

A synthesis on cave-dwelling spiders in Europe

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Running title: European cave spiders checklist

28

29 **Abstract**

30 We provide the first overview on spiders living in subterranean habitats in Europe,
31 including the first European subterranean spider checklist. In Europe there are 486 spider
32 species known to dwell in caves and other subterranean habitats, distributed across 22
33 families. Despite a few species being able to colonize caves across the whole continent,
34 approximately 90% of the species show a restricted distribution, occurring exclusively in
35 one or two countries. From a biogeographic perspective, Southern Europe emerges as the
36 main hot spot of subterranean spider diversity, showing the highest richness of endemic
37 species. Compared to other temperate regions of the world, some families appear to be
38 well represented and other poorly represented (or lacking) in European subterranean
39 habitats. Overall, it appears that the taxonomical knowledge on subterranean spiders in
40 Europe is sufficient, but not evenly distributed. As this checklist represents a useful
41 baseline for advances in this field, we point out specific areas of interest for future
42 research.

43 I. INTRODUCTION

44 Following the description of the first blind cave-dwelling vertebrate *Proteus anguinus*
45 (Amphibia, Proteidae) (Laurenti 1768) and the first cave-obligate invertebrate *Leptodirus*
46 *hochenwartii* (Coleoptera, Leiodidae) (Schmidt 1832), interest in subterranean biology
47 gradually increased (Camacho 1992). Soon after the birth of modern spelebiology, Jørgen
48 Schiödte (1812–1884), Emil Racoviță (1868–1947) and René Jeannel (1879–1965)
49 recognized the potential of cave ecosystems, defining them as ideal settings in which to
50 find evidence for the Darwinian evolution theories, and where to investigate biogeographic
51 patterns of species diversification. These early insights allowed scientists to consider
52 caves ideal ecological and evolutionary laboratories (Poulson and White 1969).

53 From an evolutionary perspective, a breadth of studies focused on morphological and
54 physiological adaptations to the subterranean environment, on cryptic species diversity in
55 caves and on speciation processes (reviewed in Proudlove and Wood 2003; Porter et al.
56 2007; Culver and Pipan 2009a; 2015; Juan et al. 2010; Wilkens 2010). However, the role
57 of caves as ecological laboratories is as yet not fully explored, especially when considering
58 macroecological and biogeographic patterns at a continental or global scale (reviewed in
59 Culver et al. 2013). Theoretically, the subterranean domain gathers accumulated
60 convergent adaptations in filtered subsamples of regional species pools (e.g., Gibert and
61 Deharveng 2002; Derkarabetian et al. 2010; Protas and Jeffery 2012; Fišer et al. 2013; Liu
62 et al. 2017). It has been suggested that the factors driving the biogeographic patterns of
63 phylogenetic distant taxa should also be convergent (Culver et al. 2013), which often
64 allows the generalization of results obtained from a single group of subterranean
65 organisms to other taxa. In spite of that, the analysis of patterns and processes of
66 biological diversity and diversification in subterranean environments is very incomplete for
67 a number of reasons. Foremost, compared with epigeal habitats, caves and other

68 subterranean habitats constitute challenging working environments, making it difficult to
69 assemble a suitable amount of data (Culver et al. 2006; 2013; Zagamajster et al. 2010;
70 Christman et al. 2016; Mammola and Leroy 2017). Secondly, in most regions all
71 troglobionts are invertebrates, fungi or bacteria, invariably underrepresented in ecology
72 and conservation studies (Cardoso et al. 2011); on the other hand, the paucity of species,
73 compared with epigean communities, can make it simpler to understand how subterranean
74 communities assemble and function. Furthermore, whilst state-of-art synthesis for certain
75 cave-dwelling taxa have been published in recent years (e.g. Vanderwolf et al. 2013;
76 Falasco et al. 2015; Du Preez et al. 2017; Mammola and Isaia 2017a), overviews on most
77 subterranean arthropods are still missing.

78 Araneae (spiders) is a very diverse group of arthropods comprising nearly 47,000 extant
79 (World Spider Catalog—WSC, 2017) and nearly 1,300 fossil (Dunlop et al. 2016)
80 described species. According to available approximations, worldwide spider species
81 belonging to at least 48 families have representatives underground (Mammola and Isaia
82 2017a). Recent syntheses suggest that the core of this diversity is found in temperate
83 regions (Reddell 2005), although a comparison with tropical regions may be equivocal due
84 to the fact that these areas have not been sufficiently studied, and to the lack of
85 comprehensive works on tropical cave spiders (see Peck 1999; Bloom et al. 2014;
86 Mammola and Isaia 2017a). While Culver and Pipan (2009a) reported about 30 species of
87 eyeless troglobiont tropical spiders, it is likely that a deep survey of taxonomic papers
88 would certainly disclose remarkable levels of diversity. For instance, cave-dwelling species
89 are abundant in tropical pholcids (e.g. Peck 1990; Gertsch and Peck 1992; Machado et al.
90 2011; Yao et al. 2015, 2016), with approximately 40 genera with troglophile species,
91 several genera with troglobionts (e.g. *Micropholcus*, *Ciboneya*, *Khorata*, *Pholcus*, *Uthina*),

92 and at least three genera including entirely eyeless species (*Aymaria*, *Anopsicus*,
93 *Metagonia*) (B. A. Huber, pers. comm. 2017).

94 Morphological and physiological adaptations in subterranean spiders are directly related to
95 progressive or regressive evolution and often include reduction or loss of cuticular
96 pigments, regression or loss of the eyes-apparatus, thinning of the integuments, elongation
97 of legs, heavy spination, reduction of the metabolic rate leading to higher resistance to
98 starvation, alteration of the circadian rhythm, reduction in fecundity, delayed maturity,
99 slower development, and the tendency to lay a smaller number of eggs (reviewed in
100 Mammola and Isaia 2017a). Phylogenetic studies suggest that these troglobiomorphic
101 traits have evolved several times independently in many spider lineages (e.g. Arnedo et al.
102 2007; Ledford et al. 2011).

103 Contrary to other continents, Europe has been sufficiently studied in its subterranean
104 fauna. Although not exhaustive, we provide the first comprehensive checklist of European
105 subterranean species of spiders. Our aims are to: i) synthesize the scientific knowledge on
106 spiders inhabiting caves and other subterranean habitats across Europe and ii) review the
107 current knowledge on their origin and geographic distribution. A glossary of the main terms
108 and acronyms related to the subterranean biology adopted in this text is presented in Table
109 1.

110

111 **II. HISTORICAL BACKGROUND**

112 The first descriptions of European spiders associated with caves date back to the second
113 half of the eighteenth century, when Clerck (1757) and Scopoli (1763) described some
114 poorly adapted species of *Nesticus* (Nesticidae), *Harpactea* (Dysderidae), *Metellina*
115 (Tetragnathidae) and *Holocnemus* (Pholcidae). A few decades later, Latreille (1804)
116 described the troglophile *Meta menardi* (Tetragnathidae), from specimens collected in

117 caves '[...] de la ville du Mans' in the Loire region (France). The latter species is well
118 known among cavers as a ubiquitous cave-dweller in the twilight zone of most European
119 caves.

120 The description of the first troglobiont spider was published in 1857, when Jørgen Matthias
121 Christian Schiödte (1812–1884) described *Stalita taenaria* (Dysderidae) from the Postojna
122 cave in Slovenia. According to the original description, *S. taenaria* shows some marked
123 troglobiomorphic traits, being eyeless—'*oculi nulli*'—and fully depigmented—'*abdomine*
124 *niveo*' (Schiödte 1847: 80).

125 These early insights into the subterranean habits of spiders were followed by several
126 descriptions of cave-dwelling species across Southern Europe (e.g., Keyserling 1862;
127 Simon 1872; Pavesi 1873; Simon 1881) (Figure 1). A significant leap forward in the
128 number of described European species is due to the French arachnologist Eugène Simon
129 (1848–1924), who named numerous cave adapted species—especially in the genus
130 *Troglohyphantes* (Simon 1884)—in his famous book "*Les arachnides de France*".

131 The beginning of the twentieth century saw a significant increase in European
132 spelobiological studies (Camacho 1992). During his entire career, Simon provided 58 valid
133 descriptions of cave-dwelling species (Simon 1901, 1907, 1910, 1911, 1914, 1929). Along
134 with Simon, the French speleobiologist Jean Baptiste Louis Fage (1883–1964) focused on
135 a variety of cave spider genera (Fage 1912, 1913, 1919, 1945), describing 27 valid
136 species and providing important insights on their origin and adaptations (Fage 1919,
137 1931). Concurrently, the diversity of subterranean spiders was being disclosed by
138 Władysław Jan Kulczyński (1854–1919) and Josef Kratochvíl (1909–1992) in the Balkans
139 (Kulczyński 1914; Kratochvíl 1934, 1935, 1936, 1938, 1939, 1948) and by Ludovico di
140 Caporiacco (1901–1951), Edouard Dresco (1907–2001) and Carl Friedrich Roewer (1881–

141 1963) in Italy (e.g. Caporiacco 1936, 1938, 1939, 1941; Dresco 1949, 1954, 1956, 1959;
142 Roewer, 1931, 1953).

143 In the second half of the twentieth century, Christa L. Deeleman-Reinhold and Paolo
144 Marcello Brignoli (1942–1986) described numerous European cave-dwelling species and
145 published some important syntheses on their origin and distribution (e.g., Brignoli 1970,
146 1971; Deeleman-Reinhold 1977, 1981). Subsequently, Carles Ribera and Christo
147 Deltchev, among others, focused mostly on the fauna of the Iberian and the Balkan
148 peninsulas (Ribera 1978, 2008, 2011; Deltchev 1979, 1988, 2004).

149 From the 1980s onward, subterranean spiders have been discovered in habitats other
150 than caves (Novak et al. 2012; Mammola et al. 2016c). In particular, subterranean spiders
151 have been collected extensively in the deep strata of taluses in central Europe (Růžička
152 1990, 1996; Růžička and Thaler 2002; Růžička and Klimeš 2005; Laška et al. 2011;
153 Rendoš et al. 2012, 2013; Růžička and Dolanský 2016) and in *Milieu Souterrain*
154 *Superficiel* (MSS) across the Iberian Peninsula (e.g., Ortuño et al. 2013; Jiménez-Valverde
155 et al. 2015), Romania (Nae and Ilie, 2004; Nae, 2008) and Bulgaria (Deltchev et al. 2011).

156 These independent discoveries testified the natural occurrence of subterranean spiders in
157 the network of fissures (scree, rock cracks, etc.), the size of which is not commensurable
158 with the human scale (Culver and Pipan 2009b, 2014; Mammola et al. 2016c).

159 In the last few years, several new species have been described in southern Europe (e.g.,
160 Isaia and Pantini 2008, 2010; Wang and Li 2010a, 2011; Deltchev and Čurčić 2011;
161 Gasparo 2011; Ribera and López-Pancorbo 2011; Bosmans and Gasparo 2015; Ribera
162 and Mas 2015; Mammola et al. 2016b; Wu et al. 2016; Isaia et al. 2017; Pavlek and Ribera
163 2017), including the first European record of Symphytognathidae (Cardoso and Scharff
164 2009). Studies on European subterranean spiders continues to gain momentum and it is
165 reasonable to expect that new species will be discovered in the future, as proven by the

166 accumulation curve of species descriptions, which is far from reaching the asymptote
167 (Figure 1).

168

169 **III. THE CHECKLIST OF EUROPEAN SUBTERRANEAN SPIDERS**

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171 We relied on the online taxonomic resources on spiders (Nentwig et al. 2017; WSC 2017)
172 and the associated literature data in order to compile the checklist of the European
173 subterranean spiders. In the absence of detailed information on the epigean/hypogean
174 distribution and the natural history of the taxa of interest (Trajano and Carvalho 2017), we
175 based the ecological classification of species (troglonbionts or troglonbioniles as defined in
176 Table 1) on troglonbionmorphic traits reported in the original description of each species.
177 When available, ecological information was also considered. We acknowledged that in
178 many circumstances boundaries between categories can be vague; however, we intended
179 to provide a general indication of the degree of subterranean adaptation of European
180 spiders, which can be useful to delineate general patterns and considerations.

181 Regarding the countrywide distribution of each species, we relied on Nentwig et al. (2017),
182 whereas we derived the global distribution from the WSC (2017). We included all
183 European countries, as defined in Spiders of Europe (Nentwig et al. 2017). However, we
184 excluded the Azores, Madeira, and Canary Islands from the checklist as their insularity
185 leads to different processes which shape regional diversity.

186 The comprehensive checklist is reported in the Supporting information Table S1. Overall,
187 we identified 195 troglonbiont (Figure 2) and 291 troglonbionile species (Figure 3), distributed
188 altogether in 92 genera across 22 families (Table 2). A number of these species are poorly
189 described, given that many descriptions (ca. 60 species) are based on a single sex and/or
190 lack diagnostic illustrations.

191 Around 90% of European cave spiders show a restricted distribution, being found
192 exclusively in one country. The remaining 10% have a more widespread distribution,
193 ranging across multiple countries. At least three cave-dwelling species are alien to Europe
194 (see section V).

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197 **IV. BIOGEOGRAPHY OF SUBTERRANEAN SPIDERS**

198 Although modern biogeographical studies on subterranean spiders based on statistic
199 inference are virtually absent, previous authors made some contributions on the matter,
200 focusing on the general species-distribution patterns in Europe (e.g., Brignoli 1970,
201 1971a,b, 1972, 1973; Deeleman-Reinhold 1978, 1981; Deeleman-Reinhold and Deeleman
202 1980; Deltchev 1978, 2011; Koponen 1993; Ribera and Juberthie 1994; Gasparo and
203 Thaler 2000; Ribera 2004; Cardoso 2012a).

204 The diversity of subterranean spiders is unevenly distributed in Europe (Figure 4). It has
205 been suggested that past climatic events of biogeographical importance played the most
206 important role in determining the European pattern of subterranean spider biodiversity.
207 Traditionally, the theory of relicts and refuges, or climate relict hypothesis (Holsinger 1988;
208 Botosaneanu and Holsinger 1991), has been used to explain subterranean radiation in
209 temperate regions (reviewed in Culver and Pipan 2010). This theory suggests that long-
210 term climatic changes, in particular the Pleistocene glaciations (1.806–0.011 Mya),
211 prompted the colonization of the subterranean habitat and caused the obliteration of
212 surface-dwelling populations. The dramatic impacts due to ice masses north of the Alps
213 and the Carpathians (Holdhaus 1932; see paleo-reconstructions in Ehlers et al. 2011)
214 explain the low diversity of troglobiont spiders at northern latitudes (Růžička et al. 2013).
215 Accordingly, spider faunal assemblages in Northern Europe primarily consist of species

216 showing minor exaptations to the subterranean life, which possibly recolonized the
217 subterranean habitat after the glacial retreat (Růžička 1999; Figure 4a). Many of these
218 species are indeed widely distributed in Europe—e.g. *Palliduphantes pallidus* (O. Pickard-
219 Cambridge), *Meta menardi*, *Metellina merianae* (Scopoli), *Nesticus cellulanus* (Clerck) and
220 *Porrhomma convexum* (Westring)—reaching northern latitudes up to Fennoscandia and
221 the Arctic circle (e.g., Hippa and Koponen 1988; Koponen 1993; Fritzén and Koponen
222 2011). According to different authors (Ransy and Dethier 2006; Carter et al. 2010), the only
223 troglobiomorphic spider found at northern latitudes is *Porrhomma rosenhaueri* (L. Koch),
224 with scattered records from across central and eastern Europe (e.g. Thaler and Plachter
225 1983; Ransy and Dethier 2006; Růžička et al. 2011, 2013; Staudt et al. 2013; Nentwig et
226 al. 2017).

227 Meanwhile, glaciation cycles prompted the migration of cold-adapted species in Southern
228 Europe and simultaneously shaped the distribution of several preexistent troglobiont
229 species in the Alps and the Pyrenees, which survived in refugial areas found in the
230 periphery of the ice shields. For instance, this pattern is well exemplified by
231 troglobiomorphic species of *Troglohyphantes* in the Alps, occurring almost exclusively in
232 areas devoid from glaciers (Mammola et al 2015; Mammola et al. 2017a). On the other
233 hand, glacial dynamics fail to elucidate the diversity of troglobiomorphic species of
234 Dysderidae, Nesticidae and Leptonetidae in the Mediterranean basin, such as in the
235 Balkans, southern Italy, southern Iberian Peninsula and most Mediterranean islands. Other
236 climatic events, such as the Messinian Salinity Crisis (Culver and Pipan, 2010), seem to be
237 responsible for having driven the speciation process.

238 In general, biogeographic factors alone appear insufficient to explain the European pattern
239 of diversity. For instance, Culver et al. (2006) demonstrated the existence of a mid-latitude
240 ridge of high subterranean diversity in Europe, which is likely related to long-term surface

241 productivity. Thus, a higher surface productivity would parallel a higher radiation of spiders
242 in subsurface habitats. According to different authors (e.g. Christman and Culver 2001;
243 Niemiller and Zigler 2013), habitat availability—measured as the amount of caves in an
244 area—is also correlated to subterranean species richness. It is evident that highest
245 diversity of troglobiont spiders is concentrated in the karstic regions, which have a more
246 abundant and directly accessible habitat (see Christman and Culver 2001; Christman et al.
247 2005). This pattern is not only very clear, but also remarkable in the Dinarides, one of the
248 most important European karstic hot-spot (Bregović and Zigmajster 2016). However, it
249 remains unclear whether this is a true biological pattern or a sampling artifact (Christman
250 et al. 2016). In addition, the scarcity of studies investigating MSS (Mammola et al. 2016c),
251 as well as the paucity of speleobiological prospections in non-carbonate substrates across
252 Europe, may represent a further problem in determining a general pattern.

253 The majority of troglobiont spiders in Europe show a very restricted distribution range
254 when compared to epigean spiders (Cardoso, 2012). On the other hand, troglophiles
255 generally show wider ranges of distribution (see Supporting information Table S1). In fact,
256 several troglophile spiders are widespread in European caves (Deltchev 2011). These are
257 mostly Linyphiidae (e.g., *Palliduphantes pallidus*, *Porrhomma convexum*), Nesticidae [e.g.,
258 *Nesticus cellulanus*, *Kryptonesticus eremita* (Simon)] and Tetragnathidae (e.g., *Meta*
259 *menardi*, *Metellina meriana*). Although these species show some subterranean
260 adaptations and are commonly reported in caves, they are also able to disperse outside,
261 colonizing numerous extra-cave habitats with similar microclimatic conditions.

262 Cardoso (2012a) pointed out that spider species richness in caves is orders of magnitude
263 lower than in neighbouring epigean habitats. While associations of troglobiont and
264 troglophile spiders are frequent, the coexistence of multiple troglobionts in the same cave
265 is less common. Some remarkable examples have been documented in Europe, especially

266 in the Dinarides. For instance, Culver and Sket (2000) reported the presence of 9 arachnid
267 species coexisting in the Postojna-Planina hypogean system in Slovenia, and 10 in the
268 Pesteria de la Movile cave in Romania (Culver and Sket 2000).

269 The co-occurrence of two or more congeneric species within a single cave is even rarer,
270 and it is often mediated by niche partitioning. In Alpine *Pimoa* (Pimoidae), the coexistence
271 of species was observed for the troglophiles *P. delphinica* and *P. graphitica*, with
272 individuals of the two species sharing the same caves and showing evidence of
273 interspecific gene flow (Mammola et al. 2016b). There are some cases of *Porrhomma*
274 (Linyphiidae) coexisting in the same cave or MSS (e.g., Růžička 1990; Bedek et al. 2013;
275 Růžička and Dolanský 2016). Furthermore, the presence of two congeneric
276 *Troglohyphantes* has been recorded in a few caves in Slovenia, Croatia (Deeleman-
277 Rehinold 1978), and in the Western Italian Alps (Isaia and Pantini 2010; Isaia et al. 2011,
278 2017). Typically, the co-occurrence of more species of *Troglohyphantes* occurs exclusively
279 between phylogenetically distant lineages with different degrees of troglomorphism (Isaia
280 et al. 2017).

281

282

283 **V. TAXONOMIC ACCOUNT**

284 Such as other cave-dwelling taxonomic groups (Gibert and Deharveng 2002),
285 subterranean spiders represent filtered subsamples of regional species pools. However,
286 with the notable exception of the Iberian Peninsula (Cardoso 2012a), the extent of the
287 epigean/hypogean community turnover has never been determined.

288 Currently, 63 families of spiders have been reported in Europe (Nentwig et al. 2017; Figure
289 5), of which *circa* one third has representatives underground, either troglophiles or
290 troglobionts (Figure 6). The taxonomic disharmony in European cave species

291 assemblages is reflected, among other examples, by the lack of cave-adapted
292 Mygalomorphs. Mygalomorphs are represented in Europe by three families of trap-door
293 spiders (Ctenizidae, Nemesiidae, Cyrtaucheniidae), with the addition of a few species of
294 Theraphosidae. Tentatively, Mygalomorphs are among the largest European spiders, a
295 factor that may have hindered their adaptation to energy-poor environments. Moreover, it
296 is likely that many caves lack appropriate substrates in which to dig burrows. Conversely,
297 in other world regions various species of cave Mygalomorphs have been reported
298 (Mammola and Isaia, 2017a), especially in the tropics (e.g. Bertani et al. 2013; Maroquín
299 2014; Fonseca-Ferreira et al. 2017), where energy inputs in caves are generally higher.
300 Unsurprisingly, families mostly relying on sight for preying, such as active and ambush
301 hunters (e.g. Lycosidae, Oxyopidae, Salticidae and Thomisidae), are also lacking in
302 European caves as well as in the rest of the world (Mammola and Isaia 2017a). Notable
303 exceptions are three species of eyeless Lycosidae, two in Hawaii (Gertsch 1973a) and one
304 in French Polynesia (Framenau and Lehtinen 2014). In addition, it has been suggested that
305 an active lifestyle is not a good adaptation to cave life, as it requires much energy
306 compared to a sit-and wait strategy (e.g. Cardoso 2012a). An exception is found in
307 Dysderidae which, despite displaying an active hunting lifestyle, are particularly diversified
308 in Southern European caves and Shallow Subterranean Habitats (SSHs) (e.g., Deeleman-
309 Reinhold and Deeleman 1988; Gasparo and Thaler 2000; Arnedo et al. 2007; Cardoso
310 2012a; Macías-Hernández et al. 2016).

311 In comparison to other temperate regions, in European subterranean habitats some
312 families are well represented while others are not. A clear example can be found in the
313 family Dictynidae, which had notable radiations in the North American (e.g. Paquin and
314 Dupérré 2009; Hedin 2015) and Asian karstic areas (e.g. Li and Wang 2017), while they
315 are almost lacking in European subterranean habitats.

316 Conversely, the Dysderidae, Leptonetidae, Linyphiidae, and Nesticidae—including most
317 European troglobionts—are ubiquitously found across karstic areas in southern Europe
318 and other temperate regions worldwide (e.g., Brignoli 1970; Gertsch 1974, 1984; Lehtinen
319 and Saaristo 1980; Miller 2005; Reddell 2005; Ledford et al. 2011, 2012; Lin et al. 2016).

320 The Dysderidae are renowned for their occurrence in subterranean habitats and include
321 numerous troglobionts, especially in the Dinaric karst and in the Iberian Peninsula (e.g.,
322 Deeleman-Reinhold & Deeleman, 1988; Gasparo & Thaler, 2000). Troglobiont-rich genera
323 include *Dysdera*, *Folkia*, *Harpactea*, *Mesostalita*, *Minotauria*, *Parastalita*, *Rhode*,
324 *Speleoharpactea*, *Stalagtia*, and *Stalita*.

325 The Linyphiidae include numerous species associated with caves and several troglobionts
326 in the genus *Antrohyphantes* (Balkan peninsula), *Centromerus* (Iberian Peninsula, Italy,
327 Balkans), *Lepthyphantes* (Iberian Peninsula, Romania), *Palliduphantes* (Balkans, Italy,
328 Spain), *Troglohyphantes* (Alps, Balkans, Cantabrian Mountains, Carpathian, Pyrenees),
329 and *Typhlonypbia* (Dalmatia). The genus *Troglohyphantes*, in particular, is the European
330 spider taxon that underwent the largest radiation in caves (Deeleman-Rehinold 1978;
331 Deltchev 2008; Isaia et al. 2011, 2017). It currently includes 127 species (WSC, 2017), of
332 which at least 72 are troglobionts.

333 Leptonetidae are commonly found in subterranean habitats across the Mediterranean
334 basin (Brignoli 1970). Most of the species are troglophiles, but troglobionts can be found in
335 France (*Leptoneta*), Iberian Peninsula (*Teloleptoneta* and *Leptoneta*), Italy
336 (*Protoleptoneta*), and the Balkan Peninsula (*Barusia*, *Cataleptoneta*, *Leptonetela*, and
337 *Sulcia*).

338 Nesticidae are renowned for their hypogean adaptations, being often found in underground
339 ecosystems in the Mediterranean basin (Ribera et al. 2014). Troglobiont-rich genera
340 include *Carpathonesticus*, *Kryptonesticus*, *Nesticus* and *Typhlonesticus*, the latter

341 consisting exclusively of troglobionts. Notably, in Europe both Leptonetidae and Nesticidae
342 appear to be more diverse in subterranean than in epigean habitats (Figure 6).

343 Hahniidae, Liocranidae, Pholcidae, Agelenidae, Telemidae and Symphytognathidae also
344 include a number of troglobionts. Hahniidae include a few anophtalmic species in the
345 genus *Hahnia* and *Iberina*, which are found in the Pyrenees, Romania and Caucasus.
346 Troglobiomorphic Liocranidae are found in the genus *Agroecina* (Romania) and
347 *Cybaeodes* (Sicily and Iberian Peninsula). Other troglobionts are found in Agelenidae
348 (*Hadites* and *Histopona*) and Pholcidae (*Stygopholcus* and *Hoplopholcus*).

349 The troglobiont spiders listed so far belong to genera (or at least families) sharing the
350 same geographic area with congeneric surface-dwelling species. This pattern suggests
351 that, from a phylogenetic point of view, most European cave species did not originate from
352 deep, ancient cladogenetic events. Exceptions are found in Telemidae and
353 Symphytognathidae, which are monospecific in Europe. For this reason, *Telema tenella*
354 Simon (Telemidae) and *Anapistula ataecina* (Symphytognathidae) are considered the only
355 true relict species in European caves, ancient representatives of families with tropical
356 origins which once occupied Europe (Fage 1931; Cardoso and Scharff 2009). *T. tenella* is
357 found in the Oriental Pyrenees and in the province of Gerona (Juberthie 1985; Ribera and
358 Mateos 2000; Wang et al. 2012). Worldwide, the genus *Telema* consists of an additional
359 39 species, found in Guatemala (Gertsch 1973b) and East- and Southeast-Asia (WSC,
360 2017), including several cave-dwelling representatives (e.g., Zu and Chen 2002; Chen and
361 Zu 2009; Lin et al. 2009, Wang and Li 2010b; Zhang and Li 2014). *A. ataecina* was
362 recently discovered in few caves of the Frade cave system in Portugal (Cardoso and
363 Scharff 2009). The genus includes subterranean species from Western Australian caves
364 (e.g., Harvey 1998).

365 Finally, at least three cave-associated species are alien to Europe, namely *Psilochorus*
366 *simoni* (Berland) (Pholcidae), *Nesticella mogera* (Yaginuma) and *Eidmannella pallida*
367 (Emerton) (Nesticidae) (Nentwig 2015; Mammola 2017; Nentwig et al. 2017). *P. simoni* is
368 native to North America and it has been introduced in Europe at least once, being now
369 established in several European countries (Fürst and Blandenie 1993; Nentwig et al.
370 2017). It is commonly found in caves and other artificial habitats, especially mines
371 (Kostanjšek and Ramšak 2005; Isaia et al. 2011). *Nesticella* spiders are of Asian descent.
372 *N. mogera* was recently recorded in a few European countries (e.g., Kielhorn 2009; Bielak-
373 Bielecki and Rozwałka 2011; Nentwig et al. 2017). *E. pallida* is a cosmopolitan species of
374 tropical and subtropical areas, having been accidentally introduced into greenhouses and
375 similar habitats (Nentwig et al. 2017). It is now commonly found in caves and greenhouses
376 of the Madeira, Canary and Balearic Islands and in the southeastern Iberian Peninsula
377 (Ribera, unpublished data). To our knowledge, no studies have been conducted to attest
378 potential negative impacts on native spider communities in caves.

379

380 VII. FUTURE LINES OF RESEARCH

381 Several questions concerning the biogeography of subterranean spiders in Europe remain
382 mostly unanswered. In this perspective, the checklist of European cave-dwelling spiders
383 herein provided aims at setting a baseline for speleobiological, arachnological and
384 biogeographical studies. We report a number of long-standing questions, hoping to
385 stimulate future research on subterranean spiders.

386

387 i) *Phylogeographical patterns*. Research is needed to shed light on the diversification and
388 origin of the European cave fauna and to understand which are the closest extant relatives
389 of cave obligate species. In particular, establishing empirical phylogenetic patterns of cave

390 species using broad taxonomic samples—both cave and epigean species—appears to be
391 a promising line of enquiry.

392

393 ii) *Ecological drivers of subterranean spiders*. It is still unclear whether species richness
394 and diversity of subterranean spiders in European subterranean habitats are driven by
395 macro-scale (e.g. latitude, past glacial dynamics, macroclimate) or micro-scale parameters
396 (e.g. geology, cave dimension, trophic resources).

397

398 iii) *Functional groups*. In terms of foraging guilds (*sensu* Cardoso et al. 2011), a functional
399 disharmony is often observed in cave-dwelling spiders, with entire guilds being scarcely
400 represented, if not absent, in caves. With the exception of the Iberian Peninsula (Cardoso,
401 2012) there are, however, no studies on functional assemblages of subterranean spider
402 communities.

403

404 iv) *Competition and niche partitioning*. Being top-predators, several species of spiders
405 compete with each other for space and resources in subterranean habitats. In Europe, it
406 has been demonstrated that, at a local scale, there is competition between congeneric
407 *Meta* spiders (Mammola and Isaia 2014), in *M. menardi* and *Metellina merianae* (Bourne
408 1976, 1977; Novak et al. 2010) and in *M. menardi* and *Pimoa graphitica* (Mammola et al.
409 2016a). However, further studies have to be conducted to better understand how
410 competition between cave-dwelling spiders influences the large scale distribution,
411 especially in high dispersal troglophile species (Mammola et al. 2015; Mammola and Isaia,
412 2017b).

413

414 v) *Other interspecific relationships*. According to Culver and Pipan (2009a), the peculiar
415 conditions found in subterranean habitats limit the risk of predation. However, other
416 asymmetrical interspecific interactions, such as parasitoidism (e.g. Dipterans and
417 Hymenopterans) and parasitism (e.g. fungi and other pathogens), have been rarely
418 investigated. Moreover, the effect of interspecific relationships on distributional patterns
419 (e.g. overlap between parasites/parasitoids and their hosts) has never been considered.

420

421 vi) *Effects of future climate change on distribution patterns*. Climatic-driven changes in the
422 distribution range of most subterranean species have been seldom studied (e.g.,
423 Brandmayr et al. 2013; Brandmayr and Pizzolotto 2016; Sánchez-Fernández et al. 2016;
424 Mammola and Leroy 2017). Regarding spiders, significant latitudinal shifts are expected
425 within high dispersal species (Mammola 2017; Mammola and Isaia 2017b). On the other
426 hand, contractions in the distribution range can be expected within most restricted
427 cryophilic *taxa* (Mammola et al. 2017a). Ecological hypotheses about the effect of climate
428 change on organisms dwelling in stable habitats, such as caves, represent a challenging
429 and fast-moving field of research.

430

431 vii) *Assessing the conservation status of subterranean spiders*. The status of conservation
432 of most subterranean spiders is unknown, given that a few species have been assessed
433 according to the IUCN criteria (Cardoso 2010; Cardoso and Hilton-Taylor 2015; IUCN
434 2017; Borges et al. 2016; Mammola et al. 2017b; Cardoso et al. 2017). Of these, most
435 assessments are now outdated, having been made before the adoption of the current
436 criteria in 2001, and thus not comparable with the current criteria. Therefore, there is an
437 urgent need for IUCN assessments of European subterranean species and the

438 development of specific conservation programmes (Martín et al. 2010; Borges et al. 2012;
439 Cardoso et al. 2011, 2016, 2017; Cardoso 2012b; Mammola and Isaia 2017a).

440

441 **VIII. CONCLUSIONS**

442 In a recent review on the status of biodiversity studies in subterranean habitats, Culver and
443 colleagues argued that (2013:49) "[...] *perhaps the time is right for a large-scale global*
444 *assessment of subterranean biodiversity*". With respect to subterranean spiders, we
445 believe that the current paucity of information on the distribution of most species—
446 especially in the tropics—delays global understanding of their diversity and its thorough
447 comparison across different biogeographic areas . On a more positive note, this work
448 demonstrates that information found in literature can be extracted and summarized in
449 order to provide a reliable baseline to unravel biogeographic patterns—at least in areas
450 where the subterranean fauna is relatively well documented. This is also possible thanks
451 to the extensive online spider taxonomic catalogues (Nentwig et al. 2017; WSC 2017), with
452 current nomenclature, updated synonymies, associated literature and distributional data—
453 however, such data is currently missing for most large arthropod orders and classes.
454 Although most macroecological questions about subterranean spiders are still
455 unanswered, there is a strong potential for fast advancements in our understanding of their
456 diversity patterns, processes and of the evolution of life in caves.

457

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464

465 **CONFLICT OF INTEREST**

466 The authors disclose any actual or potential conflict of interest

467

468 **SUPPORTING INFORMATION**

469 **Table S1.** Checklist of the European subterranean spiders.

470

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1086 **TABLES**

1087 **Table 1.** Definition of main terms and acronyms related to the subterranean biology
 1088 adopted in this text.

Term	Acronym	Definitions adopted herein	Reference(s)
Troglobiomorphism	-	The complex of morphological and physiological adaptations to the subterranean environmental conditions.	Juberthie and Decu 1994
Troglobiont	TB	An organism strictly bound to the hypogean habitat, clearly exhibiting subterranean adaptations.	Sket 2008
Troglophile	TF	Organisms which are able to maintain stable subterranean populations (eutroglophile) or are inclined to inhabit subterranean habitats, being however intimately associated with epigean habitats for some biological functions (subtroglophile).	
Trogloxene	-	An epigean species occurring accidentally underground.	
Shallow—or Superficial—Subterranean Habitats	SSH	The aphotic subterranean habitats close to the surface, harboring species with troglobiomorphic traits, namely hypotelminorheic habitats, epikarst, lava tubes, deep leaf litter, deep soil strata and the MSS.	Culver and Pipan 2009b, 2014
<i>Milieu Subterrain Superficiel</i>	MSS	A terrestrial SSH represented by the underground network of empty air-filled voids and cracks harboring species with troglobiomorphic traits.	Mammola et al. 2016c

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1096 **Table 2.** Spider families occurring in subterranean habitats across Europe, with current
 1097 number of genera and species. Total number of genera for each family are derived from
 1098 Spiders of Europe (Nentwig et al. 2017).

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Family	Hypogean elements		Total in Europe		Notes
	Gen.	Sp.	Gen.	Sp.	
Agelenidae	5	40	19	220	Mainly troglaphiles. Troglaphionts in <i>Histoona</i> and <i>Hadites</i> .
Amaurobiidae	1	3	4	39	Some troglaphiles in <i>Amaurobius</i> .
Anapidae	2	3	3	5	Some weakly adapted species in MSS habitats.
Cybaeidae	1	1	4	15	<i>Cybaeus vignai</i> is the only species showing troglaphiomorphic traits.
Dictynidae	3	4	19	69	Some troglaphile species in the genus <i>Cicurina</i> , <i>Chorizomma</i> and <i>Mastigusa</i> .
Dysderidae	16	56	22	372	Many troglaphiont species mostly distributed in the Mediterranean basin.
Filistatidae	1	1	3	11	<i>Filistata insidiatrix</i> often at the cave entrance.
Hahniidae	2	3	8	34	Troglaphionts in <i>Hahnia</i> and <i>Iberina</i> .
Leptonetidae	8	60	8	69	Numerous genera with troglaphiles and troglaphionts.
Linyphiidae	28	222	217	1231	Several troglaphiont-rich genera (e.g. <i>Centromerus</i> and <i>Troglaphyphantes</i>).
Liocranidae	2	5	12	53	Troglaphionts in <i>Cybaeodes</i> and <i>Agraecina</i> .
Mysmenidae	1	1	3	4	<i>Trogloneta granulum</i> in bare-colluvial MSS.
Nesticidae	6	50	7	55	Different genera, all mostly related to caves. Troglaphiles and troglaphionts.
Pholcidae	6	20	12	44	Mostly troglaphiles. Troglaphiomorphic species in <i>Hoplopholcus</i> and <i>Stygopholcus</i> .
Pimoidae	1	4	1	4	Only represented in Europe by the genus <i>Pimoa</i> , troglaphile.
Segestriidae	1	2	2	18	Two species of <i>Segestria</i> found in caves.
Sicariidae	1	1	1	2	<i>Loxosceles rufescens</i> often associated with caves and other SSH.
Sparassidae	1	1	5	15	<i>Heteropoda variegata</i> often associated with caves.
Symphytognathidae	1	1	1	1	Only represented in Europe by <i>Anapistula ataecina</i> (relict species, troglaphiont).
Telemidae	1	1	1	1	Only represented in Europe by <i>Telema tenella</i> (relict species, troglaphiont).
Tetragnathidae	2	3	4	32	Troglaphiles in <i>Meta</i> and <i>Metellina</i> , widespread in European caves.
Theridiidae	3	5	46	228	Troglaphile species in <i>Episinus</i> , <i>Robertus</i> and <i>Rugathodes</i>
Total (22)	93	486	402	2522	See Supporting information Table S1 for the complete checklist.

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1103 **FIGURES LEGEND**

1104 **Figure 1.** Number of subterranean spider species described from 1757 to 2015.

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1106 **Figure 2.** Examples of the diversity of spiders in European subterranean habitats—
1107 troglobionts. **a)** *Hadites tegenarioides* Keyserling (Agelenidae); **b)** *Stalagtia*
1108 *hercegovinensis* (Nosek) (Dysderidae); **c)** *Stygopholcus absoloni* (Kulczyński) (Pholcidae);
1109 **d)** *Troglohyphantes* sp. (Linyphiidae) **e)** *Stalita pretneri* Deeleman-Reinhold (Dysderidae);
1110 **f)** *Sulcia* sp. (Leptonetidae)—note the typical violet reflexes on the legs, a useful character
1111 for distinguishing Leptonetidae in the field; **g)** *Typhlonesticus absoloni* (Kratohvíl)
1112 (Nesticidae); **h)** *Typhlonyphia* sp. (Linyphiidae). Photo credits/by curtesy of: **a,d,h:** Tin
1113 Rožman; **b,c,e,f,g)** Martina Pavlek.

1114

1115 **Figure 3.** Examples of the diversity of spiders in European subterranean habitats—
1116 troglophiles. **a)** *Loxosceles rufescens* (Dufour) (Siicaridae); **b)** *Palliduphantes pallidus* (O.
1117 P.-Cambridge) (Linyphiidae); **c)** *Pimoida graphitica* Mammola, Hormiga and Isaia
1118 (Pimoidae); **d)** *Nesticus cellulanus* (Clerck) (Nesticidae) **e)** *Porrhomma convexum*
1119 (Westring) (Linyphiidae); **f)** *Meta menardi* (Latreille) (Tetragnathidae); **g)** *Hoplopholcus*
1120 *labyrinthi* (Kulczyński) (Pholcidae); **h)** *Tegenaria* sp. (Agelenidae). Photo credits/by curtesy
1121 of: **a–c,f,h:** Francesco Tomasinelli (**b** and **f** in Isaia et al. 2011) **d:** Enrico Lana (in Isaia et
1122 al. 2011); **e:** Mauro Paschetta (in Isaia et al. 2011); **g:** Fulvio Gasparo (in Nentwig et al.
1123 2017).

1124

1125 **Figure 4.** Distribution of troglophilic (**a**) and troglobitic (**b**) spiders in Europe. For each
1126 country, shades of grey indicate number of species (see legend).

1127

1128 **Figure 5.** Family charts of European spiders and cave-dwelling spiders, with reference to
1129 troglobionts and troglophiles.

1130

1131 **F**

1132 **i**

1133 **g**

1134 **u**

1135 **r**

1136 **e**

1137

1138 **6**

1139 **.**

1140

1141 **P**

1142 **r**

1143 **o**

1144 **p**

1145 **o**

1146 **r**

1147 **t**

1148 **i**

1149 **o**

1150 **n**

1151

1152 **o**

1153 **f**

1154

1155 **e**