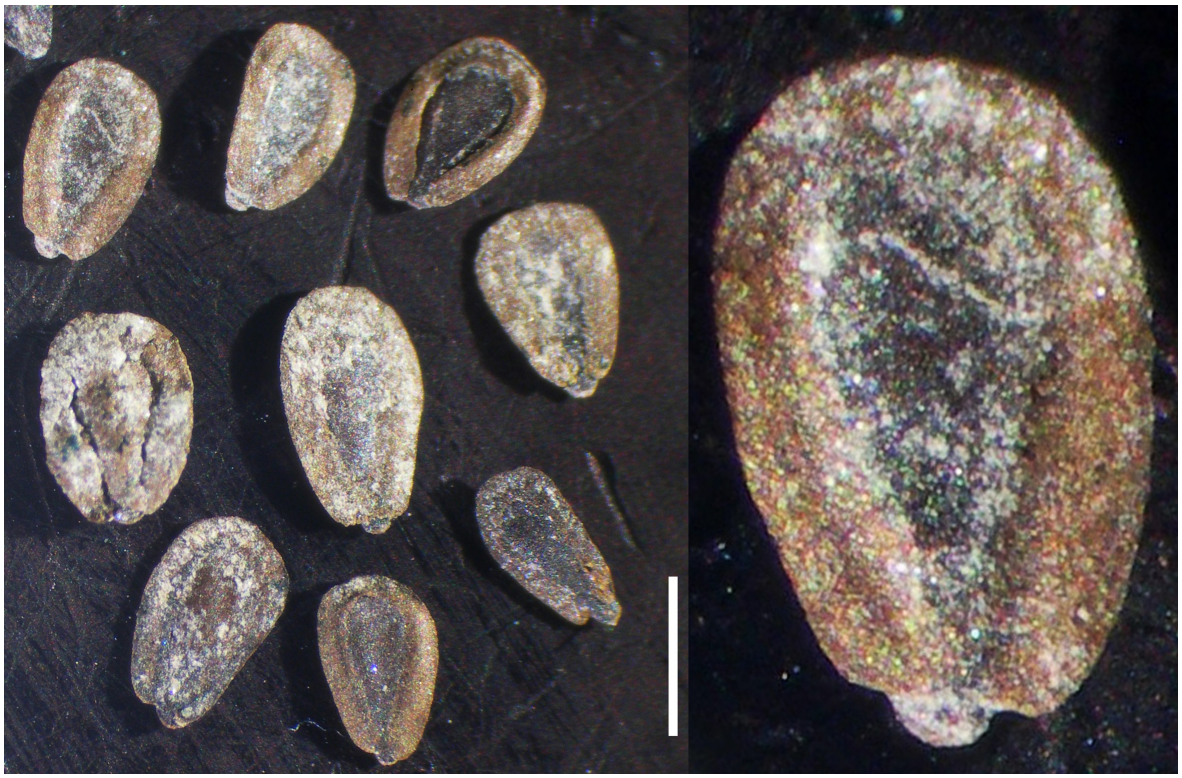

FIGURE 5. *Lycopus* cf. *pliocenicus* from the early Pliocene of Ca' Viettone (Martinetto et al. 2018), Northern Italy, nutlets in dorsal view (CCN2406, CENOFITA collection of the Turin University). Scale bar 1 mm. The nutlet at the top left corner is enlarged in the right portion of the image.

The present evidence suggests these two possibilities: a) the Italian fossils from the Ca' Viettone and Stura di Lanzo-Nole Canavese sites may actually indicate past occurrence of *L. americanus* in Europe; b) they may belong to a European fossil-species. The first possibility would need further evidence and may be confusing for phylogenetic and phytogeographic analyses. Moreover, these fossils can be distinguished from *L. americanus* for a slightly larger nutlet size (length 1.35–1.70 versus 1.00–1.40 mm) and, therefore, the second possibility is preferred. Indeed, these Italian fossils match all the known characters of *L. pliocenicus*, but the state of relevant collar characters (open/close, subequal/unequal) in the type material of such fossil-species is unknown. For this reason, the use of open nomenclature (*L.* cf. *pliocenicus*) is preferred for the Italian fossils. Additional fossil specimens from Villafranca d'Asti-RDB Quarry (Tab. 1), dated around 3.2 Ma, agree in all the detectable characters with the above-cited ones of the Ca' Viettone and Stura di Lanzo-Nole Canavese sites, and are also assigned to *L.* cf. *pliocenicus.* Some other Pliocene and all the Early Pleistocene (2.6 to 0.8 Ma) fossils are problematic (Tab. 1: listed as *L.* sp. indet., see Sigovini et al. 2016), mainly because of the scarcity of remains. A fossil from Pietrafitta, which was doubtfully attributed to *L.* cf. *exaltatus* (Martinetto *et al.* 2014), does not show convincing diagnostic characters for that species (e.g., unequal collar), so that here it is reinterpreted as *Lycopus* sp. indet. The abundant samples from sediments younger than 0.2 Ma (Fig. 4) showed a combination of characters typical of the *L. europaeus*-type and, in consideration of the context of the fossil sites, can be confidently assigned to *L. europaeus*. Only in one site (NVE58, Altino) a nutlet of the *L. exaltatus*-type was found (Fig. 4) in association with much more abundant nutlets of the *L. europaeus*-type and with intermediate forms, thus suggesting a broad intraspecific morphological variation (as observed in extant samples MCC0708 and MCC2547, see above), rather than the unlikely occurrence of *L. exaltatus* in this fossil assemblage.

Ecology and distribution in Italy:—The habitat of *Lycopus* species is mostly confined to wetlands and river banks (Henderson 1962, Moon & Hong 2006, Euro+Med 2006-2015). *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 fringe communities, banks of ponds and rivers, and shaded streams (Akhani 2014). Today in Italy these habitats are more common in the

northern and central part of the country and, interestingly, most of the palaeobotanical records of *Lycopus* are from the Northern Italian regions. Only a few traces are available from the northern part of Central Italy, whereas no records are available from the southern regions, Sicily and Sardinia. Despite we can invoke preservation biases and uneven intensity of archaeo- and palaeobotanical investigations among the causes of such missing evidence, the ecological and phytogeographical, besides taphonomic and collection, features may explain why the records are concentrated in the northern regions of the country.

Conclusions

Taxonomical and chronological overview of the Italian fossils:—The overview of the collections and field studies highlights significant and diffused *Lycopus* records since 4 Ma from different Italian localities. All those Italian fossil assemblages which showed a good preservation of the diagnostic characters could be assigned to only two (out of nine) morphological types of nutlets, either to the *L. europaeus*-type or to the *L. americanus*-type.

The fossil record of *Lycopus* in Italy starts with a rich assortment of nutlets of *L*. cf. *pliocenicus* dated to the late Zanclean (late early Pliocene) and this taxon also occurs in the Piacenzian (late Pliocene). The deposits dated from 2.6 to 0.2 Ma provided a limited number of fossil nutlets, often incomplete, which are treated as *Lycopus* sp. indet., whereas 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 assemblage assigned to this species dates back to 0.2–0.1 Ma (Cava Campitello: Tab. 1), whereas the Holocene record is widespread and includes several archaeological sites as well.

Future development:—The possible phylogenetic relationships of the Pliocene *L.* cf. *pliocenicus* from Italy with the extant 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, our detection of *L. americanus*-type nutlets in the Neogene of Europe, and back to the early Oligocene in West Siberia (Dorofeev 1963, Nikitin 2006) may be significant. It should be investigated whether the five above-cited extant species, sharing very similar fruit morphology (non-tuberculated corky crest, apparent scutum), may have diverged from a common ancestor with nutlet characters very similar to those of the extant *L. americanus*. Of course, the remains of this putative ancestor could be represented by the early Oligocene plant which produced the above-cited West Siberian fossil nutlets. This lineage may have later expanded its range down to southern Europe (*L.* cf. *pliocenicus* of the Italian Pliocene). The presently available fossil record, alone, does not permit to assess whether the extant European *L. exaltatus*, missing any reliable fossil record, might have originated from such a lineage. Rather, the almost complete morphological correspondence of the nutlets of the extant *L. americanus* with some Eurasian fossils mildly suggest that it could be a descendant of that lineage through a possible range expansion to North America. In facts, early Miocene fossils of the *L. americanus*-type occur in the Russian Far East (*Lycopus parvulus*, Nikitin 2006, p. 16), i.e. right on the pathway from West Siberia to Alaska through the Beringian land bridge (Wen et al. 2016). Based on palaeobotanical evidence, the evolution of *L. europaeus* may well have taken place in Eurasia, where the *L. europaeus* nutlet type is documented at least since the Miocene in West Siberia, and where nutlet assemblages morphologically identical to the extant ones of *L. europaeus* occur since the Pliocene. We hope that our assessment of diagnostic characters and morphological types of nutlets will facilitate future analyses on fossil assemblages and comparisons with extant taxa, and we suggest that the integration of such analyses with molecular phylogeny could progressively fill the gaps in our knowledge of the distribution of *Lycopus* taxa through time and space.

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