

## New amphisbaenian lizards from the Early Paleogene of Europe and their implications for the early evolution of modern amphisbaenians

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**ABSTRACT.** Three new amphisbaenian lizard taxa are described from the Early Paleogene of Western Europe. Two new basal forms, *Polyodontobaena belgica* gen. et sp. nov. from the Early Paleocene of Hainin (Belgium) and *Camptognathosaurus parisiensis* gen. et sp. nov. from the Late Paleocene of Rivecourt-Petit Pâtis and Cernay-lès-Reims (France), are characterised by a dentary lacking a strong angle at the symphysis and bearing 10 to 12 massively built and conical teeth. These two taxa form the new family Polyodontobaenidae. A third new amphisbaenian, *Blanosaurus primeocaenus* gen. et sp. nov., is also described from the Early Eocene of Dormaal (Belgium), Condé-en-Brie and Prémontré (France) and represents the oldest modern amphisbaenian lizard of Europe, tentatively assigned to Blanidae. It is characterised by a reduction of tooth number and by the presence of a strong angle at the symphysis. Palaeobiogeographic considerations suggest a first hypothesis that the Eocene forms would have evolved from the Paleocene species. The second hypothesis would be that as for the lizard *Scincoideus haininensis*, primitive amphisbaenians were present in Europe from the Paleocene, whereas beginning in the Early Eocene only modern forms with typical reduced dentition (fewer than 10 teeth) are present. The origin of these modern forms is very likely related with the dispersal of the first modern mammals.

**KEYWORDS:** Hainin, Dormaal, Belgium, France, Paleocene, Eocene

### Introduction

Amphisbaenians are burrowing, wormlike limbless lizards living in neotropical areas; their greatest species diversity is in Africa and South America but they are also present in Europe, around the Mediterranean Sea (Kearney, 2003; Augé, 2005; Pianka & Vitt, 2003). The size range of the different species is from 10 to 80 cm (adult body length) and most of the amphisbaenians are within a range of 25 to 40 cm (Grzimek, 2003). The most well-known species *Amphisbaenia alba* is the largest and can reach 73.5 to 85 cm in snout-vent length (Montero & Gans, 1999; Grzimek, 2003). The amphisbaenian skull is short and robustly built, the dentary is reduced and bears 5 to 9 teeth (Kearney, 2003). They live in a variety of habitats (deserts, tropical rainforests, woodlands) and usually dig burrows in loose sandy soil but may also be present under rocks or in termite nests (Grzimek, 2003). All amphisbaenians are limbless except *Bipes*, whose exhibit forelimbs, are highly specialized for digging and resemble those of moles. It is however not clear whether this is retention or if *Bipes* regained these limbs (Kearney & Stuart 2004). According to Macey et al. (2004), loss of limbs in the Rhineuridae, and the lineage leading to the Amphisbaenidae and Trogonophidae is independent and the forelimbs of bipedidae have arisen secondarily. Moreover, according to Wiens et al. (2006), limb loss and fossoriality occurred at least 25 times during squamate evolution.

Phylogenetic relationships among the amphisbaenians have been revised by Kearney (2003) and afterwards by Vidal et al. (2008). This infra-order is now divided in 6 families and 23 genera including more than 150 species. Bipedidae is represented today only by the genus *Bipes*, restricted to Mexico. Trogonophidae are represented by 4 Recent genera living in North Africa, Somalia and the Middle East. Blanidae, represented today by the genus *Blanus*, is known in Europe (e.g. *B. cinereus* and *B. mariae*), Middle East (*Blanus strauchi*) and the North of Africa (e.g. *Blanus mettetali*). Fossil forms are known from the Miocene in Europe. Recently, Cadeidae has been erected based on molecular divergence with Blanidae (Vidal et al., 2008; Vidal & Hedges, 2009) and only includes the genus *Cadea* which is restricted to Cuba. Amphisbaenidae is the most diversified family with 19 genera and 133 extant and fossil species (Augé, 2005). Extant taxa are living in South America (e.g. *Amphisbaena*, *Mesobaena*), and in Africa (e.g. *Ancylocranium*, *Baikia*, *Chirindia*). After Blanidae has been split from Amphisbaenidae by Kearney (2003), only *Lophocranium rusingensis* from the Lower Miocene of Kenya was still included in the family Amphisbaenidae. This

family is therefore not present in Europe (Charig & Gans, 1990). Finally, Rhineuridae currently represented only by the genus *Rhineura*, is the most diversified family in terms of fossils. They are solely present in North America since the Paleocene (Estes, 1983). In Europe, in summary, Amphisbaenia are represented by amphisbaenids and blandides whereas in North-America, their presence is attested by rhineurids and bipedids.

In this paper we describe and discuss the characters of three new taxa from the Early Paleogene of Western Europe. The first one, attributed to a new basal amphisbaenian, is from the Early Paleocene locality Hainin in southern Belgium (reference-level MP1-5, Schmidt-Kittler 1987; see De Bast 2013, p. 965). The second is another primitive amphisbaenian from the Late Paleocene Rivecourt-Petit Pâtis and Cernay-lès-Reims localities of Northern France (MP6). The third new taxon has been discovered in several Early Eocene localities of eastern Belgium (Dormaal, MP7) and northern France (Condé-en Brie, MP8+9; Prémontré, MP10), and represents the oldest modern amphisbaenian of Europe.

Abbreviations: DIIC RS and DIII RS: layers DII and DIII of the Dormaal locality from the Richard Smith Dormaal collection; HA: Hainin collection, I.G. number: 30.562; IRSNB R: Royal Belgian Institute of Natural Sciences, Type and Figures collection Reptilia; KMMA/MRAC: Royal Museum for Central Africa (RMCA), Tervuren, Belgium; MNHN CB, CR or PMT: respectively Condé-en-Brie, Cernay-lès-Reims and Prémontré localities, collections houses at the Natural History Museum of Paris, France; RIV PP: Rivecourt-Petit Pâtis, collection houses at the Compiègne Museum, France.

### Systematic Paleontology

Class Diapsida Osborn 1903  
Order Squamata Opper 1811  
Suborder Lacertilia Owen 1842  
Infraorder Amphisbaenia Gray, 1844

Polyodontobaenidae fam. nov.

Type-genus: *Polyodontobaena* gen. nov.

Diagnosis: Differs from all other amphisbaenian families in having a long dentary bearing numerous teeth (10 to 12), in the absence of an angle at the mandibular symphysis and in its posterior teeth, which are massively built and conical and decrease in size towards the anterior end of the bone.

Included genera: *Polyodontobaena* gen. nov. and *Camptognathosaurus* gen. nov.

*Polyodontobaena* gen. nov.

Etymology: From the Greek Poly- (numerous), odous- (teeth), baena (head) by reference to the numerous teeth of this amphisbaenian.

Type-species: *Polyodontobaena belgica* sp. nov.

Diagnosis: Differs from other amphisbenians in that the dentary does not form a strong angle at the intermandibular symphysis and bears 12 pleurodont and heterodont teeth. In the posterior part of the jaw, teeth are more massively built and conical and decrease in height towards the anterior end of the bone. The horizontal lamina stops posteriorly after the last tooth.

*Polyodontobaena belgica* sp. nov.

(Figs. 1-2, 5A-B)

Etymology: From Belgium, where the specimens were discovered.

Holotype: IRSNB R 283 (HA 605), a nearly complete left dentary.

Paratype: IRSNB R 284 (HA 606), a right dentary.

Referred specimens: 13.7-14 (01), 16.4-15.10 (01) and HA 607-639 (37 trunk vertebrae including HA 607/IRSNB R 285); HA 640-642 (3 cervical or caudal vertebrae including HA 640/IRSNB R 286).

Type horizon and locality: Early Paleocene Hainin Formation, continental "Montian", MP1-5, Hainin, Mons Basin, Hainaut Province, Belgium.

Diagnosis: The same as for the genus.

Description: IRSNB R 283 (HA 605) and IRSNB R 284 (HA 606) are two robust dentaries (Fig. 1). Lingually, the Meckelian

groove is open. The bone is anteriorly shallow and does not form a strong angulation at the level of the intermandibular symphysis. Posteriorly, the bone is deeper and bears a well-developed intramandibular septum extending to the posterior end of the tooth row (Fig. 1A2 et B2). Ventrally the septum is fused to the dentary wall whereas the posterior border presents a wide notch. Teeth are pleurodont, conic, short, massive and slightly anteriorly oriented. Two-thirds of their height projects above the dental parapet, and a small foramen opens at the base of each tooth. The horizontal lamina has a thick lingual terminus that ends posteriorly beyond the last tooth. A narrow subdental gutter is present. The left dentary (IRSNB R 283) is 6 mm long and 2 mm high (Fig. 1A). It lacks only the anterior and posterior extremities and was likely about 7 mm long when it was complete. It has 12 loci, three of which preserve complete teeth. Two slightly striated apices are still present (Fig. 2A). Labially, this specimen is not ornamented but presents four aligned foramina (Fig. 1A3). The right dentary fragment (IRSNB R 284) is 3 mm long, 1.5 mm high and was probably about 6 mm long when it was complete (Fig. 1B). The posterior extremity and the anterior part of the bone are missing. Five tooth loci are preserved. The teeth are slightly thinner than in IRSNB R 283, and four apices are preserved. Posterior teeth (Fig. 2C) resemble those of IRSNB R 283 (Fig. 2A), whereas the more anterior teeth (Fig. 2B) are slightly labio-lingually compressed and posteriorly curved. Moreover, the striae of the apices are stronger than on the teeth of IRSNB R 283 (Fig. 2B). Three foramina are present on the labial side of IRSNB R 284 (Fig. 1B3).

Forty procoelous vertebrae belonging to amphisbenians were identified in Hainin (Fig. 5A-B). In dorsal view, the neural arch is constricted at mid-length, and its anterior border is U-shaped. The zygapophyses are oval and the prezygapophyses are distinct from the neural arch. In ventral view, the subcentral foramina are situated in the anterior part of the centrum. In lateral view, the neural arch is high and the neural spine is not well-developed, forming only a narrow line on the neural arch length. In anterior and posterior views, the cotyle and the condyle are depressed. Two forms of vertebrae are recognized. The first one (Fig. 5A) presents in ventral view slightly medially constricted borders of the centrum and well-developed subcentral foramina. In lateral

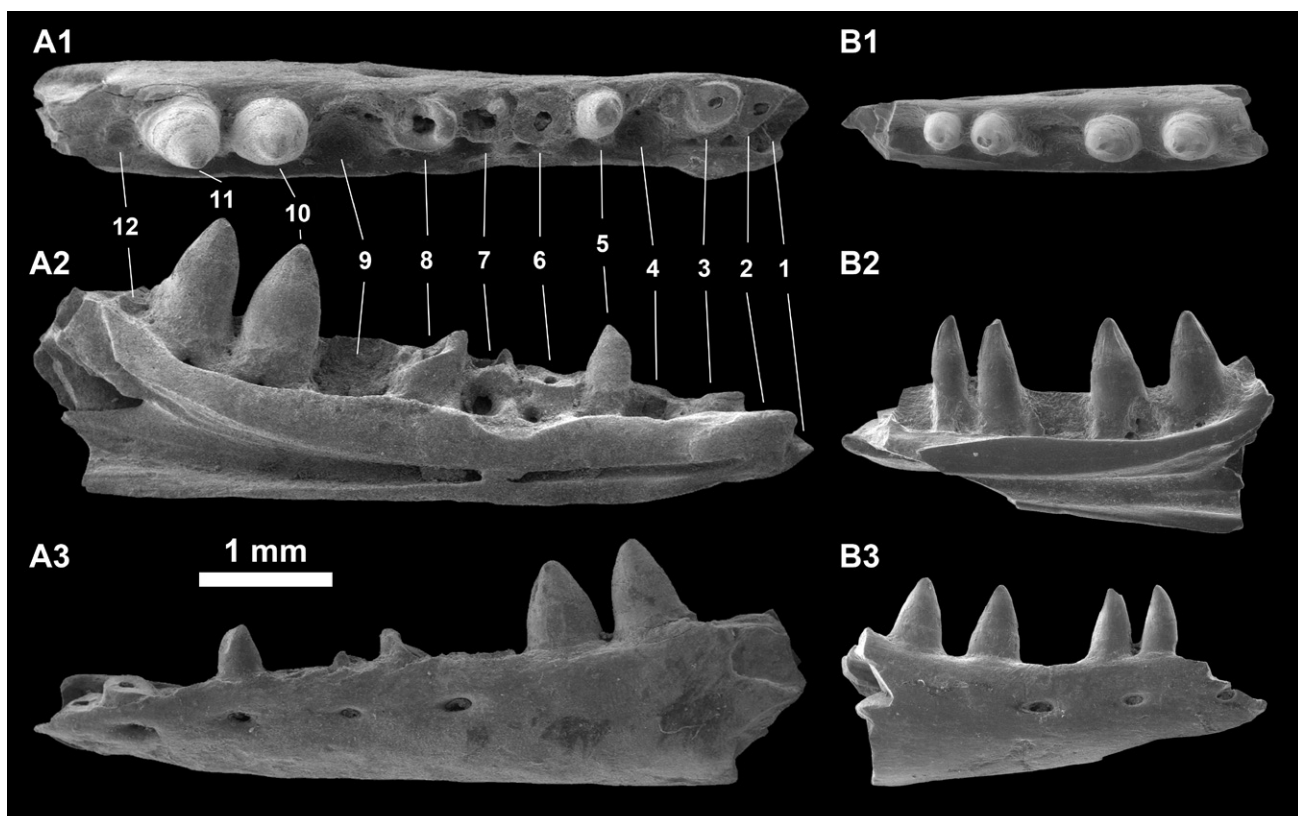
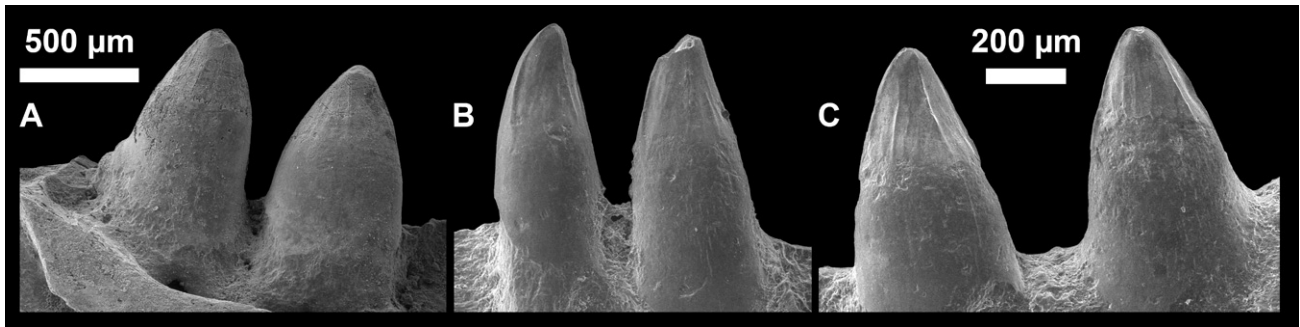


Figure 1. *Polyodontobaena belgica* gen. et sp. nov. (Early Paleocene, MP1-5, Hainin, Belgium) A. IRSNB R 283/HA 605, left dentary in dorsal (A1), lingual (A2) and labial (A3) views. B. IRSNB R 284/HA 606, right dentary in dorsal (B1), lingual (B2) and labial (B3) views.



**Figure 2.** *Polyodontobaena belgica* gen. et sp. nov. (MP1-5, Hainin, Belgium) **A.** IRSNB R 283/HA 605, detail of the posterior teeth. **B-C.** IRSNB R 284 /HA 606, detail of the anterior (**B**) and posterior teeth (**C**).

view, the ventral border of the centrum is nearly horizontal and the crest between the prezygapophyses and the postzygapophyses is ventrally curved. The paradiapophysis is well developed and is situated directly below the prezygapophysis. In anterior and posterior views, the zygapophyses are about 30 degrees above the horizontal. The second form of vertebrae (Fig. 5B) is smaller than the first form. In ventral view, the lateral borders are parallel and the subcentral foramina are reduced. In lateral view, the ventral border of the centrum is slightly concave. The paradiapophysis is reduced, slightly posteriorly displaced, and is laterally expanded to form transverse processes. The crest between the zygapophyses is strait. In anterior and posterior views, the zygapophyses are about 25 degrees above the horizontal.

**Discussion:** Vertebrae and dentaries from Hainin have been easily associated as they are the only bones showing amphisbaenian morphologies.

The first form of vertebrae corresponds to trunk vertebrae by the medially compressed centrum, the well-developed paradiapophysis, the high neural arch, and the distance between the prezygapophyses that is larger than between the postzygapophyses (Wu, Brinkman & Russell, 1996). The second form corresponds to cervical vertebrae presenting transverse processes (personal observations on *Amphisbaena alba*, IRSNB 3394).

Short and small dentaries, and vertebrae presenting a low neural spine, a flat centrum with sub-parallel borders and well-developed diapophyses, are typical for the amphisbaenians (Augé 1990a). The specimens from Hainin cannot belong to the Trogonophidae because these latter are acrodont (Rage, 1988) whereas the specimens from Hainin are pleurodont. They cannot nor belong to the rhineurids because in dorsal view the vertebrae of the latter family bear longitudinal striae and the posterior border of the neural arch is denticulate (Estes, 1983), which is not the case on the Hainin specimens. Moreover, in rhineurids, the coronoid overlaps the dentary (Kearney, 2003) whereas, compared with extant taxa, the posterior part of the dentaries from Hainin likely overlaps the coronoid. Also, in rhineurids, the articular surface between the dentaries slightly pointed posteroventrally (Kearney et al, 2005) which is not the case in Hainin specimens. The three other amphisbaenian families, Bipedidae, Blanidae and Amphisbaenidae, are not well described for their osteological characters. However, bipedids (Smith, 2009: fig. 10I), blanids (Fig. 4D) and amphisbaenids (Montero & Gans, 1999: fig. 47 and personal observations on an *Amphisbaena alba* specimen, IRSNB 3394, IG 6135) all have a dentary presenting a strong angle at the posterior end of the mandibular symphysis, which is not the case on the Hainin specimens. Moreover, most of the fossil amphisbaenians described in Europe are typically compared with the recent blandid genus *Blanus* (Augé, 1990a). The Hainin specimens resemble *Blanus* in the posteriorly curved teeth apices but differs from this genus by having nearly twice longer dentaries (7 mm versus 3-4 mm) bearing more teeth (12 versus 8). Moreover, the horizontal lamina of the Hainin dentaries ends posteriorly after the last tooth and the anterior part of the bones is not curved whereas on *Blanus*, the lamina goes posteriorly over a length corresponding to about two teeth and the anterior part of the dentary presents a strong angle (Augé & Rage, 2000). For these reasons, the Hainin specimens do not belong to *Blanus*.

Two other fossil amphisbaenian genera are described in Europe: *Omoioityphlops* and *Palaeoblanus*. The former includes two species. The first one, *O. priscus* Rochebrune 1884 is based on five articulated vertebrae from the Upper Eocene or Oligocene of France and has been considered as a *nomen dubium* by Estes (1983), since amphisbaenian vertebrae are not diagnostic to the genus or species level. A second species was nevertheless established as *O. gracilis* Roček 1984 from the Lower Miocene (MN4) of Dolnice (Czech Republic) based on dentaries and vertebrae. The size of this species is its main diagnostic character as its dentaries are only 3.5 mm long (Roček, 1984) whereas the Hainin dentary IRSNB R 283 is about twice as large (6 mm long). The specimens from Hainin can therefore not be attributed to the genus *Omoioityphlops*. Moreover, Venczel & Sanchiz (2006) and Venczel & Ştiucă (2008) considered the genus *Omoioityphlops* as a synonym of *Blanus* based on their general morphology. This idea has already been suggested by Estes (1983). *Omoioityphlops* seems therefore not to be a valid genus. The genus *Palaeoblanus* is known only from one species, *P. tobieni* from the Lower Miocene (MN1) of Germany (Schleich, 1988). This taxon shares with the Hainin specimens the absence of a strong angle at the symphysis. However, the dentary of *P. tobieni* is shorter (4-5 mm), bears only 8 homodont teeth, and the first anterior tooth is the most developed (Augé & Rage, 2000) which is not the case on the Hainin dentaries. These latter cannot therefore belong to *Palaeoblanus tobieni*.

The Hainin dentaries are characterized by a long bone reaching about 7 mm long and bearing 12 teeth, by the absence of an angle at the symphysis and by posterior teeth that are massively build, conic and are decreasing in size towards the anterior part of the bone. These characters permit attribution of this amphisbaenian from Hainin to a new genus and species and the erection of a new family.

#### *Camptognathosaurus* gen. nov.

**Etymology:** From the Greek kamptos- (curved), gnathos- (jaw), saurus (lizard) by reference to the curved dentary of this amphisbaenian.

**Type-species:** *Camptognathosaurus parisiensis* sp. nov.

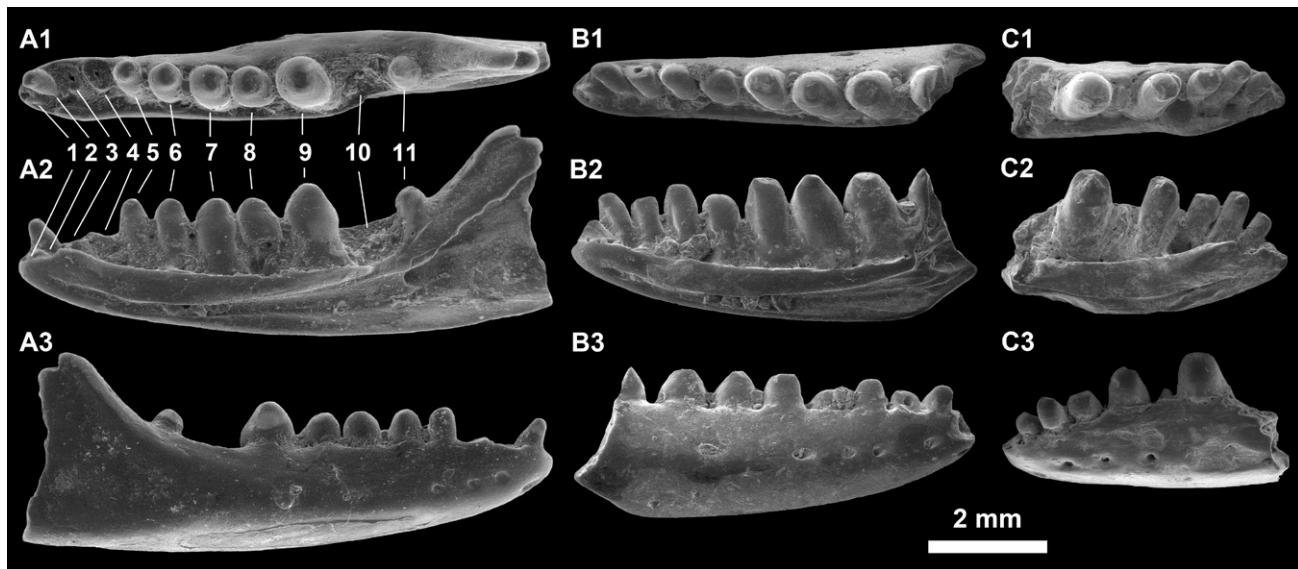
**Diagnosis:** Differs from all other amphisbaenians except *Polyodontobaena belgica* in having a dentary that does not form a strong angle at the posterior end of the intermandibular symphysis. Differs from *Polyodontobaena belgica* in having a taller, more robust dentary with a smoothly curved ventral border; and only 11 teeth that are more bulbous and project above the dental parapet nearly the half of their height.

#### *Camptognathosaurus parisiensis* sp. nov.

(Fig. 3)

**Etymology:** From the Paris Basin where the specimens were discovered.

**Holotype:** RIV PP 413, a nearly complete right dentary from Rivecourt-Petit Pâtis, Paris Basin, France.



**Figure 3.** *Camptognathosaurus parisiensis* gen. et sp. nov. **A.** RIV PP 413 (MP6b, Rivecourt-Petit Pâtis, France), right dentary in dorsal (A1), lingual (A2) and labial (A3) views. **B.** CR 17420 (MP6a, Cernay-lès-Reims, France), nearly complete right dentary in dorsal (B1), lingual (B2) and labial (B3) views. **C.** CR 17425 (MP6, Cernay-lès-Reims, France), anterior part of a left dentary in dorsal (C1), lingual (C2) and labial (C3) views.

Referred specimens: Rivecourt, Carrière Petit Pâtis, Paris Basin, France: RIV PP 414, a fragmentary right dentary and RIV PP 415, a poorly preserved left dentary; Cernay-lès-Reims, Carrière Lemoine, Paris Basin, France: about fifteen dentaries and maxillae including MNHN CR 17420, a well-preserved right dentary, MNHN CR 17421, posterior part of a right dentary and MNHN CR 17425, anterior part of a left dentary.

Type horizon and locality: latest Paleocene, MP6b, Rivecourt-Petit Pâtis, Paris Basin, France.

Diagnosis: The same as the genus.

Description: The best preserved specimen is a right dentary, RIV PP 413, from the locality of Rivecourt-Petit Pâtis (Paris Basin, France; Smith et al. in press; Fig. 3A). It is a robust bone, 9 mm long and 3 mm high in its most posterior part. It lacks only the posterior extremity. As in *Polyodontobaena belgica*, the Meckelian groove is open and the anterior part of the dentary lacks a strong angulation at the posterior end of the intermandibular symphysis. However, the ventral border is not straight as in *P. belgica* but is smoothly curved. Posteriorly, RIV PP 413 is tall and bears a well-developed intramandibular septum extending to the posterior end of the tooth row and a posteriorly oriented coronoid process (Fig. 3A2). The teeth are pleurodont, conical, short, massive and slightly anteriorly oriented. Nearly half of their height projects above the dental parapet, and a replacement pit opens at the base of several teeth. Three other fragments from the locality of Cernay-lès-Reims (Paris Basin, France) are attributed to the same taxon: MNHN CR 17420, a right dentary lacking its posterior part (Fig. 3B), MNHN CR 17421, a posterior part of a right dentary, and MNHN CR 17425, the anterior part of a left dentary (Fig. 3C). On these specimens, the horizontal lamina has a thick lingual terminus that extends posteriorly beyond the last tooth (Fig. 3B2). In dorsal view, a subdental gutter is present but is narrower than in *P. belgica* (Fig. 3A1, 4B1, 4C1 compared with Fig. 1A1, 1B1). Also, the symphysis (Fig. 3A1, 4B1) seems more anteriorly developed than in *P. belgica* (Fig. 1A1). Labially, the dentary is not ornamented but has 5 aligned foramina (Fig. 3A3) that are more closely spaced than in the holotype of *P. belgica* (Fig. 1A3).

RIV PP 413 clearly has 11 loci for teeth, and eight of them are preserved. Apices are not striated on RIV PP 413 (Fig. 3A2) and MNHN CR 17420 (Fig. 3B2). However, striae are clearly visible on MNHN CR 17421 and MNHN CR 17425 (Fig. 3C2). On the latter specimen, a small striated lingual cusp is also present.

Discussion: As in *Polyodontobaena belgica*, the specimens

described from the localities of Rivecourt-Petit Pâtis and Cernay-lès-Reims are typical for the amphisbaenians and do not belong to any known families because teeth are pleurodont and there is no clear angulation in the anterior part of the dentary. For the same reasons, the specimens cannot be attributed to *Blanus*, *Omoiotyphlops* or *Palaeoblanus*. Indeed, teeth are heterodont, the dentaries are long (9 mm long), the horizontal lamina of the dentaries ends posteriorly behind the last tooth, and the angulation of the ventral margin is lacking in the anterior part of the bones.

The dentaries from the two French localities are similar to those of Hainin in having a long bone bearing more teeth than usual, in the absence of an angle at the symphysis and in the shape of the posterior teeth, which are massively built and conical and decrease in size towards the anterior end of the bone. However, *Camptognathosaurus parisiensis* differs from the Belgian specimens in having a taller, more robust dentary and a smoothly curved ventral border; teeth are more bulbous and do not extend so far above the dental parapet. These characters permit attribution of the amphisbaenian from Rivecourt-Petit Pâtis and Cernay-lès-Reims to a new genus and species in the same family as *Polyodontobaena belgica*.

Family Blanidae Kearney 2003

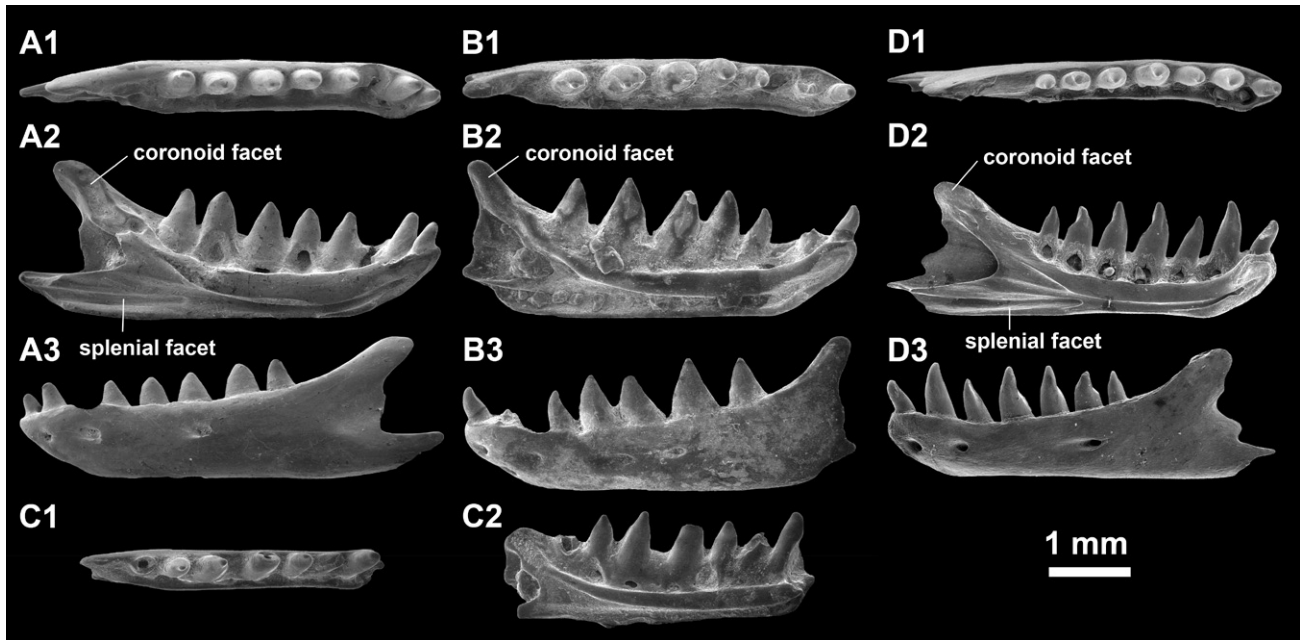
*Blanosaurus* gen. nov.

Etymology: By reference to the extant amphisbaenian genus *Blanus*, which the new genus resembles, and *saurus* (lizard).

Type-species: *Blanosaurus primeocaenus* sp. nov.

Diagnosis: Differs from the Polyodontobaenidae in having a strong angle at the the mandibular symphysis of the dentary and in bearing 8 teeth; differs from Trogonophidae in having pleurodont teeth; differs from Rhineuridae in lacking longitudinal striae on the vertebrae and a denticulate neural arch and in having a coronoid process not overcomng the dentary; differs from Amphisbaenidae by lacking the ventral extension of the symphyseal articular facet; and differs from Bipedidae by having 8 loci for teeth. Differs from *Palaeoblanus* in lacking a strong angle at the symphysis, in having conical and labio-lingually compressed teeth with a first prominent tooth. It further differs from *Blanus* in having a taller Meckelian groove and in presenting an intermandibular septum extending anteriorly and reaching or surpassing the level of the posterior end of the tooth row.

*Blanosaurus primeocaenus* sp. nov.  
(Fig. 4A-C, 5C)



**Figure 4.** A–C. *Blanosaurus primeocaenus* gen. et sp. nov. A. IRSNB R 287/DIII RS26 (MP7, Dormaal, Belgium), left dentary in dorsal (A1), lingual (A2) and labial (A3) views. B. PMT 103 (MP10, Prémontré, France), left dentary in dorsal (B1), lingual (B2) and labial (B3) views. C. CB 1616 (MP8+9, Condé-en-Brie, France), incomplete left dentary in dorsal (C1) and lingual (C2) views. D. *Blanus strauchi* (Recent, Sagalassos, Turkey) KMMA/MRAC A1-079-R-0006, reversed right dentary in dorsal (D1), lingual (D2) and labial (D3) views.

**Etymology:** From the Latin *Primus* (early) and *Eocaenus* (Eocene) in reference to the presence of the species in the early Eocene.

**Holotype:** IRSNB R 287 (DIII RS26), a nearly complete left dentary.

**Referred specimens:** Dormaal, Vlaamse Brabant, Belgium: about 60 dentaries and fragmentary dentaries, from the levels DIIC and DIII of the private collection of one of us (R.S.) including IRSNB R 113 (left dentary); and more than one hundred of vertebrae including IRSNB R 114 (dorsal vertebra) and IRSNB R 288 (DIIC RS15, trunk vertebra); Condé-en-Brie, Paris Basin, France: two dentaries including MNHN CB 1616 and CB 16461, and nine trunk vertebrae including MNHN CB 1615; Prémontré, Paris Basin, France: four dentaries including MNHN PMT 99 and PMT 100 (left dentaries) and 24 vertebrae including MNHN PMT 101 and PMT 102 (two trunk vertebrae).

**Type horizon and locality:** earliest Eocene Dormaal Member of the Tienen Formation, Landen Group, MP7, Dormaal, Belgium.

**Diagnosis:** The same as the genus.

**Description:** The left dentary IRSNB R 287 is the best-preserved (Fig. 4A). It is 5 mm long and 2 mm high at its most posterior end. It is lacking only the third tooth (from anterior). Like in *Polyodontobaena belgica*, the Meckelian groove is open but contrary to *P. belgica*, the anterior part of the dentary forms an angulation at the posterior end of the mandibular symphysis. The ventral border of the bone is straight and horizontal until the level of the coronoid process. A strong splenial facet is present in the postero-ventral region of the dentary. This posterior part of the bone is tall and bears a well-developed intramandibular septum extending to the posterior end of the tooth row (Fig. 4A2). The teeth are pleurodont, labio-lingually compressed, short and slightly anteriorly oriented. Nearly half their height projects above the dental parapet, and a replacement pit is open at the base of two teeth. The horizontal lamina has a thick lingual terminus that does not extend posteriorly beyond the tooth row. In dorsal view, a subdental gutter is present of about the same width as on *P. belgica*. Labially, IRSNB R 287 is smooth (not ornamented) and has 3 aligned foramina (Fig. 4A3). The last foramen is more widely separated from the anterior ones than in *P. belgica* and *Camptognathosaurus parisiensis*. The surangular notch is

distinctive; the dorsal part of the coronoid process is dorsally oriented while the ventral part of the dentary is horizontal and posteriorly oriented. Eight teeth are clearly present on IRSNB R 287, but in the posterior part of the bone a small hole is present as a remnant of a ninth small tooth. Moreover, on 16 dentaries where a tooth count can be done, 15 of them presents 8 teeth and only one presents a much reduced ninth tooth. Some of the Dormaal specimen presents striated apices.

About one hundred procoelous vertebrae belonging to amphisbaenians were identified in Dormaal (Fig. 5C). In dorsal view, the neural arch is constricted at mid-length, and its anterior border is U-shaped. The zygapophyses are oval and the prezygapophyses are distinct from the neural arch. In ventral view, the subcentral foraminae are situated in the anterior part of the centrum. This latter has slightly medially constricted borders. In lateral view, the neural arch is low and the neural spine is not well developed, forming only a narrow line on the neural arch length. The ventral surface of the centrum is slightly concave and the interzygapophyseal ridge is nearly horizontal. The paradiapophysis is well developed and situated directly below the prezygapophysis. In anterior and posterior views, the cotyle and the condyle are dorso-ventrally flattened. The zygapophyses are about 30 degrees above the horizontal.

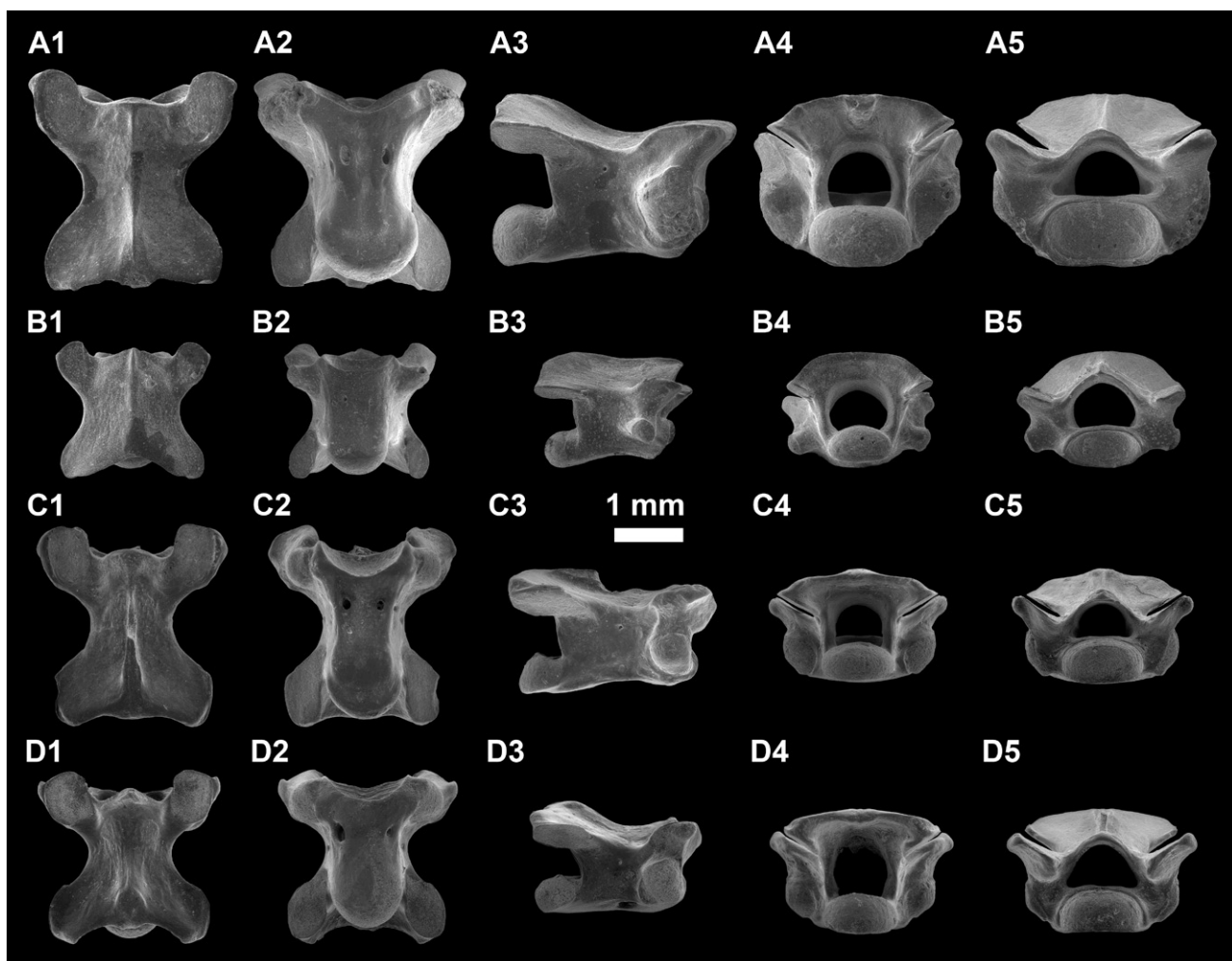
**Discussion:** Vertebrae and dentaries from Dormaal have been easily associated as they are the only bones showing amphisbaenian morphologies. As *Polyodontobaena belgica* and *Camptognathosaurus parisiensis*, the specimens from Dormaal cannot belong to the Trogonophidae or Rhineuridae. They are closer to the Bipedidae, Blanidae and Amphisbaenidae in having a strong angle at the the mandibular symphysis. However, the Dormaal taxon differs from the Amphisbaenidae by having a dorso-ventrally oriented symphyseal articular facet on the dentary that projects ventrally and forms a kind of protuberance (Montero & Gans, 1999: fig. 47 and personal observations on an *Amphisbaena alba* specimen, IRSNB 3394). This complex structure is not present on the Dormaal dentaries. The Dormaal taxon resembles bipedids and blandid in having the intermandibular septum extending anteriorly and reaching or surpassing the level of the posterior end of the tooth row; a strong splenial facet in the postero-ventral region of the dentary; and the posterior part of the dentaries likely overcoming the coronoid (see Smith, 2009: fig. 10I for a drawing of *Bipes biporus*; Fig. 4D). The vertebrae of the Dormaal taxon are also similar to those

of *Bipes biporus* (Augé, 2012: fig. 4a) and of *Blanus cinereus* (Augé, 2012: fig. 4e) and have a completely different morphology than those of rhineurids, trogonophids and amphisbaenids (Augé, 2012: fig. 4b-d). However, bipedids have only 6 teeth whereas the Dormaal taxon has 8 teeth. A comparison between Dormaal specimens and the genus *Blanus* (Blanidae) was already mentioned in several publications (Estes, 1983; Hecht & Hoffstetter, 1962; Augé, 1990a, 1990b). Augé (1990a) indicates some differences between the Dormaal specimens and two recent species of *Blanus*. Following this author, the Dormaal specimens differ from the species *Blanus cinereus*, *B. antiquus* and also from *Paleoblanus tobieni* by having a dorso-ventrally wider Meckelian groove. Indeed, the ventral border of the *B. cinereus* dentaries (see Blain, 2009, fig. 10.1) is more developed dorsally and the Meckelian groove opens therefore more medially. Moreover, the intermandibular septum of *Blanus strauchi* extends anteriorly but not reaches or surpasses the level of the posterior end of the tooth row as on the Dormaal specimens (Fig. 4).

The Dormaal specimens cannot be attributed to the European fossil genera *Omoiothylops* and *Palaeoblanus*. Indeed, *Omoiothylops priscus* was considered as a *nomen dubium* by Estes (1983); *O. gracilis* has only 3.5 mm long dentaries (Roček, 1984) and *Palaeoblanus* lacks the strong angle at the symphysis level, presents conical teeth, and has a first prominent tooth (Schleich, 1988). The Dormaal taxon resembles *Anniealexandria gansi* in the general shape of the dentary (Smith, 2009). However, the dentaries of this latter taxon have 9 teeth whereas most of the Dormaal specimens have only 8 teeth. Moreover, the dentary

from the Early Eocene (MP8+9) of Mutigny (Paris Basin, France) attributed to *Anniealexandria* sp. by Augé (2012) clearly presents a heterodont dentition (Augé, 2012: fig. 2), which is not the case in the homodont Dormaal dentaries (Fig. 4). This homodonty precludes also an attribution of the Dormaal taxon to *Louisamphisbaena* Augé, 2012 (tentatively attributed to Blanidae), which moreover has 7 widely spaced teeth on the dentary (*versus* 8 closely spaced teeth on Dormaal specimens). The Dormaal dentaries also clearly differ from those from *Polyodontobaena belgica* and *Camptognathosaurus parisiensis* mainly in having fewer tooth loci (8 *versus* 12 and 11 respectively on the *P. belgica* and *C. parisiensis*) and by presenting a strong angulation at the symphyseal level (*versus* no angulation or a smoothly curved dentary respectively on the *P. belgica* and *C. parisiensis*).

The Dormaal specimens are therefore here attributed to a new genus and species, tentatively attributed to the family Blanidae. Indeed, similarities with the Bipedidae have to be kept in mind even if this latter family is only present in Mexico and is usually excluded for geographic and stratigraphic reasons (Delfino, 1997; Augé, 2012). Both families have been considered as being basal in phylogenetic analysis (Kearney, 2003). However, Macey et al. (2004) placed Rhineuridae at the base of the tree, and Bipedidae have been placed as the sister taxon to Amphisbaenidae plus Trogonophidae. This hypothesis has been confirmed and followed by subsequent authors (e.g. Müller et al., 2011; Gauthier et al., 2012; Pyron et al., 2013). In this new configuration, Amphisbaenians are closely related to Lacertidae.



**Figure 5.** Comparison of vertebrae morphology of *Polyodontobaena belgica* gen. et sp. nov., *Blanosaurus primeocaenus* gen. et sp. nov., and *Blanus strauchi*. **A.-B.** *Polyodontobaena belgica* gen. et sp. nov. **A.** IRSNB R 285/HA 607 (MP1-5, Hainin, Belgium), first form of vertebra (trunk) in dorsal (**A1**), ventral (**A2**), right lateral (**A3**), posterior (**A4**) and anterior (**A5**) views. **B.** IRSNB R 286/HA 640 (MP1-5, Hainin, Belgium), second form of vertebra (cervical or caudal) in dorsal (**B1**), ventral (**B2**), right lateral (**B3**), posterior (**B4**) and anterior (**B5**) views. **C.** *Blanosaurus primeocaenus* gen. et sp. nov. IRSNB R 288/DIIC RS15 (MP7, Dormaal, Belgium), trunk vertebra in dorsal (**C1**), ventral (**C2**), right lateral (**C3**), posterior (**C4**) and anterior (**C5**) views. **D.** *Blanus strauchi* (Recent, Sagalassos, Turkey) KMM/AMRAC A1-079-R-0006, trunk vertebra in dorsal (**D1**), ventral (**D2**), right lateral (**D3**), posterior (**D4**) and anterior (**D5**) views.

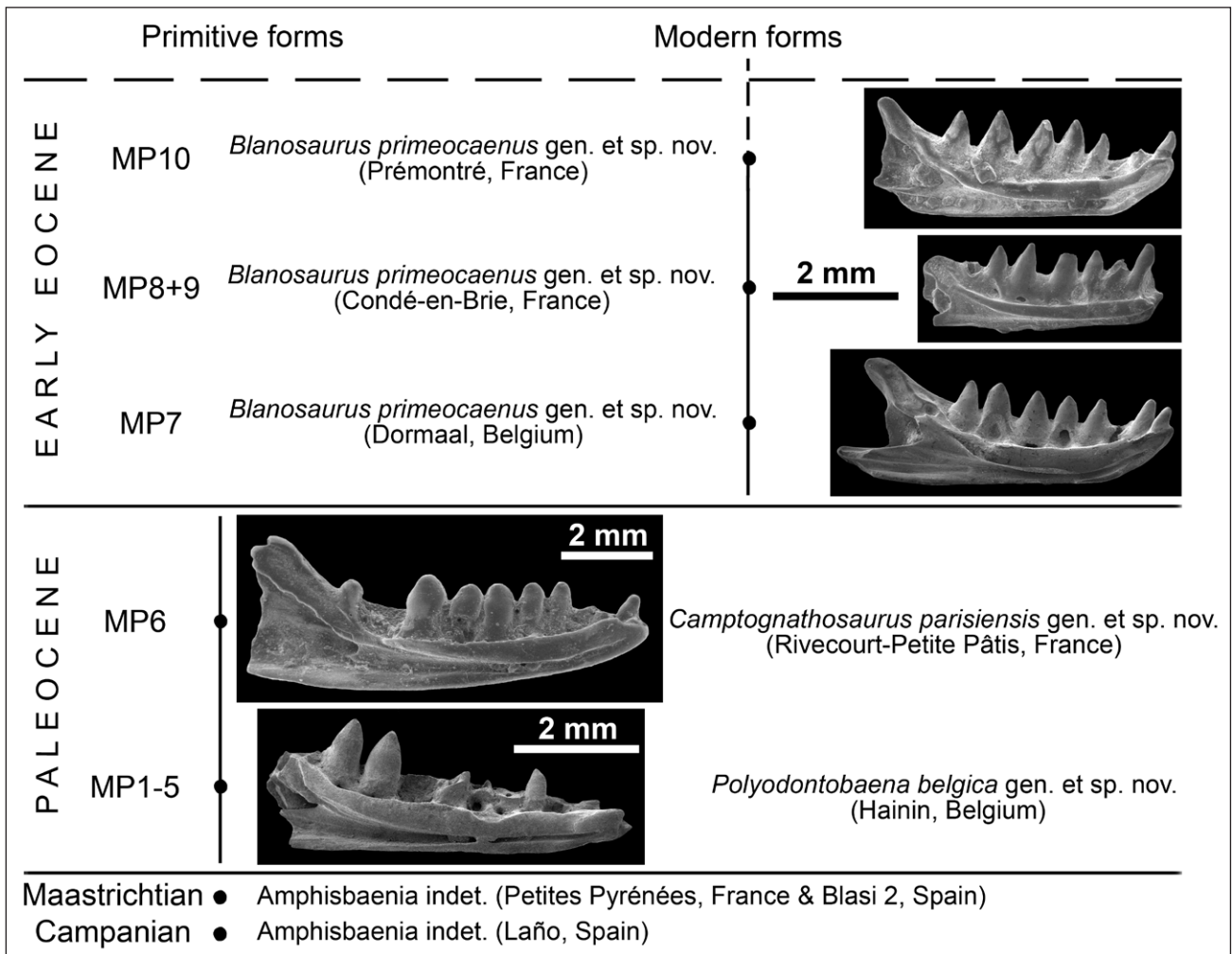


Figure 6. Stratigraphic distribution of amphisbaenians in Europe based on Paleocene and Early Eocene specimens described in this paper.

Smith (2009) indicated that the North American species *Anniealexandria gansi* presents similarities with *Bipes*. These two taxa have been considered with *Blanus*, Amphisbaenidae, and Trogonophiidae as being ‘higher’ amphisbaenians presenting four synapomorphies: (1) reduction or loss of the anterolateral process of the coronoid; (2) posterior extension of the intramandibular septum at least to the end of the tooth row; (3) presence of a strong facet for the splenial on the ventromedial face of the intramandibular septum; (4) increased height of the dentary posteriorly. The Hainin taxon resembles ‘higher’ amphisbaenians in presenting the two first characters. However, a low tooth count and the lack of an angulation at the symphysis are more consistent with a basal position for Polyodontobaenidae. These characters are conflictual and the accurate phylogenetic position of the Hainin taxon is therefore difficult to establish. Moreover, Macey et al. (2004) considered taxa found in Laurasian regions (Rhineuridae and Bipedidae) as basal. However, these authors did not split Blanidae from Amphisbaenidae as established by Kearney (2003).

Finally, some specimens from the Early Eocene of both French localities of Condé-en-Brie (MP8+9, Fig. 4C) and Prémontré (MP10, Fig. 4B) present exactly the same characteristics as the Dormaal specimens. In Condé-en-Brie, a left dentary (MNHN CB 1616, Fig. 4C), an incomplete dentary (MNHN CB 16461) and nine trunk vertebrae (MNHN CB 1615) have already been described (Augé 1990b). They are therefore also attributed to *Blanosaurus primeocaenus*.

### Biogeographic considerations

The origin and affinities of the amphisbaenians remain obscure. Following Kearney (2003), it has probably to be found in the Jurassic of Gondwana based on their current abundance in Africa and South America today. However, a western Mediterranean

or Laurasian origin has also been mentioned (Kearney, 2003). More recently, Macey et al. (2004) and Hembree (2006) suggest that amphisbaenians originated before the Late Triassic breakup of the Pangea, Vidal et al. (2008) proposed that African Amphisbaenidae crossed the South Atlantic by rafting late in the Paleogene to invade South America and Hipsley et al. (2009) suggest that amphisbaenians separated from lacertids during the Late Cretaceous. Finally, molecular phylogenies indicate the following relationship of the taxa (Vidal et al., 2008; Pyron et al., 2013): [Rhineuridae [Bipedidae [Cadeidae, Blanidae [Amphisbaenidae, Trogonophiidae]]]]. This pattern transposed in terms of areas would be: [North-America [North-America [North-America, Europe [Africa-South-America, Africa]]]] and indicate that basal clades originated in North-America.

In Europe, the presence of amphisbaenians have been suggested based on isolated vertebrae coming from the Campanian of Laño in Spain (Rage, 1999), and the Maastrichtian of the Petites Pyrénées in France (Gheerbrant et al., 1997). However, these two attributions are tentative and these vertebrae could likely belong to anguids (Blain, 2010; Augé, 2012). The presence of amphisbaenians in the Early Paleocene of Hainin was first mentioned by Groessens-Van Dyck (1986, p.59) and based on our study it represents the oldest amphisbaenian formally identified in Europe. As previously mentioned, *Polyodontobaena belgica* gen. et sp. nov. and *Camptognathosaurus parisiensis* gen. et sp. nov. present an especially primitive morphology while *Blanosaurus primeocaenus* appears to present a modern pattern. Following Wu et al. (1996), amphisbaenians usually bear less than 10 teeth but this character varies within the suborder. A great number of teeth (9 loci) are described in *Oligodontosaurus wyomingensis* and also for *Amphisbaena alba*. Same authors defined that it is a basal condition within the amphisbaenians. This indicates that the Hainin amphisbaenian that bears 12 loci is more primitive that these two taxa even if tooth reduction could have taken place

independently in different amphisbaenian lineages (Smith, 2009). The amphisbaenians from the Eocene that resemble *Blanus* seem to be more derived.

In order to understand the evolution of the amphisbaenians in Europe, comparative studies have been done on specimens from the Paleocene of Hainin (MP1-5, Belgium), Cernay-lès-Reims (MP6a, France), Rivecourt-Petit Pâtis (MP6b, latest Paleocene, France) and from the Lower Eocene of Dormaal (MP7, Belgium), Condé-en-Brie (MP8+9, France) and Prémontré (MP10, France). This study allowed considering two main hypotheses. The first one is that the Eocene forms would have evolved from Paleocene species. However, Polyodontobaenidae and Blanidae are morphologically different and some “intermediate” forms or more fossils would have to be found to support this hypothesis. The second hypothesis would be that as for the lizard *Scincoidea haininensis* (Folie et al. 2005), primitive amphisbaenians were present during the Paleocene, and have been replaced at the beginning of the Eocene or at least before the Paleocene-Eocene Thermal Maximum by modern taxa bearing reduced jaws (Fig. 6). As already mentioned by several authors (e.g. Augé, 2003; Folie et al., 2005), numerous herpetological genera and families occur indeed for the first time in the European fossil record at the earliest Eocene of Dormaal (MP7). These occurrences are very likely related with the dispersal of the first modern mammals in Europe around the Paleocene-Eocene Thermal Maximum (Smith, 2000; Smith et al., 2006). The modern amphisbaenian taxa are thus likely blaniids and maybe bipedids but no fossil bipedids have been recorded yet. The North-American fossil amphisbaenians are rhineurids and present a very different morphology than the European amphisbaenids. The only exception seems to be *Anniealexandria* from the earliest Eocene of Wyoming (W-0) that does not resemble to a rhineurid. Moreover, this genus and *Blanosaurus* from the earliest Eocene of Belgium (MP7) are present simultaneously on both continents. Therefore, it is difficult to establish the biogeographic origin for these genera. A possibility would be a dispersal from Africa or Asia. Unfortunately, fossils from these two continents are not sufficiently well known to test this hypothesis. Until now, two amphisbaenians (*Tadrosaurus gheerbranti* and another undetermined taxon) have been described from the Late Paleocene of Morocco (Augé & Rage, 2006) but these taxa are morphologically distinct from the Paleocene Polyodontobaenidae and the Eocene Blanidae of Europe.

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