

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

3

4 Marco Isaia^{1*}, Stefano Mammola¹, Paola Mazzuca², Miquel A. Arnedo² & Paolo Pantini³
5

6 1) Department of Life Sciences and Systems Biology, Università di Torino. Via Accademia
7 Albertina, 13. I-10123 Torino, Italy.

8 2) Department of Evolutionary Biology, Ecology and Environmental Sciences & Biodiversity
9 Research Institute, Universitat de Barcelona. Av. Diagonal 643, Barcelona 08028, Catalonia, Spain.

10 3) Museo civico di Scienze Naturali “E. Caffi”. Piazza Cittadella, 10. I-24129 Bergamo, Italy.

11 * **Corresponding author:** marco.isaia@unito.it

12

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

14

15

16

17

18

19

20

21

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

36

37

38

39

40

41

42

43

44

45

46

Index

47	
48	INTRODUCTION
49	MATERIAL & METHODS
50	Molecular methods
51	Taxonomy
52	RESULTS
53	Molecular analyses
54	TAXONOMIC ACCOUNT
55	<u>Lucifuga complex</u>
56	Troglolyphantes albopictus Pesarini, 1989 (= <i>T. aldae</i> Pesarini 2001 new synonymy)
57	<u>Troglolyphantes apenninicus Isaia, Mammola & Pantini new species</u>
58	<u>Troglolyphantes lucifer Isaia, Mammola & Pantini new species</u>
59	Troglolyphantes lucifuga (Simon, 1884) (= <i>T. sarae</i> Pesarini, 2011 new synonymy)
60	Troglolyphantes pluto di Caporiacco, 1938
61	Troglolyphantes sciakyi Pesarini, 1989
62	<u>Caporiaccoi complex</u>
63	Troglolyphantes caligatus Pesarini, 1989
64	Troglolyphantes dominici Pesarini, 1988
65	Troglolyphantes iulianae Brignoli, 1971
66	Troglolyphantes zaroni Pesarini, 1988
67	<u>Diurnus complex</u>
68	Troglolyphantes juris Thaler, 1982
69	<u>Henroti complex</u>
70	Troglolyphantes henroti Dresco, 1956
71	Troglolyphantes vignai Brignoli, 1971
72	<u>Microcymbium complex</u>
73	Troglolyphantes microcymbium Pesarini, 2001
74	<u>Orpheus complex</u>
75	Troglolyphantes bolognai Brignoli, 1975 (= <i>T. bonzanoi</i> Brignoli, 1979 new synonymy)
76	Troglolyphantes konradi Brignoli, 1975
77	<u>Polyophtalmus complex</u>
78	Troglolyphantes fagei Roewer, 1931
79	<u>Ruffoi complex</u>
80	Troglolyphantes ruffoi di Caporiacco, 1936
81	<u>Sordelli complex</u>
82	Troglolyphantes gestroi Fage, 1933
83	Troglolyphantes lessinensis di Caporiacco, 1936
84	Troglolyphantes regalini Pesarini, 1989
85	<u>New data on other subterranean spiders</u>
86	Turinyphia clairi (Simon, 1884) (Araneae, Linyphiidae)
87	Typhlonesticus morisii (Brignoli, 1975) (Araneae, Nesticidae)
88	DISCUSSION
89	DNA barcode analysis
90	Ecology and natural history of the Italian species
91	SUPPLEMENTARY MATERIALS
92	ACKNOWLEDGEMENTS
93	REFERENCES

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 1st and 2nd codon partitions together and 3rd partition apart—as the best
227 partition scheme. The preferred evolutionary model for the 1st + 2nd codon partition was HKY+I+G
228 and for the 3rd 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 *Caporiaccoi*,
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 Mondolé 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 epigyne, 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, Province 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 epigeal habitats in the Austrian and Eastern Italian Alps. Specimens found in Bus

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

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

971 **REFERENCES**

972 Arnedo, M. A., Oromi, P., Múrria, C., Macías-Hernández, N., & Ribera, C. (2007). The dark side of
973 an island radiation: systematics and evolution of troglobitic spiders of the genus *Dysdera*
974 Latreille (Araneae: Dysderidae) in the Canary Islands. *Invertebrate Systematics*, *21*, 623–
975 660. doi: 10.1071/IS07015

976

977 Arnò, C., & Lana, E. (2005). *Ragni cavernicoli del Piemonte e della Valle d'Aosta*. Torino:
978 Associazione Gruppi Speleologici Piemontesi.

979

980 Borges, P. A. V. & Wunderlich, J. (2008). Spider biodiversity patterns and their conservation in the
981 Azorean archipelago, with descriptions of new species. *Systematics and Biodiversity*, *6*, 249–
982 282. doi: 10.1017/S1477200008002648

983

- 984 Brignoli, P. M. (1971). Note su ragni cavernicoli italiani (Araneae). *Fragmenta entomologica*, 7, 121–
985 229.
- 986
- 987 Brown, S.D.J., Collins, R.A., Boyer, S., Lefort, M.-C., Malumbres-Olarte, J., Vink, C.J., &
988 Cruickshank, R.H. (2012). Spider: An R package for the analysis of species identity and
989 evolution, with particular reference to DNA barcoding. *Molecular Ecology Resources* 12,
990 562-565.
- 991
- 992 Culver, D. C., & Pipan, T. (2014). *Shallow Subterranean Habitats. Ecology, Evolution, and*
993 *Conservation*. Oxford: University Press.
- 994
- 995 Deeleman-Reinhold, C. L. (1978). Revision of the cave-dwelling and related spiders of the genus
996 *Troglohyphantes* Joseph (Linyphiidae), with special reference to the Yugoslav species. *Opera*
997 *Academiae Scientiarum et Artium Slovenica (Classis IV) Ljubljana*, 23(6), 1–221.
- 998
- 999
- 1000 Deltshev, C., Lazarov, C., Naumova, C., & Stoev, C. (2011). A survey of spiders (Araneae) inhabiting
1001 the euedaphic soil stratum and the superficial underground compartment in Bulgaria.
1002 *Arachnologische Mitteilungen*, 40, 33–46. doi: 10.5431/aramit4005
- 1003
- 1004 Dresco, E. (1956). Note sur quelques araignées cavernicoles du genre *Troglohyphantes* et description
1005 d'espèces nouvelles. *Congrès International de Spéléologie I*, 3, 295–300.
- 1006

- 1007 Dresco, E. (1959). Catalogue raisonné des araignées et des opilions des grottes du Canton du Tessin
1008 (Suisse). *Annales de Spéléologie*, 14, 359–390.
- 1009
- 1010 Domingo-Quero, T., & Alonso-Zarazaga, A. M. (2010). Soil and litter sampling, including MSS.
1011 *Abc Taxa*, 8(1), 173–212.
- 1012
- 1013 Fage, L. (1919). Etudes sur les araignées cavernicoles. III. Sur le genre *Troglohyphantes*.
1014 Biospeleologica XL. *Archives de Zoologie Expérimentale et Générale (Biospelologica XL)*, 58,
1015 55–148.
- 1016 Fage, L. (1931). Araneae, 5e série, précédée d'un essai sur l'évolution souterraine et son
1017 déterminisme. *Biospeologica, LV. Archives de Zoologie Expérimentale et Générale*, 71, 91–
1018 291.
- 1019 Gasparo, F. (1997). Miscellanea biospeologica. Parte I: Friuli. *Atti e Memorie della Commissione*
1020 *Grotte "E. Boegan"*, 34, 17–48.
- 1021
- 1022 Gasparo, F. (2001). Note su *Troglohyphantes iulianae*, con descrizione del maschio (Araneae,
1023 Linyphiidae). *Fragmenta Entomologica*, 33, 1–7.
- 1024
- 1025 Goloboff, P. A., Farris, J. S. & Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis.
1026 *Cladistics*, 24, 774–786. doi: 10.1111/j.1096-0031.2008.00217.x.
- 1027
- 1028 Hänggi, A. (1990). Beiträge zur Kenntnis der Spinnenfauna des Kt. Tessin III-Für die Schweiz neue
1029 und bemerkenswerte Spinnen (Arachnida: Araneae). *Mitteilungen der Schweizerischen*
1030 *Entomologischen Gesellschaft*, 63, 153–167.

1031

1032 Isaia, M., & Pantini, P. (2008). A new species of *Troglohyphantes* (Araneae, Linyphiidae) from the
1033 western Italian Alps. *Journal of Arachnology*, 35, 427–431. doi: 10.1636/H07-16.1

1034

1035 Isaia, M., & Pantini, P. (2010). New data on the spider genus *Troglohyphantes* (Araneae, Linyphiidae)
1036 in the Italian Alps, with the description of a new species and a new synonymy. *Zootaxa*, 2690,
1037 1–18. doi: 10.11646/zootaxa.2690.1.1

1038

1039 Isaia, M., Lana, E. & Pantini, P. (2010). Ecology and distribution of the genus *Troglohyphantes*
1040 Joseph, 1881 in the Western Italian Alps. In: W. Nentwig, M. Schmidt-Entling, & C. Kropf
1041 (Ed.), *European Arachnology 2008* (pp. 89–97). Bern: Natural History Museum.

1042

1043 Isaia, M., Paschetta, M., Lana, E., Pantini, P., Schönhofer, A. L., Christian, E., & Badino, G. (2011).
1044 *Subterranean arachnids of the Western Italian Alps (Arachnida: Araneae, Opiliones,*
1045 *Palpigradi, Pseudoscorpiones)*. Torino: Museo di Scienze Naturali.

1046

1047 Jiménez-Valverde, A., Gilgado, J. D., Sendra, A., Pérez-Suárez, G., Herrero-Borgoñón, J. J., &
1048 Ortuño, V. M. (2015). Exceptional invertebrate diversity in a scree slope in Eastern Spain.
1049 *Journal of Insect Conservation*, 19, 713–728. doi: 10.1007/s10841-015-9794-1

1050

1051 Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., ...
1052 Drummond, A. (2012). Geneious Basic: an integrated and extendable desktop software
1053 platform for the organization and analysis of sequence data. *Bioinformatics*, 28(12), 1647-
1054 1649. doi: 10.1093/bioinformatics/bts199

1055

1056 Lanfear, R., Calcott, B., Ho, S. Y. W., & Guindon, S. (2012). PartitionFinder: Combined Selection
1057 of Partitioning Schemes and Substitution Models for Phylogenetic Analyses. *Molecular*
1058 *Biology and Evolution*, 29, 1695–1701. doi: 10.1093/molbev/mss020.

1059

1060 Laška, V., Kopecký, O., Růžička, V., Mikula, J., Vele, A., Šarapatka, B., & Tuf, I. H. (2011). Vertical
1061 distribution of spiders in soil. *Journal of Arachnology*, 39(3), 393-398. doi: 10.1636/P09-75.1

1062

1063 Lessert, R. de (1910). *Catalogue des invertébrés de la Suisse. Fasc. 3, Araignées*. Geneva: Musée
1064 d'Histoire Naturelle de Genève.

1065

1066 López, H., & Oromí, P. (2010). A pitfall trap for sampling the mesovoid shallow substratum (MSS)
1067 fauna. *Speleobiology Notes*, 2, 7–11.

1068

1069 Mammola, S., & Isaia, M. (2016). The ecological niche of a specialized subterranean spider.
1070 *Invertebrate biology*, 135(1), 20–30. doi: 10.1111/ivb.

1071

1072 Mammola, S., Isaia, M., & Arnedo, M. A. (2015). Alpine endemic spiders shed light on the origin
1073 and evolution of subterranean species. *PeerJ*, 3, e1384. doi: 10.7717/peerj.1384

1074

1075 Mammola, S., Giachino, P. M., Piano, E., Jones, A., Barberis, M., Badino, G., & Isaia, M. (2016).
1076 Ecology and sampling techniques of an understudied subterranean habitat: the Milieu
1077 Souterrain Superficiel (MSS). *The Science of Nature*, 103, 88. doi:10.1007/s00114-016-1413-

1078 9

1079

1080 Marazzi, S. (2005). *Atlante orografico delle Alpi. SOIUSA. Suddivisione orografica internazionale*
1081 *unificata del Sistema Alpino*. Scarmagno: Priuli & Verlucca.

1082

1083 Meier R., Shiyang K., Vaidya G., Ng PK. DNA barcoding and taxonomy in diptera: a tale of high
1084 intraspecific variability and low identification success. *Systematic Biology*, 55, 715–728

1085

1086 Nae, A. (2008). Data concerning the Araneae fauna from the aninei mountains Karsik Area (Banat,
1087 Romania). *Travail Institutul de Speologie "E. Racovitza"*, 47, 53–63.

1088

1089 Nentwig W., Blick, T., Gloor, D., Hänggi, A., & Kropf, C. (2016). Spiders of Europe. Retrieved
1090 from: www.araneae.unibe.ch

1091

1092 Novak, T., Šajna, N., Antolinc, E., Lipovšek, S., Devetak, D., & Janžekovič, F. (2014). Cold tolerance
1093 in terrestrial invertebrates inhabiting subterranean habitats. *International Journal of*
1094 *Speleology*, 43(3), 265–272. doi: 10.5038/1827-806X.43.3.3.

1095

1096 Pantini, P., & Isaia, M. (2016). Checklist of the Italian spiders (Version April 2016). Retrieved from:
1097 <http://www.museoscienzebergamo.it/>

1098

1099 Paradis E., Claude J. & Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R
1100 language. *Bioinformatics* 20: 289-290

- 1101
- 1102 Pesarini, C. (1988a). Due nuove specie di *Troglohyphantes* delle Prealpi Lombarde (Araneae
1103 Linyphiidae). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia
1104 Naturale di Milano*, 129, 89–100.
- 1105
- 1106 Pesarini, C. (1988b). Osservazioni su alcuni *Troglohyphantes* della fauna Italiana, con descrizione di
1107 due nuove specie (Araneae Linyphiidae). *Atti della Società Italiana di Scienze Naturali e del
1108 Museo Civico di Storia Naturale di Milano*, 129, 237–247.
- 1109
- 1110 Pesarini, C. (1989). Note su alcune specie italiane di *Troglohyphantes* Joseph, con descrizione di sei
1111 nuove specie (Araneae Linyphiidae). *Atti della Società Italiana di Scienze Naturali e del
1112 Museo Civico di Storia Naturale di Milano*, 130, 229–246.
- 1113
- 1114 Pesarini, C. (2001) Note sui *Troglohyphantes* italiani, con descrizione di quattro nuove specie
1115 (Araneae Linyphiidae). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di
1116 Storia Naturale di Milano*, 142, 109–133.
- 1117
- 1118 Pesarini, C. (2011). *Troglohyphantes sarae*, nuova specie della Val d'Aosta (Araneae, Linyphiidae).
1119 *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di
1120 Milano*, 152, 63–68.
- 1121
- 1122 Rambaut A, Suchard MA, Xie D & Drummond AJ (2014) Tracer v1.6. Retrieved from:
1123 <http://beast.bio.ed.ac.uk/Tracer>

1124

1125 Ribera, C., Elverici, M., Kunt, K. B., & Özkütük, R. S. (2014). *Typhlonesticus gocmeni* sp. n., a new
1126 cave-dwelling blind spider species from the Aegean region of Turkey (Araneae, Nesticidae).
1127 *ZooKeys*, *419*, 87–102. doi: 10.3897/zookeys.419.5739.

1128

1129 Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. L., Darling, A., Höhna, S., ... Huelsenbeck,
1130 J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice
1131 across a large model space. *Systematic Biology*, *61*, 539–542. doi: 10.1093/sysbio/sys029

1132

1133 Růžička, V., & Thaler, K. (2002). Spiders (Araneae) from Deep Screes in the Northern Alps (Tyrol,
1134 Austria). *Verein Innsbruck*, *89*, 137–141.

1135

1136 Růžička, V., & Klimeš, L. (2005). Spider (Araneae) communities of scree slopes in the Czech
1137 Republic. *Journal of Arachnology*, *33*, 280–289. doi: 10.1636/04-44.1.

1138

1139 Růžička, V., & Dolanský, J. (2016). Catching of spiders in shallow subterranean habitats in the Czech
1140 Republic. *Arachnologische Mitteilungen*, *51*, 43–48. doi: 10.5431/aramit5106.

1141

1142

1143 Růžička, V., Šmilauer, P., & Mlejnek, R. (2013). Colonization of subterranean habitats by spiders in
1144 Central Europe. *International Journal of Speleology*, *42*, 133–140. doi: 10.5038/1827-
1145 806X.42.2.5.

1146

1147 Schenkel, E. (1933). Beitrag zur Kenntnis der schweizererischin Spinnenfauna. V. Teil. Spinnen aus

1148 dem Saas-Tal (Wali) und von der Gegend zwischen Trins und Flims (Graubünden). *Revue*
1149 *Suisse de Zoologie*, 40(2), 11–29.

1150

1151 Simon, E. (1929). Les arachnides de France. Synopsis générale et catalogue des espèces françaises
1152 de l'ordre des Araneae, 3e partie. *Paris*, 6, 533–772.

1153

1154 Sket, B. (2008). Can we agree on an ecological classification of subterranean animals? *Journal of*
1155 *Natural History*, 42, 1549–1563. doi: 10.1080/00222930801995762.

1156

1157 Stamakis, A. (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with
1158 thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690. doi:
1159 10.1093/bioinformatics/btl446

1160

1161 Thaler, K. (1967). Zum Vorkommen von *Troglohyphantes*-Arten in Tirol und dem Trentino (Arachn.,
1162 Araneae, Linyphiidae). *Berichte des Naturwissenschaftlich-Medizinischen Vereins in*
1163 *Innsbruck*, 55, 155–173.

1164

1165 Thaler, K. (1982). Zwei weitere Deckennetzspinnen der Ostalpen: *Troglohyphantes tauriscus* n. sp.
1166 und *T. juris* n. sp. (Arachnida: Aranei, Linyphiidae). *Archives des Sciences, Genève*, 35,
1167 161–172.

1168

1169 Thomsen, P.F. & Willerslev, E. 2015. Environmental DNA – An emerging tool in conservation for
1170 monitoring past and present biodiversity. *Biological Conservation*, 183, 4-18.

1171

1172 World Spider Catalog, (2016). World Spider Catalog. Natural History Museum Bern (Version 16.5).

1173 Retrieved from: <http://wsc.nmbe.ch>

1174 **Tables**

1175

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

Species	Pesarini's complexes (2001)
<i>Troglohyphantes bolognai</i> , <i>T. konradi</i> , <i>T. pedemontanus</i>	<i>Orpheus</i>
<i>T. albopictus</i> , <i>T. lucifuga</i> , <i>T. pluto</i> , <i>T. sciakyi</i> , <i>T. apenninicus</i> n.sp., <i>T. lucifer</i> n.sp., <i>T. subalpinus</i>	<i>Lucifuga</i>
<i>T. nigraerosae</i> , <i>T. vignai</i>	<i>Henroti</i>
<i>T. juris</i> , <i>T. sbordonii</i>	<i>Diurnus</i>
<i>T. bornensis</i> , <i>T. lanai</i> , <i>T. microcymbium</i> , <i>T. cavadinii</i>	<i>Microcymbium</i>
<i>T. caligatus</i> , <i>T. caporiaccoi</i> , <i>T. comottii</i> , <i>T. dominici</i> , <i>T. iulianae</i> , <i>T. spatulifer</i> , <i>T. zanoni</i>	<i>Caporiaccoi</i>
<i>T. gestroi</i> , <i>T. lessinensis</i> , <i>T. regalini</i> , <i>T. sordellii</i>	<i>Sordellii</i>
<i>T. fatalis</i> , <i>T. ruffoi</i>	<i>Ruffoi</i>
<i>T. fagei</i> , <i>T. poleneci</i> , <i>T. scientificus</i>	<i>Polyophtalmus</i>
<i>T. exul</i> , <i>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
1255

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.