



HAL
open science

Resampling Bouché's historical localities reveals three new species and helps identifying a new genus of earthworms (*Oligochaeta*, *Hormogastridae* and *Lumbricidae*) in Southeastern France

Sylvain Gérard, Daniel Fernández Marchán, Alejandro Martínez Navarro, Mickaël Hedde, Thibaud Decaëns

► To cite this version:

Sylvain Gérard, Daniel Fernández Marchán, Alejandro Martínez Navarro, Mickaël Hedde, Thibaud Decaëns. Resampling Bouché's historical localities reveals three new species and helps identifying a new genus of earthworms (*Oligochaeta*, *Hormogastridae* and *Lumbricidae*) in Southeastern France. *Zoosystema*, 2023, 45 (23), pp.749-768. 10.5252/zoosystema2023v45a23 . hal-04915765

HAL Id: hal-04915765

<https://hal.science/hal-04915765v1>

Submitted on 28 Jan 2025

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Resampling Bouché's historical localities reveals three new species and helps identifying**
2 **a new genus of earthworms (Oligochaeta, Hormogastridae and Lumbricidae) in**
3 **Southeastern France.**

4 **Le rééchantillonnage des localités historiques de Bouché permettent la découverte de trois**
5 **nouvelles espèces et d'un nouveau genre de vers de terre (Oligochaeta, Hormogastridae**
6 **et Lumbricidae) dans le Sud-Ouest de la France.**

7 Sylvain Gérard^{1,2*}, Daniel Fernández Marchán^{2,3}, Alejandro Martinez Navarro³, Mickaël
8 Hedde¹, Thibaud Decaëns²

9 ¹ Eco&Sols, Institut Agro Montpellier, INRAE, IRD, CIRAD, Univ Montpellier, Montpellier,
10 France

11 ² CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

12 ³ Biodiversity, Ecology and Evolution Department, Faculty of Biology, Universidad
13 Complutense de Madrid, Madrid, Spain

14 * Corresponding author

15

16 The present paper has not been submitted to another journal, nor will it be in the 6 months after
17 initial submission to *Zoosystema*. All co-authors are aware of the present submission.

18

19 **ABSTRACT**

20 Southern France has been highlighted as an important hotspot of earthworm diversity
21 mostly by the work of Marcel Bouché, who sampled more than 1300 localities in mainland
22 France including Corsica in the 1960s. We resampled some of the Bouché's localities and
23 conducted molecular phylogenetic analysis. It leads to the identification of a new Lumbricidae
24 genus (*Flabellodrilus* n. gen.), for which *Allolobophora bartolii* should be the type species,
25 improving the clarity of the catch all genus *Allolobophora*. It also allowed us to discover two
26 new species of Lumbricidae (*Flabellodrilus luberonensis* n. sp. and *Allolobophora delitescens*
27 n. sp.), and one new species of Hormogastridae (*Vignysa callasensis* n. sp.). These three new
28 species underline the great earthworm diversity of southeastern France. Their discovery in a
29 previously well-sampled area further suggests that these species have narrow geographic ranges
30 and small populations. They also seem to be specialized for open habitats that are declining in
31 the French Mediterranean landscape. These different characteristics suggest a relatively high
32 risk of extinction for these three new species.

33 **KEYWORDS**

34 Earthworms, new species, *Flabellodrilus* n. gen., *Allolobophora*, *Vignysa*, France

35 **RÉSUMÉ**

36 Le sud de la France est considéré comme un point chaud de diversité pour les vers de
37 terre, comme mis en évidence par le travail de Marcel Bouché, qui a échantillonné plus de 1300
38 localités en France métropolitaine incluant la Corse dans les années 1960. Nous avons ré-
39 échantillonné certaines de ces localités et réalisé des analyses phylogénétiques moléculaires.
40 Ce travail nous a conduit à identifier un nouveau genre de Lumbricidae (*Flabellodrilus* n. gen.)
41 dont l'espèce type devrait être *Allolobophora bartolii*, ce qui apporte plus de clarté pour le genre
42 "fourre-tout" *Allolobophora*. Cela nous a également permis de découvrir deux nouvelles
43 espèces de Lumbricidae (*Flabellodrilus luberonensis* n. sp. et *Allolobophora delitescens* n. sp.),

44 ainsi qu'une nouvelle espèce d'Hormogastridae (*Vignysa callasensis* n. sp.). Ces trois nouvelles
45 espèces soulignent l'importante diversité de vers de terre dans le sud-est de la France. Leur
46 découverte dans une région précédemment bien échantillonnée suggère une aire de répartition
47 géographique restreinte et de petites populations pour ces espèces. Elles semblent par ailleurs
48 spécialisées dans les habitats ouverts qui tendent à diminuer dans les paysages méditerranéens
49 français. Ces différentes caractéristiques suggèrent un risque d'extinction relativement élevé
50 pour ces trois nouvelles espèces.

51 **MOTS CLES**

52 Vers de terre, espèces nouvelles, *Flabellodrilus* n. gen., *Allolobophora*, *Vignysa*, France

53

54 INTRODUCTION

55 South West Europe is recognised as a diversity hotspot for earthworms, with France,
56 Spain and Italy being the most diverse countries at the continent scale in terms of number of
57 species (Brown *et al.* 2023; Misirlioglu *et al.* 2023; DriloBASE taxo). South Western Europe
58 is also considered to be the origin and one of the centers of diversification of the family
59 Lumbricidae Rafinesque-Schmaltz, 1815 (Omodeo & Rota 2008), and the only area of
60 particular genera (e.g. *Scherotheca* Bouché, 1972, *Gatesona* Qiu & Bouché, 1998a,
61 *Proselodrilus* Bouché, 1972) and of the whole family Hormogastridae Michaelsen, 1900
62 (Marchán *et al.* 2018).

63 At a smaller scale, Southern France has a regional diversity and a proportion of endemics
64 higher than anywhere else in the country (Bouché 1972; Rota 1994; Qiu & Bouché 1998b,
65 1998c, 1998d, 1998f; Marchán *et al.* 2020). This was in particular highlighted by the historical
66 work of Bouché (1972) who sampled earthworms in 1363 localities in mainland France and
67 Corsica Island during the 1960s. This extensive sampling served as a basis for his monography
68 of French earthworms (i.e. “Lombriciens de France”) in which he synthesized all the knowledge
69 of the time and described a number of species new to science. Since this major publication, it
70 was commonly admitted that France was one of the temperate countries with the best known
71 earthworm fauna. Fifty years later, the project #Vers2022 aimed at resampling Bouché’s
72 localities to assess how earthworm distribution and community patterns have changed after 50
73 years of global change. The sampling effort carried out as part of this project also provided
74 fresh samples that are now used to build molecular phylogenies and to search for undescribed
75 species. This resulted in the discovery of several species new to science like for instance in the
76 genus *Scherotheca* (Marchán *et al.* 2022, 2023a, 2023b).

77 In this study, we describe one new genus (*Flabellodrilus* n. gen) and two new species of
78 Lumbricidae (*Flabellodrilus luberonensis* n. sp., *Allolobophora delitescens* n. sp.), and one new

79 species of Hormogastridae (*Vignysa callasensis* n. sp.) that were discovered during the re-
 80 sampling of Bouché's localities in southeastern France.

81 **MATERIAL and METHODS**

82 EARTHWORM SAMPLING

83 The specimens of the newly described species were sampled as part of the #Vers2022
 84 project. The descriptions of the localities are given in Table 1, along with the other species
 85 found in those samples. The sampling method consisted of soil digging and hand-sorting. The
 86 specimens were then washed with water and fixed in 99% ethanol for long-time storing and
 87 molecular analyses.

88 TABLE 1. – List, geolocation and habitat cover of the type localities of three new earthworm
 89 species in Southeastern France (Provence–Alpes–Côte d'Azur).

Species	Location	Coordinates (lat/long)	Code in Bouché (1972)	Habitat	Other species in the sample
					<i>Aporrectodea</i>
	Vaucluse				<i>balisa</i>
<i>Flabellodrilus</i>	department,	43.963°N,		Mediterranean	<i>Aporrectodea</i>
<i>luberonensis</i>	Saint-	5.337°E	ECORDRE_0527	shrubland	<i>rubra</i>
n. sp.	Saturnin-				<i>Aporrectodea</i>
	les-Apt				<i>trapezoides</i>
					<i>Octolasion</i>
					<i>cyaneum</i>
<i>Allolobophora</i>	Var	43.573°N,		Mediterranean	<i>Aporrectodea</i>
<i>delitesca</i> n.	department,	6.530°E	ECORDRE_0496	grassland in	<i>caliginosa</i>
sp.	Callas				

				an old olive	<i>Aporrectodea</i>
				grove	<i>rubra</i>
					<i>acidicola</i>
					<i>Flabellodrilus</i>
					<i>bartolii</i>
					<i>Octolasion</i>
					<i>cyaneum</i>
					<i>Scherotheca</i>
					<i>rhodana</i>
					<u><i>Allolobophora</i></u>
					<u><i>chlorotica</i></u>
					<u><i>Aporrectodea</i></u>
					<u><i>caliginosa</i></u>
<i>Vignysa</i>	Var				<u><i>Aporrectodea</i></u>
<i>callasensis</i> n.	department,	43.587°N,	ECORDRE_0503	Riparian	<u><i>rosea</i></u>
sp.	Callas	6.538°E		grassland	<u><i>Scherotheca</i></u>
					<u><i>porotheca</i></u>
					<u><i>Scherotheca</i></u>
					<u><i>rhodana</i></u>

90

91 MORPHOLOGICAL DESCRIPTIONS

92 Ethanol-fixed specimens were firstly studied following a classical morpho-anatomical
93 description workflow. The following characters were used to describe the external morphology:
94 body shape, body pigmentation, body length (after ethanol fixation), body mass, diameter

95 (preclitellar, clitellar and postclitellar regions), number of segments, type of prostomium,
96 arrangement of setae, position of clitellum, position of genital markings, position and shape of
97 tubercula pubertatis, position of male pores, position of ovipores, spermathecal pores and
98 nephridial pores. A few specimens of each species were dissected, and their internal anatomy
99 was described using the following characters: thickness of the septa, position of gizzard,
100 position of crop, position and shape of calciferous glands, position of esophagus-intestine
101 transition, position and shape of typhlosole, position of hearts, shape of nephridia, type of testis
102 sacs, position and shape of seminal vesicles, position and shape of spermathecae.

103 We then compared the morpho-anatomical characters of studied specimens to those of
104 already known species in the genera concerned. When a series of specimens differed from
105 already known species by at least one morpho-anatomical character of specific diagnostic value,
106 we considered it represented a species putatively new to science.

107 DNA AND PHYLOGENETIC ANALYSES

108 A few specimens of each possibly new species were used for DNA analyses. Total
109 genomic DNA was extracted from ventral integument samples of approximately 5 x 5 mm by
110 using the SpeedTools Tissue DNA Extraction kit (Biotools). Regions of the nuclear gene 28S
111 rRNA and mitochondrial 16S rRNA, 12S rRNA, NADH dehydrogenase (ND1) and cytochrome
112 oxidase subunit 1 (COI) were amplified by polymerase chain reaction (PCR), using the primers
113 described in Pérez-Losada *et al.* (2009) and Folmer *et al.* (1994). PCR reactions were carried
114 out using a GeneAmp Multicycler Ep gradient (Eppendorf) with the following conditions: an
115 initial denaturation step (5 min at 94°C); 40 cycles (35 for ND1) consisting in denaturation at
116 95 °C for 30 s, annealing (ranging from 45 °C to 55 °C) for 45 s, and extension at 72 °C for 1
117 min; and a final extension step (5 min at 72 °C). The amplified PCR products were purified
118 using the Multiscreen PCRµ96 purification kit (Millipore) and sequenced in Macrogen (Spain).

119 Sequences were aligned with MAFFT v.7 (Kato & Standley 2013) with default settings
120 and concatenated with BioEdit (Hall 1999), resulting in a matrix of 3,210 base pairs for each
121 species. Sequences reported by Domínguez *et al.* (2015), Pérez-Losada *et al.* (2009, 2011),
122 Paoletti *et al.* (2016), de Sosa *et al.* (2019) and Marchán *et al.* (2020), including representatives
123 of most of the Lumbricini (*sensu* Marchán *et al.* 2022) genera were downloaded from GenBank
124 and used as a reference dataset. The species included are listed in Suppl. Material 1.

125 All the DNA sequences obtained in this study are available in GenBank, under accession
126 numbers X (to be provided). COI sequences (new and datamined from GenBank), together with
127 metadata, are publicly available in the dataset DS-EWNSPSG (doi xxxxxxxx) in the Barcode
128 of Life Datasystem (BOLD, Ratnasingham & Hebert 2007).

129 In order to perform phylogenetic analyses, the best fitting evolutionary model for each
130 partition was selected with jModelTest v. 2.1.3 (Darriba *et al.* 2012) by applying the Akaike
131 information criterion (AIC; Akaike 1973) and the Bayesian information criterion (BIC;
132 Schwarz 1978). The best-fitting evolutionary models were GTR+I+G for COI, 28S, and ND1,
133 GTR+G for 12S and HKY+I+G were chosen for 16S. Parameters were set to 50 million
134 generations and sampled every 5,000th generation (10,000 trees). Two independent runs each
135 with four chains were performed and 20% of the trees were discarded as burn-in. The remaining
136 trees were combined and summarized on a 50% majority-rule consensus tree. Clade support
137 values over 70% and 90% (for Bootstrap and Posterior probability respectively) were
138 considered high. Uncorrected average pairwise distances between the studied species for the
139 molecular markers COI were calculated in MEGA 11 (Tamura *et al.* 2021) in order to support
140 their status as separate species.

141 SPECIES DESCRIPTIONS

142 When a species considered as putatively new to science based on its morphology was
143 further confirmed as distinct from its nearest neighbors by the molecular phylogenetic analysis,
144 we proceeded to its formal description. We then compiled a table containing the collection data
145 of all the studied specimens for each species, and a second table describing the morpho-
146 anatomical characters of each of them. We used the R Markdown (Allaire *et al.* 2022) scripts
147 proposed by Decaëns *et al.* (2023) to automatically (1) write the information about collection
148 data of holotypes and paratypes, and (2) generate a standardized description of each species
149 including external morphological characters and internal anatomy.

150 **ABBREVIATIONS**

151 MNHN: Museum national d'Histoire naturelle, Paris

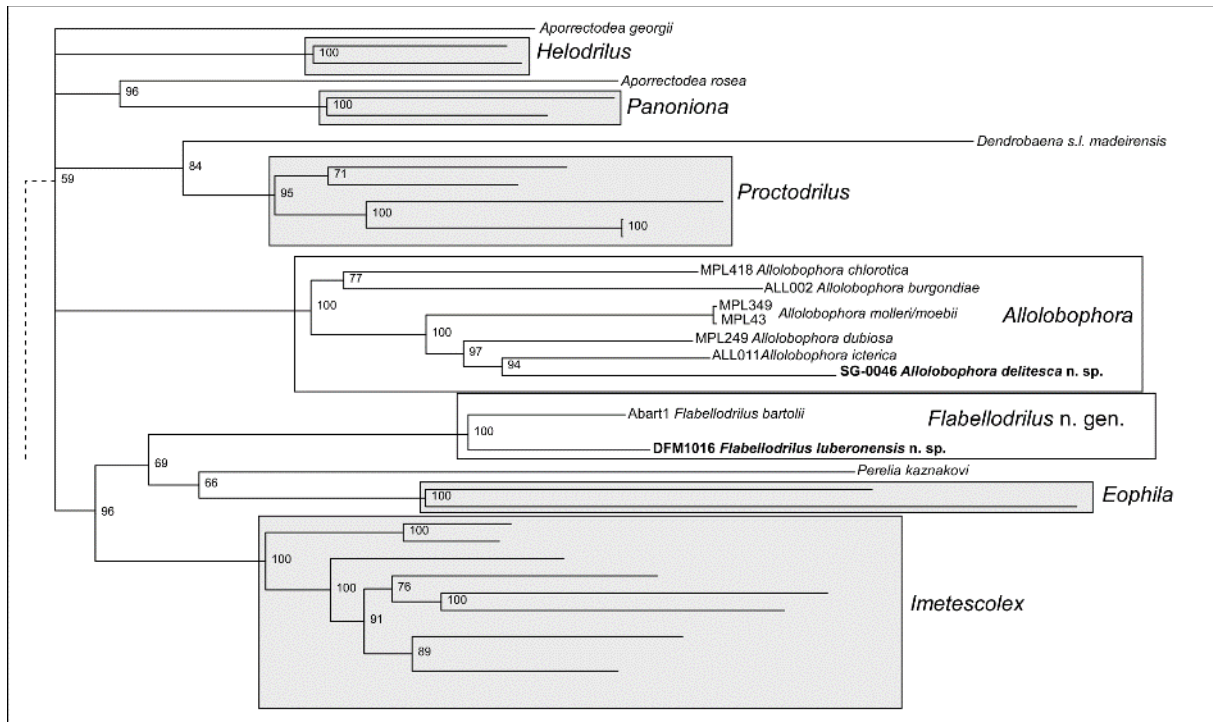
152 Eco&Sols: Eco&Sols collection, Montpellier

153 **RESULTS**

154 The morpho-anatomical analysis of the samples revealed three sets of specimens
155 belonging to three different species putatively new to science that were initially assigned to the
156 genera *Allolobophora* Eisen, 1874 (Lumbricidae) for two of them, and *Vignysa* Bouché, 1970
157 (Hormogastridae) for the third one. We obtained a complete set of genes (i.e. COI, 16S, ND1,
158 12S, 28S) for one specimen in each Lumbricidae species, and COI DNA barcodes for four
159 specimens of *Vignysa*. These sequences and others datamined from GenBank and other projects
160 were used to produce 1) a phylogenetic tree of the Lumbricidae genera closely related to
161 *Allolobophora*, based on the concatenated sequence of COI-16S-ND1-12S-28S molecular
162 markers (Fig. 1), and 2) a DNA barcode tree of the genus *Vignysa* (Fig. 2). Both of these trees
163 confirmed the separation of the three species from their nearest neighbors, and highlighted their
164 relationships with closely related species.

165 Some individuals collected in Callas and assigned to the genus *Allolobophora* based on
166 their morphology, appeared clearly separated from other species in the genus as highlighted by
167 the position of the specimen SG-0046 in Fig. 1. This species, which we describe under the name
168 *Allolobophora delitescens* n. sp., is closely related to *Allolobophora icterica* Savigny, 1826 in
169 the reconstructed phylogeny.

170 Another specimen from a second set of individuals initially assigned to *Allolobophora*
171 (i.e. DFM-1016) appeared closely related to *Allolobophora bartolii* Bouché, 1972, although
172 different enough to be considered as belonging to a separate species (Fig. 1). These two sister
173 species form a clade which is separated enough from its nearest neighbors to be considered as
174 a distinct genus. We propose here to describe this new genus under the name *Flabellodrilus* n.
175 gen. with *Flabellodrilus bartolii* n. comb. as type species, and we describe the newly discovered
176 species under the name *Flabellodrilus luberonensis* n. sp.. The moderately low support for the
177 nodes connecting *Flabellodrilus* n. gen., *Perelia* Easton, 1983 (represented by *Perelia*
178 *kaznakovi* (Michaelsen, 1910)) and *Eophila* Rosa, 1893 makes it complicated to know the exact
179 relative position of these genera, but they appear to belong to a well-supported clade together
180 with *Imetescolex* Szederjesi, Marchán & Csuzdi, 2022, and clearly separated from
181 *Allolobophora sensu stricto* as defined by Bouché (1972).

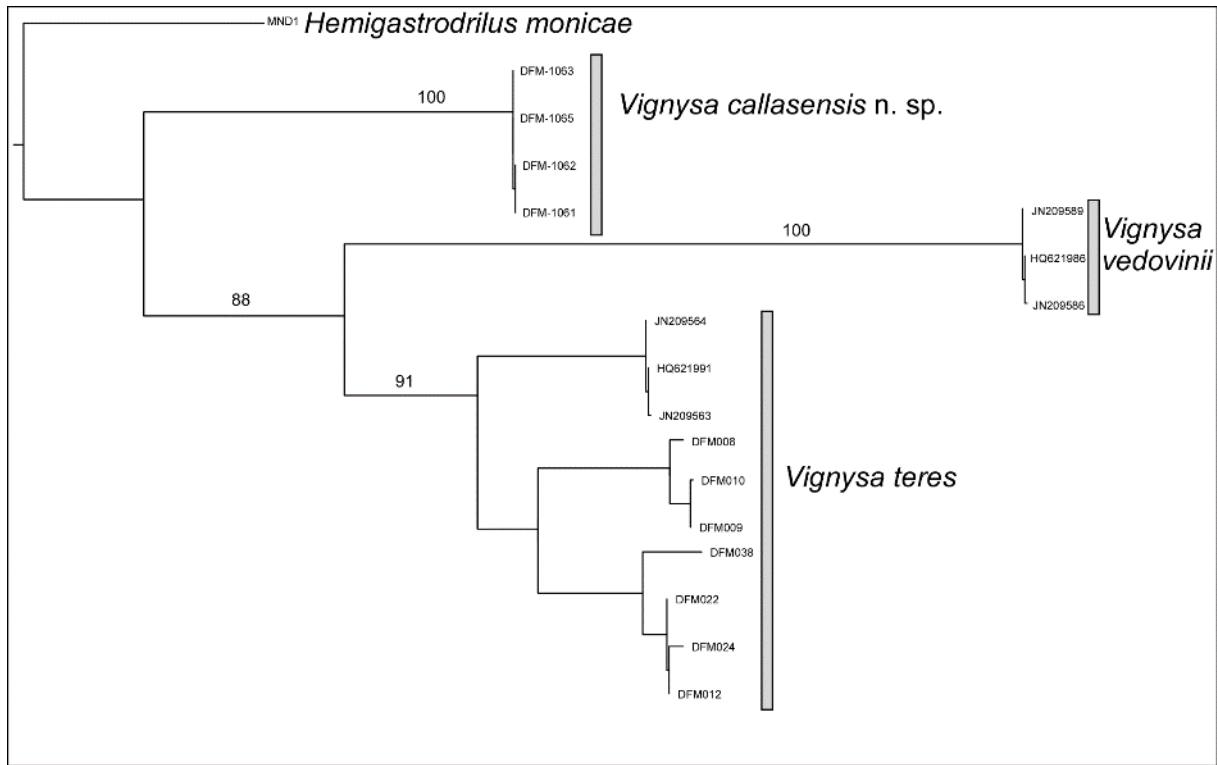


182

183 FIG. 1. – Multilocus phylogenetic tree focused on *Allolobophora*-related Lumbricidae genera (the full
 184 phylogenetic tree is shown in Suppl. Material 1). The tree was obtained from Bayesian inference based
 185 on the concatenated sequences of the COI-16S-ND1-12S-28S molecular markers. Posterior probability
 186 values are shown beside nodes. White boxes show target genera while grey boxes indicate closely related
 187 genera (species labels shown in Suppl. Material 1).

188

189 Finally, the four specimens of the *Vignysa* species appeared clearly separated from the
 190 two previously known species within the genus (Fig. 2). We propose to describe these
 191 specimens under the name *Vignysa callasensis n. sp.*



192

193 FIG. 2. – DNA barcode tree of the genus *Vignysa*. The tree was obtained from Bayesian inference based
 194 on the sequences of COI barcodes. Posterior probability values are shown above branches. Grey bars
 195 delimit individuals belonging to each species.

196

197 Uncorrected average pairwise distances between the new species and their closest
 198 relatives are 12.4% for *F. luberonensis* n. sp. versus *F. bartolii* (Table 2), 18.5% for *V.*
 199 *callasensis* n. sp. versus *Vignysa teres* (Dugès, 1828) (Table 3), and 15% for *A. delitescens* n.
 200 sp. versus *Allolobophora dubiosa* (Örley, 1881) (Table 2). These distances are within the range
 201 of divergence usually found among well-established lumbricid species, thus supporting the
 202 delimitation of the three new species obtained from both morpho-anatomical characters and
 203 phylogenetic analyses.

204 TABLE 2. – Uncorrected average pairwise distances (in percentage) calculated for the COI barcodes
 205 between the newly described Lumbricidae species and their closest relatives.

	<i>All. delitescens sp. nov.</i>	<i>All. chlorotica</i>	<i>All. dubiosa</i>	<i>All. molleri</i>	<i>All. monchicana</i>	<i>All. burgondiae</i>	<i>All. icterica</i>	<i>Fl. bartolii</i>	<i>Fl. luberonsensis sp.nov.</i>	<i>Fla</i>
<i>All. delitescens sp. nov.</i>										
<i>All. chlorotica</i>	17.20									
<i>All. dubiosa</i>	15.01	18.21								
<i>All. molleri</i>	15.85	18.89	14.84							
<i>All. monchicana</i>	16.02	18.89	16.36	10.62						
<i>All. burgondiae</i>	18.21	18.55	18.21	17.88	16.53					
<i>All. icterica</i>	16.02	18.55	16.36	16.36	16.36	16.36				
<i>Fl. bartolii</i>	18.38	20.74	18.38	17.54	18.72	19.39	18.38			
<i>Fl. luberonsensis sp.nov.</i>	19.39	19.90	17.54	20.40	20.24	18.89	18.38	12.14		
<i>Flabellodrilus sp.</i>	16.69	18.72	17.88	18.04	19.06	17.03	17.20	10.29	11.47	
<i>Eo. gestroi</i>	19.56	19.73	19.73	17.71	21.42	17.71	20.07	16.19	16.53	
<i>Eo. tellini</i>	19.39	18.89	19.90	20.91	20.74	20.07	19.73	17.37	17.71	
<i>Pe. kaznakovi</i>	20.24	18.21	20.40	21.59	20.57	19.56	19.73	16.69	18.04	

206

207 TABLE 3. – Uncorrected average pairwise distances (in percentage) calculated for the COI barcodes
 208 between the newly described Hormogastridae species and their closest relatives.

	<i>V. teres</i>	<i>V. callasensis</i> sp. nov.	<i>V. vedovinii</i>
<i>Vignysa teres</i>	10.0		
<i>Vignysa callasensis</i> sp. nov.	18.5	0.0	
<i>Vignysa vedovinii</i>	19.6	20.0	0.0

209

210

211

212 **TAXONOMY**

213

Phylum ANNELIDA Lamarck, 1802

214

Class CLITELLATA Michaelsen, 1919

215

Sub-class OLIGOCHAETA Grube, 1850

216

Order CRASSICLITELLATA Jamieson, 1988

217

Family LUMBRICIDAE Rafinesque, 1815

218

Genus *Flabellodrilus* Gérard, Decaëns & Marchán n. gen.

219

TYPE SPECIES. – *Allolobophora bartolii* Bouché, 1972: 454

220

ETYMOLOGY. – The genus name is derived from the fan-shaped clitellum of the two species

221

currently attributed to this genus (flabellum, a: fan).

222

DIAGNOSIS. – Medium-sized worms with faint brown pigmentation (sometimes absent) and

223

mid-segmental dark dots in the cephalic region. Prostomium epilobous, no transversal furrows.

224

Setae closely paired. First dorsal pore in 5/6. Male pores in ½ 15 with well-developed

225

porophores. Spermathecal pores in 9/10, 10/11, double (rarely in (8/9)9/10-12/13, simple or

226

double). Nephridial pores aligned. Clitellum moderately posterior between XXXII and XLIV.

227

Calciferous glands in X–XIV with diverticula in X. Typhlosole with four lamellae.

228

Spermathecae double in X and XI, globular and intracoelomic (rarely simple or double in

229

(IX)X-XIII. Two pairs of seminal vesicles in XI–XII. Nephridial bladders sigmoid with a sub-

230

terminal constriction followed by a loop.

231

DIFFERENTIAL DIAGNOSIS. – *Flabellodrilus* can be differentiated from closely related genera by

232

some morpho-anatomical characters. It differs from *Allolobophora* by the more anterior

233

position of the clitellum, pigmentation (faint brown with pigmentary dots vs frequently green),

234 repetition of spermathecae (double vs simple), number of seminal vesicles (two pairs in XI and
235 XXII *versus* four pairs in IX to XII) and shape of nephridial bladders (sigmoid with subterminal
236 constriction *versus* U-shaped). It differs from *Panionia* Mršić & Šapkarev, 1988 by the more
237 posterior position of the clitellum, pigmentation (faint brown vs absent), repetition of
238 spermathecae (double *versus* double-multiple) and shape of nephridial bladders (sigmoid with
239 subterminal constriction and loop *versus* sigmoid with subterminal constriction and bag-like
240 distension). *Flabellodrilus* differs from *Eophila* by its generally smaller size, its pigmentation
241 (faint brown with pigmentary dots *versus* purplish-brown in bands or light grey) and repetition
242 of spermathecae (double *versus* simple), and from *Imetescorex*, *Helodrilus* and *Proctodrilus* by
243 the presence of nephridial bladders in all segments. Finally, the loosely defined genus *Perelia*
244 is similar to *Flabellodrilus* in the shape of their nephridial bladders, but they differ in their
245 pigmentation (pigmentary dots not documented in *Perelia*) and in the repetition of their
246 spermathecae (double *versus* simple).

247 INCLUDED SPECIES. –

248 *Flabellodrilus bartolii* n. comb. (Bouché, 1972: 454)

249 *Flabellodrilus luberonensis* n. sp.

250 DIVERSITY AND DISTRIBUTION. – The genus *Flabellodrilus* is composed of two species
251 distributed in the Provence sedimentary basin, at the east of the Rhône river, and in the external
252 Alps (Barronies and Nice Prealps).

253 REMARKS.- The subspecies *Allolobophora bartolii meougensis* (Bouché, 1970) is significantly
254 different from *Flabellodrilus bartolii* n. comb. In the position of the clitellum and position and
255 repetition of spermathecae (8/9–12/13 *versus* 9/10–10/11, simple *versus* double). It thus appears
256 likely that it constitutes a separate species from *F. bartolii*. In the absence of detailed morph-

257 anatomical analysis and molecular data, we conservatively maintain this subspecies as
258 *Flabellodrilus bartolii meougensis* n. comb. (Bouché, 1970).

259

260 *Flabellodrilus luberonensis* Gérard, Decaëns & Marchán n. sp.

261 (Figs. 3, 4)

262 TYPE MATERIAL. – **Holotype. France** • One adult specimen; Provence–Alpes–Côte d’Azur,
263 Vaucluse, D943, 84490 Saint–Saturnin–les–Apt, in the soil; latitude/longitude:
264 43.963°N/5.337°E; elevation: 434 m asl; 25 November 2021; T. Decaëns, D. F. Marchán leg.;
265 deposited at MNHN (BOLD Sample ID: DFM-1016).

266 **Paratypes. France** • Four adult specimens; same data as Holotype; deposited as follow: two
267 specimens at Eco&Sols (BOLD Sample ID: DFM-1017, DFM-1020), two specimens at MNHN
268 (BOLD Sample ID: DFM-1018, DFM-1019).

269 **Other material. France** • Nine sub-adult specimens; same data as Holotype; deposited at
270 Eco&Sols.

271 ETYMOLOGY. – The species name is derived from the massif of Luberon where the type
272 specimens were found.

273 DESCRIPTION

274 *External morphology.* (Fig. 3A, B)

275 Body shape cylindrical. Body pigmentation absent, mid-segmental dark dots in the cephalic
276 region. Average body length after ethanol fixation: 80 mm (range: 70 to 100 mm; n= 3 adult
277 specimens). Average body mass: 1.163 g (range: 0.855 to 1.398 g; n= 3). Average diameter:
278 4.6 mm in the preclitellar region (range: 4.2 to 5.4 mm; n = 5), 5.8 mm in the clitellum (range:
279 5.2 to 6.8 mm; n = 5), 4.6 mm in the postclitellar region (range: 4.2 to 5.2 mm; n = 5). Average

280 number of segments: 283 (range: 187 to 353; n = 3). Prostomium of closed epilobic type. Setae
281 closely paired. Setal arrangement: aa:ab:bc:cd:dd = 14:2:8:1:32. Clitellum in XXXII–XLII
282 (XLIII). Genital markings in XI–XII, randomly unpaired in XVI–XXVIII, intraclitellar in
283 XXXIV, in ab. Tubercula pubertatis: protruding band in XXXV–XL. Male pores: one pair in
284 XV. Ovipores: one pair in 1/2 XIV, at 1 x ab dorsally from b. Spermathecal pores not visible.
285 Nephridial pores not visible.

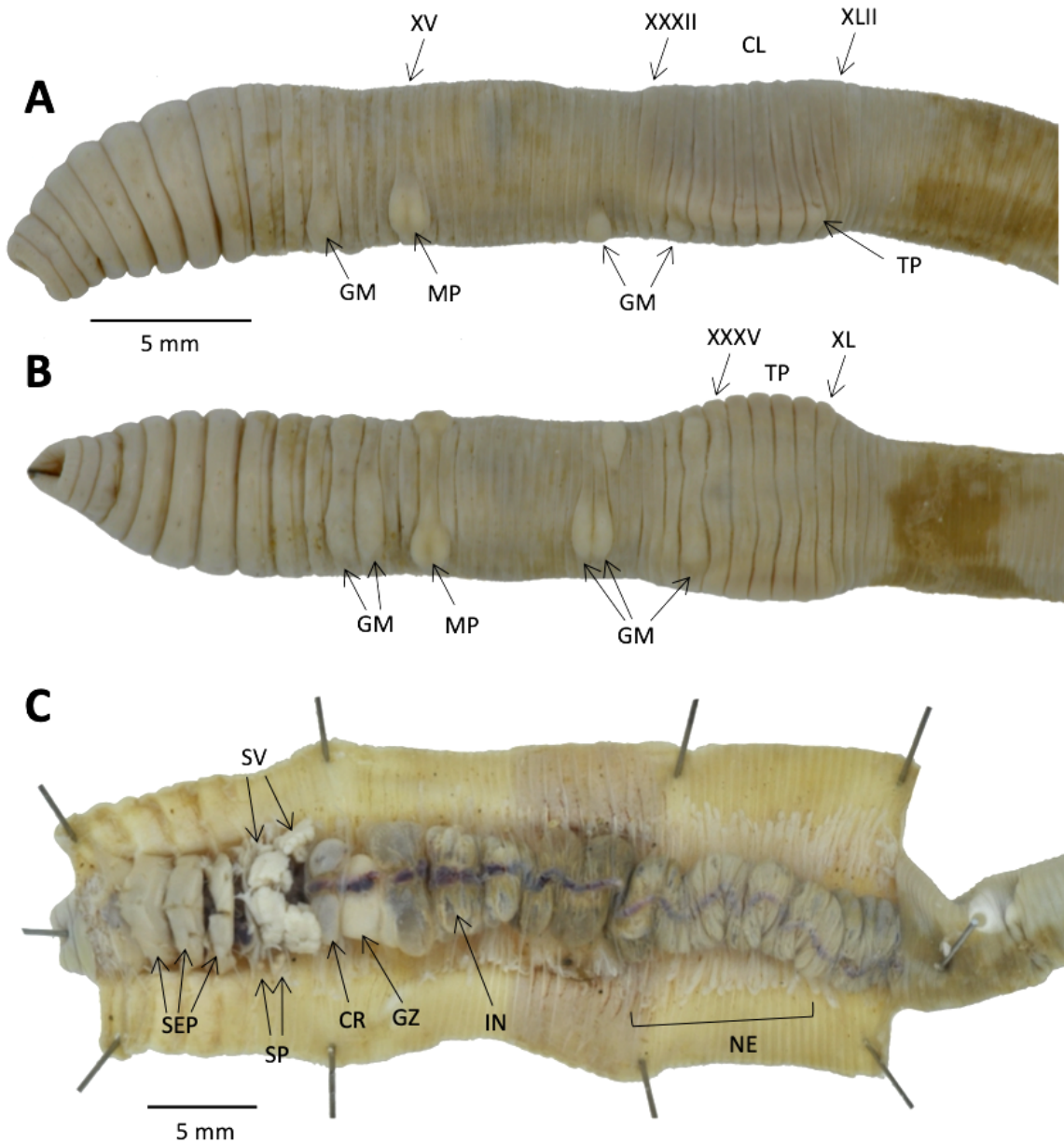
286 *Internal anatomy.* (Fig. 3C, 4)

287 Septa: thickened from 5/6 to 9/10, otherwise membranous. Crop in XV–XVI. Muscular gizzard
288 in XVII–XVIII followed by a membranous pouch in XIX, with an average size (width x length)
289 of 3.55 x 2.10 mm. Calciferous glands: in X–XIV, forming a pair of spherical lobes in X.
290 Esophagus-intestine transition in XV. Typhlosole starts in XX, forming four folded lamellae.
291 Hearts: in VI–XI. Excretory apparatus: one pair of holonephridia per segment, nephridial
292 vesicles sigmoid with a sub-terminal constriction followed by a loop (Fig. 4). Seminal vesicles:
293 two pairs in XI–XII, large and lobulated. Spermathecae: two pairs in X–XI, intracoelomic,
294 sessile and double (Fig. 3C).

295 ECOLOGY. – *F. luberonensis* n. sp. was found in a Mediterranean shrubland (garrigue) soil at
296 low elevation (434 m asl).

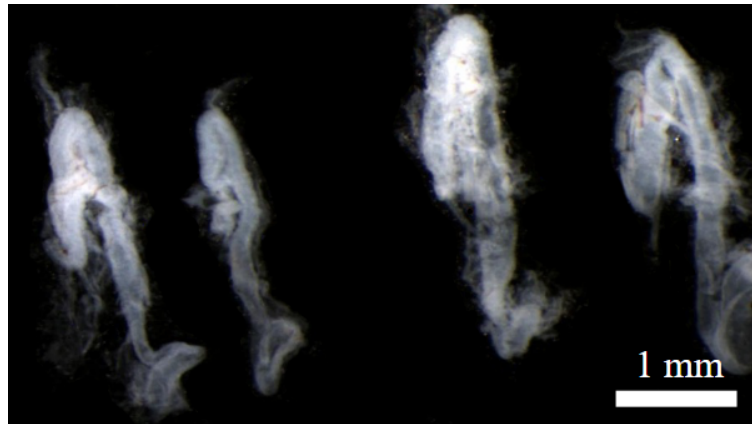
297 DISTRIBUTION. – *F. luberonensis* n. sp. is only known from the type locality, near the city of
298 Saint-Saturnin-les-Apt, between the massif of Luberon and the Vaucluse mountains in the
299 Vaucluse department (Provence-Alpes-Côte d’Azur, France) (Fig. 5). It is located in the
300 Luberon Regional Natural Park (Parc Naturel Régional du Luberon).

301 REMARKS. – This species can be distinguished from its closest relative *F. bartolii* n. comb. by
302 the position of its clitellum and tubercula pubertatis (Table 4) and by their remarkably high
303 genetic distance (12.14% uncorrected pairwise COI distance).



304

305 FIG. 3. – *Flabellodrilus luberonensis* n. sp.: A) External view of the anterior body; B) Lateral
 306 view of the anterior body; C) Dissection of the anterior body. All images from the Holotype
 307 specimen and © T. Decaëns; CL= clitellum, CR= crop, GM= genital marks, GZ= gizzard, IN=
 308 intestine, MP= male pore, NE= nephridia, SEP= septa, SP= spermathecae, SV= seminal
 309 vesicles, TP= tubercula pubertatis.



310

311 Fig. 4. – Pre-clitellar nephridia of *Flabellodrilus luberonensis* n. sp. © D.F. Marchán

312

313 **Genus *Allolobophora* Eisen, 1874**

314 TYPE SPECIES. – *Enterion chloroticum* Savigny, 1826: 182

315 DIAGNOSIS. – Small-to-medium-sized species with green pigmentation (sometimes absent).

316 Prostomium epilobous, no transversal furrows. Setae closely paired. First dorsal pore in 4/5

317 (rarely 3/4, 5/6, 7/8). Male pores in ½ XV with well-developed porophores. Presence of

318 spermatophores. Spermathecal pores in variable position and number between 7/8 and 10/11,

319 simple. Nephridial pores irregularly distributed (*en solfège*). Clitellum moderately posterior to

320 extremely posterior, starting between XXVIII and LXXIII and ending between XXXVI and

321 LXXVIII. Calciferous glands in X–XV with diverticula in X. Typhlosole usually trifold

322 (sometimes bifid or with 4 lamellae). Variable number of simple spermathecae, usually three

323 or four pairs. Four pairs of seminal vesicles in IX–XII. Nephridial bladders U-shaped (incurvate

324 and reclinate or proclinate).

325 INCLUDED SPECIES. –

326 *Allolobophora chlorotica* (Savigny, 1826: 182)

327 *Allolobophora burgondiae* Bouché, 1972: 272

328 *Allolobophora icterica* (Savigny, 1826: 182)

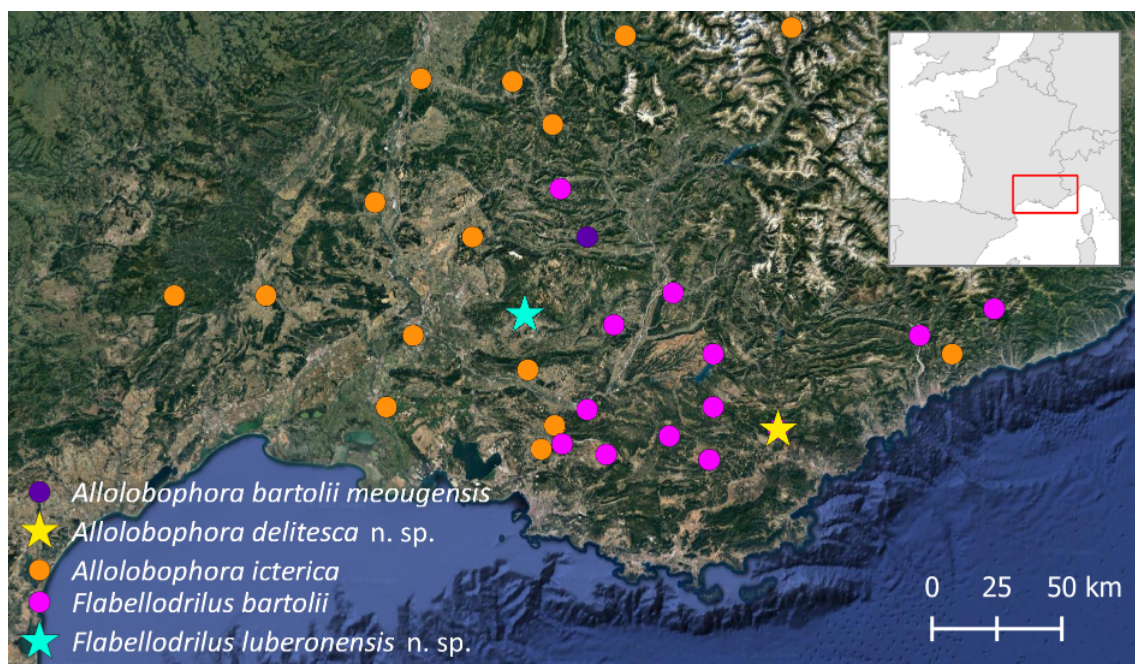
329 *Allolobophora molleri* Rosa, 1889: 3

330 *Allolobophora moebii* Michaelsen, 1895

331 *Allolobophora dubiosa* (Örley, 1881: 603)

332 *Allolobophora delitescens* n. sp.

333 DIVERSITY AND DISTRIBUTION. – The genus *Allolobophora* as redefined by Navarro *et al.* (2023)
334 comprises seven species natively distributed in the Iberian Peninsula, France, Morocco,
335 Algeria, Italy, Belgium, Czech Republic, Germany, Romania, Switzerland, The Netherlands,
336 United Kingdom, Bulgaria, Croatia, Hungary, Moldova, Montenegro, Russia, Serbia, Slovakia,
337 Turkey and Ukraine. However, their geographic origin appears to be located between the
338 Iberian Peninsula, Maghreb and the perialpine region (including France, Switzerland and the
339 Western Balkans). The species attributed to *Heraclescolex* Qiu & Bouché, 1998e in the genus
340 original description likely belong to *Allolobophora* and are mainly distributed in Portugal,
341 western Spain and Morocco.



343 FIG. 5. – Distribution of newly described Lumbricidae species, *Flabellodrilus luberonensis* n.
344 sp. and *Allolobophora delitescens* n. sp. (stars), and their closest relatives (circles) in Southern
345 France. All species within the genus *Flabellodrilus* n. gen. are represented.

346

347 *Allolobophora delitescens* Gérard, Decaëns & Marchán n. sp.

348 (Figs. 6, 7)

349 TYPE MATERIAL. – **Holotype. France** • One adult specimen; Provence–Alpes–Côte d’Azur,
350 Var, 83830 Callas, in the soil; latitude/longitude: 43.573°N/6.530°E; elevation: 305 m asl; 28
351 November 2021; T. Decaëns, D. F. Marchán, S. Gérard, R. Della Vedova leg.; deposited at
352 MNHN (BOLD Sample ID: SG-0024).

353 **Paratypes. France** • One adult and one sub-adult specimens; same data as Holotype; deposited
354 as follow: one specimen at Eco&Sols (BOLD Sample ID: SG-0046), and one specimen at
355 MNHN (BOLD Sample ID: SG-0047).

356 ETYMOLOGY. – The species name is derived from the present participle of the latin verb
357 *delitescere, is, ere*, which can be translated to the intransitive verb “to hide”. This is a reference
358 to the fact that Marcel Bouché did not find this species despite his sampling in 1968 at the type
359 locality.

360 DESCRIPTION

361 *External morphology.* (Fig. 6A, 6B)

362 Body shape cylindrical. Body pigmentation absent. Average body length after ethanol fixation:
363 85 mm (range: 72 to 98 mm; n= 2 adult and 1 subadult specimens). Average body mass: 0.918
364 g (range: 0.639 to 1.197 g; n = 2). Average diameter: 4.7 mm (range: 4.6 to 4.7 mm; n= 2) in
365 the preclitellar region, 5.0 mm (range: 4.9 to 5.0 mm; n= 2) in the clitellum, 4.5 mm (range: 4.1

366 to 4.8 mm; n= 2) in the postclitellar region. Average number of segments: 201 (range: 200 to
367 202; n= 2; 1 subadult specimen with 211 segments). Prostomium of closed epilobous type.
368 Setae closely paired. Setal arrangement aa:ab:bc:cd:dd = 11:1:6:1:29. Clitellum in (XXXV)
369 XXXVI–(XLVI) XLVII. Genital markings in intraclitellar in XXXVII–(XXXVIII) XXXIX.
370 Tubercula pubertatis: thin band in XL–XLVI. Male pores: one pair in XV. Ovipores: one pair
371 in 1/2 XIV, at 1 x ab dorsally from b. Spermathecal pores not visible. Nephridial pores not
372 visible.

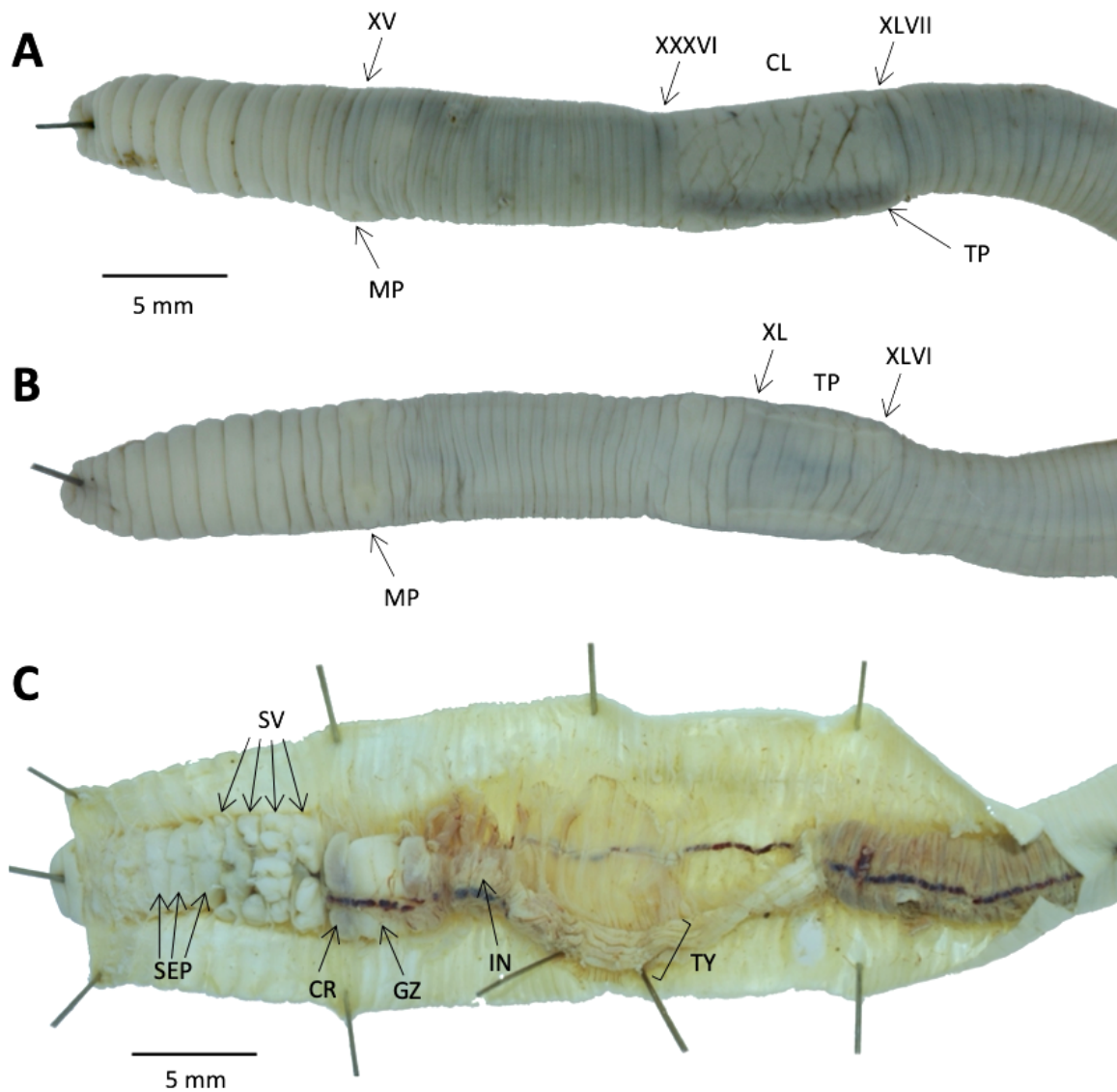
373 *Internal anatomy.* (Fig. 6C, 7)

374 Septa: thickened from 6/7 to 10/11, otherwise membranous. Crop in XV–XVI. Muscular
375 gizzard in XVII–XVIII, followed by a membranous pouch in XIX, with an average size (width
376 x length) of 3.80 x 2.25 mm. Calciferous glands: in X–XIV, forming two kidney-shaped lobes
377 in X. Esophagus-intestine transition in XV. Typhlosole start in XIX, forming five lamellae.
378 Hearts: in VI–XI. Excretory apparatus: one pair of holonephridia per segment, nephridial
379 vesicles U-shaped (Fig. 7). Seminal vesicles: four pairs in IX–XII, smaller in IX–X, large
380 lobulated in XI–XII. Spermathecae: three pairs in 8/9, 9/10, 10/11, small globular and
381 intraseptal, simple (a single case of a double spermathecae).

382 ECOLOGY. – *A. delitescens* n. sp. was found in a Mediterranean grassland, previously an olive
383 tree orchard, surrounded by pine forests, at a low elevation (305 m asl).

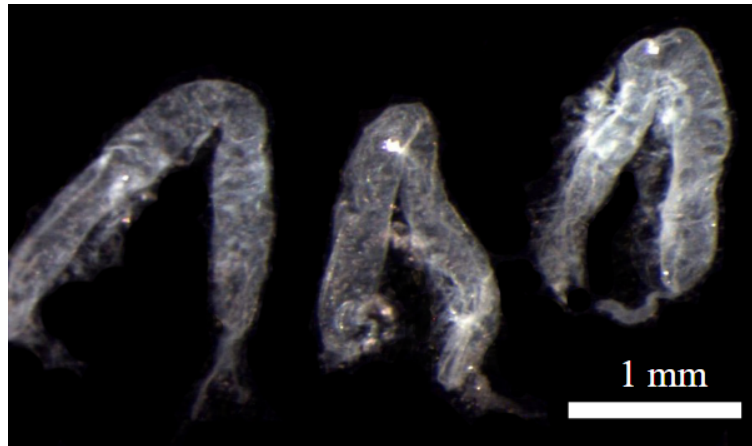
384 DISTRIBUTION. – *A. delitescens* n. sp. is only known from its type locality, near the city of
385 Callas, in the sedimentary basin north to the Esterel massif in the Var department (Provence-
386 Alpes-Côte d'Azur, France) (Fig. 5).

387 REMARKS. – *A. delitescens* n. sp. can be distinguished from its closest relatives *A. icterica* and
388 *A. dubiosa* by the position of the clitellum, tubercula pubertatis and typhlosole type, and by its
389 absence of pigmentation and smaller size in the latter case (Table 4).



390

391 FIG. 6. – *Allobophora delitescens* n. sp.: A) External view of the anterior body; B) Lateral view of the
 392 anterior body; C) Dissection of the anterior body. All images from the Holotype specimen and © T.
 393 Decaëns; CL= clitellum, CR= crop, GM= genital marks, GZ= gizzard, IN= intestine, MP= male pore,
 394 SEP= septa, SV= seminal vesicles, TP= tubercula pubertatis, TY= typhlosole.



395

396 FIG. 7. – Pre-clitellar nephridia of *Allolobophora delitescens* n. sp.. © D.F. Marchán.

397 TABLE 4. – Main morphological characters distinguishing the newly described species *Flabellodrilus*
 398 *luberonensis* n. sp., *Allolobophora delitescens* n. sp. and their closest relatives.

Characters	<i>Flabellodrilus</i> <i>luberonensis</i> n. sp.	<i>Flabellodrilus</i> <i>bartolii</i>	<i>Allolobophora</i> <i>delitescens</i> n. sp.	<i>Allolobophora</i> <i>icterica</i>	<i>Allolobophora</i> <i>dubiosa</i>
Length	70–100 mm	60–120 mm	70–98 mm	70–90 mm	120–250 mm
N. segments	187–353	280–394	200–211	140–200	120–303
Weight	0.85–1.24 g	0.85–1.49 g	0.64–1.2 g	0.3–1.33 g	2.96–3.47 g
Pigmentation	Absent, dark spots	Brown-yellow, dark spots	Absent	Absent	Dark green to greenish brown
Papillae	XI–XII, XVI–XXVIII, XXXIV	X, XI, XXXIII–XLIV	XXXVII, (XXXVIII), XXXIX	XI, XLIV, XLV	Unknown
Spermathecal pores	9/10, 10/11 double	9/10, 10/11 double	8/9, 9/10, 10/11 simple in c	(7/8)8/9, 9/10, 10/11 simple in c	8/9, 9/10, 10/11 simple in c
Clitellum	XXXII–XLII (XLIII)	(XXXIII) XXXIV–XLIII (XLIV)	(XXXV) XXXVI–(XLVI) XLVII	(XXXIII) XXXIV–XLIII (XLIV)	(XXXVI) XXXVII–XLVII (XLVIII)
Tubercula pubertatis	XXXV–XL	(XXXV) XXXVI–XLI	XL–XLVI	(XXXV) XXXVI–XLII (XLIII)	(XLIII) XLIV–XLVII (XVIII)
Typhlosole	Four lamellae	Four lamellae	Five lamellae	Bifid	Bifid

Nephridial bladders	Sigmoid, bag-like distension	Sigmoid, bag-like distension	U-shaped	U-shaped	U-shaped
Seminal vesicles	XI, XII	XI, XII	IX - XII	IX - XII	IX - XII
Spermathecae	Double, oval in X, XI	Double, oval in X, XI	Simple, intraseptal in 8/9, 9/10, 10/11	Simple, intraseptal to intracoelomic, in (VIII), IX, X, XI	Simple in 8/9, 9/10, 10/11

399

400

Family HORMOGASTRIDAE Michaelsen, 1900

401

Genus *Vignysa* Bouché, 1970

402

TYPE SPECIES. – *Lumbricus teres* Dugès, 1828: 289

403

DIAGNOSIS. – Small-to-medium-sized species without cutaneous pigmentation. Prostomium

404

prolobous. Transversal furrows on segments I-II. Setae closely paired. Male pores in 15/16 with

405

well-developed porophores. Spermathecal pores in 9/10, 10/11, simple. Nephridial pores

406

aligned. Clitellum between XIV and XXIX (1/2 XXX). Two gizzards in VI–VII. Typhlosole

407

lire or Y shaped. Two pairs of spermathecae, disc shaped or tubular. Two pairs of seminal

408

vesicles in XI–XII. Nephridial bladders fish-hook shaped with caeca from the first segments.

409

INCLUDED SPECIES. –

410

Vignysa teres (Dugès, 1828: 289)

411

Vignysa vedovinii Rota, 1994: 27

412

Vignysa callasensis n. sp.

413

DIVERSITY AND DISTRIBUTION. – This genus currently comprises three species occurring in

414

South-Eastern France, from Montpellier (Hérault, Occitanie) to the north of Fréjus (Var,

415

Occitanie), and from the Mediterranean Sea to the 44th north parallel (Fig. 8).



416

417 FIG. 8. – Distribution of *Vignysa callasensis* n. sp. (star) and its closest relatives (circles) in
 418 Southern France. All species of the genus *Vignysa* are represented.

419

420 ***Vignysa callasensis* Gérard, Decaëns & Marchán n. sp.**

421 **(Figs. 9, 10, 11)**

422 **TYPE MATERIAL.** – **Holotype. France** • One adult specimen; Provence–Alpes–Côte d’Azur,
 423 Var, 83830 Callas, in the soil; latitude/longitude: 43.587°N/6.538°E; elevation: 340 m asl; 28
 424 November 2021; T. Decaëns, D. F. Marchán, S. Gérard, R. Della Vedova leg.; deposited at
 425 MNHN (BOLD Sample ID: DFM-1062).

426 **Paratypes. France** • 8 adult specimens; same data as Holotype; deposited as follow: 4
 427 specimens at Eco&Sols (BOLD Sample ID: DFM-1061, DFM-1065, SG-0057, SG-0058), 4
 428 specimens at MNHN (BOLD Sample ID: DFM-1064, DFM-1063; SG-0059, SG-0060).

429 **Other material. France** • 10 adult and 11 sub-adult specimens; same data as Holotype;
 430 deposited at Eco&Sols.

431 ETYMOLOGY. – The name of the species is derived from the city of Callas in the Var department
432 (Provence-Alpes-Côte d’Azur, France) where the type specimens were found.

433 DESCRIPTION

434 *External morphology.* (Fig. 9A, B)

435 Body shape cylindrical. Body pigmentation absent. Gut content visible in transparency.
436 Average body length after ethanol fixation: 95 mm (range: 82 to 150 mm; n= 9 adult
437 specimens). Average body mass: 0.984 g (range: 0.850 to 1.260 g; n= 11). Average diameter:
438 4.0 mm in the preclitellar region (range: 3.5 to 4.8 mm; n= 11), 4.5 mm in the clitellum (range:
439 4.0 to 5.4 mm; n= 11), 4.9 mm in the postclitellar region (range: 4.0 to 5.5 mm; n=11). Average
440 number of segments: 162 (range: 157 to 167; n= 7). Prostomium of prolobous type. Setae
441 closely paired. Setal arrangement aa:ab:bc:cd:dd = 18:2:8:1:25. Clitellum in XV–XXIII,
442 beginning unclear. Genital markings in XII–XIV and XX–XXIII, in ab. Tubercula pubertatis:
443 thin band in XVII–XXIII, more marked in XX–XXIII. Male pores: one pair in XV. Ovipores
444 not visible. Spermathecal pores not visible. Nephridial pores not visible.

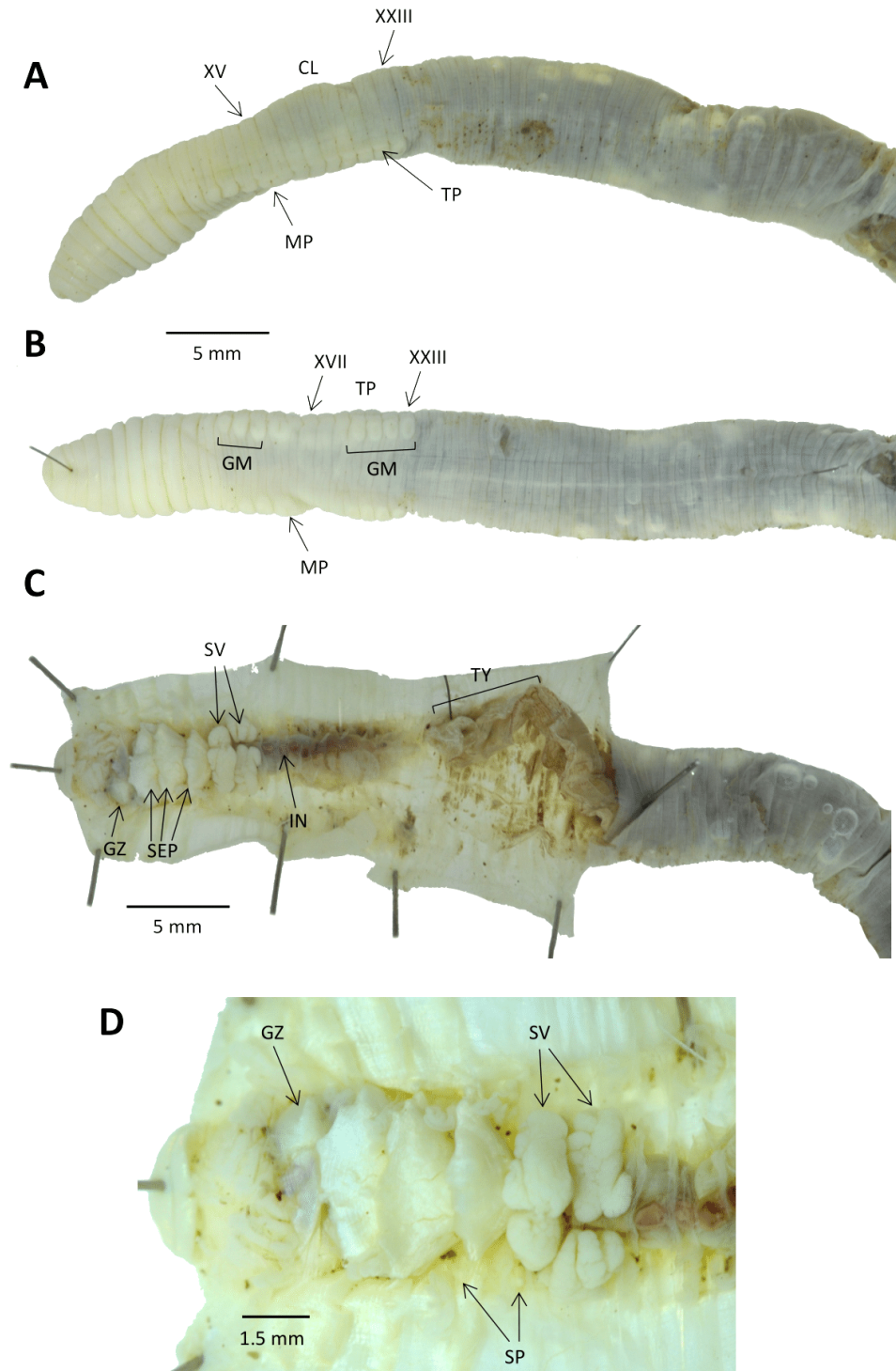
445 *Internal anatomy.* (Fig. 9C, D)

446 Septa: thickened from 7/8 to 9/10, otherwise membranous. Crop: missing. Gizzard: two
447 globular gizzards in VI–VII, of 1.5 mm in diameter. Calciferous glands: absent. Esophagus-
448 intestine transition in XIII. Typhlosole start in XX or XXII, formed by a “Y” shaped large
449 lamellae. Hearts: in VI–XI. Excretory apparatus: one pair of holonephridia per segment,
450 nephridial vesicles boat-hook shaped (bent cecum) in preclitellar segments, open V shaped in
451 the rest of the body. Seminal vesicles: two pairs in XI–XII, large and lobulated. Spermathecae:
452 two pairs in IX–X (9/10, 10/11), intracoelomic, tubular and folded, simple.

453 ECOLOGY. – *Vignysa callasensis* n. sp. was found in a riparian grassland near La Risse stream,
454 at a low elevation (340 m asl).

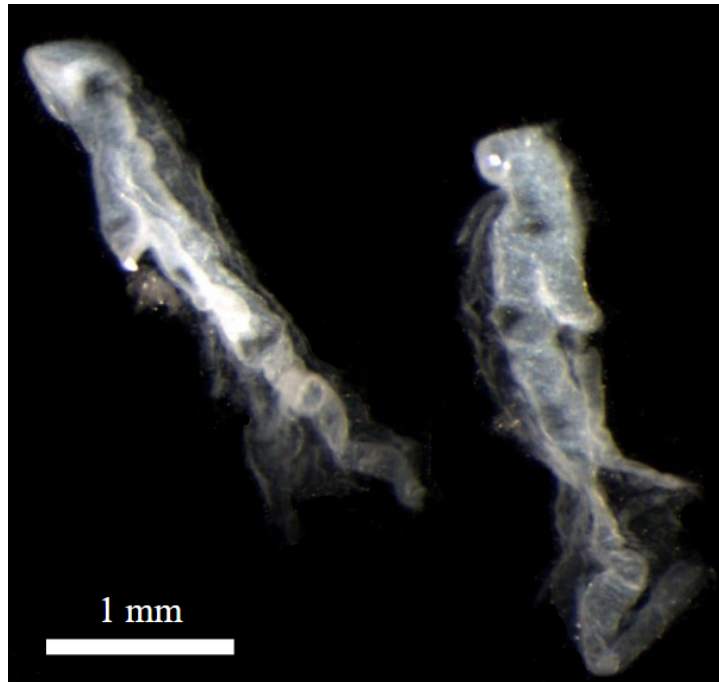
455 DISTRIBUTION. – *Vignysa callasensis* n. sp. was found near the city of Callas, in the sedimentary
456 basin North to Esterel, in the Var department (Provence-Alpes-Côte d’Azur, France).

457 REMARKS. – This species is the smallest species of the genus *Vignysa*: 0.850–1.260 g and 157–
458 167 segments *versus* 1.400–2.700 g and 205–232 segments for *Vignysa teres* (Bouché 1972;
459 personal data), and 3.500–4.800 g and 372–396 segments for *Vignysa vedovinii* (Rota 1994)
460 (see Table 5). It is also the easternmost species within the genus. Alive, it has a viscous texture
461 (Fig. 11) and tends to break easily. The absence of blood vesicles (the same as in *V. vedovinii*)
462 suggests that this trait is an apomorphy of *V. teres*.



463

464 FIG. 9. – *Vignysa callasensis* n. sp.: A) External view of the anterior body; B) Lateral view of the anterior
 465 body; C) Dissection of the anterior body; D) Detail of the anterior body dissection showing the
 466 spermathecae. All images from the Holotype specimen and © T. Decaëns; CL= clitellum, GM= genital
 467 marks, GZ= gizzard, IN= intestine, MP= male pore, SEP= septa, SV= seminal vesicles, TP= tubercula
 468 pubertatis, TY= typhlosole.



469

470 FIG. 10. – Pre-clitellar nephridia of *Vignysa callasensis* n. sp. © D.F. Marchán.



471

472 FIG. 11. – Living specimen of *Vignysa callasensis* n. sp. © S. Gérard.

473 TABLE 5. – Main morphological characters distinguishing the newly described species *Vignysa*
 474 *callasensis* n. sp. and their closest relatives.

Characters	<i>Vignysa callasensis</i> n. sp.	<i>Vignysa teres</i>	<i>Vignysa vedoninii</i>
Length	88–150 mm	170–200 mm	110–130 mm
N. segments	160–163	205–232	372–396
Weight	0.85–1.26 g	1.4–2.7 g	3.5–4.8 g
Papillae	XII, XIV, XX–XXIII	(XIV) XV, XVI (XVII), XXII–XXV	XVI–XVIII, XXIV– XVII (XXVII, XXVIII)

Spermathecal pores	9/10, 10/11 simple	9/10, 10/11 simple	9/10, 10/11 simple
Clitellum	XV–XXIII	(1/2 XIII, XIV) 1/2 XIV–XXV	(XIV) XV–XXIX (1/2 XXX)
Tubercula pubertatis	(XVII) XX–XXIII	XXI–XXIV	XXIII, XIV–XXVII (XXVIII, XXIX)
Spermathecae	Simple, tubular in IX, X	Simple, tubular in IX, X	Simple, disc-shaped, in IX, X

475

476 **DISCUSSION**

477 TAXONOMY AND PHYLOGEOGRAPHY

478 Beyond its contribution to the knowledge of the earthworm fauna of France, our work
479 provides new insights into the understanding of the taxonomy and phylogeny of the genera
480 *Allolobophora* and *Vignysa*.

481 The limits of the genus *Allolobophora*, and the number of species it contains, are still
482 not agreed upon in the literature. Depending on the authors, the genus comprises 69 species
483 (DriloBASE taxo), 51 species and subspecies (Blakemore 2008) or 57 species and subspecies
484 (Brown *et al.* 2023; Misirlioğlu *et al.* 2023). The relevance of the genus has also been and is
485 still highly discussed, *Allolobophora* being considered as a catch-all genus, and demonstrated
486 to be polyphyletic in phylogenetic trees (Navarro *et al.* 2023). Some authors proposed to
487 separate it between *Allolobophora sensu stricto* and *Allolobophora sensu lato* (Bouché 1972;
488 Easton 1983; Csuzdi & Zicsi 2003). Marchán *et al.* (2021) elevated the subgenus *Gatesona*
489 proposed by Qiu & Bouché (1998a) to the genus level, and Popović *et al.* (2022) assigned
490 several Balkanic *Allolobophora* species to a redefined *Cernosvitovia*. Later, Navarro *et al.*
491 (2023) separated the genus *Allolobophora* into 4 distinct genera: *Allolobophora*, *Panoniona*,
492 *Lucquesia* Navarro *et al.*, 2023 and *Vosgesia* Navarro *et al.*, 2023. They also synonymised the
493 genus *Heraclescolex* with *Allolobophora*, and finally proposed to move *Aporrectodea icterica*

494 to the genus *Allolobophora*, a new taxonomic assignment which is strongly supported by our
495 results.

496 Here, we propose to remove *A. bartolii* from the *Allolobophora* genus, and to assign it
497 to the new genus *Flabellodrillus* n. gen., along with the new species *F. luberonensis* n. sp.. This
498 new cut within the genus *Allolobophora*, together with the previous revision by Navarro *et al.*
499 (2023), result in the restriction of the genus to seven species forming a monophyletic group and
500 corresponding broadly to the *Allolobophora sensu stricto* of Bouché (1972). The addition of *A.*
501 *delitescens* n. sp. further reinforce the monophyletic property of *Allolobophora*. These
502 taxonomic acts and the phylogenetic analyses that support them highlight the artificial character
503 of the “catch-all” group *Allolobophora sensu lato*, which is progressively split into several small
504 genera generally comprising species of restricted geographical distribution. There are still
505 several Balkanic species of *Allolobophora* which likely belong to *Cernovitovia* due to their
506 morphological and biogeographic affinities (see Popović *et al.* 2022), but others such as
507 *Allolobophora asconensis* Bretscher, 1900, *Allolobophora festae* Rosa, 1892, *Allolobophora*
508 *marcuzzii* Omodeo, 1952 or *Allolobophora schneideri* Michaelsen, 1900 (which are Italian
509 species) or the Caucasian *Allolobophora pseudonematogena* Perel, 1967, *Allolobophora*
510 *brunnecephala* Kvavadze, 1985 and *Allolobophora immaculata* Omodeo and Rota, 1989 are
511 more controversial: a strong effort to include these species in molecular phylogenetic analyses
512 would allow to eliminate *Allolobophora sensu lato* once and for all.

513 The family Hormogastridae is endemic of Western Mediterranean region, being present
514 only in Algeria, France, Italy, Malta, Spain and Tunisia with nine genera (Marchán *et al.* 2018
515 ; Rota *et al.* 2017). The genus *Vignysa* is endemic to South-Eastern France (Bouché 1972; Rota
516 1994) and comprises three species including the one described herein (Blakemore 2008; Brown
517 *et al.* 2023; Misirlioğlu *et al.* 2023; DriloBASE taxon). All are restricted to France: *V. teres*
518 occurs in several localities of the Hérault department (Occitanie), *V. vedovinii* has been found

519 in two localities of Bouches-du-Rhône and Var departments (Provence-Alpes-Côte d'Azur),
520 and *V. callasensis* n. sp. is known only from its type locality in the Var department (Fig. 8). The
521 distribution of the three species seems to be non-overlapping, but this will require further
522 occurrence data to be confirmed. The basal position of *V. callasensis* n. sp. in the DNA barcode
523 phylogenetic tree (Figure 2) indicates that the genus *Vignysa* could have originated in Provence,
524 a region that has been previously highlighted for its high rate of earthworm endemism (Bouché
525 1972; Marchán *et al.* 2020). However, this assumption should be treated with caution as it is
526 only based on a barcode tree whose topology reliability can be questioned. Analyses will need
527 to be strengthened by using multi-locus data and by including if possible other species in
528 neighboring genera before robust conclusions can be drawn.

529 DIVERSITY IN SOUTH-EASTERN FRANCE.

530 We describe here three new species and one new genus, which are, as far as we know,
531 all endemic from South-Eastern France. We found these new taxa in a region previously
532 intensively sampled by M. Bouché (Bouché 1972). This underlines the remarkably high
533 earthworm diversity in this region, which already counted several endemic species before our
534 contribution (e.g. *Aporrectodea balisa* (Bouché, 1972); *Cataladrilus porquerollensis* Marchán
535 & Decaëns, 2020; *Eumenoscolex pereli* (Bouché, 1972); *F. bartolii*; *Kritodrilus calarensis*
536 (Tetry, 1944); *Kritodrilus micrurus* Zicsi & Csuzdi, 1999; *Scherotheca dugesi* (Rosa, 1895);
537 *Scherotheca porotheca* Bouché, 1972; *Scherotheca portrosana* Marchán & Decaëns, 2020;
538 *Scherotheca sanaryensis* (Tetry, 1942) for Lumbricidae, together with *Boucheona gallica*
539 (Rota, 1994) and the genus *Vignysa*). This supports the hypothesis of South-Western Europe
540 being the origin and the center of diversification of the family Hormogastridae (Marchán *et al.*
541 2018) and one of the center of diversification of the familie Lumbricidae (Omodeo & Rota
542 2008). It also highlights that South-Western Europe, and more especially of South-Eastern
543 France, can be considered as a biodiversity hotspot for earthworms.

544 These high levels of endemism and diversity of earthworm could be explained by the
545 geological and climatic history of the region. South-Eastern France is composed of a huge
546 variety of geological substrates, with various ages and composition (Chantraine *et al.* 1996). It
547 is composed of three main geological structures: (1) relics of the Variscan orogeny from late
548 Paleozoic (Esterel, Maures and Tanneron massifs), associated with late Paleozoic sediments;
549 (2) Mesozoic sediments and pre-Alps sedimentary massifs; and (3) Cenozoic sediment in the
550 Rhone and Durance basins. The whole structure is located between late Paleozoic mountains
551 (Central Massif in the West and North-West) and younger mountains from Mesozoic (Alps in
552 East, Pyrenees in South-West). This high diversity of geological substrates can explain a
553 complex evolutionary history, with different physico-chemical soil properties driving a
554 diversification of adaptive traits in earthworms. Mathieu & Davies (2014) also suggested that
555 glaciations in the late Pleistocene acted as an environmental filter, with Southern France
556 providing habitat refuges for earthworm populations.

557 The discovery of three new species in that region was actually expected. M. Bouché
558 carried a quite intensive sampling in the region, but he favored good spatial coverage over
559 intensive sampling at each locality (ECORDRE_0496 and ECORDRE_0503 were done the
560 same day together with 13 other sites, whereas ECORDRE_0527 was done together with 11
561 other sites (Bouché, 1972)). However, the non-detection of these species can also be explained
562 by their absence of the locality at that time. Earthworm can have a really patchy distribution,
563 even at the very local scale, making them hard to collect. They could also have changed their
564 local distribution in response to climate and land use changes that have occurred over the past
565 five decades. Finally, they could be present at that time, but at a juvenile stage, making them
566 undetectable without molecular analysis.

567 This highlights the importance of resampling previously surveyed localities when
568 seeking to establish species lists and discover potential new taxa, like the work of Marchán *et*

569 *al.* (2023) in Corsica. Further studies should also aim at intensifying sampling in non-previously
570 sampled localities in South-Eastern France, as for instance in the Saint-Baume mountain, the
571 Plaine des Maures and the Esterel massif. Given the high diversity and the high proportion of
572 species with narrow geographical distribution, this will undoubtedly result in the discovery of
573 additional species new to science as has been the case in previous works in Port-Cros and
574 Porquerolle Islands (Marchán *et al.* 2020), in Corsica (Marchán *et al.* 2023), and in
575 southwestern France (Marchán *et al.* 2023).

576

577 CONSERVATION

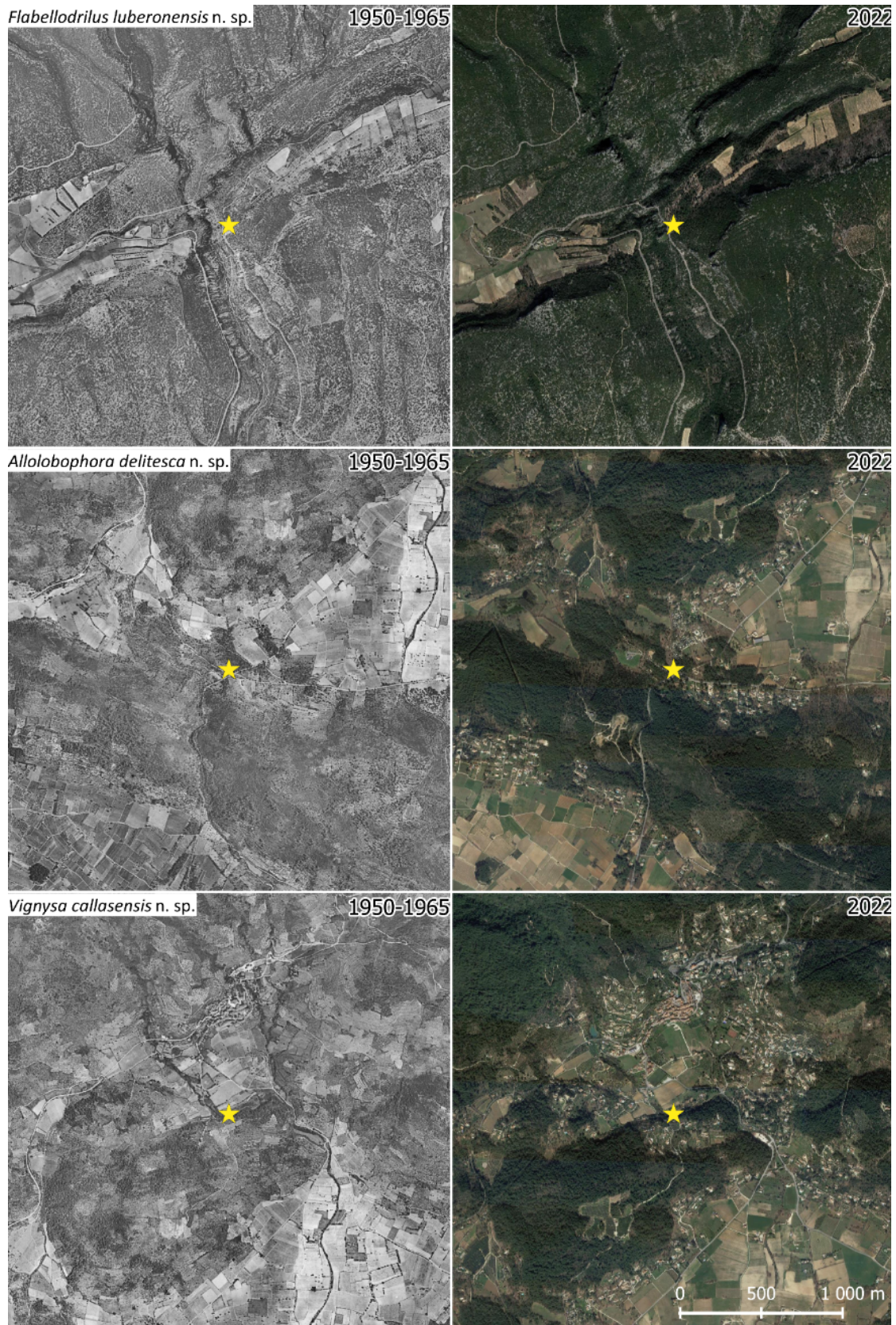
578 The three species described in this work were found in open landscapes. Until more
579 specimens of these species are found, we can say they are open habitat specialists. This is the
580 case for many endemic species of South-Eastern France. For instance, *A. balisa*, *C.*
581 *porquerollensis*, *E. pereli*, *K. micrurus*, *S. dugesi*, *S. porotheca* and *V. vedovinii* are considered
582 as strict open habitat specialists. Other species such as *F. bartolii*, *K. calarensis*, and *V. teres*,
583 even not being strict specialists, are mostly found in open habitats. The specialization to open
584 habitats from endemic species in the Mediterranean region is also observed in other taxa, such
585 as birds (Blondel & Aronson 1999).

586 However, open landscapes are decreasing in the Mediterranean region. Since the middle
587 of the nineteenth century, the abandonment of traditional agro-pastoral practices and the
588 decrease of the use of wood for charcoal led most habitats to experience secondary successions
589 and the progressive afforestation of Mediterranean grasslands and scrublands (Barbero *et al.*
590 1990; Blondel & Aronson 1999; Chauchard *et al.* 2007). More recently, these habitats have also
591 decreased in surface due to the expansion of housing urbanization in the second half of the
592 twentieth century, especially in South-Eastern France (Daligaux 2001; Baccaïni & Sémécurbe
593 2009). The type localities of the three new species, all open habitats (*i.e.* grasslands for *V.*

594 *callasensis* n. sp. and *A. delitescens* n. sp., garrigue for *F. luberonensis* n. sp.) have undergone
595 such a transition, visible from old (1950-1960) and current satellite pictures in Fig 12.

596 This historical decrease of open landscapes has led to a decrease in biodiversity,
597 especially on rare and endemic species (Preiss *et al.* 1997; Blondel & Aronson 1999; Labaune
598 & Magnin 2002; Höchtl *et al.* 2005). We can therefore argue that this open habitat loss at a fast
599 pace represents a major threat on those newly described specialist species.

600 The threats these species are facing raise the question of their conservation. One of the
601 major tools for assessing the conservation status of a species is the IUCN red list. The species
602 described herein were only found in their type localities, in an already strongly sampled region.
603 It can be an indication of small populations with a narrow distribution range. Thus, they match
604 the IUCN red list (IUCN Standards and Petitions Committee 2022) criterion D (very small
605 population size), especially criterion D2 (very restricted distribution) and first part of criterion
606 B (small range area). However, the loss of the habitat where they were found and the
607 Mediterranean region being highly threatened by climate change (MedECC 2020) could be
608 indicators of their decline, matching the second part of criterion B (decline). We can then make
609 the hypothesis that they face an extinction risk, and could be listed as Vulnerable species
610 according to the IUCN red list. More sampling should be conducted in their area to better know
611 their repartition range and population size, since they are only known in their type localities.
612 Genetic diversity could also be measured to know if populations are fragmented, as it has been
613 done for *Compostelandrilus cyaneus* (Briones & Díaz Cosín, 1993) by Marchán & Domínguez
614 (2022).



615

616 FIG. 12. – Satellite pictures around type localities of *Flabellodrilus luberonensis* n. sp., *Allolobophora*
 617 *delitescens* n. sp. and *Vignysa callasensis* n. sp. in the 1950-1965 period (left) and in 2022 (right).

618 (1950-1965 satellite pictures © IGN (Institut national de l'information géographique et forestière)
619 2022;© Google 2022).

620

621 **CONCLUSION**

622 The description of three new species in South-Eastern France in a resampling of Bouché's
623 plots (Bouché 1972) highlights the tremendous diversity in this region, which could still host a
624 high number of species yet to be discovered. In a region facing global change pressures like
625 urbanization, habitat and land use changes and climate mutations, it also stresses that their
626 conservation is not guaranteed and deserves consideration.

627 Moreover, these descriptions and the phylogenetic evidence on which they rely help to
628 better understand the systematics of the historically catch-all genera *Allolobophora*, and
629 improved our understanding of the diversity and distribution of the endemic genus *Vignysa*.

630 **CONFLICT OF INTEREST**

631 The authors do not have any conflicts of interest to declare.

632 **ACKNOWLEDGMENTS**

633 The authors would like to thank Raphaël Della Vedova for his help during the fieldwork.
634 This work benefited from financial support from the GloWorms project. DFM was funded by
635 a Make Our Planet Great Again Postdoctoral grant from Campus France (mopga-postdoc-3—
636 6111272103) and María Zambrano Postdoctoral Fellowship from the Spanish Government.

637 **REFERENCES**

638 AKAIKE H. 1973. — Maximum likelihood identification of Gaussian autoregressive moving
639 average models. *Biometrika* 60 (2): 255–265. <https://doi.org/10.1093/biomet/60.2.255>

- 640 ALLAIRE J.J., XIE Y., MCPHERSON J., LURASCHI J., USHEY K., ATKINS A., WICKHAM H.,
641 CHENG J., CHANG W. & IANNONE R. 2022. — rmarkdown: Dynamic Documents for R.
642 R package version 2.10.
- 643 BACCAÏNI B. & SEMECURBE F. 2009. — La croissance périurbaine depuis 45 ans. Extension et
644 densification. *INSEE première* 1240: 1–4.
- 645 BARBERO M., BONIN G., LOISEL R. & QUÉZEL P. 1990. — Changes and disturbances of forest
646 ecosystems caused by human activities in the western part of the mediterranean basin.
647 *Vegetatio* 87 (2): 151–173. <https://doi.org/10.1007/BF00042952>
- 648 BLAKEMORE R.J. 2008. — An updated list of valid, invalid and synonymous names of
649 Criodriloida and Lumbricoidea (Annelida: Oligochaeta: Criodrilidae,
650 Sparganophilidae, Ailoscolecidae, Hormogastridae, Lumbricidae, Lutodrilidae). *A*
651 *Series of Searchable Texts on Earthworm Biodiversity, Ecology and Systematics from*
652 *Various Regions of the World.*
- 653 BLONDEL J. & ARONSON J. 1999. — *Biology and Wildlife of the Mediterranean Region.*
654 Oxford University Press.
- 655 BOUCHE M.B. 1970. — Remarques sur quelques Lumbricina de France et consequences de la
656 decouverte des nouveaux taxons Vignysinae (Subfam. nov) et Diporodrilidae (Fam.
657 nov.). *Pedobiologia* 10: 246–256.
- 658 BOUCHE M.B. 1972. — *Lombriciens de France. Ecologie et Systématique.* INRA Editions.
- 659 BRETSCHER K. 1900. — Mitteilungen über die Oligochœtenfauna der Schweiz. *Revue suisse*
660 *de zoologie. Annales de la société zoologique suisse* 8: 1–44.

- 661 BRIONES M. & DIAZ COSIN D.J. 1993. — *Eophila cyanea* n. sp.(Lumbricidae, Oligochaeta), a
662 new earthworm species from the Iberian Peninsula. *Graellsia* 47: 73–76.
- 663 BROWN G.G., JAMES S.W., LAPIED E., DECAËNS T., REYNOLDS J.W., MISIRLIOĞLU M.,
664 STOJANOVIĆ M., PHILLIPS H. & CAMERON E. 2023. — A checklist of megadrile
665 earthworm (Annelida: Clitellata) species and subspecies of the world. *Zenodo*.
666 <https://doi.org/10.5281/zenodo.7301848>
- 667 CHANTRAINE J., AUTRAN A., CAVELIER C. & CLOZIER L. 1996. — Carte géologique de la
668 France à l'échelle du millionième. BRGM.
- 669 CHAUCHARD S., CARCAILLET C. & GUIBAL F. 2007. — Patterns of Land-use Abandonment
670 Control Tree-recruitment and Forest Dynamics in Mediterranean Mountains.
671 *Ecosystems* 10 (6): 936–948. <https://doi.org/10.1007/s10021-007-9065-4>
- 672 CSUZDI C. & ZICSI A. 2003. — Earthworms of Hungary (Annelida: Oligochaeta;
673 Lumbricidae). Budapest: Hungarian Natural History Museum. 271 p.
- 674 DALIGAUX J. 2001. — La périurbanisation en Provence: visages d'hier et d'aujourd'hui,
675 interrogations pour demain. Le cas du Var et des Bouches-du-Rhône. *Géocarrefour* 76
676 (4): 289–302.
- 677 DARRIBA D., TABOADA G.L., DOALLO R. & POSADA D. 2012. — jModelTest 2: more models,
678 new heuristics and parallel computing. *Nature Methods* 9 (8): 772–772.
679 <https://doi.org/10.1038/nmeth.2109>
- 680 DECAËNS T., BARTZ M.C., GOULPEAU A., MARCHÁN D.F., MAGGIA M.E., LAPIED E., FEIJO
681 A.M. & JAMES S.W. 2023. — Earthworms (Oligochaeta, Clitellata) of the Mitaraka

682 range, French Guiana: commented checklist with description of one genus and
683 eighteen species new to science. Submitted to *Zoosystema*.

684 DOMÍNGUEZ J., AIRA M., BREINHOLT J.W., STOJANOVIC M., JAMES S.W. & PÉREZ-LOSADA M.
685 2015. — Underground evolution: New roots for the old tree of lumbricid earthworms.
686 *Molecular Phylogenetics and Evolution* 83: 7–19.
687 <https://doi.org/10.1016/j.ympev.2014.10.024>

688 DRILOBASE TAXO. Available at: <http://taxo.drilobase.org> [Accessed: 16 January 2023].

689 DUGES A.-L. 1828. — *Recherches sur la circulation, la respiration et la reproduction des*
690 *Annélides abranches*. C. Thuau.

691 EASTON E.G. 1983. — A guide to the valid names of Lumbricidae (Oligochaeta). In: Satchell
692 J.E. (ed.) *Earthworm Ecology: From Darwin to Vermiculture*: 475–487. Springer
693 Netherlands, Dordrecht.

694 EISEN G. 1874. — Om Skandnaviens Lumbricider. *Öfversigt af Kongliga Vetenskaps-*
695 *Akademiens Förhandlingar* 30 (8): 43–56.

696 FOLMER O., BLACK M., HOEH W., LUTZ R. & VRIJENHOEK R. 1994. — DNA primers for
697 amplification of mitochondrial Cytochrome C oxidase subunit I from diverse
698 metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.

699 GOOGLE 2022 — Available at: <http://google.com/maps> [Accessed: 13 December 2022].

700 GRUBE A.E. 1850. — Die Familien der Anneliden. In: *Archiv für Naturgeschichte*: 275–276,
701 281. Nicolai, Berlin.

702 HALL T.A. 1999. — BioEdit: a user-friendly biological sequence alignment editor and analysis
703 program for Windows 95/98/NT. *In: Nucleic acids symposium series: 95–98.*
704 ([London]: Information Retrieval Ltd., c1979-c2000.).

705 HÖCHTL F., LEHRINGER S. & KONOLD W. 2005. — “Wilderness”: what it means when it
706 becomes a reality—a case study from the southwestern Alps. *Landscape and Urban*
707 *Planning* 70 (1): 85–95. <https://doi.org/10.1016/j.landurbplan.2003.10.006>

708 IUCN STANDARDS AND PETITIONS COMMITTEE 2022. — Guidelines for Using the IUCN Red
709 List Categories and Criteria. Version 15.1.

710 JAMIESON B.G.M. 1988. — On the phylogeny and higher classification of the Oligochaeta.
711 *Cladistics* 4 (4): 367–401. <https://doi.org/10.1111/j.1096-0031.1988.tb00520.x>

712 KATOH K. & STANDLEY D.M. 2013. — MAFFT Multiple Sequence Alignment Software
713 Version 7: Improvements in performance and usability. *Molecular Biology and*
714 *Evolution* 30 (4): 772–780. <https://doi.org/10.1093/molbev/mst010>

715 LABAUNE C. & MAGNIN F. 2002. — Pastoral management vs. land abandonment in
716 Mediterranean uplands: impact on land snail communities. *Global Ecology and*
717 *Biogeography* 11 (3): 237–245. <https://doi.org/10.1046/j.1466-822X.2002.00280.x>

718 LAMARK J.-B. de 1802. — Recherches sur l’organisation des corps vivants: précédé du
719 discours d’ouverture du cours de zoologie donné dans le Muséum d’Histoire naturelle.
720 Fayard.

721 MARCHÁN D.F., DECAËNS T., DÍAZ COSÍN D.J., HEDDE M., LAPIED E. & DOMÍNGUEZ J. 2020.
722 — French Mediterranean islands as a refuge of relic earthworm species: *Cataladrilus*
723 *porquerollensis* sp. nov. and *Scherotheca portcrosana* sp. nov. (Crassiclitellata,

- 724 Lumbricidae). *European Journal of Taxonomy* 701: 1–22.
725 <https://doi.org/10.5852/ejt.2020.701>
- 726 MARCHÁN D.F. & DOMÍNGUEZ J. 2022. — Evaluating the conservation status of a North-
727 Western Iberian earthworm (*Compostelandrilus cyaneus*) with insight into its genetic
728 diversity and ecological preferences. *Genes* 13 (2): 337.
729 <https://doi.org/10.3390/genes13020337>
- 730 MARCHÁN D.F., DOMÍNGUEZ J., HEDDE M. & DECAËNS T. 2023. — The cradle of giants:
731 insight into the origin of *Scherotheca* (Lumbricidae, Crassiclitellata) with description
732 of eight new species from Corsica, France. *Zoosystema*, in press.
- 733 MARCHÁN D.F., FERNÁNDEZ R., SOSA I. DE, SÁNCHEZ N., DÍAZ COSÍN D.J. & NOVO M. 2018.
734 — Integrative systematic revision of a Mediterranean earthworm family:
735 Hormogastridae (Annelida, Oligochaeta). *Invertebrate Systematics* 32 (3): 652–671.
736 <https://doi.org/10.1071/IS17048>
- 737 MARCHÁN D.F., GÉRARD S., HEDDE M., ROUGERIE R. & DECAËNS T. 2022. — An updated
738 checklist and a DNA barcode library for the earthworms (Crassiclitellata, Oligochaeta)
739 of Corsica, France. *Zoosystema* 44 (17): 439–461.
740 <https://doi.org/10.5252/zoosystema2022v44a17>
- 741 MARCHÁN D.F., JIMÉNEZ S., DECAËNS T. & DOMÍNGUEZ J. 2021. — Systematic revision of
742 *Gatesona* (Crassiclitellata, Lumbricidae), an endemic earthworm genus from the
743 Massif Central (France). *PLOS ONE* 16 (9): e0255978.
744 <https://doi.org/10.1371/journal.pone.0255978>
- 745 MARCHÁN D.F., NOVO M., DOMÍNGUEZ J., DA SILVA A., MARTÍNEZ A., HEDDE M., GÉRARD S.
746 & DECAËNS T. 2023. — The best is yet to come: six new species within a large-bodied

- 747 earthworm genus (*Scherotheca*, Lumbricidae) in a densely sampled region
748 (Southwestern France). *Zoological Journal of the Linnean Society*, in press.
- 749 MARCHÁN D.F., NOVO M., SÁNCHEZ N., DOMÍNGUEZ J., DÍAZ COSÍN D.J. & FERNÁNDEZ R.
750 2020. — Local adaptation fuels cryptic speciation in terrestrial annelids. *Molecular*
751 *Phylogenetics and Evolution* 146: 106767.
752 <https://doi.org/10.1016/j.ympev.2020.106767>
- 753 MATHIEU J. & DAVIES J.T. 2014. — Glaciation as an historical filter of below-ground
754 biodiversity. *Journal of Biogeography* 41 (6): 1204–1214.
755 <https://doi.org/10.1111/jbi.12284>
- 756 MEDECC 2020. — Climate and environmental change in the Mediterranean Basin – Current
757 situation and risks for the future. First Mediterranean Assessment Report. [Cramer,
758 W., Guiot, J., Marini, K. (eds.)] Union for the Mediterranean, Plan Bleu, UNEP/MAP,
759 Marseille. <https://doi.org/10.5281/zenodo.4768833>
- 760 MICHAELSEN W. 1895. — Zur Kenntnis der Oligochaeten. *Abhandlungen und Verhandlungen*
761 *des Naturwissenschaftlichen Vereins, Hamburg* 13: 1–37.
- 762 MICHAELSEN W. 1900. — Oligochaeta. *Das Tierreich* 11: 1–575.
- 763 MICHAELSEN W. 1910. — Die Oligochaeten fauna der vorderindischceylonischen region.
764 *Abdruck Verhandlungen der Naturwissenschaftlichen Vereins, Hamburg* 19 (5): 1–
765 108.
- 766 MICHAELSEN W. 1919. — Über die Beziehungen der Hirudineen zu den Oligochaeten.
767 *Mitteilungen aus dem Naturhistorischen Museum Hamburg* 36: 131–153.

- 768 MISIRLIOĞLU M., REYNOLDS J.W., STOJANOVIĆ M., TRAKIĆ T., SEKULIĆ J., JAMES S.W.,
769 CSUZDI C., DECAËNS T., LAPIED E., PHILLIPS H., CAMERON E. & BROWN G.G. 2023. —
770 Earthworms (Clitellata, Megadrili) of the world: an updated checklist of valid species
771 and families, with notes on their distribution. *Zootaxa*, in press.
- 772 MRŠIĆ N. & ŠAPKAREV J.A. 1988. — Revision of the genus *Allolobophora* Eisen, 1874 (sensu
773 POP 1941) (Lumbricidae, Oligochaeta). *Acta Musei Macedonici Scientiarum*
774 *Naturalium* 19: 1–38.
- 775 NAVARRO A.M., PINADERO S.J., DECAËNS T., HEDDE M., NOVO M., TRIGO D. & MARCHÁN
776 D.F. 2023. — Catch-all no more: integrative systematic revision of the genus
777 *Allolobophora* (Crassiclitellata, Lumbricidae) with the description of two new relict
778 earthworm genera. *Journal of Zoological Systematics and Evolutionary Research*, in
779 press.
- 780 OMODEO P. 1952. — Materiali zoologici raccolti dal Dr. Marcuzzi sulle Alpi Dolomitiche.
781 *Archivio Zoologico Italiano* 37: 29–59.
- 782 OMODEO P. & ROTA E. 2008. — Earthworm diversity and land evolution in three
783 Mediterranean districts. *Proceedings of the California Academy of Sciences. Fourth*
784 *Series* 59 (I–5): 65–83.
- 785 ÖRLEY L. 1881. — A magyarországi Oligochaeták faunája. I. Terricolae. *Mathematikai és*
786 *Természettudományi Közlemények* 16: 562–611.
- 787 PAOLETTI M.G., BLAKEMORE R.J., CSUZDI C., DORIGO L., DREON A.L., GAVINELLI F.,
788 LAZZARINI F., MANNO N., MORETTO E., PORCO D., RUZZIER E., TONIELLO V.,
789 SQUARTINI A., CONCHERI G., ZANARDO M. & ALBA-TERCEDOR J. 2016. — Barcoding
790 *Eophila crodabepis* sp. nov. (Annelida, Oligochaeta, Lumbricidae), a large stripy

- 791 earthworm from Alpine foothills of Northeastern Italy similar to *Eophila tellinii*
792 (Rosa, 1888). *PLOS ONE* 11 (3): e0151799.
793 <https://doi.org/10.1371/journal.pone.0151799>
- 794 PÉREZ-LOSADA M., BREINHOLT J.W., PORTO P.G., AIRA M. & DOMÍNGUEZ J. 2011. — An
795 earthworm riddle: Systematics and phylogeography of the Spanish Lumbricid
796 *Postandrilus*. *PLOS ONE* 6 (11): e28153.
797 <https://doi.org/10.1371/journal.pone.0028153>
- 798 PÉREZ-LOSADA M., RICOY M., MARSHALL J.C. & DOMÍNGUEZ J. 2009. — Phylogenetic
799 assessment of the earthworm *Aporrectodea caliginosa* species complex (Oligochaeta:
800 Lumbricidae) based on mitochondrial and nuclear DNA sequences. *Molecular*
801 *Phylogenetics and Evolution* 52 (2): 293–302.
802 <https://doi.org/10.1016/j.ympev.2009.04.003>
- 803 POPOVIĆ F.J., STOJANOVIĆ M.M., DOMÍNGUEZ J., SEKULIĆ J.M., TRAKIĆ T.B. & MARCHÁN
804 D.F. 2022. — Molecular analysis of five controversial Balkanic species of
805 *Allolobophora* Eisen, 1873 (Lumbricidae, Clitellata) with emendation of the genus
806 *Cernosvitovia* OMODEO, 1956. *Zootaxa* 5116 (3): 351–372.
807 <https://doi.org/10.11646/zootaxa.5116.3.3>
- 808 PREISS E., MARTIN J.-L. & DEBUSSCHE M. 1997. — Rural depopulation and recent landscape
809 changes in a Mediterranean region: Consequences to the breeding avifauna.
810 *Landscape Ecology* 12 (1): 51–61. <https://doi.org/10.1007/BF02698207>
- 811 QIU J.-P. & BOUCHE M.B. 1998AA. — Le genre *Allolobophora* Eisen, 1874 (Oligochaeta:
812 Lumbricidae), ses avatars et sa définition moderne. *Documents Pédozoologiques et*
813 *Intégrologiques* 4 (8): 86–97.

- 814 QIU J.-P. & BOUCHE M.B. 1998b. — *Zophoscolex*, un nouveau genre de Lumbricidae
815 (Annelida: Oligochaeta) d'Iberie et de France. *Documents Pédozoologiques et*
816 *Intégrologiques* 4 (4): 20–36.
- 817 QIU J.-P. & BOUCHE M.B. 1998c. Révision du genre *Proselodrilus* Bouché, 1972
818 (Oligochaeta: Lumbricidae); description de 16 taxons nouveaux pour la science.
819 *Documents Pédozoologiques et Intégrologiques* 4 (5): 37–64.
- 820 QIU J.-P. & BOUCHE M.B. 1998d. — Révision morphologique, chorologique et taxonomique
821 du genre *Scherotheca* Bouché, 1972 (Oligochaeta: Lumbricidae). *Documents*
822 *Pédozoologiques et Intégrologiques* 4 (12): 117–139.
- 823 QIU J.-P. & BOUCHE M.B. 1998e. — *Heraclescolex*, un nouveau genre de Lumbricidae
824 (Annelida: Oligochaeta). *Documents Pédozoologiques et Intégrologiques* 4 (13): 140–
825 152.
- 826 QIU J.-P. & BOUCHE M.B. 1998f. — *Eumenescolex*, un nouveau genre de Lumbricidae
827 (Annelida: Oligochaeta). *Documents Pédozoologiques et Intégrologiques* 4 (1): 3–7.
828 <https://doi.org/10.13140/RG.2.2.21733.24806>
- 829 RAFINESQUE C.S. 1815. — *Analyse de la nature, ou tableau de l'univers et des corps*
830 *organisés*. Self published, Palermo.
- 831 RATNASINGHAM S. & HEBERT P.D.N. 2007. — BOLD: The Barcode of Life Data System
832 (<http://www.barcodinglife.org>). *Molecular Ecology Notes* 7 (3): 355–364.
833 <https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- 834 ROSA D. 1889. — Note sui Lombrichi iberici. *Bollettino dei Musei di Zoologia ed Anatomia*
835 *Comparata della R. Università di Torino* 63 (4): 3.

- 836 ROSA D. 1892. — Descrizione dell'*Allolobophora smaragdina* nuova specie di Lumbricide.
837 *Bollettino dei Musei di Zoologia ed Anatomia Comparata della R. Università di*
838 *Torino* 7 (130): 1–2.
- 839 ROSA D. 1893. — Revisione dei lumbricidi. *Bollettino dei Musei di Zoologia ed Anatomia*
840 *Comparata della R. Università di Torino* 8 (160): 10.
- 841 ROSA D. 1895. — *Allolobophora dugesii* nuova specie di Lumbricide europeo. *Bollettino dei*
842 *Musei di Zoologia ed Anatomia Comparata della R. Università di Torino* 10 (205): 1–
843 3.
- 844 ROTA E. 1994. — Contribution to the taxonomy of the Hormogastridae (Annelida:
845 Oligochaeta) with description of two new species from southern France. *Journal of*
846 *Natural History* 28 (1): 27–36. <https://doi.org/10.1080/00222939400770031>
- 847 ROTA E., SCHEMBRI P.J., OMODEO P. 2017. — Earthworms of Malta (Annelida:
848 Clitellata: Acanthodrilidae, Hormogastridae, Lumbricidae). *Zootaxa* 4311 (2): 287-
849 291. <https://doi.org/10.11646/zootaxa.4311.2.11>
- 850 *Savigny J.-C. & Cuvier G.* 1826. — Analyse des travaux de l'Académie royale des Sciences
851 pendant l'année 1821, partie physique [Zoology from p. 172]. *Mémoires de*
852 *l'Académie (royale) des sciences de l'Institut (imperial) de France*: 176–184.
- 853 SCHWARZ G. 1978. — Estimating the dimension of a model. *The Annals of Statistics* 6 (2):
854 461–464.
- 855 DE SOSA I., DÍAZ COSÍN D.J., CSUZDI C., PAOLETTI M.G. & MARCHÁN D.F. 2019. — Placing
856 *Eophila tellinii* (Oligochaeta, Lumbricidae) in a molecular phylogenetic context

857 advances the century-old controversy around the problematic genus. *European*
858 *Journal of Soil Biology* 94: 103114. <https://doi.org/10.1016/j.ejsobi.2019.103114>

859 SZEDERJESI T., MARCHÁN D.F., CSUZDI C., SARBU S.M., PAVLÍČEK T., KRÍZSIK V., MARTIN P.
860 & DOMÍNGUEZ J. 2022. — Three in one: molecular phylogeny of the genus *Helodrilus*
861 (Crassiclitellata: Lumbricidae) with a description of two new genera and two new
862 species. *Zoological Journal of the Linnean Society*: zlac069.
863 <https://doi.org/10.1093/zoolinnea/zlac069>

864 TAMURA K., STECHER G. & KUMAR S. 2021. — MEGA11: Molecular Evolutionary Genetics
865 Analysis Version 11. *Molecular Biology and Evolution* 38 (7): 3022–3027.
866 <https://doi.org/10.1093/molbev/msab120>

867 TETRY A. 1942. — Description d'une nouvelle forme française de Lombricien : *Eophila*
868 *dugesi* (Rosa) f. *sanaryensis* Tetry. *Revue scientifique* 80 (3210–3211): 323–324.

869 TETRY A. 1944. — *Octolasion calarensis* n. sp. Un nouvel Oligochete Francais. *Bulletin du*
870 *Muséum national d'Histoire naturelle* 2 (16): 179–182.

871 ZICSI A. & CSUZDI C. 1999. — Weitere Angaben zur Regenwurmfauna Frankreichs mit
872 Beschreibung fünf neuer Arten (Oligochaeta: Lumbricidae). *Revue Suisse de Zoologie*
873 106: 983–1003. <https://doi.org/10.5962/bhl.part.80111>

874

