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Spiders in caves

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Authors contribution

SM conceived the study, led the writing, prepared figures; MI revised the manuscript, prepared figures. Both authors gave final approval for publication.

Competing interests

We have no competing interests.

24 **Abstract**

25 World experts of different disciplines, from molecular biology to macro-ecology, recognize the value
26 of cave ecosystems as ideal ecological and evolutionary laboratories. Among other subterranean
27 taxa, spiders stand out as intriguing model organisms for their ecological role of top-predators, their
28 unique adaptations to the hypogean medium and their sensitivity to anthropogenic disturbance.
29 Since the description of the first eyeless spider (*Stalita taenaria*), an array of papers on
30 subterranean spider biology, ecology and evolution has been published, but a comprehensive
31 review on these topics is still lacking. We provided a general overview of the spider families
32 recorded in hypogean habitats worldwide, we reviewed the different adaptations of hypogean
33 spiders to subterranean life, and we summarized the information gathered so far about their origin,
34 population structure, ecology, and conservation status. Finally, we pointed out the limits of the
35 knowledge we currently have regarding hypogean spiders, aiming to stimulate future research.

36

37

38 **Keywords:** Araneae, Subterranean Biology, Evolution, Hypogean habitat

39 **I.BACKGROUND**

40 Spiders are a very diverse group of arthropods dating back to the Late Carboniferous [1],
41 and comprising more than 46,000 described species [2]. They are considered one of the
42 most successful groups of organisms in terms of evolutionary radiation [3,4] and ecological
43 plasticity [5], as they have virtually colonized all terrestrial habitats, including subterranean
44 ones.

45 A number of spider taxa underwent remarkable diversification in hypogean habitats (Figure
46 1), showing unique adaptations and exhibiting a wide variety of functional and
47 morphological diversity [6,7]. The smallest female spider ever described (*Anapistula*
48 *ataecina* Cardoso & Scharff; ~0.4 mm [8]) as well as the largest one (*Heteropoda maxima*
49 Jäger; legspan of ~30 cm [9]) provide two appropriate examples of the extraordinary
50 morphological diversity of subterranean spiders.

51 The peculiar habits of hypogean spiders have been intriguing scientists for a long time, as
52 they served as models for physiological [10–12], ecological [13–17], ethological [18,19]
53 and biogeographical studies [20–22]. However, compared to other hypogean organisms,
54 the potential of subterranean spiders is still under-expressed. The paucity of studies is
55 related to the general lack of a state-of-the-art on subterranean spider biology, ecology
56 and evolution, conceivably hindering advances in knowledge.

57 In this review, we present a collection of information about spiders colonizing subterranean
58 habitats—especially caves—and discuss their relevance in the understanding of cave life
59 evolution and the ecology of subterranean animal communities.

60

61

62

63 (1) Terminology and acronyms

64 We define *troglobiomorphism*—or *troglobiomorphic* traits/features—as the complex of
65 morphological and physiological adaptations to the subterranean environment [23].

66 Despite the fact that ecological categorizations often oversimplify real cases and
67 boundaries between categories can be vague, for the sake of this review, we use the
68 traditional biospeleological categories [24] to characterize the level of subterranean
69 adaptation:

70 i) a *troglobiont*—or *troglobite*—exhibits distinct adaptations to the subterranean
71 environment, such as depigmentation and eye regression;

72 ii) a *troglophile* generally shows moderate adaptations to subterranean conditions.

73 Although it strongly relies on hypogean habitats, its life-cycle is not exclusively linked to
74 the specific conditions found in these environments.

75 iii) a *trogloxene* is found in caves due to indirect causes.

76 Superficial Subterranean Habitats (SSHs) [25] are aphotic subterranean habitats close to
77 the surface, harboring species with troglobiomorphic traits, namely hypotelminorheic
78 habitats, epikarst, lava tubes, deep leaf litter, soil strata and the MSS—*Milieu Souterrain*
79 *Superficiel*. MSS is defined as the underground network of empty air-filled voids and
80 cracks developing within multiple layers of rocky fragments, usually covered by topsoil
81 [26].

82

83 II. TAXONOMY AND PHYLOGEOGRAPHY

84 The first scientific descriptions of spiders associated with caves date back to the second
85 half of the eighteenth century [2], when Clerck (1709–1765), Scopoli (1723–1788) and

86 Latreille (1762–1833) described some poorly adapted species of *Nesticus* (Nesticidae),
87 *Harpactea* (Dysderidae), *Meta* (Tetragnathidae) and *Holocnemus* (Pholcidae).
88 The description of the first true troglobiont spider dates back to 1857, when Schiödte
89 (1812–1884) described *Stalita taenaria* (Dysderidae) from the Postojnska cave in
90 Slovenia. *S. taenaria* shows remarkable troglbiomorphic traits, namely the absence of
91 eyes and a pronounced cuticular depigmentation [27]. The early insights into the world of
92 subterranean spiders paved the way for generations of scientists to disclose the huge
93 diversity hidden in caves and other subterranean habitats around the globe.
94 According to available estimations, ~1,000 troglbiomorphic spider species have been
95 described to date and classified as troglbionts [6,7]. In addition, a countless number of
96 species have been reported to be associated with caves. During our bibliographic survey,
97 we recorded spiders showing subterranean adaptations in at least 48 families—out of the
98 113 currently listed [2] (Table 1).
99 The appearance of troglbiomorphic features occurred multiple times during the 380
100 millions years of spider evolution, in mygalomorph and araneomorph families scattered all
101 over the spider tree of life (Figure 2). As well as most hypogean taxa [28], troglbiomorphic
102 spiders represent filtered subsamples of regional epigean species pools [17]. However
103 there are genera and families without epigean relatives, like Trogloraptoridae [29].
104 In terms of foraging guilds (*sensu* [30]), a functional disharmony is often observed, with
105 entire guilds being scarcely represented, if not absent, in caves—e.g., sensing web
106 weavers, ambush hunters. Aside from the notable exception of the Iberian Peninsula [17],
107 there are no extensive compilations about functional groups in subterranean spiders,
108 making it difficult to draw any general pattern.
109 Subterranean spiders are distributed in all continents but Antarctica. As for other
110 taxonomic groups [31], the core of the diversity is found in temperate regions—especially

111 in the northern hemisphere. In the tropics, around 40 species of eyeless spiders are
112 currently known, having been reported from caves in Central and South America [32–38],
113 Caribbean [39], Hawaii [40], Galapagos [41], Asia and Oceania [42–45]. In this regard, cave
114 fauna in the tropics is probably understudied [46] and it is likely that the number of tropical
115 troglobiont spiders will grow in the near future [39].

116

117 **III.SUBTERRANEAN ADAPTATIONS**

118 Species under the same selective pressure evolve convergent adaptive traits. Being
119 subjected to strong environmental filters, hypogean habitats are a remarkable example of
120 this phenomenon [47]. The primary limiting factors for subterranean species are the lack of
121 solar radiation and the scarcity of food resources—see [48] for an in-depth discussion. The
122 process of adaptation implies the evolution of well-defined and often convergent biological
123 traits [49,50]. Indeed, troglobiomorphic spiders share adaptive features found in other
124 groups of cave animals, supposedly due to of the strong and similar selective pressures
125 acting underground [51].

126 We here discuss the details on these adaptations, grouping them according to morphology,
127 physiology and behaviour.

128

129 **(1)Morphology**

130 Morphological adaptations in subterranean spiders are directly related to progressive or
131 regressive evolution. They include reduction or loss of cuticular pigments, eye regression
132 or loss, thinning of integuments, legs elongation and heavy spinulation [37,38,52–61].

133 Evidence suggest that pigmentation is the first character undergoing regression during the
134 process of adaptation to the subterranean environment (reviewed in [62]), whereas the

135 loss of pigment around the eyes and the progressive eye reduction represent a second
136 step in the adaptation process [53,61]. Given that in most spiders visual perception plays a
137 minor role in hunting and mating, eye reduction, rather than of other sensory organs, is
138 common [63]. Obvious exceptions include spider families relying on sight for prey capture
139 [40,55], such as Lycosidae—which include three troglobionts [45],—or Salticidae, which
140 lack troglobionts.

141 Compared to their epigeal relatives, cave species often develop longer legs [53,55,57,58].
142 However, caution should be exercised in generalizing this pattern, as leg elongation is
143 apparently a morphological feature depending on habitat size [64] and may not occur in
144 spiders inhabiting small interstices—see Ecology.

145 An interesting related aspect refers to intraspecific variation in troglomorphic traits, such
146 as eye reduction and depigmentation. For instance, intraspecific polymorphism was
147 documented in *Neoleptoneta* [65], *Cicurina* [66], *Troglohyphantes* [67] and *Porrhomma*
148 [60,61]. Variability in troglomorphic traits was documented both at a regional and local
149 scale, but a reasonable explanation for these patterns has never been provided. For
150 example, Ledford et al. [65] observed a range of variation between the populations of two
151 different species of *Tayshaneta* (Leptonetidae) found in central Texas along a latitudinal
152 gradient, "*from darkly pigmented, large-eyed individuals to lightly pigmented, reduced-*
153 *eyed forms to depigmented, blind individuals*". At a local scale individuals of
154 *Kryptonesticus eremita* (Simon) (Nesticidae) found in caves show variability in
155 pigmentation patterns within a single population depending on the distance from the
156 entrance [68].

157

158

159 (2)Physiology

160 Physiological adaptations pertain reduction of the metabolic rate, higher resistance to
161 starvation, alteration in circadian rhythm, reduction in fecundity, delayed maturity, slower
162 development, and the tendency to lay a smaller number of eggs, though larger [52–54,69].
163 However, quantitative studies aiming to shed light on these adaptations are scarce.

164 Observations conducted on different species kept in captivity showed a delayed
165 maturation of juveniles and longer life span [53,57,69], up to 12 years in *Telema tenella*
166 [69]. The eggsac of the latter species contains an extremely reduced number of eggs—3
167 or 4, rarely less—of relative large dimension (~0.4 mm [69]). Data referring to other
168 families align these results [8,52,70,71].

169 Deeleman-Reinhold [53] provided a comprehensive analysis on this topic, comparing size
170 and number of eggs/eggsacs in twenty regressed and non-regressed species of
171 *Troglohyphantes*. She observed fewer eggs in regressed species (mean=12.3 mm vs.
172 mean=16.8 mm in non-regressed species) of slightly larger size (mean=0.36 mm vs.
173 mean=0.41mm in non-regressed species). For comparison, a number of eggs/eggsacs
174 one order of magnitude higher has been documented in troglophile species able to
175 disperse outside caves [14,72,73].

176 Experimental and field data suggest that hypogean spiders have fine-tuned their
177 physiological tolerance to the constant and narrow temperature and relative humidity
178 ranges of their habitats over time. With the thinning of the integuments, subterranean
179 organisms are more prone to desiccation, and thus are preferentially associated with
180 humid microhabitats [74]. Experiments on adults and spiderlings of *Lycosa howarthi*
181 Gertsch provided evidence of a pronounced sensitivity to saturation deficit [10,11].

182 Moreover, several in-field studies statistically demonstrated that spiders prefer specific—
183 and often stable—climatic conditions [13–15,75]. Novak *et al.* [12] tested lower lethal
184 temperatures in various trogloniles and troglobionts, including spiders. He concluded that
185 while trogloniles retained their ability to withstand temperature variations, most
186 troglobionts lost their thermoregulatory mechanisms due to regressive evolution.
187 Accordingly, it has been suggested that subterranean ecosystems may present ideal
188 opportunities to study mechanisms underlying the responses to changes in climate, owing
189 to the fact that species within these ecosystems are often adapted to constant
190 temperatures [75].

191

192 **(3)Behavior**

193 Little is known about the behavior of subterranean species, as in most cases the rarity of
194 species often precludes anything but empirical observations. Documented observations in
195 spiders—mostly anecdotal [7]—primarily refer to reproductive behaviour [18,70,72,76].
196 Complex courtships were documented in trogloniles [18,72], whereas maternal care was
197 observed in troglobiontic Nesticidae [70,77]. Sociality in cave spiders was never
198 documented [19]. Non-territorial 'subsociability', in the form of free movements of the spiders
199 inside and between interconnected webs, was tentatively proposed for *Goeldia zygierae*
200 Almeida-Silva, Brescovit & Dias (Titanocidae), a troglonile inhabiting Brazilian caves
201 [72].

202

203 **IV.ORIGIN—SUBTERRANEAN EVOLUTION**

204 Available phylogenetic studies suggest that troglobiomorphic traits have evolved several
205 times independently [59,65] (Figure 2).

206 The origin of troglobionts is generally explained by two major theories. The theory of active
207 colonization [78] or adaptive shift hypothesis [10], puts emphasis on the process of active
208 colonization of the hypogean domain, being the species driven by the opportunity to
209 occupy new, unexploited ecological niches. Active colonization generally refers to
210 hypogean speciation in tropical areas [41], but the same theory applies in temperate
211 regions.

212 On the other hand, the theory of relicts and refuges, or climate relict hypothesis [79,80],
213 puts emphasis on long-term climatic changes, such as glaciation cycles, indicating them
214 as the main factors prompting the colonization of the subterranean habitat, meanwhile
215 causing the obliteration of surface-dwelling populations [81]. Climate relict hypothesis
216 explains the origin of troglobiont spiders in temperate regions [20–22,60,75,82]. This point
217 of view is supported by the fact that tropical caves—not involved in Pleistocene glaciations
218 (1.806–0.011 Mya)—are not as rich in species as the ones in temperate areas. However, it
219 is worth noticing that these two theories are not incompatible, and it is likely that in some
220 cases they both played a role in hypogean speciation.

221 Whichever the causes and mechanisms, the processes are similar to primary successions
222 over time. At first, generalist pioneer species begin the colonization, being then gradually
223 replaced by specialized and competitive elements, highly efficient in resources
224 exploitation. Subterranean habitats are characterized by a constant flux of invaders and
225 migrants [47], with the colonization process starting from transitional zones in the vicinity of
226 the surface [56], including the SSHs [25]. In the first phases, organisms with adaptive traits
227 suitable for subterranean life—exaptations—are generally favoured. For example eye
228 reduction, depigmentation, and highly developed chemoreceptors in moss-, soil-, and litter-
229 dwelling spider species [21,53,60,65,83] generally promote the colonization of
230 subterranean habitats.

231 When the process of colonization advances, spiders move deeper in the subterranean
232 domain, facing changes in the environmental conditions, which act as environmental
233 filters. The attainment of mechanisms that may be more efficient in the regulation of hydric
234 balance and metabolism, combined with the ability to carry out the entire life cycle in
235 darkness, implies a complete adaptation to the subterranean conditions. At this point,
236 troglophiles undergo further selective pressures, fine-tuning their adaptive traits and
237 determining true subterranean specialization. Segregation mechanisms hindering gene
238 flow between epigeal and hypogean populations—allopatry or parapatry—seem to play a
239 major role in the speciation process [84]. Arnedo *et al.* [59] documented a compelling case
240 of coexistence of sister-species pairs of *Dysdera* in lava tubes in the Canary Island. They
241 hypothesized that trophic segregation is the cause of the high level of sympatry between
242 these species. The case of the Canarian cave-dwelling *Dysdera* supports the hypothesis
243 of a sympatric speciation within the terrestrial hypogean environment and, apparently, is
244 the only such case documented in literature. Conversely, sympatric speciation was
245 observed in Mexican cave fish [85,86] and Australian stigobitic diving beetles [87,88].

246

247 **V. DISPERSAL AND GENETIC STRUCTURING**

248 Troglobiomorphic spider species exhibit lower physiological tolerance, which hampers their
249 dispersal ability via non-subterranean habitats. Moreover, caves and other subterranean
250 habitats are generally concentrated in certain geological areas—e.g. karst—and are often
251 isolated from each other by non-suitable habitats. These considerations raise the
252 questions of the ability of subterranean species to disperse and the genetic structure of the
253 populations.

254 Many authors have attempted to answer these questions, using crickets, beetles,
255 crustaceans and fish (reviewed in [84,89]). Studies on troglophile spiders have often

256 uncovered moderate gene flows between populations and relatively shallow population
257 structures [22,73,90]—but see [91]—suggesting the existence of extra-cave dispersal [92].
258 When considering troglobionts a different picture emerges. Studies conducted so far
259 uncovered pronounced genetic structuring and low gene flow—if any—between cave
260 populations, as found with *Nesticella* [82], *Nesticus* [90,93], *Troglohyphantes* [22], and
261 *Telema* [94]. Although sometimes it is difficult to separate speciation from population
262 structuring [95], the lack of gene flow supports the 'caves as islands' scenario *sensu* [93],
263 in which dispersal is virtually absent.

264 However, Paquin and Hedin [66] found shared haplotypes in isolated cave populations of
265 *Cicurina*, which can be interpreted either as ancestral molecular polymorphism or as
266 ongoing gene flow across species boundaries. Similar results were obtained by [65] when
267 studying populations of *Neoleptoneta*.

268 In this respect, it is worth remembering that subterranean habitats are often connected
269 through the networks of cracks, voids and other SSHs, which may enhance the dispersal
270 of subterranean species [25,26].

271

272 **VI. POPULATION STRUCTURE**

273 Generalizations on population size of troglobionts are often trivial, as it is likely to depend
274 on the carrying capacity of the single cave system. Furthermore, caves are connected with
275 rock-fissures and other microcavernous habitats inaccessible to men—unless by indirect
276 means,—which often precludes correct population estimations. However, in some
277 circumstances, protocols for monitoring populations in caves have been successfully
278 applied [92,96].

279 As a rule of thumb, larger populations are expected in prey-rich tropical caves rather than
280 in temperate oligotrophic caves. Population structures in caves are usually skewed toward
281 juveniles, with values up to two thirds juveniles in Tetragnathidae [13,14], or even more in
282 Dyctinidae [97]. Female-biased sex ratio was also documented in numerous species. In
283 *Troglohyphantes* adult females outnumber adult males with ratios from 2.5:1 to 10:1, or
284 more [15,53]. In *Cicurina* spp., the estimated ratio of adult females/males is *circa* 10:1 [97],
285 and in *Stalita taenaria* 4:1 [98]. Ratios for troglophile species align these results, as in
286 *Meta* ssp. (from 3:1 to 5:1 [14]), *Kryptonesticus eremita* (3:1 [98]), and *Pimoa graphitica*
287 Mammola, Hormiga & Isaia (3:1 [16]).

288 When considering subadult spiders, some evidence suggests that sexes are actually not
289 skewed towards females [53,57]. The longer life span of females and the high mortality
290 rates of males after the last molt may explain these patterns.

291

292 **VII.ECOLOGY**

293 **(1)Habitat and microhabitat**

294 Hypogean spiders are primarily found in caves and artificial subterranean sites—mines,
295 bunkers, cellars, subways. Troglobiomorphic species have also been collected in SSHs,
296 such as lava tubes [40,59,74], the MSS (reviewed in [26]), and other dark, moist habitats
297 like deep soil and leaf litter strata, and animal burrows [54] (Figure 3).

298 The spatial distribution of spiders within caves—in terms of linear distance from the
299 entrance—appears to be related to the degree of subterranean adaptation. The less
300 adapted species are preferentially found close to the entrance. Orb-weaver spiders are
301 associated with cave walls and roofs of the twilight zone [64], characterizing the so-called
302 “entrance spiders” [83]. Conversely, space- and sheet-weavers and ground hunters

303 generally colonize cave floors, especially rocky debris [99]. The presence of spiders in
304 millimetric and centimetric interstices—MSS and other SSHs—deserves some further
305 comments, since it can be limited by the habitat size. According to available data, such a
306 habitat seems preferentially colonized by spiders spinning small webs or by active ground
307 dwellers. Conversely, orb weavers naturally prefer wider interstices—i.e. caves [26,64,99].
308 In fact, large orb-weavers have also been documented in SSHs characterized by large
309 voids, such as bare stony debris and boulder fields [61,100], as they offer enough 3-
310 dimensional space.

311

312 **(2) Predation and diet**

313 Being top-predators, spiders in caves are preferentially found in prey-rich areas, where
314 they maximize food intake [14–16,101]. Many subterranean spiders also evolved unusual
315 foraging behaviors and feeding habits, in order to comply with the general low prey
316 availability. In resource-deprived environments, space and sheet webs [30] are favoured,
317 given their high efficiency in catching prey. On the other hand, orb webs targeting flying
318 insects are rare, and are preferentially found in the twilight zone, where the availability of
319 flying prey is usually higher.

320 For the same reason, many cave lineages widen their diets and loose trophic
321 specialization [28]. Detritivores, small-sized predators, and external animals blundering
322 underground are among the most frequent prey captured by cave spiders. Anecdotic
323 captures of vertebrates by subterranean spiders have also been reported, with prey such
324 as fish [102], amphibians and reptiles [103].

325 *Meta menardi* well exemplifies the diet of a subterranean spider, as demonstrated by
326 numerous studies [13,14,16,104]. Arthropods comprise the bulk of the diet, but unusual
327 prey such as Gastropoda and even conspecifics of smaller size are also consumed.

328 On the other hand, exceptions have been observed in *Dysdera* spp., which are regarded
329 as specialist woodlouse hunters [59]. In this respect, Cardoso [17] hypothesized that
330 *Dysdera* may switch from specialist to generalist during the transition from the epigean to
331 the hypogean habitat.

332

333 **(3)Cave communities**

334 The richness of spider species in caves is orders of magnitude lower than in epigean
335 ecosystems, each cave having a limited capacity to host a considerable number of species
336 [17]. The association of troglobiont and troglophile spiders is common, as different species
337 usually exploit distinct ecological niches. Coexistence of multiple troglotic species in the
338 same cave is less frequent. For instance, coexistence of three troglotic species has been
339 documented in the Southern Alps [99] and in the Iberian Peninsula [17]. Furthermore,
340 Bloom and colleagues [39] documented in the tropics an unique occurrence of two
341 troglotic species within a single cave in Hispaniola. The occurrence of two or more congeneric
342 spider species in a single subterranean system is even rarer , and is often mediated by
343 niche partitioning. As far as we are aware, occurrence of two congeneric species has been
344 documented in *Cicurina* [55,57,105], *Dysdera* [59], *Pimoa* [73] and *Troglohyphantes*
345 [53,67].

346

347

348

349 **(4)Ecological niche and interspecific competition**

350 Poulson and White [106] suggested that microclimate, habitat structure and food
351 availability are the main factors which determine subterranean biodiversity rather than
352 other factors such as competition and niche-based processes. However, Poulson [101]
353 demonstrated that two linyphiid spiders have been able to exploit distinct spatial niches in
354 North American caves, in order to avoid competition. In recent year, it is becoming clear
355 that niche-based processes operating in subterranean ecosystems are more common than
356 previously thought [48].

357 There is a consistency, across studies, in stating that the linear distance from the cave
358 entrance is the environmental gradient over which the niche diversification is generally
359 achieved. Whether the spatial distribution of spider species is driven by competition alone,
360 or by its combination with other driving forces—trophic availability, microclimatic conditions
361 —coexisting species tend to occupy distinct areas of the cave, thus reducing niche
362 overlaps [15,16,101,107]. Other mechanisms enhancing niche partitioning include the
363 trophic niche differentiation [13], spatial segregation [108], temporal niche shifts [13], and
364 conditional differentiation [14, 22].

365

366 **VIII.CONSERVATION**

367 Hypogean fauna is highly susceptible to disturbance [47], and spiders are not an
368 exception. Scientific evidence indicates that subterranean spiders are vulnerable to
369 anthropic disturbance [109], and numerous authors stressed out the importance of
370 protecting their habitats [17,71,94,96,110].

371 There are several intrinsic factors related to the biology of troglobionts that determine a
372 higher vulnerability in hypogean species compared to their superficial counterparts:

373 i) the small range of distribution of most species implies higher vulnerability. The eight
374 species of subterranean spiders assessed according to the IUCN criteria [111], have often
375 fulfilled the extent of occurrence (EOO) and area of occupancy (AOO) criterias of the
376 threatened species;

377 ii) low dispersal implies a reduced ability to shift distribution in face of habitat disruption.
378 Moreover, the genetic pool in a single subterranean population is often reduced;

379 iii) the physiological specialization of most troglobionts implies a higher risk of extinction,
380 especially in case of climatic alterations—e.g. global warming [75].

381 iv) the reduced carrying capacity of most subterranean systems implies the occurrence of
382 simplified ecological communities in the cave ecosystem, which leads to a higher risk of
383 disruption of the trophic web. Moreover, most spiders are directly susceptible to variations
384 in trophic availability, which in turn, depend upon events outside the cave [112].

385 v) the population structure and reproductive peculiarity of most subterranean spider
386 species, expose them to additional disturbance. For example, observations on *Hickmania*
387 *troglydites* (Higgins & Petterd) (Austrochilidae) indicated that the population abundance
388 and mean body size in tourist caves are noticeably displaced in comparison to natural
389 caves [109].

390 It is clear that the conservation of subterranean spiders is often complicated by the lack of
391 information about their distribution and auto-ecology [70]. As a direct consequence,
392 assessing species diversity and population abundances may be difficult, and thus
393 determining the status of conservation of the different species.

394 Furthermore, the current species hypothesis regarding speciose *taxa* are often far for
395 being solid [66,71,91,95,97], which is a crucial factor hindering the conservation of cryptic
396 and restricted species [113].

397 Given the lack of detailed information, general measures of conservations should include:

398 i) avoidance of extensive collections of rare species.

399 ii) avoidance of any form of disruption of subterranean habitats, including artificial
400 modification which could alter the local microclimate;

401 iii) listing troglobiont spiders as legally protected species, in order to increase the tutelage
402 of their habitats;

403 iv) promoting IUCN assessment of troglobiont species [114].

404 Subterranean spiders represent remarkable model organisms and their study offers unique
405 possibilities to shed light on adaptive, ecological and evolutionary processes. For this
406 reasons alone, underground habitats have to be prioritised and protected. Although self-
407 evident, it should be plainly stated that increasing the knowledge about cave spiders will in
408 turn increase the awareness of the cave natural heritage, which will have positive
409 feedbacks on their tutelage.

410

411 **IX.CONCLUSIONS**

412 1) Worldwide, ~1,000 subterranean spiders across 48 families have been described so far
413 (Table 1). However, recent descriptions of new species, or even entire new families [29], in
414 regions where the cave fauna is relatively well-known, show that in the hypogean habitats
415 there are still a lot of surprises in store. By some estimates, only one third of the spider
416 species have been described [115], and it is expected that a significant portion of this
417 estimated diversity pertains to the hypogean ecosystems—especially in the tropics [39].

418

419 2) A significant number of subterranean spiders is poorly described, as many species
420 descriptions are based on a single sex and/or lack diagnostic illustrations. In addition,

421 several new species have been described in non-peer-reviewed journals and this practice
422 continues to date.

423

424 3) The process of morphological, physiological and behavioural adaptation to the
425 subterranean domain in spiders is only partially understood and our knowledge mostly
426 relies on sporadic observations and anecdotic information. The use of modern
427 investigation tools, such as molecular techniques and statistical inference, is a stimulating
428 endeavour that would allow to shed further light on this topic.

429

430 4) Among other *taxa*, the suitability of hypogean spiders as model organisms in biological,
431 ecological and evolutionary studies has been widely demonstrated over the past few
432 decades.

433

434 5) Whilst the conservation status of many caves is acceptable, it would be useful to list
435 troglobiont spiders as legally protected species and assess their conservation status
436 according to the latest IUCN criteria.

437

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