



General palaeontology, Systematics, and Evolution (Vertebrate Palaeontology)

Amphibians and squamate reptiles from the late Pleistocene of the “Caverne Marie-Jeanne” (Hastière-Lavaux, Namur, Belgium): Systematics, paleobiogeography, and paleoclimatic and paleoenvironmental reconstructions



Amphibiens et reptiles squammates du Pléistocène supérieur de la caverne Marie-Jeanne (Hastière-Lavaux, Namur, Belgique) : systématique, paléobiogéographie, et reconstitutions paléoclimatique et paléoenvironnementale

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ABSTRACT

Archeological sites usually provide important information about the past distribution of small vertebrate fauna, and by extension about past terrestrial environments and climate in which human activities took place. In this context, Belgium has an interesting location in northwestern Europe between the fully studied zooarcheological records of Germany and England. We present here the revision of the late Pleistocene (Marine Isotope Stages 3 and 2) collection of the “Caverne Marie-Jeanne” (Hastière-Lavaux, Namur), studied by Jean-Claude Rage in the 1970s and the revision of the whole “indeterminate” small vertebrate materials from the “Caverne Marie-Jeanne” stored in the Royal Belgian Institute of Natural Sciences (RBINS) Quaternary collections in search of more herpetofaunal remains. It is now by far the largest late Pleistocene collection at RBINS with more than 20,500 recognized bones of amphibians and reptiles and covering the last 60,000 years. The faunal list comprises two urodeles (*Lissotriton* gr. *L. vulgaris* and *Salamandra salamandra*), four anurans (*Bufo* gr. *B. bufo-spinosus*, *Epidalea calamita*, *Rana temporaria* and *Rana* cf. *R. arvalis*), three lizards (*Lacerta* cf. *L. agilis*, *Zootoca vivipara* and *Anguis* gr. *A. fragilis*), and three snakes (*Natrix* gr. *N. natrix*, *Coronella austriaca*, and *Vipera berus*). This study represents the first fossil record

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in Belgium for *L. gr. L. vulgaris*, *R. arvalis*, *Z. vivipara*, *N. gr. N. natrix* and *C. austriaca*. As a whole, this assemblage suggests a patchy humid landscape under colder and dryer climatic conditions in comparison with present ones. This study also underlines the necessity of a primary separation in larger taxonomical categories by the specialist itself.

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R É S U M É

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Les sites archéologiques fournissent généralement des informations importantes sur la distribution passée des faunes de petits vertébrés, et par extension sur les environnements terrestres et les climats passés dans lesquels les activités humaines se sont déroulées. Dans ce contexte, la Belgique jouit d'un emplacement intéressant dans le Nord-Ouest de l'Europe, entre les importants registres zooarchéologiques allemands et anglais. Nous présentons ici la révision de la collection du Pléistocène supérieur (stades isotopiques marins 3 et 2) de la caverne Marie-Jeanne (Hastière-Lavaux, Namur) étudiée par Jean-Claude Rage dans les années 1970 et la révision de l'ensemble des petits vertébrés « indéterminés » de la caverne Marie-Jeanne préservés dans les collections quaternaires de l'Institut royal des sciences naturelles de Belgique (IRSNB), en cherchant de plus amples restes d'herpétofaune. Il s'agit maintenant, et de loin, de la plus grande collection pour le Pléistocène supérieur à l'IRSNB, avec plus de 20 500 ossements reconnus d'amphibiens et de reptiles, couvrant les 60 000 dernières années. La liste faunique comprend deux urodèles (*Lissotriton* gr. *L. vulgaris* et *Salamandra salamandra*), quatre anoues (*Bufo* gr. *B. bufo-spinosus*, *Epidalea calamita*, *Rana temporaria* et *Rana* cf. *R. arvalis*), trois lézards (*Lacerta* cf. *L. agilis*, *Zootoca vivipara* et *Anguis* gr. *A. fragilis*) et trois serpents (*Natrix* gr. *N. natrix*, *Coronella austriaca* et *Vipera berus*). Cette étude représente la première mention fossile de *L. gr. L. vulgaris*, *R. arvalis*, *Z. vivipara*, *N. gr. N. natrix* et *C. austriaca* en Belgique. Dans son ensemble, cet assemblage suggère un paysage humide en mosaïque sous des conditions climatiques plus froides et plus sèches par rapport au présent. Cette étude souligne également la nécessité d'une séparation primaire en grandes catégories taxonomiques par le spécialiste lui-même.

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1. Introduction

Archeological sites usually provide important information about the past distribution of small vertebrate fauna, when archeologists have taken care to recover such tiny remains. Behind the biological information about the occurrence of some taxa currently absent from a territory (because of climate change and/or habitat destruction), such data are also useful for archeologists as, by comparison with their present distribution, small vertebrates are complementary to the large fauna for the reconstruction of past environments and climate in which human activities took place (Bailon and Rage, 1992). In Europe, Jean-Claude Rage has been the precursor of such studies (Rage, 1968, 1972, 1974), leading to a renewal of paleoherpetological studies for the northwestern European Pleistocene and the training of young researchers who still continue his work today.

In this context, Belgium has an interesting location in northwestern Europe (Fig. 1), in between the fully studied zooarcheological record of Germany and England, because its southern half (Walloon Region) contains a great number of late Pleistocene cave sites that have delivered one of the largest collection of Neanderthal remains and Mousterian lithic industries in Europe (e.g., Pirson et al., 2018; Toussaint, 1996; Toussaint and Pirson, 2007; Toussaint et al., 2004). Among the materials recovered from such 19th-century excavations, small vertebrate remains can

generally also been identified. Unfortunately, besides their historical interest, most of them are clearly lacking a well-defined stratigraphic context. One of the exceptions among these ancient excavations is the “Caverne Marie-Jeanne” excavated by the Royal Belgian Institute of Natural Sciences (RBINS) more recently (1943) and with well-stratified deposits (Fig. 2; Ballmann et al., 1980). As in many other places in the world, studies on the Pleistocene herpetofauna from Belgium, when compared with mammals, have been relatively scarce. To our knowledge, four main late Pleistocene sites have mentioned fossil remains of amphibians and reptiles so far: two of them are the already-mentioned the “Caverne Marie-Jeanne” (Ballmann et al., 1980) and “Grotte Walou” (de Wilde, 2011), where a general faunal list has been published with reference to amphibians and reptiles, and more recently, the Scldina and Sous-Saint-Paul caves, where fossil herpetofauna has been fully described, illustrated and interpreted (Blain et al., 2014).

According to the preliminary study of the small vertebrates [in Ballmann et al. (1980) and mentioned in Holman (1998) and Sanchíz (1998)], the “Caverne Marie-Jeanne” was shown as an interesting site for Pleistocene amphibians and reptiles with a quite diverse fauna including at least nine taxa: *Salamandra* sp., *Bufo* s.l., *Epidalea* cf. *calamita*, *Pelophylax* cf. *esculentus*, *Rana temporaria*, *Anguis* sp., *Lacerta* sp., Colubridae indet. and *Vipera* sp. However, this material was still undescribed nor illustrated and not

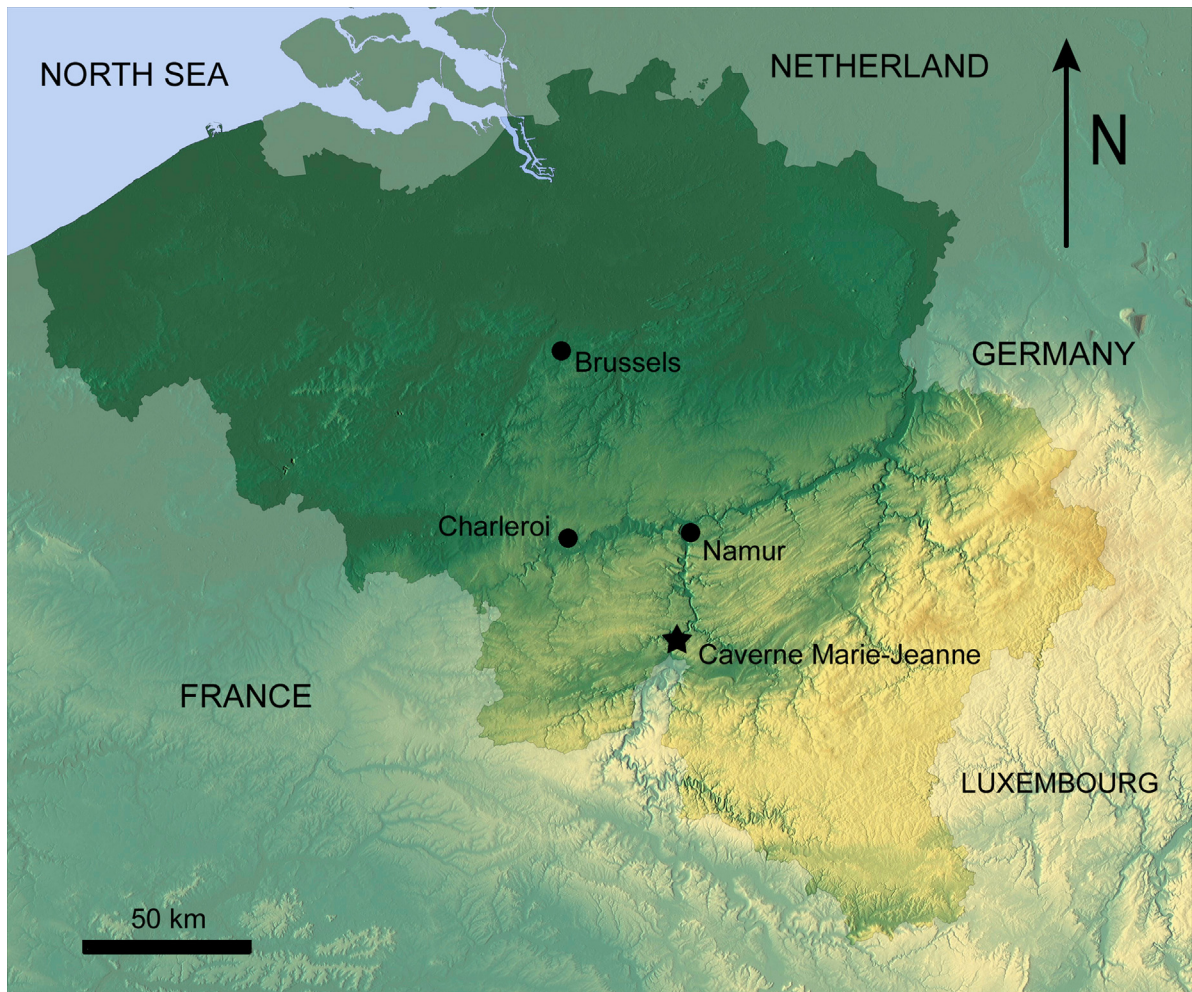


Fig. 1. Geographical location of the “Caverne Marie-Jeanne” (Hastière-Lavaux, Belgium).

Fig. 1. Localisation géographique de la caverne Marie-Jeanne (Hastière-Lavaux, Belgique).

fully interpreted in terms of paleoenvironment and paleoclimate. The present study thus corresponds to (1) the revision of the “small fraction of” the fossil herpetofauna from the “Caverne Marie-Jeanne” studied by Jean-Claude Rage (MNHN, Paris) for the publication of [Ballmann et al. \(1980\)](#) and provisionally housed in his office (J.-C. Rage, personal communication in 2015) since then, and which now has been returned to the RBINS for its final conservation; (2) the whole revision of the “indeterminate” small vertebrate materials (labelled as “small mammal postcranial”; [Fig. 3](#)) from the “Caverne Marie-Jeanne” stored in the RBINS Quaternary collections in search of more herpetofaunal remains; (3) to propose a paleoenvironmental and paleoclimatic reconstruction for the latest Pleistocene of Belgium based on the whole identified herpetological material.

Such publication thus aims to bring further data on the history of modern herpetofauna from Belgium and inside a northwestern European framework, in between the continental European and British fossil records, and also to reconstruct the paleoenvironmental and paleoclimatic

conditions of this region during the late Pleistocene. We dedicate this research to the memory of Jean-Claude Rage (1943–2018), for his pioneering works on the Quaternary amphibians and reptiles from France and Belgium.

2. The site

The “Caverne Marie-Jeanne” (50°13'0"N/4°47'6"E) is an archeological site situated in southeastern Belgium, in the Ardennes region ([Fig. 1](#)). The cave, which is formed in the Early Carboniferous (Tournaisian) marine limestones, 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; Brace et al., 2012](#)). The Meuse River is 1.5 km from the site, and the slope to reach the river is strongly inclined (2%). The overlying plateau is located directly beside the cave (5 m), with a subvertical escarpment of approximately 13 m high. The excavations at this site took place during the summer of 1943 under the direction of M. Gilbert (RBINS).

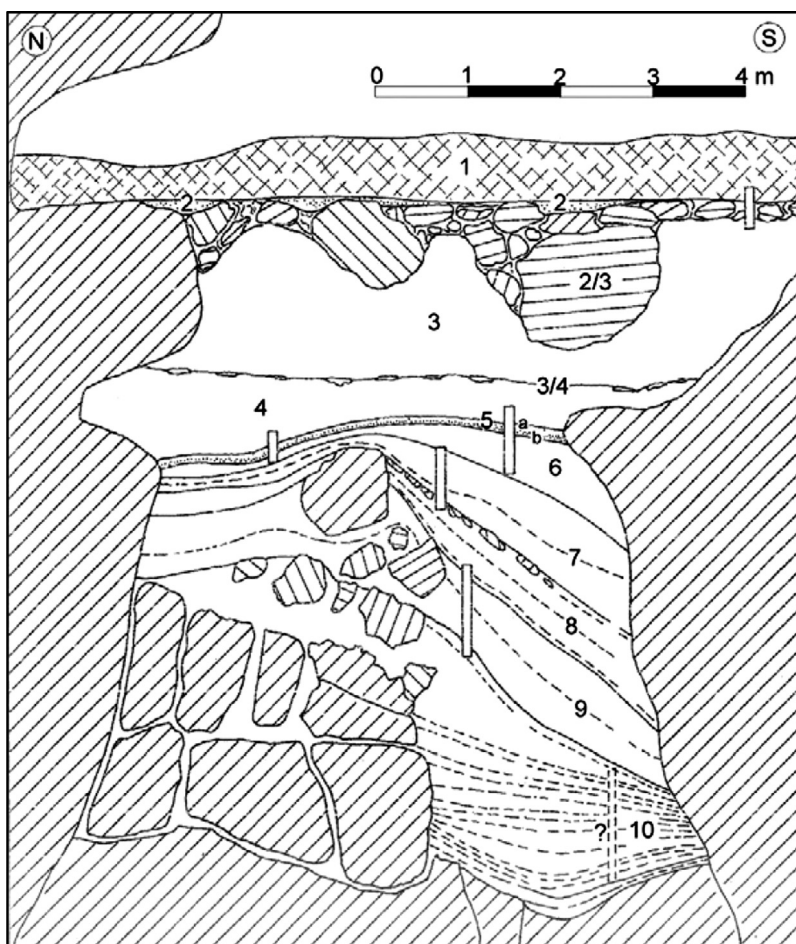


Fig. 2. Stratigraphic sequence of the “Caverne Marie-Jeanne” (Hastière-Lavaux, Belgium) according to Ballmann et al. (1980). See the text for the explanation of the different levels.

Fig. 2. Séquence stratigraphique de la caverne Marie-Jeanne (Hastière-Lavaux, Belgique) selon Ballmann et al. (1980). Voir le texte pour l’interprétation des différents niveaux.



Fig. 3. The Quaternary vertebrate collections of the Royal Belgian Institute of Natural Sciences (Brussels). On the left: view of a compactus with the drawers; on the right, example of “miscellaneous” small vertebrate remains preserved in glass tubes and labelled “small mammals post-cranial remains”.

Fig. 3. Les collections de vertébrés quaternaires de l’Institut royal des sciences naturelles de Belgique (Bruxelles). À gauche : vue d’un compactus avec les tiroirs; à droite, un exemple de restes de petits vertébrés « en vrac » conservés dans des tubes en verre et étiquetés comme « restes postcrâniens de micromammifères ».

During this field campaign, about 40 m³ of sediment were extracted and screened-washed, recovering a large collection of bones and several plant, mollusk, and archeological remains (Ballmann et al., 1980).

These remains are housed at the RBINS under the General Inventory number 14,138 given on 4 September 1943. During excavation campaigns, ten layers were evidenced in the cave (Fig. 2). At the base of the stratigraphic sequence, layers 10 to 7 are sterile. Then layers 6 to 2 delivered a large collection of faunal remains and lithic tools with some Mousterian artefacts that have been identified mainly in layer 3. These fossiliferous layers are principally composed of silty sands. Among large mammals, *Crocota crocuta spelaea*, *Coelodonta antiquitatis*, *Equus cf. remagensis*, *Cervus elaphus*, *Bison priscus*, and *Bos primigenius* are the most abundant taxa (Ballmann et al., 1980). The recent revision of the small mammal fauna has revealed a total of 31 species including rodents, insectivores, and bats (López-García et al., 2017), with the predominance of the narrow-headed vole (*Microtus gregalis*), the common vole (*Microtus arvalis*), and the Arctic lemming (*Dicrostonyx torquatus*) in the lower layers (6 to 4) by contrast to layer 2, where the Common vole (*M. arvalis*), the Common mole (*Talpa europaea*), the narrow-headed vole (*M. gregalis*), the common shrew group (*S. gr. araneus*), the European water vole (*Arvicola amphibius*), and the Arctic lemming (*D. torquatus*) are the most abundant species.

The geological interpretation of the cave suggested that, during the formation of layers 10 to 7, the cave was closed and then, 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 large mammal accumulation from the “Caverne Marie-Jeanne” seems to indicate that the cavity probably functioned as a hyena den or hibernation place. Finally, the uppermost layer 1 is composed of clayey soil mixed with organic remains where fossil and modern faunal remains have been recovered (Ballmann et al., 1980). Numeric dating of the stratigraphic sequence of the “Caverne Marie-Jeanne” (Brace et al., 2012) shows that the lower layers (6 to 4) are dated between ca. 50–40 kyr B.P., and thus pertain to Marine Isotope Stage (MIS) 3, whereas the overlying layer 2 gives somewhat divergent dating comprised between 14,850–13,925 and 25,456–24,497 cal yr. B.P. and thus pertains to MIS 2.

3. Material and methods

3.1. Amphibians and reptiles from the “Caverne Marie-Jeanne”

The specimens here described are part of the rich Quaternary vertebrate collections of the RBINS. The latter have been sorted and inventoried in 2017 and 2018 with the help of technicians, trainees, and students, and are now composed of more than 1,600 drawers, which represent one third of all the fossil vertebrate collections of the RBINS. They are now isolated from other collections and stored

all together in a large compactus (Fig. 3). Among them, 43 drawers contain remains from the “Caverne Marie-Jeanne” and 15 of these drawers contain miscellaneous microvertebrate remains that have been specifically screened for micromammal and herpetological remains, respectively.

The material from the “Caverne Marie-Jeanne” consists mainly of disarticulated bone fragments probably collected (we lack information on the recovery techniques) by screen-washing with a 1-mm mesh screen, to judge by the dimensions of the bone remains (López-García et al., 2017). The fossil material was processed, sorted, classified by the technicians hired at RBINS and then deposited in the collections. As already said in the introduction, a “small part” of the herpetofaunal remains have been sent in the 1970s to J.-C. Rage (MNHN, Paris) for their identification (in Ballmann et al., 1980). It is important to stress here that J.-C. Rage never had access to the whole material and did not sort by himself the amphibians and reptiles. Such a situation clearly distorted the assemblage at least for the skeletal representation, as observed by Rage himself (Ballmann et al., 1980), as for example there were no snake vertebrae at all (the most common element in snakes), but only a few jaws. This situation leads us to organize the complete revision of the “miscellaneous” small vertebrate remains (preserved in glass tubes and labelled “small mammals post-cranial remains”; Fig. 3) from the “Caverne Marie-Jeanne” in search of the missing skeletal parts, which were in many cases the diagnostic element for an attribution to species levels (see below vertebrae for newts, salamanders, and snakes). As a result, the studied fossil assemblage from the “Caverne Marie-Jeanne” currently includes some 20,500 bones, corresponding to a minimum of 1,430 identified individuals and representing at least 12 taxa (Table 1).

3.2. Systematic study

The systematic nomenclature used basically follows Speybroeck et al. (2010) and Lescure and De Massary (2012). The osteological nomenclature follows Estes (1981) and Sanchíz (1998) for amphibians, Rauscher (1992) for lizards and Szyndlar (1984, 1991) for snakes. The general taxonomical criteria follow Szyndlar (1984), Bailon (1991, 1999), Barahona Quintana (1996), Barahona and Barbadillo (1997), Holman (1998), Gleed-Owen (1998), Ratnikov (2001), Ratnikov and Litvinchuk (2007), and Blain (2005, 2009). Comparisons were drawn using the dry skeleton collections of the “Museo Nacional de Ciencias Naturales” (Madrid, Spain), of the “Muséum national d’histoire naturelle” (“Anatomie comparée”, Paris, France), of the Department of Paleontology, Faculty of Natural Sciences of the Charles University (Prague, Czech Republic), the Royal Belgian Institute of Natural Sciences (Brussels, Belgium), the Royal Museum for Central Africa (Tervuren, Belgium), the Paleontology Museum of the University of Tübingen (Germany), and the Blain Herpetological collection deposited at IPHES (Tarragona, Spain). Measurements were made with scaled drawings using a binocular microscope with a camera lucida.

Table 1

Amphibians and reptiles represented in the "Caverne Marie-Jeanne" (Hastière-Lavaux, Belgium) in number of remains (NR) and minimum number of individuals (MNI).

Tableau 1

Amphibiens et reptiles de la caverne Marie-Jeanne (Hastière-Lavaux, Belgique) selon le nombre de restes (NR) et le nombre minimum d'individus (MNI).

	Level 1		Level 2		Level 3		Level 4		Level 5		Level 6		TOTAL	
	NR	MNI	NR	MNI	NR	MNI	NR	MNI	NR	MNI	NR	MNI	NR	MNI
<i>Lissotriton vulgaris</i> group							1	1					1	1
<i>Salamandra salamandra</i>			17	7			6	2	20	6	2	2	45	17
<i>Bufo</i> gr. <i>bufo-spinosus</i>	219	54	3685	350	58	16	665	100	44	18	34	7	4705	545
<i>Epidalea calamita</i>			3	1			6	4	3	3	6	2	18	10
<i>Rana temporaria</i>	29	10	1346	157	18	6	1997	270	836	143	654	89	4880	675
<i>Rana</i> cf. <i>R. arvalis</i>			36	14			12	4	2	2			50	20
<i>Anura</i> indet.			7544				1674		41		20		9279	
<i>Lacerta</i> cf. <i>L. agilis</i>			6	2					2	1	1	1	9	4
<i>Zootoca vivipara</i>			220	87			391	14	64	26	26	4	701	131
<i>Anguis fragilis</i> s.l.			18	3			241	4	38	5	29	2	326	14
<i>Natrix</i> gr. <i>N. natrix</i>							4	1	1	1	2	1	7	3
<i>Coronella austriaca</i>			3	2			44	1	11	2	5	1	63	6
<i>Vipera berus</i>			3	2			121	2	48	4	19	1	191	9
<i>Ophidia</i> indet.			17				174		13		18		222	
TOTAL	248	64	12898	625	76	22	5336	403	1123	211	816	110	20497	1435

Table 2

Distribution by habitats of the amphibians and reptiles from the “Caverne Marie-Jeanne” (Hastière-Lavaux, Belgium). Abbreviations: OD: open-dry; OH: open-humid; Wo: woodland and woodland-edges; R: rocky and stony; Wa: water and water-edges.

Tableau 2

Distribution par habitats des amphibiens et reptiles de la caverne Marie-Jeanne (Hastière-Lavaux, Belgique). Abréviations : OD : ouvert et sec; OH : ouvert et humide ; Wo : forêt et lisières de forêt ; R : rocheux et pierreux ; Wa : milieux aquatiques et riverains.

	OD	OH	Wo	R	Wa
<i>Lissotriton vulgaris</i> group		0.1	0.8		0.1
<i>Salamandra salamandra</i>		0.2	0.7		0.2
<i>Bufo bufo</i>	0.1	0.3	0.4		0.2
<i>Epidalea calamita</i>	0.75			0.25	
<i>Rana temporaria</i>		0.4	0.4		0.2
<i>Rana arvalis</i>		0.6	0.2		0.2
<i>Lacerta agilis</i>	0.5		0.2	0.3	
<i>Zootoca vivipara</i>		0.5	0.25	0.25	
<i>Anguis fragilis</i>	0.1	0.5	0.25	0.15	
<i>Natrix helvetica</i>		0.45	0.2	0.1	0.25
<i>Coronella austriaca</i>	0.35		0.25	0.4	
<i>Vipera berus</i>	0.3	0.3	0.1	0.3	

Abbreviations: IRSNB: Institut royal des sciences naturelles de Belgique.

3.3. Habitat weighting

A paleoenvironmental reconstruction has been done using the habitat weighting method applied to amphibians and reptiles (see [Blain et al., 2008](#)), distributing each taxon in the habitat(s) where it is possible to find it at present in northwestern Europe ([Table 2](#)). Because late Pleistocene amphibians and reptiles can be considered specifically identical to modern populations, the current species habitat distribution may be used for the habitat weighting. The habitats were divided into five types: open land in which dry and wet meadows are distinguished, woodland with woodland-margin and scrubland areas, areas surrounding water, and rocky areas. Each species was given a maximum possible score of 1.00, which was broken down according to the habitat preference of that species, so that, if an animal occurred in more than one habitat type, its score was proportional to its habitat preference. The distribution data are from [de Witte \(1942\)](#), [Duguet and Melki \(2003\)](#), and [Jacob et al. \(2007\)](#).

3.4. Paleoprecipitation tool ([Böhme et al., 2006](#))

The reconstruction of mean annual precipitation (MAP) follows [Böhme et al. \(2006\)](#). This method is based on the relative abundance of six herpetological (excluding non-fossorial snakes) ecophysiological groups (aquatic, heliophobe, semiaquatic + woodland, peri-aquatic, fossorial + arboreal, heliophile) and represents a regression analysis with annual precipitation as the dependent variable and the relative frequencies of the groups as explanatory variables ([Böhme et al., 2006](#)). By constructing a normalized index using regression coefficients, the mean annual precipitation (MAP) is calculated by the equation

$$MAP = -35.646 + 2402.289$$

$$* \left(\sum \text{indexes} / \text{number of species} \right)$$

Based on [Böhme et al. \(2006\)](#), the amphibians and reptiles described as fossils in Caverne Marie-Jeanne have been classified in the ecophysiological groups as follow: semiaquatic + woodland (*Rana arvalis*; Index = 0.513), peri-aquatic (*Lissotriton* gr. *L. vulgaris*, *Salamandra*, *Bufo* gr. *B. bufo-spinosus*, *Epidalea calamita*, and *Rana temporaria*; index = 0.3918), fossorial + arboreal (*Anguis* gr. *A. fragilis*; index = 0.0917), and heliophile (*Lacerta agilis* and *Zootoca vivipara*; index = 0).

3.5. Bioclimatic model ([Hernández-Fernández, 2001b](#))

The bioclimatic model is based on the hypothesis that a significant correlation between the climate and the mammals communities exists. According to [Hernández-Fernández \(2001a, b\)](#), [Hernández-Fernández and Peláez-Campomanes \(2005\)](#), and [Hernández-Fernández et al. \(2007\)](#), any mammal assemblages can be included in ten climatic types, that can be distributed using the Climatic Restriction Index ($CRI_i = 1/n$, where n is the number of climatic zones where the species are represented and i is the climatic zone where the species appears): I, Equatorial; II, tropical with summer rains; II/III, transition tropical semiarid; III, subtropical arid; IV, subtropical with winter rains and summer droughts; V, warm-temperate; VI, typical temperate; VII, arid-temperate; VIII, cold-temperate (boreal); IX, Arctic.

After obtaining the distribution of a small mammal fossil assemblage according to each climatic groups, the Bioclimatic Component (BC; representation level by level of each of the available climates) can be calculated using the following formula:

$$BC_i = \left(\sum CRI_i \right) \times 100/S,$$

where S is the number of species per unit. From the BC, a mathematic modelling has been elaborated using a multiple linear regression ([Hernández-Fernández and Peláez-Campomanes, 2005](#)) that allows one, by means of a series of functions, to estimate various climatic parameters. Based on this method, two climatic factors will be estimated here: the mean annual temperature (MAT) and

the mean annual precipitation (MAP). Only rodents have been included in the analysis.

3.6. Quantified Ecology (Jeannet, 2010)

The Quantified Ecology method is based on giving climato-ecological values, stemming from randomly collected geographic and climatic data provided by the remote climatic stations over thirty years, for each one of some 150 Eurasian and North tropical species (amphibians, reptiles, small mammals including insectivores and bats) in relation with their climatic and ecological potentialities (Jeannet, 2010). For each species, the climatic data provided by remote stations and averages thereof, are associated with that of other species of the same level. The values obtained for each parameter are given in Jeannet (2010). Then, just by obtaining the mean of all the species represented in a site or a level, this method permits to calculate various climatic and environmental parameters, from whose here we will only use the mean annual temperature (MAT) and mean annual precipitation (MAP). In order to compare with other proxies, amphibians and reptiles have been separated from the small mammals (rodents, insectivores, and bats).

3.7. Modern climate data

The reconstructed climatic parameters are compared with the modern climatic data (1980–2010) from the meteorological station of Hastière-Lavaux (50°4' N, 4°49' E), situated at 98 m a.s.l. (climate-data.org). For the area around the “Caverne Marie-Jeanne”, the current data show that the mean annual temperature (MAT) = 9.9 °C, and the mean annual precipitation (MAP) = 840 mm.

4. Systematic description

AMPHIBIA Linnaeus, 1758

As a whole, amphibians are represented by 18,980 remains (i.e. 92.6% of the whole material) and have been referred to six taxa belonging to caudates and anurans.

CAUDATA Scopoli, 1777

SALAMANDRIDAE Goldfuss, 1820

Lissotriton gr. *L. vulgaris* (Linnaeus, 1758)–Palmate or smooth newt (Fig. 4A)

A unique presacral vertebra (Fig. 4A) is attributed to the *Lissotriton vulgaris* group [i.e. *L. vulgaris*, *L. helveticus* (Razoumosky, 1789) and *L. italicus* (Peracca, 1898)] in the level 4 of the “Caverne Marie-Jeanne”. This vertebra is opisthocoelous, small in size (centrum length, CL = 1.81 mm), weakly elongated (length/width ratio, L/W = 1.7) and possesses well-differenced bifurcated transverse processes visible in lateral view. The neural arch is markedly vaulted (ratio neural arch height/vertebra height = 0.42). In dorsal view, the anterior margin of the neural arch is somewhat slightly concave, its posterior limit reaching the anterior third of the prezygapophyseal articular facets. The well-differentiated neural spine is long, of

moderate height, thin anteriorly but slightly enlarged posteriorly, and horizontal in lateral aspect on all its length. It does not reach the anterior margin of the neural arch and posteriorly is bifurcated with a moderately deep and wide median notch. In ventral view, the condyle is robust and shows no postcondylar constriction. On the ventral surface of the centrum, the ventral crests are well developed, but show some variation in their extension. The subcentral foramina are large and, in addition, several other small foramina are also present.

Among the West-European small-sized salamandrids, the species *Triturus marmoratus* Latreille, 1800, *Triturus pygmaeus* Wolterstorff, 1905, *Ichthyosaura alpestris* (Laurenti, 1768), *Lissotriton boscai* Lataste and Tournerville in Blanchard, 1879, *Lissotriton vulgaris* and *L. helveticus* have presacral vertebrae with a well-developed neural spine that is high along its whole length (i.e. Ratnikov and Litvinchuk, 2007). In *Triturus*, unlike in *Lissotriton*, the interzygapophyseal constriction is more pronounced, the posteromedial notch of the neural arch is weak, and the neural spine is not bifurcated posteriorly. The vertebrae of *T. cristatus* and *T. marmoratus* are relatively longer than *I. alpestris*, and both are longer and slenderer than in *L. vulgaris* and *L. helveticus* (Gleed-Owen, 1998). *Ichthyosaura alpestris* has relatively narrow vertebrae, with a more elongate appearance than in *L. vulgaris* or *L. helveticus* (Gleed-Owen, 1998). The subcentral foramina are large in the genus *Lissotriton*, whereas in other genera they are generally smaller or absent (Ratnikov and Litvinchuk, 2007). By its overall shape, this fossil vertebra matches well with the genus *Lissotriton*.

Holman and Stuart (1991) and Holman (1998) suggested that *L. vulgaris* can be separated from *L. helveticus*, when viewed dorsally, by the size of a U-shaped notch in the neural arch, this notch being deeper and more W-shaped in *L. vulgaris* than in *L. helveticus*. Gleed-Owen (1998) verified this character, but relates the size of this notch to the slopes of the posterior neural arch ascending at different angles in the two species. The steeper angle in *L. vulgaris* creates a level platform at the apex (with a deeper notch). In *L. helveticus*, the sides converge to a peak that gives the neural spine a triangular appearance in anterior view (with a smaller notch). Gleed-Owen (1998) also remarks that not all specimens are as distinctly pointed, relating to position in the vertebral column. This last morphology is the one that seems to appear on our fossil vertebra, in posterior view, with the slopes of the posterior neural arch ascending more weakly than in *L. helveticus*, however. The notch seems also to be moderately deep in dorsal view, i.e. more similar to what is observed in *L. helveticus* than to what is observed in *L. vulgaris*. However, the height of the neural spine in lateral view is relatively lower than what is observed in *L. helveticus* and more similar to what is observed in *L. vulgaris*. As stressed by Gleed-Owen (1998) and thereafter by Böhme (2010), there appears to be some ambiguity in the character proposed by Holman and Stuart (1991), and confident diagnosis might not be possible in all cases, thus leading here to a cautious attribution at the level of the group of species only.

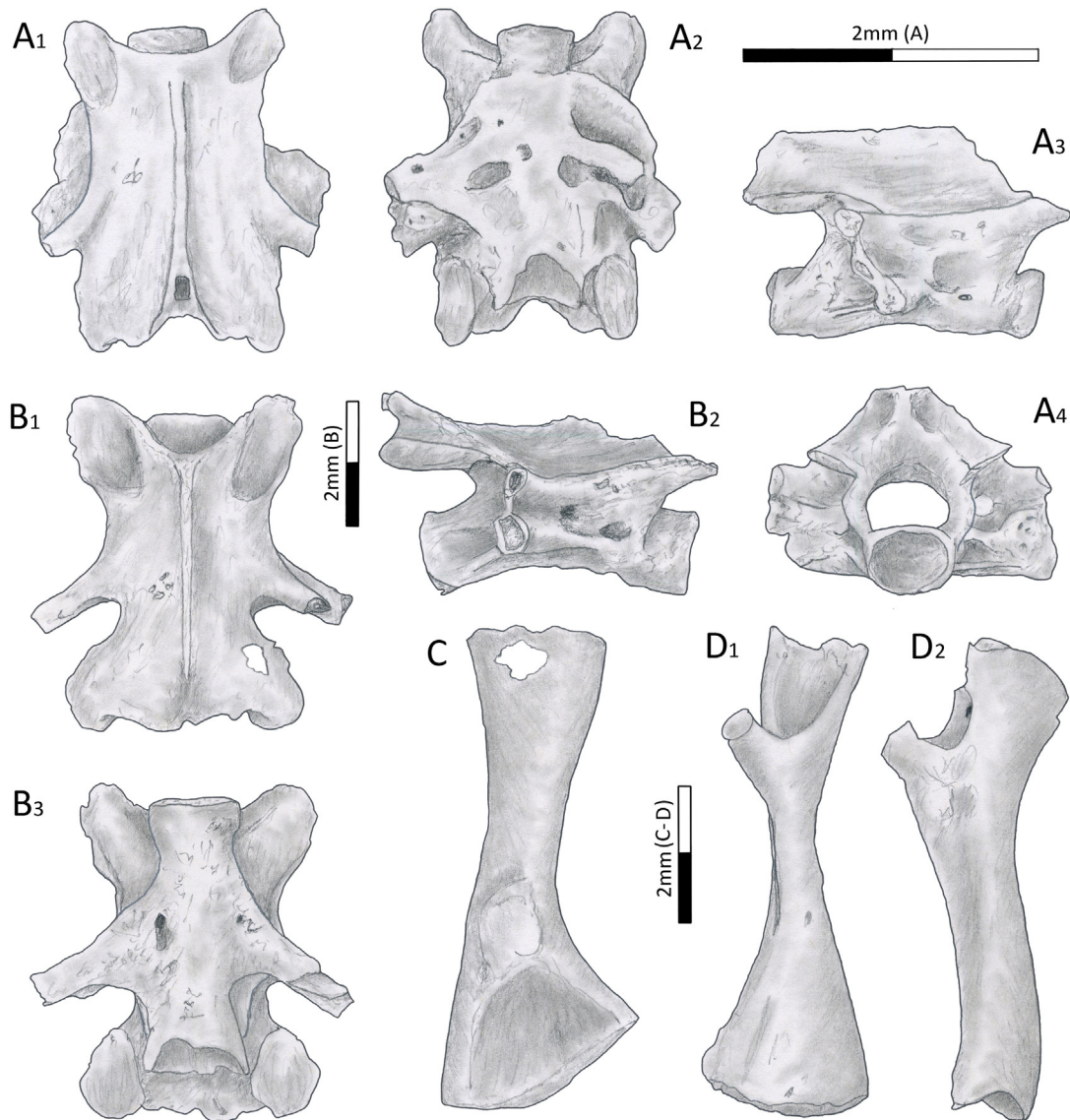


Fig. 4. Fossil caudates from the late Pleistocene of the “Caverne Marie-Jeanne” (Hastière-Lavaux, Namur). **A:** *Lissotriton* gr. *L. vulgaris*, presacral vertebra (IRSNB A 08) in dorsal (A1), ventral (A2), right lateral (A3) and posterior (A4) views; **B–D:** *Salamandra* (Linnaeus, 1758). **B:** presacral vertebra (IRSNB A 09) in dorsal (B1), right lateral (B2) and ventral (B3) views; **C:** left ilium (IRSNB A 10) in lateral view; **D:** femur (IRSNB A 11) in ventral (D1) and lateral (D2) views.

Fig. 4. Urodèles fossiles du Pléistocène supérieur de la caverne Marie-Jeanne (Hastière-Lavaux, Namur). **A :** *Lissotriton* gr. *L. vulgaris*, vertèbre présacrée (IRSNB A 08) en vues dorsale (A1), ventrale (A2), latérale droite (A3) et postérieure (A4) ; **B–D :** *Salamandra* (Linnaeus, 1758) ; **B :** vertèbre présacrée (IRSNB A 09) en vues dorsale (B1), latérale droite (B2) et ventrale (B3) ; **C :** ilion gauche (IRSNB A 10) en vue latérale ; **D :** fémur (IRSNB A 11) en vues ventrale (D1) et latérale (D2).

Salamandra salamandra (Linnaeus, 1758)–Fire salamander (Fig. 4B–D)

A total of 45 elements have been attributed to the fire salamander: 23 presacral vertebrae, one postsacral vertebra, 7 humeri, 12 femurs, one left ilium, and one tibia. The presacral vertebrae (Fig. 4B) differ from those of the previous salamandrid by their larger size (total length, taken from the anterior margin of the prezygapophyses to the posterior margin of the postzygapophyses, comprised between 5 and 7 mm). They are opisthocelous,

with bifurcated transverse processes. The neural arch is dorsoventrally flattened, with a deeply concave anterior margin, at the level of the middle part of the prezygapophyseal articular facets and a small medial notch in its posterior margin. The neural spine is long, low, and narrow, and is well developed in the middle part of the neural arch only. In ventral view, two small subcentral foramina are visible on the centrum and located anteriorly. All these characters are typical of the genus *Salamandra* (i.e. Estes, 1981; Ratnikov and Litvinchuk, 2007; Sanchíz and Młynarski, 1979). The postsacral vertebra is characterized by the presence of only

one slightly dorsoventrally flattened rib-bearer. Other elements (Fig. 4C–D), less diagnostic, have been attributed to the genus *Salamandra*, mainly based on their size and because their morphology does not differ from the one of that species.

Various southern former sub-species within the *S. salamandra* group have recently been elevated at the species rank: *Salamandra atra* Laurenti, 1768 (from the French Alps to Albany), *Salamandra corsica* Savi, 1838 (Isle of Corsica, France), *Salamandra lanzai* Nascetti, Andreone, Capula, and Bullini, 1988 (in the Alps between France and Italy), and *Salamandra longirostris* Jogger and Steinfartz, 1994 (southernmost Iberian Peninsula) (Speybroeck et al., 2010). No osteological criteria have been provided yet that would permit to diagnose these new species. Consequently, the fossil remains from “Marie-Jeanne” are attributed based on the modern geographical distribution of *S. salamandra*, the only species of that group currently living in northern Europe.

ANURA Duméril, 1805

Anuran remains are very common in the layers of the “Caverne Marie-Jeanne” (18,934 remains, i.e. 92.4% of the total). Among them, some 9279 fossil remains (mainly incomplete elements) have been referred to only as indeterminate anurans.

BUFONIDAE Gray, 1825

Bufo gr. *B. bufo-spinosus* (Linnaeus, 1758) – Common toad (Fig. 5A–P)

A total of 4705 bones have been attributed to the common toad: 35 maxillae; 4 frontoparietals, 15 sphenetmoids, 43 pterygoids, 56 squamosals, 2 parasphenoids, 9 prootic-exoccipitals, 4 angulars, 8 atlas, 19 vertebrae, 137 sacra, 176 urostyles, 3 suprascapulars, 6 parascapulars, 293 scapulae, 30 clavicles, 282 coracoids, 730 humeri, 766 radio-ulnae, 842 ilia, 396 femurs, 784 tibiofibulae, 30 tarsals, and 35 phalanxes. The species determination of this taxon rests mostly on the morphology of cranial and post-cranial elements, in accordance with the criteria established by Böhme (1977), Sanchíz (1977), Bailon and Hossini (1990), Bailon (1991, 1999), and Ratnikov (2001). The maxillae (Fig. 5A) have no teeth, like in all bufonids. The frontoparietals (Fig. 5B) are rectangular, unfused between them and also unfused with the prootic and exoccipital, with a flat dorsal surface and with a well-developed occipital canal. The sphenetmoids (Fig. 5C) are wider than long, with short antero-lateral processes, and without any sella amplificans. In dorsal view, the postero-dorsal margin of the posterior chamber is concave and wide. The pterygoids (Fig. 5D) have three branches of similar width, with no dilatation between the maxillary and posterior branches. The squamosals (Fig. 5E) present a moderately developed *lamina alaris* and a reduced transverse branch. The atlases (Fig. 5F) have an ogival-shaped neural canal with two anterior condyles and a posterior condyle

(procoelous). The neural arch is short and the neural crest is wider posteriorly. The sacral vertebrae (Fig. 5G) have one anterior cotyle and two well-distinct posterior condyles. The transverse processes are moderately elongated, and the neural arch bears a neural crest with no opened fossette at the base of the transverse processes. The urostyles (Fig. 5H) have two anterior well-distinct and slightly dorso-ventrally flattened cotyles. The neural crest is moderately high and the neural canal is subtriangular. The scapulae (Fig. 5I) are higher than wide and present a robust glenoid process, detached and clearly visible in dorsal view. The small supraglenoid fossa is absent. The coracoids (Fig. 5J) are robust, with a short distal extremity. The clavicles (Fig. 5K) are straight and robust. The radio-ulnae (Fig. 5L) are short and robust with a poorly pronounced neck. The humeri (Fig. 5M) have a straight and rather robust diaphysis. The humeral condyle is circular, displaced radially, and generally weakly ossified. The radial epicondyle is poorly developed. In male, the medial crest (*crista medialis*) is flat and restricted to the distal part of the epiphysis. The ilia (Fig. 5N) do not have a dorsal crest, but a relatively low *tuber superior*, with a rounded unilobed dorsal limit. As a variation of the general *B. gr. bufo-spinosus* morphology, some of the ilia from the second layer of the “Caverne Marie-Jeanne” present a bilobate dorsal limit of the *tuber superior*, but without the typical preacetabular fossa observed in genus *Bufo*. The femurs (Fig. 5O) are relatively long, robust and sigmoid, with a femoral crest (or deltoid crest) that is divided and forms a triangular surface. The tibiofibulae (Fig. 5P) are somewhat short and robust, with relatively wide extremities. The other bony elements, which are often incomplete, display the general morphology of the bufonids. The separation of these elements into species has often been performed on the basis of their size, *B. gr. bufo-spinosus* being generally larger than *E. calamita*.

Epidalea calamita (Laurenti, 1768) – Natterjack toad (Fig. 5Q–U)

The natterjack toad is rather scarce in the “Caverne Marie-Jeanne”, even if occurring in quite all layers. It is represented by a few elements: three sacral vertebrae, one scapula, four humeri, six ilia, one femur, and three tibiofibulae. The sacral vertebrae (Fig. 5Q) differ from the bufonid described above in having the two posterior condyles more or less joined together and a fossette that opens posteriorly and laterally at the base of the transverse processes. The only scapula (Fig. 5R) is characteristic of *E. calamita* by the presence of a small supraglenoid fossa above the glenoid apophysis. Humeri (Fig. 5S and T) have a more robust and curved diaphysis than the elements attributed to *B. gr. bufo-spinosus*, and the condyle and epicondyles are more developed. Ilii (Fig. 5U) differ from *B. gr. bufo-spinosus* in having a higher and pointed dorsal prominence (*tuber superior*) and by the presence of a well-developed lateroventral excrescence (*calamita* blade or *calamita* ridge) on the ilial shaft. Finally, one femur and three tibiofibulae have been also carefully attributed to

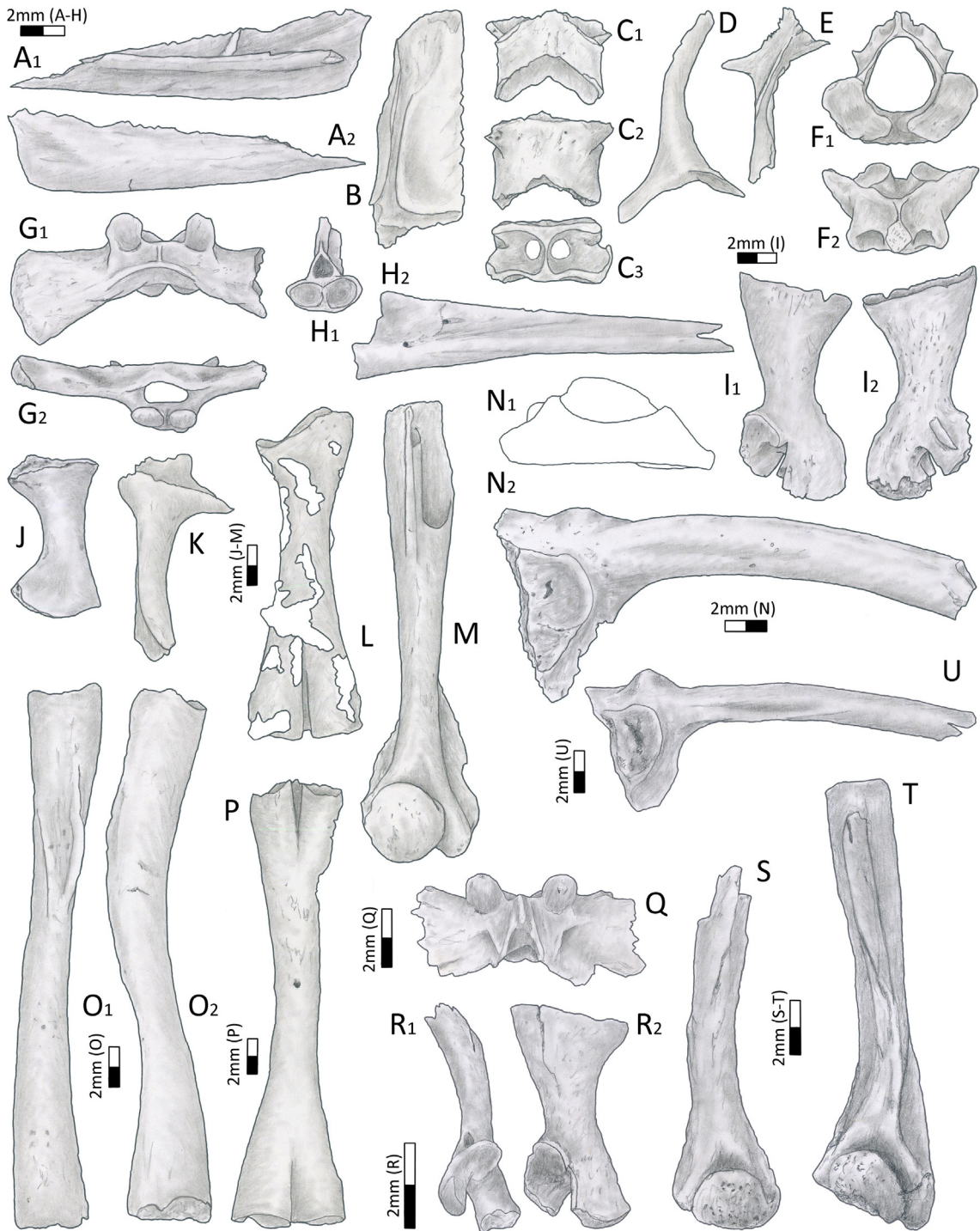


Fig. 5. Fossil toads from the late Pleistocene of the “Caverne Marie-Jeanne” (Hastièrre-Lavaux, Namur, Belgium). **A–P:** *Bufo* gr. *B. bufo-spinosus*, **A:** left maxilla (IRSNB A 12) in medial (A1) and lateral (A2) views; **B:** right frontoparietal (IRSNB A 13) in ventral view; **C:** sphenethmoid (IRSNB A 14) in dorsal (C1), ventral (C2) and anterior (C3) views; **D:** right pterygoid (IRSNB A 15) in ventral view; **E:** left squamosal (IRSNB A 16) in medial view; **F:** atlas (IRSNB A 17) in anterior (F1) and dorsal (F2) views; **G:** sacrum (IRSNB A 18) in dorsal (G1) and posterior (G2) views; **H:** urostyle (IRSNB A 19) in anterior (H1) and left lateral (H2) views; **I:** right scapula (IRSNB A 20) in dorsal (I1) and ventral (I2) views; **J:** coracoid (IRSNB A 21) in ventral view; **K:** clavicle (IRSNB A 22) in ventral view; **L:** radio-ulna (IRSNB A 23) in medial view; **M:** right humerus of male (IRSNB A 24) in ventral view; **N:** right ilium (IRSNB A 25) in posterior (N1) and lateral (N2) views; **O:** femur (IRSNB A 26) in ventral (O1) and lateral (O2) views; **P:** tibiofibula (IRSNB A 27) in lateral view; **Q–T:** *Epidalea calamita*, **Q:** sacrum (IRSNB A 28) in dorsal view;

E. calamita based on their smaller size and the presence of a narrow and straight femoral crest on the femur.

RANIDAE Rafinesque-Schmaltz, 1814

Rana temporaria Linnaeus, 1758 – Common frog (Fig. 6A–K)

The common frog is represented by 4880 bones: 18 premaxillae, 241 maxillae, 16 sphenetmoids, 9 pterygoids, 4 squamosals, 1 parasphenoid, 7 exoccipitals, 16 angulars, 28 atlases, 796 vertebrae (including 73 eighth vertebrae), 136 sacra, 6 fused 8th vertebra and sacrum, 272 urostyles, 20 parasterna, 172 scapulae, 195 coracoids, 733 humeri, 478 radio-ulnae, 604 ilia, 219 femurs, 504 tibiofibulae, 34 tarsals, and 371 phalanxes. Premaxillae and maxillae are toothed. The sphenetmoids (Fig. 6A) are as long as wide, with short antero-lateral processes, and without any sella amplificans. The difference with *B. bufo* is small and relies on the postero-dorsal margin of the posterior chamber, which is somewhat deeper. Pterygoids are slenderer than those of bufonids and present an internal branch much shorter than the posterior one. The squamosals do not have any *lamina alaris* and the anterior and posterior ends of the transverse branch have a similar development. The atlases and vertebrae possess a small centrum and the lateral walls of the neural arch are generally slenderer than in bufonids. The 8th vertebra is amphicoelous. The sacral vertebrae (Fig. 6B) have one anterior condyle and two posterior condyles, and the transverse processes are robust and cylindrical. The urostyles (Fig. 6C) have two anterior well distinct and circular cotyles. The neural crest is high and the neural canal generally narrow. The scapulae (Fig. 6D) are higher than wide and, in dorsal view, unlike bufonids, the glenoid process is partially hidden by the acromial process. On the ventral surface of the bone, a long internal crest is visible. The coracoids (Fig. 6E) are robust, with a well-developed and flattened distal extremity. The humeri (Fig. 6F) have a straight diaphysis. The humeral condyle is circular, in line with the main axis of the diaphysis, and generally well ossified. The radial epicondyle is poorly developed. In male, the medial crest, in medial view, is curved at the level of the ulnar epicondyle and then flat and characteristically very long on the diaphysis. The radio-ulnae (Fig. 6G) are somewhat slenderer than those of bufonids, with a well pronounced neck, and the proximal extremity (*oleocranium*) is generally much more ossified than in bufonids. The ilia (Fig. 6H–J) are characterized by

the presence of a long ilial crest, a short ischial process (*pars ascendens*), a well-developed *tuber superior* and a posteromedial surface that is smooth and without any interilial sulcus. The ilial crest in most of the ilia attributed to *R. temporaria* is low, like in brown frogs (genus *Rana*) and not as vertical as in green frogs (genus *Pelophylax*). In addition, the junction surface with the ischio-pubis (*corpus ossis ilii*) is narrow: acetabulum diameter on thickness ratio (*d/t*, *sensu* Gleed-Owen, 2000) comprised between 2.83 and 4.16, like in the genus *Rana*, where the values of *d/t* lie between 2.75 and 4.00, whereas in genus *Pelophylax* *d/t* is comprised between 2.12 and 2.88 (Gleed-Owen, 2000). Within the genus *Rana*, attribution at the species level is rather difficult, but factors such as size or robustness may suggest an assignation to *R. temporaria*. Also, the height of the ilial crest is generally lower in *R. temporaria*, whereas it is higher in other western European species (Bailon, 1999; Blain and Arribas, 2017; Esteban and Sanchíz, 1985, 1991; Gleed-Owen, 1998, 2000). Femurs have no femoral crest. Finally, other bones (especially tibiofibulae Fig. 6G, tarsals, and phalanxes) present a size and a certain slenderness, when compared with bufonids, that match with an attribution to *R. temporaria*.

Rana cf. *R. arvalis* Nilson, 1842 – Moor frog (Fig. 7A–E)

Among the former collection, two fossil ilia were reported by J.-C. Rage (in Ballmann et al., 1980) to pertain to the edible frog ("*Rana* cf. *esculenta*") in layer 5 of the "Caverne Marie-Jeanne". These ilia (Fig. 7A–B) have a somewhat higher dorsal crest and above all a much more vertical *tuber superior* than usually reported in *R. temporaria*. However, their *d/t* values, respectively 3.25 and 3.8, fall well within the range of genus *Rana*. The dorsal crest reaches its highest point at the level of the *tuber superior*, as reported by Böhme (1977), Bailon (1999), Ratnikov (2001), and Ratnikov and Blain (2018) for *R. arvalis*, whereas in *Rana dalmatina* Fitzinger, 1839 the dorsal crest is higher than the *tuber superior*. The dorsal margin of the dorsal crest may be somewhat eroded and does not present the typical continuously high and rounded crest morphology that, according to the consulted comparative material, must correspond to *R. arvalis* juveniles. In consulted adults of *R. arvalis wolterstorffi*, the dorsal crest is sometimes a little bit depressed anteriorly to the *tuber superior*, as it occurs on the fossils of the "Caverne Marie-Jeanne". Additionally, in comparison with the ilia attributed to *R. temporaria*,

R: right scapula (IRSNB A 29) in posterior (R1) and dorsal (R2) views; S: left humerus of female (IRSNB A 30) in ventral view; T: right humerus of male (IRSNB A 31) in ventral view.

Fig. 5. Crapauds fossiles du Pléistocène supérieur de la caverne Marie-Jeanne (Hastièrre-Lavaux, Namur, Belgique). **A–P** : *Bufo* gr. *B. bufo-spinosus*, A : maxillaire gauche (IRSNB A 12) en vues médiale (A1) et latérale (A2) ; B : frontopariétal droit (IRSNB A 13) en vue ventrale ; C : sphénethmoïde (IRSNB A 14) en vues dorsale (C1), ventrale (C2) et antérieure (C3) ; D : ptérygoïde droit (IRSNB A 15) en vue ventrale ; E : squamosal gauche (IRSNB A 16) en vue médiale ; F : atlas (IRSNB A 17) en vues antérieure (F1) et dorsale (F2) ; G : vertèbre sacrée (IRSNB A 18) en vues dorsale (G1) et postérieure (G2) ; H : urostyle (IRSNB A 19) en vues antérieure (H1) et latérale gauche (H2) ; I : scapula droite (IRSNB A 20) en vues dorsale (I1) et ventrale (I2) ; J : coracoïde (IRSNB A 21) en vue ventrale ; K : clavicule (IRSNB A 22) en vue ventrale ; L : radio-ulna (IRSNB A 23) en vue médiale ; M : humérus droit de mâle (IRSNB A 24) en vue ventrale ; N : ilion droit (IRSNB A 25) en vues postérieure (N1) et latérale (N2) ; O : fémur (IRSNB A 26) en vues ventrale (O1) et latérale (O2) ; P : tibio-fibula (IRSNB A 27) en vue latérale ; **Q–T** : *Epidalea calamita*, Q : vertèbre sacrée (IRSNB A 28) en vue dorsale ; R : scapula droite (IRSNB A 29) en vues postérieure (R1) et dorsale (R2) ; S : humérus gauche de femelle (IRSNB A 30) en vue ventrale ; T : humérus droit de mâle (IRSNB A 31) en vue ventrale.

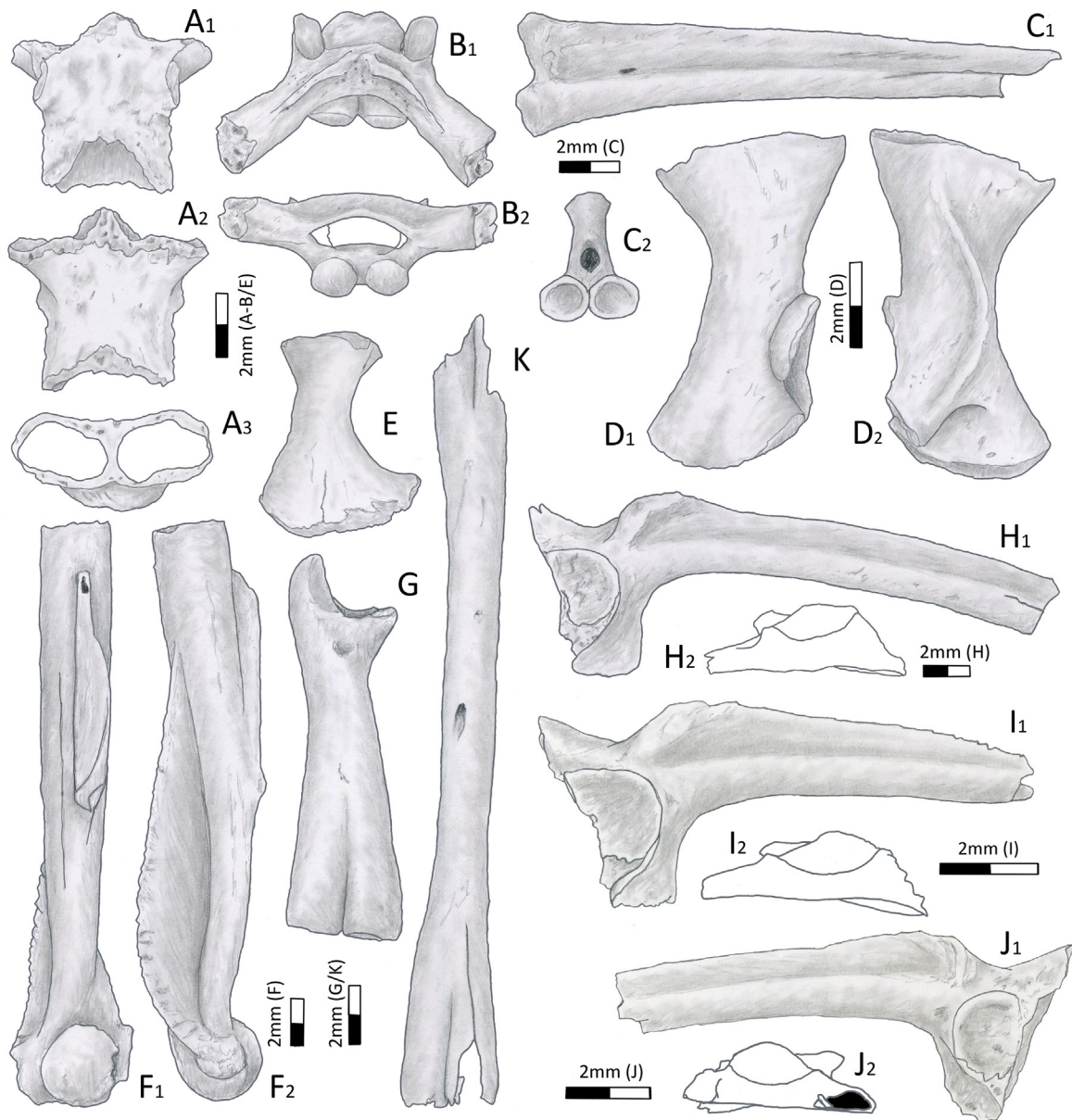


Fig. 6. Fossil Common frogs (*Rana temporaria*) from the late Pleistocene of the “Caverne Marie-Jeanne” (Hastière-Lavaux, Namur, Belgium). A: Sphenethmoid (IRSNB A 32) in dorsal (A1), ventral (A2) and anterior (A3) views; B: sacrum (IRSNB A 33) in dorsal (B1) and posterior (B2) views; C: urostyle (IRSNB A 34) in left lateral (C1) and anterior (C2) views; D: left scapula (IRSNB A 35) in dorsal (D1) and ventral (D2) views; E: coracoid (IRSNB A 36) in ventral view; F: left humerus of male (IRSNB A 37) in ventral (F1) and medial (F2) views; G: radio-ulna (IRSNB A 38) in medial view; H: right ilium (IRSNB A 39) in lateral (H1) and posterior (H2) views; I: right ilium (IRSNB A 40) in lateral (I1) and posterior (I2) views; J: left ilium (IRSNB A 41) in lateral (J1) and posterior (J2) views; K: tibiofibula (IRSNB A 42) in lateral view.

Fig. 6. Grenouilles rouges fossiles (*Rana temporaria*) du Pléistocène supérieur de la caverne Marie-Jeanne (Hastière-Lavaux, Namur). A : Sphénethmoïde (IRSNB A 32) en vues dorsale (A1), ventrale (A2) et antérieure (A3) ; B : vertèbre sacrée (IRSNB A 33) en vues dorsale (B1) et postérieure (B2) ; C : urostyle (IRSNB A 34) en vues latérale gauche (C1) et antérieure (C2) ; D : scapula gauche (IRSNB A 35) en vues dorsale (D1) et ventrale (D2) ; E : coracoïde (IRSNB A 36) en vue ventrale ; F : humérus gauche de mâle (IRSNB A 37) en vues ventrale (F1) et médiale (F2) ; G : radio-ulna (IRSNB A 38) en vue médiale ; H : ilion droit (IRSNB A 39) en vues latérale (H1) et postérieure (H2) ; I : ilion droit (IRSNB A 40) en vues latérale (I1) et postérieure (I2) ; J : ilion gauche (IRSNB A 41) en vues latérale (J1) et postérieure (J2) ; K : tibio-fibula (IRSNB A 42) en vue latérale.

the junction surface with the ischio-pubis seems to be somewhat thinner and, probably due in part to the more vertical orientation of the *tuber superior*, the supra-acetabular fossa looks deeper. Consequently, these two ilia have been cautiously attributed to *R. arvalis*.

During the revision of the collections at RBINS, more ilia have been referred to *R. arvalis* as well as various scapulae and humeri. Consequently, the Moor Frog is now represented in the “Caverne Marie-Jeanne” by a total of 50 bones: 4 scapulae, 33 humeri, and 13 ilia.

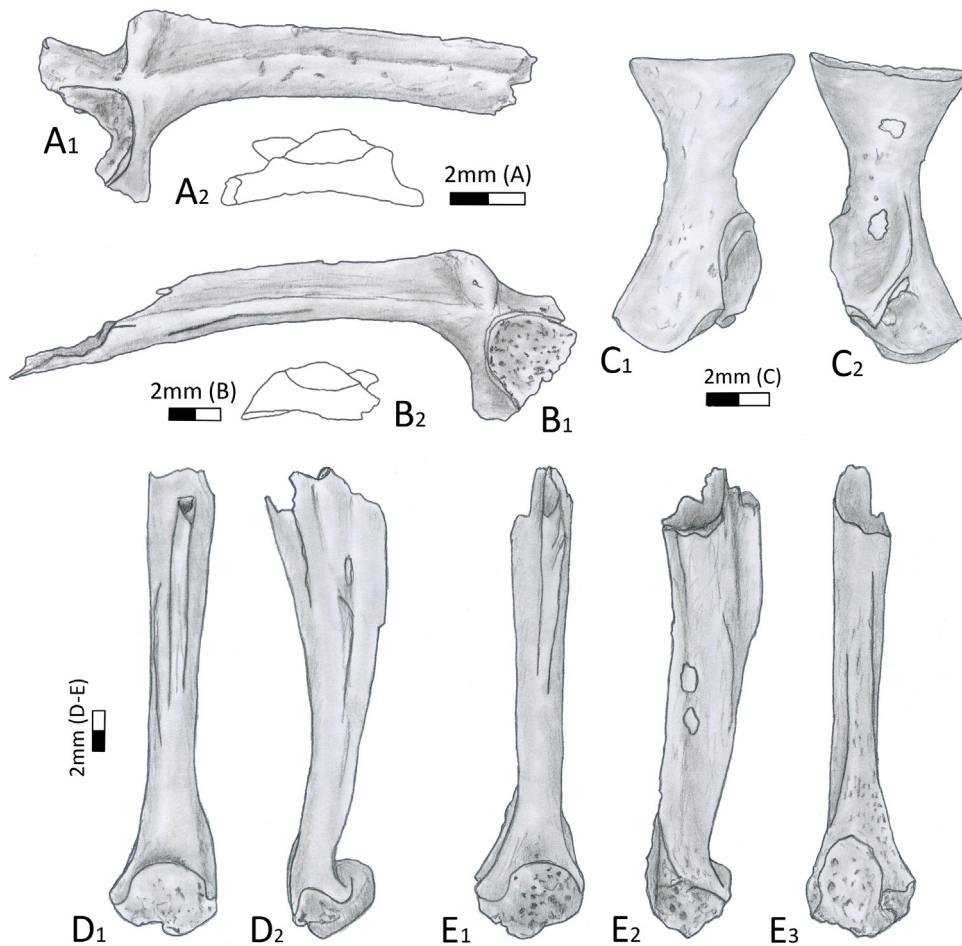


Fig. 7. Fossil Moor frogs (*Rana* cf. *R. arvalis*) from the late Pleistocene of the “Caverne Marie-Jeanne” (Hastière-Lavaux, Namur, Belgium). A: Right ilium (IRSNB A 43) in lateral (A1) and posterior (A2) views; B: left ilium (IRSNB A 44) in lateral (B1) and posterior (B2) views; C: left scapula (IRSNB A 45) in dorsal (C1) and ventral (C2) views; D: left humerus of female (IRSNB A 46) in ventral (D1) and medial (D2) views; E: left humerus of male (IRSNB A 47) in ventral (F1), medial (F2) and dorsal (F3) views.

Fig. 7. Grenouilles des champs fossiles (*Rana* cf. *R. arvalis*) du Pléistocène supérieur de la caverne Marie-Jeanne (Hastière-Lavaux, Namur, Belgique). A : ilion droit (IRSNB A 43) en vues latérale (A1) et postérieure (A2) ; B : ilion gauche (IRSNB A 44) en vues latérale (B1) et postérieure (B2) ; C : scapula gauche (IRSNB A 45) en vues dorsale (C1) et ventrale (C2) ; D : humérus gauche de femelle (IRSNB A 46) en vues ventrale (D1) et médiale (D2) ; E : humérus gauche de mâle (IRSNB A 47) en vues ventrale (F1), médiale (F2) et dorsale (F3).

The morphology of the supplementary ilia is similar to the ones already described. The scapulae (Fig. 7C) attributed to *R. arvalis* are somewhat slender than those referred to *R. temporaria*, with a narrower neck and a head representing no more than half of the total bone length. According to Ratnikov (2001), *Pelophylax lessonae* (Camerano, 1882) and *R. arvalis* have very similar scapulae, but the anterior margin in *P. lessonae* is more convex, the neck is comparatively wider, and the internal crest is shorter. The humeri (Fig. 7D–E) are clearly referable to the genus *Rana* based on the morphology of the lateral and medial crests, which are deflexed dorsally (Bailon, 1999; Ratnikov, 2001). According to Ratnikov (2001), the morphology of these two crests allows us to distinguish *R. arvalis* from *R. temporaria*: *R. arvalis* has almost equally developed medial and lateral crests with converging proximal ends, whereas the medial crest in *R. temporaria* is

appreciably higher and longer than the lateral one. The distance between the proximal ends is comparatively weaker in *R. arvalis* than in *R. temporaria* (Ratnikov and Blain, 2018).

REPTILIA Laurenti, 1768
SQUAMATA Oppel, 1811
LACERTILIA Günther, 1867

“Lizards” are relatively scarce in the assemblage from the “Caverne Marie-Jeanne”, with 1036 remains (5% of all the material). Two lacertids and an anguid lizard have been identified.

LACERTIDAE Batsch, 1788
Lacerta cf. *L. agilis* Linnaeus, 1758 – Sand Lizard (Fig. 8A–C)

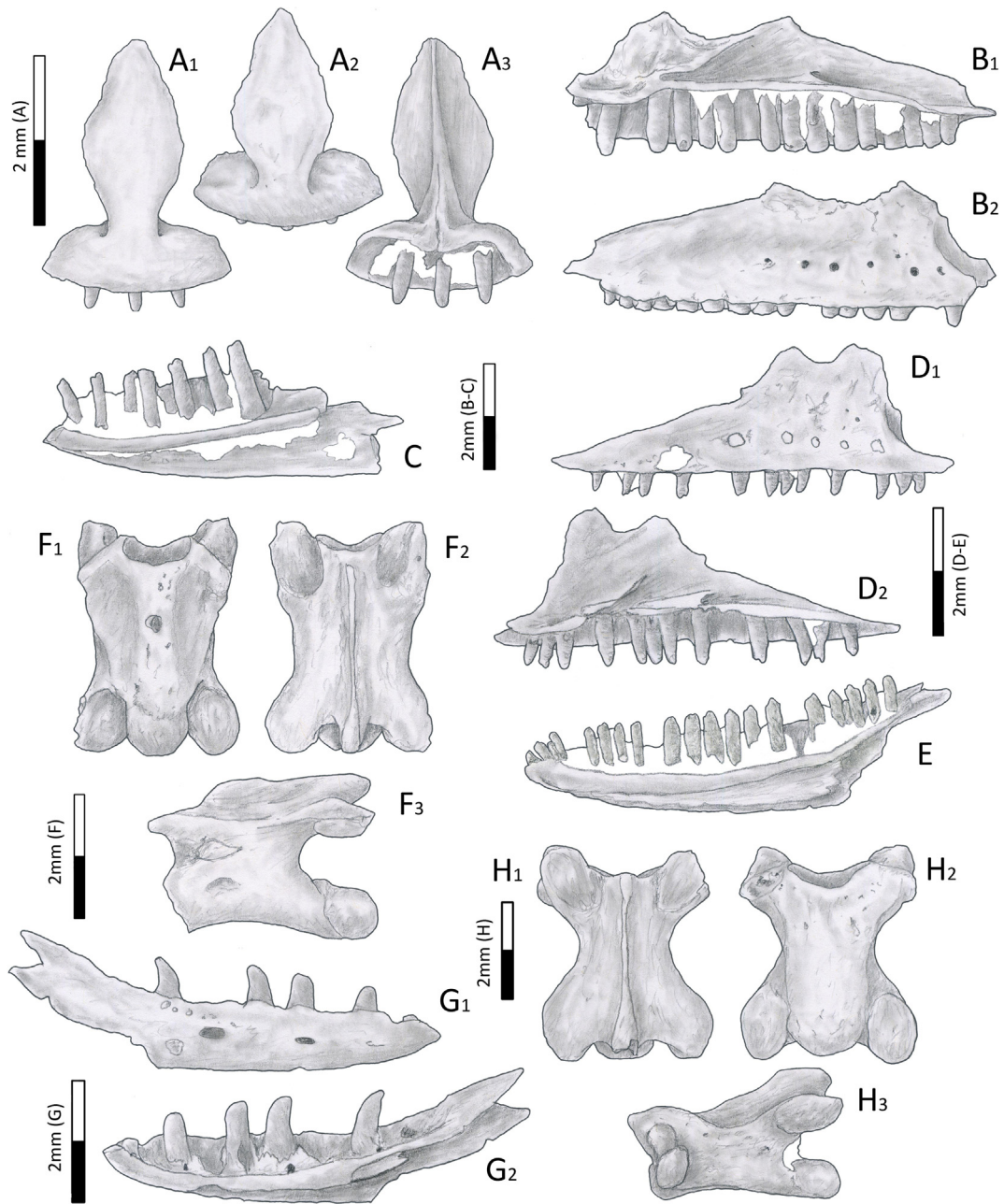


Fig. 8. Fossil lizards from the late Pleistocene of the “Caverne Marie-Jeanne” (Hastière-Lavaux, Namur, Belgium). **A–C:** *Lacerta* cf. *L. agilis*, A: premaxilla (IRSNB R 378) in anterior (A1), antero-dorsal (A2) and posterior (A3) views; B: right maxilla (IRSNB R 379) in medial (B1) and lateral (B2) views; C: right dentary (IRSNB R 380) in medial view; **D–F:** *Zootoca vivipara*, D: right maxilla (IRSNB R 381) in lateral (D1) and medial (D2) views; E: right dentary (IRSNB R 382) in medial view; F: trunk vertebra (IRSNB R 383) in ventral (F1), dorsal (F2) and left lateral (F3) views; **G–H:** *Anguis* gr. *A. fragilis*, G: right dentary (IRSNB R 384) in lateral (G1) and medial (G2) views; H: trunk vertebra (IRSNB R 385) in dorsal (H1), ventral (H2) and left lateral (H3) views.

Fig. 8. Lézards fossiles du Pléistocène supérieur de la caverne Marie-Jeanne (Hastière-Lavaux, Namur, Belgique). **A–C:** *Lacerta* cf. *L. agilis*, A : prémaxillaire (IRSNB R 378) en vues antérieure (A1), antéro-dorsale (A2) et postérieure (A3) ; B : maxillaire droit (IRSNB R 379) en vues médiale (B1) et latérale (B2) ; C : dentaire droit (IRSNB R 380) en vue médiale ; **D–F:** *Zootoca vivipara*, D : maxillaire droit (IRSNB R 381) en vues latérale (D1) et médiale (D2) ; E : dentaire droit (IRSNB R 382) en vue médiale ; F : vertèbre dorsale (IRSNB R 383) en vues ventrale (F1), dorsale (F2) et latérale gauche (F3) ; **G–H:** *Anguis* gr. *A. fragilis*, G : dentaire droit (IRSNB R 384) en vues latérale (G1) et médiale (G2) ; H : vertèbre dorsale (IRSNB R 385) en vues dorsale (H1), ventrale (H2) et latérale gauche (H3).

Among the lacertid material from the “Caverne Marie-Jeanne”, there are two size categories. The largest one, comprising one premaxilla, five maxillae, two dentaries and one scapula-coracoid, is referred to the Sand Lizard. The only premaxilla (Fig. 8A) is medium sized, with the maximum width of the premaxilla shelf equal to 2.3 mm. In anterior view, the posterodorsal process is short and leaf-shaped with no ornamentation. Seven or eight tooth positions are visible in posterior view, with three preserved teeth. This premaxilla can be referred to a subadult specimen of *Lacerta agilis* by the following combination of characters. The short and wide leaf-shaped margins of the posterodorsal process are characteristics of adult specimens of *L. agilis*; whereas in *Zootoca vivipara* (Lichtenstein, 1823) and *Lacerta bilineata* Daudin, 1802 this process is generally long and narrow leaf-shaped, and unlike *Podarcis muralis* (Laurenti, 1768), where it is more variable (Barahona, 1996; Barahona and Barbadillo, 1997). However, ornamentation is lacking on the posterior portion of the posterodorsal process, which may suggest that the specimens was not fully adult. The number of tooth positions is rather ambiguous, as it is equal to seven in *P. muralis* and *Z. vivipara*; and usually in higher number in *L. bilineata* and *L. agilis* (Barahona, 1996; Barahona and Barbadillo, 1997; personal observations). However, here again, it must be due to the not fully-adult characters of the fossil. Finally, the size of the fossil estimated by the maximum width of the premaxilla shelf enters the range of *L. agilis* (1.9–2.5 mm), whereas it is slightly smaller than *L. bilineata* (more than 2.4 mm) and much larger than *Z. vivipara* (1.2–1.5 mm) and *P. muralis* (1.6–2.0 mm). The maxillae (Fig. 8B) are somewhat incomplete, ever lacking the dorsal process. They bear pleurodont, isodont, cylindrical, and mono- or bicuspid teeth. A small step is visible on the posterior process like in *P. muralis*, *L. bilineata*, and *L. agilis*, whereas in *Z. vivipara* there is no step (Barahona, 1996; Barahona and Barbadillo, 1997). Finally, the length of the maxillary shelf in our fossils (between 7.1 and 8.0 mm) enters the range of adults of *L. agilis* and *L. bilineata* (more than 7 mm); whereas *P. muralis* (4.8–6.0 mm) is usually smaller and well outside the range of *Z. vivipara* (4.3–4.6 mm). The fragments of dentary (Fig. 8C) possess the morphological characteristics of the Lacertidae, bearing pleurodont, isodont, cylindrical, and mono- or bicuspid and with a Meckelian sulcus open along its entire length. The posterior part of the element is not represented. These elements are cautiously attributed to *L. agilis* on the basis of their size (probably equal or superior to 10 mm for the complete dentary). The dentaries of *P. muralis* and *Z. vivipara* are generally smaller, and those of *L. bilineata* are somewhat more robust (Rauscher, 1992; and personal observations). A scapulo-coracoid is also referred to the size category of *L. agilis*.

Zootoca vivipara (Lichtenstein, 1823) – Viviparous Lizard (Fig. 8D–F)

A total of 701 bones have been attributed to the viviparous lizard: 34 maxillae, 203 dentaries, 317 vertebrae, 74 sacra, 7 caudal vertebrae, 1 scapulo-coracoid, 22

humeri, 11 femora, 3 tibiae, and 29 hemipelves. These bones are much smaller than the fossils attributed to the previous lacertid. The maxillae (Fig. 8D) bear pleurodont, isodont, cylindrical and mono- or bicuspid teeth. The anterior projection of the dorsal process is poorly developed, a characteristic of adults of *Z. vivipara* and juveniles from other species (Barahona, 1996; Barahona and Barbadillo, 1997). There is no step on the posterior process like in *Z. vivipara* and differing from *P. muralis*, *L. bilineata*, and *L. agilis*, where a step is always present (Barahona, 1996; Barahona and Barbadillo, 1997; personal observations). Finally, the length of the maxillary shelf in our fossils (around 5.2 mm in the best-preserved elements) is somewhat higher than the range of *Z. vivipara* (4.3–4.6 mm) given by Barahona and Barbadillo (1997). The dentaries (Fig. 8E) possess pleurodont, isodont, cylindrical, and mono- or bicuspid, a Meckelian sulcus open along its entire length and, in lateral view, the impression of the coronoid is well visible. In some elements, the ventral posterior projection seems to be longer than the dorsal posterior projection, like in *Z. vivipara*, and in opposition to what is observed in *L. bilineata* and *L. agilis*, where these two projections are almost the same size (Barahona Quintana (1996); Barahona and Barbadillo, 1997; personal observations) and the notch on the posterior margin of the bone is no so deep as seen in *Z. vivipara* and *P. muralis*. When compared with *P. muralis*, the ventral posterior projection is more robust on our fossils than in this species, and in a similar way than on the consulted specimens of *Z. vivipara*. This character is also visible in Rauscher (1992). Finally, the length of the dental shelf has been estimated on the best-preserved elements from the “Caverne Marie-Jeanne” to be roughly comprised between 4.8 and 5.6 mm and thus entering the range of adult *Z. vivipara* (5.2–5.5 mm) and slightly smaller than the range of *P. muralis* (5.7–6.9 mm) and *L. agilis* (6 mm), but well outside of the range of *L. bilineata* (more than 8.4 mm). A large amount of procoelous small (centrum length comprised between 1.4 and 3.2 mm) vertebrae are represented in the “Caverne Marie-Jeanne”. These vertebrae (Fig. 8F) are more or less elongated and with a small interzygapophyseal constriction. The neural spine is long, thin and low. Posteriorly, it ends as a short interzygapophyseal point. In ventral view, the centrum is cylindrical, with a rather wide hemal keel with indistinct lateral edges. The cotyle and condyle are slightly flattened dorso-ventrally. Like the other less diagnostical elements (scapulo-coracoid, humeri, femora, tibiae and hemipelves), these vertebrae have been referred to *Z. vivipara* due to their small size.

ANGUIDAE Gray, 1825

Anguis gr. *A. fragilis* Linnaeus, 1758 – Slow Worm (Fig. 8G–H)

The Slow Worm is discretely represented in the “Caverne Marie-Jeanne” by some 326 elements: 2 maxillae, 19 dentaries, 173 trunk vertebrae, 131 caudal vertebrae, and one rib. No osteoderm, usually abundant in other contemporary localities, has been found during the whole

revision of the fossil materials stored at RBINS. Maxillae are small and bear large, conical, monocuspid teeth, strongly curving posteriorly at the tip. Teeth are well spaced from each other and do not show striae. The tooth positions are equal to 6 on the best-preserved element. Dentaries (Fig. 8G) are small and distinctly curved dorsally in the posterior portion. They bear teeth similar to those of the maxillae. Tooth positions are comprised between 7 and 9 on the best-preserved elements. In lateral view, the dental crest covers less than a half of the length of the teeth. The intramandibular septum ends by the last tooth position or slightly anteriorly. No surangular spine can be seen on the posterior margin of the bone. The trunk vertebrae (Fig. 8H) are small (CL < 3 mm) and procoelous, with a posterior condyle and anterior cotyle that are dorsoventrally flattened. In lateral view, the neural spine is long and moderately high, and posteriorly it forms an interzygapophyseal tip that does not go beyond the posterior limit of the postzygapophyses. The articular surfaces of the pre- and postzygapophyses are more or less oval, moderately forward-directed and upward-inclined. In ventral view, the centrum, which is longer than wide, has a flat ventral surface and has lateral margins that are parallel for more than half of their length. When present, the sub-central foramina are small and are located on the anterior half of the vertebra. The caudal vertebrae show greater elongation than the trunk vertebrae, hemapophyses fused to the centrum on its posterior half, and the transverse processes that are well developed and dorsoventrally flattened. Some centra show the line of autotomy. The trunk vertebrae are distinguished from those of other anguines (*Ophisaurus* and *Pseudopus*) mainly by their smaller size, but also by their relatively elongated shape and the lateral margins of the centrum, which are more or less parallel. The fossils from the “Caverne Marie-Jeanne” do not display any morphological difference with those of the present-day *A. fragilis* group, comprising the newly erected species, but still not diagnosed osteologically: *A. cephalonion* Werner, 1894, *A. colchica* (Nordmann, 1840), *A. fragilis* Linnaeus, 1758, *A. graeca* Bedriaga, 1881, and *A. veronensis* Pollini, 1818 (Gvoždík et al., 2013).

SERPENTES Linnaeus, 1758

Only 483 snake remains (2.4% of all the material) have been found in the “Caverne Marie-Jeanne”. These are mainly represented by small-sized vertebrae. Members of the families Natricidae, Colubridae and Viperidae have been identified.

NATRICIDAE Bonaparte, 1840

Natrix gr. *N. natrix* (Linnaeus, 1758) – Grass Snake (Fig. 9A)

Seven trunk vertebrae have been referred to the Grass Snake group, including *Natrix helvetica* (Lacépède, 1789) (Britain, France, Netherlands, Belgium, Germany and Switzerland), *Natrix* (Linnaeus, 1758) (central and eastern Europe, southernmost Scandinavian Peninsula and Balkan

Peninsula) and its Iberian representative *N. astreptophora* (Seoane, 1885) (Kindler and Fritz, 2018; Kindler et al., 2017, 2018a, b; Pokrant et al., 2016). The trunk vertebrae have a somewhat sigmoid hypapophysis, and the neural arch is convex in posterior view. The condyle and the cotyle are small and circular. Their centrum length is comprised between 3.4 and 5.2 mm. The trunk vertebrae attributed to *Natrix* gr. *N. natrix* are distinguished above all by the morphology of the centrum, this being generally flat or concave and the lateral margins are clearly marked, whereas in *Natrix maura* (Linnaeus, 1758) the centrum is slightly convex and with lateral margins that are more or less diffuse (Szyndlar, 1984). In addition, the morphology of the extremity of the hypapophysis and the paradipophysis (i.e. diapophysis plus parapophysis) is robust and blunt like in *N. gr. N. natrix* whereas in *N. maura* these extremities are more gracile and pointed (Szyndlar, 1984).

COLUBRIDAE Oppel, 1811

Coronella austriaca Laurenti, 1768 – Smooth Snake (Fig. 9B–C)

A total of 45 elements have been attributed to the smooth snake in the “Caverne Marie-Jeanne”: 3 dentaries, 13 anterior trunk vertebrae, 43 trunk vertebrae, and 4 caudal vertebrae. The fossil trunk vertebrae (Fig. 9B) are small in size (CL < 4 mm), do not have a hypapophysis, and have a neural arch that is markedly flattened dorsoventrally, as in the genus *Coronella*. The precondylar constriction is particularly well marked, a characteristic of the genus *Coronella* that usually differs from the case of juveniles/adults of all the other colubrids (Blain, 2005, 2009). The prezygapophyseal processes are relatively wide at the base and with blunted ends like in *C. austriaca*, and differing from *Coronella girondica* (Daudin, 1803), where these processes are generally narrower and pointed (Bailon, 1991; Szyndlar, 1984). Finally, in ventral view, the parapophyses are somewhat longer than the diapophyses, like in *C. austriaca*, whereas in *C. girondica* they have a similar length (Bailon, 1991; Szyndlar, 1984). Dentaries (Fig. 9C) are somewhat well preserved. Dentaries are straight and slender. In dorsal view, the anterior end of the bone is strongly curved inside. The bone is generally isodontic, except 2–3 minute anteriormost teeth. A complete dentary has 26 tooth positions. The somewhat elongate small mental foramen lies at the level of the 9th tooth. The compound notch on the lateral surface is situated at the level of the 14th tooth. Meckel's groove opens widely into compound notch, and anteriorly completely closed by the 11th or 12th tooth.

VIPERIDAE Oppel, 1811

Vipera berus (Linnaeus, 1758) – Adder (Fig. 9D–F)

The adder is by far the most represented snake in the “Caverne Marie-Jeanne”, with a total of 191 fossil remains: 1 venom fang, 2 left dentaries, 17 anterior trunk vertebrae, and 171 trunk vertebrae. The trunk vertebrae (Fig. 9E) show the typical characteristics of the family: presence of

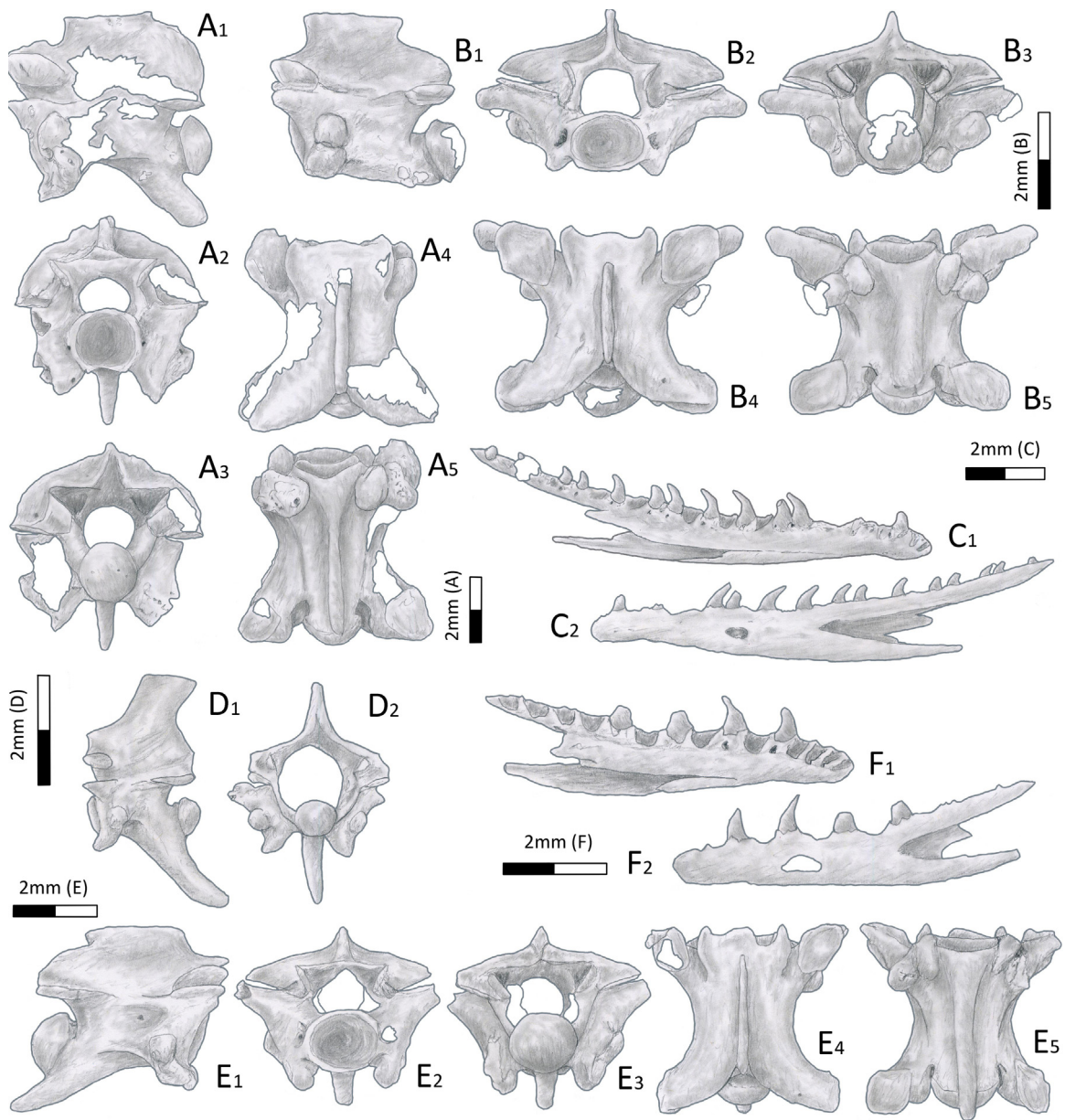


Fig. 9. Fossil snakes from the late Pleistocene of the “Caverne Marie-Jeanne” (Hastière-Lavaux, Namur, Belgium). **A:** *Natrix* gr. *N. natrix*, anterior trunk vertebra (IRSNB R 386) in left lateral (A1), anterior (A2), posterior (A3), dorsal (A4), and ventral (A5) views; **B–C:** *Coronella austriaca*, B: trunk vertebra (IRSNB R 387) in left lateral (B1), anterior (B2), posterior (B3), dorsal (B4) and ventral (B5) views; C: left dentary (IRSNB R 388) in medial (C1) and lateral (C2) views; **D–F:** *Vipera berus*, D: anterior trunk vertebra (IRSNB R 389) in left lateral (D1) and posterior (D2) views; E: trunk vertebra (IRSNB R 390) in right lateral (E1), anterior (E2), posterior (E3), dorsal (E4) and ventral (E5) views; F: left dentary (IRSNB R 391) in medial (F1) and lateral (F2) views.

Fig. 9. Serpents fossiles du Pléistocène supérieur de la caverne Marie-Jeanne (Hastière-Lavaux, Namur, Belgique). **A :** *Natrix* gr. *N. natrix*, vertèbre dorsale antérieure (IRSNB R 386) en vues latérale gauche (A1), antérieure (A2), postérieure (A3), dorsale (A4) et ventrale (A5) ; **B–C :** *Coronella austriaca*, B : vertèbre dorsale (IRSNB R 387) en vues latérale gauche (B1), antérieure (B2), postérieure (B3), dorsale (B4) et ventrale (B5) ; C : dentaire gauche (IRSNB R 388) en vues médiale (C1) et latérale (C2) ; **D–F :** *Vipera berus*, D : vertèbre dorsale antérieure (IRSNB R 389) en vues latérale gauche (D1) et postérieure (D2) ; E : vertèbre dorsale (IRSNB R 390) en vues latérale droite (E1), antérieure (E2), postérieure (E3), dorsale (E4) et ventrale (E5) ; F : dentaire gauche (IRSNB R 391) en vues médiale (F1) et latérale (F2).

a straight and distally pointed hypapophysis; neural arch dorsoventrally flattened; centrum convex in transverse section and not well-marked lateral margins; developed and round condyle and cotyle; and upwardly inclined articular surface of the zygapophyses. The trunk vertebrae from the “Caverne Marie-Jeanne” are somewhat small with a

centrum length shorter than 4 mm. The vertebral morphology permits two groups to be differentiated within the European vipers: the “*Vipera aspis* complex” and the “*Vipera berus* complex”. The neural spine of the trunk vertebrae is very low and the hypapophysis is sigmoid-shaped, with an obtuse apex like in the “*V. berus* complex”

(Szyndlar, 1984). European members of the “*V. berus* complex” [*V. berus* (Linnaeus, 1758), *Vipera ursinii* (Bonaparte, 1835) and *Vipera seoanei* Latastei, 1879] display homogeneous vertebra morphology and are hardly distinguishable from one another (Szyndlar, 1984; Szyndlar and Rage, 1999). Nevertheless, the morphology of the fossil vertebrae fits well with *V. berus*, the only adder currently present in northern Europe. The anterior trunk vertebrae are characterized by a hypapophysis that is usually shorter than the centrum and a relatively low neural spine (Fig. 9D). The only venom fang is long, tubular and slightly curved, and on its anterior surface the suture of the venom canal is not visible, like in viperids (Jackson, 2002). The two dentaries are much shorter and straighter than the dentary of *Coronella austriaca* previously described. Teeth are badly preserved, but one of them shows some 14 tooth positions (Fig. 9F). In dorsal view, the anterior end of the bone is more or less curved inside. The mental foramen, filled with sediment in the two specimens, is well elongated and lies at the level of the 7th and 8th teeth. The compound notch on the lateral surface approaches by the 11th tooth. Meckel’s groove opens into compound notch at the level of the 9th tooth, and is anteriorly reduced to a narrow slit or completely closed (Fig. 9F).

5. Discussion

5.1. Paleobiogeography

According to Jacob et al. (2007) in the Walloon Region (roughly the southern half of Belgium) where the “Caverne Marie-Jeanne” is located, there are currently represented one salamander (*Salamandra salamandra*), four newts (*Ichthyosaura alpestris*, *Triturus cristatus*, *Triturus helveticus* and *Triturus vulgaris*), ten anurans (*Bombina variegata*, *Alytes obstetricans*, *Pelobates fuscus*, *Bufo*, *Epidalea calamita*, *Hyla arborea*, *Rana temporaria*, *Pelophylax lessonae*, *Pelophylax ridibundus*, and *Pelophylax kl. esculentus*), no endemic chelonians, four lizards (*Lacerta agilis*, *Podarcis muralis*, *Zootoca vivipara*, and *Anguis fragilis*), and three snakes (*Natrix helvetica*, *Coronella austriaca*, and *Vipera berus*). In its totality, the herpetofaunal assemblage of the “Caverne Marie-Jeanne” documents at least 12 amphibians and squamate reptiles (i.e., 54.5% of the current diversity observed in Wallonia), with two salamandrids (40.0% of the current diversity), four anurans (but documenting three of the current anurans, i.e. 30.0% of the current diversity), three lizards (75.0% of the current diversity), and three snakes (i.e. the whole current diversity).

Rana arvalis is the only species represented in the “Caverne Marie-Jeanne” that is currently absent from the area, and constitutes its first fossil mention in Belgium. In northwestern Europe, the species has already been mentioned in the middle Pleistocene (Bailon and Rage, 1992; Rage, 1972) and Neolithic (Arbogast et al., 2010) from France, in the Middle Pleistocene of the Netherlands (Holman, 1998; Schouten, 2016) and in the middle and late Pleistocene from Britain and Germany (Holman, 1998; Roček and Šandera, 2008; Sanchíz, 1998). All late Pleistocene records, except for one (Zdrody in Poland; Baluk et al., 1979; Młynarski and Szyndlar, 1989), which

is very close to the southern limits of the ice-sheet cover during the Last Glacial Maximum, come from areas that were not covered with ice (Roček and Šandera, 2008). According to Gleed-Owen (1998), there are no cold-stage records for *R. arvalis* in Britain, as the late Pleistocene occurrences have been recorded in Shropham 1 (MIS 5e; Holman and Clayden, 1990) and Swanton Morley (MIS5e; Holman, 1987). In Germany, records for *R. arvalis* come from Burgtonna near Langensalza (MIS 5e, central Germany; Heinrich and Jaeger, 1978; Młynarski et al., 1978; Böhme, 1989), Pottenstein (MIS 5, southern Germany; Brunner, 1938, 1956), and Teufelsbrücke (MIS 3/2, central Germany; Böhme, 1980). Thus, the record from the “Caverne Marie-Jeanne” may represent one of the latest fossil record for the species in western Europe before the Last Glacial Maximum. Such record may be interesting, as remains of *Rana* cf. *arvalis/dalmatina* have been identified from the Holocene (Middle Saxon) Fenland sites at Goshberton (Lincolnshire) and Terrington St. Clement (Norfolk), whereas today both are absent from the British islands (Gleed-Owen, 1998) and thus may suggest that southern Belgium may have been a northern refugia for *R. arvalis* during the latest Pleistocene, when molecular studies seem to suggest a southern refugia in the Carpathian Basin (Babik et al., 2004). The “Caverne Marie-Jeanne” also represents the first fossil record in Belgium for *Lissotriton* gr. *L. vulgaris*, *Zootoca vivipara*, *Natrix* gr. *N. natrix*, and *Coronella austriaca*. The *Lissotriton vulgaris* group was already described from the middle Pleistocene of the Netherlands (Holman, 1998; Schouten, 2016) and from the middle and late Pleistocene of Germany (Holman, 1998) and Britain (Gleed-Owen, 1998). In Britain, *L. vulgaris* is even present during the latest Pleistocene (MIS 2) in Potter’s Cave and the *L. vulgaris* group in Roger’s Cave (Gleed-Owen, 1998). *L. vulgaris* is the only newt to have reached Ireland before its isolation from Britain, perhaps due to its ability to breed in a wider range of ponds or to be more cold tolerant than *L. helveticus*, which seems to have reached Britain later (Gleed-Owen, 1998). In northern France, *L. cf. L. helveticus* has been recorded in the Neolithic of Mesnil-Aubry (Bailon, 2012). *Z. vivipara* has been described in the Middle Pleistocene of the Netherlands (Holman, 1998; Schouten, 2016), in the middle Pleistocene to Holocene of Germany (Holman, 1998) and in the British late Pleistocene (including MIS 2) and Holocene (Gleed-Owen, 1998). *N. gr. N. natrix* has been mentioned as a fossil in the early Pleistocene, middle Pleistocene and Holocene of the Netherlands (Glastra, 1983; Holman, 1998; Schouten, 2016; Villa et al., 2018; Wijngaarden-Bakker and van Troostheide, 2003), in the middle Pleistocene to Holocene of Germany (Holman, 1998), in the middle Pleistocene, early late Pleistocene, and Holocene of Britain (Holman, 1998; Gleed-Owen, 1998), and in northern France in the Neolithic of Val-de-Reuil (Arbogast et al., 2010). However, this group seems to have not been recorded up to now in any latest Pleistocene (MIS 3 and MIS 2) site in northwestern Europe. Like for *R. arvalis*, its occurrence in the “Caverne Marie-Jeanne” may thus represent its latest fossil record in northwestern Europe before the Last Glacial Maximum. However, its absence in the upper layers from the “Caverne Marie-Jeanne” (levels 1 to 3) is in accordance with molecular data that suggest for

Table 3

Comparison between the different herpetofaunal assemblages of the “Caverne Marie-Jeanne” (CMJ) with the typical herpetological associations for Pleistocene climatic cycles in central Europe (after Böhme, 1996, 2000, 2010). This table has been used as a data matrix for the cluster and the principal component analyses (see Fig. 10).

Tableau 3

Comparaison entre les différents assemblages herpétofauniques de la caverne Marie-Jeanne (CMJ) et les associations herpétofauniques typiques des cycles climatiques du Pléistocène en Europe centrale (d'après Böhme, 1996, 2000, 2010). Ce tableau a été utilisé comme matrice de données pour les analyses de cluster et en composantes principales (voir Fig. 10).

Species	CMJ4-6 (MIS 3)	CMJ2 (MIS 2)	Late glacial	Early interglacial	Interglacial climate optima	Late interglacial and interstadial	Latest interglacial to early glacial	Glacial
<i>Salamandra salamandra</i>	x	x			x			
<i>Triturus cristatus</i>				x	x			
<i>Triturus vulgaris</i>	gr.			x	x	x		
<i>Bombina bombina</i>					x			
<i>Pelodytes punctatus</i>								
<i>Pelobates fuscus</i>					x	x		
<i>Bufo bufo</i>	x	x	x	x	x	x		
<i>Epidalea calamita</i>	x	x				x		
<i>Bufotes viridis</i>						x	x	
<i>Hyla arborea</i>					x	x		
<i>Rana dalmatina</i>				x	x			
<i>Rana temporaria</i>	x	x		x	x	x	x	x
<i>Rana arvalis</i>	cf.	cf.	x	x		x		
<i>Pelophylax</i> sp.					x	x		
<i>Emys orbicularis</i>					x			
<i>Anguis fragilis</i>	x	x		x	x	x		
<i>Lacerta agilis</i>	x	x		x		x		
<i>Lacerta viridis</i>					x			
<i>Zootoca vivipara</i>	x	x		x			x	
<i>Natrix</i> gr. <i>N. natrix</i>	x			x	x	x		
<i>Vipera berus</i>	x	x	x	x			x	
<i>Coronella austriaca</i>	x	x		x		x		
<i>Zamenis longissimus</i>					x			

the western representative of the group (*Natrix helvetica*) a refugium located in southern France (Kindler et al., 2018a).

Finally, *C. austriaca* is known in northwestern Europe in the middle Pleistocene and Holocene of Britain (Gleed-Owen, 1998), in the middle Pleistocene to Holocene of Germany (Holman, 1998) and in northern France in the Neolithic of Val-de-Reuil (Arbogast et al., 2010). As this species has never been mentioned in the Netherlands, the record of the “Caverne Marie-Jeanne” represents an interesting mention for northwestern Europe.

When compared with the modern herpetofauna from Belgium, the “Caverne Marie-Jeanne” lacks *Ichtyosaura alpestris*, *Triturus cristatus*, *Bombina variegata*, *Alytes obstetricans*, *Pelobates fuscus*, *Hyla arborea*, *Pelophylax lessonae*, *Pelophylax kl. esculentus*, and *Podarcis muralis*, which are still undescribed as fossils in Belgium. When compared with other Pleistocene sites from Belgium, the “Caverne Marie-Jeanne” also lacks the genus *Pelodytes* and *Zamenis longissimus* described in the MIS 5 of Scladina Cave (Blain et al., 2014).

When compared with the British fossil record, the “Caverne Marie-Jeanne” (together with the Scladina Cave) interestingly documents the persistence during MIS 3 and 2 of *Salamandra*, a species that has never been recorded during the late Pleistocene and is not present in the British Isles today. As reported by Gleed-Owen (1998), the preference of *S. salamandra* for wooded upland areas, and its absence from lowland continental areas bordering the North Sea,

seems to suggest that a Pleistocene crossing via a low-lying land-bridge would be unlikely.

Finally, on the one hand, when compared with Central Europe typical herpetological faunal associations for Pleistocene climatic cycles (Böhme, 1996, 2000, 2010), the “Caverne Marie-Jeanne” lacks species only recorded during interglacial climate optima such as *Bombina*, *Emys orbicularis*, *Lacerta viridis* and *Zamenis longissimus*, with the exception of *Salamandra* (Table 3). On the other hand, the “Caverne Marie-Jeanne” documents species never present during Interglacial climate optima (*Zootoca vivipara* and *Vipera berus*) and species not recorded during the Glacial and the late Glacial periods (*S. salamandra*, *Anguis fragilis*, *Natrix* gr. *N. natrix* and *Coronella austriaca*). Here again, the presence of *S. salamandra* during MIS 3 and 2 in Belgium is interesting, as it may suggest peculiar environmental conditions (favoring the persistence of broadleaved forest) that would have constituted a refugium for the species in northwestern Europe outside interglacial periods, even if phylogenetic data suggest southernmost refugia in the Iberian Peninsula and the Balkan (Steinfartz et al., 2000). Principal component analysis of the composition of level 4 to 6 (MIS 3) and of level 2 (MIS 2) from the “Caverne Marie-Jeanne” in comparison with the central European herpetological associations (Fig. 10) suggests that: (1) these two assemblages are strongly similar and (2) they both better match the composition of “Early Interglacial” and “Late interglacial and interstadial” herpetofaunal assemblages from central Europe.

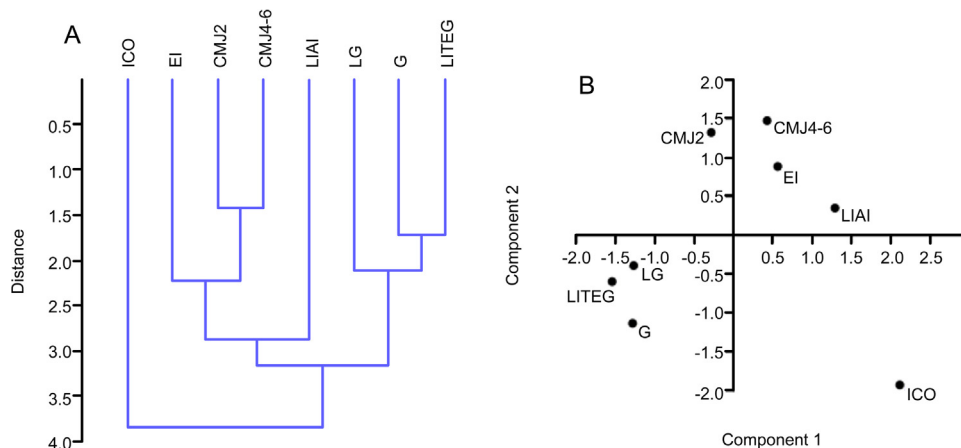


Fig. 10. Comparison according to cluster (A) and principal component (B) analyses between the composition of the different herpetofaunal assemblages of the “Caverne Marie-Jeanne” and the typical herpetological associations for Pleistocene climatic cycles in Central Europe (after Böhme, 1996, 2000, 2010). Abbreviations: CMJ2, “Caverne Marie-Jeanne” level 2; CMJ4-6, “Caverne Marie-Jeanne” levels 4 to 6; LG, late Glacial; EI, early Interglacial; ICO, Interglacial climate optima; LIAI, late Interglacial and Interstadial; LITEG, latest Interglacial to early Glacial; G, Glacial.

Fig. 10. Comparaison selon les analyses de cluster (A) et en composantes principales (B) entre la composition des différents assemblages herpétofauniques de la caverne Marie-Jeanne et les associations herpétofauniques typiques des cycles climatiques du Pléistocène en Europe centrale (d'après Böhme, 1996, 2000, et Böhme, 2010). Abréviations : CMJ2 : caverne Marie-Jeanne, niveau 2 ; CMJ4-6 : caverne Marie-Jeanne, niveaux 4 à 6 ; LG : Glaciaire final ; EI : début de l'Interglaciaire ; ICO : optimum climatique de l'Interglaciaire ; LIAI : Interglaciaire final et Interstadiaire ; LITEG : Interglaciaire final à début du Glaciaire ; G : Glaciaire.

5.2. Reconstruction of the environment and climate

Paleoenvironmental reconstructions based on the habitat weighting method (Fig. 11A; Table 4), show that there is no important difference between levels, as already observed from the study of the small mammals (López-García et al., 2017). They suggest that, during the latest Pleistocene, 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%) probably near from a river or a lake. Aquatic habitats are well represented (comprised between 16 and 20% of the landscape), even if there is no typical aquatic species in the herpetofaunal assemblages. On the contrary, dry and rocky/stony environments are rather poorly represented, even if slightly more extended in the upper part of the sequence.

The several quantitative paleoclimatic methods applied here to the different levels of the “Caverne Marie-Jeanne” (Fig. 11B–C; Table 5) are relatively concordant in characterizing the climatic conditions during MIS 3 and 2, clearly colder than the present ones (between -2.9 and up to -9.6°C lower than modern MAT) and possibly reveal lower rainfall (between 140 and 330 mm lower than modern MAP). Reconstruction based on small mammals (BM) gives lower temperature estimates than the other methods and higher estimates for precipitations (even higher than current level), especially for the lower levels (levels 4 to 6). The other methods (applied on small mammals and herpetofauna) confirm the cold conditions, but against the previous reconstruction (BM in López-García et al., 2017), which suggests dryer conditions. Among the different levels, level 2 seems to be slightly colder than levels 4 to 6, with the exception of the QE(AR) reconstruction, but not particularly wetter nor dryer, with the exception of the BM(MM)

reconstruction, where level 2 is suggested to be slightly dryer than levels 4 to 6.

Such paleoenvironmental and paleoclimatic homogeneity among the different levels from the “Caverne Marie-Jeanne” is certainly due to the fact that, apart from the presence of a newt (*L. vulgaris* group) and the absence of *L. agilis* in level 4, and from the absence of *R. arvalis* in level 6 and of *N. gr. N. natrix* in level 2, the faunal list is very similar between levels having delivered enough remains (levels 2, 4, 5, and 6). The only striking difference lies in the inversion of the dominant anuran taxon between levels 4–6 and level 2. *Rana temporaria* dominates the level-4–6 assemblages (representing always more than 71% of the anurans), whereas it is *B. bufo* s.l. that dominates the level-2 assemblage (67% of the anurans). This data was already observed by J.-C. Rage in the previous study (Ballmann et al., 1980) and it was suggested that level 2 was more humid than levels 4 to 6 due to the higher hygrophily of *B. bufo*. Both anurans are ubiquitous, with a very large modern distribution in Europe, and are present in a large variety of biotopes. It is true that for breeding *B. bufo* s.l. prefers permanent and deep-water points, with an abundant aquatic vegetation, whereas *R. temporaria* prefers shallow sunny water points rich in nutrients (Jacob et al., 2007). Formerly, this frog was very common everywhere in Wallonia (Boulenger, 1922; de Selys-Longchamps, 1842; de Witte, 1942). It was probably the most common amphibian, as testified by the importance of their catches for consumption by the local populations (Gosse, 1979). However, this status has evolved and the most abundant amphibian in areas with little forest, where human pressure is considerable, is probably now the common toad (Jacob and Kinet, 2007). For Pleistocene times, strong human pressure on anuran populations can be reasonably discarded and such change in the anuran composition can be linked with some

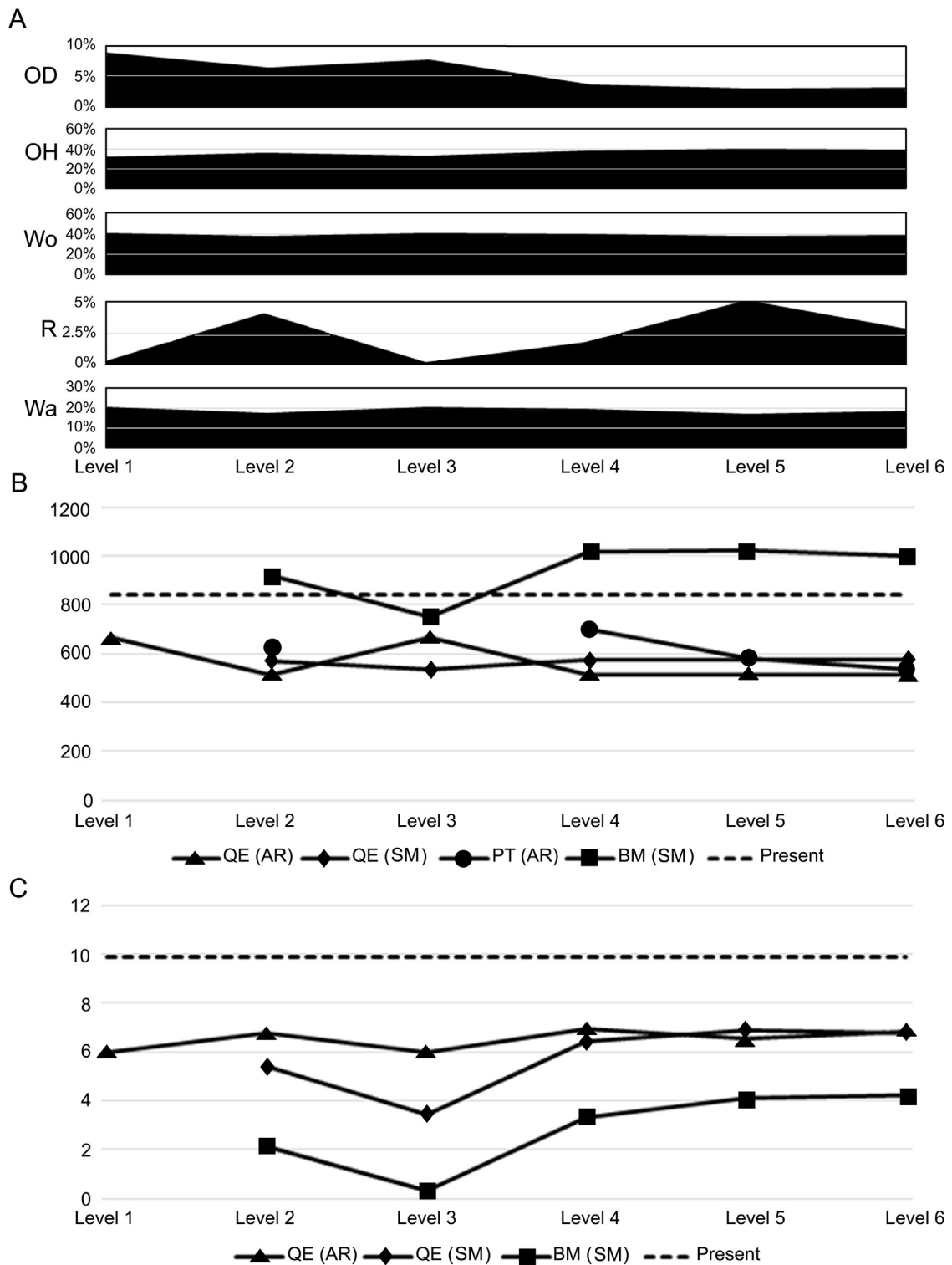


Fig. 11. Paleoenviromental and paleoclimatic reconstructions for the late Pleistocene of the “Caverne Marie-Jeanne” (Hastière-Lavaux, Belgium). A: Landscape reconstruction; B: mean annual precipitation (in mm); C: mean annual temperature (in °C). Abbreviations: OD: open-dry; OH, open-humid; Wo: woodland and woodland-edges; R: Rocky and Stony; Wa: water and water-edges; QE: quantified ecology; PT: paleoprecipitation tool; BM: bioclimatic model; AR: amphibians and reptiles; SM: small mammals.

Fig. 11. Reconstitutions paléoenvironnementale et paléoclimatique du Pléistocène supérieur de la caverne Marie-Jeanne (Hastière-Lavaux, Belgique). A : Reconstitution du paysage ; B : précipitation moyenne annuelle (en mm) ; C : température moyenne annuelle (en °C). Abréviations : OD : ouvert et sec ; OH : ouvert et humide ; Wo : forêt et lisières de forêt ; R : rocheux et pierreux ; Wa : milieux aquatiques et riverains ; QE : écologie quantifiée ; PT : outil de paléoprécipitation ; BM : Modèle Bioclimatique ; AR : amphibiens et reptiles ; SM : petits mammifères.

Table 4

Paleoenvironmental reconstructions of the successive layers from the “Caverne Marie-Jeanne” using the habitat weighting method. Abbreviations: OD: open-dry; OH: open-humid; Wo: woodland and woodland-edges; R: rocky and stony; Wa: water and water-edges.

Tableau 4

Reconstitutions paléoenvironnementales des niveaux successifs de la caverne Marie-Jeanne à partir de la méthode de la pondération des habitats. Abréviations : OD : Ouvert et sec ; OH : Ouvert et humide ; Wo : forêt et lisières de forêt ; R : Rocheux et pierreux ; Wa : milieux aquatiques et riverains.

	Level 1	Level 2	Level 3	Level 4	Level 5	Level 6
OD	8.6%	6.1%	7.4%	3.4%	2.7%	3.0%
OH	31.5%	35.7%	32.7%	37.5%	39.0%	38.1%
Wo	39.9%	37.4%	39.9%	38.8%	37.1%	38.3%
R	0.0%	3.9%	0.0%	1.5%	4.9%	2.6%
Wa	20.0%	16.9%	20.0%	18.8%	16.2%	18.1%

Table 5

Paleoclimatic reconstructions of the successive layers from the “Caverne Marie-Jeanne” using quantified ecology (Jeannet, 2010), paleoprecipitation tool (Böhme et al., 2006) and bioclimatic model (Hernández-Fernández, 2001b) methods applied to the small vertebrates assemblages. Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature; QE, quantified ecology, PT, paleoprecipitation tool; BM, bioclimatic model; AR, amphibians and reptiles; SM, small mammals. Modern climatic data (1980–2010) are from www.climate-data.org.

Tableau 5

Reconstitutions paléoclimatique des niveaux successifs de la caverne Marie-Jeanne d'après les méthodes de l'écologie quantifiée (Jeannet, 2010), outil de paléoprécipitation (Böhme et al., 2006) et du modèle bioclimatique (Hernández-Fernández, 2001b), appliquées aux assemblages de petits vertébrés. Abréviations : MAP, précipitation moyenne annuelle ; MAT : température moyenne annuelle ; QE : écologie quantifiée ; PT : outil de paléoprécipitation ; BM, modèle bioclimatique ; AR : amphibiens et reptiles ; SM : petits mammifères. Les données climatiques modernes (1980–2010) sont extraites du site www.climate-data.org.

MAP (in mm)	Level 1	Level 2	Level 3	Level 4	Level 5	Level 6
QE (AR)	665	511.1	665	515.5	513.7	511.1
QE (SM)		569.2	535.6	574.3	578.1	573.3
PT (AR)		580.2		697.8	580.2	533.7
BM (SM)		921	752	1018	1023	1000
1980–2010	840	840	840	840	840	840
MAT (in °C)	Level 1	Level 2	Level 3	Level 4	Level 5	Level 6
QE (AR)	6.0	6.8	6.0	7.0	6.6	6.8
QE (SM)		5.4	3.4	6.4	6.9	6.8
BM (SM)		2.2	0.3	3.4	4.1	4.2
1980–2010	9.9	9.9	9.9	9.9	9.9	9.9

ecological change, maybe with the extension, distribution, or quality of the vegetal cover linked with humidity.

Modern herpetological surveys realized in Poland (Białowieża Primeval Forest; Pikulik et al., 2001) bring interesting arguments for environments where *R. temporaria* is the dominant species. Summer abundance and habitat distribution surveys showed that frogs and toads were widely, but not evenly, distributed between the various habitats. The highest densities were recorded along a brook located entirely in the old-growth forest with no open marshes along its course. Medium-sized and small forest rivers and wet alder-ash forests growing along them were also densely populated by amphibians. Amphibians were uncommon in dryer forest. The common frog was shown as the most ubiquitous species, with peak numbers recorded in the smallest forest brooks within forested valley, whereas the common toad was occupying the broadest range of habitats, being the only species inhabiting dryer forests as well as wet places. Thus, the abundance of *B. bufo* in level 2 can be linked with an increase of dry forested habitats. Interestingly, according to the same study (Pikulik et al., 2001), edible frogs occurred primarily in the largest rivers with wide, unforested valleys. Thus, the absence of any waterfrogs in the “Caverne Marie-Jeanne” may be significant for the absence of such environmental conditions nearby the cavity. Among the amphibians represented in

the “Caverne Marie-Jeanne”, *S. salamandra* also gives interesting information about the presence in the environment of forested areas, as today this species is typical from mixed or broadleaved woodlands and shows greater abundance within forested hilly landscapes (de Wavrin and Graitson, 2007).

Besides amphibians, the reptiles represented as fossils in the “Caverne Marie-Jeanne” usually live in biotopes with a great environmental heterogeneity, alternating open areas with bushy environment or woodland edges, thus providing abundant resources and numerous refugia for escaping and thermoregulation. Some of them would prefer humid meadows, as *Z. vivipara*, *A. fragilis*, and *N. natrix* s.l., while others would prefer dryer and sunny environments, as *L. agilis* and *C. austriaca*. Finally, the viper *V. berus* prefers dense herbaceous vegetation, dotted with small clear areas with no particular preference between dry or humid environments.

The last representative of the herpetofaunal assemblage from the “Caverne Marie-Jeanne”, even if poorly represented – always less than 1% of the anurans – is the natterjack toad *E. calamita*. It is a heliophile species that 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 as a pioneer species that

can quickly colonize newly created habitats and disappear just as quickly when vegetation becomes too dense. In Wallonia, the species has disappeared today from primary habitats. It is assumed that these were mainly in the major river bed, where floods ensured the presence of shoals of sand and gravel with flooded depressions. The low abundance of this species in the “Caverne Marie-Jeanne” is another argument for characterizing the environments existing during MIS 3 and MIS 2 as relatively stable and forested.

Such results are coherent with other proxies as the large-mammal assemblage (especially with the herbivores) that suggested (Ballmann et al., 1980) globally cold, dry and open environmental conditions (cold steppe) for the lower levels (6 to 4), with the presence of species such as *Mammuthus primigenius*, *Rangifer tarandus*, *Vulpes lagopus*, and *Ochotona pusilla*. The mollusks indicate an environment alternating between dry and humid conditions, under progressive cooling (Ballmann et al., 1980). In level 5, the mollusk association indicates interstadial conditions, exemplified by the presence of three species with southern affinities, *Pyramidula rupestris*, *Abida secale*, and cf. *Helicella profuga*. In level 4, only one species with southern affinities survive. For level 2, despite an increase in species richness, no southern species are recorded. It is to remember here that the climatic and environmental interpretations by Ballmann et al. (1980) were based only on a small part of the collection from the “Caverne Marie-Jeanne” and that their conclusions may be valid from a qualitative point of view, but have to be taken cautiously into consideration when dealing with quantitative interpretations. Finally, the proxy bringing the more complete information up to date is small mammals. Small mammals (López-García et al., 2017) have suggested for the MIS 3 levels a mixed habitat dominated by open woodland formations (between 30.2% and 32.7%) and dry meadows (between 18.6% and 27.3%). Small mammals also document a high component of humid meadows, but never exceeding 20%. For level 2, woodlands are reconstructed to have been more extended (40.1%) followed by humid meadows (i.e. 21.6%). Dry meadows, in this case, do not exceed 20%. This last proxy seems to suggest a reverse tendency for decreasing moisture than the one proposed here from the herpetofaunal assemblages. However, these environmental changes are subtle and do not seem to affect significantly the structure of the reconstructed landscape. Such small disagreement between proxies can also be due to a taphonomic bias. As shown by the taphonomic study of the small mammals (López-García et al., 2017), the main potential accumulators are *Bubo bubo* and *Falco tinnunculus*, and the relative abundances of their preys is usually reliable with the habitat where they hunt. However, the diurnal and moderately selective habits of the falconiforms, identified as the principal accumulators for levels 6 to 4, suggest that the relative abundances of the taxa present in the association should be treated with caution.

6. Conclusions

The revision of the late Pleistocene (Marine Isotope Stages 3 and 2) collection of the “Caverne Marie-Jeanne” (Hastière-Lavaux, Namur) stored in the Royal Belgian Institute of Natural Sciences (RBINS) Quaternary collections has been done in order to complete the preliminary study (Rage in Ballmann et al., 1980) on the fossil amphibians and reptiles from this site and to propose a paleoenvironmental and paleoclimatic reconstruction for the latest Pleistocene of Belgium. Our conclusions are given below.

- 1) More than 20,500 recognized bones of amphibians and reptiles have been identified and catalogued. The faunal list comprises now two urodeles (*Lissotriton* gr. *L. vulgaris* and *Salamandra salamandra*), four anurans (*Bufo* gr. *B. bufo-spinosus*, *Epidalea calamita*, *Rana temporaria*, and *Rana* cf. *R. arvalis*), three lizards (*Lacerta* cf. *L. agilis*, *Zootoca vivipara* and *Anguis* gr. *A. fragilis*) and three snakes (*Natrix* gr. *N. natrix*, *Coronella austriaca* and *Vipera berus*). Thus, the previous faunal list has been actualized, with five new taxa (*L.* gr. *L. vulgaris*, *R.* cf. *R. arvalis*, *Z. vivipara*, *N.* gr. *N. natrix*, and *C. austriaca*), one removal (*Pelophylax* cf. *esculentus*), and updated thanks to the recovery of new diagnostic elements, like vertebrae for snakes and urodeles.
- 2) This study reports the first fossil record in Belgium for *L.* gr. *L. vulgaris*, *R. arvalis*, *Z. vivipara*, *N.* gr. *N. natrix*, and *C. austriaca*. *Rana arvalis* is the only species represented in the “Caverne Marie-Jeanne” that is currently absent from the area.
- 3) The amphibian and reptile assemblages from the “Caverne Marie-Jeanne” are strongly similar across the different levels and match with the composition of “early Interglacial” and “late Interglacial and Interstadial” herpetofaunal assemblages from central Europe, with the exception of *S. salamandra*, which is usually only recorded during interglacial climate optima in central Europe, but was still present in the “Caverne Marie-Jeanne” during MIS 3 and 2. The “Caverne Marie-Jeanne” also lacks *Pelodytes* and *Zamenis longissimus*, present in Belgium during the interglacial period (MIS 5), as documented in Scladina Cave (Sclayn, Namur, Belgium).
- 4) As a whole, amphibians and reptiles suggest a patchy humid landscape under colder and dryer climatic conditions in comparison with present ones. Mixed or broadleaved forest areas seem to have been well represented during MIS 3 and 2, especially in the valleys along the rivers. The replacement as the dominant anuran of the common frog by the common toad along the sequence may suggest an environmental change in the composition or structure of the forested areas between MIS 3 and MIS 2 towards dryer conditions.
- 5) Finally, even if the former study by Ballmann et al. (1980) was only based on a small fraction of the material and nor remains neither individuals were quantified, this work also underlines the necessity of a primary

separation in larger categories by the specialist himself, in order to pick in the whole material the diagnostic elements permitting better systematical attribution.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.crpv.2019.04.006>.

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