

AMPHIBIAN AND REPTILE REMAINS FROM THE UPPER TRIASSIC OF SAINT-NICOLAS-DE-PORT (EASTERN FRANCE) AND THEIR BIOSTRATIGRAPHIC SIGNIFICANCE

E. BUFFETAUT

U.A. 720 du CNRS, Laboratoire de Paléontologie des Vertébrés,
Université Paris VI, 4 place Jussieu, 75230 Paris Cedex 05, France

and

G. WOUTERS

230 chaussée de la Hulpe, 1170 Boitsfort, Belgium

(Received September 17, 1985)

The fossil vertebrate locality of Saint-Nicolas-de-Port, near Nancy in eastern France, is well known for having yielded an assemblage of early mammal teeth. It is usually referred to the "Rhaetian" following local lithostratigraphic usage. Amphibian remains from Saint-Nicolas-de-Port include intercentra, dermal plates and a clavicle of pliosaurids (cf. *Plagiosaurus*), and a palatine fragment referred to a capitosaurid. The reptiles are represented by teeth of the phytosaur *Rattiodon rathioneyeri* (Huene), the prosauropod *Platosaurus* sp., and procompsognathid coelurosaur. The age assignment to the Rhaetian is not satisfying, because the Rhaetian stage is of doubtful status and is being abandoned by an increasing number of stratigraphers, and should not be used in the Germanic Realm because of the impossibility of proper correlation with the Alpine Realm. Our comparison of the amphibian and reptile assemblage from Saint-Nicolas-de-Port with faunas from the Keuper of Germany shows that there are close resemblances with the assemblage from levels referred to the Knollenmergel at Halberstadt in central Germany. It thus seems likely that the Saint-Nicolas-de-Port fauna is of late Middle Keuper age. Its place in the standard marine-based stratigraphic scale may be close to the boundary between Middle and Late Norian (the Rhaetian being considered as the equivalent of the Late Norian).

INTRODUCTION

Fossil vertebrate remains have been reported in the late Triassic beds of the vicinity of Saint-Nicolas-de-Port (Meurthe-et-Moselle, eastern France) since the 19th century. As early as 1851, Levallois mentioned the occurrence of bones in the so-called "grès infra-liasique." In 1862, he added that there is "une couche à débris de poissons et de sauriens" in the grès infra-liasique south of Saint-Nicolas-de-Port (Levallois, 1862, p. 273). Later, in 1928, Corroy mentioned Saint-Nicolas-de-Port among the main vertebrate localities of the Upper Keuper of Lorraine. In 1971, Langier wrote (p. 64):

Cette carrière a livré une faune d'une grande richesse, comprenant des maxillaires, des dents appartenant à plusieurs groupes de Vertébrés, des vertèbres dorsales et caudales, phalanges, griffes, os longs pourvus d'une cavité médullaire. Il est possible de suivre l'évolution de la denture d'une espèce, grâce aux divers stades de croissance qui ont été retrouvés (embryons de *Ceratodus*). Enfin, il sera possible de confirmer l'existence des Mammifères par une étude d'histologie osseuse comparée.

He also announced a detailed study of these vertebrate remains, which has not been published.

Interest in the Saint-Nicolas-de-Port locality has much increased since the washing and screening of large amounts of sediment by one of us (G.W.) and P. Coupatez (Brussels) has led to the discovery of mammal teeth (Russell *et al.*, 1976). Papers have been published on the mammals (Sigogneau-Russell, 1978, 1983a, 1983b) and on the dipnoans (Martin *et al.*, 1981) of the locality. However, the amphibian and reptile remains, although abundant, have been mentioned only in a preliminary faunal list (Sigogneau-Russell *et al.*, 1979). The aim of the present paper is to describe the amphibian and reptile material in the Wouters collection (now in the Institut royal des Sciences naturelles, Brussels), and to try to use it for biostratigraphic purposes. So far, the age of the locality has not been established with sufficient precision. It is usually referred to the "Rhaetian," but, as will be seen below, the use of this stage name is, to say the least, disputable, and can be misleading. We have tried to compare the amphibian and reptile faunal assemblage from Saint-Nicolas-de-Port with well known late Triassic faunas from Germany, in order to determine its stratigraphic position more accurately.

The fossils described below belong to the Wouters collection in the Institut royal des Sciences naturelles de Belgique (Brussels), under general inventory number IG 26857. They have been collected in a quarry south of the town of Saint-Nicolas-de-Port (actually on the territory of Rosières-aux-Salines). A location map and a synthetic section have been published by Laugier (1971). There is also a detailed section in Al Khatib's thesis (1976).

The Saint-Nicolas-de-Port quarry shows a succession of sand, sandstone and clay beds, with intercalated bone-beds. The main bone-bed is at the base of the section, and most of the fossils described in the present paper come from it. Al Khatib (1976) has found that the sands show some granulometric characters of river and beach deposits, and has interpreted the Saint-Nicolas-de-Port sediments as deposited in very shallow marine conditions, very close to the continent.

SYSTEMATIC DESCRIPTION

Class Amphibia
Order Temnospondyli
Suborder Plagiosauria
Family Plagiosauridae
cf. Plagiosaurus

The Plagiosauridae are represented by abundant remains (Figure 1, A to F). More than 50 vertebral centra are present in the collection; they are nearly cylindrical, with concave anterior and posterior articular faces. Their length varies from 5 to 16 mm. These fossils are usually much worn, and show few morphological details. The dorsal face is usually flattened, and sometimes shows a median groove bordered by the insertion surfaces for the neural arch (which has been lost in all specimens). On some centra, one or two pairs of articular facets, in a dorsolateral position, can be seen; ribs articulated on them. These vertebral centra show the typical morphology of plagiosaurid intercentra; they strongly resemble, for instance, those found in 1917 during military excavations in the Keuper of Bénamont Wood (near Lunéville, eastern France) and described by Piveteau in 1928. There are also many resemblances with the abundant plagiosaurid intercentra found in the Upper Ladinian Kupferzell locality, in Baden-Württemberg (Wild, 1980), and kept in the Staatliches Museum für Naturkunde in Stuttgart.

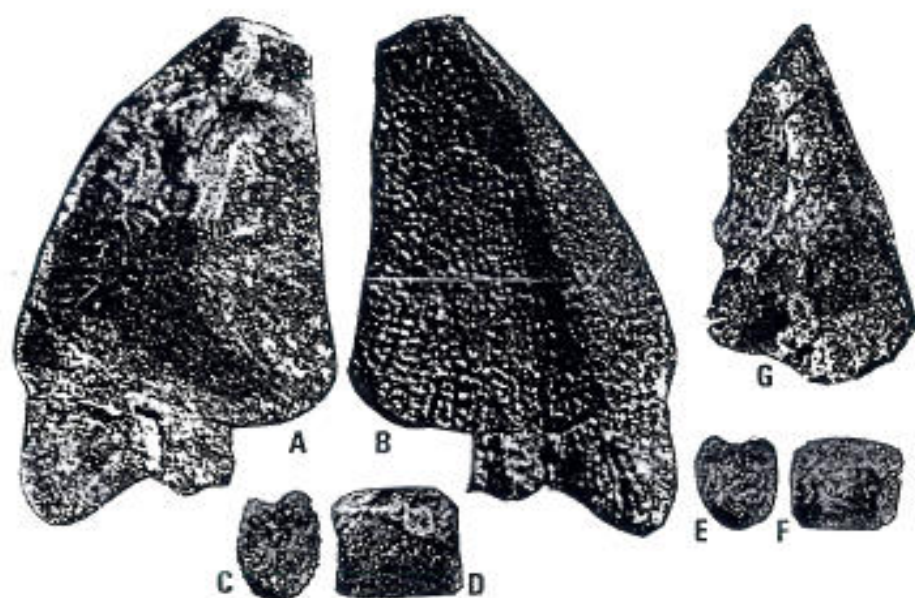


FIGURE 1 Amphibian remains from the late Triassic of Saint-Nicolas-de-Port (Meurthe-et-Moselle, eastern France). A, B: left clavicle of cf. *Plagiosaurus*, a2616, in dorsal (A) and ventral (B) views; C, D, E, F: plagiosaurid intercentra a2614 (C, D) and A (2615) in anterior (C, E) and left lateral (D, F) views; G: fragment of the left palatine of a capitosaurid (?) a2617. All specimens $\times 1$. Collection: Institut royal des Sciences naturelles de Belgique (Brussels). Photographs by C. Abrial.

An incomplete clavicle (a2616, Figure 1, A-B) from Saint-Nicolas-de-Port also belongs to a plagiosaurid. Its posterior and anteriormost parts are broken. The ventral and lateral faces of this bone show a dense ornamentation of rounded tubercles changing into irregular ridges toward the ends of the bone. The ventral and lateral faces meet at nearly right angle anteriorly; this angle becomes more open posteriorly. The lateral face, as preserved, is shaped like a right-angled triangle. The dorsal face shows, in its anterolateral part, a strong ventrally directed process, more or less perpendicular to the ventral "plate" of the bone; posteriorly to this process, there is a vast triangular surface limited by the lateral edge and by an oblique ridge, which meet at the base of the process. Farther forward, and medially, there is another triangular surface, with its summit pointing toward the process; it seems to be the articular surface for the lateral process of the interclavicle. The most anteromedial part of the bone is broken. This bone is remarkably similar to the clavicle of *Plagiosaurus depressus* from the Keuper of Halberstadt figured by Jaekel (1914, Figure 29). As shown by Nilsson (1937), Jaekel's interpretation of the shoulder girdle of the Plagiosauridae is probably erroneous, because Jaekel mistook the anterior part for the posterior part. According to Nilsson's interpretation, the specimen from Saint-Nicolas-de-Port would be a left clavicle. A detailed comparison with the various Plagiosauridae known from the middle and upper Triassic is not very easy, because the clavicle has not always been described in much detail. By its general shape, the specimen from Saint-Nicolas-de-Port is reminiscent of the plagiosaurid clavicles from Kupferzell, which have been referred to *Plagiosernum* Fraas (Wild, 1980), but it differs from them by the implantation of the dorsal process.

which is higher, more upright and narrower in the form from Saint-Nicolas-de-Port. Comparison with *Gerrothorax rhaeticus*, described by Nilsson (1937, 1946) from the "Rhaetian" of Sweden, is more difficult, because the clavicles of this animal are not completely preserved. Nevertheless, Nilsson (1937) remarks that in *Gerrothorax rhaeticus* the posterior part of the clavicle is definitely weaker than in *Plagiosaurus depressus*, with a different outline. As far as can be ascertained, the clavicle from Saint-Nicolas-de-Port shows a well developed posterior part, as in *Plagiosaurus depressus* from Halberstadt. Of all described plagiosaurid clavicles, that of *Plagiosaurus depressus* resembles the Saint-Nicolas-de-Port specimen most closely, as far as morphology and proportions are concerned. This is the reason why we refer the specimen to the genus *Plagiosaurus*.

A few specimens bearing the same ornamentation as the clavicle described above can also be referred to plagiosaurids. One of them, very fragmentary, could be a skull bone, the others probably are dermal plates. The Plagiosauridae are known to have been covered with an armour of ornamented dermal plates (Huene, 1922a; Nilsson, 1937, 1946; Wild, 1978, 1980). One of the plates from Saint-Nicolas-de-Port, elongated and with a concavo-convex cross-section, seems to be a ventrolateral plate of the type described by Nilsson (1946) in *Gerrothorax rhaeticus*; these plates formed a longitudinal row along the body.

In the absence of skull remains, an identification of the plagiosaurid material is not easy. The morphology of the vertebrae and dermal plates does not allow a safe identification at the generic level. The plagiosaurid material from Saint-Nicolas-de-Port is thus referred to *Plagiosaurus* on the basis of the clavicle.

Suborder Stereospondyli
Superfamily Capitosauroidae
Family Capitosauridae?

The locality has also yielded a skull bone fragment of a large amphibian, which is apparently a fragment of a left palatine. Its morphology indicates that it is unlikely to belong to a plagiosaurid. The specimen (a2617, Figure 1G) shows a flat, smooth dorsal surface, and a lateral surface at right angles with the dorsal surface. The lateral surface is covered with irregular sinuous grooves, and seems to be a sutural surface for the maxilla. The ventral face exhibits strong reliefs. In the anterior region, there is the posterolateral part of a vast rounded depression, about 1 cm deep, which may be a pit for the insertion of a very large tooth ("palatine tusk pit" of Welles and Cosgriff, 1965). Just behind it, there is a broken tooth, the section of which shows a distinct labyrinthodont structure; what remains of this tooth indicates a diameter of at least 1 cm at the level of the break. Posterolaterally to this tooth, there was a row of smaller labyrinthodont teeth; two of them, represented only by their insertion areas, are visible, with diameters which decrease toward the rear.

This bone fragment obviously does not allow a very accurate identification. It does not resemble the palatine of the Plagiosauridae, but is rather reminiscent of that of some capitosaurids, such as *Cyclotosaurus* and *Mastodonsaurus*, in which there is, behind the choana, a pit containing a very large tooth, followed by a tooth row of variable length, in which the teeth become smaller toward the rear. In the Metoposauridae, there is also a pair of large teeth on the palatine, followed by a row of smaller teeth, but this tooth row is more lateral than posterior relative to the choana. The specimen from Saint-Nicolas-de-Port seems to be more reminiscent of the capitosaurid condition. Its fragmentary state does not warrant an identification at the generic level, and we therefore refer to it as an indeterminate capitosaurid.

Class Reptilia
 Subclass Archosauria
 Order Thecodontia
 Family Phytosauridae
 Genus *Rutiodon* Emmons
Rutiodon ruetimeyeri (Huene, 1911)

Phytosaurs are the most abundant reptiles in the collection, but they are represented almost solely by isolated teeth. These are often reduced to their crowns, the hollow, thin-walled root being damaged or completely destroyed. Among these phytosaur teeth, three main morphological types can be distinguished.

- large laterally compressed teeth with a somewhat blade-like outline in lateral and medial view (Figure 2, G to L). 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 one and a posterior one). This type of teeth is common in the posterior part of the jaws of phytosaurs with a robust skull, such as the European *Nicrosaurus kapffi* (Meyer, 1861).
- very strong recurved teeth, with an almost circular cross-section and serrated carinae; their enamel is sometimes more or less fluted (Figure 2, C to F).
- 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 toward the apex (Figure 2, A-B).

The occurrence of these three types of teeth in the locality does not necessarily indicate that three distinct types of phytosaurs are represented there. A more or less marked heterodonty is usually observable in these animals. Moreover, among the phytosaur teeth found at Saint-Nicolas-de-Port, there are specimens of intermediate shape showing a transition from one type to another. In the absence of more complete evidence, it is thus simpler to admit that a single type of phytosaur with a heterodont dentition is present at Saint-Nicolas-de-Port. Comparison with complete phytosaur skulls shows that compressed and serrated teeth come from the posterior part of the jaws, and long slender teeth from the anterior part, the teeth with a subcircular cross-section and serrated carinae occupying an intermediate position. This condition can notably be observed in *Nicrosaurus kapffi*, from the Stubensandstein (middle Keuper) of Württemberg. However, in this form there are hardly any fluted teeth. Fluted teeth have been described by Huene (1922) in specimens from Salzgitter and Halberstadt (in central Germany) and Niederschönthal (in Switzerland), which he called *Angistorhinopsis ruetimeyeri*, and which Gregory (1962) and Westphal (1976) place in the genus *Rutiodon*. The description given by Huene (1922) of the teeth of *Rutiodon ruetimeyeri* perfectly fits the teeth from Saint-Nicolas-de-Port. This is the reason why we think this species is present in the locality.

A large bone fragment, 12.5 cm long and with a roughly triangular cross-section, may also be referred to a phytosaur (Figure 2 R). One of its faces, probably the medial face, is covered with fine striations indicating a sutural surface, which are oblique relative to the longitudinal axis of the specimen. The lateral face, which makes an acute angle with the medial face, bears deep irregular grooves. The third face corresponds to a break. The medial surface is strongly reminiscent of median sutural surfaces between the premaxillae of phytosaurs. The specimen may thus be a fragment of the premaxilla of a large phytosaur with a robust snout. In lateral view, the dorsal edge of the bone rises sharply enough at about mid-length. This would

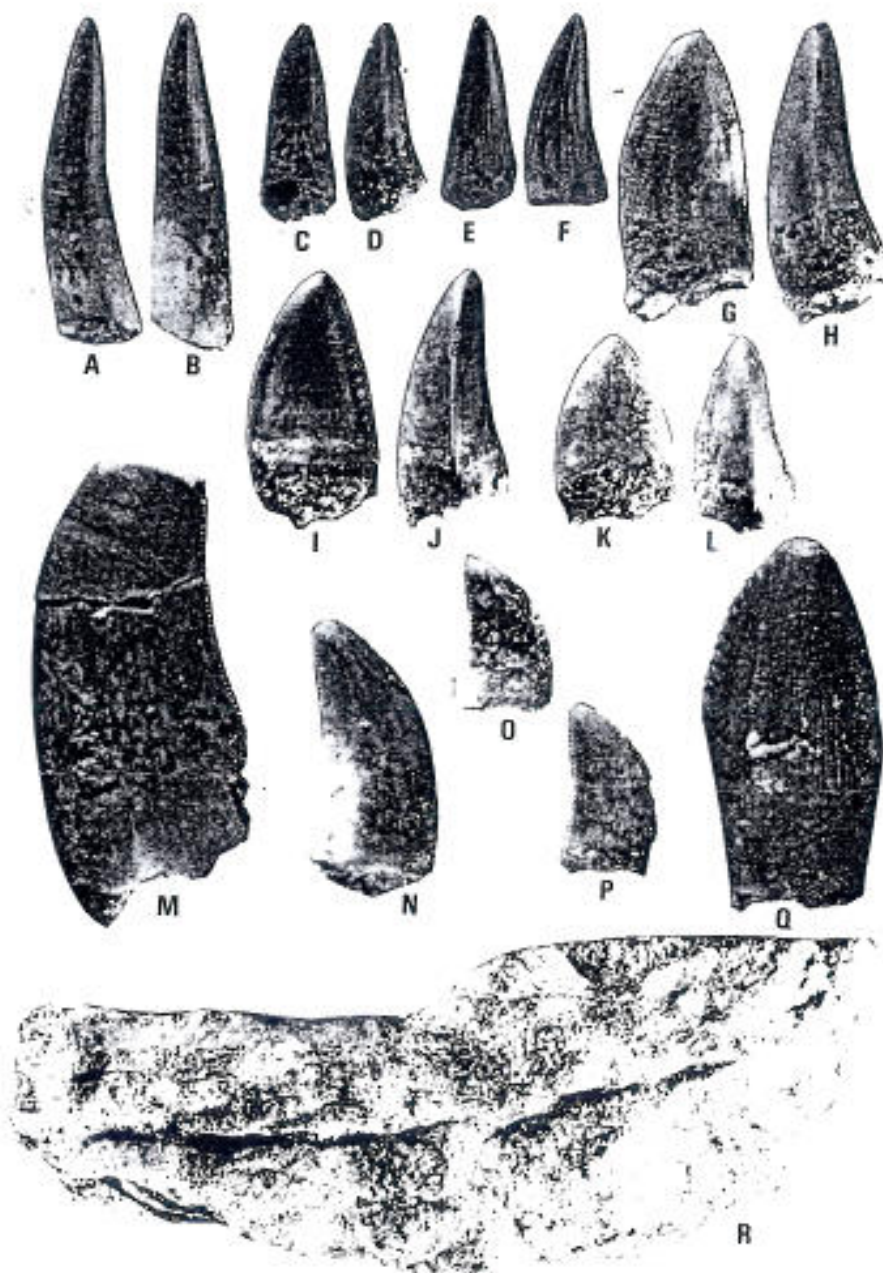


FIGURE 2 Reptile remains from the late Triassic of Saint-Nicolas-de-Port (Meurthe-et-Moselle, eastern France). A to L: teeth of the phytosaur *Ruetimeyeria* (Huene), from the anterior (A, B: a2618), middle (C, D: a2619, E, F: a2620), and posterior (G, H: a2621, I, J: a2622, K, L: a2623) part of the jaw; M to P: coelurosaur teeth (Procompsognathidae) a2624 (M), a2625 (N), a2626 (O) and a2627 (P); Q: tooth of *Plateosaurus* sp., a2628; R: fragment of the left premaxilla of a phytosaur, a2628, in lateral view. A to L and R: $\times 1$; M to O: $\times 3$. Collection: Institut royal des Sciences naturelles de Belgique. Photographs by C. Abrial.

indi
and
who
riet.
elev
Tl
plate
radi
anin

Di
de-Pe
cylinc
anter
the or
poste
wide)
The a
separ
depre
face.
This
in Pla
famous
Stuttg
have b
the iso
also yie
too inc
used th

A las
carnivo
ved tow
carina i
the crow
the root
long; on
A pre
type occ
saurs. S

indicate a rostrum fairly low in its anterior part, but rising sharply more posteriorly, and therefore different from that of *Nicrosaurus kapffi*, which is elevated along its whole length. The Saint-Nicolas-de-Port specimen is more reminiscent of *Rutiodon ruetimeyeri*, although in the latter, as reconstructed by Huene (1922b), the posterior elevation is more gradual.

The locality has also yielded a few incomplete and water-worn phytosaur dermal plates. They show an ornamentation consisting of wide grooves with a more or less radial arrangement. The considerable thickness of these plates indicates large animals, which is in agreement with the size of the teeth.

Order Saurischia
Suborder Sauropodomorpha
 infraorder Prosauropoda
 Family Plateosauridae
 Genus *Plateosaurus* Meyer
 Plateosaurus sp.

Dinosaur teeth are definitely less abundant than phytosaur teeth at Saint-Nicolas-de-Port. Among them, several are characteristically leaf-shaped (Figure 2 Q). The cylindrical root is usually broken. The crown is clearly separated from it by its greater anteroposterior development and by its marked lateral compression. In lateral view, the outline of the crown is triangular, with a slightly rounded apex. The anterior and posterior edges form carinae which bear coarse serrations (each one is about 0.5 mm wide); these are not very numerous, and oblique relative to the axis of the crown. The anterior carina is usually slightly shorter than the posterior one. The carinae are separated from the center of the lateral and medial faces by faintly marked depressions; each face thus shows a median convexity, better defined on the lateral face. These teeth are not very large (height of the crown: about 1 cm).

This dental morphology is frequent among prosauropod dinosaurs, and especially in *Plateosaurus*, as confirmed by comparison with skulls of this dinosaur from the famous Trossingen locality kept in the Staatliches Museum für Naturkunde in Stuttgart. As many species of *Plateosaurus* showing a very similar dental morphology have been described from the Upper Keuper of Europe, it is not possible to identify the isolated teeth from Saint-Nicolas-de-Port at the species level. The locality has also yielded a jaw fragment containing a tooth of the type described above, but it is too incomplete and poorly preserved to be of any systematic use. We have therefore used the designation *Plateosaurus* sp.

Suborder Theropoda
 Infraorder Coelurosauria
 Family Procompsognathidae
 Procompsognathidae indet.

A last group of teeth found at Saint-Nicolas-de-Port indicates the presence of small carnivorous dinosaurs. They are small, laterally compressed, pointed teeth, recurved toward the rear, with serrated carinae (Figure 2, M to P). While the posterior carina is well developed, with distinct serrations, along almost the whole height of the crown, the anterior carina is distinct near the apex and becomes fainter toward the root, being replaced by a rounded edge. Several of these teeth are less than 1 cm long; one of them, however, is 22 mm long, although its apex is broken (Figure 2 M).

A precise identification is difficult, because in the late Triassic teeth of this general type occurred in several groups, notably primitive crocodylians and theropod dinosaurs. *Saltoposuchus longipes* Huene, 1921, from the Stubensandstein (middle

Keuper of Germany) and *Terrestrisuchus gracilis* Crush, 1984, from Welsh fissure fillings, considered by Crush (1984) as primitive crocodylians (suborder Sphenosuchia), both possess compressed teeth with serrated carinae. However, they also occur in coelurosaurs such as *Halticosaurus orbitoangulatus* Huene, 1932 and *Procompsognathus triassicus* Fraas, 1913, both from the Stubensandstein of Pfaffenhofen, in Württemberg (Huene, 1921, 1932). The marked rearward curvature of the teeth from Saint-Nicolas-de-Port is apparently more reminiscent of these coelurosaurs (and especially of the posterior teeth of *Procompsognathus*) than of the Sphenosuchia. We therefore refer them to indeterminate procompsognathids.

The list of the amphibians and reptiles hitherto identified from Saint-Nicolas-de-Port is thus the following:

Amphibia:

cf. *Plagiosaurus*
Capitosauridae?

Reptilia:

Rutiodon ruetimeyeri
Plateosaurus sp.
indeterminate Procompsognathidae

THE AGE OF THE SAINT-NICOLAS-DE-PORT LOCALITY

The vertebrate-bearing beds of Saint-Nicolas-de-Port are usually referred to the stratigraphic unit locally known as "Grès à *Avicula contorta*" (or "Grès infra-liassique"), which is itself considered as belonging to the "Rhétien inférieur" (the "Rhétien supérieur" being represented in this part of eastern France by the "Argiles de Levallois"). As pointed out by Schuurman (1977, p. 160),

the terms "Rhétien inférieur" (Lower Rhaetian) and "Rhétien supérieur" (Upper Rhaetian) have been applied on the basis of the local stratigraphy and have no chronostratigraphical significance.

Moreover, the problem is further complicated by the fact that at Saint-Nicolas-de-Port the fossiliferous beds have not yielded the supposedly characteristic *Rhaetavícula contorta*, and are not overlain by the Argiles de Levallois (Sigogneau-Russell, 1983a). Nevertheless, Sigogneau-Russell (1983a, 1983b) has argued that the Saint-Nicolas-de-Port vertebrate fauna is indeed of Rhaetian age, for local stratigraphic reasons, and because the Grès à *Avicula contorta* is referred to the early to middle Rhaetian on palynological evidence by Schuurman (1977).

However, this age assignment is not fully satisfying. As noted by Clemens (1980, p. 65) in his review of "Rhaeto-Liassic" mammals from Germany and Switzerland, "how the time of deposition of the bonebeds at Saint-Nicolas-de-Port relates to that of the Swiss and German bonebeds remains unclear." Part of this obscurity is undoubtedly due to terminological problems linked to the use of the term "Rhaetian," and it therefore seems useful to discuss briefly the status and significance of the Rhaetian, before we attempt to place the Saint-Nicolas-de-Port amphibian and reptile assemblage in the succession of late Triassic vertebrate faunas.

Although it has long been placed at the base of the Jurassic system by many stratigraphers (especially in France), the Rhaetian stage was introduced in 1861 by Gumbel to designate the uppermost Triassic, with the Kössener Schichten of the northern Alps as stratotype. In recent years, however, the significance of the term "Rhaetian" has been questioned by an increasing number of stratigraphers, because

it has been found that the so-called Rhaetian ammonoid fauna cannot properly be distinguished from that of the Upper Norian (see discussion in Wiedmann *et al.*, 1979; Tozer, 1984). According to Tozer (1984, p. 14), it thus appears that "the scope of the Norian, as it has been used throughout the 20th century, almost certainly overlaps that of stratotype Rhaetian," which leads to the conclusion that "in view of their probable overlap, Upper Norian and Rhaetian are best treated as synonymous substages." At the moment, there is no general agreement as to the status of the Rhaetian: the IUGS Subcommittee on Trias Stratigraphy has favoured the retention of the Rhaetian stage in an enlarged form including the previous Sevatian, or Upper Norian (Wiedmann *et al.*, 1979), but several authors think the Rhaetian stage should be altogether abandoned (Tozer, 1979, 1984; Palmer, 1983), although the term "Rhaetian" may still be used to designate a marly facies of the uppermost Triassic (Fabricius, 1974). Although attempts have been made to redefine the Rhaetian on a palynological basis (Visscher and Schuurman, 1979), Fisher and Dunay (1981) have concluded that it is not possible to give "a palynological identity to the redefined Rhaetian stage" (p. 130), and that "the palynological evidence does not appear to support any conception of an 'expanded' Rhaetian, but it is consistent with Tozer's (1979) proposal" (p. 133).

In the case of the Germanic Realm (to which Saint-Nicolas-de-Port belongs), the situation is further complicated by the difficulty of correlation with the Alpine Realm. The IUGS Subcommittee has rejected the use of the term Rhaetian in the Germanic Realm, because the so-called Rhaetian of the Germanic Realm "can by no means be correlated with the Alpine Realm" (Wiedmann *et al.*, 1979, p. 133). The Subcommittee has recommended that "Upper Keuper" or "Rhaetkeuper" should be used instead (Richter-Bernburg, 1979). Consequently, recent stratigraphic subdivisions of the German Upper Triassic (Gwinner, 1980) no longer mention the Rhaetian, but use the term "Oberer Keuper" instead. Incidentally, this decision strongly restricts the usefulness of the Rhaetian as a standard stratigraphic unit.

Because of the many uncertainties concerning the status and significance of the Rhaetian, especially in the Germanic Realm, it seems that to assign the Saint-Nicolas-de-Port fauna to the Rhaetian on the basis of local lithostratigraphic usage is misleading and does not actually tell much about the place of this faunal assemblage in the succession of late Triassic faunas.

We have tried to use a different approach, based on a comparison of the amphibians and reptiles from Saint-Nicolas-de-Port with those from better known localities in the Germanic Realm. At the moment, the mammal remains from Saint-Nicolas-de-Port do not seem to be of much use for correlation purposes because of uncertainties concerning the age of other continental European Triassic mammal localities, such as the bone-beds of southwestern Germany and northern Switzerland (see review in Clemens, 1980), or the newly discovered Habay-la-Vieille haramiyid locality in Belgium (Wouters *et al.*, 1984). These localities are usually referred to the Rhaetian, and the correlation problems they pose are rather similar to that of Saint-Nicolas-de-Port. As to the vertebrate-bearing fissure fillings of Wales and western England, their ages are still a matter of controversy. It may be mentioned here that the recent discovery of a therian mammal in the Emborough fissure has thrown serious doubt on the supposed fundamental distinction between the faunas of fissures filled before and after the "Rhaetic" transgression (Fraser *et al.*, 1985; Fraser, this volume). Generally speaking, it seems very difficult at the moment to define a characteristic Rhaetian vertebrate fauna.

A first result of our comparison of the Saint-Nicolas-de-Port amphibians and reptiles with faunal assemblages from the Keuper of Germany is that the Saint-

Nicolas-de-Port fauna is what may be called a "classical" late Triassic fauna, with stegocephalians, phytosaurs and *Plateosaurus*. In Germany, such assemblages are known from the Stubensandstein and the Knollenmergel. According to Benton (1984), dinosaurs do not appear there below the Unterer Stubensandstein, become more abundant in the Mittlerer Stubensandstein, and finally come to "dominate" the faunas in the Oberer Stubensandstein and the Knollenmergel. The occurrence of plateosaurs and procompsognathids at Saint-Nicolas-de-Port thus indicates that the locality is probably not older than the Unterer Stubensandstein, which itself belongs to the upper part of the Middle Keuper (Gwinner, 1980), and may be correlated, with some uncertainty, with the Middle Norian (Benton, 1984). Moreover, the occurrence of the phytosaur *Rutiodon ruetimeyeri* at Saint-Nicolas-de-Port suggests that the locality is more recent than the Stubensandstein, since this species does not seem to be present among the abundant phytosaur remains from that unit, but is known from younger levels. *Rutiodon ruetimeyeri*, being the form identified with the greatest precision in our material from Saint-Nicolas-de-Port, is of special importance for correlation purposes. It has been reported from levels referred to the "Rhät" in central Germany (Salzgitter) and Switzerland (Niederschönthal), and is also known to occur at Halberstadt in central Germany (now in the German Democratic Republic). Although Gregory (1969) and Westphal (1976) have referred the Halberstadt finds of *Rutiodon ruetimeyeri* to the "Rhät," following Huene's original age assignment, it does seem that the phytosaur remains from Halberstadt actually come from beds now considered as equivalent to the Knollenmergel.

In fact, the whole assemblage of amphibians and reptiles from Saint-Nicolas-de-Port shows close resemblances with the fauna from the famous Baerecke quarry at Halberstadt (see Jaekel, 1914; Kuhn, 1939). In this quarry, fossil vertebrates occur in several levels of the section, which have been listed and numbered by Kuhn (1939). Kuhn's section comprises 29 levels, numbered from top to bottom. Fossil vertebrates also found at Saint-Nicolas-de-Port occur in levels 15 to 20; the closest resemblances seem to be with bed 18, a blue clay which has yielded *Plateosaurus*, *Halticosaurus*, phytosaurs and plagiosaurids, as well as turtles and metoposaurids. The phytosaur *Rutiodon ruetimeyeri* is recorded by Kuhn (1939) from bed 20. According to Kuhn (1939), the beds below level 16 correspond to the Knollenmergel, while those above it are referred to the "Rät," but the distinction is only based on the occurrence of more massive sandstone beds from level 16 upward, and may be of doubtful significance. In any case, there does not seem to be an important faunal change between the beds referred to the Knollenmergel and those referred to the Rät. It seems to be widely accepted today that the *Plateosaurus* beds at Halberstadt are indeed the equivalent of the Knollenmergel, and that they belong to the uppermost Middle Keuper (Hahn, 1973; Clemens *et al.*, 1979). Interestingly, they have yielded a haramiyid tooth (Hahn, 1973), which may be an additional resemblance with Saint-Nicolas-de-Port.

The available palaeontological evidence therefore suggests that the vertebrate fauna from Saint-Nicolas-de-Port is of roughly the same age as that from the *Plateosaurus* beds at Halberstadt. However, it must be admitted that little is known about the stratigraphic range of this type of fauna, because latest Triassic and earliest Jurassic continental vertebrate localities are still not very abundant in Europe. One cannot exclude the possibility that the vertebrate fauna of the Upper Keuper was similar to that of the uppermost Middle Keuper. However, the presence of a common species of phytosaur, *Rutiodon ruetimeyeri*, in the *Plateosaurus* beds of Halberstadt and at Saint-Nicolas-de-Port suggests that the age difference between these localities cannot be very great, because as shown by Gregory (1969), phyto-

sauers have evolved rapidly in the late Triassic, and phytosaur species are usually short-lived (which makes them useful for correlation purposes).

To sum up, it seems likely that the Saint-Nicolas-de-Port vertebrate fauna corresponds to the top of the Middle Keuper. Because of the above-mentioned correlation problems, it is of course more difficult to place it in the standard, marine-based, stratigraphic scale. If we accept that the "Rhaetian" is the equivalent of the Upper Norian, it seems that the Saint-Nicolas-de-Port fauna should be placed close to the boundary between the Middle Norian and the Upper Norian.

STRATIGRAPHIC CONCLUSIONS

1) Previous attributions of the Saint-Nicolas-de-Port vertebrate faunal assemblage to the Rhaetian are not satisfying, because the Rhaetian as a stage is of doubtful significance, and should not be used in the Germanic Realm.

2) Comparison of the Saint-Nicolas-de-Port amphibians and reptiles with those from other late Triassic vertebrate localities in the Germanic Realm reveals close similarities with the assemblage from the *Plateosaurus* beds of Halberstadt, which are referred to the uppermost Middle Keuper.

3) A provisional correlation with the standard marine stratigraphic scale suggests that the Saint-Nicolas-de-Port fauna may be placed at the top of the Middle Norian (the Rhaetian being considered as the equivalent of the Upper Norian).

4) Much correlation work remains to be done before the latest Triassic vertebrate localities of Europe can safely be placed in their proper stratigraphic succession. The establishment of a biostratigraphic scale based on vertebrates (including early mammals) for this time interval seems to be an essential step toward the solution of many of the remaining problems.

ACKNOWLEDGEMENTS

We thank Professor Paul Sartelet (Brussels) for the loan of the Saint-Nicolas-de-Port amphibian and reptile material after it was acquired by the Institut royal des Sciences naturelles de Belgique.

Comparison with material from the Keuper of Germany has been made with the kind permission of Dr. Rupert Wild (Stuttgart) and Professor Frank Westphal (Tübingen).

REFERENCES

- Al Khatib, R. (1976). *Le Rhénan de la bordure orientale du Bassin de Paris et le "Calcaire à Gryphes" de la région de Nancy. Etude pétrographique et sédimentologique*. Thesis, Université de Nancy, 278 pp.
- Benton, M. J. (1984). Fossil reptiles of the German Late Triassic and the origin of the dinosaurs. In: Reif, W. E. and Westphal, F., *Third Symposium on Mesozoic Terrestrial Ecosystems*, Attempto-Verlag, Tübingen, 13-18.
- Clemens, W. A. (1980). Rhaeto-Liassic mammals from Switzerland and West Germany. *Zitteliana*, 5, 51-92.
- Clemens, W. A., J. A. Lillegraven, E. H. Lindsay and G. G. Simpson (1979). Where, when, and what—A survey of known Mesozoic mammal distribution. In: Lillegraven, J. A., Kielan-Jaworowska, Z. and Clemens, W. A. *Mesozoic Mammals*, University of California Press, Berkeley, Los Angeles, London, 7-58.
- Corroy, G. (1928). Les Vertébrés du Trias de Lorraine et le Trias lorrain. *Ann. Paléont.*, 17, 11-56.
- Crush, P. J. (1984). A late upper Triassic sphenosuchid crocodylian from Wales. *Palaeontology*, 27, 131-157.

Sédimentologie du Rhétien de Meuse
(1979) Science de la Terre
(Nouveaux Annales)

- Fabricius, F. (1974). Die stratigraphische Stellung der Rhät-Fazies. *Schriften. erdwiss. Komm. österr. Akad. Wiss.* 2, 87-94.
- Fisher, M. J. and R. E. Dunay (1981). Palynology and the Triassic/Jurassic boundary. *Rev. Palaeobot. Palynol.* 34, 129-135.
- Fraser, N. C., G. M. Walkden and V. Stewart (1985). The first pre-Rhaetic therian mammal. *Nature* 314, 161-163.
- Gregory, J. T. (1962). The genera of phytosaurs. *Am. J. Sci.* 260, 652-690.
- Gregory, J. T. (1969). Evolution und interkontinentale Beziehungen der Phytosauria (Reptilia). *Paläont. Z.* 43(1/2), 37-51.
- Gümbel, C. W. (1861). *Geognostische Beschreibung des bayerischen Alpengebirges und seines Vorlandes*. Perthes, Gotha, 950 pp.
- Gwinner, M. P. (1980). Eine einheitliche Gliederung des Keupers (Germanische Trias) in Süddeutschland. *Neues Jb. Geol. Paläont. Mh.* 4, 229-234.
- Hahn, G. (1973). Neue Zähne von Haramiyiden aus der deutschen Ober-Trias und ihre Beziehungen zu den Multituberculaten. *Palaeontographica*, A 142, 1-15.
- Huene, F. von (1921). Neue Pseudosuchia und Coelurosaurier aus dem Württembergischen Keuper. *Acta zool., Stockh.* 2, 329-403.
- Huene, F. von (1922a). Beiträge zur Kenntnis der Organisation einiger Stegocephalen der schwäbischen Trias. *Acta zool., Stockh.* 3, 397-460.
- Huene, F. von (1922b). Neue Beiträge zur Kenntnis der Parasuchia. *Jb. preuss. geol. Landesanst.* 42, 59-160.
- Huene, F. von (1932). Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monogr. Geol. Paläont.* 1(4), 1-368.
- Jaekel, O. (1914). Über die Wirbeltierfunde in der oberen Trias von Halberstadt. *Paläont. Z.* 1, 155-215.
- Kuhn, O. (1939). Beiträge zur Keuperfauna von Halberstadt. *Paläont. Z.* 21, 258-286.
- Laugier, R. (1971). Le Lias inférieur et moyen du Nord-Est de la France. *Sci. Terre Mém.* 21, 1-300.
- Levallois, J. (1851). Aperçu de la constitution géologique du département de la Meurthe. *Annls Mines* 19, 635-667.
- Levallois, J. (1862). Aperçu de la constitution géologique du département de la Meurthe. *Mém. Acad. Stanislas*, 246-301.
- XX Martin, M., D. Sigogneau-Russell, P. Couppez and G. Wouters (1981). Les Cératodontidés (Dipnoi) du Rhétien de Saint-Nicolas-de-Port (Meurthe-et-Moselle). *Geobios* 14(6), 773-791.
- Nilsson, T. (1937). Ein Plagiosauride aus dem Rhät Schonen. *Meddel. Lunds geol. minor. Instn.* 72, 1-75.
- > Nilsson, T. (1946). A new find of *Gerrhosaurus rhaeticus*, a plagiosaurid from the Rhaetic of Scania. *Acta Univ. Lund* 2(42), 1-42.
- Palmer, A. (1983). The Decade of North American Geology 1983 geologic time scale. *Geology* 11, 503-504.
- XX Piveteau, J. (1928). Etudes sur quelques Amphibiens et Reptiles fossiles. Un Amphibien stégocéphale du Trias de Lunéville. *Annls Paléont.* 17, 23-29.
- Richter-Bernburg, G. (1979). Bemerkungen zum Begriff Rhaet. *Newsl. Stratigr.* 8(2), 151-152.
- X Russell, D., D. Russell and G. Wouters (1976). Une dent d'aspect mammalien en provenance du Rhétien français. *Geobios*, 9(4), 377-392.
- Schuurman, W. M. L. (1977). Aspects of Late Triassic palynology. 2. Palynology of the "Grès et Schiste à *Avicula concolor*" and "Argiles de Levallois" (Rhaetic) of northeastern France and southern Luxembourg. *Rev. Palaeobot. Palynol.* 23(3), 159-253.
- X Sigogneau-Russell, D. (1978). Découverte de Mammifères rhétiens (Trias supérieur) dans l'est de la France. *C. r. hebdom. Séanc. Acad. Sci., Paris*, D287, 991-993.
- Sigogneau-Russell, D. (1983a). Caractéristiques de la faune mammalienne du Rhétien de Saint-Nicolas-de-Port (Meurthe-et-Moselle). *Bull. Inf. Géol. Bass. Paris* 20(2), 51-53.
- Sigogneau-Russell, D. (1983b). Nouveaux taxons de Mammifères rhétiens. *Acta palaeont. pol.* 28, 233-249.
- XX XX Sigogneau-Russell, D., H. Cappetta and P. Taquet (1979). Le gisement rhétien de Saint-Nicolas-de-Port et ses conditions de dépôt. *7e Réun. Ann. Sc. Terre*, 429.
- Tozer, E. T. (1979). Latest Triassic ammonoid faunas and biochronology, Western Canada. *Geol. Surv. Canada Paper* 79-1B, 127-135.
- Tozer, E. T. (1984). The Trias and its ammonoids: the evolution of a time scale. *Geol. Surv. Canada Misc. Rept.* 35, 1-171.
- Visscher, H. and W. M. L. Schuurman (1979). Palynology and the Rhaetic problem. *Newsl. Stratigr.* 8(2), 148-150.
- X Welles, S. P. and J. Cosgriff (1965). A revision of the labyrinthodont family Capitosauridae. *Univ. Calif. Publ. Geol. Sci.* 54, 1-148.

- Westphal, F. (1976). Phytosauria. *Handbuch der Paläoherpetologie*, Gustav Fischer Verlag, Stuttgart and New York 13, 99-120.
- Wiedmann, J., F. Fabricius, L. Krystyn, J. Reitner and M. Urlichs (1979). Über Umfang und Stellung des Rhaet. *Neuwl. Stränge*, 8(2), 133-148.
- Wild, R. (1978). Die Saurier von Kupferzell. Vorläufige Ergebnisse der Fossilgrabung beim Autobahnbau. *Württembergisch Franken*, 181-196.
- Wild, R. (1980). The fossil deposits of Kupferzell, Southwest Germany. *Mesozoic Vertebrate Life* 1, 15-18.
- Wouters, G., D. Sigogneau-Russell and J. C. Lepage (1984). Découverte d'une dent d'Haramiyidé (Mammalia) dans des niveaux rhétiens de la Gaume (en Lorraine belge). *Bull. Soc. Belg. Géol.* 93(4), 351-355.