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THE LOWER VERTEBRATES FROM THE EOCENE AND OLIGOCENE OF THE PHOSPHORITES DU QUERCY (FRANCE): AN OVERVIEW

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Abstract - The Phosphorites du Quercy (southwestern France) consist of more than 100 fossiliferous fissure-fill sites. Lower vertebrates from these localities include some fishes and amphibians, but mostly are reptiles. The precise provenances and geological ages of fossils collected during the nineteenth and the beginning of the twentieth centuries ('old collections') are unknown. The new excavations, which have produced the 'new collections', have shown that the ages range from the early Eocene (MP 8+9) to the early Miocene (MN 3), but almost all localities range from the late middle Eocene (MP 16) to the late Oligocene (MP 28). The list of all taxa of lower vertebrates from the Phosphorites is provided. In addition to species of undetermined geographic origin (probably European), the faunas from the Eocene include forms with North and South American affinities. The middle and late Eocene faunas contain endemic species. At the Eocene-Oligocene transition, a prominent event (the 'Grande Coupure') led to the extinction of most of the species present during the Eocene. Almost all taxa with American affinities died out at that time. During the Oligocene, the invasion of migrants probably from Asia and presumed local evolution of the few taxa that survived the 'Grande Coupure', replaced the former European-American faunas.

Résumé - Les Phosphorites du Quercy correspondent à plus de cent gisements. Les vertébrés inférieurs de ces gisements comprennent surtout des amphibiens et reptiles, les poissons étant extrêmement rares. Les reptiles sont beaucoup plus nombreux que les amphibiens. Les gisements précis et l'âge géologique des fossiles trouvés au XIXème et au début du XXème siècles («anciennes collections») ne sont pas connus. Les nouveaux travaux sur les Phosphorites («nouvelles collections») ont montré que les âges vont de l'Eocène inférieur (MP 8+9) au Miocène inférieur (MN 3), mais presque tous les gisements sont compris entre l'Eocène moyen tardif (MP 16) et l'Oligocène supérieur (MP 28). La liste de tous les taxons de vertébrés inférieurs des Phosphorites est donnée. Les faunes éocènes comprennent des taxons d'origine géographique non déterminée (probablement européenne) auxquels s'ajoutent des formes à affinités nord et sud américaines ainsi que, pour l'Eocène moyen et supérieur, des espèces marquées par l'endémisme. A la limite Eocène-Oligocène, un événement marquant, la «Grande Coupure», a conduit à l'extinction de la plus grande partie des amphibiens et reptiles; pratiquement toutes les espèces à affinités américaines ont été éliminées par cet événement. Pendant l'Oligocène, les quelques taxons qui avaient survécu à la Grande Coupure, une probable spéciation locale et, surtout, des immigrations d'origine asiatique probable ont formé de nouvelles faunes qui ont remplacé celles de l'Eocène, lesquelles étaient de nature euro-américaine.

Key Words - Amphibians, Reptiles, Eocene, Oligocene, Phosphorites du Quercy, France.

Mots clés - Amphibiens, Reptiles, Eocène, Oligocène, Phosphorites du Quercy, France.

INTRODUCTION

The Phosphorites du Quercy (hereafter referred to as 'the Phosphorites') are phosphatic sediments that in-fill fissures in limestone plateaus of the Quercy region (southwestern France). These fissure-fills often contain fossil vertebrates, and they have produced rich and diverse faunas. The fossils are generally disarticulated, well-preserved bones. Collections from the Phosphorites were obtained during two separate periods : (1) from the late 1860s to the beginning of the twentieth century, and (2) from the late 1960s to present.

The Phosphorites were discovered in 1865 (Gèze, 1938), and they were worked for phosphate until the beginning of the twentieth century. During this first phase, the quarries were worked by non-paleontologists (quarrymen), consequently most of the fossils were destroyed or lost. Most specimens recovered lack provenance data. Moreover, when a provenance was recorded for a specimen, only a toponym was provided (e.g. Caylux, Lamandine, Bach, etc), which does not correspond to identified fossiliferous sites, as they are only village names close to the fossiliferous sites. The fossils collected during that period make up the 'old collections'. A number of taxa were erected on the basis of specimens from these collections.

Paleontological investigation of the fissure-fills began in the 1960's by the Université des Sciences et Techniques du Languedoc at Montpellier and the Université Paris 6, with the support of the CNRS. Today, numerous localities are known. They have been dated from the early Eocene to the early Miocene (see below). The fossils recovered from these localities are collectively referred to as the 'new collections'.

Lower vertebrates (i.e., fishes, amphibians, reptiles) from all localities have not been studied yet. The present article is an updated overview of our present knowledge.

1. THE 'OLD COLLECTIONS'

As mentioned above, the precise provenance and the geological age of the fossil vertebrates from the old collections are unknown. Nevertheless, despite this situation, 30 genera (four amphibian and 26 reptile genera) and 43 species (six amphibian and 37 reptile species) have been named based on specimens from the old collections (Tabl. 1, 2). Among these taxa, 11 genera and five species are not valid because they are junior synonyms or junior homonyms. Although the names of 37 species are taxonomically valid, 13 of these species are regarded as *nomina dubia* (Tabl. 2) because they are based upon specimens that are not sufficiently informative from a paleoanatomical point of view. Consequently, it is not possible to identify these species in the new collections. Five of the valid and well-defined species, based on the old collections, have not been found in the new collections. These include: *Arambourgia gaudryi* (crocodilian); '*Placosaurus*' *europaeus* (lizard); '*Palaeopython*' *neglectus*, '*Paleryx*' *cayluxi,* and *Plesiotortrix edwardsi* (snakes). *A. gaudryi*, '*P.*' *europaeus*, '*P.*' *neglectus* and *P. edwardsi* are each known only by their type specimen, which comes from the old collections. '*P.*' *cayluxi*, known only by the holotype (now lost), was recovered from the Phosphorites. However, a distorted vertebra from the late middle Eocene of Robiac (MP 16; southeastern France) may belong to this species.

Also, there have been some misidentifications of taxa among specimens from the early collections. For example, *Necrodasypus* was described as a mammal but, in fact, it is a lizard (*Placosaurus*). The anuran *Thaumastosaurus* was first interpreted as a lizard, and some lizards were mistaken for snakes.

It should be added that peculiar specimens were found during the old excavations. These specimens, generally called 'mummies', are in fact natural casts that show the external morphology. Such 'mummies' include one salamander, a few anurans and snakes. The new excavations have not produced additional mummies.

2. THE 'NEW COLLECTIONS'

The second wave of collecting (from the late 1960's to present), has resulted in the discovery and rediscovery of numerous fissure-fills. Excavations have yielded rich and diverse vertebrate faunas. Implementation of screen-washing techniques has resulted in the recovery of many small specimens. Fossils collected during the new excavations are here referred to as the 'new collections'. All fissure-fills have been precisely dated. Presently, more than 100 fossiliferous localities have been recovered and dated. Their ages range from the early Eocene (standard level MP 8+9; locality of Pasturat; Astruc *et al.*, 2003) to the early Miocene (zone MN 3; locality of Crémat; Sigé *et al.*, 1991). However, nearly all of them range from MP 16 (late middle Eocene) to MP 28 (late Oligocene) (about standard levels MP and zones MN, see Schmidt-Kittler, 1987 and Steininger, 1999).

About 80 species of lower vertebrates have been identified, but not all of them have been described. Some of them are provisionally identified by a letter (e.g., 'Salamandridé F', 'Boidae C',...). Moreover, some uncertainties remain; for example: is *Megalotriton* aff. *M. filholi* from Oligocene localities of the Phosphorites a species distinct from *M. filholi* that has been identified in the Eocene, or is *Anguis* sp. (or any genus whose species is or are not identified) represented by one or more species (Tabl. 3)?

Nineteen species based on the old collections have been found during the new excavations; therefore, the stratigraphical ranges of these species are now established (Tabl. 3). Ten genera and 22 species have been erected on the basis of specimens collected during the new excavations (Tabl. 1, 2).

3. SYSTEMATIC ACCOUNT

The fauna from the Phosphorites is skewed towards the terrestrial component. Reptiles largely outnumber other groups of lower vertebrates. In terms of the minimum number of species, reptiles presently comprise about 83.5% of the fauna of lower vertebrates (lizards: 40.5%, snakes: 31%, chelonians: 8.3%, crocodilians: 3.6%). But, it should be kept in mind that chelonians and crocodilians have not been thoroughly studied. Further works will perhaps increase the number of species in these groups, but probably not significantly. The proportion of amphibians is clearly lower, only about 15.4% of the species of lower vertebrates belong to amphibians (salamanders: 8.3%, anurans: 7.1%). Few fishes have been recovered, and they have not been identified. However, at least one species of fish was present, which comprises about 1% of the fauna. Because of uncertainties regarding the stratigraphic ranges of chelonians and crocodilians, it is not possible to compare percentages of taxa from the Eocene to those from the Oligocene. Parenthetically, the lower vertebrates from the only known Miocene locality of the Phosphorites have not been studied, so its faunal composition cannot be compared to those of the Eocene and Oligocene faunal complexes at this time.

Provisional lists of lower vertebrate fossil taxa were published by de Bonis *et al.* (1973) and Crochet *et al.* (1981).

3.1. FISHES

Fishes are very rare in the Phosphorites. In terms of number of specimens, they represent a very small component of the lower vertebrate fauna (less than 1%). Fish taxa have been listed as coming from only two localities. Curiously, these localities are the oldest and youngest ones: early Eocene of Pasturat (indeterminate fishes; Astruc *et al*., 2003) and early Miocene of Crémat (Cyprinidae indeterminate; Sigé *et al*., 1991). Fishes are also known from some other localities of the Phosphorites but they have not been published.

3.2. AMPHIBIA

Salamanders and anurans are present in the fissure-fills of the Phosphorites, however, the Albanerpetontidae (Allocaudata) have not been recovered. The Albanerpetontidae are salamander-like amphibians of uncertain affinities. They are known in Europe from the Middle Jurassic to the Pliocene (Venczel & Gardner, 2005). Apparently, their paleoenvironmental requirements are not inconsistent with presence in the Phosphorites. On the other hand, it should be noted that they have not been recovered from the Eocene, at worldwide scale, and that only recently they have been reported from the Oligocene of Germany (Böhme & Ilg, 2003; Wiechman, 2003). However, these Oligocene albanerpetontids have not been formally described. Taking this in account, the absence of albanerpetontids from the Phosphorites is not so surprising.

3.2.1. Caudata

Salamanders (Caudata) are somewhat common in the Phosphorites. Although they have not been thoroughly studied, they are of interest from both a biostratigraphic and paleobiogeographic point of view.

Salamanders from the Phosphorites were possibly first reported by Filhol (1873a). In that paper he described a 'mummy' tetrapod and referred to it as a large-sized lizard. However, this account perhaps pertains to a 'mummy' he subsequently assigned to an indeterminate salamander (Filhol, 1877: figs 419-420). But, the fact that Filhol (1873a) regarded the fossil as a large-sized animal casts some doubts on this possibility. The first unequivocal salamander (*Megalotriton filholi*) from the Phosphorites was reported by Zittel (1890). Later, De Stefano's (1903a) redescribed *M. filholi* and named two new taxa, *Megalotriton portisi* and *Heteroclitotriton zitteli* (Tabl. 1, 2).

Aside from taxa based on the old collections, salamanders from the Phosphorites were reported and/or described only by Rage & Vergnaud-Grazzini (1978), Estes (1981), Augé & Rage (1995), and Duffaud (2000). Up to seven species may be present, only three of them being named (Table 3). They all belong to the Salamandridae.

Tabl. 1. **GENERA** BASED ON SPECIMENS FROM THE **OLD COLLECTIONS** OF THE PHOSPHORITES	
ORIGINAL DESCRIPTION	PRESENT STATUS (SYNONYMY)
Caudata:	
Megalotriton Zittel, 1890	unchanged
Heteroclitotriton De Stefano, 1903	*Salamandra* Laurenti, 1768
Anura:	
Thaumastosaurus De Stefano, 1903	unchanged
Enigmatosaurus Nopcsa, 1908	*Thaumastosaurus* De Stefano, 1903
Crocodylia:	
Arambourgia Kälin, 1939	unchanged
Lacertilia:	
Pseudolacerta De Stefano, 1903	unchanged
Palaeochamaeleo De Stefano, 1903	*Uromastyx* Merrem, 1820
Quercygama Augé & Smith, 1997	unchanged
Cadurcogekko Hoffstetter, 1946	unchanged
Cadurcosaurus Filhol, 1882	*Dracaenosaurus* Pomel, 1846
Pseudeumeces Hoffstetter, 1944	unchanged
Brevisaurus Augé, 2005	unchanged
Ayalasaurus Augé, 2005	unchanged
Necrodasypus Filhol, 1894	*Placosaurus* Gervais, 1852
Protrachysaurus De Stefano, 1903	*Placosaurus* Gervais, 1852
Proiguana Filhol, 1876	'*Placosaurus*' Gervais, 1852
Paraplacosauriops Augé & Sullivan, 2006	unchanged
Necrosaurus Filhol, 1876	unchanged
Palaeovaranus Filhol, 1877	*Necrosaurus* Filhol, 1876
Odontomophis de Rochebrune, 1884	*Necrosaurus* Filhol, 1876
Palaeosaurus Filhol, 1873 - non *Palaeosaurus* von Meyer, 1831	*Necrosaurus* Filhol, 1876
Eurheloderma Hoffstetter, 1957	unchanged
Omoiotyphlops de Rochebrune, 1884	unchanged
Serpentes:	
Palaeopython de Rochebrune, 1880	unchanged
Scytalophis de Rochebrune, 1880 - non *Scytalophis* Kaup, 1856	*Rageophis* Wallach, 1986
Palaelaphis de Rochebrune, 1884	unchanged
Plesiotortrix de Rochebrune, 1884	unchanged
Tachyophis de Rochebrune, 1884	unchanged
Rageophis Wallach, 1986	unchanged
Cadurceryx Hoffstetter & Rage, 1972	unchanged
GENERA BASED ON SPECIMENS FROM THE **NEW COLLECTIONS** OF THE PHOSPHORITES	
Lacertilia:	
Cadurciguana Augé, 1987	unchanged
Escampcerta Augé, 2005	unchanged
Graciliceria Augé, 2005	unchanged
Quercycerta Augé, 2005	unchanged
Mediolacerta Augé, 2005	unchanged
Orthoscincus Augé, 2005	unchanged
Eocordyla Augé, 2005	unchanged
Serpentes:	
Eoanilius Rage, 1974	unchanged
Cadurcoboa Rage, 1978	unchanged
Platyspondylia Rage, 1974	unchanged

Table 1. List of genera erected on the basis of specimens from the Phosphorites du Quercy (mainly based on Augé 2005, Estes 1981 and 1983, Rage 1984b, Rocek & Lamaud 1995, Wallach 1986).

Tabl. 2. **SPECIES** BASED ON SPECIMENS FROM THE PHOSPHORITES DU QUERCY

	ORIGINAL DESCRIPTION	PRESENT STATUS (SYNONYMY)
SPECIES BASED ON SPECIMENS FROM THE **OLD COLLECTIONS**	**Caudata:**	
	Megalotriton filholi Zittel, 1890	unchanged
	Megalotriton portisi De Stefano, 1903	*Megalotriton filholi* Zittel, 1890
	Heteroclitotriton zitteli De Stefano, 1903	*Salamandra sansaniensis* Lartet, 1851
	Anura:	
	Thaumastosaurus bottii De Stefano, 1903	unchanged
	Bufo serratus Filhol, 1876	unchanged, *nomen dubium*
	Rana plicata Filhol, 1876	unchanged, *nomen dubium*
	Chelonii:	
	Testudo phosphoritarum Bergounioux, 1935	*Cheirogaster phosphoritarum* (Bergounioux, 1935)
	Ptychogaster (?) *cayluxensis* Lydekker, 1889	*Temnoclemmys cayluxensis* (Lydekker, 1889)
	Crocodylia:	
	Alligator gaudryi De Stefano, 1905	*Arambourgia gaudryi* (De Stefano, 1905)
	Lacertilia:	
	Lacerta lamandini Filhol, 1877	*Geiseltaliellus lamandini* (Filhol, 1877)
	Palaeochamaeleo europaeus De Stefano, 1903	*Uromastyx europaeus* (De Stefano, 1903)
	Agama galliae Filhol, 1877	*Quercygama galliae* (Filhol, 1877)
	Cadurcogekko piveteaui Hoffstetter, 1946	unchanged
	Plestiodon cadurcense Filhol, 1877	*Pseudeumeces cadurcensis* (Filhol, 1877)
	Cadurcosaurus sauvagei Filhol, 1882	*Dracaenosaurus croizeti* Gervais, 1852
	Brevisaurus smithi Augé, 2005	unchanged
	Ayalasaurus tenuis Augé, 2005	unchanged
	Lacerta mucronata Filhol, 1877	*Pseudolacerta mucronata* (Filhol, 1877)
	Varanus ? margariticeps Gervais, 1876	*Placosaurus margariticeps* (Gervais, 1876), *nomen dubium*
	Plestiodon quercyi Filhol, 1882	*Paraplacosauriops quercyi* (Filhol, 1882)
	Necrodasypus galliae Filhol, 1894	*Placosaurus galliae* (Filhol, 1894), *nomen dubium*
	Proiguana europeana Filhol, 1876	'*Placosaurus*' *europaeus* (Filhol, 1876)
	Iguana europaeana Filhol, 1877	'*Placosaurus*' *europaeus* (Filhol, 1876)
	Propseudopus cayluxi De Stefano, 1903	*Placosaurus cayluxi* (De Stefano, 1903), *nomen dubium*
	Protrachysaurus gaudryi De Stefano, 1903	*Placosaurus gaudryi* (De Stefano, 1903), *nomen dubium*
	Placosaurus leenhardti Leenhardt, 1926	*Paraplacosauriops quercyi* (Filhol, 1882)
	Palaeosaurus cayluxi Filhol, 1873	*Necrosaurus cayluxi* (Filhol, 1873)
	Eurheloderma gallicum Hoffstetter,1957	unchanged
	Omoiotyphlops priscus de Rochebrune, 1884	unchanged, *nomen dubium*
	Typhlops edwardsi de Rochebrune, 1884	*Omoiotyphlops priscus* de Rochebrune, 1884, *nomen dubium*
	Serpentes:	
	Python cadurcensis Filhol, 1876	*Palaeopython cadurcensis* (Filhol, 1876)
	Palaeopython filholi de Rochebrune, 1880	unchanged
	Palaeopython neglectus de Rochebrune, 1884	'*Palaeopython*' *neglectus* de Rochebrune, 1884
	Coluber lafonti Filhol, 1877	*Rageophis lafonti* (Filhol, 1877), *nomen dubium*
	Plesiotortrix edwardsi de Rochebrune, 1884	unchanged
	Palaelaphis antiquus de Rochebrune, 1884	unchanged, *nomen dubium*
	Palaelaphis robustus de Rochebrune, 1884	unchanged, *nomen dubium*
	Pylmophis gracilis de Rochebrune, 1884	'*Pylmophis*' *gracilis* de Rochebrune, 1884, *nomen dubium*
	Tachyophis nitidus de Rochebrune, 1884	unchanged, *nomen dubium*
	Elaphis boulei De Stefano, 1905	unchanged, *nomen dubium*
	Paleryx cayluxi De Stefano, 1905	'*Paleryx*' *cayluxi* De Stefano, 1905
	Natrix mlynarskii Rage, 1988	unchanged
	Cadurceryx filholi Hoffstetter & Rage, 1972	unchanged
SPECIES BASED ON THE **NEW COLLECTIONS**	**Lacertilia:**	
	Cadurciguana hoffstetteri Augé, 1987	unchanged
	Pseudolacerta quercyini Augé, 2005	unchanged
	Cadurcogekko rugosus Augé, 2005	unchanged
	Lacerta filholi Augé, 1988	unchanged
	Mediolacerta roceki Augé, 2005	unchanged
	Escampcerta amblyodonta Augé, 2005	unchanged
	Gracilicerta sindexi Augé, 2005	unchanged
	Quercycerta maxima Augé, 2005	unchanged
	Orthoscincus malperiensis Augé, 2005	unchanged
	Eocordyla mathisi Augé, 2005	unchanged
	Ophisaurus roqueprunensis Augé, 1992	*Dopasia roqueprunensis* (Augé, 1992)
	Dopasia frayssensis Augé, 2005	unchanged
	Placosaurus estesi Sullivan & Augé, 2006	unchanged
	Serpentes:	
	Eoanilius europae Rage, 1974	unchanged
	Bavarioboa bachensis Szyndlar & Rage, 2003	unchanged
	Bavarioboa vaylatsae Szyndlar & Rage, 2003	unchanged
	Bavarioboa crocheti Szyndlar & Rage, 2003	unchanged
	Cadurcoboa insolita Rage, 1978	unchanged
	Platyspondylia lepta Rage, 1978	unchanged
	Platyspondylia sudrei Rage, 1988	unchanged
	Dunnophis cadurcensis Rage, 1974	unchanged
	Coluber cadurci Rage, 1974	unchanged

Table 2. List of species erected on the basis of specimens from the Phosphorites du Quercy (mainly based on Augé 2005, Estes 1981 and 1983, Rage 1984b, Szyndlar & Rage 2003).

Tabl. 3. LOWER VERTEBRATES FROM THE NEW EXCAVATIONS OF THE PHOSPHORITES DU QUERCY		
Taxa	**Stratigraphic ranges in the Phosphorites**	**Global stratigraphic ranges**
CAUDATA		
Salamandridae		
Megalotriton filholi Zittel, 1890 *	MP 18-19	identical
Megalotriton aff. *M. filholi*	MP 21-23	identical
Salamandra sansaniensis Lartet, 1851	MP 22-25	MP17-21?, MP22-MN7
'Salamandridé C' in Duffaud, 2000	MP 10/11? and MP 16-19	MP 6?, MP 7-19
Chelotriton paradoxus Pomel, 1853	MP 25	MP 25-MN 7+8
'aff. *Triturus*' = 'Salamandridé F' in Duffaud, 2000	MP 16-17	identical
'*Triturus*' = 'Salamandridé G' in Duffaud, 2000	MP 18-23	identical
ANURA		
Discoglossidae		
Latonia aff. *L. vertaizoni* (Friant, 1944)	MP 22-23	identical
Pelobatidae		
Eopelobates aff. *E. anthracinus* Parker, 1929	MP 19-21	MP 19-30/MN 1, MN 4?
Pelobates sp.	MP 22-23	MP 22-Recent
Pelodytidae		
cf. *Pelodytes*	MP 16-19	MP 13?, MP 16-Recent
Ranidae		
cf. *Rana*	MP 16-23	MP 16-Recent
Leptodactylidae		
Thaumastosaurus bottii De Stefano, 1903 *	MP 16-19, MP 20?	identical
CHELONII		
Chelydridae		
Chelydropsis sanctihenrici Broin, 1977	MP 28	MP 26-28
Testudinidae		
Temnoclemmys cayluxensis (Lydekker, 1889) *	MP 28	identical
Temnoclemmys aff. *T. cayluxensis*	MP 16	identical
Cheirogaster phosphoritarum (Bergounioux, 1935) *	MP 28	identical
Provencemys laurenti (Bergounioux, 1934)	MP 23	MP 23-28
Dithyrosternum sp.	MP 19	identical
'*Ergilemys*' sp.	MP 18-28	MP 18-MN 6
'*Palaeochelys* s.l.-*Mauremys*' group indet.	MP 18	MP 7-Recent
CROCODYLIA		
Diplocynodontidae		
Diplocynodon sp.	MP 18 and MP 28	Middle Eocene-Miocene
LACERTILIA		
Iguanidae		
Cadurciguana hoffstetteri Augé, 1987 *	MP 16-19	identical
Geiseltaliellus lamandini (Filhol, 1877) *	MP 16?, MP 17-19	identical
Pseudolacerta mucronata (Filhol, 1877) *	MP 16?, MP 17-19	identical
Pseudolacerta quercyini Augé, 2005 *	MP 16-19	identical
Agamidae		
Uromastyx europaeus (De Stefano, 1903) *	MP 22	identical
Quercygama galliae (Filhol, 1877) *	MP 23? and MP 25	identical
Gekkonidae		
Cadurcogekko piveteaui Hoffstetter, 1946 *	MP 16-19	identical
Cadurcogekko rugosus Augé, 2005 *	MP 17 and 18 or 19	identical
Lacertidae		
Plesiolacerta lydekkeri Hoffstetter, 1942	MP 16-21	MP 14-21
Escampcerta amblyodonta Augé, 2005 *	MP 17-19	identical
Gracilicerta sindexi Augé, 2005 *	MP 16-19	identical
Quercycerta maxima Augé, 2005 *	MP 17	identical
Lacerta filholi Augé, 1988 *	MP 22-28	MP 22-MN 2
Mediolacerta roceki Augé, 2005 *	MP 23-28	MP 23-30
Pseudeumeces cadurcensis (Filhol, 1877) *	MP 25-28	MP 25-28, MP 30?
? Teiidae		
Brevisaurus smithi Augé, 2005 *	MP 17	identical
? Cordylidae		
Eocordyla mathisi Augé, 2005 *	MP 16-17	identical

Table 3. List of lower vertebrates found in the Phosphorites du Quercy during the new excavations. Asterisks denote species erected on the basis of specimens from the Phosphorites (see table 2) (mainly based on Augé 2005, Augé & Sullivan 2006, Broin 1977, Duffaud 2000, Hervet 2004, Rage 1984b, Sullivan & Augé 2006, Szyndlar & Rage 2003).

Tabl. 3 (continued). LOWER VERTEBRATES FROM THE NEW EXCAVATIONS OF THE PHOSPHORITES DU QUERCY		
Taxa	**Stratigraphic ranges in the Phosphorites**	**Global stratigraphic ranges**
LACERTILIA (continued)		
Scincidae		
Ayalasaurus tenuis Augé, 2005 *	MP 18 or 19	identical
Orthoscincus malperiensis Augé, 2005 *	MP 17	identical
Scincomorpha, families indeterminate		
Scincoidea indeterminate 'Forme B' in Augé, 2005	MP 17-19	identical
Scincomorpha indeterminate 'Forme B' in Augé, 2005	MP 17	identical
Anguidae		
Anguis sp.	MP 16-25	MP8+9?, MP 14-Recent
Placosaurus estesi Sullivan & Augé, 2006 *	MP 17	identical
Paraplacosauriops quercyi (Filhol, 1882) *	MP 16	identical
Dopasia roqueprunensis Augé, 1992 *	MP 23-28	MP 21-28
Dopasia coderetensis Augé, 2005	MP 23	MP 23-30
Dopasia frayssensis Augé, 2005 *	MP 28	identical
Helvetisaurus picteti (Hoffstetter, 1942)	MP 17-19	identical
Varanidae		
cf. *Saniwa* ?	MP 19	MP 1/5-Middle Oligocene
Necrosauridae		
Necrosaurus cayluxi (Filhol, 1873) *	MP 16-19	identical
Necrosaurus eucarinatus (Kuhn, 1940)	MP 17-19	MP 12-19
Helodermatidae		
Eurheloderma gallicum Hoffstetter, 1957 *	MP 16-19	identical
? Amphisbaenidae		
gen. and sp. indeterminate	MP 16-28	identical
Lacertilia *incertae sedis*		
gen. and sp. indeterminate	MP 17	identical
SERPENTES		
Scolecophidia, family indeterminate		
gen. and sp. indeterminate	MP10/11 and MP 16-18	identical
Aniliidae		
Coniophis sp.	MP 16-19	Albian-Upper Eocene
Eoanilius europae Rage, 1974 *	MP 16-19, MP 20?	identical
Eoanilius aff. *E. oligocenicus* Szyndlar, 1994	MP 22	MP 22-28
Boidae		
Palaeopython cadurcensis (Filhol, 1876) *	MP 16-19	identical
Palaeopython filholi de Rochebrune, 1880 *	MP 19-20	identical
Bavarioboa bachensis Szyndlar & Rage, 2003 *	MP 26	identical
Bavarioboa vaylatsae Szyndlar & Rage, 2003 *	MP 26	identical
Bavarioboa crocheti Szyndlar & Rage, 2003 *	MP 28	identical
Cadurcoboa insolita Rage, 1978 *	MP 14-20	identical
Cadurceryx filholi Hoffstetter & Rage, 1972 *	MP 16-19, MP 20?	MP13?, MP16-19, MP20?
Bransateryx vireti Hoffstetter & Rage, 1972	MP 25-28	MP 22-MN 2
'Boidae C' in Crochet et al., 1981	MP 16-21	identical
'Boidae D' in Crochet et al., 1981	MP 17? and MP 19	identical
'Boidae F' in Crochet et al., 1981	MP 23	identical
'Boidae H' in Crochet et al., 1981	MP 22	identical
'Boidae K' in Crochet et al., 1981	MP16?, MP17-19, MP20?	identical
'Boidae L' in Crochet et al., 1981	MP 16-19	identical
Tropidophiidae		
Dunnophis matronensis Rage,1973	MP 10/11-MP 13	MP 7-13
Dunnophis cadurcensis Rage, 1974 *	MP 16-19	identical
Platyspondylia sudrei Rage, 1988 *	MP 16-19, MP 20?	identical
Platyspondylia lepta Rage, 1974 *	MP 28	MP 28-30
Russellophiidae		
gen. and sp. indeterminate	MP 16	identical
Colubridae		
Coluber cadurci Rage, 1974 *	MP 21-25	MP 21-30, MN 2?
Natrix mlynarskii Rage, 1988 *	MP 22	identical

Table 3. List of lower vertebrates found in the Phosphorites du Quercy during the new excavations. Asterisks denote species erected on the basis of specimens from the Phosphorites (see table 2) (mainly based on Augé 2005, Augé & Sullivan 2006, Broin 1977, Duffaud 2000, Hervet 2004, Rage 1984b, Sullivan & Augé 2006, Szyndlar & Rage 2003)

3.2.2. Anura

Frogs have been recovered from numerous localities, but they are not common. The first fossil frogs from the Phosphorites were reported by Filhol (1873a) who described, but did not name, an incomplete 'mummified' frog from the old collections. Subsequently, he named it *Rana plicata* (Filhol, 1876) and provided illustrations (Filhol, 1877). In 1876, Filhol also described *Bufo serratus*, which is based on another 'mummified' specimen; the latter species was figured later as *Bufo servatus* (Filhol, 1877). These two taxa are regarded as *nomina dubia* (*nomina vana* according to Sanchiz, 1998). Aside from these 'mummies', only one taxon (*Thaumastosaurus bottii*) was based on a specimen from the old collections. De Stefano (1903b) named *Thaumastosaurus* on an incomplete skull (specimen is now lost), and he regarded it as a problematic lizard (*incertae sedis*). On the basis of De Stefano's illustrations, Hoffstetter (1945) later demonstrated that *Thaumastosaurus* (= *Enigmatosaurus*) is a frog. Moreover, he suggested that it is member of the Pelobatidae, though subsequent evaluations of material from the new collections demonstrate that it is a leptodactylid frog (Rage, 1981; Rocek & Lamaud, 1995).

In addition to *Thaumastosaurus*, the new collections have yielded discoglossids, pelobatids, pelodytids, and ranids (Tabl. 3). More recently, Sanchiz (1998: 154) reported microhylids and rhacophorids from Escamps, a late Eocene locality (MP 19) of the Phosphorites; but these specimens were not described, so the presence of these two families (Microhylidae and Rhacophoridae) is questionable. Taxa pertaining to the extinct Palaeobatrachidae (Late Cretaceous-Pleistocene), rather common in other European Cenozoic localities, are not present in the fissure-fills of the Phosphorites. Like the fishes, palaeobatrachids were highly aquatic animals, so their absence in the terrestrial-dominated environment of the Phosphorites is not surprising. It should be noted that the earliest representatives of the living genus *Pelobates* occur in the early-middle Oligocene (MP 23), perhaps the early Oligocene (MP 22) of the Phosphorites (Duffaud, 2000). Similarly, the Phosphorites have produced the earliest ranid (MP 16, late middle Eocene); these fossils cannot be distinguished from the living *Rana*, but assignment to this genus has not been demonstrated (Rage, 1984a). A pelodytid occurs as early as the level MP 16 in the Phosphorites (Crochet *et al.*, 1981; Rage 1988). This pelodytid cannot be definitely distinguished from the extant genus *Pelodytes*. It perhaps documents the earliest representative of the family, but a doubtful pelodytid was reported from an older level (MP 13), outside the Phosphorites (Duffaud & Rage, 1997).

3.3. REPTILIA

Reptiles are represented by chelonians, crocodiles, and squamates (lizards and snakes). Small forms (i.e. squamates) largely outnumber large taxa (chelonians and crocodiles). Numerous taxa were erected on the basis of specimens from the old collections. Chelonians and crocodiles have not been adequately studied, while squamates have been the subject of many papers (references are listed in Augé, 2005; Rage, 1984b; Szyndlar & Rage, 2003).

3.3.1. Chelonii

Although remains of chelonians are relatively common in the Phosphorites (mainly as disarticulated carapace and plastral elements) they have been rarely studied. Chelonians from the Phosphorites were first noted by Gervais (1876), but he did not provide any detailed identifications. De Stefano (1905) described two forms referred to as *Ocadia* sp. and *Ptychogaster* sp. Two species were subsequently based on specimens from the old collections: *Testudo phosphoritarum* Bergounioux, 1935 (today referred to the genus *Cheirogaster*) and *Ptychogaster cayluxensis* Lydekker, 1889 (presently referred to the genus *Temnoclemmys*). Additional specimens of these two species have been found during the new excavations and thus have been dated (Lapparent, 2000, 2002). No new taxa have been established based on specimens from the new collections.

At least seven species are currently recognized from the Phosphorites; however, they have not all been identified (Tabl. 3). At species level, only *Temnoclemmys* aff. *T. cayluxensis* has been identified from the Eocene part of the Phosphorites (Broin, 1988). The other species, including *Temnoclemmys cayluxensis*, have been reported from Oligocene localities (Tabl. 3).

Remark: The most recent review of chelonians from the Phosphorites is that of Claude and Tong (this volume). There are a few taxonomic disagreements between the latter work which was based on a part of the material, and the present report that reviewed only bibliographic data antedating Claude and Tong's study.

3.3.2. Crocodylia

Crocodiles were first, and briefly, reported from the Phosphorites by Gervais (1876). Filhol (1877) referred a fragmentary mandible to *Diplocinodon gracile* (sic), (i.e., *Diplocynodon gracilis* Vaillant, 1872). This taxon was later cited in some articles (e.g., De Stefano, 1905). Berg (1966) questioned the validity of the species and Buffetaut (1978) doubted this assignment. De Stefano (1905) described *Alligator gaudryi* on the basis of a nearly complete skull. Kälin (1939) erected the genus *Arambourgia* for the reception of the species, but this genus is considered by some to be synonymous with *Allognathosuchus* Mook, 1921 (see Buffetaut, 1978). However, Brochu (2004) separated the two genera. According to Kälin (1939) the provenance of *A. gaudryi* would be Memerlin, but this cannot be definitely accepted. If the type locality is really Memerlin, then the geological age of this skull (the only known specimen referred to the species) is late Eocene (MP 18 or 19; Rémy *et al*., 1997). Berg (1966: 75) referred one tooth from the old collections to *Pristichampsus*. But, Rossmann (1988: 111) regarded it only as a possible pristichampsine.

Additional crocodiles have been recovered in the new collections, but they are not common and are very fragmentary consisting mostly of isolated teeth, vertebrae, and osteoderms. Material in the new collections confirm the presence of *Diplocynodon*, but species-level identification is not possible. *Diplocynodon* sp. is known from the late Eocene and late Oligocene levels of the Phosphorites (Buffetaut, 1978).

In summary, two, perhaps three distinct taxa are known from the Phosphorites: the alligatorid *A. gaudryi*, the diplocynodontid *Diplocynodon*, and perhaps an indeterminate pristichampsine.

3.3.3. Squamata

By far, the squamates (lizards and snakes) represent the greatest part of the faunas of lower vertebrates, both in terms of numbers of taxa and specimens from the fissure-fills of the Phosphorites. Squamates were identified from the Phosphorites as early as 1873. Filhol (1873a) reported on a 'mummified' portion of a snake and, as noted previously, also on a 'mummy' that may be either a lizard or a salamander. He also erected *Palaeosaurus cayluxi*, a fossil lizard, but without describing it (Filhol, 1873b). Gervais (1873) assigned a vertebra to the snake genus *Palaeophis*, a highly aquatic snake, but the figure that Gervais published demonstrates the vertebra belongs to the boid *Palaeopython*.

More recently, there have been a number of studies that deal, in part or in full, with lizards from the Phosphorites, most notably those of Estes (1983), Augé (2005) and Sullivan & Augé (2006). As far as snakes are concerned, two articles (Rochebrune, 1884; Rage, 1974) were solely devoted to fossil Serpentes from the Phosphorites. Snakes from these localities have been also described in various other studies that are listed in Rage (1984b) and Szyndlar & Rage (2003).

Based on the current evidence, lizards from the Phosphorites include more than 30 valid species (Table 3). However, some species have yet to be identified and named (e.g., *Anguis* sp., 'genus and species indeterminate', etc). At least 10 families of lizards have been identified from the Phosphorites: Iguanidae, Agamidae, Gekkonidae, Lacertidae, Scincidae, Anguidae, Varanidae, Necrosauridae, Helodermatidae, one family of amphisbaenians (?Amphisbaenidae), and perhaps Cordylidae. It is possible that some indeterminate taxa may belong to other families (Augé, 2005).

Snakes are less numerous than lizards. Twenty-five species have been identified. Several of them have not been named yet (e.g., *Coniophis* sp., 'Boidae C', etc). These snakes belong to at least six families: 'Aniliidae', Boidae, Tropidophiidae, Russellophiidae, Colubridae, and an indeterminate family of scolecophidians. More than half of these species belong to the Boidae (Tabl. 3).

4. DISCUSSION

4.1. STRATIGRAPHY

It has been widely held that amphibians and reptiles have little stratigraphic significance. But, Holman (1976) and Sullivan & Holman (1996) for North America, and Rage (1984c) for Europe, have demonstrated that this assertion is largely untrue. In addition, thanks to the number of localities and to their extensive stratigraphic range, the Phosphorites have even shown that herpetofaunas may be indicative of precise stratigraphic levels. In the Phosphorites, only some species can be used as precise stratigraphic markers, i.e., species with short stratigraphic ranges (see Tabl. 3), but assemblages of species may be characteristic; that is to say, stratigraphy founded on herpetofaunas is based on appearances and extinctions of taxa, not on evolution of lineages. These assemblages permit us to identify intervals of four or three standard levels, or in some cases even one standard level.

4.2. PALEOGEOGRAPHY

Several taxa from the Phosphorites have affinities with North American taxa. These include the glyptosaurines *Placosaurus*, *Paraplacosauriops* (Anguidae), *Eurheloderma* (Helodermatidae), the tropidophiid snake *Dunnophis*, Teiidae, if *Brevisaurus smithii* really belongs to this family, and perhaps the varanid *Saniwa* (Augé, 2005; Augé & Sullivan, 2006; Rage, 1984b; Sullivan & Augé, 2006). In addition, some taxa have South American affinities. These include the leptodactylid frog *Thaumastosaurus* and the boine snake *Palaeopython* (Rage, 1981, 1999; Rocek & Lamaud, 1995). Moreover, iguanid lizards and tropidophiid snakes may either demonstrate close relationships with North America or more remote affinities with South America (Rage, 1999). Except for the helodermatids that apparently were still present in the Oligocene of the Phosphorites (Augé 2005), all these forms with North and/or South American affinities are restricted to the Eocene part of the Phosphorites.

After the Eocene, migrant taxa reached Europe and were present in the Oligocene. Their geographic origin is uncertain, but the arrival of the first immigrant taxa coincided with the opening of the Turgai barrier (an epicontinental sea) that separated Europe from Asia. In addition, the Oligocene lower vertebrate immigrants arrived with mammals of Asiatic origin. None of the amphibians and reptiles suggests African origins. Therefore, as mammals, amphibians and reptiles that reached Europe during the Oligocene likely came from Asia.

4.3. HISTORY OF THE FAUNA

Two faunal complexes can be distinguished in the Phosphorites: (1) an Eocene faunal complex (from MP 10 or MP 11 to MP 20); and (2) an Oligocene faunal complex (from MP 21 to MP 28). These faunas differ from one another and are separated by a significant hiatus called the 'Grande Coupure', which may be translated as the 'Great Break'.

The faunas from the earliest levels of the Phosphorites (MP 8+9, MP 11 to 15) are poorly known. As far as the herpetofaunas are concerned, only MP 10 or MP 11, MP 13, and MP 14 have been documented. The faunas from the period MP 16-MP 19 are very rich and diverse, squamates being the most numerous. The lower vertebrate faunal assemblages from the Eocene include forms that share affinities with taxa from North and South America (see above) as well as some local endemic species. Aside from these taxa, species of indeterminate geographic affinities are also present; they are probably European. The American taxa are 'hold-overs' from the early Eocene, a period during which North America and Europe were still united. South American taxa likely reached Europe through North America, due to the terrestrial connection that linked South and North America during the Late Cretaceous-early Paleocene. On the other hand, Europe definitely separated from North America by the late early Eocene ; since the Turgai Sea still separated it from Asia, Europe was isolated. This isolation was probably the cause of the presence of peculiar forms that may be regarded as endemic to Europe (at least western Europe) during the middle and late Eocene: the large salamandrid *Megalotriton*, the strange snakes *Cadurceryx*, '*Paleryx*' *cayluxi*, and perhaps *Platyspondylia*, a problematic tropidophiid snake peculiar to Europe.

The standard level MP 20 is very poor, and the few taxa it has produced are not distinct from those of MP 19. But, between MP 19 (latest Eocene) and MP 21 (beginning of the Oligocene), a pronounced faunal turnover, the 'Grande Coupure', took place. Forty-four or 45 species of amphibians and reptiles were present in the Phosphorites before the 'Grande Coupure' (Table 3). Only four to six of them (i.e., 9.1% to 13.3%) survived this event. More specifically, squamates showed the greatest turnover; only 5.3% of the species survived. Among the taxa with American affinities, only the Helodermatidae apparently remained in existence there after the 'Grande Coupure'.

During the earliest Oligocene (MP 21), the faunas of amphibians and reptiles were poor and not diverse. They were subsequently increased by immigrations and presumably autochthonous evolution. Several taxa probably came from Asia (see above). Thus, European-Asiatic faunas replaced the former European-American faunas after the 'Grande Coupure'.

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