

Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern France)

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ABSTRACT

Numerous isolated cynodont teeth have been collected from the Late Triassic of Saint-Nicolas-de-Port (north-eastern France). The material is very diversified and the following taxa are recognized: *Pseudotriciconodon wildi* Hahn, Lepage *et* Wouters, 1984; *Tricuspes tuebingensis* E. v. Huene, 1933; *Tricuspes sigogneauae* Hahn, Hahn *et* Godefroit, 1994; *Tricuspes tapeinodon* n.sp.; *Meurthodon gallicus* Sigogneau-Russell *et* Hahn, 1994; *Hahnia obliqua* n.g., n.sp.; *Gaumia longiradicata* Hahn, Wild *et* Wouters, 1987; *Lepagia gaumensis*, Hahn, Wild *et* Wouters, 1987; *Maubeugia lotharingica* n.g., n.sp.; *Rosieria delstatei* n.g., n.sp. and aff. *Microscalenodon*. This cynodont fauna mainly includes small insectivorous forms, more particularly represented by Dromatheriidae; tiny herbivorous are represented by rare dwarf Traversodontidae. The study of the palaeogeographical and stratigraphic distribution of the Late Triassic to Early Jurassic cynodonts indicates that the fauna discovered in Saint-Nicolas-de-Port is characteristic of the Late Norian-Rhaetian period and is actually the most representative of this period for Western Europe. Granulometric analysis of the bone-bed reveals that they accumulated in a nearshore shallow marine environment.

KEY WORDS

Cynodontia,
Late Triassic,
Saint-Nicolas-de-Port,
dental morphology.

RÉSUMÉ

De nombreuses dents isolées de cynodontes ont été découvertes dans le Trias supérieur de Saint-Nicolas-de-Port (nord-est de la France). Le matériel étudié est très diversifié et les taxa suivants sont représentés : *Pseudotricodon wildi* Hahn, Lepage et Wouters, 1984 ; *Tricuspes tuebingensis* E. v. Huene, 1933 ; *Tricuspes sigogneauae* Hahn, Hahn et Godefroit, 1994 ; *Tricuspes tapeinodon* n.sp. ; *Meurthodon gallicus* Sigogneau-Russell et Hahn, 1994 ; *Hahnia obliqua* n.g., n.sp. ; *Gaumia longiradicata* Hahn, Wild et Wouters, 1987 ; *Lepagia gaumensis*, Hahn, Wild et Wouters, 1987 ; *Maubeugia lotharingica* n.g., n.sp. ; *Rosieria delsatei* n.g., n.sp. et aff. *Microscalenodon*. La faune de cynodontes est surtout composée de petits insectivores, représentés notamment par les Dromatheriidae ; de minuscules herbivores, formes naines de la famille des Traversodontidae, sont également présents. L'étude de la répartition paléogéographique et stratigraphique des cynodontes du Trias supérieur et du Jurassique inférieur montre que la faune de Saint-Nicolas-de-Port est caractéristique de la période Norien supérieur-Rhétien ; c'est incontestablement la faune la plus représentative de cette période pour l'Europe de l'Ouest. L'analyse granulométrique du sédiment du *bone-bed* a révélé qu'il s'était accumulé dans un environnement marin proche du rivage.

MOTS CLÉS

Cynodontia,
Trias supérieur,
Saint-Nicolas-de-Port,
morphologie dentaire.

INTRODUCTION

In 1851, Levallois recorded fossil bones from the "grès infra-liasique" in the vicinity of Saint-Nicolas-de-Port (Meurthe-et-Moselle, north-eastern France; Fig. 1). In 1862, he mentioned the presence of a layer rich in fish and saurian remains to the south of this town. In 1928, Corroy mentioned Saint-Nicolas-de-Port among the most important upper Keuper localities of Lorraine.

In 1971, Laugier gave the stratigraphic log in a sand quarry opened in 1922, 2.5 km south-east of Saint-Nicolas-de-Port. This quarry falls partly within the boundary of the adjacent village Rosières-aux-Salines. He also documented the diversity and abundance of the fauna discovered there. The stratigraphy and the sedimentology of this section was studied in detail by Al Khatib (1976).

The first mammal-like tooth was discovered in 1975 by G. Wouters, a Belgian collector. This tooth was subsequently described by Russell *et al.* (1976). Since then, several tons of sediments have been washed and screened by G. Wouters, teams from the Muséum national d'Histoire naturelle (Paris) and from the Institut

royal des Sciences naturelles de Belgique and several amateur collectors. Attention was particularly paid to mammal teeth discovered in this quarry: these have been described in a series of papers by a team lead by D. Sigogneau-Russell (Sigogneau-Russell 1978, 1983a, 1983b, 1983c, 1989, 1990; Frank *et al.* 1984, 1986; Sigogneau-Russell *et al.* 1986; Hahn *et al.* 1989, 1991). Amphibian and reptile material has been described by Buffetaut & Wouters (1986), Cuny & Ramboer (1991) and Cuny (1993). Fish remains have been studied by Sigogneau-Russell *et al.* (1979), Martin *et al.* (1981) and Duffin (1993). Synthetic faunal lists are given by Cuny (1993) and Duffin (1993).

Until now, little work has been completed about the cynodont teeth discovered in Saint-Nicolas-de-Port, in spite of their abundance and their scientific interest. The double-rooted mammal-like tooth described by Russell *et al.* (1976) was subsequently named *Meurthodon gallicus* Sigogneau-Russell et Hahn, 1994 and referred to the family "Therioherpetidae" (Sigogneau-Russell & Hahn 1994). Hahn *et al.* (1994) described teeth of *Tricuspes sigogneauae* Hahn, Hahn et Godefroit, 1994 and reviewed the systematic position of the family Droma-

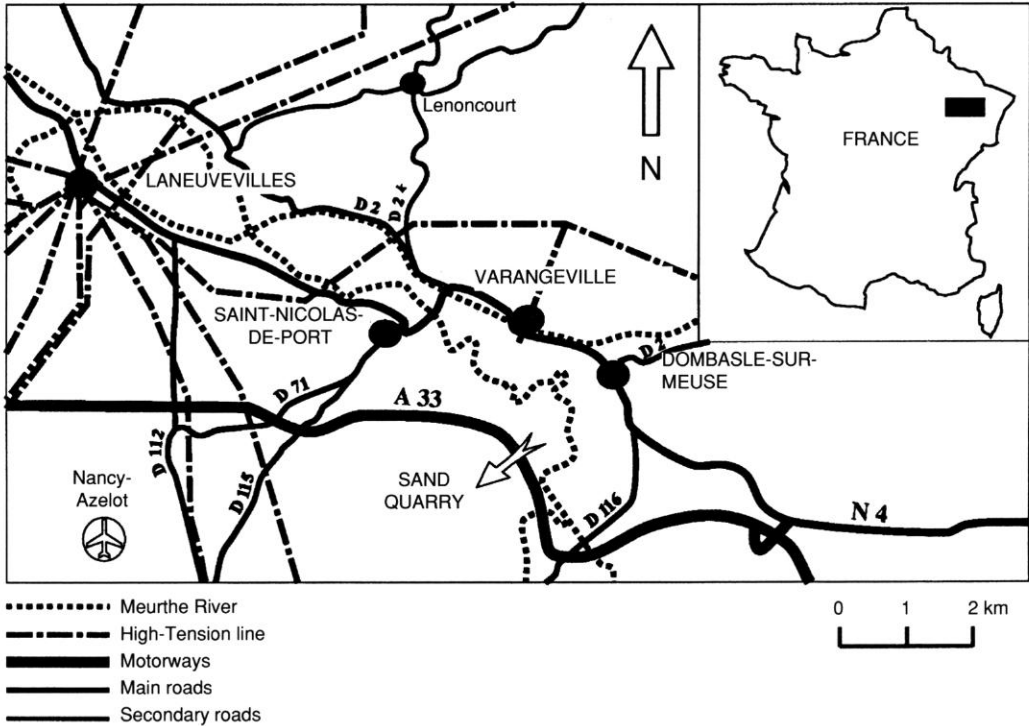


FIG. 1. — Locality sketch map for Saint-Nicolas-de-Port.

theriidae. The purpose of the present paper is to describe the cynodont remains discovered in Saint-Nicolas-de-Port, on the basis of the whole currently available material. The collections are housed in the Institut royal des Sciences naturelles de Belgique (Brussels: IRSNB) and in the Muséum national d'Histoire naturelle (Paris: MNHP). The fossils were collected by G. Wouters, D. Sigogneau-Russell, J.-C. Lepage, D. Delsate and P. Godefroit.

GEOLOGICAL SETTING

Laugier (1971, fig. 19) described the geological section exposed in the quarry of Saint-Nicolas-de-Port. The base of the section is formed by schistose marls of the Keuper. It is overlain by four sedimentary cycles. Bone-beds can be observed at the base of each cycle, followed by sands and sandstones, finally by clays. The bone-beds decrease in thickness through the sequence. The

basal conglomerate, above the Keuper marls, reaches a thickness of 1.05 m.

Unfortunately, the quarry is now being used as a city dump and the section described by Laugier cannot be observed any longer. Recent excavations and new sections demonstrate that the geological structure of the quarry is much more complex than described by Laugier. Most of the deposits are lenticular and show, therefore, important lateral variations. Furthermore, correlations between close sections are very difficult to establish.

Most of the vertebrate material discovered since 1975 at Saint-Nicolas-de-Port has been found in only one bone-bed. Figure 2 illustrates the geological section observed in this part of the quarry. The bone-bed is an intra-formational conglomerate which varies in thickness from 0.2 to 1 m. It is formed by coarse sands and small pebbles. It lays upon more than 7 m of alternating marly clays and sands. The bone-bed is capped by nearly 3 m of compact sandstones. Recent excavations exploited other bone-beds in other parts of

the quarry. The sampled sediments have still to be screened and sorted. It is interesting to notice that, nowadays, Keuper marls cannot be obser-

ved in any of the recent sections of the quarry. The age of the Saint-Nicolas-de-Port quarry has been much disputed. Lack of international agree-

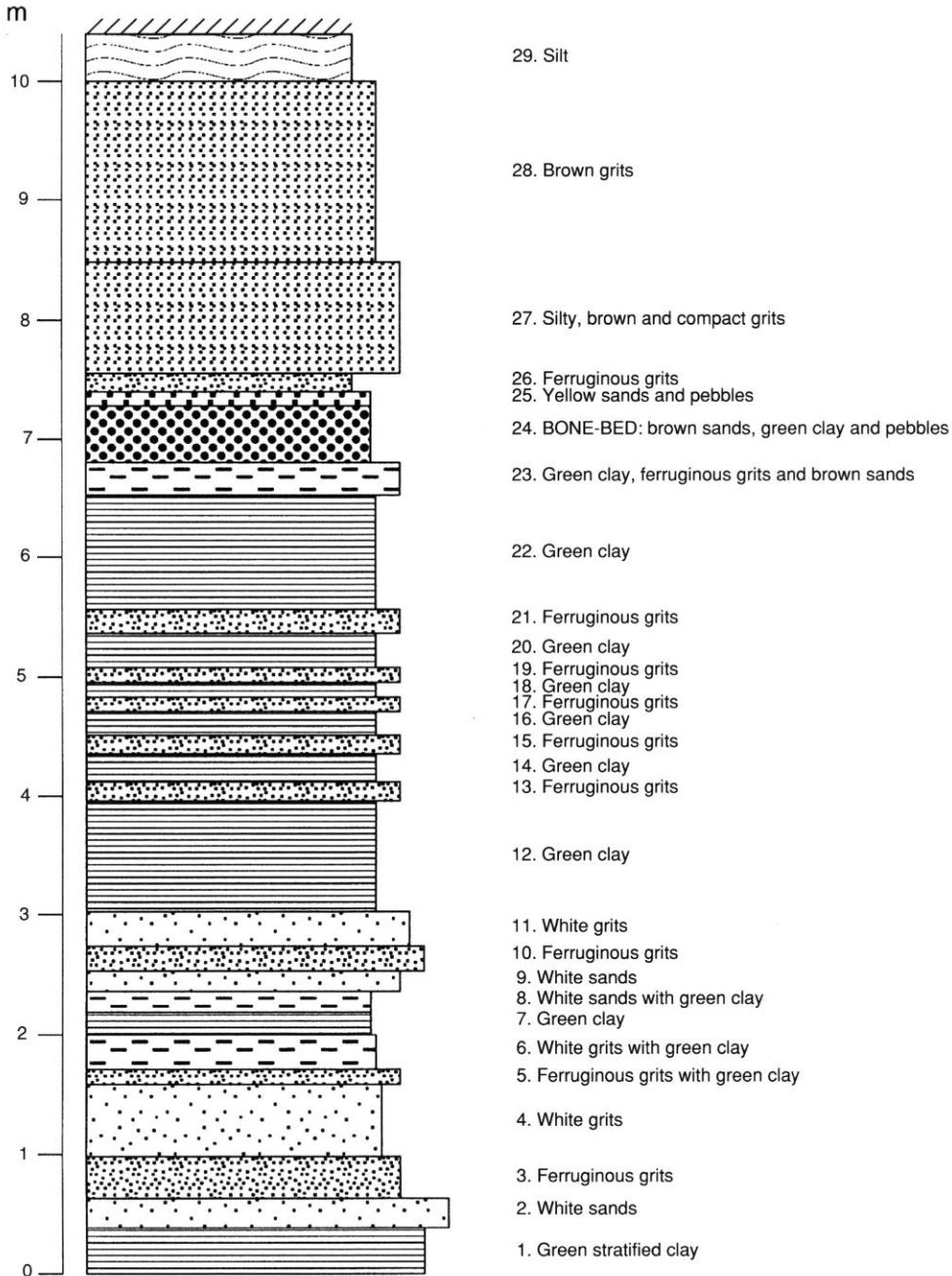


FIG. 2. — Stratigraphic log of the Upper Triassic section at Saint-Nicolas-de-Port.

ment on the status of the Rhaetian Stage limits the discussion. Moreover, palynological samplings in the quarry are, at the present time, unprofitable. From a lithological point of view, the sediments are regarded as Lower Rhaetian in age (Laugier 1971; Al Khatib 1976; Sigogneau-Russell 1983a). Buffetaut (1985), Buffetaut & Wouters (1986), Cuny & Ramboer (1991), Duffin (1993) and Cuny (1993) argue for a slightly older age: the vertebrate fauna from Saint-Nicolas-de-Port shows close similarities to that of the Knollenmergel at Halberstadt in central Germany (Upper Norian).

Granulometric analysis of the sediments (Al Khatib 1976) reveals that they accumulated in a nearshore shallow marine environment. The sands have some characters of river or beach deposits.

SYSTEMATIC PALAEOONTOLOGY

The systematics of the Cynodontia adopted by Battail (1991) is followed in the present paper. Concerning the family Dromatheriidae, the classification proposed by Hahn *et al.* (1994) is followed. As the taxa treated in the present paper are defined exclusively on dental characters, it is usually difficult to settle with certainty the polarity of these traits. For that reason, it has been decided to include both apomorphic and plesiomorphic characters in the diagnoses of Cynodontia *incertae sedis* taxa: therefore, these do not follow strictly the cladistic principles.

Order THERAPSIDA Broom, 1905

Infraorder CYNODONTIA Owen, 1861

CYNODONTS WITH SECTORIAL POST-CANINE TEETH

ORIENTATION OF THE TEETH

The orientation of isolated teeth in cynodonts with sectorial teeth is discussed by Peyer (1956), Russell *et al.* (1976) and Hahn *et al.* (1984, 1987, 1994). The most convex side is conventionally and somewhat arbitrarily regarded as the labial side, on both the upper and lower post-

canines. The distal inclination of the cusps, when present, determines the mesial and distal sides of the teeth. The accessory cusps are usually more numerous or better developed on the distal half of the crown than on the mesial half. When wear is developed, it is possible to distinguish the upper teeth from the lower ones: wear develops on the lingual side of the former and on the labial side of the latter. When wear is not developed or when the lingual and labial sides of the crown are symmetrical, it is thus impossible to settle whether the specimen belongs to the upper or to the lower tooth row.

Family DROMATHERIIDAE Gill, 1872

REMARK

The cladogram of the Dromatheriidae proposed by Hahn *et al.* (1994) shows that this group is clearly paraphyletic, as the ancestry of the mammals lies within it.

Genus *Pseudotriciconodon*

Hahn, Lepage *et* Wouters, 1984

Pseudotriciconodon Hahn, Lepage *et* Wouters, 1984: 358.

TYPE SPECIES. — *Pseudotriciconodon wildi* Hahn, Lepage *et* Wouters, 1984.

OTHER REFERRED SPECIES. — *Pseudotriciconodon chatterjeei* Lucas *et* Oakes, 1988. Identification of this taxon as a cynodont has been questioned by Sues & Olsen (1990), but without argumentation.

DIAGNOSIS. — Crown of postcanine teeth tricuspid to pentacuspid and very narrow ($2.4 < \text{ratio "length/width" of the crown} < 4.2$); labial and lingual sides of the crown nearly parallel. Cutting edge perfectly straight. Base of the crown not constricted. Root semielliptical in outline, about 1.5 times as high as the crown; tip of the root sometimes divided by a short furrow; pulpal canal small, elliptical in shape and sometimes double.

Pseudotriciconodon wildi

Hahn, Lepage *et* Wouters, 1984
(Figs 3, 4)

Pseudotriciconodon wildi Hahn, Lepage *et* Wouters, 1984: 358, pl. 1, figs 1, 2; pl. 2, figs 2-6; pl. 3, figs 1-6. — Clemens 1986: 238. — Hahn *et al.* 1987: 17,

pl. 5, fig. 2. — Lucas & Oakes 1988: 447. — Battail 1991: 88. — Hahn *et al.* 1994: 142, fig. 2a. — Sigogneau-Russell & Hahn 1994: 206, fig. 10.10d.

HOLOTYPE. — MNHL “R.M. 1”, in the Muséum national d’Histoire naturelle de Luxembourg.

LOCUS TYPICUS. — “Rinckebierg” (Medernach, Great-Duchy of Luxembourg).

STRATUM TYPICUM. — Bone-bed included within the Steinmergel-Gruppe (Norian, Upper Triassic).

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: IRSNB R156, IRSNB R157, IRSNB 28114/68, IRSNB 28114/100, IRSNB 28114/638, IRSNB 28114/737, IRSNB 28114/739, IRSNB 28114/752, IRSNB 28114/811, IRSNB 28114/859, IRSNB 28114/870, IRSNB 28114/905, IRSNB 28114/906, IRSNB 28114/994, MNHP SNP25, MNHP SNP54, MNHP SNP115L, MNHP SNP61W, MNHP SNP63, MNHP SNP68W, MNHP SNP75W, ? MNHP SNP83W, MNHP SNP198W, MNHP SNP288W, MNHP SNP295W, MNHP SNP300W, MNHP SNP306W, ?MNHP SNP337W, MNHP SNP351W, MNHP SNP423W, MNHP SNP425W.

DIAGNOSIS. — 0.9 mm < length of the crown of postcanine teeth < 3.1 mm; 0.35 mm < width of the crown of postcanine teeth < 0.95 mm.

DESCRIPTION

Classification

Hahn *et al.* (1984) base their classification of the

postcanine teeth in *Pseudotricodon wildi* on the number and the arrangement of the accessory cusps. Six categories can be distinguished.

Group I:

1 anterior and 1 posterior accessory cusps.

Group II:

1 anterior and 2 posterior accessory cusps.

Group III:

1 anterior and 3 posterior accessory cusps.

Group IV:

2 anterior and 2 posterior accessory cusps.

Group V:

2 anterior and 3 posterior accessory cusps.

Group VI:

? anterior and 2 posterior accessory cusps.

Measurements

The measurements taken on the postcanine teeth of *Pseudotricodon wildi* are shown in table 1. The orientation of the teeth and the measurements are illustrated by Hahn *et al.* (1984, fig. 1).

Crown

In occlusal view, the crown appears elongated antero-posteriorly and quite narrow labio-lingually: in the specimens discovered in Saint-Nicolas-de-Port, the ratio “length/width” of the crown varies between 2.45 and 4.45. Both the lingual and the labial sides of the crown are

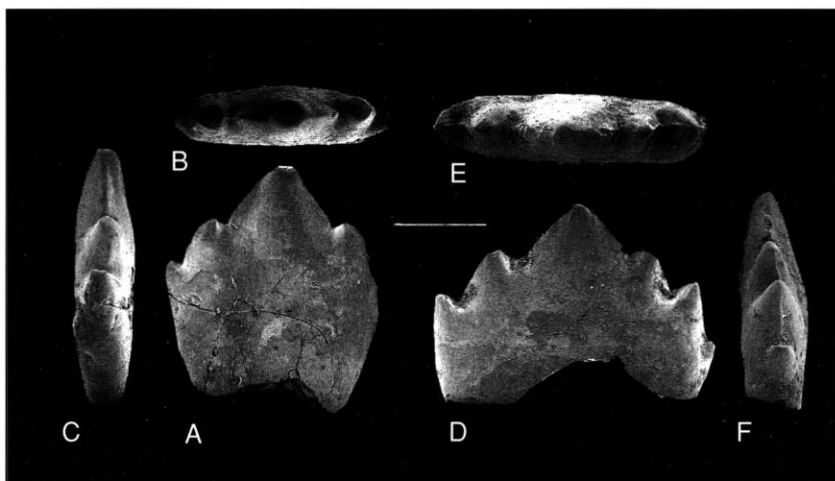


FIG. 3. — Postcanine teeth of *Pseudotricodon wildi*, from the Late Triassic of Saint-Nicolas-de-Port. **A-C**, IRSNB R156; **A**, lateral view; **B**, occlusal view; **C**, posterior view. **D-F**, IRSNB R157; **D**, lateral view; **E**, occlusal view; **F**, posterior view. Scale bar: 1 mm.

nearly straight, slightly convex at the level of the main central cusp. All the cusps are in line with the antero-posterior axis of the crown. The cutting edge is very sharp and perfectly straight. In anterior and posterior views, all the cusps are nearly perfectly straight, without marked curve towards the lingual side of the crown. In lateral view, the main cusp occupies a median

position. It has the outline of an isosceles triangle; its anterior and posterior edges are straight or slightly convex. It is flanked by one to two anterior and one to three posterior accessory cusps of decreasing heights. All are triangular, sharp and clearly separated from each other. Their vertical axes usually diverge slightly from the main cusp; they can be curved towards the

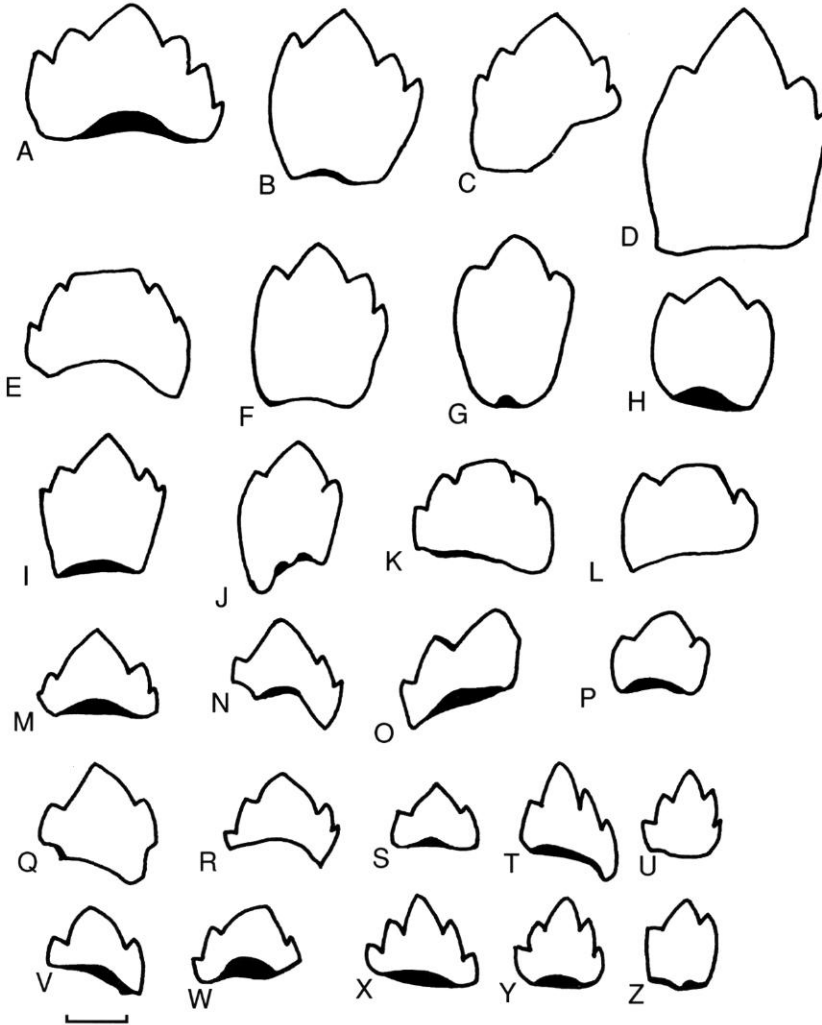


FIG. 4. — Outline of postcanine teeth of *Pseudotricynodon wildi*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, IRSNB R157; **B**, IRSNB R156; **C**, IRSNB 28114/859; **D**, IRSNB 28114/739; **E**, IRSNB 28114/906; **F**, MNHP SNP300W; **G**, IRSNB 28114/737; **H**, MNHP SNP306W; **I**, MNHP SNP63W; **J**, IRSNB 28114/68; **K**, IRSNB 28114/905; **L**, IRSNB 28114/752; **M**, IRSNB 28114/870; **N**, IRSNB 28114/627; **O**, IRSNB 28114/766; **P**, IRSNB 28114/100; **Q**, MHNP SNP115L; **R**, MNHP SNP425W; **S**, MHNP SNP68W; **T**, MNHP SNP75W; **U**, MNHP SNP351W; **V**, IRSNB 28114/811; **W**, IRSNB 28114/994; **X**, MNHP SNP423W; **Y**, MNHP SNP295W; **Z**, MNHP SNP288W. Scale bar: 1 mm.

median axis of the crown.

The wear on the cusps is apical but very erratic: it does not form clearly defined facets. It is therefore usually impossible to distinguish upper and lower postcanines. The crown has no basal cingulum and no basal groove separating the crown from the root.

Root

The root is about 1.5 times as high as the crown. Its outline is semielliptical in lateral view. Its median portion is slightly depressed in comparison with the anterior and the posterior borders. The pulpal foramen, when it can be observed, is elliptical and elongated antero-posteriorly. Neither bipartition of the root nor undoubling of the pulpal canal can be observed in the teeth discovered in Saint-Nicolas-de-Port. In anterior view, the root is very compressed labio-lingually, like the crown.

TABLE 1. — Measurements (in mm) of the postcanine teeth of *Pseudotriciconodon wildi*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown. For the signification of the groups, see text.

Group	Number	Lc	Wc	Hc	L/W
I	IRSNB 28114/737	1.95	0.55	1.1	3.55
	IRSNB 28114/68	1.65	0.6	1.15	2.75
	IRSNB 28114/628	2.1	0.55	1.4	3.82
	IRSNB 28114/752	2	0.5	>1.65	4
	IRSNB 28114/8111	1.7	0.7	1.3	2.43
	RSNB 28114/100	1.65	0.55	1	3
	MNHP SNP54	1.5	0.37	1.1	4.05
	MNHP SNP 115L	1.65	0.5	1.15	3.3
	MNHP SNP61W	2.37	0.9	-	2.63
	MNHP SNP68W	1.35	0.55	-	2.45
	MNHP SNP288W	1.1	0.25	0.9	4.4
	MNHP SNP306W	1.9	0.45	1.15	4.22
	II?	IRSNB 28114/994	?1.8	0.65	1.3
II	IRSNB R156	2.45	0.75	1.85	3.27
	IRSNB 28114/739	2.85	0.95	2.25	3
	MNHP SNP75W	1.42	0.55	-	2.58
	MNHP SNP300W	2.18	0.55	1.45	3.96
IV	IRSNB 28114/859	2.25	0.7	1.5	3.21
	IRSNB 28114/905	2.25	0.6	>1.6	3.75
	IRSNB 28114/870	?2	0.7	1.45	?2.86
	IRSNB 28114/906	2.55	0.85	>2	3
	MNHP SNP63W	2	0.45	1.4	4.44
	MNHP SNP295W	1.35	0.45	1.05	3
	MNHP SNP351W	1.15	0.4	1.1	2.88
	MNHP SNP423W	1.75	0.6	-	2.92
MNHP SNP425W	1.7	0.55	-	3.09	
V	IRSNB R157	3.1	0.75	2.1	4.13

DISCUSSION

Small teeth with fundamentally tricuspid crowns and undivided roots are also known, in Triassic times, in *Tanystropheus*, *Macrocnemus* (Prolacertilia) and *Eudimorphodon* (Pterosauria). Hahn *et al.* (1984) list the features distinguishing the teeth of these animals. Differences can particularly be observed in the structure of the root, but also in the ornamentation of the enamel or in the proportions of the crown. During the Late Triassic, *Pseudotriciconodon* and *Eudimorphodon* lived together in Saint-Nicolas-de-Port (Godefroit & Cuny, in prep.), as in Medernach (Great-Duchy of Luxemburg, Hahn *et al.* 1984) and in the Chinle Formation of New Mexico, USA (Murry 1986; Lucas & Oakes 1988).

In contemporary Morganucodontidae (real mammals), the root in premolars and molars is completely divided; moreover, the crown is surrounded by well developed cingula.

Ornithischian dinosaurs from Late Triassic assemblages of North America also possess multicuspoid triangular teeth (Hunt & Lucas 1994). In these animals the crowns are more massive and usually recurved (at least in the premaxillary teeth). The cusps are more numerous and much less distinct. The root is higher and separated from the crown by a well developed neck.

The genus *Pseudotriciconodon* is now unanimously referred to the Family Dromatheriidae (Carroll 1988; Lucas & Oakes 1988; Battail 1991; Hahn *et al.* 1994; Sigogneau-Russell & Hahn 1994); this attribution is based on the partial bipartition of the root observed in some specimens, on the triconodont organization of the crown and on the combined absence of cingula and constriction between the crown and the root.

The teeth from Saint-Nicolas-de-Port differ from *Pseudotriciconodon chatterjeei*, from the Chinle Formation of New Mexico, by the absence of distinct striations on the enamel and by their larger size. They are both morphologically and morphometrically closer to *Pseudotriciconodon wildi*, from Medernach.

Figure 5 shows the relative evolution of the length (x axis, in Ln) and of the width (y axis, in Ln) of the dental crowns in *Pseudotriciconodon wildi*. The allometric parameters have been estimated, using

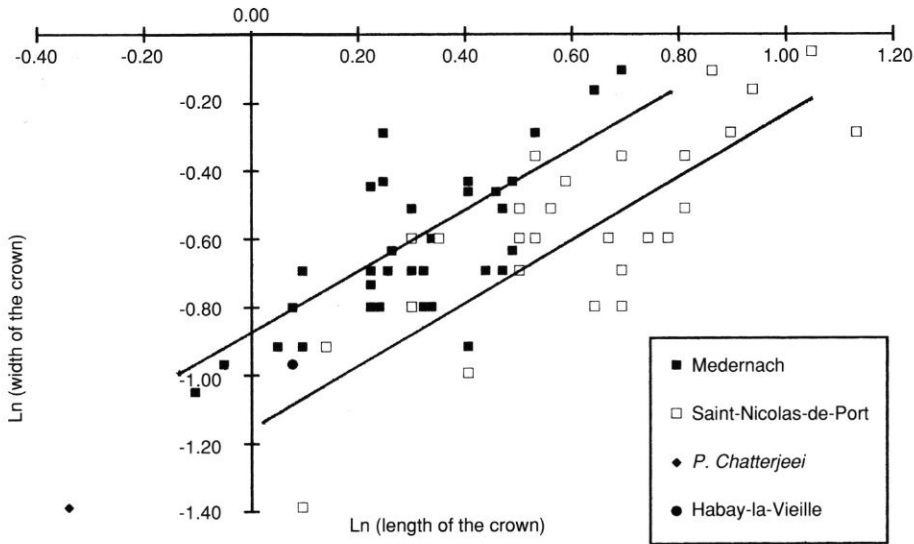


Fig. 5. — Dispersion diagram of the postcanine teeth in *Pseudotriciconodon*.

Teissier's (1948) formulas (both the length and the width of the crown are here regarded as dependent variables), separately for the populations from Medernach and Saint-Nicolas-de-Port. The allometry coefficient is similar in both population: $b = 0.90$ and 0.92 , respectively in the populations from Saint-Nicolas-de-Port and Medernach. The isometry between the variables can therefore reasonably be concluded. On the other hand, the characteristic ratio differs in the two populations: $a = 0.31$ and 0.40 , respectively in the populations from Saint-Nicolas-de-Port and Medernach. In average, the teeth discovered in Saint-Nicolas-de-Port seem narrower than those from Medernach. This difference cannot be considered as statistically significant because Pearson's correlation coefficients between the variables are not sufficiently high: $r = 0.80$ for the teeth from Saint-Nicolas-de-Port and 0.73 for the teeth from Medernach. Nevertheless, this observation is quite interesting because it reflects a more general morphometrical trend: Tessier (1936) and Chevais (1937) have actually compiled examples in which local races of a same species do not differ in "b" value, but can be distinguished in "a" value. The proportions of the studied organ differ in these populations, but the differences are preserved without change

during the life of the animal (at least, in mature specimens). Therefore, the study of dental allometry in *Pseudotriciconodon wildi* shows that the morphometrical differences observed between the teeth discovered in Saint-Nicolas-de-Port and Medernach can be interpreted as normal variations between two local (geographically and/or stratigraphically) faunas of a same species. There is no morphological or morphometrical evidence now available to support a systematic distinction between these populations.

Genus *Tricuspes* E. von Huene, 1933

Tricuspes E. von Huene, 1933: 82.

TYPE SPECIES. — *Tricuspes tuebingensis* E. von Huene, 1933.

OTHER REFERRED SPECIES. — *Tricuspes sigogneauae* Hahn, Hahn *et* Godefroit, 1994; *Tricuspes tapeinodon* n.sp.

DIAGNOSIS. — Accessory cusps sometimes developed on the anterior (E/e) or on the posterior (D/d) border of the molar crown. Cusps not perfectly aligned but arranged in a V-like manner: the anterior and posterior cusps are set in a slightly more lingual position than the more central cusps and the crown has an arched aspect in occlusal view. Axis of the crown perfectly vertical.

Crown separated from the root by a marked constriction. Root subdivided in its full length, but both portions remain in close contact with one another.

***Tricuspes tuebingensis* E. von Huene, 1933**
(Fig. 6A-C)

Tricuspes tuebingensis E. von Huene, 1933: 82, pl. 1, fig. 7a, b. – Kuhn 1965: 85.

Tricuspes tuebingensis – Hopson & Kitching 1972: 82. – Clemens *et al.* 1979: 10. – Clemens 1980: 66, pl. 10, figs 1, 2a-c. – Battail 1991: 89. – Hahn *et al.* 1994: 148, fig. 3.

? Schneidezahn S_1 – E. von Huene 1933: 84, pl. 1, fig. 9a-d.

HOLOTYPE. — An isolated right molariform preserved in the Geologisch-Paläontologischen Institut der Universität Tübingen (Germany) and figured, among others, by Clemens (1980, pl. 10, figs 1, 2a-c).

LOCUS TYPICUS. — Gaisbrunnen, north of Tübingen (Württemberg, Germany).

STRATUM TYPICUM. — “Rhätbonebed”, included in Rhaetian sandstones. Upper Triassic.

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: IRSNB R158 (upper molariform).

DIAGNOSIS. — Molariform teeth with a tiny accessory cusp *m* in postero-lingual position; crown rather high:

ratio “length/height” of the crown = 1.53 in IRSNB R158 and < 1.5 in the holotype. Accessory cusps D/d and E/e, when present, incorporated in the cutting edge of the crown.

DESCRIPTION

Measurements

Length of the crown = 2.75 mm; width of the crown = 1.06 mm; height of the crown = 1.8 mm.

Crown

The nomenclature of the cusps in *Tricuspes* is illustrated by Hahn *et al.* (1994, fig. 5). The enamel is perfectly smooth. In occlusal view, the crown is rather elongated: the ratio “length/width” of the crown = 2.59. The labial side is very convex antero-posteriorly and the lingual side, slightly concave. The crown is formed by five very distinct cusps. Contrary to *Pseudotriciconodon*, these are not perfectly aligned, but they are arranged in a V-like manner: cusps B and C are set in a more lingual position than cusp A; in the same way, accessory cusps D and E are set in a slightly more lingual position than cusps C and B. The cutting edge is not as developed as in *Pseudotriciconodon*. The base of the crown is clearly constricted.

In lingual view, the crown is not very high (ratio “length/height” of the crown = 1.55) and domi-

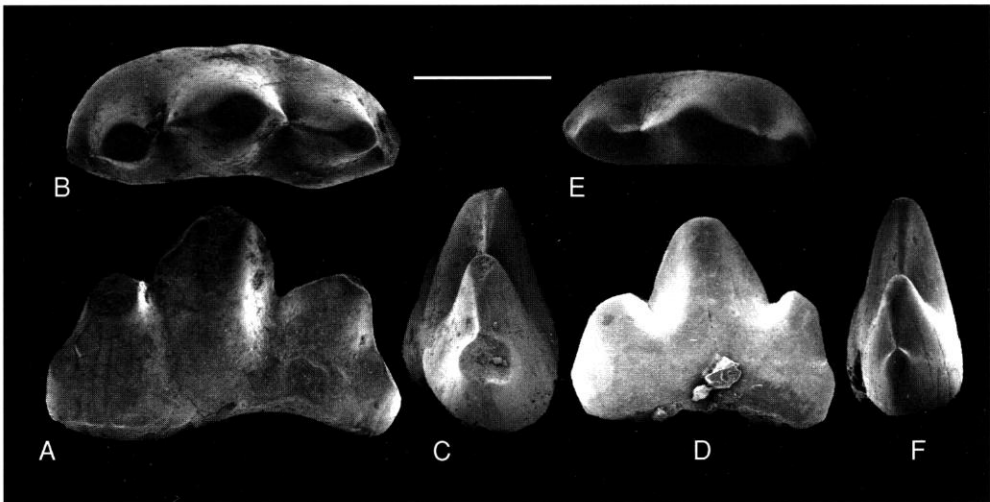


FIG. 6. — A-C, IRSNB R158, upper postcanine tooth of *Tricuspes tuebingensis*, from the Late Triassic of Saint-Nicolas-de-Port; lingual view; B, occlusal view; C, posterior view. D-F, IRSNB R159, upper postcanine tooth of *Tricuspes sigogneauae*, from the Late Triassic of Saint-Nicolas-de-Port; D, lingual view; E, occlusal view; F, anterior view. Scale bar: 1 mm.

nated by the median cusp A. The anterior and posterior edges of this cusp are clearly convex and separated from cusps B and C by distinct notches. Its vertical axis slopes slightly backwards. Anterior cusp B is lower than posterior cusp C. The latter slopes more backwards than cusp A; cusp B slopes somewhat forwards. Cusp B is flanked anteriorly by a low, bulbous accessory cusp E; cusp C is posteriorly flanked by a very eroded accessory cusp D. These accessory cusps are incorporated in the cutting edge of the crown. A tiny, very eroded accessory cusp m is visible on the lingual side of the crown, just below cusp C. Wear facets affect the lingual side of the apex of the cusps. This tooth is thus an upper molariform. On cusp A, the wear facet is triangular and very concave. Cusp B is more affected by wear than cusp C. Accessory cusp D, as mentioned above, is very eroded.

Root

The root is not preserved in IRSNB R158.

DISCUSSION

Tricuspes tuebingensis is known by one lower (holotype) and one upper (IRSNB R158) molariform teeth. These teeth differ from those of *Tricuspes sigogneauae* (see below) in the presence of a tiny accessory cusp m on the postero-lingual portion of cusp c. Accessory cusps d and e, although eroded, are also better developed in IRSNB R158 than in *Tricuspes sigogneauae* (see Hahn *et al.* 1994, figs 5-9) and are clearly located on the cutting edge of the crown. IRSNB R158 differs from the holotype by its crown proportionally lower and longer. This character, correlated to the development of accessory cusps d

and e, probably reflects a more distal position in the tooth row of the former. Hahn *et al.* (1994) did not observe significant differences in the proportions of lower and upper molariform teeth in *Tricuspes sigogneauae*.

Tricuspes sigogneauae

Hahn, Hahn *et Godefroite*, 1994

(Fig. 6D-F)

Tricuspes sigogneauae Hahn, Hahn *et Godefroite*, 1994: 149, figs 5-13.

Tricuspes cf. *tuebingensis* Clemens, 1980: 71, pl. 10, fig. 5a-c.

HOLOTYPE. — MNHP SNP49LW, a lower molariform figured by Hahn *et al.* (1994, fig. 5).

PARATYPES. — 6 upper molars, 7 lower molars and 4 premolars preserved in the MNHP and the IRSNB (see Hahn *et al.* 1994, tabs 2-4, for catalogue numbers).

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

STRATUM TYPICUM. — "Rhaetian" sandstones. Upper Triassic.

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: IRSNB R159, IRSNB 28114/193, MNHNP SNP55, MNHP SNP24W, ? MNHP SNP98W, MNHP SNP289W, MNHP SNP343W, MNHP SNP345W.

DIAGNOSIS. — Molariform teeth without accessory cusp m in postero-lingual position; crown high: ratio "length/height" of the crown < 1.3. Accessory cusps D/d and E/e, when present, not incorporated in the cutting edge of the crown, but located on its anterior and posterior wall.

TABLE 2. — Measurements (in mm) of the new molariform teeth of *Tricuspes sigogneauae*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown; **LL**, lower left; **LR**, lower right; **UL**, upper left; **UR**, upper right.

Number	Position	Lc	Wc	Hc	Lc / Wc	Root	Cusps
IRSNB 28114/193	LL	2.92	1.16	2.8	2.52	+	3
MNHNP SNP289W	LR	1.86	0.77	1.75	2.42	-	3 (?)
MNHNP SNP24W	UL	2.56	1.1	1.95	2.33	-	+3+
MNHNP SNP55	UR	1.67	0.68	1.36	2.46	-	3
IRSNB R159	UR	2.17	0.8	1.75	2.71	-	+3+
MNHNP SNP343W	UR	1.13	0.5	1	2.26	-	(?) 3
MNHNP SNP345W	UR	-	0.87	2	-	-	+3 (?)

DESCRIPTION

The molariform teeth of this species were very accurately described by Hahn *et al.* (1994). The new material discovered in Saint-Nicolas-de-Port does not give new morphological informations. Table 2 gives a summary of the main morphological and morphometrical informations collected from the new molariforms of *Tricuspes sigogneauae*. The classification of the teeth, following the development of the accessory cusps, was created by Hahn *et al.* (1994) and is explained below (description of *Tricuspes tapeinodon*).

DISCUSSION

Hahn *et al.* (1994, figs 13, 14) attribute four pre-molariform teeth to *Tricuspes sigogneauae*. These are regarded, in the present paper, as belonging to *Cynodontia incertae sedis*.

***Tricuspes tapeinodon* n.sp.**
(Figs 7, 8)

Tricuspes sp. indet. – Hahn *et al.* 1994: 154, *partim*, fig. 16.

HOLOTYPE. — IRSNB R161, an upper right molariform.

PARATYPES. — IRSNB R160, IRSNB 28114/35, IRSNB 28114/80, IRSNB 28114/106, IRSNB

28114/107, IRSNB 28114/108, IRSNB 28114/109, IRSNB 28114/827, IRSNB 28114/988, MNHP SNP160W.

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

DERIVATIO NOMINIS. — *tapeinos* (Greek) = low, and *odous* (Greek) = tooth.

STRATUM TYPICUM. — “Rhaetian” sandstones. Upper Triassic.

DIAGNOSIS. — Crown of the molariform teeth very low: ratio “length/height” of the crown > 1.55. Median cusp A/a not much higher than cusps B/b and C/c. No accessory cusp m in postero-lingual position. Accessory cusps d and e, when present, incorporated in the cutting edge of the crown.

DESCRIPTION

Classification

As proposed by Hahn *et al.* (1994) in *Tricuspes sigogneauae*. 3: both accessory cusps D/d and E/e absent; + 3: E/e present, D/d absent; 3+: E/e absent, D/d present; + 3+: both D/d and E/e present.

Measurements

The measurements taken on the molariform teeth of *Tricuspes tapeinodon* are shown in table 3.

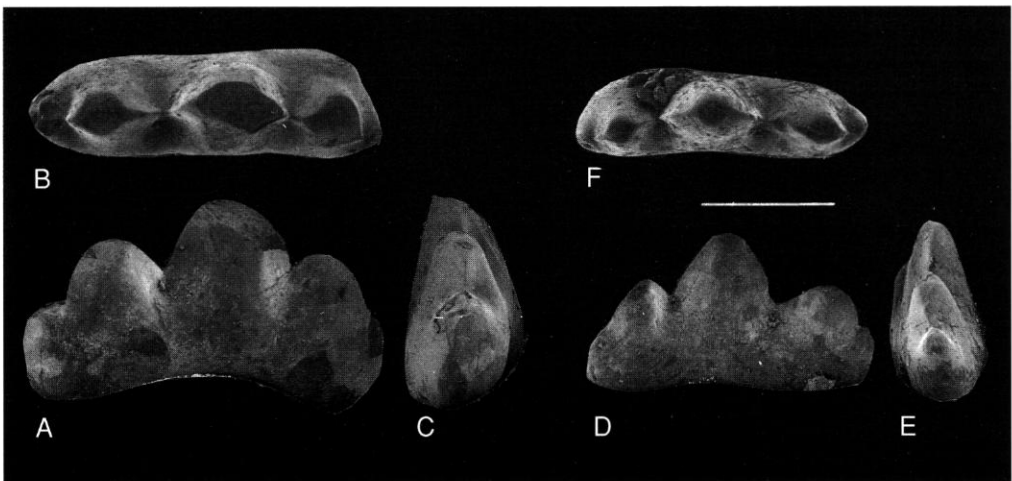


FIG. 7. — Molariform teeth of *Tricuspes tapeinodon*, from the Late Triassic of Saint-Nicolas-de-Port. **A-C**, IRSNB R161, upper post-canine; **A**, lingual view; **B**, occlusal view; **C**, anterior view. **D-F**, IRSNB R160, ? lower postcanine; **D**, lingual view; **E**, posterior view; **F**, occlusal view. Scale bar: 1 mm.

Crown

The enamel is always perfectly smooth. The crown is composed of three main cusps. The highest (A/a) is set in a submedian position and flanked by an anterior cusp (B/b) and a posterior cusp (C/c). Two accessory cusps are sometimes developed on the anterior and posterior portion of the crown (respectively E/e and D/d). In occlusal view, the crown is proportionally long and narrow: the ratio "length/width" of the crown varies between 2.25 and 3.8, on the teeth currently studied. The crown has a pronounced arched aspect: its labial side is very convex antero-posteriorly and its lingual side, slightly concave; at the level of the central cusp, the lingual side of the crown is nevertheless somewhat convex. As usual in *Tricuspes*, the cusps are not perfectly aligned, but set in a V-like manner. The cutting edge joining the cusps together is less developed than in *Tricuspes tuebingensis* or *Tricuspes sigogneauae*. The anterior and posterior ends of the crown are tapering.

In lingual view, the crown is very low: the ratio "length/height" of the crown varies between 1.55 and 2.25 in the material referred to this species. The main cusp A/a is not much higher than cusps B/b and C/c. Cusps B/b and C/c are usually subequal in size and it is therefore more difficult to distinguish the anterior and the posterior ends of the crown than in *Tricuspes tuebingensis* or in *Tricuspes sigogneauae*. They are more rounded and stocky than cusp A/a and their vertical axis can be somewhat divergent. The cusps are well separated from each other by deep notches.

The accessory cusps D/d and E/e, when present, are incorporated in the cutting edge, as in *Tricuspes tuebingensis*, and not rejected on the anterior and posterior walls of the crown, as in *Tricuspes sigogneauae*.

There is no trace of cingulum or accessory cusp m, as in *Tricuspes tuebingensis*. The crown was apparently separated from the root by a constriction.

Wear facets are not always as well marked as in *Tricuspes sigogneauae* and it is therefore sometimes difficult to distinguish the lower from the upper molariform teeth. Wear erodes the upper teeth on their lingual and the lower teeth on their labial side.

In IRSNB R160 (lower molariform), the apices of cusps A, B and C are truncated by wear and have thus a bevel-edged aspect. Cusp A bears a second elliptical wear facet, from the apical facet to its base.

In IRSNB 28114/108 (upper molariform), the apices of cusps A, B and C are slightly blunt by small circular wear facets. The lingual side of the crown bears, below cusp b, a wide facet reminiscent of a contact facet with the contiguous tooth in the dental row.

The lingual side of IRSNB 28114/109 (upper molariform) has a very extensive, mat and slightly concave wear facet, extending from the anterior edge of cusp B to the anterior edge of cusp C and from the base of the crown to the apices of the cusps. A second wear facet, at the base of the posterior side of cusp C, can be inter-

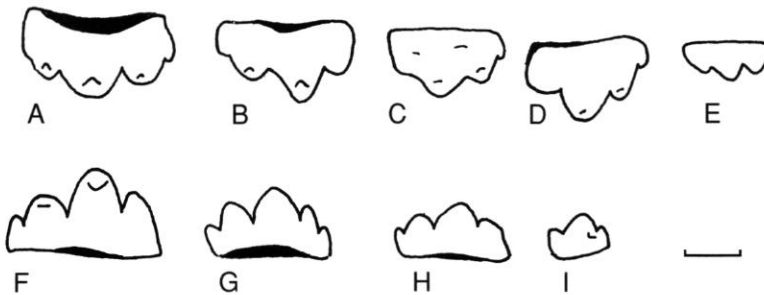


FIG. 8. — Outline of molariform teeth of *Tricuspes tapeinodon*, from the Late Triassic of Saint-Nicolas-de-Port. A, IRSNB R161; B, IRSNB 28114/80; C, IRSNB 28114/108; D, MNHP SNP160W; E, IRSNB 28114/109; F, IRSNB 28114/106; G, IRSNB R160; H, IRSNB 28114/107; I, IRSNB 28114/35. Scale bar: 1 mm.

TABLE 3. — Measurements (in mm) of the molariform teeth of *Tricuspes tapeinodon*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown; **LL**, lower left; **LR**, lower right; **UL**, upper left; **UR**, upper right.

Number	Position	Lc	Wc	Hc	Lc / Wc	Root	Cusps
IRSNB 28114/35	? LL	1.15	0.4	0.74	2.87	-	3
IRSNB 28114/107	? LL	2.28	0.6	1.02	3.8	-	+3
IRSNB 28114/106	LR	2.87	0.85	1.5	3.38	-	3+
IRSNB R160	? LR	2.27	0.7	1.33	3.24	-	+3+
IRSNB 28114/80	UL	2.62	0.82	1.46	3.19	-	3+
IRSNB 28114/827	UL	-	0.98	1.5	-	-	+3 (?)
MNHP SNP160W	UL	>2.3	0.72	-	>3.26	-	+3 (?)
IRSNB R161	UR	2.83	0.9	1.62	3.14	-	+3+
IRSNB 28114/108	UR	2.15	0.95	1.27	2.26	-	3+
IRSNB 28114/109	UR	1.65	0.67	0.75	2.46	-	3

preted as a contact facet with the contiguous posterior tooth in the dental row. It seems, therefore, that the teeth of the same row were aligned, which permits one-to-one occlusion between teeth of the opposite rows.

The labial side of IRSNB 28114/106 (lower molariform) bears three wear facets. The first one erodes the posterior edge of cusp b and the anterior edge of cusp a. The second one is continuous on the posterior edge of cusp a and on the anterior edge of cusp c. The third facet affects the posterior edge of cusp c and the anterior edge of cusp d.

Root

The root is not preserved in the molariform tooth referred to *Tricuspes tapeinodon*.

DISCUSSION

Figure 9 compares the distribution of the length (x axis, in Ln) and of the width (y axis, in Ln) of the molariform teeth in the three species recognized in the genus *Tricuspes*. It appears that *T. tapeinodon* has, in average, proportionally narrower dental crowns than *T. sigogneauae*. This result can be considered as significant because

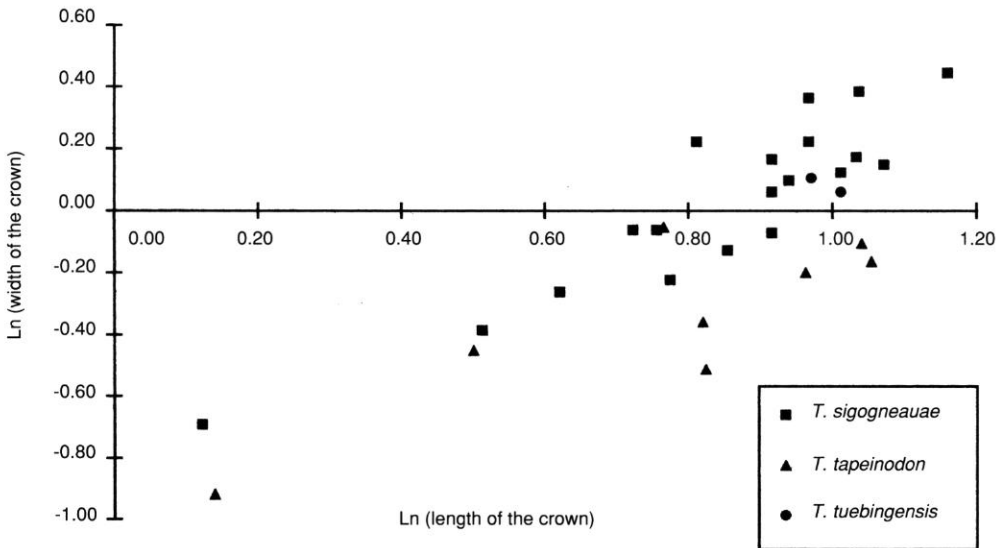


Fig. 9. — Dispersion diagram of the molariform teeth in *Tricuspes*.

Pearson's correlation coefficients are sufficiently high: $r = 0.91$ and 0.84 , respectively in *T. sigogneauae* and *T. tapeinodon*. The allometry coefficient, estimated by Teissier's (1948) formula differs between these species ($b = 1.16$ in *T. sigogneauae* and 0.9 in *T. tapeinodon*), which confirms their taxonomic distinction. There is no evidence, at our present state of knowledge, to support a generic distinction of *Tricuspes tapeinodon*.

Genus *Meurthodon*

Sigogneau-Russell *et* Hahn, 1994

Meurthodon Sigogneau-Russell *et* Hahn, 1994: 212.

TYPE SPECIES. — *Meurthodon gallicus* Sigogneau-Russell *et* Hahn, 1994.

DIAGNOSIS. — As for the only currently recognized species *Meurthodon gallicus* Sigogneau-Russell *et* Hahn, 1994.

Meurthodon gallicus

Sigogneau-Russell *et* Hahn, 1994
(Figs 10, 11)

Meurthodon gallicus Sigogneau-Russell *et* Hahn, 1994: 212, figs 10.11. — Hahn *et al.* 1994: 142, fig. 2f.

Tricuspes sp. indet. — Hahn *et al.* 1994: *partim* 154, fig. 15.

"Dent d'aspect mammalien" (Russell *et al.* 1976: 377, pl. 1, figs 1-3).

"... probably representative of a cynodont reptile..." (Clemens 1979: 11).

"Advanced mammal-like reptile" (Clemens 1980: 62).
"French mammal (?)" (Gow 1980: 480, fig. 10).

HOLOTYPE. — MNHP SNP1W.

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

STRATUM TYPICUM. — "Rhaetian" sandstones. Upper Triassic.

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: MNHP SNP1W, IRSNB R162, IRSNB R163, IRSNB 281141/5, IRSNB 28114/17, IRSNB 28114/40, IRSNB 28114/45, IRSNB 28114/56, IRSNB 28114/746, IRSNB 28114/754, IRSNB 28114/814, IRSNB 28114/902, IRSNB 28114/993, MNHP SNP51DD, MNHP SNP64W, MNHP SNP115W, MNHP SNP200W, MNHP SNP210W, MNHP SNP514W.

DIAGNOSIS. — Crown of postcanine teeth asymmetrical and tetracuspoid. The second cusp is always the largest and the first cusp is usually the smallest. The three posterior cusps are clearly inclined backwards. Small erratic cingular elements on some teeth. Crown

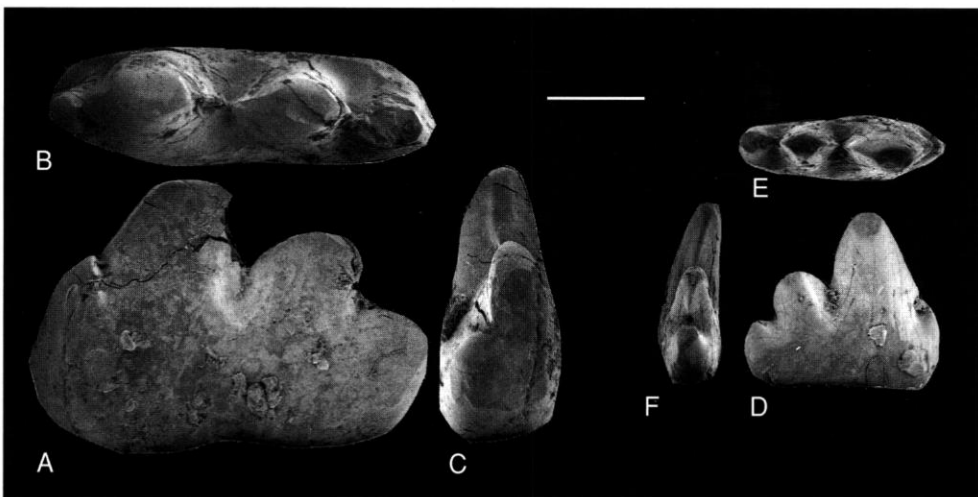


FIG. 10. — Postcanine teeth of *Meurthodon gallicus*, from the Late Triassic of Saint-Nicolas-de-Port. **A-C**, IRSNB R162, lower postcanine; **A**, lateral view; **B**, occlusal view; **C** posterior view. **D-F**, IRSNB R163, upper postcanine; **D**, lateral view; **E**, occlusal view; **F**, posterior view. Scale bar: 1 mm.

clearly separated from the root by a sulcus. Roots completely subdivided and fully separated on the distal three quarters of their length.

DESCRIPTION

Preliminary remark

Until now, the holotype (MNHP SNP1W) was the only known specimen of *Meurthodon gallicus*. The original description of this tooth (Russell *et al.* 1976) is particularly detailed. Therefore, the following description points only to differential characters observed in new material referred to this species.

Measurements

The measurements taken on the postcanine teeth of *Meurthodon gallicus* are shown in table 4.

General characters of the crown

The crown is tetracuspid and the cusps are very compressed labio-lingually. The second cusp is always the highest. Its is flanked by a small anterior cusp and by two posterior cusps of decreasing sizes. The three posterior cusps slope backwards. The crowns of some teeth (IRSNB 28114/005, IRSNB 28114/902) are proportionally less long, but higher than in MNHP SNP1W. This feature can reflect the relative position of the tooth in the jaw: the most slender teeth have a pronounced premolariform aspect.

First cusp

The first cusp is always quite small. Its axis is nearly perfectly vertical, but can sometimes slope backwards (IRSNB 28114/40). It is usually adjacent to the second cusp, but can be separated from it by a more or less deep groove. It is sometimes slightly displaced towards the lingual side of the crown (IRSNB 28114/5, IRSNB R163, IRSNB 28114/814, MNHN SNP115W). The first cusp of MNHP SNP1W, IRSNB 28114/40, IRSNB 28114/056, IRSNB R162, MNHP SNP64W and MNHP SNP210W bears, on its anterior lingual side, a well marked flat triangular facet. This suggests a contact between contiguous teeth and thus, a mesio-distal overlapping of the teeth (Russell *et al.* 1976). In IRSNB R162, a tiny accessory cusp, at the base of the labial side of the first cusp, is prolonged backwards by a brief ridge.

Second cusp

The second cusp is always by far the highest. Its labial side is more convex than its lingual side. Its apex is rounded. It slopes backwards: its vertical axis forms an angle of 60° to 70° with the horizontal axis of the crown. Its posterior margin is always less oblique than its anterior margin. Both are made thinner, cutting, usually pinched at the base and more rounded at the top. The cusp can be slightly curved towards the lingual side of the crown (IRSNB 28114/5, IRSNB 28114/17, IRSNB R163). At the level of the junction with the third cusp, both the labial and the lingual sides of the crown bear a concave dimple. The labial one is always better marked.

Third cusp

The third cusp is nearly identical to the second. It is usually still more inclined backwards (MNHP SNP1W, IRSNB R163, IRSNB 28114/40, IRSNB 28114/56, IRSNB 28114/902). It is always smaller than the second cusp and higher than the first and the fourth. Its anterior and posterior margins are cutting, too, particularly at their base. Its labial and lingual sides also bear small facets, at the level of the junction with the fourth cusp.

Fourth cusp

The fourth cusp is usually higher than the first one (MNHP SNP1W, IRSNB 28114/5, IRSNB 28114/17, IRSNB R163, IRSNB 28114/45, IRSNB 28114/56, MNHP SNP64W, MNHP SNP210W), but can sometimes be somewhat smaller (IRSNB 28114/902, IRSNB 28114/993, MNHP SNP200W). It is always less inclined backwards than the third: its slope is approximately the same than that of the second cusp. Its apex is usually more sharp-pointed than that of the second and the third cusps. Its anterior margin is sharper than its posterior margin, which participates in the posterior border of the crown. The posterior border of the fourth cusp bears, in IRSNB 28114/5 and IRSNB R163, a well marked triangular mat facet, probably corresponding to the overlapping area with the contiguous posterior tooth in the dental series. In IRSNB 28114/040, a posterior swelling forms a tiny posterior accessory cusp.

Base of the crown

The base of the crown is distinctly constricted by a sulcus separating it from the root. Under the cusps, the labial side of the crown is usually convex antero-posteriorly; the lingual side is flat to slightly concave. The labial side sometimes presents a concavity between the second and the third cusp (MNHP SNP 1W, IRSNB 28114/5, IRSNB 28114/56). Between these cusps, the base of the lingual side of the crown bears a dimple in continuity with the separation line of the roots.

The labial side of IRSNB R162 bears, under the junction between the third and the fourth cusp, a small swelling which can be interpreted as the rough shape of a cingulum. If the orientation proposed above is correct, the presence of cingular elements on the labial side should indicate, by analogy with the Morganucodontidae, that this tooth is an upper postcanine. The presence of wear facets on the labial side of the cusps contradicts this interpretation (see below). Such a swelling can be observed on the lingual side of IRSNB 28114/17, under the junction between

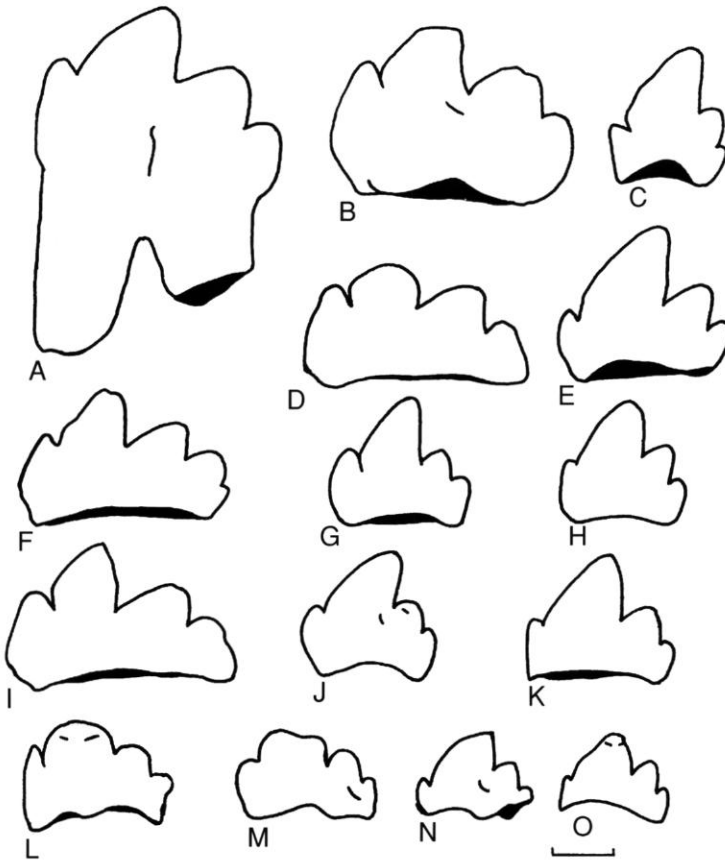


FIG. 11. — Outline of postcanine teeth of *Meurthodon gallicus*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, MNHP SNP1W; **B**, IRSNB R162 (lower postcanine); **C**, IRSNB 28114/902; **D**, IRSNB 28114/40; **E**, MNHP SNP210W; **F**, MNHP SNP64W; **G**, IRSNB 28114/993; **H**, IRSNB R163 (upper postcanine); **I**, IRSNB 28114/746; **J**, IRSNB 28114/17 (lower postcanine); **K**, MNHP SNP514W; **L**, IRSNB 28114/56 (lower postcanine); **M**, IRSNB 28114/45 (lower postcanine); **N**, MNHP SNP51DD; **O**, MNHP SNP20W. Scale bar: 1 mm.

the second and the third cusp. With the lingual dimple between the second and the third cusp, this swelling delimits a small lingual basin. A tiny accessory cusp can be observed on the lingual side of IRSNB 28114/5, under the junction between the second and the third cusp. These last two teeth, which present cingular elements only on their lingual side, are therefore probably lower postcanines.

Wear facets

Russell *et al.* (1976) did not observe clearly defined wear facets in MNHP SNP1W. The flat anterior facet on the first cusp is nevertheless interpreted, as mentioned above, as a contact area with the contiguous tooth. The flatter upper half of the fourth cusp is similarly regarded as a contact area with the posterior tooth. These facets indicate that the teeth of the same row were aligned, which is an important prerequisite to one-to-one occlusion (Crompton & Luo 1993; Luo 1994). However, several other teeth present clearly defined wear facets.

Two elongated, semielliptical and concave facets are present on the labial side of the second and third cusps, in IRSNB 28114/5. The facet extends nearly as far as the base of the second cusp. If the orientation proposed is correct, this tooth is therefore a lower postcanine.

In IRSNB 28114/56, wear facets are also located on the lingual side of the second and third cusps. The first facet truncates the top of the second cusp. The second facet is long and oblique forwards: it reaches the base of the third cusp. This tooth is therefore probably a lower postcanine.

In IRSNB 28114/17, the labial side of the apex is truncated by an elliptical wear facet, which confirms its attribution to the lower dental series. In IRSNB R162, a wear facet extends on the anterior side of the apex of the second cusp, replacing its natural cutting edge by a narrow, flat and elongated facet, and, on its labial side, forming a small triangular area. The interpretation of this tooth is difficult: both the cingular elements and the wear facet are present on the same side and the cusps are not curved. If the orientation of this tooth is correct, it is thus a lower postcanine with tiny external cingular elements.

MNHP SNP 115W has been identified by

Hahn *et al.* (1994, fig. 15) as *Tricuspes* sp. In fact, it presents all the diagnostic characters of *Meurthodon gallicus*. The labial side of its last three cusps possesses well marked wear facets. Thus, it is probably a lower postcanine.

MNHP SNP 200W also possesses a well marked elongated wear facet on the labial side of its second cusp, which permits its attribution to the lower dental series.

Two wear facets can be observed on the lingual side of IRSNB R163. The first, triangular in shape, is located at the apex of the second cusp; the second facet is elongated on the third cusp. This is therefore probably an upper postcanine.

Roots

The roots can only be observed on the holotype and have been described in detail by Russell *et al.* (1976).

DISCUSSION

Russell *et al.* (1976) discuss in detail the affinities of the holotype MNHP SNP1W and emphasize the close resemblance of this tooth with those of the Late Triassic cynodont *Therioherpeton carogni* Bonaparte *et* Cabrera, 1975 and with those of *Sinoconodon rigneyi* Patterson *et* Olson, 1961. The latter genus is now clearly recognized as a true mammal, forming the sister-group of a monophyletic taxon that includes all the other

TABLE 4. — Measurements (in mm) of the postcanine teeth of *Meurthodon gallicus*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown.

Number	Lc	Wc	Hc	Lc/Wc
MNHP SNP1W	4.25	1.32	3.05	3.22
IRSNB 28114/005	2.17	0.8	> 2	2.71
IRSNB 28114/017	2.32	0.8	2.23	2.9
IRSNB R163	2.25	0.72	2.12	3.12
IRSNB 28114/040	3.9	1.1	> 2.1	3.54
IRSNB 28114/045	2.42	0.9	-	2.69
IRSNB 28114/056	2.6	0.87	> 1.85	2.99
IRSNB R162	4.25	1.35	2.9	3.15
IRSNB 28114/746	3.95	1.07	2.4	1.65
IRSNB 28114/754	2.98	0.9	-	3.31
IRSNB 28114/902	2	0.88	2.37	2.27
IRSNB 28114/993	2.48	-	2.1	-
MNHP SNP64W	3.53	0.97	2.25	3.64
MNHP SNP200W	1.85	0.8	1.43	2.31
MNHP SNP210W	3.02	1.01	2.7	2.99
MNHP SNP514W	2.67	0.89	2.17	3

mammals (Crompton & Luo 1993; Wible & Hopson 1993; Lucas & Luo 1993; Luo 1994). Sigogneau-Russell & Hahn (1994) group *Therioherpeton* and *Meurthodon* within the family Therioherpetidae. This family is thought to form the sister-group of the Dromatheriidae. Hahn *et al.* (1994) gather both genera within the family Dromatheriidae.

The new specimens discovered in Saint-Nicolas-de-Port permit a better understanding of the dental variability in *Meurthodon*. The postcanine teeth of *Meurthodon* are compared in detail with those of *Therioherpeton* and *Sinoconodon*, in order to clarify the affinities of the genus:

1. The presence of wear facets on the labial side or on the lingual side of the crowns attests that the material referred to *Meurthodon* includes upper and lower postcanines morphologically identical. This seems to be a usual character in the Dromatheriidae. The upper and lower postcanines seem also very similar in *Sinoconodon*. In *Therioherpeton*, the upper and the lower postcanines seem to be constructed following the same plan, but the poor preservation of the material prevents more precise comparisons.

2. In *Sinoconodon*, postcanine teeth lack differentiation into premolariform and molariform teeth (Crompton & Sun 1985). In adult dental formula, the single canine is separated from the first postcanine by a long diastema (Patterson & Olson 1961). The anterior postcanines are lost without replacement, resulting in an increasingly large postcanine diastema during ontogeny. At least two postcanines are added to the posterior end of the tooth row and at least one postcanine was replaced in older specimens (Crompton & Luo 1993). In *Therioherpeton*, the crowns of the anterior postcanines are not preserved, but the size of their alveolae are smaller than in the posterior molariform teeth. Their postcanine dentition was thus probably subdivided into premolariform and molariform teeth. Bonaparte & Barberena (1975) observed an alternate tooth replacement in this genus. In *Meurthodon*, only isolated teeth have been discovered: this prevents the identification of premolariform teeth in this genus (see below). Nevertheless, some teeth have a more slender

aspect than others: this can reflect their relative position in the dental series. The tooth replacement pattern is unknown in *Meurthodon*.

3. In *Meurthodon*, the roots of molariform teeth are fully separated on three quarters of their length, but fused proximally below the crown. In *Therioherpeton*, they are separated on the whole length, but connected by a thin sheet of dentine. In *Sinoconodon*, like in *Meurthodon*, the postcanine roots are divided only along their distal parts (Luo 1994, fig. 6.6).

4. In *Meurthodon*, the presence of small facets on the anterior and posterior parts of the crown reveals the contact between contiguous postcanines. In *Therioherpeton*, the distal postcanines have an oblique implantation, like in the Tritheledontidae: the anterior margin of the distal postcanine is placed antero-lingually to the posterior margin of the mesial tooth. The adjacent postcanines of *Sinoconodon* do not interlock with one another (Crompton & Luo 1993).

5. The postcanines of *Meurthodon* show wear facets. They do not seem constant, like in the Morganucodontidae or later mammals, indicating that the relations between lower and upper postcanines were not yet clearly defined. A stronger wear seems to affect the cusps of *Therioherpeton* (see Bonaparte & Barberena 1975). In *Sinoconodon*, the postcanine crowns lack wear facets, which is probably correlated to the absence of one-to-one alignment of the corresponding upper and lower molariforms (Crompton & Luo 1993; Luo 1994).

6. Tiny and very inconstant cingular elements can be observed on *Meurthodon* postcanines. *Therioherpeton* lacks cingulum or cingular accessory cusps. Some of the best preserved postcanines of *Sinoconodon* possess a faint labial cingulum on the uppers and a more distinct one on the posterolingual surface of the lowers (Crompton & Sun 1985; Crompton & Luo 1993).

7. In these three genera, the crown is laterally compressed and fundamentally tetracuspoid: the second cusp is the highest and the decreasing size of the distal cusps is regular. The cusps are proportionally higher and better defined in *Meurthodon* than in *Therioherpeton*, but this may be a result of a stronger wear in the latter genus (Sigogneau-Russell & Hahn 1994). The cusps do

not present backwards slope in *Therioherpeton*. The first cusp is independent from the second and the last two cusps are closer side by side than in *Meurthodon* (Russell *et al.* 1976). A fifth anterior accessory cusp can be observed on some postcanines in *Sinoconodon* (see Patterson & Olson 1961; Crompton & Sun 1985). The first cusp is usually better separated from the second than in *Meurthodon*. The last three cusps are also usually less inclined.

Comparisons with the advanced cynodont *Therioherpeton* and the primitive mammal *Sinoconodon*, whose dentition is most similar, reveal that the postcanine teeth of *Meurthodon* present a mosaic of plesiomorphic (low development of cingular elements) and apomorphic (better separated roots, wear facets, ? contacts between adjacent postcanines) characters. As this taxon is currently known only by its postcanine teeth, it is not possible to decide whether *Meurthodon* is a very advanced cynodont or a true early mammal. Waiting for further evidence, this genus is provisionally and questionably classified within the Dromatheriidae, as suggested by Hahn *et al.* (1994). This seems the most conservative course, in the present state of knowledge. Morphometrically, the dispersion diagram of the

postcanine teeth in *Meurthodon gallicus* shows a negative allometry between the width and the length of the crowns (Fig. 12): the allometry coefficient b , calculated according Tessier's (1948) formula, is 0.63. Pearson's correlation coefficient is high ($r = 0.89$) and this result can therefore be regarded as correct. This negative allometry reflects the cutting function of the postcanine teeth in *Meurthodon*. The correlation between the length and the height of the postcanine crowns is too low ($r = 0.63$) to permit a correct estimation of the allometry coefficient between these variables.

CYNODONTIA INCERTAE SEDIS
Genus *Habnia* n.g.

TYPE SPECIES. — *Habnia obliqua* n.sp.

DERIVATIO NOMINIS. — Dedicated to Prof. Dr. G. Hahn, for his contribution to the knowledge of Late Triassic cynodonts and early mammals from Lorraine.

DIAGNOSIS. — As for the only currently recognized species *Habnia obliqua* n.sp.

DISCUSSION

See under *Habnia obliqua* n.sp.

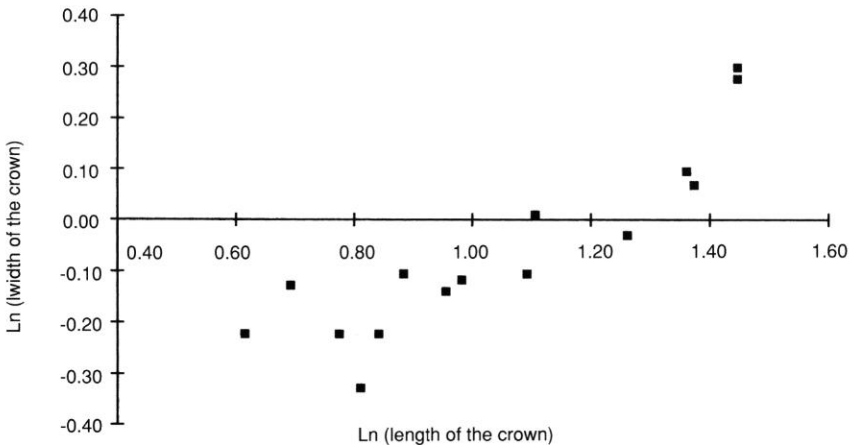


FIG. 12. — Dispersion diagram of the postcanine teeth in *Meurthodon*.

Hahnia obliqua n.sp.

(Fig. 13)

HOLOTYPE. — IRSNB R164, a left upper postcanine, with its root nearly completely preserved.

PARATYPES. — MNHP SNP50DD, a complete lower right postcanine; IRSNB 28114/102, MNHP SNP23 and MNHP SNP57, crowns without roots of upper postcanines.

DERIVATIO NOMINIS. — *obliquus*, -a, -um (lat.) = oblique. Refers to the vertical axis of the crown, inclined backwards.

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

STRATUM TYPICUM. — "Rhaetian" sandstones. Upper Triassic.

DIAGNOSIS. — Ratio "length/width" of the crown > 3. Vertical axis of the crown inclined backwards. Main cusp slightly curved towards the lingual side. Labial side of the crown clearly more convex than the lingual side. Elongated wear facets along the anterior and posterior cutting edges, on the upper postcanines. Base of the crown not constricted. Root semielliptical in outline, 1.5 to 2 times as high as the crown. Pulpal canal narrow and elliptical in outline.

DESCRIPTION

Measurements

Table 5 shows the measurements taken on the postcanine teeth of *Hahnia obliqua* from Saint-Nicolas-de-Port.

Crown

The crown is tricuspid and the enamel, perfectly smooth. In occlusal view, the crown is very compressed labio-lingually: 3 < ratio "length/width" of the crown < 3.65. The labial side is convex antero-posteriorly, while the lingual side is slightly concave. As in *Pseudotriciconodon*, the three cusps are perfectly aligned on the mesio-distal axis of the crown. Nevertheless, the edge is not as sharp as in the latter genus. On the upper postcanines, the edge is particularly blunt between the main cusp and the mesial cusp. The apex of the main cusp is rejected to the lingual side.

In anterior view, the main cusp is not perfectly straight, as in *Pseudotriciconodon*, but curved towards the lingual side, particularly in its upper portion.

In lingual view, the vertical axis of the crown is inclined backwards, forming an angle of approximately 15° with the vertical axis of the root. The

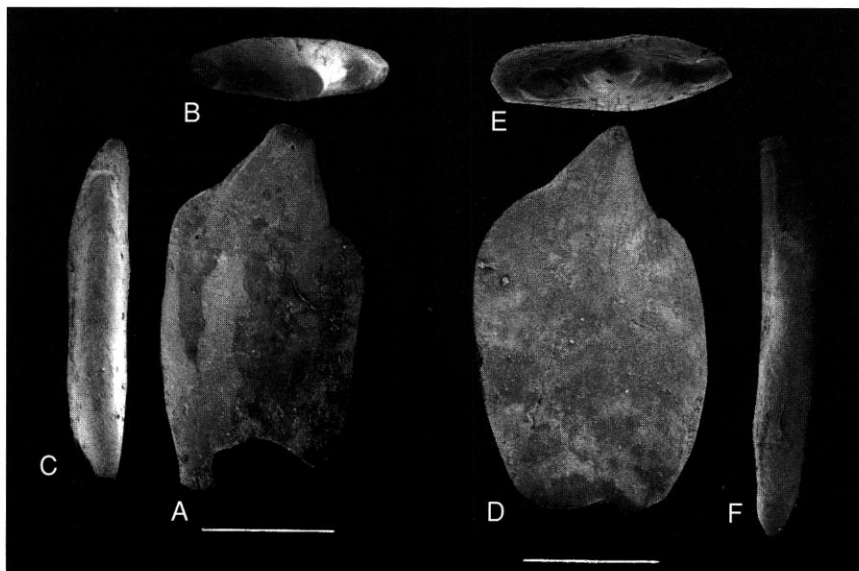


FIG. 13. — Postcanine teeth of *Hahnia obliqua*, from the Late Triassic of Saint-Nicolas-de-Port. A-C, IRSNB R164, upper postcanine; A, lateral view; B, occlusal view; C, anterior view. D-F, MNHP SNP50DD, lower postcanine; D, lateral view; E, occlusal view; F, posterior view. Scale bar: 1 mm.

TABLE 5. — Measurements (in mm) of the postcanine teeth of *Hahnia obliqua*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown; **Hr**, height of the root.

Number	Lc	Wc	Hc	Hr
IRSNB R164	1.6	0.45	1.15	2.1
IRSNB 28114/102	1.25	0.4	> 1.2	-
MNHP SNP50DD	1.82	0.5	1.25	1.9
MNHP SNP23	2.3	0.75	-	-

main cusp has a triangular outline; its anterior and posterior edges are straight, but its apex is always somewhat blunt. It is flanked by a pair of very blunt triangular accessory cusps. These are not well separated from the main cusp. Because of the backwards slope of the crown, the distal accessory cusp seems lower than the mesial cusp. In the upper postcanines, a well marked wear facet runs along the posterior edge, on the lingual side of the main cusp. This looks like an elongated, very narrow and mat surface. In IRSNB 28114/102 and MNHP SNP23, a second wear facet is present on the anterior edge of the main cusp; it is less marked and less long (stopping below the apex of the main cusp) than the first one. This facet is absent from IRSNB R164, but the anterior edge of the main cusp is very blunt. A third small facet is present on the lingual side of the apex of the main cusp. In MNHP SNP50DD, identified as a lower postcanine, a small wear facet is present on the labial side of the main cusp, in the middle of the anterior edge. There is no constriction between the crown and the root.

Root

The root is nearly complete in IRSNB R164 and complete in MNHP SNP50DD. In IRSNB R164, the root is nearly 2 times as high as the crown; in MNHP SNP50DD, the ratio "height of the root/height of the crown" = 1.5. In basal view, it is very compressed labio-lingually. Its labial side is slightly convex antero-posteriorly; the upper portion of its lingual side is flat and the lower portion is slightly concave. The pulpal foramen is small and elliptical in outline. It does not show any evidence of bipartition.

In lateral view, the root has a semi-elliptical outline. It gradually and symmetrically gets narrow towards the tip.

DISCUSSION

By their general morphology, these teeth are reminiscent of the small carnivorous cynodonts from the Upper Triassic: the crown is tricuspid, smooth, very narrow labio-lingually, with a cutting edge and without cingulum; the root is high and semielliptical in shape (Hahn *et al.* 1984). The affinities with the different families of Triassic carnivorous cynodonts are nevertheless difficult to establish. The main characters of the postcanine teeth in these families are reviewed below and compared with those of *Hahnia obliqua*.

Thrinaxodontidae

(Late Permian of South Africa and Russia, Early Triassic of South Africa)

In contrast with *Hahnia obliqua*, the postcanine teeth of the *Thrinaxodontidae* are not strictly sectorial, but possess an internal cingulum with small cusps (Hopson & Kitching 1972; Battail 1991). The lingual side of the upper postcanines does not bear marked wear facets.

Galesauridae

(Late Permian and Early Triassic of South Africa) Like in *Hahnia*, the postcanine teeth of the *Galesauridae* are devoid of cingulum. Nevertheless, in *Cynosaurus* Schmidt, 1927, they are less compressed labio-lingually and the anterior accessory cusp is less detached. In *Galesaurus* Owen, 1860, the postcanines are very compressed labio-lingually, but, in contrast with *Hahnia*, the main cusp is very curved backwards and there is no anterior accessory cusp (Battail 1991). The teeth do not bear marked wear facets (Crompton 1972).

Cynognathidae

(Early Triassic and Early Middle Triassic of South Africa and South America)

The *Cynognathidae* form a monogeneric family (Battail 1991). The postcanine teeth of *Cynognathus* Seeley, 1895 are similar to those of *Hahnia*: the crown is very compressed labio-lingually, devoid of cingulum and formed by a

high central cusp flanked by several accessory cusps perfectly aligned antero-posteriorly, forming a cutting edge. The vertical axis of the crown slopes backwards. The lingual side of the upper postcanines and the labial side of the lower postcanines bear marked wear facets (Crompton 1972). The root is undivided, but can be slightly depressed by a longitudinal furrow. Nevertheless, differences can be observed: in *Cynognathus*, the main cusp is curved backwards and somewhat serrated, especially in younger specimens.

Chiniquodontidae

(Lower Triassic of South Africa and Argentina, Middle Triassic of Tanzania, Argentina and Brazil, Upper Triassic of Argentina and Brazil)

In the Chiniquodontidae, the root of the postcanine teeth is never subdivided and can be separated from the crown by a well marked constriction. The presence of wear facets attests constant contacts between upper and lower postcanines, like in *Habnia*. The crowns of postcanine teeth are strictly sectorial, following the complete disparition of the cingulum, in *Probelesodon lewisi* Romer, 1969 and *Probainognathus jensei* Romer, 1970 (Battail 1989). The crowns of the postcanines, in *Probainognathus*, although very worn, are quite different from those of *Habnia*: the main cusp, low and weakly developed, is flanked by an anterior and a posterior cusp poorly developed. The edge formed by these cusps is sinuous and devoid of sharp points. Only the most posterior postcanines are tricuspid in *Probelesodon*: the anterior accessory cusp is always very low and poorly separated from the main cusp. The latter is very curved backwards.

Tritheledontidae

(Late Triassic of Argentina, Early Jurassic of South Africa and the USA)

In the Tritheledontidae, the crowns of the postcanine teeth are always less compressed labio-lingually than in *Habnia* and usually bear a cingulum (see Gow 1980).

Dromatheriidae

(Middle Triassic of Argentina, Late Triassic of Europe and the USA)

The postcanines of *Habnia* are very similar to those of *Pseudotriciconodon*: the crown is tricuspid, strictly sectorial without cingulum and very compressed labio-lingually; the cusps are perfectly aligned following the antero-posterior axis of the crown, forming a cutting edge; there is no constriction between the crown and the root; the root is semielliptical in outline and very compressed; the pulpal foramen is small and elliptical in outline. Marked wear facets are absent from *Pseudotriciconodon* postcanines, but are observed in *Tricuspes*. The backwards slope of the crown is an uncommon feature in species currently referred to the Dromatheriidae. The only true diagnostic character of the family Dromatheriidae is the subdivision of the root in posterior postcanines. This feature is not present in the two complete teeth currently discovered in *Habnia*. Nevertheless, the subdivision of the base of the root is very rare in the primitive Dromatheriidae *Pseudotriciconodon*.

Small carnivorous cynodonts incertae sedis

(Late Triassic of Europe)

In *Lepagia* Hahn, Wild *et* Wouters, 1987 and *Gaumia* Hahn, Wild *et* Wouters, 1987, the postcanine teeth are fundamentally tricuspid and strictly sectorial, without cingulum, like in *Habnia*. The root is always undivided. Contrary to *Habnia*, the crown is never inclined backwards, the main cusp is not curved to the lingual side and does not bear marked wear facets, in both genera. Moreover, the crown is well separated from the root by a marked constriction.

In the current state of knowledge, the phylogenetical position of *Habnia* within the infraorder Cynodontia seems difficult to establish. The structure of the postcanine teeth is similar to those of Cynognathidae, but the attribution to this family is very dubious, for want of true diagnostic characters in the postcanines: the *Cynognathus* Zone in South Africa (Spathian to Anisian, see Shishkin *et al.* 1995) and the Upper Triassic in Saint-Nicolas-de-Port are actually separated by a space of time of about 25 Ma. The postcanines of *Habnia* resemble those of the Dromatheriidae, too, but there is no trace of bipartition of the root in the material currently

discovered. Waiting for further evidences, *Hahnia* is thus referred to *Cynodontia incertae sedis*.

Genus *Gaumia* Hahn, Wild *et* Wouters, 1987

Gaumia Hahn, Wild *et* Wouters, 1987: 11.

TYPE SPECIES. — *Gaumia longiradicata* Hahn, Wild *et* Wouters, 1987.

OTHER REFERRED SPECIES. — *Gaumia* ? *incisa* Hahn, Wild *et* Wouters, 1987.

DIAGNOSIS. — Crown of the postcanine teeth “trico-dont”, more or less narrow, with the labial and lin-

gual sides nearly symmetrical. Axis of the crown perfectly vertical. Cusps not curved and more or less symmetrically arranged, the central cusp being the highest; cutting edge perfectly straight. No cingulum. Base of the crown constricted. Root triangular in outline and very high, at least 1.5 times as high as the crown. Tip of the root undivided; pulpal canal small and rounded to elliptical in outline.

Gaumia longiradicata Hahn,
Wild *et* Wouters, 1987
(Figs 14, 15)

Gaumia longiradicata Hahn, Wild *et* Wouters, 1987: 12, pl. 4, fig. 1, pl. 5, fig. 1. — Battail 1991: 89. — Sigogneau-Russell & Hahn 1994: 206, fig. 10.10b.

HOLOTYPE. — IRSNB “R.M.35”.

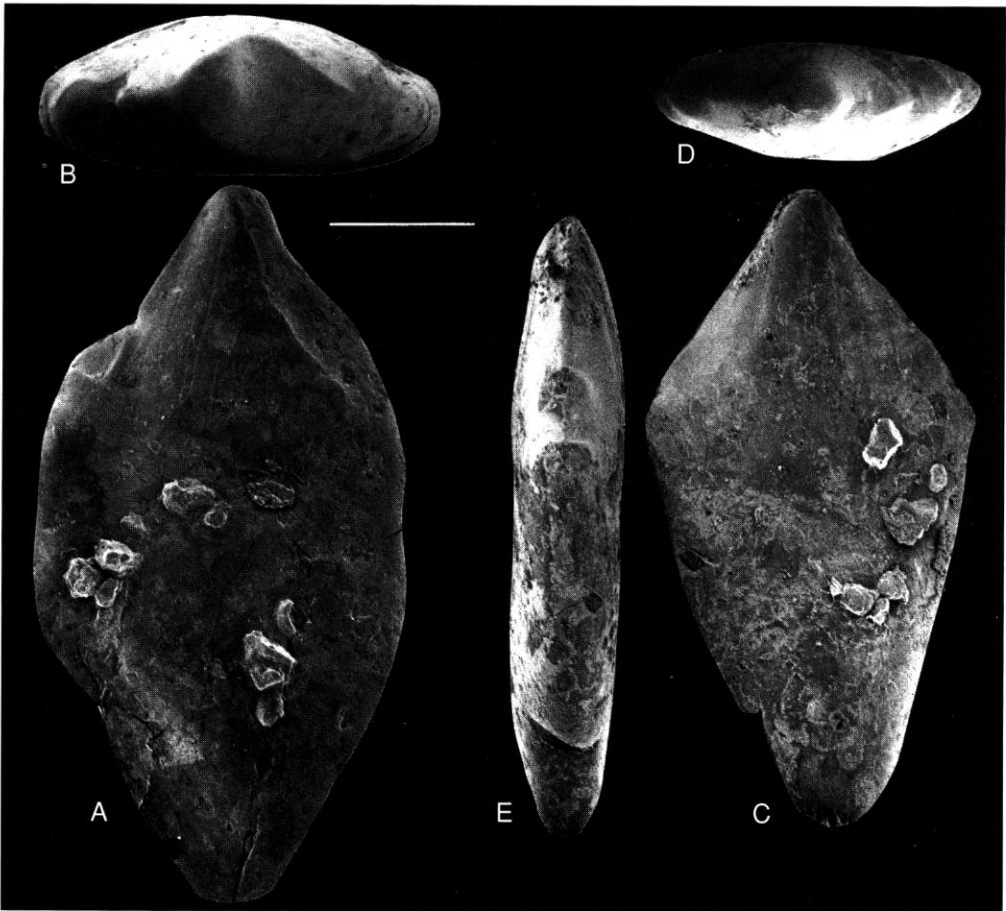


FIG. 14. — Postcanine teeth of *Gaumia longiradicata*, from the Late Triassic of Saint-Nicolas-de-Port. **A, B**, IRSNB R165; **A**, lateral view; **B**, occlusal view. **C-E**, IRSNB R166; **C**, lateral view; **D** occlusal view; **E**, ? anterior view. Scale bar: 1 mm.

PARATYPE. — IRSNB "R.M.36".

LOCUS TYPICUS. — Side of the highway E25-E411, at Habay-la-Vieille (Belgian Lorraine).

STRATUM TYPICUM. — Bone-bed "HLV-2", Grès de Mortinsart (Rhaetian, Upper Triassic).

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: IRSNB R165, IRSNB R166, IRSNB 28114/047, IRSNB 28114/055, IRSNB 28114/088, IRSNB 28114/090, IRSNB 28114/093, IRSNB 28114/646, IRSNB 28114/982, ? IRSNB 28114/771, MNHP SNP131L, MNHP SNP430W.

DIAGNOSIS. — Crown of postcanine teeth tri- to pentacuspoid and relatively thick: $2.1 < \text{ratio "length/width" of the crown} < 2.75$. First pair of accessory cusps (or median accessory cusps) not clearly individualized; second pair (lateral accessory cusp) more clearly separated. Smooth enamel on all cusps.

DESCRIPTION

Classification

The postcanine teeth of *Gaumia longiradicata* discovered in Saint-Nicolas-de-Port are classified according to the number and the position of the

accessory cusps, as in *Pseudotriciconodon wildi* (see above). The estimate of the number of accessory cusps is not always easy because these are usually weakly differentiated.

Measurements

The measurements taken on the postcanine teeth of *Gaumia longiradicata* discovered in Saint-Nicolas-de-Port are shown in table 6.

Crown

In *Gaumia longiradicata*, the postcanine crowns are perfectly smooth. In occlusal view, the crown is thicker than in *Pseudotriciconodon wildi* or in *Gaumia ? incisa*: $2.1 < \text{ratio "length/width" of the crown} < 2.75$. Both the labial and the lingual sides of the crown are convex at the level of the main cusp. The width of the crown progressively decreases towards the anterior and posterior ends. The cusps are perfectly aligned on the antero-posterior axis of the crown. Their edge, perfectly median and straight, is not as sharp as in *Pseudotriciconodon wildi* or in *Gaumia ? incisa*.

In anterior view, the main cusp is perfectly

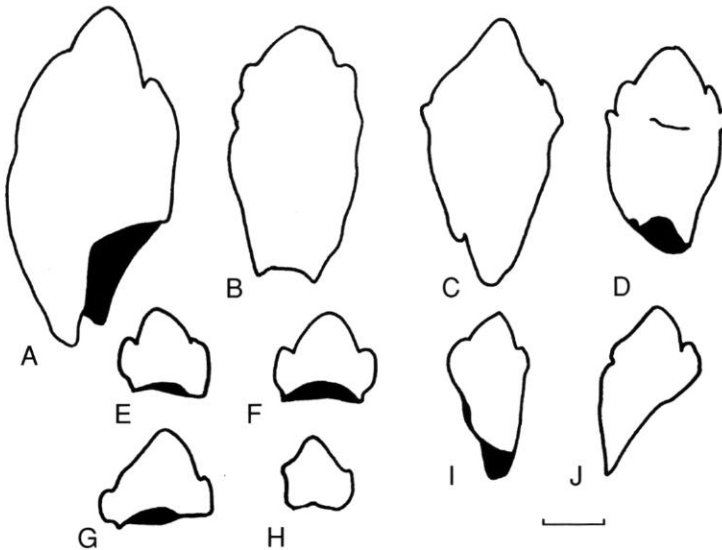


FIG. 15. — Outline of postcanine teeth of *Gaumia longiradicata*, from the Late Triassic of Saint-Nicolas-de-Port. A, IRSNB R165; B, IRSNB 28114/47; C, IRSNB R166; D, IRSNB 28114/982; E, IRSNB 28114/90; F, IRSNB 28114/93; G, IRSNB 28114/55; H, IRSNB 28114/88; I, IRSNB 28114/646; J, MNHP SNP131L. Scale bar: 1 mm.

TABLE 6. — Measurements (in mm) of the postcanine teeth of *Gaumia longiradicata*, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown; **Hr**, height of the root. For the signification of the groups, see text.

Group	Number	Lc	Wc	Hc	Hr	Lc/Wc	Hr/Hc
I	IRSNB 28114/047	1.95	0.75	1.4	2.75	2.6	1.96
	IRSNB 28114/088	1.2	0.5	0.85	-	2.4	-
	IRSNB 28114/090	1.5	0.65	1.2	-	2.31	-
	IRSNB 28114/093	1.7	0.8	1.3	-	2.12	-
	IRSNB 28114/646	1.9	0.7	1.1	>1.6	2.71	>1.5
	MNHP SNP131L	1.67	0.61	? 1.18	-	2.73	-
	MNHP SNP430W	1.32	0.53	-	-	2.49	-
?	IRSNB R165	1.6	0.71	2	3.3	2.26	1.65
II	IRSNB 28114/055	1.9	0.75	1.8	-	2.53	-
IV	IRSNB 28114/982	1.95	0.75	1.5	>1.9	2.6	>1.27
IV ?	IRSNB R166	2.3	0.9	1.8	2.65	2.56	1.47

straight, not curved to the lingual side of the crown.

In lateral view, the main cusp has a triangular outline and is specially broad: its base occupies nearly the full length of the crown. Its borders are straight to slightly concave. Its apex is less sharp than in *Pseudotricodon wildi*. The median pair of accessory cusps is set along the lower third of the main cusp. These are not very developed and always very blunt: they can be separated from the main cusp by an indentation which is not very deep (IRSNB 28114/093,

IRSNB R165), or can be presented as a vague undulation of the edges of the main cusp (IRSNB 28114/047, IRSNB 28114/646). When the lateral accessory cusps are present, they are set at the base of the crown, quite anteriorly and/or posteriorly. These lateral accessory cusps are very small (less than one tenth of the height of the main cusp), narrow, but better differentiated than the median accessory cusps.

Wear is apical and very erratic, as in *Pseudotricodon wildi*. It does not form clearly marked wear facets. The crown and the root are

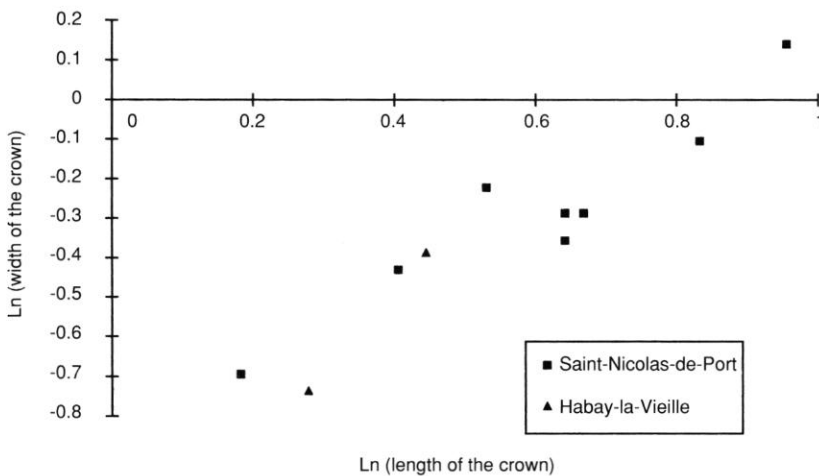


FIG. 16. — Dispersion diagram of the postcanine teeth in *Gaumia longiradicata*.

clearly separated by a constriction.

Root

The root is preserved in IRSNB 28114/047, IRSNB 28114/646, IRSNB R165, IRSNB 28114/982, IRSNB R166 and MNHP SNP131L. In anterior view, the root is less narrow and thus, more robust than in *Pseudotriconodon wildi*. This explains the higher proportion of preserved roots in *Gaumia longiradicata*. The root is much higher than the crown: the ratio "height of the root/height of the crown" varies between 1.47 (IRSNB R166) and 1.96 (IRSNB 28114/047). It has, in lateral view, a subtriangular outline: its length lessens quickly and symmetrically towards the tip. Its anterior and posterior borders are straight (IRSNB 28114/913) to slightly convex (IRSNB 28114/047, IRSNB R165, IRSNB 28114/982). The tip of the root is rounded and pierced by a small rounded to elliptical pulpal foramen: this pulpal canal is never double, as in *Pseudotriconodon wildi*.

In IRSNB R166, the anterior (?) border of the root is naturally truncated at the level of its lower third. A small lunulate foramen is visible at the level of the truncature. As this feature can be observed in only one specimen, it is not possible to know whether this represents a second pulpal foramen or more simply an isolated anomaly of the root.

DISCUSSION

Gaumia resembles *Pseudotriconodon* in the general aspect of the crown of its postcanines. However, the base of the crown is constricted and the root is higher and subtriangular in outline. The absence of bipartition of the root suggests that *Gaumia* is not a member of the family Dromatheriidae. The presence of a second pulpal foramen in IRSNB R166 needs to be confirmed by future discovery of additional specimens showing this feature. The absence of true apomorphies in the postcanine dentition of *Gaumia* leads to consider this genus as a *Cynodontia incertae sedis* (see Hahn *et al.* 1987; Battail 1991).

The postcanine teeth discovered in Saint-Nicolas-de-Port can be referred to the species

Gaumia longiradicata Hahn, Wild *et* Wouters, 1987: their crown is relatively thick and the enamel is perfectly smooth on all cusps. These teeth cannot be morphometrically distinguished from the type material discovered in Habay-la-Vieille (Fig. 16). In this species, the length and the width of the crown are isometrical ($b = 0.99$; $r = 0.94$). The dental crowns referred to *Gaumia* ? *incisa* Hahn, Wild *et* Wouters, 1987 are significantly narrower and enamel ridges are present on the lingual side of the main cusp. Peyer (1956, pl. 9, figs 18, 27, 34, 44 and 47) describes several teeth from the Upper Triassic of Hallau (Switzerland) that can be referred to the genus *Gaumia*. They are characterized by few indistinct enamel ridges on both the lingual and the labial sides of the main cusp: they probably belong to a new undescribed species (Sigogneau-Russell & Hahn 1994).

Genus *Lepagia* Hahn, Wild *et* Wouters, 1987

Lepagia Hahn *et al.*, 1987: 5.

TYPE SPECIES. — *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987.

DIAGNOSIS. — As for the only currently recognized species, *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987.

Lepagia gaumensis

Hahn, Wild *et* Wouters, 1987
(Figs 17, 18)

Lepagia gaumensis Hahn *et al.*, 1987: 7, fig. 2, pl. 1, fig. 1, pl. 2, figs 1, 2. — Battail 1991: 89. — Sigogneau-Russell & Hahn 1994: 206, fig. 10, 10a.

"Zähne von wahrscheinlich synapsiden Reptilien, Gruppe a" (Peyer 1956: 56, *partim*, pl. 5, fig. 66, pl. 10, fig. 68).

"Zahn eines synapsiden Reptiles" (Kindlimann 1984: 3, fig. 4).

HOLOTYPE. — IRSNB "R.M.28".

PARATYPES. — IRSNB "R.M.29" and IRSNB "R.M.30".

LOCUS TYPICUS. — Side of the speedway E25-E411, at Habay-la-Vieille (Belgian Lorraine).

STRATUM TYPICUM. — Bone-bed “HLV-2”, Grès de Mortinsart (Rhaetian, Upper Triassic).

NEW HYPOTYPES. — From Saint-Nicolas-de-Port: IRSNB R167, IRSNB 28114/051, ? IRSNB 28114/104.

DIAGNOSIS. — Crown of the postcanine teeth long, narrow ($2.5 < \text{ratio “length/width” of the crown} < 3.7$) and tricuspid to pentacuspoid; labial and lingual sides of the crown slightly convex and nearly parallel; cutting edge of the cusps perfectly straight. Crown asymmetrical in lateral view. Axis of the crown perfectly vertical. No cingulum. Base of the crown very constricted. The root, nearly rectangular in lateral view and subequal in height to the crown, does not taper distally. Pulpal canal restricted to a long and narrow slit. Horizontal ramus of the mandible very low. Splenial very thin, extending halfway up on the lingual side of the dentary.

DESCRIPTION

Orientation

As in *Pseudotriciconodon wildi* (see above).

Measurements

Measurements taken on the postcanine teeth of *Lepagia gaumensis* discovered in Saint-Nicolas-de-Port are shown in table 7.

Crown

The crown is perfectly smooth in IRSNB 28114/051 and IRSNB R167; some indistinct enamel ridges are present on the labial side of the apex of the main cusp, in IRSNB 28114/104. In occlusal view, the crown is rather long and narrow: the ratio “length/width” of the crown varies between 2.5 and 3.5 in the teeth discovered in Saint-Nicolas-de-Port. The labial and lingual borders are nearly parallel: the labial side is somewhat more convex than the lingual one. The cusps are perfectly aligned following the antero-posterior axis of the crown; they form a sharp cutting edge.

In anterior view, the main cusp is perfectly straight and not curved towards the lingual side.

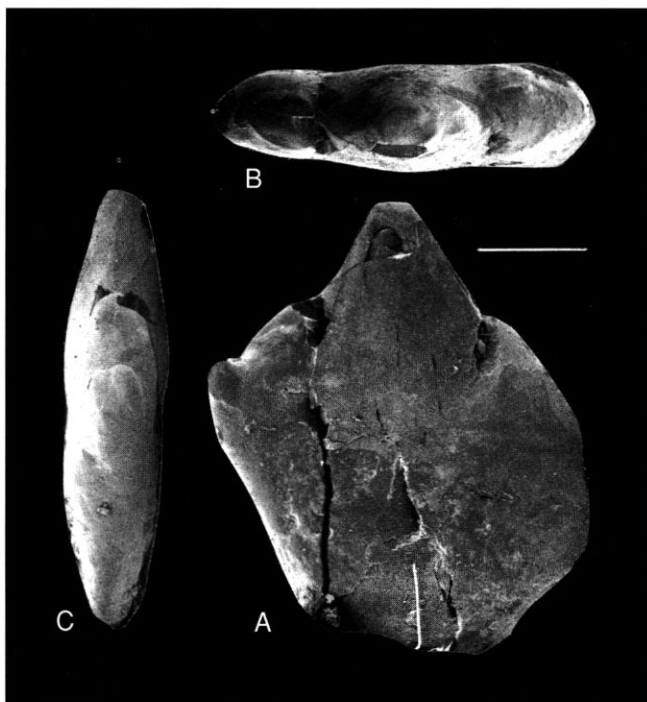


FIG. 17. — IRSNB R167, postcanine tooth of *Lepagia gaumensis*, from the Late Triassic of Saint-Nicolas-de-Port. A, lateral view; B, occlusal view; C, ? anterior view. Scale bar: 1 mm.

TABLE 7. — Measurements (in mm) of the postcanine teeth of *Lepagia gaumensis*, from the Late Triassic of Saint-Nicolas-de-Port. Lc, length of the crown; Wc, width of the crown; Hc, height of the crown; Hr, height of the root. For the signification of the types, see text.

Group	Number	Lc	Wc	Hc	Hr	Lc/Wc	Hr/Hc
? II	IRSNB 28114/051	1.25	0.5	? 0.95	1	2.5	1.05
IV	IRSNB R167	3.65	1.05	2.7	1.7	3.47	0.63
	IRSNB 28114/104	2.65	0.85	1.8	-	3.12	-

In lateral view, the crown is more irregular, less symmetrical than in *Pseudotriciconodon* or *Gaumia*. The main cusp, triangular in shape, is proportionally less high and its apex is less sharp than in the latter genera. It is flanked by one or two anterior, and by one or two posterior accessory cusps. In IRSNB 28114/104 and IRSNB R167, which possess two pairs of accessory cusps, the anterior accessory cusps are set higher on the edge of the main cusp than the posterior accessory cusps. The first pair of accessory cusps (median accessory cusps) is rather large, but not very sharp; on the other hand, the second pair (lateral accessory cusps) is smaller, but sharper. The crown of IRSNB 28114/051 is very eroded. Its main cusp seems slightly inclined backwards; the anterior accessory cusp is small but very sharp, whereas the posterior one appears as a vague undulation of the posterior edge of the main cusp.

As in *Pseudotriciconodon* and *Gaumia*, wear is erratic on the apex of the cusps and does not form clearly defined facets. There is no trace of cingulum. The crown and the root are separated by a well marked constriction.

Root

The root is undivided and never clearly higher than the crown: the ratio “height of the root/height of the crown” is about 1.05 in IRSNB 28114/051 and 0.63 in IRSNB R167. In anterior view, it is always very narrow. In lateral view, the root of IRSNB R167 has an irregular trapezoidal outline. Its length is greater than its height. Its anterior border is straight and oblique backwards and its posterior border is clearly convex. The root of IRSNB 28114/051 is proportionally higher; its anterior and posterior borders are slightly convex and nearly parallel.

The tip of the root is well preserved in IRSNB R167. It is long and nearly straight. The pulpal foramen is restricted to a long, very narrow and undivided slit.

DISCUSSION

IRSNB 28114/051 and IRSNB R167 are similar to the postcanine teeth of *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987 from the Rhaetian of Habay-la-Vieille (Belgian Lorraine) and Hallau (Switzerland): the crown is asymmetrical and irregular, there is a well marked constriction

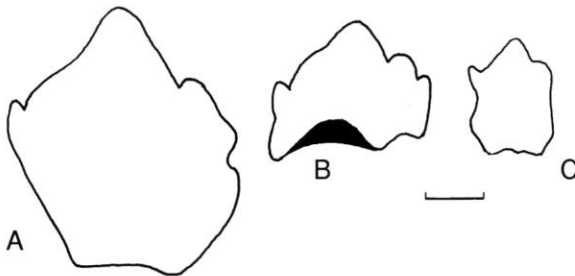


FIG. 18. — Outline of postcanine teeth of *Lepagia gaumensis*, from the Late Triassic of Saint-Nicolas-de-Port. A, IRSNB R167; B, IRSNB 28114/104; C, IRSNB 28114/51. Scale bar: 1 mm.

between the crown and the root, the root is proportionally low and subtrapezoidal, the pulpal canal is a long and narrow slit.

The identification of IRSNB 28114/104 is more problematical because of its broken root. The shape of the crown resembles that of *Lepagia gaumensis*, but erratic enamel ridges can be observed on the labial side of the apex of the main cusp. Nevertheless, this character is too poorly expressed to justify the creation of a new species. Waiting for further evidence, this tooth is tentatively identified as *Lepagia gaumensis*.

Hahn *et al.* (1987) compare the mandible of *Lepagia gaumensis* with that of *Probainognathus*: in both taxa, the splenial is very narrow and extends

halfway up on the lingual side of the dentary. As a result of this comparison, *Lepagia* is grouped within the family Chiniquodontidae. Battail (1989) observed a comparable reduction of the splenial in all the other families of advanced cynodonts, correlatively to the development of the dentary. Moreover, the horizontal ramus of the mandible is much lower in *Lepagia* than in the Chiniquodontidae and is rather reminiscent of the mandible of the Dromatheriidae. Nevertheless, the root of the postcanine teeth is not subdivided in *Lepagia*, as in the Dromatheriidae. Thus, in the current state of our knowledge, it is not possible to state precisely the systematic position of *Lepagia gaumensis* within the Cynodontia.

TABLE 8. — Measurements (in mm) of the cynodont premolariform teeth, from the Late Triassic of Saint-Nicolas-de-Port. **Lc**, length of the crown; **Wc**, width of the crown; **Hc**, height of the crown. For the signification of the forms, see text.

Form	Number	Lc	Wc	Hc	Lc/Wc	Lc/Hc
1	IRSNB 28114/029	1.4	0.65	-	2.15	-
	IRSNB 28114/032	1.45	0.58	1.9	2.5	0.76
	IRSNB 28114/039	1.13	0.68	1.43	1.66	0.79
	IRSNB 28114/114	1.25	0.55	-	2.27	-
	IRSNB 28114/116	1.4	0.65	-	2.15	-
	IRSNB 28114/118	1.05	0.6	1.2	1.75	0.87
	IRSNB 28114/119	1.25	0.7	1.47	1.79	0.85
	IRSNB 28114/120	1.65	0.88	2.3	1.87	0.71
	IRSNB R168	2.4	1.2	3.95	2	0.61
	IRSNB 28114/755	1.9	0.85	-	2.24	-
	IRSNB 28114/765	1.87	1	2.48	1.87	0.75
	IRSNB 28114/904	2.15	1.25	2.82	1.72	0.76
	IRSNB 28114/911	1.12	0.57	>1.58	1.96	> 0.7
	IRSNB 28114/973	1.5	0.98	1.83	1.53	0.82
	IRSNB 28114/000	2.13	1.25	?	1.7	?
	IRSNB 18114/925	1.68	1	?	1.68	?
	MNHP SNP83DD	2.37	1.15	3.27	2.06	0.72
	MNHP SNP58W	1.52	0.7	-	2.17	-
	MNHP SNP136W	0.95	0.53	1.05	1.79	0.9
	MNHP SNP159W	1.32	0.5	1.5	2.64	0.88
	MNHP SNP214W	1.73	0.98	-	1.76	-
	MNHP SNP215W	1.28	0.64	1.57	2	0.82
	MNHP SNP282W	0.73	0.35	1.05	2.09	0.7
	MNHP SNP328W	0.7	0.32	0.77	2.18	0.91
	MNHP SNP342W	0.88	0.48	-	1.83	-
	MNHP SNP395W	2.04	1.1	3.11	1.85	0.66
	MNHP SNP402W	2.21	-	3.24	-	0.68
	MNHP SNP404W	1.57	0.77	-	2.04	-
	MNHP SNP443W	0.58	0.33	0.68	1.76	0.85
	MNHP SNP451W	1.3	0.51	-	2.55	-
	MNHP SNP468W	2.15	1.16	3.28	1.85	0.66
	2	IRSNB R169	1.5	0.65	-	2.3
MNHP SNP95L		1.07	0.35	-	3.05	-
MNHP SNP12W		2.19	1.19	-	1.84	-
MNHP SNP85W		1.39	0.68	1.49	2.04	0.93
3	IRSNB R170	2.15	1	3.8	2.15	0.57
	IRSNB R171	2.25	1.05	1.9	2.14	1.18
4	IRSNB 28114/877	0.75	0.18	-	4.17	-
5	IRSNB 28114/877	0.75	0.18	-	4.17	-
6	MNHP SNP484W	1.8	0.47	1.42	3.83	1.27

PREMOLARIFORM TEETH INCERTAE SEDIS

Teeth with a slender crown composed by a high anterior cusp and by a small posterior accessory cusp are described and discussed in the present chapter. Biometrical data observed on these teeth are shown in table 8. Six categories can be distinguished, on the basis of the general morphology of their crown.

Form 1
(Figs 19A, B, 20)

MATERIAL EXAMINED. — Specimens discovered in Saint-Nicolas-de-Port: IRSNB R168, IRSNB 28114/000, IRSNB 28114/029, IRSNB 28114/032, IRSNB 28114/039, IRSNB 28114/114, IRSNB 28114/116, IRSNB 28114/118, IRSNB 28114/119, IRSNB 28114/120, IRSNB 28114/755, IRSNB 28114/765, IRSNB 28114/904, IRSNB 28114/911,

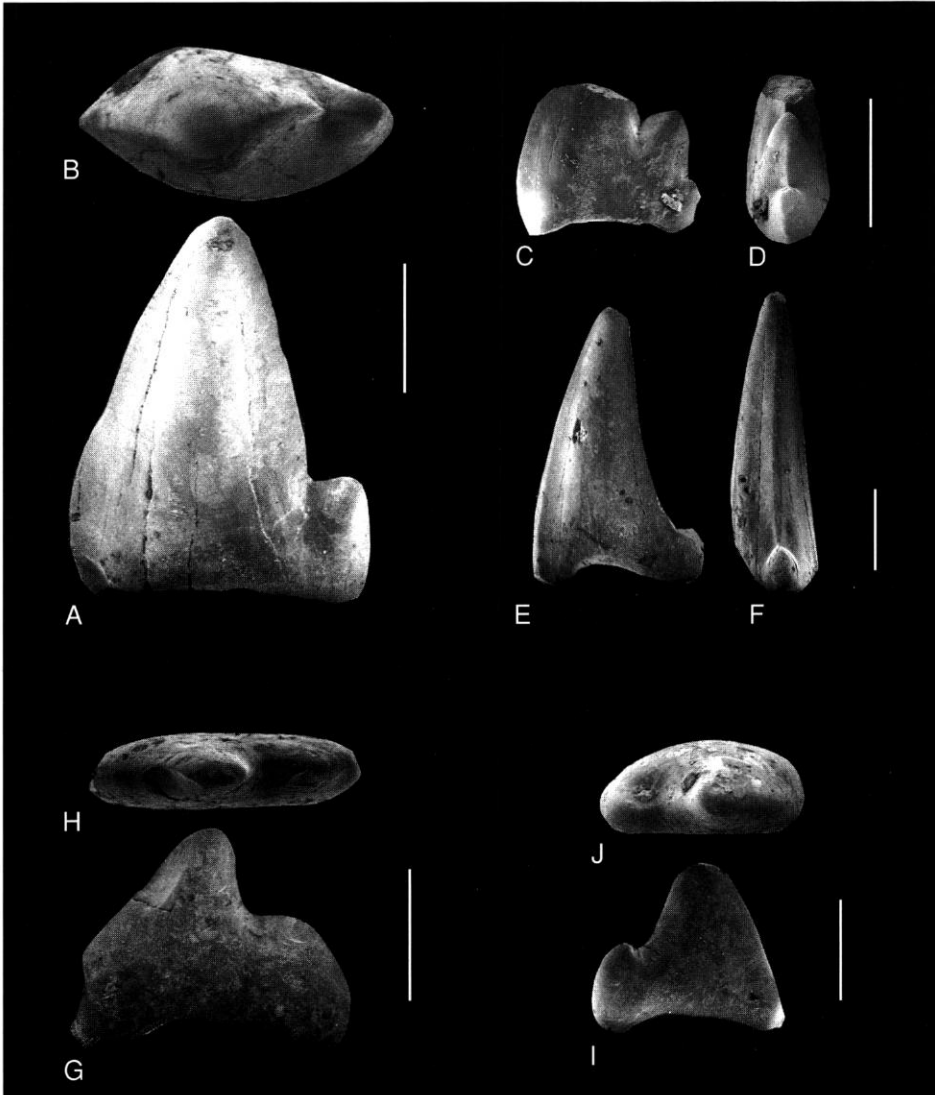


FIG. 19. — Cynodont premolariform teeth, from the Late Triassic of Saint-Nicolas-de-Port. **A, B**, IRSNB R168, form 1; **C, D**, IRSNB R169, form 2; **E, F**, IRSNB R170, form 3; **G, H**, MNHP SNP484W, form 6; **I, J**, IRSNB R171, form 4. **A, C, E, G, I**, lateral views; **B, H, J**, apical views; **D, F**, posterior views. Scale bars: 1 mm.

IRSNB 28114/925, IRSNB 28114/973, MNHP SNP72DD, MNHP SNP83DD, MNHP SNP58W, MNHP SNP136W, MNHP SNP159W, MNHP SNP214W, MNHP SNP215W, MNHP SNP282W, MNHP SNP328W, MNHP SNP342W, MNHP SNP395W, MNHP SNP402W, MNHP SNP404W, MNHP SNP443W, MNHP SNP451W, MNHP SNP468W.

DESCRIPTION

Premolariform teeth of form 1 are, by far, the most numerous. The crown is rather slender ($0.61 < \text{ratio "length/height" of the crown} < 0.93$), but their base is relatively robust ($1.53 < \text{ratio "length/width" of the crown} < 2.55$).

The main cusp is high and has a triangular outline in lateral view. It is curved backwards and slightly towards the lingual side. Its apex is rather sharp on the highest crowns, but more rounded on the smallest teeth. Nevertheless, it must be noted that the apex of the cusp can be partially eroded. Its anterior border is very convex: its base is usually thinner than its apical portion which can form a flattened edge. Its posterior edge is less convex, but very sharp along its whole height. Its labial side is convex antero-posteriorly. Its lingual side forms a central convex ridge, flanked by an anterior and a posterior concave third. The posterior concavity is usually better marked than the anterior one.

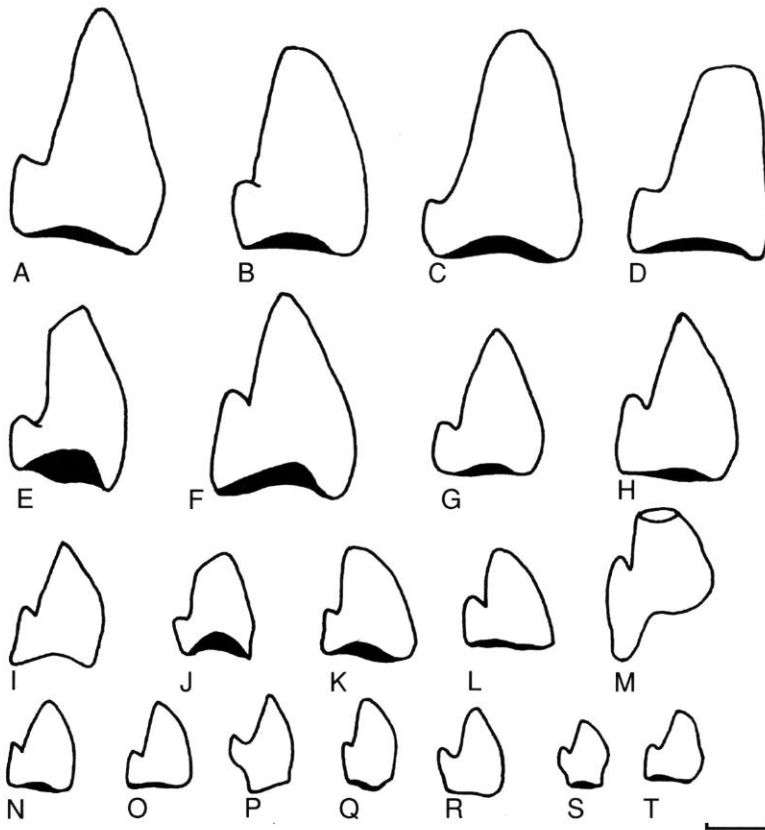


FIG. 20. — Outline of cynodont premolariform teeth (form 1), from the Late Triassic of Saint-Nicolas-de-Port. **A**, IRSNB R168; **B**, MNHP SNP395W; **C**, MNHP SNP468W; **D**, MNHP SNP492W; **E**, MNHP SNP58W; **F**, MNHP SNP83DD; **G**, IRSNB 28114/765; **H**, IRSNB 28114/904; **I**, IRSNB 28114/32; **J**, IRSNB 28114/29; **K**, IRSNB 28114/973; **L**, IRSNB 28114/648; **M**, MNHP SNP214W; **N**, IRSNB 28114/39; **O**, IRSNB 28114/119; **P**, MNHP SNP342W; **Q**, MNHP SNP382W; **R**, MNHP SNP136W; **S**, MNHP SNP443W; **T**, MNHP SNP78. Scale bar: 1 mm.

The posterior accessory cusp is always very reduced and triangular in lateral view. Its maximum height can reach the third of the height of the main cusp. Its apex is not very sharp. Its vertical axis usually slopes backwards.

Wear can affect the apex of the cusps, but does not form clearly defined facets. The crown is distinctly separated from the root by a constriction, particularly well marked on the anterior and the posterior sides of the teeth (MNHP SNP342W, MNHP SNP443W, MNHP SNP451W). The root is not preserved in the premolariform teeth discovered in Saint-Nicolas-de-Port.

DISCUSSION

Premolariform teeth of form 1 appear, at first sight, morphometrically heterogeneous: the small crowns seem proportionally much lower than the taller ones. Figure 22 shows the relative growth of the length (in Ln) and the height (in Ln) of the crown in the premolariform teeth discovered in Saint-Nicolas-de-Port. The coefficient of correlation calculated for the teeth of form 1 is astonishingly high: $r = 0.985$. The allometry coefficient b , calculated according to Teissier's (1948) formula, is 1.21. The apparent morphometrical heterogeneity of these teeth can therefore be easily explained by the positive allometry between the length and the height of the crown: the height grows more quickly than the length. Figure 23 shows that the length and the width of

the crown, in the premolariform teeth of form 1, can be regarded as isometrical: $b = 1.05$; $r = 0.94$. In conclusion, it can be assumed that the morphometrical variability observed in these teeth reflects ontogenetical differences and/or the position in the jaw, instead of taxonomic heterogeneity.

Form 2 (Figs 19C, D, 21A-C)

MATERIAL EXAMINED. — Specimens discovered in Saint-Nicolas-de-Port: IRSNB R169, MNHP SNP 95L, MNHP SNP12W, MNHP SNP85W.

DESCRIPTION

The premolariform teeth grouped in form 2 differ from the other forms by a second small accessory cusp, posteriorly. It is very reduced and reaches only the quarter of the height of the first accessory cusp. The proportions of the crown are similar to those observed in the premolariform teeth of form 1 (see Table 8, Figs 22, 23). The asymmetry between the lingual and the labial sides of the main cusp is less marked than in the premolariform teeth of form 1. In anterior view, the main cusp is slightly curved towards the lingual side of the tooth. Hahn *et al.* (1994) describe a well defined wear facet on the labial side of MNHP SNP12W: this is therefore a lower premolariform tooth. The base of the anterior

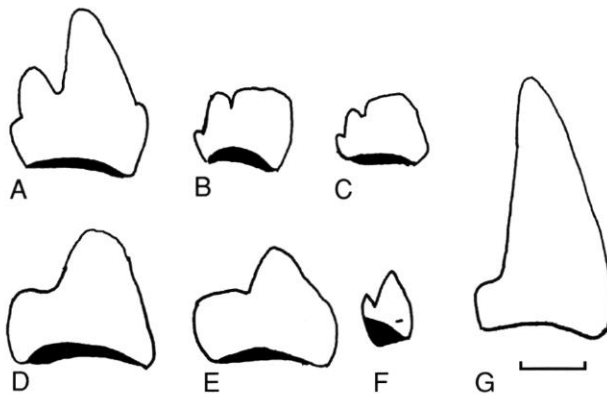


FIG. 21. — Outline of cynodont premolariform teeth, from the Late Triassic of Saint-Nicolas-de-Port. **A**, MNHP SNP85W (form 2); **B**, IRSNB R169 (form 2); **C**, MNHP SNP95L (form 2); **D**, IRSNB R1471 (form 4); **E**, MNHP SNP484W (form 6); **F**, IRSNB 28114/877 (form 5); **G**, IRSNB R170 (form 3). Scale bar: 1 mm.

border of the main cusp is very sharp in IRSNB R169. In MNHP SNP85W, a small swelling on the base of the anterior edge of the main cusp can tentatively be interpreted as the rough shape of an anterior accessory cusp. The base of the crown is clearly separated from the root by a constriction, as in the premolariform teeth of form 1. The root is not preserved in the known material.

DISCUSSION

Hahn *et al.* (1994) refer SNP 12W to *Tricuspes sigogneauae*. This identification is mainly based on the position of the second accessory cusp, on the posterior wall of the crown. Nevertheless it seems that, in the present case, this character mainly reflects the low development of this cusp. Thus, because of the important diversity of the cynodont fauna from Saint-Nicolas-de-Port, this identification is doubtful, in the absence of jaw fragments associating both premolariform and molariform teeth (see below).

The morphological differences observed between the premolariform teeth of form 1 and form 2 can perhaps be interpreted as differences of position in the tooth row: premolariform teeth of form 1 should be set in a more anterior position than premolariform teeth of form 2.

Form 3 (Figs 19E, F, 21G)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R170.

DESCRIPTION

IRSNB R170 is characterized by its very high, slender and caniniform crown: the ratio “length/height” of the crown is 0.57 (see Fig. 22). On the other hand, the ratio “length/width” of the crown, which is 2.15, has a usual value, as in the premolariform teeth of form 1 or 2. Both the labial and the lingual sides of the main cusp are nearly symmetrically convex. The main cusp has, in lateral view, a triangular outline and is curved backwards. Its apex is slightly blunt. Its posterior edge is very sharp. Its anterior border forms a flattened edge, on its whole height. Along the anterior border of its lingual side, it bears a long, elliptical and flatten wear facet. If the orientation proposed for this tooth is correct, it is thus an upper premolariform. The posterior accessory cusp is tiny: it is only represented by a small swelling at the base of the posterior border of the main cusp. The root is not preserved.

DISCUSSION

The very slender aspect of the crown (see

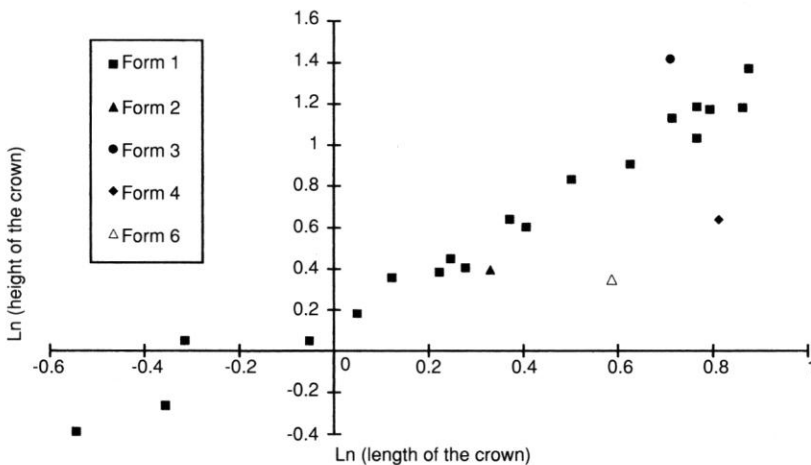


FIG. 22. — Dispersion diagram (length/height) of the cynodont premolariform teeth.

Fig. 22) and the tiny posterior accessory cusp distinguish IRSNB R170 from the other premolariform teeth discovered in Saint-Nicolas-de-Port. These differences could reflect a more anterior position of this specimen in the tooth row of the animal. Nevertheless the presence of a well marked wear facet, not observed in the premolariform teeth of forms 1 and 2, indicates that this tooth probably belongs to another taxon.

Form 4
(Figs 19I, J, 21D)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R171.

DESCRIPTION

Contrary to IRSNB R170, this tooth is very stocky: the ratio “length/height” of the crown is 1.18. The ratio “length/width” of the crown, which is 1.14, is usual, as in the other forms of premolariform teeth previously described. The labial and lingual sides of the crown are quite asymmetrical: the labial side is very convex antero-posteriorly and the lingual one, straight. The main cusp is low, stocky and triangular in outline. Its apex is rounded and bears a small elliptical wear facet, showing the dentine, on its labial

side. If the orientation proposed for this tooth is correct, IRSNB R171 is thus a lower premolariform. Both the anterior and posterior edges of the main cusp are not very sharp. The posterior accessory cusp, weakly developed and very rounded, reaches the quarter of the height of the main cusp. At the junction between the two cusps, the labial side of the crown bears a small dimple. The root is not preserved.

DISCUSSION

Figure 22 shows that this tooth is morphometrically different from the other premolariform teeth discovered in Saint-Nicolas-de-Port (except MNHP SNP484W) because of its low and stocky crown. The very rounded apex of the cusps is an unusual feature, too.

Form 5
(Fig. 21F)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB 28114/877.

DESCRIPTION

This fragmentary dental crown is very small and extremely thin: the ratio “length/width” of the crown is 4.17. The main cusp has, in lateral

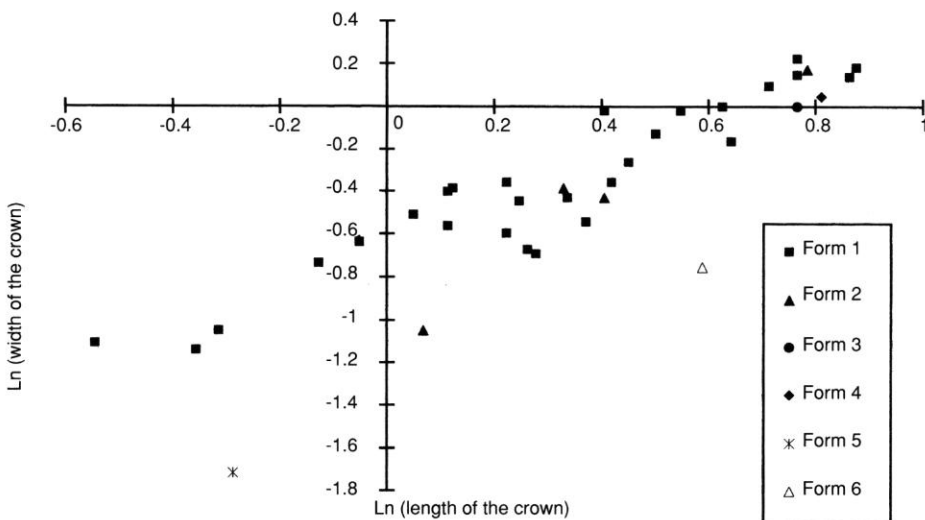


Fig. 23. — Dispersion diagram (length/width) of the cynodont premolariform teeth.

view, a triangular outline and is rather elongated antero-posteriorly. Its apex is very sharp and both its anterior and posterior edges are extremely sharp, too. The anterior edge is slightly longer than the posterior one and, therefore, the main cusp slopes slightly backwards. The posterior accessory cusp is triangular and very sharp, too. It reaches the half of the height of the main cusp. The base of the crown is broken, but seems particularly high.

DISCUSSION

IRSNB 28114/877 differs from the other premolariform teeth discovered in Saint-Nicolas-de-Port because of its extremely narrow crown (see Fig. 23) and its very sharp edges.

Form 6 (Figs 19G, H, 21E)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: MNHP SNP484W.

DESCRIPTION

MNHP SNP484W is characterized by its proportionally long, low and narrow crown: the ratio “length/width” of the crown is 3.83 and the ratio “length/height” of the crown, 1.27. Both the labial and the lingual sides of the crown are symmetrically antero-posteriorly convex. The edge is sharp on the whole length of the crown. The main cusp is short, not very high and triangular in outline. Both its anterior and posterior cutting edges are slightly convex. Its apex is rather rounded. The posterior accessory cusp is quite low and rounded, but very elongated antero-posteriorly. At the base of the anterior edge of the crown, an elliptical flattened surface, showing the dentine, probably represents a contact facet with the anterior adjacent crown in the tooth row. The base of the crown seems constricted.

DISCUSSION

MNHP SNP484W is clearly different from the other premolariform teeth discovered in Saint-Nicolas-de-Port: the proportions of the crowns are unusual (see Figs 22, 23), the main cusp is very short and low, the accessory cusp is propor-

tionally very long and the contact area, at the base of the crown, is not present in the other specimens. Consequently, it probably belongs to another taxon.

AFFINITIES OF PREMOLARIFORM TEETH FROM SAINT-NICOLAS-DE-PORT

Premolariform teeth similar to those discovered in Saint-Nicolas-de-Port have been described in primitive pterosaurs, Triassic cynodonts and early mammals.

Pterosaurs

Teeth similar to premolariforms discovered in Saint-Nicolas-de-Port are described in the pterosaur *Eudimorphodon ranzii* (Wild 1978). These are formed by a main cusp slightly curved backwards, with a sharp-pointed apex and a very sharp edge, and by a small posterior accessory cusp. Nevertheless, the enamel bears numerous longitudinal ridges and the crown is less compressed labio-lingually. “Premolariform” teeth of *Eudimorphodon* are preserved in the Upper Triassic of Saint-Nicolas-de-Port, too (Godefroit & Cuny, in prep.).

Cynodonts

The general pattern of premolariform teeth discovered in Saint-Nicolas-de-Port can be observed in several groups of Triassic cynodonts.

Thrinaxodontidae. In *Thrinaxodon liorhinus* Seeley, 1895, from the Early Triassic of South Africa, the most anterior upper postcanines are compressed labio-lingually and bicuspid, with an anterior main cusp and a posterior accessory cusp. Nevertheless, these always bear a well developed lingual cingulum (Battail 1991).

Galesauridae. In *Galesaurus* Owen, 1860, from the Early Triassic of South Africa, both the upper and the lower postcanines are compressed labio-lingually, bicuspid, without distinct anterior accessory cusp and without cusped cingulum (Battail 1991). Nevertheless, they differ from the premolariform teeth from Saint-Nicolas-de-Port in their main cusps very curved backwards and in their posterior accessory cusp proportionally higher.

Cynognathidae. In *Cynognathus crateronotus*

Seeley, 1895, from the Early Triassic and Early Middle Triassic of South Africa, the postcanine teeth are always compressed labio-lingually, very sharp and devoid of cingulum. In the largest specimens, the most anterior postcanines are very similar to the premolariform teeth from Saint-Nicolas-de-Port, with a high main cusp slightly curved backwards and a small posterior accessory cusp. Nevertheless these teeth are clearly larger in *Cynognathus*. The juvenile specimens have a more complex postcanine structure (Battail 1991).

Chiniquodontidae. Sectorial and bicuspid postcanine teeth can be observed in *Probelesodon lewisi* Romer, 1969 and *Probainognathus jenseni* Romer, 1970, from the Middle Triassic of Argentina. In *Probainognathus*, the main cusp is very low and not very developed and, moreover, the edge of the crown is sinuous, without well defined accessory cusp. The postcanine teeth of *Probelesodon* are typically bicuspid: only the most posterior postcanines possess an anterior accessory cusp. Nevertheless, the main cusp is always more curved backwards than in the premolariform teeth from Saint-Nicolas-de-Port.

Tritheledontidae. If bicuspid dental crowns are present in *Pachygelenus monus* Watson, 1913, *Tritheledon riconoi* Broom, 1912 and *Diarthrognathus broomi* Crompton, 1958, from the Late Triassic of South Africa, these teeth are never as strictly sectorial as in the premolariform teeth from Saint-Nicolas-de-Port.

Dromatheriidae. The postcanine teeth of the Dromatheriidae are always strictly sectorial, without developed cingulum and with a cutting edge. In *Dromatherium sylvestre* Emmons, 1857, from the Late Triassic of the United States, some postcanines seem typically bicuspid: the posterior accessory cusp is either smaller than the main cusp or almost of the same size. The root is always double and, contrary to the premolariform teeth discovered in Saint-Nicolas-de-Port (at least in the forms 1, 2 and 6), there is no constriction between the crown and the root. It is interesting to observe that, in *Dromatherium*, these "pre-molariform" teeth are set more posteriorly than the tricuspid teeth. Premolariforms are not recorded in other species, only known by very fragmentary material or by isolated teeth. As

explained above, the premolariform teeth attributed to *Tricuspes sigogneauae* by Hahn *et al.* (1994) are here more cautiously referred to *Cynodontia* indet.

Early mammals

Morganucodontidae. (Rhaetian and Early Liassic of Western Europe, Groenland, China and South Africa). Morganucodontidae are represented in Saint-Nicolas-de-Port by isolated molars of *Brachyostrodon coupatezi* Sigogneau-Russell, 1983 and *Brachyostrodon maior* Hahn, Sigogneau-Russell *et* Godefroit, 1991. Other taxa are also present but have not been described yet. In the Morganucodontidae, the premolariform teeth present a similar structure as those discovered in Saint-Nicolas-de-Port.

In *Morganucodon* Kühne, 1949 the premolars are formed by two cusps, as in the premolariforms discovered in Saint-Nicolas-de-Port. Nevertheless, the crown is less narrow labio-lingually and the anterior side is rounded and sometimes even bulbous. The main cusp is more elongated antero-posteriorly. A weak cingulum seems always present. The root is double (Mills 1971; Kermack *et al.* 1973; pers. obs.).

In *Megazostrodon rudnerae* Crompton *et* Jenkins, 1968, pm2 and PM4 are bicuspid and they seem devoid of cingulum. Nevertheless, they clearly differ from premolariform teeth discovered in Saint-Nicolas-de-Port by their more stocky and bulbous appearance (see Crompton 1974, figs 4-6).

In *Erythrotherium parringtoni* Crompton, 1964, pm2 and pm3 resemble the premolariform teeth from Saint-Nicolas-de-Port in being bicuspid and apparently devoid of cingulum. Nevertheless, as in the other Morganucodontidae, these teeth look less sectorial and more bulbous.

Kuehneotheriidae. (Rhaetian and Early liassic of Western Europe, Groenland and India). Theria are represented, in Saint-Nicolas-de-Port, by the Woutersiidae *Woutersia* Sigogneau-Russell, 1983 and by other undescribed Kuehneotheriidae. Premolars are known in the Kuehneotheriidae *Kuehneotherium praecursoris* Kermack, Kermack *et* Mussett, 1968. They differ from the premolariform teeth discovered in

Saint-Nicolas-de-Port by their more elongated and more curved main cusp and also by the frequent presence of a small anterior accessory cusp and of cingular elements.

CONCLUSIONS

From the preceding comparisons, it appears that the premolariform teeth discovered in Saint-Nicolas-de-Port have evident affinities with the cynodonts. In the other groups of reptiles, only the pterosaur *Eudimorphodon* has dental crowns with a similar structure, but with numerous and well marked enamel ridges. In the early mammals Morganucodontidae and Kuehneotheriidae, the crowns of the premolars are more bulbous and usually possess cingular elements.

The premolariform teeth from Saint-Nicolas-de-Port do not show clear diagnostical characters allowing their strict identification at the family level. The attribution of several premolariform teeth to the species *Tricuspes sigogneauae*, proposed by Hahn *et al.* (1994), is here regarded as doubtful. The absence of preserved root is particularly determinant. The morphological and morphometrical variability of the crown permits the distinction of six "forms". This heterogeneity probably reflects the presence of several taxa in this material. If dromatheriids had alternating (and continuous) replacements like in *Therioherpeton*, it can not be excluded that premolariform teeth represent, in fact, replaced deciduous teeth, which must be numerous in the fossil sample.

GOMPHODONT CYNODONTS

Family TRAVERSODONTIDAE von Huene, 1936

PRELIMINARY REMARKS

Hopson (1984, 1985) thinks that the Traversodontidae represent a paraphyletic group: he believes that the ancestry of the family Tritylodontidae lies within it. Therefore, the Traversodontidae are not strictly monophyletic, but rather represent a grade group. On the other hand, Battail (1991) recognizes the Traversodontidae as a monophyletic group: the Tritylodontidae should form the sister-group of the Traversodontidae.

It is interesting to note that the Traversodontidae, known by complete skull material, are relatively small forms in the late Early Triassic (*Pascualgnathus*, *Andescynodon*...), medium-sized forms in the early Middle Triassic (*Scalenodon*, *Massetognathus*...) and large to very large forms in the late Middle Triassic and in the early Late Triassic (*Exaeretodon*, *Ischignathus*, *Scalenodontoides*...). It is therefore rather surprising to find, in deposits dated from the very end of the Triassic, tiny teeth which, on the basis of their structure, seem to be attributable to traversodontids. It cannot be excluded, however, that the taxonomic position of these forms might be re-evaluated, should more complete material reveal major anatomical differences with the typical, well known Traversodontidae.

Genus *Maubeugia* n.g.

TYPE SPECIES. — *Maubeugia lotharingica* n.sp.

DERIVATIO NOMINIS. — Dedicated to Dr. P.-L. Maubeuge, for his contribution to the knowledge of the geology and palaeontology of the Lorraine area and for his active participation in the exploration of the quarry of Saint-Nicolas-de-Port.

DIAGNOSIS. — As for the only currently recognized species *Maubeugia lotharingica* n.sp.

DISCUSSION

See below.

Maubeugia lotharingica n.sp.

(Figs 24, 25)

HOLOTYPE. — IRSNB R172, a left upper postcanine, with its root nearly completely preserved.

DERIVATIO NOMINIS. — *lotharingicus*, -a, -um (lat.) = from Lorraine (north-eastern France).

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

STRATUM TYPICUM. — "Rhaetian" sandstones. Upper Triassic.

DIAGNOSIS. — Traversodontidae known by only one upper postcanine tooth, with the following characters: crown very small (width = 0.80 mm) with an ovoid

outline in occlusal view (ratio "length/width" of the crown = 0.80); labial side longer, but less convex than the lingual side. Main labial cusp somewhat higher than the lingual one. Transverse ridge set behind the middle of the crown, but not merged with the posterior cingulum; anterior basin consequently larger than the posterior basin. Well developed central cusp on the transverse ridge, close to the labial main cusp and separated from the lingual cusp by an embayment. Large antero-labial accessory cusp connected to the main labial cusp by a prominent ridge. Both anterior and posterior "cingula" very low and very poorly expressed.

DESCRIPTION

Orientation

The orientation of IRSNB R172 proposed here is mainly based on comparisons with the upper postcanines of *Scalenodon charigi* Crompton, 1972 and *Boreogomphodon jeffersoni* Sues et Olsen, 1990, which closely resemble this tooth. In the Traversodontidae, the upper postcanines are clearly wider (labio-lingually) than long (mesio-distally). As in advanced Traversodontidae, the transverse ridge of IRSNB R172 is set behind the middle of the tooth and the anterior basin is therefore better developed than the posterior one. The buccal side is longer and less convex than the lingual side. A tall accessory cusp is set on the antero-labial margin of the crown. Thus, IRSNB R172 is a left upper postcanine.

Measurements

Length of the crown (= maximum mesio-distal diameter) = 0.65 mm; width of the crown (= maximum labio-lingual diameter) = 0.80 mm.

Crown

In occlusal view, the crown is subovoid in outline, wider than long (the ratio "length/width" of the crown = 0.81). The labial border is longer, but less convex than the lingual one; the anterior border is more convex than the posterior one. Three cusps are arranged to form a transverse row. The lingual cusp seems the widest and the central cusp is by far the smallest. The central cusp is closer to the labial cusp. The three main cusps are connected together by a transverse ridge. This ridge is set in a posterior position, behind the middle of the crown. A very large accessory cusp, nearly as wide as the labial cusp,

is set on the antero-labial margin of the crown. The edges of both the main and the accessory labial cusps form a continuous ridge, parallel to the labial side of the crown. Very low ridges, respectively parallel to the anterior and the posterior margins of the crown, connect, on one hand, the accessory labial to the lingual cusps and, on the other hand, the main labial to the lingual cusps. A wide anterior basin is surrounded by the lingual side of the accessory labial cusp, by the antero-lingual side of the main labial cusp, by the anterior side of the central cusp and by the antero-labial side of the lingual cusp. A smaller and less well defined posterior basin occupies a corresponding position behind the transverse ridge: it is surrounded by the postero-lingual side of the main labial cusp, by the posterior side of the central cusp and by the postero-labial side of the lingual cusp.

In labial view, the main and the accessory labial cusps are separated from each other by a shallow indentation. The accessory cusp is somewhat lower than the main one. Their apices are very rounded. At the level of their junction, the anterior side of the crown forms a very small basin. The crown is separated from the root by a well marked constriction.

In lingual view, the lingual cusp seems lower than the main labial cusp, and its apex seems less rounded. At the base of the crown, a small, elliptical and deep depression can be observed. This is probably due to post-mortem distortion of the specimen.

In anterior view, the crown has a bell-mouthed outline. Both labial and lingual sides are convex dorso-ventrally; the lingual wall is somewhat more convex than the labial one. The main labial cusp is the highest. It is connected to the central cusp by a prominent ridge with anterior wall nearly vertical. The central cusp is separated from the lingual cusp by a rather deep indentation. The transverse ridge passes on the labial side of the lingual cusp. The crest connecting the accessory labial cusp to the lingual cusp ("anterior cingulum") is quite low and forms tiny undulations. The constriction between the crown and the root is very clearly marked.

In posterior view, the posterior wall of the portion of the transverse ridge connecting the labial

and the central cusps is less vertical than the anterior wall. The ridge connecting the main labial and the lingual cusps ("posterior cingulum") is very low and not very developed.

Root

The tip of the root is broken. Complete, the root was probably much higher than the crown. In lingual view, it is subrectangular in shape: its anterior and posterior sides are straight and nearly parallel. In anterior view, the root is gently tapering to the tip. The posterior border is more oblique than the anterior one.

DISCUSSION

The morphology of the upper postcanines is very variable in the Traversodontidae: therefore, they are very useful to establish the phylogenetical relationships of the different genera within this

family (Battail 1989). Thus, it is interesting to compare IRSNB R172 with the upper postcanines in currently known traversodonts.

Pascualgnathus Bonaparte, 1966

Andescynodon Bonaparte, 1969

Rusconiiodon Bonaparte, 1970

(Lower Triassic of Argentina)

The upper postcanines of these small and primitive Traversodontidae share several plesiomorphic characters (Battail 1989). Contrary to IRSNB R172, the transverse ridge connecting the labial and the lingual cusps is set anteriorly, in the anterior part of the crown. The posterior basin is consequently larger than the anterior one. There is no trace of central cusp. An accessory cusp is present, posteriorly to the main labial cusp. Both the anterior and the posterior cingula are well developed.

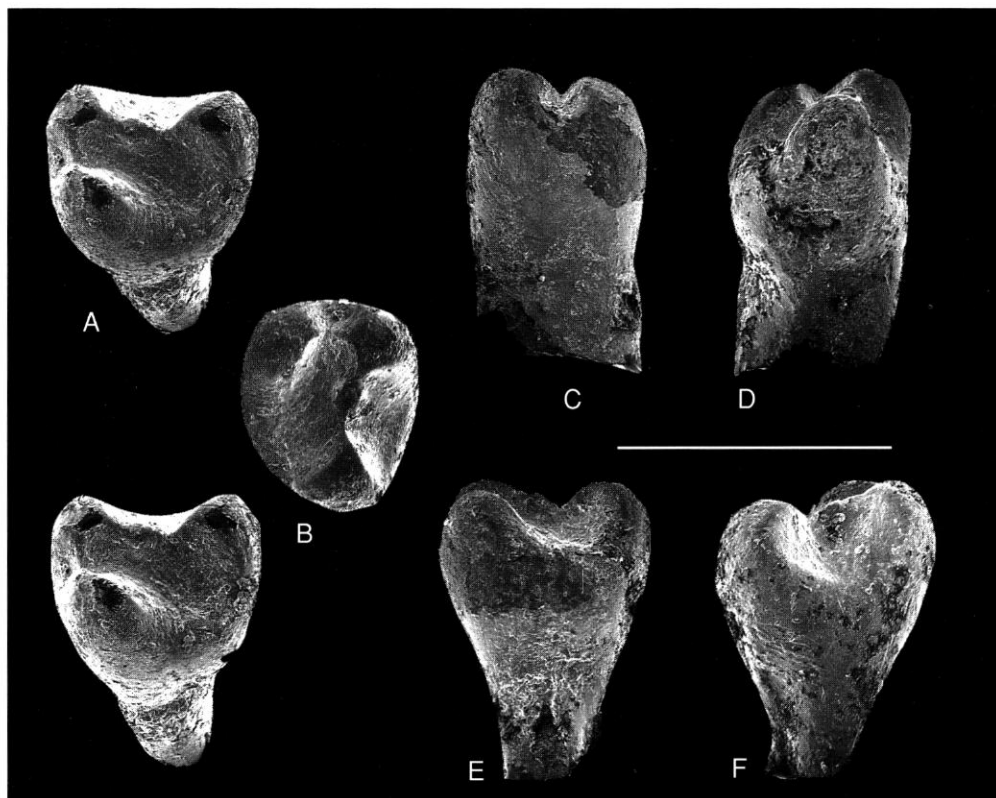


FIG. 24. — IRSNB R172, left upper postcanine of *Maubeugia lotharingica*, from the Late Triassic of Saint-Nicolas-de-Port. A, stereophotographs; B, occlusal view; C, labial view; D, lingual view; E, anterior view; F, posterior view. Scale bar: 1 mm.

Scalenodon Crompton, 1955

(Middle Triassic of Tanzania, Zambia and ? Russia)

The different species in the genus *Scalenodon* (*sensu* Battail 1991) differ mainly from each other in the structure of their postcanine teeth. The differences observed in the Tanzanian species are summarized by Crompton (1972, table 1). The transverse ridge is always set posteriorly, behind the middle of the crown, like in IRSNB R172. The anterior basin is therefore much larger than the posterior basin. In several species, the transverse ridge, quite posteriorly set, merges with the posterior cingulum and the posterior basin is consequently lost. Except in *Scalenodon charigi* Crompton, 1972, the transverse ridge supports a well developed central cusp. The anterior and posterior cingula are

more or less developed in the different species of *Scalenodon*. Antero-labial and/or antero-lingual accessory cusps are occasionally present. The upper postcanines of *Scalenodon* differ from IRSNB R172 in several details. The crown, much larger, is always proportionally wider. The labial side is usually more convex than the lingual one. The central cusp is set more lingually: it is connected to the lingual cusp by a prominent ridge and separated from the labial cusp by a deep embayment.

Massetognathus Romer, 1967

(Middle Triassic of Argentina)

In *Massetognathus*, the transverse ridge is set quite posteriorly and merges with the posterior cingulum; it supports a central cusp, close to the lingual cusp. The posterior basin is consequently

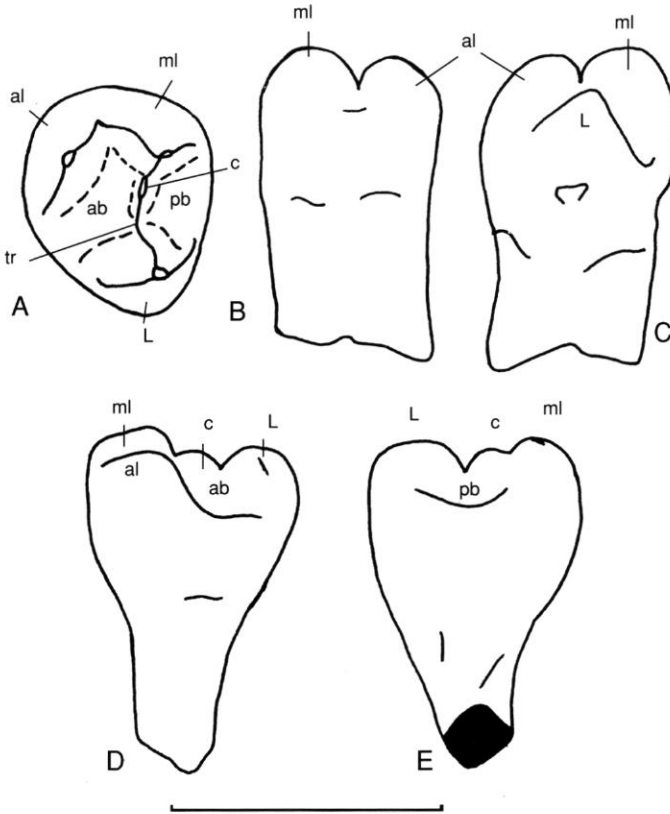


FIG. 25. — IRSNB R172, left upper postcanine of *Maubeugia lotharingica*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **ab**, anterior basin; **al**, antero-labial cusp; **c**, central cusp; **L**, lingual cusp; **ml**, main labial cusp; **pb**, posterior basin; **tr**, transverse ridge. Scale bar: 1 mm.

lost, but the anterior basin is enlarged. A large accessory cusp is set anteriorly and slightly lingually to the labial main cusp. The lingual wall of the crown looks therefore oblique. The labial side of the crown is very convex antero-posteriorly.

Traversodon von Huene, 1936

(Upper Triassic of Brazil)

In this large Traversodontidae, the upper postcanines are proportionally much wider than in IRSNB 28114/113. The transverse ridge connecting the labial and the lingual cusps is set behind the middle of the crown and the anterior basin is somewhat larger than the posterior one. Contrary to IRSNB 28114/113, the lingual cusp is much higher than the labial one and there is neither central cusp nor accessory cusp.

Gomphodontosuchus von Huene, 1928

(Upper Triassic of Brazil)

In this genus, the transverse ridge connecting the lingual and the labial main cusps forms the posterior wall of the crown and is devoid of central cusp. A labial and a lingual accessory cusps are set on the anterior margin of the crown and connected to the corresponding main cusp by a low ridge. The labial cusps are clearly set more anteriorly than the lingual ones. The anterior basin surrounded by these four cusps is particularly enlarged, but not very deep.

Exaeretodon Cabrera, 1943

(Upper Triassic of Argentina, Brazil and India)

Ischignathus Bonaparte, 1963

(Upper Triassic of Argentina)

The upper postcanines of these large Traversodontidae are formed by two main cusps connected by a low posterior transverse ridge, concave posteriorly and oblique. The main labial cusp is set much more anteriorly than the main lingual cusp. An accessory lingual cusp is set in front of the main lingual cusp. An accessory labial cusp forms an anterior lobe accommodated in the posterior concavity of the anterior adjacent tooth. Therefore, the crown of the upper postcanines has, in occlusal view, a characteristic geniculate outline. An accessory posterior cusp can occasionally be developed. The central cusp is apparently absent. The anterior basin is more or

less enlarged in the different species.

Arctotraversodon Sues, Hopson *et* Shubin, 1992

(Upper Triassic of Canada)

The upper postcanines of this large Traversodontidae are very large and very compressed mesio-distally. The transverse ridge connecting the labial and the lingual cusps forms the posterior wall of the crown and supports a prominent central cusp. It is close to the lingual cusp and separated from the labial cusp by a deep embayment. There is no anterior accessory cusp. The anterior cingulum is well developed.

Microscalenodon Hahn, Lepage *et* Wouters, 1988

(Upper Triassic of Belgium)

The upper postcanines of *Microscalenodon* are, as IRSNB R172, very small. The crown is very compressed mesio-distally and its morphology is quite simple: a large lingual cusp and a small labial cusp are connected by a transverse ridge forming the posterior wall of the crown, without central cusp, accessory cusp and anterior cingulum.

Boreogomphodon Sues *et* Olsen, 1990

(Upper Triassic of the USA)

The upper postcanines of this genus closely resemble IRSNB R172. They are very small, less than 5 mm wide. The labial side is longer and less convex than the lingual one. The transverse ridge, set behind the middle of the crown, supports a well developed central cusp. A large antero-labial accessory cusp is connected to the main labial cusp by a prominent ridge. The anterior ridge ("anterior cingulum") connecting the accessory labial cusp to the lingual cusp is very low and poorly developed. Nevertheless, they differ in several details. The crown is proportionally wider in *Boreogomphodon*. The transverse ridge is set more posteriorly and the posterior basin is consequently lost. The central cusp is close to the lingual cusp and separated from the labial cusp by a deep embayment.

From these detailed comparisons with the upper postcanines in the different genera of Traversodontidae, it appears that IRSNB R172 shows an original set of morphological characters

justifying its attribution to a separate new genus:

- The crown is ovoid in occlusal view and not very compressed mesio-distally.
- The transverse ridge is set behind the middle of the crown, but does not participate in the posterior wall of the crown. The anterior basin is larger than the posterior basin.
- The transverse ridge supports a well developed central cusp, close to the labial cusp and separated from the lingual cusp by a deep embayment.
- The antero-labial accessory cusp is particularly well developed and connected to the main labial cusp by a prominent ridge.
- The tooth is very small.

In the structure of its upper postcanines, *Maubeugia* more closely resembles *Scalenodon* and *Boreogomphodon* than any other taxon. Figure 26 illustrates the possible phylogenetic relationships between the different genera of Traversodontidae. Although discovered in Late Triassic out-

cropp, *Maubeugia* looks, in the structure of its upper postcanines, rather “primitive”. This cladogram, modified from Battail (1989, fig. 128), only reflects the modifications in the structure of the upper postcanines and is, therefore, very restrictive. A more definitive assessment of the phylogeny of the Traversodontidae must await an analysis of the whole skeleton in these gomphodont cynodonts.

Genus *Rosieria* n.g.

TYPE SPECIES. — *Rosieria delsatei* n.sp.

DERIVATIO NOMINIS. — From the type locality Rosières-aux-Salines.

DIAGNOSIS. — As for the only currently recognized species *Rosieria delsatei* n.sp.

DISCUSSION

See under *Rosieria delsatei* n.sp.

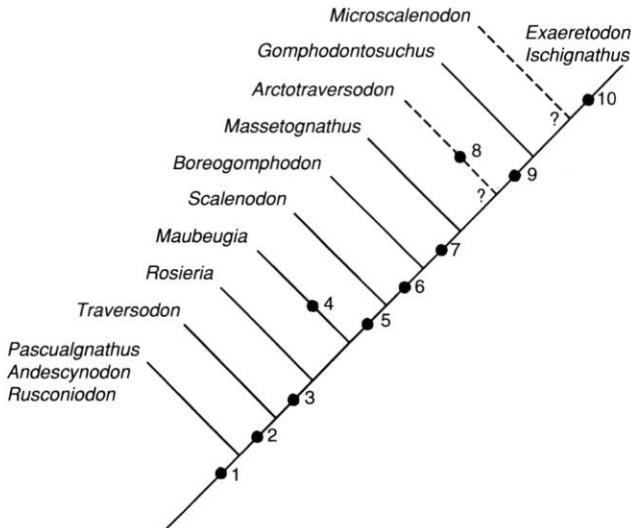


FIG. 26. — Possible phylogeny of the Traversodontidae, following the modifications of the structure of their upper postcanines (after Battail 1989, modified). 1, upper postcanines mainly formed by one main lingual cusp and one main labial cusp, connected together by a transverse ridge; presence of cingula in front of and behind the transverse ridge; presence of one postero-labial accessory cusp. 2, disparition of the postero-labial accessory cusp; transverse ridge set behind the middle of the crown. 3, formation of a basin in front of the transverse ridge; apparition of one antero-labial accessory cusp. 4, central cusp connected to the main labial cusp. 5, central cusp connected to the lingual cusp. 6, transverse ridge merging with the posterior cingulum. 7, antero-labial accessory cusp displaced medially. 8, upper postcanines very compressed mesio-distally. 9, development of a central basin; apparition of one antero-lingual accessory cusp. 10, transverse ridge concave backwards; geniculate outline of the upper postcanines.

***Rosieria delsatei* n.sp.**
(Figs 27, 28)

HOLOTYPE. — IRSNB R173, an upper left postcanine, root not preserved.

DERIVATIO NOMINIS. — Dedicated in honour to Dr. D. Delsate, for his active palaeontological field-work in Lorraine and adjacent areas.

LOCUS TYPICUS. — Quarry at Rosières-aux-Salines, region of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France).

STRATUM TYPICUM. — “Rhaetian” sandstones. Upper Triassic.

DIAGNOSIS. — Traversodontidae known by one upper postcanine tooth, with the following characters: crown very small (width = 1.22 mm) with a subrectangular outline, in occlusal view (ratio “length/width” of the crown = 2.2); labial side straight and lingual side convex. Main lingual cusp much higher than the labial one. Transverse ridge set behind

the middle of the crown: it does not participate in the posterior wall of the crown; anterior basin consequently much larger than the posterior basin. No central cusp on the transverse ridge. Small antero-labial accessory cusp connected to the main labial cusp by a prominent ridge. Both anterior and posterior cingula not developed.

DESCRIPTION

Orientation

The orientation of IRSNB R173 proposed here is mainly based on the presence of an accessory cusp, assumed to be set in antero-labial position, as in the advanced Traversodontidae (see Battail 1989, fig. 123). If this orientation is correct, the lingual side of the crown is more convex than the labial one, as in most Traversodontidae, and the lingual cusp is clearly higher than the labial one, as in *Traversodon* von Huene, 1936, *Scalenodon angustifrons* (Parrington, 1946), or *Microscalenodon* Hahn, Lepage *et* Wouters, 1988.

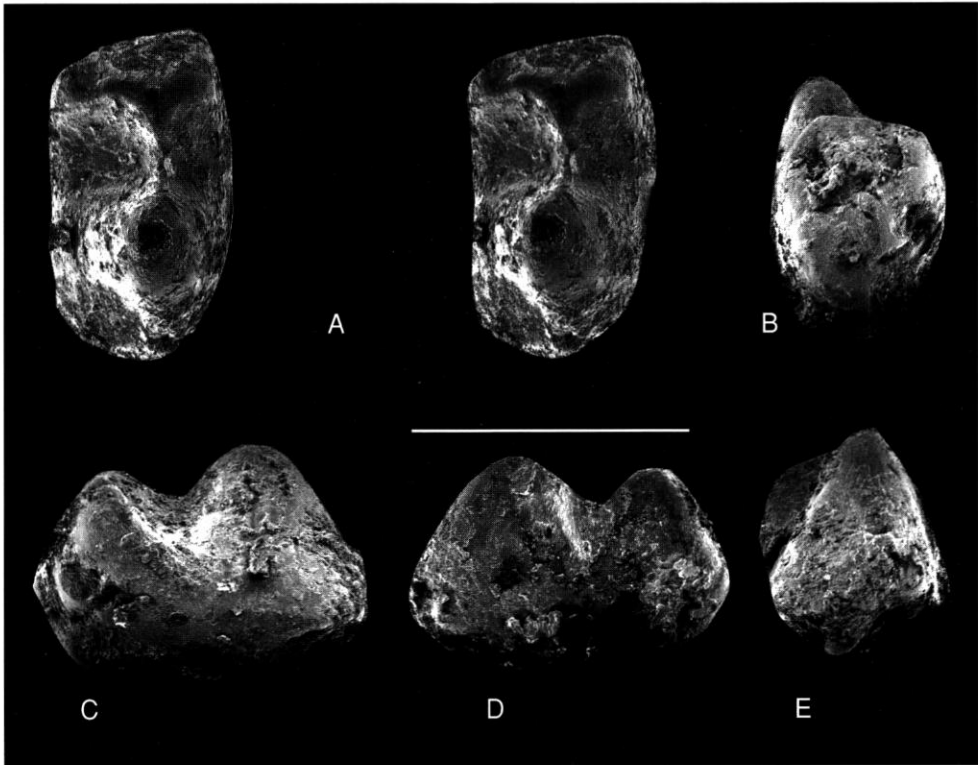


FIG. 27. — IRSNB R173, left upper postcanine of *Rosieria delsatei*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, stereophotographs, occlusal view; **B**, labial view; **C**, anterior view; **D**, posterior view; **E**, lingual view. Scale bar: 1 mm.

Moreover, the transverse ridge is set behind the middle part of the crown, as in all advanced Traversodontidae. Thus, IRSNB R173 is a left upper postcanine.

Measurements

Length of the crown = 0.55 mm; width of the crown = 1.22 mm.

Crown

The crown of IRSNB R173 is very small. In occlusal view, it is elongated (ratio "length/width" of the crown = 0.45) and subrectangular in outline. The labial border is nearly straight, whereas the lingual border is very convex. Both the anterior and posterior borders are slightly concave and nearly parallel. The crown is formed by two main cusps connected by a cutting transverse ridge. The main lingual cusp is much larger than the labial one. The transverse ridge is set behind the middle of the

crown and does not support any central cusp. This ridge delimits a large anterior basin and a small posterior basin. A small antero-labial cusp is connected to the main labial cusp.

In labial view, the main and the accessory labial cusps are connected by a high ridge: their limit is not clear. The main labial cusp is clearly higher than the accessory one. Their apex is very rounded.

In lingual view, the lingual cusp has a piriform outline. Its base is very broad and both its anterior and posterior borders are sigmoid. Its apex is rounded.

In anterior view, both the labial and lingual borders of the crown are very convex. The lingual cusp is much wider and higher than the main labial cusp. The transverse ridge connecting these cusps is very high and its anterior wall is not as vertical as the posterior one. The anterior basin is not limited by an anterior cingulum.

In posterior view, the posterior wall of the trans-

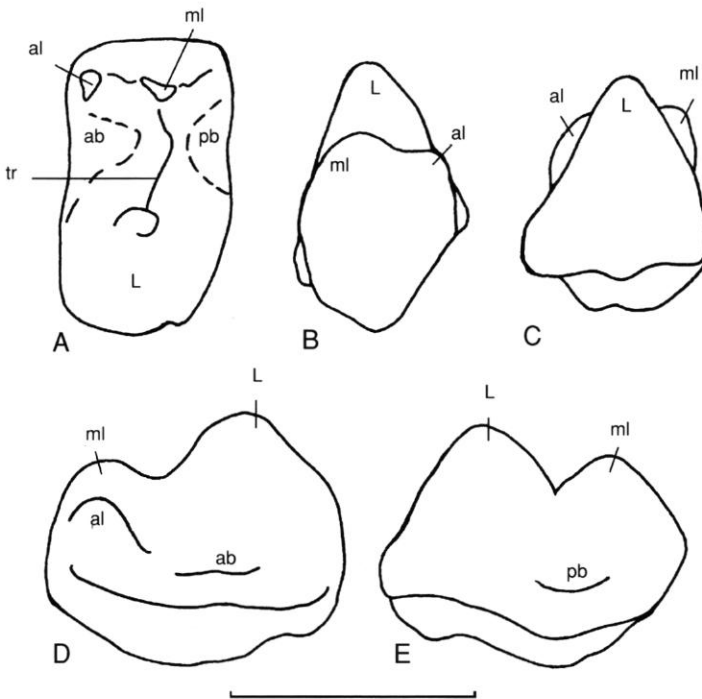


FIG. 28. — IRSNB R173, left upper postcanine of *Fosieria delstaei*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **ab**, anterior basin; **al**, antero-labial cusp; **L**, lingual cusp; **ml**, main labial cusp; **pb**, posterior basin; **tr**, transverse ridge. Scale bar: 1 mm.

verse ridge connecting the lingual and the main labial cusps is nearly vertical. The posterior basin, very poorly developed, forms a small depression at the level of the junction between the lingual and the labial cusps; it is not limited posteriorly by a posterior cingulum. A constriction delimits the crown and the root.

Root

The root is not preserved in IRSNB R173.

DISCUSSION

IRSNB R173 differs from IRSNB R172, referred to the new species *Maubeugia lotharingica*, in its proportionally wider outline, in its lingual cusp much higher than its main labial cusp and in lacking a central cusp. Moreover, the antero-labial accessory cusp is clearly less developed than in the latter: however, the development of this cusp is highly variable in the tooth row of the Traversodontidae (see Crompton 1972).

It resembles IRSNB R406, discovered in the Rhaetian of Habay-la-Vieille and referred to *Microscalenodon nanus* Hahn, Lepage *et* Wouters, 1988, in its small size, in its proportionally wide crown, in its lingual cusp much higher than its labial cusp and in lacking a central cusp. It differs from the latter in retaining a small posterior basin and an antero-labial accessory cusp.

IRSNB R173 resembles the upper postcanine teeth of *Scalenodon angustifrons* (Parrington, 1946), from the Middle Triassic of Tanzania, in the elongated outline of its crown, in its lingual cusp clearly higher than its labial one, in the presence of an antero-labial accessory cusp, in its transverse ridge set posteriorly, behind the middle of the crown, and in retaining a small posterior basin. It differs, however, from the latter in its smaller size and in lacking a central cusp as well as a cingulum.

The new tooth from Saint-Nicolas-de-Port resembles the upper postcanines of *Traversodon* von Huene, 1936 in its lingual cusp much higher than its labial cusp, in the absence of accessory cusp and in the presence of a posterior basin distinctly smaller than the anterior one. It differs in its smaller size and in the presence of a well developed antero-labial accessory cusp, absent in *Traversodon*. Moreover, the transverse ridge seems

set more posteriorly in IRSNB R173.

Contrary to the upper postcanine teeth of *Massetognathus* Romer, 1967, *Gomphodontosuchus* von Huene, 1928, *Ischignathus* Bonaparte, 1963, *Exaeretodon* Cabrera, 1943, *Boreogomphodon* Sues *et* Olsen, 1990 and *Arctotraversodon* Sues, Hopson *et* Shubin, 1992, the transverse ridge of IRSNB R173 does not form the posterior wall of the crown and the anterior basin is consequently less enlarged than in the former genera.

In conclusion, the crown of IRSNB R173 presents an original set of characters justifying its attribution to a new genus of Traversodontidae: *Rosieria*. Figure 26 shows that the upper postcanines of *Rosieria* can easily be derived from those of *Traversodon* by simple addition of an antero-labial accessory cusp and by slight backwards movement of the transverse ridge. In the same way, the postcanine teeth of *Scalenodon* and *Maubeugia* can be derived from those of *Rosieria*, by doubling of the lingual or the labial cusp, respectively.

Genus aff. *Rosieria* (Figs 29, 30)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R174, a left upper postcanine.

DESCRIPTION

Orientation

As in IRSNB R173.

Measurements

Length of the crown = 0.65 mm; width of the crown = 1.05 mm.

Crown

In occlusal view, the crown is very elongated labio-lingually (ratio "length/width" of the crown = 0.62) and subelliptical in outline. The lingual border is more convex than the labial one and the anterior border, much more convex than the posterior one: the latter is nearly perfectly straight. The crown is formed by two cusps

connected together by a transverse ridge. The lingual cusp is much larger than the labial one. The transverse ridge is relatively low, in the middle of the crown. It is set behind the middle of the crown and does not support any central cusp. This transverse ridge delimits a small posterior basin and a larger anterior basin. The posterior basin is limited posteriorly by a low, poorly developed and straight posterior cingulum. The anterior cingulum limiting the anterior basin is very poorly expressed, too, but very convex. There is no evidence of an accessory cusp.

In lingual view, the lingual cusp has a piriform outline: its base is broad and its apex rounded. Its anterior border is slightly concave, but its posterior border is nearly straight. There is no clear constriction between the crown and the root.

In labial view, the labial cusp has a triangular outline: both its anterior and posterior borders are nearly straight. Its posterior border is more oblique than its anterior border. Its apex is rather rounded.

In anterior view, the lingual cusp is much wider and somewhat higher than the labial one. The



FIG. 29. — IRSNB R174, left upper postcanine of aff. *Rosieria*, from the Late Triassic of Saint-Nicolas-de-Port. A, occlusal view; B, labial view; C, lingual view; D, anterior view; E, posterior view. Scale bar: 1 mm.

transverse ridge forms a deep notch, at the level of the junction between these cusps. The slope of the anterior wall of the transverse ridge is not very marked. The anterior cingulum is very low. In posterior view, the posterior basin looks very small. The posterior wall of the transverse ridge is more vertical than the anterior one. The posterior cingulum is very short and very low.

Root

The root of IRSNB R174 is robust, but very eroded. It was at least 1.5 times as high as the crown. In lingual view, it has a semielliptical outline. Its vertical axis is oblique, set at an angle of about 30° with the vertical axis of the crown. Its anterior side is more convex than its posterior one. In anterior view, the root has a triangular outline. Both its labial and lingual sides are slightly convex. The lingual side is longer than the labial one. The tip of the root is very rounded and set at the level of the junction between the cusps of the crown.

DISCUSSION

IRSNB R174 is reminiscent of IRSNB R173, referred to the newly defined species *Rosieria del-satei*, in its small and elongated crown, in its lingual cusp larger and higher than its labial one, in its transverse ridge set behind the middle of the crown, without central cusp, and in the retention of a small posterior basin. It differs mainly in the absence of a small antero-labial accessory cusp. In this character, it rather resembles *Traversodon*. However, the absence of this accessory cusp on an isolated tooth is, in advanced Traversodontidae, a negative character without actual phylogenetical significance. In *Scalenodon*, for example, the development of the anterior accessory cusps and of the cingula is variable within the dental row of a same animal (see Crompton 1972). For this reason, it cannot be excluded that IRSNB R174 belongs to the same species or, at least, to the same genus as IRSNB R173. That is the reason why the former postcanine is provisionally referred to aff. *Rosieria*, waiting for further evidence.

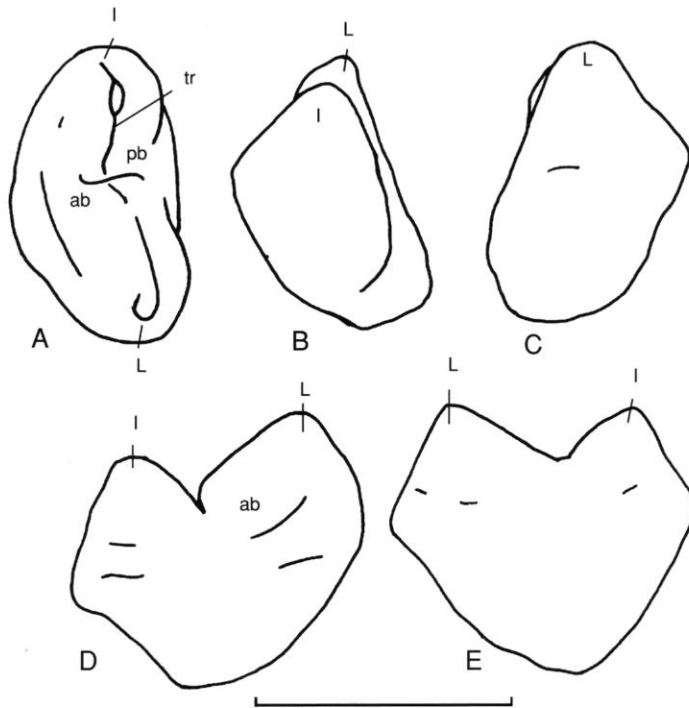


FIG. 30. — IRSNB R174, left upper postcanine of aff. *Rosieria*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **ab**, anterior basin; **L**, lingual cusp; **I**, labial cusp; **pb**, posterior basin; **tr**, transverse ridge. Scale bar: 1 mm.

Genus aff. *Microscalenodon*
(Figs 31, 32)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R175, a left upper postcanine.

DESCRIPTION

Orientation

See Hahn, Lepage & Wouters 1988.

Measurements

Length of the crown: 0.58 mm; width of the crown: 1.15 mm.

Crown

In occlusal view, the crown is proportionally very wide (ratio “length/width” of the crown = 0.5) and subrectangular in outline. The labial border is shorter and more convex than the lingual one, which is an unusual character in the Traversodontidae. The posterior border is perfectly straight and the anterior border, somewhat convex. The morphology of the crown is quite

simple: two cusps connected together by very poorly developed anterior and posterior ridges (“cingula”). The lingual cusp is by far the largest; the labial cusp is very short antero-posteriorly, but rather elongated labio-lingually. The ridges delimit a large central basin. There is no evidence of a transverse ridge: it is merged probably with the posterior ridge, forming the posterior wall of the crown. There is neither central nor accessory cusps.

In lingual view, the lingual cusp is not very high and has a piriform outline: its base is large antero-posteriorly and its apex is very rounded.

In labial view, the labial cusp is very low and triangular in outline. It clearly slopes towards the anterior side. Its apex is rounded, too.

In anterior view, the lingual cusp is distinctly higher than the labial cusp. The anterior ridge is nearly non-existent. The central basin gently slopes from the posterior wall to the anterior base of the crown.

In posterior view, the posterior ridge is clearly higher than the anterior one and forms the posterior wall of the crown.

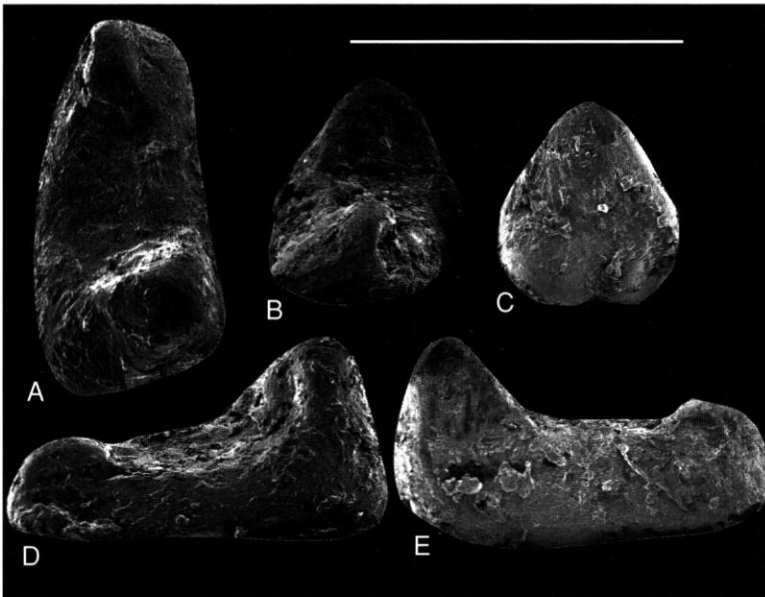


FIG. 31. — IRSNB R175, left upper postcanine of aff. *Microscalenodon*, from the Late Triassic of Saint-Nicolas-de-Port. A, occlusal view; B, labial view; C, lingual view; D, anterior view; E, posterior view. Scale bar: 1 mm.

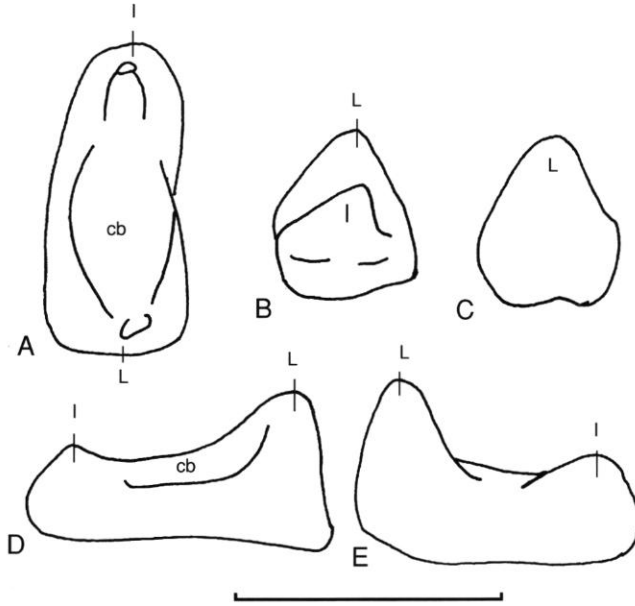


FIG. 32. — IRSNB R175, left upper postcanine of aff. *Microscalenodon*, from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **cb**, central basin; **L**, lingual cusp; **I**, labial cusp. Scale bar: 1 mm.

Root

The root is not preserved in this specimen.

DISCUSSION

IRSNB R175 resembles *Microscalenodon nanus* Hahn, Lepage *et* Wouters, 1988 in the quite simple structure of its crown, without transverse ridge, central and accessory cusps. Moreover, the anterior and the posterior sides of the crown are nearly parallel, the lingual cusp is very rounded and the central basin gently slopes from the posterior wall to the anterior base of the crown. It differs from IRSNB R406, the holotype and only upper postcanine currently referred to *Microscalenodon nanus*, in its crown proportionally lower, in its labial cusp less developed and in lacking an extended wear facet on its occlusal side. In the current state of our knowledge, for want of material, we cannot form a correct estimate of the dental variation within the species *Microscalenodon nanus*. That is the reason why IRSNB R175 is tentatively referred to aff. *Microscalenodon*.

Family TRAVERSODONTIDAE, gen. and sp. indet.
(Figs 33, 34)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R176, a left lower postcanine.

DESCRIPTION

Orientation

In the Traversodontidae, the lower postcanines are formed by a transverse ridge supporting two main cusps on the anterior half of the crown and by a low basin on the posterior half of the crown. The labial main cusp is usually higher than the lingual one.

Measurements

Length of the crown = 1.32 mm; width of the crown = 1.13 mm.

Crown

In occlusal view, the crown has a subtrapezoidal outline. It is proportionally longer than wide: the

ratio “length/width” of the crown = 1.17. The posterior half of the labial border and the posterior border are very convex. The lingual border is nearly perfectly straight. The anterior border is slightly concave and very oblique. The anterior half of the crown is formed by two large cusps connected together by an anterior transverse ridge. The labial cusp is much longer (mesio-distally), but somewhat less wide (labio-lingually) than the lingual cusp. In front of the transverse ridge, the labial cusp bears a poorly developed swelling. A tiny anterior depression is limited by the anterior wall of the transverse ridge and by the lingual side of the anterior swelling of the

labial cusp. The posterior half of the crown forms a talon, not very large and distinctly narrower than the anterior part of the crown. The posterior talon forms a central valley elongated antero-posteriorly and surrounded by a ridge which bears a broad lingual accessory cusp, adjoining the main lingual cusp.

In anterior view, the crown has a bell-shaped outline. The labial cusp is distinctly higher than the lingual cusp. The transverse ridge connecting these cusps is not very high. The anterior depression has a triangular outline. The crown and the root are separated by a well marked constriction. In posterior view, the central valley of the poste-

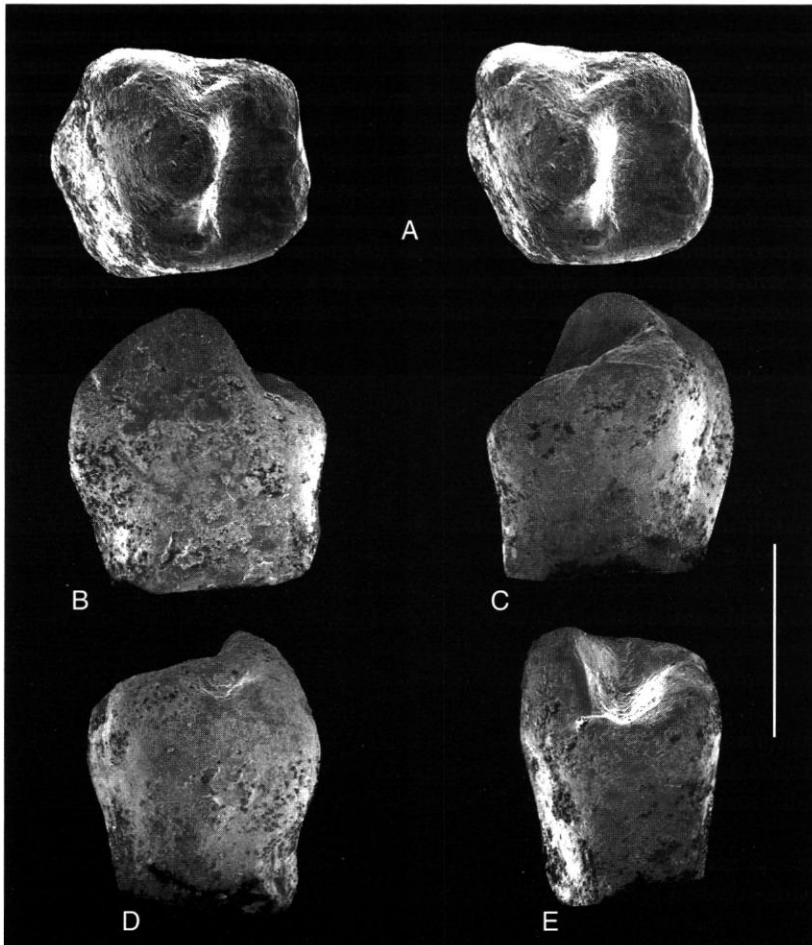


FIG. 33. — IRSNB R176, left lower postcanine of Traversodontidae indet., from the Late Triassic of Saint-Nicolas-de-Port. **A**, stereophotographs, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. Scale bar: 1 mm.

rior talon gently slopes from the transverse ridge to the posterior wall of the crown. The posterior portion of the ridge surrounding the valley is particularly low.

In labial view, the large labial cusp has a triangular outline. It is broader than high. Its anterior border is convex; its posterior border is shorter and straight. Therefore, this cusp somewhat slopes backwards. Its apex is very eroded. The lingual part of the talon looks proportionally very short. The crown is separated from the root by a well marked constriction, as in anterior view.

In lingual view, the main and the accessory lingual cusps are so closely united and their apex are so eroded that they form a quasi-continuous and straight ridge which slopes obliquely downwards from the main to the accessory cusp. The anterior swelling of the labial cusp lies in front of the level of the anterior border of the main lingual cusp.

Root

The tip of the root is broken. At the level of the fracture, the root has, in basal view, an ovoid outline. Its anterior border is shorter, but more convex than its posterior border; its lingual border is more convex than its labial border. The pulpal canal is very small and rounded.

DISCUSSION

IRSNB R176 has the typical traversodont pattern of a transverse ridge supporting two main cusps on the anterior half of the crown and a narrower talon on its posterior half. If the upper postcanines are very variable and, thus, phylogenetically useful in the Traversodontidae, the lower postcanines are much more constant and less diagnostic.

The lower postcanines of the primitive Traversodontidae *Pascualgnathus* Bonaparte, 1966 and *Andescynodon*, Bonaparte, 1969 differ

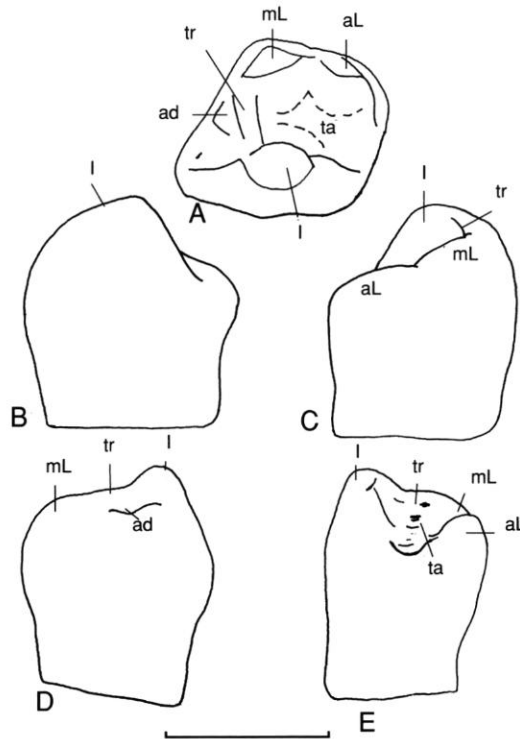


FIG. 34. — IRSNB R176, left lower postcanine of Traversodontidae ind., from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **ad**, anterior depression; **aL**, accessory lingual cusp; **l**, labial cusp; **mL**, main lingual cusp; **ta**, talonid; **tr**, transverse ridge. Scale bar: 1 mm.

from IRSNB R176 in the presence of a postero-labial accessory cusp, connected to the main labial cusp by a low ridge, and in the lack of a postero-lingual accessory cusp on the talon of their crown. Moreover, the posterior basin is more enlarged than in the latter. There is no trace of anterior swelling on the anterior side of the main labial cusp.

In the lower postcanines of *Scalenodon* Crompton, 1955, a small accessory cusp, equivalent to the anterior swelling of the labial cusp observed in IRSNB R176, is developed on the antero-labial side of the crown. However, a posterior accessory cusp is present on the labial side of the talon, rather than on the lingual side, as in IRSNB R176. Moreover, the posterior basin is more enlarged than in the latter.

In *Massetognathus* Romer, 1967, the posterior talon is lower and its basin is more enlarged than in IRSNB R176. Both the labial and lingual ridges of the talon are crenulated, but there is neither well developed posterior accessory cusp nor anterior swelling of the labial cusp.

The lower postcanines of *Gomphodontosuchus* von Huene, 1928, *Exaeretodon* Cabrera, 1943, *Ischignathus* Bonaparte, 1963 and *Scalenodontoides* Crompton *et* Ellenberger, 1957 differ from IRSNB R176 in possessing the following derived characters:

- The lingual cusp is distinctly inclined obliquely backwards.
- The labial cusp is broader than the lingual cusp.
- Except in *Ischignathus*, the labial cusp is set anteriorly with respect to the lingual cusp.
- There are two accessory cusps: a postero-lingual one and a postero-labial one.

The lower postcanine referred to *Microscalenodon nanus* Hahn, Lepage *et* Wouters, 1988 resembles IRSNB R176 in its very small size and in the proportions of its main cusps. Nevertheless, an accessory cusp is developed on the postero-labial side of the crown, the talon and the posterior basin are distinctly more developed and the labial cusp does not bear any anterior swelling.

From these comparisons with the lower postcanines in the different genera of Traversodonti-

dae, it can be concluded that IRSNB R176 shows an original set of morphological characters:

- The antero-labial cusp is longer (mesio-distally) but less wide (labio-lingually) than the antero-lingual cusp.
- The antero-labial cusp supports an anterior swelling.
- There is a broad postero-lingual accessory cusp.
- The talon is not very enlarged: it forms a central valley elongated antero-posteriorly.
- The tooth is very small.

In the absence of more complete material, correspondences with the genera *Maubeugia* and *Rosieria*, defined on isolated upper postcanines from the same locality, are impossible to establish. That is the reason why IRSNB R176 is referred to Traversodontidae indet.

Family aff. TRAVERSODONTIDAE,
gen. and sp. indet.
(Figs 35, 36)

MATERIAL EXAMINED. — Specimen discovered in Saint-Nicolas-de-Port: IRSNB R177.

DESCRIPTION

Orientation

IRSNB R177 shows morphological affinities with the upper postcanines of the Traversodontidae (see discussion). The marked slope of the main cusps permits to distinguish the anterior and posterior sides of the crown. If the interpretation proposed here is correct, the small accessory cusp would be set on the antero-labial border of the crown, as in advanced Traversodontidae. Therefore, it is identified as a right upper postcanine.

Measurements

Length of the crown = 1.39 mm; width of the crown = 1.5 mm.

Crown

In occlusal view, the crown of IRSNB R177 is subtrapezoidal and very elongated antero-posteriorly: the ratio “length/width” of the crown is 0.93. The lingual border is long and very convex;

the labial one is shorter and slightly concave. Both the anterior and posterior borders are nearly straight and oblique: the posterior border is longer than the anterior one. The crown is divided into two parts by an antero-posterior furrow. The lingual part is the widest and is fully covered by a very large lingual cusp. The labial side of the crown is formed by two labial cusps. The posterior labial cusp is the largest: it is connected to the apex of the labial cusp by a transverse ridge, set behind the middle of the crown. The antero-labial accessory cusp is connected to the main labial cusp by a small ridge and connected to the lingual one by a poorly developed anterior cingulum. The transverse ridge, connecting the lingual and the main labial cusps, delimits an anterior and a posterior valley. The anterior valley is surrounded by the antero-labial side of the lingual cusp, the anterior wall of the transverse ridge, the antero-lingual side of the main labial cusp, the lingual side of the accessory labial cusp and the posterior wall of the anterior cingulum. The posterior valley is distinctly smaller than the anterior one: it is limited by the postero-labial side of the lingual cusp, the posterior wall of the transverse ridge and the postero-lingual side of the main labial cusp.

There is no evidence of a posterior cingulum. In anterior view, the lingual cusp is by far the highest: the main labial cusp reaches the half of its height and the accessory labial cusp, the third of the main labial cusp. Both the lingual and the main labial cusps are somewhat inclined towards the labial side of the crown. The transverse ridge is deeply notched by the antero-posterior furrow. The anterior cingulum is very low and is also notched by the antero-posterior furrow. The postero-lingual side of the main labial cusp is less vertical than the antero-labial side of the lingual cusp. In posterior view, the postero-labial side of the main cusp is nearly perfectly vertical; the postero-lingual side of the main labial cusp is more oblique. The posterior valley is opened posteriorly: it is not limited by a posterior cingulum. The posterior ridge of the lingual cusp is well marked. In lingual view, the lingual cusp is subtriangular in outline and clearly inclined backwards. The anterior border is oblique, forming an angle of about 45° with the base of the crown, and somewhat convex. The posterior border is shorter, more vertical and very slightly concave. The apex of the cusp is very rounded. In labial view, the main labial cusp has almost

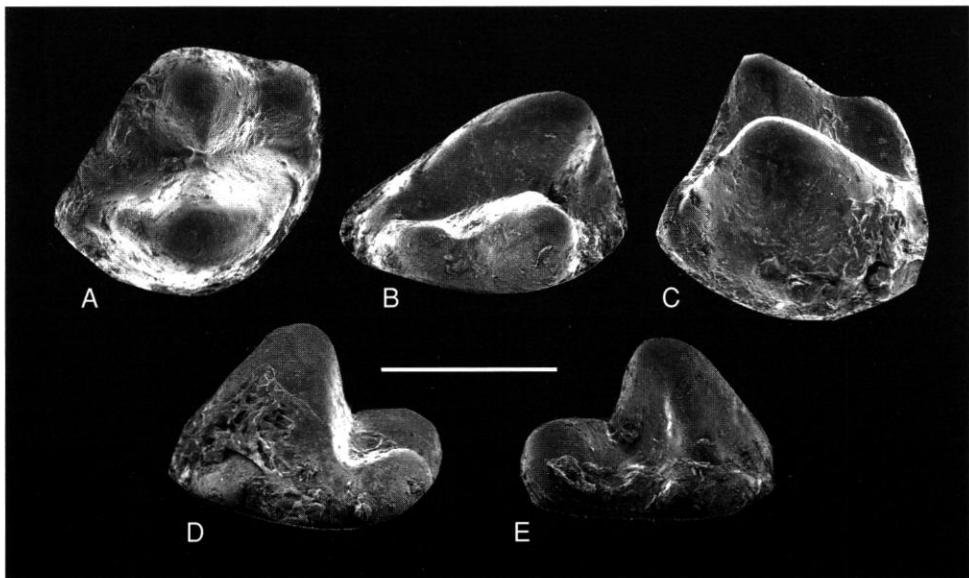


FIG. 35. — IRSNB R177, right upper postcanine of ? Traversodontidae indet., from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. Scale bar: 1 mm.

the same outline as the lingual cusp. It is inclined backwards and its apex is rounded too. The accessory labial cusp, very low, is placed against it: the ridge connecting the two labial cusps is low and poorly developed.

Root.

The root is not preserved in IRSNB R177.

DISCUSSION

IRSNB R177 is undoubtedly reminiscent of the upper postcanine teeth of the advanced Traversodontidae in the general organisation of its crown. A large lingual cusp is connected to the main accessory cusp by a transverse ridge set behind the middle of the crown and delimiting an anterior and a smaller posterior valley. An accessory cusp is set in front of the main labial cusp and the anterior valley is closed by an anterior cingulum. The organisation of the cusps is similar to IRSNB R174, referred to the newly defined genus *Rosieria*. Nevertheless, it differs from the upper postcanines of all currently known Traversodontidae in being longer (mesio-distally) than wide (labio-lingually).

In its proportions, IRSNB R177 more closely

resembles the lower postcanines of the Traversodontidae. Nevertheless, its morphological organization is quite different. The lower postcanines of the Traversodontidae are rather constant indeed (see Battail 1989): a high transverse ridge supports two cusps on the anterior half of the crown and a low basin forms the posterior half. An accessory cusp is usually present on the postero-labial portion of the crown.

In certain respects, IRSNB R177 is reminiscent of the postcanine of the Haramiyidae. This group, only known by isolated teeth, is very abundant in Saint-Nicolas-de-Port (Sigogneau-Russell 1989, 1990). The Haramiyidae are tentatively identified as primitive allotherian mammals (see Butler & Macintyre 1994 for an extended discussion of Haramiyidae affinities). As in IRSNB R177, the dental crowns of the Haramiyidae are elongated antero-posteriorly and they are divided into two rows of cusps by a deep antero-posterior furrow. However, the "accessory cusps" are more numerous on the anterior part of the lower postcanines and on the posterior part of the upper ones. Moreover, the posterior slope of the dominating cusps is never as marked as in IRSNB R177.

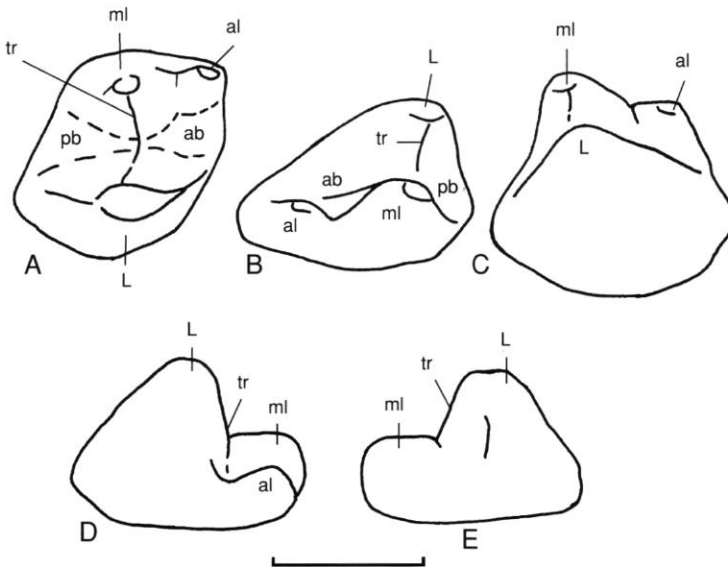


FIG. 36. — IRSNB R177, right upper postcanine of ? Traversodontidae indet., from the Late Triassic of Saint-Nicolas-de-Port. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, anterior view; **E**, posterior view. **ab**, anterior basin; **al**, antero-labial cusp; **L**, lingual cusp; **ml**, main labial cusp; **pb**, posterior basin; **tr**, transverse ridge. Scale bar: 1 mm.

It can be concluded that IRSNB R177 most closely resembles the upper postcanines of the Traversodontidae: the general organization of the cusps is similar to the new defined genus *Rosieria*. Because of its very unusual proportions, it is cautiously referred to familia aff. Traversodontidae, waiting for the discovery of more complete material.

PALAEOBIOGEOGRAPHY OF LATE TRIASSIC AND EARLY JURASSIC CYNODONTS

FOSSIL LOCALITIES AND HORIZONS

Table 9 gives a synthetic correlation, modified from Lucas & Hunt (1994), of Late Triassic and Early Jurassic formations discussed in the text.

Ischigualasto Formation

(San Juan Province, Argentina)

Age. Late Carnian (Hunt 1991; Hunt & Lucas 1991). Early to Late Carnian (Battail 1993).

Taxa discovered. Traversodontidae: *Exaeretodon frenguelli* Cabrera, 1943; *Exaeretodon vincei* (Bonaparte, 1963); *Ischnognathus sudamericanus* (Bonaparte, 1963).

Chiniquodontidae: *Chiniquodon theotonicus* von Huene, 1936.

Upper part of the Los Colorados Formation

(La Rioja Province, Argentina)

Age. Late Norian (Bonaparte 1972; Lucas & Hunt 1994).

Taxa discovered. Tritheledontidae: *Chalimimia musteloides* Bonaparte, 1978.

Remark. Bonaparte (1972) identified postcranial bones as cf. *Tritylodon*. Lucas & Hunt (1994) suspect that they pertain to *Chalimimia*.

Upper Santa Maria Formation

(Rio Grande do Sul, Brazil)

Age. Late Carnian (Hunt 1991; Hunt & Lucas 1991). Early Carnian (Battail 1993).

Taxa discovered. Traversodontidae: *Traversodon stahleckeri* von Huene, 1936; *Gomphodontosuchus brasiliensis* von Huene, 1928; *Exaeretodon frenguelli* Cabrera, 1943.

Dromatheriidae: *Therioherpeton cargini* Bonaparte et Barberena, 1975.

Chiniquodontidae: *Chiniquodon theotonicus* von Huene, 1936; *Belesodon magnificus* von Huene, 1936.

Lower Elliot Formation

(Morobong Hill, Lesotho)

Age. Late Carnian or Early Norian (Hopson 1984).

Taxon discovered. Traversodontidae: *Scalenodontoides macrodentes* Crompton et Ellenberger, 1957.

Upper Elliot and Clarens Formations

(South Africa and Lesotho)

Age. Hettangian to Sinemurian (Olsen & Galton 1984).

Taxa discovered. Tritheledontidae: *Pachygenelus monus* Watson, 1913; *Diarthrognathus broomi* Crompton, 1958; *Tritheledon riconoi* Broom, 1912.

Tritylodontidae: *Tritylodon longaeus* Owen, 1884 (*sensu* Sues 1986b).

Remark. *Pattisia likhoelensis* Lees et Mills, 1983, from Lesotho, is certainly a Tritheledontidae, possibly a synonym of *Pachygenelus monus* (Lucas & Hunt 1994).

Maleri Formation

(Andhra Pradesh, India)

Age. Late Carnian (Hopson 1984; Battail 1991).

Taxon discovered. Traversodontidae: *Exaeretodon statisticae* Chatterjee, 1982.

Remark. Battail (1991) considers that *Exaeretodon statisticae* might be a junior synonym of *Exaeretodon frenguelli*.

Bull Canyon Formation

(Eastern New Mexico, USA)

Age. Early to Middle Norian (Lucas & Hunt 1994, fig. 20.5).

Taxon discovered. Dromatheriidae: *Pseudotriacodon chatterjeei* Lucas et Oakes, 1988.

Remark. The identification of this taxon as a cynodont has been questioned by Sues & Olsen (1990), but without justification.

Kayenta Formation

(North-eastern Arizona, USA)

Age. Late Sinemurian – Early Pliensbachian

	SERIES	Stage	Argentina	Brazil	Southern Africa	India	Western North Amer.	Eastern North Amer.	United Kingdom	France	Belgium Luxemb.	Switzerland	Germany	China
178	EARLY JURASSIC	Toarcian												
187		Pliensbachian					Navajo Ss. 10		Windsor Hill Fissure 16					
194,5		Sinemurian			Upper Elliot and Clarens Fm 5		Kayenta Fm 8 La Boca Fm 9		St. Brides's Island					Lufeng Fm
203,5		Hettangian						Mc Coy Brook Fm 14						
208	UPPER TRIASSIC	Rhaetian										Hallau Bone-bed 20	Rhätanstein 21	
210		Norian	Los Colorados Fm 2				Bull Canyon Fm 7			St.-Nicolas de-Port 17				
222					Lower Elliot Fm 4						Medernach 18			
229		Carnian	Ischigualasto Fm 1	Upper Santa Maria Fm 3		Maleri Fm 6		Cumnock 12 Wolfville Fm 13						
								Turkey Barnch Fm 11						

TABLE 9. — Stratigraphic position of the Late Triassic and Early Jurassic formations where cynodonts have been discovered (after Lucas & Hunt 1994, modified).

(Peterson & Pipiringos 1979; Clark & Fastovsky 1986; Sues 1986b).

Taxa discovered. Tritylodontidae: *Kayentatherium wellsi* Kermack, 1982; *Oligokyphus* sp.; *Dinnebitodon amarali* Sues, 1986; *Nearctylodon broomi* Lewis, 1986.

La Boca Formation

(Tamaulipas, north-eastern Mexico)

Age. ? Early Jurassic (Clark *et al.* 1991, 1994). New radiometric dates indicate that this formation would be Middle Jurassic in age (Luo, pers. comm.).

Taxon discovered. Tritylodontidae: *Bocatherium mexicanum* Clark *et* Hopson, 1985.

Navajo Sandstones

(Arizona, USA)

Age. Pliensbachian (Marzolf 1990).

Taxon discovered. Tritylodontidae: Tritylodontid indet. (Winkler *et al.* 1991).

Turkey Branch Formation

(Richmond Basin, Virginia, U.S.A.)

Age. Early to Middle Carnian (Sues & Olsen 1990; Sues *et al.* 1994).

Taxa discovered. Traversodontidae: *Boreogomphodon jeffersoni* Sues *et* Olsen, 1990.

Dromatheriidae: *Microconodon tenuirostris* Osborn, 1886.

Cummock Formation

(Sanford Basin, North Carolina, USA)

Age. Late Carnian (Sues *et al.* 1994; Lucas & Hunt 1994).

Taxa discovered. Dromatheriidae: *Dromatherium sylvestre* Emmons, 1857; *Microconodon tenuirostris* Osborn, 1886.

Wolfville Formation of the Fundy Group

(Minas Basin, Nova Scotia, Canada)

Age. Late Carnian or Carno-Norian (Hopson 1984).

Taxon discovered. Traversodontidae: *Arcto-traversodon plemmyridon* (Hopson, 1984).

Mc Coy Brook Formation of the Fundy Group

(Nova Scotia, Canada)

Age. Early Jurassic (Shubin *et al.* 1991):

? Hettangian (Lucas & Hunt 1994).

Taxon discovered. Tritheledontidae: *Pachygenelus* cf. *monus*.

Remark. ? *Pachygenelus milleri* Chatterjee, 1983, from the Dockum Formation (Upper Triassic) of Near Post (Western Texas, USA) is regarded by Shubin *et al.* (1991) as doubtful because it lacks diagnostic cynodont characters: teeth are fused to the jaw and there are no cingula on the post-canine teeth.

Pant 4 Quarry of St. Bride's island

(Glamorgan, U.K.)

Age. Hettangian to Early Sinemurian (Evans & Kermack 1994).

Taxon discovered. Tritylodontidae: *Oligokyphus* cf. *major*.

Windsor Hill Fissure

(Somerset, UK)

Age. Pliensbachian (Kühne 1956).

Taxon discovered. Tritylodontidae: *Oligokyphus major* Kühne, 1956.

Remarks. Kühne (1956) described originally two species, *O. major* and *O. minor*, which are probably sexual dimorphs (Sues 1985). A tritylodontid *incertae sedis* is present at the nearby Holwell Quarry (Savage 1971).

Saint-Nicolas-de-Port

(Meurthe-et-Moselle, France)

Age. Late Norian (Buffetaut & Wouters 1986; Cuny & Ramboer 1991; Cuny 1993) or Early Rhaetian (Sigogneau-Russell 1983a).

Taxa discovered. Dromatheriidae: *Pseudotriconodon wildi* Hahn, Lepage *et* Wouters, 1984; *Tricuspes tuebingensis* E. von Huene, 1933; *Tricuspes sigogneauae* Hahn, Hahn *et* Godefroit, 1994; *Tricuspes tapeinodon* n.sp.; *Meurthodon gallicus* Sigogneau-Russell *et* Hahn, 1994.

Traversodontidae: *Maubeugia lotharingica* n.g., n.sp.; *Rosieria delsatei* n.g., n.sp.; genus aff. *Microscalenodon*.

Cynodontia *incertae sedis*: *Hahnia obliqua* n.g., n.sp.; *Gaumia longiradicata* Hahn, Wild *et* Wouters, 1987; *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987.

Remark. Godefroit (1997) describes a Late Triassic fauna in the nearby and contempora-

neous locality of Varangéville. This fauna includes teeth of indeterminate advanced cynodonts.

Medernach

(G.-D. Luxemburg)

Age. ? Middle Norian (Hary & Muller 1967; Cuny *et al.* 1995).

Taxa discovered. Dromatheriidae: *Pseudotricodon wildi* Hahn, Lepage *et* Wouters, 1984; "cf. *Tricuspes tuebingensis*" (= *Tricuspes* aff. *sigogneauae*).

Cynodontia *incertae sedis*: *Gaumia* cf. *incisa*.

Habay-la-Vieille

(Gaume, Belgium)

Age. Early Rhaetian (Bock 1987).

Taxa discovered. Dromatheriidae: *Pseudotricodon* ? sp.

Traversodontidae: *Microscalenenodon nanus* Hahn, Lepage *et* Wouters, 1988.

Cynodontia *incertae sedis*: *Gaumia longiradicata* Hahn, Wild *et* Wouters, 1987; ? *Gaumia incisa* Hahn, Wild *et* Wouters, 1987; *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987.

Hallau Bone-bed

(Kanton Schaffhausen, Switzerland)

Age. For Clemens (1980), the Hallau Bone-bed postdates the Upper Norian (Knollenmergel), but is no younger than the Lower, but not Lowermost, Hettangian (the bone-bed is overlain by a marl containing the ammonite *Psiloceras johnstoni*). Therefore, the Hallau local fauna is probably of Rhaetian age.

Taxa discovered. Dromatheriidae: *Tricuspes sigogneauae* Hahn, Hahn *et* Wouters, 1994.

Cynodontia *incertae sedis*: *Gaumia* sp.; *Lepagia gaumensis* Hahn, Wild *et* Wouters, 1987.

Rhätensandstein bone-beds of Württemberg

(Germany)

Age. Probably not older than Upper Norian and not younger than Lower Hettangian (Clemens 1980).

Taxa discovered. Dromatheriidae: *Tricuspes tuebingensis* E. von Huene, 1933.

Tritylodontidae: *Oligokyphus triserialis* Hennig, 1922 (*sensu* Sues 1985); *Tritylodon fraasi*

Lydekker, 1887; *Chalepotherium plieningeri* (Ameghino, 1903).

Lower Lufeng Formation

(Western Yunnan, China)

Age. Hettangian to Pliensbachian (Chen *et al.* 1982; Luo & Wu 1995).

Taxa discovered. (according to Luo & Wu 1994). Tritylodontidae: *Bienotherium yunnanense* Young, 1940; *Bienotherium minor* Young, 1947; *Bienotherium magnum* Chow, 1962; *Oligokyphus lufengensis* Luo *et* Sun, 1993; *Lufengia delicata* Chow *et* Hu, 1959; *Yunnanodon brevirostre* (Cui, 1976); *Dianzhongia longistrata* Cui, 1981.

PALAEOGEOGRAPHICAL SKETCH OF ADVANCED CYNODONTS AND AFFINITIES OF THE SAINT-NICOLAS-DE-PORT CYNODONT FAUNA

Three successive stages can be distinguished in the Late Triassic and Early Jurassic cynodont assemblages worldwide: the Late Carnian/Early Norian assemblages, the Late Norian/Rhaetian assemblages and the Liassic assemblages. The Late Carnian/Early Norian assemblages are particularly well represented in South America (Argentina and Brazil), but elements have also been discovered in southern Africa, India and eastern North America. These assemblages are dominated by Traversodontidae. With the exception of *Boreogomphodon*, all are large or giant herbivorous cynodonts. The Chiniquodontidae apparently disappeared at the end of the Carnian. The Dromatheriidae appeared during the Carnian. They are very small cynodonts with perfectly sectorial postcanine teeth. This Late Carnian/Early Norian cynodont assemblages can be included within the B-type assemblages, defined by Romer (1966).

The Late Norian/Rhaetian cynodont assemblages are well represented in Western Europe, on the western margin of the Germanic Realm. The fauna discovered in Saint-Nicolas-de-Port is the most representative of this type of cynodont assemblages. These are dominated by small car-

nivorous or insectivorous cynodonts with sectorial postcanine teeth (Dromatheriidae or *Cynodontia incertae sedis*). The Traversodontidae are very rare and only represented by dwarf forms. The cynodont fauna from Saint-Nicolas-de-Port appears very similar with those from Medernach (three genera in common), Habay-la-Vieille (three or four genera in common) and Hallau (three genera in common).

From a palaeoecological point of view, it is interesting to observe that, in Saint-Nicolas-de-Port, small herbivorous Traversodontidae co-exist with two groups of herbivorous allotherian mammals: the Haramiyidae and the Theroteinidae. All these small herbivorous groups probably had different dietary specializations, allowing their sympathy. For Sigogneau-Russell & Hahn (1994), the haramiyid teeth, which are rarely strongly worn, may be indicative of a diet based on soft plant matter; the low cusps and delicate roots of the theroteinid molars perhaps suggest a diet based on rather softer vegetables. The stout root and the high cusps of the dwarf traversodontid postcanine teeth suggest a diet based on harder vegetables. The wear pattern of the postcanine teeth is unfortunately insufficiently known, in this group, to confirm this hypothesis. In the same way, the Dromatheriidae co-exist with morganucodontid mammals in Saint-Nicolas-de-Port, as in Hallau (Peyer 1956) and Medernach (Cuny *et al.* 1995). Both groups are characterized by triconodont cutting teeth and probably occupied similar ecological niches. Sigogneau-Russell & Hahn (1994) suggest that the Dromatheriidae ("chinquodontoids") were probably too small to be carnivorous: perhaps they fed on insects with hard elytrae. In Saint-Nicolas-de-Port, the most frequent morganucodontid, *Brachyozostrodon*, is characterized by its relatively large and very stocky molars, indicating that it fed on larger preys: it was probably a small carnivorous.

The cynodont fauna discovered in the Rhätsandstein bone-beds from Germany has a intermediate composition between the typical Late Norian-Rhaetian assemblages and the Liassic ones. *Tricuspes* is the only dromatheriid discovered in this area, whereas at least three

genera of tritylodontids have been discovered. These are the oldest Tritylodontidae currently recognized.

Outside Western Europe, the Late Norian Los Colorados Formation of Argentina has yielded the oldest known Tritheledontidae: *Chalimimia*. The presence of *Pseudotriconodon* in the Norian Bull Canyon Formation of New Mexico is doubtful (Sues & Olsen 1990).

Traversodontids and dromatheriids are absent from the Liassic cynodont assemblages. These are characterized by the presence of Tritylodontidae and/or Tritheledontidae. Liassic tritylodontids have a pangean palaeogeographical distribution: they are known from Europe, North America, China and South Africa. This reflects the apparent cosmopolitanism of tetrapod faunas at that period, as already noted by Shubin *et al.* (1981), Olsen & Galton (1984) and Lucas & Hunt (1994). Nevertheless, at the generic level, the Liassic tritylodontids appear more endemic. Out of ten tritylodontid genera recognized in the Early Jurassic (the Rhätsandstein bone-beds from Germany are provisionally regarded as Late Triassic in age), eight have currently only been discovered in a limited palaeogeographical area. *Dinnebitodon*, from the Kayenta Formation (USA), and *Yunnanodon*, from the Lower Lufeng Formation, are very similar and probably represent sister-taxa by dental apomorphies (Luo pers. comm.). If this taxonomic similarity is taken into consideration, the endemism of tritylodonts would be lower. However, as the stratigraphic position of each formation is not clearly established, definitive palaeogeographical conclusions are very hazardous for that period. The genus *Oligokyphus* has a wide palaeogeographical distribution: remains have been discovered in Germany, the United Kingdom, China and North America. Stratigraphically, it probably ranges from the Rhaetian to the Pliensbachian. The Upper Elliot and Lower Clarens Formations of southern Africa have yielded three tritheledontid genera. Outside southern Africa, a jaw fragment of the tritheledontid *Pachygelenus cf. monus* has been discovered in the ? Hettangian Mc Coy Brook formation of Nova Scotia.

CONCLUSIONS

The Late Triassic cynodont fauna discovered in Saint-Nicolas-de-Port is unique in terms of the diversity of the fauna. The following taxa are represented: *Pseudotriciconodon wildi* Hahn, Lepage et Wouters, 1984; *Tricuspes tuebingensis* E. von Huene, 1933; *Tricuspes sigogneauae* Hahn, Hahn et Godefroit, 1994; *Tricuspes tapeinodon* n.sp.; *Meurthodon gallicus* Sigogneau-Russell et Hahn, 1994; *Hahnia obliqua* n.g., n.sp.; *Gaumia longiradicata* Hahn, Wild et Wouters, 1987; *Lepagia gaumensis*, Hahn, Wild et Wouters, 1987; *Maubeugia lotharingica* n.g., n.sp.; *Rosieria delsatei* n.g., n.sp. and aff. *Microscalenodon*. Small carnivorous or insectivorous cynodonts are particularly numerous and diversified (eight species). They are represented by the family Dromatheriidae and by *Cynodontia incertae sedis*. It has been previously shown that Dromatheriidae probably represent the sister-taxon of Mammalia (Hahn et al. 1994). Herbivorous cynodonts are rare and probably represented by dwarf forms of the family Traversodontidae. Although very advanced, these traversodonts are characterized by a primitive dental morphology. The study of the palaeogeographical and stratigraphic distribution of Late Triassic to Early Jurassic advanced cynodonts indicates that the fauna discovered in Saint-Nicolas-de-Port is characteristic of the Late Norian-Rhaetian period.

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REFERENCES

- Al Khatib R. 1976. — *Le Rhétien de la bordure orientale du Bassin de Paris et le "Calcaire à Gryphées" de la région de Nancy. Étude pétrographique et sédimentologique*. Unpublished Ph. D. thesis, Université de Nancy I, 278 p.
- Ameghino F. 1903. — Los diprotodontes del orden de los plagiolacoideos y el origen de los roedores y de los polimastodontes. *Anales del Museo nacional de Buenos Aires* 1(3): 81-192.
- Battail B. 1989. — *Les Cynodontes: systématique, phylogénie, contexte biostratigraphique*, volume 2. Unpublished Ph. D. thesis. Université de Paris VI, Muséum national d'Histoire naturelle, 483 p.
- 1991. — Les Cynodontes (Reptilia, Therapsida) : une phylogénie. *Bulletin du Muséum national d'Histoire naturelle*, 4^e série, C 13 (1-2) : 17-105.
- 1993. — On the Biostratigraphy of Triassic therapsid-bearing formations, in Lucas S. G. & Morales M. (eds), *The non-marine Triassic, New Mexico Museum of Natural History & Science Bulletin* 3: 31-35.
- Bock H. 1987. — *Ein Modell zur Beckenausdehnung und Fazieszonierung am Westrand der Eifeler Nord-Süd Zone während der Trias und zur Transgression des Unteren Lias am Ardennensüdrand*. Unpublished Ph. D. thesis. Aachen Universität, 417 p.
- Bonaparte J. F. 1963. — Descripción de *Ischignathus sudamericanus* n.g., n.sp., nuevo cinodonte gonfodonte del Triásico Medio superior de San Juan, Argentina. *Acta geologica lilloana* 4: 111-128.
- 1966. — Sobre nuevos terápsidos triásicos hallados en el centro de la Provincia de Mendoza, Argentina. *Acta geologica lilloana* 8: 91-100.
- 1969. — Dos nuevas faunas de reptiles triásicos de Argentina: 283-306, in *Gondwana stratigraphy. IUGS Symposium, Buenos Aires 1967*. Unesco, Paris.
- 1970. — Annotated list of the South American Triassic tetrapods: 665-682, in *Second Gondwana Symposium, South Africa 1970. Proceedings and papers*. Unesco, Paris.
- 1972. — Los tetrápodos del sector superior de la formación Los Colorados, La Rioja, Argentina (Triásico Superior). *Opera Lilloana* 22: 1-183.
- 1978. — El Mesozoico de América del Sur y sus Tetrápodos. *Opera lilloana* 26: 1-596.
- Bonaparte J. F. & Barberena M. C. 1975. — A possible mammalian ancestor from the Middle Triassic of Brazil (Therapsida-Cynodontia). *Journal of Paleontology* 49 (5): 931-936.
- Broom R. 1912. — On a new type of cynodont from the Stormberg. *Annals of the South African Museum* 5 (17): 334-336.
- Buffetaut E. 1985. — The age of the Saint-Nicolas-de-Port vertebrate locality (Triassic of eastern France). *Terra Cognita* 5: 2, 3.
- Buffetaut E. & Wouters G. 1986. — Amphibian and reptile remains from the Upper Triassic of Saint-Nicolas-de-Port (Eastern France) and their biostratigraphic significance. *Modern Geology* 10: 133-145.
- Butler P. M. & Macintyre G. T. 1994. — Review of

- the British Haramiyidae (? Mammalia, Allotheria), their molar occlusion and relationships. *Philosophical Transactions of the Royal Society of London B* 345: 433-458.
- Cabrera A. 1943. — El primer hallazgo de terapsidos en la Argentina. *Notas del Museo de La Plata, Paleontologia* 8 (5): 317-331.
- Carroll R. L. 1988. — *Vertebrate paleontology and evolution*. Freeman and Co, New York, 698 p.
- Chatterjee S. 1982. — A new cynodont reptile from the Triassic of India. *Journal of Paleontology* 56: 203-214.
- 1983. — An ictidosaur fossil from North America. *Science* 220: 1151-1153.
- Chen P., Li W., Chen J., Wang Z., Shen Y. & Sen D. 1982. — Stratigraphical classification of Jurassic and Cretaceous in China. *Scientia Sinica B25*: 1227-1248.
- Chevais S. 1937. — Croissance et races locales de *Corophium volutator*. *Travaux de la station biologique de Roscoff* 15 : 99-132.
- Chow M. 1962. — A tritylodontid specimen from Lufeng, Yunnan. *Vertebrata Palasiatica* 6: 365-367 [in Chinese].
- Chow M. & Hu C. C. 1959. — A new tritylodont from Lufeng, Yunnan. *Vertebrata Palasiatica* 3: 9-12 [in Chinese].
- Clark J. M. & Fastovsky D. E. 1986. — Vertebrate biostratigraphy of the Glen Canyon Group of northern Arizona: 285-301, in Padian K. (ed.), *The beginning of the age of Dinosaurs*. Cambridge University Press.
- Clark J. M. & Hopson J. A. 1985. — Distinctive mammal-like reptile from Mexico and its bearing on the phylogeny of the Tritylodontidae. *Nature* 315: 398-400.
- Clark J. M., Montellano M., Hopson J. A. & Hernandez R. 1991. — Mammals and other tetrapods from the Early Jurassic La Boca Formation, northeastern Mexico. *Journal of vertebrate Paleontology* 11 (supplement to No. 3): 23A.
- Clark J. M., Montellano M., Hopson J. A., Hernandez R. & Fastovsky D. E. 1994. — An Early or Middle Jurassic tetrapod assemblage from the La Boca Formation, north-eastern Mexico: 295-302, in Fraser N. C. & Sues H.-D. (eds), *In the shadow of the dinosaurs. Early Mesozoic tetrapods*. Cambridge University Press.
- Clemens W. A. 1980. — Rhaeto-Liassic mammals from Switzerland and West Germany. *Zitteliana* 5: 51-92.
- 1986. — On Triassic and Jurassic mammals: 237-246, in Padian K. (ed.), *The beginning of the age of dinosaurs*. Cambridge University Press.
- Clemens W. A., Lillegraven J. A., Lindsay E. H. & Simpson G. G. 1979. — Where, when and what. — A survey of known Mesozoic mammals distribution: 7-58, in Lillegraven J. A., Kielan-Jaworowska Z. & Clemens W. A. (eds), *Mesozoic mammals: the first two-thirds of mammalian history*. University of California Press, Berkeley.
- Corroy G. 1928. — Les vertébrés du Trias de Lorraine et le Trias lorrain. *Annales de Paléontologie* 17 : 11-56.
- Crompton A. W. 1955. — On some Triassic cynodonts from Tanganyika. *Proceedings of the zoological Society of London* 125: 617-669.
- 1958. — The cranial morphology of a new genus and species of ictidosaurian. *Proceedings of the zoological Society of London* 130 (2): 183-216.
- 1964. — A preliminary description of a new mammal of the Upper Triassic of South Africa. *Proceedings of the zoological society of London* 142 (3): 441-452.
- 1972. — Postcanine occlusion in cynodonts and tritylodontids. *Bulletin of the British Museum of natural History (Geology)* 21 (2): 27-71.
- 1974. — The dentitions and relationships of the Southern African Triassic mammals, *Erythrotherium parringtoni* and *Megazostrodon rudnerae*. *Bulletin of the British Museum of natural History (Geology)* 24 (7): 397-437.
- Crompton A. W. & Ellenberger F. 1957. — On a new cynodont from the Molteno Beds and the origin of the tritylodontids. *Annals of the South African Museum* 44 (1): 1-13.
- Crompton A. W. & Jenkins F. A. 1968. — Molar occlusion in Late Triassic mammals. *Biological reviews* 34: 427-458.
- Crompton A. W. & Luo Z. 1993. — Relationships of the Liassic mammals, *Sinoconodon*, *Morganucodon oebleri* and *Dinnetherium*: 30-44, in Szalay F. S., Novacek M. J. & McKenna M. C. (eds), *Mammal phylogeny*. Springer-Verlag, New York.
- Crompton A. W. & Sun A. 1985. — Cranial structure and relationships of the Liassic mammal *Sinoconodon*. *Zoological journal of the Linnean Society* 85: 99-119.
- Cui G. 1976. — *Yunnaniamia*, a new tritylodont genus from Lufeng, Yunnan. *Vertebrata Palasiatica* 14: 85-90 [in Chinese].
- 1981. — A new genus of Tritylodontoidea. *Vertebrata Palasiatica* 19: 5-10 [in Chinese].
- Cuny G. 1993. — *Évolution des faunes de vertébrés à la limite Trias-Jurassique en France et au Luxembourg : implications à l'Europe occidentale*. Unpubl. Ph. D. thesis. Université de Paris VI, 206 p.
- Cuny G., Godefroit P. & Martin M. 1995. — Microrestes de vertébrés dans le Trias Supérieur du Rinckebierg (Medernach, G-D Luxembourg). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 196: 5-67.
- Cuny G. & Ramboer G. 1991. — Nouvelles données sur la faune et l'âge de Saint-Nicolas-de-Port. *Revue de Paléobiologie* 10 (1) : 69-78.
- Duffin C. J. 1993. — Late Triassic shark teeth (Chondrichthyes, Elasmobranchii) from Saint-Nicolas-de-Port (north-east France) in Herman J.

- & Van Waes H. (eds), *Elasmobranches et stratigraphie*, Professional Paper 264 : 7-32.
- Emmons E. 1857. — *American geology*, pt. 6. Albany, Sprague, 152 p.
- Evans S. E. & Kermack K. A. 1994. — Assemblages of small tetrapods from the Early Jurassic of Britain: 271-283, in Fraser N. C. & Sues H.-D. (eds), *In the shadow of the dinosaurs. Early Mesozoic tetrapods*. Cambridge University Press.
- Franck R. M., Sigogneau-Russell D. & Hemmerle J. 1986. — Ultrastructural study of triconodont (Prototheria, Mammalia) teeth from the Rhaeto-Liassic, in Russell D., Santoro J.-P. & Sigogneau-Russell D. (eds), *Teeth revisited: proceedings of the VIIth International Symposium on Dental Morphology, Paris. Mémoires du Muséum national d'Histoire naturelle, série C 53* : 101-108.
- Franck R. M., Sigogneau-Russell D. & Voegel J. C. 1984. — Tooth ultrastructure of Late Triassic Haramiyidae. *Journal of dental Research* 63 (3): 661-664.
- Godefroit P. 1997. — Reptilian, therapsid and mammalian teeth from the Upper Triassic of Varangéville (northeastern France). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 67: 83-102.
- Gow C. E. 1980. — The dentitions of the Trithelodontidae (Therapsida: Cynodontia). *Proceedings of the Royal Society of London B* 208: 461-481.
- Hahn G., Hahn R. & Godefroit P. 1994. — Zur Stellung der Dromatheriidae (Ober-Trias) zwischen den Cynodontia und den Mammalia. *Geologica et Palaeontologica* 28: 141-159.
- Hahn G., Lepage J.-C. & Wouters G. 1984. — Cynodontier-Zähne aus der Ober Trias von Medernach, Groosherzogtum Luxemburg. *Bulletin de la Société belge de Géologie* 93 (4) : 357-373.
- 1988. — Traversodontiden-Zähne (Cynodontia) aus der Ober-Trias von Gaume (Süd-Belgien). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 58 : 171-186.
- Hahn G., Sigogneau-Russell D. & Godefroit P. 1991. — New data on *Brachyzostrodon* (Mammalia; Upper Triassic). *Geologica et Palaeontologica* 25: 237-249.
- Hahn G., Sigogneau-Russell D. & Wouters G. 1989. — New data on Theroteinidae. — their relations with Paulchoffatiidae and Haramiyidae. *Geologica et Palaeontologica* 23: 205-215.
- Hahn G., Wild R. & Wouters G. 1987. — Cynodontier-Zähne aus der Obertrias von Gaume (Süd-Belgien). *Mémoires pour servir d'explication aux cartes géologiques de minières de la Belgique* 24 : 1-33.
- Hary A. & Müller A. 1975. — Zur stratigraphischen Stellung des Bonebeds von Medernach (Luxemburg). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1967 (6): 333-342.
- Hennig E. 1922. — Die Säugerzähne des württembergischen Rhät-Lias-Bonebeds. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 46: 181-267.
- Hopson J. A. 1984. — Late Triassic traversodont cynodonts from Nova Scotia and southern Africa. *Palaeontologia Africana*, 25: 181-201.
- 1985. — Morphology and relationships of *Gomphodontosuchus brasiliensis* von Huene (Synapsida, Cynodontia, Tritylodontoidea) from the Triassic of Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1985 (5): 285-299.
- Hopson J. A. & Kitching J. W. 1972. — A revised classification of cynodonts (Reptilia Therapsida). *Palaeontologia Africana* 14: 1-85.
- Huene E. von 1933. — Zur Kenntnis des Württembergischen Rätbonebeds mit Zahnfunden neuer Säuger und säugerähnlicher Reptilien. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 89: 5-128.
- Huene F. von 1928. — Ein Cynodontier aus der Trias brasiliens. *Zentralblatt für Mineralogie, Geologie und Paläontologie B* 1928: 251-270.
- 1936. — *Die fossilen Reptilien des südamerikanischen Gondwanalandes. Ergebnisse der Sauriergrabungen in Südbrasilien 1928/1929, Lieferung 2*. Verlag F. F. Heine, Tübingen, 332 p.
- Hunt A. P. 1991. — The early diversification pattern of dinosaurs in the Late Triassic. *Modern Geology* 16: 43-60.
- Hunt A. P. & Lucas S. G. 1991. — A new rhynchosaur from the Upper Triassic of West Texas, and the biochronology of Late Triassic rhynchosaurs. *Palaeontology* 34: 927-938.
- 1994. — Ornithischian dinosaurs from the Upper Triassic of the United States: 227-241, in Fraser N. C. & Sues H.-D. (eds), *In the shadow of the dinosaurs. Early Mesozoic tetrapods*. Cambridge University Press.
- Kermack D. M. 1982. — A new tritylodont from the Kayenta Formation of Arizona. *Zoological journal of the Linnean Society* 76: 1-17.
- Kermack D. M., Kermack K. A. & Musset F. 1968. — The Welsh pantothere *Kuehneotherium praecursoris*. *Journal of the Linnean Society (Zoology)* 47 (312): 407-423.
- Kermack K. A., Musset F. & Rigney H. W. 1973. — The lower jaw of *Morganucodon*. *Zoological journal of the Linnean Society* 53: 83-175.
- Kindlimann R. 1984. — Ein bisher unbekannt gebliebener Zahn eines synapsiden Reptils aus dem Rät von Hallau (Kanton Schaffhausen, Schweiz). *Mitteilungen der naturforschenden Gesellschaft in Schaffhausen* 32: 3-11.
- Kuhn O. 1965. — Therapsida (Supplementum 1). *Fossilium Catalogus I: Animalia*, 110: 1-200.
- Kühne W. G. 1949. — On a triconodont tooth of a new pattern from a fissure-filling in South Glamorgan. *Proceedings of the zoological Society of London* 119: 345-350.

- 1956. — *The Liassic therapsid Oligokyphus*. British Museum Natural History, London, 149 p.
- Laugier R. 1971. — Le Lias inférieur et moyen du Nord Est de la France. *Sciences de la Terre, Mémoire* 21 : 1-300.
- Lees P. M. & Mills R. 1983. — A quasi-mammal from Lesotho. *Acta palaeontologica polonica* 28: 171-180.
- Levallois J. 1851. — Aperçu de la constitution géologique du département de la Meurthe. *Annales des Mines* 19 : 635-667.
- 1862. — Aperçu de la constitution géologique du département de la Meurthe. *Mémoires de l'Académie Stanislas* 1862 : 246-301.
- Lewis E. 1986. — *Nearctylodon broomi*, the first nearctic tritylodont: 295-303, in Hotton III N., McLean P. D., Roth J. J. & Roth E. C. (eds), *The ecology and biology of mammal-like reptiles*. Smithsonian Institution Press, Washington and London.
- Lucas S. G. & Hunt A. P. 1994. — Chronology and paleobiogeography of mammalian origins: 335-351, in Fraser N. C. & Sues H.-D. (eds), *In the shadow of the dinosaurs. Early Mesozoic tetrapods*. Cambridge University Press.
- Lucas S. G. & Luo Z. 1993. — *Adelobasileus* from the Upper Triassic of West Texas: the oldest mammal. *Journal of vertebrate Paleontology* 13 (3): 309-334.
- Lucas S. G. & Oakes W. 1988. — A Late Triassic cynodont from the American South West. *Palaeontology* 31: 445-449.
- Luo Z. 1994. — Sister-group relationships of mammals: 98-128, in Fraser N. C. & Sues H.-D. (eds), *In the shadow of the dinosaurs. Early Mesozoic tetrapods*. Cambridge University Press.
- Luo Z. & Sun A. 1993. — *Oligokyphus* (Cynodontia: Tritylodontidae) from the Lower Lufeng Formation (Lower Jurassic) of Yunnan, China. *Journal of vertebrate Paleontology* 13: 477-482.
- Luo Z. & Wu X.-C. 1994. — The small tetrapods of the Lower Lufeng Formation, Yunnan, China: 251-270, in Fraser N. C. & Sues H.-D. (eds), *In the shadow of the dinosaurs. Early Mesozoic tetrapods*. Cambridge University Press.
- 1995. — Correlation of vertebrate assemblage of the Lower Lufeng Formation, Yunnan, China: 83-88, in Sun A. & Wang Y. (eds), *Sixth Symposium on Mesozoic terrestrial ecosystems and biota, short papers*. China Ocean Press, Beijing.
- Lydekker R. 1887. — *Catalogue of the fossil Mammalia in the British Museum* (5). British Museum – Natural History, London, 345 p.
- Martin M., Sigogneau-Russell D., Coupatez P. & Wouters G. 1981. — Les Ceratodontidés (Dipnoi) du Rhétien de Saint-Nicolas-de-Port (Meurthe et Moselle). *Geobios* 14 (6) : 773-791.
- Marzolf J. E. 1990. — Reconstruction of extensionally dismembered early Mesozoic sedimentary basins; south-eastern Colorado Plateau to the eastern Mojave Desert. *Geological Society of America Memoir* 176: 477-500.
- Mills J. R. E. 1971. — The dentition of *Morganucodon*: 26-63, in Kermack D. M. & Kermack K. A. (eds), *Early mammals*. Academic Press, London.
- Murry P. A. 1986. — Vertebrate paleontology of the Dockum Group, western Texas and eastern New Mexico: 109-137, in Padian K. (ed.), *The beginning of the age of dinosaurs*. Cambridge University Press.
- Olsen P. E. & Galton P. M. 1984. — A review of the reptile and amphibian assemblages from the Stormberg of Southern Africa with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia Africana* 25: 87-110.
- Osborn F. 1886. — A new mammal from the American Triassic. *Science* 8: 540.
- Owen R. 1860. — On some reptilian fossils from South Africa. *Quarterly journal of the geological Society of London* 16: 49-63.
- 1884. — On the skull and dentition of a Triassic mammal (*Tritylodon longaeus*) from South Africa. *Quarterly journal of the geological Society of London* 40: 146-152.
- Parrington F. R. 1946. — On the cranial anatomy of cynodonts. *Proceedings of the zoological Society of London* 116: 181-197.
- Patterson B. & Olson E. C. 1961. — A triconodontid mammal from the Triassic of Yunnan: 129-191, in Vandebroek G. (ed.), *International Colloquium on the evolution of lower and nonspecialized mammals*. Koninklijke vlaamse Akademie voor Wetenschappen, Letteren en Schone Kunsten van België, Brussels.
- Peterson F. & Pipiringos G. N. 1979. — Stratigraphic relations of the Navajo Sandstones to Middle Jurassic formations, southern Utah and northern Arizona. *United States geological Survey professional paper* 1035-B: 1-43.
- Peyer B. 1956. — Über Zähne von Haramiyiden, von Triconodonten und von wahrscheinlich synapsiden Reptilien aus dem Rhät von Hallau, Kt. Schaffhausen, Schweiz. *Schweizerische palaeontologische Abhandlungen* 72: 1-72.
- Romer A. S. 1966. — The Chañares (Argentina) Triassic reptile fauna. I. Introduction. *Breviora* 247: 1-14.
- 1967. — The Chañares (Argentina) Triassic reptile fauna. III. Two new gomphodonts, *Massetognathus pascuali* and *M. terugii*. *Breviora* 264: 1-25.
- 1969. — The Chañares (Argentina) Triassic reptile fauna. V. A new chiniquodontid cynodont, *Probelesodon lewisi*. — Cynodont ancestry. *Breviora* 333: 1-24.
- 1970. — The Chañares (Argentina) Triassic reptile fauna. VI. A cynodont with an incipient squamosal-dentary jaw articulation. *Breviora* 344: 1-18.
- Russell D., Russell D. & Wouters G. 1976. — Une dent d'aspect mammalien en provenance du

- Rhétien français. *Geobios* 9 (4) : 377-392.
- Savage R. J. G. 1971. — *Tritylodontid incertae sedis*. *Proceedings of the Bristol naturalists' Society* 32: 80-83.
- Schmidt K. P. 1927. — New reptilian generic names. *Copeia* 163: 58, 59.
- Seeley H. G. 1895. — Researches on the structure, organization and classification of the fossil Reptilia. Part IX, section 1. On the Therosuchia. *Philosophical Transactions of the Royal Society of London*, series B 185 (21): 987-1018.
- Shishkin M. A., Rubidge B. S. & Hancox P. J. 1995. — Vertebrate biozonation of the Upper Beaufort Series of South Africa. — a new look on correlation of the Triassic biotic events in Euramerica and Southern Gondwana: 39-41, in Sun A. & Wang Y. (eds), *Sixth Symposium on Mesozoic terrestrial ecosystems and Biota, short papers*. China Ocean Press, Beijing.
- Shubin N. H., Crompton A. W., Sues H.-D. & Olsen P. E. 1991. — New fossil evidence on the sister-group of mammals and early Mesozoic faunal distributions. *Science* 251: 1063-1065.
- Sigogneau-Russell D. 1978. — Découverte de Mammifères rhétiens (Trias supérieur) dans l'Est de la France. *Comptes rendus de l'Académie des Sciences de Paris*, série D 287 : 991-993.
- 1983a. — Caractéristiques de la faune mammalienne du Rhétien de Saint-Nicolas-de-Port. *Bulletin d'information des géologues du Bassin de Paris* 20 (2) : 51-53.
- 1983b. — Nouveaux taxons de mammifères rhétiens. *Acta Palaeontologica Polonica* 28: 233-249.
- 1983c. — A new therian mammal from the Rhaetic locality of Saint-Nicolas-de-Port (France). *Zoological Journal of the Linnean Society* 78: 175-186.
- 1989. — Haramiyidae (Mammalia, Allotheria) en provenance du Trias supérieur de Lorraine. *Palaeontographica*, A 206 (4/6) : 137-198.
- 1990. — Reconnaissance formelle d'une nouvelle espèce dans l'hypodigme français des Haramiyidae (Mammalia, Allotheria). *Bulletin du Muséum national d'Histoire naturelle*, 4^e série, C 12 (1) : 85-88.
- Sigogneau-Russell D., Cappetta H. & Taquet P. 1979. — Le gisement rhétien de Saint-Nicolas-de-Port et ses conditions de dépôt. *7^e réunion annuelle des Sciences de la Terre (Lyon)* : 429.
- Sigogneau-Russell D., Frank R. & Hemmerlé J. 1986. — A new family of mammals from the lower part of the French Rhaetic: 99-108, in Padian K. (ed.), *The beginning of the age of Dinosaurs*. Cambridge University Press.
- Sigogneau-Russell D. & Hahn G. 1994. — Upper Triassic microvertebrates from Central Europe: 197-213, in Fraser N. C. & Sues H.-D. (eds), *In the shadow of the Dinosaurs. Early Mesozoic tetrapods*. Cambridge University Press.
- Sues H.-D. 1985. — First record of the tritylodont *Oligokyphus* (Synapsida) from the Lower Jurassic of western North America. *Journal of vertebrate Paleontology* 5: 328-335.
- 1986a. — *Dinnebitodon amarali*, a new tritylodontid (Synapsida) from the Lower Jurassic of western North America. *Journal of Paleontology* 60: 758-762.
- 1986b. — Relationships and biostratigraphic significance of the Tritylodontidae (Synapsida) from the Kayenta Formation of northeastern Arizona: 279-284, in Padian K. (ed.), *The beginning of the age of Dinosaurs*. Cambridge University Press.
- Sues H.-D., Hopson J. A. & Shubin N. H. 1992. — Affinities of ? *Scalenodontoides plemmyridon* Hopson, 1984 (Synapsida: Cynodontia) from the Upper Triassic of Nova Scotia. *Journal of vertebrate Paleontology* 12: 168-171.
- Sues H.-D. & Olsen P. E. 1990. — Triassic vertebrates of Gondwanan aspect from the Richmond Basin of Virginia. *Science* 249: 1020-1023.
- Sues H.-D., Olsen P. E. & Kroeler P. A. 1994. — Small tetrapods from the Upper Triassic of the Richmond Basin (Newark Supergroup), Virginia: 161-170, in Fraser N. C. & Sues H.-D. (eds), *In the shadow of the Dinosaurs. Early Mesozoic tetrapods*. Cambridge University Press.
- Teissier G. 1936. — Croissance comparée des formes locales d'une même espèce. *Mémoires du Musée royal d'Histoire naturelle de Belgique*, série 2, 3 : 627-634.
- 1948. — La relation d'allométrie, sa signification statistique et biologique. *Biometrics* 1 (4): 14-53.
- Watson D. M. S. 1913. — On a new cynodont from the Stormberg. *Geological Magazine* V (10) 4: 145-148.
- Wible J. R. & Hopson J. A. 1993. — Basicranial evidence for early mammal phylogeny: 45-62, in Szalay F. S., Novacek M. J. & McKenna M. C. (eds), *Mammal phylogeny*. Springer-Verlag, New York.
- Wild R. 1978. — Die Flugsaurier (Reptilia, Pterosauria) aus der oberen Trias von Cene bei Bergamo, Italien. *Bolletino della Società Paleontologica Italiana* 17 (2): 176-256.
- Winkler D. A., Jacobs L. L., Ongleton J. D. & Downs W. R. 1991. — Life in a sand sea: biota from Jurassic interdunes. *Geology* 19: 889-892.
- Young C. C. 1940. — Preliminary notes on the mesozoic mammals from Lufeng, Yunnan, China. *Bulletin of the geological Society of China* 20 (2): 93-111.
- 1947. — Mammal-like reptiles from Lufeng, Yunnan, China. *Proceedings of the zoological Society of London* 117: 537-597.

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