ARCHOSAURIFORM TEETH FROM THE UPPER TRIASSIC OF SAINT-NICOLAS-DE-PORT (NORTHEASTERN FRANCE)

by

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ABSTRACT

The Late Triassic locality of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France) has yielded numerous isolated teeth belonging to archosauriform reptiles. The following tooth groups can be identified: heterodont phytosaurs, the pterosaur *Eudimorphodon*, the prosauropod dinosaur *Plateosaurus*, three types of putative ornithischian teeth and 13 types of carnivorous Archosauriformes indet. Apparent venom-conducting teeth belonging to a new taxon of ?Archosauriformes (*Graoullyodon hacheti* nov. gen. nov. sp.) are also described. From a palaeogeographical point of view, the ornithischian teeth from Saint-Nicolas-de-Port (if their attribution is confirmed) are the oldest fossils of this group in Europe.

The biostratigraphic distribution of the tooth forms mostly suggests a Late Norian or Early Rhaetian (depending on current interpretations) age of the deposits, but do not provide more precisions than fossils previously described from the area. The dietary habits and, consequently, the palaeoecological relationships of the different vertebrate groups discovered at Saint-Nicolas-de-Port are tentatively established: the ornithischian and prosauropod teeth reflect a herbivorous diet, whereas the other archosauriform teeth are probably from carnivores or omnivores.

RESUME

De nombreuses dents isolées de reptiles archosauriformes ont été découvertes dans le Trias supérieur de Saint-Nicolas-de-Port (Meurthe-et-Moselle, France). Les groupes suivants y sont représentés: des phytosaures hétérodontes, le ptérosaure *Eudimorphodon*, le dinosaure prosauropode *Plateosaurus*, trois types de dents rapportées provisoirement à des dinosaures ornithischiens et 13 types de dents appartenant à des Archosauriformes carnivores indét. Sont également décrites des dents appartenant à un nouveau taxon d'?Archosauriformes apparamment venimeux, *Graoullyodon hacheti* nov. gen. nov. sp. D'un point de vue paléogéographique, les dents d'ornithischiens trouvées à Saint-Nicolas-de-Port, si cette identification est confirmée, sont les plus anciens fossiles de ce groupe actuellement découverts en Europe.

La distribution biostratigraphique des différents types de dents suggère un âge Norien supérieur ou Rhétien (suivant les interprétations actuelles) des dépôts, mais ne fournit pas plus de précisions que les fossiles précédemment décrits dans cette région. Le régime alimentaire et, par conséquent, les relations paléoécologiques des différents groupes de vertébrés découverts à Saint-Nicolas-de-Port sont théoriquement établis: la morphologie dentaire des ornithischiens et des prosauropodes reflète un régime alimentaire herbivore, tandis que les autres types de dents d'Archosauriformes appartiennent à des carnivores ou à des omnivores.

INTRODUCTION

The sand quarry of Saint-Nicolas-de-Port is situated 10 km ESE of Nancy (Meurthe-et-Moselle, France; Figure 1). Since the middle of the nineteenth century, fossil bones have been recorded from the "grès infra-liasique" in this area (Levallois, 1862). Today, this locality is famous for its numerous teeth of Late Triassic mammals, including those of Haramiyidae (Sigogneau-Russell, 1989, 1990), Theroteinidae (Sigogneau-Russell *et al.*, 1986: Hahn *et al.*, 1989), Morganucodontidae (Sigogneau-

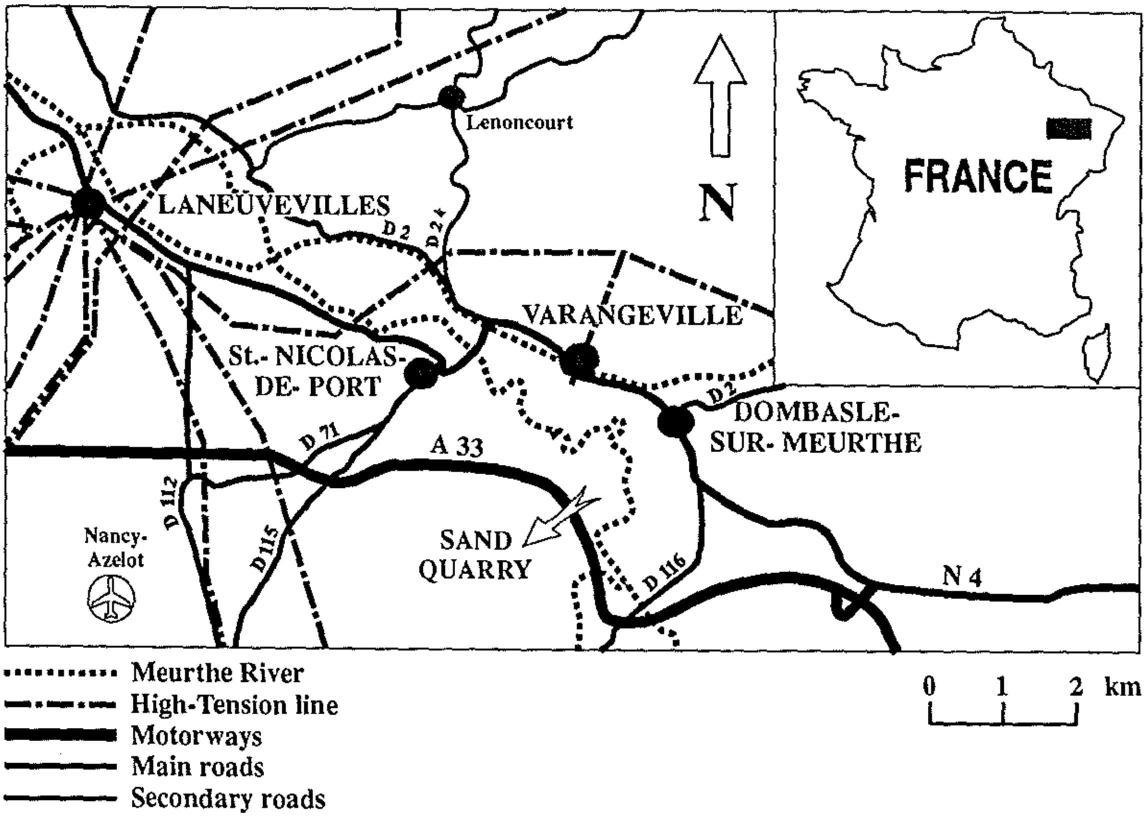

Figure 1.— Locality sketch map for Saint-Nicolas-de-Port.

Russell, 1983a; Hahn *et al.*, 1991), Woutersiidae (Sigogneau-Russell, 1983b; Sigo gneau-Russell and Hahn, 1995), Kuehneotheriidae (Sigogneau-Russell and 1994) and docodonts (Sigogneau-Russell and Godefroit, 1997). Shark and fish material has been described by Sigogneau-Russell *et al.* (1979), Martin *et al.* (1981), Cuny and Ramboer (1991), Cuny (1993) and Duffin (1993). Amphibian and reptile remains have been described by Buffetaut and Wouters (1986), Cuny and Ramboer (1991) and Cuny (1993), but the greatest part of the material remains undescribed.

Figure 2 is the stratigraphic log of the Upper Triassic section at the place where the main bone-bed was discovered. The persistent difficulty with Upper Triassic vertebrate sites is dating and correlation with other faunas. The age of Saint-Nicolas-de-Port is disputed: some place the fossiliferous bed at the base of the Rhaetian (Maubeuge, 1955; Laugier, 1971; Sigogneau-Russell, 1983c; Hahn *et al.,* 1989), while others advocate a slightly older, latest Norian, age (Buffetaut and Wouters, 1986; Cuny and Ramboer, 1991; Cuny, 1993; Duffin, 1993).

The object of the present paper is to describe the archosauriform teeth discovered at Saint-Nicolas-de-Port and to assess their contribution to discussions about the evolution of early ornithischian dinosaurs, the stratigraphic position and correlation of the fauna and the ecosystem.

All the specimens described in this paper are preserved in the collections of the

Department of Palaeontology in the Institut royal des Sciences naturelles de Belgique (IRSNB).

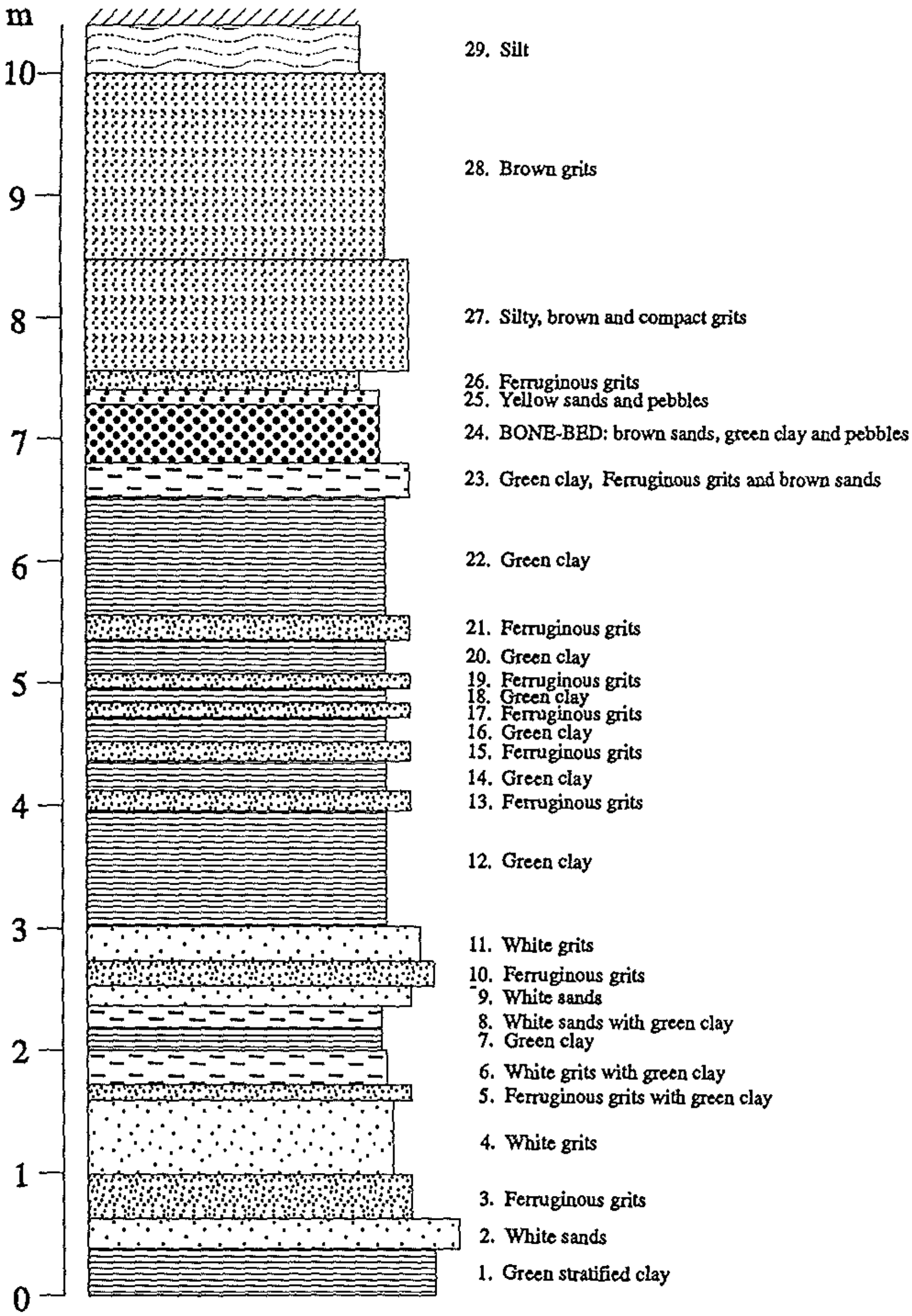

Figure 2.— Stratigraphic log of the Upper Triassic section at Saint-Nicolas-de-Port.

DENTAL CHARACTERS OF THE ARCHOSAURIFORMES

The Archosauria include the living crocodiles and birds, as well as the fossil dinosaurs, pterosaurs and several related lineages of basal archosaurs. Archosaurs are defined cladistically as a monophyletic group and are characterized, among others, by skeletal characters (Benton, 1985; Gauthier, 1986; Evans, 1988; Benton and Clark, 1988; Sereno, 1991b; Juul, 1995). Following Sereno (1991b), Archosauria can be divided into Crurotarsi and Ornithodira, characterized by different types of ankle joint and by other post-cranial synapomorphies. Crurotarsi include Phytosauria (=Parasuchia; Doyle and Sues, 1995), Ornithosuchidae and Suchia (*Gracilisuchus* + Aetosauria + Rauisuchia + Poposauridae + Crocodylomorpha). Ornithodira include *Scleromochlus*, Pterosauria and Dinosauromorpha (including birds). Archosauriformes is a monophyletic clade regrouping Archosauria with the basal groups Proterosuchidae, Erythrosuchidae, *Euparkeria* and Proterochampsidae.

During the Late Triassic Period, archosauriforms became ecologically very diversified and evolved numerous dental adaptations. In order to clarify the scope of the present paper, it is advisable first to define the dental characters of the archosauriforms.

Romer's (1956, p. 589) diagnosis of Archosauria (which we would now call Archosauriformes) includes dental characters: "Teeth, in general, typically thecodont, in most groups conical and pointed medio-laterally, with the development of anterior and posterior keels, frequently serrate". The following remarks can be made about this definition:

1) Charig and Sues (1976) state that the basal archosauriforms Proterosuchidae and Erythrosuchidae have subthecodont dental insertion. However, Juul (1995) reports a typical thecodont dentition in several genera of both families. For Gauthier *et al.* (1988), premaxillary teeth implanted in deep sockets are apomorphic in Archosauriformes; maxillary and dentary teeth in deep sockets characterize Archosauriformes minus Proterosuchidae. Unfortunately, the character "deep sockets" is too vaguely phrased to be useful, as it is not possible to obtain a quantitative expression of the relative lengths of root to crown in many archosauriforms (Juul, 1995). Typical thecodont dentitions can also be observed in other amniote lineages: diadectids, pareiasaurs, Triassic ichthyosaurs, thalattosaurs, sauropterygians, placodonts, mosasaurs and therapsids.

2) In most Archosauriformes, the crown is formed by a single conical cusp. Secondary modifications occur in several groups. The primitive pterosaur *Eudimorphodon* has multicuspid sectorial cheek teeth, similar to those of advanced cynodonts (Wild, 1978; see below). Serrations of the edges can be developed into prominent denticules in herbivorous dinosaurs (Galton, 1986b; Hunt and Lucas, 1994). Clark *et al.* (1989) described complex, mammal-like teeth in a Cretaceous crocodilian from Malawi.

3) According to Benton (1985) and Benton and Clark (1988), labiolingually compressed marginal teeth are diagnostic for the Archosauriformes ("Archosauria"). Evans (1988) and Juul (1995), however, propose that this character potentially applies at a more general level that includes Archosauriformes and Prolacertiformes, the next

closest sister-taxon of Archosauriformes within Archosauromorpha. However, this character independently evolved in some Late Triassic to Early Jurassic sphenodontids (Fraser and Walkden, 1983), in Squamata (see Edmund, 1969) and in numerous cynodonts (Battail, 1989). On the other hand, teeth are not clearly compressed in numerous phytosaurs (see below), crocodilians, pterosaurs and dinosaurs, which can be seen as secondary modifications.

4) For Evans (1988), Gauthier *et al.* (1988) and Juul (1995), the presence of serrated marginal teeth is an autapomorphy of the clade Archosauriformes among the diapsid reptiles. However, serrations are (certainly secondarily) absent from the teeth of numerous archosaurs, including stagonolepidids, some theropod dinosaurs (Stromer, 1915; Antunes and Sigogneau, 1992), pterosaurs (Wellnhofer, 1978) and most crocodilians.

The most spectacular example of a squamate possessing a typical archosaurian dentition is the Komodo Dragon (*Varanus komodoensis* OUWENS, 1912). This extant varanid possesses blade-like, recurved, compressed and serrated "tyrannosaur-like" teeth; they only differ from the teeth of carnivorous archosaurs by their pleurodont implantation.

However, taking the remarks above into account, Romer's (1956) definition is a useful description of the "generalized archosauriform tooth" and permits the recognition of archosauriform teeth in the fossil samples discovered at Saint-Nicolas-de-Port.

DESCRIPTIONS AND COMPARISONS

Total tooth height often cannot be measured accurately because of wear and breakage, or differences in tooth curvature. In theropod dinosaurs, the fore-aft basal length (FABL) of the tooth has a relatively constant relationship to the total length and can be easily measured in numerous specimens (Currie *et al.*, 1990). The labio-lingual basal width (LLBW) is taken perpendicular to the FABL. Although the absolute value of tooth measurements is taxonomically meaningless in reptiles, because of the presumably indeterminate growth of these animals and of the continuous replacement of their teeth, the ratio FABL/LLBW is a good estimate of the degree of labio-lingual compression of the teeth.

***Monophyletic hierarchy*: Archosauriformes: Archosauria: Crurotarsi: Phytosauria: Phytosauridae indet. (type 1)**

Phytosaurs are by far the most abundant reptiles in the collections and are represented by several hundred isolated teeth. These have previously been described by Buffetaut and Wouters (1986), Cuny and Ramboer (1991) and Cuny (1993). The size of these teeth varies between 5 and 80 mm. Three types of teeth can be distinguished (Buffetaut and Wouters, 1986):

- **Anterior teeth (Plate 1, A):** "*Very strong recurved teeth, with an almost circular cross-section and serrated carinae; their enamel is sometimes more or less fluted*".

- **Intermediate teeth (Plate 1, B):** "*Long slender teeth, with a nearly circular cross-section and non-serrated carinae. They often show a double curvature, and their enamel is often definitely fluted, the fluting disappearing towards the apex.*" These teeth are usually much smaller than the anterior teeth.

- **Posterior teeth (Plate 1, C):** "*Large laterally compressed teeth with a somewhat blade-like outline in lateral and medial view. The convex labial face is more curved anteroposteriorly than the concave lingual face. The enamel is nearly smooth. There are two finely serrated (about three serrations per mm) carinae (an anterior and a posterior one)*". The serrations are equally dense on both carinae. Cuny (1993) notes that the serrations are smaller at the base of the crown than towards the apex.

The presence of specimens of intermediate shape, showing a transition from one type to another, indicates the presence of a single type of large phytosaur with a heterodont dentition at Saint-Nicolas-de-Port. Moreover, the ratio of the different kinds of teeth (anterior: 16%, intermediate: 39% and posterior: 46%, see Cuny, 1993) fits quite well with the ratio observed in some skull reconstructions of heterodont phytosaurs such as that of *Leptosuchus adamanensis* given by Camp (1930) (anterior teeth: 8%, intermediate: 50% and posterior: 42%) or that of "*Angistorhinopsis*" *ruetimeyeri* given by Huene (1922) (anterior teeth: 6%, intermediate: 48% and posterior: 46%). The high percentage of anterior teeth found at Saint-Nicolas-de-Port could certainly be explained by the difficulty in differentiating between anterior and intermediate teeth in some cases and by collecting bias.

Three heterodont phytosaurs are quite well known in the European Upper Triassic: "*Belodon*" *plieningeri*, *Nicrosaurus kapffi* and "*Angistorhinopsis*" *ruetimeyeri*. *Nicrosaurus kapffi* shows no fluted teeth (Buffetaut and Wouters, 1986) whereas the description given by Huene (1922) for the teeth of "*Angistorhinopsis*" *ruetimeyeri* HUENE, 1911, from the Middle Keuper of Württemberg, perfectly fits the teeth from Saint-Nicolas-de-Port. That is why Buffetaut and Wouters (1986) referred these teeth to this species. Buffetaut and Wouters (1986), Cuny and Ramboer (1991) and Cuny (1993) follow Gregory (1962) and Westphal (1976) in referring the species *ruetimeyeri* to the genus *Rutiodon*. In the meantime, Long and Murry (1995) have reviewed the genus *Rutiodon* and proposed that this genus is represented in North America by the sole species *Rutiodon carolinensis* EMMONS, 1856, which is characterized by its homodont dentition. However Doyle and Sues (1995) consider the genus *Rutiodon* as a metataxon "*pending a thorough phylogenetic reassessment of the interrelationships of phytosaurs*". In the present state of the art, "*Angistorhinopsis*" *ruetimeyeri* shows no diagnostic characters, and, pending a revision, should be considered as an undetermined phytosaurid (*sensu* Doyle and Sues, 1995). Moreover, Meyer (1865) indicated that fluted teeth also occur in his "*Belodon*" *plieningeri*. So, it appears that no dental character permits the attribution of teeth from Saint-Nicolas-de-Port to either "*Angistorhinopsis*" *ruetimeyeri* or "*Belodon*" *plieningeri* and we have to consider them as belonging to an undetermined Phytosauridae (*contra* Cuny and Ramboer, 1991 and Cuny, 1993). The fragment of premaxilla and dermal plates described by Buffetaut and Wouters (1986) do not settle this problem.

Hunt (1989a) has suggested that the kind of heterodont dentition described here is an ecological adaptation of the phytosaurs to a generalist predatory way of life.

Phytosauridae indet. (type 2)

Referred specimens: IRSNB R169, IRSNB 28114/54, IRSNB 28114/167, IRSNB 28114/168, IRSNB 28114/938, IRSNB 28114/986, IRSNB 28114/1002.

Description (Plate 1, D-E):

These triangular blade-like teeth are very similar to the posterior teeth of the heterodont Phytosauridae described above, but are distinctly smaller (FABL < 5 mm). The base of the crown is moderately labiolingually compressed (FABL /LLBW = 1.4 - 1). The labial side is always more convex than the lingual one, both vertically and horizontally. The enamel is usually smooth. Both the anterior and the posterior carinae are symmetrically serrated (11-15 serrations per mm). The serrations are usually nearly perpendicular to the carina.

Discussion:

This could indicate the presence of juvenile specimens in the material discovered at Saint-Nicolas-de-Port rather than another heterodont phytosaurian species. However, anterior and intermediate teeth of similar size have not been identified in the material currently discovered at Saint-Nicolas-de-Port. Thus, it is difficult to settle the question of the presence of more than one species of Phytosauridae at Saint-Nicolas-de-Port.

Monophyletic hierarchy: Archosauria: Ornithodira: Pterosauria: Eudimorphodontidae:

Genus *EUDIMORPHODON* ZAMBELLI, 1973

Referred specimens: IRSNB R182, IRSNB R183, IRSNB 28114/102, IRSNB 28114/165, IRSNB 28114/166, IRSNB 28114/605, IRSNB 28114/632, IRSNB 28114/711.

Description (Plate 1, H-K):

The crown of these teeth usually has a typical "triconodont" structure, with a main central cusp and one or two anterior and posterior, small and well-differentiated accessory cusps. The crowns in IRSNB R183 and IRSNB 28114/711 are bicuspid, with an anterior main cusp and a small posterior accessory cusp. The cusps are always perfectly aligned along the anteroposterior axis of the crown, forming a sharp cutting edge. The crown is well compressed labiolingually (FABL / LLBW = 1.9 - 2.3). The labial side is usually more convex than the lingual one. The main cusp is usually perfectly vertical, but clearly slopes posteriorly in IRSNB 28114/166. The crown is ornamented by numerous and well marked longitudinal ridges on both the labial and lingual sides.

Discussion:

Cheek teeth of the pterosaur *Eudimorphodon* closely resemble those of advanced cynodonts, especially those of *Pseudotriconodon*, in their typical "triconodont" structure (Hahn *et al.*, 1984). However, postcanine teeth of *Pseudotriconodon* are more compressed labiolingually (FABL / LLBW = 1.78 - 2.3 in *Eudimorphodon* [Cuny *et al.*, 1995]; 2.4 - 4.2 in *Pseudotriconodon* [Godefroit and Battail, 1997]) and devoid of enamel ridges, although a species of *Eudimorphodon, E. rosenfeldi,* possesses also perfectly smooth teeth (Dalla Vecchia, 1995). Moreover, the root, when preserved, is clearly longer in *Pseudotriconodon* than in *Eudimorphodon.* In the general structure of their crowns, IRSNB 28114/117 and IRSNB 28114/711 resemble the cynodont premolariform teeth discovered at Saint-Nicolas-de-Port (see Godefroit and Battail, 1997). Nevertheless, their enamel is ornamented with numerous longitudinal ridges whereas it is smoother in cynodonts. Anterior teeth of *Eudimorphodon* are sometimes bicuspid, similar to IRSNB R183 and IRSNB 28114/711 (Wild, 1978).

Monophyletic hierarchy: Ornithodira: Dinosauromorpha: Dinosauria: Saurischia: Sauropodomorpha: Prosauropoda: Plateosauridae:

Genus *PLATEOSAURUS* MEYER, 1837

Referred specimens: IRSNB R184, IRSNB 28114/94, IRSNB 28114/97, IRSNB 28114/170, IRSNB 28114/171, IRSNB 28114/172, IRSNB 28114/173, IRSNB 28114/174, IRSNB 28114/619, IRSNB 28114/643, IRSNB 28114/746.

Description (Plate 1, F-G):

These teeth are not very large (crown height: 2-11 mm). Their crowns are characteristically subtriangular and leaf-shaped in lateral view. They are symmetrical and straight in anterior and posterior views. The apex is slightly rounded and usually worn. The base is moderately compressed labiolingually (FABL/LLBW = 1.55 - 2.1). The anterior and posterior edges of the crown form carinae; the anterior carina is usually slightly shorter than the posterior one. They bear 7 to 16 coarse denticles, oblique to the apex. The carinae are separated from the middle of the crown by marked depressions. Therefore, each side bears a median convexity, better defined on the labial side than on the lingual one. On several crowns, the denticles are completely worn and four large and well-marked wear facets are present along the cutting edges. The root is cylindrical in cross-section and usually separated from the crown by a marked constriction.

Discussion:

Similar teeth have been described by Buffetaut and Wouters (1986), Cuny and Ramboer (1991) and Cuny (1993). These authors noticed the great resemblance of these teeth to those of the prosauropod *Plateosaurus*, common in the Upper Triassic of Germany and France. According to Galton (1990), and contrary to Gauffre (1993), the presence of well-marked wear surfaces on the teeth discovered at Saint-Nicolas-de-Port proves that this is not characteristic of the yunnanosaurids within the prosauropods. Sander (1992, Figure10f) illustrated a plateosaur tooth with a well-marked apical wear surface.

Monophyletic hierarchy: Dinosauria: ?Ornithischia *incertae sedis*

Sereno (1986, 1991a) and Hunt and Lucas (1994) distinguish the following synapomorphies in the isolated teeth of the basal Ornithischia: (1) low, triangular tooth crown in lateral view; (2) recurvature absent from maxillary and dentary teeth; (3) well-developed neck separating crown from root; (4) prominent large denticles arranged at 45 degrees or greater to the mesial and distal edges; (5) premaxillary teeth distinct from dentary/maxillary teeth; (6) maxillary and dentary teeth asymmetrical in mesial and distal views. The combination of these six characters seems a good description of the generalized ornithischian tooth. In most prosauropods, the tooth crowns are proportionally higher and the lingual and labial sides are nearly symmetrical. Nevertheless, according to Gauffre (1993), the teeth of prosauropod dinosaurs can sometimes be confused with those of primitive ornithischians, as these characters, taken separately, can be observed in both groups:

- the prosauropod *Lufengosaurus* also has low triangular crowns (Young, 1947).

- the neck separating the crown and the root is also well-developed in numerous prosauropods, including *Plateosaurus* (Galton, 1990; Sander, 1992: Figure 10f).

- The number of denticles is also low in some prosauropods: 5 to 7 on some *Massospondylus* teeth (Crompton and Attridge, 1986).

The posterior teeth of heterodont phytosaurs differ from those of primitive ornithischians in their much smaller denticles perpendicular to the edges and in the absence of a neck separating the crown from the root.

?Ornithischia (type 1): genus aff. *TECOVASAURUS*

Referred specimen: IRSNB R185.

Description (Plate 2, A-B):

This tooth crown is subtriangular in lateral view, low (height of the crown /FABL = 0.91) and laterally compressed (FABL/LLBW = 2.09). The labial side is more rounded than the lingual one. It is quite asymmetrical in lateral view: the anterior edge is convex and the posterior one concave. The posterior portion of the tooth is longer than the anterior one. There are ?8 denticles on the anterior edge and 10 on the posterior edge, arranged at about 45 degrees to the edges, and they do not reach the base of the crown. The anterior denticles are very worn. The apex is somewhat rounded. The base of the lingual side is ornamented with small ridges, which do not reach the apical portion of the crown. The root is not preserved on this specimen, but appears to have been separated from the crown by a constriction.

Discussion:

This tooth is tentatively referred to an ornithischian dinosaur, as the crown is low, subtriangular in lateral view, asymmetrical in anterior view and probably separated from the root by a distinct neck. Moreover, the denticles are well developed and arranged at about 45 degrees to the mesial and distal edges. This tooth resembles *Tecovasaurus murryi* HUNT and LUCAS, 1994, from the upper Carnian of the United States, in being markedly asymmetical in lateral view, with a convex anterior edge and a longer concave posterior edge. The anterior denticles do not reach the base of the crown. However, this tooth differs from *Tecovasaurus* in the presence of small longitudinal ridges at the base of the lingual side and in the number of denticles: ?8 on the anterior edge and 10 on the posterior edge in IRSNB R185, compared to five on the posterior edge and up to 12 on the anterior edge in *Tecovasaurus murryi*. This tooth probably belongs to a new undescribed species closely allied to *Tecovasaurus murryi* HUNT and LUCAS, 1994. The material (one isolated tooth) is too poor and inadequate to create a new taxon. Moreover, as the type material of *Tecovasaurus murryi* consists of five isolated teeth (see Hunt and Lucas, 1994), it is currently impossible to estimate the dental variation within this genus. Therefore, IRSNB R185 is referred to as aff. *Tecovasaurus*, awaiting further evidence.

?Ornithischia indet. (type 2)

Referred specimens: IRSNB R186, IRSNB 28114/2.

Description (Plate 2, C-D):

The crown of these dentary or maxillary teeth is triangular in outline, not very high (height of the crown/FABL = 1 - 1.15) and about twice as long as wide (FABL / LLBW = 2 - 2.18). The crown is very slightly recurved posteriorly. The labial side is clearly more convex than the lingual one. The anterior and posterior edges each bear about 15 small denticles along their full height. These are arranged at about 45 degrees to the edges of the crown. The apex is rather acute. Although the enamel appears smooth on the labial side, it forms delicate ridges on the lingual one.

The root is not preserved on either of the specimens. In IRSNB R186, it was clearly separated from the crown by a distinct neck.

Discussion:

These teeth could belong to an ornithischian: the crown is triangular in lateral view, asymmetrical in anterior or posterior view, the denticles are arranged at about 45 degrees to the edges and the crown and root are separated by a neck (Sereno, 1986, 1991a; Hunt and Lucas, 1994). They differ from the teeth of all ornithischian dinosaurs currently described from the Late Triassic and Early Jurassic:

- In *Fabrosaurus australis* GINSBURG, 1964 (*sensu* Hunt and Lucas, 1994, including *Lesothosaurus diagnosticus* GALTON, 1978), the dentary/maxillary crowns have fewer (4 to 7) and larger denticles. A faint cingulum and a median ridge can be observed on both sides of the crown. The enamel is perfectly smooth on both sides (Thulborn, 1970).

- In Heterodontosauridae, the crown of the cheek teeth is chisel-shaped, with denticles restricted to the uppermost third of the crown (Weishampel and Witmer, 1990b).

- In basal Thyreophora of the Lower Jurassic, the apex of the crown caps a broadly rounded eminence that divides the smooth lingual side into subequal mesial and distal regions. The labial side is nearly flat. A maximum of six denticles can be observed on the anterior and posterior edges of the crown (Coombs *et al.*, 1990). Cingula are present.

- The teeth of *Pisanosaurus mertii* CASAMIQUELA, 1967 are poorly known and not well preserved. They appear to lack a cingulum and denticles have not been described. Maxillary teeth curve lingually from their base; dentary crowns are relatively straight and vertical (Bonaparte, 1976; Weishampel and Witmer, 1990a).

- *Technosaurus smalli* CHATTERJEE, 1984 possesses dentary/maxillary teeth with very prominent denticles, forming anterior and posterior "accessory cusps"; longitudinal striations are present on both sides of the lower constricted part of the crown (Hunt and Lucas, 1994).

- In *Lucianosaurus wildi* HUNT and LUCAS, 1994, the base of the crown varies for the mesial and distal margins of the crown. A posterior accessory cusp is sometimes present. On both the lingual and labial sides, there are fine longitudinal striations.

- The dentary/maxillary crowns of *Tecovasaurus murryi* HUNT and LUCAS, 1994 are clearly asymmetrical in lateral view. Moreover, the denticles are less numerous and the mesial ones do not reach the base of the crown. The enamel is perfectly smooth.

- *Pekinosaurus olseni* HUNT and LUCAS, 1994 is characterized by proportionally lower and broader dentary/maxillary teeth, with ridges on the apical half of the crown.

- In *Revueltosaurus callenderi* HUNT, 1989, the proportions of the dentary/maxillary teeth are comparable to those of IRSNB 28114/2 and IRSNB R186, but they are clearly much larger. The denticles are less numerous and do not reach the base of the crown, but this can be related to the size of the crown. The enamel lacks longitudinal ridges.

- *Galtonia gibbidens* (COPE, 1878) is currently known only from premaxillary teeth.

IRSNB 28114/2 and IRSNB R186 also closely resemble some teeth referred to *Azendohsaurus laaroussii* from the Upper Triassic of Morocco. Gauffre (1993) shows that this dinosaur is a prosauropod and not an ornithischian, as suggested by Galton (1984) and Hunt and Lucas (1994). The only difference is the nearly symmetrical aspect of the crown, in anterior or posterior view, in *Azendohsaurus* (P.G., personal observations).

From the preceding comparisons, it appears that IRSNB 28114/2 and IRSNB R186 probably belong to an ornithischian, but a primitive prosauropod similar to *Azendohsaurus* cannot be ruled out. The structure of these teeth is very plesiomorphic, compared to those of other Late Triassic or Early Jurassic ornithischian dinosaurs (lack of cingulum, numerous small denticles). The only apomorphy observed on these teeth is the presence of delicate ridges on the lingual side of the crown, an apomorphy shared with IRSNB R185. It is currently difficult to estimate the variability and, therefore, the systematic importance of such a character in primitive ornithischians, because the dental structure of these animals is too incompletely known. Pending the discovery of further material, we refer these teeth to ?Ornithischia indet. and it is not impossible that IRSNB R185, IRSNB R186 and IRSNB 28114/2 belong to the same taxon.

?Ornithischia indet. (type 3)

Referred specimen: IRSNB R202.

Description (Plate 2, L-M):

The crown of this tooth is triangular in lateral view, extremely low (height of the crown/FABL = 0.39, approximately) and very compressed labiolingually (FABL/LLBW = 0.26, approximately). It is slightly asymmetrical in apical view: the labial side is somewhat more convex than the lingual one. The anterior and posterior cutting edges form an obtuse angle of about 120 degrees. Each edge bears well-developed denticles (10 on the completely preserved edge) arranged at about 45 degrees to the edge. The anteriormost and posteriormost denticles are larger and more prominent than the median ones. The enamel is smooth: only post-mortem crevices can be observed. There is no cingulum. The root is broken, but it was separated from the crown by a distinct neck.

Discussion:

This tooth probably belongs to an ornithischian dinosaur: the crown is low, triangular in lateral view, the denticles are prominent and arranged at about 45 degrees to the cutting edges, the labial and lingual sides are slightly asymmetrical and the root is separated from the crown by a distinct neck. This tooth is unusual in its extremely low crown, indicating that it probably belongs to a new taxon. However, this character may also reflect a posterior position in the jaws.

Monophyletic hierarchy: Archosauriformes indet.

The remainder of the descriptive section of this paper is devoted to specimens that appear to be archosauriform (see above), but cannot be identified more precisely. Several of these teeth apparently belong to new taxa, but we have not proposed new binominals for each distinct micromorph. New taxa spawned on the basis of isolated teeth are too often a source of confusion in the nomenclature of reptiles (see Padian (1990), Ostrom and Wellnhofer (1990) and Sereno (1991a) for examples). It is impossible to assess whether the variability observed reflects ontogeny, sexual dimorphism, position in the tooth row, populational variation, or taxonomic distinction. A new binomen has been chosen for a type of ?Archosauriformes teeth with a very distinctive structure (see below).

Archosauriformes indet. (Type 1)

Referred specimens: IRSNB R187, IRSNB R188, IRSNB 28114/134, IRSNB 28114/135, IRSNB 28114/141, IRSNB 28114/142, IRSNB 28114/144a, ?IRSNB 28114/145, IRSNB 28114/146, IRSNB 28114/147a, IRSNB 28114/779, IRSNB 28114/A2624, IRSNB 28114/A2629.

Description (Plate 2, E-G):

These caniniform teeth have a pointed crown, recurved posteriorly. They are strongly labiolingually compressed: FABL / LLBW = 2.1 - 3.5. The labial side of the crown is always slightly more convex than the lingual side. The posterior carina is well developed and bears distinct serrations along almost the whole height of the crown. These serrations are perfectly perpendicular to the carina. Their density (4 - 7.5 per mm) partially depends on the size of the crown, as usual in carnivorous tetrapods with serrated teeth (Farlow *et al.*, 1989). The anterior carina forms a cutting edge near the apex of the crown and gradually becomes a rounded edge towards the root. Serrations are present on the apical third or half of the anterior edge: the anterior serrations always look less well-marked than the posterior ones, which is due to differential wear. The enamel is not perfectly smooth, but criss-crossed by very thin ripples, usually better marked on the lingual side of the crown.

The root is always resorbed on the specimens found in Saint-Nicolas-de-Port; sometimes there is a well-preserved resorption cavity. This indicates that these teeth were shed by the animals as part of the normal replacement process.

Discussion:

Similar teeth have previously been described from Saint-Nicolas-de-Port by Buffetaut and Wouters (1986) and Cuny and Ramboer (1991) and cautiously referred to theropod dinosaurs, because of their close resemblance to the teeth of *Procompsognathus triassicus* FRAAS, 1913. The skull of *Procompsognathus* is now referred to the sphenosuchian *Saltoposuchus* (Sereno and Wild, 1992). In *Saltoposuchus*, the anterior serrations are offset to the lingual side of the crown (Sereno and Wild, 1992), a character that is not present in the teeth from Saint-Nicolas-de-Port.

These teeth closely resemble those of the theropod *Liliensternus liliensterni* (HUENE, 1934) from the Knollenmergel of Bezirk Suhl, Germany. Similar teeth, referred to *cf. Liliensternus*, have also been discovered in the Knollenmergel of Frick, Trossingen and Halberstadt, in Germany (Sander, 1992). Nevertheless, it appears that caniniform, recurved and labiolingually compressed teeth, with fine crenulations along the distal portion of the anterior carina and the whole posterior carina, can be observed in several independent lineages of Archosauriformes: Proterosuchidae and Erythrosuchidae (Charig and Sues, 1976; Juul, 1995), Sphenosuchia (Crush, 1984; Sereno and Wild, 1992), Rauisuchia (Chatterjee, 1985; Benton, 1986; Chatterjee and Majumdar, 1987), Ornithosuchidae (Walker, 1964), Herrerasauridae (Sues, 1990), Ceratosauria (Welles, 1984; Colbert, 1989; Rowe and Gauthier, 1990) and later theropods (Currie *et al.*, 1990). Thus, a more precise identification seems impossible in the present state of our knowledge: it would require detailed comparisons with the teeth of the different groups of Late Triassic carnivorous Archosauriformes, with precise data about such features as the proportions and symmetry of the crown, the density and distribution of the serrations and enamel ornamentation. These teeth and the following are therefore attributed to Archosauriformes indet.

Archosauriformes indet. (Type 2)

Referred specimens: IRSNB R189, ?IRSNB 28114/141.

Description (Plate 2, H-I):

IRSNB R189 is a slender, pointed caniniform tooth which is recurved posteriorly. It is proportionally higher and clearly less compressed than teeth of type 1: FABL / LLBW = 1.53. Both the lingual and the labial sides are symmetrically convex. The anterior edge is rounded along its whole height and does not bear serrations. A serrated carina is developed along the apical two-thirds of the posterior edge; the basal third of this edge is rounded. The serrations are very worn: their density cannot be correctly estimated. A long and narrow matt surface runs along the posterior edge, on the ?lingual side of the tooth: this is probably a wear facet. The enamel is perfectly smooth.

IRSNB 28114/141 is a broken tooth similar to IRSNB R189. The posterior serrations (4,25 per mm) are perfectly perpendicular to the carina and extend further towards the base of the crown than in IRSNB R189.

Archosauriformes indet. (Type 3)

Referred specimen: IRSNB R190.

Description (Plate 2, J-K):

This tooth is remarkable for its blade-like crown. It is very high, slender (FABL / LLBW = 1.74), slightly recurved and curved towards the lingual side. The labial side is much more convex anteroposteriorly than the lingual one. The anterior edge forms an unserrated carina along its whole height. The posterior carina is sharper: its basal two-thirds are delicately serrated (about 15 serrations per mm), while the apical third is unserrated. The serrations look slightly oblique. The enamel is perfectly smooth on both sides.

Discussion:

The distribution of the serrations along the basal two-thirds of the posterior edge is unusual in carnivorous archosaurs. Usually, serrations occur along the distal part of this edge or along its whole height.

Archosauriformes indet. (Type 4)

Referred specimen: IRSNB R191, IRSNB 28114/137.

Description (Plate 3, A-B):

The apical portion of the teeth is broken. The crown is caniniform, recurved posteriorly, slightly curved to the lingual side and clearly less compressed labiolingually than teeth of type 1: FABL / LLBW = 1.37 - 1.62. The labial side is much more convex anteroposteriorly than the lingual one. The preserved portion of the anterior edge is very rounded, without serrations. The posterior edge forms a well developed serrated carina. The serrations (about 8 per mm) are not perfectly perpendicular to the carina, but slightly oblique. The enamel forms longitudinal ridges, more numerous, finer and better marked on the lingual side of the crown.

Archosauriformes indet. (Type 5)

Referred specimen: IRSNB R192.

Description (Plate 3, C-D):

This caniniform tooth is 2.3 times higher than long and strongly recurved. Its labial and lingual sides are symmetrically convex. The base is labiolingually compressed (FABL / LLBW = 1.76), but the section of the tooth becomes progressively rounded towards the apex. The anterior edge is rounded and the posterior one forms a small carina along its whole height. There is no trace of serrations along this carina. The apex is acute. The enamel is fluted on both the labial and the lingual sides.

Archosauriformes indet. (Type 6)

Referred specimen: IRSNB R193.

Description (Plate 3, E-F):

This hooked tooth, proportionally low and stout, is not very compressed labiolingually (FABL / LBW = 1.4). It is strongly recurved posteriorly and slightly lingually. Both the labial and the lingual sides are nearly symmetrically convex. Both the anterior and the posterior edges form well-developed, but unserrated carinae. The enamel is smooth on the labial side of the crown; it forms longitudinal ridges on the lingual side.

Discussion:

In Archosauriformes, premaxillary teeth are often of a different shape than the maxillary and dentary ones. For example, in the ceratosaur *Coelophysis bauri* from the Chinle Formation of Arizona and New Mexico and in *Syntarsus rhodesiensis* from the Forest Sandstone of Zimbabwe, the premaxillary teeth lack serrations and are less compressed labiolingually than the maxillary teeth (Colbert, 1989). Moreover, Colbert (1989) noted that in small individuals of *C. bauri* these teeth are ribbed, which is quite similar to the teeth of our Archosauriformes indet. type 5. But in another ceratosaur, *Dilophosaurus wetherilli*, from the Kayenta Formation, the premaxillary teeth are serrated (Welles, 1984). Among Sphenosuchia, *Dibothrosuchus elaphros* and *Platyognathus hsui* bear premaxillary teeth that are less compressed labiolingually than maxillary and dentary teeth and that lack serrations (Wu and Chatterjee, 1993; Wu and Sues, 1996). In the ornithosuchid *Ornithosuchus longidens*, the premaxillary teeth have a less compressed cross-section than the maxillary teeth, but are serrated (Walker, 1964). In the rauisuchid *Postosuchus kirkpatricki*, the premaxillary teeth are more slender and conical than the maxillary and dentary teeth, with a higher density of serrations (Chatterjee, 1985). There are also some variations in the dentary teeth. In *Coelophysis bauri*, the first seven dentary teeth lack serrations; the eighth tooth has posterior serrations, while the succeeding dentary teeth have both anterior and posterior serrations (Colbert, 1989). In the sphenosuchid *Terrestrisuchus gracilis*, the anterior dentary teeth lack serrations and are less labiolingually compressed than the more posterior ones, which have posterior serrations only. Maxillary teeth of this species have both anterior and posterior serrations (Crush, 1984). In *Ornithosuchus longidens*, the first two dentary teeth are less compressed than the more posterior ones (Walker, 1964). Thus, teeth of types 2 to 6, not very compressed labiolingually and with or without serrated edges, may be interpreted as premaxillary teeth or anterior dentary teeth. However, as little is known about the variation of premaxillary tooth shape among Archosauriformes, this is not of taxonomic significance.

Archosauriformes indet. (Type 7)

Referred specimens: IRSNB R194, IRSNB 28114/85, IRSNB 28114/87, IRSNB 28114/110, IRSNB 28114/130, IRSNB 28114/162, IRSNB 28114/163.

Description (Plate 3, G-H):

The crown of these teeth is as long as high (PHC / FABL = 0.95 - 1.18), but clearly recurved and curved slightly towards the lingual side. They are very compressed labiolingually (FABL / LLBW = 1.87 - 2.64). The labial side is convex both horizontally and vertically. The lingual side is flat horizontally and slightly concave vertically. The apex is usually acute, but sometimes worn. Both the anterior and posterior edges are very trenchant. In IRSNB 28114/085, IRSNB 28114/110, IRSNB 28114/162 and IRSNB R194, a small accessory cusp is present at the base of the posterior cutting edge. In IRSNB 28114/87 and IRSNB 28114/130, both the anterior and posterior edges bear two or three tiny denticles on their basal half. There is no trace of a denticle in IRSNB 28114/163, but the posterior edge is worn. The enamel is always perfectly smooth on the labial side of the crown. On the other hand, it forms dense and well marked longitudinal ridges on the lingual side. The root is not preserved on any of the specimens currently known and was separated from the crown by a constriction.

Discussion:

These specimens are reminiscent of some premolariform teeth attributed to cynodonts from the same locality (Godefroit and Battail, 1997). In the latter, the enamel is perfectly smooth on both sides, the anterior edge never bears denticles and the main cusp is not inclined to the lingual side. "Premolariform" teeth of the pterosaur *Eudimorphodon* (see above) are more massive and their enamel is ornamented on both sides.

Similar teeth have been described from the upper Norian of Medernach in Luxembourg (Cuny *et al.*, 1995: Figure 6h-i) and tentatively referred to phytosaurs. Nevertheless, the crown is too compressed labiolingually to be a posterior tooth of a heterodont phytosaur and it does not bear fine crenulations along its cutting edges.

Archosauriformes indet. (Type 8)

Referred specimens: IRSNB R195 ?IRSNB 28114/151.

Description (Plate 3, I-J):

IRSNB R195 is a portion of a high, strongly labiolingually compressed blade-like tooth (FABL / LLBW = 2.57). It is quite straight vertically. Its labial side is slightly convex and its lingual face nearly flat. Both its anterior and posterior edges are very cutting and finely crenulated (about 11 crenulations per mm). The enamel forms some large but indistinct ripples on both sides.

IRSNB 28114/151 is the apical portion of a blade-like tooth similar to IRSNB R195: perfectly straight, very compressed (FABL / LLBW = 2.38), with the enamel forming large but indistinct ripples. Both edges are very sharp, but do not show any crenulation. However, it must be noted that the edges of IRSNB 28114/151 look worner than those of IRSNB R195, which could explain the absence of the small crenulations.

Archosauriformes indet. (Type 9)

Referred specimens: IRSNB R196, IRSNB 28114/140.

Description (Plate 4, A-B):

These teeth are characterized by their high, perfectly straight, triangular and very compressed (FABL / LLBW = 1.86 - 2.45) crown. The labial side is slightly more convex than the lingual one. The anterior and posterior edges are very sharp and irregular. Although they are worn in IRSNB 28114/140, the cutting edges of IRSNB R196 bear very small, indistinct and oblique serrations. The apex of the crown is very acute. The enamel is perfectly smooth on both sides.

Archosauriformes indet. (Type 10)

Referred specimen: IRSNB R197.

Description (Plate 3, K-L):

This small crown is triangular in outline, as long as high and strongly compressed labiolingually (FABL / LLBW = 2.92). The apex is rather rounded. The labial and the lingual sides are symmetrically nearly flat anteroposteriorly and vertically. The edges are sharp and bear tiny and very worn serrations (about 10 serrations per mm).

Archosauriformes indet. (Type 11)

Referred specimens: IRSNB R198.

Description (Plate 4, C-D):

This apical fragment is triangular in lateral view and not recurved. The crown was probably elongated anteroposteriorly. Its apex is rather acute and its edges form a slightly convex, very sharp and unserrated carina. It is very compressed labiolingually: both the labial and the lingual sides are symmetrically convex anteroposteriorly. The enamel is perfectly smooth on both sides.

Archosauriformes indet. (Type 12)

Referred specimen: IRSNB R199.

Description (Plate 4, E-F):

The crown of this complete tooth is triangular in outline, low (height of the crown / FABL = 0.86) and very compressed labiolingually (FABL / LLBW = 2.27). The apex is slightly curved posteriorly and lingually. The labial side is convex both horizontally and vertically. The lingual side is formed by a median rib flanked by anterior and posterior concave facets running along the edges. Both the anterior and posterior edges form pronounced carinae: the anterior one is unserrated, but the posterior one bears six worn and indistinct denticles halfway up the apex of the crown. With the exception of post-mortem cracks, the enamel is smooth.

The root of this specimen is partially resorbed, forming a large resorption cavity. Like the crown, it is very compressed labiolingually. Its distal side is very concave.

Archosauriformes indet. (Type 13)

Referred specimen: IRSNB R200.

Description (Plate 4, G-H):

This is the apical part of a crown which was probably not very compressed labiolingually and not recurved. Although broken, the apex was probably not very acute. The labial and the lingual sides are nearly symmetrically convex. The anterior and posterior edges form very trenchant but unserrated carinae. The enamel is ornamented by thin longitudinal ridges on both sides.

Monophyletic hierarchy: ?Archosauriformes *incertae sedis*

Genus *GRAOULLYODON* nov.

Diagnosis: As for the type species, *Graoullyodon hacheti* nov. sp. (monospecific genus).

Derivatio nominis: *Graoully*, mythical monster of the Metz area (see Bellard (1965-66) for a historical study of the Graoully legend) and *odous* (Greek), tooth.

Type species: *Graoullyodon hacheti* sp. nov.

Graoullyodon hacheti sp. nov.

Diagnosis: Tooth crowns caniniform and triangular in cross-section. Anterior side with an infolded median groove. Trenchant posterior edge, with a dozen prominent denticles arranged obliquely along the edge.

Holotype: IRSNB R201.

Paratypes: IRSNB 28114/149 and IRSNB 28114/35.

Derivatio nominis: In honour of Dr. Michel Hachet, Curator of the Musée municipal de Toul, who so kindly received our team during the excavations at Saint-Nicolas-de-Port.

Locus typicus: Quarry of Saint-Nicolas-de-Port, in Rosières-aux-Salines (Meurthe-et-Moselle, France).

Stratum typicum: Bone-bed assigned to the "Rhaetian" sandstones (Late Triassic).

Description (Plate 4, I-L):

These caniniform teeth are rather low and stout (FABL / LLBW = 1) and triangular in cross-section. The anterior side is nearly perfectly flat labiolingually and slightly convex from top to bottom. It bears an infolded enamel-lined median groove. This groove becomes narrower and shallower towards the tip of the crown and disappears at the level of its apical third. The anterolabial and anterolingual edges of the tooth are rather rounded and do not bear crenulations. The lingual side is slightly concave both vertically and horizontally and the labial side is symmetrically convex, so that the apex is somewhat displaced to the posterolingual side of the tooth. The posterior edge, somewhat more acute than the others, bears a dozen rather prominent denticles arranged obliquely along the posterior edge. The enamel is perfectly smooth. There is a resorption cavity at the base of the tooth.

Discussion:

The attribution of this tooth to the ?Archosauriformes is based on the presence of prominent denticles on the posterior edge and on the presumed thecodont implantation. The groove on the anterior side of these teeth is reminiscent of the venom groove along the anterior edge of the poison fangs of many extant snakes and *Heloderma*. By analogy, it is possible that this structure also served in venom conduction. Apparent venom-conducting teeth have also been described in another Late Triassic archosauriform: *Uatchitodon kroehleri* SUES, 1991 is characterized by its strongly labiolingually compressed, recurved, serrated and blade-like dental crowns, bearing deeply infolded median grooves on both their labial and lingual sides (Sues, 1991; Sues *et al.*, 1994). The earliest record of what appears to be an oral venom-delivery apparatus in tetrapods is represented by the therocephalian therapsid *Euchambersia*, from the Upper Permian of South Africa: a deep lateral recess on the maxilla opens onto the palate just behind the large canine (Mendrez, 1975). Therefore, it appears that an oral venom-conducting apparatus independently appeared in several amniote lineages (therapsids, archosauriforms and squamates).

DISCUSSION AND CONCLUSIONS

Late Triassic ornithischian evolution

Ornithischians are rare components of Late Triassic vertebrate assemblages and are mainly known from isolated teeth. Dutuit (1972) described *Azendohsaurus laaroussi*, a fragmentary jaw and associated teeth, from the early late Carnian (Hunt and Lucas, 1994) of Morocco. Galton (1984), however, noted that one of the associated teeth clearly shows ornithischian characters and he described additional specimens from the Upper Triassic of Morocco. Thulborn (1974) and Gauffre (1993) reexamined the specimen and suggested that it represents, in fact, a prosauropod. *Pekinosaurus olseni*, based on isolated teeth from the Late Carnian Pekin Formation of North Carolina, is a presumed ornithischian from the late Carnian (Hunt and Lucas, 1994). *Pisanosaurus mertii* CASAMIQUELA, 1967, from the Ischigualasto Formation in Argentina, is also from the late Carnian. Galton (1983) mentioned a partial maxilla from the late Carnian Wolfville Formation of Nova Scotia (Canada). *Galtonia gibbidens* and *Tecovasaurus murryi* are based on isolated teeth from North America that occur in strata dated as latest Carnian (Hunt and Lucas, 1994). *Lucianosaurus wildi* and *Revueltosaurus callenderi* are isolated teeth discovered in early to middle Norian strata in North America (Padian, 1990; Hunt and Lucas, 1994). A right dentary from the same age represents *Technosaurus smalli* (Chatterjee, 1984).

If their attribution is confirmed, the ornithischian teeth discovered in Saint-Nicolas-de-Port could be the oldest representatives of this group in Europe. Cuny *et al.* (in prep.) describe a presumed ornithischian tooth from the Rhaetian of Lons-le-Saunier (Jura, France) and the tooth of *"Plateosaurus" ornatus* from the Rhaetian bone-bed of Schlößlesmühle, near Tübingen (Württemberg, Germany) may in fact belong to an ornithischian dinosaur (Huene, 1907-08). Notwithstanding doubts about the precise age of Saint-Nicolas-de-Port (see below), these latter specimens are definitely younger than those from Saint-Nicolas-de-Port. However, those teeth are the only presumed ornithischian fossils discovered to date in the late Norian-Rhaetian formations.

Because of the rarity and poor preservation of much of the material referred to Triassic ornithischian dinosaurs, very little of substance can be said about their early evolution. These small to medium-sized herbivorous dinosaurs were at least present in North and South America by the Carnian and possibly in Europe by the Norian. However, this apparent biogeographical distribution is almost certainly the result of a lack of data for other areas. During the Early Jurassic, ornithischian dinosaurs became relatively common and diverse. This may be related to the extinction of other low-browsing herbivores, such as aetosaurs, at the end of the Triassic (Hunt and Lucas, 1994).

The age of the Saint-Nicolas-de-Port quarry

The age of Saint-Nicolas-de-Port has been debated by numerous authors. Stratigraphers and mammal workers argued for an early Rhaetian age (Laugier, 1971, Sigogneau-Russell, 1983c), but Buffetaut and Wouters (1986), Cuny and Ramboer

(1991) and Duffin (1993) placed the beds in the uppermost middle Keuper (late Norian) because of the great resemblance of their amphibians and reptiles to those discovered in the famous Baerecke quarries at Halberstadt (Germany). It is not the purpose of this paper to discuss all the arguments developed by the different authors in favour of one or the other hypothesis. Nevertheless, some remarks can be made based on the study of the archosauriform teeth.

One of the most important arguments developed by Buffetaut and Wouters (1986) is the presence of the phytosaur *"Angistorhinopsis" ruetimeyeri* at Saint-Nicolas-de-Port and at Halberstadt. In the latter locality, this phytosaur is recorded at the top of the sequence, above the plateosaur beds, in layers referred to the "Rhät" by Huene (1922) and Kuhn (1939). On the other hand, Buffetaut and Wouters (1986) claimed that these beds can be included in the underlying Knollenmergel, but they do not provide support for this view. It has been shown above that the teeth discovered at Saint-Nicolas-de-Port do not necessarily belong to the species *"Angistorhinopsis" ruetimeyeri* and that such a heterodont dentition can also be observed in other species of phytosaurs (*"Belodon" plieningeri*) and other heterodont phytosaurs. Although phytosaurs are good biostratigraphic indicators for the Upper Triassic (Lucas and Hunt, 1989, 1993; Hunt, 1991; Hunt and Lucas, 1991; Benton, 1994), the biostratigraphic value of isolated phytosaur teeth from Saint-Nicolas-de-Port as an indicator of an upper Norian age for that locality remains uncertain. It requires precise informations about the age of the phytosaur-bearing beds at Halberstadt, about the systematic status of *"Angistorhinopsis" ruetimeyeri* and *"Belodon" plieningeri* and about the interspecific variation of the teeth in heterodont phytosaurs. However, to our knowledge, fluted phytosaurian teeth seem to be unknown in other European "Rhaetian" sites.

For Buffetaut and Wouters (1986), Cuny and Ramboer (1991) and Cuny (1993), the presence of numerous *Plateosaurus* teeth in Saint-Nicolas-de-Port suggests a late Norian age for this locality. Indeed, it appears that most *Plateosaurus* specimens have been discovered in the Knollenmergel or in equivalent formations of western Europe (Galton, 1985, 1986a, 1990; Sander, 1992). Rhaetian prosauropod material seems rare and hardly diagnostic in the German Basin (Cuny, 1993, 1995).

Other taxa reported here from Saint-Nicolas-de-Port have broader stratigraphic ranges. Specimens very similar to the "Archosauriformes type 1" teeth from Saint-Nicolas-de-Port are described from the Knollenmergel of Germany (Sander, 1992). Nevertheless, it has been shown that similar teeth can also be found in numerous archosaurian lineages and are, therefore, poor biostratigraphic indicators. The pterosaur *Eudimorphodon* was first decribed from the middle Norian (Benton, 1994) of Cene, Italy (Wild, 1978). Teeth of *Eudimorphodon* were subsequently described in the Norian of Friuli, Italy (Dalla Vecchia, 1995), in the late Norian of Medernach (Luxembourg; Hahn *et al.*, 1984; Cuny *et al.*, 1995) and in the Dockum Formation (late Carnian - early Norian) of North America (Murry, 1986). Clemens (1980), on the basis of figures given by Peyer (1956), tentatively referred some isolated teeth from the Rhaetian site of Hallau (Switzerland) to *Eudimorphodon*, but this record was never confirmed (see Fraser and Unwin, 1990). The early ornithischian *Tecovasaurus*, tentatively identified at Saint-Nicolas-de-Port, was first described from the late Carnian of Texas and Arizona (Hunt and Lucas, 1994).

It can be concluded that, although the archosaurian fauna overall resembles that from the late Norian of Germany, the temporal resolution of isolated archosaurian teeth is not fine enough to draw precise conclusions about the age of the Saint-Nicolas-de-Port quarry. The solution to this problem would require the discovery of more complete material, which would permit more precise identifications of the animals. Moreover, a consensus is needed on the status of the Rhaetian stage.

The Saint-Nicolas-de-Port vertebrate community

An ecological community can be defined as a group of organisms living together within a definite locality. This community is characterized by a trophic structure with food webs linking plants, primary, secondary and tertiary consumers. In the community, each animal occupies an ecological niche. For Elton (1927), the niche is the place of the animal in the biotic environment, its relations to food and enemies. The niche of an animal can be defined to a large extent by its size and food habits.

In palaeontology, recognition of fossil communities is rather difficult and depends largely on taphonomic conditions of fossilization. Moreover, it is usually difficult to decide upon the precise diet of an extinct animal, which depends on both ecological and morphological factors. If tooth morphology and the body size are regarded as important characters in analyzing the diet of an animal, these criteria need to be used with caution because they do not provide conclusive evidence for a particular type of diet.

The mixture of terrestrial, marine and freshwater vertebrates within the Saint-Nicolas-de-Port community suggests a deltaic or a coastal palaeoenvironment. This is confirmed by the sedimentological study of the section by Al Khatib (1976). The marine vertebrates are dominant within the bone-bed. Although they are very numerous, they are not very diverse. They are represented by sharks (*Lissodus*, *Rhomphaiodon*: Duffin, 1993), Perleidiformes, Pycnodontiformes and Actinopterygii (Cuny, 1993). It is possible that some of these fishes are fresh-water animals. The pterosaur *Eudimorphodon* is usually regarded as a coastal fish-eater and indeed fossilized stomach remains of an individual from the Norian of Cene (Italy) shows that *Eudimorphodon* preyed on small fishes such as *Parapholidophorus*. Juvenile individuals had a different dentition and probably ate insects (Wild, 1978; Wellnhofer, 1978, 1991).

The lungfishes (Ceratodontiformes) are represented by *Ptychoceratodus phillipsi* and by *Ceratodus kaupi* (Martin *et al.*, 1981). *C. kaupi* was an ubiquitous animal, living in marine as well as in freshwater environments. *P. phillipsi* is regarded as a littoral species (Martin *et al.*, 1981). The living ceratodontid *Neoceratodus* from Australia has an omnivorous diet: young specimens feed on insect larvae and planktonic crustaceans, while larger individuals eat frogs, tadpoles, fishes, shrimps, earthworms, snails and aquatic plants (Allen, 1989).

Late Triassic temnospondyl amphibians occur largely in floodplain channels and in lacustrine deposits (Milner, 1994). They are represented at Saint-Nicolas-de-Port by the Capitosauroidea, Metoposauridae and Plagiosauridae (Buffetaut and Wouters, 1986; Cuny and Ramboer, 1991; Cuny, 1993). The latter were undoubtedly suction-gulpers, living permanently on the bottom (Milner, 1994). Capitosauroids were large and crocodile-like temnospondyls, growing up to 3 m in length. Along with the Metoposauridae, they probably filled the niche of amphibious predators, feeding on freshwater fishes but also on terrestrial vertebrates (Benton, 1979; Hunt *et al.*, 1993). Phytosaurs were also crocodile-like amphibious macropredators. Their lifestyle was not basically different from that of living crocodilians (Westphal, 1976). Coprolites and

	Abundance	Size	Habitat	Ecological niche	Diet
Capitosauroidea ind.	**	M/L	Fresh-water	Aquatic/terrestrial predators	Fishes and other vertebrates
Metoposauridae ind.	**	M	Fresh-water	Aquatic/terrestrial predators	Fishes and other vertebrates
Plagiosauridae ind.	****	M	Fresh-water	Fully aquatic predators	Fishes
Rutiodontidae ind.	****	L	Fresh-water	Aquatic/ terrestrial predators	Fishes and other vertebrates
?Rutiodontidae ind.	**	M	Fresh water	Aquatic/terrestrial predators	Fishes and other vertebrates
Eudimorphodontidae					
Eudimorphodon	**	M	Coastal	Coastal fishers	Fishes
Plateosauridae					
Plateosaurus	**/***	L	Lowland	Large herbivores	Vegetation
?Ornithischia ind. 1-3	*/**	M	Lowland	Small / medium herbivores	Vegetation
Archosauriformes ind. 1	***	M	Lowland	Top predators	Medium/large vertebrates
Archosauriformes ind. 2-13	*/**	S/M	Lowland	Small/medium predators	Small/medium vertebrates
Graoullyodon	*	S	Lowland	Small predator	Small/medium vertebrates
Sphenodontia ind.	**	S	Lowland	Insectivores	Insects
Lepidosauromorpha ind.	*	S	Lowland	Insectivores	Small insects
"Chiniquodontoidea"					
Pseudotriconodon	***	S	Lowland	Insectivores	Large insects
Meurthodon	**	S	Lowland	Insectivores, small predators	Large insects, small vertebrates
Tricuspes	**	S	Lowland	Insectivores	Large insects
Gaumia	**	S	Lowland	Insectivores	Large insects
Lepagia	*	S	Lowland	Insectivores	Large insects
Hahnia	*	S	Lowland	Insectivores	Large insects
Traversodontidae					
Maubeugia	*	S	Lowland	Small omnivores	Insects, soft plant matter,...
Rosieria	*	S	Lowland	Small omnivores	Insects, soft plant matter,...
Microscalenodon	*	S	Lowland	Small omnivores	Insects, soft plant matter,...
Haramiyidae					
Thomasia	***	S	Lowland	Small herbivores	Soft plant matter
Theroteinidae					
Theroteinus	**	S	Lowland	Small herbivores	Soft fruits
Morganucodontidae					
Brachyzostrodon	**	S	Lowland	Insectivores	Large insects
Morganucodon	**	S	Lowland	insectivores	Large insects
Woutersiidae					
Woutersia	*/**	S	Lowland	Insectivores	Large insects
Kuehneotheriidae					
Kuehneotherium	*	S	Lowland	Insectivores	Large insects
Docodonta					
Delsatia	*	S	Lowlands	Insectivores	Large insects

Figure 3.— Ecological niche of the different tetrapod taxa represented in Saint-Nicolas-de-Port. *: very rare; **: rare; ***: common; ****: abundant. S: small (< 60 cm); M: medium-sized (60cm < size < 3m); L: large (> 3 m)

stomach contents show that they ate fishes and small reptiles. They could lie partially submerged in water or walked on land in order to catch preys (Chatterjee, 1978; Benton, 1979).

Fossils of terrestrial vertebrates are not very common in Saint-Nicolas-de-Port, but they appear very diverse. We have no direct evidence of the type of vegetation present either in the form of macroscopic plant material or palynomorphs. However, the vegetation must have been well developed in the vicinity, in order to provide the basic

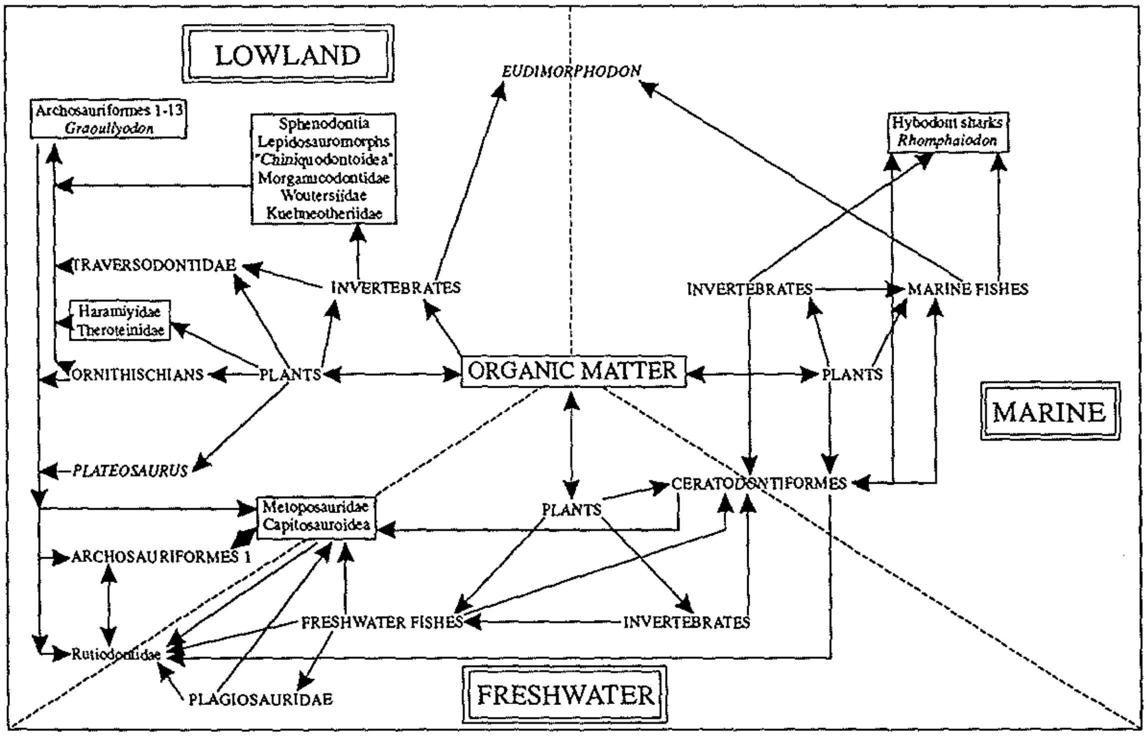

Figure 4.— Possible trophic relationships within the Saint-Nicolas-de-Port vertebrate community.

trophic support for such a variety of animals. Small herbivores are represented by allotherian mammals.

Teeth of the haramiyid *Thomasia* are rarely strongly worn, which may indicate a diet of soft plant matter. Those of the theroteinid *Theroteinus* have low cusps and delicate roots that suggest a diet of rather soft plants (Sigogneau-Russell and Hahn, 1994). Early ornithischians were small to medium-sized herbivores; because wear facets are poorly developed on the teeth of Late Triassic ornithischians (see also Hunt and Lucas, 1994), it can be deduced that they also fed on rather soft matter. *Plateosaurus* was a large herbivore, reaching 7 m in length. Its teeth often show extensive wear surfaces: it could probably eat tougher plant material. The long neck of this animal extended the vertical feeding range so that vegetation could be reached at higher levels (Bakker, 1978; Galton, 1986b).

Insects were probably quite abundant and provided nutrition for the juvenile forms of numerous reptiles, but also for numerous small adults. These include Sphenodontia and an indeterminate lepidosauromorph (Cuny, 1993), small "chiniquodontoid" (*sensu* Sigogneau-Russell and Hahn, 1994) cynodonts (Godefroit and Battail, 1997), Morganucodontidae, Woutersiidae, Kuehneotheriidae and Docodonta (Sigogneau-Russell, 1983a, b; Hahn *et al.*, 1991; Sigogneau-Russell and Hahn, 1994, 1995; Sigogneau-Russell and Godefroit, 1997). The great diversity of small herbivores and insectivores may have led to the diversification of small to medium-sized predators, represented by the Archosauriformes indet. types 2-13 described in the present paper, characterized by their sharp and usually serrated teeth. *Graoullyodon*, with its venom-conducting caniniform teeth, was probably an important predator in this community. Archosauriformes indet. type 1 were medium-sized predators, the largest fully terrestrial ones in the fauna, which probably dominated the terrestrial ecosystem.

A summary of the ecological characteristics of the different tetrapod taxa represented at Saint-Nicolas-de-Port is presented in Figure 3. The diagram in Figure 4 represents the theoretical relationships within the Late Triassic community of vertebrates from Saint-Nicolas-de-Port.

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CAPTIONS OF THE PLATES

PLATE 1

Archosauriformes teeth from the Late Triassic of Saint-Nicolas-de-Port. A-C: scale bars = 1 cm; D-M: scale bars = 1 mm.

A: IRSNB R178, anterior tooth of Phytosauridae type 1.

B: IRSNB R 179, intermediate tooth of Phytosauridae type 1.

C: IRSNB R180, posterior tooth of Phytosauridae type 1.

D-E: IRSNB R181, tooth of Phytosauridae form 2 in lateral (D) and anterior or posterior (E) views.

F-G: IRSNB R184, tooth of *Plateosaurus* in lingual (F) and labial (G) views.

H-I: IRSNB R182, tooth of *Eudimorphodon* in labial (H) and posterior (I) views.

J-K: IRSNB R183, tooth of *Eudimorphodon* in lateral (J) and posterior (K) views.

L-M: IRSNB R202, ?ornithischian (type 3) tooth in lateral (L) and apical (M) views.

PLATE 2

Archosauriformes teeth from the Late Triassic of Saint-Nicolas-de-Port. Scale bars = 1 mm.

A-B: IRSNB R185, tooth of aff. *Tecovasaurus* in lingual (A) and posterior (B) views.

C-D: IRSNB R186, ?ornithischian (type 2) tooth in lingual (C) and posterior (D) views.

E: IRSNB R187, Archosauriformes indet. (type 1) tooth in lateral view.

F-G: IRSNB R188, Archosauriformes indet. (type 1) tooth in lateral views, with detail (G) of the crenulations.

H-I: IRSNB R189, Archosauriformes indet. (type 2) tooth in lateral views, with detail (I) of the posterior wear facet.

J-K: IRSNB R190, Archosauriformes indet. (type 3) tooth in lingual (J) and posterior (K) views.

PLATE 3

Archosauriformes teeth from the Late Triassic of Saint-Nicolas-de-Port. Scale bars = 1 mm.

A-B: IRSNB R191, Archosauriformes indet. (type 4) tooth in lateral views, with detail (B) of the posterior crenulations.

C-D: IRSNB R192, Archosauriformes indet. (type 5) tooth in lateral (C) and posterior (D) views.

E-F: IRSNB R193, Archosauriformes indet. (type 6) tooth in labial (E) and lingual (F) views.

G-H: IRSNB R194, Archosauriformes indet. (type 7) tooth in labial (G) and lingual (H) views.

I-J: IRSNB R195, Archosauriformes indet. (type 8) tooth in lateral (I) and anterior or posterior (J) views.

K-L: IRSNB R197, Archosauriformes indet. (type 10) tooth in lateral (K) and anterior or posterior (L) views.

PLATE 4

Archosauriformes teeth from the Late Triassic of Saint-Nicolas-de-Port. Scale bars = 1 mm.

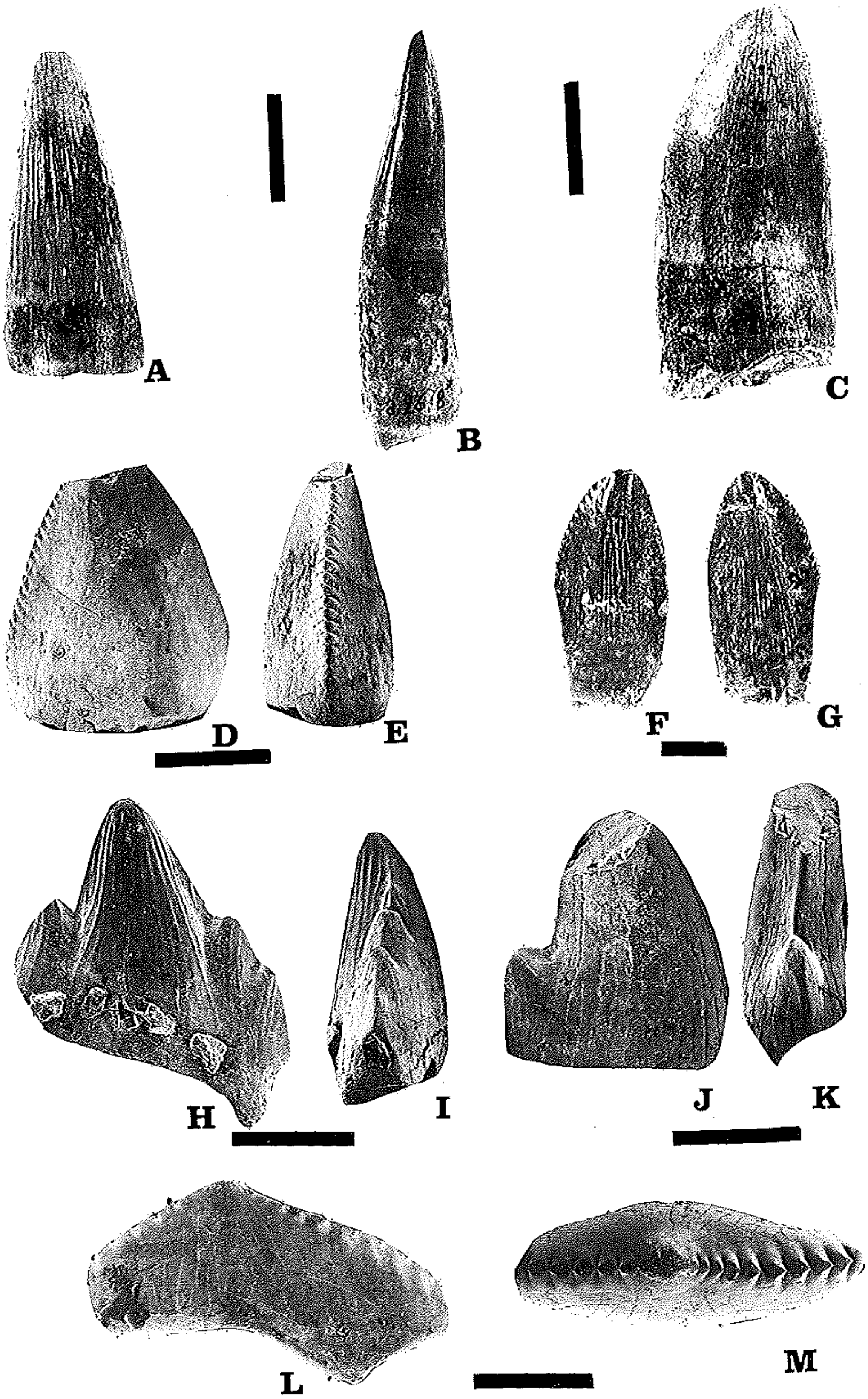
A-B: IRSNB R196, Archosauriformes indet. (type 9) tooth in lateral views, with detail (B) of the crenulations.

C-D: IRSNB R198, Archosauriformes indet. (type 11) tooth in lateral (C) and apical (D) views.

E-F: IRSNB R199, Archosauriformes indet. (type 12) tooth in labial (E) and posterior (F) views.

G-H: IRSNB R200, Archosauriformes indet. (type 13) tooth in lateral (G) and anterior or posterior (H) views.

I-L: IRSNB R201, tooth of *Graoullyodon hacheti*, in anterior (I), lingual (J), posterior (K) and antero-lingual (L) views, anterior groove indicated by an arrow.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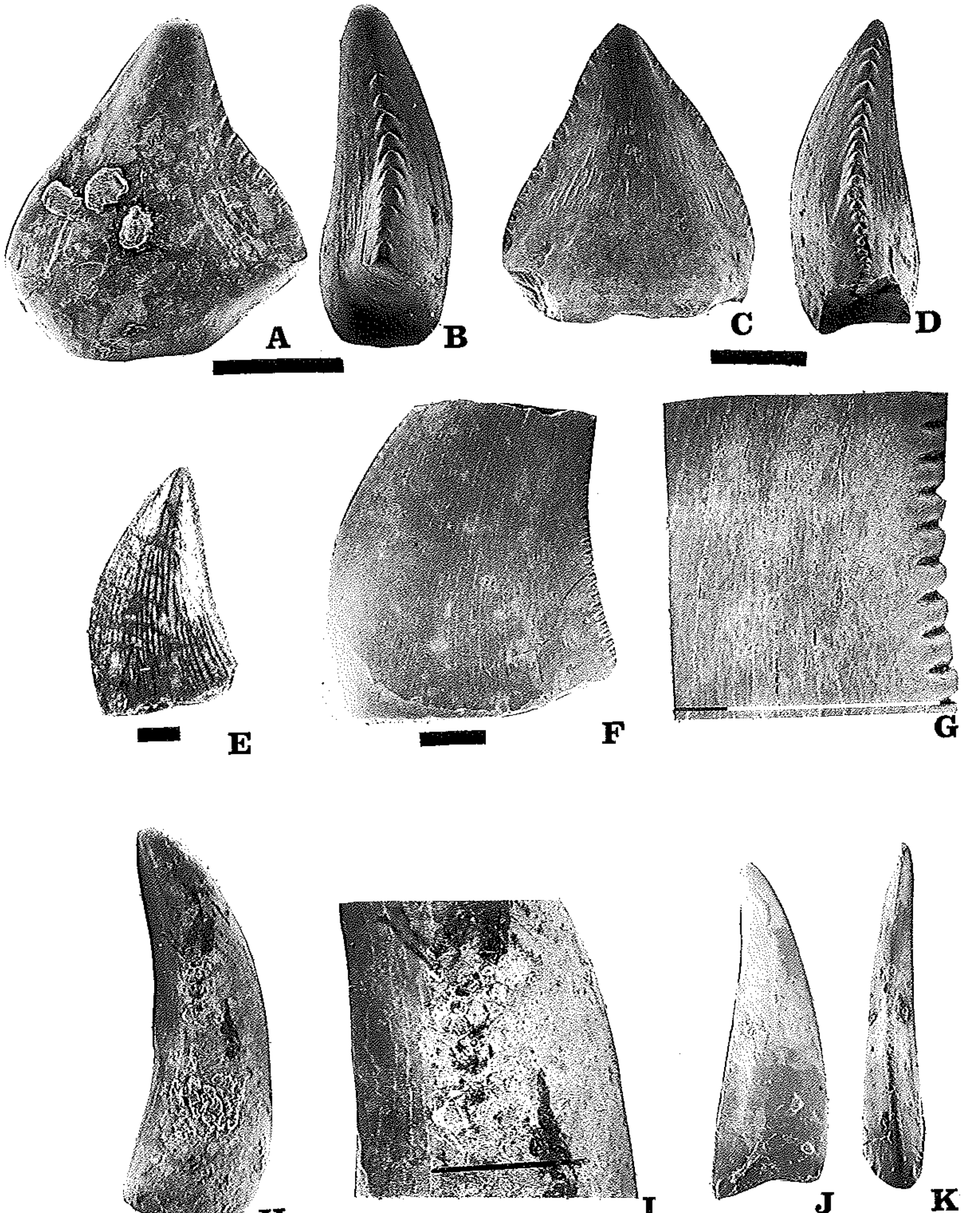
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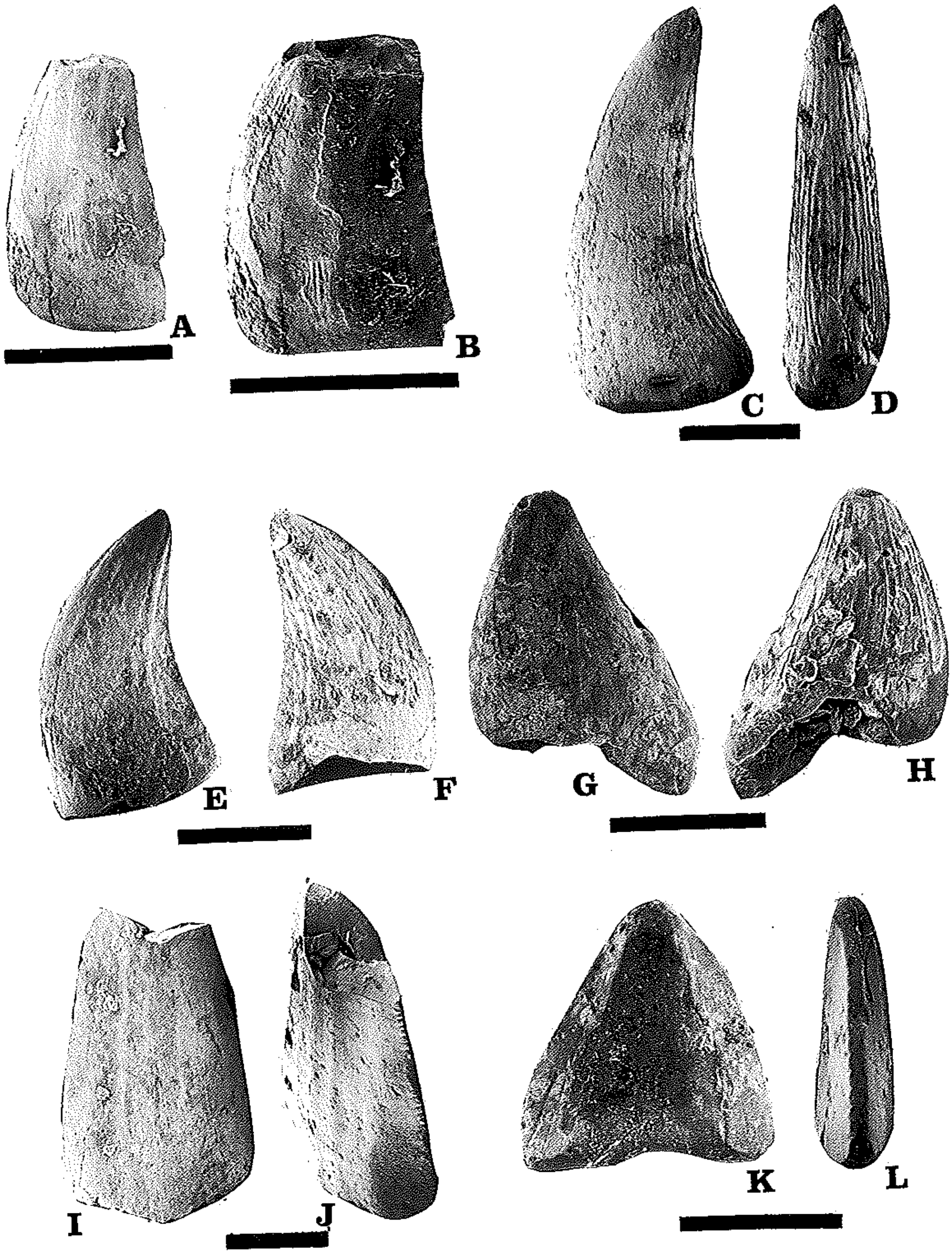

PLATE 4