Archaeological and Anthropological Sciences (2021) 14:5
https://doi.org/10.1007/s12520-021-01481-3

ORIGINAL PAPER

The last interglacial-glacial cycle in the Meuse Valley (southern Belgium) inferred from the amphibian and reptile assemblages: implications for Neanderthals and anatomically modern humans

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Received: 8 April 2021 / Accepted: 28 November 2021 / Published online: 10 December 2021

Abstract

The Meuse and its tributary valleys contain numerous Late Pleistocene cave sites that have yielded one of the largest collections of Neanderthal and Mousterian lithic industries in Europe. Today, it is an important north–south migratory corridor for flora and fauna, generating rich biotopes. The Quaternary collections of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium) are here used to complement our knowledge of the successive herpetofaunal assemblages in Belgium during the last interglacial-glacial cycle (marine isotope stages 5 to 1). Herpetofauna from 18 caves are described for the first time. In total, 17 taxa (10 amphibians and seven reptiles) are identified, three of which correspond to their first fossil record for Belgium (*Alytes obstetricans*, *Pelobates fuscus*, and *Hyla arborea*). The thermophilic snake *Zamenis longissimus* is documented for the first time in the Holocene (Atlantic/Subboreal period) of Belgium. After marine isotope stage (MIS) 5, the Belgian herpetofauna was still reasonably diverse during MIS 3, but it seems to be represented only by the common frog *Rana temporaria* and a viper during MIS 2. Paleoenvironmental and paleoclimatic reconstructions are proposed for a selection of the chronologically best-constrained sites, using the quantified ecology method. More specifically, the late Magdalenian of the Trou de Chaleux is reconstructed as particularly cold and dry. The seasonal contrast reaches its maximum during this period. The quantitative parameters calculated in this study provide a new paleoecological context for understanding the conditions with which the successive human species had to cope in Northwestern Europe during the last interglacial-glacial cycle.

Keywords Herpetofauna · Paleobiogeography · Paleoenvironment · Paleoclimatology · Last interglacial-glacial cycle · Northwestern Europe

Introduction

The Meuse (in French) or Maas (in Dutch) is a major European river, with a total length of 925 km, rising in France and flowing through Belgium and the Netherlands before draining into the North Sea from the Rhine-Meuse-Scheldt delta. The Meuse Valley is oriented south-north for most of its course, but it goes from west to east between Namur and Liège and goes northeast to the Dutch border, then west to the sea (Fig. 1). It is today an important migratory corridor for flora and fauna (Coen 1987). Through the Meuse Valley, sub-Mediterranean plant species can travel far north (Crépin 1860; Devos 1870; Lambinon et al. 1993). In the same way, southern insects and animals such as the wall lizard (*Podarcis muralis*) take advantage of this passage to reach more northern sites (Parent 1979). Whereas the Condrusian plateau (a lenticular natural region extending from west to east, south of Namur and Liège) has an oceanic climate, the different valleys enjoy very different microclimates. In many places, there are numerous limestone slabs facing south and/or facing north. The microclimatic contrast

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This article is part of the Topical Collection on *Microvertebrate Studies in Archaeological Contexts: Middle Paleolithic to early Holocene past environments*

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Fig. 1 Location of Belgium in Europe (A), the Meuse Valley and its tributaries (B), and detailed map (C) with indication of the localities studied here. (1) Sous-Saint-Paul and Scladina; (2) Walou; (3) Marie-Jeanne; (4) Goyet; (5) Montaigle (Trou du Chêne, Trou du Sureau, Trou du Château, and Trou de l'Érable); (6) Furfooz (Trou de Praules, Trou des Nutons, Trou du Frontal and Trou Reuviau); (7) Trou de Chaleux; (8) Trou Balleux; (9) Trou Magrite; (10) Trou de La Naulette and Trou des Blaireaux; (11) Caverne de Freyr; (12) Cavernes du Bay-Bonnet; (13) Grotte la Chefalize. We have not been able to localize the locality named "Puit artésien de l'atelier central."

between such slabs is very great: the north-facing slopes are very shady and cold, whereas the south-facing slopes are very sunny, hot, and dry. Such sites, with their south-facing limestone cliffs, are important steps in these migrations. The very peculiar stationary conditions that prevail in these areas mean that they can include species adapted to rigorous and contrasting climates, i.e., sub-Mediterranean, steppe, and dealpine species (i.e., whose area of habitat is centered on the Mediterranean mountains) on the sunny rocks, and mid-European mountain species on the shaded sides. Such peculiar conditions must have also been in place during the Pleistocene, generating rich biotopes around the archaeological sites.

Indeed, the Meuse and tributary valleys contain a great number of Late Pleistocene cave sites that have yielded one of the largest collections of Neanderthal remains and Mousterian lithic industries in Europe (Otte 1979; Cahen and Haesaerts 1984; Toussaint et al. 2011). The first description of Pleistocene finds from Belgian cave sites dates from the 1830s (Schmerling 1833). Some 30 years later, Edouard Dupont undertook major excavations in numerous prehistoric caves in the south of Belgium. He discovered important bone accumulations dating mostly to the last glacial (Dupont 1873). The material included large quantities of remains from herbivores and carnivores, artifacts, bone tools, and ivory ornaments, which were stored in the Royal Belgian Institute of Natural Sciences (RBINS). When E. Dupont became a director of the institute in 1868 (Vivé and Versailles 1996), he apparently did not have much time to study the fossil assemblages he excavated, although the archives of the institute contain many of his unpublished notes dating from 1905 to 1906. New interest in this bone material was kindled in the 1990s, resulting in publications on, among other things, the dating and the archaeozoology of Belgian Magdalenian caves (Charles 1996, 1998; Germonpré 1997), the systematics and osteometry of foxes (Germonpré and Sablin 2004) and dogs and wolves (Germonpré et al. 2009), cave bear paleobiology (Germonpré and Sablin 2001; Germonpré 2004), and the ancient DNA of giant deer (Hughes et al. 2006), Arctic foxes (Dalen et al. 2007), and lemmings (Brace et al. 2012). Among the material recovered from the nineteenth-century excavations, small-vertebrate remains have also been identified. Unfortunately, despite their historical interest, most of these sites lack a well-defined stratigraphic context. Part of the material housed at the RBINS has recently been revised, giving rise to publications on fish (Van Neer et al. 2007), amphibians and reptiles (Blain et al. 2019), birds (Goffette et al. 2020), and small mammals (López-García et al. 2017a). The present study is a revision of the Quaternary collections at the RBINS in search of Belgian Pleistocene and Holocene sites that may have yielded fossil remains of amphibians and reptiles. It thus aims to complete the zooarchaeological study of the Belgian Quaternary fossil record and to provide further data on the history of the modern herpetofauna of the continental part of Northwestern Europe, in relation to the paleoclimatic and paleoenvironmental changes that occurred in this region during the last interglacial-glacial cycle.

Material and methods

RBINS collections and contextualization of the herpetofaunal material

For this study, we had access to material from 18 cave sites in southern Belgium, housed in the Quaternary collections of the Royal Belgian Institute of Natural Sciences, Brussels, Belgium (Table 1; Supplementary Online Material [SOM] Appendix 1). As these sites were excavated mainly in the nineteenth century or at the beginning of the twentieth, they usually lack a clear stratigraphical or chronological context (apart from general considerations on the associated large-mammal fauna: "Âge du Renne," "Âge du Mammouth," or "Époque Néolithique"). Many of the RBINS specimens come from the historical collection of the geologist Edouard Dupont who, as the director of the RBINS from 1868 to 1909, gave a significant impulse to research exploration in Belgium. The collected specimens sometimes lack a specific general inventory number (I.G.). However, they have been placed on special plaster structures (the "planchettes"), presenting the bones by taxonomic group or locality.

Any information associated with the remains in the drawers and boxes has been annotated during the revision of the RBINS collections. Extensive bibliographical research has been undertaken, on Internet but also directly in the RBINS library and general archives, to ascertain which excavation campaign the material was from. Despite the impossibility of ensuring that the remains encountered during our revision of the collections had not been mixed at some stage of the recovery, donation, and/or storage process, we have tried to evaluate whether each of these assemblages is ecologically and taphonomically coherent with its "historical" chronological attribution (i.e., the labels associated with the material). We have also revised the context of the excavation and noted any information relating to the sedimentological context, the numerical dating where available, other faunal studies (large mammals, birds, fishes, and paleoanthropology), and the cultural attribution of the artifacts encountered in each layer (mainly described in Otte 1979), which may provide contextual information on the chronological attribution as well as the likelihood of the material having been mixed or not.

In addition to the RBINS Quaternary collections, we include here the results from six unpublished Holocene samples from Scladina Cave, which we had on loan from 2013 to 2015 and have now returned to be housed in the Scladina Cave Archaeological Center (Sclayn, Belgium).

Systematic study

The revision of the RBINS Quaternary collections in search of herpetofaunal remains was undertaken in accordance with the indications of the catalog and by looking directly in each drawer for boxes containing miscellaneous small-vertebrate remains. Remains identified as pertaining to an amphibian or a reptile were separated from the miscellaneous material and stored apart. New register numbers were given to these new samples to isolate them clearly. In some cases, the bones were exhibited to the public at the Museum of Natural Sciences. In this context, some bones were fixed with organic glue on green cardboard; these were displayed on larger plaster trays designed to be stored in the rooms of the museum. In most cases, the bones were not separated from their original presentation, but only identified anatomically and taxonomically, and counted. However, for some interesting elements, this situation hampered any proper study, as the bones could not be removed. To perform the present description, we carefully detached some of the bones from their support. Pictures were taken using a Zeiss Axiocam ERc 5 s camera mounted on a Zeiss Stemi 2000-c stereo microscope in combination with a Volpi Intralux® 5100 fiber optic light source, during our time spent studying the RBINS collections. Additional pictures were taken at the RBINS using a Canon EOS 700D camera connected to a photo-stacking system. Stacking of the pictures was performed using Zerene software. At the IPHES-CERCA, pictures were processed with the DinoCapture 2.0 software, using photographs from the AM4115TL Dino-Lite Edge digital microscope when the snake material from Scladina Cave and the Trou du Frontal was on loan. Anurans are represented in Fig. 2 and snakes in Figs. 3, 4, and 5, in accordance with taxonomic classification.

The systematic nomenclature basically follows Speybroeck et al. (2020). Osteological nomenclature follows Sanchiz (1998) and Bailon (1999) for amphibians and Szyndlar (1984a, 1991) for snakes. The general taxonomic criteria follow Szyndlar (1984a), Bailon (1991, 1999), Barahona Quintana (1996), Barahona and Barbadillo (1997), Holman (1998), Gleed-Owen (1998), and Blain (2005, 2009). Comparisons were drawn using the dry skeleton collections of the Museo Nacional de Ciencias Naturales (Madrid, Spain), the Royal Belgian Institute of Natural Sciences (Brussels, Belgium), the Royal Museum for Central Africa (Tervuren, Belgium), and the Blain Herpetological Collection deposited at IPHES-CERCA (Tarragona, Spain). Measurements were made with scaled drawings using a binocular microscope with a camera lucida.

Data on the distribution and ecology of Belgian amphibians and reptiles come primarily from De Witte (1942), Duguet and Melki (2003), and Jacob et al. (2007).

Statistics

Some 44 herpetofaunal assemblages chronologically dated to between Marine Isotope Stage (MIS) 7/6 (i.e., 300–130 ka) and the Bronze Age (ca. 3,500 BP) were compiled into a data matrix (SOM Table S1). Overall, there is a good distribution of levels throughout the studied period, and all the archaeological cultures known for this region are represented: the Mousterian associated with *Homo neanderthalensis* and the Aurignacian, Perigordian, Magdalenian, Tardenoisian, Chalcolithic, and Bronze Age that are linked to anatomically modern humans (*Homo sapiens*). For each sample, all the represented species were included. Species were grouped into rows, whereas the archaeo-paleontological samples were grouped into columns. Therefore, in the binary data base, the presence of a taxon is marked by "1" and its absence by "0." Some corrections were applied to the data matrix in order to reduce dispersion and facilitate interpretation. The family-level citations of Ranidae indet. and Colubridae indet. are excluded, to avoid statistical deviations due to the low level of determination, although they are included in the subsequent discussion. For the same reason, the citation of cf. *Vipera* sp. from the Trou de Chaleux ("1er niveau ossifère") was assigned to *Vipera berus*, the only species of Viperidae present in the regional sequence. To compare the Belgian fossil record with the typical herpetofaunal successions suggested by G. Böhme (1996, 2000) and M. Böhme (2010) for Central Europe, we added to the data matrix such typical herpetological assemblages adapted to Northwestern Europe for each of the Pleistocene climate periods in the last interglacial-glacial cycle. In addition, the modern composition of the southern Belgian herpetofauna is added to the data matrix by way of comparison with current interglacial conditions, including the northern parsley frog *Pelodytes punctatus* in the concurrence of species, since its current distribution borders the Belgian territory (Jacob et al. 2007).

Correspondence analysis is applied to the data matrix. This is the recommended method for comparison of assemblages (assigned to columns) with the taxa they include (assigned to rows) in an equivalent way (Greenacre 2010). This will underline the relationships of proximity between taxa of different associations, grouping them closely in contrast to the more atypical taxa, which will appear in an eccentric position in relation to the rest of the set, making it possible to infer whether or not the resulting herpetofaunal groups are based on chronostratigraphic criteria whose origins are related to possible biogeographic changes. Moreover, hierarchical clustering is used to support the results of the correspondence analysis. This generates a dendrogram revealing the relationships of similarity between the different assemblages included in the data matrix (SOM Fig. S1). In addition, the Jaccard similarity index is applied, since this

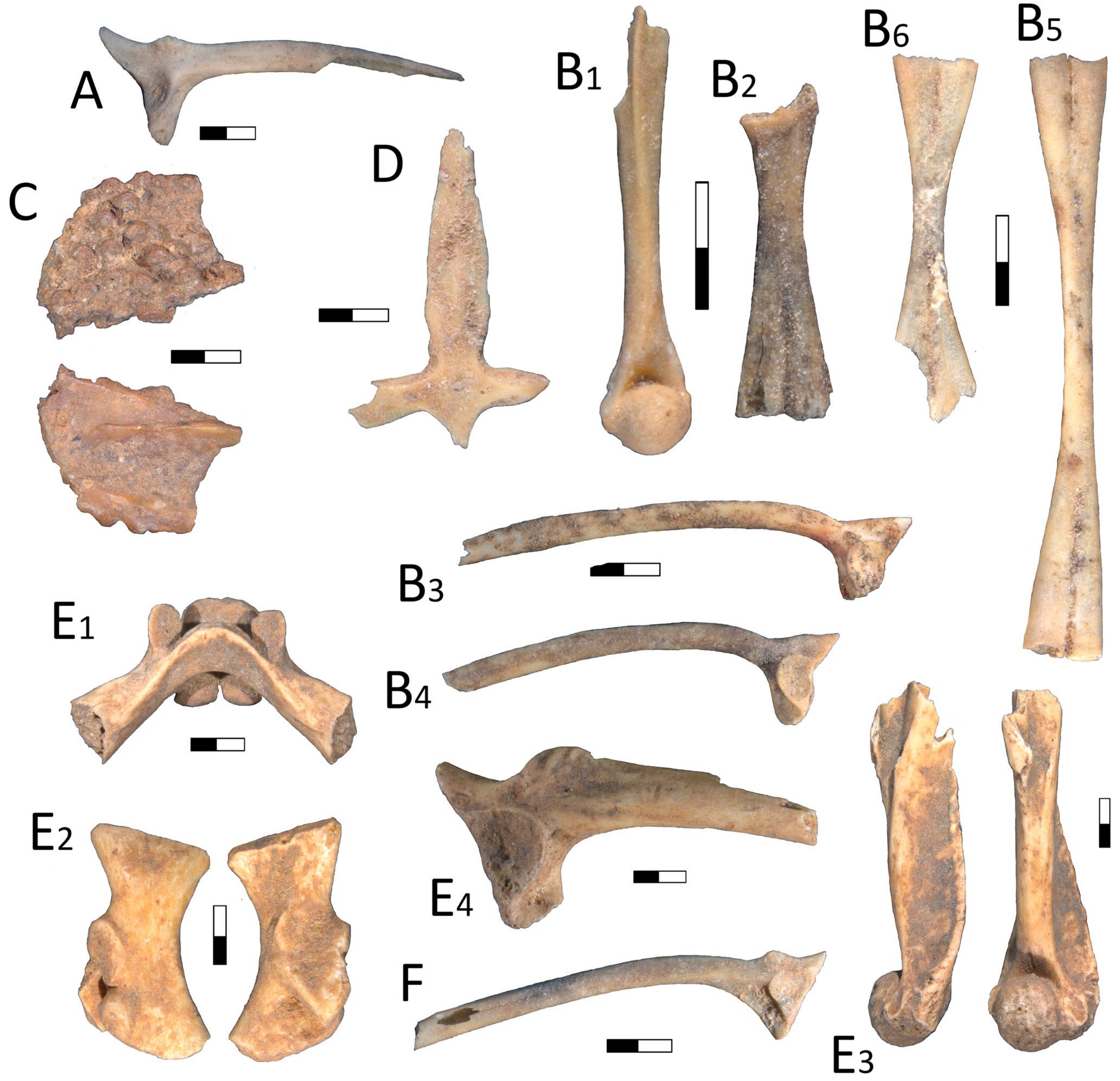

Fig. 2 Fossil anurans from the Late Pleistocene-Holocene of Belgium. (A) *Alytes obstetricans* from the Chalcolithic/Bronze Age? of the Trou du Frontal (Furfooz, Namur), right ilium (IRSNB A 48) in lateral view; (B) *Pelodytes punctatus* from indeterminate chronology of Grotte la Chefalize (Jemeppe-sur-Sambre, Namur), (B_1) left humerus of female (IRSNB A 49) in ventral view, (B_2) radioulna (IRSNB A 50), (B_3) left ilium (IRSNB A 51) in lateral view, (B_4) left ilium (IRSNB A 52) in lateral view, (B_5) tibiofibula (IRSNB A 53), and (B_6) tarsal (IRSNB A 54); (C) cf. *Pelobates fuscus* from the Tardenoisian (latest Pleistocene) of the Trou du Chêne (Haut-le-Wastia, Namur), a fragment of cranial bone with dermal ornamentation (maxilla?) (IRSNB A 55) in dorsal and ventral views; (D) *Rana* cf. *arvalis* from the Holocene? of "Puit artésien de l'atelier central," parasphenoid (IRSNB A 57) in ventral view; (E) *Rana temporaria* from the late Magdalenian of the Trou de Chaleux (Houyet, Namur), (E_1) sacrum (IRSNB A 61) in dorsal view, (E_2) right scapula (IRSNB A 62) in dorsal and ventral views, (E_3) right humerus of male (IRSNB A 63) in posterior and ventral views, (E_4) ilium (IRSNB A 64) in lateral view; (F) *Hyla arborea* from the Holocene? of "Puit artésien de l'atelier central," left ilium (IRSNB A 65) in lateral view. All scales = 2 mm

is recommended for clustering binary data, to give more importance to joint occurrences in the assemblages (Hammer et al. 2001). Furthermore, the "unweighted pair-group average" is applied to the data matrix, resulting in the union in the dendrogram of different groups based on the average distance between their members. The Paleontological

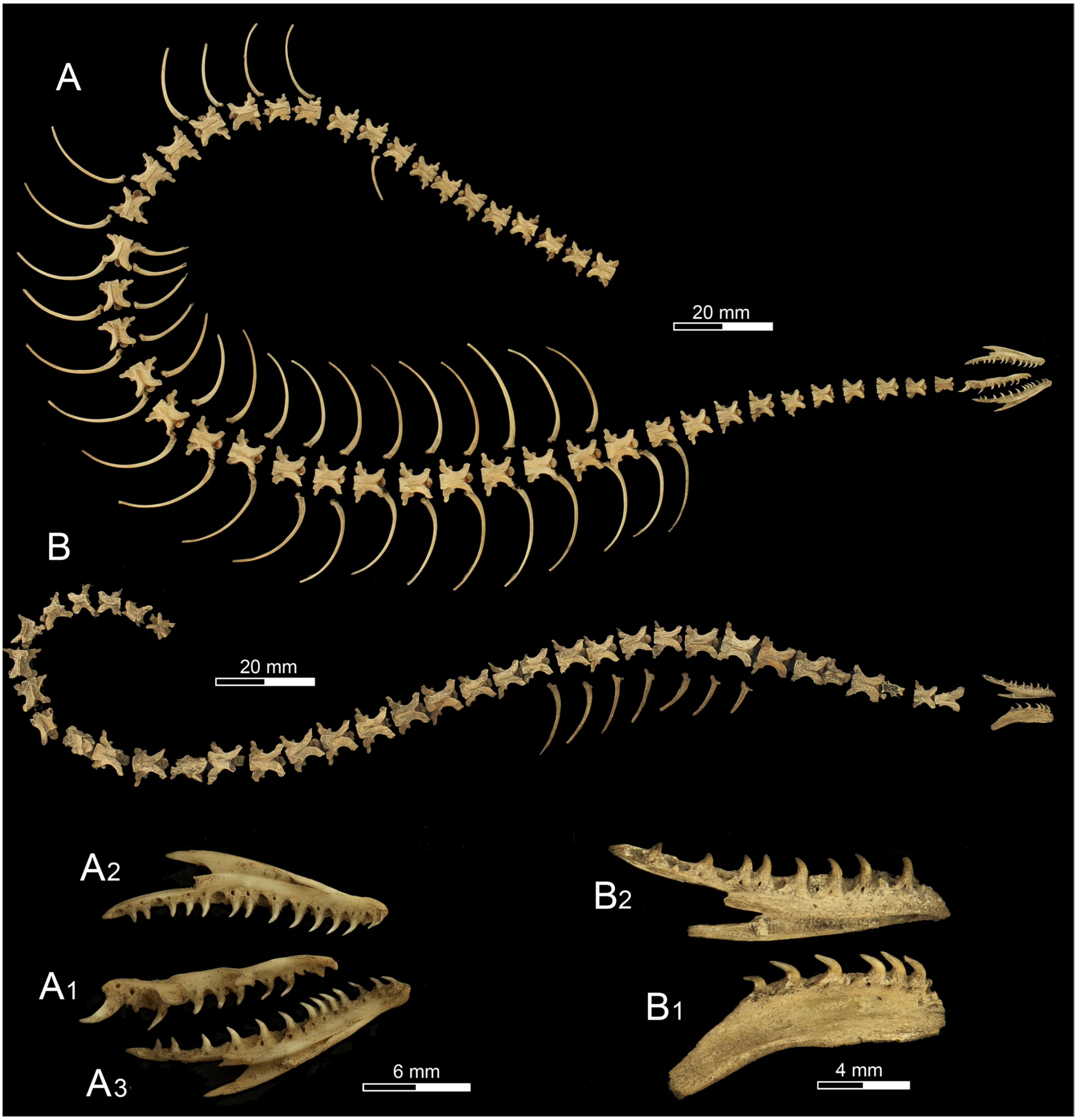

Fig. 3 Fossil grass snakes (*Natrix natrix* s.l.) from the Late Pleistocene-Holocene of Belgium. (A) "Planchette 2188" (IRSNB R 441) from the Chalcolithic/Bronze Age of the Trou du Frontal (Furfooz, Namur). (B) "Planchette 2626" (IRSNB R 442) with uncertain chronology from the Trou Reuviau (Furfooz, Namur). Larger views of cranial elements are presented for the left maxilla (IRSNB R 441a) (A_1), and right (IRSNB R 441b) (A_2) and left (IRSNB R 441c) (A_3) dentaries for the first specimen (A); and for the right pterygoid (IRSNB R 442a) (B_1) and left dentary (IRSNB R 442b) (B_2) for the second specimen (B). Note that here we represent two specimens of *Natrix natrix* s.l., whose bones were glued in 1904 on dark green cardboard, and which were displayed on larger plaster trays designed to be exhibited to the public in the rooms of the Museum of Natural Sciences (Brussels)

Statistics program (PAST4.03) is used for all statistical approaches (Hammer et al. 2001).

Paleoclimatic and paleoenvironmental reconstructions

In order to propose quantitative data on environment and

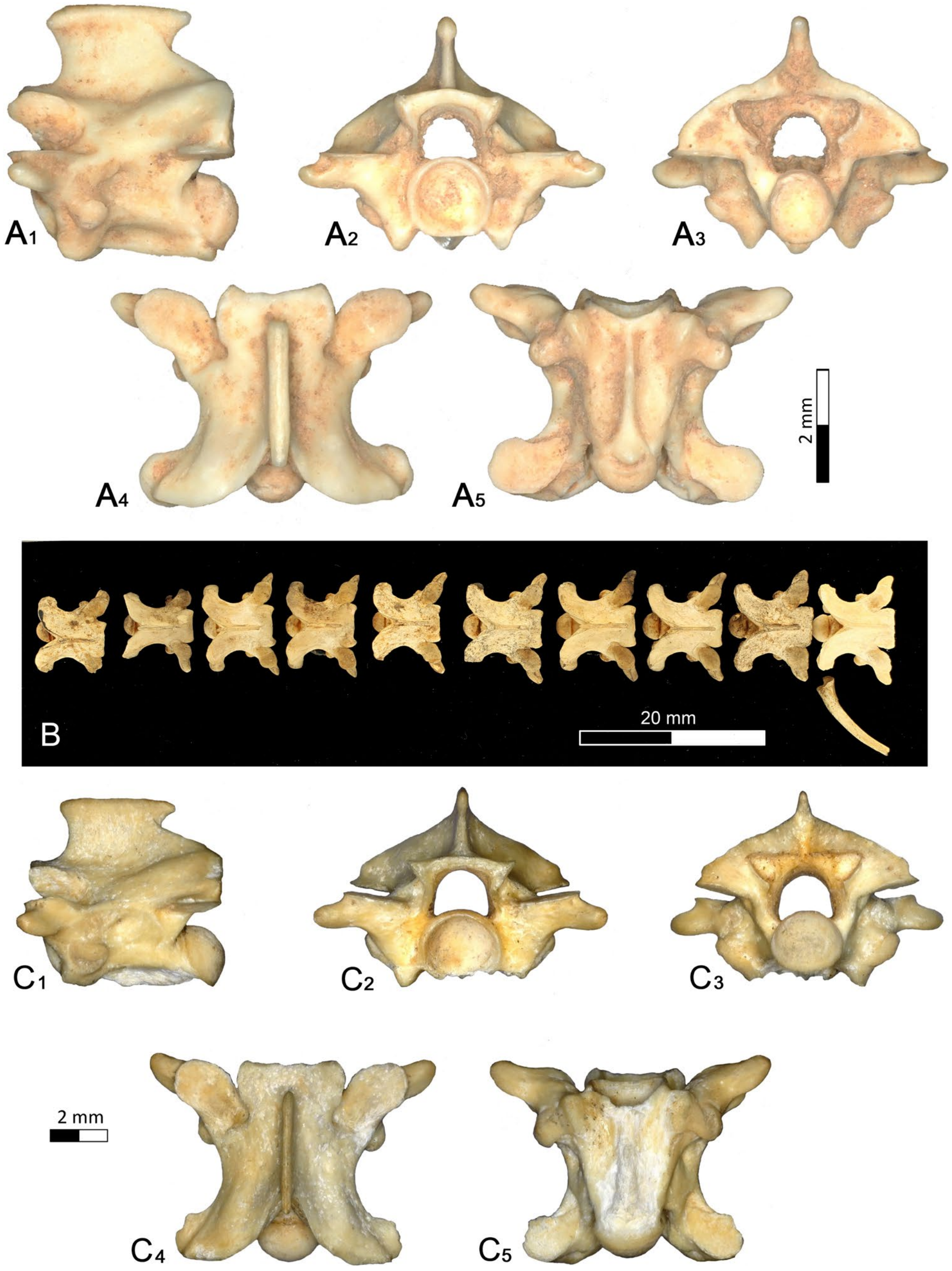

Fig. 4 Fossil Aesculapian snakes (*Zamenis longissimus*) from the Late Pleistocene-Holocene of Belgium. (A) trunk vertebra (IRSNB R 443) from the "Holocene burrow infillings" of Scladina Cave (Sclayn, Namur), in left lateral (A_1), anterior (A_2), posterior (A_3), dorsal (A_4), and ventral (A_5) views; (B) set of ten glued trunk vertebrae and a rib (IRSNB R 444) from the Chalcolithic/Bronze Age? of the Trou du Frontal (Furfooz, Namur) glued on "Planchette 2188"; and (C) unglued trunk vertebra (IRSNB R 444a, the last one on the right in Fig. 4B), in left lateral (C_1), anterior (C_2), posterior (C_3), dorsal (C_4), and ventral (C_5) views

climate for a selection of the chronologically best-constrained sites/samples, we used the quantified ecology method (Jeannet 2010, 2018), based on absence/presence. This method has been shown to give reasonably accurate results in paleoclimatic reconstructions (remaining relatively unaffected by faunal impoverishment), even though, as in many other paleoclimatic methods based on the provision of a mean value for a taxon, the results are slightly biased towards Eurasian mean values, thus smoothing over potential paleoclimatic and paleoenvironmental variations (Blain and Jiménez-Arenas, unpublished data).

The quantified ecology method is based on giving climato-ecological values, stemming from randomly collected geographic and climatic data provided by remote climatic stations over 30 years, for each species in relation to its climatic and ecological potentialities (Jeannet 2010). For higher taxonomic ranks (excluding the family level), we simply take the mean of the different taxa included in the category, as for the *Lissotriton vulgaris* group (i.e., we took the mean of *L. vulgaris* + *L. helveticus*). For each species, the averages from the climatic data provided by remote stations are associated with those for other species at the same level. The values obtained for each parameter are given in Jeannet

Fig. 5 Fossil viper (cf. *Vipera* sp.) from the late Magdalenian of the Trou de Chaleux (Houyet, Namur). (A) left dentary (IRSNB R 445), in occlusal (A_1), medial (A_2), and lateral (A_3) views

(2010). However, in a few cases (especially concerning mean annual precipitation, MAP), the values published in the supplementary material (Jeannet 2010) present some problems (likely due to the software used to design the table); these values have consequently been recalculated from the raw data. Such mistakes were not detected for Caverne Marie-Jeanne in Blain et al. (2019), and this may explain some differences between the present values and the former estimates (see SOM Tables S2–S12 for details on the calculations and parameters used in this study). The mean of all the species represented at a site and/or in a level, therefore, makes it possible to estimate various climatic parameters, such as the mean annual temperature (MAT), mean annual precipitation (MAP), mean temperature of the warmest month (MTW), mean temperature of the coldest month (MTC), maximum extreme temperature (MaxET), minimum extreme temperature (MinET), and the number of rain days per year (YR), snow days per year (YS), and frost days per year (YF).

In addition to the climatic parameters, Jeannet (2010) also proposed certain quantifications for environmental parameters. The quantified ecology method deliberately avoids the use of the minimum number of individuals (MNI), judged not always to be representative of the environment (Jeannet 2010). It thus proposes to weigh the preference of each species for forested and humid environments, mean values representing a proxy for the extension of wooded (%forested) and humid (%humid) environments around the archaeological localities. We applied this method to our Belgian assemblages to provide a paleoenvironmental point of view (see SOM Tables S2–S12 for details of the calculations and weighting used in this study), even though, in the light of the modern ecological bibliography, we do not fully agree with some of the weighting values given by Jeannet (2010). For example, *Rana temporaria* is given a score of 0 for woodland preference, whereas according to various publications this species is today strongly associated with wooded environments in southern Belgium (Jacob and Kinet 2007). We are confident, however, that Marcel Jeannet gave his weighting based on his own experience of Late Pleistocene small vertebrates rather than based on modern ecological studies.

Finally, as a control for the method, we also included in our analysis the herpetofaunal successions from Central Europe, modified from Böhme (2010).

Recent climatic data are taken from two online webpages: climate-data.org based on a 1980–2010 database, and meteobelgique.be based on a 1900–1960 database.

Bufo bufo vs. Rana temporaria index

In order to investigate the dominance pattern between *Rana temporaria* and *Bufo bufo*, as has been shown for Caverne Marie-Jeanne (Rage in Ballmann et al. 1980; Blain et al. 2019), the minimum number of individuals (MNI) for these two species was calculated (see SOM Tables S2–S12). MNI is based on the number of remains, laterality, and sex described in SOM Appendix S1. Only sites with a certain degree of chronological precision are included. This index is established as:

$$\text{Index} = \text{Bb}/(\text{Bb} + \text{Rt})$$

where Bb is the minimum number of individuals for *Bufo bufo* s.l. and Rt is the minimum number of individuals for *Rana temporaria*.

Finally, the relation between this index and the climatic and environmental parameters was analyzed with ordinary least squares (OLS) regression models. These analyses were conducted with R (R Core Team) taking on a significance level of $\alpha = 0.05$.

Results

Fossil herpetofaunal assemblages and chronocultural contextualization

A total of 18 unpublished sites, corresponding to 62 samples/layers, are presented here (SOM Appendix S1). In its entirety, this represents a total number of 5563 identified remains and roughly corresponds to 621 individuals (MNI). We added published sites to this analysis, leading to a total of 22 sites (44 layers/samples; Table 1), covering the whole Late Pleistocene and ranging from MIS 7/6 to MIS 1. The sites are organized chronologically (i.e., following the order of the oldest level represented in the site), for some of them using the available numerical dating (14C) and their cultural attribution. As most of the skeletal remains are redundant,

Table 1 Distribution of the amphibian and reptile occurrences from the Late Middle Pleistocene to Holocene archaeo-paleontological sites and various layers in southern Belgium. Data for Sous-Saint-Paul and Scladina (layers VI-Vocre) are from Blain et al. (2014), for Caverne Marie-Jeanne from Blain et al. (2019), and for Walou from de Wilde (2011a, b). For Walou, "?" means attribution was originally made at genus level only. Central European assemblages have been adapted from Böhme (2010): "x" means the taxon was not included originally, as it has no fossil record in Central Europe

Code	**Sites**	**Lissotriton vulgaris group**	Salamandra salamandra	Alytes obstetricans	cf. Pelobates fuscus	Pelodytes punctatus	Bufo bufo s.l	Epidalea calamita	Rana temporaria	Rana cf. arvalis	Ranidae indet	Hyla arborea	Anguis fragilis	Lacerta agilis	Zootoca vivipara	Natrix natrix s.l	Coronella austriaca	Zamenis longissimus	Colubridae indet	Vipera berus	cf. Vipera sp.
	Mousterian (> 43 ka)																				
1	Sous-Saint-Paul					x	x		x												
2	Walou DI/DII						?		?												
3	Scladina (layers VI-Vocre)		x			x	x		x				x					x		x	
4	Walou CIV						?		?												
5	Caverne Marie-Jeanne (layer 6)		x				x	x	x				x	x	x	x	x			x	
6	Caverne Marie-Jeanne (layer 5)		x				x	x	x	x			x	x	x	x	x			x	
7	Caverne Marie-Jeanne (layer 4)	x	x				x	x	x	x			x		x	x	x			x	
8	Scladina (layer I)								x					x							
9	Walou CIII and CII						?		?												
10	Goyet ("niv. inf. en dessous 2e niv. du Moustérien")						x		x												

Table 1 (continued)

Code	**Sites**	**Lissotriton vulgaris group**	Salamandra salamandra	Alytes obstetricans	cf. Pelobates fuscus	Pelodytes punctatus	Bufo bufo s.l	Epidalea calamita	Rana temporaria	Rana cf. arvalis	Ranidae indet	Hyla arborea	Anguis fragilis	Lacerta agilis	Zootoca vivipara	Natrix natrix s.l	Coronella austriaca	Zamenis longissimus	Colubridae indet	Vipera berus	cf. Vipera sp.
11	Goyet ("Salle du Mouton—2e niveau moustérien")						x		x												
12	Goyet ("Salle du Mouton—1er niveau moustérien")								x												
	Mousterian or Aurignacian																				
13	Goyet ("Salle du Mouton—terre noire")						x	x	x												
	Aurignacian (43–26 ka)																				
14	Walou CI						?		?												
15	Goyet ("Salle du Mouton—terre jaune")						x	x	x												
	Perigordian (35–20 ka)																				
16	Trou du Chêne ("3eme niveau ossifère")						x		x												

Table 1 (continued)

Code	**Sites**	**Lissotriton vulgaris group**	Salamandra salamandra	Alytes obstetricans	cf. Pelobates fuscus	Pelodytes punctatus	Bufo bufo s.l	Epidalea calamita	Rana temporaria	Rana cf. arvalis	Ranidae indet	Hyla arborea	Anguis fragilis	Lacerta agilis	Zootoca vivipara	Natrix natrix s.l	Coronella austriaca	Zamenis longissimus	Colubridae indet	Vipera berus	cf. Vipera sp.
17	Trou du Sureau (“2ième niveau”)								x												
18	Walou B5						?		?												
	Perigordian or Magdalenian																				
19	Caverne Marie-Jeanne (layer 2)		x				x	x	x	x			x	x	x		x			x	
20	Trou de Praules (“1er niveau ossifère”)						x		x												
	Magdalenian (17–12 ka)																				
21	Trou de Chaleux (“1er niveau ossifère”)								x												x
22	Trou du Château (Montaigle)								x												
	Magdalenian or Tardenoisian																				

Table 1 (continued)

Code	**Sites**	**Lissotriton vulgaris group**	Salamandra salamandra	Alytes obstetricans	cf. Pelobates fuscus	Pelodytes punctatus	Bufo bufo s.l	Epidalea calamita	Rana temporaria	Rana cf. arvalis	Ranidae indet	Hyla arborea	Anguis fragilis	Lacerta agilis	Zootoca vivipara	Natrix natrix s.l	Coronella austriaca	Zamenis longissimus	Colubridae indet	Vipera berus	cf. Vipera sp.
23	Trou du Chêne (“2e niveau ossifère”)								x												
	Tardenoisian (10–5 ka)																				
24	Trou du Chêne (“argile à blocaux”)				x		x		x												
25	Trou Balleux						x														
	Chalcolithic / Bronze Age																				
26	Trou du Frontal (“1er niveau ossifère”)			x			x		x							x		x			
	Holocene indeterminate																				
27	Scladina (“terriers holocènes”)		x				x		x									x			
28	Trou Magrite de Pont-à-Lesse						x		x												
	Indeterminate																				

Table 1 (continued)

Code	**Sites**	**Lissotriton vulgaris group**	Salamandra salamandra	Alytes obstetricans	cf. Pelobates fuscus	Pelodytes punctatus	Bufo bufo s.l	Epidalea calamita	Rana temporaria	Rana cf. arvalis	Ranidae indet	Hyla arborea	Anguis fragilis	Lacerta agilis	Zootoca vivipara	Natrix natrix s.l	Coronella austriaca	Zamenis longissimus	Colubridae indet	Vipera berus	cf. Vipera sp.
29	“Puit artésien de l’atelier central”						x		x	x	x	x	x								
30	Trou des Nutons (“1er niveau ossifère”)						x				x										
31	Trou de La Naulette (“3ieme niveau ossifère”)						x				x										
32	Trou des Blaireaux (“1er niveau ossifère”)						x														
33	Trou Reuviau						x		x							x					
34	Caverne de Freyr (“Dépôt en place”)						x														
35	Caverne de Freyr (“Dépôt remanié”)						x		x												
36	Cavernes du Bay-Bonnet						x		x												
37	Trou de l’Érable (Montaigle)						x														

Table 1 (continued)

Code	**Sites**	**Lissotriton vulgaris group**	Salamandra salamandra	Alytes obstetricans	cf. Pelobates fuscus	Pelodytes punctatus	Bufo bufo s.l	Epidalea calamita	Rana temporaria	Rana cf. arvalis	Ranidae indet	Hyla arborea	Anguis fragilis	Lacerta agilis	Zootoca vivipara	Natrix natrix s.l	Coronella austriaca	Zamenis longissimus	Colubridae indet	Vipera berus	cf. Vipera sp.
38	Grotte la Chefalize, Salle I					x	x		x										x		
39	Grotte la Chefalize, Salle II						x		x												
40	Goyet (“Grotte 1 annexe—terre noire”)								x												
41	Goyet (“Grotte 1—terre noire”)						x		x												
42	Goyet (“Grotte 1—terre jaune”)						x														
43	Goyet (“Grotte 3 entre les deux couloirs”)								x												
44	Goyet (“Couloir entre les Grottes 3 et 4”)								x												
	Central European assemblages																				
	Late glacial						x			x										x	
	Early interglacial	x					x		x	x			x	x	x	x	x			x	

Table 1 (continued)

Code	**Sites**	**Lissotriton vulgaris group**	Salamandra salamandra	Alytes obstetricans	cf. Pelobates fuscus	Pelodytes punctatus	Bufo bufo s.l	Epidalea calamita	Rana temporaria	Rana cf. arvalis	Ranidae indet	Hyla arborea	Anguis fragilis	Lacerta agilis	Zootoca vivipara	Natrix natrix s.l	Coronella austriaca	Zamenis longissimus	Colubridae indet	Vipera berus	cf. Vipera sp.
	Interglacial climate optima	x	x	(x)	x	(x)	x		x			x	x			x		x			
	Late interglacial and interstadial	x			x		x	x	x	x		x	x	x		x	x				
	Latest interglacial to early glacial								x						x					x	
	Glacial								x												

we here only describe the rare species in the Belgian fossil record.

Grotte Sous-Saint-Paul (Sclayn, Namur)

The Grotte Sous-Saint-Paul is located below Scladina Cave in the village of Sclayn (Namur Province; Fig. 1); its sedimentary filling is separated from the Late Pleistocene sequence of Scladina by a major hiatus (Haesaerts 1992; Pirson 2007; Pirson et al. 2008, 2014). The stratigraphic sequence of Sous-Saint-Paul cave (Otte et al. 1983; Haesaerts 1992) has not recently been reviewed. A chronostratigraphic interpretation (Pirson 2007; Pirson et al. 2008, 2014) suggests that layers VII to X probably date back to MIS 6–7, i.e., between 300 and 130 ka. Thirteen U/Th dates from a reworked stalagmitic floor from either layer VIII, VII, or VI (see Pirson et al. 2008) gave a mean age of 138 ka (Gewelt et al. 1992). The herpetofaunal assemblage for levels X, IX, and VII (Table 1-1) has been described in Blain et al. (2014). It is constituted by anurans only: the parsley frog (*Pelodytes punctatus*), the common toad (*Bufo bufo*), and the European common brown frog (*Rana temporaria*).

Walou (Trooz, Liège)

Located about 10 km southeast of the city of Liège (Liège Province; Fig. 1), Walou Cave (Trooz) opens to the northwest and overhangs by 25 m the Magne river, a tributary of the Vesdre River. Excavations were carried out there from 1985 to 1990 by M. Dewez (Université catholique de Louvain, Belgium) and then from 1996 to 2004 by C. Draily (Service Public de Wallonie, Namur). Numerous prehistoric occupations have been identified in the cave (Draily 2011). The Walou stratigraphic sequence is certainly one of the best-documented for the Late Pleistocene of the Belgian karst. Based on an interdisciplinary approach, the chronostratigraphic and paleoenvironmental framework of the occupations is well established. The sequence is 12 m thick and covers the last 150,000 years. Out of a total of about 45 layers, 25 have yielded archaeological material: 14 are attributed to the Middle Paleolithic, five to the Upper Paleolithic, two to the Mesolithic, and one to the Neolithic (three are undetermined). All the industries were made of flint collected in a reworked position, presumably in the vicinity of the cave.

The data concerning the herpetofauna come from two chapters of the same monograph: de Wilde (2011a) provides the stratigraphic distribution of the anuran remains (apparently no squamate has been identified), whereas de Wilde (2011b) proposes a very summary identification of these remains, attributed to *Bufo* sp. and *Rana* sp. There is no way to know whether these two genera were found together or not in all the stratigraphic levels where anurans are mentioned.

Here, we consider that these two genera are present in all the levels where anurans are recorded. Moreover, to be consistent with the data presented here for other sites, we attribute these remains to the species *Bufo bufo* and *Rana temporaria*. The chronological attribution for each of these levels is based on Draily (2011). For his part, de Wilde (2011a—pp. 15–16: tables 7 and 8) identified anuran remains in levels DI/DII (MIS 5/6; Tables 1–2), CIV (MIS 4; Tables 1–4), CIII (MIS 4/early 3), and CII (MIS 3; Tables 1–9), CI (late MIS 3, around 30–42 ka, Aurignacian; Tables 1–14), and B5 (MIS 2, 21 to 26 ka, Gravettian; Tables 1–18).

Grotte de Scladina (Sclayn, Namur)

Scladina Cave is located in a small tributary valley of the Meuse River, in the village of Sclayn (Namur Province; Fig. 1). It consists of a large gallery 6 m high and 6–20 m wide, connected to other caves such as Sous-Saint-Paul Cave located several meters below. After 30 years of almost permanent fieldwork, excavations in Scladina Cave have reached more than 40 m in length beyond the entrance. Initially discovered by speleologists in 1971, the cave has undergone several multidisciplinary research campaigns since 1978, focusing mainly on archaeology, archaeozoology, large and small mammals, palynology, stratigraphy, and sedimentology (e.g., Otte 1992; Otte et al. 1998). More than 17,500 lithic artifacts have been collected, corresponding to four main Mousterian occupations (Bonjean et al. 2011). Thousands of faunal remains have also been found throughout the sequence, including a fragment of maxilla and a nearly complete mandible of a juvenile Neanderthal, unearthed from 1990 onwards (Bonjean et al. 1997; Otte et al. 1993; Toussaint et al. 1994) and dated to 127 + 46/ − 32 ka by gamma spectrometry (Toussaint et al. 1998).

A detailed description of the geology of Scladina Cave can be found in Pirson (2007) and Pirson et al. (2008). Although the stratigraphic sequence now appears considerably more complex than previously described (see Pirson 2007, for historiographical details), the old nomenclature has been retained here (Bastin et al. 1986; Cordy 1992), corresponding to the sector investigated on the terrace by J.-M. Cordy. However, a general correlation with the main lithostratigraphic units of the new stratigraphic record can be established. The chronostratigraphic interpretation of layers Vocre to VI is MIS 5 (i.e., 130–74 ka) and of layer I is MIS 3 (43,150 + 950/ − 700 BP (GrA-32581); 40,210 + 400/ − 350 BP (GrA-32635); Pirson 2007; Pirson et al. 2008, 2014). All the layers from the terrace have provided lithic artifacts, but only two main Mousterian occupations have been identified. The first one is complex 5 (where layer VB is included, but with an indeterminate age within MIS 5), and the second one is unit 1A (where layer I is included, MIS 3 in age) (Bonjean et al. 2009; Di Modica and Bonjean 2004; Otte et al. 1988).

The first studies of the small-vertebrate assemblages of Scladina Cave were undertaken by Jean-Marie Cordy in the 1980s and mainly focused on rodents, insectivores, and lagomorphs (Bastin et al. 1986; Cordy 1992). López-García et al. (2017b) revised these previous faunal lists and completed the assemblage with a study of the bats. Blain et al. (2014) described the herpetofaunal assemblages. This latter study identified the fire salamander (*Salamandra salamandra*), the parsley frog (*Pelodytes punctatus*), the common toad (*Bufo bufo*), the European common brown frog (*Rana temporaria*), the slow worm (*Anguis fragilis*), the Aesculapian snake (*Zamenis longissimus*), and the common European adder (*Vipera* cf. *berus*) in layers Vocre to VI–VIa (Tables 1, 2, 3). However, Level I (MIS 3; Tables 1–8) only yielded a few remains of *R. temporaria* and the sand lizard (*Lacerta* cf. *agilis*). In addition to these Pleistocene assemblages, Scladina also provided Holocene deposits in the upper part of the stratigraphic sequence inside the cave, mainly corresponding to the filling of rabbit or badger burrows. This miscellaneous material has obviously not been dated and was not included in the study by Blain et al. (2014). Various samples (as separate burrows) have been studied for the present study (Tables 1–27). Sample G4; SC-1982–122 (cutting across layers VIII to X; at a depth of 615–700 cm) has yielded a large amount of *Bufo bufo*, and four vertebrae and one humerus of *S. salamandra*. Sample D33; SC-1991–174 (cutting across layer Ia; at a depth of 302–312 cm) yielded *B. bufo* and *Rana* sp. Samples B34; SC-1992–112 (cutting across layer I), C37; SC-1994–510 (cutting across layer 40; at a depth of 270–280 cm), and H-20; SC-1982–50 (cutting across layer I + II) only provided remains of *B. bufo*. Finally, SC-1987–350 furnished *B. bufo*, two ilia of *R. temporaria*, and three vertebrae of *Z. longissimus*.

Even without any precise context within the Holocene, the three trunk vertebrae attributed to the Aesculapian snake (among them IRSNB R 443; Fig. 4A) from one of the Holocene burrow infillings in Scladina Cave is relevant, as this snake has only been recorded in Belgium in the lower layers (MIS 5) of Scladina (Blain et al. 2014). The fossil trunk vertebrae possess a centrum length respectively of 5.8, 5.2, and 5.0 mm. They do not bear any hypapophyses on the centrum and are characterized by a deep and rounded haemal keel that is spatulate at the caudal end (Fig. 4A5). The prezygapophyseal processes are relatively short, except for one of them which is slightly more elongated and more angulated dorsoventrally (probably due to intracolumnar variation) and shows a rounded tip. All three trunk vertebrae fit with the morphology of *Zamenis longissimus* as described by Szyndlar (1984a, 1991) and Bailon (1991). No comparisons have been made with *Zamenis lineatus* (formerly included with *Z. longissimus*), but this snake can be ruled out given that its geographical distribution is restricted to southern Italy and Sicily (Razzetti and Zanghellini 2006).

Table 2 Climatic (in °C for temperature and mm for precipitation), atmospheric (in days per year), and environmental (in %) parameters calculated by the quantified ecology method applied to the amphibians and reptiles from the Late Middle Pleistocene to Holocene of southern Belgium and Central European herpetofaunal successions, modified from Böhme (2010). *MAT*, Mean annual temperature; *MAP*, mean annual precipitation; *MTW*, mean temperature of the warmest month; *MTC*, mean temperature of the coldest month; *MaxET*, maximum extreme temperature; *MinET*, minimum extreme temperature; *YR*, the number of rain days per year; *YS*, snow days per year; *YF*, frost days per year; *%forested*, extension of wooded environments; *%humid*, extension of humid environments; *SD*, standard deviation; *Bb vs. Rt index*, *Bufo bufo* vs. *Rana temporaria* index; *LG*, late glacial; *EI*, early interglacial; *ICO*, interglacial climate optimum; *LII*, late interglacial and interstadial; *LIEG*, latest interglacial to early glacial; *G*, glacial. See Table 1 for the numerical correspondence of the sites/samples

Sites	MAT		MAP		MTW		MTC		MaxET		MinET		YR		YS		YF		%forested		%humid		Bb vs. Rt index
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
1	8.2	3.9	710.0	7.8	20.2	1.5	−3.7	9.1	36.1	2.0	−21.6	8.5	143.0	9.5	63.7	50.3	122.0	71.9	30.0	43.6	70.0	8.7	0.9
3	8.4	4.6	672.9	9.3	20.3	2.0	−2.6	7.8	36.2	1.5	−21.6	11.7	136.0	11.4	63.1	52.9	120.4	60.2	45.7	36.4	42.1	30.7	0.8
5	6.8	3.7	614.0	6.3	20.1	1.6	−5.7	5.7	35.7	1.4	−27.0	9.1	138.7	9.3	82.5	38.1	146.3	43.9	38.0	32.6	46.0	31.7	0.1
6	6.6	3.6	607.3	6.4	20.2	1.5	−6.6	6.2	35.7	1.3	−28.0	9.2	140.7	11.1	85.6	37.6	152.5	46.5	38.2	30.9	48.6	31.3	0.1
7	6.8	3.8	615.5	7.0	20.0	1.5	−5.9	6.6	35.4	1.2	−26.9	9.8	140.9	11.1	83.5	39.6	157.3	49.7	37.7	30.9	56.8	32.0	0.3
8	6.6	1.5	635.0	3.5	20.8	1.3	−7.6	0.9	35.8	2.8	−26.8	3.3	145.5	10.6	72.0	12.7	162.0	4.2	20.0	28.3	42.5	46.0	0.0
10	6.0	0.7	665.0	0.7	20.8	1.4	−9.0	1.1	35.7	2.7	−26.4	2.7	143.5	13.4	92.0	15.6	163.5	2.1	40.0	56.6	67.5	10.6	0.5
11	6.0	0.7	665.0	0.7	20.8	1.4	−9.0	1.1	35.7	2.7	−26.4	2.7	143.5	13.4	92.0	15.6	163.5	2.1	40.0	56.6	67.5	10.6	0.5
12	5.5		660.0		19.8		−8.2		33.8		−24.5		153.0		81.0		165.0		0.0		75.0		0.0
13	7.2	2.2	660.0	1.0	20.3	1.3	−6.3	4.7	35.6	1.9	−24.9	3.3	143.0	9.5	80.7	22.5	153.7	17.1	30.0	43.6	70.0	8.7	0.8
15	7.2	2.2	660.0	1.0	20.3	1.3	−6.3	4.7	35.6	1.9	−24.9	3.3	143.0	9.5	80.7	22.5	153.7	17.1	30.0	43.6	70.0	8.7	0.8
16	6.0	0.7	665.0	0.7	20.8	1.4	−9.0	1.1	35.7	2.7	−26.4	2.7	143.5	13.4	92.0	15.6	163.5	2.1	40.0	56.6	67.5	10.6	0.0
17	5.5		660.0		19.8		−8.2		33.8		−24.5		153.0		81.0		165.0		0.0		75.0		0.0
19	6.8	3.7	614.0	6.3	20.2	1.6	−6.4	6.5	35.9	1.3	−27.5	9.6	141.3	11.5	83.4	38.9	152.0	49.0	39.0	32.5	46.0	31.7	0.7
20	6.0	0.7	665.0	0.7	20.8	1.4	−9.0	1.1	35.7	2.7	−26.4	2.7	143.5	13.4	92.0	15.6	163.5	2.1	40.0	56.6	67.5	10.6	0.7
21	2.9	3.7	585.0	10.6	18.5	1.8	−10.9	3.8	34.7	1.2	−33.3	12.4	144.0	12.7	115.0	48.1	187.5	31.8	30.0	42.4	42.5	46.0	0.0
22	5.5		660.0		19.8		−8.2		33.8		−24.5		153.0		81.0		165.0		0.0		75.0		0.0
23	5.5		660.0		19.8		−8.2		33.8		−24.5		153.0		81.0		165.0		0.0		75.0		0.0
24	6.4	0.9	643.3	3.8	21.5	1.5	−8.7	0.9	36.5	2.3	−27.2	2.4	143.7	9.5	90.0	11.5	160.3	5.7	26.7	46.2	70.0	8.7	0.0
25	6.5		670.0		21.8		−9.7		37.6		−28.3		134.0		103.0		162.0		80.0		60.0		1.0
26	8.2	3.6	676.0	8.8	20.8	1.4	−3.9	6.8	36.0	2.0	−22.0	9.5	135.0	10.8	62.4	49.0	129.8	43.7	44.0	32.1	57.0	32.5	0.4
27	9.1	3.6	690.0	4.7	21.6	1.3	−3.2	6.8	36.5	1.9	−18.5	9.3	133.0	14.9	54.3	44.5	122.0	48.0	55.0	44.3	46.3	32.5	
28	6.0	0.7	665.0	0.7	20.8	1.4	−9.0	1.1	35.7	2.7	−26.4	2.7	143.5	13.4	92.0	15.6	163.5	2.1	40.0	56.6	67.5	10.6	0.7
29	7.0	2.4	634.0	5.4	20.6	1.0	−6.6	6.7	36.0	1.7	−27.4	6.4	147.4	10.2	84.4	26.0	155.4	41.3	46.0	34.4	62.0	21.7	0.5
LG	3.6	3.1	573.3	8.5	20.1	2.5	−12.9	2.9	36.4	1.1	−36.2	7.1	143.3	15.3	123.0	23.6	195.7	29.3	60.0	20.0	48.3	34.0	
EI	6.1	3.2	606.0	7.0	20.0	1.5	−7.4	5.8	35.5	1.5	−29.4	8.0	142.8	8.6	90.6	34.4	167.6	43.5	34.5	23.1	51.0	36.0	
ICO	9.3	2.9	677.3	7.4	20.7	1.5	−1.5	6.0	36.2	1.7	−20.4	8.1	137.1	10.3	53.1	38.6	124.3	50.9	43.2	34.5	62.3	28.0	
LII	7.6	2.2	630.0	5.2	20.7	1.2	−5.4	5.2	36.0	1.6	−26.2	6.0	143.7	7.8	75.6	25.3	153.0	38.2	32.3	27.9	58.6	32.0	
LIEG	2.8	2.6	566.7	8.1	18.5	1.3	−11.1	2.7	34.6	0.9	−34.4	9.0	144.0	9.0	117.0	34.2	191.7	23.6	26.7	30.6	55.0	39.1	
G	5.5		660.0		19.8		−8.2		33.8		−24.5		153.0		81.0		165.0		0.0		75.0		

Table 3 Values of correlations between climatic parameters and the *Bufo bufo* vs. *Rana temporaria* index. *Adj-R*$_2$, adjusted R^2; *Slope*, sign of the slope; *p*-value of the regression model. As the significance value was established at $\alpha = 0.05$, all correlations with higher *p*-value are considered not significant and are not taken into account. Significant correlations are highlighted in bold

	Bufo bufo vs. *Rana temporaria* Index		
	Adj.r^2	*p*-value	Slope
MAT	**0.34**	**0.002**	0.178
MAP	0.22	0.012	0.006
MTW	0.189	0.019	0.249
MTC	0.129	0.047	0.069
MaxET	**0.394**	**$<<$0.001**	0.252
MinET	0.102	0.071	0.048
%forested	**0.433**	**$<<$0.001**	0.013
%humid	−0.036	0.657	−0.003

Caverne Marie-Jeanne (Hastière-Lavaux, Namur)

Caverne Marie-Jeanne is an archaeological site situated in southeastern Belgium, in the Ardennes region (Fig. 1). The cave is located in a small valley, 25 m above the right bank of a small tributary (Féron) of the Meuse River, near the town of Hastière-Lavaux (Ballmann et al. 1980). The excavations at this site took place during the summer of 1943 under the direction of M. Gilbert (RBINS). During the excavation campaigns, ten layers were brought to light within the cave. At the base of the stratigraphic sequence, layers 10 to 7 are sterile. Layers 6 to 2 yielded a large collection of faunal remains and lithic tools with some Mousterian artifacts, identified mainly in layer 3. The geological interpretation of the cave suggested that, during the formation of layers 10 to 7, the cave was closed whereas from layers 6 to 2, it was connected with the outside. The scarcity of the lithic tools suggests that the cave was probably not inhabited by humans, but that tools were probably accidentally introduced. According to the faunal list and taphonomic studies, the cave probably functioned as a hyena den or hibernation place. Numerical dating of the stratigraphic sequence of Caverne Marie-Jeanne (Brace et al. 2012) shows that the lower layers (6 to 4) are dated to between ca. 50 and 40 kyr BP and thus pertain to MIS 3, whereas the overlying layer 2 gives somewhat divergent datings ranging between 14,850 and 13,925 and 25,456–24,497 cal year BP and thus suggests a mix of materials pertaining to late MIS 3 and MIS 2 (López-García et al. 2017a).

During the 1943 field campaign, about 40 m^3 of sediments was extracted and screen-washed, recovering a large collection of bones and several plant, mollusk, and archaeological remains (Ballmann et al. 1980). These remains are housed at the RBINS under general inventory number (I.G.) 14,138, donated on 4 September 1943. The herpetofaunal assemblage has already been described in Blain et al. (2019) and is now composed of some 20,500 recognized bones of amphibians and reptiles. The faunal list for the lower layers (levels 4–6; Tables 1–5, 6, and 7) comprises two urodeles (*Lissotriton* gr. *L. vulgaris* and *Salamandra salamandra*), four anurans (*Bufo bufo*, *Epidalea calamita*, *Rana temporaria*, and *Rana* cf. *arvalis*), three lizards (*Lacerta* cf. *agilis*, *Zootoca vivipara*, and *Anguis* gr. *A. fragilis*), and three snakes (*Natrix natrix*, *Coronella austriaca*, and *Vipera berus*). The upper layer (level 2; Tables 1–19) has a similar composition but without *Lissotriton* gr. *L. vulgaris* and *Natrix natrix*. One of the main differences lies in the inversion of the dominant anuran taxa between levels 4 and 6 and level 2. *R. temporaria* dominates the level 4–6 assemblages (always representing more than 71% of the anurans), whereas *B. bufo* dominates the level 2 assemblage (67% of the anurans). Blain et al. (2019) proposed that this replacement may be related to an environmental change in the composition or structure of the forested areas between MIS 3 and MIS 2 with the onset of drier conditions.

Cavernes de Goyet (Mozet, Namur)

The network of caves and galleries known as "Cavernes de Goyet" is located at an altitude of 130 m above sea level in a carboniferous limestone cliff on the right bank of the Samson River, in the commune of Mozet, 3 km southeast of Namêche and 10 km southeast of Namur (Ulrix-Closet 1975; Otte 1979; Cahen and Haesaerts 1984; Fig. 1). The main cave is about 15 m above the river (Stevens et al. 2009). Discovered by Dupont (1869a, b), only the third cave has yielded human remains and has been the subject of a more detailed report (Dupont 1872a). Numerous subsequent excavations failed to reveal any human bones. Dupont described five ossiferous levels in the third cave (1872a), giving a list of the species present (Rutot 1910). Only the upper levels 1, 2, and 3 contained industry (Dupont 1872a). The stratigraphy has been reworked, and the series are not homogeneous (de Sonneville-Bordes 1961). A typological analysis, however, recognized the presence of Mousterian, Aurignacian, Perigordian, and Magdalenian industries. Most Mousterian tools are of the Quina type (Ulrix-Closset 1975). The industry of the ancient Upper Paleolithic was analyzed by Otte (1979).

The history of the excavations, summarized in Otte (1979), is complex. Discovered in 1869 by Dupont (Dupont 1869a), these caves have since then continued to attract excavators of all qualifications. Dupont probably undertook his work in all five caves, but above all, he published the results obtained from his exploration of the third one, which was the richest. After excavations by Tihon in 1891, the Service des

Fouilles des Musées du Cinquantenaire (A. de Loët and E. Rahir) in 1907, and many amateurs who returned the excavated material in 1908–1909, important work was undertaken inside the various caves at the beginning of 1936 with the aim of promoting their use as a tourist attraction. This was due to Kaiser, the concessionaire of the caves who sold part of the discovered materials to the RBINS (Angelroth 1937; de Bournonville 1955; Otte 1979). The RBINS thus carried out important excavations in 1937 and 1938, particularly in the third cave. A Middle Paleolithic level was discovered (de Bournonville 1955), and these excavations were extended to caves 2, 3, and 4. They focused on the "Salle du Mouton," the galleries numbered 1 to 6, the "central corridor," the "well," and the terrace. Although no publication ensued, it seems that these works only encountered reworked grounds, except for the probable Mousterian level mentioned above (Eloy 1943; Blouard 1946; Eloy 1952–1953). The material that is studied here comes from these excavations. Specimens are registered under I.G. 12,096, from 22 December 1938.

From the labels kept in the RBINS drawers, Otte (1979) infers that during the 1937 and 1938 excavations, two especially concentrated levels were encountered in the "Salle du Mouton." The upper one was made up of "yellow sediment" (terre jaune) and the lower one was 1.50 m thick and subdivided into three sections, of "black sediment" (terre noire). The artifacts examined by Otte (1979) from these two layers belong almost exclusively to the Aurignacian "yellow sediment," whereas those from the "black sediment" comprise a mixture of Mousterian and Aurignacian pieces. Accelerator mass spectrometry (AMS) dates on selected bone elements cover a period between 12,500 and 39,000 years BP (Germonpré 1997, 2004; Germonpré and Sablin 2001; van Strydonck et al. 2001).

Accordingly, we here consider the samples labeled "niv. inf. en dessous 2e niv. du Moustérien" (Tables 1–10), "Salle du Mouton—2e niveau Moustérien" (Tables 1–11), and "Salle du Mouton—1er niveau Moustérien" (Tables 1–12) to be possible Mousterian samples. The samples from "Salle du Mouton—terre noire" (Tables 1–13) are considered a mixture of Mousterian and Aurignacian, and the samples from "Salle du Mouton—terre jaune" (Tables 1–15) are considered to be Aurignacian. Other samples from the first cave and diverse corridor areas (Tables 1–40 to 44) are not interpreted in terms of chronology. However, it should here be stressed that a Magdalenian chronology is possible for some of these latter, undetermined samples, as the youngest two layers from Goyet contained Magdalenian artifacts. These artifacts found in the Goyet Caves include bone needles, a biserial bone harpoon, a necklace composed of 26 teeth and two bone fragments, a necklace composed of 180 fossil remnants of *Turitella* shells, a "bâton de commandement" (command stick), and fragments of ochre (Dewez 1987; Dupont 1873; van Wetter 1920). A 14C dating of the fauna also gave a Magdalenian age (Germonpré 1997; Stevens et al. 2009). However, the presence of badger and domesticated pig in these upper layers shows that some mixing with later and possibly earlier material has occurred (Germonpré 2001).

In total, the Cavernes de Goyet only document three anuran species: *Bufo bufo*, *Epidalea calamita*, and *Rana temporaria* (Table 1). The "Mousterian" samples from Goyet yielded rather scarce elements of anurans referred at genus level to *Bufo* and *Rana* (probably *B. bufo* and *R. temporaria*). The samples attributed to the Aurignacian/Mousterian ("Salle du Mouton, terre noire") furnished all three species. Notes on labels suggest that within this level *E. calamita* is only represented in the lower part of the level, by various humeri, one ilium, and one tibiofibula. The middle part of this level included the remains of *B. bufo* and *Rana* sp. (probably *R. temporaria*). The upper part only provided two right female humeri of *R. temporaria*. The two "Aurignacian" samples ("terre jaune sup." with bones and silex and worked bones) yielded a particularly abundant number of skeletal elements pertaining to the common toad *B. bufo* (number of remains, NR = 266; minimum number of individuals, MNI = 63), a left male humerus of *E. calamita*, and several remains of *R. temporaria* (number of remains = 32; minimum number of individuals = 13). Finally, samples without a chronological context provided a few remains of *B. bufo* or *R. temporaria*, and both in some cases (Table 1; SOM Appendix S1).

Trou du Chêne (Haut-le-Wastia, Namur)

The caves of Montaigle are part of the Bois de Foy, in the commune of Haut-le-Wastia (Fig. 1). They are located in an almost vertically rising limestone wall (60 m high and 75 m long; Dupont 1868). At the base of the cliff flows the Flavion river. Of the eight caves explored in 1867 by Dupont, only two yielded Paleolithic material: the Trou du Chêne ("Oak Hole") and the Trou du Sureau ("Elder Hole"). These caves were named after the flora that grew in front of the entrance (Dupont 1868).

The Trou du Chêne, in Montaigle, is a small cave located in the same rock face and a few meters west of the Trou du Sureau. Its shape is semi-circular; it has a depth of 8 m and a width (at the entrance) of 5 m. It is approximately 35 to 40 m above the Flavion river (Dupont 1868, 1868–1869; Otte 1979). This cave has a terrace in common with the western entrance to the Trou du Sureau. It was excavated, along with the other shelters in the Montaigle massif, by Edouard Dupont in 1867. The latter (Dupont 1868) recognized four layers (from bottom to top): (a) gravelly sands; (b) sandy-clay deposits; (c) sandy-clay deposits with rolled pebbles and, in places, stones cemented by limestone infiltrations and scree; (d) blocky clay (angular pebbles). The three upper deposits extended to both the cave and the terrace where the connection with the stratigraphy of the Trou du Sureau (Dupont 1868) was established. Of the material deposited at the RBINS, the Trou du Chêne ("3e niveau ossifère") furnished the following arvicoline rodents: *Arvicola amphibius*, *Alexandromys oeconomus*, *Lasiopodomys gregalis*, and *Microtus arvalis* (López-Garcia, unpublished data), mainly characteristic of stable watercourses (*Arvicola*) and open-humid environments (*Alexandromys** and *Lasiopodomys**).

The herpetofauna studied here come from the third and second levels. According to Otte (1979), the lower layer ("third level") certainly dates to the Upper Paleolithic. There is no evidence to attribute it to the Aurignacian. Rather, the presence of a spine point fragment suggests that it dates to the Upper Perigordian (Otte 1979). Here, we consequently attribute this level to the Perigordian age. The overlying level ("second level") could, given its industry, be related to the Mesolithic (Tardenoisian). However, Otte (1979) suggested that Dupont combined the layer of frost-bearing and frost-fractured rubble containing late-glacial rodent bones with the Mesolithic level of occupation that probably lay over this deposit. Thus, the herpetofauna from this level may be related to the Magdalenian more than to the Tardenoisian. The upper level dates, at least in part, to the Neolithic (pottery shards and temperate fauna).

All the material is detailed in the Appendix (SOM Appendix S1). Samples attributed to the Perigordian ("3^{e} niveau ossifère") document the presence of the anurans *Bufo bufo* and *Rana temporaria* (Tables 1–16). *R. temporaria* (NR = 196; MNI = 11) is much more abundant than *B. bufo* (NR = 2; MNI = 1). Samples attributed to the Magdalenian or Tardenoisian (2^{e} niveau ossifère) only furnished abundant remains (NR = 407; MNI = 54) of *Rana temporaria* (Tables 1–23). Finally, Tardenoisian samples ("argile à blocaux") yielded cf. *Pelobates fuscus* in addition to *B. bufo* and *R. temporaria* (Tables 1–24). In these samples, *R. temporaria* (NR = 276; MNI = 66) is much more represented than *B. bufo* (NR = 2; MNI = 1).

A single bone fragment documents the probable presence of the common spadefoot (*Pelobates fuscus*) in the Trou du Chêne (Fig. 2C). This fragment is distinctive in that it bears dense dermal ornamentation on the external surface of the bone. On the inner side of the bone, two well-separated subparallel crests are visible. The morphology of these crests may indicate that this element was part of a maxilla, but the fossil is too incomplete to rule out definitively that it might be a fragment of frontoparietal or squamosal, bones that also bear dermal ornamentation in pelobatids.

Trou du Sureau (Haut-le-Wastia, Namur)

The Trou du Sureau ("Elder Hole"; Fig. 1) is the largest of the Montaigle caves (Otte 1979). It is located at an altitude of 33 m above the Flavion river. It was formed between two limestone sections separated by a fault. The two entrances, one to the south, the other to the west, are separated by a massive pillar. A back wall forms a slight overhang, forming an outside shelter of 33.5-m length. The two entrances are currently very large, being more than 6 m high. The Trou du Sureau was excavated in 1867 by Dupont, together with the Trou du Lierre ("Ivy Hole") and the Trou du Chêne. In 1948, excavations were resumed by the RBINS (J. de Heinzelin and collaborators).

Dupont (1868) established a stratigraphy composed of 12 levels, numbered from bottom to top. Layer 11 contained, towards the base, industry, and fauna. Large mammals were represented by a few elements from reindeers and horses. The carnivore material pertained to the red fox, large canids, stone marten, stoat, weasel, polecat, and badger (Dupont, unpublished notes in Van Neer et al. 2007). Dupont (1873) mentions an assemblage for this cave, which he describes as an unusual accumulation of small mammals, terrestrial birds (575 individuals), anurans, shells, and freshwater fish. Due to the high number of remains, the material was only partially sampled and in a random way. Van Neer et al. (2007) described the fish material from the Trou du Sureau as mainly graylings, brown trout, burbots, and unidentified cyprinids. A hearth (with burnt bones and carved flint) occupied the central part of the cave. This assemblage corresponds to the "second ossiferous level." During the 1948 excavations, J. de Heinzelin observed an upper layer composed of frost-fractured limestone blocks embedded in the breccia, which contained microfauna that could correspond to the second level of Dupont. No dates are available for the second bone horizon, but Dupont assigned it to the "Age du Renne." Typical pleniglacial species such as mammoth, cave bear, or cave hyena, found in the deeper horizons of the cave, are lacking in this assemblage (Dupont, unpublished notes in Van Neer et al. 2007). This level has been attributed by Otte (1979) to the late glacial and more precisely to a short Perigordian occupation. The latter author proposes a correspondence between the layers of the Trou du Chêne and those of the Trou du Sureau that differs from that of Dupont: the Perigordian layer ("3rd level" of Trou du Chêne) would correspond to level 2 of the Trou du Sureau; the two upper layers (Mesolithic and Neolithic) would be mixed in level 1 of the Trou du Sureau, according to the study of lithic industries.

The herpetofaunal remains studied here stem from the Dupont excavation. Abundant material of the common brown frog *Rana temporaria* (NR = 123; MNI = 9) is all that has been described in the Trou du Sureau (Tables 1–17; SOM Appendix S1).

Trou de Praules (Furfooz, Namur)

The Trou de Praules is one of three caves along the Lesse river, explored by Edouard Dupont during the months of

March and April 1866 (Dupont 1868). It is located 500 m upstream from Furfooz (Fig. 1), on the left bank, about 30 m above the Lesse river. The cave is 6 m wide and 3.5 m long in the middle. The height between the rocky floor and the ceiling averages only 2 m. The Quaternary sediments at the base, immediately on the limestone floor, consist of a thin layer of stratified clay-sand deposits with rolled pebbles and gravel arranged in non-continuous veins. The sequence continues with yellow clays with blocks ("argiles jaunes à blocaux"), less than one meter thick and containing, mostly at the base, bones (bear, wolf, fox, horse, reindeer, and goat), and some flints. Dupont therefore attributed this level to the Age of the Reindeer. Here, we place this assemblage within the Perigordian or Magdalenian (Table 1).

The first ossiferous layer from the Trou de Praules has furnished a few remains attributed to anurans. *Bufo bufo* is represented by 30 bones corresponding to five individuals, whereas a few elements (three radioulnae and four phalanxes) have been associated with the genus *Rana* (probably *R. temporaria*) (Tables 1–20; SOM Appendix S1).

Trou de Chaleux (Houyet, Namur)

The Trou de Chaleux is located in a limestone cliff on the right bank of the Lesse river, 6 km southeast of Dinant and 1 km southwest of Furfooz (Ulrix-Closset 1975; Cahen and Haesaerts 1984; Otte 1994; Fig. 1). It is situated about 15 m above the Lesse river (Otte 1994). The site, excavated by van Beneden, Hauzeur, and Dupont in 1865, was later the subject of two detailed descriptions (Dupont 1865, 1867c). A geological section is given by Dupont (1865), who also provides an inventory of the species found, including large mammals (many displaying cut marks and anthropogenic breakage), birds, fish, and numerous artifacts (Dupont 1867c, 1871, 1873). The very abundant lithic material has been attributed to the upper Magdalenian (de Sonneville-Bordes 1961). The human remains, housed at the RBINS (Planchette 2602), consist of a fragment of parietal, four isolated teeth, seven ribs, four fragments of scapula, four long bones of the arm, four bones of the leg, and bones of the hand and foot (Cahen and Haesaerts 1984).

New excavations were undertaken at the end of the twentieth century on the terrace in front of the cave. M. Otte and colleagues unearthed remains from a Magdalenian occupation, including mammals (Otte 1994). Detailed reviews of the excavations at the Trou de Chaleux can be found in Otte (1994) and Charles (1998). Dewez (1987) presents an exhaustive analysis of the Magdalenian artifacts, including large collections of lithic and bone industries as well as figurative art. The three best-represented mammals are horse, fox, and muskox (Charles 1998; Germonpré 1997). In addition to mammal remains, the cave also yielded bird and fish remains (Dupont 1873; Van Neer et al. 2007). The presence of bird taxa such as the snowy owl (*Bubo scandiacus*) and ptarmigans (*Lagopus* sp.) is also clearly associated with Arctic environments and is consistent with an attribution to the late Magdalenian (Goffette et al. 2020).

Several AMS dates are available, with calibrated ages ranging from 15,733 cal BP to 14,134 cal BP (Germonpré et al. 2009; Stevens et al. 2009; Goffette et al. 2020), situating the main deposit of the mammal assemblage from the Trou de Chaleux, identified by Dupont as the "1er niveau ossifère," at the transition from Greenland Stadial 2 to Greenland Interstadial 1 (Bølling-Allerød Interstadial). The more recent excavations verified the chronological homogeneity of the Magdalenian layer excavated by Dupont. However, part of the assemblage is clearly much younger, as attested by a radiocarbon-dated prehistoric pig humerus with cut marks (OxA-4193: 3,060 ± 85 BP) (Charles 1998), and the presence of six bones of the chicken (*Gallus gallus* f. *domestica*), which obviously represent a more recent intrusion (Goffette et al. 2020).

The herpetofaunal remains recovered at the Trou de Chaleux during the excavation by E. Dupont in 1865 and stored at the RBINS are exclusively composed of the common brown frog *Rana temporaria*, which is present in great abundance (NR = 1988; MNI = 142; Fig. 2E). There is also the rare presence of a viper (cf. *Vipera* sp.), documented by a left dentary and, by association, probably also one rib (Tables 1–21; SOM Appendix S1). The dentary (IRSNB R 445; Fig. 5), of which a length of 9.5 mm is preserved, is short and straight, as in vipers (Fig. 5A). The tooth number can be estimated to be 14 or 15, based on the alveolar counting method. In dorsal view, the anterior end of the bone is more or less curved inside. In medial view, Meckel's groove is anteriorly completely closed. In lateral view, the mental foramen, filled with sediment, is well elongated and lies close but slightly anterior to the midpoint of the dentary length.

Trou du Château (Haut-le-Wastia, Namur)

The Trou du Château ("Castle Hole") is one of the Montaigle caves (Fig. 1). No information has been found about its excavation, and the RBINS catalog is unclear about the provenance of its remains. Labels associated with this material indicate only that the biochronology was suggested to be of the "Reindeer Age." Here, we thus tentatively classify the site as probably Magdalenian. This site only furnished a few remains of *Rana temporaria* (NR = 16; MNI = 3; Tables 1–22). In addition, a few non-diagnostic elements have been attributed to Anura indet. (SOM Appendix S1).

Trou Balleux (Walsin, Namur)

The Trou Balleux is located in Hulsonniaux (Fig. 1), on the left bank of the Lesse river, 280 m downstream from the hamlet of Chaleux (Cahen and Haesaerts 1984). Its opening is 45 m above the level of the river. The site was excavated by Dupont in 1866, by Goffin in 1894, and also in the 1980s (Depaepe 1988). Dupont (1867c) gives a record of the stratigraphy and mentions human occupations in "two different periods." Dupont discovered remains from beaver, red deer, roe deer, horse, bison, sheep/goat, and pig (unpublished notes in Germonpré et al. 2009). A few human bones were also collected by Dupont in 1867 (Planchette 2490), and more elements, including a skull, along with some elements of industry, were collected in 1894 (I.G. 6183; Cahen and Haesaerts 1984). The species present point to a postglacial age for this assemblage (Germonpré et al. 2009). A 14C dating based on a deer bone from the 1894 excavation gives a date of 10,110 ± 120 BP (Dewez 1981), i.e., between 12,127 and 11,257 cal BP and corresponding to the Lateglacial-Holocene transition and the beginning of the Preboreal.

For this site, the material available at the RBINS is from the excavation by Dupont (Planchette 2490) and only includes remains of *Bufo bufo* (NR = 53; MNI = 9) (Tables 1–25; SOM Appendix S1).

Trou du Frontal (Furfooz, Namur)

The Trou du Frontal ("Frontal Hole") is part of the Furfooz cave complex, already mentioned as including the Trou de Praules, and located 500 m upstream from Furfooz (Fig. 1). It is located 16 m above the Lesse river on its left bank. It was probably explored at the same time as the Trou de Praules by Edouard Dupont during the months of March and April 1866 (Dupont 1866). This cave yielded a Magdalenian assemblage, including remains of horse and reindeer (Germonpré et al. 2009). The carnivores in the faunal assemblage comprise red fox, Arctic fox, large canids, brown bear, stone marten, stoat, weasel, polecat, badger, and cat (Dupont, unpublished notes in Germonpré et al. 2009). Along with mammals, bird and fish remains were also discovered at the Trou du Frontal (Dupont 1873; Van Neer et al. 2007). Furthermore, a significant proportion of postglacial material was also excavated by Dupont in the 1860s, including a high number of pig and sheep/goat remains.

A dating of the layer attributed to the Magdalenian gave 10,720 ± 120 BP (Lv-1135), but the dating made at the request of the RBINS on human ribs 4,430 ± 30 BP (GrN-10 179) confirms the recent character of the bones, which was suggested by their relatively high nitrogen content (Twiesselmann 1971; Cahen and Haesaerts 1984).

Among the material stored at the RBINS (labeled as first ossiferous layer, yellow clays with blocks, Reindeer Age), the following taxa of amphibians and reptiles have been identified: the midwife toad (*Alytes obstetricans*), common toad (*Bufo bufo*), European common brown frog (*Rana temporaria*), European grass snake (*Natrix natrix*), and the Aesculapian snake (*Zamenis longissimus*) (Tables 1–26). *B. bufo* (NR = 95; MNI = 16) and *R. temporaria* (NR = 93; MNI = 21; SOM Appendix S1) are equally abundant. The thermophilous character of *Z. longissimus*, only recorded from the MIS 5 and Holocene layers of Scladina Cave (see the "Grotte de Scladina (Sclayn, Namur)" section), does not fit well with attribution to the Magdalenian, and consequently, this assemblage is tentatively attributed to the postglacial material from the Chalcolithic period (between 5,070 and 4,876 cal BP).

A. obstetricans is represented by a nicely preserved ilium (Fig. 2A). The ilium shaft is rather straight. It does not have a dorsal crest, and the superior tubercle is well developed, with a slightly rectangular lateral outline, and located for the most part over the acetabular cavity. Posteriorly, the ischial process (*pars ascendens*) is long, and the pubic process (*pars descendens*) is reduced. In the posterior view, the bone shows a moderately developed tubercle and interiliac groove. The posteromedial face is smooth. All these features permit an attribution to generic level only. However, based on biogeographical information, this element can be referred to as the midwife toad (*A. obstetricans*), the only species of the genus still living today in southern Belgium (De Witte 1942; Duguet and Melki 2003; de Wavrin and Graitson 2007).

A probable single individual of the grass snake group (*Natrix natrix* s.l.) has been reconstituted and glued onto a wooden plate (Planchette 2188, Fig. 3A). This specimen is constituted by one left maxilla, two dentaries (left and right), 39 trunk vertebrae, five caudal vertebrae, and some 40 ribs. As can be observed in Fig. 3A, this snake has been wrongly reconstituted, with the ribs glued contrary to the anatomical orientation in a living specimen, and the cranial elements have been glued at the continuation of the caudal vertebrae. The left maxilla, presented in medial view (Fig. 3A1), is elongated and 14.2 mm long. It is clearly opisthomegadontic, with one of the preserved last teeth being considerably larger than the six preserved previous ones. The prefrontal process projects laterally, and a tip on its intero-posterior end protrudes backward. The ectopterygoid process is tapered and projects intero-anteriorly. The morphology of this maxilla is similar to the one figured for *Natrix natrix* by Szyndlar (1984a: Fig. 44.13). The right and left dentaries are exposed in medial view (Fig. 3A2 and A3). Their total preserved length is respectively 15.4 and 15.7 mm, and both bear 13 preserved teeth. The dentition is isodontic, with long, backward-curved teeth. Meckel's groove opens widely into a compound notch and anteriorly is completely closed. Although it does not seem to be as elongated as figured by Szyndlar (1984a), it falls within the variability of what has been observed in the representatives of the genus *Natrix* hosted in the IPHES-CERCA osteological collections. Viper dentaries are usually much shorter than those of other snakes, with only 14 or 15 tooth positions, and colubrine snake dentaries (genera *Zamenis* and *Hierophis*) are strongly proterodontic (Szyndlar 1984a). A detached trunk vertebra of specimen IRSNB R 444a permitted us to complete the description (Fig. 4C). This trunk vertebra has a somewhat sigmoid hypapophysis, and the neural arch is convex in posterior view. The condyle and the cotyle are small and circular. The attribution to *Natrix natrix* s.l. is based above all on the morphology of the centrum, which is flat or concave with clearly marked lateral margins, whereas in *Natrix maura* the centrum is slightly convex with somewhat diffuse lateral margins (Szyndlar 1984a). In addition, the morphology of the extremity of the hypapophysis and the paradiapophysis (i.e., diapophysis plus parapophysis) is robust and blunt, as in *N. natrix* s.l. (Szyndlar 1984a). The grass snake group currently includes *Natrix helvetica* (Britain, France, Netherlands, Belgium, Germany, and Switzerland), *Natrix natrix* (central and eastern Europe, southernmost Scandinavian Peninsula, and the Balkan Peninsula), and its Iberian representative *Natrix astreptophora* (Kindler and Fritz 2018; Kindler et al. 2017, 2018a, b; Pokrant et al. 2016). Although these species have not been fully separated from an osteological point of view, the fossils from the Trou du Frontal may pertain to *Natrix helvetica*, the only living representative of the group in Belgium.

Finally, on the same "Planchette 2188," ten trunk vertebrae (centrum length estimated to be around 4.0 mm) and one rib are attributed to *Zamenis longissimus* (specimens IRSNB R 444; Fig. 4B). In order to describe these vertebrae, the anteriormost one has been carefully removed from its support (Fig. 4C). This trunk vertebra does not bear a hypapophysis on the centrum, as in "colubrine" snakes, and is characterized by a deep and rounded haemal keel that is spatulate at the caudal end. The prezygapophyseal processes are relatively short and show a slender and pointed tip (as on specimen IRSNB R 443; Fig. 4A; Bailon 1991; Szyndlar 1984a). The zygosphene is straight anteriorly. All these characters refer to this vertebra to the species *Z. longissimus*.

Trou Magrite (Pont-à-Lesse, Namur)

The Trou Magrite is situated in a rocky limestone massif, on the right bank of the Lesse river, between Walsin and Pont-à-Lesse, 5 km southeast of Dinant (Fig. 1). It is 150 m from the river and opens 26 m above it (Ulrix-Closset 1975). The site is composed of a high outer rock shelter covering a large terrace, a lower and an upper mouth, a vestibule, a broad main chamber, and a small rear room at the base of a now-blocked chimney that was probably once open to the plateau above (Gautier et al. 1997; Jimenez et al. 2016). The excavations were mainly carried out by Dupont in 1864–1865, reaching the bedrock in 1867 (Dupont 1865, 1867a, 1872a). After Dupont, many researchers continued to visit the site and carry out excavations there, such as Rahir in 1908 (Rahir 1928) and Rutot in 1913–1914 (Angelroth 1939), but notably without publishing the results of their research. Dupont found four ossiferous levels (Dupont 1867a; Rutot 1910), but he gave only one list of species, although he reported significant differences between the lower and upper levels (Dupont 1872a). Dupont states simply that reindeer and horse were more abundant in the "upper levels," whereas mammoth, rhinoceros, and other extinct species were more abundant in the "lower levels" (Dupont 1867a, 1868–1869). The lithic tools are very rich, but the objects from the various levels have been brought together: they relate to the Mousterian, Aurignacian, and Perigordian, as well as a facies from the end Upper Paleolithic (de Sonneville-Bordes 1961; Ulrix-Closset 1975; Otte 1979). The presence of human remains is mentioned by Dupont in a synoptic table (Dupont 1872a). Preserved at the RBINS, the material consists of a child's upper jaw bearing five teeth, one occipital fragment, one isolated tooth, four fragments of an upper limb, six fragments of a lower limb, and one vertebra (Cahen and Haesaerts 1984).

The material studied here comes from Dupont's excavations. The associated label, signed by Dupont in October 1906, indicates a Neolithic attribution for these materials, with the occurrence of "*Arvicola amphibius*, *Arvicola agrestis*, *Mus sylvaticus*, *Myoxus glis*, *Talpa europaea*, birds, anuran, fish, and terrestrial shells." This assemblage is tentatively attributed to the Holocene (Tables 1–28). As regards herpetological remains, only *Bufo bufo* and *Rana temporaria* are documented at the Trou Magrite (Table 1; SOM Appendix S1), with *B. bufo* being somewhat more abundant (NR = 28; MNI = 5) than *R. temporaria* (NR = 8; MNI = 2).

Unknown locality labeled "Puit artésien de l'atelier central"

Apart from the label associated with this interesting herpetofaunal assemblage (Tables 1–29; SOM Appendix S1), no information is available concerning the stratigraphy, chronology, or other contextual features. However, the site is relatively important from a paleoherpetological point of view, as it documents the first fossil record in Belgium for *Hyla arborea* and one of the few mentions for *Rana arvalis* and *Anguis fragilis*. This assemblage yielded a total of 353 remains, from which *B. bufo* (NR = 65; MNI = 11) is the most highly represented species, followed by *R. temporaria* (NR = 23; MNI = 10) and *R. arvalis* (NR = 46; MNI = 6).

The moor frog (*Rana* cf. *arvalis*) is represented by one squamosal, seven parasphenoids, and 38 vertebrae. The only squamosal has a typical T morphology, with the anterior and posterior extremities of the transverse process presenting a somewhat similar development. Attribution to the species level within the genus *Rana* is difficult because of very small distinctions and high intraspecific variability (Ratnikov and Blain 2020). The anterior process is wide, with a sharp bend on the lower edge as in *R. arvalis*, whereas *R. temporaria* has a narrow and long anterior process (Ratnikov and Blain 2020). The parasphenoids (Fig. 2D) are thin, and their total length is greater than the distance between the ends of the lateral processes. They have a wide anterior process. The width of the lateral processes, though incomplete, seems to be considerably less than the width of the anterior process. This latter character permits a cautious attribution to *R. arvalis*, whereas in *R. temporaria* the lateral processes are somewhat wider (Ratnikov and Blain 2020). Of the fossil material, some 38 vertebrae have been tentatively referred to *R. arvalis*, based on their well-expressed dorsal flattening and their lesser robustness than usually observed in *R. temporaria* (Ratnikov and Blain 2020). The neural arches have shorter laminae and narrower pedicles than in *R. temporaria*, and the medial part of the neural arch in the trunk vertebrae protrudes towards the back and upwards. Six of these vertebrae, being amphicoelous, have been identified as having the eighth position in the column.

The European tree frog (*Hyla arborea*) is represented by a single almost complete right ilium with all its anterior branches preserved (Fig. 2F). Small in size, it has no dorsal crest but has a globose, laterally curved superior tubercle, and a ventrally enlarged pubic process (*pars descendens*; Bailon 1999). This ilium thus clearly pertains to the genus *Hyla*. Osteologically, the morphology of the superior tubercle permits us to rule out attribution to the Mediterranean tree frog *Hyla meridionalis*, where the superior tubercle is more or less circular in lateral view, whereas in the other European species of the genus, *Hyla molleri*, *Hyla arborea* sensu stricto, *Hyla orientalis*, and *Hyla intermedia*, this superior tubercle is dorsoventrally flattened (Holman 1992, 1998). Based on biogeographical arguments, this ilium is referred here to as the current species *Hyla arborea* sensu stricto, the only representative of the genus today in Northwestern Europe (Stock et al. 2012).

The slow worm (*Anguis fragilis*) is represented by a single particularly well-preserved caudal vertebra. This vertebra is elongated and dorsoventrally flattened, and as usual in anguid lizards, its centrum, in ventral view, has a flat ventral surface. Hemapophyses are fused to the centrum on its posterior half, and the transverse processes are well developed and dorsoventrally flattened. Given its small size and the biogeographical context, other anguine genera such as *Ophisaurus* and *Pseudopus* can be ruled out. This fossil vertebra does not display any morphological differences with respect to those of the present-day *A. fragilis* group, which comprises newly erected species but is still not diagnosed osteologically: *A. cephallonica*, *A. colchica*, *A. fragilis*, *A. graeca*, and *A. veronensis* (Gvoždik et al. 2013).

Trou des Nutons (Furfooz, Namur)

The Trou des Nutons or Caverne de Gendron is a cave located 2,500 m as the crow flies from the Furfooz caves. It is located on the right bank of the Lesse river, about 70 m above it. The cave is 14 m long and 2.5 m wide. Dupont (1868) described various levels. The first ossiferous layer corresponds to his yellow clays with blocks (“argile jaune à blocaux”) and a more superficial layer (“compost formed by the decomposition of leaves”). It was in this “humus” layer, located 8 m from the entrance and covered by a 60-cm-thick stalagmite, that Dupont discovered some 17 human skeletons. The pottery associated with these burials was studied by G. de Mortillet, who suggested that it was from the “transition between Stone and Bronze Ages” (Dupont 1868). The lower layer was attributed to the Age of the Reindeer by Dupont (1868). In this first ossiferous layer, Germonpré et al. (2009) studied the partly associated skeleton of a large canid that Dupont had identified as a wolf. The skull has been given an AMS age of 21,800 ± 90 BP, whereas the main bone horizon produced Magdalenian artifacts, and a cut-marked horse phalanx has been dated by AMS to 12,630 years BP (Charles 1998). The material is latest Pleistocene in age but has probably been mixed.

The herpetofauna studied here (I.G. 2530 from 20 October 1865) comes from the first ossiferous layer. It yielded a very few bones from two anuran taxa: a left ilium and a tibiofibula from *Bufo bufo* and two very large tibiofibulae (maximum length = 37 mm) from an indeterminate ranid (Ranidae indet., maybe pertaining to the genus *Pelophylax*) (Tables 1–30; SOM Appendix S1).

Trou de La Naulette (Walsin, Namur)

The Trou de La Naulette (or Caverne de la Naulette) is a large cave that opens on the left bank of the Lesse river, 2 km northwest of Hulsonniaux and 6 km southeast of Dinant (Fig. 1). It is located about 500 m upstream from the Trou du Blaireau and 25 m above the river. Its opening is only a few meters wide and it is over 60 m in length. Its width averages 10 m (Dupont 1866; Cahen and Haesaerts 1984).

The report of the first excavations carried out in 1866 was published the same year (Dupont 1866). The essential data, including a geological section, are given in successive publications by Dupont (1866, 1867b, 1871, and 1872a) and Rutot

(1910). The test pit made by Dupont would have revealed an 11-m stratigraphy with 15 levels. There were three ossiferous levels according to Dupont (1867b). The lowest level (the first ossiferous level) yielded only a fragmentary hyena maxilla. The second ossiferous level provided "few but admirably preserved remains." The species documented by Dupont were wolf, brown bear, fox, badger, bat, marmot, water rat, mammoth, rhinoceros, horse, reindeer, wild boar, chamois, common deer, mouflon, and fish. It is probably this level that yielded a Neanderthal mandible and ulna in 1866 (Dupont 1866), a canine in 1867 (Dupont 1867c), and a right metacarpal III in 1872 (Dupont 1872a; Cahen and Haesaerts 1984). The mandible, ulna, and right metacarpal are preserved at the RBINS (Planchette 2569). The anatomical features of this mandible have made it possible to attribute it to a Neanderthal, probably related to the Mousterian culture (Cahen and Haesaerts 1984). A paleoanthropological study suggests that the morphology of the human jaw may place it among the early Neanderthals, showing similarities with morphologies usually observed around 120,000 years ago (Pirson and Toussaint 2011). Finally, the upper level (third ossiferous level—layer 2) yielded only a few bones, mostly the jaws of an undetermined ruminant.

The material studied here at the RBINS (I.G. 5039) was deposited on 25 December 1883 by Edouard Dupont and corresponds to "rock and fossil samples collected in 1883 during the geological map survey." The associated label indicates that these remains come from the third (and uppermost) ossiferous level. The label mentions Mammoth Age, but its upper position in the stratigraphy and the uncertainty concerning the systematic attribution of the ruminant (sheep or mouflon) preclude any chronological attribution of these remains.

Whatever the case, the identified paleoherpetological remains are very scarce and consist of a right humerus from a female *Bufo bufo* and two large-sized (total length = 33 mm) tibiofibulae from a frog (Ranidae indet.) (Tables 1–31; SOM Appendix S1).

Trou des Blaireaux (Vaucelles, Namur)

The Trou des Blaireaux ("Badger Hole") is located about 500 m upstream from the Trou de La Naulette, 2 km northwest of Hulsonniaux and 6 km southeast of Dinant (Fig. 1). The cave is 20 m deep and not very wide and ends in a badgers' burrow. Its transverse diameter is about 6 m. It is 75 m above the level of the Lesse river, on its left bank. Dupont (1868) described three layers in the cave. The first is composed of yellow sediment. The second layer—also called "first ossiferous level" on the RBINS labels—is made up of yellow clays with blocks ("argile jaune à blocaux"). This is the only layer where some evidence of human occupation has been found (Dupont 1866). The recovered bones are few and document horse, elk, fox, badger, feral cat, and heather rooster. Finally, a third layer at the base is composed of alternating clayey and sandy sediments ("lehm").

The material identified in the RBINS Quaternary collections proceeds from the second layer. Apart from the attribution of this layer to the Reindeer Age by Dupont, no further chronological data have been proposed for this second level. We regard the chronology as uncertain. As regards the herpetofauna, only *Bufo bufo* (NR = 34; MNI = 4) has been recovered from this locality (Tables 1–32; SOM Appendix S1).

Trou Reuviau (Furfooz, Namur)

This cave is located 1 km south of Furfooz, on the right bank of the Lesse river, and 6 km southeast of Dinant (Fig. 1). It is open to the west, at an altitude of 34 m above the river, from which it is about 500 m away. The cave itself is 3.5 m deep, 1.8 m wide, and 1.8 m high. It is preceded by a small terrace (Rahir 1914; Otte 1979).

The first and most important excavations were carried out by Dupont in 1864 or 1865 (Dupont 1865; Twiesselmann 1952). According to Rahir (1914), excavations also took place later, in 1866–1868. Dupont probably excavated most of the deposits, both in the cave and on the terrace (Otte 1979). Dupont (1865) recognized the succession of the following deposits: above the bedrock, there was a layer of yellow clay, with angular boulders, containing faunal remains but no industry. Above it, "loose deposits" with Roman tiles and "some other objects" were encountered. Dupont therefore observed only one "ossiferous" level located in the yellow clay with blocks ("argile jaune à blocaux"). Dupont (1867b, 1872b) included the occupation of the lower level in the "Reindeer Age." Based on the industry, A. de Loë (1912) attributed it to the "Gravette type: Upper Aurignacian." Thereafter, it was generally considered to be a Magdalenian occupation only (Twiesselmann 1952; de Sonneville-Bordes 1961).

Dupont (1867b) reported remains of brown bear, wild boar, horse, fox, reindeer, and water rat in the yellow clay with blocks. In the RBINS collections, a series of bones exhibit determinations made by Dupont (in 1905 and 1907, according to the labels). This fauna includes, without indication of level, the following: snow fox, common fox, cat, badger, hare, horse, wild boar, capridae, roe deer, musk ox, bison, elk deer, and chamois. Twiesselmann (1952) cites the following species: *Ursus arctos*, *Felis lynx*, *Rangifer tarandus*, *Canis lupus*, and *Dicrostonyx torquatus*. Otte (1979) points out the absence of archaic species generally associated with early Upper Paleolithic cultures (mammoth, rhinoceros, and cave bears). On the other hand, according to the same author, the fauna clearly presents species belonging to a recent period, which testify to the mixing between levels. Additionally, according to Otte (1979), the prehistoric material of the underlying level has undergone major disturbance and contains a mixture of at least two Upper Paleolithic industries: Mousterian, some Aurignacian objects, and a more recent industry (Upper Perigordian or Magdalenian). Finally, occupation in the Neolithic period appears very likely, disturbing the earlier levels.

The Trou Reuviau furnished remains of *Bufo bufo* (NR = 18; MNI = 5), *Rana temporaria* (NR = 5; MNI = 2), and a set of elements glued on a cardboard and certainly corresponding to a single individual of the grass snake *Natrix natrix* (Fig. 3B), composed of one right pterygoid, one left dentary, 32 trunk vertebrae, four caudal vertebrae, and seven ribs (Tables 1–33; SOM Appendix S1). The fragment of right pterygoid (preserved length = 14 mm) is presented in ventral view (Fig. 3B1). It corresponds to the posterior part of this element. Six similarly long and strongly backward-curved teeth are preserved. The morphology of the posterior process, oriented posterolaterally, is rather short, and with its straight lateral margins, it is characteristic of *Natrix*, whereas in *Zamenis longissimus* it is usually much longer and wider with curved lateral margins, and the dentition is proterodontic (Szyndlar 1984a). The dentary is exposed in medial view (Fig. 3B2). Its total preserved length is 16 mm. The number of tooth positions cannot be counted exactly because of the erosion of the anteriormost part of the element. However, the dentition seems to be somewhat isodontic, with long, backward-curved teeth. Meckel's groove opens widely into compound notch, and anteriorly is completely closed. As with previously described fossil dentaries, this bone does not seem to be as elongated as figured by Szyndlar (1984a). However, it falls within the variability observed in representatives of the genus *Natrix* hosted in the IPHES-CERCA osteological collections. The trunk vertebrae, as already described above for genus *Natrix*, have a somewhat sigmoid hypapophysis, and the neural arch is convex in posterior view. Though hardly visible due to the glue, the morphology of the extremity of the hypapophysis and the paradiapophysis is robust and blunt, as in *N.* gr. *N. natrix*. As in the Trou du Frontal, this specimen can be related to the current species *Natrix helvetica*, the only living representative of the group in Belgium.

Caverne de Freyr (Waulsort, Namur)

Some herpetofaunal remains have been identified among the material labeled as being from the Caverne de Freyr (I.G. 4916 from 15 December 1882); these correspond to "rock and fossil samples collected in 1882 during the geological map survey by M.E. Dupont." This cave is located on the property of the Castle of Freyr, on the left bank of the Meuse River, between the cities of Waulsort and Anseremme (Fig. 1).

According to the labels associated with this material, Dupont collected fossils partly from the in situ sediment and partly from the reworked sediment. Both collections were attributed to the Age of the Mammoth. The material is reasonably abundant but documents only a few species. In the in situ sediment, where Dupont mentions the presence of *Rhinoceros tichorhinus*, only *Bufo bufo* (NR = 338; MNI = 35) has been documented (Tables 1–34; SOM Appendix S1). The reworked sediment yielded a more diverse faunal list according to Dupont (*Felis catus*, *Felis lynx*, *Gulo borealis*, *Canis lupus*, *Canis lagopus*, *Canis vulpes*, *Arctomys marmotta*), but as far as amphibians and reptiles are concerned only *B. bufo* (NR = 9; MNI = 2) and *Rana temporaria* (NR = 51; MNI = 4) are represented (Tables 1–35; SOM Appendix S1). This material is considered here to be of uncertain chronology.

Cavernes du Bay-Bonnet (Trooz, Liège)

The site of the Bay-Bonnet caves (also known as Grottes de Fonds-de-Forêt) consists of two caves 8 m apart located in the commune of Forêt, on the left bank of the Magne river, a tributary of the Vesdre river, 12 km southeast of Liège (Rutot 1909; Ulrix-Closset 1975; Cahen and Haesaerts 1984; Pirson and Toussaint 2011). These caves are located about 100 m from the river and 18 m above the riverbed (Rutot 1909; Toussaint et al. 2004). The upstream cave, or "first cave," is the larger. Facing west, it consists of an angled gallery about 30 m long, sometimes referred to as the "Hamal-Nandrin" hall or corridor, which leads to a large hall called "Schmerling." It is this corridor which, in 1895, yielded some Neanderthal bone and dental remains.

These caves were first excavated by Schmerling ("Trous de Sottais") in 1829–1830. F. Tihon resumed excavation and exhumed a right femur and a Neanderthal tooth in 1895 in the upstream cave (Tihon 1898). The femur is currently in deposit at the RBINS. Subsequent excavations have not yielded any human remains (Ulrix-Closset 1975; Otte 1979). The few geologists involved carried out more precise surveys, such as Rutot in the upstream cave (Rutot 1909) and Fourmarier during excavations in the 1930s at the Fonds de Forêt (Hamal-Nandrin et al. 1934). The excavation of the terrace by Hamal-Nandrin et al. (1934) suggests the presence of two ossiferous levels: a first Magdalenian (?) level and a second Mousterian level. Finally, in 2003, M. Toussaint carried out several test pits (Pirson and Toussaint 2011).

The various stratigraphic observations were compared by Twiesselmann (1961), Ulrix-Closset (1975), and Otte (1979). No precise conclusions seem to have been drawn from the study of the fauna collected at Bay-Bonnet (Ulrix-Closset 1975). The product of the excavations (industries) by Tihon has been brought together into a single group;

the presence of Mousterian, Aurignacian, Perigordian, and Magdalenian industries has been mentioned (de Sonneville-Bordes 1961; Ulrix-Closset 1975; Otte 1979). However, according to Toussaint et al. (2004), the Mousterian lithic material is homogeneous and of the Quina type (Charentian). He suggests that the Neanderthal remains would have come from this level and attributes an age of 35–40 ka to them.

There is no information associated with the material we accessed from the RBINS, nor any indication of what excavation or ossiferous level these elements would have come from. The preservation of these bones, however, suggests a fairly recent age (Holocene?) and may therefore be due to a reworking rather than belonging to ancient levels (Mousterian-Gravettian).

This site has furnished a very few remains of *Bufo bufo* (NR = 5; MNI = 1) and *Rana temporaria* (NR = 9; MNI = 3; Tables 1–36; SOM Appendix S1). This material is here considered to be of uncertain chronology.

Trou de l'Érable (Haut-le-Wastia, Namur)

The Trou de l'Érable ("Maple Hole") is, like the Trou du Chêne and Trou du Sureau described above, part of the Montaigle complex of caves (Fig. 1). The label associated with the material mentions that it comes from the first ossiferous layer (yellow clay with blocks, "argile jaune à blocaux"), attributed to the Reindeer Age by Dupont. No additional indication has been found concerning the age of this material, which is here thus considered to be of uncertain chronology.

An abundance of *Bufo bufo* (NR = 224; MNI = 18) has been documented at the Trou de l'Érable (Tables 1–37; SOM Appendix S1).

Grotte la Chefalize (Jemeppe-sur-Sambre, Namur)

Some herpetological material labeled as being from La Chefalize Cave has been recovered within the RBINS Quaternary collections. According to the general inventory (I.G.) number, this cave is located in the municipality of Jemeppe-sur-Sambre in the Province of Namur. Other locality names given on the label (Onoz-Spy) refer to ancient municipalities that were merged under the name Jemeppe-sur-Sambre in 1977. This material comes from an "Exploration of the Institute; bones of Pleistocene mammals and other vertebrates from an Onoz-Spy cave," and it was deposited at the RBINS on 1 September 1970 (I.G. 17,467). The labels associated with the material refer to a quarry ("carrière Glume") and to two different rooms inside the cave.

No information from archaeological or geological sources has been found concerning this site. In the municipality of Jemeppe-sur-Sambre, there is an old, 6-ha quarry called "Vaux quarry," "Delsipée quarry," or "Onoz quarry" (SPWARNE 2020). Located in the Orneau Valley, the site was exploited from 1902 to 1966 as a quarry and lime kilns, then became a landfill site for household, inert, and industrial waste until 1987 and subsequently a place where used tires were clandestinely deposited. Since its remediation in 2004, the site has regained its wild and natural character and now serves as a refuge for flora and fauna of interest (SPWARNE 2020).

The material from the first room (Tables 1–38; SOM Appendix S1) included the rather abundant remains of the parsley toad *Pelodytes punctatus* (NR = 27; MNI = 6), with four ilia, four humeri, two radioulnae, 12 tibiofibulae, and five tibiale-fibulare. The common toad *Bufo bufo* (NR = 17; MNI = 8) is much less well represented than the common brown frog *Rana temporaria* (NR = 335; MNI = 38). In addition, the cervical vertebra of a colubrid snake (Colubridae indet.) has also been documented.

As noted above, *Pelodytes punctatus* is particularly well represented for a Belgian site, and its fossils are quite well preserved (Fig. 2B). The humeri (Fig. 2B1) present a slender and straight shaft in ventral view. The condyle is slightly moved outward in relation to the main axis of the diaphysis. The radioulnae (Fig. 2B2) are short and somewhat robust, as in the species *P. punctatus* and *Pelodytes ibericus*, whereas in *Pelodytes caucasicus* they seem to be more robust (Sanchiz et al. 2002). The ilia (Fig. 2B3–4) lack a dorsal crest and present a generally well-curved ilial shaft. The superior tubercle, if present, is very reduced (see Fig. 2B4). The development of the acetabulum is similar in morphology to that observed in *P. punctatus*, whereas in *P. caucasicus* and *P. ibericus* it is more extended (Sanchiz et al. 2002). The tibiofibulae (Fig. 2B5) possess the *P. punctatus* morphology, being less robust than *P. caucasicus* in the central region (Sanchiz et al. 2002). Finally, the tibiale-fibulare (Fig. 2B6) are relatively slender, as in *P. punctatus*, whereas they are usually more robust in *P. caucasicus* and *P. ibericus* (Sanchiz et al. 2002).

The presence of *P. punctatus* makes this site (room I) very interesting, because to date this anuran has only appeared during "warm stages" (MIS 5) at Scladina and Sous-Saint-Paul caves (Table 1). However, due to the lack of associated information, this material is here considered to be of uncertain chronology.

The material from the second room (Tables 1–39; SOM Appendix S1) yielded only cf. *Bufo bufo* (NR = 1; MNI = 1) and *Rana temporaria* (NR = 61; MNI = 9).

Statistical analyses of the fossil assemblages

The most represented species of herpetofauna are *Rana temporaria* (present in 39 assemblages, 88.63% of the total) and *Bufo bufo* (35 assemblages, 79.54%). Other taxa are present in a much lower number of concurrences (between one and six assemblages). The least representative taxa are *Lissotriton vulgaris, Alytes obstetricans*, cf. *Pelobates fuscus*, and *Hyla arborea* (one assemblage, 2.27%).

The first correspondence analysis permits two groups to be distinguished among the represented taxa (Fig. 6A). The first group is formed by the dominant species, *Rana temporaria* and *Bufo bufo*. These are Eurosiberian/generalist taxa tolerating cold conditions. The second group is composed of the remaining taxa. All of them are hygrophilous and/or generalist taxa, tolerant of Eurosiberian and/or temperate influences. Internally, this group shows a tendency towards colder

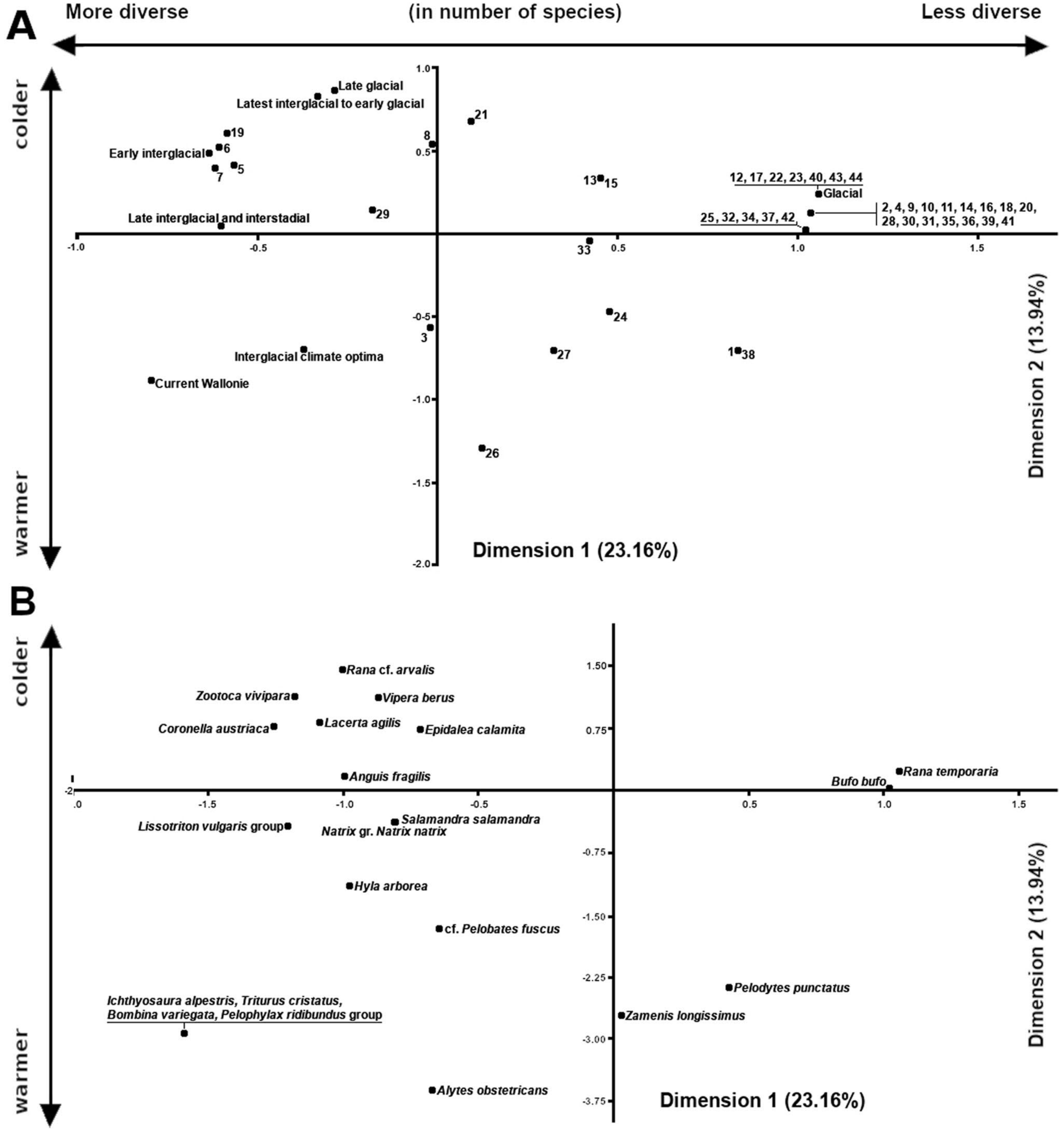

Fig. 6 Statistical analyses of the Late Pleistocene to Holocene herpetofaunal assemblages from Belgium. (A) Correspondence analysis of the herpetofaunal assemblages by site/sample. (B) Correspondence analysis of the species occurring. See Table 1 for the numerical correspondence of the sites/samples

and drier conditions in the higher values of the vertical axis (such as *Epidalea calamita*, *Lacerta agilis*, *Zootoca vivipara*, or *Vipera berus*) and towards warmer and more humid conditions in the lower values (such as *Alytes obstetricans*, cf. *Pelobates fuscus*, *Hyla arborea*, or *Zamenis longissimus*).

The second correspondence analysis (Fig. 6B) indicates a similar pattern. The dominant role of *Rana temporaria* and *Bufo bufo* in the Belgian fossil record has generated a large grouping of assemblages, which is associated with the "glacial" stage for the Central European model, in the right zone following the horizontal axis of the graph. The rest of the samples are located in intermediate positions among this large grouping, following a vertical dispersion axis, from the samples closest to the optimal interglacial conditions in the lower values of the vertical axis to other samples more closely linked to early or late glacial scenarios, according to the Central European model.

The results of the correspondence analyses are confirmed by the hierarchical analysis, with a high cophenetic correlation coefficient (0.9144) and obtaining the same relation of similarity between the different assemblages (SOM Table S1).

Paleoclimatic and paleoenvironmental reconstructions

The reconstructed mean annual temperature (MAT) ranges between 2.9 and 9.1 °C (Table 2, Fig. 7). The highest values correspond to the "warm stage" sites of Sous-Saint-Paul (Fig. 7: no. 1; MIS 7/6), Scladina (Fig. 7: no. 3; layers VI-Vocre), the mid-Holocene sites of the Trou du Frontal (Fig. 7: no. 26; "first ossiferous level"), and the undated Holocene burrows from Scladina (Fig. 7: no. 27). This last sample reaches up to 9.1 °C, a value very similar to the current temperature in southern Belgium (around 9.6–9.8 °C; climate-data.org). MIS 3 sites show fluctuating values of between 5.5 and 7.2 °C, whereas MIS 2, particularly the second part of it (the late Magdalenian of the Trou du Chaleux; Fig. 7: no. 21), has the lowest values of the whole sequence with 2.9 °C (i.e., 6.9 °C lower than present local values at Houyet). Compared with the herpetofaunal successions from Central Europe (modified from Böhme 2010), our highest reconstructed MATs are quite similar to the value obtained for the "interglacial climate optimum" (9.3 °C), whereas the lowest temperature (Trou du Chaleux; Fig. 7: no. 21) falls within the range of the lowest values obtained for the "latest interglacial to early glacial" (2.8 °C) and the "late glacial" (3.6 °C). Other herpetofaunal assemblages give values of between 5.5 and 7.6 °C. Curiously, the "glacial" period shows a somewhat warmer MAT than the "early and late glacial."

The results for the mean annual precipitation (MAP) do not show great variation between sites. The rainfall levels are always between 585 and 710 mm (Table 2, Fig. 7), i.e., much lower than current values in southern Belgium (around 800–850 mm; climate-data.org). The highest value corresponds to Sous-Saint-Paul (MIS 7/6; Fig. 7: no. 1), and the lowest to the late Magdalenian of the Trou du Chaleux (Fig. 7: no. 21). Such a range of values is also coherent with the herpetofaunal successions from Central Europe, where MAP ranges from 566.7 mm ("latest interglacial to early glacial"), followed by the "late glacial" value (573.3 mm), up to 677.3 mm (the "interglacial climate optimum"). Such a low degree of variation may explain why in the correspondence analyses (Fig. 6), the humidity factor does not affect the fossil assemblages.

An approach to seasonality may also focus on the mean temperature of the warmest month (MTW) and the mean temperature of the coldest month (MTC) values (Table 2, Fig. 7). The differences between the sites for MTC are much higher than for MTW. MTW oscillates between 18.5 and 21.8 °C (i.e., 3.3 °C), whereas MTC varies between – 2.5 and – 10.9 °C (i.e., 8.4 °C). Seasonality (the contrast between summer and winter temperatures) is thus reconstructed to have been higher than in the Meuse Valley today. Indeed, the present-day MTW is around 17.5 °C, and MTC is between 1.7 and 2.2 °C (i.e., a variation of 0.5 °C; climate-data.org). Thus, MTW seems always to have been slightly higher than at present, and MTC markedly lower than at present. The minimum MTC is obtained for the Trou du Chaleux (Fig. 7: no. 21; – 10.9 °C; i.e., 12.6 °C lower than at present), whereas the highest reconstructed MTCs correspond to the "warm stages" (MIS 7/6, 5 and 1; respectively Fig. 7: nos. 1, 3, 26, and 27). Compared with the herpetofaunal successions from Central Europe (modified from Böhme, 2010), the lowest MTC is similar to "latest interglacial to early glacial" (– 11.1 °C) and "late glacial" (– 12.9 °C) conditions (Table 2). Here again, the "glacial" period shows a somewhat warmer MTC than the "early and late glacial."

The maximum extreme temperature (MaxET) does not show major variations over the different periods represented here. The values range between 33.8 and 37.6 °C (Table 2). Warmer extremes (between 36 and 37 °C) correspond to "warm stages" (MIS 5 and MIS 1), although some levels of MIS 3/2 also reach quite similar values (i.e., layer 2 from Caverne Marie-Jeanne; Fig. 7: no. 19). The lowest values (33.8 °C) correspond to Goyet ("Salle du Mouton—1er niveau moustérien," MIS 3; Fig. 7: no. 12) and to MIS 3/2 sites such as the Trou du Sureau (2^{e} niveau; Fig. 7: no. 17), the Trou du Château (Fig. 7: no. 22), and the Trou du Chêne ("2^{e} niveau ossifère"; Fig. 7: no. 23). The values obtained are similar to those reconstructed for Central European herpetofaunal successions, with "glacial" assemblages having the lowest value (33.8 °C; Table 2: G). Unlike MaxET, the minimum extreme temperature (MinET) presents a large range of variation, with the coldest extreme obtained for the

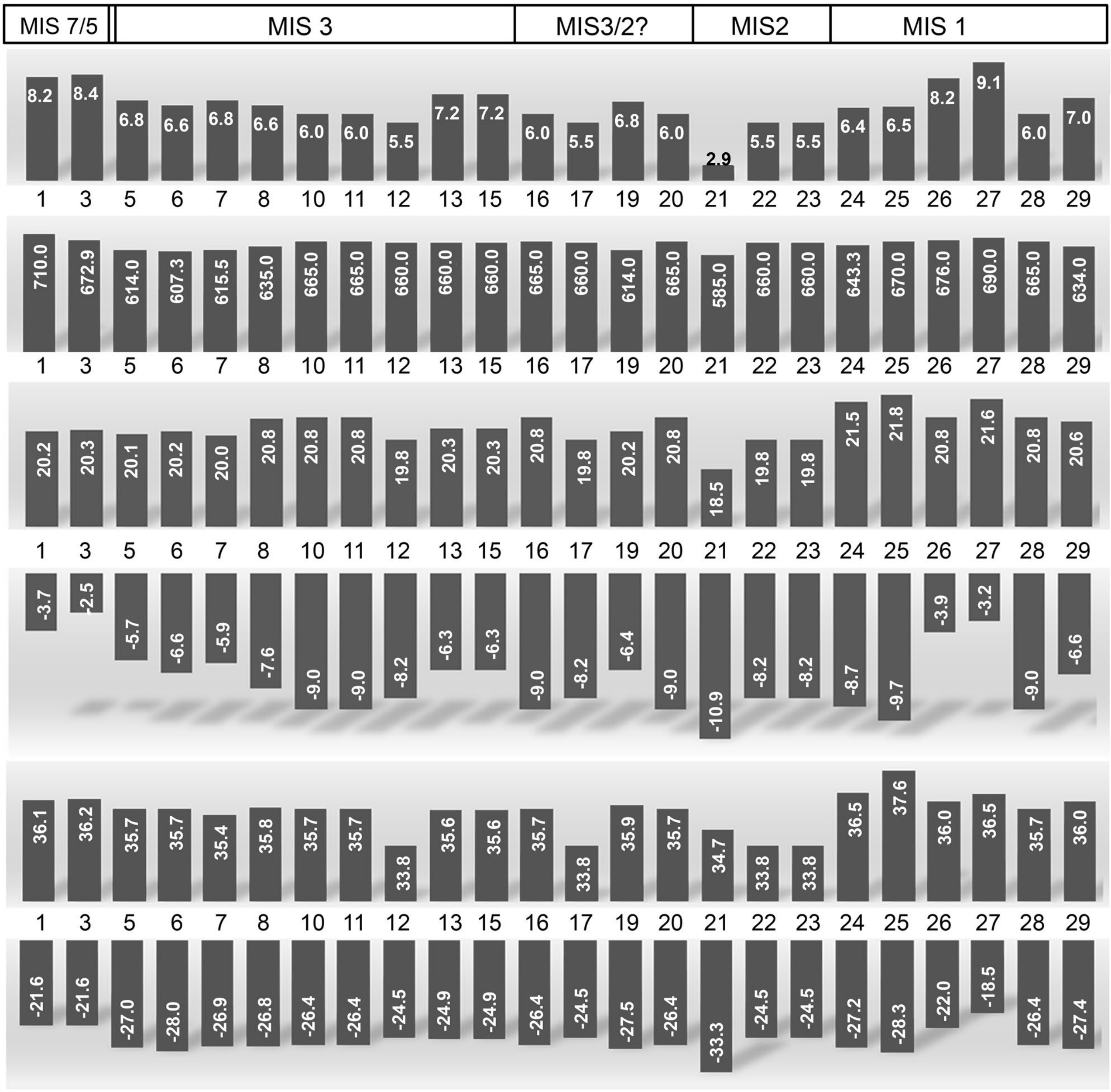

Fig. 7 Paleoclimatic reconstructions for a selection of Belgian Late Pleistocene localities from MIS 7/5 to the Holocene. Abbreviations: MAT, mean annual temperature (in °C); MAP, mean annual precipitation (in mm); MTW, mean temperature of the warmest month, MTC, mean temperature of the coldest month, MaxET, maximum extreme temperature (in °C); MinET, minimum extreme temperature (in °C). See Table 1 for the numerical correspondence of the sites/samples

late Magdalenian of the Trou de Chaleux (− 33.3 °C; Fig. 7: no. 21). Such a value is consistent with the values obtained for the "late glacial" (− 36.2 °C; Table 2: LG) and "latest interglacial to early glacial" (− 34.4 °C; Table 2: LIEG) periods. The mildest extremes were reconstructed for interglacial and Holocene sites (− 18.5 to − 22 °C) such as Sous-Saint-Paul (Fig. 7: no. 1), Scladina (layers VI–Vocre; Fig. 7: no. 3), the Trou du Frontal ("1er niveau ossifère"; Fig. 7: no. 26), and the Holocene burrows of Scladina (Fig. 7: no. 27). Such values are concordant with the "interglacial climate optimum" (− 20.4 °C; Table 2: ICO). Again, the "glacial" herpetofaunal assemblage from Central Europe does not correspond to the lowest value for MinET.

The number of rain days per year (YR; Table 2; Fig. 8) oscillates between 133 and 153, somewhat fewer than today (between 170 and 180 days; meteobelgique.be). The highest values are obtained for late MIS 3 and MIS 2 sites such as Goyet (Salle du Mouton—1er niveau moustérien, MIS 3; Fig. 8: no. 12), the Trou du Sureau (2^{e} niveau; Fig. 8: no. 17), the Trou du Château (Fig. 8: no. 22), and the Trou du Chêne (2^{e} niveau ossifère; Fig. 8: no. 23). In accordance with the low differences observed for MAP, YR does not vary a lot, unlike the parameters for the number of snow days per year (YS) and the number of frost days per year (YF). As YS and YF are temperature-related, these two parameters show rather marked variations. YS oscillates between 54.3 (Fig. 8: no. 27) and 115 (Fig. 8: no. 21), and YF between 120.4 (Fig. 8: no. 3) and 187.5 (Fig. 8: no. 21; Table 2). Today, in the region under study, YS ranges between 20 and 30 days, and YF between 70 and 110 days, showing major variation from the littoral (in the north) to inner Belgium (in the south) (meteobelgique.be). Both YS and YF show their highest value for the late Magdalenian of the Trou du Chaleux (Fig. 8: no. 21), the coldest site in the sequence. During MIS 5 (and 6/7?), YS and YF are rather low with only 63 days for YS and 120–122 days for YF (Fig. 8: no. 1 and 3). During MIS 3 and MIS 2, values oscillate between 72 and 92 days for YS and 146.3 and 165 days for YF, reaching, as noted above, a peak (115 days and 187.5 days respectively) during the late Magdalenian (Trou de Chaleux; Fig. 8: no. 21). Finally, the Holocene presents a main range of values similar to MIS 3, with the lowest values of the whole sequence (YS = 54.3 and YF = 122; Fig. 8: no. 27) for the warm reconstructed climate of the Holocene burrows of Scladina. Higher values for YS and YF are estimated for the Holocene assemblages of the Trou Balleux (Fig. 8: no. 25) and the Trou Magrite (Fig. 8: no. 28), sites that show a lower temperature reconstruction relative to other Holocene

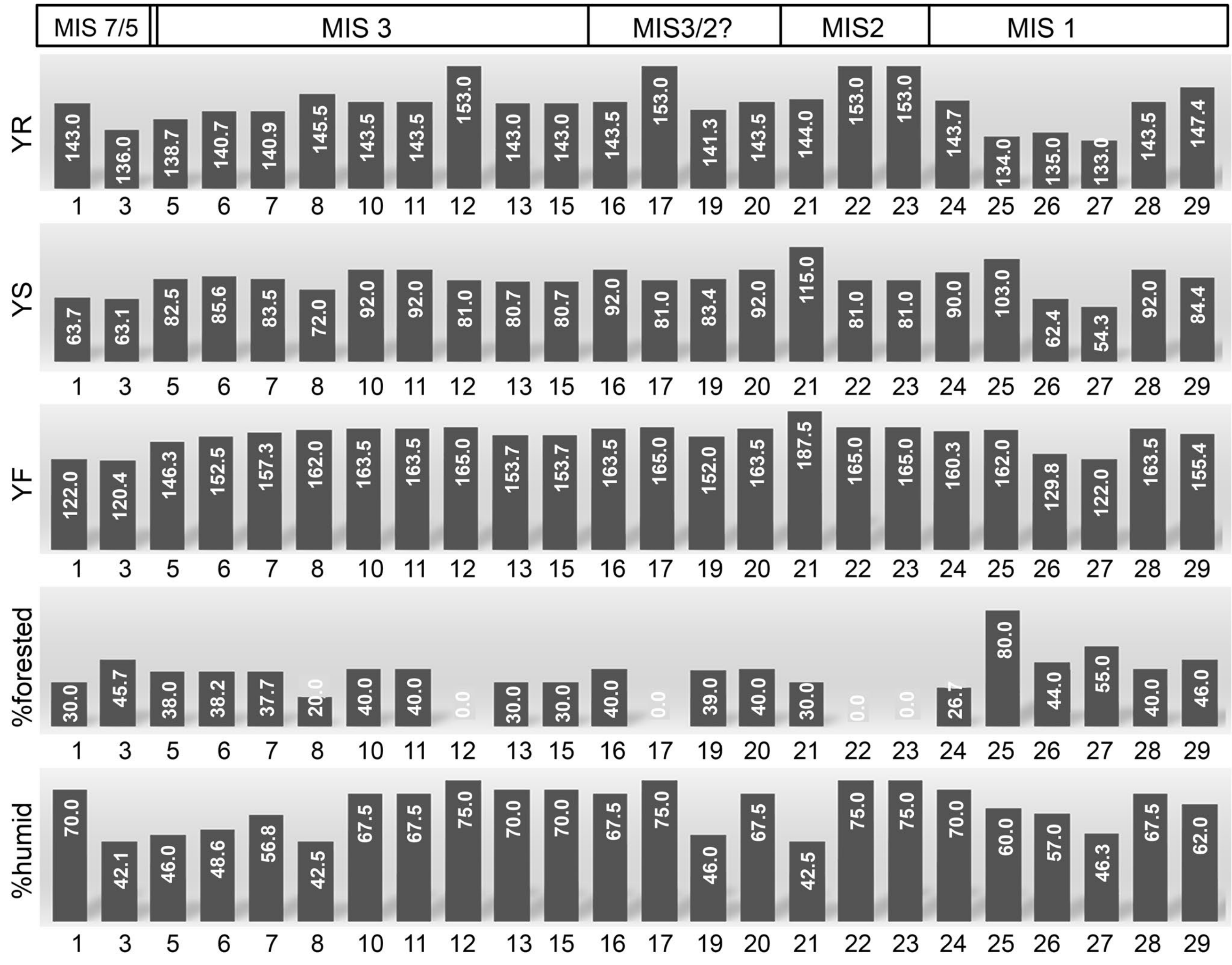

Fig. 8 Paleoatmospheric and paleoenvironmental reconstructions for a selection of Belgian Late Pleistocene localities from MIS 7/5 to the Holocene. Abbreviations: YR, number of rain days per year; YS, number of snow days per year; YF, number of frost days per year; %forested, percentage of species with preference for wooded environments, and %humid, percentage of species with preference for humid environments. See Table 1 for the numerical correspondence of the sites/samples

sites, although this is certainly due to the incompleteness of the fossil record. Finally, compared with Central European herpetofaunal assemblages, the obtained values are concordant with an "interglacial climate optimum" for the Holocene burrows of Scladina (Fig. 8: no. 27) and to a lesser extent for Sous-Saint-Paul (Fig. 8: no. 1) and Scladina (layers VI-Vocre; Fig. 8: no. 3) and with "latest interglacial to early glacial" or "late glacial" conditions for the late Magdalenian of the Trou de Chaleux (Table 2; Fig. 8: no. 21). Again, the lowest estimated temperatures are not obtained for the "glacial" period but for the preceding and following ones.

Apart from a peak for the Trou Balleux (due to the presence only of *Bufo bufo* s.l.; Fig. 8: no. 25), the percentage of species with a preference for wooded environments (%forested; Table 2; Fig. 8) varies between virtually 0% (assemblages with only *Rana temporaria*) and 55%. The highest values (> 40%) are obtained for the Holocene and Scladina Cave (layers VI-Vocre; Fig. 8: no. 3) whereas, for MIS 3 and MIS 2, %forested is generally somewhat lower, albeit reaching 40% for some sites. Compared with the Central European assemblages (Table 2), the method seems to display some discrepancies for the cold and dry reconstructed "late glacial," presenting the highest percentage of species with a preference for forested environments (60%). Nevertheless, it seems to make sense when reconstructing "glacial" environments as very open (0.0%) and the "interglacial climate optimum" as the second most forested period (43.2%). Such data thus raise certain concerns when it comes to interpreting assemblages with only one or two environmentally tolerant species.

Finally, the last parameter is the percentage of species with a preference for humid environments (%humid), which oscillates between 42.1 and 75% (Table 2; Fig. 8: nos. 3 and 12, 17, 22, 23). No evident pattern can be distinguished among these variations, probably again due to the apparently low variations in reconstructed rainfall, apart from the fact that the last part of MIS 3 and MIS 2 seems to have been more humid than other periods. Such results are concordant with what is reconstructed for the Central European assemblages (Table 2), characterizing the "glacial" as the most humid period (75%; but again only based on the presence of *R. temporaria*) followed by the "interglacial climate optimum" (62.3%).

The duo Bufo bufo—Rana temporaria

The change in dominance between *Rana temporaria* and *Bufo bufo* is an interesting pattern already underlined for Caverne Marie-Jeanne (Rage in Ballmann et al. 1980; Blain et al. 2019). In the present study including numerous sites and a broader chronological range, the *Bufo bufo* vs. *Rana temporaria* index shows notable variations over the period considered (Fig. 9). It is higher during "warm stages" (MIS 7/6, 5, and MIS 1), highly variable during the fluctuating MIS 3, and very low during MIS 2, especially during the Magdalenian and also probably during the earliest part of the Holocene.

According to the statistical analyses, climate and environmental parameters seem not to be major determining factors for this index. However, there is a certain (not high) positive correlation with MAT, MaxET, and the vegetation cover (%forested; Table 3). The remaining climatic correlations have an adjusted r^2 of under 0.3 or are not significant (have a p-value over 0.05). According to the correlations, the *Bufo bufo* vs. *Rana temporaria* Index seems to be influenced by the temperature and terrestrial environment, suggesting that when temperatures are warm/temperate and the environment is forested *B. bufo* dominates over *R. temporaria*, whereas the latter species becomes dominant under cold climatic conditions and in open environments. The higher correlation with woodland extension (%forested) is not surprising, as the quantified ecology method weighted these species in

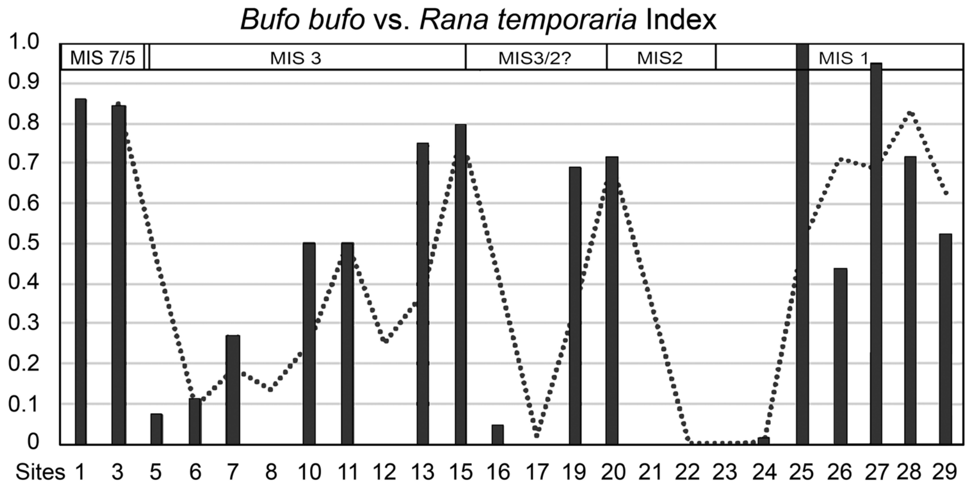

Fig. 9 Chronological evolution of the *Bufo bufo* vs. *Rana temporaria* Index. The dotted line represents a tendency curve (mean = 2). See Table 1 for the numerical correspondence of the sites/samples

completely opposite ways (and not in accordance with the modern ecology of *R. temporaria*). However, the correlation with temperature is rather interesting as it is not influenced by such an evident opposite weighting of the two species. Again, temperature seems to play a greater role in explaining the herpetofaunal pattern than precipitation does.

Discussion

Evolution of the herpetofaunal assemblages in Belgium

The dominant herpetological association for the Late Pleistocene to Holocene fossil record from Belgium is mainly composed of the duo *Bufo bufo* and *Rana temporaria*. At least 26 of the documented samples from the Mousterian, Aurignacian, Perigordian, Magdalenian, Tardenoisian, and indeterminate Holocene consist of only one or both species. The predominance of both species thus covers the entire studied period, as also occurs in other areas such as the northern Iberian Peninsula, with the concurrence of *Alytes obstetricans*, *Epidalea calamita*, *Bufo bufo* s.l., *Rana temporaria*, *Anguis fragilis*, and *Vipera* sp. for the same chronology, both at the glacial maximum and in post-glacial Latest Pleistocene and Holocene levels (Bisbal-Chinesta and Blain 2018). In Central Europe, the concurrence of *Bufo bufo* and *Rana temporaria* occurs during the "early interglacial," "interglacial climate optimum," and "late interglacial and interstadial" stages, along with species typical of temperate Eurosiberian conditions (Böhme 2010). During the "latest interglacial to early glacial" stage, the species are limited to *Bufotes viridis*, *Rana temporaria*, *Zootoca vivipara*, and *Vipera berus*, decreasing in the "glacial" stage where only *Rana temporaria* is represented, and followed by a new increase in the number of species during the "late glacial" stage with the concurrence of *Bufo bufo*, *Rana arvalis*, and *Vipera berus* (Böhme 2010). The predominance of *B. bufo* and *R. temporaria* in the Belgian fossil record is possibly more related to their abundance in terms of the number of individuals in past ecosystems and not to the composition of the herpetofaunal communities being limited to these two species. Both anurans are common and highly resistant to multiple climatic conditions, from mild to very cold, until they reach sub-Arctic latitudes (Garcia-Porta et al. 2012; Cogălniceanu et al. 2017).

In the Belgian fossil record, the assemblages with the highest richness (in the number of species) come from the Mousterian layers 4, 5, and 6 (Tables 1–5 to 7) of Caverne Marie-Jeanne, with some 12 taxa: *Lissotriton vulgaris* s.l., *Salamandra salamandra*, *B. bufo* s.l., *Epidalea calamita*, *R. temporaria*, *Rana* cf. *arvalis*, *Anguis fragilis*, *Lacerta agilis*, *Zootoca vivipara*, *Natrix natrix* s.l., *Coronella austriaca*, and *Vipera berus*. The herpetofaunal association of the Mousterian layers "VI-Vocre" of Scladina (Tables 1–3) also presents a high number of species in concurrence: *Salamandra salamandra*, *Pelodytes punctatus*, *B. bufo* s.l., *R. temporaria*, *Anguis fragilis*, *Zamenis longissimus*, and *Vipera berus*. These Mousterian assemblages are typically "warm stages" and even in the case of layers VI-Vocre of Scladina they may suggest warmer conditions than at present due to the combined appearance of *Pelodytes punctatus* and *Zamenis longissimus*.

The northern parsley frog (*Pelodytes punctatus*) is a generalist anuran that shows a preference for open landscapes in Northwestern Europe, such as coastal dune areas or partially forested areas, avoiding dense woodlands (Toxopeus et al. 1993; Boyer and Dohogne 2008), although it depends especially on the existence of water bodies for its reproduction (Richter-Boix et al. 2007). The Aesculapian snake (*Zamenis longissimus*) prefers sunny forested habitats such as bushlands and deciduous woodlands, although it also uses open spaces for thermoregulation (Levièvre et al. 2010a, b). Both species are probably the Mediterranean in origin and are not currently living in Belgium. *P. punctatus* has populations in the French provinces bordering southern Belgium (Jacob et al. 2007). In the case of *Z. longissimus*, the nearest populations are in northeastern France (not far from the source of the Meuse River), although there are near-relict populations in western Germany, in the localities of Schlangenbad and Hirschhorn (Musilová et al. 2007, 2010). This colubrid reappears during the Holocene, in the samples from the Holocene burrows of Scladina Cave (Tables 1–27), together with *Salamandra salamandra*, *Bufo bufo* s.l., and *Rana temporaria*, and from the "first ossiferous level" of the Trou de Frontal (Tables 1–26), ascribed to the Atlantic/Subboreal period, in concurrence with *Alytes obstetricans*, *B. bufo* s.l., *R. temporaria*, and *Natrix natrix* s.l.

The absence of urodeles is remarkable in the layers chronoculturally assigned to glacial phases. *Lissotriton vulgaris* s.l. and *Salamandra salamandra* are only cited from the oldest Mousterian levels of Scladina (VI-Vocre) and from the three Mousterian levels of Caverne Marie-Jeanne (layers 4, 5, and 6), but not in the other Pleistocene samples until their reappearance in the most recent level of Scladina and in the assemblage of the Trou du Frontal, assigned to the mid-Holocene (Atlantic/Subboreal). This phenomenon has also been described for the northern Iberian Peninsula, where there is an almost total absence of urodeles during MIS 3 and MIS 2, where they reappear after the last glacial maximum (Bisbal-Chinesta and Blain 2018). The possible exception is the herpetofaunal assemblage from level 2 of Caverne Marie-Jeanne (Tables 1–19), with an imprecise chronocultural ascription between the Perigordian and the Magdalenian. Urodeles appear in a concurrence composed of *Salamandra salamandra*, *Bufo bufo* s.l., *Epidalea calamita*, *Rana temporaria*, *Rana* cf. *arvalis*, *Anguis fragilis*, *Lacerta agilis*, *Zootoca vivipara*, *Coronella austriaca*, and *Vipera berus*. This diverse association of herpetofauna from Caverne Marie-Jeanne may represent the first post-glacial concurrence if it belongs to the advanced Magdalenian or, if older, it may provide evidence of the existence of humid glacial refuges in southern Belgium in a generally cold and dry environmental context.

Last but not least, the present study provides new data that shed light on the formation of the extant herpetofauna of Belgium, at a time when most of the native species were in regression or disappearing mainly due to landscape anthropization rather than due to climate change (Jacob and Graitson 2007). Seven species of reptiles (belonging to four families) and 14 species of amphibians (six families) are indigenous to southern Belgium. The Walloon fauna includes all the Belgian-Dutch species, with the exception of the moor frog (*Rana arvalis*), whose existence has never been demonstrated in Wallonia, although it inhabits part of the Campine lowlands and peat bogs (Antwerp province) (Bauwens and Claus 1996; Parent 1997). Unfortunately, the sample (Tables 1–29) within the RBINS Quaternary collections, where this species is quite well represented, is provided neither with chronological nor even geographical information. However, as already demonstrated by Blain et al. (2019), this species formed part of the Walloon herpetofauna during the Late Pleistocene, as evidenced in layers 5, 4, and 2 of Caverne Marie-Jeanne (Tables 1–6, 7, 19). The recent extirpation of two amphibians in Belgium seems to be confirmed, as there has been no mention of the common spadefoot toad (*Pelobates fuscus*) since 1987–1990 and of the European tree frog (*Hyla arborea*) since 1993, at the end of a process that began before 1940 (Jacob and Graitson 2007). In our dataset, *H. arborea* s.l. is mentioned in the unlocated sample from "Puit artésien de l"atelier central" (Tables 1–29), and there is a probable mention for *P. fuscus* in the Early Holocene (Tardenoisian) of the Trou du Chêne ("argile à blocaux"; Tables 1–24). In addition to these extirpated species, other taxa are undergoing a significant recent regression of their regional range. Thus, in recent decades, the natterjack toad (*Epidalea calamita*) has disappeared from the Ardennes, the grass snake (*Natrix helvetica*) has probably become extinct (in its native state) in central Belgium, and the common European adder (*Vipera berus*) has suffered a marked contraction of its range (Jacob and Graitson 2007). Though not very abundant, *E. calamita* is present in a few Late Pleistocene sites but has not been documented in any Holocene sample so far (Table 1). *Natrix natrix* s.l. is well documented during the Late Pleistocene and in one Holocene locality (Table 1). Finally, *V. berus* is also mentioned frequently in Late Pleistocene sites, possibly up until MIS 2, but it does not so far have any Holocene record. As a result of the lack of detailed studies of Holocene cave deposits, most of the extant amphibians and reptiles from Belgium have yet to be described as fossils or subfossils. This applies to the Alpine newt (*Ichthyosaura alpestris*), northern crested newt (*Triturus cristatus*), yellow fire-bellied toad (*Bombina variegata*), agile frog (*Rana dalmatina*), water frogs (*Pelophylax* sp.), and the common wall lizard (*Podarcis muralis*). Curiously, the latter is the only native species that has locally extended its range in southern Belgium during the last 150 years, due to its anthropophilic character. This extension must have occurred mainly at the end of the nineteenth century (Graitson 2000; Jacob and Graitson 2007), and this may be an explanation for its absence in the Belgian fossil record.

Environment and climate during the last interglacial-glacial cycle in Belgium

The last interglacial-glacial cycle between 130 and 14 ka ago (MIS 5–2; Lisiecki and Raymo 2005) is characterized by well-pronounced climate fluctuations. These climate fluctuations involved major re-organizations in the atmosphere, oceans, cryosphere, and biosphere, including the expansion and retreat of ice sheets and displacements in vegetation zones at sub-continental scales. A wealth of terrestrial proxy-based climate records for the Late Pleistocene are available from long terrestrial lake and loess sequences in Northern Europe (Helmens 2014), based on pollen, macrofossils, oxygen isotopes, cladocerans, beetles, and chironomids. Environmental and climate conditions during MIS 5 (ca. 130–70 ka BP) are known to be markedly different from those during MIS 4–2 (ca. 70–15 ka BP). MIS 5 is characterized in Northern Europe by three long forested intervals (corresponding to MIS 5e, 5c, 5a) interrupted by two short, relatively cold and dry intervals (MIS 5d and 5b). The time interval encompassing MIS 4–2 shows open vegetation. It is characterized by two glacial maxima (MIS 4 and 2) with sub-continental-scale glaciation over Northern Europe and dry conditions in strongly continental Eastern European settings. MIS 3 is characterized by high-amplitude climate oscillations, with mild climate conditions in early MIS 3, possibly interrupted by glaciation during a major part of MIS 3 until ca. 35 ka BP. Late MIS 3 and MIS 2 were cold with the most extreme or peak glacial conditions during MIS 2. Helmens (2014) suggests that the climate variability in Central and Northern Europe during the last interglacial-glacial cycle was mostly in degrees of continentality, with major shifts in winter temperature and precipitation values, and summer temperatures remaining largely unchanged.

Marine isotope stage 5

Two localities document the herpetofaunal assemblages from the "warm stages" in Belgium: Scladina (Tables 1, 2,

3) and (though slightly older) Sous-Saint-Paul (Tables 1-1). Together, the taxa represented in layers Vocre to VI of Scladina Cave are thought to fit well with a variety of climatic conditions, maybe warmer conditions than at present in the case of layer Vocre (Blain et al. 2014). These species reflect multiple environments, including a slow-water stream within a forest area and humid meadows. These various environments may be correlated with climatic fluctuations during MIS 5. *Zamenis longissimus* is the most thermophilic species in the faunal list, and taking into account its modern distribution in Europe, it has been suggested that temperatures may have been 1 to 2 °C higher than at present in southern Belgium during the formation of layer Vocre (Blain et al. 2014). The new climate estimates based on the application of the quantified ecology method to the herpetofaunal assemblages from Scladina (layers VI-Vocre) are consistent with these previous data, even though the reconstructed MATs are not as high as previously thought (8.4 °C) and are effectively cooler than modern values (9.6–9.8 °C). MAP (672.9 mm) suggests a lower rainfall during MIS 5 than today (Table 2).

In accordance with the higher abundance of small-mammal remains compared to herpetofaunal remains, various periods have been identified within MIS 5 at Scladina Cave (López-García et al. 2017b). Layer VI of Scladina has been attributed to MIS 5c (Pirson 2007). The small-mammal assemblage from this layer shows a relatively high percentage of forest formations (around 55%) in relation to open land, with a low percentage of local aquatic environments. The reconstructed mean annual temperature (MAT) is lower and mean annual precipitation (MAP) higher than the modern climate (López-García et al. 2017a, b). Both pollen (detecting a climatic optimum) and large mammals (dominated by red and roe deer) suggest that this layer should be attributed to a temperate period (Bastin 1992; Cordy 1992; Simonet 1992). The rather limited diversity of the herpetofaunal assemblage recovered from this layer (*Bufo bufo* s.l., *Anguis fragilis*, and *Vipera* cf. *berus*; Blain et al. 2014) also suggests a good representation of wet forested areas with dense herbaceous vegetation, alternating laterally with more open environments, such as humid meadows and forest edges or scrubby environments.

Layer VB possibly reflects a mixing of several distinct layers, as suggested by Pirson (2007). Even so, the small-mammal results obtained for this layer suggest, in general, cold and relatively drier environmental and climatic conditions (López-García et al. 2017b). In this layer, *Pelodytes punctatus* has been identified, together with *Bufo bufo* s.l., *Rana temporaria*, and *Vipera berus* (Blain et al. 2014). Such an assemblage may suggest effectively drier conditions (reconstructed here as having a rainfall some 100–150 mm lower than today), with a larger representation of open or semi-open, even arid landscapes. This layer also corresponds to the highest representation of *R. temporaria* even though *B. bufo* s.l. still predominates. *P. punctatus* is also represented in layer VII of Sous-Saint-Paul, with a possible chronology constrained stratigraphically to be older than MIS 5c (considered MIS 7/6). Interestingly, this species is also represented in Grotte la Chefalize (Salle I; Tables 1–38), but the lack of stratigraphic and biochronological information precludes the possibility of knowing whether this site is fairly recent (Holocene) or from the Latest Middle/Earliest Late Pleistocene. Future study of its mammalian assemblages housed at the RBINS may possibly cast some light on this no longer existing site.

Finally, layer Vocre of Scladina Cave corresponds to a relatively dry, temperate, interstadial period with well-represented forest formations (Bastin 1992; Cordy 1992; Simonet 1992) and has been correlated with MIS 5a (Pirson 2007; López-Garcia et al. 2017b). This layer furnished a quite rich herpetofaunal assemblage, with the occurrence of *S. salamandra*, *R. temporaria*, *A. fragilis*, and *Z. longissimus* (Blain et al. 2014). Quantitative analysis of the small mammals from layer Vocre suggested a predominance of forest formations (71%) in relation to open environments and relatively low values for water-edge areas. As for layer VI, the climate has been reconstructed as cooler (but weighted by the occurrence of the thermophilic bat *Miniopterus schreibersii*) and more humid than today. The representation of species with open dry requirements, such as *Crocidura* sp., *Lagurus lagurus*, or *Spermophilus citellus*, is rather low (2.4%) by contrast with the representation of species associated with humid environments, such as *Alexandromys oeconomus* (9.52%) or *Talpa europaea* (4.76%) (López-García et al. 2017b). Such results are thought to be in accordance with the paleoclimatic and paleoenvironmental interpretation of the paleopedological record of Western Europe. This interpretation suggests for MIS 5c and MIS 5a a slightly lower MAT than today and a vegetation mainly composed of boreal to temperate forest (Haesaerts et al. 1999, 2011, 2016; Vancampenhout et al. 2013). Such a reconstruction is consistent with the ecology of the Aesculapian snake (*Z. longissimus*), which generally avoids open environments and prefers warm, moderately humid, deciduous woodlands and scrubby areas, and of the fire salamander (*S. salamandra*), which prefers deciduous forests in hilly areas, since it hides in fallen leaves and around mossy tree trunks. At present, *Z. longissimus* appears to prefer humid regions and is often associated with river valleys, favoring the south-facing slopes of hills descending into river valleys (Gomille 2002). In addition, these snakes are known to use the more shaded and humid forests in the northernmost part of their distribution area, as they do further south. Indeed, in France *Z. longissimus* is the only species of snake known to inhabit the interior of forests, where hardly any ground vegetation is present (Doré 1986). For its part, *S. salamandra* does not seem to be very discriminating with respect to water, as it only needs small brooks or ponds with clean water in its habitat for the development of its larvae.

The climate was reconstructed applying the bioclimatic model (Hernández-Fernández 2001) to the rodent and insectivore assemblage from layer Vocre of Scladina. This gives 3.7 °C for MAT (i.e., 6 °C lower than today) and 979 mm for MAP (i.e., 149 higher than today; López-García et al. 2017b). The thermal ecology of *Z. longissimus* conflicts with such a cold temperature reconstruction for layer Vocre. The optimum temperature for activity observed in German populations is 20–22 °C (Heimes 1988), and animals are rarely recorded below 16 °C or above 25 °C. Other observations of Ukrainian populations (Ščerbak and Ščerban 1980) have put the minimum temperature for activity as starting from 19 °C and the optimum as 21–26 °C. Its northernmost distribution limit in Europe corresponds to a MAT above 7.3 °C, as at Karlovy Vary (Czech Republic; climate-data.org), with an MAP ranging between 600 and 1000 mm. The newly reconstructed MATs (8.4 °C) for Scladina (layers VI-Vocre) obtained in this study are thus concordant with such minimum temperature requirements for *Z. longissimus* (at least supporting a small northern population); they are effectively cooler than modern values, as predicted by the small-mammal and paleopedological studies.

Marine isotope stage 4

The only data for MIS 4 come from level CIV of Walou cave (Tables 1, 2, 3, 4), where only *Bufo* sp. and *Rana* sp. have been mentioned (de Wilde 2011a, b). This prevents us from making any reliable inferences about the climate and environment at that time.

Marine isotope stage 3

Interest in MIS 3 has been stimulated by the extreme variability of this period (Allen et al. 1999), and the questions raised by archaeological research into the extinction of the Neanderthals and the transition from the Mousterian to Aurignacian cultures. MIS 3 (ca. 60–30 ka BP) is characterized by a series of alternations between stadial (“cold”) and interstadial (“warm”) conditions, corresponding to a dynamic that alternates between forest development and the expansion of semi-arid areas. Most of the information comes from southern Europe, such as that from Lago Grande di Monticchio (Italy; Allen et al. 1999, 2000), whereas in Northern Europe deposits representing cold intervals are predominantly devoid of biotic remains (Huntley et al. 2003). Consequently, much of the information about the climate evolution of MIS 3 in Northwestern Europe comes from loess deposits, which provide a high-resolution terrestrial archive (e.g., Pirson et al. 2009; Haesaerts et al. 2011, 2016).

Although MIS 3 is represented here by a quite large number of samples (Tables 1, 2, 3, 4, 5 to 15), the poor chronological resolution of many of the samples prevents any precise analysis of the paleoenvironmental and paleoclimatic changes that occurred within this fluctuating period. However, reconstructed values can provide an overview of the varying conditions during this period, and Caverne Marie-Jeanne (layers 6 to 4) may represent a good example of the prevailing interstadial conditions, as it documents the boreal climatic conditions around interstadial 12 (IS 12; ca. 47 ka) (López-Garcia et al. 2017a).

According to the small mammals (López-Garcia et al. 2017a), the reconstructed MATs vary between 4.2 (layer 6) and 3.3 °C (layer 4), i.e., MATs were between 6.6 and 5.7 °C lower than the current climate. On the other hand, the reconstructed MAPs are always higher than at present, ranging between 1000 and 1022 mm, i.e., some 160–180 mm higher than current values. The small-mammal paleoecology suggests a mixed habitat dominated by open woodland formations (around 30%) and a lateral variation from dry (between 18 and 27%) to humid (never exceeding 20%) meadows. The malacofauna from Caverne Marie-Jeanne indicates some variations in humidity, with a relatively cool and dry interstadial environment for layer 5 contrasting with probably cooler and more humid conditions for layer 4 (Ballmann et al. 1980). The large-mammal assemblages also suggest cold climatic and generally dry environmental conditions for layers 6 to 4, with the presence of species such as *Mammuthus primigenius* (woolly mammoth), *Rangifer tarandus* (reindeer), *Vulpes lagopus* (Arctic fox), and *Ochotona pusilla* (steppe pika) (Ballmann et al. 1980). Finally, at a regional level, loess-based paleoenvironmental interpretations also suggest cold (boreal) climatic conditions for IS 12 (Haesaerts et al. 2016).

On the other hand, the quantitative analysis of the amphibians and reptiles proposed by Blain et al. (2019) suggested that the landscape was patchy around the site, with a large representation of humid meadows (between 30 and 40% of the total landscape) and forested habitats (between 37 and 40%), likely in the area around a river or a lake. Aquatic habitats are well represented (comprising between 16 and 20% of the landscape), and dry and rocky/stony environments are rather poorly represented, even though there is no typically aquatic species in the herpetofaunal assemblages. However, such discrepancies must basically be a matter of scale, i.e., regional versus local environments. This is more evident when the climate reconstruction is considered, as the herpetofauna suggests a clearly cooler MAT (3.1 to 3.3 °C lower than modern values) and a somewhat drier MAP (225–240 mm lower than at present). Again, the climate reconstructed on the basis of amphibians and reptiles suggests milder conditions than those for small mammals and above all much drier conditions. The humidity fluctuations observed based on the malacofauna are also reflected by the herpetofauna, layer 5 being slightly drier than layer 4 (Table 2; Fig. 7).

Interestingly, one of the less represented species in the herpetofaunal assemblage from Caverne Marie-Jeanne, always amounting to less than 1% of the anurans, is the natterjack toad, *Epidalea calamita*. This heliophilous species frequents open habitats characterized by low and sparse vegetation and the presence of shallow, often temporary, water points. It shows a preference for soft, mostly sandy substrates. It is reputed to be a pioneer species that can quickly colonize newly created habitats and quickly disappear when vegetation becomes too dense (Duguet and Melki 2003). In the Walloon region, the species has today disappeared from its primary habitats (Graitson and Denoël 2007). It is assumed that these were mainly in the major riverbed, where floods ensured the presence of shoals of sand and gravel with flooded depressions. From a climatic point of view, this species, unlike *Bufo bufo* s.l. and *Rana temporaria*, has a much more reduced distribution. It is found throughout Western and Central Europe, the British Isles and Scandinavia, from Portugal to the Baltic countries. Its occurrence during MIS 3 in Belgium is also attested by two samples from Goyet (Salle du Mouton, "terre noire" and "terre jaune"; Tables 1–13 and 15). This species gives a temperate signal for paleotemperature reconstructions of these two layers from Goyet attributed either to the Mousterian or Aurignacian.

The last sample documenting MIS 3 is the Mousterian layer I of Scladina Cave (Tables 1–8). The 14C dates for unit 1A and 1B, where layer I is included (1B-GRH: 43,150 + 950/ − 700 BP (GrA-32581); 1A-GK: 40,210 + 400/ − 350 BP (GrA-32635); Pirson 2007; Pirson et al. 2008; López-García et al. 2017b), may suggest that within MIS 3, there is a correlation with interstadials 11 or 10 (ca. 40–43 ka). Layer I has been interpreted as a dry interstadial period with steppe and woodland, with large-mammal species dominated by horse, red deer, woolly rhinoceros, and bovids (Bastin 1992; Cordy 1992; Simonet 1992). According to the small-mammal assemblage (López-García et al. 2017b), layer I is characterized by a landscape more or less similar to Caverne Marie-Jeanne (layers 6 to 4), with a good representation of open environments (33.3%), forest formations (29.8%), and water streams (15.5%). A paleoclimatic reconstruction based on the bioclimatic model suggests a MAT of − 1.0 °C and a MAP equal to 711.2 mm, i.e., − 10.7 °C and − 118.8 mm respectively lower than modern values. Such lower values are thought to be supported by the relatively high representation of strictly cold species, such as *Lagurus lagurus* (4.75%), *Lemmus lemmus* (9.52%), and *Dicrostonyx torquatus* (4.76%) (López-García et al. 2017b). Again, the reconstruction based on the herpetofaunal assemblages gives a warmer temperature (MAT = 6.6 °C; Table 2) than that for the small mammals, but in this case, the reduced number of species may generate some uncertainty as to the robustness of our reconstruction. The sand lizard (*Lacerta agilis*) is a widespread Eurasian species that today in Northern Europe reaches as far as the southernmost part of the Fennoscandian Peninsula (southern Sweden) and Estonia. Such areas are characterized by an MAT higher than 4 °C, whereas the small-mammal MAT (− 1.0 °C) would correspond to the Arctic tundra (i.e., the region of the Barents Sea).

Marine isotope stage 2

Only a few localities document MIS 2: the Magdalenian sites of the Trou de Chaleux ("first ossiferous level"; Tables 1–21) and the Trou du Château (Tables 1–22), and the Magdalenian or Tardenoisian site of the Trou du Chêne ("2nd ossiferous level"; Tables 1–23). These sites record the occurrence of only one anuran species, the brown frog (*Rana temporaria*), but often abundantly (140 individuals for the Trou de Chaleux and 55 for the Trou du Chêne; see SOM Table S13). In addition, a viper (cf. *Vipera* sp.) is also represented in the Trou de Chaleux.

Of these three sites, the chronologically best constrained is without any doubt the Trou de Chaleux (Houyet, Namur), with calibrated ages ranging from 15,733 to 14,134 cal BP, situating the main deposit, identified by Dupont as the "1er niveau ossifère," at the transition of Greenland Stadial 2 to Greenland Interstadial 1 (Bølling-Allerød Interstadial; Germonpré et al. 2009; Stevens et al. 2009; Goffette et al. 2020). The large-mammal assemblage from the Trou de Chaleux is mainly derived from an exploitation by Magdalenian people for food, skins, and ornaments. Bones of horse, reindeer, red deer, muskox, and brown bear show anthropogenic modifications (Charles 1998). The species most commonly exploited by the Magdalenian group at the Trou de Chaleux was the horse. Partly butchered horse carcasses were brought to the cave and carved up at the site for meat, marrow, tendons, and ligaments. The same treatment was applied to reindeer and muskox carcasses (Charles 1998). Foxes were skinned, and their meat filleted (Charles 1998). Several fox and bear canines display an anthropogenic perforation of the root (Charles 1998; Germonpré and Hämäläinen 2007; Germonpré et al. 2013); they were probably used by the Magdalenian people as ornaments (Van Wetter 1920). Leaving aside any bias caused by selective hunting by Magdalenian populations, the three best-represented mammals are horse, fox, and muskox (Charles 1998; Germonpré 1997), suggesting very open, cold, and dry conditions.

A recent study of the avifauna from the Trou de Chaleux (Gofette et al. 2020) described the presence of species characteristic of a cold environment such as the snowy owl

(*Bubo scandiacus*), ptarmigans (genus *Lagopus*), and pine grosbeak (*Pinicola enucleator*), which are mainly found today in the Arctic or sub-Arctic regions (e.g., Fennoscandia) or, in the case of the rock ptarmigan (*Lagopus muta*), in mountainous areas acting as interglacial refugia (Stewart et al. 2010). Other taxa, such as the loon (*Gavia arctica/stellata*), whooper swan (*Cygnus cygnus*), red-breasted merganser (*Mergus serrator*), common scoter (*Melanitta nigra*), godwits (genus *Limosa*), and plovers (genus *Pluvialis*) are also expected as breeding species in a cold environment. In contrast, several species are today characteristic of more temperate climates, such as the gray partridge (*Perdix perdix*) and the tawny owl (*Strix aluco*). Most of the bird taxa from the Trou de Chaleux are typical of an open landscape. Today, many species favor tundra, steppes, or grasslands and are regularly found associated in Pleistocene assemblages as inhabitants of the mammoth steppe, which covered much of Eurasia during glacial periods (Tyrberg 1991). However, a few species are characteristic of forested environments, such as the western capercaillie (*Tetrao urogallus*) and the tawny owl, indicating the presence of forested areas in the vicinity of the cave, as part of the transitional landscape characterizing the Late Glacial at the onset of the Holocene (Damblon 1994; Verbruggen 1999). Indeed, the presence of the pine grosbeak, a cold-tolerant species needing trees to breed, suggests that forests were indeed present during the Late Glacial (Cramp and Perrins 1994). A high proportion of bird species favoring ponds or large water bodies is also recorded, including ducks, geese, swans, loons, and waders.

Our reconstructions fit quite well with other such proxies. According to the quantified ecology method, the Trou de Chaleux corresponds to the coldest reconstructed MAT (2.9 °C, i.e., 6.9 °C lower than today) of all the sites studied, together with the lowest MAP (585 mm, i.e., 264 mm lower than at present in Houyet). Seasonality is also reconstructed as having been much higher than at present, with much lower MTC than today (Table 2, Fig. 7). Similar values can be found today in the sub-Arctic area of central Sweden, southern Finland, and in a large strip across the Russian territories corresponding to Taiga. For such a cold climate, it is therefore interesting to go further in its description to give an idea of the challenging conditions that the Magdalenian population of the Trou de Chaleux had to face. The MaxET is among the lower ones, at 34.7 °C, but is not the lowest reconstructed here, whereas the MinET, reaching − 33.3 °C, indeed corresponds to the lowest temperature reconstructed for the whole sequence (Table 2; Fig. 7). By way of comparison, the warmest registered summers (an instrumental record) for Belgium are 2003 and 1976. Whereas 2003 had the warmest summer temperature, the heatwave was particularly long in 1976, with maximum temperatures over 30 °C for 16 consecutive days in the city of Uccle (meteobelgique.be). On the other hand, particularly intense cold snaps in Belgium were recorded during winter 1962–1963 (the longest, from December to March), in 1956 (the coldest), and more recently as well (January and February 1985, February 1986, 1987, 2009, and 2013). During such cold snaps, temperatures can drop to − 18 °C in the city of Uccle and as far as − 30 °C further inland (city of Rochefort, January 1940; meteobelgique.be). The number of rainy days per year faced by the Magdaleanian population (YR = 144; Table 2) was somewhat lower than today (170–180 days; meteobelgique.be). However, the number of snow and frost days per year was much higher than today, with YS for the Trou de Chaleux equal to 115 days (Table 2) as opposed to 20–30 days at present (meteobelgique.be), and with YF reaching the value of 187.5 days (Table 2) as opposed to 70–110 days today in the Meuse and Lesse valleys (meteobelgique.be). Finally, the paleoenvironment based on amphibians and reptiles is also reconstructed as dry (%humid = 42.5%) and rather open (%forested = 30%), even though, as stressed above, the modern ecology of *Rana temporaria* in Belgium is strongly associated with wooded environments (Jacob and Kinet 2007). The viper represented at the Trou de Chaleux (probably *Vipera berus*) today shows a certain preference for dense herbaceous vegetation, dotted with small clear areas, with no particular preference between dry and humid environments (Paquay and Graitson 2007).

During this period, the *Bufo bufo* vs. *Rana temporaria* index is rather low, thus suggesting a predominance of *R. temporaria* over *B. bufo*. Such a change in the dominant anuran species has been proposed to be linked with an ecological change, for example in the extension, distribution, or quality of the vegetatation cover associated with humidity (Blain et al. 2019). Modern herpetological surveys carried out in Poland (Białowieža Primeval Forest; Pikulik et al. 2001) show that peak numbers of *R. temporaria* are recorded in the smallest forest brooks within forested valleys, whereas the common toad occupies a broader range of habitats, being the only species to inhabit drier forests as well as wet places. Such data thus suggest that, although *R. temporaria* is able to live in temperate forest environments today, it would be more adapted than *B. bufo* to cool and humid environmental conditions such as those that seem to have been prevalent during MIS 2.

Holocene (marine isotope stage 1)

Again, the poor chronological attribution of the Holocene samples, mainly due to their reworked conditions, precludes any deep study of MIS 1. However, two periods are worthy of comment here. The first corresponds to the early Preboreal (documented in the Trou Balleux), and the second may correspond to the latest part of the Atlantic or to the beginning of the Subboreal (documented in the Trou du Frontal and possibly Scladina).

The sample from the Trou Balleux (Tables 1–25) has been dated to between 12,127 and 11,257 cal BP, corresponding to the beginning of the Preboreal period. The climate has been reconstructed as still rather cool (−3 °C lower than present temperatures) and drier, together with a highly forested environment (%forested = 80%; Table 2, Fig. 8). According to Dutch high-resolution multi-proxy records (Bos et al. 2007), such a reconstruction may be correlated with the Friesland phase, occurring around 11.5 ka. However, as our reconstruction is only based on the occurrence of one ubiquitous species (*Bufo bufo* s.l.), doubts can be raised about such a result. Nevertheless, the fact that *B. bufo* appears again, subsequently to the Magdalenian samples (Tables 1–21, 22, and 23) where it was absent, is, in itself, a sign that the temperatures in Northern Europe probably recovered at the beginning of the Holocene. Interestingly, during the same cultural period (Tardenoisian), the sample from the Trou du Chêne ("argile à blocaux"; Tables 1–24), with similar temperature estimates, furnished the first fossil record for *Pelobates fuscus* in Belgium, together with *B. bufo* s.l. and *Rana temporaria*.

On the other hand, two sites are of interest insoafar as they document temperatures as warm as interglacial conditions. This is the case for the Holocene samples from Scladina (Tables 1–27) and the Trou du Frontal ("first ossiferous level"; Tables 1–26), where the occurrence of *Zamenis longissimus* constitutes a thermophilic signal, together with the first fossil record for Belgium of the midwife toad (*Alytes obstetricans*) in the Trou du Frontal. Holocene MAP reconstructions remain low compared to present values (800–850 mm; climate-data.org) in the Meuse Valley. MaxET values correspond to the highest estimated values of the whole sequence, with a decrease in the number of rainy days and with forest environments reaching higher values than in any previous interglacial or interstadial sample (Fig. 7).

The mention of *Zamenis longissimus* in Scladina and the Trou du Frontal represents its first Holocene record for Belgium. This species was previously cited in the Late Pleistocene (MIS 5c) of Scladina Cave (Blain et al. 2014). As the Holocene burrows of Scladina correspond to a mix of material and partially reworked Pleistocene sediment with modern elements (Dominique Bonjean, personal communication), they do not prove the Holocene nature of this snake. By contrast, for the Trou du Frontal, even though, as noted above, it may represent a mix of Late Glacial (10 ka) and Holocene (4.4 ka) material, the Holocene attribution of this snake seems to be more secure. According to Musilová et al. (2010), the northern extension of this colubrid is linked to conditions warmer than at present that prevailed during the mid-Holocene, approximately 5,000–8,000 years ago, and the present-day distribution in the southern half of Europe is a remnant of this much wider Holocene range. Indeed, Holocene fossil remains of *Z. longissimus* have been described as far north as northern Germany (Peters 1977a, b), southern Poland (Szyndlar 1984a, b; Berto et al. 2021), and Denmark (Ljungar 1995). This latter record corresponds to the northernmost fossil record yet found, and it has been estimated to date to between 6150 and 5950 cal BP (Ljungar 1995). This occurrence thus corresponds with the Atlantic Period (9050–5700 years BP), the climatic optimum of the Holocene, when mean annual temperatures are thought to have been globally 2–2.5 °C higher than today (Dahl-Jensen et al. 1998). At that time, for example, another reptile, the pond turtle *Emys orbicularis*, occurred even in Sweden, close to 59°N (Sommer et al. 2007). Phylogenetic and demographic analyses of *Z. longissimus* have identified two major clades that expanded from their respective western and eastern refugia after the last glacial maximum and contributed approximately equally to the present range (Musilová et al. 2010b). Snakes from the relic northern populations belong to the eastern clade, showing that it was primarily the snakes from the eastern refugium, probably the Balkans, that occupied Central and Northern Europe during the Holocene climatic optimum. Consequently, if the dating (5,070–4,876 cal BP) obtained from a human rib from the Trou du Frontal (Twiesselmann 1971; Cahen and Haesaerts 1984) is also valid for *Z. longissimus*, the Trou du Frontal probably represents one of the very last occurrences of this thermophilic species in Belgium and probably also in Northern Europe, during the latest part of the Atlantic or the beginning of the still-warm (and warmer than at present) Subboreal periods.

Implications for human settlements in the Meuse Valley

As reconstructed here, the Neanderthals lived under various climatic and environmental conditions, from the warm climate of Scladina (layers VI-Vocre) to the cold conditions documented in the last Mousterian level of Goyet ("Salle du Mouton—1er niveau moustérien"). According to the data estimated here, the Neanderthals benefited from relatively wooded, humid biotopes in southern Belgium, with constant rainfall.

One of the major issues in recent prehistory is the replacement of the Neanderthals by Anatomically Modern Humans (i.e., the so-called Middle to Late Paleolithic transition). No significant differences are observed in the paleoclimate and paleoenvironmental range between Mousterian and Aurignacian samples (Figs. 7 and 8), as has already been demonstrated in the southern peninsulas of Europe (e.g., López-García et al. 2011, 2015; Rey-Rodríguez et al. 2016; Jovanovic et al. 2020). Interestingly, however, the last sample to be considered Middle Paleolithic (Tables 1–12) has been reconstructed as potentially having a very reduced extension of woodland under cold conditions. Woodland areas have been stressed as an important feature of the landscapes occupied by Neanderthals (López-García et al. 2019), and the disappearance of large forest tracts may have made them vulnerable. The last Neanderthals from Europe in Gorham's cave (Gibraltar, UK) have been associated with a short peak of increasing aridity at the end of Heinrich Event 2 (at around 24.5 ka) in the Iberian Peninsula (Blain et al. 2013). A pulse of extreme aridity has also been proposed by Shea (2008) as a cause of the local extinction of the Neanderthals of the Levant at 45 ka. It is still too early to argue for a similar pattern in southern Belgium, as humidity and rainfall seem to have been constant over this period, and this hypothesis thus needs to be tested with a sequence that is chronologically better constrained.

Finally, paleoecological reconstructions have here been undertaken for the late Magdalenian populations of southern Belgium. The Trou de Chaleux is one of the northernmost sites of the distribution of Magdalenian culture, together with Goyet and the Trou des Nutons (Belgium), Teufelsbrücke, Oelknitz, and Kniegrote (Germany), and Kulna and Pekarna (Czech Republic) (Djindjian et al. 1999). At the Trou de Chaleux, the Magdalenian people were apparently well prepared to cope with a particularly cold climate and rather open environmental conditions, under which they were able to hunt on horse, reindeer, red deer, and muskox for food, skins, and ornaments (Charles 1998).

Conclusions

The Quaternary collections of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium) have been used to complement our previous knowledge of the successive herpetofaunal assemblages in Belgium during the last interglacial-glacial cycle and to provide new paleoclimatic and paleoenvironmental reconstructions for this time period, thus making it possible to better define the conditions in which the successive human populations lived in the Meuse Valley. The conclusions are as follows:

1. The search for amphibian and reptile fossil remains undertaken at the RBINS identified some 31 unpublished assemblages from southern Belgium, corresponding to 18 caves/sites.
2. In total, 17 taxa (10 amphibian and seven reptile) have been identified, three of which correspond to their first fossil record in Belgium (*Alytes obstetricans*, *Pelobates fuscus*, and *Hyla arborea*). The thermophilous snake species *Zamenis longissimus* is documented for the first time in the Holocene of Belgium (Atlantic/Subboreal period).
3. From a chronological point of view and taking into account the considerable uncertainty concerning mixing and dating for some sites, this new dataset sheds new light on MIS 2, where most of the Magdalenian assemblages furnished abundant remains of only one anuran species (*Rana temporaria*) and additionally one snake (cf. *Vipera* sp.) at the Trou de Chaleux.
4. Paleoclimatic reconstructions using the quantified ecology method on the chronologically best constrained assemblages permit quantitative data to be proposed for climatic and atmospheric aspects of southern Belgium during the last interglacial-glacial cycle. The temperature (MAT) oscillated between 2.9 and 9.1 °C. The highest values correspond to "warm stage" assemblages (MIS 7/6, MIS 5a–c, and the mid-Holocene). MIS 3 assemblages show fluctuating values of between 5.5 and 7.2 °C, whereas MIS 2, particularly the second part of MIS 2 (Late Magdalenian), exhibits the lowest values of the whole sequence, at 2.9 °C (i.e., 6.9 °C lower than present values). The mean temperature of the coldest month (MTC) and minimum extreme temperature (MinET) present a large range of variation, with the coldest values again obtained for MIS 2 (− 10.9 and − 33.3 °C respectively). Similarly, the reconstructed number of snow (YS) and frost (YF) days per year reach their maximum values (115 and 187.5 days respectively) during the late Magdalenian. The seasonal contrast is thus at its maximum, as MTW values are somewhat lower, but summer is still quite warm temperate.
5. Concerning rainfall, neither mean annual precipitation (MAP) nor the number of rainy days per year (YR) demonstrates major variations between the different periods. Rainfall levels are always between 585 and 710 mm, i.e., much lower than current values in southern Belgium (at around 800–850 mm). The highest value corresponds to the MIS 7/6 and the lowest to the late Magdalenian.
6. As far as the paleoenvironment is concerned, the quantified ecology method (based only on absence/presence data) suggests that there were important variations in forest cover (%forested) ranging from virtually 0% (assemblages with only *Rana temporaria*) to 55%. The highest values (> 40%) are obtained for interglacial periods (Holocene and MIS 5a–c) whereas for MIS 3 and MIS 2 the woodland cover is generally somewhat lower. Finally, no evident pattern is distinguished for the extension of humid environments (%humid), probably due to the apparently low variation in reconstructed rainfall, as well as the fact that the last part of MIS 3 and MIS 2 seem to have shown more humid environments than other periods.
7. The variation observed in the dominance of *Bufo bufo* over *Rana temporaria* during the period studied here seems to be influenced by the temperature and terrestrial

environment. The evidence is that when temperatures are warm/temperate and the environment is forested, *B. bufo* dominates over *R. temporaria*, whereas the latter species becomes dominant under cold climatic conditions and in open environments.

8. As far as human populations are concerned, the climate and environmental reconstructions show that Neanderthals thrived under different conditions and that the last recorded occurrence in the studied sequence is correlated with cold conditions but above all with an important reduction in forest cover. Subsequent Aurignacian conditions were not particularly different from Mousterian ones. Finally, the climate conditions for the late Magdalenian populations living in the northernmost part of their distribution area were particularly cold (in terms of temperature and days of snow and frost). The landscape was rather open, even though some proxies locally suggest a certain representation of woodland patches.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12520-021-01481-3.

Acknowledgements HAB acknowledges Dr. Mietge Germonpré (RBINS) and Quentin Gofette (RBINS) for sharing relevant information about some of the Belgian caves studied here and the general context. Special thanks are due to Mrs. Carole Paleco (RBINS), the Synthesys staff in Brussels for administrative gestion, and Alain Drèze (RBINS) for logistical support. The pictures were photo-stacked by Julien Lalanne (RBINS). We kindly thank Thierry Smith (RBINS) for access to his Zeiss camera and stereo microscope and Dominique Bonjean (Scladina Cave Archaeological Center) for the loan of the Holocene material in 2013-2015 and for permission to include part of the Holocene material from Scladina in this study. Rupert Glasgow revised the English texts. Finally, we thank the invited editor A. Blanco-Lapaz (Senckenberg, Tübingen, Germany) and the three referees Prof. J.R. Stewart (Bournemouth University, United Kingdom), Prof. V.Y. Ratnikov (Voronezh State University, Russia), and Dr. Elisa Luzi (University of Tübingen, Germany) for their comments on an earlier version of this manuscript.

Author contribution All authors contributed to the study's conception and design. Preparation of the material, data collection and analysis, and funding acquisition were performed by Hugues-Alexandre Blain, Cécilia Cousin, and Annelise Folie. The first draft of the manuscript was written by Hugues-Alexandre Blain, and all the authors commented on previous versions of the manuscript. All the authors read and approved the final manuscript.

Funding The study of the RBINS Quaternary collections was possible thanks to three Synthesys Grants BE-TAF-4385, BE-TAF-5469, and BE-TAF-1329 to HAB. This paper is also part of projects 2017SGR-859 (Gov. of Catalonia, AGAUR), and CGL2016-80000-P (Spanish Ministry of Economy and Competitiveness). AMM was supported by the Agència de Gestió d'Ajuts Universitaris i de Recerca (AGAUR) and the Departament d'Empresa i Coneixement de la Generalitat de Catalunya (grant 2019FI_B00487). JMLG was supported by a Ramón y Cajal contract (grant RYC-2016–19386). The Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA) received financial support from the Spanish Ministry of Science and Innovation through the "María de Maeztu" program for Units of Excellence (CEX2019-000945-M).

Synthesys, BE-TAF-4385, Hugues-Alexandre Blain, BE-TAF-5469, Hugues-Alexandre Blain, BE-TAF-1329, Hugues-Alexandre Blain, Agència de Gestió d'Ajuts Universitaris i de Recerca, 2017SGR-859, Hugues-Alexandre Blain, 2019FI_B00487, Almudena Martínez Monzón, Ministerio de Economía, Industria y Competitividad, Gobierno de España, CGL2016-80000-P, Hugues-Alexandre Blain, Ministerio de Ciencia, Innovación y Universidades, RYC-2016–19386, Juan Manuel López García.

Data availability The archaeological material studied here is housed in the Quaternary collections of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium).

Declarations

Ethics approval Not applicable.

Competing interests The authors declare no competing interests.

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