



## Review

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## Spiders in caves

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

## 1. Background

Receiving poor energy inputs and being light-deficient, caves are generally considered extreme environments, characterized by low abundance and diversity of organisms. Because of their extraordinary adaptations, cave-dwelling animals offer unique study opportunities for pushing forward our current understanding of evolutionary and ecological processes [1,2]. Among other subterranean taxa, spiders are distinctive for their ecological role of top predators [3–5], and for the variety of functional adaptations [6], therefore representing undervalued models for the understanding the evolution of life in extreme habitats. Accordingly, subterranean spiders have served as models for physiological [7–9], ecological [4,5,10–12], ethological [13,14] and biogeographic studies [15–17], among others.

However, compared with other animal groups, the potential of spiders as model organisms is still under-expressed. It is possible that the paucity of studies is related to the difficulty of working in subterranean habitats and to the rarity of most subterranean species, which pose major impediments to data collection and analysis. In addition, the general lack of a state of the art on subterranean spider biology, ecology and evolution conceivably hinders advances in knowledge. In this review, we present a collection of information about spiders colonizing subterranean habitats—especially caves—and discuss their relevance in the understanding of cave life evolution and the ecology of subterranean animal communities.

### (a) Terminology and acronyms

We use the term *troglobiomorphism* to distinguish the suite of adaptations, especially morphological, to subterranean life [18]. Despite the fact that ecological categorizations often oversimplify real cases and boundaries between categories can be vague, for the sake of this review, we use the traditional speleobiological nomenclature [19] to indicate ecological distributions of species:

- (1) a *troglobiont* is strongly bound to hypogean habitats;
- (2) a *troglophile* is able to maintain hypogean populations, but relies on epigeal habitats for some biological functions;

- (3) a *trogloxene* occurs only sporadically in a hypogean habitat and is unable to establish stable subterranean populations.

The acronym SSH refers to *shallow subterranean habitats* [20], i.e. the aphotic subterranean habitats close to the surface, harbouring species with troglobiomorphic traits, namely hypotelminorheic habitats, epikarst, lava tubes, deep leaf litter, soil strata and the *milieu souterrain superficiel* (MSS; see [21]).

We considered the terms ‘hypogean’ and ‘subterranean’ as synonyms.

## 2. Taxonomy and phylogeography

Spiders are a very diverse group of arthropods dating back to the Late Carboniferous [22], and comprising more than 46 500 described species [23]. They are considered one of the most successful groups of organisms in terms of evolutionary radiation [24] and ecological plasticity [25], as they have virtually colonized all terrestrial habitats, including subterranean ones.

A number of spider taxa underwent remarkable diversification in subsurface habitats (figure 1), showing unique adaptations and exhibiting a wide variety of functional and morphological diversity [26,27]. The smallest spider ever described (*Anapistula ataecina* Cardoso & Scharff; approx. 0.4 mm [28]) as well as the largest one (*Heteropoda maxima* Jäger; legspan of approx. 30 cm [29]) provide two appropriate examples of the extraordinary morphological diversity of subterranean spiders.

The description of the first troglobiont spider dates back to 1847, when Schiödte (1812–1884) described *Stalita taenaria* (Dysderidae) from the Postojna cave in Slovenia. *S. taenaria* shows remarkable troglobiomorphic traits, namely the absence of eyes—‘oculi nulli’—and a pronounced cuticular depigmentation—‘abdomine niveo’ [30].

The discovery of a spider showing extraordinary adaptations to the subterranean environment, paved the way for future generations of scientists to disclose the huge biological diversity hidden in subterranean habitats around the world.

According to available estimates [26,27], around 1000 troglobiomorphic spiders have been classified as troglobionts. In addition, a countless number of species have been reported to be associated with caves. During our bibliographic survey, we recorded spiders showing subterranean adaptations in at least 48 families (table 1)—out of the 113 currently listed [23].

The appearance of troglobiomorphic features occurred multiple times during the 380 Myr of spider evolution, in families scattered all over the spider tree of life (figure 1). As well as most hypogean taxa [31], troglobiomorphic spiders represent filtered subsamples of regional epigeal species pools [4]. However, there are genera and families without epigeal relatives, like Trogloraptoridae [32].

In terms of foraging guilds (*sensu* [31]), a functional disharmony is often observed, with entire guilds being scarcely represented, if not absent, in caves—e.g. sensing web weavers, ambush hunters. Aside from the notable exception of the Iberian Peninsula [4], there are no extensive compilations about functional groups in subterranean spiders, making it difficult to draw any general pattern.

Subterranean spiders are distributed in all continents but Antarctica (table 1). As for other taxonomic groups [33], the core of the diversity is found in temperate regions—especially in the Northern Hemisphere. In the tropics, around 40 species

of eyeless spiders are currently known, having been reported from caves in Central and South America [34–39], Caribbean [40], Hawaii [41], Galápagos [42], Asia and Oceania [43–46]. In this regard, cave fauna in the tropics is probably understudied [47], and it is likely that the number of tropical troglobiont spiders will grow in the near future [40].

## 3. Subterranean adaptations

Species under the same selective pressure evolve convergent adaptive traits. Being subjected to strong environmental filters, hypogean habitats are a remarkable example of this phenomenon [1]. The primary limiting factors for subterranean species are the lack of solar radiation and the scarcity of food resources—but see [48] for an in-depth discussion. The process of adaptation implies the evolution of well-defined and often convergent biological traits [49]. Indeed, troglobiomorphic spiders share adaptive features found in other groups of cave animals, supposedly due to the strong and similar selective pressures acting underground [1].

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

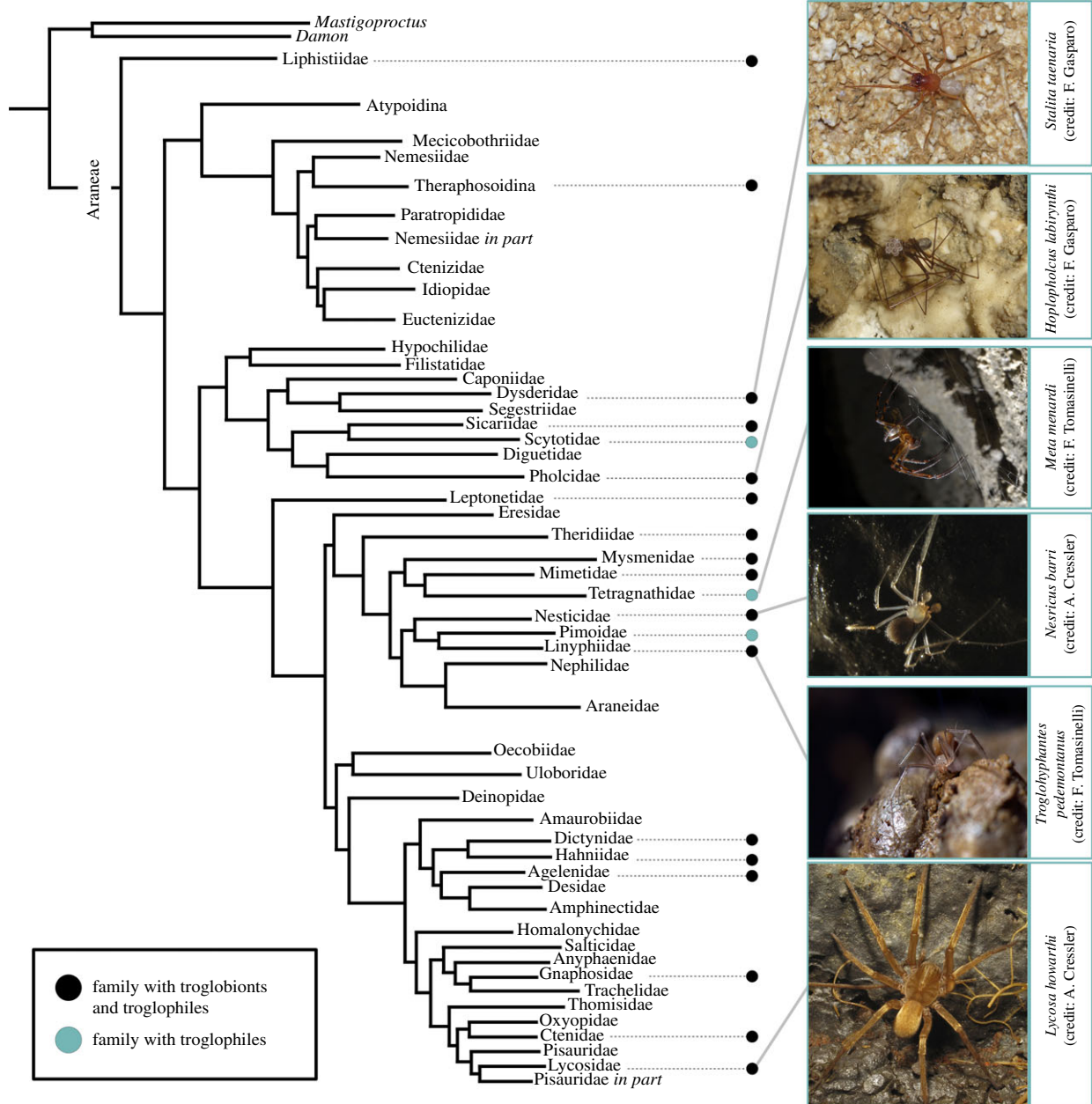
### (a) Morphology

Morphological adaptations are directly related to progressive or regressive evolution. They include reduction or loss of cuticular pigments, eye regression or loss, thinning of integuments, leg elongation and heavy spination [38,39,50–59].

Data referring to the European species of *Troglohyphantes* (Linyphiidae) suggest that pigmentation is the first character undergoing regression in the process of subterranean adaptation [51], whereas the loss of pigment around the eyes and the progressive eye reduction represent a second step in the adaptation process [51,59]. Tentatively, this is possibly related to the minor role played in spiders by visual perception and the consequent negligible development of eye apparatus in most epigeal species, a feature that could represent a pre-adaptation to life in darkness. Conversely, evidence suggests that the presence of pigments in epigeal populations is selectively maintained [60]. Exceptions include spider families relying on sight for prey capture [41,53], such as Lycosidae, which in fact include only three troglobionts [46], or Salticidae, which lack troglobionts.

Compared with their epigeal relatives, cave species often develop longer legs [51,53–55]. However, caution should be exercised in generalizing this pattern, as leg elongation is apparently a morphological feature depending on habitat size [20] and may not occur in spiders inhabiting small interstices—see Ecology.

An interesting related aspect refers to intraspecific variation in troglobiomorphic traits, such as eye reduction and depigmentation. Intraspecific polymorphism was documented in *Neoleptoneta* (Leptonetidae) [61], *Cicurina* (Dictynidae) [62], *Troglohyphantes* [63] and *Porrhomma* (Linyphiidae) [58,59]. Variability in troglobiomorphic traits was documented both at a regional and local scale, but a reasonable explanation for these patterns has never been provided. For example, [61] observed a range of variation between the populations of two different species of *Tayshaneta* (Leptonetidae) found in central Texas along a latitudinal gradient, ‘from darkly pigmented, large-eyed individuals to lightly pigmented, reduced-eyed forms to depigmented, blind individuals’. At a local scale,



**Figure 1.** Appearance of troglobiomorphic features during the evolution of spiders. Tree topology according to [24]—not all spider families are included. (Online version in colour.)

individuals of *Kryptonesticus eremita* (Simon) (Nesticidae) found in caves show variability in pigmentation patterns within a single population depending on the distance from the entrance [64].

### (b) Physiology

Physiological adaptations pertain to reduction of the metabolic rate, higher resistance to starvation, alteration in circadian rhythm, reduction in fecundity, delayed maturity, slower development and the tendency to lay a smaller number of eggs, though larger [50–53,65]. However, quantitative studies aiming to shed light on these adaptations are scarce and, as far as we are aware, no studies accounted for phylogenetic effects, making difficult to generalize results across families.

Observations conducted on different species kept in captivity pointed towards a delayed maturation of juveniles and longer lifespan [51,54,65]. A reduced number of eggs/cocons (less than 10) was also documented for several troglobionts

[28,50,65–67]. For comparison, a number of eggs/eggsacs one order of magnitude higher was documented for troglaphile species able to disperse outside the cave habitat [68,69]. Deeleman-Reinhold [51] provided a comprehensive analysis on this topic focusing on the genus *Troglohyphantes*, comparing size and number of eggs/eggsacs in 20 regressed and non-regressed species. She observed fewer eggs in regressed species (mean = 12.3 mm versus mean = 16.8 mm in non-regressed species) of slightly larger size (mean = 0.36 mm versus mean = 0.41 mm in non-regressed species).

Experimental and field data suggest that hypogean spiders have fine-tuned their physiological tolerance to the constant and narrow temperature and relative humidity ranges of their habitats over time [70]. With the thinning of the integuments, subterranean organisms are more prone to desiccation, and thus are preferentially associated with humid microhabitats [3]. Experiments on adults and spiderlings of *Lycosa howarthi* Gertsch (Lycosidae) provided evidence of a pronounced sensitivity to saturation deficit [7,8].

**Table 1.** List of the spider families including troglobiont/troglophile species.

family	distribution	notes
<b>ORTOGNATHA</b>		
Barychelidae	Cuba, Dominican Republic	troglobionts in <i>Troglathele</i> and <i>Trichopelma</i>
Cyrtacheniidae	Guinea	<i>Acontius stercoricola</i> is the only troglobiont in the family
Dipluridae	Central and South America, Philippines, Australia	troglophiles and troglobionts in <i>Euargus</i> , <i>Harmonicon</i> , <i>Masteria</i> and <i>Troglodiplura</i>
Hexatelidae	New Zealand	<i>Hexathele cavernicola</i> is the only troglobiont in the family
Liphistiidae	Malaysia, Thailand	troglobionts in <i>Liphistius</i>
Microstigmatidae	Ecuador	<i>Spelocteniza ashmolei</i> is the only troglobiont in the family
Theraphosidae	Mexico, Brazil	troglobionts in <i>Tmesiphantes</i> and <i>Hemirrhagus</i>
<b>LABIDOGNATHA</b>		
Agelenidae	Europe, USA, China	various troglobiomorphic genera (e.g. <i>Coelotes</i> , <i>Histopona</i> , <i>Draconarius</i> )
Amaurobiidae	Europe	some troglophiles in <i>Amaurobius</i>
Anapidae	South Africa, Korea	troglobionts in <i>Crozetulus</i> and <i>Conculus</i>
Austrochilidae	Tasmania	<i>Hickmania troglodytes</i> is the only troglophile in the family
Ctenidae	Dominican Republic, Java, Cuba, Australia, South Africa	troglobionts in <i>Ciba</i> and <i>Janusia</i>
Cybaeidae	Holarctic	troglobionts in <i>Cybaeus</i> and <i>Cybaeozyga</i>
Cycloctenidae	Australia, Tasmania	troglobionts in <i>Cycloctenus</i> and <i>Toxopsiella</i>
Dyctinidae	Europe, USA, Mexico, Japan	troglobionts in <i>Cicurina</i>
Dysderidae	Mediterranean basin, Canary Islands	various degree of adaptation in several genera
Gnaphosidae	Cuba, southeast Asia	troglobionts in <i>Herpyllus</i> , <i>Hongkongia</i> and <i>Micythus</i>
Grandungulidae	Australia, New Zealand	cave-dwelling species in various genera
Hahniidae	Europe	troglobionts in <i>Hanhia</i> , <i>Iberina</i>
Holarchaeidae	Tasmania and New Zealand	cave-dwelling species in <i>Holarchaea</i>
Leptonetidae	Holarctic, Mexico, South America	numerous troglobionts and troglophiles
Linyphiidae	Holarctic, Africa, Australia, Central America	numerous troglobionts and troglophiles
Liocranidae	Europe, North Africa, Canary Islands	cave-dwelling species in <i>Brachyanillus</i> , <i>Liocranum</i> and <i>Agraecina</i>
Lycosidae	Hawaii, French Polinesia	three troglobitic species in <i>Adelocosa</i> , <i>Lycosa</i> and <i>Nukuhiva</i>
Mimetidae	Sri Lanka	<i>Mimetus strinatii</i> is the only troglobiont in the family
Mysmenidae	Mexico, Tasmania, China (?)	troglobionts in <i>Maymena</i> and <i>Trogloneta</i>
Nesticidae	Holarctic, Brazil, Africa, Oceania	numerous troglobionts and troglophiles
Ochyroceratidae	North and South America, Antilles, Asia, Africa	cave-dwelling species in several genera
Oonopidae	Mexico, Cuba, China, Ecuador, India, Iran	troglobionts in several genera (e.g. <i>Dysderoides</i> , <i>Gamasomorpha</i> , <i>Wanops</i> )
Orsolobidae	New Zealand	<i>Anopsolobus subterraneus</i> is the only troglobiont in the family
Pholcidae	Northern and Southern Hemispheres	numerous troglobiomorphic species
Phyxelididae	South Africa	cave-associated species and one troglobiont ( <i>Phyxelida makapanensis</i> )
Pimoidae	Holarctic	troglophiles especially in <i>Pimoida</i>
Prodidomidae	Galápagos Islands, Brazil	troglobiont in <i>Lygromma</i>
Scytotidae	Philippines	cave-associated species in <i>Scytodes</i>
Sicariidae	Africa, South America	cave-associated species and few troglobionts in <i>Loxosceles</i>
Sparassidae	Asia, East Africa	troglobiomorphic species in <i>Sinopoda</i> and <i>Berlandia</i>
Stiphidiidae	Australia, Tasmania	troglobionts in several genera (e.g. <i>Baiami</i> , <i>Stiphidion</i> , <i>Tartarus</i> )
Symphytognathidae	Australia, Europe (Portugal)	troglobionts in <i>Anapistula</i>
Syntaxidae	Tasmania	species with troglobiomorphic traits in <i>Tupua</i>
Telemidae	North-Central America, Europe, Asia, South Africa	troglobionts in several genera (e.g. <i>Apneumonella</i> , <i>Telema</i> , <i>Telemofila</i> , <i>Usofila</i> )

(Continued.)

Table 1. (Continued.)

family	distribution	notes
Tetrablemmidae	Mexico, China, Japan, Sumatra	numerous troglaphiles
Tetragnathidae	Holarctic, Tasmania	troglaphiles in <i>Meta</i> , <i>Metellina</i> , <i>Okileucauge</i> and <i>Orsinome</i>
Theridiidae	USA, Oceania, Europe, Galápagos Islands	troglaphiles and troglabionts in various genera
Theridiosomatidae	Venezuela, Sri Lanka	cave-dwelling species, especially in <i>Plato</i>
Trochanteridae	Oceania	troglabionts in <i>Desognanops</i> and <i>Olin</i>
Troglooraptoridae	caves in Oregon (northwest USA)	monospecific family ( <i>Troglooraptor marchingtoni</i> , troglaphile)
Zoropsidae	Oregon (USA)	troglabionts in <i>Phanotea</i> and <i>Tengella</i>

Moreover, Novak *et al.* [9] tested lower lethal temperatures in various troglaphiles and troglabionts, including spiders. They concluded that while troglaphiles retained their ability to withstand temperature variations, most troglabionts lost their thermoregulatory mechanisms due to regressive evolution.

Although these pieces of evidence are compelling, in lack of correction for phylogeny the figures remain crude. Specifically, it remains unresolved whether differences in thermal tolerance are adaptive or are due to phylogenetic relatedness [71].

### (c) Behaviour

Little is known about the behaviour of subterranean species, as in most cases the rarity of species often precludes anything but sporadic observations. Documented observations in spiders—mostly anecdotal [27]—primarily refer to reproductive behaviour [13,66,68,72]. Complex courtships were documented in troglaphiles [13,68], whereas maternal care was observed in troglabiont Nesticidae [66,73]. Sociality in cave spiders was never documented [14]. Non-territorial ‘subsociability’, in the form of free movements of the spiders inside and between interconnected webs, was tentatively proposed for *Goeldia zygierae* Almeida-Silva, Brescovit & Dias (Titanocidae), a troglaphile inhabiting Brazilian caves [68].

## 4. Origin: subterranean evolution

Available phylogenetic studies suggest that troglabiomorphy has evolved several times independently [56,61]. The origin of troglabionts is generally explained by two major theories. The theory of active colonization [74] or adaptive shift hypothesis [7], puts emphasis on the process of active colonization of the hypogean domain, being the species driven by the opportunity to occupy new, unexploited ecological niches. This theory generally refers to hypogean speciation in tropical areas [42,75].

The theory of relicts and refuges, or climate relict hypothesis [76,77], puts emphasis on long-term climatic changes, such as glaciation cycles, indicating them as the main factors prompting the colonization of the subterranean habitat, meanwhile causing the obliteration of surface-dwelling populations [78]. To date, the climate relict hypothesis has been mostly used to explain the radiation of troglabiont spiders in temperate regions [16,17,59,70,79]. However, it is worth noticing that the two theories are not incompatible, and it is likely that in some cases they both played a role in hypogean speciation.

Whichever the causes and mechanisms, the processes are similar to primary successions over time. At first, generalist pioneer species begin the colonization, being then gradually replaced by specialized and competitive elements. Subterranean habitats are characterized by a constant flux of invaders and migrants [1], with the colonization process starting from transitional zones in the vicinity of the surface [57], including the SSHs [20]. In the first phases, organisms with adaptive traits suitable for subterranean life—exaptations—are generally favoured. For example, eye reduction, depigmentation and highly developed chemoreceptors in moss-, soil- and litter-dwelling spider species [16,51,58,61,80] generally promote the colonization of subterranean habitats.

When the process of colonization advances, spiders move deeper in the subterranean domain, facing environmental changes that act as ecological filters. The attainment of mechanisms that may be more efficient in the regulation of hydric balance and metabolism, combined with the ability to carry out the entire life cycle in darkness, implies a complete adaptation to the subterranean conditions. At this point, troglaphiles undergo further selective pressures, fine-tuning their adaptive traits and determining true subterranean specialization.

Segregation mechanisms hindering gene flow between epigeal and hypogean populations—allopatry or parapatry—seem to play a major role in the speciation process [81]. Arnedo *et al.* [56] documented a compelling case of coexistence of sister-species pairs of *Dysdera* (Dysderidae) in lava tubes in the Canary Islands. They hypothesized that trophic segregation is the cause of the high level of sympatry between these species, supporting the only documented case of sympatric speciation within the terrestrial hypogean environment. Conversely, sympatric speciation was observed in freshwater subterranean ecosystems in Mexican cave fish [82,83] and Australian hypogean diving beetles [84,85].

## 5. Dispersal and genetic structuring

Troglabionts often exhibit lower physiological tolerance, which hampers their dispersal ability via non-subterranean habitats. Moreover, caves and other subterranean habitats are generally concentrated in certain geological areas—e.g. karst—and are often isolated from each other by non-suitable habitats. These considerations paved the way for the use of caves as ideal systems in which to study isolation and population structuring.

Many authors have attempted to address these issues, using crickets, beetles, crustaceans and fish [81,86]. In spiders,



**Figure 2.** Breadth of habitats colonized by subterranean spiders across the world. (a) Natural caves; (b) deep strata of mountain screes and boulder fields; (c) mines and quarries; (d) *milieu souterrain superficiel* (MSS); (e) man-made military fortifications; (f) cellars; (g) shallow subterranean habitats (SSH) such as deep soil and litter strata. By courtesy of: (a,c) Mauro Paschetta; (b) Federico Pianciola; (d) Jacopo Orlandini; (e,f,g) Dino Mammola. (Online version in colour.)

studies on troglophiles have often uncovered moderate gene flows between populations and relatively shallow population structures [17,69,87]—but see [88]—suggesting the existence of extra-cave dispersal [89].

When considering troglobionts a different picture emerges. Studies uncovered pronounced genetic structuring and low gene flow—if any—between cave populations, as found with Nesticidae [15,79,87,90], Linyphiidae [17] and Telmidae [91]. Although it is difficult to separate speciation from population structuring [92], the lack of gene flow supports the ‘caves as islands’ scenario *sensu* [90], in which dispersal is virtually absent.

However, Paquin & Hedin [62] found shared haplotypes in isolated cave populations of *Cicurina*, which can be interpreted either as ancestral molecular polymorphism or as ongoing gene flow across species boundaries. Similar results were obtained with *Neoleptoneta* [61].

In this respect, it is worth remembering that subterranean habitats are often connected through the networks of cracks, voids and other SSHs, which may enhance the dispersal of subterranean species [20,21].

## 6. Population structure

Generalizations on population size of subterranean species are often trivial, as it is likely to depend on the carrying capacity of the single cave system. Furthermore, caves are connected with rock fissures and other habitats inaccessible to men [20,21], which often precludes correct population estimations. However, in some circumstances, protocols for monitoring spider populations in caves have been successfully applied [89,93].

As a rule of thumb, larger populations are expected in prey-rich tropical caves rather than in temperate oligotrophic caves. Population structures in caves are usually skewed towards juveniles, with values up to two-thirds juveniles in Tetragnathidae [10,11], or even more in Dycytinidae [94]. Female-biased sex ratio was also documented in numerous species. In *Troglolyphantes*, adult females outnumber adult males with ratios from 2.5 : 1 to 10 : 1, or more [12,50]. In *Cicurina* spp., the estimated ratio of adult females/males is around 10 : 1 [94], and in *S. taenaria* 4 : 1 [95]. Ratios for troglophile species align these results, as in *Meta* ssp. (Tetragnathidae) (from 3 : 1 to 5 : 1; [5,12]), *Kryptonesticus eremita* (3 : 1; [95]) and *Pimoida graphitica* Mammola *et al.* (Pimoidae) (3 : 1; [69]).

When considering subadult spiders, some evidence suggests that sexes are actually not skewed towards females [51,54]. The longer lifespan of females and the high mortality rates of males after the last moult may explain these patterns. In the case of *Anapistula ataccina* (Symphytognathidae), parthenogenesis was also proposed to explain strongly biased sex ratios [28], although it remains to be proven.

## 7. Ecology

### (a) Habitat and microhabitat

Troglobiomorphic spiders are mostly reported from subterranean habitats accessible to man, such as caves and artificial sites—mines, bunkers and cellars. Moreover, other habitats such as lava tubes [3,41,56], the MSS [21] animal burrows and other dark, moist SSHs [51] (figure 2) proved to be suitable for hosting communities of subterranean spiders.

The spatial distribution of spiders within caves—in terms of linear distance from the entrance—appears to be related to the degree of subterranean adaptation. The less adapted species are preferentially found close to the entrance. Orb-weaver spiders are associated with cave walls and roofs of the twilight zone [96], characterizing the so-called ‘entrance spiders’ [80]. Conversely, space- and sheet-weavers and ground hunters generally colonize cave floors, especially rocky debris [97]. The presence of spiders in millimetric and centimetric interstices—MSS and other SSHs—deserves some further comments, because it can be limited by the habitat size. According to available data, such a habitat seems preferentially colonized by spiders spinning small webs or by active ground dwellers. Conversely, orb-weavers prefer wider interstices—i.e. caves [21,96,97]. In fact, large orb-weavers have also been documented in SSHs characterized by large voids, such as boulder fields [59], offering enough three-dimensional space.

### (b) Predation and diet

Being top predators, spiders are preferentially found in prey-rich areas, where they maximize food intake [5,11,12,98]. Many subterranean spiders also evolved unusual foraging behaviours and feeding habits, in order to comply with the general low prey availability. In resource-deprived environments, space and sheet webs are favoured, given their high efficiency in catching prey. On the other hand, orb webs targeting flying insects are rare, and are preferentially found in the twilight zone, where the availability of flying prey is usually higher.

For the same reason, many cave lineages widen their diets and lose trophic specialization [31]. Detritivores, small-sized predators and external animals blundering underground are among the most frequent prey captured by cave spiders. Occasional captures of vertebrates by subterranean spiders have also been reported, with prey, such as fish [99], amphibians and reptiles [100].

*Meta menardi* well exemplifies the diet of a subterranean spider, as demonstrated by numerous studies. Arthropods comprise the bulk of the diet, but unusual prey such as Gastropoda and even conspecifics of smaller size are also consumed [5,11,12,101].

On the other hand, exceptions have been observed in *Dysdera* spp., which are regarded as specialist woodlouse hunters [56]. In this respect, Cardoso [4] hypothesized that *Dysdera* may switch from specialist to generalist during the transition from the epigeal to the hypogean habitat.

### (c) Cave communities and interspecific competition

The richness of spider species in caves is orders of magnitude lower than in epigeal ecosystems, each cave having a limited capacity to host a considerable number of species [4]. The association of troglobiont and troglophile spiders is common, as different species usually exploit distinct ecological niches. Coexistence of multiple troglobionts in the same cave is less frequent [4,40,56,97], and often mediated by niche partitioning.

There is a consistency, across studies, in stating that the linear distance from the cave entrance is the environmental gradient over which the niche diversification is generally achieved. Whether the spatial distribution of spider species is driven by competition alone, or by its combination with other driving forces—e.g. trophic availability, microclimatic conditions—coexisting species tend to occupy distinct areas of the cave,

thus reducing niche overlaps [5,12,98,102]. Other documented mechanisms enhancing niche partitioning include the trophic niche differentiation [10], spatial segregation [103], temporal niche shifts [10] and conditional differentiation [11].

## 8. Conservation

Hypogean fauna is highly susceptible to disturbance [1], and spiders are not an exception. In fact, recently numerous authors stressed the importance of protecting their habitats [4,67,91,93,104].

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

- (1) the small range of distribution of most species implies higher vulnerability. Eight species of subterranean spiders assessed according to the IUCN criteria [105], have often fulfilled the criteria of the threatened species;
- (2) low dispersal implies a reduced ability to shift distribution in face of habitat disruption. Moreover, the genetic pool in a single subterranean population is often reduced;
- (3) the physiological specialization of most troglobionts implies a higher risk of extinction, especially in case of climatic alterations—e.g. global warming [70];
- (4) the reduced carrying capacity of most subterranean systems implies the occurrence of simplified ecological communities in the cave ecosystem, which leads to a higher risk of disruption of the trophic web. Moreover, most spiders are directly susceptible to variations in trophic availability, which in turn, depend upon events outside the cave [106];
- (5) the population structure and reproductive peculiarity of most subterranean spider species, expose them to additional disturbance. For example, observations on *Hickmania troglodytes* (Higgins & Petterd) (Austrochilidae) indicated that the population abundance and mean body size in tourist caves are noticeably displaced in comparison to natural caves [107].

It is clear that the conservation of subterranean spiders is often complicated by the lack of information about their distribution and auto-ecology [66]. As a direct consequence, assessing species diversity and population abundances may be difficult, and thus determining the status of conservation of the different species.

Furthermore, the current species hypothesis regarding speciose taxa are often far from being solid [62,67,88,92,94], which is a crucial factor hindering the conservation of cryptic and restricted species [108].

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

- (1) minimizing the impacts on rare species—e.g. avoiding collecting using indiscriminate methods such as massive use of pitfall traps.
- (2) minimizing the alterations of local microclimate;
- (3) promoting IUCN assessment of troglobiont species [109];
- (4) listing troglobiont spiders as legally protected species, in order to increase the tutelage of their habitats.

Although self-evident, it should be plainly stated that increasing the knowledge about cave spiders will in turn increase

the awareness of the cave natural heritage—both in cavers and visitors of touristic caves—which will have positive feedback on their tutelage.

## 9. Conclusion

- (1) Worldwide, approximately 1000 subterranean spiders across 48 families have been described so far (table 1). However, recent descriptions of new species, or even entire new families [32], in regions where the cave fauna is relatively well known, show that in the hypogean habitats there are still a lot of surprises in store. By some estimates, only one-third of the spider species have been described [110], and it is expected that a significant portion of this estimated diversity pertains to the hypogean ecosystems—especially in the tropics [40].
- (2) The process of adaptation to the subterranean domain in spiders is only partially understood and our knowledge mostly relies on sporadic observations. Comparative studies supported by modern investigation tools—and accounting for phylogenetic effects—represent stimulating endeavours that would allow further light to be shed on this topic.
- (3) In the last 20 years, the use of a molecular approach to study subterranean spiders has proven to be a promising field of research, aiming to disclose biogeographic patterns of species diversification [16,17,79], delimit species boundaries [91,92] and unravel the role of dispersal in highly isolated populations [15,90].

- (4) When compared with surface ecosystems, subterranean environments exhibit lower biodiversity and simplified trophic webs, harbouring specialized biocoenoses of considerable scientific interest. In this context, the role of spiders as top-predators represents a stimulating feature to revisit classical ecological concepts such as species interactions and niche dynamics. In recent years, subterranean spiders have also proved to be effective models for macro-ecological studies at the regional scale [4], e.g. acting as potential bioindicator of the effects of global warming on subterranean communities [70].
- (5) Caves are fragile ecosystems and their fauna is susceptible to disturbance and environmental alterations. While the conservation status of many caves is acceptable, it would be useful to list troglobiont spiders as legally protected species and assess their conservation status according to the latest IUCN criteria.

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