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**Advances in the systematics of the spider genus Troglodyphantes (Araneae, Linyphiidae)**

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*Original Citation:*

*Availability:*

This version is available <http://hdl.handle.net/2318/1610505> since 2017-05-15T09:05:05Z

*Published version:*

DOI:10.1080/14772000.2016.1254304

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(Article begins on next page)

1 **Advances in the systematics of the spider genus *Troglohyphantes* (Araneae,**  
2 **Linyphiidae)**

3

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13 **Running title:** Advances in *Troglohyphantes* systematics

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22 **ABSTRACT**

23 With 128 described species and 5 subspecies, the spider genus *Troglohyphantes* (Araneae,  
24 Linyphiidae) is a remarkable example of species diversification in the subterranean environment. In  
25 this paper, we conducted a systematic revision of the *Troglohyphantes* species of the Italian Alps,  
26 with a special focus on the *Lucifuga* complex, including the description of two new species (*T.*  
27 *lucifer* n. sp. and *T. apenninicus* n. sp). In addition, we provided new diagnostic drawings of the  
28 holotype of *T. henroti* (*Henroti* complex) and established three new synonymies within the genus.  
29 The molecular analysis of the animal DNA barcode confirms the validity of this method of  
30 identification of the Alpine *Troglohyphantes* and provides additional support for the morphology-  
31 based species complexes. Finally, we revised the known distribution range of additional  
32 *Troglohyphantes* species, as well as other poorly known alpine cave-dwelling spiders.

33

34 **Keywords:** cave-dwelling fauna, endemism, taxonomy, Italian spiders, species complexes, DNA  
35 barcoding

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94 **INTRODUCTION**

95 The linyphiid spider genus *Troglohyphantes* Joseph, 1881 is presently known to include 128 species  
96 and 5 subspecies (World Spider Catalog, 2016), which are generally found in a variety of habitats  
97 such as caves, mines, soil litter, rocky debris, and other moistly and shaded retreats (Fage, 1919;  
98 Deeleman-Reinhold, 1978; Isaia et al., 2011; Isaia, Lana, & Pantini, 2010). The genus is primarily  
99 distributed in the European mountain range, from the Cantabric Mountains in the West to the  
100 Balkans and Caucasus in the East. Four additional species are found in Northern Africa (Atlas) and  
101 two in the Canary Islands (World Spider Catalog, 2016). The systematics and the distribution of the  
102 genus has been studied in a variety of works, with major focus on the Balkan peninsula (Deeleman-  
103 Rehinold, 1978), the Pyrenees (Fage, 1919; 1931) and the Alps (Deeleman-Rehinold, 1978; Isaia et  
104 al., 2011; Isaia & Pantini, 2010; Pesarini, 1988a, 1988b, 1989, 2001). In general, *Troglohyphantes*  
105 species are rare and show narrow distributions. In several cases, they have been reported just from a  
106 single or few localities.

107 Because of the high speciosity of this genus, several authors have proposed to assemble the  
108 different species in groups based on either phenetic grounds—overall similarity—or authoritative,  
109 non-quantitative, phylogenetic hypotheses. The first classification was proposed by Fage (1919)  
110 who sorted 21 species—mainly pyrenaic and alpine—into 5 “*Groupes*” (I–V). Diagnoses were  
111 based on morphological characters, mostly pertaining to the morphology of male palps and  
112 epygines. In 1978 Deeleman-Reinhold revisited Fage’s classification and included 101 species—96  
113 of which are presently valid species—which were classified in three series (A, B and C) according  
114 to the epyginal morphology. Each series was further subdivided into 12 groups named after the  
115 more representative species and based on male palp morphology. However, especially in series B,  
116 boundaries between groups remained vague, sometimes including species of difficult placement. In  
117 spite of that, most of the authors describing new *Troglohyphantes* species after 1978, classified  
118 them following Deeleman-Reinholds’s criteria.

119 A preliminary attempt to classify Italian species was proposed by Thaler (1967) and Brignoli

120 (1971). Stemming from these early works, Pesarini (2001) retrieved Deeleman-Reinhold's  
121 classification and used it as a baseline to sort the Italian species into 11 "*Complexes*", partly  
122 overlapping with the extant classifications. Because of the high diversity of the genus in Italy,  
123 Pesarini (2001) further created some specific complexes for the Italian fauna, which included Italian  
124 species only.

125 When considering these three classifications and the work of further authors, more than 80% (109  
126 out of 132) of the genus diversity is indeed classified within at least one of the available diagnostic  
127 criteria. The highest number of species is classified according to Deeleman-Reinhold's criteria (99  
128 species, 75%) and covers mostly Alpine and Dinaric species. Fage's classification follows, covering  
129 a similar geographic range (88 species, 66%), while Pesarini's mostly focuses on Alpine species (38  
130 species, 28%). Overlaps and geographic coverages of the three classifications are illustrated in Fig.  
131 1 and detailed in Supplementary material Table S1.

132 However, in the absence of a proper morphological or molecular phylogenetic quantitative  
133 evaluation, the delimitations of the species groups remains speculative.

134 Knowledge of the genus in Italy has grown considerably in the last decades, mainly due to the  
135 contributions of Pesarini (1988a, 1988b, 1989, 2001) and studies conducted by our research team  
136 (Isaia & Pantini, 2008, 2010; Isaia et al., 2010, 2011; Mammola, Isaia, & Arnedo, 2015; Mammola  
137 & Isaia, 2016). However, even from a merely taxonomic standpoint, knowledge of *Troglohyphantes*  
138 spiders is far from being exhaustive and it is probable that more species have yet to be described.

139 One of the most speciose group in Italy is Deeleman-Reinhold's *Orpheus* group, which includes  
140 nine species from the Alps, one from the Massif Central and two from the Pyrenees. Pesarini (2001)  
141 splitted the *Orpheus* group in two complexes—*Lucifuga* and *Orpheus*. The two complexes differ  
142 mainly in the general shape of the *lamella characteristica* and have subtle differences in the  
143 epigynal structure. The *Orpheus* complex includes four species that exhibit troglomorphic  
144 adaptations, such as depigmentation and eye reduction.

145 In the present study, we focused on the *Lucifuga* complex. We described two new species—*T.*  
146 *lucifer* n. sp. and *T. apenninicus* n. sp.—, provided a detailed overview of the remaining species  
147 included in the group to facilitate their identification and proposed several nomenclatural changes.  
148 Furthermore we provided new data on species belonging to other complexes (*Caporiacoi*,  
149 *Diurnus*, *Henroti*, *Microcymbium*, *Orpheus*, *Polyophtalmus*, *Ruffoi* and *Sordelli*) and refined their  
150 distribution ranges, illustrated the holotype of *T. henroti* and provided new faunistic data on rare,  
151 stenoendemic cave-dwelling spiders collected during our recent surveys. Finally, we used a DNA  
152 barcoding approach to help in species delimitation and facilitate identification of Italian species.

153

## 154 **MATERIAL AND METHODS**

### 155 **Molecular methods**

156 Sequences for the mitochondrial cytochrome *c* oxidase subunit I gene—hereinafter *cox1*, the  
157 Animal DNA barcode—were obtained following the protocols described in Mammola et al. (2015).  
158 We were able to sample half of the known diversity of *Troglohyphantes* in Italy (17 out of 37  
159 species). For each species considered in the molecular analysis, we have reported the relative DNA  
160 code in Supplementary Material Table S2.

161 Sequences were edited and managed using Geneious R9 (Kearse et al., 2012). The alignment of the  
162 sequences was trivial, as they showed no evidence of indel mutations.

163 Parsimony analysis of the *cox1* matrix was conducted with TNT v.1.1 (Goloboff, Farris, & Nixon,  
164 2008) using 1,000 iterations of Wagner trees, followed by TBR branch swapping, and clade support  
165 assessed with 1,000 Jackknife resampling replicates—removal probability 36%. The best  
166 partitioning schemes and substitution models were assessed simultaneously with PartitionFinder  
167 v.1.0.1 (Lanfear, Calcott, Ho, & Guindon, 2012) under a Bayesian information criterion (BIC).

168 Maximum Likelihood (ML) analysis was conducted in RAxML v.7.4.2 (Stamatakis, 2006). We  
169 inferred the best ML tree and bootstrap support, automatically determining a sufficient number of

170 bootstrap replicates, using the MRE convergence criteria. Bayesian (BI) analysis was conducted in  
171 MrBayes v.3.2 (Ronquist et al., 2012) with two independent runs of 2 million generations with four  
172 Markov chains (one cold, three heated), sampling every 1,000 generations. The chain convergence  
173 (ASDSF), the correct mixing (EES) and the number of generation to discard as burn-in were  
174 monitored with Tracer v.1.6 (Rambaut, Suchard, Xie, & Drummond, 2014). The first 25% of trees  
175 in each run were discarded as burn-in. In all analyses the Canarian species *Troglohyphantes oromii*  
176 (Ribera & Blasco, 1986) was used as an outgroup to root the trees.

177 The ability of the animal barcode to identify species in Italian *Troglohyphantes* was investigated by  
178 means of distance metrics (Meier, Shiyang, Vaidya, & Ng, 2006), as implemented in the R package  
179 SPIDER 1.3 (Brown et al., 2012). Genetic distances were corrected using the Kimura 2 parameters  
180 model, as widely applied in Barcoding analyses, and using the R package APE 3.4 (Paradis, Claude,  
181 & Strimmer, 2004). First, we used the nearest neighbour criterion to assign a query sequence to the  
182 same species as its closest sequences in the reference library. We then inferred the threshold values  
183 that minimised the identification error rates—ie. false negatives or false positives—by optimising  
184 the SPIDER function *thereshOptm* testing threshold divergence values from 0.1 to 15%. The  
185 presence of a barcoding gap was visualized by plotting the maximum intraspecific divergence to the  
186 smallest interspecific divergence.

187

## 188 **Taxonomy**

189 Except otherwise stated, specimens are stored in 75% ethanol at the Museo Civico di Scienze  
190 Naturali “E. Caffi” of Bergamo (Italy). Additional materials are stored in:

191 i) Marco Isaia’s collection (CI) at Dipartimento di Scienze della Vita e Biologia dei Sistemi,  
192 University of Torino, Italy;

193 ii) Fulvio Gasparo's private collection (CG);

194 iii) the Natural History Museum of Bern (NHMB);

195 iv) the Museo Civico di Storia Naturale di Milano (MCSNM);



196 v) the Muséum National d'Histoire Naturelle de Paris (MNHN).  
197 All specimens were hand collected, except otherwise stated.  
198 We studied materials using a Leica M80 stereoscopic binocular microscope. Illustrations of  
199 pedipalps and epigynes were made by Elena Pelizzoli using a *camera lucida*. Paolo Pantini  
200 provided the diagrams of the female internal genitalia, using *camera lucida* on cleared epygines. All  
201 measurements are in mm. Anatomical terms follow Deeleman-Reinhold (1978).  
202 The summary bibliography, the relevant literature and the synonyms for each of the species here  
203 presented refers to the World Spider Catalog (2016).  
204 The toponomastics and classification of the different sectors and sub-sectors of the Alps follows the  
205 standard partition of the alpine chain (SOIUSA; Marazzi, 2005). Whenever appropriate/applicable,  
206 the speleological cadastral codes of the caves are given in squared brackets [regional code and  
207 number].  
208 The following abbreviations are used in the text: ALE = anterior lateral eyes; AME = anterior  
209 median eyes; MSS = *Milieu Souterrain Superficiel* (*sensu* Mammola et al., 2016); PLE = posterior  
210 lateral eyes; PME = posterior median eyes; SA = Suprategular apophysis; SSD = Subterranean  
211 Sampling Device; SSH = Shallow Subterranean Habitat (*sensu* Culver & Pipan, 2014); TLL = total  
212 leg length; TmI = position of trichobothrium on metatarsus of first leg.

213

## 214 **RESULTS**

### 215 **Molecular analyses**

216 The new sequences obtained in the present study are available in GenBank® (KT831559–  
217 KT831596; see Supplementary materials Tables S2).

218 We generated 48 sequences of 676 bp of the *cox1* DNA barcode, corresponding to 43 unique  
219 haplotypes. The mean interspecific genetic divergence (K2P) across the Italian *Troglyphantes*  
220 individuals was 16.8% (sd=0.023). The comparison of the minimum interspecific divergences, with  
221 the maximum intraspecific divergences revealed the existence of a barcoding gap (Supplementary

222 Material Fig. S1), with an optimum threshold divergence estimated between 7 and 7.6%. The  
223 nearest neighbour criterion resulted in a 100% identification success in species represented by more  
224 than one sequence.

225 The parsimony analysis yielded three trees of 1132 steps. Partitionfinder selected the simple  
226 codon—i.e. two partitions 1<sup>st</sup> and 2<sup>nd</sup> codon partitions together and 3<sup>rd</sup> partition apart—as the best  
227 partition scheme. The preferred evolutionary model for the 1<sup>st</sup> + 2<sup>nd</sup> codon partition was HKY+I+G  
228 and for the 3<sup>rd</sup> codon partition the TrN+G—a GTR was implemented in MrBayes instead. We used  
229 unlinked GTR+G models for the RAxML analysis. The results of the analyses conducted under the  
230 different phylogenetic inference methods are summarized in Fig. 2. All species showed exclusive  
231 haplotypes that formed supported clades. As expected by using a single, highly variable gene, deep  
232 relationships were poorly supported and some differed across methods. However, all complexes  
233 proposed by Pesarini (2001) were recovered and mostly supported as monophyletic, except for the  
234 *Microcymbium* complex, which was recovered as paraphyletic with regards to the *Caporiacoi*,  
235 *Sordellii* and *Henroti* complexes.

236

## 237 **TAXONOMIC ACCOUNT**

### 238 **Lucifuga complex**

239 The *Lucifuga* complex so far comprises seven species (Pesarini, 2001, Isaia and Pantini, 2010):  
240 *Troglohyphantes albopictus* Pesarini, 1989, restricted to Colli Euganei and Colli Berici—formally  
241 outside of the alpine chain, a few km south of the Prealps of Veneto; *T. aldae* Pesarini, 2001 only  
242 recorded in the type locality—Asiago plateau, Prealps of Veneto; *T. lucifuga* (Simon, 1884)—from  
243 Lanzo Valley to Tessin and Wallis; *T. pluto* di Caporiacco, 1938, endemic to the Corsaglia Valley  
244 and high Tanaro Valley—Ligurian Alps; *T. sarae* Pesarini, 2011, endemic to Val d'Aosta; *T. sciakyi*  
245 Pesarini, 1989, endemic to the Central Lombard Prealps; *T. subalpinus* Thaler, 1967, restricted to  
246 Northern Tyrol and Lower Austria (Fig. 3). Together with the species of the *Orpheus* complex, all  
247 species included in the *Lucifuga* complex belong to the *Orpheus* group *sensu* Deeleman-Reinhold

248 (1978). With *T. subalpinus* (Austria) and *T. lucifuga* (Italy and Switzerland) as the only exceptions,  
249 all species included in this complex are Italian endemic.

250 The complex is characterized by the peculiar dorso-flattened *lamella characteristic*, with the two  
251 branches (*sensu* Deeleman-Rehino, 1978) fused for most of their length. In this complex, the  
252 *lamella characteristic* is not entirely visible from a lateral view and requires detachment—or at  
253 least bulb expansion. The scape of the epygine is always pedunculated —“*palette*” *sensu* Fage,  
254 1919. All the species belonging to this group present an abdominal pattern, which is rather reduced  
255 in *T. pluto*.

256 Here we provided comparative plates illustrating the diversity of the species belonging to this  
257 complex (Figs. 4, 5, 6, 7, 8, 9). Moreover, we described two new species and proposed two  
258 synonymies within the complex. Accordingly, the complex still includes seven species: *T.*  
259 *albopictus*, *T. apenninicus* n. sp., *T. lucifer* n. sp., *T. lucifuga*, *T. pluto*, *T. sciakyi* and *T. subalpinus*.

260

261 ***Troglohyphantes albopictus* Pesarini, 1989 (= *T. aldae* Pesarini 2001, new synonymy)**

262 Figs. 4.1, 5.1, 6.1, 6.2, 7.1, 8.1, 9.1

263 *Material examined*

264 Italy, Veneto, Province of Padova: Rovolon, Colli Euganei, 22.IV.1988, leg. Zanon (male holotype of *T. albopictus*;  
265 MCSNM). Province of Vicenza: Valle Scalon (Altopiano di Asiago), in military bunkers, 30.V.1989, leg. Comotti e  
266 Baldan (male holotype of *T. aldae*; MCSNM); Mt. Grappa, 10.X.1969 Buche leg. 1♀ 2juv; same locality, 28.IX.1977,  
267 Buche leg. 2♂♂; Recoaro, Monti Lessini, Fongara, m 850, 28.IV.1984, Thaler leg. 1♂ 1♀ 1juv; Campodalbero, m  
268 1200, 27.IV.1984 Thaler leg. 2♂♂ 3♀♀ 1juv; Nanto, Colli Berici, 25.IV.1985, Thaler leg. 1♂ 1♀; Schio, Sant'Antonio,  
269 Pian delle Fugazze, Rifugio Balasso (1000m), 10.X.1969, 1♂. Trentino Alto Adige, Province of Trento: Borgo  
270 Valsugana, Val di Sella, m 900-1200, 30.IX.1977, 2♂♂ 3♀♀ 3juv

271

272 *Notes*

273 The examination of the holotype of *Troglohyphantes albopictus*, the material from other localities  
274 and the holotype of *T. aldae*, allowed the comparison of *lamella characteristic* (Figs. 6.1, 6.2),  
275 suggesting that *T. aldae* Pesarini 2001 is a junior synonym of *T. albopictus* Pesarini 1989.

276 Accordingly, the range of distribution of *T. albopictus* now comprises Colli Euganei, Colli Berici  
277 and the Prealpi Venete—Asiago plateau.

278

279 ***Troglohyphantes apenninicus* Isaia, Mammola & Pantini new species**

280 Figs. 4.2, 5.2, 6.3, 7.2, 8.2, 9.2, 10

281 *Type series*

282 **Holotype.** Italy, Toscana, Province of Pistoia: Abetone, 10.66270 E 44.14500 N, 15.X.1975, Thaler leg. 1♂.

283 **Paratypes.** Italy, Toscana, Province of Massa: Apuane Alps, Mount Sumbra, 10.27900 E 44.07800 N, 04.VI.1988,

284 Thaler leg. 2 juv Province of Pistoia: Abetone, 10.662700 E 44.14500 N, 15.X.1975, Thaler leg. 4♂♂ 6♀♀ 6juv

285

286 *Diagnosis*

287 Males of *Troglohyphantes apenninicus* are primarily distinguished from other species of

288 *Troglohyphantes* by the shape of the *lamella characteristic* —better viewed if extracted (Fig.

289 6.3),—flattened dorso-ventrally, with the external branch ending with a sharp tooth pointed

290 upwards, almost parallel to the longer axis of the external branch. In comparison with the sister

291 species, in *T. albopictus* (Fig. 6.1), *T. lucifer* n.sp. (Fig. 6.4), and *T. lucifuga* (Figs. 6.5, 6.6) the

292 external branch tapers in a subtriangular apex, bent at the top towards the internal branch.

293 Conversely in *T. apenninicus* (Fig. 6.3), *T. sciaky* (Fig. 6.8), *T. pluto* (Fig. 6.7) and *T. subalpinus*

294 (Fig. 6.9) the apex is not bent, being smaller in *T. subalpinus*, pointed and slender in *T. pluto* and

295 enlarged at its base in *T. sciaky*. The shape of the cymbium (Fig. 5) is also diagnostic, ending

296 proximally with three stout apophysis: the internal apophysis is similar to *T. albopictus* (Fig. 5.1)

297 but stouter, the median apophysis is subtriangular—smaller and more pointed than *T. albopictus* and

298 bigger than the other species of the complex,—and the external apophysis is similar to *T.*

299 *albopictus*.

300 Females are best diagnosed by the epyginum viewed ventrally, by combining the shape of the

301 scape—rhomboidal—with the margins of the pedunculated part—curved,—although differences

302 across species of the *Lucifuga* complex can be very subtle (Fig. 7). In *T. apenninicus* n.sp. the  
303 epyginal plate forms a rhomboidal scape, narrowed at its base and enlarged distally (Figs. 7.2,  
304 10.3). In comparison with other species, the scape is almost round in *T. albopictus* (Fig. 7.1) and  
305 trapeizoidal—more enlarged at the base—in *T. pluto* (Fig. 7.5) and *T. sciaky* (Fig. 7.6). The margins  
306 of the proximal part of the scape—connecting the scape to the upper part of the epygyne—are  
307 curved, unlike the parallel margins found in *T. albopictus* (Fig. 7.1), *T. lucifer* n. sp. (Fig. 7.3) and *T.*  
308 *lucifuga* (Fig. 7.4). Viewed laterally, the scape appears similar to *T. sciaky* (Fig. 8.6), more arched  
309 than in the other species of the complex—especially *T. albopictus* (Fig. 8.1), *T. lucifer* n. sp. (Fig.  
310 8.3) and *T. lucifuga* (Fig. 8.4). The identification of females in absence of males remains doubtful  
311 in most cases.

312

### 313 *Description*

314 Male holotype: prosoma 1.37 long, 1.10 wide, yellowish. Thoracic region slightly swollen,  
315 yellowish. Cephalic region slightly elevated, interspersed with black bristles between the eyes.  
316 Clypeus slightly indented under the eyes, then convex, 0.31 long. Eyes normally developed, with  
317 pigment and black margins. AME smallest. PLE as large as PME, ALE slightly larger than PLE.  
318 ALE and PLE almost contiguous. PLE–PME distance = 0.03, ALE–AME distance = 0.04, PME–  
319 PME distance = 0.06. Eye diameters AME 0.06, PME and PLE 0.07, ALE 0.10.  
320 Sternum heart-shaped, brownish with flimsy darkened anterior edges. Chelicerae 0.65 long,  
321 brownish, with ca. 30 lateral stridulatory ridges and armed with three teeth on the anterior side of the  
322 chelicerae, and five small, aligned teeth on the internal side. Legs brownish, uniform in colour. Leg  
323 I: femur 2.88, patella 0.34, tibia 3.13, metatarsus 2.66, tarsus 1.66, TLL 10.66; leg II: femur 2.69,  
324 patella 0.31, tibia 2.72, metatarsus 2.50, tarsus 1.44, TLL 9.66; leg III: femur 2.03, patella 0.31, other  
325 articles missing; leg IV: femur 2.81, patella 0.31, tibia 2.69, metatarsus 2.50, tarsus 1.38, TLL 9.69.  
326 Abdomen 1.90 long, 1.35 wide; greyish with a dark pattern (Fig. 10.2). Palp (Fig. 10.1): femur 1.28,  
327 patella 0.38, tibia 0.31, total palpal length 1.97. Cymbium faintly convex, roughly rectangular when

328 seen from above, ending proximally with three stout apophysis, the external and the medial  
329 subtriangular, the internal subrectangular (Fig. 5.2). Posterior part of paracymbium subtriangular, the  
330 apical part gradually narrowed anteriorly. *Lamella characteristic* flattened dorso-ventrally, better  
331 visible after extraction (Fig. 6.3). External and internal branches fused over most of their length. The  
332 internal branch is attached to the radix, made up of two lobes, the smaller branch is short and rounded  
333 and the longer one is enlarged distally and separated from the external branch by a depression.  
334 Fickert's gland absent. External branch of the lamella, ending with a sharp tooth, darkened at its end,  
335 pointed upwards, almost parallel to the longer axis of the external branch. Distal suprategular  
336 apophysis (median apophysis *sensu* Deelman-Reinhold, 1978) directed upwards, with a sharp end.  
337 Tip of the embolus spiculate. Spination (Tibia and Metatarsus III absent): femur I–II with one dorsal  
338 spine; femur III–IV with no spine. Patella I–IV with one dorsal spine. Tibia I with two dorsal, two  
339 prolateral, two retrolateral and two ventral spines. Tibia II with two dorsal, two retrolateral spines,  
340 one ventral and one prolateral; Tibia III absent; tibia IV with two dorsal, one retrolateral and one  
341 prolateral spine. Metatarsus I, II, IV with one dorsal spine. Patella of the Palp with one long, curved  
342 spine. TmI: 0.21. Trichobothrium on Mt IV absent.

343

344 *Female* (paratype from same locality as holotype): prosoma yellowish, 1.31 long, 1.06 wide. Cephalic  
345 region grey-yellowish. Carapace, ocular area, clypeus, and sternum similar to the male in all features.  
346 Clypeus 0.25 long, chelicerae 0.50 long. Anterior margin of the chelicerae armed with three teeth on  
347 the anterior side of the chelicerae, and five small, aligned teeth on the internal side. PLE–PME  
348 distance = 0.03, ALE–AME distance = 0.04, PME–PME distance = 0.06, AME–AME almost  
349 contiguous, ALE–PLE contiguous. Eye diameters: AME 0.06, PME 0.07, ALE 0.10, PLE 0.09.  
350 Abdomen greyish, 1.53 long, 1.18 wide, with a dark pattern. Leg I: femur 2.69, patella 0.38, tibia  
351 2.97, metatarsus 2.22, tarsus 1.41, TLL 9.66; leg II: femur 2.47, patella 0.34, tibia 2.25, metatarsus  
352 2.06, tarsus 0.91, TLL 8.03; leg III: femur 2.06, patella 0.34, tibia 1.56, metatarsus 1.63, tarsus 0.81,  
353 TLL 6.50; leg IV: femur 2.59, patella 0.34, tibia 2.50, metatarsus 2.00, tarsus 1.22, TLL 8.66. Female

354 palp: femur 1.13, patella 0.25, tibia 0.75, tarsus 0.44, total palp length 3.50. Spination: Patella of the  
355 palp with one dorsal spine, pedipalpal claw present; Tibia of the palp with one dorsal, two prolateral  
356 and one retrolateral spine; Tarsus of the palp with three ventral and two prolateral spines, and one  
357 retrolateral spine. Femur I–II with one dorsal spine; femur III–IV with no spine. Patella I–IV with  
358 one dorsal spine. Tibia I with two dorsal, two prolateral, two retrolateral and two ventral spines. Tibia  
359 II with two dorsal, one ventral, two retrolateral and one prolateral spine; Tibia III with two dorsal,  
360 one prolateral and one retrolateral spine; tibia IV with two dorsal, one retrolateral and one prolateral  
361 spine. Metatarsus I–IV with one dorsal spine. Position of TmI: 0.21. Trichobothrium on Mt IV absent.  
362 Epigynum strongly protruding (Figs. 7, 8). Epyginal plate strongly incised, forming a rhomboidal  
363 scape, narrowed at its base, enlarged medially and converging distally. Lateral lobes emerging at the  
364 posterior end of the epygine (Figs. 7.2, 10.3). Scape arched from a lateral view (Figs. 8.2, 10.4),  
365 covering entirely the inner part of the epygine (“*languette interne*” according to Fage, 1919); stretcher  
366 tongue-shaped bent upwards toward the scape, bearing a pitted knob at its end, clearly visible from a  
367 ventral point of view. Internal genitalia as in Fig. 9.2.

368

### 369 *Etymology*

370 The species epithet derives from the Latin *Apenninum*, the Apennine mountain range, in which the  
371 type series was collected.

372

### 373 *Distribution*

374 The species is currently known to occur in two localities of the Tuscan Apennines: Abetone (Pistoiese  
375 mountains) and Mount Sumbra (Apuan Alps). The species was collected by Konrad Thaler in epigeal  
376 localities. No indications about the habitat were given.

377

378

379 ***Troglohyphantes lucifer* Isaia, Mammola & Pantini new species**

380 Figs. 4.3, 5.3, 6.4, 7.3, 8.3, 9.3, 11, 12

381 *Type series*

382 **Holotype.** Italy, Piemonte, Province of Torino: Roure, Tana del Diavolo [Pi 1591], 7.1220669 E 45.0263401 N,  
383 12.IX.2014, Isaia & Mammola leg. 1♂ (CI 2566).

384 **Paratypes.** Italy, Piemonte, Province of Torino: Almese, Viù, Colle del Lys, 7.36146 E 45.17751 N, 9.06.2016, Isaia,  
385 Mammola & Palermo leg. 3♂♂ 6♀♀ (CI 2883-2884); Gravere, Balma Fumarella [Pi 1597], 7.034559 E 45.125928 N,  
386 13.VI.2014, Mammola & Piano leg. 1♀ (CI 2727).

387

388 *Material examined*

389 Italy, Piemonte, Province of Torino: Almese, Viù, Colle del Lys, 10.X.1972, Thaler leg. 7♂♂ 9♀♀ 6juv; same locality,  
390 same data, Thaler leg. 3♂♂ 5♀♀; same locality, same data, Thaler leg. 1♂ 1♀; same locality, same data, Thaler leg. 7♂♂  
391 8♀♀ 2juv; same locality, same data, Thaler leg. 4♂ 9♀♀; same locality (in an abandoned house), 9.VI.2016, Isaia,  
392 Mammola & Palermo leg. 1♂ 2♀♀ (CI); same locality (in rocky debris), same data, Isaia, Mammola & Palermo leg. 2♂♂  
393 4♀♀ (CI); Giaveno, W Forno, 09.X.1972, Thaler leg. 2♂ 7♀ 4juv; Bruzolo, Seinerer mineshaft, 30.IX.2016, Isaia &  
394 Mammola leg. 1♀ (CI); Novalesa, Grotta del Ghiaccio di Bosconero [Pi 1580], 15.VII.2006, Lana E. leg. 1♂; same  
395 locality, 18.II.2016, Isaia & Mammola leg. 2♂♂ 6♀♀ (CI); Mezenile, Borna Maggiore del Pugnetto [Pi 1501],  
396 17.VI.2006, Isaia leg. 1juv (CI 1033); same locality, 29.I.2010, Isaia leg. 1♀ (CI 1057); Same locality, 17.VII.2015,  
397 Mammola & Piano leg. 1♂ 2♀♀ (CI 2725); Mezenile, Tana del Lupo [Pi 1502], 17.XII.14, Isaia & Mammola leg. 2♂♂  
398 1♀ (CI 2613); Mezenile, "Cavernetta 5" [Pi], 11.III.2016, Mammola & Isaia leg. 1♀; Mezenile, Pugnetto beech forest,  
399 1.VII.2012–1.VII.2013, SSD in MSS 0.60 m deep, Isaia & Piano leg. 4 juv (CI 2381); same locality, same data, SSD in  
400 MSS 0.80 m deep, Isaia & Piano leg. 1♀ (CI); Mezenile, Pugnetto beech forest (leaf litter), 12.IX.2013, Isaia leg. 3♀♀  
401 (CI 2561).

402

403 *Other material*

404 Italy, Piemonte, Province of Torino: Mezenile, Borna Maggiore del Pugnetto [Pi 1501] (Isaia *et al.*, 2010, 2011 sub *T.*  
405 *lucifuga*); Mezenile, Borna Inferiore del Pugnetto [Pi 1502] (Isaia *et al.*, 2010, 2011 sub *T. lucifuga*); Novalesa, Grotta  
406 del Ghiaccio di Bosconero [Pi 1580] (Isaia *et al.*, 2010, 2011 sub *T. lucifuga*); Novalesa, Boira dal Farfujet o Balma dei  
407 Folletti [Pi 1620] (Arnò & Lana, 2005 sub Linyphiidae indet.; Isaia *et al.*, 2010, 2011 sub *T. lucifuga*).

408

409 *Diagnosis*

410 Males of *Troglohyphantes lucifer* n. sp. are primarily distinguished from other species of  
411 *Troglohyphantes* by the shape of the *lamella characteristic*, better viewed if extracted (Fig. 6.4).

412 The new species is close to *T. lucifuga* and other species of the *Lucifuga* complex, from which it is



413 distinguishable by the presence of three teeth-like apophysis on the *lamella characteristic* (Fig. 6.4),  
414 two on the external branch and one on the internal branch. Compared to the other species, the teeth-  
415 like apophysis on the external branch are unique to *T. lucifer* n.sp. and are absent in other species of  
416 the complex. The shape of the cymbium, ending proximally with three stout apophysis and rounded  
417 at the proximal border (Fig. 5.3), is also diagnostic. Compared to other species, the internal apophysis  
418 is long and slender, with parallel margins—i.e. almost rectangular if compared to other species within  
419 the group,—with a rounded apex. Females are best diagnosed by the epyginum viewed ventrally  
420 (Figs. 7.3, 11.3), although differences across species of the *Lucifuga* complex can be very subtle (Figs.  
421 7, 8). Compared to other species, the epyginal plate is strongly incised, forming a trapezoidal scape  
422 (Fig. 7.3). The margins of the proximal part of the scape—connecting the scape to the upper part of  
423 the epygyne—are parallel, similar to *T. albopictus* (Fig. 7.1), *T. apenninicus* n. sp. (Fig. 7.2) and *T.*  
424 *lucifuga* (Fig. 7.4). Viewed laterally, the scape appears similar to *T. albopictus* (Fig. 8.1) and *T.*  
425 *lucifuga* (Fig. 8.4), and less arched than the other species of the complex. The identification of females  
426 in absence of males remains doubtful in most cases—see also diagnosis of *T. apenninicus*.

427

#### 428 *Description*

429 *Male holotype* (CI2566): prosoma 1.25 long, 1.12 wide, yellowish. Thoracic region slightly swollen,  
430 yellowish with grey shades. Cephalic region elevated, interspersed with black bristles between the  
431 eyes, with few small black bristles forming the eye region and continuing backwards in three  
432 longitudinal rows converging at the thoracic furrow. One bristle just below AME. Carapace with  
433 darker margins. Clypeus slightly indented under the eyes, then convex, 0.59 long. Eyes normally  
434 developed, with pigment and black margins. AME smallest. ALE slightly bigger than PME and PLE.  
435 ALE and PLE contiguous. PLE–PME distance = 0.04, ALE–AME distance = 0.04, PME–PME  
436 distance = 0.04. Eye diameters AME 0.06, PME 0.07, ALE 0.09, PLE 0.07. Sternum heart-shaped,  
437 yellowish with flimsy darkened anterior edges. Chelicerae light brownish, 0.62 long, with ca. 30  
438 lateral stridulatory ridges and armed with three anterior teeth. Legs yellowish, uniform in colour. Leg

439 I: femur 3.19, patella 0.72, tibia 3.28, metatarsus 2.91, tarsus 1.72, TLL 11.81; leg II: femur 3.00,  
440 patella 0.75, tibia 3.13, metatarsus 2.81, tarsus 1.56, TLL 11.25; leg III: femur 2.19, patella 0.41, tibia  
441 1.97, metatarsus 1.72, tarsus 1.09, TLL 7.38; leg IV: femur 2.94, patella 0.66, tibia 2.78, metatarsus  
442 2.66, tarsus 1.38, TLL 10.41. Abdomen greyish with faint pattern (Fig. 11.2), 2.03 long, 1.31 wide.  
443 Palp (Fig. 10a): femur 0.63, patella 0.19, tibia 0.19. Cymbium faintly convex, roughly rectangular  
444 when observed from above, ending proximally with three stout apophysis, rounded at the proximal  
445 border (Fig. 5.3).

446 Posterior part of paracymbium subtriangular, apical part gradually narrowed anteriorly (Fig. 11.1).

447 *Lamella characteristic* similar to *T. lucifuga* (Fig. 6.5, see Isaia *et al.*, 2011: p. 132, fig. 2.51a),  
448 flattened dorso-ventrally, better visible from a dorsal view after extraction (Fig. 6.4). External and  
449 internal branch fused over most of their length. The internal branch attached to the radix, made up of  
450 two lobes, the smaller branch short and rounded and the longer one enlarged distally, bearing on the  
451 outer margin two characteristic teeth-like apophysis, darkened at their tips—see also the paragraph  
452 on the synonymy *T. sarae* = *T. lucifuga*—: one placed medially, sharp and well defined, tapering, and  
453 pointing towards the internal branch; the other shorter, smaller and less pointed, placed in the notch  
454 between the latter and the distal apex of the external branch of the lamella. Fickert's gland absent.

455 External branch of the lamella, ending with a sharp tooth, darkened at its end, pointed towards the  
456 internal branch, nearly perpendicular to the longer axis of the external branch. Suprategular apophysis  
457 directed upwards, with a sharp end (Fig. 11.1). Tip of the embolus spiculate. Spination: femur I with  
458 two prolateral spines; Femur II–IV with no spine. Patella I–IV with one dorsal spine. Tibia I with one  
459 dorsal, two ventral, and one retrolateral spine; Tibia II with one dorsal, one ventral, one retrolateral  
460 and one prolateral spine; tibia III with one prolateral, one dorsal and one retrolateral spine; Tibia IV  
461 with one dorsal, two prolateral, and three retrolateral spines. Metatarsus I–IV with one dorsal spine.  
462 Patella of the palp with one long, curved spine. TmI: 0.2. Trichobothrium on Mt IV absent.

463

464 *Female* (paratype from Pugnetto CI 2727): prosoma 1.23 long, 1.00 wide, slightly darker than male.

465 Cephalic region light-brownish. Carapace, ocular area, clypeus, and sternum are similar in all features  
466 to the analogous male body parts. Dark brown sternum with dark margins. Anterior margin of the  
467 chelicerae armed with three teeth. Clypeus 0.23 long, chelicerae 0.47 long. PLE–PME distance =  
468 0.06, ALE–AME distance = 0.04, PME–PME distance = 0.06, AME–AME distance = 0, ALE–PLE  
469 distance = 0. Eye diameters: AME 0.04, PME, AME and PLE = 0.07. Abdomen greyish with black  
470 pattern (Fig. 12), 2.5 long, 1.87 wide. Leg I: femur 2.50, patella 0.50, tibia 3.22, metatarsus 2.72,  
471 tarsus 1.53, TLL 10.47; leg II: femur 2.66, patella 0.56, tibia 2.81, metatarsus 2.50, tarsus 1.38, TLL  
472 9.91; leg III: femur 2.19, patella 0.34, tibia 1.88, metatarsus 1.88, tarsus 0.81, TLL 7.09; leg IV: femur  
473 2.72, patella 0.38, tibia 2.50, metatarsus 2.41, tarsus 1.25, TLL 9.25. Female palp: femur 0.66, patella  
474 0.13, tibia 0.38, tarsus 0.78, total palp length 1.94. Spination (CI 2381): Femur I with one prolateral  
475 spine; Femur II–IV with no spine. Patella I–IV with one dorsal spine. Tibia I–II with two dorsal, one  
476 prolateral, two ventral and three retrolateral spines; Tibia III with two dorsal, one prolateral and one  
477 retrolateral spine. Tibia IV with two dorsal, two ventral and one retrolateral spine. Metatarsus I–IV  
478 with one dorsal spine. Patella of the palp with one dorsal spine, pedipalpal claw present; Tarsus of  
479 the palp with four dorsal, three retrolateral and three prolateral spines. TmI: 0.2. Trichobothrium on  
480 Mt IV absent.

481 Epigynum strongly protruding, with trapezoidal scape (Fig. 11.3), arched from a lateral view (Fig.  
482 11.4). Scape diverging distally, with a short stem. Tips of the lateral lobes visible in normal position  
483 (Fig. 11.3). Epyginal plate incised, forming a trapezoidal scape, enlarged medially and converging  
484 distally. Lateral lobes emerging at the posterior end of the epygine (Fig. 11.3). Scape arched from a  
485 lateral view (Fig. 11.4), covering entirely the inner part of the epygine (“*languette interne*” according  
486 to Fage, 1919); stretcher tongue-shaped almost straight, abruptly bent upwards toward the scape,  
487 bearing a pitted knob at its end clearly visible from a ventral point of view. Internal genitalia as in  
488 Fig. 9.3.

489

490 *Etymology*

491 The species epithet derives from the name of the type locality *Tana del Diavolo*—Devil’s lair. Lucifer  
492 is the classical traditional Jewish-Christian name assigned to the Devil after the interpretation of a  
493 Bible verse from Isaiah. More precisely, Lucifer is the name of the Devil before the Fall from heaven  
494 “*to the depth of the pit*” (Isaiah 14: 15). The epithet also recalls the previous misidentifications of  
495 *Troglohyphantes lucifer* with *T. lucifuga*.

496

#### 497 *Distribution*

498 The species is known to be found in several localities of a small sector of the Northern Cottian Alps  
499 —Viù, Susa and Chisone Valley.

500

#### 501 *Notes*

502 This species was firstly collected in an unspecified epigeal habitat by Konrad Thaler in 1972, in the  
503 nearby of Colle del Lys and Giaveno—Cottian Alps. The majority of the recent material listed in this  
504 contribution was collected on floors and walls of the twilight zone of natural caves as well as in block  
505 fields in beech forests. Further specimens were collected in MSS during recent biospeleological  
506 investigations at the hypogean complex of Pugnetto—Mezzenile, Lanzo valley, Graian Alps, North-  
507 western Alps. MSS was sampled using Subterranean Sampling Devices (SSD; Domingo-Quero &  
508 Alonso-Zarazaga, 2010; López & Oromí, 2010) installed at a depth of 0.40–0.80 m.

509

#### 510 ***Troglohyphantes lucifuga* (Simon, 1884) (= *T. sarae* Pesarini, 2011 new synonymy)**

511 Figs. 4.4, 5.4, 6.5, 6.6, 7.4, 8.4, 9.4

#### 512 *Material examined*

513 Italy, Valle d'Aosta, Province of Aosta: Val di Rhêmes, Vandalettaz, 15.X.2006, Fantoni & De Angelis leg. 1♂ (Paratype  
514 of *T. sarae*; MCSNM); Brusson, 09.V.1995, Lana leg. 1♂ 4♀♀ (CI 1055); La Salle, Borna d'la Glace [Ao 2001],  
515 09.IX.1995, Lana leg. 5♂♂, 7♀♀ (CI 1062); same locality, 16.IX.2014; Isaia & Mammola leg 3♂♂ (CI 2567); Petosan,  
516 21.X.2009, Lana leg. 2♂♂, 4♀♀ (CI 1063); St. Rhemy, Fortino presso St.Rhemy, 07.IX.2008, Lana leg. 1♂ 1♀ (CI

517 1067); Verrogne, Fessura di Verrogne [Ao 2017], 09.IX.1995, Lana leg. 4♂♂ 4♀♀ 1juv (CI 1069); same locality,  
518 16.IX.2014; Isaia & Mammola leg 1♂ (CI 2568); Sarre, Mezz'Abisso [Ao 2071], 26.X.2008, Lana leg. 1♂ 1♀ (CI 1073);  
519 Sarre, Grotta della Soldanella [Ao 2072], 26.X.2008, Lana leg. 1♂ 3♀♀ (CI 1074). Piemonte, Province of Verbania:  
520 Macugnaga, Moraine of Belvedere glacier (Mount Rosa), 24/09–12.X.2014, pitfall trap, Tampucci leg. 1♂ 3♀♀;  
521 Sambughetto, Caverna delle Streghe di Sambughetto [Pi 2051], 01.X.2013, Isaia & Mammola leg. 2♂♂ (CI 2573).  
522 Province of Vercelli: Borgosesia, Buco della Bondaccia [Pi 2505], 27.I.2008, Isaia leg. 1♂ 2♀♀ (CI 1054); Valduggia,  
523 Bell'Ingresso [Pi 2539], 17.VI.2009, Lana leg. 1♂ (CI 1071); Valduggia, Bocc d'la Mocia [Pi 2541], 17.VI.2009, Lana  
524 leg. 1♂ (CI 1070). Province of Novara: Alagna, Alpi Pile, 03.X.1971, Thaler leg. 2♂♂ 3♀♀ 1juv; same locality, same  
525 data, Thaler leg. 1♀; same locality, same data, Thaler leg. 3♂♂ 10juv; Alagna, Quarone (Roccapietra), 03.X.1971 Thaler  
526 leg. 1♀ 6juv; Province of Biella: Biella, Santuario di Oropa, 11.X.1972, Thaler leg. 5♂♂, 3♀♀. Province of Torino:  
527 Brosso, Buca del Ghiaccio della Cavallaria [Pi 1609], 07.XI.2014, Isaia & Mammola leg. 3♂♂ 2♀♀ 3juv (CI 2607);  
528 Sparone, Grotta la Custreta [Pi 1593], 07.XI.2014, Isaia & Mammola leg. 2♂ 3♀ (CI 2610); Ceres, Borna del Servais B,  
529 24.IX.2014, Mammola & Paschetta leg. 1♂ 1♀ 2juv (CI 2571); same locality, 14.X.2009, Isaia & Paschetta leg. 1♂ (CI  
530 1061); same locality, 29.IX.2002, Lana leg. 1♂ 1♀ (CI 1077); Ingria, Torrente Soana, 10.X.1972, Thaler leg. 3♂♂, 5♀♀  
531 1 juv; same locality, same data, Thaler leg. 2♂♂ 5♀♀ 3 juv

532

### 533 *Notes*

534 The comparison of specimens of *T. lucifuga* from different localities of Val d'Aosta and Piemonte  
535 with type material of *T. sarae* Pesarini 2011—described on specimens from Val di Rhêmes and  
536 Valsavaranche, Val d'Aosta—suggests that the latter is a junior synonym of *T. lucifuga*.  
537 Specifically, the observation of the detached *lamella characteristic* revealed a clear  
538 correspondence between the two species (Figs. 6.5, 6.6). The diagnosis of *T. sarae* was based on the  
539 presence of two small and squat teeth on the medial part of the outer margins of the internal and the  
540 external branches of the lamella (Pesarini, 2011, p. 65, f. 3). By examining the detached lamella  
541 (Fig. 6.5) of different specimens of *T. lucifuga* and comparing them with the type material of *T.*  
542 *sarae* (Fig. 6.6), two weak longitudinal bumps were observed on the dorsal part of the branches of  
543 the internal and external lamella, which determine two apparent discontinuities in the profiles of the  
544 distal margins of the lamella. Such discontinuities, identical in *T. sarae*, appear like small teeth from  
545 a lateral point of view, which may explain Pesarini's wrong diagnosis. On this base, we propose *T.*  
546 *sarae* Pesarini, 2011 as junior synonym of *T. lucifuga* (Simon, 1884).

547 *Troglohyphantes lucifuga* is generally found in the outer part of caves, but also in epigean habitats,  
548 such as moist shaded places, deep leaf litter and other SSHs. The species is widely distributed in the  
549 North-Western Italian Alps—Val d’Aosta and Northern Piemonte. The presence of this species in  
550 Switzerland is testified by historical records (Dresco, 1959; Lessert, 1910; Schenkel, 1933) in  
551 Wallis (Bourg Saint Pierre and Zermatt) and Tessin (Frasco).

552

553 ***Troglohyphantes pluto di Caporiacco, 1938***

554 Figs. 4.5, 5.5, 6.7, 7.5, 8.5, 9.5

555 *Material examined*

556 Italy, Piemonte, Province of Cuneo: Frabosa Sottana, Balma Ghiacciata del Mondolè [Pi 102], 22.IX.2015, Isaia,  
557 Mammola & Ladame leg. 5♀♀ 9 juv (CI 2644); Roccaforte Mondovì, Grotta dei Partigiani della Tura [Pi 286], 11.X.2015 Lana  
558 leg. 1♀ (CI); same locality, 22.V.2016, Chesta & Lana leg. 1♂ 1♀; same locality, 9.VIII.2016, Lana leg 1♀ (CI); same locality,  
559 22.VIII.2016, Lana leg 1♀ (CI); same locality, 18.VIII.2016, Giachino & Lana leg 1♂ 2juv (CI); Roccaforte Mondovì, Grotticella  
560 della Tura [Pi n.c.], 12.VIII.2016, Chesta & Lana leg. 1♀ (CI); same locality, 22.VIII.2016, Chesta & Lana leg. 1♂ (CI); Roccaforte  
561 Mondovì, Plutonis Antrum [Pi n.c.], 16.VII.2016, Chesta & Lana leg 2♂♂ 2♀♀ (CI); same locality, 11.VI.2016, Chesta & Lana leg.  
562 1♂ (CI).

563

564 *Notes*

565 The species presence was previously recorded in four localities in the Corsaglia valley (Isaia et al.,  
566 2011). Remarkably, the population of Balma Ghiacciata del Mondolè [Pi 102] is found in the  
567 twilight zone of the cave, opening in mount Mondolè at 2,071 m asl—Artesina, Province of Cuneo,  
568 Italy. The cave is characterized by a very cool microclimatic condition, sustaining a perennial  
569 snowfield near the entrance.

570

571 ***Troglohyphantes sciakyi*** Pesarini, 1989

572

573 Figs. 4.6, 5.6, 6.8, 7.6, 8.6, 9.6

574 *Material examined*

575 Italy, Lombardia, Province of Bergamo: Roncobello, Pozzo del Castello [Lo 1310], 31.XII.1989, Comotti & Baldan leg.

576 2♂♂ 2♀♀ 2juv; Castione della Presolana, Passo della Presolana, Monte Scanapa (1600m), 29.IX.1971, 4♂♂ 4♀♀ 7juv

577

578 *Notes*

579 New records for this rare species, previously known to be found in eight localities (Isaia & Pantini,

580 2010; Pesarini, 1989).

581

582

583 **Caporiaccoi complex**

584 The *Caporiaccoi* complex comprises seven Italian species, of which distributions are mostly

585 centred in the Central Lombardian Prealps: *T. caligatus* Pesarini, 1989, *T. caporiaccoi* Brignoli,

586 1971, *T. comottii* Pesarini, 1989, *T. dominici* Pesarini, 1988, *T. iulianae* Brignoli, 1971, *T. spatulifer*

587 Pesarini, 2001 and *T. zanoni* Pesarini, 1988. *T. caporiaccoi* is the only species in this complex

588 showing troglobiomorphic features (Isaia & Pantini, 2010).

589 The complex is characterized by small species (total length around 3 mm) bearing a well developed

590 dorsal median process on the cymbium. The epigine, which is very enlarged at the base, has a

591 subtriangular scape (“*clavus*” *sensu* Brignoli, 1971).

592 Despite its affinity with Deeleman-Reinhold’s *Diurnus* group, the complex does not overlap with

593 any of the previous classifications and the species included herein are all Italian endemic.

594

595 ***Troglohyphantes caligatus* Pesarini, 1989**

596 *Material examined*

597

598 Italy, Lombardia, Province of Como: between Lasnigo and Barni, m 600, 1.X.1971, 2♂♂ 6♀♀ 3juv; Grotta Tacchi [Lo

599 2029], Zelbio, 19.V.1985, Comotti & Baldan leg. 6♀♀; Pian del Tivano, Grotta Tacchi, 7.V.2016, Isaia, Mammola,

600 Barzagli, Manenti & Santinelli leg. 2♂♂ 3♀♀ (CI).

601

602 *Notes*

603 A rare species for which we provide new records collected in Triangolo Lariano—Province of

604 Como. The species was known to be found in Monte San Primo (Triangolo Lariano, Italy) (Pesarini,  
605 1989) and Monte Generoso (Switzerland) (Hänggi, 1990).

606

607

608 ***Troglohyphantes dominici* Pesarini, 1988**

609

610 *Material examined*

611 Italy, Lombardia, Province of Bergamo: Colzate, pendici Monte Alben, sopra Baite del Sedernello, m 1300, 13.VI.1990,  
612 Valle leg. 1♂ 1♀; Gazzaniga, Valle Platz, m 850, XI.1984 Comotti & Valle leg. 1♂.

613

614 *Notes*

615 New records of this species, of which distribution is centred on the Alps and Prealps of Bergamo.

616

617 ***Troglohyphantes iulianae* Brignoli, 1971**

618 *Material examined*

619 Italy, Liguria, Province of Savona: between Pontinvrea and Giusvalla, m 500, 1.X.1972, 1♂ 5♀ 3juv (NHMB).

620 Toscana, Provincia of Lucca: Castelnuovo, Torrente Turrite Secca, 10.406700 E, 44.108500 N., 16.X.1975, Thaler leg.  
621 (NHMB).

622

623

624 *Notes*

625 New records of the presence of this species in the Tuscanian Apennines. Previously observed in a  
626 few localities in the Ligurian Alps (Brignoli, 1971; Gasparo, 2001; Isaia et al., 2011) and in the  
627 Apuan Alps (Pesarini, 2001).

628

629 ***Troglohyphantes zanoni* Pesarini, 1988**

630

631 *Material examined*

632 Italia, Lombardia, Province of Bergamo: Costa Imagna, Pozzo delle Pozzette [Lo 1372], 25.III.1984, Comotti leg. 1♂

633 1♀; Rota d'Imagna, Tomba dei Polacchi [Lo 1003], 1.X.1987, Comotti & Valle leg. 1♂; Villa d'Ogna, m 550, wood,

634 VII-VIII.1985, Pisoni & Valle leg. 2♂♂; Val Taleggio, between Taleggio and Sottoc Chiesa, m 700, 30.IX.1971, Buche

635 leg. 2♂♂ 2♀♀; Treviglio, Parco del Roccolo, m 155, wood, 3.X – 6.XI.2011, pitfall trap, Leoni leg. 1♂; same locality,

636 6.XI – 15.XII.2011, pitfall trap, Leoni leg. 1♂; same locality, 15.III – 19.IV.2012, Leoni leg. 1♂; same locality, 26.VII –

637 21.X.2012, Leoni leg. 1♀; Province of Lecco: Rongio, Grotta Ferrera [Lo 1502], Barzaghi, Isaia, Mammola &

638 Santinelli leg. 1♂ 4♀♀ (CI).



639

640 *Notes*

641 This epigean species shows a disjunct distribution in the Prealps of Bergamo-Brescia and Colli  
642 Euganei, possibly related to the fragmentation of the original forest of the Po plain (*Quercus-*  
643 *Carpinetum*) (Isaia & Pantini, 2010). This hypothesis is supported by the findings of new  
644 populations in a small patch of residual forest in the Po Plain near Treviglio—Parco del Roccolo.  
645 Interestingly, there are records of the species presence in the Tomba dei Polacchi cave [Lo 1003],  
646 the type locality of *T. caporiaccoi* (*Caporiaccoi* complex). The coexistence of two species of  
647 *Troglohyphantes* seems to occur only in distantly related groups, as hypothesized by Deeleman-  
648 Reinhold (1978).

649

650 **Diurnus complex**

651 In Italy, the *Diurnus* complex comprises the troglobiomorphic species *T. sbordonii* Brignoli, 1975  
652 which is found in several localities in Giulie Alps, Giulie Prealps and Carnic Prealps and *T. juris*  
653 Thaler, 1982, endemic to the Carnic Prealps. The species of this complex share the features of the  
654 homonym Deeleman-Reinhold's group (including three Slovenian species, see Supplementary  
655 Material, Table S1), namely the presence of a remarkable dorsal medial apophysis and the simple  
656 structure of the cymbium, lacking the two basal divergent processes.

657

658 ***Troglohyphantes juris* Thaler, 1982**

659 *Material examined*

660

661 Italy, Friuli Venezia Giulia, Province of Pordenone: Montereale Valcellina, inghiottitoio Val di Pai [Fr 469],  
662 20.VIII.1987, Comotti leg. 1♂.

663

664 *Notes*

665 A new record of this rare species, previously found in very few localities (Thaler, 1982; Pesarini,  
666 1989).

667

668 **Henroti complex**

669 The *Henroti* complex comprises *Troglohyphantes vignai* Brignoli, 1971 (Cottian and Ligurian  
670 Alps), *T. nigraerosae* Brignoli, 1971 (Graian Alps, from Gran Paradiso massif to the Lanzo  
671 valleys) and *T. henroti* Dresco, 1956, a French endemic species from Isère and Drôme. The complex  
672 entirely overlaps the homonym Deeleman-Reinhold's group. Species within this complex are  
673 characterized by a well-developed, simple structure of the external branch of the *lamella*  
674 *characteristica* and by the triangular scape of the epygine, wide and enlarged at the base.

675

676 ***Troglohyphantes henroti* Dresco, 1956**

677 Fig. 13

678 *Material examined*

679 France, Drôme Department: Maison Forestiere, Lente, 24 .IX.1947 Negre & Henrot leg. (male holotype; MNHN);  
680 Grotté des Feès, Col de la Machine, 02.07.1950 Henrot leg. (female paratype; MNHN).

681

682 *Notes.*

683 The species can be found in a few localities of the municipalities of Presles (Isère Department) and  
684 Bouvante (Drôme Department), both within the Auvergne-Rhône-Alpes region (Dresco, 1956). The  
685 species is illustrated partially in Dresco (1956) and Deeleman-Reinhold (1978). Given the lack of  
686 complete diagnostic drawings, we provided new illustrations of the male holotype (Fig. 13.1) and  
687 the female paratype (Figs. 13.2, 13.3), for future comparative aims.

688

689 ***Troglohyphantes vignai* Brignoli, 1971**

690 *Material examined*

691 Italy, Piemonte, Province of Cuneo: Frabosa Soprana, Grotta Beppe Bessone (=lo Zucco) [Pi 3303], 22.V.2015, Isaia &  
692 Mammola leg. 1♂, 1♀, 1juv (CI).

693

694 *Notes*

695 The species can be found in Cottian and Ligurian Alps with a remarkable distribution gap in the

696 Maritime Alps. We here provided a new record of the species presence in the Ligurian Alps—  
697 subsection Alpi del Marguareis,—that slightly widens the range of the distribution of this species  
698 eastwards. It is worth noticing that the district of Alpi del Marguareis shows the highest diversity of  
699 *Troglohyphantes* within the Western Alps—*T. konradi*, *T. vignai*, *T. pluto*, *T. pedemontanus*, *T.*  
700 *iulianae* and *T. bolognai*.

701

### 702 **Microcymbium complex**

703 The *Microcymbium* complex comprises four isolated species, all characterized by very small  
704 distribution ranges: *T. microcymbium* Pesarini, 2001 (two caves in Prealps of Bergamo), *T.*  
705 *bornensis* Isaia & Pantini, 2008 (Pugnetto cave complex, Graian Alps), *T. lanai* (Fenera massif,  
706 Pennine Alps), and *T. cavadinii* Pesarini, 1989 (two caves in the Prealps of Bergamo).

707

### 708 ***Troglohyphantes microcymbium* Pesarini, 2001**

#### 709 *Material examined*

710 Italy, Lombardia, Province of Bergamo: Sant’Omobono, Grotta di Nala di Cà Maquela [Lo 1135], 10.VI.2016,  
711 Santinelli, Manenti, Barzaghi leg. 2♀♀, 1 juv (CI); Province of Lecco: Mandello del Lario, Grotta I Ching [Lo 5079],  
712 20.VIII.2008, Aimar leg. 1♂.

713

#### 714 *Notes*

715 Previously found exclusively in the type locality—Sant’Omobono (BG), Grotta Nala di Ca’  
716 Maquela [Lo 1135].

717

### 718 **Orpheus complex**

719 The *Orpheus* complex comprises four troglobiomorphic species distributed in SW-Alps:

720 *Troglohyphantes bolognai* Brignoli, 1975 (one cave in Ligurian Alps), *T. bonzanoi* Brignoli, 1979

721 (one cave in Ligurian Alps), *T. konradi* Brignoli, 1975 (seven caves in Maritime Alps) and *T.*

722 *pedemontanus* (Gozo, 1908) (three caves in Ligurian Alps). The whole complex is part of

723 Deeleman-Reinhold's *Orpheus* group, which includes species from the Alps, the Pyrenees, one  
724 species from Massif Central and one from Caucasus. The complex gets its name from *T. orpheus*  
725 (Simon, 1884), a French endemic species of the departments of Aude, Ariège and Pyrénées-  
726 Orientales (Simon, 1929). The distal portion of the *lamella characteristic* is not—or only  
727 partially—flattened dorso-ventrally.

728 According to the nomenclature change here provided, the complex now includes three species: *T.*  
729 *bolognai*, *T. konradi* and *T. pedemontanus*.

730

731 ***Troglohyphantes bolognai* Brignoli, 1975 (= *T. bonzanoi* Brignoli, 1979 new synonymy)**

732 *Material examined*

733 Italy, Liguria, Province of Imperia: Pieve di Teco, Sgarbu du Ventu [Li 619], (type locality of *T. bonzanoi*), 27.XII.2014,  
734 Isaia & Mammola leg. 1♀ (CI 2600); same locality, 09.XII.2015, Isaia & Mammola leg. 4♂♂, 5♀♀, 3 juv (CI 2645);  
735 Badalucco, Tana Bertrand [Li 104] (type locality of *T. bolognai*), 04.IV.2014, Isaia & Mammola leg. 2♀♀, 5 juv (CI  
736 2564); same locality, 27.XII.2014, Isaia & Mammola leg. 1♂ 1♀ (CI 2609).

737

738 *Notes*

739 This troglobiomorphic species description was based on one female, collected in the Tana di  
740 Bertrand cave [Li 104] in Badalucco, Province of Imperia, Liguria (holotype stored at Museum of  
741 Verona, P.M. Brignoli's collection, not examined here). Our collection of topotypic material—  
742 including the so far unknown male—allowed the comparison with topotypic males of *T. bonzanoi*, a  
743 troglobiomorphic species from Sgarbu du Ventu cave [Li 619] (holotype stored at Museum of  
744 Verona, P.M. Brignoli's collection, not examined here), a few kilometres away from the type  
745 locality of *T. bolognai*. The *lamella characteristic* of the two species was found to be identical. On  
746 this base we propose the synonymy *Troglohyphantes bonzanoi* Brignoli, 1979 = *T. bolognai*  
747 Brignoli, 1975. The synonymy is also supported by molecular base (see Fig. 2).

748

749 ***Troglohyphantes konradi* Brignoli, 1975**

750 *Material examined*

751 France, Alpes Maritime: Brigue, Blockhouses in the nearby of Balconi di Marta, 12.VIII.2016, Beikes & Isaia leg. 1♀ (CI).

752

753 *Notes*

754 This record attest for the first time the presence of this species in France.

755

756 ***Polyophtalmus complex***

757 The *Polyophtalmus* complex includes *Troglohyphantes fagei*, which is widely distributed in the  
758 Eastern Alps, the troglobiomorphic *T. scientificus* Deeleman-Rheinold, 1978, endemic to the Giulie  
759 Prealps and Giulie Alps, and *T. poleneci* Wiehle, 1964, doubtfully recorded by Pesarini (2001) in  
760 Monte Matajur (Giulie Prealps). The complex gets its name from Deeleman-Reinhold's homonym  
761 group, which mostly includes Balkanic species (see Supplementary materials Table S1). The female  
762 is characterised by the shape of the scape, squat and enlarged at the base. The male paracymbium  
763 bears a peculiar "pocket" (*sensu* Deeleman-Reinhold, 1978) and the cymbium lacks dorsal  
764 processes.

765

766 ***Troglohyphantes fagei* Roewer, 1931**

767 *Material examined*

768 Italy, Veneto, Province of Treviso: Susegana, Bus de le Fade [V 1271], m 215, 28.IV.1990, Gasparo leg. 1♂ 1♀ (CG).

769 Friuli Venezia Giulia, Province of Udine: Torreano, Foran di Landri [Fr 46], m 425, 19.V.1993 Gasparo leg. 1♀

770 (Gasparo 1997: 20, sub *Troglohyphantes* sp.) (CG).

771

772 *Notes*

773 Mostly found in epigean habitats in the Austrian and Eastern Italian Alps. Specimens found in Bus

774 de le Fade [V 1271] are characterized by pronounced microphthalmy.

775

776 **Ruffoi complex**

777 The *Ruffoi* complex comprises *Troglohyphantes ruffoi* di Caporiacco, 1936 (Prealps of Garda Lake,  
778 Prealps of Vicenza and Colli Berici) and *T. fatalis* Pesarini, 1988 (Prealps of Belluno and Colli  
779 Euganei). Deeleman-Reinhold's included *T. ruffoi* in the *Polyophtalmus* group, but according to  
780 Pesarini (2001), *T. ruffoi* and *T. fatalis* have to be considered in a separate complex. Species  
781 belonging to this group are characterized by the narrowed epyginal scape of the female and by the  
782 presence of two robust spines on the pedipalp tibia of the male. The *lamella characteristic* bears  
783 well-developed apical apophysis.

784

785 ***Troglohyphantes ruffoi* di Caporiacco, 1936**

786 *Material examined*

787 Italy, Veneto, Province of Vicenza: Arsiero, Riofreddo Valley, 4.VI – 27.VI.2001, pitfall trap, Busato leg. 1♂ 2♀♀ (CI).

788

789 *Notes*

790 New record of this species, found in both epigean and hypogean localities of Southern Trentino and  
791 Monti Lessini (Pesarini, 2001).

792

793 **Sordellii complex**

794 The *Sordellii* complex was firstly defined by Thaler (1967) and then retrieved by Pesarini (2001). It  
795 includes four species: *Troglohyphantes sordellii* (Pavesi, 1875) and *T. gestroi* Fage, 1933 (both  
796 endemic to the Prealps of Lugano and Lombardian Prealps), *T. lessinensis* (endemic to Lessini  
797 Mountains), and *T. regalini* Pesarini, 1989 (recorded in a few caves in the area of the Sebino  
798 Bergamasco), the latter being the only troglobiomorphic species within the complex. The complex  
799 only include Italian species showing affinities with Deeleman-Reinhold's *Polyophtalmus* group.

800 This complex is characterized by a sub-rectangular epyginal scape and by the peculiar wrench-  
801 shaped *lamella characteristic* and the absence of dorsal processes on the cymbium.

802

803 ***Troglohyphantes gestroi* Fage, 1933**

804 *Material examined*

805 Italy, Lombardia, Province of Brescia: Altopiano di Cariadeghe, Bus del Budrio [Lo 71], 10.III.2016, Santinelli leg.

806 1♀.

807

808

809 ***Troglohyphantes lessinensis* di Caporiacco, 1936**

810 *Material examined*

811 Italy, Veneto, Province of Vicenza: Cornedo Vicentino, Cereda, Grotta del Cameron, 5.VII.1987, Comotti & Baldan leg.

812 1♂ 1♀; Monte di Malo, Bus del Soglio [V 172], 5.VII.1987, 2♀♀ 2juv; same locality, 14.VIII.1988, Comotti & Baldan

813 leg. 2♂♂ 1♀ 1juv

814

815 *Notes*

816 Specimens examined are characterized by a pronounced microphthalmmy.

817

818

819 ***Troglohyphantes regalini* Pesarini, 1989**

820 *Material examined*

821 Italy, Lombardia, Province of Brescia: Marcheno, Caregno, Caia dell'Angili [Lo 405], 1.I.1990, Comotti & Baldan leg.

822 1♂ 4♀♀.

823

824 *Notes*

825 New record of this eyeless species, previously found in a few caves in the Sebino Bergamasco.

826

827 **New data on other subterranean spiders**

828 Given the rarity of these species and the general lack of information available in literature, we here

829 provide new data of occurrence of *Turinyphia clairi* (Simon, 1884) (Linyphiidae) and

830 *Typhlonesticus morisii* (Brignoli, 1975) (Nesticidae) gathered during our recent surveys.

831

832 ***Turinyphia clairi* (Simon, 1884) (Araneae, Linyphiidae)**

833 *Material examined*

834 Italy, Piemonte, Province of Cuneo: Becetto, Pertus dei Draï [Pi 1017], 16.VIII.2015, Isaia & Mammola leg. 1♂ (CI).

835 Liguria, Province of Imperia: Coscio di Arroscia, Garbo di Pian Cavallo [Li 851], 09.I.2016, Isaia & Ladame leg. 1♂

836 (CI); Monte Ceriana, Military blockhouse, 12.VIII.2016, Beikes & Isaia leg. 4♀♀ 1♂ (CI).

837

838 *Notes*

839 Rare species, found in caves and other shaded, damp habitats. In the Western Italian Alps, the

840 species was previously found in only six localities (Arnò & Lana, 2005; Isaia et al., 2011).

841 The Palearctic genus of *Turinyphia* includes four species worldwide: *T. clairi* (Southern Europe), *T.*

842 *maderiana* (Schenkel, 1938) from Madeira, *T. cavernicola* Wunderlich 2008 from Azores and *T.*

843 *yunohamensis* (Bösenberg & Strand, 1906) from Japan. *Turinyphia* species are regarded by Borges

844 and Wunderlich (2008) as relict taxa and palaeoendemic, which survived in mountain areas and

845 islands.

846

847 ***Typhlonesticus morisii* (Brignoli, 1975) (Araneae, Nesticidae)**

848 *Material examined*

849 Italy, Piemonte, Province of Cuneo: Chiusa di Pesio, Grotta Superiore delle Camoscere [Pi 250], 15.VII.1987, Comotti

850 & Baldan leg 1♀; Roccaforte Mondovì, Grotta dei Partigiani della Tura [Pi 286], 22.V.2016, Chesta & Lana leg. 1♀ (CI); same

851 locality, 7.VI.2016, Chesta & Lana leg. 2♀♀ 1juv (CI); same locality, 25.VI.2016, Chesta & Lana leg. 1♀ (CI); same locality,

852 18.VIII.2016, Giachino & Lana leg. 4♂♂ 1♂ (CI); same locality, 22.VIII.2016, Lana leg. 1♂ (CI); Roccaforte Mondovì, Grotticella

853 della Tura [Pi n.c.], 25.VI.2016, Chesta & Lana leg. 1♀; same locality, 12.VIII.2016, Chesta & Lana leg. 2♂♂ 1♀ 2juv (CI).

854 Liguria, Province of Imperia: Triora, Prospetto di Miniera del Monte Grai, 12.VIII.2016, Beikes & Isaia leg. 1♀ (CI). France, Alpes

855 Maritime: Brigue, Balconi di Marta, 12.VIII.2016, Beikes & Isaia leg. 2♂♂ 2♀♀ (CI).

856

857 *Notes*



858 Troglobiomorphic species previously found exclusively in the type locality—Sotterranei del forte A  
859 di Vernante, Opera 11 Tetto Ruinas, Vernante. *Typhlonesticus morisii* shares sister species in Spain  
860 (*T. obcaecatus*), south-eastern Alps (*T. idriacus*), Montenegro (*T. absoloni*), and Turkey (*T.*  
861 *gocmeni*) (Nentwig, Blick, Gloor, Hänggi, & Kropf, 2016; Ribera, Elverici, Kunt, & Özkütük,  
862 2014). We here provide several new records from different localities in the Ligurian Alps, including  
863 the first French record of this species.

864

## 865 **DISCUSSION**

### 866 *DNA barcode analysis*

867 The large diversity of the genus *Troglohyphantes* in Europe prompted the categorization of the  
868 species in different phenetic groups, aiming to achieve a better understanding of the distribution  
869 patterns and relationships within the genus. Despite being preliminary, our inferred gene tree, based  
870 on the Animal DNA barcode, recovers most of the species complexes concerning the Italian species  
871 proposed by Pesarini (2001) (Table 1). These results suggest that the morphological characters used  
872 to define those complexes are phylogenetically relevant. Moreover, we have shown that the species  
873 can be diagnosed based on their genetic barcode, and that DNA barcoding is an effective tool for  
874 species identification in this group. The use of DNA barcodes may greatly help to increase our  
875 taxonomic information on the group and better delimit the distribution range of the species by  
876 assigning juveniles or by identifying the presence of the species in environmental samples  
877 (Thomsen & Willerslev, 2015).

878 The gene tree affinities between lineages and the geographic distribution of the species therein,  
879 suggest a pattern of multiple cave colonization processes. This hypothesis is supported by the co-  
880 occurrence of representatives of different complexes at a sub-regional scale—sometimes also at the  
881 same locality. For example, *T. bornensis* (*Microcymbium* complex), *T. lucifer* n. sp. (*Lucifuga*

882 complex) and *T. nigraerosae* (*Henroti* complex) can be found at short distance from each other  
883 within the same valley—Lanzo. Similarly, multiple genetically distant species are present in the  
884 Prealps of Bergamo (see Isaia & Pantini, 2010) and in the SW-Alps—Ligurian Alps and Maritime  
885 Alps. Therefore, we hypothesize that species communities in *Troglohyphantes* are the result of  
886 multiple, independent colonizations, rather than a consequence of local diversification of a single  
887 common ancestor. The extant lineages could be interpreted as the result of range contractions and  
888 isolation during past climatic changes, followed by population expansions of certain species—i.e.  
889 the less troglobiomorphic—during interglacials and other favourable periods. A recent  
890 phylogeographic study on *T. vignai* (Mammola et al., 2015) revealed similar patterns, and suggested  
891 that long-term climatic changes have been the main cause of the diversification of the genus in the  
892 Western Alps.

893 Because of the high diversity of this genus, the rarity of the species and the use of a single,  
894 maternally inherited marker, our conclusions based on the molecular analysis should be considered  
895 tentative. A more thorough sampling of the species representing the diversity of the genus, and the  
896 use of multiple, unlinked DNA markers will be required to provide a well-supported hypothesis of  
897 the phylogenetic relationships within the genus. In this regards, a collaborative project aiming to  
898 provide a phylogenetic structure of European *Troglohyphantes* and to investigate the origins and  
899 diversity of this remarkable group, is currently under way.

900

#### 901 ***Ecology and natural history of the Italian species***

902 *Troglohyphantes* spiders are generally associated with dark and humid habitats, such as caves,  
903 artificial subterranean habitats and SSHs. Except for the recent study on the ecological niche of *T.*  
904 *vignai* by Mammola and Isaia (2016) and the information provided by Deeleman-Rehinold (1978),  
905 little is known about the specific preferences of *Troglohyphantes* spiders.

906 In this study, we attested for the first time in Italy the presence of *Troglohyphantes* in MSS—i.e., *T.*

907 *lucifer* n.sp. This is not surprising, especially considering that troglobiomorphic spiders have been  
908 recently documented in a variety of MSS in Europe (e.g., Arnedo, Oromi, Múrria, Macías-  
909 Hernández, & Ribera, 2007; Deltchev, Lazarov, Naumova, & Stoev, 2011; Jiménez-Valverde *et al.*,  
910 2015; Laška *et al.*, 2011; Mammola *et al.*, 2016; Nae, 2008; Růžička & Dolanský, 2016; Růžička &  
911 Klimeš, 2005; Růžička, Šmilauer, & Mlejnek, 2013; Růžička & Thaler, 2002). Unfortunately, spider  
912 research on the MSS in Italy is still in its infancy. It is most likely that extensive investigations will  
913 lead to the discovery of additional hidden biodiversity within the genus.

914 The two new species described in this paper, *T. lucifer* n.sp. and *T. apenninicus* n.sp., can be  
915 classified as trogliphiles (*sensu* Sket, 2008), having fully developed eyes and abdominal pattern  
916 (Figs. 8b, 9b). Trogliphile species of *Troglohyphantes* are usually cold adapted (Isaia *et al.*, 2010;  
917 Novak *et al.*, 2014), and possess other exaptations to the subterranean conditions—e.g. lucifugous  
918 or hygrophilic species.

919 *T. lucifer* n.sp. shows a wide ecological plasticity, being able to colonize a variety of habitats,  
920 including the twilight zone of caves and various SSHs—leaf litter, deep soil strata, MSS, rocky  
921 accumulations. The species is very similar to—and has been frequently confused with—*T. lucifuga*,  
922 both regarding morphology and ecological requirements (Isaia *et al.*, 2010, 2011; Isaia & Pantini,  
923 2010). It seems likely that *T. lucifer* represents the ecological vicariant of *T. lucifuga* in the Cottian  
924 and Southern Graian Alps. According to our records, in certain localities *T. lucifer* n. sp. is able to  
925 coexist with other *Troglohyphantes* spiders. In this regard, Deeleman-Rehinoold (1978) suggested  
926 that the co-occurrence of more species of *Troglohyphantes* is rare, and may occur exclusively in  
927 phylogenetically distant lineages. The coexistence of two unrelated congeneric species in the same  
928 cave was already observed in few caves in Slovenia (Deeleman-Rehinoold, 1978) and in Croatia  
929 (Martina Pavlek, personal communication, June 18, 2016). In the Western Italian Alps, the co-  
930 occurrence of species of the *Lucifuga* complex and others is documented for *T. lucifuga* - *T.*  
931 *nigraerosae* (*Henroti* complex), *T. lucifer* n.sp. - *T. vignai* (*Henroti* complex), *T. lucifer* n.sp. - *T.*  
932 *bornensis* (*Microcymbium* complex) and *T. lucifuga* - *T. lanai* (*Microcymbium* complex) (Isaia *et al.*,

933 2010, 2011; Isaia & Pantini, 2010; this study).

934 Since the only known records of *T. apenninicus* are uniquely represented by the type series—  
935 collected in unspecified epigean habitats in 1975 and 1988 by Konrad Thaler,—the ecology of *T.*  
936 *apenninicus* n.sp. is still unknown. Unfortunately, no information about the habitat are provided on  
937 the original labels.

938

### 939 **Supplementary Materials**

940 Table S1. *Troglohyphantes* species listed in WSC (2016). For each species, we report the current  
941 taxonomic status, the placement—if any—in the phenetic classifications according to Fage (1919),  
942 Deeleman-Reinhold (1978) and Pesarini (2001).

943 Table S2. List of specimens sequenced in this study with voucher information, DNA code and  
944 GenBank® access code.

945

946 Figure S1. Barcoding analysis of the Italian species of *Troglohyphantes*. Plot of the maximum  
947 intraspecific K2P distance against the minimum interspecific K2P distance (left). Values above the  
948 1:1 line indicate the presence of a barcode gap. Plot of false positives (in blue) and false negatives  
949 (in red) against genetic divergences, the optimal threshold laid between 7 and 7.6% K2P  
950 divergence (right).

951

### 952 **ACKNOWLEDGEMENTS**

953 This work is dedicated in memory of our estimated colleague and extraordinary natural scientist  
954 Angelo Morisi, who recently passed away after a long illness. A special thank goes to Alexandra  
955 Jones for proof-reading the paper and to Elena Pelizzoli for the illustrations. The authors would like  
956 to thank Benedetta Barzaghi, Sanne Beikes, Mike Chesta Pier Mauro Giachino, Fabio Ladame,  
957 Enrico Lana, Raul Manenti, Jacopo Orlandini, Mauro Paschetta, Elena Piano and Roberto Santinelli  
958 for fieldwork assistance. We are sincerely grateful to Francesco Tomasinelli for the photographs.

959 We are indebted to Franco Bianchi, and Martin, Giovanna, Tsojkie, Gerd, and Sanne Beikes for  
960 helping us in finding the Tana di Bertrand. Thanks to Bartolomeo Vigna for guiding us to the Balma  
961 Ghiacciata del Mondolè. A warm thank goes to Barbara Knoflach, for providing to us specimens of  
962 *Troglohyphantes* stored in Thaler's collection. Thanks to Andrea Sabbadini for providing materials  
963 stored in the Museo Civico di Storia Naturale (Milano) and to Enrico Lana, Mike Chesta, Sanne  
964 Beikes and Gianni Comotti for the craved elusive discovery of the new localities of *Typhlonesticus*  
965 *morisii* in the Ligurian Alps. We are grateful to Gustavo Hormiga, Dimitar Dimitrov and an  
966 anonymous referee for helping us for helping with improving the quality of the manuscript.

967

#### 968 **Disclosure statement**

969 No potential conflict of interest was reported by the authors.

970

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1174 **Tables**

1175

1176 **Table 1.** The Italian species of *Troglohyphantes* and their affinities to Pesarini's complexes (2001).

<b>Species</b>	<b>Pesarini's complexes (2001)</b>
<i>Troglohyphantes bolognai, T. konradi, T. pedemontanus</i>	<i>Orpheus</i>
<i>T. albopictus, T. lucifuga, T. pluto, T. sciakyi, T. apenninicus</i> n.sp., <i>T. lucifer</i> n.sp., <i>T. subalpinus</i>	<i>Lucifuga</i>
<i>T. nigraerosae, T. vignai</i>	<i>Henroti</i>
<i>T. juris, T. sbordonii</i>	<i>Diurnus</i>
<i>T. bornensis, T. lanai, T. microcymbium, T. cavadinii</i>	<i>Microcymbium</i>
<i>T. caligatus, T. caporiaccoi, T. comottii, T. dominici, T. iulianae,</i> <i>T. spatulifer, T. zanoni</i>	<i>Caporiaccoi</i>
<i>T. gestroi, T. lessinensis, T. regalini, T. sordellii</i>	<i>Sordellii</i>
<i>T. fatalis, T. ruffoi</i>	<i>Ruffoi</i>
<i>T. fagei, T. poleneci, T. scientificus</i>	<i>Polyophtalmus</i>
<i>T. exul, T. pavesii</i>	<i>Exul</i>
<i>T. excavatus</i>	<i>Croaticus</i>

1177

1178

1179

1180 **Figure captions**

1181

1182 **Fig. 1.** Venn diagram illustrating the extant classifications of the species of *Troglohyphantes*  
1183 according to Fage (1919), Deeleman-Reinhold (1978) and Pesarini (2001). Numbers in sets indicate  
1184 the number of species classified according to the different authors and pie charts refer to the  
1185 geographic coverages of the species included therein. Data used to generate the figure are reported  
1186 in Supplementary Material, Table S1.

1187

1188 **Fig. 2.** Maximum likelihood tree. Circles on internal nodes denote support values as follow: upper  
1189 left: Bayesian posterior probabilities (PP); upper right: maximum likelihood bootstraps (BS),  
1190 bottom: parsimony jackknifing (PJ). Filled box: PP>95% or BS>75 or PJ>0.75. Grey boxes: clades  
1191 recovered with support values below former thresholds. Empty sectors: clades not recovered. The  
1192 tree was rooted using *Troglohyphantes oromii* (Ribera & Blasco, 1986). Pesarini's species groups  
1193 recovered as monophyletic in dotted boxes.

1194

1195 **Fig. 3.** Distribution map of the *Lucifuga* complex.

1196

1197 **Fig. 4.** Male pedipalp—*Lucifuga* complex (E = Embolus; LC = Lamella caratteristica; PC =  
1198 Paracymbium; SA = Suprategular apophysis; Te = Tip of the embolus). (4.1) *Troglohyphantes*  
1199 *albopictus*. Male from Arcugnano (VI) (27.3–12.04.2003 Pantini legit); (4.2) *T. apenninicus* n. sp.  
1200 Holotype male (15.X.1975 Thaler legit); (4.3) *T. lucifer* n. sp. Male from Col del Lys, Almese (TO)  
1201 (10.X.1972 Thaler legit); (4.4) *T. lucifuga*. Male from Ex-miniera di Cudine, Corio (TO) (Isaia et  
1202 al., 2011 fig. 2.51A, modified); (4.5) *T. pluto*. Male from [197 Pi/CN] Abisso Artesinera, Frabosa  
1203 Sottana (CN) (Isaia et al., 2011 fig. 2.63A, modified); (4.6) *T. sciakyi*. Male from Camerata  
1204 Cornello (BG) (27/8–08.X.2010 Massareo & Zucchelli legit); (4.7) *T. subalpinus*. Male from Styria,  
1205 Muraztal S Frein (10.X.1973 Buche legit). Scale: 0.5 mm. Illustration by Elena Pelizzoli.

1206

1207 **Fig. 5.** Cymbium of the right palp—*Lucifuga* complex. (5.1) *Troglohyphantes albopictus*. Male  
1208 from Altopiano d'Asiago (VI) (05–06.1989 Comotti & Baldan legit); (5.2) *T. apenninicus* n. sp.  
1209 Holotype; (5.3) *T. lucifer* n. sp. Male from Col del Lys, Almese (TO) (10.X.1972 Thaler legit); (5.4)  
1210 *T. lucifuga*. Male from [2057 Ao/AO] Grotta VM1, Chatillon (15.V.2006 Lana legit); (5.5) *T. pluto*.  
1211 Male from [197 Pi/CN] Abisso Artesinera, Frabosa Sottana (28.VI.2008 Isaia legit); (5.6) *T. sciakyi*.  
1212 Male from Alpe Arera (BG) (17.07.2002 Fabbri, Lodovici & Valle legit); (5.7) *T. subalpinus*. Male

1213 from Styria, Muraztal S Frein (10.X.1973 Buche *legit*). Scale: 0.2mm. Illustration by Elena  
1214 Pelizzoli.

1215

1216 **Fig. 6.** *Lamella characteristic* (extracted)—*Lucifuga* complex (EB = External branch; IB =  
1217 Internal branch; Rad= Radix). (6.1) *Troglohyphantes albopictus*. Male from Arcugnago (VI)  
1218 (27.03–12.IV.2003 MSNB *legit*); (6.2) *T. aldae* = *T. albopictus*. Holotype; (6.3) *T. apenninicus* n.  
1219 sp. Holotype; (6.4) *T. lucifer* n. sp. Male from Col del Lys, Almese (TO) (10.X.1972 Thaler *legit*);  
1220 (6.5) *T. lucifuga*. Male from [2057 Ao/AO] Grotta VM1, Chatillon (15.V.2006 Lana *legit*); (6.6) *T.*  
1221 *sarae* = *T. lucifuga*. Holotype; (6.7) *T. pluto*. Male from [197 Pi/CN] Abisso Artesinera, Frabosa  
1222 Sottana (28.VI.2008 Isaia *legit*); (6.8) *T. sciakyi*. Male from Alpe Arera (BG) (17.07.2002 Fabbri,  
1223 Lodovici & Valle *legit*); (6.9) *T. subalpinus*. Male from Styria, Muraztal S Frein (10.X.1973 Buche  
1224 *legit*). Scale: 0.25mm. Illustration by Elena Pelizzoli.

1225

1226 **Fig. 7.** Epigyne, ventral view—*Lucifuga* complex. (7.1) *Troglohyphantes albopictus*. Female from  
1227 Monti Berici, Nanto (I) (Thaler *legit*); (7.2) *T. apenninicus* n. sp. Female from S. Abetone  
1228 (09.1975–10.1975); (7.3) *T. lucifer* n. sp. Female from Col del Lys, Almese (TO) (10.X.1972 Thaler  
1229 *legit*); (7.4) *T. lucifuga*. Female from [art. Pi/TO] *ex miniera di Cudine*, Corio (15.V.2006 Lana  
1230 *legit*) (Isaia et al., 2011: fig. 2.51B, modified); (7.5) *T. pluto*. Female from [197 Pi/CN] Abisso  
1231 Artesinera, Frabosa Sottana (28.VI.2008 Isaia *legit*) (Isaia et al., 2011: fig. 2.63B, modified); (7.6)  
1232 *T. sciakyi*. Female from Mare di Burrasca, Colere (BG) (09 .IX.2015 Massaro, Mazzo, Oneto &  
1233 Pantini *legit*); (7.7) *T. subalpinus*. Female from Styria, Muraztal S Frein (10.X.1973 Buche *legit*).  
1234 Scale: 0.2mm. Illustration by Elena Pelizzoli.

1235

1236 **Fig. 8.** Epigyne, lateral view—*Lucifuga* complex. (8.1) *Troglohyphantes albopictus*. Female from  
1237 Monti Berici, Nanto (I) (Thaler *legit*); (8.2) *T. apenninicus* n. sp. Female from S. Abetone  
1238 (09.1975–10.1975); (8.3) *T. lucifer* n. sp. Female from Col del Lys, Almese (TO) (10.X.1972 Thaler  
1239 *legit*); (8.4) *T. lucifuga*. Female from [art. Pi/TO] *ex miniera di Cudine*, Corio (15.V.2006 Lana  
1240 *legit*) (Isaia et al., 2011: fig. 2.51C, modified); (8.5) *T. pluto*. Female from [197 Pi/CN] Abisso  
1241 Artesinera, Frabosa Sottana (28.VI.2008 Isaia *legit*) (Isaia et al., 2011: fig. 2.63C, modified); (8.6)  
1242 *T. sciakyi*. Female from Mare di Burrasca, Colere (BG) (09.IX.2015 Massaro, Mazzo, Oneto &  
1243 Pantini *legit*); (8.7) *T. subalpinus*. Female from Styria, Muraztal S Frein (10.X.1973 Buche *legit*).  
1244 Scale: 0.2mm. Illustration by Elena Pelizzoli.

1245

1246 **Fig. 9.** Diagrams of internal female genitalia, aboral view—*lucifuga* group (s = spermathecae; cg =



1247 copulatory groove; fg = fertilization groove). (9.1) *Troglohyphantes albopictus*. Female from  
1248 Campodalbero, Vicenza (V) (Thaler legit); (9.2) *T. appenninicus* n. sp. Female from S. Abetone  
1249 (09.1975–10.1975); (9.3) *T. lucifer* n. sp. Female from Col del Lys, Almese (TO) (03.X.1972 Thaler  
1250 legit); (9.4) *T. lucifuga*. Female from Alpi Pile, Alagna (NO) (03.X.1971 Thaler legit); (9.5) *T.*  
1251 *pluto*. Female from [197 Pi/CN] Abisso Artesinera, Frabosa Sottana (28.VI.2008 Isaia legit) (Isaia  
1252 et al., 2011: fig. 2.63C, modified); (9.6) *T. sciakyi*. Female from Mare di Burrasca, Colere (BG)  
1253 (09.IX.2015 Massaro, Mazzo, Oneto & Pantini legit). Scale: 0.2mm. Illustration by Paolo Pantini  
1254  
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1256 **Fig. 10.** *Troglohyphantes appenninicus* n. sp. Holotype male and paratype female (15.X.1975 Thaler  
1257 legit). (10.1) Retrolateral view of male pedipalp (E = Embolus; LC = Lamella caratteristica; PC =  
1258 Paracymbium; SA = Suprategular apophysis; Te = Tip of the embolus). (10.2) Abdominal pattern.  
1259 (10.3) Epigyne, ventral view. (10.4) Epigyne, lateral view; Scales: a=0.5 mm; b=1 mm; c–d=0.2  
1260 mm. Illustration by Elena Pelizzoli.  
1261

1262 **Fig. 11.** *Troglohyphantes lucifer* n. sp. Male and female from Col del Lys, Almese (TO) (10.X.1972  
1263 Thaler legit). (11.1) Retrolateral view of male pedipalp (E = Embolus; LC = Lamella  
1264 caratteristica; PC = Paracymbium; SA = Suprategular apophysis; Te = Tip of the embolus). (11.2)  
1265 Abdominal pattern. (11.3) Epigyne, ventral view. (11.4) Epigyne, lateral view. Scales: a=0.5 mm;  
1266 b=1 mm; c–d=0.2 mm. Illustration by Elena Pelizzoli.  
1267

1268 **Fig. 12.** *Troglohyphantes lucifer* n. sp. Female from [1502 Pi/TO] Borna inf. del Pugno, Pugno  
1269 (TO) (11.III.2016 Isaia, Mammola, Piano, Tomasinelli leg.). (12.1) Abdominal pattern, dorsal view  
1270 (12.2–12.4). Live specimen. Photo by Francesco Tomasinelli.  
1271

1272 **Fig. 13.** *Troglohyphantes henroti* Dresco, 1956. Holotype male and paratype female (02.VII.1950  
1273 Henrot legit). (13.1) Retrolateral view of male pedipalp (E = Embolus; LC = Lamella  
1274 caratteristica; PC = Paracymbium; SA = Suprategular apophysis; Te = Tip of the embolus); (13.2)  
1275 Epigyne, ventral view. (13.3) Epigyne, lateral view. Scales: 2.1 = 0.5 mm; 2.2–2.3 = 0.2 mm.  
1276 Illustration by Elena Pelizzoli.