Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France)

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ABSTRACT

The Béon 1 vertebrate locality, formerly known as "Montréal-du-Gers" in southwestern France, has yielded a rich fauna of amphibians and squamate reptiles of late early Miocene (MN 4; Orleanian) age. It represents the first herpetofauna of that age described from Western Europe. The assemblage from Béon 1 includes 26 species (three species of salamanders, two of anurans, seven of lizards, and 14 of snakes). At least as far as snakes are concerned, the appearance of such a diversity of taxa is typical of the zone MN 4. The presence of this diverse snake assemblage at Béon 1 demonstrates that the wave of modern taxa that invaded Central Europe during MN 4 also reached Western Europe. The number and diversity of natricine snakes appear to be a characteristic of the late early Miocene (MN 4) and also of the early middle Miocene. Although a change apparently took place between the herpetofaunas from MN 4 and MN 6 in Central Europe, Béon 1 shows that the faunas were not altered significantly during that period in Western Europe. Béon 1 has produced the earliest *Pseudopus laurillardi* (Anguidae), *Python europaeus* (Boidae), *Coluber pouchetii*, *Texasophis meini*, *Neonatrix europaea*, and *Neonatrix natricoides* (Colubridae). It has also yielded one of the earliest *Varanus* (Varanidae) and perhaps the youngest *Natrix merkurensis* (Colubridae). The knowledge of the anatomy of the anguid lizard *Pseudopus laurillardi* is increased by the description of a posterior braincase. The abundance of aquatic amphibians and snakes confirms the presence of lacustrine/swampy environment.

KEY WORDS
Amphibia,
Squamata,
Reptilia,
Miocene,
France.

RÉSUMÉ

Amphibiens et squamates (reptiles) du Miocène inférieur (MN 4) de Béon 1 (Montréal-du-Gers, France).

Le gisement de vertébrés de Béon 1, préalablement connu sous le nom de « Montréal-du-Gers » (Gers, France), a fourni une riche faune d'amphibiens et de squamates (reptiles) du Miocène inférieur tardif (MN 4 ; Orléanien). C'est la première herpétofaune de cet âge décrite en Europe occidentale. La faune de Béon 1 comprend 26 espèces (trois espèces d'urodèles, deux d'anoures, sept de lézards et 14 de serpents). Au moins en ce qui concerne les serpents, l'apparition d'aussi nombreux taxons est typique de la zone MN 4. La présence de cette faune de serpents diversifiée montre que la vague de taxons modernes qui a envahi l'Europe centrale pendant MN 4 a atteint l'Europe occidentale. La diversité des Natricinae (serpents) et la quantité des spécimens correspondants apparaissent comme une caractéristique du Miocène inférieur tardif (MN 4) et du début du Miocène moyen. Alors qu'un changement semble avoir affecté les herpétofaunes d'Europe centrale entre MN 4 et MN 6, Béon 1 montre que les herpétofaunes d'Europe occidentale n'ont pas subi de changement significatif pendant cette période. Béon 1 a livré les plus anciens représentants de *Pseudopus laurillardi* (Anguidae), *Python europaeus* (Boidae), *Coluber pouchetii*, *Texasophis meini*, *Neonatrix europaea* et *Neonatrix natricoides* (Colubridae). Le gisement a aussi fourni l'un des plus anciens *Varanus* (Varanidae) et peut-être le plus récent représentant de *Natrix merkurensis* (Colubridae). La connaissance de *Pseudopus laurillardi* (Anguidae) est complétée par la description d'une partie postérieure de boîte crânienne. La fréquence des amphibiens et serpents aquatiques confirme la présence d'eaux calmes.

MOTS CLÉS
Amphibia,
Squamata,
Reptilia,
Miocène,
France.

INTRODUCTION

The late early Miocene (zone MN 4) corresponds to an important turnover in the snake fauna of Europe (Szyndlar & Böhme 1993; Ivanov 2001; Szyndlar & Rage 2003) and, to a lesser degree, anurans (Rage & Roček 2003). Several snake assemblages of MN 4 age were studied from Portugal (Quinta das Pedreiras and Quinta do Pombeiro; Antunes & Rage 1974), Spain (Córcoles; Alférez Delgado & Brea López 1981; Alférez *et al.* 1982), Germany (Petersbuch 2; Szyndlar & Schleich 1993), Austria (Oberdorf; Szyndlar 1998) and Czech Republic (Dolnice; Szyndlar 1987); moreover, Ivanov (2000) reported on the snake fauna from Vieux-Collonges (France) that is dated from the MN 4/MN 5 transition. Unfortunately, the other components of the herpetofaunas from that time are poorly known. Aside from snakes, only the faunas of lizards from Dolnice (Roček 1984) and of amphibians from Oberdorf (Sanchiz 1998a) have been studied.

Béon 1 ("Département" of Gers; southwestern France) has yielded a rich and diverse fauna of vertebrates of MN 4 age that includes amphibians and reptiles (Crouzel *et al.* 1988; Duranthon *et al.* 1999). In France, this is the only locality that has produced a rich assemblage of amphibians and squamates belonging to the zone MN 4 (apart from Vieux-Collonges that is MN 4/MN 5 in age). These amphibians and squamates are reported here. Aside from squamates, the reptiles also include crocodiles (*Diplocynodon styriacus*; Duranthon *et al.* 1999) and chelonians (*Cheirogaster* sp., *Ptychogaster* sp., and a small testudinid of the *Testudo* group; Duranthon *et al.* 1999; F. de Lapparent de Broin pers. comm.). The mammals were listed and/or studied by Crouzel *et al.* (1988), Duranthon *et al.* (1995, 1999), Antoine & Duranthon (1997), and Antoine *et al.* (2000a).

The Béon 1 locality was first reported as "Montréal-du-Gers" (Crouzel *et al.* 1988; Duranthon *et al.* 1995; Szyndlar & Rage 2002: 434). After the recovery of a second fossiliferous site – both being in the vicinity of the place known as "Béon" – the name "Montréal-du-Gers" was changed into "Béon 1" for the classical locality, whereas the second site was named "Béon 2" (Antoine & Duranthon 1997; Duranthon *et al.* 1999; Antoine *et al.* 2000a, b). Béon 2 did not yield amphibians and reptiles.

Béon 1 is assigned to the zone MN 4 of the European Neogene Mammal zones system (Mein 1975; Steininger 1999). More precisely, it is referred to the upper part of the zone (formerly, MN 4b) on the basis of mammals (Bruijn *et al.* 1992; Antoine & Duranthon 1997; Duranthon *et al.* 1999; Antoine e*t al.* 2000a, b); within "MN 4b", it is slightly older than the reference locality of La Romieu (Duranthon pers. comm.). The MN 4 age represents the middle Orleanian in terms of continental stratigraphy and part of the late Burdigalian standard stage; it lasted from *c.* 18 to *c.* 17 Ma (Steininger 1999).

The specimens studied in the present report are curated in the Muséum d'Histoire naturelle of Toulouse (MHNT), France.

SYSTEMATICS

Class AMPHIBIA Linnaeus, 1758
Order CAUDATA Scopoli, 1777
Family SALAMANDRIDAE Goldfuss, 1820
Genus *Chelotriton* Pomel, 1853

cf. ***Chelotriton*** sp.
(Fig. 1A)

MATERIAL EXAMINED. — 1 incomplete vertebra (Béon 2004 LT 1).

COMMENTS

This opisthocoelous vertebra (centrum length: 3.38 mm) is provided with divergent and widely separated rib-bearers that are united by a bony lamina up to their lateral tip. Posterior to the prezygapophysis, the anterior zygapophyseal crest dips posteroventrally and it joins the lamina that unites the rib-bearers. Numerous foramina open in the lateral walls of the vertebra. In ventral view, the centrum is cylindrical, poorly defined laterally, and slightly constricted in the middle of its length. Unfortunately, the neural spine (the morphology of which is characteristic of *Chelotriton*) is broken off.

One of the main characteristics of this vertebra is the posteroventral slope of the anterior zygapophyseal crest that joins the lamina connecting the rib-bearers. In salamandrids, this feature occurs in the living *Pleurodeles* and *Tylototriton* (but not in *Echinotriton*, that has been separated from *Tylototriton*; Nussbaum & Brodie 1982), and in the extinct European genera *Chelotriton* (middle Eocene-late Pliocene; Bailon 1989) and *Brachycormus* (late Oligocene and perhaps early Miocene; Estes 1981; Roček 1996). The size and the overall morphology of the available vertebra points to *Chelotriton*; however, this single, incomplete specimen cannot permit us to confirm this assignment.

Genus *Triturus* Rafinesque, 1815

About 40 opisthocoelous vertebrae show the combination of features that characterizes the genus *Triturus*: vertebrae opisthocoelous; condyle round, not separated from the centrum by a marked constriction; centrum without vertical ventral crests; ventral crests that connect the centrum to the ventral rib-bearers developed; dorsal and ventral rib-bearers markedly separated and united by a bony lamina; neural arch vaulted; neural spine well developed (Gonzales & Sanchiz 1986).

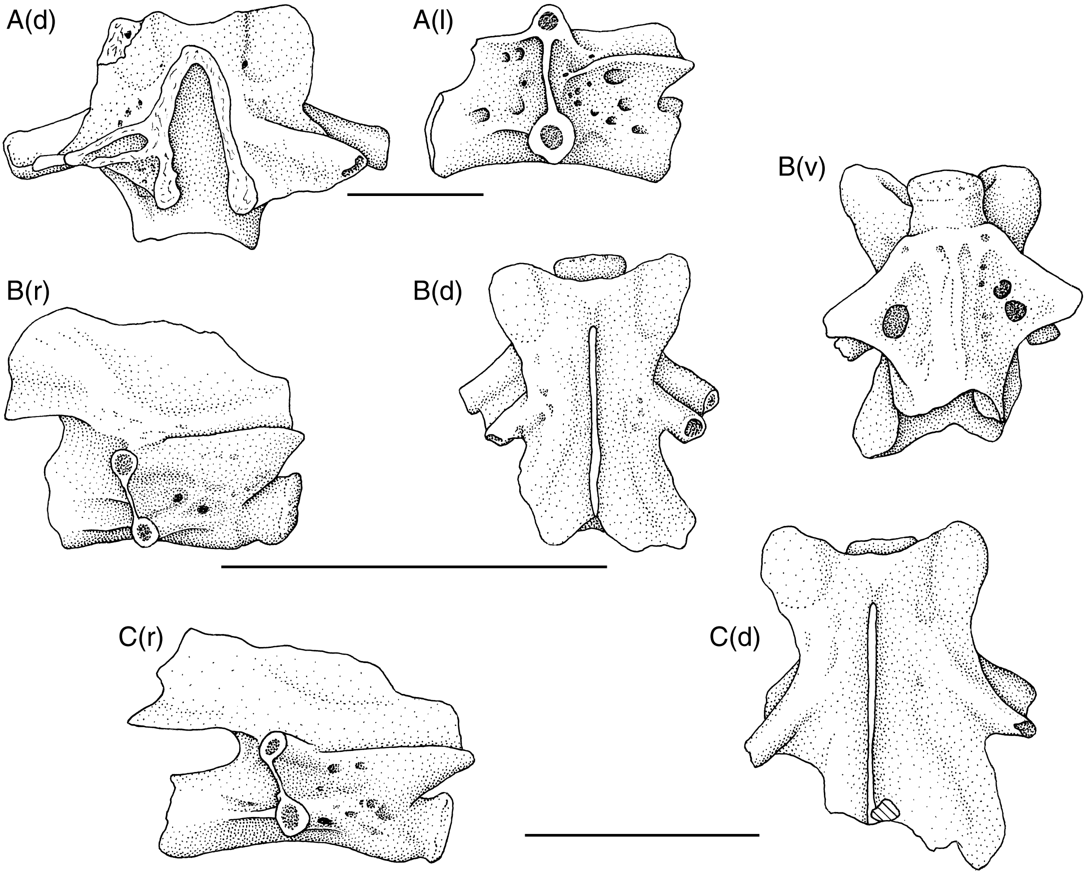

FIG. 1. — Caudata; **A**, cf. *Chelotriton* sp., trunk vertebra (Béon 2004 LT 1); **B**, *Triturus* aff. *T. helveticus* (Razoumowsky, 1789), trunk vertebra (Béon 2004 LT 2); **C**, *Triturus* cf. *T. marmoratus* (Latreille, 1800), trunk vertebra (Béon 2004 LT 5). Dorsal (**d**), left lateral (**l**), right lateral (**r**), and ventral (**v**) views. Scale bars: 2 mm.

Triturus aff. *T. helveticus* (Razoumowsky, 1789) (Fig. 1B)

MATERIAL EXAMINED. — 21 trunk vertebrae (Béon 2004 LT 2-4).

COMMENTS

This species is represented by tiny vertebrae (average length of centrum: 1.47 ± 0.13 mm). The neural spine is long, high, thin, and sometimes slightly forked posteriorly. The median notch in the posterior border of the neural arch is moderately deep and wide. The neural arch is vaulted; the ratio neural arch height/vertebra height is 0.43 ± 0.03. The size of the ventral crests shows variation. The subcentral foramina are generally large.

The height of the neural spine and the clearly vaulted neural arch show that these vertebrae belong to the subgenus usually named "*Palaeotriton*" (*sensu* Bolkay 1928). The overall vertebral morphology is similar to that of *Triturus* aff. *T. helveticus* reported from the middle Miocene (MN 6) of Sansan by Rage & Hossini (2000). This *Triturus* from Béon 1 appears to be the earliest representative of the *T. helveticus* group.

Triturus cf. ***T. marmoratus*** (Latreille, 1800)
(Fig. 1C)

MATERIAL EXAMINED. — 10 trunk vertebrae (Béon 2004 LT 5, 6).

COMMENTS

The vertebrae are clearly larger than those referred to as *Triturus* aff. *T. helveticus* (centrum length: from 2.52 to 3.21 mm; average: 2.84 ± 0.27 mm) and the t-test comparing the length of the centrum of this form to that of the preceding taxon is significant at the 5% level. The neural arch is moderately vaulted; the ratio neural arch height/vertebra height is 0.37 ± 0.025 and the t-test comparing this ratio to that of the vertebrae of *T.* aff. *T. helveticus* is highly significant at the 1% level. The neural spine is long, low and thin. The ventral crests appear to be weakly developed. The subcentral foramina are smaller and more numerous than in *T.* aff. *T. helveticus*.

The low neural spine demonstrates that this form belongs to the subgenus *Triturus* (i.e. *Neotriton* Bolkay, 1928). Although low, the neural spine is higher than that of species of the *T. cristatus* group, which shows that the form from Béon 1 should be assigned to the *T. marmoratus-T. vittatus* assemblage. In addition, the posterior part of the dorsal border of the neural spine is not flattened and lacks pits; therefore, these vertebrae do not belong to *T. vittatus* (Jenyns, 1835). However, the vertebrae from Béon 1 are smaller than those of the living *T. marmoratus* and it should be noted that *T. pygmaeus* (Wolterstorff, 1905), that was long regarded a subspecies of *T. marmoratus*, is now regarded as a species (García París *et al.* 2001). Unfortunately, the vertebrae of *T. pygmaeus* are poorly known. Therefore, the specimens from Béon 1 are provisionally referred to as *Triturus* cf. *T. marmoratus*.

Estes (1981) identified the earliest member of the *T. marmoratus* group (as *Triturus* cf. *T. marmoratus*) in the latest Oligocene (MP 30; early Miocene according to Estes) of Coderet, France.

Triturus sp.

MATERIAL EXAMINED. — 1 atlas (Béon 2004 LT 7), 7 trunk vertebrae (Béon 2004 LT 8), 1 humerus (Béon 2004 LT 9), and 3 femora (Béon 2004 LT 10).

In addition to some damaged trunk vertebrae, the above atlas, humerus, and femora do not appear to be useful for purposes of identification within the genus.

Order ANURA Rafinesque, 1815
Family DISCOGLOSSIDAE Günther, 1858
Genus *Latonia* Meyer, 1843

Latonia aff. ***L. ragei*** Hossini, 1993
(Fig. 2)

MATERIAL EXAMINED. — 1 incomplete premaxilla (Béon 2004 LT 11), 8 incomplete maxillae (Béon 2004 LT 12, 13), 1 oticoccipital (Béon 2004 LT 14), 3 presacral vertebrae (Béon 2004 LT 15), 1 sacral vertebra (Béon 2004 LT 16), 1 coracoid (Béon 2004 LT 17), 2 humeri (Béon 2004 LT 18, 19), and 1 ilium (Béon 2004 LT 20).

DESCRIPTION

Premaxilla

The bone bears teeth but it lacks sculpture. On the *lamina horizontalis*, the *pars maxillaris* is less developed than the *pars palatina* that strongly protrudes medially. On the medial face, a deep depression is located at the base of the *pars facialis*.

Maxilla

All specimens lack sculpture. The *lamina horizontalis* is thick with a rounded medial border. The tooth row terminates beyond the posterior end of the *lamina horizontalis*. A broad and shallow posterior depression occurs on the medial face of the bone; in one specimen (Fig. 2B), a second, smaller and more posterior depression is present.

Oticoccipital

In dorsal view, the lateral prootic process (*ramus lateralis*; Špinar 1978) is elongate and slender, the sutural surface for the frontoparietal is striated, and the posterior prootic crest (*prominentia ducti semicircularis posterioris*; Roček 1994) forms a strong prominence directed posteromedially. In posterior view, the condyle is close to the medial border of the bone. The supracondylar fossa is deep and limited medially by a vertical ridge. The *fenestra ovalis* appears as the lateral aperture of a transverse elongate bony tube.

Vertebrae
The vertebrae are opisthocoelous. In presacrals, the centrum is cylindrical; as a result, the condyle and condyle are round. The neural arch is long, of the imbricate type, and provided with a strong neural spine that ends posteriorly as an interzygapophyseal point. The sacral processes of the sacral vertebra are incomplete, but they are directed posterolaterally. Apparently, they were moderately widened distally, as in the living *Discoglossus*.

Coracoid
The *pars glenoidalis* is well developed whereas the damaged *pars epicoracoidalis* appears to be moderately widened.

Humerus
The condyle is shifted laterally and the *fossa cubitalis* is shallow. The margin of the lateral crest is slightly deflected ventrally. Only one humerus is provided with a medial crest; in its proximal part, the border of the latter crest forms a medial, slightly prominent curve.

Ilium
The posterior part of the only available ilium is damaged. In posterior view, an interiliac groove is present while the interiliac tubercle is partly broken off. The shaft bears a low and medially bent dorsal crest. The posterior part of the crest forms the *tuber superius* that is low and slightly globulous.

COMMENTS
These specimens display a combination of features that unquestionably points to discoglossids: *pars palatina* of premaxilla long; medial face of the *pars facialis* of the premaxilla with a deep depression; maxilla toothed and high; lateral prootic process of oticoccipital elongate; *fenestra ovalis* at the lateral extremity of a bony tube; vertebrae opisthocoelous; centrum cylindrical; *pars glenoidalis* of coracoid expanded but *pars epicoracoidalis* moderately widened; condyle of humerus shifted laterally; interiliac tuber and interiliac groove present.
Several traits demonstrate that the discoglossid from Béon 1 belongs to the *Discoglossus-Latonia* assemblage: *lamina horizontalis* of maxilla thickened; lateral prootic process of oticoccipital slender; neural spines of vertebrae well developed; overall morphology of humerus similar; presence of a dorsal crest and a *tuber superius* on the ilium. The presence of a deep supracondylar fossa on the oticoccipital, the strong posteromedial projection of the posterior prootic crest, the presence of a broad depression on the medial face of the maxilla, the projection of the tooth row posterior to the *lamina horizontalis*, the medial curve of the border of the medial crest of the humerus, and the weakly prominent *tuber superius* of the ilium are consistent with *Latonia* and rule out referral to the living genus *Discoglossus*.
Latonia is known in Europe from the late Oligocene to the early Pleistocene (Delfino 2002; Rage & Roček 2003). The absence of sculpture distinguishes the species from Béon 1 from *Latonia gigantea* (Lartet, 1851) that is known from the early Miocene (MN 4) to the early Pliocene (MN 15) (Rage & Hossini 2000; Roček & Rage 2000). This character and the posterolaterally directed and moderately widened sacral processes of the sacral vertebra are reminiscent of *L. ragei*, a species known from the latest Oligocene (MP 30; Hossini 1993) to the early Miocene (MN 4; Sanchiz 1998a). *L. vertaizoni* (Friant, 1944) (late Oligocene) is the only other species in which the lack of sculpture on the maxilla is confirmed (Roček 1994); but the anterior border of the sacral processes of this species is perpendicular to the vertebral axis, whereas in the species from Béon 1 this border is directed posterolaterally. The comparison with *L. seyfriedi*, the type species of the genus (MN 7+8, middle Miocene), is not possible because it is represented only by articulated specimens whose ventral face only is observable; consequently, it is impossible to determine whether sculpture is present on the maxilla (Roček 1994).

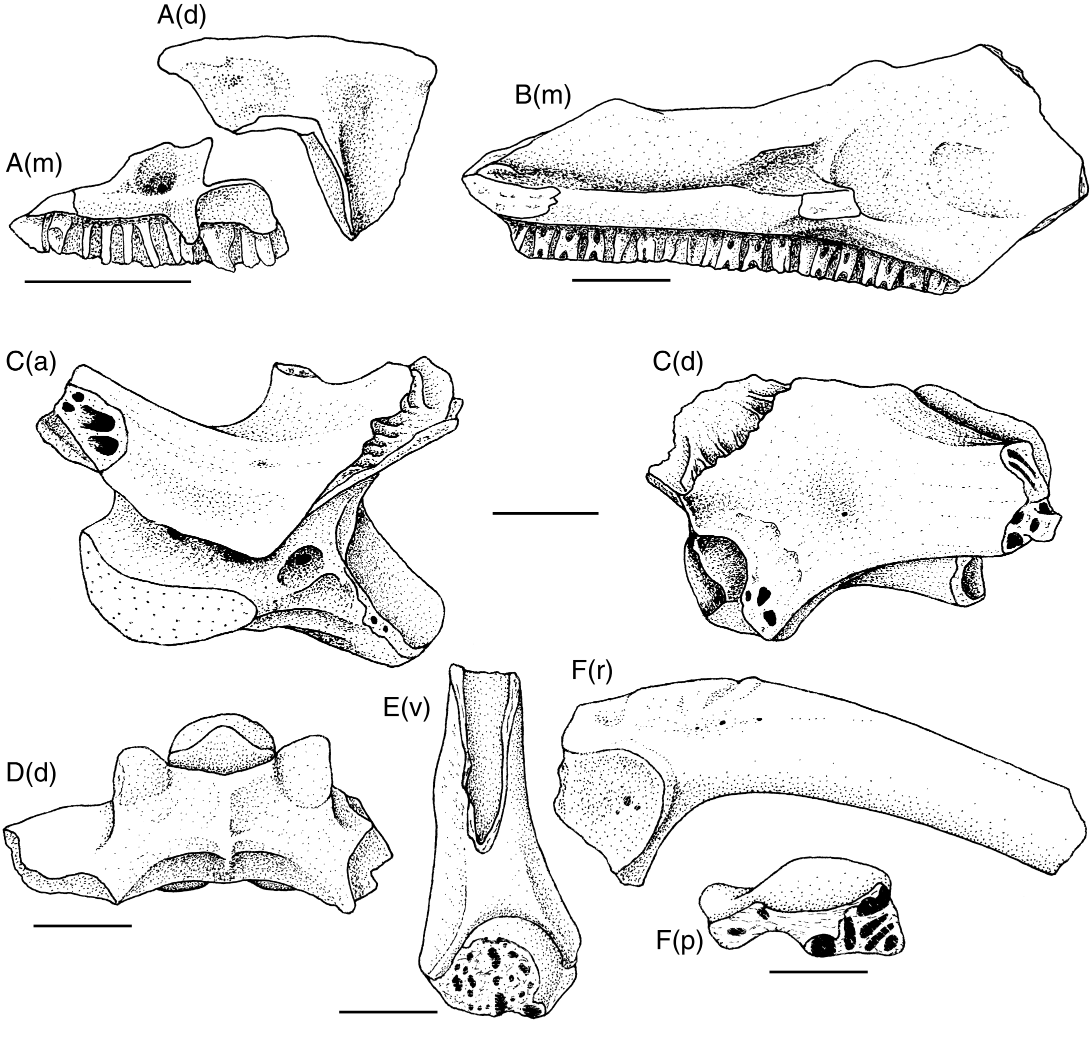

FIG. 2. — *Latonia* cf. *L. ragei* Hossini, 1993; **A**, left premaxilla (Béon 2004 LT 11); **B**, right maxilla (Béon 2004 LT 12); **C**, right oticoccipital (Béon 2004 LT 14); **D**, sacral vertebra (Béon 2004 LT 16); **E**, left humerus of a male (Béon 2004 LT 18); **F**, right ilium (Béon 2004 LT 20). Anterior (**a**), dorsal (**d**), medial (**m**), posterior (**p**), right lateral (**r**), and ventral (**v**) views. Scale bars: 2 mm.

The specimens from Béon 1 are smaller than those representing *L. ragei* at Coderet (MP 30) and Laugnac (MN 2), both localities in France. The snout-vent length of the individuals from Béon 1 was about 9 to 13 cm whereas those from Coderet and Laugnac reached about 18 cm. In addition, in the fossils from Coderet and Laugnac, the posterior prootic crest, medial crest of the humerus, and *tuber superius* of the ilium are more robust, the depression of the medial face of the maxilla is deeper and more distinctly limited, and the sacral processes are directed slightly more posteriorly. In summary, the discoglossid from Béon 1 is close to *L. ragei*, but because of some differences, it cannot be referred to this species without reservation. However, the specimens from Béon 1 being smaller, the differences are perhaps only of ontogenetic nature.

REMARKS

Roček (1994) suggested that *Latonia vertaizoni* is present at Coderet (MP 30). This opinion was based on the absence of sculpture on the maxilla. But in the sacral vertebrae from Coderet, the sacral processes are not perpendicular to the vertebral axis, therefore they cannot belong to *L. vertaizoni*; they are directed posterolaterally as in *L. ragei*. There is no significant difference between the specimens from Laugnac (MN 2), the type locality of *L. ragei*, and those from Coderet. Therefore, as stated by Hossini (1993) the *Latonia* species from Coderet is *L. ragei*; this species is not restricted to the early Miocene.
Böhme (2002) reported *L. ragei* from MN 5 localities in Austria; thus the Austrian fossils would represent the youngest record of the species. But the identification rests on fragmentary remains scattered in several sites, therefore it cannot be accepted without reservation.

Family RANIDAE Rafinesque-Schmaltz, 1818
Genus *Rana* Linnaeus, 1758
Synklepton *Rana esculenta* Linnaeus, 1758

Rana sp.
(Fig. 3A-C)

MATERIAL EXAMINED. — 2 angulosplenials (Béon 2004 LT 21), 6 presacral vertebrae (Béon 2004 LT 22), 6 sacral vertebrae (Béon 2004 LT 23), 6 humeri (Béon 2004 LT 24-26), and 1 ilium (Béon 2004 LT 27).

DESCRIPTION

The specimens clearly show the characteristics of the genus *Rana*. More specifically, several features are typical of species belonging to the "green frogs group", or "water frogs" (i.e. synklepton *Rana esculenta* sensu Dubois & Günther 1982). The *processus coronoideus* of the angulosplenial forms a well developed vertical lamina whose dorsal edge is convex; its extent is similar to that of green frogs. Moreover, the lateral surface of the angulosplenial that is located below the *sulcus Meckeli*, at the level of the *processus coronoideus*, is nearly vertical and limited ventrally by an elongate external mandibular ridge as in green frogs (Bailon 1999). The vertebrae and humeri show all of the characteristics of the genus *Rana*. All available humeri are small, they likely belonged to juvenile individuals (Fig. 3A, B). The only available ilium is damaged (Fig. 3C), but the depth of the supracetabular fossa and the thickness of the ilio-ischiatic face also point to green frogs (Bailon 1991, 1999).

COMMENTS

Green frogs are comparatively frequent in Tertiary localities. The earliest fossils were reported from the early Oligocene (Sanchiz *et al.* 1993), perhaps the late Eocene (Rage 1984a; Holman & Harrison 1999). Several species from the Miocene of Europe likely belong to this assemblage (Rage & Roček 2003), but Sanchiz (1998b) regarded all of them as *nomina dubia*.
Today, the green frogs group includes true species and hybridogenetic "species" that form a complex assemblage. Dubois & Günther (1982) named this assemblage "Synklepton *Rana esculenta*". The morphology of these frogs is very homogeneous and the osteology of several recently recognized living species is unknown. Consequently, it is practically impossible to distinguish extinct species within this complex.

Class REPTILIA McCartney, 1802
Order SQUAMATA Merrem, 1820
Suborder LACERTILIA Owen, 1842
Infraorder SCLEROGLOSSA
Estes, de Queiroz & Gauthier, 1988
Family GEKKONIDAE Gray, 1825

Unidentified genus and species
(Fig. 3D)

MATERIAL EXAMINED. — 2 incomplete dentaries (Béon 2004 LT 28, 29).

COMMENTS

These specimens display the typical features of the family: *sulcus Meckeli* closed; teeth numerous, pleurodont, isodont, slender, and unicuspid. However, the anterior teeth appear to be uncommonly pointed. Identification below family level is impossible.

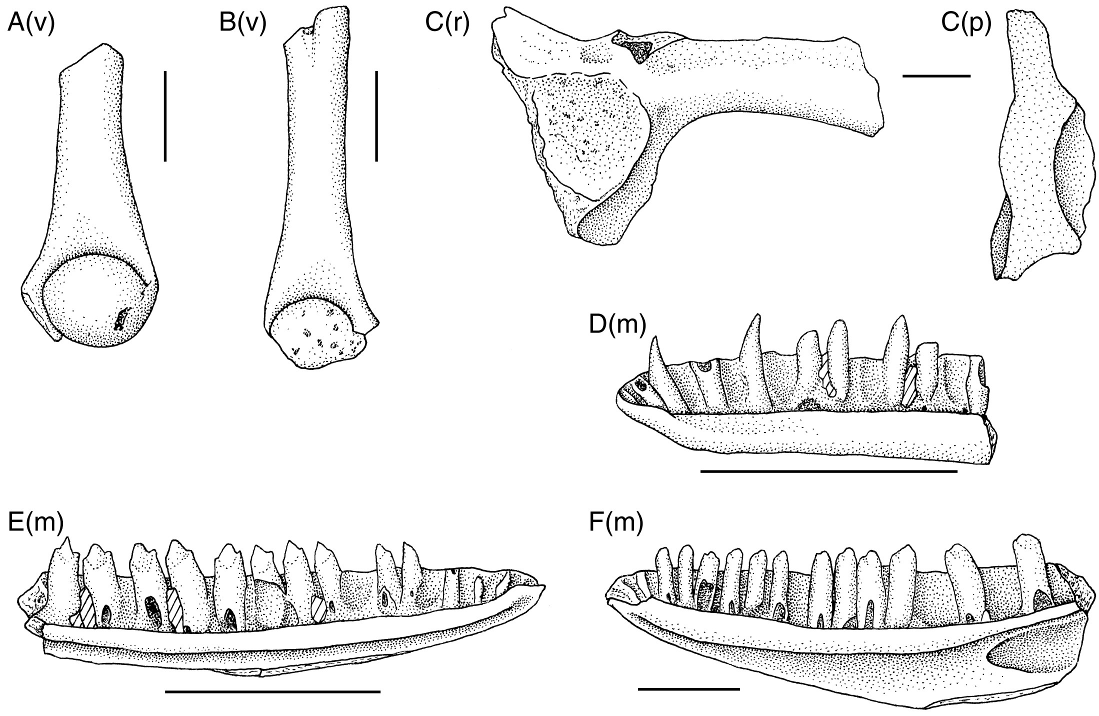

FIG. 3. — **A**-**C**, *Rana* sp. synkl. *R. esculenta* Linnaeus, 1758; **A**, left humerus of a female (Béon 2004 LT 24); **B**, right humerus of a female (Béon 2004 LT 25); **C**, right ilium (Béon 2004 LT 27); **D**, gekkonid lizard, right dentary (Béon 2004 LT 28); **E**, lacertid lizard, unidentified genus and species 1, left dentary (Béon 2004 LT 30); **F**, lacertid lizard, unidentified genus and species 2, right dentary (Béon 2004 LT 32). Medial (**m**), posterior (**p**), right lateral (**r**), and ventral (**v**) views. Scale bars: 2 mm.

Family LACERTIDAE Bonaparte, 1831

As is typical for lacertids, the *sulcus Meckeli* is widely open in the posterior part of the bone and it gradually narrows anteriorly, where it opens ventromedially. The tooth row, *lamina horizontalis*, and ventral border of the dentary are arched ventrally. Teeth are cylindrical, pleurodont, isodont, and generally bi- or tricuspid. Two morphological types appear to be present at Béon 1.

Unidentified genus and species 1
(Fig. 3E)

MATERIAL EXAMINED. — 5 dentaries (Béon 2004 LT 30, 31).

COMMENTS

This lacertid is represented by slender dentaries whose *lamina horizontalis* and ventral border are weakly arched ventrally. The *lamina horizontalis* does not clearly thicken anteriorly and the teeth are generally tricuspid. The weakly arched *lamina horizontalis* and ventral border are reminiscent of *Miolacerta tenuis* Roček, 1984 from Dolnice, Czech Republic (early Miocene, MN 4) and *Edlartetia sansaniensis* (Lartet, 1851) from the middle Miocene (MN 6) of Sansan, France (Augé & Rage 2000). However, in the latter species, the teeth are bicuspid and some are narrowed below the apex. Tricuspid teeth are characteristic of *Miolacerta tenuis* but the available material does not permit us to securely refer the fossils from Béon 1 to this species.

Unidentified genus and species 2
(Fig. 3F)

MATERIAL EXAMINED. — 2 dentaries (Béon 2004 LT 32, 33).

COMMENTS

This lizard is represented by dentaries larger than those of the preceding species. The dentaries are clearly arched and the teeth are bicuspid. In addition, the *lamina horizontalis* is thicker than in the other species, mainly anteriorly. These dentaries cannot be assigned to a described species.

Indeterminate lacertids

MATERIAL EXAMINED. — 2 premaxillae (Béon 2004 LT 34), 4 fragments bearing teeth (Béon 2004 LT 35), 1 humerus (Béon 2004 LT 36), 1 femur (Béon 2004 LT 37).

Within lacertilians, identification of premaxillae and long bones is often difficult. However, the overall morphology of the specimens from Béon 1 appears to be consistent with the Lacertidae and different from that of the other families present in the locality. It is not possible to determine to which of the above lacertid types they belong.

Family ANGUIDAE Gray, 1825
Genus *Pseudopus* Merrem, 1820

Pseudopus laurillardi (Lartet, 1851)
(Fig. 4A, B)

Anguis ? *Laurillardi* Lartet, 1851: 40.

Ophisaurus ? *laurillardi* – Estes 1983: 143.

Pseudopus laurillardi – Augé & Rage 2000: 276-278, figs 9-13.

Pseudopus laurillardi was redescribed by Augé & Rage (2000) on the basis of cranial bones from the middle Miocene (MN 6) of Sansan, France. The material from Béon 1 includes a posterior part of braincase, i.e. a skeletal element previously unknown for the species, and additional characters can be observed on the dentary. Therefore, an emended diagnosis is proposed.

MATERIAL EXAMINED. — Posterior part of a braincase (Béon 2004 LT 38), 1 right dentary (Béon 2004 LT 39), 44 trunk vertebrae (Béon 2004 LT 40-42; Béon 93 E3 SN 1; Béon 98 déblais SN 1), 3 sacral vertebrae (Béon 2004 LT 43), 82 caudal vertebrae (Béon 2004 LT 44-47; Béon 93 E3 SN 2), 16 osteoderms (Béon 2004 LT 48).

EMENDED DIAGNOSIS. — *Pseudopus laurillardi* differs from the three other species of the genus (*P. apodus* (Pallas, 1775), *P. pannonicus* (Kormos, 1911), *P. moguntinus* (Boettger, 1875)) in having larger anterolateral processes of the parietal. It is distinguished from *P. apodus* and *P. pannonicus* in having a more ventrally arched dentary, a *lamina horizontalis* of the dentary strongly projecting medially, a broad *sulcus dentalis*, a weak angulation between the alveolar surface of the parapet and the subdental shelf, a thicker ventral border of the trigeminal notch, a more developed interfenestral crest, more concave posteromedial surfaces of paroccipital processes, and straight dorsal ridges (instead of curved ridges) on the posterior braincase. It further differs from *P. apodus* by its more weakly striated teeth and more robust dentary. Apparently, it further differs from *P. moguntinus* in having a short groove on the lateroventral margin of the anterior part of the dentary.

DESCRIPTION

The dentary from Béon 1 compares favorably with the neotype, i.e. a left dentary (designated by Augé & Rage 2000) and all other dentaries of *P. laurillardi* from Sansan. The dentary from Béon 1 is slightly smaller than the neotype but it falls within the range of variation of the species. In both specimens, the ventral border and *lamina horizontalis* are markedly arched ventrally, the teeth are blunt, amblyodont, and their apices are weakly striated, and the anterior inferior alveolar foramen is located beneath the 6th tooth from the rear. In addition, other features not reported in Augé and Rage's description occur in the two specimens: the bone is robust and its lateral surface is clearly convex in cross section; the *lamina horizontalis* prominently extends medially, has a rounded medial border and dorsally it forms a subhorizontal subdental shelf that is slightly separated from the alveolar surface of the parapet by a weak angulation. As a consequence of the strong medial extension of the *lamina horizontalis*, the tooth row is clearly separated from the medial border of the *lamina*. A broad *sulcus dentalis* is present. On the lateroventral margin of the anterior part of the bone, a short and shallow groove runs anteroposteriorly. The smaller dentaries from Sansan perhaps lack the latter groove.

A posterior part of braincase is referred to *P. laurillardi*. The type locality, Sansan, did not yield braincases. On the whole, the specimen from Béon 1 is similar to the posterior braincase of the only living species of the genus, *P. apodus*, that ranges from Croatia to Central Asia and the middle East. Four features are worth mentioning. On the dorsal face of the braincase of *P. laurillardi*, each dorsal ridge (dr, Fig. 4B) that joins the base of each paroccipital process to the *processus ascendens* of the supraoccipital is straight. The part of the prootic that is ventral to the trigeminal notch is thick and, consequently, the ventral border (vb, Fig. 4B) of the notch forms an elongate and relatively broad subtriangular surface that faces dorsolaterally. The interfenestral ridge, between the oval fenestra and occipital recess (= round fenestra), appears to be well developed, and the posteromedial surfaces (pms, Fig. 4B) of the paroccipital processes are clearly concave.

Vertebrae show the typical morphology of anguines; they are assigned to *P. laurillardi* because their size is consistent with the above skull bones, their centrum more clearly widens anteriorly than in vertebrae of *Ophisaurus* (see below), and their ventral surface is nearly flat. Osteoderms are referred to *P. laurillardi* only on the basis of their size.

COMMENTS

According to Augé & Rage (2000), the dentary of *P. laurillardi* differs from that of *P. apodus* by having weaker striae on the apices of teeth and by the more anteriorly located anterior inferior alveolar foramen. They also stated that *P. laurillardi* differs from *P. moguntinus* (= *Propseudopus fraasi* Hilgendorf, 1883) (latest Oligocene-middle Miocene of Central Europe) and *P. pannonicus* (late Miocene-middle Pleistocene of Central and Eastern Europe) by its smaller size. The position of the anterior inferior alveolar foramen does not appear to be a reliable feature because in *P. apodus* it sometimes occurs beneath the limit between the 5th and 6th teeth (from the rear) or even entirely below the 6th tooth as in *P. laurillardi* (Roček 1980: fig. 1). But, following the study of the material from Béon 1, we may add some other features that characterize the dentary of *P. laurillardi*. It is more robust than that of *P. apodus* and more arched than that of *P. apodus* and *P. pannonicus*. Moreover, in *P. laurillardi* the dorsal surface of the *lamina horizontalis* (i.e. the subdental shelf) is subhorizontal; in other words, there appears to be a weak angulation between the alveolar surface of the parapet and the subdental shelf, which is unusual in anguines; in *P. apodus* and *P. pannonicus*, the alveolar surface and the subdental shelf form a single oblique surface, without any angulation. According to the illustrations of the dentary of *Propseudopus fraasi* (i.e. *Pseudopus moguntinus*) in Hilgendorf (1885), an angulation is perhaps present also in this species. Finally, the strong medial projection of the *lamina horizontalis* and the presence of a *sulcus dentalis* clearly distinguish *P. laurillardi* from *P. apodus* and *P. pannonicus*. These two features appear to be present in *P. moguntinus*.

Several traits of the braincase should be added to the features that characterize *P. laurillardi*. A conspicuous difference between the posterior braincase of *P. laurillardi* and those of *P.* cf. *P. pannonicus* from Montoussé 5 (late Pliocene, France; Bailon 1991), *P. pannonicus*, and *P. apodus* is that in *P. laurillardi*, the dorsal ridges (dr, Fig. 4B) are straight, whereas they are medially concave in the other forms. Moreover, *P. laurillardi* differs from *P. apodus* and *P. pannonicus* in having thicker ventral borders of the trigeminal notches (vb, Fig. 4B), more developed interfenestral ridges, and more concave posteromedial surfaces of the paroccipital processes (pms, Fig. 4B). The distinction between *P. laurillardi* and the poorly known *P. moguntinus* cannot be easily established. However, aside from its larger size and smaller anterolateral processes of parietal, *P. moguntinus* apparently lacks the short groove that runs anteroposteriorly on the ventrolateral

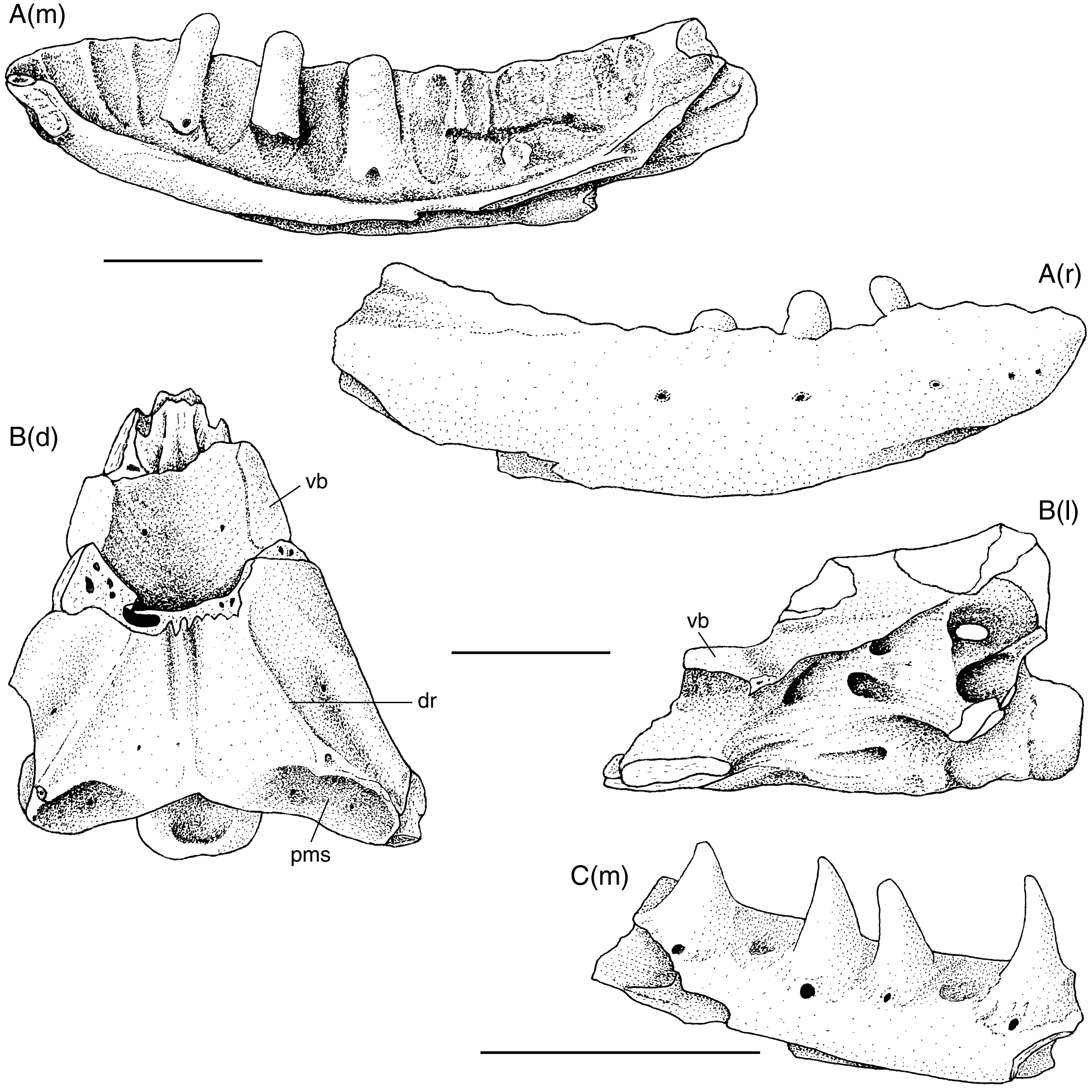

FIG. 4. — **A**, **B**, *Pseudopus laurillardi* (Lartet, 1851); **A**, right dentary (Béon 2004 LT 39); **B**, posterior part of a braincase (Béon 2004 LT 38); **C**, *Ophisaurus* sp., left dentary (Béon 2004 LT 49). Dorsal (**d**), left lateral (**l**), medial (**m**), and right lateral (**r**) views. Abbreviations: **dr**, dorsal ridge; **pms**, posteromedial surface of paroccipital process; **vb**, ventral border of trigeminal notch. Scale bars: A, B, 5 mm; C, 2 mm.

margin of the dentary (Hilgendorf 1885), even on large specimens; this groove occurs in *P. laurillardi*, *P. apodus*, and *P. pannonicus*. Augé & Rage (2000) suggested that *P. moguntinus* might be referred to the synonymy of *P. laurillardi*, but the few above characters will have to be considered when the former species is revised.

Finally, the parietal provides a feature that markedly distinguishes *P. laurillardi* from the other species: the anterolateral processes of the parietal (improperly termed "prefrontal processes" in Augé & Rage 2000, partly following Fejérváry-Lángh 1923) of *P. apodus*, *P. moguntinus*, and *P. pannonicus* are smaller than those of *P. laurillardi*. However, only one parietal is known from Sansan (Augé & Rage 2000); this bone has not been found at Béon 1. *Pseudopus laurillardi* has been found only at Béon 1 (MN 4) and Sansan (MN 6).

Genus *Ophisaurus* Daudin, 1803

Ophisaurus sp.
(Fig. 4C)

MATERIAL EXAMINED. — 1 fragmentary left dentary (Béon 2004 LT 49), and perhaps 1 pterygoid (Béon 2004 LT 50) and 20 vertebrae (Béon 2004 LT 51, 52).

COMMENTS

On the dentary, the subdental shelf and alveolar surface of the parapet form a single, inclined surface; as a result, the implantation of teeth is subpleurodont. The *lamina horizontalis* does not project medial to the bases of teeth. The teeth are conical; their apices are pointed, slightly recurved and not striated. Such teeth are reminiscent of those of *Ophisaurus* (*sensu* Klembara 1979, 1981; i.e. *Dopasia* Gray, 1853 included) of the European type. But a more precise identification is impossible.

One pterygoid and 20 vertebrae or so, that display the anguine morphology, are tentatively assigned to this taxon on the basis of size consistency. Moreover, the centrum is less widened anteriorly and the ventral surface more convex than in *Pseudopus*, and the subcentral ridges are slightly concave in ventral aspect.

Family VARANIDAE Gray, 1827
Genus *Varanus* Merrem, 1820

Varanus sp.
(Fig. 5)

MATERIAL EXAMINED. — 1 axis (Béon 2004 LT 53), 2 trunk (Béon 2004 LT 54, 55) and 1 sacral (Béon 2004 LT 56) vertebrae.

COMMENTS

The referral of these vertebrae to the Varanidae is based on the following features: axis elongate and provided with a robust hypapophysis; extremity of the hypapophysis somewhat expanded and bearing two articular surfaces; trunk vertebrae with a well demarcated *pars tectiformis* on the anterior part of the neural arch; ventral surface of centrum widened anteriorly and convex ventrally in cross section; condyle strongly depressed, its articular surface facing mainly dorsally (Hoffstetter 1969; Hoffstetter & Gasc 1969; Estes 1983).

In Western Europe, two varanid genera have been reported from the Miocene: *Iberovaranus* Hoffstetter, 1969, from the late early, and perhaps early middle Miocene of the Iberian Peninsula (Hoffstetter 1969; Antunes & Rage 1974; Rage & Augé 1993) and the extant *Varanus* known from the early Miocene (MN 4, see below) to the early/late Pliocene (Hoffstetter 1969; Estes 1983; Bailon 1991, 1992; Rage & Augé 1993). *Iberovaranus* differs from *Varanus* in having more elongate neural arches, narrower condyles, and less pronounced precondylar constriction (Hoffstetter 1969). The vertebrae from Béon 1 show the typical morphology of *Varanus*; more specifically, the precondylar constriction is very characteristic.

Remains of *Varanus* found in the Miocene of Western Europe have been either allocated to *Varanus hofmanni* Roger, 1898 (MN 6, middle Miocene of Germany; Roger 1898; Hoffstetter 1969) or doubtfully referred to this species (early to late Miocene of Spain and France; Hoffstetter 1969; Alférez Delgado & Brea López 1981). But these varanids have not been really studied.

Specimens from Béon 1 are approximately similar to those from Artenay (early part of MN 4, France) that represent the oldest *Varanus* in Europe (see below). However, trunk vertebrae from Artenay are slightly larger than those from Béon 1 and anterior trunk vertebrae have slightly less concave subcentral ridges in ventral aspect.

The paucity of the material does not permit us to draw definite conclusions. Pending a revision of *Varanus hofmanni*, the specimens from Béon 1 are referred to as *Varanus* sp.

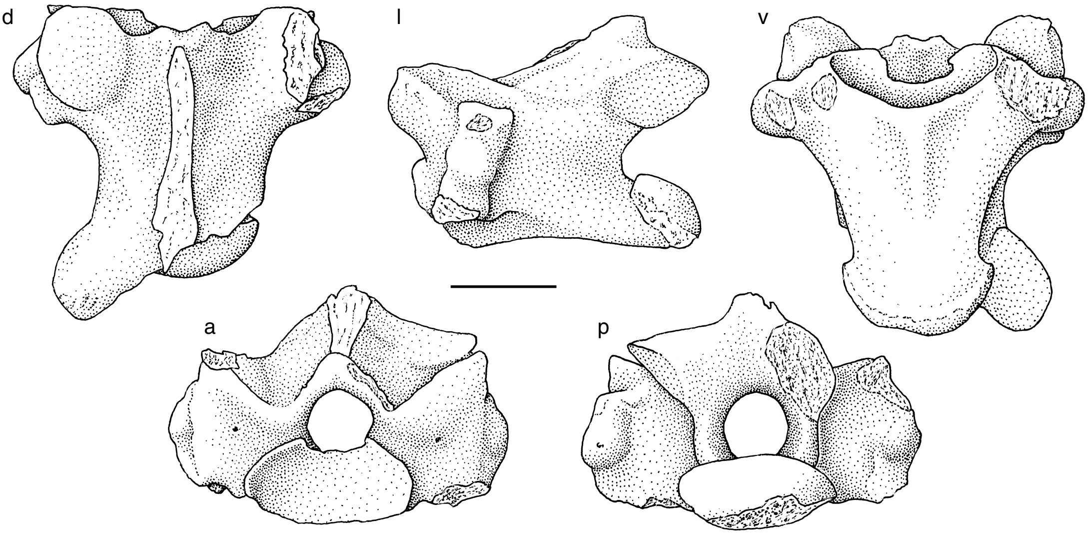

FIG. 5. — *Varanus* sp., trunk vertebra (Béon 2004 LT 54), in anterior (**a**), dorsal (**d**), left lateral (**l**), posterior (**p**), and ventral (**v**) views. Scale bar: 5 mm.

REMARKS ON THE OLDEST RECORDS OF *VARANUS*

Varanus sp. from Béon 1 is one of the oldest representatives of the genus in Europe. Artenay (MN 4, France), that is slightly older than Béon 1, produced the earliest European *Varanus*. Hoffstetter (1969) reported that the latter appears to be morphologically close to the vertebrae from Vieux-Collonges (MN 4/5, France) and La Grive (MN 7+8, France) referred to as *Varanus* cf. *V. hofmanni*. *Varanus* was also reported (as *V.* ? *hofmanni*) from Córcoles, Spain, a locality that is approximately contemporaneous with Béon 1 (Alférez Delgado & Brea López 1981); but it should be noted that the identification of the Spanish fossil rests on a single caudal vertebra. Since no other *Varanus* has been reported from the Orleanian of the Iberian Peninsula, while *Iberovaranus* is known from this stage and in this area, it may be entertained whether the specimen from Córcoles really belongs to *Varanus*.

In Africa also, *Varanus* is present in the early Miocene. According to Hoffstetter (1969) and Estes (1983), the genus is present in the early Miocene (without precision) of Kenya, but Clos (1995) and Rage (2003a) reported *Varanus* from levels that may be equated with the European Agenian or Orleanian (approximately the Aquitanian and Burdigalian in terms of international reference stages). The oldest African locality that yielded *Varanus* is Songhor (Kenya). According to Clos (1995), the specimens from this locality are reminiscent of *V. rusingensis* Clos, 1995, from Rusinga (Kenya), a slightly younger locality. Songhor is located at about 19.5-19.9 Ma; therefore, according to Pickford & Senut (1999) it would correlate to the upper part of the European zone MN 2, i.e. to the late Agenian (= late Aquitanian).

In Australia, a varanid (probably *Varanus*) was present as early as the latest Oligocene in the Hiatus A locality (Scanlon pers. comm.). That Australian fossil, if really *Varanus*, is the earliest known representative of the genus. Since it seems doubtful that *Varanus* originated in Australia, this suggests that older *Varanus* are probably present in Asia.

But, in Asia, all pre-Miocene reports of *Varanus* are questionable. The genus was doubtfully reported from the middle Eocene (now regarded early Eocene; Averianov & Godinot 1998) of Kyrgyzstan by Reshetov *et al.* (1978). But, this genus only appears in a faunal list, without any description.

Zerova & Ckhikvadze (1986) rightly questioned this report; they identified the fossil as a "vertebra of a large lizard, probably related to Varanidae". Alifanov (1993) reported *Varanus* sp. from the middle Eocene and early Oligocene of Mongolia. Figures of the dorsal and ventral faces of a vertebra from the middle Eocene are given but the specimens from the early Oligocene are not described. The figures do not demonstrate that the fossil from the Eocene belongs to *Varanus*. Therefore, the oldest confirmed remains of *Varanus* from Asia are vertebrae of *V. pronini* Zerova & Ckhikvadze, 1986, from the middle Miocene (without more precision) of Kazakhstan (Zerova & Ckhikvadze 1986).

SCLEROGLOSSA *incertae sedis*
AMPHISBAENIA Gray, 1844

Indeterminate amphisbaenian

MATERIAL EXAMINED. — 4 trunk vertebrae (Béon 2004 LT 57).

COMMENTS

The vertebrae show features that are found in both the Amphisbaenidae and Blanidae (the latter family has been erected recently by Kearney 2003): vertebrae markedly depressed; neural spine faint or absent; zygosphene-zygantrum system absent; paradiapophyses globular; ventral surface of centrum only slightly convex in cross-section, without any trace of ridge. Vertebrae do not permit further identification.

SERPENTES Linnaeus, 1758
Infraorder SCOLECOPHIDIA
Duméril & Bibron, 1844

Indeterminate scolecophidian

MATERIAL EXAMINED. — 1 trunk vertebra (Béon 2004 LT 58).

COMMENTS

A tiny, incomplete vertebra represents a scolecophidian (length from prezygapophysis to postzygapophysis: 1.2 mm). It displays a combination of characters that is characteristic of the group: vertebra depressed; long axis of prezygapophyseal facet clearly oriented anteriorly but prezygapophyseal process directed more transversely (as shown by its preserved base); paradiapophyses blocky and lacking any trace of subdivision; posterior median notch in the neural arch absent (inferred from the preserved part of the neural arch).

The vertebral morphology is very homogeneous within the group and identification is impossible, even at family level. Only one extinct species was described from Europe: *Typhlops grivensis* Hoffstetter, 1946, from the middle Miocene (MN 7+8) of France; its generic assignment may be questioned (Rage 1984b).

In Europe, scolecophidians are known from the earliest to the late Eocene (Crochet *et al.* 1981; Rage 1984b) but they are lacking in most of the Oligocene. They are again present in the latest Oligocene, at La Colombière, France (MP 30; unpublished). During the Miocene, the group extended from Western to Eastern Europe (Szyndlar 1985, 1991a; Hír *et al.* 2001), but during the Pliocene it was restricted to southern Europe, from Spain to Greece (Bailon 1991; Szyndlar 1991a). In Europe, the only living species inhabits the Balkan and eastern Caucasian regions (Darevsky 1997).

Infraorder ALETHINOPHIDIA Nopcsa, 1923
Family BOIDAE Gray, 1825
Genus *Python* Daudin, 1803

Python europaeus Szyndlar & Rage, 2003
(Fig. 6A)

python – Rage 1987: 63.

Python sp. – Ivanov 2000: 561-563; 2001: 564, tab. 1; 2002: 531, fig. 12, tab. 1.

Python europaeus Szyndlar & Rage, 2003: 68-72, figs 31-33.

MATERIAL EXAMINED. — 33 trunk vertebrae (Béon 2004 LT 59; Béon 93 E3 SN 3, 4; Béon 98 E3 3023, 3040, 3053, 3056; Béon 98 F1 3049) and 1 caudal vertebra (Béon 2004 LT 60).

COMMENTS

Python europaeus was described recently on the basis of specimens from Vieux-Collonges (MN 4/5, early/middle Miocene transition) and "old levels" from La Grive (MN 5, early middle Miocene), both localities in France (Szyndlar & Rage 2003). The assignment of this species to *Python* rests mainly on one single palatine from Vieux-Collonges, but the vertebrae also show a combination of features that is characteristic for this genus: haemal keel well defined by subcentral grooves or depressions that reach the cotyle, but only its posterior part projects below the centrum (Scanlon & Mackness 2001); neural arch markedly vaulted and upswept above the zygantrum; zygapophyseal facets weakly inclined; paracotylar foramina absent. Within *Python*, the vertebrae of *P. europaeus* are characterized by their low neural spines. The vertebrae from Béon 1 are quite similar to those from Vieux-Collonges and La Grive. The largest vertebra from Béon 1 (centrum length: 11.1 mm) is slightly larger than those from Vieux-Collonges and La Grive (centrum lengths: 10.1 and 10.7 mm respectively) but, on the whole, the size is similar in the three localities. Only one difference may be noted: at Béon 1, the central lobe of the zygosphene, when present, is more prominent than in the other localities. *P. europaeus* is restricted to the late early and early middle Miocene (MN 4 and MN 5) of France. Béon 1 has yielded the earliest representatives of the species.

Family COLUBRIDAE Oppel, 1811
"Colubrines"
Genus *Coluber* Linnaeus, 1758

Coluber pouchetii (Rochebrune, 1880)

pars *Coluber sansaniensis* Lartet, 1851: 40.

Tamnophis Pouchetii – Rochebrune 1880: 281, pl. 12, fig. 9.

Sansanosaurus pouchetii – Kuhn 1939: 21.

Coluber pouchetii – Rage 1981: 540, 541, fig. 1B. — Augé & Rage 2000: 296-298, figs 26-28.

MATERIAL EXAMINED. — 12 trunk vertebrae (Béon 2004 LT 61).

COMMENTS

Coluber pouchetii, a large species, was revised and redescribed by Rage (1981) and Augé & Rage (2000) on the basis of material from Sansan (MN 6). In Europe, other extinct large species referred to *Coluber* are *C. dolnicensis* Szyndlar, 1987, from the early Miocene of Merkur-North (MN 3) and Dolnice (MN 4), Czech Republic (Szyndlar 1987; Ivanov 2002), *C. caspioides* Szyndlar & Schleich, 1993, from the early Miocene of Merkur-North (MN 3), Petersbuch 2 (MN 4, Germany) and perhaps Oberdorf (MN 4, Austria) (Szyndlar & Schleich 1993; Szyndlar 1998; Ivanov 2002), and *C. suevicus* (Fraas, 1870) from Steinheim (MN 7+8, Germany) and apparently Merkur-North (Szyndlar & Böhme 1993; Ivanov 2002).

In addition to their large size, these four species share some other traits: anterior border of zygosphene more or less straight between the lateral lobes, with sometimes a small median notch; neural arch weakly depressed to weakly vaulted (except in the overgrown *C. suevicus*); posterior borders of neural arch nearly straight or even straight in posterior view; neural spine not low. Moreover, two peculiar characters suggest that *C. pouchetii* and *C. dolnicensis* might be closely related. In both species, the diapophysis is shifted posteriorly with regard to the parapophysis and the haemal keel forms a step in the anterior part of the centrum. However, the step is present in all vertebrae of *C. dolnicensis* whereas it clearly occurs only in the posterior trunk region of *C. pouchetii*; in the mid- and anterior trunk regions of the latter species it is weak or absent. *C. pouchetii* further differs from *C. dolnicensis* in having slightly shorter vertebrae and longer prezygapophyseal processes. In *C. caspioides* and *C. suevicus*, the diapophysis is not clearly shifted posteriorly and the step of the haemal keel is lacking. *C. pouchetii* further differs from *C. caspioides* in having a lower neural spine and from *C. suevicus* in having longer prezygapophyseal processes.

It should be noted that the Pliocene of Punta Nati (Balearic Islands) has yielded a species of *Coluber* that displays the two characters that are common to both *C. dolnicensis* and *C. pouchetii*. Moreover, as in the latter species, in the Balearic form the step of the haemal keel is restricted to the posterior trunk region (Bailon *et al.* in press). But because of some differences, Bailon *et al.* (in press) did not assign this snake to *C. pouchetii*; they only referred it to the "*C. dolnicensis-C. pouchetii* group".

Coluber pouchetii is known only from Béon 1 (MN 4) and Sansan (MN 6).

Genus *Texasophis* Holman, 1977

Texasophis is an extinct genus known only by trunk vertebrae. The latter are elongate, relatively depressed, and their neural arch is moderately vaulted. The neural spine is low, the prezygapophyseal processes short, the haemal keel clearly limited, and the subcentral ridges are well marked. *Texasophis* has been reported from the Oligocene and Miocene of Europe and North America.

Texasophis meini Rage & Holman, 1984

undescribed species of *Texasophis* – Holman 1984: 225, fig. 2.

Texasophis meini Rage & Holman, 1984: 91-93, fig. 2. — Szyndlar 1987: 63, 65; 1991a: 112. — Augé & Rage 2000: 300.

MATERIAL EXAMINED. — 16 trunk vertebrae (Béon 2004 LT 62, 63; Béon 98 F1 3076).

COMMENTS

The most typical feature of this species is its well limited, oblong to oblanceolate (*sensu* Auffenberg 1963) haemal keel, whose ventral surface is flat. In the type locality, La Grive M, the width of the haemal keel shows variation; the holotype has one of the widest keel. Most vertebrae from Béon 1 have wide haemal keels, some being wider than that of the holotype, whereas at Sansan they are generally narrower. However, the specimens from Béon 1 fall within the limits of the intraspecific variation.

T. meini is known from France (MN 6 and MN 7+8) (Rage & Holman 1984; Augé & Rage 2000; Ivanov 2002), Germany (MN 5; Szyndlar pers. comm.), Hungary (MN 6 or 7+8) (Gál *et al.* 1999), and Ukraine (MN 9; Szyndlar 1991a and pers. comm.). In Central Europe the genus is represented by *T. bohemiacus* that extends from the early Oligocene (MP 22) in Germany to the late early Miocene (MN 4) in the Czech Republic (Szyndlar 1987). This species is clearly distinguished from *T. meini* by its narrow haemal keel. Vieux-Collonges (MN 4/5) also yielded *Texasophis* but although the locality is stratigraphically intermediate between Béon 1 and Sansan, the species is perhaps not *T. meini*. It was referred to as *Texasophis* sp. (Ivanov 2000).

Indeterminate colubrines

MATERIAL EXAMINED. — 41 trunk vertebrae (Béon 2004 LT 64).

Identification of these incomplete vertebrae is difficult. Apparently, they do not resemble described taxa from the locality.

Subfamily NATRICINAE Bonaparte, 1838
Genus *Natrix* Laurenti, 1768

Natrix sansaniensis (Lartet, 1851)

pars *Coluber sansaniensis* Lartet, 1851: 40.

Pylmophis sansaniensis – Rochebrune 1880: 282, 283, pl. 12, fig. 11.

Pilemophis sansaniensis – Lydekker 1888: 251.

Natrix sansaniensis – Rage 1981: 538-540, fig. 1A; 1984b: 48, 49, fig. 3A. — Augé & Rage 2000: 288-299, figs 21, 22. — Ivanov 2002: 523-525, fig. 7.

pars *Natrix* aff. *N. sansaniensis* – Szyndlar & Schleich 1993: 17-20, fig. 4A-H.

MATERIAL EXAMINED. — 144 trunk vertebrae (Béon 2004 LT 65-68; Béon 91 E3 SN 1).

Comments

Natrix sansaniensis was revised and redescribed by Rage (1981) and Augé & Rage (2000). The species appears as a typical member of *Natrix*. It is mainly characterized by its high neural spines and the peculiar morphology of its hypapophyses (unusual combination of a curved anteroventral border and a pointed tip).

N. sansaniensis was reported from Sansan (MN 6, France), the type locality, and Merkur-North (MN 3, Czech Republic) (Augé & Rage 2000; Ivanov 2002). The species is perhaps present in the early middle Miocene of Vieux-Collonges (*Natrix* aff. *N. sansaniensis*; Ivanov 2000). *Natrix* cf. *N. sansaniensis* was reported from La Grive M (MN 7+8; France) by Ivanov (2002) and from Mátraszölös 1 (MN 6 or 7+8; Hungary) by Gál *et al.* (1999). Moreover, numerous vertebrae from Petersbuch 2 (MN 4; Germany) were referred to as *Natrix* aff. *N. sansaniensis* by Szyndlar & Schleich (1993); but, after the description of the species *N. merkurensis* by Ivanov (2002) it may be supposed that a part of the vertebrae assigned to the fossil from Petersbuch 2 really belongs to *N. sansaniensis* (see below: *Natrix merkurensis*).

***Natrix* cf. *N. longivertebrata* Szyndlar, 1984**

Material examined. — 1 trunk vertebra (Béon 2004 LT 69).

Comments

A single, incomplete specimen displays the characteristic traits of *N. longivertebrata*: vertebra elongate; centrum narrow, elongate, and limited by strong subcentral ridges; hypapophysis prolonged anteriorly by a salient ridge; prezygapophyseal processes stout and dorsoventrally flattened; neural arch depressed; neural spine very low, overhanging anteriorly and whose dorsal edge slopes posteriorly; parapophyseal processes strong and clearly directed anteriorly. Despite the fact that all these characters are observable, this single, damaged specimen cannot be assigned to *N. longivertebrata* without reservation. Vertebrae of *N. longivertebrata* were illustrated by Szyndlar (1984: fig. 29; 1991b: fig. 3) and Bachmayer & Szyndlar (1985: fig. 2).

N. longivertebrata is closely related to the living *N. natrix* (Szyndlar 1991b; Ivanov 1999). It is known from the Pliocene (MN 14 to MN 16) of Hungary, Poland, and Moldova (Szyndlar 1991c; Venczel 2001). *Natrix* aff. *N. longivertebrata* was reported from the middle Miocene of Sansan (MN 6) and La Grive L7, and perhaps La Grive L3 (MN 7+8) (Rage & Szyndlar 1986; Augé & Rage 2000). The species is perhaps present (*N.* cf. *N. longivertebrata*) in the late Miocene of Austria, Hungary, and Ukraine (Szyndlar & Zerova 1992; Venczel 1998). Consequently, if the vertebra from Béon 1 really belongs to *N. longivertebrata*, then it represents the earliest occurrence of the species.

***Natrix* aff. *N. merkurensis* Ivanov, 2002**
(Fig. 6B)

Material examined. — 24 trunk vertebrae (Béon 2004 LT 70, 71).

Comments

N. merkurensis is based on vertebrae and skull bones from Merkur-North (MN 3; Czech Republic). The vertebrae are mainly characterized by the peculiar combination of an elongate and narrow centrum that is reminiscent of *N. longivertebrata* and a neural spine as high as that of *N. sansaniensis* (Ivanov 2002).

The species might be present also at Petersbuch 2 (MN 4; Germany). A natricine from the latter locality was first regarded as a possible variant of *N. sansaniensis* by Szyndlar & Schleich (1993) who reported it as *Natrix* aff. *N. sansaniensis*. But, after having described *Natrix merkurensis*, Ivanov (2002) suggested that the snake from Petersbuch 2 belongs to the latter species. However, Szyndlar & Schleich (1993) noted that the main characteristic of the natricine from Petersbuch 2 is vertebral polymorphism and they hinted at the possible presence of more than a single species. Therefore, it may be entertained whether all vertebrae from Petersbuch 2 or only a part of them belong to *N. merkurensis*. Both *N. sansaniensis*

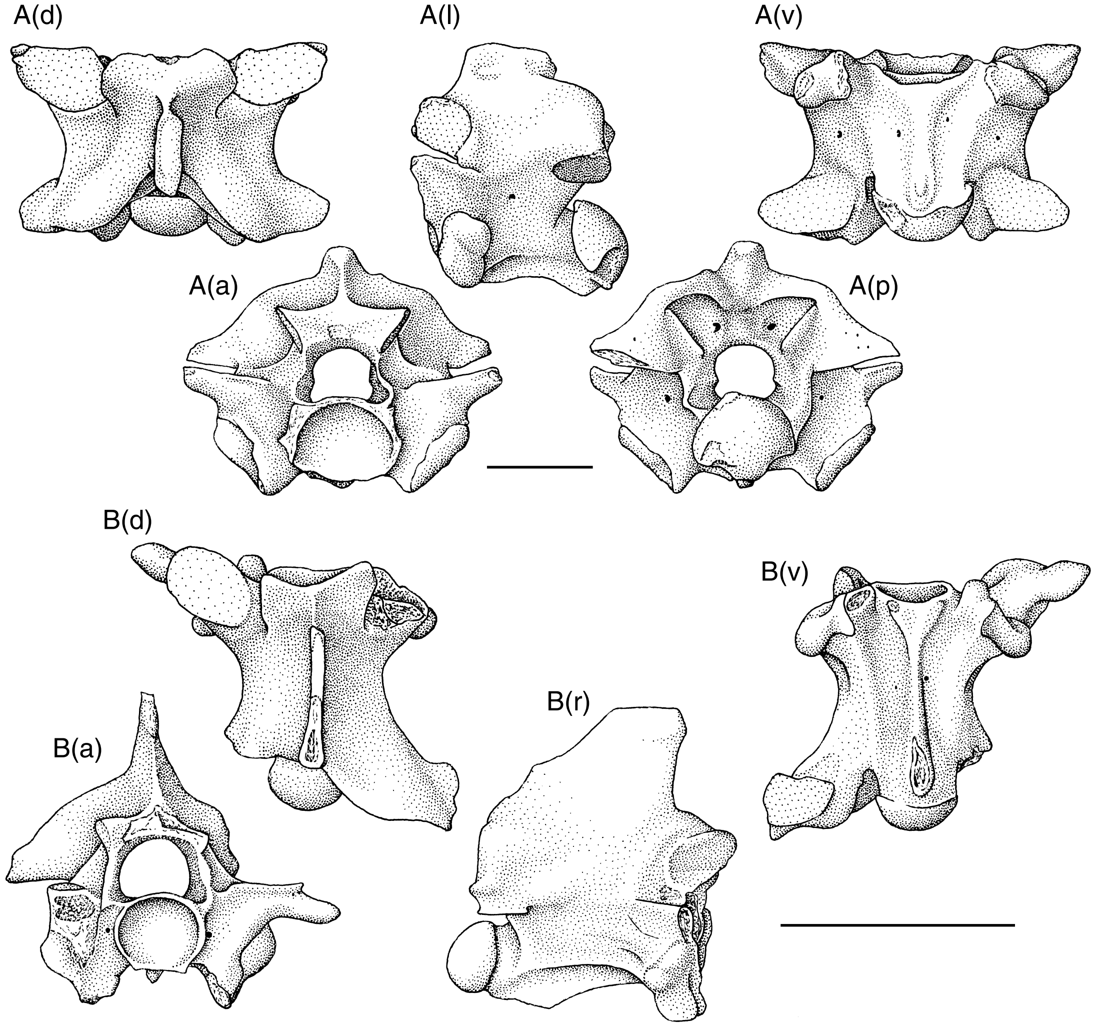

FIG. 6. — Snakes; **A**, *Python europaeus* Szyndlar & Rage, 2003, trunk vertebra (Béon 93 E3 SN 3); **B**, *Natrix* aff. *N. merkurensis* Ivanov, 2002, trunk vertebra (Béon 2004 LT 70). Anterior (**a**), dorsal (**d**), left lateral (**l**), posterior (**p**), right lateral (**r**), and ventral (**v**) views. Scale bars: 5 mm.

and *N. merkurensis* are perhaps present at Petersbuch 2.

At Béon 1, all vertebral characters, but one, are consistent with *N. merkurensis*: centrum elongate and narrow; subcentral ridges prominent; hypapophysis prolonged anteriorly by a prominent keel; neural spine high; dorsal edge of neural spine slightly forked anteriorly and posteriorly; tip of hypapophysis rounded; prezygapophyseal facets rather broad for typical *Natrix*; subcotylar tubercles present; parapophyseal processes directed anteriorly (rarely anteroventrally); epizygapophyseal spines present. The only difference is that, at Béon 1, the prezygapophyseal processes are shorter than those of *N. merkurensis* from Merkur-North; consequently, this natricine from Béon 1 is referred to as *Natrix* aff. *N. merkurensis*.

Genus *Palaeonatrix* Szyndlar, 1982

Palaeonatrix* aff. *P. lehmani
(Rage & Roček, 1983)

Dolniceophis lehmani Rage & Roček, 1983: 17-21, pls 1-2.

Palaeonatrix lehmani – Szyndlar 1987: 60, 61, fig. 5.

MATERIAL EXAMINED. — 18 trunk vertebrae (Béon 2004 LT 72, 73).

COMMENTS

On the whole, the vertebrae are reminiscent of *N. longivertebrata*. However, the base of the haemal keel extends anteriorly as a deep keel, the subcentral ridges reach the condyle, the neural arch is less depressed, and the paradiapophyses strongly project below the centrum. Vertebrae of *P. lehmani* are figured in Rage & Roček 1983 (pl. I, II, as *Dolniceophis lehmani*), Szyndlar 1987 (fig. 2), and Szyndlar & Schleich 1993 (fig. 5).

P. lehmani was reported from the early Miocene (MN 4) of Dolnice, Czech Republic, and Petersbuch 2, Germany (Szyndlar & Schleich 1993). Another species, *P. silesiaca*, is known from the middle Miocene (MN 7+8) of Poland (Szyndlar 1982).

Palaeonatrix aff. *P. lehmani* was reported from the middle Miocene (MN 6) of Sansan (Augé & Rage 2000); it could not be referred to *P. lehmani* without reservation because several specimens show tendencies toward *P. silesiaca* Szyndlar, 1982 (sizes of neural canal, condyle and cotyle). The specimens from Béon 1 do not show these tendencies; however, they differ from the typical specimens of the species in having more vaulted neural arches.

Genus *Neonatrix* Holman, 1973

Neonatrix is an extinct genus from the Miocene of North America and Europe; it perhaps extends up to the early Pliocene in Europe (Venczel 2001). Species assigned to *Neonatrix* are characterized by their small size and short hypapophyses that do not project posteriorly behind the limit of the condyle. Szyndlar & Schleich (1993) and Szyndlar & Böhme (1993) rightly questioned the validity of this genus. It might be only an artificial, polyphyletic taxon based on homoplastic features, that should be split into two or more genera. However, we retain it pending further studies.

Neonatrix europaea Rage & Holman, 1984

Neonatrix europaea Rage & Holman, 1984: 94-96, fig. 4. — Szyndlar 1987: 61. — Szyndlar & Schleich 1993: 22. — Augé & Rage 2000: 294, 295.

MATERIAL EXAMINED. — 4 trunk vertebrae (Béon 2004 LT 74).

COMMENTS

These specimens are referred to *N. europaea* on the basis of their relatively elongate shape, vaulted neural arch, large neural canal, and relatively long prezygapophyseal processes. The species was reported only from France: middle Miocene of Sansan (MN 6) and La Grive M (MN 7+8), and perhaps from the early/middle Miocene of Vieux-Collonges (MN 4/5).

Neonatrix natricoides Augé & Rage, 2000

Neonatrix natricoides Augé & Rage, 2000: 293, 294, figs 24, 25.

MATERIAL EXAMINED. — 6 trunk vertebrae (Béon 2004 LT 75).

COMMENTS

This species is clearly characterized by the marked anteroposterior extension of the hypapophysis and by the overhanging anterior and posterior edges of the neural spine. The species was previously reported only from the middle Miocene (MN 6) of Sansan (France).

Indeterminate natricines

MATERIAL EXAMINED. — 1 incomplete maxilla (Béon 2004 LT 76) and 101 trunk vertebrae (Béon 2004 LT 77-79).

One fragment of maxilla whose prefrontal process suggests *Natrix* is referred to the natricines. The vertebrae are poorly preserved. They include mostly vertebrae with elongate and well limited centra, i.e. vertebrae like those of *N. longivertebrata*, *N. merkurensis*, and *Palaeonatrix lehmani*; but they are not sufficiently complete for identification to the species level.

Family ELAPIDAE Boie, 1827
Genus *Micrurus* Wagler, 1824

Micrurus gallicus Rage & Holman, 1984

Micrurus gallicus Rage & Holman, 1984: 97-99, fig. 6. — Szyndlar & Schleich 1993: 29, 30, fig. 8. — Szyndlar & Böhme 1993: 404. — Augé & Rage 2000: 301-302.

MATERIAL EXAMINED. — 7 trunk vertebrae (Béon 2004 LT 80).

COMMENTS

Micrurus is a living elapid that inhabits the Americas. The only non-american species was originally described from the middle Miocene (MN 7+8) of La Grive (France; Rage & Holman 1984). The vertebrae are small (centrum length of the largest vertebra: 4.2 mm) and provided with a short hypapophysis. As is typical for *Micrurus*, the axis of the hypapophysis is at a very acute angle to the vertebral axis. Consequently, although short, the hypapophysis projects posteriorly beyond the tip of the condyle in various vertebrae. The neural spine is very low and long. The centrum is narrow, elongate, with a flat ventral surface. The subcentral ridges are not prominent and the subcentral grooves not clearly marked. The prezygapophyseal processes are relatively long.

The vertebrae are similar to those of *Micrurus* but the assignment to this genus has been questioned to varying degrees by Szyndlar & Schleich (1993) and Augé & Rage (2000): the vertebral morphology of various small elapids from Asia is unknown and the referral of *M. gallicus* to one of these Asiatic forms cannot be definitely ruled out. But these small elapids remain poorly known and the referral of the European species at generic level should be probably reconsidered after revision of this assemblage.

M. gallicus has been reported from the early Miocene (MN 4) of Petersbuch 2, Germany (Szyndlar & Schleich 1993) and the middle Miocene of Sansan (MN 6) and La Grive (MN 7+8), both localities in France (Rage & Holman 1984; Augé & Rage 2000). *Micrurus* aff. *M. gallicus* was reported from Vieux-Collonges (MN 4/5, France) by Ivanov (2000).

Indeterminate elapid

Unidentified genus and species

MATERIAL EXAMINED. — 3 incomplete trunk vertebrae (Béon 2004 LT 81).

COMMENTS

The vertebrae are larger than those of *Micrurus gallicus* (centrum length: 6.1 mm). They are also more robust. They probably all come from the posterior trunk region as shown by the presence of subcentral grooves and the posterior orientation of the hypapophyses. The ventral surface of the centrum is flat where not hollowed by the subcentral grooves. The neural spine is long and low, and its posterior border is overhanging. These features point to elapids, perhaps to the *Naja* group, but further identification is not possible; however, these vertebrae document the presence of a second elapid in the locality.

Family VIPERIDAE Gray, 1825
Genus *Vipera* Laurenti, 1768
"*Vipera aspis* complex"

Vipera sp.

MATERIAL EXAMINED. — 13 trunk vertebrae (Béon 2004 LT 82; Béon 93 E3 SN 5).

COMMENTS

This viper is comparatively small (centrum length of largest vertebra: 4.8 mm). All neural spines are broken away and only one posterior trunk vertebra preserves a hypapophysis. The vertebrae are not elongate, which rules out a referral to the "*berus* complex". The overall proportions of the specimens from Béon 1 are consistent with those in species of the "*Vipera aspis* complex". The hypapophysis of the posterior trunk vertebra is slightly curved posteriorly as in the living *V. aspis* (Linnaeus, 1758) and *V. latastei* Boscá, 1878. No further comparison is possible.

The *aspis* complex is an informal subdivision of the genus *Vipera* defined by Szyndlar & Schleich (1993). Aside from living forms, three extinct species were referred to this complex. *V. antiqua* Szyndlar, 1987 is known from the late early Miocene (MN 4) of the Czech Republic and Germany (Szyndlar 1987; Szyndlar & Schleich 1993). The earliest known viper, recovered from the earliest Miocene (MN 1) of Weisenau, Germany, perhaps belongs to this species (*Vipera* cf. *V. antiqua*; Szyndlar & Böhme 1993: 431). Despite the poor preservation of the fossils from Béon 1 it may be stated that they do not belong to *V. antiqua*. The hypapophysis of the posterior trunk vertebrae from Béon 1 is slightly curved whereas it is straight in *V. antiqua*. *V. meotica* Zerova, 1992 (in Szyndlar & Zerova 1992) is known from the late Miocene (MN 12 and perhaps MN 13) of Ukraine (Zerova 1992; Szyndlar & Rage 2002). It differs from the viper of Béon 1 in having narrower and higher vertebrae, and perhaps shorter centra. *V. natiensis* Bailon, Garcia-Porta & Quintana-Cardona, 2002, from the Pliocene of the Balearic Islands (Bailon *et al.* 2002), has vertebrae more depressed than those of the small viperid from Béon 1 and the anterior border of their zygosphene is slightly concave whereas it forms a median lobe at Béon 1.

Genus *Vipera* Laurenti, 1768 ("oriental complex") or *Daboia* Gray, 1842

"*Vipera* (Oriental viper) – J.-C. Rage (unpublished)" – Szyndlar & Rage 2002: 438.

MATERIAL EXAMINED. — 141 trunk vertebrae (Béon 2004 LT 83-86; Béon 93 E3 SN 6; Béon 98 déblais SN 2; Béon 98 E3 3043; Béon 98 F1 3074).

DESCRIPTION

The size of this fossil corresponds to that of vipers referred to the "oriental complex" of *Vipera* or to *Daboia* (Szyndlar & Rage 1999, 2002). The length of the centrum of the largest specimen reaches 8.6 mm. Moreover, as is typical for these large vipers the neural arch is strongly depressed, nearly flat. In several vertebrae from Béon 1, the neural arch is thickened above the postzygapophyseal facets; this "epizygapophyseal thickening" sometimes forms an epizygapophyseal spine. This character is not frequent in large vipers from the Neogene of Europe. The neural spine is preserved on some vertebrae; it is very high in the anterior and mid-trunk regions, but that of posterior trunk vertebrae is unknown.

COMMENTS

In Europe, large vipers have been reported from the late early Miocene (MN 4) to the latest Pliocene (MN 17) (Szyndlar & Rage 2002) and from the Pleistocene (Schneider 1975; Szyndlar 1991b). Szyndlar (1987) referred all the large vipers from the European Neogene to the informal subdivision "oriental vipers" of the genus *Vipera*; this complex also includes extant species. Subsequently, Szyndlar & Rage (1999, 2002) removed the genus *Daboia* from this assemblage. *Daboia* is mainly distinguished from *Vipera* of the oriental complex on the basis of skull bones. But vertebrae may be also identified: in *Daboia* the neural spine is higher than in oriental vipers; however, this difference is not always marked in fossils. For example, Szyndlar & Rage (1999) were unable to assign a large viper from Vieux-Collonges (MN 4/5, France) to either *Daboia* or the oriental complex of *Vipera* although some vertebrae preserve neural spines. At Béon 1, the neural spine of the most anterior vertebrae (transition between anterior and mid-trunk regions) is very high and reminiscent of *Daboia*. But, in the mid-trunk region, the neural spine does not appear to be higher than in species of the oriental complex. Consequently, this large viper from Béon 1 cannot be confidently referred to either *Daboia* or the oriental complex of *Vipera*, which is reminiscent of the large viper from Vieux-

Collonges. However, the form from Vieux-Collonges differs slightly from the viper from Béon 1. At Vieux-Collonges, all mid-trunk vertebrae lack an epizygapophyseal spine and, in large vertebrae, the anterior edge of the zygosphene is straight at Vieux-Collonges while it is generally concave at Béon 1. In addition, the specimens from Vieux-Collonges are larger (the centrum reaches 10.2 mm) than those from Béon 1.

The oriental complex includes six living species of *Vipera*. The range of this assemblage extends from northwestern Africa and southeastern Europe to India. Szyndlar & Rage (2002) assigned six or seven extinct species to the oriental complex. They inhabited Europe from Portugal to Georgia; to the north, they reached north central France, Bohemia, and east central Ukraine; they are known from the early Miocene (MN 4) to the late Pliocene (MN 17). Indeterminate vipers of the oriental complex were reported from Africa: latest Pliocene and Pliocene/Pleistocene transition of Morocco (Bailon 2000; Szyndlar & Rage 2002) and perhaps early Miocene (Burdigalian) of Namibia (Rage 2003a). A single living species belongs to *Daboia* (*D. russelii*); it occupies southern Asia from Pakistan to Indonesia (Golay *et al.* 1993). Only one extinct species is assigned to *Daboia*: *D. maxima* (Szyndlar, 1988) from the Pliocene (MN 15) of Spain (Szyndlar 1988). *Daboia* was perhaps also present in the early/middle Miocene of Vieux-Collonges (MN 4/5, France) and the early Miocene of Namibia (Rage 2003a).

Consequently, whatever its exact genus reference, the large viper from Béon 1 is one of the earliest representative of either *Daboia* or the oriental complex of *Vipera*.

Indeterminate viperids

MATERIAL EXAMINED. — 5 venom fangs (Béon 2004 LT 87) and 36 incomplete vertebrae (Béon 2004 LT 88; Béon 93 E3 SN 7).

The vertebrae likely belong to one of the two above viperid taxa, but their poor preservation does not enable assignment. Fangs do not provide taxonomic information within the family.

CONCLUSIONS

The fauna of amphibians and squamates produced by the early Miocene (MN 4; Orleanian) of Béon 1 is rich and diverse, which is typical of the herpetofaunas from the early/middle Miocene transition in Europe. Snakes, in particular, expanded markedly in number and diversity during MN 4 times (Szyndlar 1998; Ivanov *et al.* 2000; Ivanov 2001). Béon 1 has yielded the following taxa:

- Amphibia
  - Caudata
    - Salamandridae
      - cf. *Chelotriton* sp.
      - *Triturus* aff. *T. helveticus*
      - *Triturus* cf. *T. marmoratus*
      - *Triturus* sp.
  - Anura
    - Discoglossidae
      - *Latonia* aff. *L. ragei*
    - Ranidae
      - *Rana* sp. synkl. *R. esculenta*
- Reptilia
  - Squamata
  - Lacertilia
    - Gekkonidae
      - Unidentified gen. and sp.
    - Lacertidae
      - Unidentified gen. and sp. 1
      - Unidentified gen. and sp. 2
      - Lacertid indet.
    - Anguidae
      - *Pseudopus laurillardi*
      - *Ophisaurus* sp.
    - Varanidae
      - *Varanus* sp.
    - Amphisbaenia
      - Amphisbaenian indet.
  - Serpentes
    - Scolecophidia
      - Scolecophidian indet.
    - Boidae
      - *Python europaeus*
    - Colubridae
      - *Coluber pouchetii*
      - *Texasophis meini*
      - *Natrix sansaniensis*
      - *Natrix* cf. *N. longivertebrata*
      - *Natrix* aff. *N. merkurensis*
      - *Palaeonatrix* aff. *P. lehmani*
      - *Neonatrix europaea*
      - *Neonatrix natricoides*
    - Elapidae
      - *Micrurus gallicus*
      - Unidentified gen. and sp.
    - Viperidae
      - "*Vipera aspis* complex"
      - *Daboia* or "oriental *Vipera* complex"

TABLE 1. — Stratigraphic ranges of significant species from Béon 1. Black, ranges known prior to the recovery of the taxa at Béon 1; hatching, extensions resulting from the recovery of taxa at Béon 1.

taxa / zones	*Latonia ragei*	*Natrix merkurensis*	*Natrix sansaniensis*	*Python europaeus*	*Palaeonatrix lehmani*	*Pseudopus laurillardi*	*Coluber pouchetii*	*Neonatrix natricoides*	*Micrurus gallicus*	*Texasophis meini*	*Neonatrix europaea*
MN 9											
MN 7+8									■	■	■
MN 6			■		■	■	■	■	■	■	■
MN 5			■	■	■	▤	▤	▤	■	▤	▤
MN 4	■	▤	■	▤	■	▤	▤	▤	■	▤	▤
MN 3	■	■	■								
MN 2	■										
MN 1	■										
MP 30	■										
MP 29											

The presence, at Béon 1, of this rich and diverse snake assemblage mostly comprised of Colubridae, shows that the wave of modern snakes that spread over Central Europe by MN 4 times (Szyndlar 1998; Ivanov 2001) also reached Western Europe.

The locality has yielded one of the earliest *Varanus* in Europe and the earliest representatives of *Pseudopus laurillardi*, *Python europaeus*, *Coluber pouchetii*, *Texasophis meini*, *Neonatrix europaea*, and *Neonatrix natricoides*. The locality has perhaps also produced the youngest representative of *Natrix merkurensis*, but this identification cannot be confirmed (identified as *N.* aff. *N. merkurensis* at Béon 1).

The stratigraphic ranges of several taxa present, or presumed to be present (i.e. reported with the qualifier "aff.") at Béon 1 are restricted (Table 1): *Latonia* aff. *L. ragei*, *Pseudopus laurillardi*, *Python europaeus*, *Coluber pouchetii*, *Texasophis meini*, *Natrix sansaniensis*, *Natrix* aff. *N. merkurensis*, *Palaeonatrix* aff. *P. lehmani*, *Neonatrix europaea*, *Neonatrix natricoides*, and *Micurus gallicus*. These stratigraphic ranges are unquestionably consistent with the MN 4 age previously suggested by Antoine & Duranthon (1997), Duranthon *et al.* (1999), and Antoine *et al.* (2000a, b) on the basis of mammals.

Several species from Béon 1 indicate affinities with localities that are both relatively close geographically (southern France) and stratigraphically younger (up to MN 6, or even MN 7+8) and with more remote localities (from Central Europe) that are of same or close geological ages (MN 3 and MN 4). However, this remark rests on a limited number of significant (i.e. sufficiently rich) localities: Béon 1, Vieux-Collonges, Sansan, and La Grive in France; Petersbuch 2 (southeastern Germany), Oberdorf (southeastern Austria), Dolnice and Merkur-North (Western Czechia). In Central Europe, studied herpetofaunas from the MN 6-MN 7+8 interval are represented only by those of Devínska Nová Ves, Western Slovakia (MN 6; Ivanov 1998) and Opole, Poland (MN 7+8; Mlynarski *et al.* 1982). These two faunas appear to be different from those of the zone MN 4 in Western and Central Europe and from those of MN 6-MN 7+8 of Western Europe. Therefore, whereas in Western Europe no major changes affected the faunas during the MN 4-MN 7+8 period, a change apparently took place between MN 4 and MN 6 in Central Europe. It would be of interest to check this on the basis of other localities.

The presence of snakes with North American affinities (*Paleoheterodon*, *Texasophis*, *Neonatrix*, *Micrurus*) in the European Miocene was reported by Rage & Holman (1984) and Augé & Rage (2000). These snakes were present at La Grive (MN 7+8), Sansan (MN 6), and Vieux-Collonges (MN 4/5). Since that time, such snakes have been found in older localities of MN 4 age. Dolnice has produced *Texasophis bohemiacus* and *Neonatrix nova* (Szyndlar 1987) whereas *Micrurus gallicus* and perhaps *Neonatrix* were recovered from Petersbuch 2 (Szyndlar & Schleich 1993). Béon 1 corroborates the presence of such snakes in the zone MN 4 (*T. meini*, *N. europaea*, *N. natricoides*, *M. gallicus*). Still remaining in question is whether these snakes are really immigrants from North America or taxa of Asian origin that dispersed toward both Europe and North America during the Miocene. These two processes are not incompatible and these snakes that reached Europe might be of both North American and Asian origins (Augé & Rage 2000). Unfortunately, this question will remain unanswered until Neogene snakes from Asia are known. In addition, the possibility that similar vertebral morphologies of part of these snakes in North America and Eurasia result from convergent evolution cannot be definitely discarded.

One of the characteristics of the herpetofaunas from the late early Miocene (MN 4) of Europe is the appearance of rich assemblages of natricine snakes both in terms of number of specimens and, often, number of taxa (Szyndlar & Schleich 1993). This characteristic apparently lasted up to MN 6, at least in Western Europe. Prior to MN 4, this tendency was heralded by the fauna of Merkur-North (MN 3) in which natricines are predominant but not diverse (Ivanov 2002). Before MN 3, natricines were rare. Because the number of natricines increased suddenly in MN 4, Szyndlar & Schleich (1993) inferred that these snakes were immigrants rather than the products of local evolution. Ivanov (2001) concluded that these natricines came from the East. This is consistent with the fact that one of the natricine genera (*Neonatrix*) is regarded as a snake with North American affinities.

The absence of Bufonidae (Anura) and Erycinae (Serpentes, Boidae) is somewhat surprising because these two taxa are frequent in the Miocene of Europe. In Europe, bufonids were temporarily present during the Paleocene (Rage 2003b) but they were absent during the Eocene and Oligocene. They re-appeared in Europe in some localities of the zone MN 4 (Sanchiz 1998b; Rage & Roček 2003). But, at that time, the establishment of the group was probably not complete yet, which probably accounts for their absence at Béon 1. On the other hand, the Erycinae are subfossorial animals, therefore they are closely dependent on the environment. This is probably the cause of their local absence.

Ten of the 26 species of amphibians and squamates identified at Béon 1 were more or less aquatic (*Triturus* aff. *T. helveticus*, *Triturus* cf. *T. marmoratus*, *Latonia* aff. *L. ragei*, *Rana* synkl. *R. esculenta*, *Natrix sansaniensis*, *Natrix* cf. *N. longivertebrata*, *Natrix* aff. *N. merkurensis*, *Palaeonatrix* aff. *P. lehmani*, *Neonatrix europaea*, *Neonatrix natricoides*). The aquatic species represent 45.3% of the amphibian and squamate specimens. They are indicative of the presence of quiet water, which confirms the marshy and lacustrine environments inferred by Duranthon *et al.* (1999).

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