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# KUEHNEOTHERIIDS FROM SAINT-NICOLAS-DE-PORT (LATE TRIASSIC OF FRANCE)

Pascal GODEFROIT [1] & Denise SIGOGNEAU-RUSSELL [2]

(5 figures, 4 tables and 2 plates)

*1. Institut royal des Sciences naturelles de Belgique, Department of Palaeontology, rue Vautier 29, B-1000 Bruxelles, Belgium; E-mail: pgodefr@ kbinirsnb.be.*
*2. Muséum national d'Histoire naturelle, Laboratory of Palaeontology, 8 rue Buffon, F-75005 Paris, France; E-mail: dsigr@mnhn.fr.*

**ABSTRACT.** A morphological and morphometrical study is performed on a collection of kuehneotheriid isolated molars (uppers and lowers) from the Late Triassic of Saint-Nicolas-de-Port (Meurthe-et-Moselle, France). It is shown that individual and random variability is dominant in this hypodigm and that, for this reason, no specific trend can be recognised which could validly isolate it taxonomically from the British taxon *Kuehneotherium praecursoris*. Wear facets are analysed and a progressive wear series as well as the occlusion pattern are reconstructed.

**KEYWORDS:** Kuehneotheriidae, mammals, Late Triassic, northeastern France, molars, dental occlusion

**RESUME. Kuehneotheriidés de Saint-Nicolas-de-Port (Trias supérieur, France).** Une collection de molaires isolées (supérieures et inférieures) du Trias supérieur de Saint-Nicolas-de-Port (Meurthe-et-Moselle, France) a été soumise à une analyse morphologique et morphométrique. Cet hypodigme est caractérisé par une variabilité individuelle et aléatoire dominante et, pour cette raison, il n'est pas possible de reconnaître des caractères spécifiques permettant de distinguer d'un point de vue taxonomique cette population du taxon britannique *Kuehneotherium praecursoris*. Les facettes d'usure ont été étudiées, permettant de reconstituer le mode progressif d'usure, ainsi que le schéma occlusal.

**MOTS-CLES:** Kuehneotheriidés, mammifères, Trias supérieur, nord-est de la France, molaires, occlusion dentaire

## 1. Introduction

The genus *Kuehneotherium*, with the species *praecursoris*, was created by Kermack *et al.* (1968) for the "Welsh pantothere" from Pontalun Quarry (early Liassic of southern Wales), previously figured or even described by several authors (in particular Kermack & Mussett, 1958; Mills, 1964; Kermack *et al.*, 1965). The material consisted of isolated teeth; an upper molar was chosen as the type and one more upper molar, three lower molars, five premolars and four partial edentulous dentaries were referred to the taxon. The generic (and specific) diagnosis was based on these various elements.

In the same paper, Kermack *et al.* (1968: 26) mentioned the presence of another "pantothere", "certainly generically distinct from the Pontalun form", from Pant Quarry, also in southern Wales. Following that study, Mills (1984) tried to reconstruct the dentition of *Kuehneotherium* from the material from Pant Quarry, but he did not name what he thought to be only a distinct species of the genus. The material consisted of 76 lowers and 41 uppers. In the same paper, Mills reconstructed molar function in *Kuehneotherium*.

Prior to Kermack *et al.*'s work, Kretzoi (1960) had described *Kuehneon duchyense* for a single tooth also from Wales ("Duchy 33" of Kuehne 1950, 1958), regarded as a lower molar; on the other hand, Kermack *et al.* (1968) and Mills (1984) suggested it might be an upper molar. The tooth was damaged and rolled; it was subsequently considered as a *nomen vanum* (Simpson, 1945) and is now apparently lost.

Outside Wales, *Kuehneotherium* is known from the Late Triassic of Greenland (Jenkins *et al.*, 1994) and Luxembourg (Godefroit *et al.*, 1998). Finally, a tooth from Somerset, U.K., described by Fraser *et al.* (1985) is supposed to be of Norian age.

The sediments of the Saint-Nicolas-de-Port quarry, in northeastern France, are either latest Norian or early Rhaetian in age (see discussion in Godefroit & Cuny, 1997). This locality has yielded, along with cynodonts (Godefroit & Battail, 1997), haramiyids (Sigogneau-Russell, 1989), theroteinids (Sigogneau-Russell *et al.*, 1986; Sigogneau-Russell & Hahn, 1995), triconodonts (Sigogneau-Russell, 1983a), a possible docodont (Sigogneau-Russell & Godefroit, 1997) and a new symmetrodont (Sigogneau-Russell, 1983b), a sizeable lot of *Kuehneotherium* teeth. In the present paper we submit this material to a morphological as well as a statistical analysis in order compare it with the British taxon. The measurements taken on the studied specimens are presented in Table 1.

| LOWER MOLARS | | | UPPER MOLARS | | |
|---|---|---|---|---|---|
| **Number** | **Crown length** | **Crown width** | **Number** | **Crown length** | **Crown width** |
| IRSNB M1831 | 1.04 | 0.53 | IRSNB 28114/76 | 1.2 | 0.68 |
| IRSNB 28114/201 | 1 | 0.58 | IRSNB M1834 | 1.13 | 0.67 |
| IRSNB 28114/202 | 1.2 | 0.54 | IRSNB 28114/204 | 0.89 | 0.52 |
| IRSNB 28114/52FW | 1.45 | 0.75 | IRSNB M1833 | 1.10 | 0.49 |
| IRSNB M1832 | 1.45 | 0.80 | IRSNB 28114/60FW | 0.58 | 0.40 |
| IRSNB 28114/147FW | 0.98 | 0.52 | IRSNB 28114/73FW | 0.92 | 0.67 |
| IRSNB 28114/70DL | 0.77 | 0.48 | IRSNB 28114/83FW | ?0.70 | 0.47 |
| IRSNB 28114/78DL | 0.67 | 0.30 | MNHP SNP54W | 1.06 | 0.61 |
| IRSNB 2814/121DL | 0.82 | 0.45 | MNHP SNP266W | 1.01 | 0.60 |
| MNHP SNP284W | 0.81 | 0.46 | MNHP SNP75L | 0.99 | 0.61 |
| MNHP SNP122W | 0.90 | 0.42 | MNHP SNP28 | 0.96 | 0.57 |
| MNHP SNP10 | 0.66 | 0.38 | MNHP SNP127L | 1.27 | 0.68 |
| MNHP SNP145L | 0.86 | 0.49 | MNHP SNP26 | 1.07 | 0.72 |
| MNHP SNP538W | 1.21 | 0.60 | MNHP SNP103 | 1.38 | 0.80 |
| MNHP SNP92 | 0.89 | 0.48 | | | |
| MNHP 179W | 1.01 | 0.64 | | | |
| MNHP SNP197W | 1.09 | 0.46 | | | |
| MNHP SNP172W | 1.08 | 0.55 | | | |
| MNHP SNP83 | 0.74 | 0.45 | | | |
| MNHP SNP763 | 0.96 | 0.47 | | | |
| MNHP SNP758 | 0.86 | 0.42 | | | |
| MNHP SNP27W | 0.86 | 0.52 | | | |
| MNHP SNP113L | 0.70 | 0.36 | | | |
| MNHP SNP757 | 0.85 | 0.50 | | | |
| MNHP SNP22 | 0.78 | 0.40 | | | |
| MNHP SNP275W | 0.75 | 0.54 | | | |
| MNHP SNP624 | 0.92 | 0.55 | | | |
| MNHP SNP634 | 1.05 | 0.46 | | | |
| MNHP SNP70L | 0.72 | 0.44 | | | |
| MNHP SNP113L | 0.70 | 0.41 | | | |

**Table 1**. Measurements (in mm) of the *Kuehneotherium* lower and upper molars from the Late Triassic of Saint-Nicolas-de-Port.

*Kuehneotherium* occupies a fundamental position in mammal phylogeny as, before the discovery of *Woutersia* Sigogneau-Russell, 1983 and possibly (Butler, 1997) *Delsatia* Sigogneau-Russell & Godefroit, 1997, from Saint-Nicolas-de-Port, it was the oldest holotherian mammal known; and as such, its tooth pattern has been considered by all authors as the basis from which the dental pattern of all subsequent holotherians derived. Prothero (1981) however raised doubts as to the ancestral position of *Kuehneotherium*, a position discussed by Sigogneau-Russell & Ensom (1998) and Cifelli & Madsen (1998).

Mc Kenna & Bell (1997) follow Prothero (1981) who excludes *Kuehneotherium* from the bulk of the Holotheria on criteria which need reinvestigations. Pending this, we regard *Kuehneotherium* as a Holotheria incertae sedis.

**Abbreviations:**
SNP, material from Saint-Nicolas-de-Port housed in the Laboratoire de Paléontologie du Museum national d'Histoire naturelle, Paris; IRSNB, material housed in the Institut royal des Sciences naturelles de Belgique, Bruxelles. L, material coming from the Lepage collection; W, material coming from the Wouters collection; D, material coming from the Delsate collection: all three given to the Museum national d'Histoire naturelle, Paris. FW, material from the Fanny Wouters collection, housed in the Institut royal des Sciences naturelles de Belgique, Bruxelles. M, material from the Natural History Museum, London; C, material in the University College, London.

## 2. Systematic palaeontology

Infraclass Holotheria Wible, Rougier, Novacek, Mc Kenna & Dashzeveg, 1995
Legion incertae sedis
Family Kuehneotheriidae Kermack, Kermack & Mussett, 1968
Genus *Kuehneotherium* Kermack, Kermack & Mussett, 1968

**Emended dental diagnosis:** A primitive therian with cusps of both the lower and upper molars forming an obtuse angle (90° to 165°); slender lower molars with a high protoconid; metaconid slightly more lingual than paraconid; well-developed lingual cingulid; labial cingulid limited to the anterior part of the crown; talonid restricted to a pointed hypoconulid; kuehneocone present or absent; low and asymmetrical upper molars, with bulbous stylocone and metacone; stylocone set lower and more labially on the crown than metacone; developed labial and lingual cingula; talon limited to a small metastyle.

**Type species:** *Kuehneotherium praecursoris* Kermack, Kermack & Mussett, 1968.

**Comments:** It should be emphasised that, in our state of knowledge, no known autapomorphy diagnoses *Kuehneotherium*.

Description of the specimens from Saint-Nicolas-de-Port:

**Lower molars (Plate1).** Thirty-two lower molars from Saint-Nicolas-de-Port have been attributed to the genus *Kuehneotherium* on the basis of the following characters: crown elevated, proto-, para- and metaconid forming an obtuse triangle; presence of a lingual cingulid; labial cingulid limited to the anterior part of the tooth; small talonid with a single cusp; protoconid high, metaconid slightly more lingual than paraconid.

Apart from these common traits, the main characteristics of these teeth appears to be their extreme variability (Table 2):

- The trigonid angle varies between 90° and 160°; this could of course be attributed to a different position in the jaw, as exemplified by Mills' (1984) reconstruction of *Kuehneotherium* dentition (though this author does not give any figure for the respective angles), and the lower jaw of *Tinodon* (Crompton & Jenkins, 1967). However, we found no discontinuity in this variation in the Saint-Nicolas-de-Port sample, which renders the separation into categories quite arbitrary.
- According to Mills (1984), the relative height of the protoconid, very variable in the Saint-Nicolas-de-Port sample, also reflects the position in the jaw, the highest being situated in the middle of the series. A median vertical ridge can be developed on the lingual side of the protoconid in some specimens.
- Kermack *et al.* (1968) state that the paraconid is larger than the metaconid in M 19155, but that the two cusps are subequal in C 855. Prothero (1981) considers a high paraconid as an autapomorphy of *Kuehneotherium* but, in the Saint-Nicolas-de-Port sample, the paraconid is either slightly smaller than the metaconid or subequal in size. According to Mills (1984), it is mostly the respective position of these cusps relative to the protoconid that distinguishes the successive molars. In the Saint-Nicolas-de-Port sample, the paraconid is either higher in position than the metaconid or, in several cases, is situated at the same level; the metaconid is usually slightly more lingual relative to the protoconid than the metaconid but, in some cases, both cusps can be equally displaced lingually.
- In the Saint-Nicolas-de-Port sample, the hypoconulid varies in relative size, though being always very small, as well as in relative position, being set distolingually, distally or distolabially relative to the metaconid. In the Welsh sample, Kermack *et al.* (1968) qualify this cusp as prominent; the same is true of the British Norian tooth (Fraser *et al.*, 1985); in Mills' series (1984), its length is said to vary from $M_1$ to $M_2$, but is not given for the more posterior molars.
- Mills (1984) stated that cusps e and f are "a feature of all the lower molars"; Kermack *et al.* (1968) also mention them in the Pontalun specimens. In our sample, they can be both present, both absent or separately present or absent; when present their degree of development is equally variable.
- The lingual cingulid terminates labially at the base of the protoconid in M 19155 (Kermack *et al.*, 1968, fig. 3b) and rises slightly in the middle in the Pant specimens (Mills, 1984). In the French sample, the cingulid can be straight, elevated in the middle or

| Characters / Specimens | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| SNP27W | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 150° |
| SNP634 | 2 | 1 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 130° |
| SNP83 | 0 | ? | 1 | 1 | ? | 1 | 2 | 0 | 1 | 132° |
| SNP10 | 0 | ? | ? | 1 | 0 | 1 | 0 | 0 | 0 | - |
| SNP197W | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 158° |
| SNP758 | ? | ? | ? | ? | 2 | 1 | ? | 1 | 1 | - |
| SNP113L | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 1 | 107° |
| SNP94W | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | - |
| SNP70L | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 150° |
| SNP763 | 1 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 115° |
| SNP284W | 1 | 1 | 1 | 0 | ? | ? | ? | 1 | ? | 122° |
| SNP121L | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 130° |
| SNP92 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 125° |
| SNP624 | 0 | 1 | 1 | 1 | 2 | 2 | 1 | 2 | 1 | - |
| SNP22 | 0 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 165° |
| SNP78L | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | - |
| SNP179W | 1 | ? | ? | ? | 1 | ? | ? | 2 | 2 | ?90° |
| SNP756 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 160° |
| SNP172W | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 135° |
| SNP145L | 0 | 1 | 0 | 0 | ? | ? | ? | 1 | 1 | - |
| SNP89L | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 135° |
| SNP122W | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 94° |
| SNP538W | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0? | - |
| SNP757 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 1? | 0 | 102° |
| IRSNB M1831 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 104° |
| IRSNB28114/201 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 119° |
| IRSNB28114/202 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 2 | 0 | 136° |
| IRSNB28114/147 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | - |
| IRSNB28114/72DL | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 1 | 1 | 137° |
| IRSNB28114/121DL | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 142° |
| IRSNB28114/170DL | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 121° |
| IRSNB28114/52FW | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 157° |
| IRSNB M1832 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 140° |

**Table 2**. Morphological variability in the *Kuehneotherium* lower molars from the Late Triassic of Saint-Nicolas-de-Port.

List of the characters (non-polarized) considered: 1: Lingual side of protoconid flat (0), convex (1) or bearing a median ridge (2); 2: Paraconid smaller than metaconid (0) or as high as metaconid (1); 3: Paraconid set at the same level than metaconid (0), higher than metaconid (1), or lower than metaconid (2); 4: Trigonid symmetrical in apical view (0) or metaconid more lingual than paraconid (1); 5: Hypoconulid absent (0), small (1) or well-developed (2); 6: Cusp e absent (0) or present (1); 7: Cusp f absent or present (1); 8: Lingual cingulid straight (0), risen in the middle (1) or forming a distinct cusp g (2); 9: Labial cingulid absent (0), developed mesially (1) or developed both mesially and distally (2); 10: cusp angulation.

even form a distinct cusp g (kuehneocone) at this level. This cusp g is also developed on one *Kuehneotherium* lower molar from Luxembourg (Godefroit *et al.*, 1998).

- The labial cingulid is present mesially and distally in the Pontalun teeth, as well as in the Pant teeth interpreted by Mills (1984) as $M_3$ and $M_6$. An important variability occurs in the Saint-Nicolas-de-Port sample, this feature being totally absent, present only distally or at both ends of the tooth.
- According to Mills (1984), the roots of the Pontalun molars are better separated from each other than those of the Pant series, which remain fused for a variable but substantial part of their height. In the Saint-Nicolas-de-Port molars, the roots are rarely preserved, and if so, they are separated from each other along their full height, being either parallel to each other or slightly divergent; such a variability is also noted by Parrington (1978), who figures the only known dentulous lower jaw of *Kuehneotherium*.

**Upper molars (Plate 2).** Twenty-two teeth from Saint-Nicolas-de-Port have been identified as *Kuehneotherium* upper molars on the basis of the following characters (Kermack *et al.*, 1968; Mills, 1984): low and asymmetrical crown with cusps forming an obtuse triangle; both lingual and labial cingula developed, the latter being always fainter and straighter than the former; paracone always more convex lingually than labially; presence of two longitudinal sulci along the

| Characters / Specimens | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| SNP75L | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 127° |
| SNP761 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | - |
| SNP760 | ? | ? | 2 | 1 | 0 | 2 | 0 | 125° |
| SNP408W | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 164° |
| SNP82 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 104° |
| SNP26 | ? | ? | 2 | 1 | 0 | 1 | 1 | - |
| SNP50W | 1 | ? | 2 | 0 | 0 | 1 | 1 | - |
| SNP266W | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 139° |
| SNP85 | 0 | 1 | 0 | 0 | 1 | 2 | ? | 125° |
| SNP54W | 0 | ? | 0 | 0 | 0 | 2 | 0 | 122° |
| SNP53 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 106° |
| SNP107L | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 90° |
| SNP127L | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 150° |
| SNP28 | ? | 2 | 1 | 1 | 1 | 2 | 0 | 146° |
| SNP703 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 143° |
| IRSNB28114/73 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 112° |
| IRSNB28114/76 | 0 | 0 | ? | 0 | 0 | 2 | 0 | 110° |
| IRSNB M1834 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 144° |
| IRSNB28114/204 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 114° |
| IRSNB M1833 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 150° |
| IRSNB28114/60FW | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 115° |
| IRSNB28114/83FW | 1 | ? | ? | 0 | 0 | 2 | 0 | - |

**Table 3**. Morphological variability in the *Kuehneotherium* upper molars from the Late Triassic of Saint-Nicolas-de-Port.

List of the characters (non-polarized) considered: 1: Labial side of paracone convex (0) or bearing a median ridge (1); 2: Stylocone smaller than metacone (0), as large as metacone (1) or larger than metacone (2); 3: Metastyle absent (0) or present (1); 4: E absent (0) or present (1); 5: F absent (0) or present (1); 6: Labial cingulum faint (0), mesially incomplete (1) or complete (2); 7: "Z" absent (0) or present (1); 8: cusp angulation.

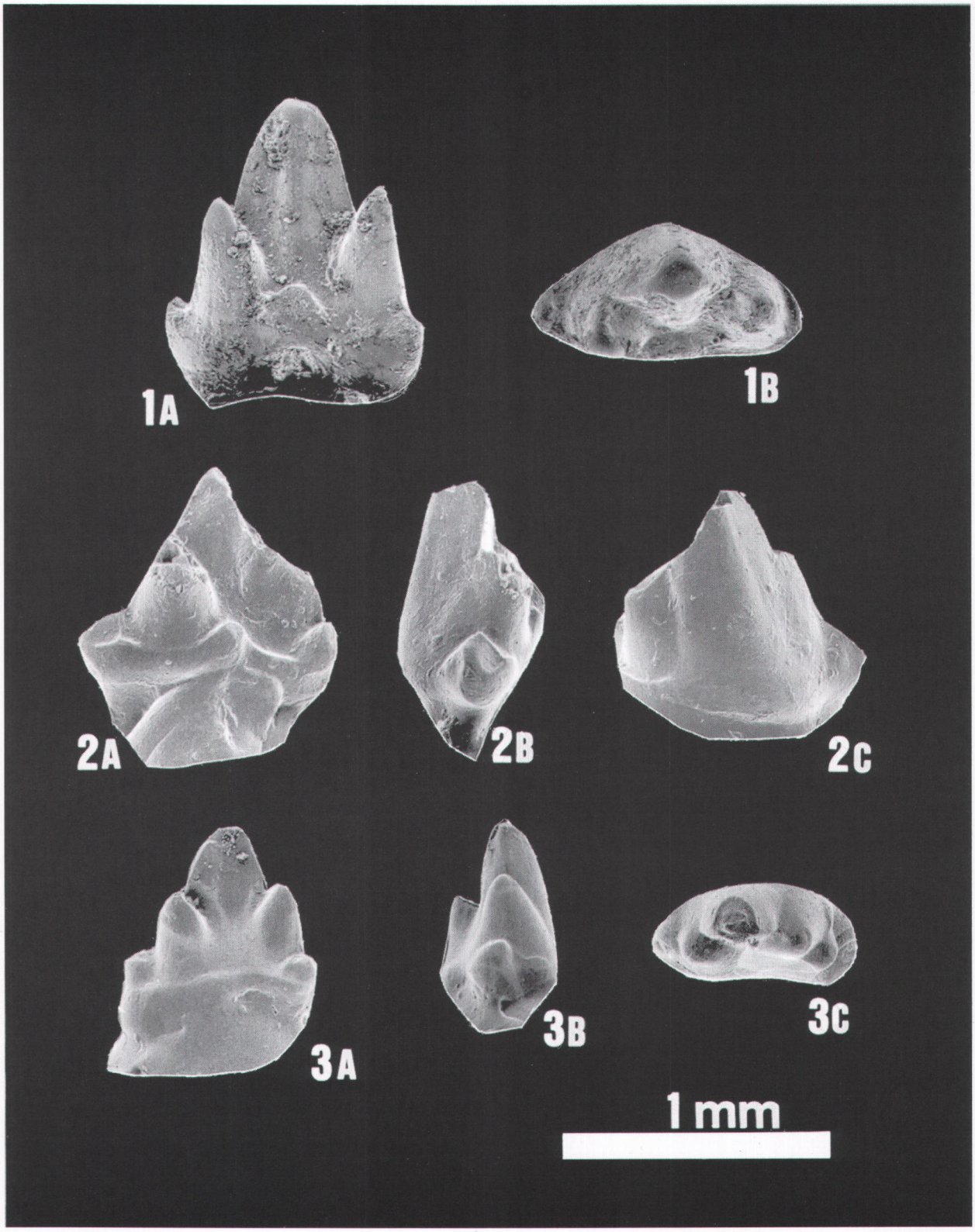
lateral borders of the cusp, so that the descending part of the pre- and postparacrista form a cutting edge; stylocone and metacone subequal and bulbous, the former being more convex labially, set lower on the crown and more labially than the latter; preparacrista consequently more nearly transverse than postparacrista.

Variability is less important than on the lower molars; it affects the following traits (Table 3):

- The trigon angle varies from 90° to 164°; as in the case of the lowers, it may be mostly an effect of the position of the tooth along the jaw.
- The paracone is more or less inclined distally; it can also be nearly vertical in some specimens. Its labial side sometimes bears a longitudinal ridge.
- The stylocone is usually smaller than the metacone, but both cusps can also be of similar size.
- Accessory cusps are represented mesially by the parastyle and cuspule F, distally by the metastyle. On the Saint-Nicolas-de-Port specimens, these can be independently present or absent, cusp-like or bulbous, but they usually remain very small; on the average, they appear less developed than on the Welsh specimens. Mills (1984) even mentions a tiny cuspule distal to the metastyle on some of the Pant molars, which has not been observed on our specimens.
- As on the Welsh molars, the lingual cingulum on the French teeth can be very erratic. It usually rises in its median part and forms a bulge against the paracone, prefiguring the prominent cusp Z of *Woutersia* (Sigogneau-Russell, 1983b). In the Pontalun sample, the lingual cingulum sometimes forms a shelf between the paracone and metacone, not observed on the Saint-Nicolas-de-Port upper molars.
- The labial cingulum is described as "beaded" or lobulated" in the Pant teeth (Mills, 1984); it appears more or less wide and presents a vertical cleft opposite the paracone. In the Saint-Nicolas-de-Port specimens, its development is variable, being sometime very faint, mainly in its mesial portion.
- As is the case for the lower molars, the two roots of the upper molars are rarely preserved in our sample; they appear either divergent or parallel.

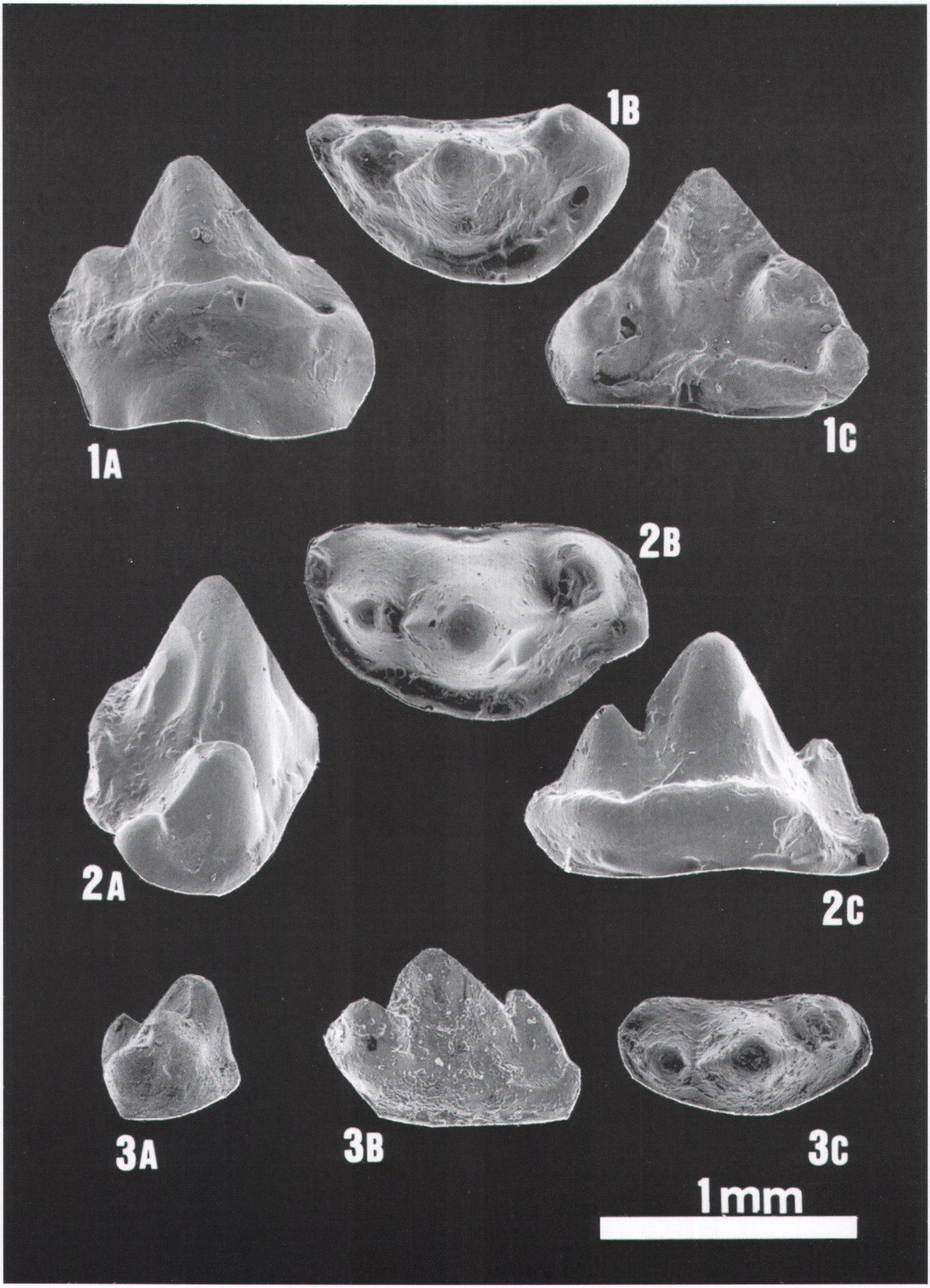
# PLATE 1

*Kuehneotherium* left lower molars from the Late Triassic of Saint-Nicolas-de-Port (France). - 1: IRSNB M1831 (A: lingual view; B: occlusal view); 2: SNP 624 (A: lingual view; B: distal view; C: labial view); 3: SNP 113L (A: lingual view; B: mesial view; C: occlusal view).


1A
1B
2A
2B
2C
3A
3B
3C
1 mm

# PLATE 2

*Kuehneotherium* left upper molars from the Late Triassic of Saint-Nicolas-de-Port (France). - 1: SNP 50W (A: lingual view; B: occlusal view; C: labial view); 2: SNP 703 (A: mesial view; B: occlusal view; C: lingual view); 3: IRSNB M 1833 (A: mesial view; B: lingual view; C: occlusal view).


1B
1A
1C
2B
2A
2C
3A
3B
3C
1mm

## Abrasion and wear:

**Lower molars (Figure 1).** Abrasion affects the apex of all the cusps, particularly that of the protoconid and the paraconid. The abrasion facet of the protoconid slopes labially and distally, that of the paraconid labially and that of the metaconid labially and mesially. A small elliptical facet usually affects the distal border of the hypoconulid. A corresponding facet can be observed at the junction between cusps e and f, confirming that adjacent lower molars interlocked in the tooth row. The configuration and phylogenetic significance of the anterior interlocking in early mammals, already discussed by Luo (1994) and Kielan-Jaworowska & Dashzeveg (1998), is reviewed in a coming paper (Sigogneau-Russell, in prep.).

Kermack *et al.* (1968) mention wear facets on the talonid and the distolabial face of the protoconid. The mode of wear in *Kuehneotherium*, as a testimony to the masticatory process, has been studied by Crompton & Jenkins (1967, 1968) and Crompton (1971). The wear pattern figured by the latter does not appear entirely satisfactory, tending to be too static and schematic. Figuration of wear in the same genus by Mills (1984) as a progressive process following different stages, appears closer to reality. It should also be added that this author observes (p. 201) "a considerable variation in the wear pattern on the different teeth of the collection partly but probably not entirely due to the position of the tooth in the series". Anyway, this progressive process can be applied to the specimens from Saint-Nicolas-de-Port: we have tentatively identified several stages. On IRSNB 28114/52FW, wear is limited along the distolabial border of the protoconid (facet 1) and remains distinct from facet 3 on the labial side of the metaconid; a small elliptical facet 2 can be observed underneath facet 3, at the level of the labial cingulum; this is more or less stage B of Mills (1984, fig.5). On SNP 94W, the bases of the proto- and metaconid facets coalesce, while a fourth facet appears along the mesiolabial edge of the protoconid. On IRSNB 28114/202 facets 1 and 3 coalesce, but are separated from facet 2; a fifth facet appears on the distolabial face of the paraconid. On IRSNB M1831 facets 1, 2, 3 are fused and so are facets 4 and 5; a sixth facet appears on the mesiolabial edge of the paraconid. Finally on SNP 78L, all facets have merged into one (stage C of Mills, 1984, fig.5). It is important to remark that facets 1 and 3 on the one hand and facets 4 and 5 on the other hand are in the same vertical plane (*contra* Crompton, 1971).

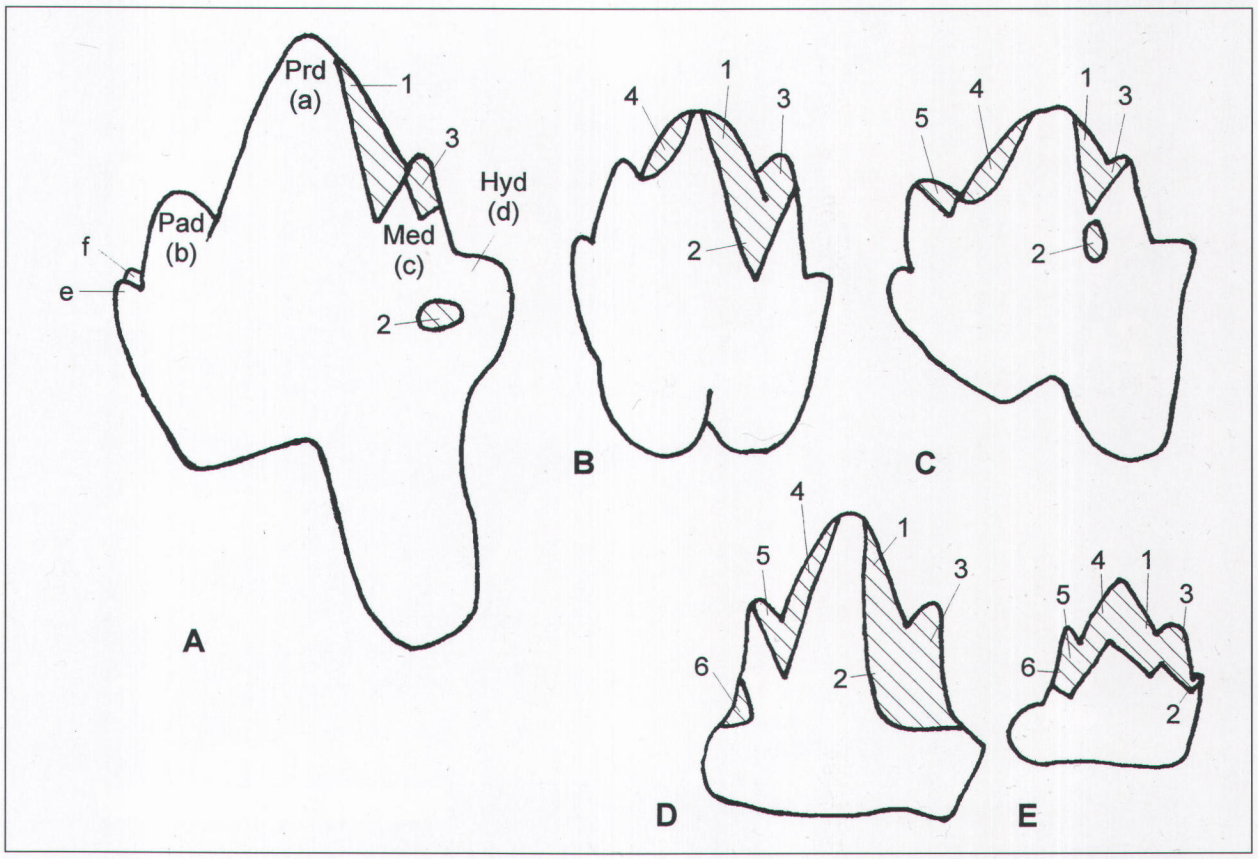



**Figure 1.** Reconstructed evolution of the wear facets in *Kuehneotherium* lower molars from the Late Triassic of Saint-Nicolas-de-Port. Labial views. A: IRSNB 28114/52FW; B: SNP 94W; C: IRSNB 28114/202; D: IRSNB M1831; E: SNP 78L. Hyd: hypoconulid; Med: metaconid; Pad: paraconid; Prd: protoconid.

**Upper molars (Figure 2).** Abrasion mainly affects the lingual side of the apex of the paracone, the orientation of the facet being variable.

In a first stage, as observed in IRSNB M1833, for example, wear affects the lingual side of the stylocone (facet I) (stage I of Mills, 1984, fig. 5). Then (IRSNB 28114/73FW) wear extends on the mesial side of the paracone (facet II) as well as on a zone below the junction stylocone-paracone (facet III) (stage B of Mills, 1984, fig. 5). In a third stage (SNP 408) facet IV affects the distolingual side of the metacone. On IRSNB M1834, two more facets are visible on the mesiolingual side of the metacone (facet V) and on the distolingual side of the paracone (facet VI). Then (IRSNB 28114/204), the mesial facets fuse at their base. Finally, distal facets fuse in a later stage, as exemplified in IRSNB 28114/76 (stage C of Mills, 1984, fig.5).

## 3. Occlusion

The occlusal relationships of upper and lower molars in *Kuehneotherium*, as deduced from wear patterns, are schematised in Figure 3. It is clearly established that wear facets first appear on the distal half of the trigonid and on the mesial half of the trigon. This results from the greater angulation between the concerned cusps, which are consequently more sollicited during mastication. Kermack *et al.* (1968) state that the protoconid wore against the stylocone; in Crompton & Jenkins's figuration (1968, fig.8), it is the mesial side of the protoconid that is shown wearing against the stylocone; while, according to Mills (1984), the same side of the protoconid wore against the distal side of the paracone and on the stylocone. Our own studies also lead to occlude the protoconid between the stylocone and metacone of the succeeding upper molars.

## 4. Specific systematics

It is not easy to distinguish intra-jaw variability from intraspecific variability on isolated teeth: both causes can account for part of the variation observed in the French *Kuehneotherium* hypodigm. As suggested by one of the reviewers (Luo), it is also probable that the studied sample includes deciduous teeth that cannot be recognised because of the important variability of the sample and of the usual poor preservation of the roots and basal part of the crown. Moreover, it cannot

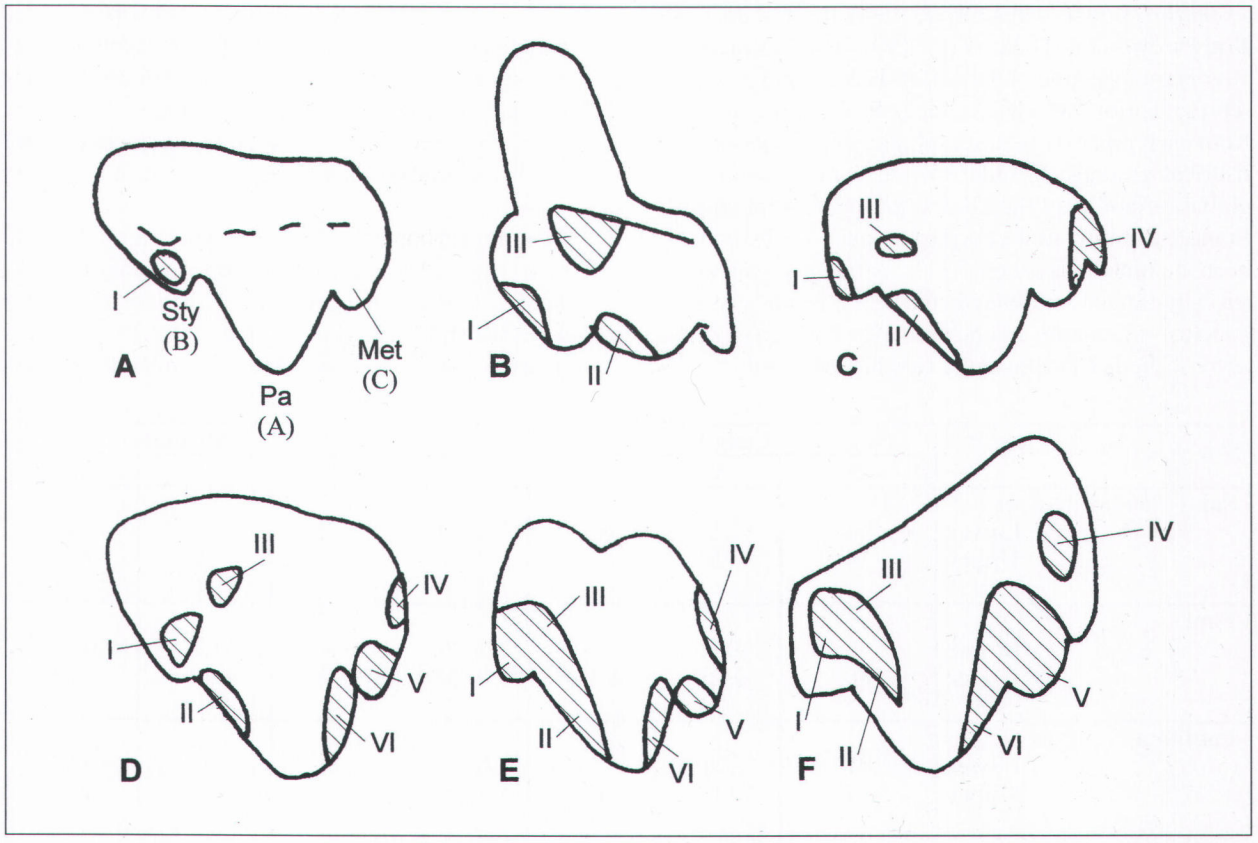



**Figure 2.** Reconstructed evolution of the wear facets in the *Kuehneotherium* upper molars from the Late Triassic of Saint-Nicolas-de-Port. Lingual views. A: IRSNB M1833; B: IRSNB 28114/73FW; C: SNP 408; D: IRSNB M1834; E: IRSNB 28114/204; F: IRSNB 28114/76. Met: metacone; Pa: paracone; Sty: stylocone.

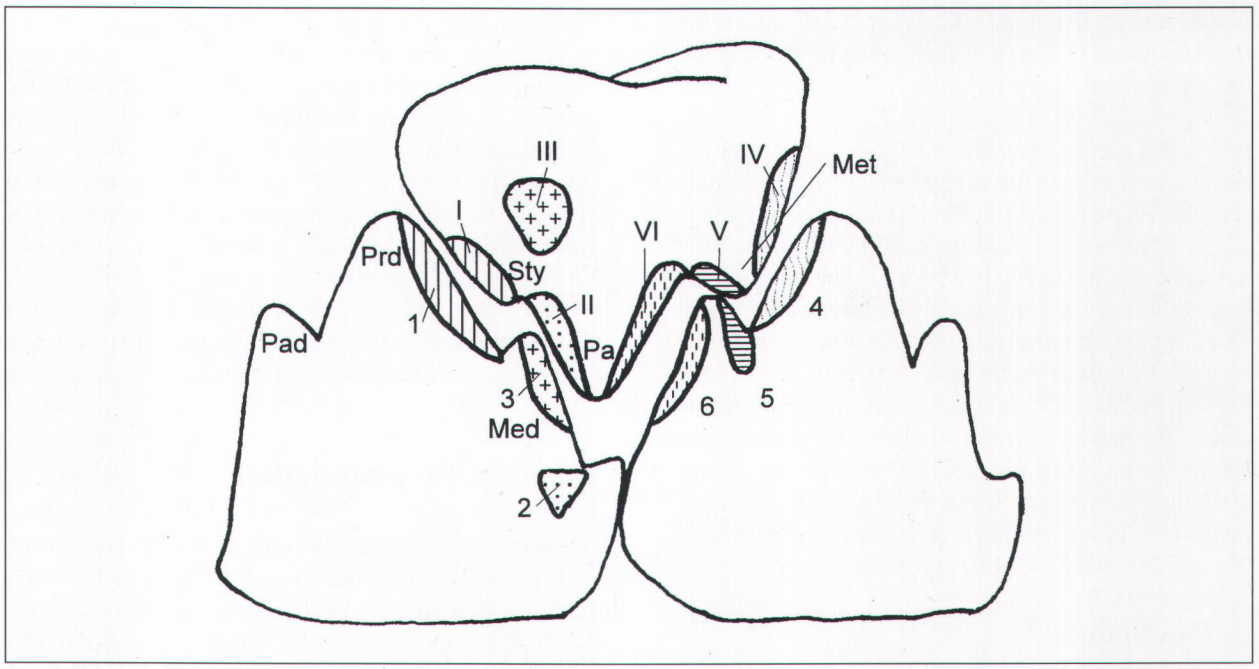



**Figure 3.** Reconstruction of molar occlusion in *Kuehneotherium*. Med: metaconid; Met: metacone; Pa: paracone; Pad: paraconid; Prd: protoconid; Sty: stylocone.

be excluded that several species are represented in this hypodigm: at the same locality, the allotherian *Thomasia* (Butler & Macintyre, 1994), the triconodont *Brachyzostrodon* (Hahn *et al.*, 1991) and the therian *Woutersia* (Sigogneau-Russell & Hahn, 1995) are all represented by two species that can be distinguished from each other on both morphological and morphometrical grounds. In order to find a structure in the global variability of the *Kuehneotherium* sample from France, a multivariate correspondance analysis has been attempted, based on the character-specimen matrices presented in Tables 2 and 3. Unfortunately, no conclusive structure can be drawn from this analysis, as most characters apparently vary independently from each other on both the upper and lower molars. Consequently, the relative importance of the different sources of variation (tooth position, intraspecific and intrageneric) on the dental morphology cannot be accurately estimated. One is therefore reduced to compare the global composition of the samples discovered within the three localities, several tooth positions and possibly several different species being mixed together.

From a morphometrical point of view, the following trends can be deduced from a comparison of the Saint-Nicolas-de-Port kuehneotheriids with those discovered in the Welsh Liassic (Figures 4-5; Table 4). Student's t-test shows that the lower molars from Saint-Nicolas-

| | Length | | | Width | | Allometry coeff. | |
|---|---|---|---|---|---|---|---|
| | n | x | s | x | s | b | a |
| **Saint-Nicolas-de-Port** | | | | | | | |
| **Lower** | 30 | 0.91 | 0.21 | 0.49 | 0.11 | 0.98 | 0.545 |
| **Upper** | 14 | 1.02 | 0.21 | 0.61 | 0.10 | 1.2 | 0.6 |
| **Pant** | | | | | | | |
| **Lower** | 40 | 0.96 | 0.10* | 0.46 | 0.10 | 1.9 | 0.49 |
| **Upper** | 46 | 0.86* | 0.10* | 0.45* | 0.07* | 1.08 | 0.53 |
| **Pontalun** | | | | | | | |
| **Lower** | 27 | 1.04* | 0.12* | 0.56* | 0.09 | 1.35 | 0.58 |
| **Upper** | 17 | 1.07 | 0.16 | 0.55 | 0.14 | 1.67 | 0.48 |

**Table 4**. Statistical comparisons of the dimensions of the *Kuehneotherium* molars from Saint-Nicolas-de-Port, Pant and Pontalun. Statistical significance of the observed differences between the mean (Student's t-test) and the standard deviation (Fisher-Snedecor's f-test) of the sample from Saint-Nicolas-de-Port and those from the Welsh localities: * = significant at 0.05 level.

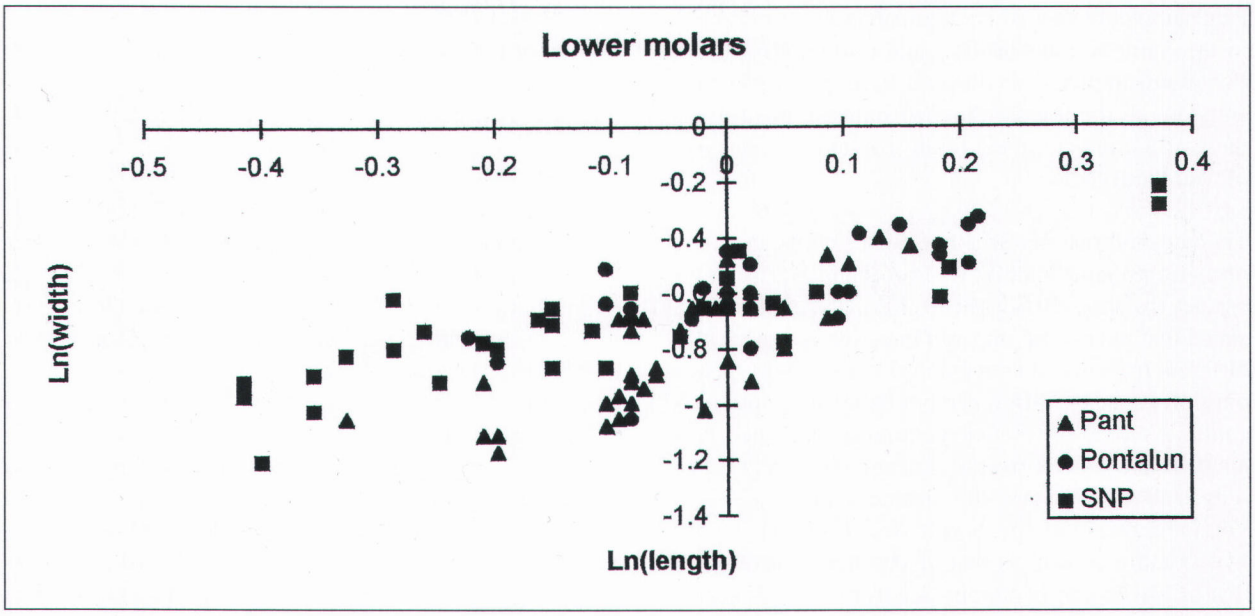



**Figure 4.** Comparisons of lower molar dimensions (in mm) in *Kuehneotherium* from Saint-Nicolas-de-Port (SNP), Pant and Pontalun.

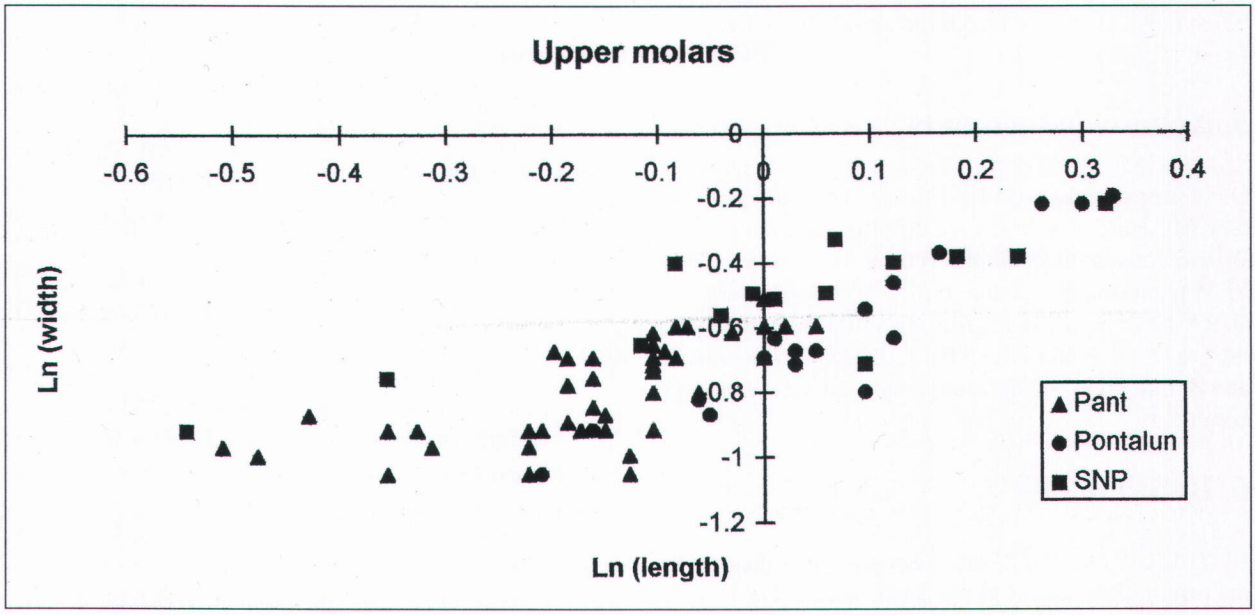



**Figure 5.** Comparisons of upper molar dimensions (in mm) in *Kuehneotherium* from Saint-Nicolas-de-Port (SNP), Pant and Pontalun.

de-Port are, in mean, significantly smaller (both mesio-distally and labio-lingually) than those from Pontalun. Fisher-Snedecor's f-test indicates that the standard deviation of the length of the lower molars is more important in the sample from Saint-Nicolas-de-Port than in the specimens from the two Welsh localities. The upper molars from Saint-Nicolas are, on the average, significantly larger, but also significantly more variable (both mesio-distally and labio-lingually) than those from Pant, but shorter than those from Pontalun.

In each sample, the allometry coefficient between the mesio-distal and the labio-lingual diameters of the molars have been calculated using Teissier's (1948) formula (both measurements are independent). Differences can be observed between the three populations. In the Saint-Nicolas-de-Port sample, the two diameters of the lower molars are isometrical, while a positive allometry can be observed in the Pontalun and particularly in the Pant sample. For the upper molars, the two diameters can be regarded as isometrical in the

Pant sample, but a positive allometry can be observed in the Saint-Nicolas-de-Port and particularly in the Pontalun samples. It is difficult to interpret these results due to the impossibility to state the position of the isolated molars in the tooth row and the presence of deciduous teeth.

The question remains whether it is possible to recognise in the Saint-Nicolas-de-Port sample a different species from the British one(s). Kermack *et al.* (1968) stated that the hypodigm from Pontalun is generically different from that at Pant Quarry. Mills (1984) speaks only of a specific difference but delayed the identification. As far as the French material is concerned, and apart from a smaller overall size and width relative to length of the lowers, the frequent presence of a kuehneocone and the lesser development of the hypoconulid as well as that of the metastyle suggest that at least some of the molars from Saint-Nicolas-de-Port could belong to a different species than those discovered in both Welsh localities. However, as long as the position of the isolated molars cannot be accurately identified, no satisfactory specific diagnosis can be established, due to a too wide variability in the different samples.

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## 6. References

BUTLER, P.M., 1997. An alternative hypothesis on the origin of docodont molar teeth. *Journal of Vertebrate Paleontology*, 17: 435-439.

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.

CIFELLI, R.L. & MADSEN, S.K., 1998. Triconodont mammals from the medial Cretaceous of Utah. *Journal of Vertebrate Paleontology*, 18 (2): 403-411.

CROMPTON, A.W., 1971. The origin of the tribosphenic molar. *In*: Kermack, K.A. & Kermack, D.M. (Eds.), Early Mammals. Academic Press: 65-87.

CROMPTON, A.W. & JENKINS, F.A. Jr., 1967. American Jurassic symmetrodonts and Rhaetic "pantotheres". *Science*, 155: 1006-1009.

CROMPTON, A.W. & JENKINS, F.A. Jr., 1968. Molar occlusion in Late Triassic mammals. *Biological Reviews*, 43 (4): 427-458.

FRASER, N.C.; WALKDEN, G.M. & STEWART, W., 1985. The first pre-Rhaetic therian mammal. *Nature*, 314: 161-163.

GODEFROIT, P. & BATTAIL, B., 1997. Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern France). *Geodiversitas*, 19 (3): 567-631.

GODEFROIT, P. & CUNY, G., 1997. Archosauriform teeth from the Upper Triassic of Saint-Nicolas-de-Port. *Palaeovertebrata*, 26 (1-4): 1-34.

GODEFROIT, P., CUNY, G.; DELSATE, D. & ROCHE, M., 1998. Late Triassic vertebrates from Syren (Luxemburg). *Neues Jahrbuch für Geologie und Paläontologie*, 210 (3): 305-343.

HAHN, G., SIGOGNEAU-RUSSELL, D. & GODEFROIT, P., 1991. New data on *Brachyzostrodon* (Mammalia; Upper Triassic). *Geologica et Palaeontologica*, 25: 237-249.

JENKINS, F.A., SHUBIN, N.H., AMARAL, W.W., GATESY, S.M., SCHAFF, C.R., CLEMMENSEN, L.B., DOWNS, W.R., BONDE, N. & OSBAECK, F., 1994. Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. *Meddedelser om Grönland, Geoscience*, 32: 3-25.

KERMACK, K.A., LEES, P.M. & MUSSETT, F., 1965. *Aegialodon dawsoni*, a new trituberculosectorial tooth from the Lower Wealden. *Proceedings of the Royal Society, B*, 162: 535-554.

KERMACK, K.A., KERMACK, D.M. & MUSSETT, F., 1968. The Welsh Pantothere *Kuehneotherium praecursoris*. *Zoological Journal of the Linnean Society*, 47: 407-423.

KERMACK, D.M. & MUSSETT, F., 1958. The jaw articulation of the Docodonta and the classification of Mesozoic mammals. *Proceedings of the Royal Society, B*, 148: 204-215.

KIELAN-JAWOROWSKA, Z. & DASHZEVEG, D., 1998. New Early Cretaceous amphilestd ('triconodont') mammals from Mongolia. *Acta Palaeontologica Polonica*, 43: 413-438.

KRETZOI, M., 1960. Zur Benemung der altesten Symmetrodonten. *Vertebrata Hungarica*, 2 (2): 307-309.

KUEHNE, W.G., 1950. A symmetrodont tooth from the Rhaeto-Lias. *Nature*, 116: 696-697.

KUEHNE, W.G., 1958. Rhaetische Triconodonten aus Glamorgan, ihre Stellung zwischen den Klassen Reptilia und Mammalia und ihre Bedeutung für die Reichart'sche Theorie. *Paläontologisches Zeitschrift*, 32: 197-235.

LUO, Z., 1994. Sister taxon relationships of mammals and the transformations of the diagnostic mammalian characters. In: Fraser, N.C. & Sues, H.-D. (eds.), In the shadow of the dinosaurs, Early Mesozoic tetrapods. Cambridge University Press: 98-128.

MILLS, J.R.E., 1964. The dentitions of *Peramus* and *Amphitherium*. *Proceedings of the Linnean Society of London*, 175: 117-133.

MILLS, J.R.E., 1984. The molar dentition of a Welsh pantothere. *Journal of the Linnean Society*, 82 (1-2): 189-205.

PARRINGTON, F.R., 1978. A further account of the Triassic mammals. *Philosophical Transactions of the Royal Society of London, B*, 282: 177-204.

PROTHERO, D.R., 1981. New Jurassic mammals from Como Bluff, Wyoming, and the interrelationships of non-tribosphenic Theria. *Bulletin of the American Museum of Natural History*, 167: 281-325.

SIGOGNEAU-RUSSELL, D., 1983a. Nouveaux taxons de mammifères rhétiens. *Acta Palaeontologica Polonica*, 228 (1-2): 233-249.

SIGOGNEAU-RUSSELL, D., 1983b. A new therian mammal from the Rhaetic locality of Saint-Nicolas-de-Port (France). *Zoological Journal of the Linnean Society*, 78: 175-186.

SIGOGNEAU-RUSSELL, D., 1989. Haramiyidae (Mammalia, Allotheria) en provenance du Trias supérieur de Lorraine (France). *Palaeontographica, A*, 206: 137-198.

SIGOGNEAU-RUSSELL, D. & ENSOM, P., 1998. *Thereuodon* (Theria, Symmetrodonta) from the Lower Cretaceous of North Africa and Europe, and a brief review of symmetrodonts. *Cretaceous Research*, 19: 445-470.

SIGOGNEAU-RUSSELL, D., FRANK, R.M. & HEMMERLE, J., 1986. A new family of mammals from the lower part of the French Rhaetic. In: Padian, K. (ed.), The beginning of the age of the dinosaurs. Cambridge University Press: 99-108.

SIGOGNEAU-RUSSELL, D. & HAHN R., 1995. Reassessment of the Late Triassic symmetrodont mammal *Woutersia*. *Acta Palaeontologica Polonica*, 40 (3): 245-260.

SIGOGNEAU-RUSSELL, D. & GODEFROIT, P., 1997. A primitive docodont (Mammalia) from the Upper Triassic of France and the possible therian affinities of the order. *Comptes rendus de l'Académie des Sciences de Paris, série IIa*, 324: 135-140.

SIMPSON, G.G., 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85: 1-340.

TEISSIER, G., 1948. La relation d'allométrie, sa signification statistique et biologique. *Biometrics*, 1 (4): 14-53.

WIBLE, J.R., ROUGIER, G.W., NOVACEK, M.J., Mc KENNA, M.C. & DASHZEVEG, D., 1995. A mammalian petrosal from the Early Cretaceous of Mongolia: implications for the evolution of the ear region and mammaliamorph interrelationships. *American Museum Novitates*, **3149**: 1-19.

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