

Amphibians and squamate reptiles from the early Upper Pleistocene of Bois Roche Cave (Charente, southwestern France)

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Abstract. The layers, ascribed to the early Upper Pleistocene (Middle Palaeolithic) of Bois Roche Cave, contain an abundant bone assemblage, as well as a few lithic artifacts, in a hyena den. The amphibians and squamate reptiles fauna consist of: *Pelobates fuscus* (Pelobatidae), *Pelodytes punctatus* (Pelodytidae), *Bufo bufo* and *Bufo calamita* (Bufonidae), *Hyla* sp. (Hylidae), *Rana temporaria* and *Rana* cf. *R. lessonae* (Ranidae), a small lacertid (Lacertidae), *Anguis fragilis* (Anguidae), *Natrix natrix* and *Coronella austriaca* (Colubridae) and a “*Vipera berus* complex” species (Viperidae). The herpetofauna may be contemporaneous of cold-temperate climatic conditions. *P. fuscus*, *R. lessonae* and “*V. berus* complex” underline more continental climatic conditions mitigated by the occurrence of species like *P. punctatus* and *B. calamita* with western Atlantic affinities. The palaeoenvironment, suggested by herpetofauna, was a very open environment, with damp meadows and small grove areas of broad-leaved trees and conifers. The proportion and distribution of species in the stratigraphic sequence allow hypotheses concerning minor climatic variations to be advanced.

Key-words: Amphibians, Reptiles, Charente region, early Upper Pleistocene, Palaeoclimate, Palaeoenvironment, Palaeobiogeography.

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I. INTRODUCTION

Bois Roche is a small cave located in the chateau of the same name in the Charente region, near the city of Cognac (Fig. 1). Entrance to the cave is provided by a short, subvertical conduit which leads into a small vaulted area, called the Vestibule, about 5 sq m total. A larger chamber, 9 × 4 m in area, called Grande Salle, with sediments nearly filling it to the ceiling was discovered by the land owner, Jean-François PORTET, and reported to the Service Archéologique of the Charente region in 1978. At the time of its discovery the cave surface was covered with bones, teeth and hyena coprolites; the paleosurface materials (including 1200 bones and teeth and 17 artifacts) were collected by

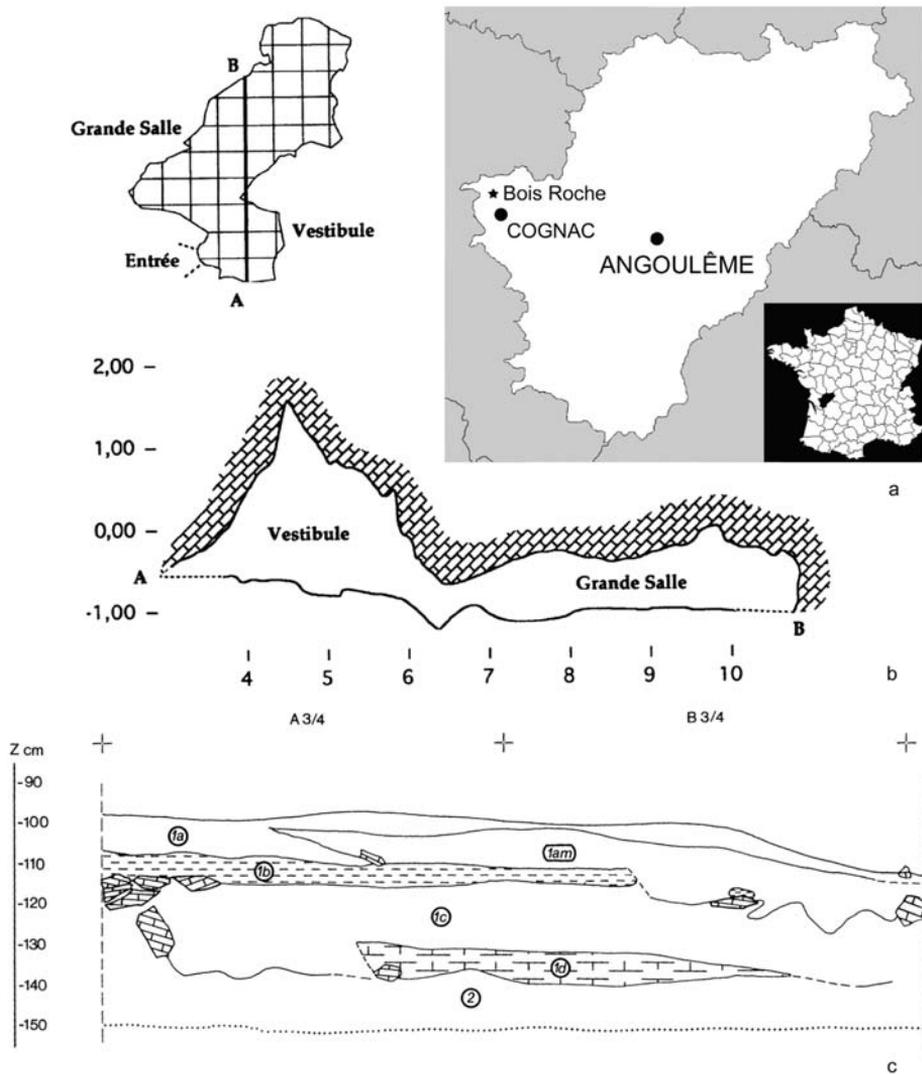


Fig. 1. a – Geographical setting; b – plan and cross-section of the cave, at the level of present-day surface; c – detail of stratigraphy (Main Chamber or Grande Salle, square A3/4 and B3/4) (from VILLA & BARTRAM 1999).

the discoverer. Test excavations were conducted in 1979 and 1981 by Bernard VANDERMEERSCH, then resumed by Laurence BARTRAM and Paola VILLA in 1995, 1997-98 and by VILLA in 1999-2000. In total an area of about 18 sq m (representing about half of the cave area at the existing surface level) has been opened down to a maximum depth of 60 to 80 cm (VILLA & BARTRAM 1996; D'ERRICO & VILLA 1997; BARTRAM & VILLA 1998; VILLA & SORESSI 2000; VILLA & D'ERRICO 2001; MARRA et al. 2004; VILLA et al. 2004).

The deposits, which slope away from the entrance toward the rear of the inner chamber, consist of two major stratigraphic units along with four subdivisions of the upper unit, as follows (from top, GOLDBERG 2001):

Unit 1a (approximately 10-15 cm) is a stony silty clay, the paleosurface unit reworked at the top (Unit 1ar) by the collecting activities of the land owner.

Unit 1am is a discontinuous layer that vary from 0 to 10 cm, whose main characteristic is to contain abundant microfauna.

Unit 1b is a lens of finely laminated brown silty clay that varies from 0 to 6 cm, deposited by running water (sheetflow). It is laterally discontinuous.

Unit 1c, ca 10 to 20 cm thick is composed of yellow-brown sandy clay silt with limestone rock fragments that range in size from granules to decimeter size blocks.

Unit 1d is a grey-brown, sinter-like layer, 5 to 15 cm thick, with localized calcitic laminae, locally eroded by burrows.

Unit 2 is a massive (up to 30-40 cm) clast-supported accumulation of clayed silt with cm to dm size blocks of limestone roof fall and abundant bones of megafauna. Lack of bedding is probably due to bioturbation by hyenas. Unit 1c and 2 are rich in rounded mm sized coprolite fragments, evident in micromorphological slides and very abundant in screen residues (BARTRAM & VILLA 1998).

Preliminary estimates based on ESR date the deposits to late OIS 5 or early OIS 4 (L. P. ZHOU, personal communication). The rodents conform to this age estimate (G. CUENCA-BESCÓS, personal communication). Evidence for a human presence is negligible consisting solely of a few Middle Palaeolithic artifacts (including nine Levallois flakes) introduced into the cave by natural transport processes such as gravity and slope wash (VILLA & SORESSI 2000). The site lacks any other evidence of human presence such as structures, hearths or ash levels.

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II. MATERIAL AND METHODS

The herpetofaunal sample consists of disarticulated and broken bone fragments collected by water-screening during the excavations that Paola VILLA and Laurence BARTRAM have conducted from 1997 to 2000 at Bois Roche Cave. This assemblage includes 40810 fragments that correspond to a minimum of 4851 specimens, representing at least twelve species (Table I). In 1997, all the sediment was water-screened using 5 mm and 1.4 mm superimposed screens; the refuse was sorted and bagged by square, layer and excavation levels of 5 cm or less, depending on the natural stratigraphy. In later seasons, the sediment was water-screened with 5 and 2 mm mesh; five-liters samples from each square and each excavation level of 5 cm were screened through 1.4 mm mesh. Micropalaeontological materials were sorted and classed in large categories by Peter ROBINSON (University of Colorado Museum).

The fragments were identified following the general criteria given by BÖHME (1977), BAILON (1999a), ESTEBAN & SANCHIZ (1985 and 1991), SANCHIZ et al. (1993), HOLMAN (1998), GLEED-OWEN (2000) and SANCHIZ et al. (2002) for Anura, and BAILON (1991) and SZYNDLAR (1984) for Squamata, using for comparisons the dry skeleton collections of the Muséum National d'Histoire Naturelle (Anatomie Comparée, Paris, France), of the Museo Nacional de Ciencias Na-

Table I

Distribution of anurans and squamate reptiles in the layers of Bois-Roche Cave (in NISP and MNIa). MNI is adjusted here according to laterality, sex and stratigraphical/spatial distribution

	1a		1am		1b		1c		1d		2		Total	
	NISP	MNIa	NISP	MNIa	NISP	MNIa	NISP	MNIa	NISP	MNIa	NISP	MNIa	NISP	MNIa
Anura														
<i>Pelobates fuscus</i>	16	9	17	12	7	5	2	1	0	0	27	17	69	44
<i>Pelodytes punctatus</i>	3507	509	12926	1007	932	149	1716	272	496	80	11236	1786	30813	3803
<i>Bufo bufo</i>	8	4	0	0	0	0	1	1	0	0	3	3	12	8
<i>Bufo calamita</i>	299	56	501	81	46	11	81	17	12	3	204	50	1143	218
<i>Hyla sp.</i>	1	1	2	2	0	0	0	0	0	0	0	0	3	3
<i>Rana temporaria</i>	345	54	427	68	99	28	6412	290	57	20	466	113	7806	573
<i>Rana cf. R. lessonae</i>	0	0	5	1	0	0	0	0	0	0	0	0	5	1
Anura indet.	10	3	11	7	11	6	6	4	0	0	20	16	58	36
Lacertilia														
Lacertidae indet.	0	0	2	2	0	0	0	0	0	0	0	0	2	2
<i>Anguis fragilis</i>	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Ophidia														
<i>Natrix natrix</i>	13	7	4	4	2	2	7	3	1	1	17	8	44	25
<i>Coronella austriaca</i>	2	1	0	0	0	0	1	1	0	0	0	0	3	2
“ <i>V. berus</i> complex”	146	17	389	14	14	4	47	10	35	4	28	9	659	58
Ophidia indet.	63	18	174	24	14	6	19	8	7	2	53	29	330	87
Total	4411	680	14318	1212	1127	211	8292	607	608	110	12054	2031	40810	4851

turales (Madrid, Spain), of the Laboratoire départemental de Préhistoire du Lazaret (Nice, France) and our personal collections.

Osteological nomenclature basically follows SANCHIZ (1998) and HOLMAN (2003) for anurans and SZYNDLAR (1984) for snakes.

All measurements have been done with a digital Measurescope Kappa MFK II on Wild M8 binocular to the nearest 0.01 mm and through camera lucida scaled drawings.

The most common species in almost all layers is the common parsley frog (*Pelodytes punctatus*) and in lesser amount the common frog (*Rana temporaria*). These species occur mainly in a discontinuous layer called 1am (COCHARD 1998) very dense in remains, and in a few small, relatively monospecific, pocket accumulations. Two pocket accumulations were found in layer 1c (in square A4, respectively 7 and 5 cm in diameter and 3 cm deep) and one in layer 2 (square C6, 12 cm in diameter and 7 cm deep). Other anuran taxa include the common spadefoot (*Pelobates fuscus*), the common European toad (*Bufo bufo*), the natterjack toad (*Bufo calamita*), an indeterminate common treefrog (*Hyla sp.*) and the pool frog (*Rana cf. R. lessonae*). An overwhelming majority of the reptil-

ian remains from Bois Roche belongs to a “*Vipera berus* complex” species. Numerous bones of this snake (659 altogether) were found in all layers. The remaining reptilian species are represented by merely 50 bones; these are a small lacertid lizard (Lacertidae indet.), the slow worm (*Anguis fragilis*), the smooth snake (*Coronella austriaca*) and the grass snake (*Natrix natrix*).

III. SYSTEMATIC PALEONTOLOGY

AMPHIBIANS

Order Anura RAFINESQUE, 1815

Family Pelobatidae BONAPARTE, 1850

Genus *Pelobates* WAGLER, 1830

Pelobates fuscus (LAURENTI, 1768)

(Fig. 2)

M a t e r i a l. The common spadefoot (*P. fuscus*) is represented at Bois Roche by 69 bone elements. Among them, cranial elements, notably maxilla, squamosal and sphenethmoid permit an easy determination of species.

D e s c r i p t i o n o f t h e m a t e r i a l. Maxilla and squamosal show a dermal ossification sculpture. The ornamentation is very discrete and far less dense than in *P. cultripes*. The maxilla is toothed; the palatine process seems well developed and shows a smoothly pronounced orbital margin. The squamosal, in lateral view, possesses a relatively developed lamella alaris, but with a surface more reduced than in *P. cultripes*.

The dorsal sphenethmoid surface is long and has well developed lateral processes and an anteriorly wide anterior process. In anterior view, the sphenethmoid is strongly flattened dorsoventrally and shows high folds in each antrum olfactorium.

Among postcranial elements, the ilium lacks a dorsal ilial crest (crista dorsalis) and a dorsal prominence (tuber superior), and shows, in medial view, a smoothly striated junctura ilioischiatrica like in *P. fuscus* whereas in *P. cultripes* the striation is more important (RAGE 1974; BAILON 1999a).

The sacrum is fused with the urostyle and possesses an anterior cotyle and a transverse process (sacral diapophysis) which even if it is incomplete, seems to be relatively wide antero-posteriorly.

Other elements show the characteristics of the genus *Pelobates*. Among them, we should note the existence of procoelous vertebrae, with a long neural arch carrying a neural spine which is low and long posteriorly. The scapula shows a processus glenoidalis partially hidden by pars acromialis and a humeral articular facet overlying the processus glenoidalis and the posterior edge of the pars acromialis. The humerus possesses a curved and solidly-built shaft, with a crista paraventralis. The spherical condyle is moved outward and the cubital fossa is radially open.

D i s t r i b u t i o n a n d h a b i t a t. The common spadefoot (*P. fuscus*) is an eurasiatic species whose westernmost distribution is constituted by Belgium, Germany and Northern Italy (DUGUET & MELKI 2003). Quite curiously, the common spadefoot is present in a residual and isolated way in the department of Indre (southwestern France, THIRION et al. 2002). This species shows a distinct preference for open areas with no or little vegetation (EGGERT 2002), or low vegetation such as orpines and mosses or Graminae and not very dense heather. Bushy areas are avoided. The decline of this species in the department of Indre could be linked to evolution of fallow land, harmful to its movements (EGGERT in THIRION et al. 2002). In this department, two male individuals have been localized by their calls in 2001, in a humid depression in the vicinity of water, while the air temperature was 9°C with a northward wind (THIRION et al. 2002).

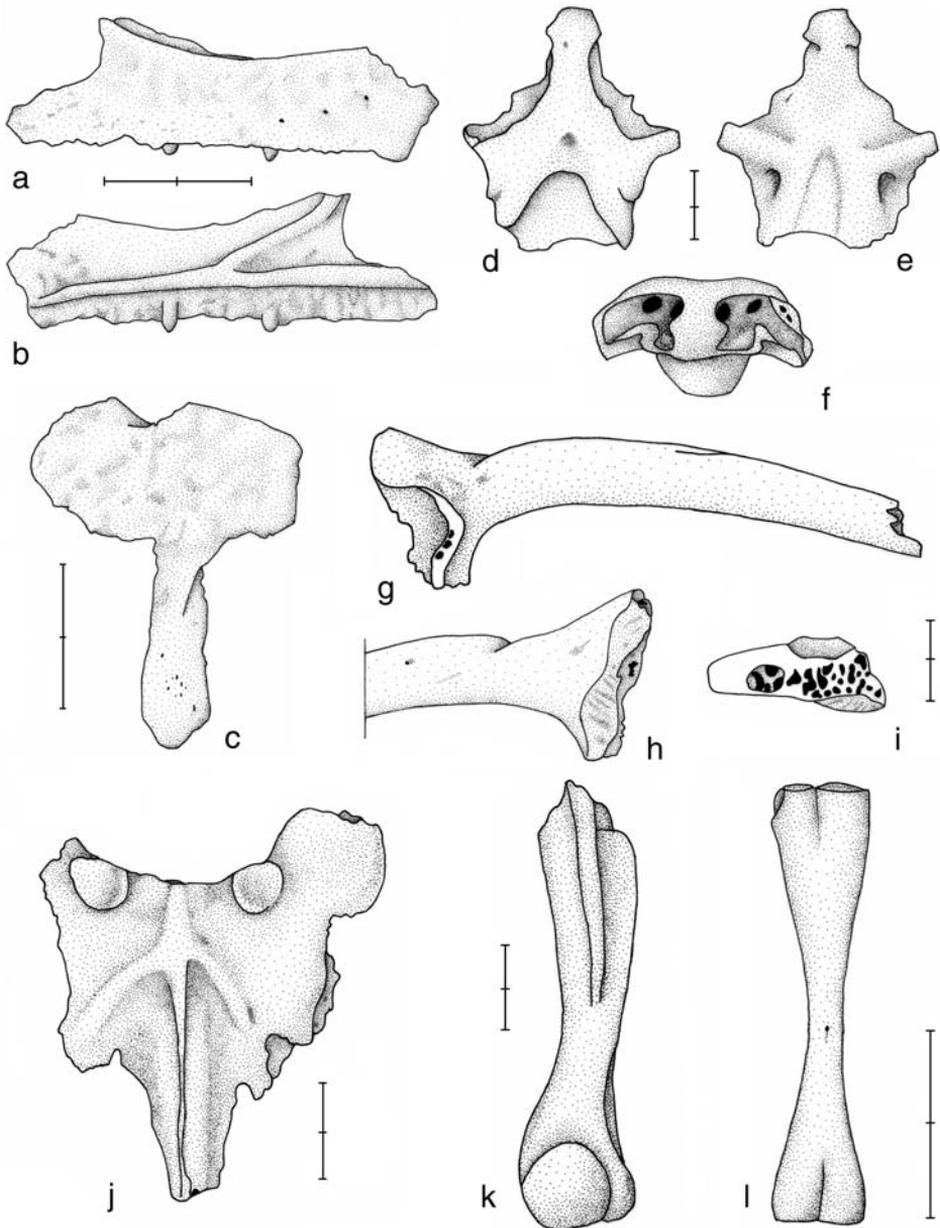


Fig. 2. *Pelobates fuscus* (LAURENTI, 1768). a, b – right maxilla (BR98-B6-2), lateral and medial views; c – right squamosal (BR98-B6-2), lateral view; d, e, f – sphenethmoid (BR97-B4-1am), dorsal, ventral and anterior views; g, h, i – ilium (BR97-B5-1a), lateral, medial and posterior views; j – sacral vertebra and urostyle (BR98-C6-2), dorsal view; k – humerus (BR98-B6-2), ventral view; l – tibiafibula (BR98-C6-2), lateral view. All scales = 2 mm.

Family Pelodytidae BONAPARTE, 1850

Genus *Pelodytes* BONAPARTE, 1838*Pelodytes punctatus* (DAUDIN, 1802)

(Figs 3, 4 and 5, Table II)

M a t e r i a l. The common parsley frog (*P. punctatus*) is by far the best represented species at Bois Roche, with 30813 elements (i.e. 75.6%) corresponding at least to 3803 individuals. All parts of the skeleton are represented, including skull and postcranial bones (Table II).

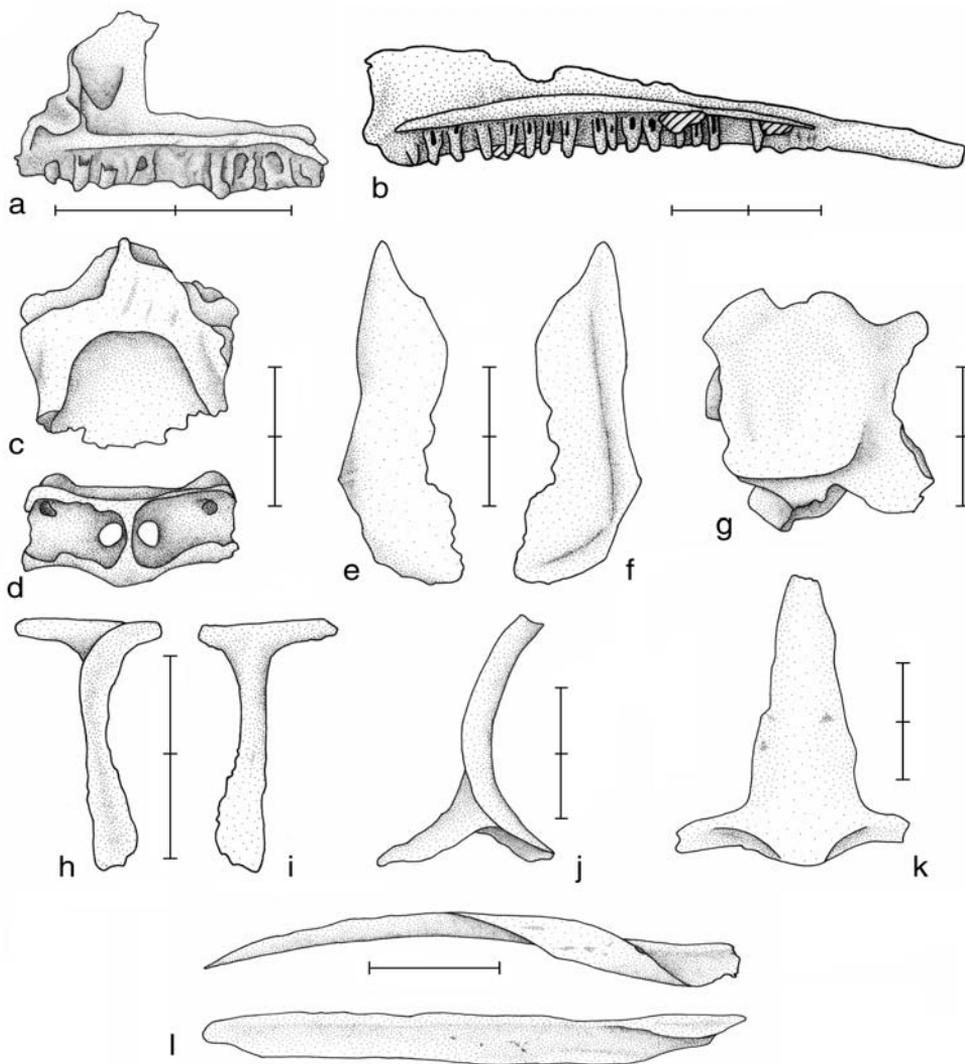


Fig. 3. *Pelodytes punctatus* (DAUDIN, 1802). BR97-B4-1am. a – premaxilla, medial view; b – maxilla, medial view; c, d – sphenethmoid, dorsal and anterior views; e, f – frontoparietal, dorsal and ventral views; g – prootic-exoccipital, dorsal view; h, i – squamosal, lateral and medial views; j – pterygoid, ventral view; k – parasphenoid, ventral view; l, m – mandible, lateral and dorsal views. All scales = 2 mm.

Table II

Distribution of *Pelodytes punctatus* elements by layers

<i>Pelodytes punctatus</i>	1a	1am	1b	1c	1d	2	Total
Premaxilla	2	119		2			123
Maxilla	9	450	3	9		5	476
Vomer		7					7
Sphenethmoid	16	96	6	1	1	68	188
Parasphenoid	1	67				1	69
Pterygoid		85					85
Frontoparietal	1	51				1	53
Squamosal		37	1			2	40
Prootic-exoccipital	18	117	1	1		36	173
Mandible	8	343	10	2		14	377
Atlas	22	65	4	14	2	71	178
Dorsal vertebrae	210	909	52	172	29	1208	2580
Sacrum	66	268	12	34	9	143	532
Urostyle	43	219	10	14	5	55	346
Scapula	14	215	2	3	1	15	250
Sternum	1	115				3	119
Ilium	533	1239	117	231	90	1413	3623
Ischium	1	34		4		11	50
Coracoid	41	321	14	19	1	70	466
Clavicle		72					72
Humerus	617	897	186	349	105	2132	4286
Radioulna	395	884	106	197	47	991	2620
Femur	249	982	92	132	30	1223	2708
Tibiofibula	920	1737	256	402	138	3414	6867
Tibiale-fibulare	340	910	60	128	38	360	1836
Phalange		2687		2			2689
Total	3507	12926	932	1716	496	11236	30813

Description of the material. The abundance and good preservation of remains attributed to this species permit detailed morphological as well as morphometric studies (Fig. 6) as established by SANCHIZ et al. (2002) and SANCHIZ (1984). Measurements have been only made on intact elements, mainly from a sample of materials sorted before water screening (to avoid breakage of delicate bones) collected by D. COCHARD in layer 1am, square B4.

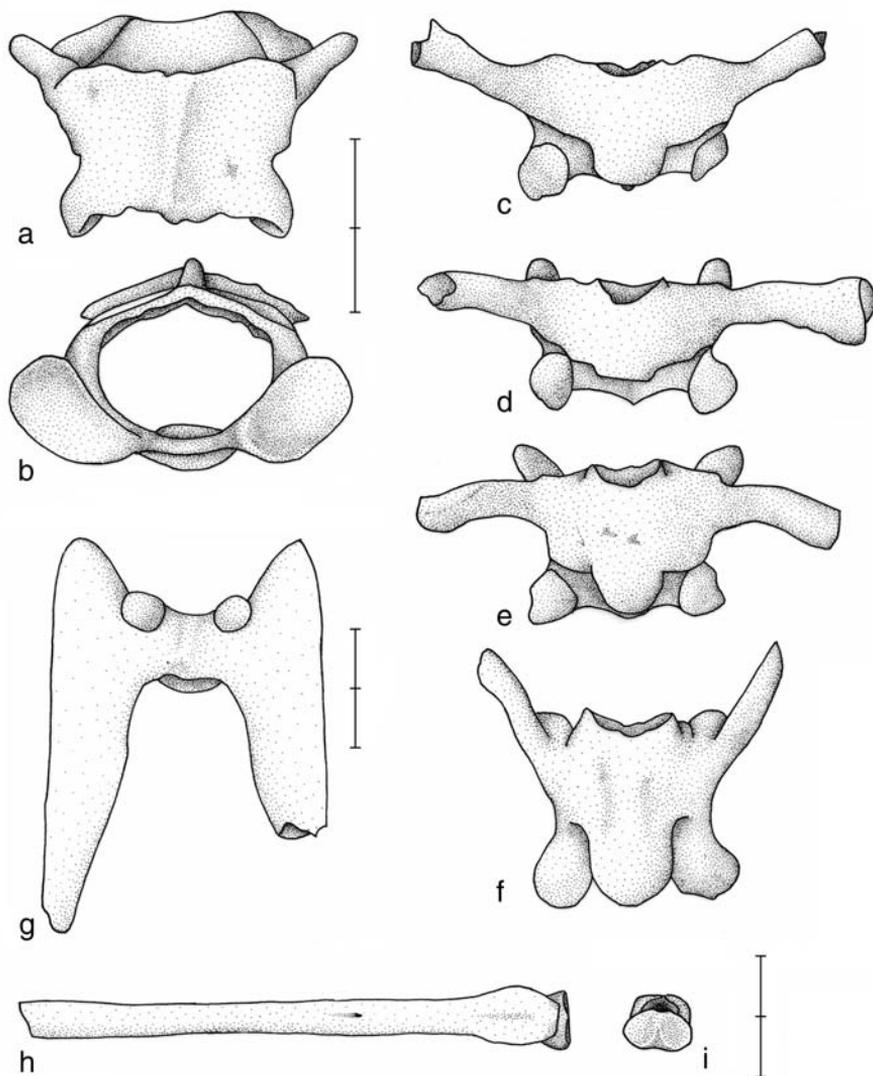


Fig. 4. *Pelodytes punctatus* (DAUDIN, 1802). BR97-B4-1am. a, b – atlas, dorsal and anterior views; c, d, e, f – dorsal vertebrae (V2, V3, V4, V5-8), ventral view; g – sacral vertebra, dorsal view; h, i – urostyle, dorsal and anterior views. All scales = 2 mm.

The premaxilla is toothed. All premaxillae are incomplete, but some of best preserved elements show approximately 14-15 tooth positions. Such a characteristic is concordant with *P. punctatus* and *P. ibericus*, whereas *P. caucasicus*, according to SANCHIZ et al. (2002), possesses 20-21 tooth positions. The interpremaxillary symphysis is weak as in *P. punctatus* and the pars facialis is broken but seems to be quite slim.

The maxilla is toothed, without dermal ossification sculpture on lateral view and possesses a relatively slender and triangular shape. The pars posterior seems relatively long and slim. No fossils show the morphology of pars palatina. The anterior margin is vertical as in *P. punctatus* and *P. iberi-*

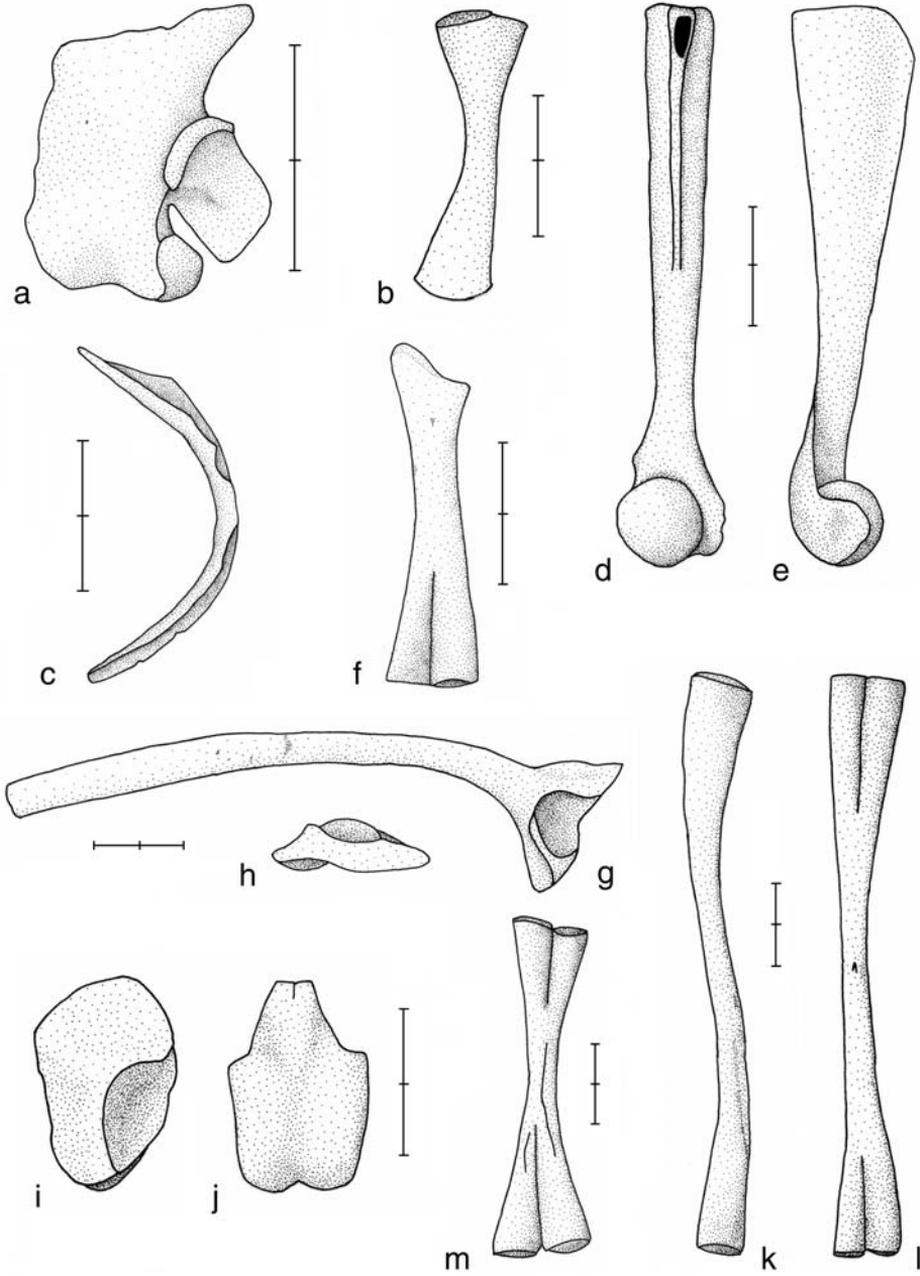


Fig. 5. *Pelodytes punctatus* (DAUDIN, 1802). BR97-B4-1am. a – scapula, dorsal view; b – coracoid, lateral view; c – clavicle, lateral view; d, e – humerus, ventral and medial views; f – radioulna, lateral view; g, h – ilium, lateral and posterior views; i, j – ischium, lateral left and symphyisial views; k – femur, lateral view; l – tibiofibula, lateral view; m – tibiale-fibulare, lateral view. All scales = 2 mm.

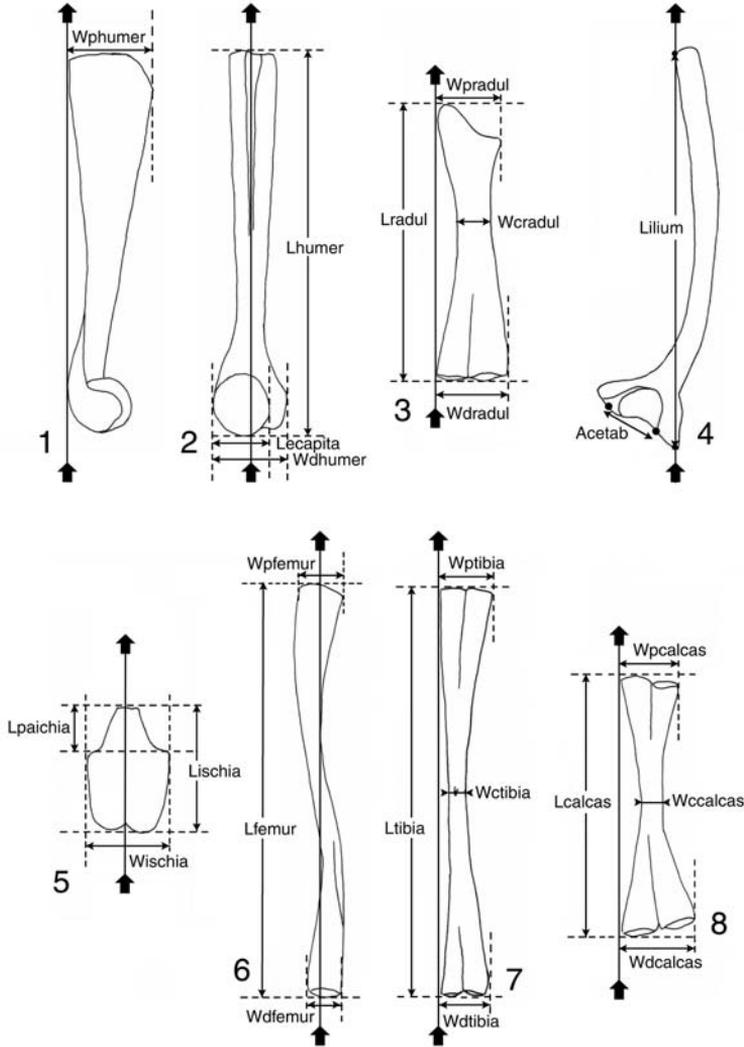


Fig. 6. Measurements of *Pelodytes punctatus* post-cranial bones used in the paper (after SANCHIZ 1984 and SANCHIZ et al. 2002). 1 and 2: Humerus. Lhumer – maximum length, Wphumer – proximal diaphysary width, Lecapita – diameter of the eminentia capitata, Wdhumer – maximum distal width. 3: Radioulna. Lradul – maximum length, Wpradul – proximal width, Wcradul – minimum central width, Wdradul – maximum distal width. 4: Ilium. Lilium – maximum length, Acetab: acetabular length. 5: Ischium. Lischia – maximum height, Wischia – maximum width, Lpaichia – dorsal height. 6: Femur. Lfemur – maximum length, Wpfemur – maximum proximal width, Wdfemur – maximum distal width. 7: Tibiofibula. Ltibia – maximum length, Wptibia – maximum proximal width, Wctibia – minimum central width, Wdtibia – maximum distal width. 8: Tibiale-fibulare. Lcalcas – maximum length, Wpcalcas – maximal proximal width, Wccalcas – minimum central width, Wdcalcas – maximum distal width.

cus, while it is slightly inclined in *P. caucasicus* (SANCHIZ et al. 2002). The most complete maxilla does not permit to count the number of tooth positions but seems to possess less than 30.

The sphenethmoid is elongated, dorsoventrally flattened with well distinct lateral processes. In anterior view it shows a slim and relatively long septum nasi with low folds in each antrum olfactorium. The morphology is concordant with *P. punctatus*, less dorsoventrally flattened than in *P. ibericus* and particularly in *P. caucasicus*.

The frontoparietal is not fused with his homologous. In ventral view, there is only one endocranial impression. The medial margin (margo sagittalis) is irregular and the prootic process is slightly developed. According to SANCHIZ et al. (2002), the degree of ossification of the medial margin permits to differentiate the 3 species of the genus: *P. caucasicus* having a well ossified medial margin whereas in *P. punctatus* and particularly in *P. ibericus* it is poorly ossified. In the Bois Roche fossils, the medial margin is poorly ossified as in *P. punctatus*. The posterolateral margin (margo prootica) is absent in the Bois Roche fossils as well as in *P. punctatus* and *P. ibericus* whereas it is well developed in *P. caucasicus* (SANCHIZ et al. 2002).

The prootic-exoccipital derives from the fusion of the prootic and the exoccipital in adults of the genus *Discoglossus*, *Pelobates*, *Pelodytes* and *Bufo* (BAILON, 1999a). According to SANCHIZ et al. (2002), within the genus *Pelodytes*, *P. caucasicus* differs from other species by a relatively larger dorsolateral sector of the prootic. In the Bois Roche fossil material, this process is slightly shorter than half of his width like in *P. punctatus* and *P. ibericus*.

The squamosal is T-shaped with a posterior end of ramus paroticus typically hook-shaped. According to SANCHIZ et al. (2002), a strong development of the ramus paroticus and ramus zygomaticus permits to differentiate *P. caucasicus* from the other genera. In our fossil material, the poor development of these rami is concordant with *P. ibericus* and *P. punctatus*.

The pterygoid is composed of three rami, among which ramus maxillaris is bent distally and is proportionally two times longer than the ramus interior and the ramus posterior which are of equal length, like in *P. punctatus* and *P. ibericus*.

The parasphenoid is a reversed cross shaped bone showing in genus *Pelodytes* a pars medialis wide at its base (BAILON 1999a). In these fossils, the lateral processes are slightly curved backward and the cultriform process of the pars medialis has the shape of a blade with borders convergent in most of its length like in *P. punctatus* and *P. ibericus* according to SANCHIZ et al. (2002).

The mandible (angulosplenic) shows a coronoid process (processus coronoideus) not very developed and medially curved in lateral view.

The atlas is procoelous, with two anterior occipital cotyles and a small and dorsoventrally flattened posterior condyle. The neural arch is relatively long and the neural spine ends in a slightly pronounced posterior point. The cotyles are well separated without any medial notch; the poor development of the atlantal neurapophysis is characteristic of *P. punctatus* according to SANCHIZ et al. (2002); *P. caucasicus* has cotyles tangent in the midline and *P. ibericus* has a neural spine that does not end in a point.

The vertebrae are nonimbricating with a reduced neural spine. According to BAILON (1999a), the transverse processes are directed anteriorly in V_2 , ventrally in V_3 and posteriorly in V_4 . The posterior vertebrae (V_{5-8}) show transverse processes at variable angle but always lesser than 90° .

The sacral vertebrae have very long diapophyses and the post-central medial edges are not straight as in *P. caucasicus* (SANCHIZ et al. 2002) but bell-shaped and more acute in their ends, like in *P. punctatus* and *P. ibericus*.

The scapula is short and strongly-built. According to SANCHIZ et al. (2002), the differences between *P. punctatus* and *P. ibericus* are subtle. In the Bois Roche fossils, the crista anterior is moderately developed with a straight anterior margin like in *P. punctatus* whereas it is well developed with a convex anterior margin in *P. ibericus*.

The coracoid shows a medial margin only slightly expanded; the anterior curvature of the bone is quite open as in *P. punctatus* and *P. ibericus* (SANCHIZ et al. 2002).

The clavicle is slender and moderately curved as in *P. punctatus*, whereas the curvature is more pronounced in *P. caucasicus* and far less so in *P. ibericus* (SANCHIZ et al. 2002).

The humerus presents a slender and straight shaft in ventral view. The condyle is slightly moved outward in relation to the diaphysary main axis. Biometrical data (Table III) suggest that the Bois Roche fossils do not differ significantly from *P. punctatus* for measurements but that they do for indexes. The stronger ventral crest (Wphumer) is quite similar to *P. caucasicus*. If, as suggested by SANCHIZ et al. (2002), the evolution within the genus shows a certain tendency towards slender humeral morphologies, the Bois Roche fossils show a unique pattern with proximal width (Iphumer) more robust than in all others species and distal width (Idhumer) and eminentia capitata width (Iechumer) clearly more slender.

The radioulna is a relatively short bone. According to SANCHIZ et al. (2002), *P. punctatus* and *P. ibericus* are similarly robust concerning this element (respectively Icradul mean: 12.66 and 12.04), whereas *P. caucasicus* which seems to be the most robust (Icradul > 13.1%). Fossils robustness show means smaller than data given by SANCHIZ et al. (2002) for *P. punctatus* and *P. ibericus* but nevertheless our fossils are included in the interval (max-min, Table III).

The ilium lacks a dorsal ilial crest (crista dorsalis); the dorsal prominence (tuber superior) if present is reduced. The ilial shaft (pars cylindrifomis) is generally well curved. According to SANCHIZ et al. (2002), the acetabulum is relatively better developed in *P. caucasicus* and *P. ibericus* (Iailium > 12.5 %) than in *P. punctatus* (Iailium < 12.5 %). The Bois Roche fossils measurements, for this index, are closer to *P. punctatus*, even if they show strongly smaller values (Table III).

The ischium, according to SANCHIZ et al. (2002), is similar among species, differing mostly in the relative length of the dorsal region that corresponds to the pars ascendens in the ilium. Concerning Ipaischia index, our fossils are closer to *P. caucasicus* whose pars ascendens is relatively short (Table III).

According to SANCHIZ et al. (2002), the femur in *P. punctatus* is significantly less robust than *P. ibericus* and *P. caucasicus* for both proximal (Ipfemur) and distal (Idfemur) indexes. The Bois Roche fossils are concordant with *P. punctatus* even if Ipfemur show smaller values (Table III).

For the tibiofibula, according to SANCHIZ et al. (2002), *P. caucasicus* is more robust than *P. ibericus* and *P. punctatus* in the central region (Wctibia), similar to *P. punctatus* in the proximal index (Wptibia), and similar to *P. ibericus* in the distal one (Wdtibia). The Bois Roche fossils do not show significant difference with *P. punctatus* for measurements; however their index values are always smaller than those of the three other species (Table III).

According to SANCHIZ et al. (2002), the tibiale-fibulare is slender in *P. punctatus* and more robust in *P. caucasicus* and *P. ibericus*. The Bois Roche indexes are smaller than those given by SANCHIZ et al. (2002) for the genus three species and seem closer to the more slender species *P. punctatus* (Table III).

In conclusion, measurements and indexes of the Bois Roche fossils are close to the values of male *P. punctatus* given by SANCHIZ et al. (2002), but generally slightly smaller. On other hand, their morphology is well concordant with *P. punctatus* even if some difference can be drawn such as the stronger ventral crest development in the humerus (Iphumer). As underlined by COCHARD (1998) in his taphonomic study, common parsley frogs fossils at Bois Roche are characterized by a strong proportion of juveniles and females (>65%): this may certainly explain such smaller index values in the Bois Roche fossils.

D i s t r i b u t i o n a n d h a b i t a t. The common parsley frog (*P. punctatus*) is a Southern species, whose modern distribution range from central Spain to Liguria to northeastern France. In the region of Poitou-Charentes, they live in humid and relatively opened areas: permanent or temporary ponds, moist meadows liable to flooding, streams and brackish swamps (THIRION et al. 2002). In alluvial context, his presence seems to be linked with the vicinity of forested areas constituting a favourable environment for wintering (DUGUET & MELKI 2003).

Table III

Statistics of *Pelodytes punctatus* post-cranial bones measurements. Abbreviations: N – number of elements, SD – standard deviation, max – maximum, min – minimum. Comparison with modern male specimens data (according to SANCHIZ et al. 2002): Pca – *Pelodytes caucasicus*, Ppu – *P. punctatus*, Pib – *P. ibericus*. P – probability after Student t test (N = P > 0.05; S = 0.05 > P > 0.01; HS = P < 0.01). Measurements definition as in Fig. 6. Indexes definition (results expressed in percentages): Iphumer = Wphumer/Lhumer; Iehumer = Lecapita/Lhumer; Idhumer = Wdhumer/Lhumer; Ipradul = Wpradul/Lradul; Icradul = Wcradul/Lradul; Idradul = Wdradul/Lradul; Iwischia = Wischia/Lischia; Ipischia = Lpaischia/Lischia; Ipfemur = Wpfemur/Lfemur; Idfemur = Wdfemur/Lfemur; Iptibia = Wptibia/Ltibia; Ictibia = Wctibia/Ltibia; Idtibia = Wdtibia/Ltibia; Ipcalcas = Wpcalcas/Lcalcas; Iccalcas = Wccalcas/Lcalcas; Idcalcas = Wdcalcas/Lcalcas. The Bois-Roche humerus sample is constituted by 8 elements of male and 55 elements of female and/or juvenile

						P		
	N	mean	SD	max	min	Pca	Ppu	Pib
Humerus								
Lhumer	63	8.62	0.970	11.44	6.61	HS	N	HS
Wphumer	63	1.91	0.214	2.46	1.38	N	HS	HS
Lecapita	63	1.32	0.149	1.75	1.07	HS	N	HS
Wdhumer	63	1.70	0.202	2.18	1.41	HS	N	N
Iphumer	63	18.13	0.709	19.58	14.84	HS	HS	HS
Iehumer	63	13.29	0.951	17.50	11.14	HS	HS	HS
Idhumer	63	16.50	0.993	20.52	15.07	HS	HS	HS
Radioulna								
Lradul	53	6.21	0.689	7.59	4.48	HS	HS	HS
Wpradul	53	1.41	0.147	1.76	1.09	HS	S	HS
Wcradul	53	0.79	0.107	1.09	0.56	HS	S	HS
Wdradul	53	1.72	0.191	2.12	1.17	HS	HS	HS
Ipradul	53	18.54	0.625	19.86	17.22	HS	HS	HS
Icradul	53	11.33	0.643	13.35	10.07	HS	HS	HS
Idradul	53	21.73	0.902	25.33	18.96	HS	HS	HS
Ilium								
Lilium	26	13.19	1.096	15.0	11.0	HS	HS	HS
Acetab	26	1.51	0.217	1.97	1.12	HS	S	N
Iailium	26	10.29	1.175	12.34	8.02	HS	HS	HS
Ischium								
Lischia	6	2.94	0.307	3.4	2.49	HS	HS	HS
Wischia	6	1.88	0.273	2.31	1.60	HS	HS	HS

Table III cont.

						P		
	N	mean	SD	max	min	Pca	Ppu	Pib
Lpaischia	6	1.07	0.065	1.15	0.99	HS	HS	HS
Iwischia	6	61.11	1.717	64.37	59.54	HS	HS	HS
Ipaischia	6	26.80	1.959	29.26	24.78	HS	HS	HS
Femur								
Lfemur	43	14.26	1.494	17.5	11.0	HS	N	HS
Wpfemur	43	1.17	0.100	1.47	0.94	HS	N	HS
Wdfemur	43	1.63	0.168	2.11	1.07	HS	HS	HS
Ipfemur	43	7.61	0.452	8.68	7.04	HS	HS	HS
Idfemur	43	10.28	0.711	11.79	8.19	HS	N	HS
Tibiofibula								
Ltibia	17	15.09	0.852	16.5	13.5	HS	N	HS
Wptibia	17	1.81	0.106	2.02	1.62	HS	N	HS
Wctibia	17	0.70	0.044	0.82	0.62	HS	N	HS
Wdtibia	17	1.91	0.104	2.10	1.68	HS	S	HS
Iptibia	17	10.71	0.447	11.76	10.06	HS	HS	HS
Ictibia	17	4.16	0.182	4.56	3.91	HS	HS	HS
Idtibia	17	11.25	0.412	11.87	10.66	HS	HS	HS
Tibiale-Fibulare								
Lcalcas	26	8.33	0.848	9.85	6.31	HS	HS	HS
Wpcalcas	26	1.92	0.220	2.31	1.41	HS	N	HS
Wccalcas	26	0.73	0.072	0.90	0.60	HS	N	HS
Wdcalcas	26	2.47	0.303	2.98	1.78	HS	S	S
Ipcalcas	26	18.73	0.729	20.56	17.48	HS	HS	HS

Family Bufonidae LAURENTI, 1768

Genus *Bufo* LAURENTI, 1768*Bufo bufo* (LINNAEUS, 1758)*Bufo calamita* (LAURENTI, 1768)

(Fig.7 a-i)

M a t e r i a l. Relatively few remains have been attributed to Bufonidae: 1076 bones to *B. calamita* and only 12 to *B. bufo*. Species determination is based on SANCHIZ (1977), BAILON & HOSSINI (1990), BAILON (1991 and 1999a) and RATNIKOV (2001) works. The few remains attrib-

uted to *B. bufo* can be distinguished from *B. calamita* by their general morphology and often by their bigger size.

D e s c r i p t i o n o f t h e m a t e r i a l. The ilium lacks a dorsal crest, the dorsal prominence is low and with a round and unilobated dorsal edge in *B. bufo*, whereas in *B. calamita* it is pointed. Moreover, in *B. calamita*, the ilial shaft (pars cylindriformis) generally shows a latero-ventral outgrowth (“*calamita* ridge”) missing in *B. bufo*.

The humerus possesses a humeral shaft which is straighter in *B. bufo* than in *B. calamita*; the condyle is moved outward in the two species and the condyle-epicondyles whole is clearly more developed in *B. calamita* than in *B. bufo*.

The scapula is higher than wide and carries a strong processus glenoidalis, separate and well visible in dorsal view. In *B. calamita*, contrary to *B. bufo*, a small supraglenoidalis fossa is present.

Finally the femur is relatively long, strongly-built and sigmoidal in shape, with a crista femoris. In *B. bufo*, the crista femoris forks and makes a triangular surface whereas in *B. calamita*, it does not and shows a cutting edge.

D i s t r i b u t i o n a n d h a b i t a t. The common European toad (*B. bufo*) has a large Eurasian distribution; although it shows a certain preference for fresh wooded areas, it has great ecological plasticity and may occupy all type of biotopes. The natterjack toad (*B. calamita*) occurs in all of France. Its terrestrial habitat is constituted by open and sparse vegetation, alternating with bare ground or loose soil areas favourable to get a lot of sunshine (DUGUET & MELKI 2003). It is one of the modern amphibians most adapted to xeric conditions.

Family Hylidae RAFINESQUE, 1814

Genus *Hyla* LAURENTI, 1768

Hyla sp.

(Fig. 7 j, k)

M a t e r i a l. An indeterminate treefrog is represented by 3 scapulas.

D e s c r i p t i o n o f t h e m a t e r i a l. These scapulas are long, slender, and have a processus glenoidalis well separate from the bone. The pars acromialis and the processus glenoidalis are narrow. This element does not permit any specific determination and consequently is adscribed only at the genus level.

Family Ranidae RAFINESQUE, 1814

Genus *Rana* LINNAEUS, 1758

“Brown Frogs Group”

Rana temporaria LINNAEUS, 1758

(Fig. 8, Table IV)

M a t e r i a l. Numerous remains, corresponding to all parts of the skeleton, are attributed to the “Brown Frogs Group”. Within this group, species determination is generally based on the frontoparietal and ilium morphology (BÖHME 1977; ESTEBAN & SANCHIZ 1985 and 1991; BAILON 1999a; GLEED-OWEN 2000; BLAIN 2005).

D e s c r i p t i o n o f t h e m a t e r i a l. The frontoparietal, in the genus *Rana*, is not fused with his homologous and, in ventral view, the endocranial impression is double (BAILON 1999a; BÖHME 1977). In the Bois Roche fossils, the frontal area is relatively wide, like in the “Brown Frogs Group” and the parietal protuberance is moved outwards. The processus lateralis is well developed and, in dorsal view, a sulcus is present between the processus paraoccipitalis and the processus lateralis. The very poor crest development is probably due to the small size of the

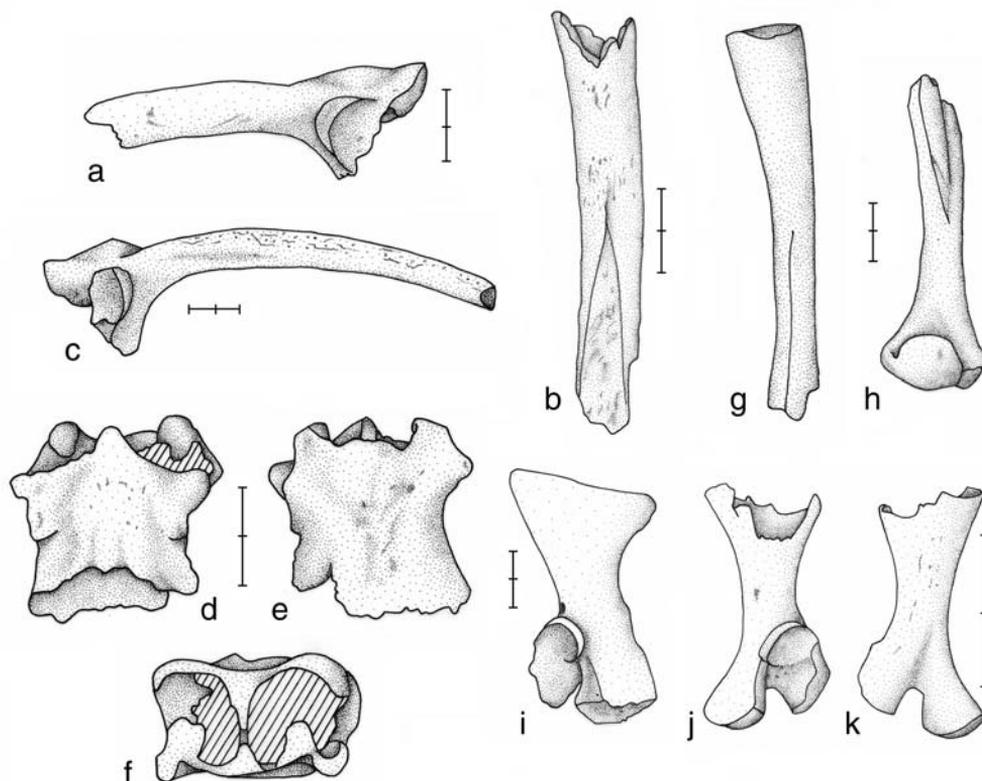


Fig. 7. *Bufo bufo* (LINNAEUS, 1758). a – ilium (BR97-B4-1a), lateral view; b – femur (BR97-B5-1a), medial view. *Bufo calamita* (LAURENTI, 1768). c – ilium (BR98-C6-2), lateral view; d, e, f – sphenethmoid (BR98-B6-2), dorsal, ventral and anterior views; h – humerus (BR98-A1/Z1-1am), ventral view; i – scapula (BR98-B6-2), dorsal view, femur (BR97-B4-1am), medial view. *Hyla* sp. j, k – scapula (BR98-Z3-1a), dorsal and ventral views. All scales = 2 mm.

bones (a juvenile characteristic). The general morphology is concordant with *R. temporaria* and permits to exclude *R. arvalis* in which the processus lateralis is poorly developed and the parietal protuberance is situated more medially than in *R. dalmatina*, *R. temporaria* (BAILON 1999a) and *R. dalmatina* which do not show a sulcus between the processus paraoccipitalis and the processus lateralis (BAILON 1999a).

The ilium, in the genus *Rana*, shows a dorsal ilial crest (crista dorsalis) on the ilial shaft (pars cylindriformis), a relatively short pars ascendens and the junctura ilioischiatia has a smooth surface (BAILON 1999a). Within the genus, the “Brown Frogs Group” presents a lower dorsal ilial crest and, in distal view, the junctura ilioischiatia surface is thicker (d/t, sensu GLEED-OWEN 2000; Fig. 9.1) in the “Water Frogs Group” ($2.12 < d/t < 2.88$) than in the “Brown Frogs Group” ($2.75 < d/t < 4.00$). At Bois Roche, the best preserved ilia show values between 2.50 and 4.00.

Within the “Brown Frogs Group”, ilia in *R. temporaria* have a lower dorsal ilial crest than in *R. dalmatina*, *R. arvalis* and *R. iberica* (BÖHME 1977; BAILON 1999a; ESTEBAN & SANCHIZ 1985). The morphology of the fossil ilia is very variable and many show characteristics exclusively attributed by some authors to *R. dalmatina* and *R. arvalis*: that is to say narrower and more posteriorly angled pars descendens (characteristic of *R. arvalis* according to GLEED-OWEN 2000), no inflexion of

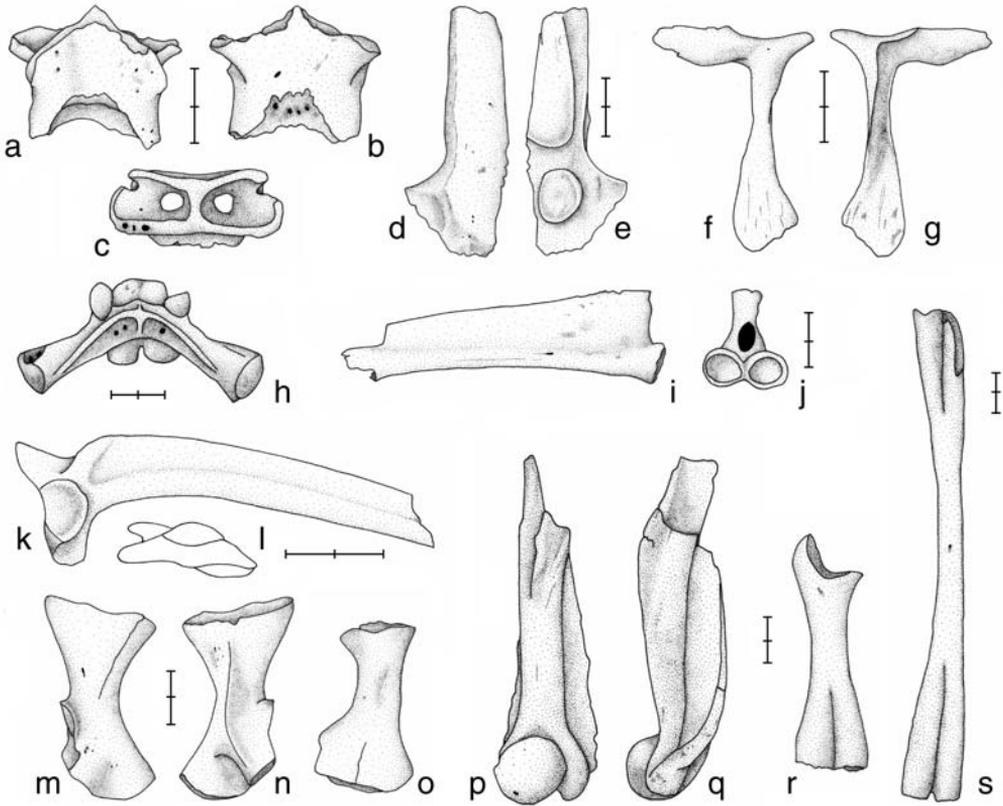


Fig. 8. *Rana temporaria* LINNAEUS, 1758. a, b, c – sphenethmoid (BR98-A4-1c-WWBQL), dorsal, ventral and anterior views; d, e – frontoparietal (BR98-A4-1c), dorsal and ventral views; f, g – squamosal (BR98-A4-1c-WWBQL), lateral and medial views; h – sacral vertebra (BR98-A4-1c-WWBQL), dorsal view; i, j – urostyle (BR98-A4-1c-WWBQL), lateral and anterior views; k, l – ilium (BR97-B4-1am), laterals and posterior views; m, n – scapula (BR98-A4-1c-WWBQL), dorsal and ventral views; o – coracoid (BR98-A4-1c-WWBQL), lateral view; p, q – humerus (BR98-A4-1c-WWBQL), ventral and medial view; r – radioulna (BR98-A4-1c-WWBQL), lateral view; s – tibiofibula (BR98-A4-1c, n°393), lateral view. All scales = 2 mm.

the dorsal ilial crest behind the dorsal prominence (characteristics of *R. dalmatina* according to ESTEBAN & SANCHIZ 1985 and GLEED-OWEN 2000). In all cases, the highest point of the dorsal ilial crest is situated at the dorsal prominence, which, according to BAILON (1999a), may not be present in *R. dalmatina*.

A few “Brown Frogs Group” remains have been assigned by COCHARD (1998) to *R. dalmatina*. Nevertheless, using ESTEBAN & SANCHIZ (1985; Fig. 9.2) biometrical methods, the P values of the Bois Roche ilia are small ($42.8 < P < 59.4$; P mean = 51.9 ± 4.15 ; n = 40) and occur (Fig. 9) some in the *R. temporaria* dispersion polygon and others either in the *R. iberica* polygon or out of any polygon (small-sized specimens). *R. dalmatina* and *R. arvalis* have P values higher than 58 (ESTEBAN & SANCHIZ 1985, 1991 and personal observations). No Iberian frogs (*R. iberica*) occur at Bois Roche.

The morphology and robustness of other elements are concordant with *R. temporaria*, even if most fossil remains seem to derive from small-sized specimens, probably juveniles.

Table IV

Distribution of *Rana temporaria* elements by layers

<i>Rana temporaria</i>	1a	1am	1b	1c	1d	2	Total
Premaxilla				100	1		101
Maxilla	4	2	1	256	2	1	266
Sphenethmoid	3			11		4	18
Parasphenoid				16			16
Pterygoid				78			78
Frontoparietal				106			106
Squamosal	11	11	1	97	1	3	124
Prootic-exoccipital				73			73
Mandible	5	4	2	204	1	3	219
Atlas	5	2	1	40	1		49
Dorsal vertebrae	76	105	14	700	9	127	1031
Sacrum	14	24	1	106	6	12	163
Urostyle	14	25	7	136	2	24	208
Scapula	14	35	6	214	1	9	279
Sternum	2		1	36			39
Ilium	39	63	7	299	4	40	452
Ischium		4		49			53
Coracoid	11	18	4	169	1	17	220
Clavicle				80		3	83
Humerus	21	24	10	347	11	62	475
Radioulna	32	17	8	319	7	41	424
Femur	15	6	12	256	3	19	311
Tibiofibula	49	37	18	397	2	78	581
Tibiale-fibulare	3	14		147		16	180
Phalange	27	36	6	2176	5	7	2257
Total	345	427	99	6412	57	466	7806

H a b i t a t a n d d i s t r i b u t i o n. The common frog (*R. temporaria*) is a cold-resistant species with a large European distribution. In southern France, the common frog is rare or absent in the plains whereas it is well represented in mountain areas appearing as a “*boreal relic*” (THIRION et al. 2002). It prefers terrestrial habitat most of the year, except during the reproduction period. In the region of Poitou-Charentes, it occurs in humid meadows, peat bogs and broad-leaved forests.

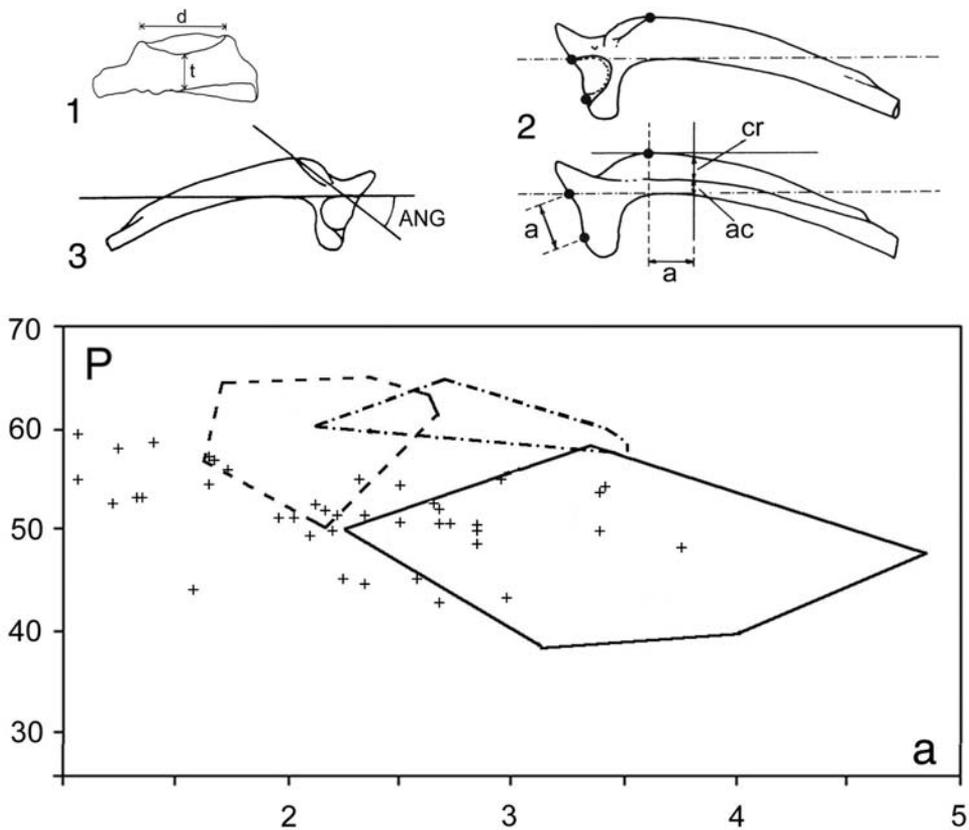


Fig. 9. Measurements of Ranidae ilia used in this paper. 1 – after GLEED-OWEN 2000; 2 – after ESTEBAN & SANCHIZ 1985; 3 – after SANCHIZ et al. 1993. Comparisons of the Bois Roche “Brown Frog Group” ilium with modern data (after ESTEBAN & SANCHIZ 1985): *R. temporaria* (continuous line; n = 16), *R. dalmatina* (dotted line and points; n = 7) and *R. iberica* (dotted line; n = 24). d – acetabular diameter in posterior view; t – junctura ilioischiatrica width; a – acetabular diameter in lateral view; ac – ilial shaft height; cr – dorsal ilial crest height; ANG – angle between tuber superior orientation and ilium main axis.

“Water Frogs Group”

Rana cf. *R. lessonae* CAMERANO, 1882

(Fig. 10)

M a t e r i a l. The “Water Frogs Group” is represented at Bois Roche by 5 elements only.

D e s c r i p t i o n o f t h e m a t e r i a l. The scapula is clearly higher than wide and the processus glenoidalis is partially hidden by the pars acromialis (BAILON 1999a). Fossil scapulas attributed to the “Water Frogs Group” are distinguished, in ventral view, by a short inner crest on the processus glenoidalis whereas in “Brown Frogs Group” it is relatively long.

The coracoid has a thick pars epicoracoidalis and a flattened and stretched pars glenoidalis. As in the “Water Frogs Group”, the central part is relatively slender.

A small-sized fragmentary ilium is present. As in the “Water Frog Group”, the junctura ilioischiatrica is thick ($d/t = 2.10$); the angle between the dorsal prominence and the iliac main axis (ANG, sensu SANCHIZ et al. 1993; Fig. 9.3) measures 44° and seems to correspond with *R. lessonae* who has high values.

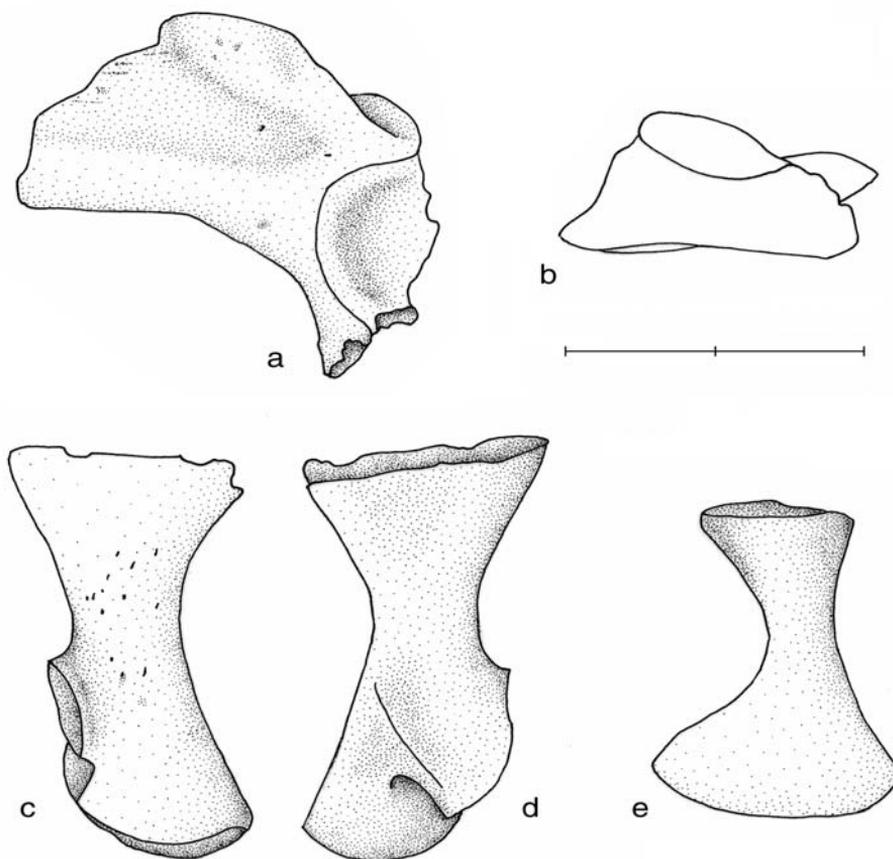


Fig. 10. *Rana* cf. *R. lessonae* CAMERANO, 1882. a, b – ilium (BR97-B4-1am), lateral and posterior views; c, d – scapula (BR98-A1/Z1-1am), dorsal and ventral views; e – coracoid (BR98-A1/Z1-1am), lateral view. Scale = 2 mm.

Habitat and distribution. *R. lessonae* is the European smallest green frog. It is a Northern Eurasian species ranging from France to the Volga basin in Russia (DUGUET & MELKI 2003). In the region of Poitou-Charentes, *R. lessonae* is scarce (THIRION et al. 2002). The species inhabits small ponds and natural marshes with aquatic vegetation. Its terrestrial habitats are represented by meadows and broad-leaved forests (DUGUET & MELKI 2003).

SQUAMATA

Lacertilia OWEN, 1842

Family Lacertidae OPPEL, 1811

Lacertidae indet.

(Fig. 11 a-c)

M a t e r i a l. Small lacertids are represented in layer 1am by only two small-sized trunk vertebrae.

D e s c r i p t i o n o f t h e m a t e r i a l. The vertebrae are procoelous, elongated, with a convex centrum having a ventral face haemal keel more or less developed. The neural

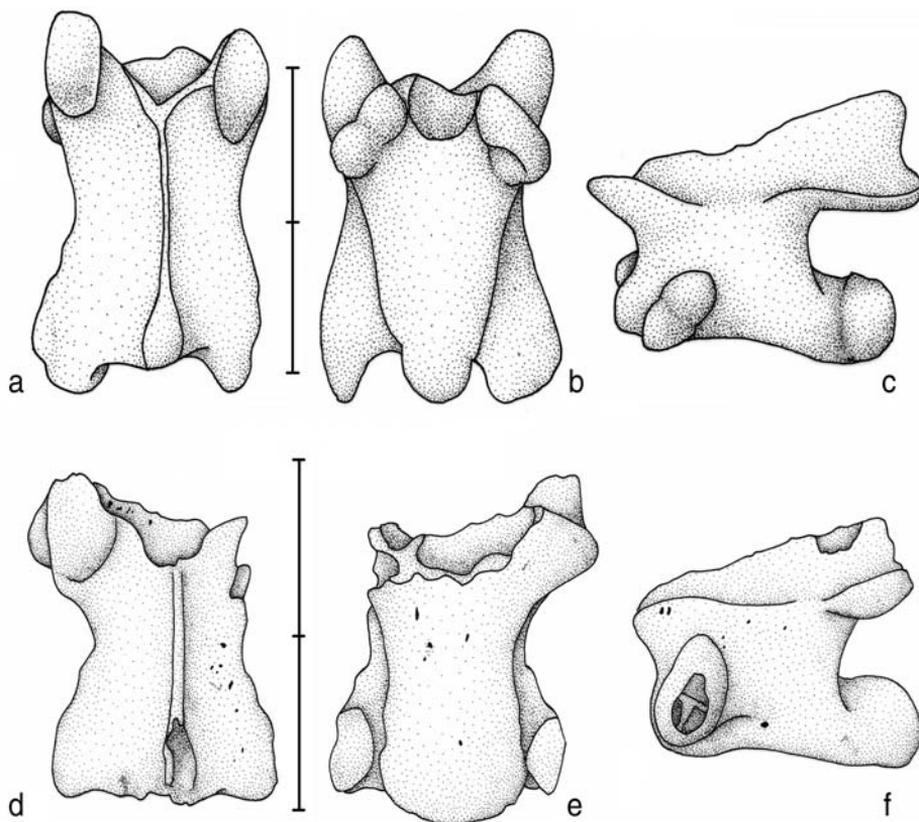


Fig. 11. Lacertidae indet. a, b, c – trunk vertebra (BR97-B4-1a/1am), dorsal, ventral and lateral views. *Anguis fragilis* LINNAEUS, 1758. d, e, f – trunk vertebra (BR97-B4-1a), dorsal, ventral and lateral views. All scales = 2 mm.

spine is long, thin, relatively developed in his posterior part and the postzygapophysis does not project over the posterior margin. The condyle and cotyle are small and slightly flattened dorsoventrally. Today in the region of Poitou-Charentes (THIRION et al. 2002), two small lacertids are present: a viviparous lizard (*Zootoca vivipara*) and the wall lizard (*Podarcis muralis*). In the absence of better material, no determination can be made and the vertebrae are attributed to a small-sized lacertid.

Family Anguidae OPPEL, 1811

Genus *Anguis* LINNAEUS, 1758

Anguis fragilis LINNAEUS, 1758

(Fig. 11 d-f)

M a t e r i a l. The slow worm (*Anguis fragilis*) is represented in Bois Roche by a single trunk vertebra.

D e s c r i p t i o n o f t h e m a t e r i a l. This small-sized vertebra (centrum length = 1.36 mm) is procoelous, dorsoventrally flattened and moderately elongated. In dorsal view the vertebra is narrower between pre- and postzygapophysis. In ventral view, the centrum is clearly longer than wide, with a flat ventral surface and the lateral margins are well marked and parallel posteriorly for more than half of their length. The subcentral foramina are not visible. In lateral view, the neural spine is long and slightly higher posteriorly; the posterior part of the neural spine

does not extend as far back as the margin of the postzygapophysis. The condyle and cotyle are dorsoventrally flattened. All these characteristics, as well as the absence of haemapophysis and the fusion of the apophysis with the centrum, permit an attribution to *A. fragilis*.

Habitat and distribution. The slow worm (*Anguis fragilis*) is a Eurasian species with a wide European distribution. It has crepuscular and nocturnal habits, and prefers strong environmental humidity.

Serpentes LINNAEUS, 1758

Family Colubridae OPPEL, 1811

« Natricinae » type trunk vertebrae, with hypapophysis

Genus *Natrix* LAURENTI, 1768

Natrix natrix (LINNAEUS, 1758)

(Fig. 12)

Material. The grass snake (*N. natrix*) is represented at Bois Roche by 44 remains.

Description of the material. The trunk vertebrae have a sigmoid-shaped and distally obtuse hypapophysis. The neural arch is strongly convex in posterior view. The neural spine is high and the condyle and cotyle are small and circular. In lateral view, the parapophysis has strongly-built and anteriorly obtuse parapophyseal processes. In ventral view, the centrum is flat with well marked lateral margins. All these characteristics according to SZYNDLAR (1984) permit an attribution to *N. natrix*.

Habitat and distribution. The grass snake (*Natrix natrix*) is a Northern European species, occurring at present in all of the Poitou-Charentes region (THIRION et al. 2002). It lives in cool and humid environments, with a preference for edges of marshes, lakes and ponds. Its minimum temperature tolerance is 8-10°C (BRUNO & MAUGERI 1992).

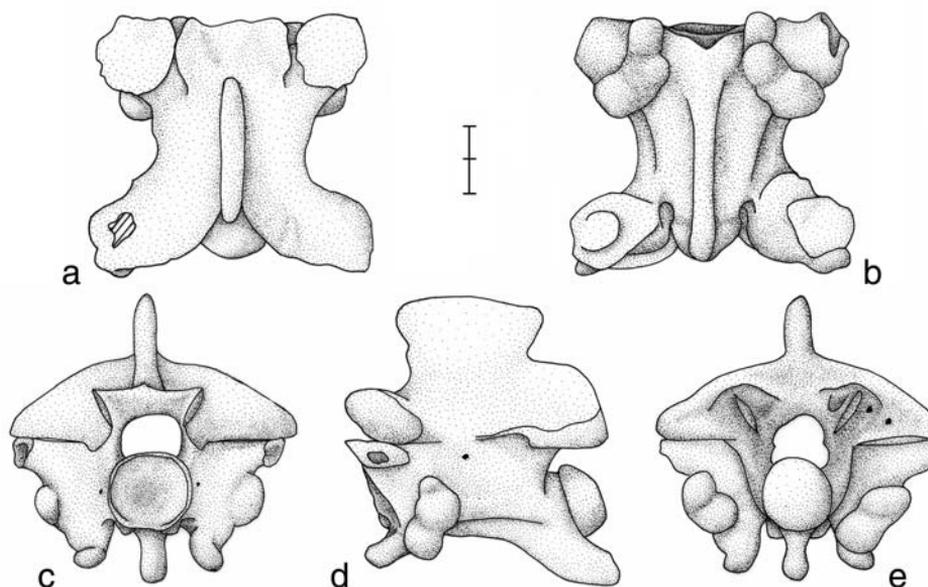


Fig. 12. *Natrix natrix* (LINNAEUS, 1758). a, b, c, d, e – trunk vertebra (BR98-B4-1c), dorsal, ventral, anterior, left-lateral and posterior views. Scale = 2 mm.

« Colubrinae » type trunk vertebrae, without hypapophyses

Genus *Coronella* LAURENTI, 1768*Coronella austriaca* LAURENTI, 1768

(Fig. 13)

M a t e r i a l. The smooth snake is represented in Bois Roche by only 3 trunk vertebrae.

D e s c r i p t i o n o f t h e m a t e r i a l. Trunk vertebrae attributed to *C. austriaca* are small-sized and have a very dorsoventrally flattened neural arch. Within the genus *Coronella*, trunk vertebrae of *C. austriaca* differ from *C. girondica* essentially by wider prezygapophyseal processes and para-diapophysis morphology: parapophysis being shorter in *C. girondica* than in *C. austriaca* (SZYNDLAR 1984; BAILON 1991).

H a b i t a t a n d d i s t r i b u t i o n. *Coronella austriaca* is a Southern European species. In the region of Poitou-Charentes, it occurs rarely (THIRION et al. 2002). In the south-western part of its distribution area, this species lives preferentially in high-lying areas and in cooler and moister environment than *Coronella girondica*. Its minimum temperature tolerance is 10°C (BRUNO & MAUGERI 1992).

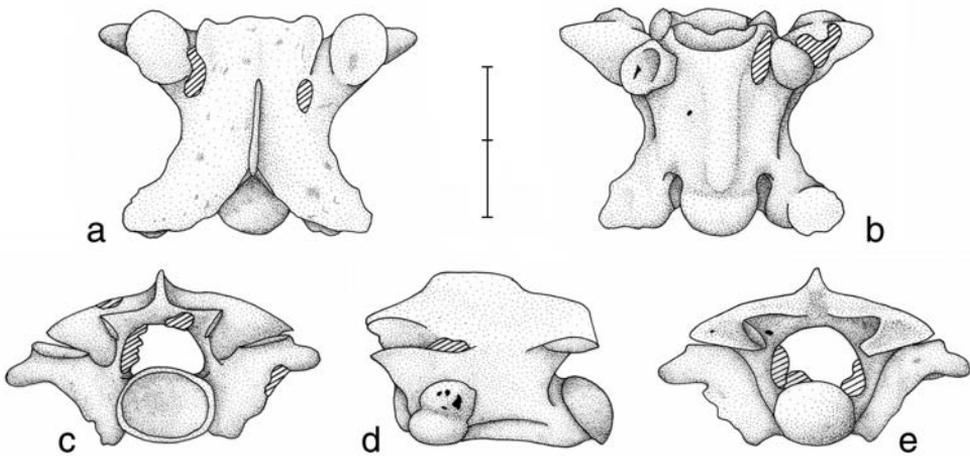


Fig. 13. *Coronella austriaca* LAURENTI, 1768. a, b, c, d, e – trunk vertebra (BR98-Z2-1c), dorsal, ventral, anterior, left-lateral and posterior views. Scale = 2 mm.

Family Viperidae OPPEL, 1811

Genus *Vipera* LAURENTI, 1768“*Vipera berus* complex”

(Fig. 14)

M a t e r i a l. The “*V. berus* complex” is represented in Bois Roche by 659 remains, mainly trunk vertebrae.

D e s c r i p t i o n o f t h e m a t e r i a l. Trunk vertebrae show the typical characteristics of the family: presence of straight and distally pointed hypapophysis, neural arch dorsoventrally flattened, centrum convex in transversal section and diffuse lateral margins, devel-

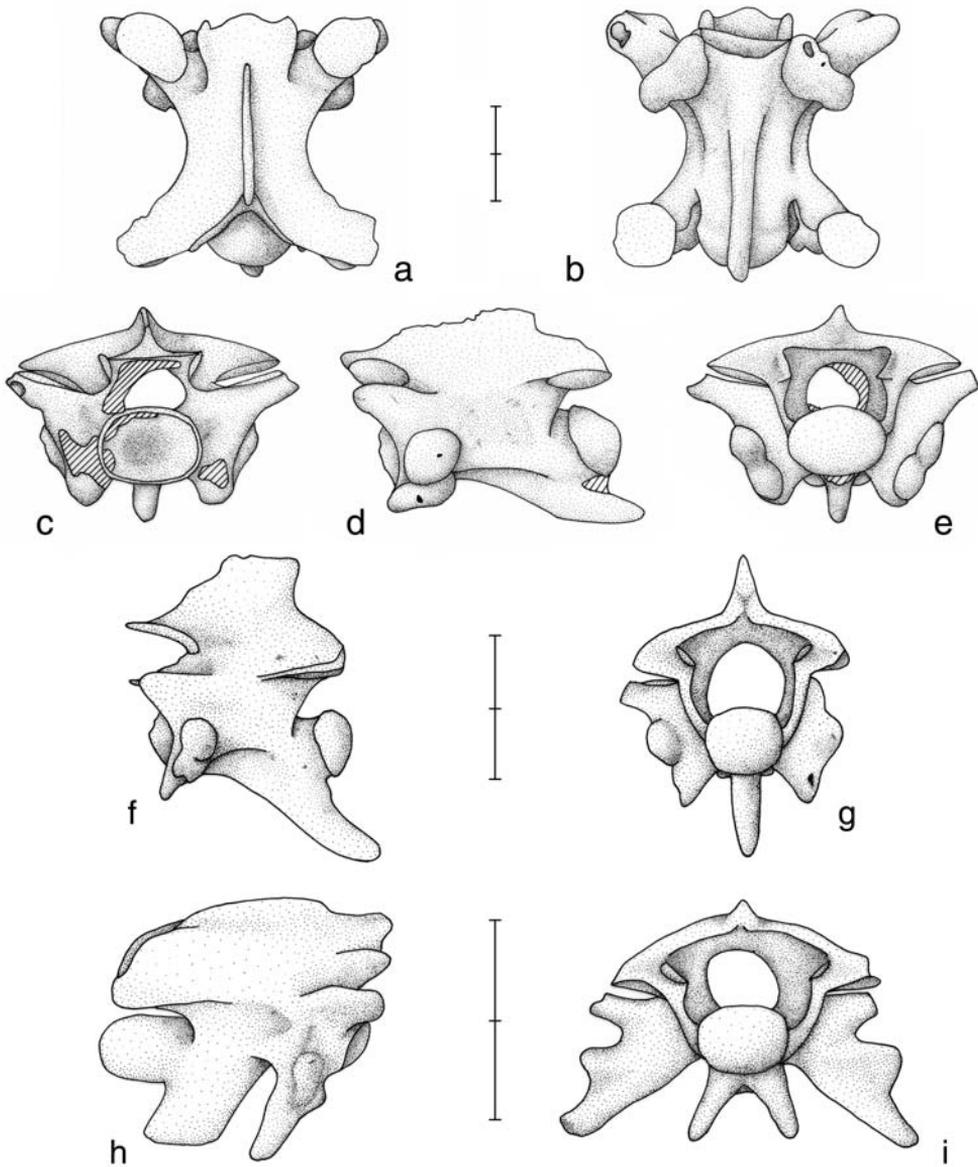


Fig. 14. “*Vipera berus* complex” species. a, b, c, d, e – trunk vertebra (BR98-B5-1c), dorsal, ventral, anterior, left-lateral and posterior views; f, g – cervical vertebra (BR97-B4-am), left-lateral and posterior views; h, i – caudal vertebra (BR97-B4-1am), right-lateral and posterior views. All scales = 2 mm.

oped condyle and cotyle, and upwards inclined prezygapophysis articular surfaces. The vertebrae morphology permits to differentiate two groups within the European vipers: “*V. aspis* complex” and “*V. berus* complex”.

“*V. berus* complex” have cervical vertebrae with a short and hook-shaped hypapophysis and lower than wide neural spine, trunk vertebrae with a very low neural spine and caudal vertebrae with pleurapophysis generally longer or equal length than haemapophysis, haemapophysis being strongly built and weak (SZYNDLAR 1984).

European members of the “*V. berus* complex” (*V. berus*, *V. ursinii* and *V. seoanei*) display homogenous vertebrae morphology and are hardly distinguishable from one another (SZYNDLAR 1984 and SZYNDLAR & RAGE 1999).

Habitat and distribution. Among the “*V. berus* complex” only the adder (*Vipera berus*) occurs in the region of Poitou-Charente. *V. seoanei* occurs low-lying areas of the French Pyrenees and in North-West of Spain and *V. ursinii* shows isolated occurrences in South-East France, Italy, Austria, Hungary, the ex-Yugoslavia and more or less continuously from Romania to Northwest China (BRUNO & MAUGERI 1992).

The adder (*V. berus*) is a European species with a very large distribution from Northern Europe to the Far East. In France, its distribution area is very fragmented and confined to the Northwest, the Vosges, the Jura and the Massif Central (GASC et al. 1997). It seems that this species has disappeared from the region of Poitou-Charentes (THIRION et al. 2002); at present it occurs only north of the Loire. Unlike the asp viper (*V. aspis*), it prefers cooler and moister environments with a minimum temperature tolerance of 8-10°C (BRUNO & MAUGERI 1992). The adder lives in swamps, peat bogs and on forest edges, both in plains and mountainous areas, up to an altitude of 3000 metres.

IV. PALAEOBIOGEOGRAPHICAL DATA OF THE BOIS ROCHE HERPETOFAUNA

The known modern distributional ranges of species present in various layers indicate unexpected patterns. At present, *Pelodytes punctatus* has a Western European range, reaching north to the English Channel and eastwards no further than the French-Belgian border, the Swiss border and coastal Northwest Italy (GASC et al. 1997). *Pelobates fuscus*, on the other hand, has an eastern distribution and does not overlap with the range of *Pelodytes punctatus*.

Several comments can be made concerning the observed differences between the fossil herpetofaunal assemblage of Bois Roche and modern distributions in the considered region. Our comments concern:

- the presence of flourishing populations of a “*Vipera berus* complex” species and common spadefoot (*Pelobates fuscus*).
- the abundance of the natterjack toad (*Bufo calamita*) in relation to the common toad (*Bufo bufo*).

The “*V. berus* complex” shows, as mentioned before, a very fragmentary modern distribution in Western Europe and especially in Southern France (BRUNO & MAUGERI 1992).

According to SZYNDLAR & RAGE (1999), species of the “*V. berus* complex” do not occur in Western Europe prior to the Quaternary and their occurrence seems to be correlated with the decline or withdrawal of members of the “*V. aspis* complex” to the south, during a climatic deterioration. In France (BAILON et al. 1988; BAILON 1991) the “*V. berus* complex” is present in the late Middle Pleistocene at the Lazaret Cave (Nice, SE France; remains attributed to *V. ursinii*) and in the late Pliocene of Montoussé 5 (Hautes-Pyrénées, SW France).

The presence of a “*V. berus* complex” species at Bois Roche is probably due to a cooler climate period whereas *V. aspis* who occurs in the early Upper Pleistocene (probably OIS 5e) layers of Arternac (Charente; BLAIN & BAILON 2003) is absent at Bois Roche.

The common spadefoot (*P. fuscus*), with the exception of a declining residual isolated population in the department of Indre and in north-eastern France (GASC et al. 1997; THIRION et al. 2002),

ranges in relatively fragmented areas including central and eastern Europe from Germany to Kazakhstan and from Estonia to Romania. As we said before, this species shows a distinct preference for open areas with no or little vegetation (EGGERT 2002). Bushy areas are avoided, and the decline of this species in the department of Indre is linked to evolution of fallow land, harmful to its movements (EGGERT in THIRION et al. 2002).

The southern limit of the common spadefoot (*Pelobates fuscus*) distribution area in France, during the period between the end of Middle Pleistocene and the beginning of the Late Pleistocene, is situated clearly to the south: Combe-Grenal in the department of Dordogne (BAILON 1991), Baume Moula-Guercy in the department of Ardèche (BAILON 1999b), Rochers de Villeneuve in the department of Vienne (SEGUIN, personal communication) and Artenac in the department of Charente (BLAIN & BAILON 2003). During this period, its occurrence is often linked with a strong occurrence of *Bufo calamita* relative to *Bufo bufo*.

The ratio of *Bufo bufo* vs. *Bufo calamita* is strongly reversed, *B. bufo* being now the most common species in the Charente region. If this observed tendency was not caused by taphonomic bias, could there be an environmental explanation?

ROMERO & REAL (1996) have shown that for south-Iberian populations, *B. bufo* is more likely to be found in areas where climate is more predictable, probably because in these areas it may exert its competitive superiority over *B. calamita*. In zones with very low climatic stability *B. calamita* is more likely to be found than *B. bufo*, probably because *B. bufo* lacks the ability to adapt to unpredictable conditions. In areas with intermediate climatic predictability, both species occur and there would be a balance between the superior competitiveness of *B. bufo* and the higher adaptability of *B. calamita*. Several authors have attributed the local differences between the distribution of *B. bufo* and *B. calamita* to differences in aridity or vegetal cover (see ROMERO & REAL 1996 for a review). *B. bufo* abundance has been reported higher in deciduous woodland zones with high precipitation, although it is not absent in arid zones. Instead *B. calamita* prefers open land and it is less frequent than *B. bufo* in woodlands, being the most common amphibian species in arid regions of Spain subject to an irregular pluviometric regimen and temperature. Such data are concordant with the reproductive success ability and strategy of these species.

Could the joint presence of species now without clear geographical equivalents indicate a particular environment for this area during Late Pleistocene? The presence of the common spadefoot and a "*V. berus* complex" species together with the natterjack toad, effectively larger than the common toad, may indicate a continental open environment, mitigated however by nearby oceanic influence as showed by the occurrence of temperate west-European thermophilic species like the common parsley frog.

V. TAPHONOMIC DATA

A taphonomic study of a common parsley frog (*Pelodytes punctatus*) sample from layer 1am has been made by COCHARD (1998), who attributed the accumulation to a catastrophic event (inundation of the cave toward the end of the period of wintering, when males and juveniles emerge from wintering before the females), based on a number of observations:

- spatial distributions and dense concentration of remains in layer 1am;
- absence of differential preservation of skeletal parts;
- absence of digestion and fragmentation due to a predator;
- overrepresentation of female specimens (more than 65%).

To assess the degree of postdepositional preservation and fragmentation of bone we can use the ratio of NISP (number of identifiable bones) to MNI (minimum number of individuals) for each species and each layers (Table V).

Table V

Ratio of NISP to MNIa for anurans by layers and species

Anura	1a	1am	1b	1c	1d	2	Total
<i>Pelobates fuscus</i>	1.8	1.5	1.4	2.0		1.6	1.6
<i>Pelodytes punctatus</i>	6.9	12.8	6.3	6.3	6.2	6.3	8.1
<i>Bufo bufo</i>	2.0			1.0		1.0	1.5
<i>Bufo calamita</i>	5.3	6.2	4.2	4.8	4.0	4.1	5.2
<i>Hyla</i> sp.	1.0	1.0					1.0
<i>Rana temporaria</i>	6.4	6.3	3.5	22.1	2.9	4.1	13.6
<i>Rana</i> cf. <i>R. lessonae</i>		5.0					5.0

A high ratio of NISP to MNI is indicative of a high degree of fragmentation and/or a high number of skeletal elements per carcass. For *Pelodytes punctatus*, there is an important difference between layer 1am and all the others: the relationship of NISP to MNI is 12926 to 1007, i.e. a ratio of 12.8 in layer 1am while it is much less in layers 1a, 1b, 1c, 1d and 2, i.e. 6.9 in layer 1a (3507/509), 6.3 in layer 1b (932/149), 6.3 in layer 1c (1716/272), 6.2 in layer 1d (496/80) and 6.3 in layer 2 (11236/1786). Likewise for *Rana temporaria* in layer 1c, the relationship of NISP/MNI is 6412 to 290, i.e. a ratio of 22.1 while it is much less in layers 1a, 1am, 1b, 1d and 2 where ratio is lower than 6.4. Since fragmentation during water-screening of these fragile bones is comparable between layers, this means that the anuran individuals in layers 1am and 1c are represented by a higher number of skeletal parts than in other layers. This is true also if we compare the relationship of NISP to MNI for other species which are generally represented by a low number of identifiable bones per MNI. This may be the result of predation and almost complete consumption by the predator of the bones of *Bufo bufo*, *Bufo calamita*, *Hyla*, and *Pelobates fuscus* or to a bad conservation in the case of natural *in situ* death. Toads are present in the diet of several carnivores and some birds of prey, as the Eagle Owls (*Bubo bubo*), but the typical bone alterations after such a relatively strong digestion are different from those observed in our fossil samples. However, the low ratio of NISP to MNI of *Rana temporaria* (in layers other than 1c) and *Pelodytes punctatus* (in layers other than 1am) may be linked with extensive destruction and consumption by the predator. In light of the observed bone alteration pattern, a part of the material, attributed to *R. temporaria*, can probably be ascribed to an accumulation of owl pellet remains, following the criteria suggested by FERNÁNDEZ-JALVO (1995) and PINTO-LLONA & ANDREWS (1999). Breakage pattern are difficult to analyze because of the material great fragility. Genus like *Rana* and *Pelodytes* are commonly preyed by nocturnal birds of prey such as the Barn Owls (*Tyto alba*) (REY et al. 1991).

In conclusion the relatively high ratio of NISP to MNI (12.8) for *Pelodytes punctatus* in layer 1am suggest an accumulation process completely different from that of other species and layers that may correspond to COCHARD's interpretation of a catastrophic accumulation by flooding. On the other hand, the relatively high ratio of NISP to MNI (22.1) for *Rana temporaria* in layer 1c suggest a better conservation of skeletal parts than in others layers.

VI. PALAEOENVIRONMENTAL AND PALAEOCLIMATIC INTERPRETATIONS

Fossil herpetofaunal assemblages can be used as accurate palaeoclimatic and palaeoenvironmental indicators. Though they collectively occupy a wide range of terrestrial and aquatic environ-

ments, individual species often have specific tolerances for temperature, vegetation cover, water quality and other factors which control their distribution (GLEED-OWEN 1999).

The abundance of herpetofaunal remains at Bois-Roche and their relatively continuous distribution permit us to make palaeoclimatic and palaeoenvironmental quantification in order to understand the evolution of faunal associations, where all groups are constituted by a set of taxa showing the same ecological and/or climatic affinities (Fig. 15).

Layer 2 shows a rather temperate environment (Fig. 15 a), relatively open (Fig. 15 b) with a pronounced humidity (Fig. 15 c) that may correspond to the climatic degradation occurring at the end of OIS 5e. The fresh period of layers 1d, 1c and 1b indicate a moist and relatively open environment with a slight increase of the shrubby vegetation, even if no typical forest species occur. Layer 1c may correspond to the coolest conditions in the sequence. Finally, layer 1a *sensu lato* (= 1a+1am) with relatively temperate conditions, although not equivalent to layer 2 values, may correspond to a short stable climatic improvement.

Few archaeological or palaeontological sites have been studied in the department of Charente from a herpetofaunal point of view and so comparisons are difficult to draw up. However, the cave of Artenac, situated about fifty kilometres to the NE contains abundant herpetofaunal remains in layers dated to the early Upper Pleistocene, probably OIS 5e (BLAIN & BAILON 2003). The Bois Roche herpetofauna does not show occurrence of more thermophilic species like those present at Artenac (*Lacerta viridis*, *Hierophis viridiflavus* and *Vipera aspis*) whose northernmost distribution boundary is situated in the vicinity of the 18°C for July temperatures isotherm.

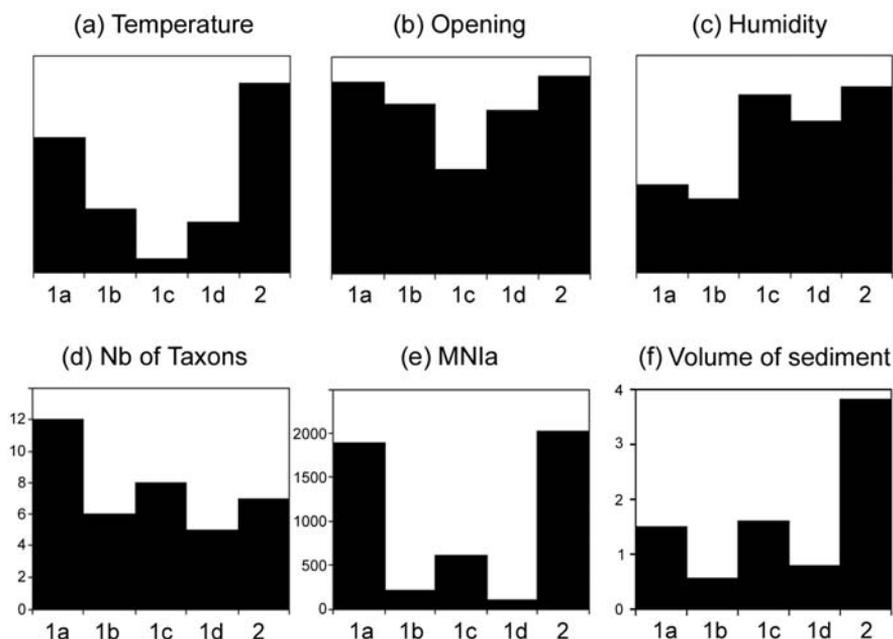


Fig. 15. Graphic representation of palaeoclimatic and palaeoenvironmental data provided by the herpetofauna. The first diagram (a) represents a factor "summer temperature". It was obtained by calculating the ratio of the Minimum Number of Individuals, adjusted by taking into account laterality (MNIA), of western European species (*P. punctatus*, *B. calamita*, *Hyla* sp., *Rana* cf. *R. lessonae* and *A. fragilis*) to the MNIA of northern European (*P. fuscus*, *B. bufo*, *R. temporaria*, *N. natrix*, *C. austriaca* and "*V. berus* complex" species). The second diagram (b) represents the ratio of MNIA of species from relatively open environment (*P. fuscus*, *P. punctatus* and *B. calamita*) to the total MNIA. The third diagram (c) shows variations in "humidity" and is the ratio of the MNIA of most hygrophilic species to the total MNIA. The fourth (d) shows the number of species, the fifth (e) shows the MNIA and the sixth (f) shows the volume of water-screened sediment in m³. In all diagrams, 1a corresponds to layers 1a and 1am.

Pelodytes punctatus and *Bufo calamita* suggest a July temperatures of at least 15°C. Based on the present northern limit of green frogs in Scandinavia and Russia, *Rana lessonae* implies a mean July temperature of at least 16°C. Both *Rana lessonae* and *Natrix natrix* require a relatively long period of summer warmth, longer than *Bufo calamita* would require. Globally, mean annual temperatures can be estimated as being at least lower of 1 to 2°C in comparison with the present in the studied area.

The majority of the species occurring at Bois Roche indicate relatively open, humid and cool environments, but favorable to a lot of sunshine (THIRION et al. 2002; DUGUET & MELKI 2003). Of all of them, *Pelobates fuscus*, and to a lesser degree *Bufo calamita* and *Coronella austriaca*, are certainly the species who need the most open and dry environment with no or few vegetation. Other species, like *Pelodytes punctatus*, *Bufo bufo*, *Rana temporaria*, *Anguis fragilis* and *Natrix natrix* suggest the presence of humid, wooded (broad-leaved or mixed) and/or shrubby little areas connected together, notably for *Pelodytes punctatus* for which such an environment constitutes a favorable place for wintering. All species suggest the immediate proximity of a stream with areas of sunny stagnant water area. The high representation of burrowing species, like *Bufo bufo*, *Bufo calamita*, *Pelobates fuscus*, *Pelodytes punctatus* and *Anguis fragilis*, points to sandy or loose soils with few stones.

CONCLUSION

The layers of Bois Roche, with an estimated date of early Upper Pleistocene (Middle Palaeolithic) have yielded the following amphibian and squamate reptile fauna: *Pelobates fuscus* (Pelobatidae), *Pelodytes punctatus* (Pelodytidae), *Bufo bufo* and *Bufo calamita* (Bufonidae), *Hyla* sp. (Hylidae), *Rana temporaria* and *Rana* cf. *R. lessonae* (Ranidae), a small lacertid (Lacertidae), *Anguis fragilis* (Anguidae), *Natrix natrix* and *Coronella austriaca* (Colubridae) and a “*Vipera berus* complex” species (Viperidae). This herpetofauna may be contemporaneous of fairly cool climatic conditions. The presence of *P. fuscus*, *R. lessonae* and “*V. berus* complex” species, now with scarce distribution area in southwestern France, indicates more continental climatic conditions mitigated by the occurrence of species with Atlantic affinities like *P. punctatus* and *B. calamita*. This herpetofauna suggests a very open environment, with damp meadows and small grove areas of broad-leaved trees and conifers.

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