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Amphibians and squamate reptiles from the lower Eocene of Silveirinha (Portugal)

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Abstract

Key-words: Amphibia; Caudata; Anura; Reptilia; Lacertilia; Serpentes; Eocene; Portugal.

Silveirinha (Portugal) has produced a diverse herpetofauna. In Europe, it is the only described assemblage of amphibians and squamate reptiles from the base of the Eocene (MP 7). The fauna includes at least two species of amphibians (belonging to the Salamandridae and perhaps the Pelobatidae) and at least 15 species of squamates (at least nine families: Iguanidae, Agamidae, Gekkonidae, one or two families of scincomorphans, Anguidae, ? Varanidae, Amphisbaenidae, Boidae, Tropidophiidae, and likely an indeterminate family of snakes). But, except for the snake *Dunnophis matronensis*, identifications at species level are not possible. The presence of iguanid lizards and of the snake *D. matronensis* in the base of the Eocene (MP 7) of Europe is confirmed. The fauna includes several squamates that show close affinities with North American *taxa*.

Resumo

Palavras-chave: Anfíbios; Caudata; Anura; Reptilia; Lacertilia; Serpentes; Eocénico; Portugal.

O sítio de Silveirinha deu herpetofauna diferenciada. Trata-se da única associação descrita na Europa de anfíbios e répteis Squamata datada do Eocénico basal (MP7). Inclui, pelo menos, duas espécies de anfíbios (Salamandridae e, talvez, Pelobatidae) e quinze de Squamata (ao menos nove famílias: Iguanidae, Agamidae, Gekkonidae, uma ou duas de scincomorfos, Anguidae, ? Varanidae, Amphisbaenidae, Boidae, Tropidophiidae e provavelmente uma família indeterminada de serpentes). Contudo, com a excepção da serpente *Dunnophis matronensis*, não são possíveis identificações a nível de espécie. Confirma-se a presença de iguanídeos e de *D. matronensis* no Eocénico basal (MP 7) da Europa. Vários Squamata evidênciam estreitas afinidades com *taxa* da América do Norte.

Introduction

In Europe, Silveirinha (Portugal) is one of the few fossiliferous localities that have yielded amphibians and/or squamates from the standard level MP 7 (lowermost Eocene). Rians and Palette (France) have produced rare lizards that remain unstudied. Meudon (Montalets Quarry), another French locality, has furnished a small fauna of amphibians and squamates that was briefly reported on by Russell *et al.* (1990). Dormaal (Belgium) and Le Quesnoy (France) have yielded comparatively rich and diverse faunas. Amphibians and squamates from Le Quesnoy, a recently discovered locality, were listed in a preliminary report but not described (Nel *et al.*, 1999). Amphibians and mainly squamates from Dormaal were studied, but not figured, by Hecht & Hoffstetter (1962). The material needs to be revised; unfortunately, it is no longer available (? misplaced). However, new excavations at Dormaal have made known additional specimens. Partly based on this new material, a brief list of amphibians and squamates was given by Godinot *et al.* (1978). Various lizards have been subsequently studied (Augé, 1990, 1995; Augé & Smith, 1997). But, apart from these lizards, the herpetofauna from Dormaal remains virtually undescribed.

Previous to the present study, Antunes & Russell (1981) listed the vertebrates from Silveirinha. As far as amphibians and squamates are concerned, they reported the following taxa (Amphibia and Squamata were identified by Sanchiz and Rage respectively): Caudata (Salamandridae); Anura (Pelobatidae: *Eopelobates* sp.;

Discoglossidae); Lacertilia (Anguidae: *Placosaurus* group; two forms belonging to indeterminate families; an indeterminate amphisbaenian); Serpentes (Boidae: indeterminate Boinae; Tropidophiidae: *Dunnophis* cf. *D. matronensis*; Russellophiidae: *Russellophis* sp.). Two of these taxa have not been found in the material on which the present study is based (specimens lost or erroneous identifications in the previous article ?). These missing taxa are the Discoglossidae and Russellophiidae. Conversely, additional material has yielded taxa of lizards that have not previously been reported from Silveirinha. The material that is available represents one of the richest fauna from the standard level MP 7.

Systematic account

Class AMPHIBIA
Order CAUDATA Scopoli, 1777
Family Salamandridae Goldfuss, 1820

Indeterminate genus and species
(Fig. 1)

1981 – Salamandridae: genre indét.; Antunes & Russell, p. 1100.

Material: 1 atlas, 33 trunk vertebrae, 3 caudal vertebrae, and 2 fragments of humeri.

Description: the atlas is represented only by its centrum. The cotyles are broad and oval, their major axis being horizontal. The odontoid process markedly projects anteriorly but it is not thick. It has two anterolateral articular facets that are circular and that clearly face ventrally.

Trunk vertebrae are well ossified but small. The length of the centrum of the largest vertebra is about 1.9 mm. The vertebrae are opisthocoelous. They are relatively elongate, those from the anterior region of the trunk (Fig. 1A) being shorter than those from the mid- and posterior trunk (Fig. 1B). The neural spine is well developed but not high. It is capped by a dermal plate that is not sculptured. The plate assumes a triangular shape in the anterior trunk vertebrae, but in more posterior vertebrae it is markedly elongate (Fig. 1B). A shallow notch indents the posterior border of the plate. On the single well-preserved anterior trunk vertebra, the neural spine reaches its maximum height about midway of its length. The anterior border of the spine is inclined. The posterior part of the neural arch rises. Its posterior border reaches the level of the top of the neural spine; consequently, in posterior aspect, the neural spine does not project above the neural arch. In mid- and posterior trunk vertebrae (Fig. 1B), the neural spine is longer anteroposteriorly and it reaches its maximum height more posteriorly. The anterior border is either inclined or vertical.

The rib-bearers are short. They are closely spaced and webbed with bone up to their lateral extremities. The rib-bearers of anterior vertebrae are thicker than those of mid- and posterior trunk ones. In the anterior trunk region, they are directed transversely whereas they are oriented posterolateraly in more posterior regions. The prezygapophyseal articular facets are broad; their anterior border is clearly convex anteriorly. A prominent zygapophyseal ridge runs from the prezygapophyses to the postzygapophyses through the dorsal rib-bearer. A prominent ventral ridge stretches along the centrum, on either side of the ventral rib-bearer. Anteriorly, the ventral ridge spreads on the ventral face of the centrum, behind the condyle, where it approaches or joins the symetrical ridge. In ventral aspect, the centrum forms an elongate bulge without any marked constriction, between the ventral ridges. It does not bear crests or basapophyses. Large subcentral foramina are present. The condyle is small with an oval and nearly flat anterior face. A small notochordal pit is present in several vertebrae. In most vertebrae, a weak constriction separates the condyle from the centrum. On each side, a spinal foramen opens dorsal to the posterior vertebrarterial foramen.

Two distal parts of humeri are available. The shaft is slender. The distal extremity is flattened dorsoventrally; in ventral view, it is at least four times as wide as the diameter of the shaft. As is usual in salamanders, the humeral ball and the extremities of the epicondyles are not preserved. The cubital fossa is broad and well-marked. The two specimens do not permit identification but their size is consistent with that of the vertebrae; they likely belong to the same taxon.

Comments: the opisthocoelous condition occurs in three families: Batrachosauroididae, Plethodontidae, and Salamandridae. The Batrachosauroididae, an extinct family (upper Cretaceous-Miocene, ? Pliocene), clearly differs from the fossils from Silveirinha. Their vertebrae have deep and narrow centra and their condyle is ring-shaped with a large notochordal pit. But, the vertebrae of the Salamandridae cannot be easily distinguished from those of the Plethodontidae. Estes (1969) shown that, within the centrum of Salamandridae, the chordal tube remains widely open whereas in Plethodontidae it is infilled with bone. On some vertebrae from Silveirinha the centrum is broken: it displays the condition that is characteristic of the Salamandridae according to Estes (1969). In addition, the comparatively large neural arch and the presence of a dermal plate on the neural spine also suggest referral to the Salamandridae. Consequently, on the basis of this combination of features, the salamander from Silveirinha is assigned to the Salamandridae.

Because of proportions, small size of the condyle, prominent ventral ridge, and morphology of the centrum the vertebrae appear to be consistent with those of the Triturinae. More specifically, they are reminiscent of an undescribed form known in the Eocene of western Europe from MP 7 to MP 16 ('Salamandridae E' *in* Duffaud, 2000).

Salamanders from the lowermost Eocene are diverse (Estes, 1981; Duffaud, 2000); unfortunately, they remain largely unstudied. At our present state of knowledge, it is

not possible to assign the salamander from Silveirinha to any taxon lower than the Salamandridae; even, the referral to the Triturinae remains doubtful.

Order ANURA Rafinesque, 1815
?Family Pelobatidae Bonaparte, 1850

Indeterminate genus and species

1981 – *Eopelobates* sp.; Antunes & Russell, p. 1100.

Material: 2 fragments of ilia.

Description and comments: both ilia are represented by the acetabular area and a short part of the shaft. The pars ascendens and descendens are broken off. The dorsal margin of one of the ilia is preserved. It shows that there is no tuber superior. Moreover, a dorsal crest is absent on the shaft.

Such a morphology (tuber superior and dorsal crest absent) is known in Pelobatidae and Pelodytidae. The relatively large size and the somewhat massive morphology point to the Pelobatidae rather than to the Pelodytidae. However, the assignment to the Pelobatidae on the basis of such features remains doubtful.

Antunes & Russell (1981) reported Eopelobates sp. from Silveirinha; Sanchiz (1998: 173) and Rocek & Rage (2000) have retained this identification. However, reliable identification of *Eopelobates* should rest on cranial bones, more specifically the frontoparietal (Duffaud, 2000; Rage & Rocek, in prep.). Therefore, assuming that the available ilia really belong to the Pelobatidae, the referral at the genus level is not possible.

Remarks about Discoglossidae: an indeterminate genus of Discoglossidae was reported from Silveirinha by Antunes & Russell (1981: 1100) and this frog was referred to as 'Discoglossinae indet.' by Sanchiz (1998: 173). But, in the available material none of the fossils may be assigned to the Discoglossidae. However, among the specimens is a well-preserved urostyle that is characteristic of the '*Discoglossus*-group'. A careful examination shows that this is not a fossil, but a recent bone that became mixed with specimens from the fossiliferous level. Consequently, on the basis of the available specimens the Discoglossidae appear to be absent at Silveirinha.

Class REPTILIA Lin. 1758
Order SQUAMATA Oppel 1811
Suborder LACERTILIA Owen, 1842
Infraorder IGUANIA Cuvier, 1817
Family Iguanidae s.l. Oppel, 1811

Today, the Iguanidae s.l. (a paraphyletic assemblage) are absent from Eurasia. Estes (1983) confirmed that the family was likely present in Europe during the Eocene. Subsequently, iguanids s.l. have been reported from the upper Cretaceous (Rage, 1999) and the Eocene (Rage & Augé, 1993; Rossmann, 2000) of Europe.

Genus *Geiseltaliellus* Kuhn, 1944

Geiseltaliellus sp.
(Fig. 2A)

Material: one posterior part of maxilla.

Description and comments: this fragment preserves eight more or less complete teeth. They are cylindrical, pleurodont, and short; they do not markedly project beyond the parapet. Teeth are tricuspid but the small anterior and posterior cusps are either worn or broken away. The maxillary foramen opens on the dorsal face of the lamina horizontalis; it is prolonged anteriorly by a depression that runs along the lateral wall of the maxilla. The posterior border of the dorsal process is markedly anterior to the extremity of the zygomatic process. This maxilla somewhat resembles that of the iguanid from the lower Eocene (MP 10) of Prémontré (France). The latter iguanid was referred to as *Geiseltaliellus* cf. *G. louisi* by Augé *et al.* (1997). But, Rossmann (2000) referred *G. louisi* to the synonymy of *Geiseltaliellus longicaudus* Kuhn, 1944, i.e. the type species from the middle Eocene of Germany. However, whatever the status of *G. louisi* may be, the only available specimen from Silveirinha does not permit a confident identification below the genus level.

Indeterminate genus and species

Material: 3 fragments of bone bearing teeth.

Description and comments: the teeth are pleurodont and comparatively elongate. Their apex is slightly compressed laterally and it slightly stretches anteroposteriorly. Such apices generally occur in iguanids, although they are sometimes present in other families.

Family Agamidae Gray, 1827
Genus *Tinosaurus* Marsh, 1872

Cf. *Tinosaurus*
(Fig. 2B)

Material: a fragment of bone bearing two teeth.

Description and comments: the teeth are acrodont, or more accurately subacrodont since their bases slightly spread on the lingual face of the bone. The teeth are long anteroposteriorly and low. They are clearly tricuspid. The central cusp is the highest one but it is not markedly larger than the anterior and posterior cusps.

This morphology is characteristic of *Tinosaurus*, a genus known from the Paleocene and Eocene of Laurasian continents. More specifically, the fossil from Silveirinha recalls T. europeocaenus, a species from the lower Eocene

of Europe (Augé & Smith, 1997). However, precise comparison between the latter species and the poorly preserved specimen from Silveirinha is not possible.

Inraorder GEKKOTA Cuvier, 1817
Family Gekkonidae Gray, 1825

Indeterminate genus and species

Material: two anterior parts of dentaries and one trunk vertebra.

Description and comments: there are no teeth preserved on the specimens but the tooth sockets show that the teeth were slender and closely spaced. The sulcus Meckeli is closed. The vertebra is amphicoelous, relatively elongate with a hourglass-shaped centrum. These features of the dentaries and vertebra are typical of gekkonids.

These fossils from Silveirinha and those reported from Dormaal (Augé, 1990) represent the earliest representatives of the family in Europe.

Infraorder SCINCOMORPHA Camp, 1923

Two taxa represent the Scincomorpha. Unfortunately, referral at family level is not possible.

Indeterminate family

Indeterminate genus 1
(Fig. 2C)

Material: four fragments of bones bearing teeth.

Description and comments: a marked sulcus dentalis is present on these fragments. The teeth are pleurodont and relatively short; they project only one-third of their height over the parapet of the jaw. They are apparently bicuspid, but the two cuspids are clearly observable on only one of the teeth. Such a bicuspid morphology frequently occurs in the Lacertidae, but these fossils are not complete enough to be referred at family level within the scincomorphan assemblage.

Indeterminate family

Indeterminate genus 2
(Fig. 2D)

Material: one fragment of bone bearing two teeth and one trunk vertebra.

Description and comments: the teeth are pleurodont and robust; they project more than one-third of their height over the parapet. The apex is relatively pointed. There is no true accessory cusp; but on one of the teeth, a shallow depression separates the apex from one of the border (? anterior or posterior) of the tooth. This morphology is reminiscent of the scincomorph Eolacerta Nöth, 1940, from the middle Eocene of Europe (Nöth, 1940; Müller, 2001).

In addition, an incomplete vertebra recalls Eolacerta. It is narrow and comparatively high. The zygapophyseal surfaces are markedly inclined above horizontal. The anterior part of the neural arch forms a narrow pseudozygosphene. The poorly preserved paradiapophyses were apparently small and rounded. The cotyle is slightly depressed. The subcentral ridges are marked and a strong haemal keel runs from the cotyle to the condyle.

Eolacerta robusta, the single species of the genus, has been reported only from the middle Eocene of Germany. However, *Eolacerta* (perhaps *E. robusta*) is present in the lower Eocene of Dormaal (MP 7, Belgium) and Prémontré (MP 10, France) (pers. obs.). *Eolacerta* has been generally referred to the Lacertidae (Estes, 1983) but Müller (2001) has recently questioned this assignment. Despite some resemblance to Eolacerta and whatever the family allocation of this genus may be, it should be noted that the fossil from Silveirinha cannot be definitely referred to any taxon within the Scincomorpha.

Infraorder ANGUIMORPHA Fürbringer, 1900
Family Anguidae Gray, 1825
Subfamily Glyptosaurinae Marsh, 1872
Tribu Glyptosaurini Marsh, 1872

In Europe, Glyptosaurini are common in the Eocene but only one genus (*Placosaurus*) has been named. It is known in the entire Eocene, from MP 7 to MP 19 (Augé, 2001). *Placosaurus* has also been reported from the upper Eocene of Asia (Sullivan, 1979). Moreover, the genus *Helodermoides* from the lower and middle Oligocene of North America should be referred to the synonymy of *Placosaurus* (Augé, 2001). In North America, the tribe ranges from the lower Eocene to the middle Oligocene, whereas in Asia it is restricted to the upper Eocene (Estes, 1983).

Indeterminate genus and species
(Figs 3A, 3 B)

1981 – forme du groupe *Placosaurus*; Antunes & Russell, p. 1100.

Material: four incomplete frontals (three posterior and probably one anterior parts), two incomplete parietals, and tens of isolated osteoderms.

Description and comments: the frontal of this taxon is a robust, unpaired bone. The dorsal face is covered with hexagonal osteoderms that display a tubercular sculpture. The frontals widen posteriorly; their interorbital portion appears to be comparatively narrow. Laterally, the notch that represents the articular facet for the prefrontal bone is clearly exposed. On the ventral face, a strong olfactory ridge runs along the lateral border of the bone; its

maximum develoment occurs midway along the length of the frontal. A specimen, that is likely an anterior part of frontal, shows that only two rows of osteoderms cover the width of this region (Fig. 3A). In ventral aspect, the descending orbital lamellae limit a shallow, elongate and oval cavity.

The parietals are thick and covered with osteoderms similar to those of the frontals (Fig. 3B). On the ventral face, the parietal ridges are relatively distant from the lateral borders of the bone. The ventral ridges that originate on the parietal processes do not reach the parietal ridges.

Tens of isolated osteoderms are available. They are hexagonal and comparatively thick, with interdigitating margins. Such osteoderms are characteristic of the skull of Glyptosaurini.

Within Glyptosaurini, referral at genus level requires well-preserved skull bones; unfortunately, none of the specimens from Silverinha is sufficiently diagnostic to be assigned to any taxon lower than the Glyptosaurini.

Tribu Melanosaurini Sullivan, 1979

The Melanosaurini are known only from Europe and North America. In Europe, they range from the lowermost Eocene (MP 7) to the upper Eocene (MP 19) (Augé, 2001). Two, perhaps three, genera of Melanosaurini have been reported from Europe: *Placosauriops* (MP 11 and MP 12, middle Eocene of Germany) and *Paraxestops* (MP 19, upper Eocene of Switzerland) (Keller *et al.*, 1991), and perhaps *Melanosaurus* from the lowermost Eocene (MP 7) of Dormaal, Belgium (Godinot *et al.*, 1978). *Placosauriops* and *Paraxestops* are restricted to Europe, but *Melanosaurus* is primarily known in North America (from the lower and ? middle Eocene) where the Melanosaurini extend from the upper Cretaceous (Campanian) to the upper Oligocene.

Cf. *Melanosaurus* Gilmore, 1928
(Figs 3C, 3D)

Material: one incomplete jugal and one fragmentary cranial bone (likely a parietal).

Description and comments: the bone that appears to be a parietal is covered with a tubercular sculpture (Fig. 3C); it lacks any trace of limits between osteoderms or scales. The tubercles are smaller than those observed in Glyptosaurini. Only the dorsal branch of the jugal is preserved (Fig. 3D). A rather robust posteroventral process was present. It shows a rough, irregular ornamentation. A prominent and sharp ridge runs along the medial face of this branch of the jugal. These features are similar to those of the jugal of *Melanosaurus* depicted by Gilmore (1928: pl. 24, fig. 3, 4). But, the available material does not permit to confidently assign the fossil from Silveirinha to this genus. The presence of *Melanosaurus* in Europe remains doubtful.

Indeterminate genus and species
(Fig. 3E)

Material: one incomplete parietal.

Description and comments

This incomplete parietal is covered with dermal plates, except the occipital area that is smooth; osteoderms are absent. The plates show a tubercular sculpture, but the tubercules are neither regularly limited nor regularly arranged, which distinguishes this bone from the Glyptosaurini. Limits between scales are clearly marked; such limits are absent in Glyptosaurini, *Melanosaurus*, and the lizard referred to as cf. *Melanosaurus*. Moreover, the tubercles are larger than those of the latter lizard from Silveirinha.

Indeterminate Glyptosaurinae

Material: some incomplete dentaries and hundreds of trunk osteoderms.

Comments: some bones do not permit us to distinguish Glyptosaurini from Melanosaurini. These bones are posterior parts of dentaries and osteoderms. The osteoderms come from the trunk region; they are rectangular with a tubercular sculpture, except on the anterior area that remains smooth.

? Subfamily Anguinae Gray, 1825

Indeterminate genus and species
(Fig. 3F)

Material: one posterior part of dentary and one trunk vertebra.

Description: within the sulcus Meckeli, the intramandibular septum extends ventrally and it fuses with the wall of the dentary. The teeth are subpleurodont, conical, and recurved; the apex is pointed, without any accessory cusp. The teeth lack plicidentine. The lamina horizontalis is not clearly distinct from the alveolar surface; it is apparently weakly developed.

The trunk vertebra is depressed. The neural spine is well-developed and the posteriormost part of its top forms a flat and triangular small surface. The cotyle and condyle are strongly depressed. The ventral face of the centrum is narrow, flat, without any keel. The subcentral ridges are marked and nearly parallel.

Comments: the implantation of the teeth, the morphology of the intramandibular septum and that of the lamina horizontalis point to the anguimorphans. Within this assemblage, the shape of the teeth recalls that of a group of Anguinae that includes the genera *Dopasia* (i.e. *'Ophisaurus' harti*) and *Anguis*; these two genera are

characterized by 'caniniform' teeth. Apart from the somewhat peculiar neural spine, the vertebral morphology is consistent with that of the living *Anguis*. More specifically, the centrum limited by subparallel subcentral ridges appears to be characteristic. But, because of the limited nature of the material the referral to the Anguinae cannot be ascertained.

? Infraorder PLATYNOTA Baur, 1890
? Family Varanidae Gray, 1827

Indeterminate genus and species

Material: one trunk vertebra.

Description: the vertebra is relatively elongate; it bears a well-developed neural spine. Anteriorly, the neural arch forms a poorly shaped pseudozygosphene. The zypapophyses do not markedly project laterally; their articular facets are clearly inclined above the horizontal. The prezygapophyseal facets are broader than the postzygapophyseal ones. The cotyle and the condyle are depressed. Their axis is inclined; as a result, the cotyle faces anteroventrally. The ventral face of the centrum does not strongly widen anteriorly; in cross section the centrum is convex ventrally but there is no marked keel. The centrum lacks a precondylar constriction.

Comments: the overall morphology of the vertebra is consistent with the Varanidae and, within this family, the presence of a pseudozygosphene is reminiscent of the genus *Saniwa*. This genus is known in the coeval locality of Dormaal (Belgium) where it is represented by the species *S. orsmaelensis* Dollo, 1923. However, in *Saniwa* the centrum markedly widens anteriorly and a precondylar constriction is present as in nearly all Varanidae. Therefore, the vertebra from Silveirinha cannot be referred to *Saniwa* and, despite some resemblance to this genus, even its assignment to the Varanidae appears to be doubtful.

Infraorder AMPHISBAENIA Gray, 1844

Amphisbaenians are common in Cainozoic localities of Europe. But their study is difficult and rare taxa only have been described.

Family Amphisbaenidae Gray, 1865

Indeterminate genus and species

1981 – Amphisbaenia: forme indét.; Antunes & Russell, p. 1100.

Material: two posterior parts of dentaries and about ten trunk vertebrae.

Description and comments: the posterior parts of the dentaries bear robust teeth the bases of which are broad. There is no accessory cusps. The sulcus Meckeli is subdivided by an intramandibular septum that extends ventrally and fuses to the lateral wall of the dentary. A strong coronoid process is directed posterodorsally.

The vertebrae are depressed. The ventral face of the centrum is flat, narrow, and well-limited by nearly parallel subcentral ridges. Some vertebrae lack a neural spine, but in others the neural spine is represented by a low keel that does not occupy the entire length of the neural arch; it does not reach the anterior and posterior borders of the arch.

The overall morphology of the vertebrae and the presence of a robust coronoid process clearly demonstrate that the specimens belong to the amphisbaenians. The morphology of the sulcus Meckeli suggests that the fossils belong to the Amphisbaenidae.

Suborder SERPENTES Linnaeus, 1758
Family Boidae Gray, 1825

Within snakes, the Boidae were the dominant group during the Paleocene and Eocene; they underwent great diversification during the Eocene. Their decline began during the Oligocene. (Rage, 1987).

Indeterminate genus and species

1981 – Boinae; Antunes & Russell, p. 1100.

Material: 16 more or less complete trunk vertebrae.

Description and comments: the boid from Silveirinha is a small form. The centrum length of the largest vertebra does not reach 7 mm. The vertebrae are short, wide, and massive. The zygosphene is rather thick and not wide. The prezygapophyses have a very short prezygapophyseal process. The paradiapophyses are weakly subdivided into para- and diapophyseal areas. Mid- and posterior trunk vertebrae bear a haemal keel, whereas a hypapophysis is present on anterior vertebrae. These features permit to refer these vertebrae to the Boidae, but other characters should be considered. The neural arch is somewhat depressed (but the vertebrae are not depressed) and the neural spine is low, which recalls the Erycinae. However, Szyndlar & Böhme (1996) have shown that these characters sometimes occur in non-erycine boids. Only caudal vertebrae permit a secure referral to the Erycinae, but such vertebrae have not been found at Silveirinha. Therefore, the available material is not sufficiently diagnotic to be referred to a taxon lower than the family.

Family Tropidophiidae Cope, 1894

The Tropidophiidae were previously regarded as a subfamily of the Boidae (Bogert, 1968; Rage, 1984). The family includes only four living genera and it is restricted to Mexico, Central America, the North of South America, and Caribbean islands. Two extinct genera have been

referred to the Tropidophiidae (McDowell, 1967): *Dunnophis* (see below) and Platyspondylia (Eocene and Oligocene of Europe).

Genus *Dunnophis* Hecht, 1959

Dunnophis is known only by vertebrae. It has been referred to the Tropidophiidae because its vertebrae closely resemble those of the living *Ungaliophis* (Bogert, 1968; McDowell, 1987).

Three species were assigned to *Dunnophis*: *D. matronensis* from the lower Eocene of Europe, *D. microechinis* from the lower or middle Eocene (Bridger Formation) of North America, and *D. cadurcensis* from the upper Eocene of Europe (Hecht, 1959; Rage, 1984). Unidentified species have been reported from the lowermost Eocene to the lowermost Oligocene. The genus is known in Europe and in North America. It is perhaps present in Africa (Paleocene of Morocco; work in progress).

Vertebrae of *Dunnophis* are mainly characterized by the following feature: vertebrae comparatively elongate and not high, centrum long and narrow, prezygapophyseal processes absent, neural spine low, neural arch relatively depressed, and hypapophyses absent on mid- and posterior trunk vertebrae.

Dunnophis matronensis Rage, 1973
(Fig. 4)

1981 – *Dunnophis* cf. *matronensis*; Antunes & Russell, p. 1100.

Material: 34 trunk vertebrae.

Description: according to Rage (1984) the vertebrae of *Dunnophis matronensis* are characterized by a zygosphene having a wide and rounded median lobe, subcentral grooves occupying only the anterior half of the centrum, and a neural spine anteroposteriorly short but prolonged anteriorly by a weak keel. On the whole, the vertebrae from Silveirinha display this morphology; however, on some of them (posterior trunk vertebrae) the subcentral grooves appear to be longer: they approach or reach the condyle. Augé *et al.* (1997) already noted that variation affects these grooves in the species. This character should be re-evaluated but the specimens from Silveirinha are too incomplete to permit such a revision. The presence of *D. matronensis* in the earliest standard level of the Eocene (MP 7) has been regarded as doubtful (Rage & Augé, 1993; Augé *et al.*, 1997). At Silveirinha, this snake was referred to as *Dunnophis* cf. *matronensis* by Antunes & Russell (1981) and an indeterminate species of *Dunnophis* was reported from Dormaal (MP 7) (Rage, 1973, 1984). Subsquently, the species has been identified, without reservation, at Le Quesnoy (France), a coeval locality (MP 7) (Nel *et al.*, 1999). The material that is now available confirms that *D. matronensis* is present at Silveirinha. But, it is still impossible to identify the species from Dormaal (material presently not located).

D. matronensis is known only in western Europe. Its stratigraphic range extends from MP 7 to MP 10 or MP 11. The precise age, MP 10 or MP 11, of the youngest locality (Viélase, France) that yielded the species is unknown (Legendre *et al.*, 1992). Therefore *D. matronensis* is known from the entire lower Eocene (MP 7 - MP 10) but it might be also present in the base of the middle Eocene (MP 11).

Indeterminate family

Indeterminate genus and species

Material: one trunk vertebra.

Description and comments: a small vertebra that lacks both prezygapophyses cannot be referred to the Boidae because it is relatively elongate and lightly built. Moreover, its elongate and narrow centrum is clearly distinct from that of boids. The wide zygosphene and narrow centrum are consistent with the vertebral morphology of the tropidophiid *Dunnophis*, but this vertebra clearly differs from those of the latter genus in having a rather well-developed neural spine that reaches the zygosphene and in having a more depressed neural arch. The absence of the prezygapophyses prevents further comparisons.

This snake is not a boid and, apparently, it does not belong to the Tropidophiidae. In the locality, it likely represents a third family that cannot be identified.

Remarks about Russellophiidae

Antunes & Russell (1981) cited *Russellophis* sp. at Silveirinha (identification by J. C. Rage). Subsequently, Rage & Augé (1993) reported *Russellophis* sp. from the lowermost Eocene (MP 7) of Portugal (i.e., implicitly from Silveirinha). However, in the available material, none of the specimens can be referred to *Russellophis*. It may be entertained whether the first identification was wrong or the specimen(s) is (are) lost. *Russellophis* cannot be regarded as a member of the fauna from Silveirinha.

Conclusions

In Europe, the herpetofauna from Silveirinha (Portugal) represents the only described assemblage of amphibians and squamates from the base of the Eocene (MP 7). Although specimens are not numerous (apart from osteoderms of Glyptosaurinae), the fauna is diverse. It includes at least two species of amphibians (two families) and 15 species of squamates (at least nine families); however, apart from *Dunnophis matronensis*, these species cannot be identified because the faunas from MP 7 are poorly known and/or the specimens from Silveirinha are not sufficiently diagnostic.

Following is the list of amphibians and squamates from the locality:

Amphibia
- CAUDATA
  - Salamandridae (one indeterminate genus and species).
- ANURA
  - ? Pelobatidae (one indeterminate genus and species).

Squamata
- LACERTILIA
  - Iguanidae (*Geiseltaliellus* sp. and one indeterminate genus and species).
  - Agamidae (cf. *Tinosaurus*).
  - Gekkonidae (one indeterminate genus and species).
  - Scincomorpha (one or two indeterminate families, two indeterminate genera and species).
  - Anguidae
    - Glyptosaurinae
      - Glyptosaurini (one indeterminate genus and species).
      - Melanosaurini (cf. *Melanosaurus* and one indeterminate genus and species).
    - ? Anguinae (one indeterminate genus and species).
  - ? Varanidae (one indeterminate genus and species).
  - Amphisbaenidae (one indeterminate genus and species).
- SERPENTES
  - Boidae (one indeterminate genus and species).
  - Tropidophiidae (*Dunnophis matronensis*).
  - ? Indeterminate family (one indeterminate genus and species).

This fauna confirms that iguanid lizards and the snake *Dunnophis matronensis* are present in the base of the Eocene (MP 7) of Europe. The locality, as also Dormaal (Belgium), has produced the earliest gekkonid lizards of Europe.

Discoglossid amphibians and russellophiid snakes, previously reported from the locality, appear to be absent.

From a palaeobiogeographic point of view, it should be noted that the Glyptosaurini, cf. *Melanosaurus* (Melanosaurini), and *Dunnophis* (Tropidophiidae) show close affinities to North American taxa. On the whole, this assemblage displays a marked Laurasian pattern. Marandat (1997) and Escarguel (1999) shown that the faunas of mammals from the lower (including MP 7) and middle Eocene of southern Europe are somewhat different from those of northern Europe. Such differences between southern and northern Europe are not perceivable on the basis of amphibians and squamates; the fauna from Silveirinha does not provide information about possible endemicity within Europe. However, our data from the lowermost Eocene are still poor and no definite conclusion can be inferred as far as palaeogeographic relations within Europe are concerned.

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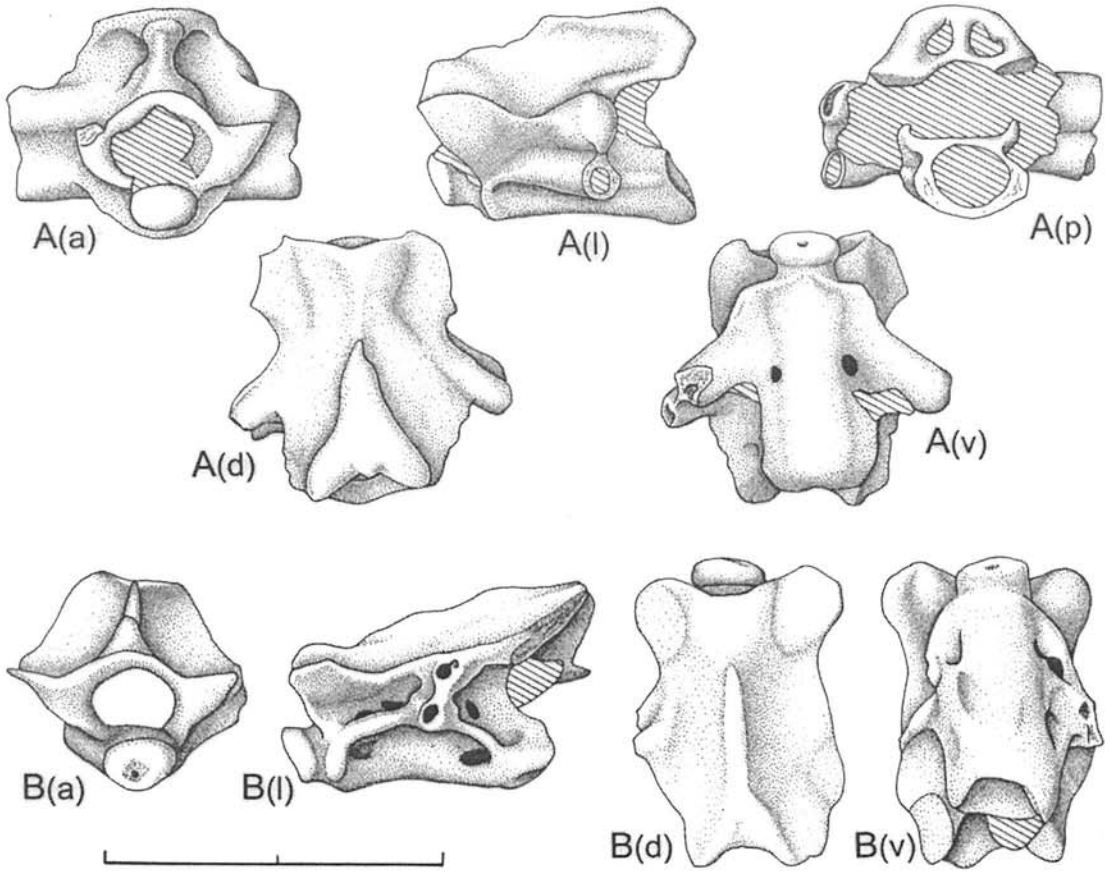
Fig. 1 – Salamandrid amphibian, indeterminate genus and species. A: anterior trunk vertebra. B: more posterior trunk vertebra. (a: anterior view; d: dorsal view; l: left lateral view; p: posterior view; v: ventral view). Scale bar represents 2 mm.

Fig. 2 – Lizards. A: *Geiseltaliellus* sp., posterior part of maxilla, medial view. B: cf. *Tinosaurus*, fragment of bone bearing teeth, medial view. C: scincomorphan, indeterminate genus 1, fragment of bone bearing teeth, medial view. D: scincomorphan, indeterminate genus 2, fragment of bone bearing teeth, medial view. Scale bars represent 2 mm.



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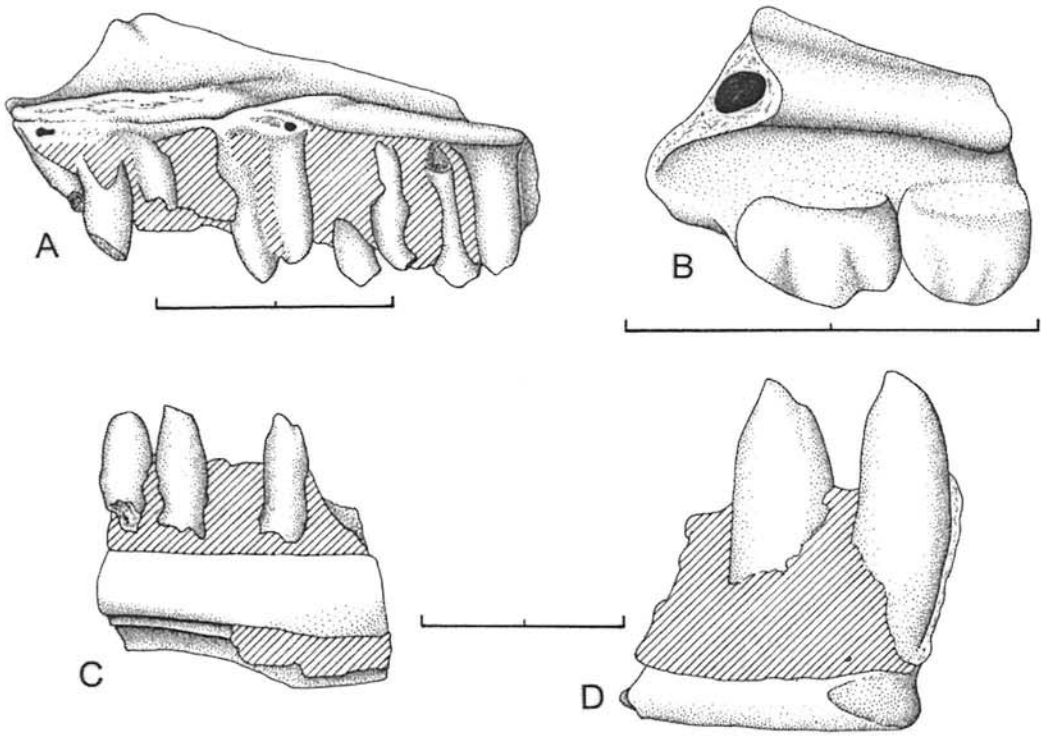

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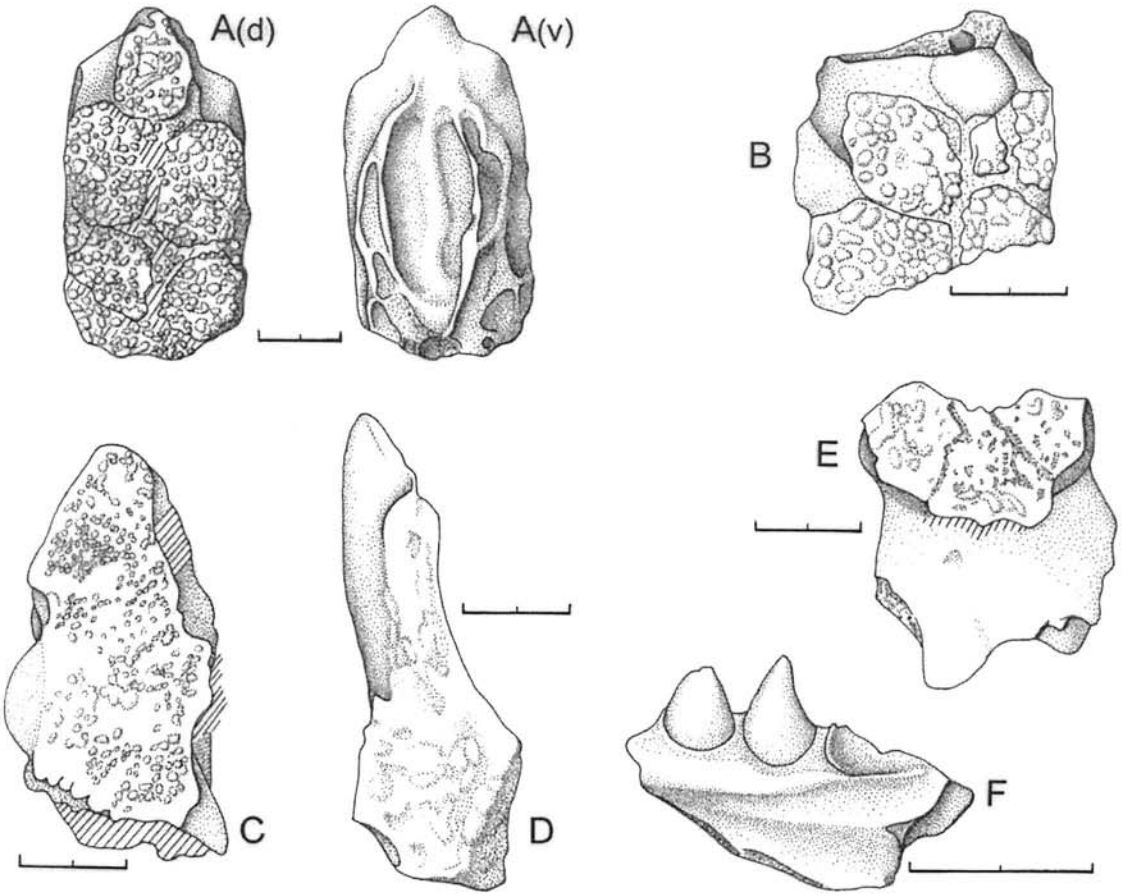
Fig. 3 – Anguid lizards. A: Glyptosaurini, indeterminate genus and species, anterior part of a frontal (d: dorsal view; v: ventral view). B: Glyptosaurini, indeterminate genus and species, fragmentary parietal, dorsal view. C: Melanosaurini, cf. *Melanosaurus*, fragmentary parietal (?), dorsal view. D: Melanosaurini, cf. *Melanosaurus*, incomplete jugal, lateral view. E: Melanosaurini, indeterminate genus and species, incomplete parietal, dorsal view. F: ? Anguinae, indeterminate genus and species, posterior part of dentary, medial view. Scale bars represent 2 mm.

Fig. 4 – Tropidophiid snake. *Dunnophis matronensis*, trunk vertebra (a: anterior view; d: dorsal view; l: right lateral view; p: posterior view; v: ventral view). Scale bar represents 2 mm



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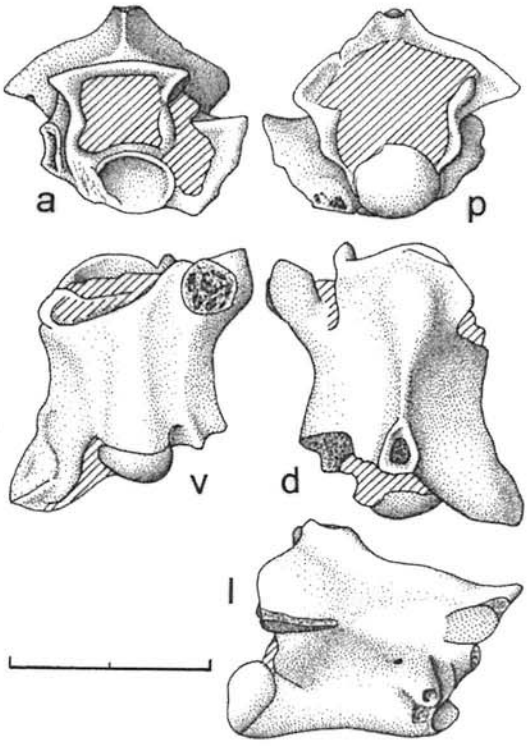

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