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Middle to Late Pleistocene herpetofauna from Scladina and Sous-Saint-Paul caves (Namur, Belgium)

L'herpétofaune du Pléistocène moyen à supérieur des grottes Scladina et Sous-Saint-Paul (Namur, Belgique)

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A B S T R A C T

For the first time, the fossil herpetofauna from the Middle and Late Pleistocene of Scladina and Sous-Saint-Paul caves (Sclayn, Belgium) is described. The amphibians and squamate reptiles are represented by one salamander (*Salamandra salamandra*), three anurans (*Pelodytes punctatus*, *Bufo bufo* and *Rana temporaria*), two lizards (*Lacerta* cf. *agilis* and *Anguis fragilis*) and two snakes (*Zamenis longissimus* and *Vipera* cf. *berus*). The occurrence of the Parsley Frog (*Pelodytes punctatus*) and the Aesculapian Snake (*Zamenis longissimus*), which are not currently represented in Belgium, is of particular interest. Scladina also represents one of the northernmost fossil mentions for the Fire Salamander (*Salamandra salamandra*) although it is within its current distribution in Europe. Finally, the presence of the Adder (*Vipera* cf. *berus*) is very probably attested in Scladina whereas today this snake is infrequent and classified as endangered in Belgium.

R É S U M É

Pour la première fois, les herpétofaunes fossiles du Pléistocène moyen et supérieur des grottes Scladina et Sous-Saint-Paul (Sclayn, Belgique) sont décrites. Les amphibiens et reptiles squamates sont représentés par une salamandre (*Salamandra salamandra*), trois anoures (*Pelodytes punctatus*, *Bufo bufo* et *Rana temporaria*), deux lézards (*Lacerta* cf. *agilis* et *Anguis fragilis*) et deux serpents (*Zamenis longissimus* et *Vipera* cf. *berus*). La présence du Pélodyte ponctué (*Pelodytes punctatus*) et de la Couleuvre d'Esculape (*Zamenis longissimus*),

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actuellement absents de Belgique, est particulièrement intéressante. Scladina représente aussi l'une des mentions fossiles les plus septentrionales pour la Salamandre tachetée (*Salamandra salamandra*), bien qu'à l'intérieur de son aire de distribution actuelle en Europe. Finalement, la présence de la Vipère péliade (*Vipera* cf. *berus*) est très probablement attestée à Scladina, alors qu'aujourd'hui ce serpent est rare et classé comme étant en voie d'extinction en Belgique.

1. Introduction

Studies of the Pleistocene herpetofauna have been relatively scarce in Belgium. To our knowledge, only two Late Pleistocene sites have been studied, the Marie Jeanne and Walou caves. The Marie-Jeanne cave (Hastière-Lavaux, Namur, Belgium) delivered the following amphibians and squamates reptiles: *Salamandra* sp. *Bufo bufo*, *Bufo* cf. *calamita*, *Rana* cf. *esculenta Rana temporaria*, *Anguis* sp., *Lacerta* sp., Colubridae indet.and *Vipera* sp. (Ballmann et al., 1980; Holman, 1998; Sanchíz, 1998); the Walou cave (Trooz, Liège, Belgium) yielded *Bufo* sp. and *Rana* sp. (De Wilde, 2011).

Scladina cave is located in a small valley of a tributary of the Meuse River, in the village of Sclayn (province of Namur, Belgium). It opens to the south-east in Visean limestone (Lives Formation). Scladina consists of a large gallery, 6 m high and 6–20 m wide, connected to other caves, as Sous-Saint-Paul cave located several meters below. The partial collapse of the ceiling of Sous-Saint-Paul created a physical connection between the sedimentary deposits of the two caves. After thirty years of an almost permanent fieldwork, excavations in Scladina cave have reached more than 40 m beyond the entrance. Initially discovered by speleologists in 1971, the cave underwent several multidisciplinary researches since 1978, dealing mainly with archaeology, archaeozoology, large and small mammals, palynology, stratigraphy and sedimentology (e.g., Otte, 1992; Otte et al., 1998). More than 17,500 lithic artefacts have been collected in the cave, corresponding to four main Mousterian occupations (Bonjean et al., 2011). Thousands of faunal remains have also been found throughout the sequence, including a fragment of maxilla and nearly complete mandible of a juvenile Neandertal child, unearthed from 1990 onwards (Bonjean et al., 1997; Otte et al., 1993; Toussaint et al., 1994), and dated to 127 + 46/−32 ka by gamma spectrometry (Toussaint et al., 1998).

The first studies of the small-vertebrate assemblages from Scladina and Sous-Saint-Paul caves were undertaken by Jean-Marie Cordy in the 1980s and mainly focused on rodents, insectivores and lagomorphs (Bastin et al., 1986; Cordy, 1992). The faunal list published in these first studies revealed a rich faunal assemblage throughout the whole Middle to Late Pleistocene sequence and consisted of some 21 taxa: 5 insectivores (*Erinaceus europaeus*, *Talpa europaea*, *Sorex araneus*, *Sorex minutus* and *Crocidura* sp.), 15 rodents (*Citellus* sp., *Cricetulus migratorius*, *Sicista betulina*, *Lagurus lagurus*, *Lemmus lemmus*, *Dicrostonyx torquatus*, *Microtus arvalis-agrestis*, *Microtus gregalis*, *Microtus oeconomus*, *Chionomys nivalis*, *Microtus* (*Terricola*) *subterraneus*, *Arvicola amphibius*, *Myodes glareolus*, *Apodemus* cf. *sylvaticus*, and *Glis glis*) and one lagomorph (*Ochotona pusilla*). The presence of indeterminate anurans and reptiles was also mentioned. The present paper thus represents the first identification and description of the fossil amphibians and squamate reptiles from Cordy's sampling of the Middle to Late Pleistocene layers of Scladina and Sous-Saint-Paul caves.

2. Material and methods

The herpetofauna fossil remains used for this study consist of disarticulated bone fragments collected by water-screening during J.-M. Cordy's sampling of the sequence at the entrance of the caves (squares F7 and C4) and stored in the collections of the Scladina Cave Archaeological Centre (Sclayn, Belgium). The studied sample included some 123 fragments, representing eight different taxa (Table 1). The systematic nomenclature used basically follows Speybroeck et al. (2010) and Lescure and De Massary, 2012. Osteological nomenclature follows Estes (1981) and Sanchiz (1998) for amphibians, Rauscher (1992) for lizards and Szyndlar (1984, 1991) for snakes. Measurements were made with scaled drawings using a binocular microscope with a camera lucida.

The studied material comes from the lower half of the Scladina cave sequence (layers I, V ochre, VB and VI/VIa) superimposing the top of the Sous-Saint-Paul cave sequence (layers VII to X). The sedimentary filling of these two caves is separated by a major hiatus (Haesaerts, 1992; Pirson, 2007; Pirson et al., 2008, 2014).

The stratigraphic sequence of Sous-Saint-Paul cave (Otte et al., 1983; Haesaerts, 1992) has not recently been reviewed. A chronostratigraphic interpretation of it (Pirson, 2007; Pirson et al., 2008, 2014) suggests that layers VII to X probably date back to the end of the Middle Pleistocene [Marine Isotope Stage (MIS) 6–7, i.e. between 300 and 130 ka].

A detailed description of the geology of the layers of Scladina cave can be found in Pirson (2007) and Pirson et al. (2008). Although the stratigraphic sequence now appears considerably more complex than previously described (see Pirson, 2007, for historiographical details), we have here decided to maintain the old nomenclature associated with the works of J.-M. Cordy (Bastin et al., 1986; Cordy, 1992). The reason for this is that the stratigraphic reappraisal was mainly undertaken inside the cave and at the present stage of research cannot be accurately correlated with the sector investigated on the terrace by J.-M. Cordy. However, a general correlation with the main lithostratigraphic units of the new stratigraphic record can be established. The chronostratigraphic interpretation of layers V ocre to VI is

Table 1
Distribution of the amphibian and squamate reptile remains identified in Scladina and Sous-Saint-Paul caves by layers.
Tableau 1
Distribution des restes d'amphibiens et de reptiles squamates identifiés dans les niveaux des grottes Scladina et Sous-Saint-Paul.

	Scladina					Sous-Saint-Paul			**Total**
	I	V ocre	VB	VB-VI	VI-VIa	VII	IX	X	
Salamandra salamandra		1							**1**
Pelodytes punctatus			1			1			**2**
Bufo bufo			9	4	34		4	14	**65**
Rana temporaria	1	3	5			3			**12**
Anura indet.			4		3				**7**
Lacerta cf. *agilis*	1								**1**
Anguis fragilis		13		1	4				**18**
Zamenis longissimus		4							**4**
Vipera cf. *berus*			2		2				**4**
Serpentes indet.		8			1				**9**
Total	**2**	**29**	**21**	**5**	**44**	**4**	**4**	**14**	**123**

MIS 5 (i.e. 130–74 ka) and of layer I is MIS 3 (i.e. 60–24 ka; Pirson, 2007; Pirson et al., 2008, 2014).

3. Systematic study

AMPHIBIA Linnaeus, 1758

Amphibians are represented by 87 remains (70.7% of all the material) and have been referred to four taxa belonging to caudates and anurans.

CAUDATA Scopoli, 1777
SALAMANDRIDAE Goldfuss, 1820
Salamandra salamandra (Linnaeus, 1758)
(Fig. 1)

Referred material: one postsacral vertebra.

Description: The vertebra is characterized by its rather large size (total length 7.7 mm between pre- and post-zygapophyses). It is assigned to the *Salamandra salamandra* group on the basis of the following characters: opisthocoelous; neural arch is dorsoventrally flattened with a deeply concave anterior margin, at the level of the middle part of the pre-zygapophyseal articular facets and a well-developed medial notch in its posterior margin; long, narrow and low neural spine, well-developed in the middle part of the neural arch only (Estes, 1981; Ratnikov and Litvinchuk, 2007; Sanchíz and Mlynarski, 1979). The presence of only one slightly dorsoventrally flattened rib-bearer is consistent with a postsacral position. In ventral view, no subcentral foramen is visible. Various southern former sub-species within the *S. salamandra* group have recently been elevated at species rank: *S. atra* (from the French Alps to Albany), *S. corsica* (Isle of Corsica, France), *S. lanzai* (in the Alps between France and Italy), and *S. longirostris* (southernmost Iberian Peninsula) (Speybroeck et al., 2010). No osteological descriptions of these new species have been yet done; consequently the fossil remains from Scladina are attributed on the basis of the geographical distribution of *S. salamandra*, the only species of that group currently living in northern Europe.

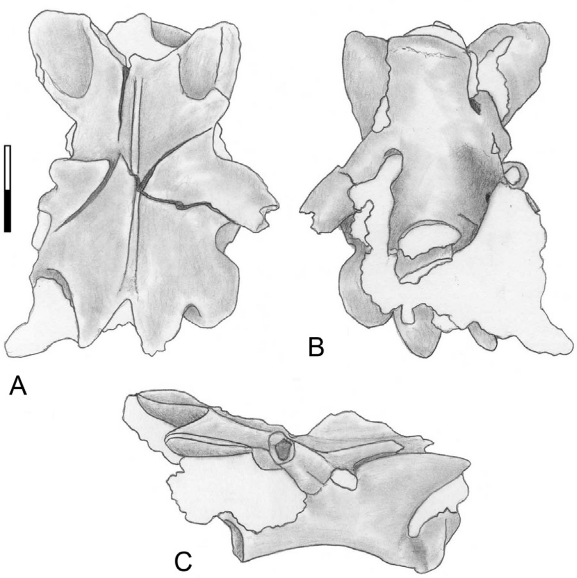

Fig. 1. *Salamandra salamandra*, A, B, C. Trunk vertebra, dorsal, ventral and right lateral views. Scale = 2 mm.
Fig. 1. *Salamandra salamandra*, A, B, C. Vertèbre dorsale, vues dorsale, ventrale et latérale droite. Échelle = 2 mm.

ANURA Duméril, 1805

Anuran remains are common in the layers of Scladina cave (86 remains). Among them, some 7 fossil remains (angulosplenial, fragments of vertebrae, fibulare and carpal) have been referred only as anurans indeterminate.

Three families are present: Pelodytidae, Bufonidae and Ranidae.

PELODYTIDAE Bonaparte, 1850
Pelodytes punctatus (Daudin, 1802)
(Fig. 2)

Referred material: one humerus and one ilium.

Description: *Humerus*. The humerus is small and presents a rather robust and straight shaft in ventral view. The condyle is more or less spherical and slightly outwardly displaced in relation to the main axis of the diaphysis. Within the genus *Pelodytes*, the robustness of this element permits attribution to *P. punctatus* (Sanchíz et al., 2002).

Ilium. The ilium is fragmentary and consists of the middle part of this element: the anteriormost part and the

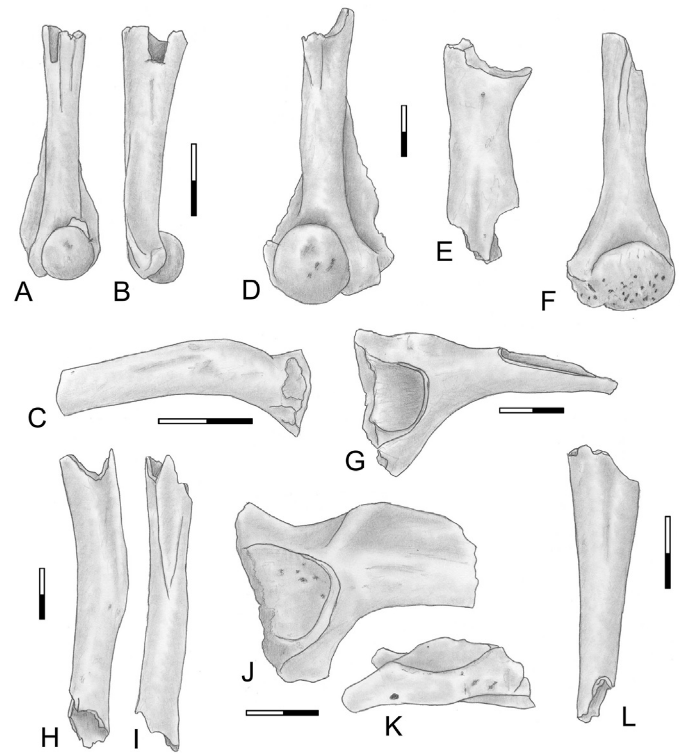

Fig. 2. *Pelodytes punctatus*. A, B. Left male humerus, ventral and mesial views. C. Left ilium, lateral view. *Bufo bufo*. D. Right male humerus, ventral view. E. Radio-ulna, lateral view. F. Left female humerus, ventral view. G. Right ilium, lateral view. H, I. Femur, dorsal and medial views. *Rana temporaria*. J, K. Right ilium, lateral and posterior views. L: Tibio-fibula, anterior view. Scale = 2 mm.

Fig. 2. *Pelodytes punctatus*. A, B. Humérus gauche de mâle, vues ventrale et mésiale. C. Ilion gauche, vue latérale. *Bufo bufo*. D. Humérus droit de mâle, vue ventrale. E. Radio-ulna, vue latérale. F. Humérus droit de femelle, vue ventrale. G. Ilion droit, vue latérale. H, I. Fémur, vues dorsale et médiale. *Rana temporaria*. J, K. Ilion droit, vues latérale et postérieure. L. Tibio-fibula, vue antérieure. Échelle = 2 mm.

acetabulum are missing. As in the genus *Pelodytes*, it lacks a dorsal ilial crest (*crista dorsalis*) and a dorsal prominence (*tuber superior*). The ilial shaft (*pars cylindriformis*) is well curved.

BUFONIDAE Gray, 1825
Bufo bufo (Linnaeus, 1758)
(Fig. 2)

Referred material: one pterygoid, one squamosal, 12 vertebrae, one sacrum, three urostyles, one scapula, one clavicle, one coracoid, four humeri, six radio-ulna, seven ilia, two femurs, four tibio-fibula, two fibulare and two carpals.

Description: The osteology of *Bufo* has been discussed in detail by several authors (e.g., Bailon, 1999; Blain et al., 2010; Böhme, 1977; Holman, 1998; Ratnikov, 2001; Sanchíz, 1977). The following discussion is limited to the most representative elements of our assemblage.

Humerus. Humeri have a shaft that is rectilinear and more or less curved in females; the condyle is laterally (radially) displaced. The humerus in *Bufo bufo* and *Bufo viridis* generally has a straighter diaphysis than in *Bufo calamita*. In male *B. bufo*, the medial crest (*crista medialis*) is flat and restricted to the distal part of the epiphysis, whereas in *B. viridis* this crest is long and dorsally curved.

Ilium. The presence of a dorsal prominence (*tuber superior*) and absence of an ilial crest (*crista dorsalis*) are characteristic of the genus *Bufo*. In *B. bufo*, the dorsal prominence is low and rounded, whereas in *B. viridis*, it is slightly higher and frequently provided with a secondary anterior tubercle and in *B. calamita*, it is higher and pointed. Moreover, in *B. viridis*, a deep pit (*fossa preacetabularis*) is present, and in *B. calamita*, a strongly developed ventrolateral crest (*calamita* blade or *calamita* ridge) is generally visible on the anterior half of the shaft.

Femur. The femur is a relatively long element and is robust and sigmoid. In *B. bufo* it usually has a low ridge (deltoid crest) that is proximally flattened and forms a triangle in medial view whereas this ridge is higher, sharper and slightly bifurcated in *B. viridis* and higher, narrow and straight in *B. calamita* (Bailon, 1999).

The other elements, which are often fragmentary, show the general morphology of the genus *Bufo*. Attribution to *B. bufo* is mainly based on their robustness rather than on their size; fossils of *B. bufo* in Scladina do not show the particularly large size (especially for females) of the southern representatives of the species.

RANIDAE Rafinesque-Schmaltz, 1814
Rana temporaria Linnaeus, 1758
(Fig. 2)

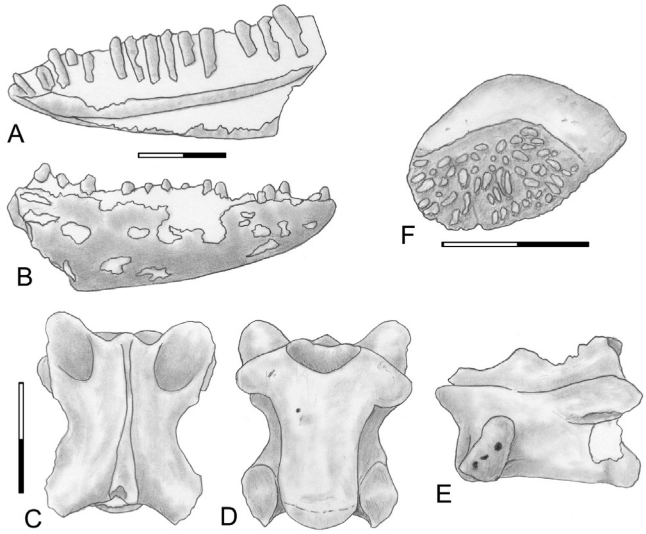

Fig. 3. *Lacerta* cf. *agilis*. A, B. Right dentary, medial and lateral views. *Anguis fragilis*, C, D, E. Trunk vertebra, dorsal, ventral and left lateral views. F. Osteoderm, external view. Scale = 2 mm.
Fig. 3. *Lacerta* cf. *agilis*. A, B. Dentaire droit, vues médiale et latérale. *Anguis fragilis*, C, D, E. Vertèbre dorsale, vues dorsale, ventrale et latérale gauche. F. Ostéoderme, vue externe. Échelle = 2 mm.

Referred material: one exoccipital, one atlas, one coracoid, three ilia, one tibio-fibula, three fibulare and three carpals.

Description: *Ilium*. Like in European ranids, ilia are characterized by the presence of an ilial crest on the shaft, a short ischial process (*pars ascendens*), a well-developed *tuber superior* and a posteromedial surface that is smooth and without any interilial *sulcus* (Bailon, 1999). The ilial crest in brown frogs (genus *Rana*) is lower and not as vertical as in green frogs (genus *Pelophylax*) and the *corpus ossis ilii* is slender (if observed on the *juncture*; *d*/*t*, *sensu* Gleed-Owen, 2000). In brown frogs, the *d*/*t* value lies between 2.75 and 4.00 whereas in green frogs *d*/*t* is between 2.12 and 2.88 (Gleed-Owen, 2000). The fossil ilia from Scladina have *d*/*t* values between 3.10 and 3.87. Within the genus *Rana*, attribution at the species level is rather difficult, but factors such as size or robustness may suggest an assignation to *Rana 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; Esteban and Sanchíz, 1985, 1991; Gleed-Owen, 1998, 2000; and personal observations).

Tibio-fibula. This element is very elongated, with relatively short longitudinal *sulci* at the distal and proximal ends. The diaphysis at the level of the *foramen nutricium* seems to be more slender in brown frogs than in green frogs.

Other elements have a size and certain slenderness that match with an attribution to *R. temporaria*. The exoccipital is not fused with the prootic, as is the case in ranids as opposed to bufonids (Bailon, 1999).

REPTILIA Laurenti, 1768

Non-avian Reptilia are represented in Scladina by lacertid and anguid lizards and ophidians.

Altogether, they only represent some 36 remains (29.3% of all the material) and have been referred to four taxa.

"Lacertilians"
LACERTIDAE Batsch, 1788
Lacerta* cf. *agilis Linnaeus, 1758
(Fig. 3)

Referred material: one dentary.

Description: A single dentary is present in layer I of Scladina cave. It possesses the morphological characteristics of the Lacertidae, bearing pleurodont, isodont, cylindrical and mono- or bicuspid teeth (most of the apices are smooth) and with a Meckelian *sulcus* open along its entire length. The posteriormost part of the element is broken. The corpus of the bone seems to be rather short and robust (total length = 7.5 mm; maximum height = 2.83 mm). Seventeen tooth positions have been preserved. No labial foramen is visible in lateral view; they are probably hidden by sediments. The element is cautiously attributed to *Lacerta agilis* on the basis of the robustness of the bone as well as its size (probably equal or superior to 10 mm for the complete dentary). The dentaries of *Podarcis muralis* and *Zootoca vivipara* are generally more slender and smaller, and those of *L.* gr. *viridis*/*bilineata* and *Timon lepidus* are more robust (Rauscher, 1992).

ANGUIDAE Gray, 1825
Anguis fragilis Linnaeus, 1758
(Fig. 3)

Referred material: one cervical vertebra, eight trunk vertebrae, eight caudal vertebrae and one osteoderm.

Description: *Vertebrae*. All the vertebrae are small (centrum length < 3 mm) and are procoelous with the condyle and cotyle dorsoventrally flattened. In lateral view, the neural spine is generally long, moderately high and, when

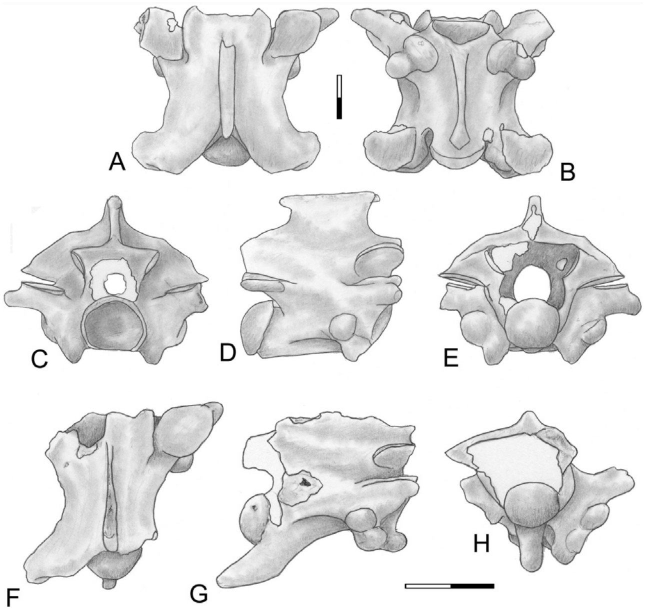

Fig. 4. *Zamenis longissimus*. A, B, C, D, E. Trunk vertebra, dorsal, ventral, anterior, right lateral and posterior views. *Vipera* cf. *berus*. F, G, H. Trunk vertebra, dorsal, right lateral and posterior views. Scale = 2 mm.

Fig. 4. *Zamenis longissimus*. A, B, C, D, E. Vertèbre troncale, vues dorsale, ventrale, antérieure, latérale et posterieure droites. *Vipera* cf. *berus*, F, G, H. Vertèbre dorsale, vues dorsale, latérale et posterieure droites. Échelle = 2 mm.

entire, it forms an interzygapophyseal point, the posterior part of which overlies the posterior edge of the neural arch. In ventral view, the centrum is generally longer than wide and possesses a flat ventral surface and two lateral margins parallel almost their entire length. The lateral foramina are not always visible but are generally small and located in the anterior half of the centrum.

The single cervical vertebra is rather short and robust, and its centrum presents the base of a posteroventrally directed hypapophysis. Of the eight caudal vertebrae, five correspond to the small anterior part of a caudal vertebra broken at the level of the autotomy suture. Three caudal vertebrae are sub-complete, more elongated than the trunk and cervical vertebrae, and show the base of two haemapophyses fused in the posterior half of their centrum and of flattened transverse processes in the anterior part of the centrum.

Osteoderm. A single left laterodorsal osteoderm is represented as a fossil in Scladina cave. It is small (maximum length = 3.1 mm) and has a somewhat semicircular shape. The anterior edge is thicker and smooth, and the posterior part of the external surface is rough and consists of a radiating network of channels and intervening ridges. The absence of a longitudinal carina and the small size of the element is consistent with attribution to *A. fragilis*. Osteoderms of the genus *Dopasia* (sensu Augé, 2005), sometimes referred as *Ophisaurus* (sensu Klembara, 2014) and *Pseudopus* are generally larger and their mediodorsal osteoderms, but not the lateral and medioventral ones, bear a longitudinal carina on the posterior part (Hoffstetter, 1962; Rauscher, 1992). Ornamentation in *Pseudopus* is generally more pronounced (Augé, 2003).

SERPENTES Linnaeus, 1758

Only 17 snake remains (13.8% of all the material) have been found in Scladina cave. These are mainly represented by vertebrae. Members of the families Colubridae and Viperidae have been identified.

COLUBRIDAE Oppel, 1811

Zamenis longissimus (Laurenti, 1768)

(Fig. 4)

Referred material: four trunk vertebrae.

Description: The fossil trunk vertebrae attain a relatively large size (centrum length between 5.9 and 4.0 mm, sensu Szyndlar, 1984) and do not bear a hypapophysis on the centrum, as in "colubrine" snakes. *Zamenis longissimus* vertebrae are characterized by a deep and rounded haemal keel that is spatulate at the caudal end. The pre-zygapophyseal processes are relatively short and show a rounded tip (but slender and pointed in the smallest specimen; Bailon, 1991; Szyndlar, 1984). As is usual in large specimens, the zygosphene is generally straight anteriorly (Szyndlar, 1991). No comparisons have been made with the recently elevated at species rank *Z. lineatus* (formerly included with *Z. longissimus*), but this snake has been disregarded on the basis of its geographical distribution restricted to southern Italy and Sicily (Razzetti and Zanghellini, 2006).

VIPERIDAE Oppel, 1811

Vipera cf. berus (Linnaeus, 1758)

(Fig. 4)

Referred material: four trunk vertebrae.

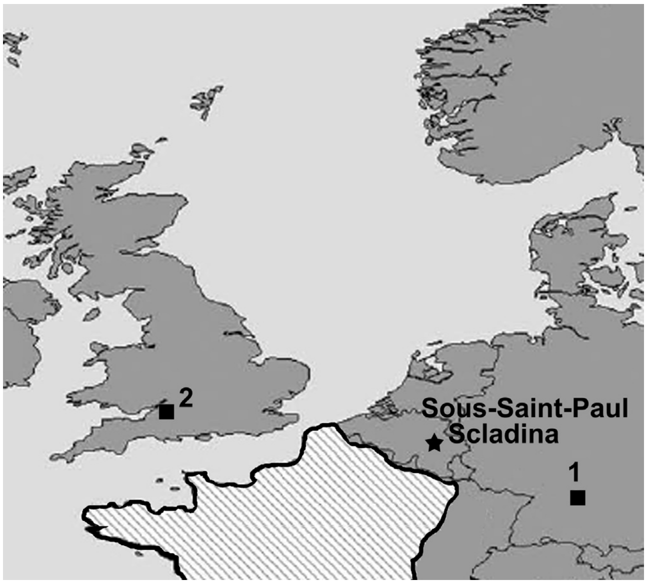

Fig. 5. Fossil record of *Pelodytes punctatus* outside its current range in northern Europe. 1: Steinbruch Schmidt, Germany, Middle Pleistocene; 2: Westbury cave, England, Middle Pleistocene.

Fig. 5. Mentions fossiles de *Pelodytes punctatus* hors de son aire de distribution actuelle en Europe du Nord. 1 : Steinbruch Schmidt, Allemagne, Pléistocène moyen ; 2 : Westbury cave, Angleterre, Pléistocène moyen.

Description: The trunk vertebrae show the typical characteristics of the family: presence of a straight and distally pointed hypapophysis; neural arch dorsoventrally flattened; centrum convex in transverse section and not well-marked lateral margins; developed condyle and cotyle; and upwardly inclined articular surface of the zygapophyses. Vertebral morphology permits two groups to be differentiated within the European vipers: the "*Vipera aspis* complex" and the "*Vipera berus* complex". Even if partially broken, 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*, *Vipera ursinii* and *Vipera seoanei*) display homogenous 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.

SERPENTES indet.

Referred material: one cervical vertebra, four trunk vertebrae, one caudal vertebra and four ribs.

All the remains without significant characters and clearly referable to the above-identified taxa or with juvenile characters have been referred to as Serpentes indeterminate.

4. Discussion

The Scladina and Sous-Saint-Paul caves assemblage provides a good opportunity to improve our understanding of the Belgian herpetofauna at the end of the Middle Pleistocene and in the Late Pleistocene. On the whole, four taxa of amphibians and four of reptiles have been identified: their presence in each sampled layer is summarized in Table 1. Scladina cave thus represents the first citation in the Belgian fossil record for the amphibian *S. salamandra*, and also the first fossil mention in the Pleistocene of Belgium, for *L.* cf. *agilis*, *Anguis fragilis*, *Z. longissimus* and *V.* cf. *berus*. Scladina and Sous-Saint-Paul caves represent the first citation in the Belgian fossil record for *P. punctatus*. Interestingly, Scladina (layer V ocre, MIS 5) also represents one of the northernmost fossil mentions for the Fire Salamander (*S. salamandra*) although it lies within its current distribution in Europe. Moreover, the probable presence of the European Adder (*V. berus*) in Scladina (layers VB and VI-VIa, MIS 5) is also noticeable because today this snake is infrequent and classified as endangered in Belgium, probably due to anthropic pressure (Ursenbacher, 2010; La biodiversité en Wallonie, 2010).

The main peculiarity of the assemblage is the coexistence of taxa still living in the area (*S. salamandra*, *B. bufo*, *R. temporaria* and *A. fragilis*) with others that today have a southern and/or western distribution, such as the Parsley Frog (*P. punctatus*) and the Aesculapian Snake (*Z. longissimus*).

P. punctatus today ranges from Spain up to the North of France, including France, Spain, Portugal and a small part of northwestern Italy (Piedmont and Liguria; Gasc et al., 1997; Duguet and Melki, 2003). In the northeastern part of its modern range, *P. punctatus* curiously does not cross the border between France and Belgium, following the political frontier exactly. In the fossil record, outside its current range *Pelodytes* sp. is known from the Middle Pleistocene of Kozi Grzbiet (Poland; Sanchíz and Szyndlar, 1984), and *P. punctatus* is recorded from the Middle Pleistocene of Steinbruch Schmidt (Stuttgart, southwestern Germany; Böttcher, 1994) and from the Middle Pleistocene (MIS 13, i.e. 528 ka) of Westbury cave (Units 11–15; Somerset,

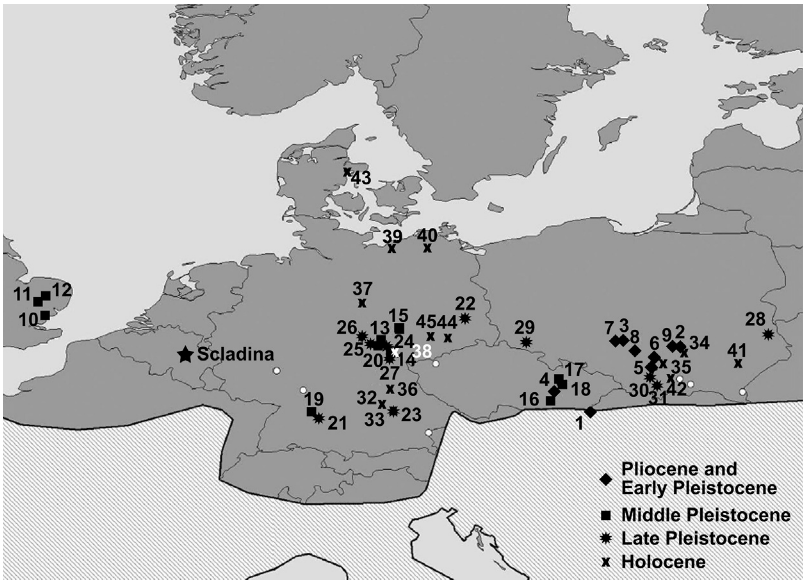

Fig. 6. Fossil record of *Zamenis longissimus* outside its current range in Northern Europe with open circles indicating isolated living populations (modified from Musilová et al., 2007). 1: Ivanovce, Slovakia; 2: Kadzielnia, Poland; 3: Zalesiaki B, Poland; 4: Malá dohoda Quarry, Czech Republic; 5: Kamyk, Poland; 6: Zabia cave, Poland; 7: Zalesiaki A, Poland; 8: Zamkowa Dolna cave, Poland; 9: Kozi Grzbiet, Poland; 10: Cudmore Grove, England; 11: Barnham, England; 12: Beeches Pit, England; 13: Weimar-Ehringsdorf, Germany; 14: Gamsenberg, Germany; 15: Neumark-Nord, Germany; 16: Stránská skála Hill, Czech Republic; 17: Mladeč caves, Czech Republic; 18: Za hájovnou cave, Czech Republic; 19: Stuttgart-Bad Cannstatt, Germany; 20: Weimar- Ehringsdorf, Germany; 21: Stuttgart-Bad Cannstatt, Germany; 22: Schönfeld-Calau, Germany; 23: Lobsing, Germany; 24: Weimar, Germany; 25: Taubach, Germany; 26: Burgtonna, Germany; 27: Gamsenberg, Germany; 28: Wierzbica, Poland; 29: Rzasnik, Poland; 30: Zytnia Skala, Poland; 31: Ciasna cave, Poland; 32: Malerfels, Germany; 33: Euerwanger Bühl, Germany; 34: Raj cave, Poland; 35: Niedostepna cave, Poland; 36: Grundfelsen Hohle, Germany; 37: Kneitlingen, Germany; 38: Gamsenberg, Germany; 39: Neukloser, Germany; 40: Pisede, Germany; 41: Jozéfow, Poland; 42: Giebultow, Poland; 43: Lystrup Enge, Germany; 44: Robschütz, Germany; 45: Klosterbuch, Germany.

Fig. 6. Mentions fossiles de *Zamenis longissimus* hors de son aire de distribution actuelle en Europe du Nord avec les cercles blancs indiquant les populations vivantes isolées (modifié de Musilová et al., 2007). 1 : Ivanovce, Slovaquie ; 2 : Kadzielnia, Pologne ; 3 : Zalesiaki B, Pologne ; 4 : Malá dohoda Quarry, République tchèque ; 5 : Kamyk, Pologne ; 6 : Zabia cave, Pologne ; 7 : Zalesiaki A, Pologne ; 8 : Zamkowa Dolna cave, Pologne ; 9 : Kozi Grzbiet, Pologne ; 10 : Cudmore Grove, Angleterre ; 11 : Barnham, Angleterre ; 12: Beeches Pit, Angleterre; 13 : Weimar-Ehringsdorf, Allemagne ; 14 : Gamsenberg, Allemagne ; 15 : Neumark-Nord, Allemagne ; 16 : Stránská skála Hill, République tchèque ; 17 : Mladeč caves, République tchèque ; 18 : Za hájovnou cave, République tchèque ; 19 : Stuttgart-Bad Cannstatt, Allemagne ; 20 : Weimar-Ehringsdorf, Allemagne ; 21 : Stuttgart-Bad Cannstatt, Allemagne ; 22 : Schönfeld-Calau, Allemagne ; 23 : Lobsing, Allemagne ; 24 : Weimar, Allemagne ; 25 : Taubach, Allemagne ; 26 : Burgtonna, Allemagne ; 27 : Gamsenberg, Allemagne ; 28 : Wierzbica, Pologne ; 29 : Rzasnik, Pologne ; 30 : Zytnia Skala, Pologne ; 31 : Ciasna cave, Pologne ; 32 : Malerfels, Allemagne ; 33 : Euerwanger Bühl, Allemagne ; 34 : Raj cave, Pologne ; 35 : Niedostepna cave, Pologne ; 36 : Grundfelsen Hohle, Allemagne ; 37 : Kneitlingen, Allemagne ; 38 : Gamsenberg, Allemagne ; 39 : Neukloser, Allemagne ; 40 : Pisede, Allemagne ; 41 : Jozéfow, Pologne ; 42 : Giebultow, Pologne ; 43 : Lystrup Enge, Allemagne ; 44 : Robschütz, Allemagne ; 45 : Klosterbuch, Allemagne.

England; Holman, 1998; Gleed-Owen, 1998, 1999). Its presence in layers Vb (MIS 5) and VII (probably MIS 6/7) of Scladina cave thus suggests a more expanded range to the northeast of its modern distribution during the Late Middle and Early Late Pleistocene (Fig. 5).

The continuous area of *Z. longissimus* covers most of France except the North (about up to the latitude of Paris), the Spanish Pyrenees and the eastern part of the Spanish north coast, Italy (except the South), all of the Balkan peninsula down to Greece and Asia Minor, and parts of central and eastern Europe up to about the 49th parallel (Gasc et al., 1997; Naulleau, 2010). Further, there are (or were in historical times) a number of isolated populations north to modern northern range limit: in western Germany (Schlangenbad, Hirschhorn and Burghausen), Switzerland (Lorrach/Basel), the Northwest of the Czech Republic (Karlovy Vary) and South Poland (Zloty potok, Zamojszczyznza, Zarzecze, Powroznik and Bieszczady; Musilová et al., 2007; Fig. 6). The northernmost historical occurrence (18th and 19th centuries) was in Vordingborg (Denmark; Boulenger, 1913; Hvass, 1942). Although some authors (e.g., Laughlin, 1962) have hypothesized that parts of the geographical distribution of the species may be the result of the intentional keeping and subsequent release of these snakes by Romans from the temples of Asclepius, the classical god of medicine, the fossil evidence shows that this snake was present north of its current distribution in Europe during the Pleistocene interglacials and the Holocene (Böhme, 2000; Gleed-Owen, 1998, 1999; Holman, 1998; Ivanov, 2007; Szyndlar, 1984).

During the Pleistocene, *Z. longissimus* was present in England during the Middle Pleistocene interglacials in Barnham (Norfolk; MIS 11, i.e. 427 ka), Beeches Pit (Suffolk; MIS 11), and Cudmore Grove (Essex; MIS 9, i.e. 334 ka; Gleed-Owen, 1998, 1999; Holman, 1998). In Germany, it was present during the Middle Pleistocene (Weimar-Ehringsdorf, Gamsenberg and Stuttgart-Bad Cannstatt), at numerous early Late Pleistocene sites often attributed to the Eemian stage (MIS 5e, i.e. 130–115 ka; van Kolfschoten, 2000), such as Schönfeld-Calau (Brandenburg), Lobsing

(Bavaria), Taubach (Thuringia), Burgtonna (Thuringia), Neumark-Nord (Saxony-Anhalt), etc., and in one layer, probably MIS 4 in age (i.e. 74 to 60 ka), from Gamsenberg (Thuringia; Böhme, 2000; Holman, 1998). In central Europe, *Z. longissimus* has been reported from the Early Pleistocene of Ivanovce (Slovakia) and the Middle Pleistocene of Stránská Skála Hill, the Mladeč caves and Za Hájovnou cave (all in Moravia; Ivanov, 2007). Finally, in Poland it is represented during the Early Pleistocene (Kadzielnia, Zalesiaki B, Kamyk and the Zabia cave), the late Early or early Middle Pleistocene (Zalesiaki A), the Middle Pleistocene (around 500 ka, Kozi Grzbiet), the early Late Pleistocene (Eemian, MIS 5e?; Rzasnik and Wierzbica I) and the Late Pleistocene (MIS 3, Weichselian) (the Zamkova Dolna cave; Szyndlar, 1984).

All this suggests that the range of *Z. longissimus* repeatedly contracted and then expanded again over the course of the Pleistocene and Holocene (Musilová, 2011; Musilová et al., 2007, 2010), very probably in relation with the alternating climatic conditions during the glacial/interglacial cycles. As a consequence, the occurrence of *Z. longissimus* in Scladina cave (layer V ocre, MIS 5) is in accordance with previous fossil mentions of the species to the north of its current distribution in northern Europe during the early Late Pleistocene (in Germany and Poland, though neither in England nor the Czech Republic), documenting for the first time the occurrence of this snake in Belgium (Fig. 6).

Together, the taxa represented in layers V ocre to VI (MIS 5, Late Pleistocene) fit well with a variety of climatic conditions, maybe warmer conditions than at present in the case of layer V ocre. These species reflect multiple environments including a slow-water stream within a forest area and humid meadows. These various environments may have formed a mosaic on the landscape or been correlated with climatic fluctuations during MIS 5. The Fire Salamander (*S. salamandra*) lives in hilly areas in European forests. It prefers deciduous forests, since it hides in fallen leaves and around mossy tree trunks. It needs small brooks or ponds with clean water in its habitat for the development of its larvae. The Common Toad (*B. bufo*) is also found largely in forested areas, especially in wet locations with dense herbaceous vegetation. The Aesculapian Snake (*Z. longissimus*) prefers warm, moderately humid, forested habitats with proper insolation and varied but not sparse vegetation that provides sufficient variation in local microclimates. It generally avoids open environments. Other taxa, such as the Slow Worm (*A. fragilis*) and the Common Frog (*R. temporaria*), may be found in more open environments, such as humid meadows and forest edges. The Parsley Frog (*P. punctatus*) is found in open or semi-open, even arid landscapes, and the common Adder (*V. berus*) is found in a variety of habitats, generally dry, cool or humid and with sparse vegetation: wastelands, heathland and gorse and forest edges or scrubby environments. *Z. longissimus* is the most thermophilous element from the faunal list, and taking into account its modern distribution in Europe, it suggests that temperatures may have been 1 to 2 °C higher than at present in southern Belgium during the formation of layer V ocre.

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References

Augé, M., 2003. La faune de Lacertilia (Reptilia, Squamata) de l'Eocène de Prémontré (Bassin de Paris, France). Geodiversitas 25, 539–574.

Augé, M., 2005. Evolution des lézards du Paléogène en Europe. Mémoires du Muséum National d'Histoire Naturelle, Volume 192. Publications scientifiques du Muséum, Paris.

Bailon, S., (Ph.D. dissertation) 1991. Amphibiens et reptiles du Pliocène et du Quaternaire de France et d'Espagne : mise en place et évolution des faunes. Université de Paris VII.

Bailon, S., 1999. Différenciation ostéologique des Anoures (Amphibia Anura) de France. In: Desse, J., Desse-Berset, N. (Eds.), Fiches d'ostéologie animale pour l'archéologie. Série C : varia. Centre de Recherches Archéologiques-CNRS, Valbonne, pp. 1–38.

Ballmann, P., de Coninck, J., de Heinzelin, J., Gautier, A., Geets, S., Rage, J.-C.I., 1980. In: Gautier, A., de Heinzelin, J. (Eds.), Les dépôts quaternaires; inventaire paléontologique et archéologique. La Caverne Marie-Jeanne (Hastière-Lavaux, Belgique). Mém. Inst. Roy. Sci. Nat. Belg. 177, 4–23.

Bastin, B., Cordy, J.-M., Gewelt, M., Otte, M., 1986. Fluctuations climatiques enregistrées depuis 125 000 ans dans les couches de remplissage de la grotte Scladina (Province de Namur, Belgique). Bull. Assoc. fr. Ét. Quat. 1–2, 168–177.

Blain, H.-A., Gibert, L., Ferràndez-Cañadell, C., 2010. First report of a green toad (*Bufo viridis* sensu lato) in the Early Pleistocene of Spain: paleobiogeographical and paleoecological implications. C.R. Palevol. 9, 487–497.

Böhme, G., 1977. Zur Bestimmung quartärer Anuren Europas an Hand von Skelettelementen. Wissenschaftliche Zeitschrift Humboldt-Universität Berlin (Math.-Nat. Reihe) 36, 283–300.

Böhme, G., 2000. Fossile Amphibie und Reptilien im Quartär Thüringens. Veröff. Nat.kd.mus. Erfurt 19, 79–97.

Bonjean, D., Toussaint, M., Otte, M., 1997. Grotte Scladina (Sclayn, Belgique) : bilan des découvertes néandertaliennes et analyse du contexte. In: Cinquième Journée d'Archéologie namuroise, Actes 5. Ed. M.R.W. – D.G.A.T.L.P, pp. 19–27.

Bonjean, D., Di Modica, K., Abrams, G., Pirson, S., Otte, M., 2011. La grotte Scladina: bilan 1971–2011. In: Toussaint, M., Di Modica, K., Pirson, S. (Eds.), Le Paléolithique moyen en Belgique. Mélanges Marguerite Ulrix-Closset. Bulletin des Chercheurs de la Wallonie, hors-série n° 4, E.R.A.U.L., 128, pp. 323–334.

Böttcher, R., 1994. Niedere Wirbeltiere (Fische, Amphibien Reptilien) aus dem Quartär von Stuttgart. Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie) 215, 1–75.

Boulenger, G.A., 1913. The snakes of Europe. Methusen & Co. Ltd, London.

Cordy, J.-M., 1992. Bio- et chronostratigraphie des dépôts quaternaires de la grotte Scladina (Province de Namur, Belgique) à partir des micromammifères. In: Otte, M. (Ed.), Recherches aux grottes de Sclayn Volume 1 : Le contexte, 27. Études et Recherches archéologiques de l'Université de Liège, pp. 79–125.

De Wilde, B., 2011. Les oiseaux, les anoures et les gastéropodes terrestres de la grotte Walou. In: Draily, C., Pirson, S., Toussaint, M. (Eds.), La grotte Walou à Trooz (Belgique), Fouilles de 1996 à 2004, volume 2 Les sciences de la vie et les datations, 21. Études et Documents Archéologie, pp. 62–65.

Duguet, R., Melki, F., 480 p 2003. Les Amphibiens de France. In: Belgique et Luxembourg. Collection Parthénope, éditions Biotope, Mèze, France.
Esteban, M., Sanchíz, B., 1985. Herpetofauna de Erralla. Munibe (Antropología y Arqueología) 37, 81–86.
Esteban, M., Sanchíz, B., 1991. Sobre la presencia de *Rana iberica* en el Pleistoceno burgales. Revista Española de Herpetologia 5, 93–99.
Estes, R., 1981. Gymnophiona, Caudata. In: Wellnhofer, P. (Ed.), Handbuch der Paläoherpetologie (Encyclopedia of Paleoherpetology), Volume 2. Gustav Fischer Verlag, Stuttgart, New York (113 p.).
Gleed-Owen, C.P., (Ph.D. dissertation) 1998. Quaternary herpetofaunas of the British Isles: Taxonomic descriptions, palaeoenvironmental reconstructions, and biostratigraphic implications. Coventry University, Coventry (550 p.).
Gleed-Owen, C.P., 1999. The palaeoclimatic and biostratigraphic significance of herpetofaunal remains from the British Quaternary. In: Andrews, P., Banham, P. (Eds.), Late Cenozoic Environments Hominid Evolution: a tribute to Bill Bishop. Geol. Soc. London, 201–215.
Gleed-Owen, C.P., 2000. Subfossil records of *Rana* cf. *lessonae*, *Rana arvalis* and *Rana* cf. *dalmatina* from Middle Saxon (c. 600-950 AD) deposits in eastern England: evidence for native status. Amphibia-Reptilia 21, 57–65.
Haesaerts, P., 1992. Les dépôts pléistocènes de la terrasse de la grotte Scladina à Sclayn (province de Namur, Belgique). In: Otte, M. (Ed.), Recherches aux grottes de Sclayn. Volume 1 : Le contexte, 27. Études et Recherches archéologiques de l'Université de Liège, pp. 33–55.
Hoffstetter, R., 1962. Observations sur les ostéodermes et la classification des Anguidés actuels et fossiles (Reptiles Sauriens). Bull. Muséum Natl. Hist. Nat. 34, 149–157.
Holman, J.A., 1998. Pleistocene amphibians and reptiles in Britain and Europe. Oxford Monographs on Geology and Geophysics, 38. Oxford University Press, New York and Oxford (254 p).
Hvass, H., 1942. Danmarks aeskulapsnoge. Naturens Verden 26, 74–86.
Ivanov, M., 2007. Herpetological assemblages from the Pliocene to Middle Pleistocene in central Europe: palaeoecological significance. Geodiversitas 29, 297–320.
Klembara, J., 2014. New finds of anguines (Squamata Anguidae) from the Early Miocene of Northwest Bohemia (Czech Republic). Paläontologische Zeitschrift, 10.1007/s12542-014-0226-4.
www.biodiversite.wallonie (consulted November 5, 2013).
Laughlin, V.L., 1962. The Aesculapian Staff and the Caduceus as Medical Symbols. Journal of the International College of Surgeons 37, 82–92.
Lescure, J., De Massary, J.-C., 2012. Atlas des Amphibiens et Reptiles de France. Biotope, Mèze & Muséum national d'histoire naturelle Paris. Collection Inventaires & Biodiversité (272 p).
Musilová, R., (Ph.D. dissertation) 2011. Ekologie a status užovky stromove (*Zamenis longissimus*) v severozapadnich Čechach. Fakulta Životniho Prostředi Česka Zemědělska Univerzita u Praze (111 p.).
Musilová, R., Zavadil, V., Kotlík, P., 2007. Isolated populations of *Zamenis longissimus* (Reptilia: Squamata) above the northern limit of the continuous range in Europe: origin and conservation status. Acta Soc. Zool. Bohem. 71, 197–208.
Musilová, R., Zavadil, V., Marková, S., Kotlík, P., 2010. Relics of the Europe's warm past: phylogeography of the Aesculapian snake. Mol. Phylogenet. Evol. 57, 1245–1252.
Otte, M. (Ed.), 1992. In: Le contexte. Études et Recherches archéologiques de l'Université de Liège, 27 (178 p.).
Otte, M., Léotard, J.-M., Schneider, A.-M., Gautier, A., Gilot, E., Aitken, M., 1983. Fouilles aux grottes de Sclayn (Namur). Helinium 23, 112–142.
Otte, M., Toussaint, M., Bonjean, D., 1993. Découverte de restes humains immatures dans les niveaux moustériens de la grotte Scladina à Andenne (Belgique). Bull. Mém. Soc. Anthropol. Paris, n.s.t. 5, 327–332.
Otte, M., Patou-Mathis, M., Bonjean, D. (Eds.), 1998. Recherches aux grottes de Sclayn. Volume 2: L'Archéologie, 79. Études et Recherches archéologiques de l'Université de Liège (437 p.).
Pirson, S., (Ph.D. dissertation) 2007. Contribution à l'étude des dépôts d'entrée de grotte en Belgique au Pléistocène supérieur. Stratigraphie, sédimentogenèse et paléoenvironnement. University of Liège & Royal Belgian Institute of Natural Sciences.
Pirson, S., Court-Picon, M., Haesaerts, P., Bonjean, D., Damblon, F., 2008. New data on geology, anthracology and palynology from the Scladina cave Pleistocene sequence: preliminary results. Mem. Geol. Surv. Belg. 55, 21–93.
Pirson, S., Court-Picon, M., Damblon, F., Balescu, S., Bonjean, D., Haesaerts, P., 2014. The palaeoenvironmental context and chronostratigraphic framework of the Scladina Cave sequence. In: Toussaint, M., Bonjean, D. (Eds.), The Juvenile Neandertal Facial Remains from Scladina Cave. Études et Recherches archéologiques de l'Université de Liège (134 p.).
Ratnikov, V.Y., 2001. Osteology of Russian toads and frogs for paleontological researches. Acta Zool. Cracov. 44, 1–23.
Ratnikov, V.Y., Litvinchuk, S.N., 2007. Comparative morphology of trunk and sacral vertebrae of tailed amphibians of Russia and adjacent countries. Russ. J. Herpetol. 14, 177–190.
Rauscher, K.L., 1992. Die Echsen (Lacertilia, Reptilia) aus dem Plio-Pleistozän von Bad Deutsch-Altenburg. Niederösterreich. Beiträge zur Paläontologie Österreich-Ungarns und des Orients 17, 81–177.
Razzetti, E., Zanghellini, S., 2006. *Zamenis longissimus* (Laurenti, 1768)/*Zamenis lineatus* (Camerano, 1891). In: Sindaco, R., Doria, G., Razzetti, E., Bernini, F. (Eds.), Atlante degli Anfibi e dei Rettili d'Italia/Atlas of Italian Amphibians and Reptiles. Edizioni Polistampa, Firenze, pp. 576–583.
Sanchíz, F.B., 1977. La familia Bufonidae (*Amphibia* Anura) en el Terciario Europeo. Trabajos Neogeno/Cuaternario 8, 75–111.
Sanchíz, B., 1998. Salientia. In: Wellnhofer, P. (Ed.), Handbuch der Paläoherpetologie (Encyclopedia of Paleoherpetology), Volume 4. Gustav Fischer Verlag, Stuttgart, New York.
Sanchíz, F.B., Mlynarski, M., 1979. Remarks on the Fossil Anurans from the Polish Pliocene. Acta Zool. Cracov. 24, 153–174.
Sanchíz, B., Szyndlar, Z., 1984. Pleistocene amphibian fauna from Kozi Grzbiet in the Holy Cross Mountains. Acta Geol. Pol. 34, 51–60.
Sanchíz, B., Tejedo, M., Sánchez-Herráiz, M.J., 2002. Osteological differentiation among Iberian *Pelodytes* (Anura, Pelodytidae). Graellsia 58, 35–68.
Speybroeck, J., Beukema, W., Crochet, P.-A., 2010. A tentative species list of the European herpetofauna (Amphibia and Reptilia) – an update. Zootaxa 2492, 1–27.
Szyndlar, Z., 1984. Fossil snakes from Poland. Acta Zool. Cracov. 28, 1–156.
Szyndlar, Z., 1991. A review of Neogene and Quaternary snakes of central and eastern Europe. Part I: Scolecophidia, Boidae. Colubrinae. Estud. geol. 47, 103–126.
Szyndlar, Z., Rage, J.-C., 1999. Oldest Fossil Vipers (Serpentes: Viperidae) from the Old World. Kaupia 8, 9–20.
Toussaint, M., Bonjean, D., Otte, M., 1994. Découverte de fossiles humains du Paléolithique moyen à la grotte Scladina à Andenne. In: Corbiau, M.-H., Plumier, J. (Eds.), Actes de la deuxième tournée d'archéologie namuroise. Facultés universitaires Notre-Dame-de-la-Paix, Namur, 26 février 1994. Ministère de la Région wallonne (DGATLP) – FUNDP (Département d'histoire de l'art et d'archéologie), Namur, pp. 19–33.
Toussaint, M., Otte, M., Bonjean, D., Bocherens, H., Falguères, C., Yokohama, Y., 1998. Les restes humains néandertaliens immatures de la couche 4A de la grotte Scladina (Andenne, Belgique). C. R. Acad. Sci. Paris, Ser. IIa 326, 737–742.
Ursenbacher, S., 2010. La vipère péliade. In: Vacher, J.-P., Geniez, M. (Eds.), Les reptiles de France, Belgique, Luxembourg et Suisse. Collection Parthénope, éditions Biotope, Mèze, France, and Muséum national d'Histoire naturelle, Paris, pp. 496–503.
van Kolfschoten, T., 2000. The Eemian mammal fauna of central Europe. Geol. Mijnbouw NJG 79, 269–271.