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

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Living specimen of *Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp. Photo: S. Gérard.

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Sylvain GÉRARD
Eco&Sols, INRAE, IRD, CIRAD, SupAgro Montpellier,
Campus SupAgro, Bâtiment 12, 2 place Viala, F-34060 Montpellier cedex 2 (France)
and CEFE, Université de Montpellier, CNRS, EPHE, IRD, 1919, route de Mende, F-34293 Montpellier cedex 5 (France)
sylvain.gerard@ens-paris-saclay.fr, sylvain.gerard57@gmail.com (corresponding author)

Daniel Fernández MARCHÁN
CEFE, Université de Montpellier, CNRS, EPHE, IRD, 1919, route de Mende, F-34293 Montpellier cedex 5 (France)
and Biodiversity, Ecology and Evolution Department, Faculty of Biology,
Universidad Complutense de Madrid, Avenida de Séneca, 2 Ciudad Universitaria E-28040 Madrid (Spain)
danifermch@gmail.com

Alejandro MARTINEZ NAVARRO
Biodiversity, Ecology and Evolution Department, Faculty of Biology, Universidad Complutense de Madrid,
Avenida de Séneca, 2 Ciudad Universitaria E-28040 Madrid (Spain), alejma21@ucm.es

Mickaël HEDDE
Eco&Sols, INRAE, IRD, CIRAD, SupAgro Montpellier,
Campus SupAgro, Bâtiment 12, 2 place Viala, F-34060 Montpellier cedex 2 (France), mickael.hedde@inrae.fr

Thibaud DECAËNS
CEFE, Université de Montpellier, CNRS, EPHE, IRD, 1919, route de Mende, F-34293 Montpellier cedex 5 (France)
thibaud.decaens@cefe.cnrs.fr

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ABSTRACT
Southern France has been highlighted as an important hotspot of earthworm diversity mostly by the work of Marcel Bouché, who sampled more than 1300 localities in mainland France including Corsica in the 1960s. We resampled some of the Bouché's localities and conducted molecular phylogenetic analyses. It leads to the identification of a new Lumbricidae Rafinesque, 1815 genus (*Flabellodrilus* Gérard, Decaëns & Marchán, n. gen.), for which *Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp. is the type species. We propose the new combination *Flabellodrilus bartolii bartolii* (Bouché, 1970) n. comb., improving the clarity of the catch-all genus *Allolobophora* Eisen, 1874. It also allowed us to discover two new species of Lumbricidae (*Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp. and *Allolobophora delitescens* Gérard, Decaëns & Marchán, n. sp.), and one new species of Hormogastridae Michaelsen, 1900 (*Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp.). These three new species underline the great earthworm diversity of southeastern France. Their discovery in a previously well-sampled area further suggests that these species have narrow geographic ranges and small populations. They also seem to be specialized for open habitats that are declining in the French Mediterranean landscape. These different characteristics suggest a relatively high risk of extinction for these three new species.

KEY WORDS
Earthworms, *Allolobophora*, *Vignysa*, France, Europe, new combinations, new species, new genus.

RÉSUMÉ
Le rééchantillonnage des localités historiques de Bouché permet la découverte de trois nouvelles espèces et d'un nouveau genre de vers de terre (Oligochaeta, Hormogastridae et Lumbricidae) dans le sud-est de la France.
Le sud de la France est considéré comme un point chaud de diversité pour les vers de terre, ainsi qu'il a été mis en évidence par le travail de Marcel Bouché, qui a échantillonné plus de 1 300 localités en France métropolitaine incluant la Corse dans les années 1960. Nous avons rééchantillonné certaines de ces localités et réalisé des analyses phylogénétiques moléculaires. Ce travail nous a conduit à identifier un nouveau genre de Lumbricidae Rafinesque, 1815 (*Flabellodrilus* Gérard, Decaëns & Marchán, n. gen.), dont l'espèce type est *Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp. Nous proposons la nouvelle combinaison *Flabellodrilus bartolii bartolii* (Bouché, 1970) n. comb., ce qui apporte plus de clarté pour le genre « fourre-tout » *Allolobophora* Eisen, 1874. Cela nous a également permis de découvrir deux nouvelles espèces de Lumbricidae (*Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp. et *Allolobophora delitescens* Gérard, Decaëns & Marchán, n. sp.), ainsi qu'une nouvelle espèce d'Hormogastridae Michaelsen, 1900 (*Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp.). Ces trois nouvelles espèces soulignent l'importante diversité de vers de terre dans le sud-est de la France. Leur découverte dans une région précédemment bien échantillonnée suggère que ces espèces ont une aire de répartition restreinte et de petites populations. Elles semblent par ailleurs spécialisées dans les habitats ouverts, qui tendent à diminuer dans les paysages méditerranéens français. Ces différentes caractéristiques suggèrent un risque d'extinction relativement élevé pour ces trois nouvelles espèces.

MOTS CLÉS
Vers de terre,
Allolobophora,
Vignysa,
France,
Europe,
combinaisons nouvelles,
espèces nouvelles,
genre nouveau.

INTRODUCTION

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

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

In this study, we describe one new genus (*Flabellodrilus* Gérard, Decaëns & Marchán, n. gen) and two new species of Lumbricidae (*Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp., *Allolobophora delitescens* Gérard, Decaëns & Marchán, n. sp.), and one new species of Hormogastridae (*Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp.) that were discovered during the re-sampling of Bouché's localities in southeastern France.

MATERIAL AND METHODS

Earthworm sampling

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

Morphological descriptions

Ethanol-fixed specimens were firstly studied following a classical morpho-anatomical description workflow. The following characters were used to describe the external morphology: body shape, body pigmentation, body length (after ethanol fixation), body mass, diameter (preclitellar, clitellar and postclitellar regions), number of segments, type of prostomium, arrangement of setae, position of clitellum, position of genital markings, position and shape of tubercula pubertatis, position of male pores, position of ovipores, spermathecal pores and nephridial pores. A few specimens of each species were dissected, and their internal anatomy was described using the following characters: thickness of the septa, position of gizzard, position of crop, position and shape of calciferous

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

Species	Location	Coordinates	Code *in* Bouché (1972)	Habitat	Other species in the sample
Flabellodrilus luberonensis Gérard, Decaëns & Marchán, n. gen., n. sp.	Vaucluse department, Saint-Saturnin-les-Apt	43°57'46"N, 5°20'13"E	ECORDRE_0527	Mediterranean shrubland (garrigue)	*Aporrectodea balisa* (Bouché, 1972) *Aporrectodea rubra* (Védovini, 1969) *Aporrectodea trapezoides* (Dugès, 1828) *Octolasion cyaneum* (Savigny, 1826)
Allolobophora delitescens Gérard, Decaëns & Marchán, n. sp.	Var department, Callas	43°34'22"N, 6°31'48"E	ECORDRE_0496	Mediterranean grassland in an old olive grove	*Aporrectodea caliginosa* (Savigny, 1826) *Aporrectodea rubra acidicola* (Bouché, 1972) *Flabellodrilus bartolii bartolii* (Bouché, 1970) n. comb. *Octolasion cyaneum* (Savigny, 1826) *Scherotheca rhodana* (Bouché, 1972)
Vignysa callasensis Gérard, Decaëns & Marchán, n. sp.	Var department, Callas	43°35'13"N, 6°32'16"E	ECORDRE_0503	Riparian grassland	*Allolobophora chlorotica* (Savigny, 1826) *Aporrectodea caliginosa* (Savigny, 1826) *Aporrectodea rosea* (Savigny, 1826) *Scherotheca porotheca* (Bouché, 1972) *Scherotheca rhodana* (Bouché, 1972)

glands, position of œsophagus-intestine transition, position and shape of typhlosole, position of hearts, shape of nephridia, type of testis sacs, position and shape of seminal vesicles, position and shape of spermathecae.

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

DNA AND PHYLOGENETIC ANALYSES

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

Sequences were aligned with MAFFT v.7 (Katoh & Standley 2013) with default settings and concatenated with BioEdit (Hall 1999), resulting in a matrix of 3 210 base pairs for each species. Sequences reported by Domínguez *et al.* (2015), Pérez-Losada *et al.* (2009, 2011), Paoletti *et al.* (2016), de Sosa *et al.* (2019) and Marchán *et al.* (2020b), including representatives of most of the Lumbricini Rafinesque-Schmaltz, 1815 (*sensu* Marchán *et al.* 2022) genera were downloaded from GenBank and used as a reference dataset. The species included are listed in the tree in Appendix 1.

All the DNA sequences obtained in this study are available in GenBank, under accession numbers 28s (OR887215, OR887216), 16s (OR887217, OR887218), 12s (OR887219, OR887220), ND1 (OR886083, OR886084). COI sequences (new and datamined from GenBank), together with metadata, are publicly available in the dataset DS-EWNSPSG (https://doi.org/10.5883/DS-EWNSPSG) in the Barcode of Life Datasystem (BOLD, Ratnasingham & Hebert 2007).

In order to perform phylogenetic analyses, the best fitting evolutionary model for each partition was selected with jModelTest v. 2.1.3 (Darriba *et al.* 2012) by applying the Akaike information criterion (AIC; Akaike 1973) and the Bayesian information criterion (BIC; Schwarz 1978). The best-fitting evolutionary models were GTR+I+G for COI, 28S, and ND1, GTR+G for 12S, and HKY+I+G were chosen for 16S. Parameters were set to 50 million generations and sampled every 5000th generation (10 000 trees). Two independent runs each with four chains were performed and 20% of the trees were discarded as burn-in. The remaining trees were combined and summarized on a 50% majority-rule consensus tree. Clade support values over 70% (Bootstrap values) and 90% (Posterior probabilities) were considered high. Uncorrected average pairwise distances between the studied species for the molecular markers COI were calculated in MEGA 11 (Tamura *et al.* 2021) in order to support their status as separate species.

SPECIES DESCRIPTIONS

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

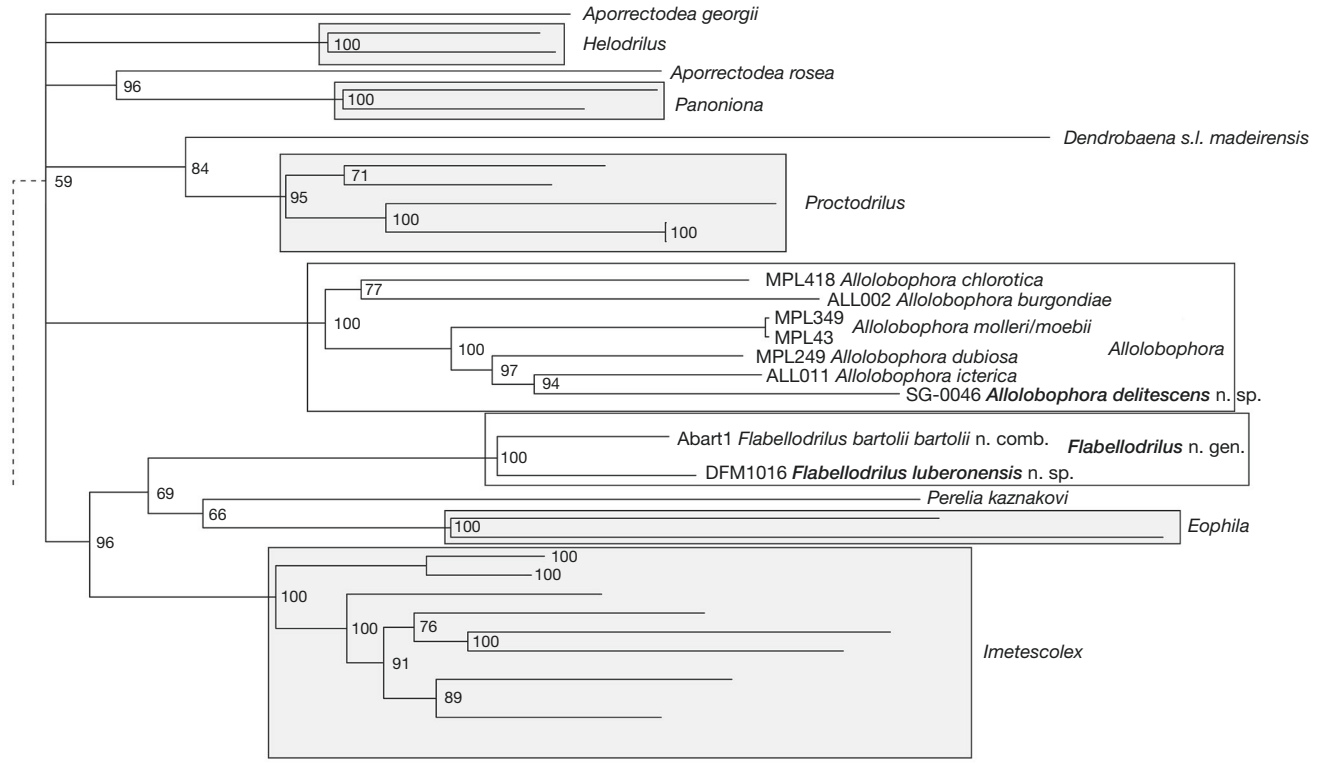

FIG. 1. — Multilocus phylogenetic tree focused on *Allolobophora*-related Lumbricidae Rafinesque, 1815 genera (the full phylogenetic tree is shown in Appendix 1). The tree was obtained from Bayesian inference based on the concatenated sequences of the COI-16S-ND1-12S-28S molecular markers. Posterior probability values are shown beside nodes. White boxes show target genera while grey boxes indicate closely related genera (species labels shown in Appendix 1).

ABBREVIATIONS

Eco&Sols	Eco&Sols collection, Montpellier;
MNHN	Muséum national d'Histoire naturelle, Paris.

RESULTS

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

Some individuals collected in Callas (Var) and assigned to the genus *Allolobophora* based on their morphology, appeared clearly separated from other species in the genus as highlighted by the position of the specimen SG-0046 in Figure 1. This species, which we describe under the name *Allolobophora delitescens* Gérard, Decaëns & Marchán, n. sp., is closely related to *Allolobophora icterica* Savigny, 1826 in the reconstructed phylogeny.

Another specimen from a second set of individuals initially assigned to *Allolobophora* (i.e., DFM-1016) appeared closely related to *Allolobophora bartolii bartolii* Bouché, 1972, although different enough to be considered as belonging to a separate species (Fig. 1). These two sister species form a clade which is separated enough from its nearest neighbors to be considered as a distinct genus. We propose here to describe this new genus under the name *Flabellodrilus* Gérard, Decaëns & Marchán, n. gen. We describe the newly discovered species under the name *Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp. and we make it the type species of *Flabellodrilus* Gérard, Decaëns & Marchán, n. gen. We also propose the new combination *Flabellodrilus bartolii bartolii* (Bouché, 1970) n. comb.The moderately low support for the nodes connecting *Flabellodrilus* n. gen., *Perelia* Easton, 1983 (represented by *Perelia kaznakovi* (Michaelsen, 1910)) and *Eophila* Rosa, 1893 makes it complicated to know the exact relative position of these genera, but they appear to belong to a well-supported clade together with *Imetescolex* Szederjesi, Marchán & Csuzdi, 2022 *in* Szederjesi *et al.*, 2022 and clearly separated from *Allolobophora* (*sensu stricto*) as defined by Bouché (1972).

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

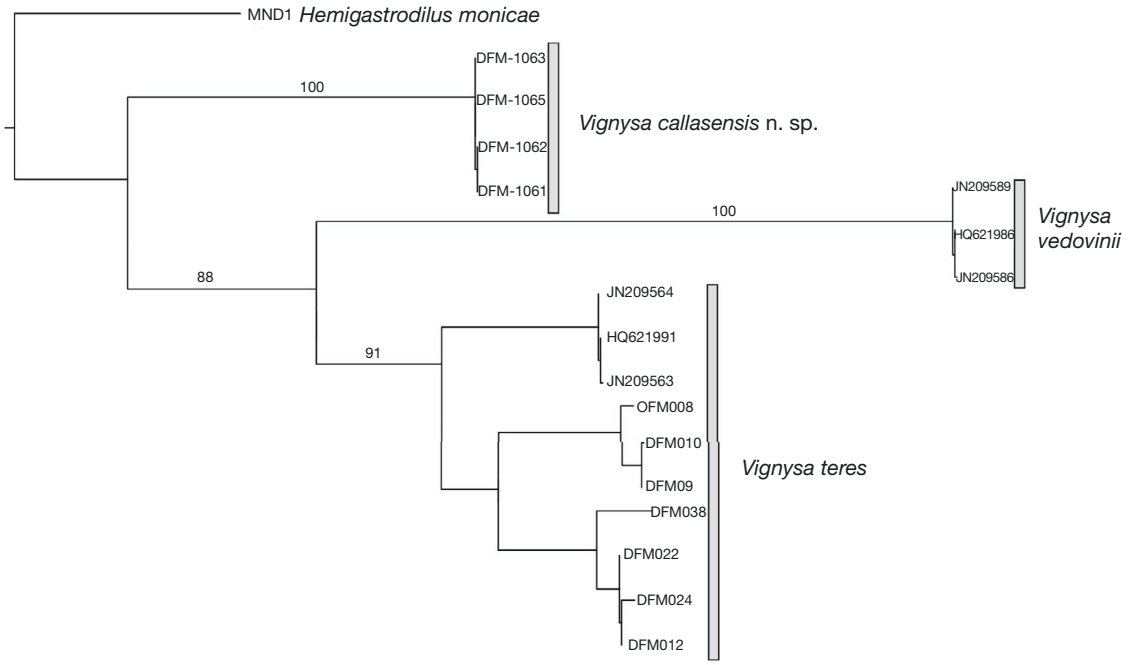

FIG. 2. — DNA barcode tree of the genus *Vignysa* Bouché, 1970. The tree was obtained from Bayesian inference based on the sequences of COI barcodes. Posterior probability values are shown above branches. Grey bars delimit individuals belonging to each species.

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

	A. chlorotica	*A. dubiosa*	*A. molleri*	*A. burgondiae*	*A. icterica*	*A. delitescens* n. sp.	*F. bartolii bartolii* n. comb.	*F. luberonensis* n. sp.	*E. gestroi*	*E. tellinii*	*P. kaznakovi*
Allolobophora chlorotica (Savigny, 1826)	–	–	–	–	–	–	–	–	–	–	–
Allolobophora dubiosa (Örley, 1881)	18.0	–	–	–	–	–	–	–	–	–	–
Allolobophora molleri Rosa, 1889	19.0	15.0	–	–	–	–	–	–	–	–	–
Allolobophora burgondiae Bouché, 1972	19.0	18.7	17.7	–	–	–	–	–	–	–	–
Allolobophora icterica (Savigny, 1826)	18.3	16.0	16.5	16.9	–	–	–	–	–	–	–
Allolobophora delitescens Gérard, Decaëns & Marchán, n. sp.	17.1	15.0	15.8	18.5	16.0	–	–	–	–	–	–
Flabellodrilus bartolii bartolii (Bouché, 1970) n. comb.	20.5	18.3	17.5	19.7	18.3	18.3	–	–	–	–	–
Flabellodrilus luberonensis Gérard, Decaëns & Marchán, n. gen., n. sp.	19.9	17.4	20.6	19.1	18.2	19.4	12.4	–	–	–	–
Eophila gestroi (Cognetti, 1905)	19.8	20.0	17.9	18.0	20.3	19.5	16.3	16.7	–	–	–
Eophila tellinii (Rosa, 1888)	19.1	20.0	20.9	20.3	19.8	19.5	17.5	17.7	17.8	–	–
Perelia kaznakovi (Michaelsen, 1910)	18.5	20.5	21.5	19.7	19.8	20.1	16.8	18.1	16.8	15.8	–

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

TABLE 3. – Uncorrected average pairwise distances (in percentage) calculated for the COI barcodes between the newly described Hormogastridae Michaelsen, 1900 species and their closest relatives.

	V. teres	*V. callasensis* n. sp.	*V. vedovinii*
Vignysa teres (Dugès, 1828)	10.0	–	–
Vignysa callasensis Gérard, Decaëns & Marchán, n. sp.	18.5	0.0	–
Vignysa vedovinii Rota, 1994	19.6	20.0	0.0

TAXONOMY

Phylum ANNELIDA Lamark, 1802
Class CLITELLATA Michaelsen, 1919
Sub-class OLIGOCHAETA Grube, 1850
Order CRASSICLITELLATA Jamieson, 1988
Family LUMBRICIDAE Rafinesque, 1815

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

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TYPE SPECIES. — *Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp.

ETYMOLOGY. — The genus name is derived from the fan-shaped clitellum of the two species currently attributed to this genus (flabellum, a: fan).

DIAGNOSIS. — Medium-sized worms with faint brown pigmentation (sometimes absent) and mid-segmental dark dots in the cephalic region. Prostomium epilobous, no transversal furrows. Setae closely paired. Male pores in 1/2 XV with well-developed porophores. Spermathecal pores in 9/10, 10/11, double (rarely in (8/9)9/10-12/13, simple or double). Nephridial pores aligned. Clitellum moderately posterior between XXXII and XLIV. Calciferous glands in X-XIV with diverticula in X. Typhlosole with four lamellae. Spermathecae double in X and XI, globular and intracoelomic (rarely simple or double in (IX)X-XIII). Two pairs of seminal vesicles in XI-XII. Nephridial bladders sigmoid with a sub-terminal constriction followed by a loop.

DIFFERENTIAL DIAGNOSIS. — *Flabellodrilus* Gérard, Decaëns & Marchán, n. gen. can be differentiated from closely related genera by some morpho-anatomical characters. It differs from *Allolobophora* by the more anterior position of the clitellum, pigmentation (faint brown with pigmentary dots in *Flabellodrilus* Gérard, Decaëns & Marchán, n. gen. vs frequently green in *Allolobophora*), repetition of spermathecae (double vs simple), number of seminal vesicles (two pairs in XI and XXII vs four pairs in IX to XII) and shape of nephridial bladders (sigmoid with subterminal constriction vs U-shaped). It differs from *Panoniona* Mršić & Šapkarev, 1988 by the more posterior position of the clitellum, pigmentation (faint brown vs absent), repetition of spermathecae (double vs double-multiple) and shape of nephridial bladders (sigmoid with subterminal constriction and loop vs sigmoid with subterminal constriction and bag-like distension). *Flabellodrilus* Gérard, Decaëns & Marchán, n. gen. differs from *Eophila* by its generally smaller size, its pigmentation (faint brown with pigmentary dots vs purplish-brown in bands or light grey) and repetition of spermathecae (double vs simple), and from *Imetescolex*, *Helodrilus* and *Proctodrilus* by the presence of nephridial bladders in all segments (absent in the latter genera). Finally, the loosely defined genus *Perelia* is similar to *Flabellodrilus* Gérard, Decaëns & Marchán, n. gen. in the shape of their nephridial bladders, but they differ in their pigmentation (pigmentary dots not documented in *Perelia*) and in the repetition of their spermathecae (double vs simple).

INCLUDED SPECIES. — *Flabellodrilus bartolii bartolii* (Bouché, 1970) n. comb. (Bouché, 1972: 454); *Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp.

DIVERSITY AND DISTRIBUTION. — The genus *Flabellodrilus* Gérard, Decaëns & Marchán, n. gen. is composed of two species distributed in the Provence sedimentary basin, at the east of the Rhône river, and in the external Alps (Barronies and Nice Prealps).

REMARKS

Flabellodrilus bartolii bartolii (Bouché, 1970) n. comb. and *Flabellodrilus bartolii meougensis* (Bouché, 1970) n. comb. are new combinations, as they were previously assigned to *Allolobophora*. Their morphology is compatible with the diagnosis of the new genus. The subspecies *Allolobophora bartolii meougensis* (Bouché, 1970) is significantly different from *Flabellodrilus bartolii bartolii* (Bouché, 1970) n. comb. in the position of the clitellum and position and repetition of spermathecae (8/9-12/13 vs 9/10-10/11, simple vs double). It thus appears likely that it constitutes a separate species from *F. bartolii bartolii* n. comb. In the absence of detailed morpho-anatomical analysis and molecular data, we conservatively maintain this subspecies as *Flabellodrilus bartolii meougensis* (Bouché, 1970) n. comb.

Flabellodrilus luberonensis
Gérard, Decaëns & Marchán, n. sp.
(Figs 3; 4)

urn:lsid:zoobank.org:act:7ACF81A1-FE52-4CB4-AC8D-9081EB9A5CB9

TYPE MATERIAL. — **Holotype**. **France** • 1 adult specimen; Provence-Alpes-Côte d'Azur, Vaucluse, D943, 84490 Saint-Saturnin-les-Apt, in the soil; 43°57'46"N, 5°20'13"E; 434 m a.s.l.; 25.XI.2021; T. Decaëns, D. F. Marchán leg.; MNHN (BOLD Sample ID: DFM-1016).
Paratypes. France • 2 adult specimens; same data as holotype; Eco&Sols (BOLD Sample ID: DFM-1017, DFM-1020) • 2 adult specimens; same data as holotype; MNHN (BOLD Sample ID: DFM-1018, DFM-1019).
Other material. France • 8 sub-adult specimens; same data as holotype; Eco&Sols.

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

ECOLOGY. — *F. luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp. was found in a Mediterranean shrubland (garrigue) soil at low elevation (434 m a.s.l.).

DISTRIBUTION. — *F. luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp. is only known from the type locality, near the city of Saint-Saturnin-les-Apt, between the massif of Luberon and the Vaucluse mountains in the Vaucluse department (Provence-Alpes-Côte d'Azur, France) (Fig. 5). It is located in the Luberon Regional Natural Park (Parc naturel régional du Luberon).

DESCRIPTION

External morphology (Fig. 3A, B)

Body shape cylindrical. Body pigmentation absent, mid-segmental dark dots in the cephalic region. Average body length after ethanol fixation: 80 mm (range: 70 to 100 mm; n = 3 adult specimens; holotype : 100 mm). Average body mass: 1.163 g (range: 0.855 to 1.398 g; n = 3; holotype: 1.398 g). Average diameter: 4.6 mm in the preclitellar region (range: 4.2 to 5.4 mm; n = 5; holotype: 5.4 mm), 5.8 mm in the clitellum (range: 5.2 to 6.8 mm; n = 5; holotype: 6.8 mm), 4.6 mm in the postclitellar region (range: 4.2 to 5.2 mm; n = 5; holotype: 4.7 mm). Average number of segments: 283 (range: 187 to353; n = 3; holotype: 309).

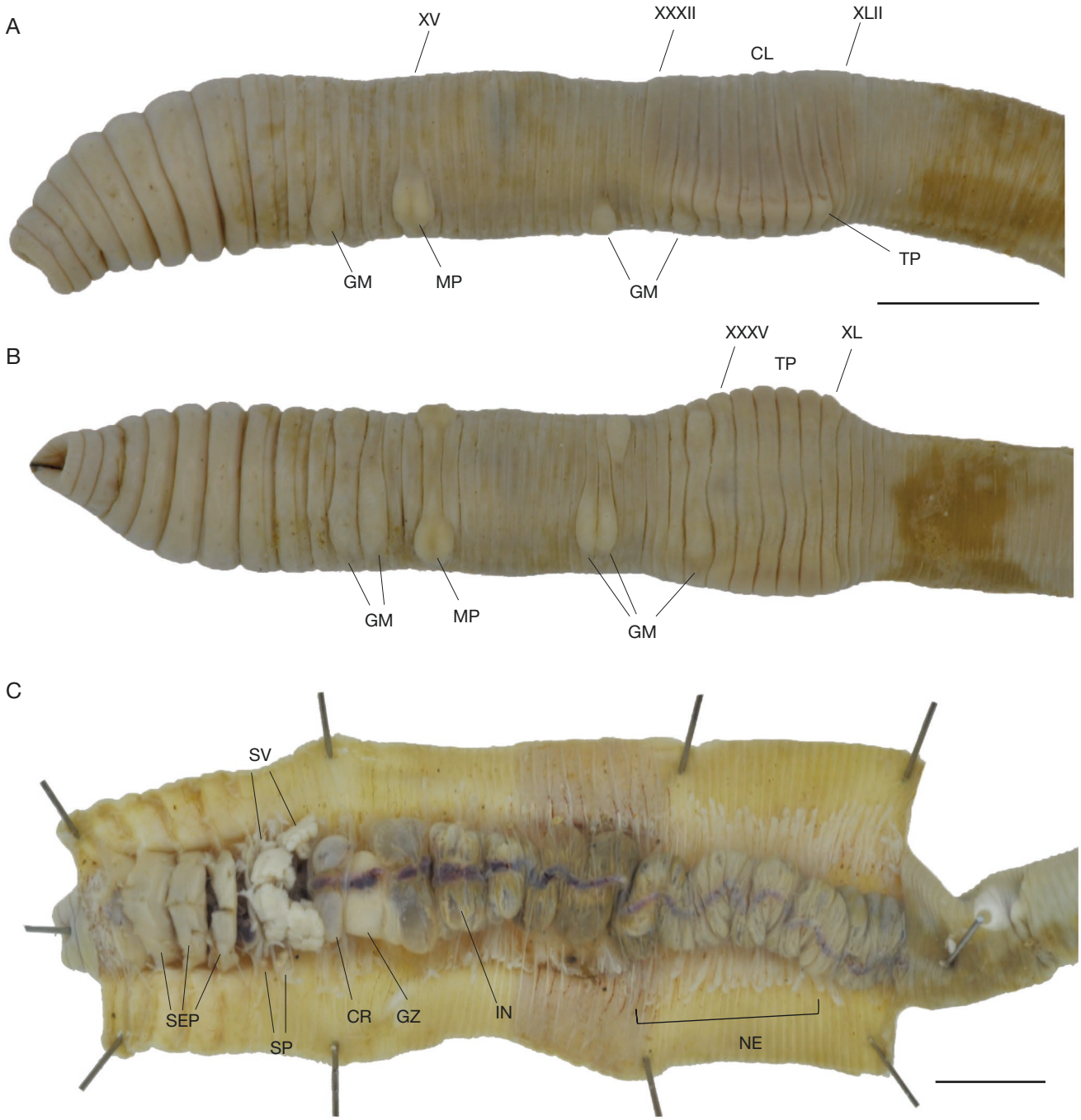

FIG. 3. — *Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp.: **A**, external view of the anterior body; **B**, lateral view of the anterior body; **C**, dissection of the anterior body. Abbreviations: **CL**, clitellum, **CR**, crop, **GM**, genital marks, **GZ**, gizzard, **IN**, intestine, **MP**, male pore, **NE**, nephridia, **SEP**, septa, **SP**, permathecae, **SV**, seminal vesicles, **TP**, tubercula pubertatis. Photos: T. Decaëns. Scale bars: 5 mm.

Prostomium of closed epilobic type. Setae closely paired. Setal arrangement: aa:ab:bc:cd:dd = 14:2:8:1:32. Clitellum in XXXII-XLII (XLIII). Genital markings in XI-XII, randomly unpaired in XXVI-XXVIII, intraclitellar in XXXIV, in ab. Tubercula pubertatis: protruding band in XXXV-XL. Male pores: one pair in XV. Ovipores: one pair in 1/2 XIV, at 1 × ab dorsally from b. Spermathecal pores not visible. Nephridial pores not visible.

Internal anatomy (Figs 3C; 4)

Septa: thickened from 5/6 to 9/10, otherwise membranous. Crop in XV-XVI. Muscular gizzard in XVII-XVIII followed by a membranous pouch in XIX, with an average size (width × length) of 3.55 × 2.10 mm. Calciferous glands: in X-XIV, forming a pair of spherical lobes in X. Œsophagus-intestine transition in XV. Typhlosole starts in XX, forming four folded lamellae. Hearts: in VI-XI. Excretory apparatus: one pair

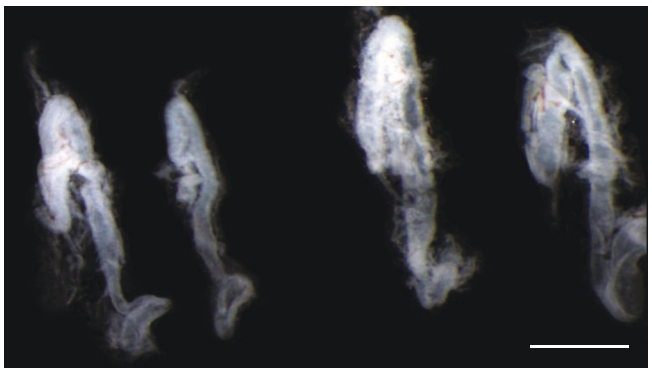

Fig. 4. — Pre-clitellar nephridia of *Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp. Scale bar: 1 mm. Photo: D. F. Marchán.

of holonephridia per segment, nephridial vesicles sigmoid with a sub-terminal constriction followed by a loop (Fig. 4). Seminal vesicles: two pairs in XI-XII, large and lobulated. Spermathecae: two pairs in X-XI, intracoelomic, sessile and double (Fig. 3C).

Remarks

This species can be distinguished from its closest relative *F. bartolii bartolii* (Bouché, 1970) n. comb. by the position of its clitellum and tubercula pubertatis (Table 4) and by their remarkably high genetic distance (12.14% uncorrected pairwise COI distance).

Genus *Allolobophora* Eisen, 1874

Type species. — *Enterion chloroticum* Savigny, 1826: 182.

Diagnosis. — Small-to-medium-sized species with green pigmentation (sometimes absent). Prostomium epilobous, no transversal furrows. Setae closely paired. First dorsal pore in 4/5 (rarely 3/4, 5/6, 7/8). Male pores in 1/2 XV with well-developed porophores. Presence of spermatophores. Spermathecal pores in variable position and number between 7/8 and 10/11, simple. Nephridial pores irregularly distributed (*en solfège*). Clitellum moderately posterior to extremely posterior, starting between XXVIII and LXXIII and ending between XXXVI and LXXVIII. Calciferous glands in X-XV with diverticula in X. Typhlosole usually trifid (sometimes bifid or with 4 lamellae). Variable number of simple spermathecae, usually three or four pairs. Four pairs of seminal vesicles in IX-XII. Nephridial bladders U-shaped (incurvate and reclinate or proclinate).

Included species. — *Allolobophora chlorotica* (Savigny, 1826: 182); *Allolobophora burgondiae* Bouché, 1972: 272; *Allolobophora icterica* (Savigny, 1826: 182); *Allolobophora molleri* Rosa, 1889: 3, *Allolobophora moebii* Michaelsen, 1895, *Allolobophora dubiosa* (Örley, 1881: 603); *Allolobophora delitescens* Gérard, Decaëns & Marchán, n. sp.

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

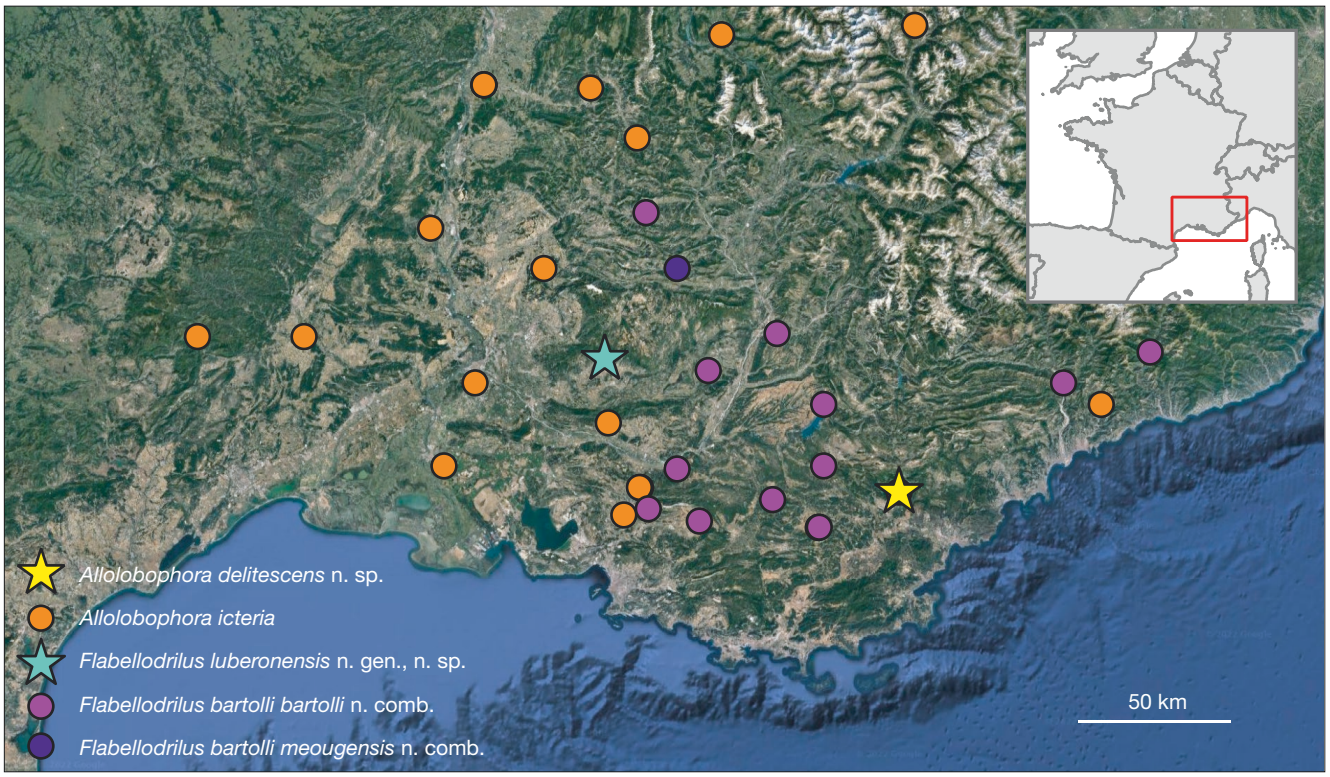

Fig. 5. — Distribution of newly described Lumbricidae species, *Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp. and *Allolobophora delitescens* Gérard, Decaëns & Marchán, n. sp. (**stars**), and their closest relatives (**circles**) in Southern France. All species within the genus *Flabellodrilus* Gérard, Decaëns & Marchán, n. gen. are represented. Credits: Google 2022.

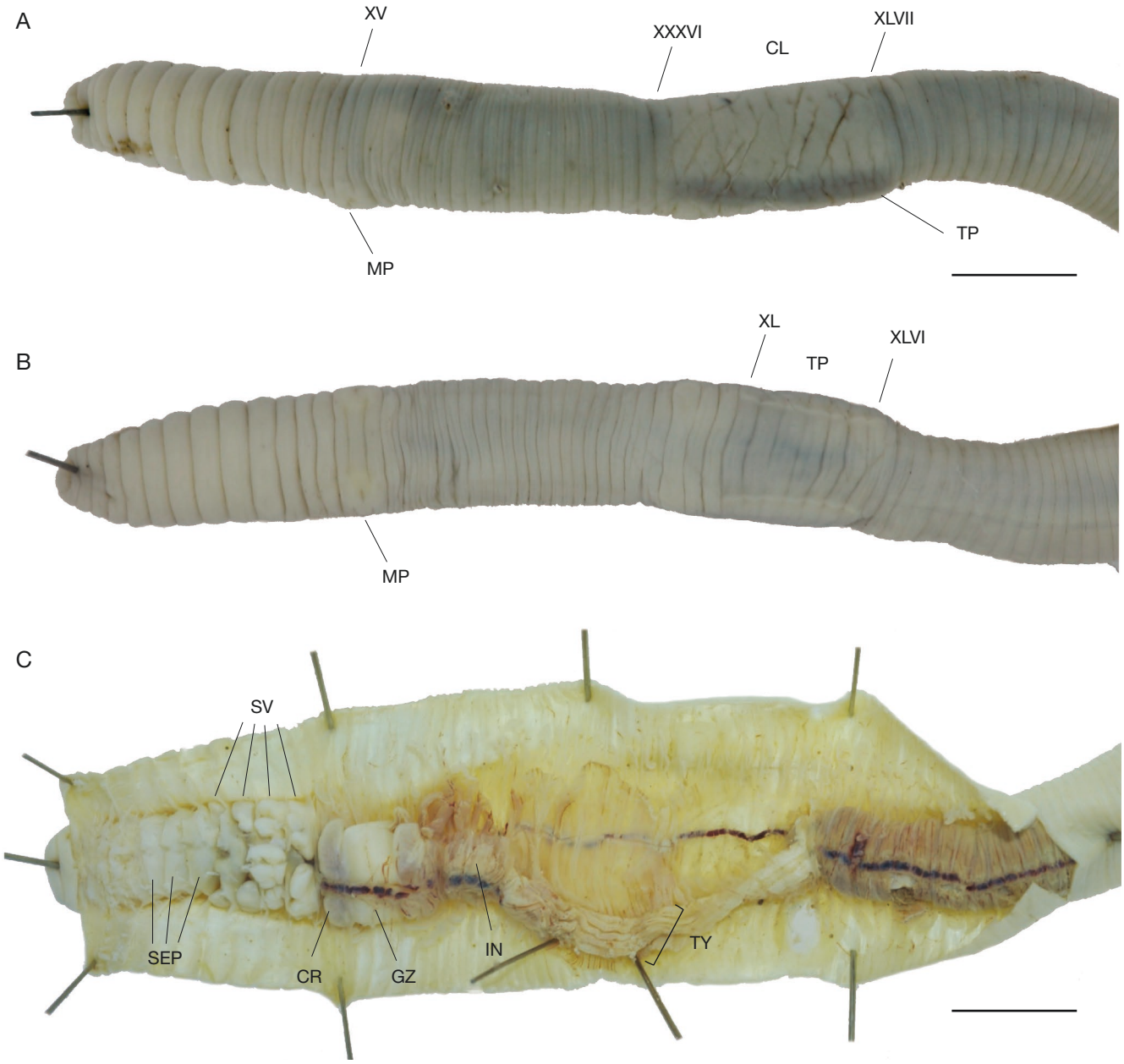

FIG. 6. — *Allolobophora delitescens* Gérard, Decaëns & Marchán, n. sp.: **A**, external view of the anterior body; **B**, lateral view of the anterior body; **C**, dissection of the anterior body. Abbreviations: **CL**, clitellum, **CR**, crop, **GM**, genital marks, **GZ**, gizzard, **IN**, intestine, **MP**, male pore, **SEP**, septa, **SV**, seminal vesicles, **TP**, tubercula pubertatis, **TY**, typhlosole. Scale bars: 5 mm. Photos: T. Decaëns.

Allolobophora delitescens
Gérard, Decaëns & Marchán, n. sp.
(Figs 6; 7)

urn:lsid:zoobank.org:act:85A16708-ADFF-4E67-AE80-B317E0E19FDD

TYPE MATERIAL. — **Holotype**. **France** • 1 adult specimen; Provence-Alpes-Côte d'Azur, Var, 83830 Callas, in the soil; 43°34'22"N, 6°31'48"E; 305 m a.s.l.; 28.XI.2021; T. Decaëns, D. F. Marchán, S. Gérard, R. Della Vedova leg.; MNHN (BOLD Sample ID: SG-0024). **Paratypes. France** • 1 adult specimen; same data as holotype; Eco&Sols (BOLD Sample ID: SG-0046) • 1 sub-adult specimen; MNHN (BOLD Sample ID: SG-0047).

ETYMOLOGY. — The species name is derived from the present participle of the latin verb *delitesco*, *is*, *ere*, which can be translated to the intransitive verb "to hide". This is a reference to the fact that Marcel Bouché did not find this species despite his sampling in 1968 at the type locality.

ECOLOGY. — *A. delitescens* Gérard, Decaëns & Marchán, n. sp. was found in a Mediterranean grassland, previously an olive tree orchard, surrounded by pine forests, at a low elevation (305 m a.s.l.).

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

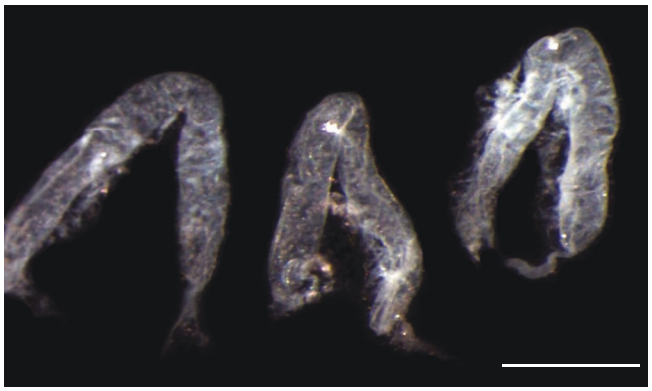

FIG. 7. — Pre-clitellar nephridia of *Allolobophora delitescens* Gérard, Decaëns & Marchán, n. sp. Scale bar: 1 mm. Photo: D. F. Marchán.

DESCRIPTION

External morphology (Fig. 6A, B)

Body shape cylindrical. Body pigmentation absent. Average body length after ethanol fixation: 85 mm (range: 72 to 98 mm; n = 2 adult specimens; holotype: 98 mm). Average body mass: 0.918 g (range: 0.639 to 1.197 g; n = 2; holotype: 1.197 g). Average diameter in the preclitellar region: 4.7 mm (range: 4.6 to 4.7 mm; n = 2; holotype: 4.7 mm), 5.0 mm in the clitellum (range: 4.9 to 5.0 mm; n = 2: holotype: 5.0 mm), 4.5 mm in the postclitellar region (range: 4.1 to 4.8 mm; n = 2; holotype: 4.8 mm). Average number of segments: 201 (range: 200 to 202; n = 2; holotype: 202; 1 subadult specimen with 211 segments). Prostomium of closed epilobous type. Setae closely paired. Setal arrangement aa:ab:bc:cd:dd = 11:1:6:1:29. Clitellum in (XXXV) XXXVI–(XLVI) XLVII. Genital markings in intraclitellar in XXXVII–(XXXVIII) XXXIX. Tubercula pubertatis: thin band in XL-XLVI. Male pores: one pair in XV. Ovipores: one pair in 1/2 XIV, at 1 × ab dorsally from b. Spermathecal pores not visible. Nephridial pores not visible.

Internal anatomy (Figs 6C; 7)

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

REMARKS

Allolobophora delitescens Gérard, Decaëns & Marchán, n. sp. can be distinguished from its closest relatives *A. icterica* and *A. dubiosa* by the position of the clitellum and tubercula pubertatis, by the type of typhlosole, and by the absence of pigmentation and the smaller size in the latter case (Table 4).

Family HORMOGASTRIDAE Michaelsen, 1900

Genus *Vignysa* Bouché, 1970

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

DIAGNOSIS. — Small-to-medium-sized species without cutaneous pigmentation. Prostomium prolobous. Transversal furrows on segments I-II. Setae closely paired. Male pores in 15/16 with well-

TABLE 4. — Main morphological characters distinguishing the newly described species *Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp., *Allolobophora delitescens* Gérard, Decaëns & Marchán, n. sp. and their closest relatives *Flabellodrilus bartolii bartolii* (Bouché, 1970) n. comb., *Allolobophora icterica* (Savigny, 1826), *Allolobophora dubiosa* (Örley, 1881), *Allolobophora monchicana* Trigo, Mascates, Briones and Diaz Cosin, 1990.

Characters	*Flabellodrilus luberonensis* n. sp.	*Flabellodrilus bartolii bartolii* n. comb.	*Allolobophora delitescens* n. sp.	*Allolobophora icterica*	*Allolobophora dubiosa*	*Allolobophora monchicana*
Length	70-100 mm	60-120 mm	70-98 mm	70-90 mm	120-250 mm	50-117 mm
N. segments	187-353	280-394	200-211	140-200	120-303	130-158
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	0.74-0.96 g
Pigmentation	Absent, dark spots	Brown-yellow, dark spots	Absent	Absent	Dark green to greenish brown	Absent
Papillae	XI-XII, XXVI-XXVIII, XXXIV	X, XI, XXXIII-XLIV	XXXVII, (XXXVIII), XXXIX	XI, XLIV, XLV	Unknown	XXII, XLVII, XLVIII
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	(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)	(XXXVII)XXXVIII(XXXIX)-XLVII(XLVIII,XLIX,L)
Tubercula pubertatis	XXXV-XL	(XXXV) XXXVI-XLI	XL-XLVI	(XXXV) XXXVI-XLII (XLIII)	(XLIII) XLIV-XLVII (XVIII)	(XXXIX)XL(XLI)-XLVI(XLVII,XLVIII,XLIX,L)
Typhlosole	Four lamellae	Four lamellae	Five lamellae	Bifid	Bifid	Bifid
Nephridial bladders	Sigmoid, bag-like distension	Sigmoid, bag-like distension	U-shaped	U-shaped	U-shaped	U-shaped
Seminal vesicles	XI, XII	XI, XII	IX-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	Simple in (8/9), 9/10, 10/11

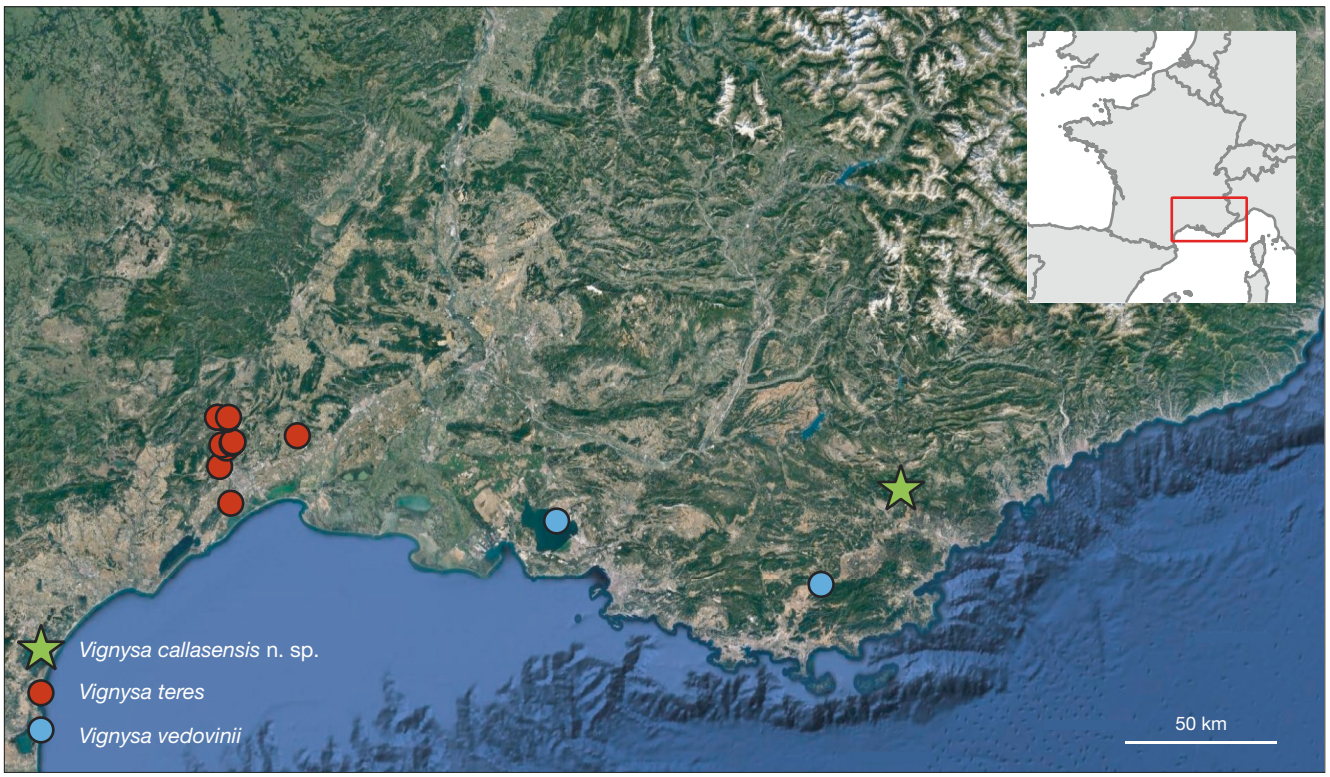

Fig. 8. — Distribution of *Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp. (**star**) and its closest relatives (**circles**) in Southern France. All species of the genus *Vignysa* Bouché, 1970 are represented. Credits: Google 2022.

developed porophores. Spermathecal pores in 9/10, 10/11, simple. Nephridial pores aligned. Clitellum between XIV and XXIX (1/2 XXX). Two gizzards in VI-VII. Typhlosole lyre- or Y-shaped. Two pairs of spermathecae, disc-shaped or tubular. Two pairs of seminal vesicles in XI-XII. Nephridial bladders fish-hook shaped with caeca from the first segments.

Included species. — *Vignysa teres* (Dugès, 1828: 289); *Vignysa vedovinii* Rota, 1994: 27; *Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp.

Diversity and distribution. — This genus currently comprises three species occurring in Southeastern France, from Montpellier (Hérault, Occitanie) to the north of Fréjus (Var, Occitanie), and from the Mediterranean Sea to the 44th north parallel (Fig. 8).

Vignysa callasensis
Gérard, Decaëns & Marchán, n. sp.
(Figs 9; 10; 11)

urn:lsid:zoobank.org:act:CF80AC3C-631B-4AE4-A58D-83632F1541B1

Type material. — **Holotype. France** • 1 adult specimen; Provence-Alpes-Côte d'Azur, Var, 83830 Callas, in the soil; 43°35'13"N, 6°32'16"E; 340 m a.s.l.; 28.XI.2021; T. Decaëns, D. F. Marchán, S. Gérard, R. Della Vedova leg.; MNHN (BOLD Sample ID: DFM-1062).
Paratypes. France • 4 adult specimens; same data as holotype; Eco&Sols (BOLD Sample ID: DFM-1061, DFM-1065, SG-0057, SG-0058) • 4 specimens; same data as holotype; MNHN (BOLD Sample ID: DFM-1064, DFM-1063; SG-0059, SG-0060).

Other material. — **France** • 10 adult and 11 sub-adult specimens; same data as holotype; Eco&Sols.

Etymology. — The name of the species is derived from the city of Callas in the Var department (Provence-Alpes-Côte d'Azur, France) where the type specimens were found.

Ecology. — *Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp. was found in a riparian grassland near La Risse stream, at a low elevation (340 m a.s.l.).

Distribution. — *Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp. was found near the city of Callas, in the sedimentary basin North to Esterel, in the Var department (Provence-Alpes-Côte d'Azur, France).

Description
External morphology (Fig. 9A, B)
Body shape cylindrical. Body pigmentation absent. Gut content visible by transparency. Average body length after ethanol fixation: 95 mm (range: 82 to 150 mm; n = 9 adult specimens; holotype: 100 mm). Average body mass: 0.984 g (range: 0.850 to 1.260 g; n = 11; holotype: 1.260 g). Average diameter: 4.0 mm in the preclitellar region (range: 3.5 to 4.8 mm; n = 11; holotype: 4.8 mm), 4.5 mm in the clitellum (range: 4.0 to 5.4 mm; n = 11; holotype: 5.3 mm), 4.9 mm in the postclitellar region (range: 4.0 to 5.5 mm; n = 11: holotype: 5.5 mm). Average number of segments: 162 (157 to 167; n = 7; holotype: 157). Prostomium of prolobous type. Setae closely paired. Setal arrangement aa:ab:bc:cd:dd = 18:2:8:1:25. Clitellum in

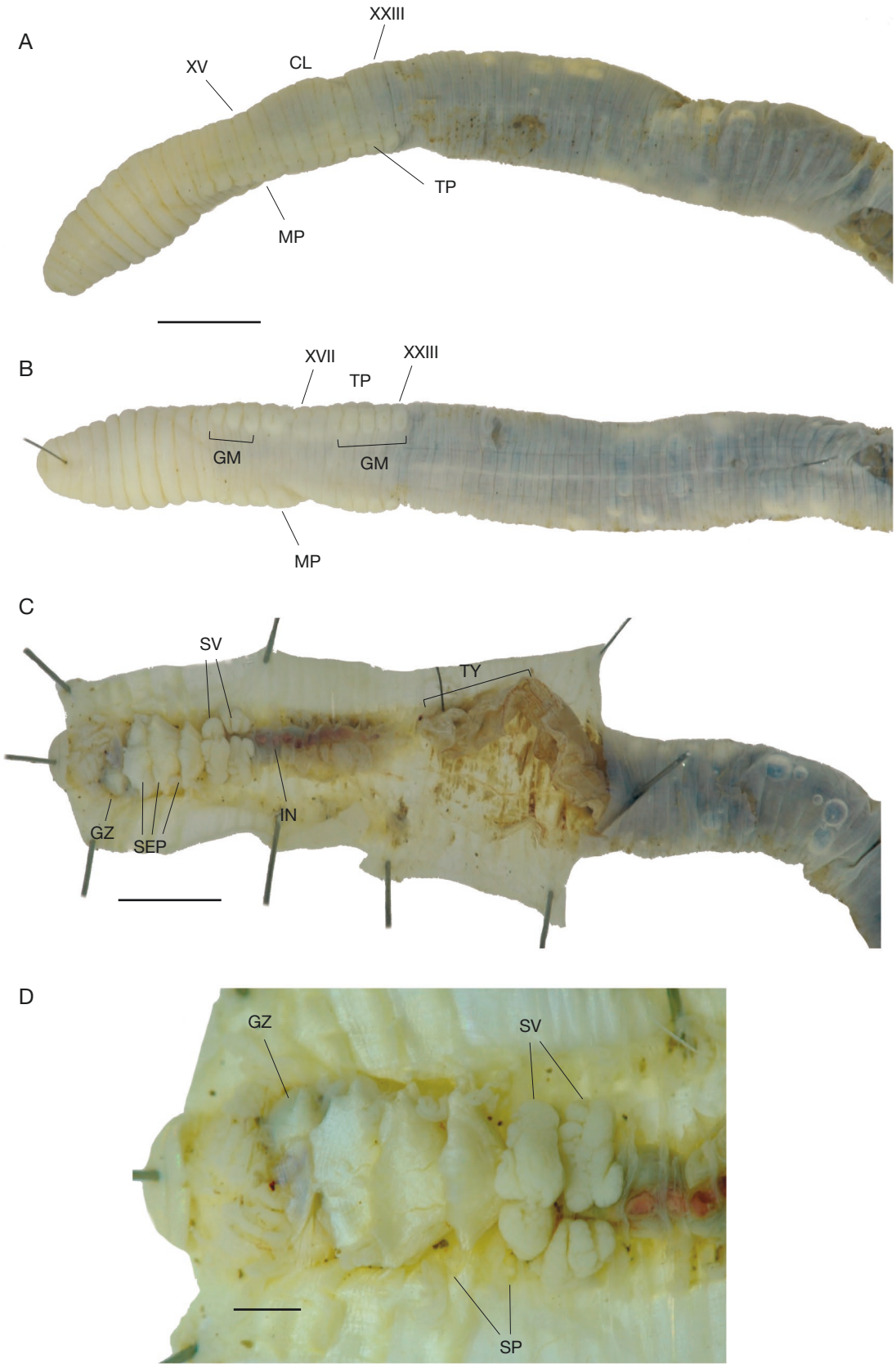

FIG. 9. — *Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp.: **A**, external view of the anterior body; **B**, lateral view of the anterior body; **C**, dissection of the anterior body; **D**, detail of the anterior body dissection showing the spermathecae. Abbreviations: **CL**, clitellum; **GM**, genital marks; **GZ**, gizzard; **IN**, intestine; **MP**, male pore; **SEP**, septa; **SV**, seminal vesicles; **TP**, tubercula pubertatis; **TY**, typhlosole. Scale bars: A-C, 5 mm, D, 1.5 mm. Photos: T. Decaëns.

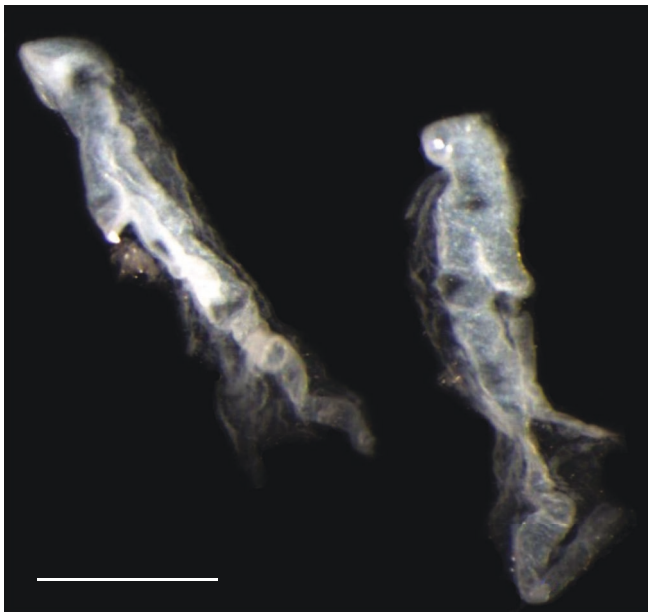

FIG. 10. — Pre-clitellar nephridia of *Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp. Scale bar: 1 mm. Photo: D. F. Marchán.

XV-XXIII, beginning unclear. Genital markings in XII-XIV and XX-XXIII, in ab. Tubercula pubertatis: thin band in XVII-XXIII, more marked in XX-XXIII. Male pores: one pair in XV. Ovipores not visible. Spermathecal pores not visible. Nephridial pores not visible.

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

REMARKS
This species is the smallest species of the genus *Vignysa*: 0.850-1.260 g and 157-167 segments vs 1.400-2.700 g and 205-232 segments for *Vignysa teres* (Bouché 1972; personal data), and 3.500-4.800 g and 372-396 segments for *Vignysa vedovinii* (Rota 1994) (see Table 5). It is also the eastern-most species within the genus. Alive, it has a viscous texture (Fig. 11) and tends to break easily. It shares with *V. vedovinii* the absence of blood vesicles.

DISCUSSION

TAXONOMY AND PHYLOGEOGRAPHY

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

The limits of the genus *Allolobophora*, and the number of species it contains, are not yet the subject of consensus in the literature. Depending on the authors, the genus comprises 69 species (DriloBASE taxo), 51 species and subspecies (Blakemore 2008) or 57 species and subspecies (Brown *et al.* 2023; Misirlioğlu *et al.* 2023). The relevance of the genus has also been and is still highly discussed, *Allolobophora* being considered as a catch-all genus, and demonstrated to be polyphyletic in phylogenetic trees (Martínez Navarro *et al.* 2023). Some authors proposed to divide it into *Allolobophora sensu stricto* and *Allolobophora sensu lato* (Bouché 1972; Easton 1983; Csuzdi & Zicsi 2003). Marchán *et al.* (2021) elevated the subgenus *Gatesona* proposed by Qiu & Bouché (1998a) to the genus level, and Popović *et al.* (2022) assigned several Balkanic *Allolobophora* species to a redefined *Cernosvitovia* Omodeo, 1956. Later, Martínez Navarro *et al.* (2023) separated the genus *Allolobophora* into four distinct genera and synonymised the genus *Heraclescolex* with *Allolobophora*. They finally proposed to move *Aporrectodea icterica* to the genus *Allolobophora*, a new taxonomic assignment which is strongly supported by our results.

Here, we propose to remove *A. bartolii* from the *Allolobophora* genus, and to assign it to the new genus *Flabellodrilus* n. gen., along with the new species *F. luberonensis* Gérard,

TABLE 5. — Main morphological characters distinguishing the newly described species *Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp. and their closest relatives.

Characters	***Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp.**	***Vignysa teres* (Dugès, 1828)**	***Vignysa vedovinii* Rota, 1994**
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, XXIV-XXVII (XXVIII, XXIX)
Spermathecae	Simple, tubular in IX, X	Simple, tubular in IX, X	Simple, disc-shaped, in IX, XI

Decaëns & Marchán, n. gen., n. sp. This new cut within the genus *Allolobophora*, together with the previous revision by Martínez Navarro *et al.* (2023), result in the restriction of the genus to seven species forming a monophyletic group and corresponding broadly to the *Allolobophora sensu stricto* of Bouché (1972). The addition of *A. delitescens* Gérard, Decaëns & Marchán, n. sp. further reinforces the monophyletic property of *Allolobophora*. These taxonomic acts and the phylogenetic analyses that support them highlight the artificial character of the "catch-all" group *Allolobophora* (*sensu lato*), which is progressively split into several smaller monophyletic genera generally comprising species of restricted geographical distribution. There are still several Balkanic species of *Allolobophora* which likely belong to *Cernosvitovia* due to their morphological and biogeographic affinities (see Popović *et al.* 2022), but others such as *Allolobophora asconensis* Bretscher, 1900, *Allolobophora festae* Rosa, 1892, *Allolobophora marcuzzii* Omodeo, 1952 or *Allolobophora schneideri* Michaelsen, 1900 (which are Italian species) or the Caucasian *Allolobophora pseudonematogena* Perel, 1967, *Allolobophora brunnecephala* Kvavadze, 1985 and *Allolobophora immaculata* Omodeo & Rota, 1989 are more controversial: a strong effort to include these species in molecular phylogenetic analyses would allow to revise *Allolobophora* (*sensu lato*) once and for all.

The family Hormogastridae is endemic of Western Mediterranean region, being present only in Algeria, France, Italy, Malta, Spain and Tunisia with nine genera (Rota *et al.* 2017; Marchán *et al.* 2018). The genus *Vignysa* is endemic to Southeastern France (Bouché 1972; Rota 1994) and comprises three species including the one described herein (Blakemore 2008; Brown *et al.* 2023; Misirlioğlu *et al.* 2023; DriloBASE taxo). All are restricted to France: *V. teres* occurs in several localities of the Hérault department (Occitanie), *V. vedovinii* has been found in two localities of Bouches-du-Rhône and Var departments (Provence-Alpes-Côte d'Azur), and *V. callasensis* Gérard, Decaëns & Marchán, n. sp. is known only from its type locality in the Var department (Fig. 8). The distribution of the three species seems to be non-overlapping, but this will require further occurrence data to be confirmed.

Diversity in Southeastern France

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

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

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

This highlights the importance of resampling previously surveyed localities when seeking to establish species lists and discover potential new taxa, like the work of Marchán *et al.* (2023a) in Corsica. Further studies should also aim at intensifying sampling in non-previously sampled localities in Southeastern France, as for instance in the Saint-Baume Mountain, the Plaine des Maures and the Esterel massif. Given the high diversity and the high proportion of species with narrow geographical distribution, this will undoubtedly result in the discovery of additional species new to science as it has been the case in previous works in Port-Cros and Porquerolle Islands (Marchán *et al.* 2020b), in Corsica (Marchán *et al.* 2023a), and in Southwestern France (Marchán *et al.* 2023b).

Fig. 11. — Living specimen of *Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp. Photo: S. Gérard.

Conservation

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

However, open landscapes are decreasing in the Mediterranean region. Since the middle of the nineteenth century, the abandonment of traditional agro-pastoral practices and the decrease of the use of wood for charcoal led most habitats to experience secondary successions and the progressive afforestation of Mediterranean grasslands and scrublands (Barbero *et al.* 1990; Blondel & Aronson 1999; Chauchard *et al.* 2007). More recently, these habitats have also decreased in surface due to the expansion of housing urbanisation in the second half of the twentieth century, especially in Southeastern France (Daligaux 2001; Baccaïni & Sémécurbe 2009). The type localities of the three new species, all open habitats (i.e., grasslands for *V. callasensis* Gérard, Decaëns & Marchán, n. sp. and *A. delitescens* Gérard, Decaëns & Marchán, n. sp., garrigue for *F. luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp.) have undergone such a transition, as shown by the comparison of old (1950-1960) and current satellite pictures in Figure 12.

This historical decrease of open landscapes has led to a decrease in biodiversity, especially on rare and endemic species (Preiss *et al.* 1997; Blondel & Aronson 1999; Labaune &

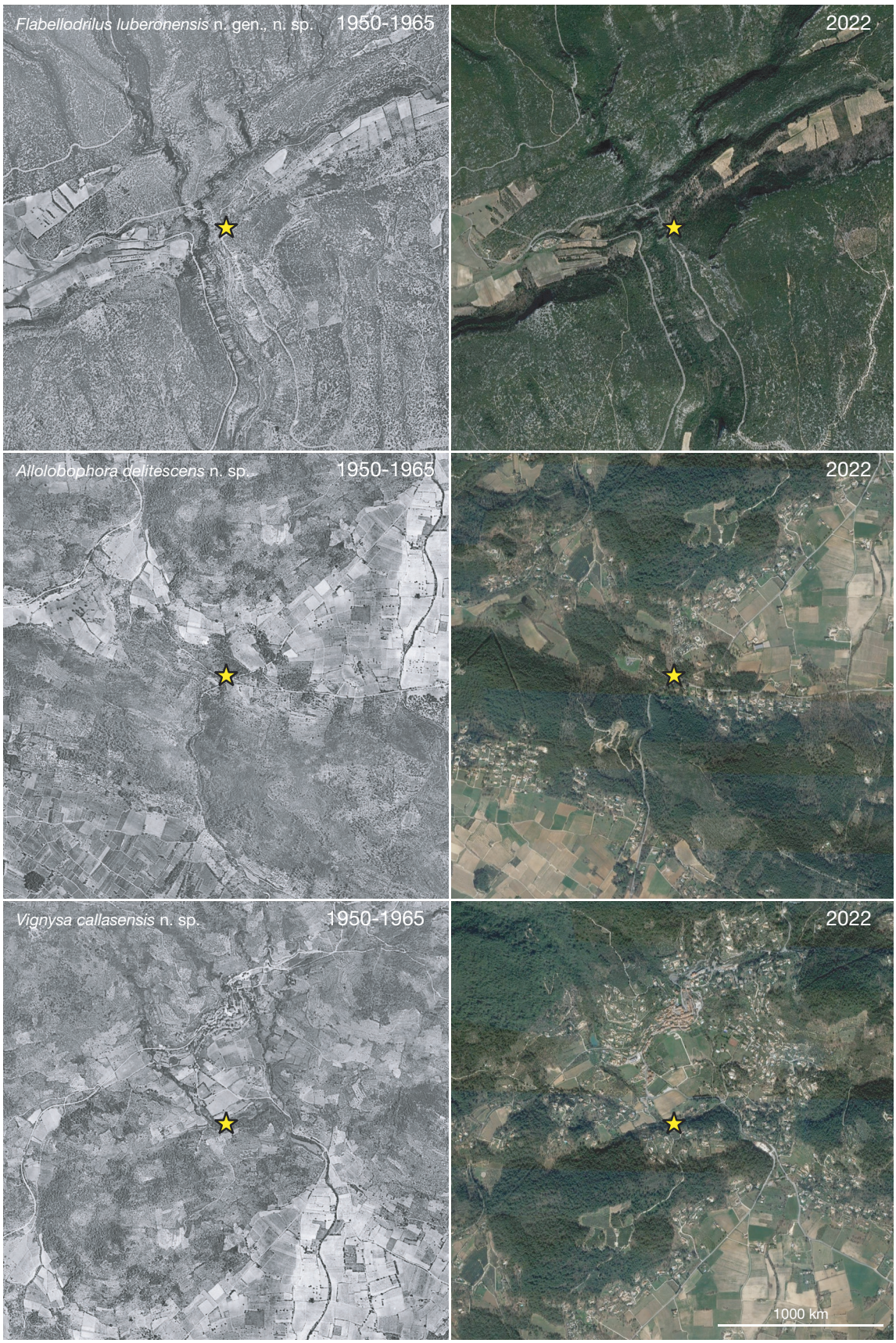

Fig. 12. — Satellite pictures around type localities of *Flabellodrilus luberonensis* Gérard, Decaëns & Marchán, n. gen., n. sp., *Allolobophora delitescens* Gérard, Decaëns & Marchán, n. sp. and *Vignysa callasensis* Gérard, Decaëns & Marchán, n. sp. in the 1950-1965 period (left) and in 2022 (right). 1950-1965: satellite pictures. Credits: Institut national de l'information géographique et forestière (IGN); Google 2022.

Magnin 2002; Höchtl *et al.* 2005). We can therefore argue that this open habitat loss at a fast pace represents a major threat on those newly described specialist species.

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

CONCLUSION

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

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

Conflict of interest

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

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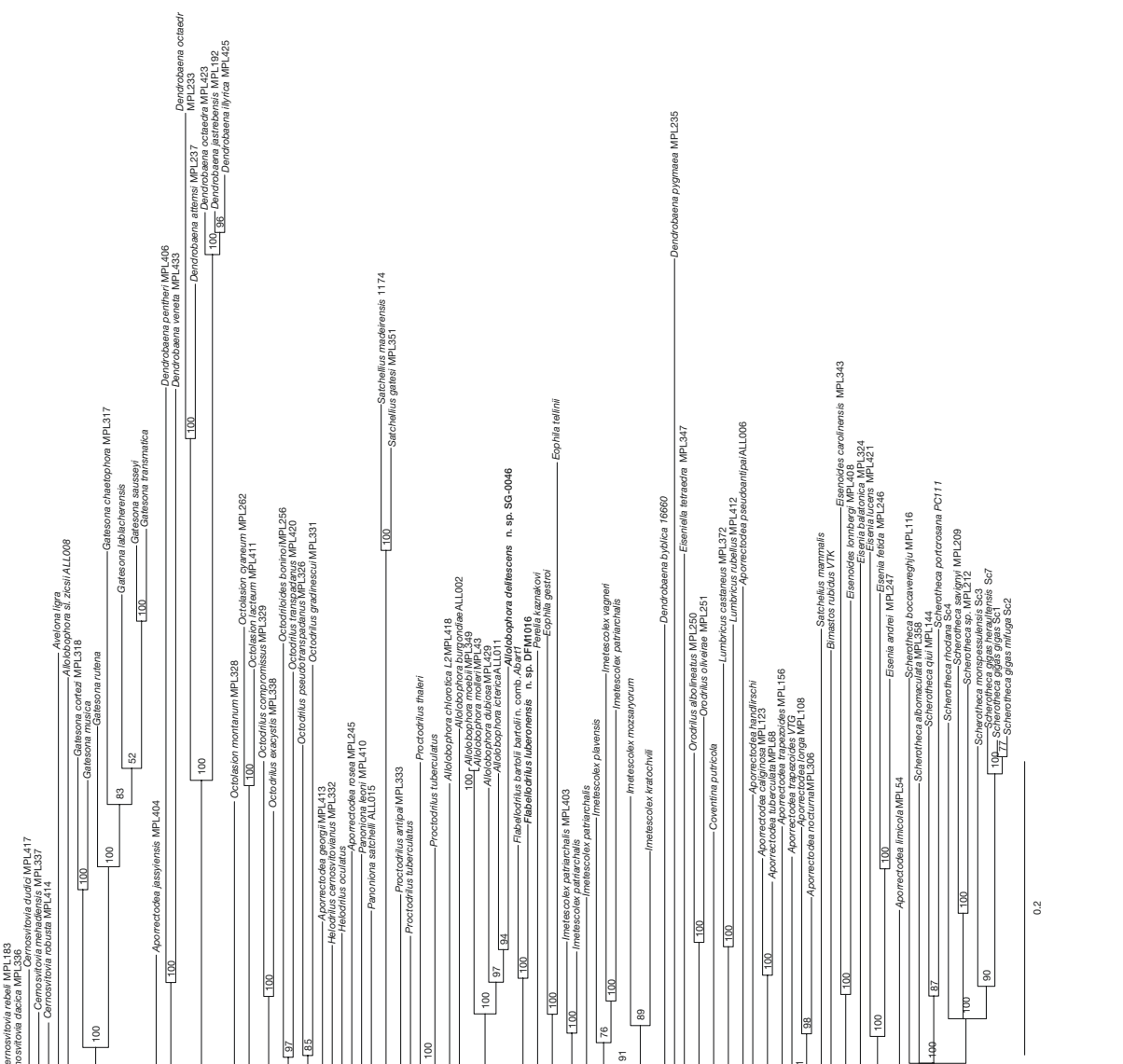

Appendix 1. — Full multilocus phylogenetic tree focused on *Allolobophora*-related Lumbricidae genera. The tree was obtained from Bayesian inference based on the concatenated sequences of the COI-16S-ND1-12S-28S molecular markers. Posterior probability values are shown beside nodes.