Reptilian, therapsid and mammalian teeth from the Upper Triassic of Varangéville (northeastern France)

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Abstract

Microvertebrate remains have been discovered at a new Late Triassic locality in Varangéville (northeastern France). The material includes reptilian (Ichthyosauria indet., Phytosauridae indet., the pterosaur aff. *Eudimorphodon*, Archosauria indet.), therapsid (advanced Cynodontia) and mammalian (Haramiyidae, Morganucodontidae, Sinoconodontidae and Woutersiidae) teeth, described in the present paper. The faunal composition, closely resembling that of the neighbouring locality of Saint-Nicolas-de-Port, suggests a coastal or a deltaic depositional environment.

Key-words: Reptiles, therapsids, mammals, teeth, Upper Triassic, Varangéville.

Résumé

Des micro-restes de vertébrés ont été découverts dans un nouveau gisement daté du Trias supérieur à Varangéville (Lorraine, France). Le matériel comprend des dents de reptiles (Ichthyosauria indet., Phytosauridae indet., le pterosaure aff. *Eudimorphodon*, des Archosauria indet.), de thérapsides (des Cynodontia évolués) et de mammifères (Haramiyidae, Morganucodontidae, Sinoconodontidae and Woutersiidae). La composition faunique, proche de celle du gisement voisin de Saint-Nicolas-de-Port, suggère un paléoenvironnement côtier ou deltaïque.

Mots-clefs: Reptiles, thérapsides, mammifères, dents, Trias supérieur, Varangéville.

Introduction

In central and western Europe, the Latest Triassic tetrapod faunas are very scanty and represented almost entirely by isolated teeth. Nevertheless, several localities have been intensively investigated during the last decades because some of them have yielded the oldest known mammalian teeth (see SIGOGNEAU-RUSSELL & HAHN, 1994). The discovery of new Late Triassic localities with mammalian teeth is of great scientific interest: it increases our knowledge of the biodiversity, the evolution, the palaeoecology and the palaeogeography of earliest mammals.

The Late Triassic mammalian assemblage of Saint-Nicolas-de-Port, in northeastern France, is the richest of this age in the world: it consists of more than 1 000 isolated teeth, representing five mammalian families. Until recently, mammals were very rare in other localities of the Paris Basin and, with rare exceptions, consisted mainly of Haramiyidae. MAUBEUGE (1955: 124) describes a bone bed in the lower Rhaetian of Varangéville. At the present time, only fish teeth have been found in this layer (pers. obs.).

In April 1995, Michel Ulrich, owner of a patch of land in the vicinity of Varangéville, drew the author's attention to the presence of fossil bones on his land. He very kindly authorized the Institut royal des Sciences naturelles de Belgique to start excavations there. The sediments were carefully washed and screened and the microremains were subsequently sorted under a binocular. This led to the discovery of a collection of isolated bones and teeth of Late Triassic vertebrates. The reptilian, therapsid and mammalian teeth, which constitute the most spectacular part of the collection, are described and discussed in the present paper. The specimens are housed in the Institut royal des Sciences naturelles de Belgique .

Abbreviations

IRSNB: collections of the Institut royal des Sciences naturelles de Belgique, in Bruxelles; MNHN: collections of the Muséum national d'Histoire naturelle de Paris; SMNS: collections of the Staatliches Museum für Naturkunde, Stuttgart.

Locality and geological setting

Varangéville (Meurthe-et-Moselle, France) is situated 10 km southeast of Nancy and 4 km north of the Saint-Nicolas-de-Port quarry (Figure 1). The fossils were collected at the base of a 2.7 m thick conglomerate, consisting of small black and rolled pebbles in a sandy cement. Such a facies indicates, in the Lorraine-Luxembourg area, the beginning of the "Rhaetian" transgression (MAU-BEUGE, 1955; LAUGIER, 1971; COUREL *et al.*, 1980). This conglomerate lies on 6 m of cross-bedded sandstones, which contain several thin conglomeratic pockets. The base of the section is formed by several meters of gypsi84



Fig. 1 -- Geographical location of the Varangéville locality (VAR) and of the Saint-Nicolas-de-Port quarry (SNP).

ferous green marls, which characterize the summit of the upper "Marnes irisées" ("middle Keuper", Norian) in the Lorraine area. The associated fauna confirms a Late Triassic age for the bone-bed: teeth of the sharks *Rhomphaiodon, Hybodus* and *Lissodus*, spines of *Nemacanthus monilifer*, teeth of the actinopterygian *Saurichthys* and bones of Capitosauridae amphibians (A.R. MILNER, pers. comm.). Reptiles, therapsids and mammals only represent a few percent of the discovered material: some archosaurian vertebrae and fragments of isolated bones and the teeth described below.

From a local lithostratigraphical point of view, the bone-bed discovered at Varangéville is typically Rhaetian. Nevertheless it must be noted that the definition of this stage in continental Europe is closely related to the transgression. It is therefore probably diachronous. For that reason, the precise age of the neighbouring Saint-Nicolas-de-Port locality is disputed. Stratigraphers and mammal workers have assigned Saint-Nicolas-de-Port to the Rhaetian (LAUGIER, 1971; SIGOGNEAU-RUSSELL, 1978; CLEMENS *et al.*, 1979; CLEMENS, 1980; SIGOGNEAU-RUS-SELL & HAHN, 1994), while other palaeontologists (BUF-FETAUT & WOUTERS, 1986; CUNY & RAMBOER, 1991; DUFFIN, 1993) argue for a slightly older, Late Norian age, because of the great resemblance of its fauna to that of the Knollenmergel at Halberstadt (Germany; JAEKEL, 1914). No consensus exists at the present time and the discussion remains open. For similar reasons, the precise age of the Varangéville locality cannot be currently asserted either, pending further evidence.

Systematic Palaeontology

The general classification of vertebrates used in this paper is not cladistic, but inspired by that of CARROLL (1988). The classification of the Ichthyopterygia is from MAZIN (1982), that of phytosaurs is inspired by DOYLE & SUES (1995), that of pterosaurs is from WELLNHOFER (1978), that of cynodonts is from CARROLL (1988) and BATTAIL (1989), amended by HAHN *et al.* (1994), that of the allotherian Haramiyidae is from BUTLER & MACINTYRE (1994), that of the eotherian Morganucodontidae is from CLEMENS *et al.*, 1979 and that of the therian Woutersiidae is from SIGOGNEAU-RUSSELL & HAHN, 1995. Class Reptilia Superorder Ichthyopterygia Order Euichthyopterygia Suborder Ichthyosauria Ichthyosauria, fam., gen. et sp. indet.

IRSNB R147 (Plate 1, Fig. 1)

The base of this broken tooth is rounded in cross-section. It flattens progressively to the apex, where the crown is mediolaterally very compressed. Its very developed anterior and posterior carinae confer to the crown a spatulate shape in lateral view. These carinae do not bear serrations and form sharp edges. The base of the crown bears very well marked, broad and longitudinal flutings, which disappear towards the apex, so that the apical portion is perfectly smooth.

Such an ornamentation is characteristic of the Ichthyosauria. In most Ichthyosauria, the teeth are rounded to slightly elliptical or quadrangular in cross-section (BAR-DET, 1990). Nevertheless, in the early Liassic ichthyosaur *Temnodontosaurus platyodon* (CONYBEARE, 1822), the dental crowns are spatulate in lateral view and their cross-section progressively flattens mediolaterally to the apex. They look very similar to IRSNB R147 (compare with GODEFROIT, 1993, fig. 16c-f, pl. 8c-d). As the ichthyosaurian material currently discovered in Varangéville consists of this single partial tooth, it has been decided to refer it to Ichthyosauria indet.

> Subclass Diapsida Infraclass Archosauromorpha Superorder Archosauria Order Crocodylotarsi Infraorder Phytosauria Family Phytosauridae Meyer, 1861 Phytosauridae, gen. et sp. indet.

IRSNB R148-149, IRSNB VAR8 (Plate 1, Figs. 2-3)

IRSNB R148 is a large and slightly mediolaterally compressed tooth with a blade-like outline in lateral view. It is slightly recurved lingually. The labial side is clearly more convex antero-posteriorly than the lingual face. The enamel is nearly smooth. Both the anterior and posterior edges form serrated (in mean, 4 serrations per mm) carinae.

IRSNB R149 and **IRSNB VAR8** are recurved teeth with a nearly circular cross-section. Their anterior and posterior edges form a non-serrated carina. Their enamel is definitely fluted, the flutings disappearing towards the apex.

IRSNB R148 perfectly fits the description of the posterior teeth and **IRSNB R149** and **IRSNB VAR8**, that of the intermediate teeth of heterodont phytosaurs. Similar teeth have been abundantly discovered in the neighbouring locality of Saint-Nicolas-de-Port. BUFFETAUT & WOU-TERS (1986) and CUNY & RAMBOER (1991) refer these teeth to the species *Rutiodon rutimeyeri*. Nevertheless, other species of Phytosauridae present a similar heterodonty, with the same tooth types differentiated along the dental series (LONG & MURRY, 1995). Waiting for further evidence on the dental morphology in heterodont phytosaurs, it has been decided to refer the specimens from Varangéville to Phytosauridae indet.

Order Pterosauria Suborder Rhamphorhynchoidea Family Eudimorphodontidae WELLNHOFER, 1978 aff. Eudimorphodon

IRSNB R150 (Plate 1, Fig. 8)

The base of this tooth is broken. The crown is formed by a high, massive, triangular, straight and mediolaterally flattened principal cusp. Its labial (?) side is slightly convex antero-posteriorly and its lingual (?) side is nearly flat. Its apex is considerably worn to its lingual (?) face. The enamel is not perfectly smooth, but slightly fluted. Both the anterior and posterior edges are cutting. The main cusp bears three triangular, prominent and well detached denticles. These are asymmetrically set on the edges of the crown.

IRSNB R150 closely resembles the two enlarged maxillary teeth of the Late Triassic early pterosaur *Eudimorphodon ranzii* ZAMBELLI, 1973. The most striking feature is the asymmetrical distribution of the three prominent denticles along the edges of the main cusp (see WILD, 1978, figs. 1 and 8).

Archosauria, fam., gen. et sp. indet.

IRSNB R151 (Plate 1, Fig. 4)

This fragmentary tooth undoubtedly belongs to a carnivorous reptile: it is caniniform, very recurved towards the rear and mediolaterally compressed. Its labial side is more convex than its lingual side. The posterior carina is very cutting and serrated (in mean, 6 serrations per mm) along the whole fragment. Serrations are perfectly perpendicular to the carina. A serrated carina is also present on the apical portion of the anterior edge; it gradually becomes fainter towards the root, being replaced by a rounded edge. The enamel is criss-crossed by very thin ripples, on both sides of the crown.

Similar teeth have been discovered in the neighbouring locality of Saint-Nicolas-de-Port (BUFFETAUT & WOU-TERS, 1986; CUNY & RAMBOER, 1991) and cautiously referred to Theropoda dinosaurs because of their close resemblance with those of *Procompsognathus triassicus* FRAAS, 1913. The skull of this species is now referred to the sphenosuchian *Saltoposuchus* (SERENO & WILD, 86

1992). Nevertheless, it appears that this kind of caniniform teeth can be observed in several independent lineages of Late Triassic archosaurs. In the current state of our knowledge, they can only be referred to Archosauria indet.

IRSNB R152 (Plate 1, Fig. 5)

The base of this small caniniform tooth is broken. It is recurved backwards and mediolaterally compressed. The labial side is convex anteroposteriorly, although the lingual side is nearly flat. The apex is acute and the anterior and posterior edges are cutting. Traces of small denticles can be distinguished at the base of the anterior edge. The enamel is perfectly smooth on the labial side; it forms dense and well marked longitudinal ridges on the lingual side.

Similar teeth have been discovered in Saint-Nicolasde-Port. (GODEFROIT & CUNY, in preparation). This type of caniniform teeth is common among carnivorous archosaurs (ROMER, 1972). The typical ornamentation of the enamel, with the presence of well marked longitudinal ridges only on the lingual face, is a character that has not been recorded in any known Late Triassic archosaur. Therefore, pending further evidence, IRSNB R152 is referred to Archosauria indet.

> Subclass Synapsida Order Therapsida Suborder Cynodontia Superfamily Chiniquodontoidea Family ? Dromatheriidae ? Dromatheriidae, gen. et sp. indet.

IRSNB R153 (Plate 1, Fig. 6)

Measurements: Length of the crown: 2.65 mm; width of the crown: 0.83 mm; height of the crown: 2.78 mm.

The crown of this tooth is very eroded and typically tricuspid. It closely resembles the isolated molariforms of Chiniquodontoidea (sensu SIGOGNEAU-RUSSELL & HAHN, 1994) described from several localities from the latest Triassic of Central Europe. In occlusal view, this crown is very compressed mediolaterally: the ratio "length / width'' = 3.19. Its presumed labial side is slightly convex while the opposite side is symmetrically concave. The three cusps are perfectly aligned anteroposteriorly, forming a cutting edge. In lateral view, the central principal cusp has the shape of an isosceles triangle. Both its anterior and posterior cutting edges are slightly sinuous; its apex is rather eroded. It is flanked by one anterior and one posterior accessory cusps that are very small and eroded. The enamel is perfectly smooth. It is removed, by post-mortem abrasion, from the base of the labial (?) side and from the median part of the lingual (?) side. There is no trace of a cingulum.

Among the Chiniquodontoidea, IRSNB R153 is clearly more laterally compressed than the postcanine crowns of Gaumia longiradicata HAHN, WILD & WOUTERS, 1987: in the latter species, the ratio "length / width" of the crown varies between 2.1 and 2.75 (GODEFROIT & BATTAIL, in press). In Gaumia? incisa HAHN, WILD & WOUTERS, 1987, the crown is as laterally compressed as in IRSNB R153, but enamel ridges are well defined on the lingual side of the main cusp. A third undescribed species of Gaumia can be recognized in the Late Triassic of Hallau (Switzerland): in this form, according to SIGOGNEAU-RUSSELL & HAHN (1994), the main cusp is characterized by few indistinct enamel ridges at its tip. In Lepagia gaumensis HAHN, WILD & WOUTERS, 1987, the postcanine crowns are usually less symmetrical in lateral view. In the genus Tricuspes E. v. HUENE, 1933, the cusps are not perfectly aligned antero-posteriorly as in IRSNB R153. IRSNB R153 more closely resembles some postcanines of Pseudotriconodon wildi HAHN, LEPAGE & WOUTERS, 1984 (compare with pl. 1, fig. 1; pl. 3, fig. 1) and Microconodon tenuirostris OSBORN, 1886 (compare with SUES et al., 1994, fig. 8.4): the crown is very compressed mediolaterally, symmetrical in lateral view and the enamel is perfectly smooth. As HAHN et al. (1994) assemble the last two genera within the family Dromatheriidae, IRSNB R153 is cautiously referred to this family, too. Nevertheless, more complete material with complete roots is needed to confirm this attribution.

Chiniquodontoidea, fam., gen. et sp. indet.

IRSNB R154 (Plate 1, Fig. 7)

Measurements: Length of the crown: 1.39 mm; width of the crown: 0.65 mm; height of the crown: > 0.95 mm.

IRSNB R154 is again a tricuspid dental crown, which undoubtedly belongs to a chiniquodontoid cynodont (*sensu* SIGOGNEAU-RUSSELL & HAHN, 1994). In occlusal view, it is not as mediolaterally compressed as in IRSNB R153: the ratio "length / width" of the crown = 2.14. The lingual and labial sides are nearly symmetrically convex and, therefore, cannot be distinguished. The edge is not as cutting as on IRSNB R153. The main cusp is set in a median position; its apex is very abraded. Both the anterior and posterior accessory cusps are conical in shape, larger and better separated from the principal cusp than on IRSNB R153; their apex is also abraded. The enamel is perfectly smooth. There is no trace of a cingulum.

Among the Chiniquodontoidea, the crown of IRSNB R154 is proportionally too wide to belong to *Pseudotriconodon wildi*: in the latter, the ratio "length / width" of the crown varies between 2.4 and 4.2 (GODEFROIT & BATTAIL, in press). The general proportions of the crown are closer to those of the postcanines of *Gaumia longiradicata*. Nevertheless, the anterior and posterior accessory cusps are less well marked in this species than in IRSNB R154. In the current state of our knowledge, this tooth cannot be precisely identified. Pending the discovery of more complete material, it is thus referred to Chinquodontoidea (*sensu* SIGOGNEAU-RUSSELL & HAHN,

1994) indet. IRSNB R153 and IRSNB R154 probably belong to different genera.

Class? Mammalia Subclass Allotheria Family Haramiyidae SIMPSON, 1947 Genus *Thomasia* POCHE, 1908 *Thomasia antiqua* (PLIENINGER, 1847)

SYNONYMY

?

- 1847 Microlestes antiquus. PLIENINGER, p. 165, pl. 1, fig. 3.
 - 1871 *Microlestes antiquus*, PLIENINGER. OWEN, p. 3, pl. 1, figs. 14-15a.
 - 1871 Microlestes Moorei, OWEN OWEN, p. 6, partim, pl. 1, fig. 10.
 - 1922 Microlestes antiquus. HENNIG, p. 181, pl. 2, figs. 1-9.
- 1928 *Microcleptes fissurae* sp. nov. SIMPSON, p. 60, figs. 15a-b; pl. 11, figs. 2-3.
 - 1928 Thomasia antiqua (PLIENINGER). SIMPSON, p. 63, fig. 16.
 - 1928 *Thomasia anglica* sp. nov. SIMPSON, p. 66, figs. 17-18; pl. 2, fig. 4.
 - 1947 Thomasia antiqua (PLIENINGER). PARRINGTON, p. 714, fig. 7; pl. 1, fig. 5.
 - 1947 *Thomasia anglica* SIMPSON. PARRINGTON, p. 712, fig. 5B, fig. 7; pl. 1, fig. 5.
 - 1956 Haramiyide (Hallau XLI). PEYER, p. 12, pl. 1, fig. 41.
 - 1973 Thomasia antiqua (PLIENINGER 1847). HAHN, p. 4, fig. 1, fig. 7.
 - 1980 Thomasia antiqua (PLIENINGER, 1847). CLEMENS, p. 68.
 - 1980 Thomasia anglica SIMPSON, 1928. CLEMENS, p. 72.
 - 1990 Haramiya butleri nov. sp. SIGOGNEAU-RUSSELL, p. 86, figs. 1-3.
 - 1994 Thomasia antiqua (PLIENINGER 1847) BUTLER & MACINTYRE, p. 49, fig. 4, fig. 5g-j, fig. 7, figs. 9-10.

HOLOTYPE

an isolated lower molar preserved in the SMNS.

LOCUS TYPICUS

Degerloch, Baden-Württemberg, Germany.

STRATUM TYPICUM

Rät-Bonebed, latest Norian to earliest Hettangian (see CLEMENS, 1980).

DIAGNOSIS see BUTLER & MACINTYRE (1994: 449).

MATERIAL FROM VARANGEVILLE IRSNB M1823, a left lower prermolariform.

DISTRIBUTION

Degerloch and Olgahain, Germany (latest Norian to earliest Hettangian); Hallau, Switzerland (latest Norian to earliest Hettangian); Saint-Nicolas-de-Port and Varangéville, France (latest Norian or earliest Rhaetian); Boisset, France (earliest Rhaetian); Holwell Quarry, U.K. (Early Jurassic).

IRSNB M1823 (Figure 2; Plate 2, Fig. 1)

Measurements: Length of the crown: 1.97 mm; width of the crown: 1.13 mm; height of the crown: 1.05 mm.

IRSNB M1823 perfectly corresponds morphologically to "*Thomasia*" type II described by SIGOGNEAU-RUSSELL (1989, figs. 17-20; pl. 2d-e) from the Upper Triassic of Saint-Nicolas-de-Port. It can therefore be interpreted as a left lower premolariform (SIGOGNEAU-RUSSELL, 1989; BUTLER & MACINTYRE, 1994). The orientation of haramiyid lower premolariforms and molariforms proposed by BUTLER & MACINTYRE (1994) is followed in the present paper: the A row ("row of 3") corresponds to the lingual side and the positive end, bearing the largest cusp of the B row, is anterior.

In occlusal view, the crown of IRSNB M1823 is ovoid and elongated antero-posteriorly. It is dominated by a large conical cusp A1 set in the axis of the crown, closing its positive end. This cusp has three sides. The lingual side is convex antero-posteriorly. The antero-labial side is flat and separated from the lingual one by a blunt angle. The postero-labial side is slightly concave: it is separated from the antero-labial side by a blunt obtuse angle and from the lingual one, by an acute angle forming a rather cutting edge. Cusp A2 is half the height of A1. Its lingual side is slightly more convex than its labial side. Its anterior side forms an edge linked to the posterior edge of A1. Both its posterior side and its apex are rounded. Cusp A3 is very low, very rounded and shows a convex posterolingual side and a concave antero-labial side.

The B row is much shorter than the A row. It is formed by 3 low and bulbous cusps. The size of these cusps



Fig. 2 — Left lower premolariform of *Thomasia antiqua* (PLIENINGER, 1847) from the Upper Triassic of Varangéville (IRSNB M1823). A: labial view; B: occlusal view. Stippled areas: abrasion facets; striated areas: attrition facets.

decreases distally. They are separated from each other by a short furrow forming a small dimple at its labial end. Their labial side is convex and their lingual side, more angulous. B3 is curved lingually, meeting A3 on the median axis of the crown.

The median basin is short, narrow and slightly oblique relative to the longitudinal axis of the crown. It is bordered anteriorly by the postero-labial side of A1 and posteriorly, by the ridge between A3 and B3. Its posterior half is notably deeper and wider than its anterior half.

The abrasion facets are better marked on the B row than on the A row. That on A1 is very small and nearly perfectly apical; that on A2 is ovoid and inclined towards the rear; that on A3 is inclined towards the rear and slightly lingually; those on B1 and B2 are inclined labially; that on B3 is inclined towards the rear and slightly labially.

The best marked attrition facet can be observed on the posterior half of the internal side of A2 (facet 3, following the nomenclature of SIGOGNEAU-RUSSELL, 1989, fig. 17). It forms a flat and semi-elliptical surface. Facet 4 is very slight and inclined towards the front: it truncates the median ridge of B1 and B2. B2 bears a second triangular attrition facet on its postero-lingual face. Facet 5 can be observed on the lingual side of A3 and B3: it fuses with facet 4 in the posterior part of the central basin.

From a morphometrical point of view, Figure 3 shows that IRSNB M1823 is similar to the lower premolariforms referred to "*Thomasia*" type II from Saint-Nicolas-de-Port. It can therefore be referred to *Thomasia antiqua* (PLIENINGER, 1847) *sensu* BUTLER & MACINTYRE, 1994.

Thomasia cf. antiqua

IRSNB M1824 (Plate 2, Fig. 2)

This is the positive end half of a typical haramiyid lower molar (compare with SIGOGNEAU-RUSSELL, 1989, figs. 3-15, pl. 1, pl. 2a-b, pl. 5a). This specimen is dominated by a large A1 cusp. The lingual side of this cusp is essentially convex anteroposteriorly but it forms posteriorly a small triangular concave facet. Its labial side is formed by a median ridge flanked by two flat areas. The junction between the lingual and the labial sides of this cusp is marked by a crest. A1 cusp slopes slightly rearwards; its apex is rather rounded. Cusp A2 is broken at its base.

Cusp B1 is situated adjacent to A1, separated from it by a deep valley. It is half the height of A1 and bulbous. Its lingual side is more convex than its labial face. Its median internal ridge, not very marked, contacts the homologous ridge on A1. The posterior edge of B1 is better marked than the anterior one. B2 is distinctly smaller and lower than B1; they are separated by a short furrow ending labially in a tiny dimple. The lingual side of B2 is much more convex than its labial face. The central basin becomes larger and deeper between A2 and B2. An accessory cusp b is set in front of B1; it is smaller than B2 and bulbous. Together with the anteriorlabial side of A1, it circumscribes a small anterior basin, which opens anteriorly.

B1 and B2 bear an elliptical abrasion facet labially.

The antero-labial side of A1 bears a triangular attrition facet. It reaches the anterior basin and it slopes towards the rear.



Fig. 3 — Morphometrical comparison of IRSNB M1823 (indicated by an arrow) with other lower premolariforms of *Thomasia* antiqua from Saint-Nicolas-de-Port (after SIGOGNEAU-RUSSELL, 1989).

The roots are broken. Nevertheless, it appears that there were two divergent roots, the anterior being elliptical in cross section and larger antero-posteriorly than labio-lingually.

Precise measurements cannot be taken on IRSNB M1824 because the crown is broken. Nevertheless, it seems morphometrically similar to specimens referred to *Thomasia antiqua* (PLIENINGER, 1847) *sensu* BUTLER & MACINTYRE, 1994.

IRSNB M1825 (Plate 2, Fig. 3)

This specimen is tentatively identified as the anterior portion of a lower left haramivid molar. It bears three cusps. The largest (A1) has a very convex lingual side; its labial side bears a large, rectangular and concave attrition facet (31, following the nomenclature of SIGOGNEAU-RUS-SELL, 1989) from the apex to the base of the cusp. It is flanked by two flat areas. The posterior edge of A1 bears two small elliptical attrition facets. Opposite to A1, cusp B1 is smaller, lower and more bulbous. Its labial side is very convex and its lingual side bears a median ridge. This contacts the anterior border of the (3_1) attrition facet to form the anterior wall of the crown. The antero-internal sides of A1 and B1 delimit a small anterior basin, which opens anteriorly. B2 is distinctly smaller than B1. The lingual side of B2, the postero-lingual side of B1 and the postero-labial side of A1 delimit the anterior portion of the rather large central basin.

As on IRSNB M1824, precise measurements cannot be taken on this specimen, because it is too incomplete, but it seems morphometrically similar to the lower molars of *Thomasia antiqua* (PLIENINGER, 1847) *sensu* BUTLER & MACINTYRE, 1994.

Subclass Eotheria Family Sinoconodontidae MILLS, 1971 aff. Sinoconodon

IRSNB M1826 (Plate 2, Fig. 4)

Measurements: Length of the crown: 3.9 mm; width of the crown: 1.1 mm; height of the crown: ?2.1 mm.

By analogy with the dentition of *Sinoconodon* PATTER-SON & OLSON, 1961, to which this tooth is tentatively attributed (see below), IRSNB M1826 is regarded as a left lower molariform: the labial side of the crown is regarded as the flattest and the lingual side bears the small "cingular" elements.

The general morphology of IRSNB M1826 is reminiscent of that of the postcanines of the Dromatheriidae (*sensu* HAHN *et al.*, 1994) cynodonts *Therioherpeton* BONAPARTE & BARBARENA, 1975 (Late Triassic of Brazil) and *Meurthodon* SIGOGNEAU-RUSSELL & HAHN, 1994 (Late Triassic of Saint-Nicolas-de-Port), as well as that of the lower molars of the early mammal *Sinoconodon* PATTERSON & OLSON, 1961 (Early Jurassic of China): the crown is very narrow (ratio "length/width" of the crown = 3.55, in IRSNB M1826) and is formed by four anteroposteriorly aligned cusps, the second being the largest. The anterior cusp (cusp b) is extremely eroded and badly preserved; it was probably small and not very well separated from cusp a, like in Meurthodon and Sinoconodon. Its antero-labial side forms a concave surface, which can be interpreted as a contact facet with the last cusp of the preceding molar: interlocking between adjacent molars is described in Therioherpeton (BONAPARTE & BARBERENA, 1975), Meurthodon (GODEFROIT & BATTAIL, in press) and Sinoconodon (PATTERSON & OLSON, 1961). The second cusp (cusp a) is by far the largest and the highest element of the crown. Its apex is broken and eroded; it clearly slopes rearwards, like in Meurthodon and Sinoconodon. Its lingual side is more convex than its labial face. It bears cutting, but eroded, anterior and posterior edges. The lingual side of the third (c) and fourth (d) cusps is preserved. Both cusps are larger and better separated than cusp b; they slightly slope rearwards, as in Meurthodon and Sinoconodon. They are conical in shape, as in Sinoconodon: in Therioherpeton and Meurthodon, cusps c and d are more compressed laterally. At the base of the posterior face of cusp d, an eroded swelling can be interpreted as a vestigial posterior cuspule. A fifth small anterior cuspule (e) is set at the base of the crown, on the antero-lingual side of cusp b. A similar cuspule can be observed in Sinoconodon (PATTERSON & OLSON, 1961), but not in Therioherpeton (BONAPARTE & BARBERENA, 1975) and Meurthodon (GODEFROIT & BATTAIL, in press). Another tiny cuspule (e') lies on the lingual side of cusp e. Cusps b, e and e' circumscribe a small and elliptical antero-lingual depression. A series of tiny and eroded cuspules is set at the base of the lingual side of the crown, beneath cusp c and at the junction between cusps c and d: CROMPTON & LUO (1993) point out the presence of a faint cingulum on the postero-lingual surface in the lower molars of Sinoconodon, in the same place as the "cingular" elements described in IRSNB M1826.

Table 1 summarizes the morphological characters observed in IRSNB M1826 and in the lower molars of *Therioherpeton*, *Meurthodon* and *Sinoconodon*. The Dromatheriidae cynodont *Pseudotriconodon*, from the Late Triassic of Western Europe and New Mexico, is here retained as outgroup: HAHN *et al.* (1994) show that the postcanines of *Pseudotriconodon* can be regarded as primitive within the Dromatheriidae and that Dromatheriidae form the sister-group of early mammals, represented by *Sinoconodon* in their phylogeny.

Figure 4 shows that IRSNB M1826 shares more characters presumed to be apomorphic with the early mammal *Sinoconodon* than with the other taxa. As this cladogram is based on few characters observed on the lower molars, it is important to point out that it probably does not reflect the exact relationships between the considered genera. Despite its fragmentary state of preservation, IRSNB M1826 is tentatively referred to genus aff. *Sinoconodon*, waiting for the discovery of better preserved fossils with complete or partial roots. It is clear that the animal to which this tooth belonged was close to the frontier beTable 1 — Comparisons of the dental characters observed in IRSNB M1826. 1: Sectorial postcanine crowns. 2: Asymmetrical crown in lateral view: 4 cusps aligned longitudinally, the second being the largest. 3: Interlocking between adjacent molars. 4: Cusps a,c and d inclined rearwards. 5: Notch separating a and c deeper than that between a and b. 6: Cusps c and d conical (1) or compressed mediolaterally (0). 7: Antero-lingual accessory cusp e. 8: Cingulum or "cingular" elements on the postero-lingual surface of the lower molars.

Character	Pseudotriconodon	Therioherpeton	Meurthodon	Sinoconodon	IRSNB M1826
1	1	1	1	1	1
2	0	1	1	1	1
3	0	1	1	1	1
4	0	0	1	1	1
5	0	0	1	1	1
6	0	0	0	1	1
7	0	0	0	1	1
8	0	0	0	1	1
Second Products				and the second second	
8	0	0	0	1	1

tween advanced cynodonts and early "true" mammals. It should be added that the attribution of the genus *Meurthodon* to the cynodont family Dromatheriidae, as established by HAHN *et al.* (1994), is uncertain, as noted elsewhere (GODEFROIT & BATTAIL, in press).

Family Morganucodontidae KÜHNE, 1958 Genus Morganucodon KÜHNE, 1949 Morganucodon sp.

IRSNB M1827 (Figure 5; Plate 3, Fig. 1)

Measurements: Length of the crown: 1.44 mm; width of the crown: 0.62 mm; height of the crown: 0.91 mm.

IRSNB M1827 is a left upper molar, as attested by the presence of a labial and a lingual cingulum. It shows the typical pattern of the Morganucodontidae: three main cusps aligned antero-posteriorly with the main cusp A being by far the largest and the highest. The labial side of A is somewhat more convex than its lingual side; both its anterior and posterior edges are cutting and its apex is rather acute. It is flanked by an anterior cusp B and a posterior cusp C that are of about equal size and distinctly separated from A by a deeply incised valley. The following characters observed in IRSNB M1827 are important for comparisons with the upper molars of Late Triassic-Liassic Morganucodontidae:

- The enamel is perfectly smooth.
- The crown is very narrow, about 2.3 times longer than wide.
- The labial cingulum is faint and nearly interrupted above cusp A. Its anterior part is short and terminates in an accessory cusp F, on the antero-labial face at the base of cusp B. The posterior portion of the labial cingulum is longer and set higher than the anterior portion. It is subdivided in four cuspules; the most posterior, cusp D, directly covers the base of the anterior side of cusp C and is distinctly smaller than the third cuspule of the row.

- The lingual cingulum is also faint and interrupted above cusp A. Its anterior portion bears three small cuspules; the anterior cuspule E is set at the base of the antero-lingual corner of B. Its posterior portion is concave and subdivided into four cuspules; the fourth, at the postero-lingual corner of the crown, is the largest and is distinctly higher than cusp D.
- The occlusion pattern is primitive. A well marked attrition facet is present on the anterior part of the lingual cingulum, at the level of the junction between cusps A and B. It is preceded by a less markedly elongated facet, at the level of the posterior portion of cusp B. It can be concluded that, when wear



Fig. 4 — Cladogram showing the relationships of IRSNB M1826 with the lower molars of *Pseudotriconodon*, *Therioherpeton*, *Meurthodon* and *Sinoconodon*. 1: Sectorial postcanine crowns. 2: Asymmetrical crown in lateral view: 4 cusps aligned longitudinally, the second being the largest. 3: Interlocking between adjacent molars. 4: Cusps a,c and d inclined rearwards. 5: Notch separating a and c deeper than that between a and b. 6: Cusps c and d conical (1) or compressed mediolaterally (0). 7: Antero-lingual accessory cusp e. 8: Cingulum or "cingular" elements on the postero-lingual surface of the lower molars.



Fig. 5 — Left upper molar of *Morganucodon* sp. from the Upper Triassic of Varangéville (IRSNB M1827). A: labial view; B: lingual view. Striated areas: attrition facets.

started, the principal cusp of the lower molar only contacted the lingual cingulum of the corresponding upper molar. Cusp a of the lower molars occluded between cusps A and B of the uppers.

The upper molars of *Brachyzostrodon* SIGOGNEAU-RUSSELL, 1983 (b) are larger and more stocky than IRSNB M1827. Their enamel is wrinkled. The lingual cingulum is always continuous (HAHN *et al.*, 1991), whereas the labial cingulum can be interrupted.

In *Megazostrodon rudnerae* CROMPTON & JENKINS, 1968, cusp D is usually much better developed, but this character is variable within the tooth row. The lingual cingulum is continuous and the labial cingulum, very well developed. The main difference can be observed in the distribution of the attrition facets and, therefore, in the relative position of the upper and lower molars during occlusion.

In *Erythrotherium parringtoni* CROMPTON, 1964, cusps D, E and F seem better developed than in IRSNB M1827, but their relative development is variable within the tooth row. Both cingula seem to be continuous. The occlusion pattern is similar to that of *Megazostrodon* (CROMPTON, 1974).

The upper molars of *Helvetiodon schutzi* CLEMENS, 1980 are larger and more massive than IRSNB M1827. Anterior cusp B is absent. The development of labial and lingual cingula and cuspules (particularly cusp E) is more extensive. Cusp D seems to be absent.

In *Dinnetherium nezorum* JENKINS, CROMPTON & DOWNS, 1983, cuspules F and E are better developed than in IRSNB M1827, forming an embrasure to receive the base of posterior cusp D, usually better developed too, of the adjacent anterior tooth. Cusp A is proportionally shorter. As in IRSNB M1827, cusp a of the lower molars occluded between cusps A and B of the uppers.

Great variability is observed in the development of cusps and cingula in the upper molars of *Morganucodon* (MILLS, 1971). Comparisons are therefore difficult. A similar development of cusp B can be observed in the most posterior molars. The cingula are present on both the labial and lingual sides of the crown. Nevertheless, they are considerably reduced on the posterior teeth of *Morganucodon watsoni* KÜHNE, 1949, especially on the labial side. So, in this species, the labial cingulum is usually interrupted or nearly interrupted as in IRSNB M1827. JENKINS *et al.* (1983) described an upper molar from the Kayenta Formation of Arizona, which they referred to *Morganucodon sp*: the lingual cingulum of this tooth shows a hiatus at its midpoint.

In *Morganucodon*, attrition starts above cusps A and B, forming wear facets identical to those observed in IRSNB M1827 (compare with CROMPTON & JENKINS, 1968, text-fig. 4,A1): cusp a of the lower molars occluded between A and B.

The dimensions of the crown are within the observed range in *Morganucodon watsoni* KÜHNE, 1949, *Morganucodon oehleri* RIGNEY, 1963 (see MILLS, 1971, table 1) and *Morganucodon peyeri* CLEMENS, 1980.

In conclusion, it can be asserted that IRSNB M1827 more closely resembles the upper molars of *Morganucodon* than those of other Late Triassic-Early Jurassic mammals, as shown in Table 2. It is much more hazar-

	IRSNB M1829	Brachyzostrodon	Morganucodon	Megazostrodon	Erythrotherium	Hallautherium
Bulbous cusps	-	++	+	++ '	-	-
Lingual cingulum between g and e	+, with one cuspule		+, with cuspules, sometimes very weak	+, with cuspules	+, without cuspules	-
Cusp b	++	++	+	+	+/-	+
Cusp e	+/-	++	+	++	+	+
Cusp g	+	++	+	++	+/-	- 1
Wrinkled enamel	-	+	-	-	-	- 4
Pecularities	labial swelling on cusp b					labial basin

Table 2 — Comparisons of IRSNB M1827 with the upper molars of Late Triassic-Early Jurassic Morganucodontidae.

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dous to assert that the poor development of the cingula and of the accessory cusps is indicative of a specific difference, because those characters are particularly variable within the genus *Morganucodon*. Therefore, IRSNB M1827 is simply referred to *Morganucodon* sp., pending further evidence.

aff. Morganucodon

IRSNB M1828 (Plate 3, Fig. 3)

Measurements: width of the crown: 0.75 mm.

This is an incomplete right lower molar consisting of the principal cusp a and the anterior portion of the crown. The roots and the posterior portion of the crown are missing.

This tooth shows similarities with the lower molars of *Morganucodon*. The main cusp a is triangular in lateral view and mediolaterally compressed; its edges are sharp and its apex is acute. Anterior cusp b is aligned with main cusp a, small and bulbous; it is separated from cusp a by a deep notch. Cusp e is well developed and separated from cusp b by a depression. In apical and anterior views, cusp b and cuspule e are not contiguous, but separated by a deep valley. Posteriorly to cuspule e, the lingual cingulum is very weak, nearly interrupted, as in *Morganucodon oehleri* (MILLS, 1971; KERMACK *et al.*, 1973). The kuehneocone, if present, is not preserved: it would therefore have been situated posteriorly to the midpoint of cusp a. Abrasion affects the apex of cusps b and e.

IRSNB M1828 differs from the lower molars of *Brachyzostrodon* in its perfectly smooth enamel, less massive morphology and less developed cusp e.

Cusp e appears less developed than in *Megazostrodon*, but this character is variable within the tooth row.

Cusp b is more developed than in *Erythrotherium*. Although the posterior portion of this molar is broken, cusp c was more deeply separated from cusp a than in the latter genus.

In *Hallautherium schalchi* CLEMENS, 1980, the anterolingual cuspule e is set more anteriorly and is less clearly separated from cusp b.

It can be concluded that IRSNB M1828 shows close similarities with the lower molars of *Morganucodon* and, more particularly, with those of *Morganucodon oehleri*. As this tooth is very fragmentary and as an important variability can be observed within the genus *Morganucodon*, this molar is tentatively referred to as aff. *Morganucodon*.

Morganucodontidae, gen. et sp. indet.

IRSNB M1829 (Figure 6; Plate 3, Fig. 2)

Measurements: preserved height of the crown: 1.48 mm. IRSNB M1829 is a damaged morganucodontid right lower molar consisting of the main cusp and the anterior end of the crown. Important differences can be observed from IRSNB M1828. Cusp a is proportionally much higher; its lingual face is subdivided longitudinally by two vertical sulci. Cusp b is also better developed and less bulbous; it slopes towards the front. At the base of its labial face, cusp b bears a distinct swelling. The lingual cingulum is well developed and bears cuspules. A tiny cuspule e forms the anterior end of the cingulum; it is located adjacent to the antero-lingual side of cusp b. On the anterior wall of the cingulum, a tiny cuspule t is set between cusp b and cuspule e. The kuehneocone g faces the postero-lingual half of cusp a; it is rather small and rounded. Between cuspules e and g, the cingulum is continuous and concave in lingual view; it bears a minor accessory cusp, just in front of the kuehneocone.

The lower molars of *Brachyzostrodon* differ from IRSNB M1829 by their wrinkled enamel. Principal cusp a is lower and more massive than in the specimen from Varangéville. Cusp b is more bulbous. Cusps e and g are better developed. The lingual cingulum is always interrupted between cuspules e and g.

In *Morganucodon*, the lingual cingulum of the lower molars is continuous between cuspules e and g, like on IRSNB M1829. Nevertheless, it is clearly less developed in *Morganucodon oehleri*. Differences exist in the proportions of the different cusps, although such characters are very variable in *Morganucodon* (see MILLS, 1971; KERMACK *et al.*, 1973). Principal cusp a is never as high as in IRSNB M1829. If the anterior cusp b is relatively well developed on the posterior lower molars, it is always smaller and more bulbous than in this specimen. Cingular cuspule e is always better developed: it is almost as large as cusp b in *Morganucodon peyeri* CLEMENS, 1980. In occlusal view, a small depression can be observed between cusps b and e. The kuehneocone g is comparatively poorly developed.



Fig. 6 — Right lower molar of Morganucodontidae indet. from the Upper Triassic of Varangéville (IRSNB M1829). Lingual view.

	IRSNB M1827	Morganucodon	Brachyzostrodon	Megazostrodon	Erythrotherium	<u>Dinnetherium</u>	Helvetiodon
Bulbous cusps	+	+	+/++	++	+	+	++
Linguat cingulum	interrupted, with cuspules	usually continuous, with cuspules	continuous, with or without cuspules	continuous, with cuspules	continuous, with cuspules	? continuous, without cuspules	continuous, with cuspules
Labial cingulum	nearly interrupted, with cuspules	+/- interrupted, with cusputes	+/- interrupted, with cuspules	variable	? continuous	? continuous, without cuspules	interrupted
Cusp B	++	variable	++	++	++	++	0
Cusp D	-	+/-	-	+	+	+	- or 0
Cusp E	+	+	+	+	++	++	++
Cusp F	+	+	variable	+	++	++	+
Wrinkled enamel	-	-	+	-	-	-	-
Attrition facets	between A and B	between A and B	between A and B	in front of B	in front of B	between A and B	?

Table 3 —	Comparisons	of IRSNB M1829	with the	lower molars of Lat	te Triassic-Early	Jurassic	Morganucodontidae
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The lower molars of *Megazostrodon rudnerae* CROMP-TON & JENKINS, 1968 are reminiscent of IRSNB M1829 in the lingual cingulum bearing one or several accessory cuspule(s) between cuspules e and g. But contrary to IRSNB M1829, the cingulum seems interrupted between cuspules e and g, on M_1 and M_2 . Cusp b is variable, but smaller. Cuspule e is better developed and better separated from cusp b. The kuehneocone is better developed, too. The lingual cingulum lies internal to cuspule e, on M_2 and internal to the kuehneocone, on M_3 .

In Erythrotherium parringtoni CROMPTON, 1964, cusp b is always poorly developed. The lingual cingulum is continuous, but devoid of cuspules. Cuspule e is not very developed. The kuehneocone is absent from M_1 . Although the posterior cusp c is broken on IRSNB M1829, it was clearly better separated from cusp a than in Erythrotherium.

The lower molars of *Hallautherium schalchi* CLEMENS, 1980 lack a lingual cingulum and a kuehneocone. A posterior basin is present on the type specimen. Cusp b is smaller and lingual cuspule e is more elongated antero-posteriorly.

Table 3 is a summary of the main characters of IRSNB M1829 and of the Rhaeto-Liassic morganucodontid genera. Dental characters in Morganucodontidae are a good example of mosaic evolution among early mammals. If IRSNB M1829 shows an unique combination of characters, this tooth is too incomplete to erect a new taxon. It is thus referred to as Morganucodontidae indet., pending further evidence.

Subclass Theria

Order Symmetrodonta

Family Woutersiidae SIGOGNEAU-RUSSELL & HAHN, 1995 Genus Woutersia SIGOGNEAU-RUSSELL, 1983(a) Woutersia mirabilis SIGOGNEAU-RUSSELL, 1983(a)

SYNONYMY

1983(a) Woutersia mirabilis sp. nov. - SIGOGNEAU-RUS-SELL, p. 180, figs. 1-5. 1995 Woutersia mirabilis SIGOGNEAU-RUSSELL 1983 -SIGOGNEAU-RUSSELL & HAHN, p. 246, fig. 1, fig. 3a-c,?figs. 7-8, fig. 9a,?figs. 9b-c, fig. 10a.

HOLOTYPE

MNHP SNP101, a left lower molar.

LOCUS TYPICUS

Saint-Nicolas-de-Port, Meurthe-et-Moselle, France.

STRATUM TYPICUM

"Rhaetian" bone bed, latest Norian or earliest Rhaetian.

DIAGNOSIS

see SIGOGNEAU-RUSSELL & HAHN (1995:180).

DISTRIBUTION

Saint-Nicolas-de-Port and Varangéville, France (latest Norian or earliest Rhaetian).

MATERIAL FROM VARANGEVILLE IRSNB M1830, a left lower molar.

IRSNB M1830 (Figure 7; Plate 3, Fig. 4)

Measurements: Length of the crown: 1.53 mm; width of the crown: 1 mm; height of the crown: 1.28 mm.

IRSNB M1830 is a complete dental crown, which closely resembles the lower molars of *Woutersia*, from the Late Triassic of Saint-Nicolas-de-Port:

- The crown is stocky and compact and it bears three main cusps forming an angle of about 150°.
- Main cusp a is relatively lower than in *Kuehneotherium praecursoris* KERMACK, KERMACK & MUSSETT, 1968 and subdivided longitudinally by two vertical sulci.
- Posterior cusp c set more lingually and better detached from cusp a than anterior cusp b.



Fig. 7 — Left lower molar of *Woutersia mirabilis* SIGOGNEAU-RUSSELL, 1983 (a) from the Upper Triassic of Varangéville (IRSNB M1830). A: lingual view; B: labial view; C: occlusal view. Stippled areas: abrasion facets; striated areas: attrition facets.

- A large median cusp g is developed on the lingual cingulum.
- The antero-lingual accessory cusp e is nearly as large as cusps b and c and shifted anteriorly with respect to cusp b.

- The lingual cingulum, at the base of cusp c, is short and a short labial cingulum can be observed at the base of cusp b.
- Abrasion has removed the apex of all the cusps.
- A large, but poorly marked triangular attrition facet affects the posterior half of cusp a and the anterior half of cusp c, reaching the level of the basal third of the crown. Below cusp c, a small and elliptical labial facet can be distinguished at the level of the cingulum.

IRSNB M1830 closely resembles the lower molars of *Woutersia mirabilis* SIGOGNEAU-RUSSELL, 1983 (a) in the proportions of its crown (see Figure 8). The tooth from Varangéville mainly differs from MNHNP SNP 101, the type lower molar of *Woutersia mirabilis*, by the complete absence of cusp d and, consequently, of the talonid. Nevertheless, this character has subsequently been mentioned for IRSNB RAS706, another molar of *Woutersia mirabilis* from Saint-Nicolas-de-Port (SI-GOGNEAU-RUSSELL and HAHN, 1995). The presence of cuspule h between cusps c and g, which also characterizes IRSNB M1830, can also be observed on IRSNB 28114/ 163, an undescribed lower molar from Saint-Nicolas-de-Port, which undoubtedly also belongs to *Woutersia mirabilis*.

Differences are more marked when compared to the species *Woutersia butleri* SIGOGNEAU-RUSSELL & HAHN, 1995: this species is characterized by smaller teeth (see Figure 8), with c less lingual relative to a and b and c bigger with respect to a. In the holotype MNHN SNP517, g and e are separated from cusps a and b by a deep valley and are completely encircled by the lingual cingulum.



Fig. 8 — Morphometrical comparison of IRSNB M1830 (indicated by an arrow) with other molars of *Woutersia* from Saint-Nicolas-de-Port (after SIGOGNEAU-RUSSELL and HAHN, 1995).

Discussion and conclusions

The great majority of fossils discovered at Varangéville belongs to marine animals: several thousands of fragmentary or complete teeth of hybodont sharks and actinopterygian fishes and one ichthyosaurian tooth. However, numerous bones from this locality belong to aquatic, but non-marine vertebrates (capitosaurid amphibians, phytosaurs), or living close by the water (*Eudimorphodon*). Finally, terrestrial animals (carnivorous archosaurs, cynodonts and mammals) are also represented, but are much rarer. This faunal composition and the predominance of coarse elements in the conglomerate suggest a deltaic or a coastal palaeoenvironment. The composition of the reptile fauna discovered at Varangéville seems globally very similar to that of Saint-Nicolas-de-Port: presence of phytosaurids (BUFFE-TAUT & WOUTERS, 1986), of the pterosaur *Eudimorphodon* (GODEFROIT & CUNY, in preparation), of several types of small archosaurian carnivorous (BUFFETAUT & WOU-TERS, 1986) and of dromatheriid cynodonts (GODEFROIT & BATTAIL, in press). *Eudimorphodon*, Dromatheriidae, small indeterminate phytosaurs and different types of small carnivorous archosaurs have also been described at Medernach (G.-D. Luxembourg; HAHN *et al.*, 1984; CUNY *et al.*, 1995). In the Late Triassic of Hallau (Switzerland), *Eudimorphodon* and "chiniquodontoid" (*sensu* SIGOGNEAU-RUSSELL & HAHN, 1994) cynodonts also co-

Table 4 — Occurence of Mammals in the Late Triassic of Europe.

Abbreviations for the localities: VAR = Varangéville (France); SNP = Saint-Nicolas-de-Port (France); BOI = Boisset (France); MED = Medernach (G.-D. Luxemburg); HLV = Habay-la-Vieille (Belgium); ATT = Attert (Belgium); Hal = Hallau (Switzerland); HBS = Halberstadt (Germany); GRBB = Rhaetian bone-beds of the Tübingen-Stuttgart area (Germany); EMB = Emborough (U.K.).

Abbreviations for the genera: B. = Brachyzostrodon; Hal. = Hallautherium; Helv. = Helvetiodon; K. = Kuehneotherium; M. = Morganucodon; T. = Thomasia; Th. = Theroteinus; W. = Woutersia.

Taxa	<u>VAR</u>	<u>SNP</u>	<u>BOI</u>	MED	<u>HLV</u>	ATT	HAL	HBS	GRBB	<u>EMB</u>
Haramiyidae T. antiqua T. moorei T. hahni T. woutersi	X	X X	x		X	x	X X	x	X	
Theroteinidae Th. nikolai		х								
Paulchoffatiidae Mojo usuratus					x					
Morganucodontidae M. peyeri M. sp. Helv. schutzi Hal. schalchi B. coupatezi B. maior	X	X X X		X			X X X			
Sinoconodontidae aff. Sinoconodon	x									
Woutersiidae W. mirabilis W. butleri	x	X X								
Kuehneotheriidae K. praecursoris K. sp. ?Kuehneotheriidae ind.		X X	x		x					x

existed (CLEMENS, 1980; SIGOGNEAU-RUSSELL & HAHN, 1994).

Table 4 compares the composition of mammalian faunas in Late Triassic localities of western Europe. Haramiyidae are particularly well represented. BUTLER & MACINTYRE (1994) distinguish four species. Thomasia antiqua (PLIENINGER, 1847), identified at Varangéville, is also represented at Saint-Nicolas-de-Port, Hallau, in the Tübingen-Stuttgart area (BUTLER and MACINTYRE, 1994) and at Boisset (CUNY, 1993). A second species, Thomasia moorei (OWEN, 1871), coexisted at Saint-Nicolas-de-Port and at Hallau. These two species have a poor stratigraphic value: they have also been discovered in Early Jurassic fissures of Holwell quarry, England (BUTLER & MACINTYRE, 1994). The species Thomasia woutersi BUTLER & MACINTYRE, 1994 is limited to the Rhaetian of Attert and Habay-la-Vieille, in southern Belgium (BUTLER & MACINTYRE, 1994; DELSATE, 1996). The species Thomasia hahni BUTLER & MACINTYRE, 1994, from the Middle Keuper of Halberstadt (Germany), is slightly older (HAHN, 1973).

The family Theroteinidae is confined to Saint-Nicolasde-Port, with a single species, *Theroteinus nikolai* SIGOGNEAU-RUSSELL, FRANK & HEMMERLE, 1986. The Paulchoffatiidae are known from a single tooth, *Mojo usuratus* HAHN, LEPAGE & WOUTERS, 1987, from Habay-la-Vieille.

Morganucodontidae are known from four Late Triassic localities, in western Europe. Morganucodon peyeri CLEMENS, 1980 is based on upper molariform teeth from Hallau. The genus Morganucodon is also present at Varangéville (this paper), Saint-Nicolas-de-Port (SIGOG-NEAU-RUSSELL & HAHN, 1994) and probably at Medernach (CUNY et al., 1995, fig. 8g-j). This genus is also known from the Early Jurassic of England (Morganucodon watsoni KÜHNE, 1949) and China (Morganucodon oehleri RIGNEY, 1963 and Morganucodon heikuopengensis (YOUNG, 1978)). CLEMENS (1980) described two monospecific genera that can be referred to the Morganucodontidae, Helvetiodon and Hallautherium, from the Late Triassic of Hallau. Brachyzostrodon SIGOGNEAU-RUSSELL, 1983 (b) is represented by two species at Saint-Nicolas-de-Port. A tooth, referred to as cf. ?Brachyzostrodon has been discovered in the Late Triassic of East Greenland (JENKINS et al., 1994).

The family Sinoconodontidae is currently known, in the Late Triassic of Europe, by one single molar from Varangéville, referred in the present paper to as aff. *Sinoconodon*. Nevertheless, it has been shown that this tooth presents close similarities to the molars of *Meurthodon gallicus* SIGOGNEAU-RUSSELL & HAHN, 1994 from Saint-Nicolas-de-Port and currently referred to the cynodont family Dromatheriidae. The genus *Sinoconodon* PATTERSON & OLSON, 1961 is known by specimens discovered in the Early Jurassic Dark Red Beds of the Lower Lufeng Formation, in Yunnan, China (Luo & WU, 1994).

The families Woutersiidae and Kuehneotheriidae are regarded as the earliest therian mammals by numerous authors (e.g., HOPSON & CROMPTON, 1969; PROTHERO, 1981; SIGOGNEAU-RUSSELL & HAHN, 1994), but this opinion is not shared by ROWE (1993). Anyway, representants of these families are extremely rare in Late Triassic outcrops. The genus Woutersia occurs at Saint-Nicolasde-Port (Woutersia mirabilis SIGOGNEAU-RUSSELL, 1983 (a) and Woutersia butleri SIGOGNEAU-RUSSELL & HAHN, 1995) and at Varangéville (Woutersia mirabilis). Kuehneotherium KERMACK, KERMACK & MUSSETT, 1968 occurs in the Late Triassic of Saint-Nicolas-de-Port (SIGO-GNEAU-RUSSELL & HAHN, 1994) Emborough, U.K. (FRA-SER et al., 1985) and East Greenland (JENKINS et al., 1994). This genus extends to the early Liassic of St. Bride's Island fissures, U.K (EVANS & KERMACK, 1994). A new docodont genus from Saint-Nicolas-de-Port is described by SIGOGNEAU-RUSSELL & GODEFROIT (in press). One "therian" tooth was discovered in Habayla-Vieille (SIGOGNEAU-RUSSELL & HAHN, 1994), but is apparently lost.

From these faunal comparisons, it appears that the reptilian, therapsid and mammalian fauna discovered at Varangéville more closely resembles that from the neighbouring Saint-Nicolas-de-Port quarry than those from other Late Triassic European localities. Differences between the Varangéville and Saint-Nicolas-de-Port faunas perhaps reflect minor ecological and/or taphonomic conditions or small differences in the stratigraphic position of the bone beds. Nevertheless, discovery biases can also explain these differences: if, since 1976, more than 1000 mammal teeth have been discovered in Saint-Nicolas-de-Port, but research at Varangéville has just begun.

The discovery of a new fossil assemblage in the Late Triassic of Varangéville confirms that the north-east margin of the Paris Basin is one of the main areas in the world for the study of the earliest mammals. Intensive prospecting and new excavations are still in progress in this area and will probably contribute to a better knowledge of these interesting primitive forms.

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Explanation of plates

Plate 1

Reptilian and therapsid teeth from the Upper Triassic of Varangéville (France)

- 1: Ichthyosauria indet. (IRSNB R147). x 0.45. Labial view.
- 2: Phytosauridae indet. (IRSNB R148). x 0.7. A: labial view; B: lingual view.
- 3: Phytosauridae indet. (IRSNB R149). x 0.5. Labial view.
- 4: Archosauria indet. (IRSNB R151). x 14. Lateral view.
- 5: Archosauria indet. (IRSNB R152). x 47. A: lingual view; B: labial view.
- 6: ?Dromatheriidae indet. (IRSNB R153). x 16. A: labial view; B: occlusal view.
- 7: Chiniquodontoidea indet. (IRSNB R154). x 37. A:?lingual view; B: occlusal view.
- 8: aff. Eudimorphodon (IRSNB R150). x 25. Lateral view.

Plate 2

Mammalian teeth from the Upper Triassic of Varangéville (France)

- 1: Stereophotographs of a left lower premolariform of *Thomasia antiqua* (PLIENINGER, 1847) (IRSNB M1823). x 32. A: labial view; B: occlusal view.
- 2: Stereophotographs of a left lower molar of Thomasia cf. antiqua (IRSNB M1824). x 26. A: labial view; B: occlusal view.
- 3: Stereophotographs of a left lower molar of Thomasia cf. antiqua (IRSNB M1825). x 35. Occlusal view.
- 4: Left lower molar of aff. Sinoconodon (IRSNB M1826). x 13. A: lingual view; B: occlusal view (stereophotographs).

PLATE 3

Mammalian teeth from the Upper Triassic of Varangéville (France)

- 1: Left upper molar of *Morganucodon* sp. (IRSNB M1827). x 38. A: labial view; B: lingual view; C: occlusal view (stereophotographs).
- 2: Right lower molar of Morganucodontidae indet. (IRSNB M1829). x 35. A: lingual view; B: labial view; C: occlusal view (stereophotographs).
- 3: Right lower molar of aff. Morganucodon (IRSNB M1828). x 35. A: lingual view; B: occlusal view (stereophotographs).
- 4: Left lower molar of *Woutersia mirabilis* SIGOGNEAU-RUSSELL, 1983 (a) (IRSNB 1830). x 27. A: lingual view; B: labial view; C: occlusal view (stereophotographs).



Plate 2



