Earliest known European mammals: A review of the Morganucodonta from Saint-Nicolas-de-Port (Upper Triassic, France)

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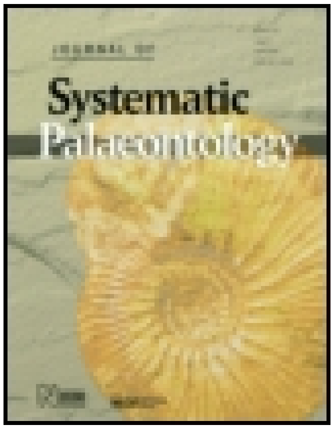

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The Rhaetian locality of Saint-Nicolas-de-Port (France) has yielded the most abundant and diverse mammalian assemblage known from the Late Triassic. Most of the material remains undescribed. We review here the morganucodonts from Saint-Nicolas-de-Port. We identify the upper and lower molariforms of the genus *Brachyzostrodon*. We also identify in the site *Morganucodon peyeri*, previously known from the Late Triassic of Hallau (Switzerland), as well as the genera *Paceyodon* and *Paikasigudodon*. The description of the new species *Megazostrodon chenali* sp. nov. extends the stratigraphical and geographical range of the genus, previously known from the Early Jurassic of southern Africa. Finally, another new morganucodont, *Rosierodon anceps* gen. et sp. nov., is described. The Morganucodonta is recognized as the most diverse order of Late Triassic mammals. Current fossil data suggest that Europe was the centre of initial diversification of morganucodonts at the end of the Triassic, and that morganucodonts were not much affected by the extinction event at the Triassic/Jurassic transition.

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Keywords: teeth; Early Jurassic; Rhaetian; Triassic/Jurassic transition; mammalian origins; occlusion

Introduction

The Triassic/Jurassic transition, which is marked by one of the five known major Phanerozoic mass extinctions (Raup & Sepkoski 1982), remains poorly known in the continental domain (Benton 1994; Fraser & Sues 1994). Therefore, the earliest known mammalian microfaunas are sometimes considered to have a relatively stable composition from the Late Triassic into the Early Jurassic (Kielan-Jaworowska *et al*. 2004). In the same way, the fossil record is very scarce from the late Early Jurassic to the early Middle Jurassic (Kielan-Jaworowska *et al.* 2004), this period giving evidence for a second wave of diversification exemplified by the first occurrence of docodonts and of crown-group Mammalia with theriiforms and australosphenidans (Luo 2007). The early evolutionary history of mammals is certainly linked to Late Triassic and Early Jurassic biotic events but the question needs to be addressed in greater detail.

The fossil record indicates that the evolutionary history of mammals began in the Late Triassic. Indeed, the oldest known mammalian fossil is the tooth of *Gondwanadon* Datta & Das, 1996, from the Carnian Tiki Formation of India (Datta & Das 1996). The mammalian affinity of *Gondwanadon* might be questionable (Kielan-Jaworowska *et al.* 2004), but other Carnian remains are known, such as the basicranium of *Adelobasileus* Lucas & Hunt, 1990 from the Dockum Formation of Texas (Lucas & Luo 1993) and the tooth of *Tikitherium* Datta, 2005 from the same formation as *Gondwanadon* but slightly younger (Datta 2005). The Norian records a first diversification of mammals, with the occurrence of morganucodonts, haramiyids and ‘symmetrodonts’ in Great Britain (Fraser *et al.* 1985; but see Whiteside & Marshall 2008), Germany (Hahn 1973), Greenland (Jenkins *et al.* 1994, 1997) and Luxembourg (Cuny *et al*. 1995). Rhaetian mammals are known from Belgium (Wouters *et al*. 1985; Hahn *et al*. 1987; Duffin & Delsate 1993; Sigogneau-Russell & Hahn 1994; Delsate 1995), Great Britain (Parrington 1941; Butler & Macintyre 1994), France (Cuny 1993a; Sigogneau-Russell & Hahn 1994; Godefroit 1997; Sigogneau-Russell & Godefroit 1997), Germany (Plieninger 1847; Huene 1933; Clemens & Martin in press), Luxembourg (Cuny *et al*. 1995; Godefroit *et al*. 1998), Poland (Świło *et al.* in press) and Switzerland (Clemens 1980). They comprise the same main groups, but with a greater generic diversity (Supplemental Table 1).

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Morganucodonta Kermack, Musset & Rigney, 1973 is the most diverse order of early mammals, with 16 genera (Kielan-Jaworowska *et al*. 2004; Clemens 2011; this article). They are known from the Carnian (?) to Bathonian and have a Pangean distribution (USA, Greenland, Europe, China, India and southern Africa) (Supplemental Table 2) (Kielan-Jaworowska *et al*. 2004). A possible additional genus, *Purbeckodon* Butler, Sigogneau-Russell & Ensom, 2012, based on six upper molariform teeth and three possible lower molariform teeth, has been found in the Early Cretaceous of England (Supplemental Table 2) (Butler, Sigogneau-Russell & Ensom, 2012). Morganucodonts are small, slender animals, generally insectivorous and probably weighing less than 100 g (Kielan-Jaworowska *et al*. 2004). They are characterized by molariforms of triconodont morphology (Kermack *et al.* 1973). Their dental formula includes three or four incisors, one canine, four or five premolars, and three, four or five molars in the half jaw (e.g. Mills 1971; Kermack *et al*. 1973; Crompton 1974). *Morganucodon* Kühne, 1949 is the best-known genus, represented by hundreds of teeth, more or less complete jaws, and cranial and post-cranial remains from the Rhaetian of France (Sigogneau-Russell & Hahn 1994; Godefroit 1997) and Switzerland (Clemens 1980) (Supplemental Table 1), and the Early Jurassic of Britain (Parrington 1971; Kermack *et al*. 1973, 1981; Jenkins & Parrington 1976), China (Rigney 1963; Kermack *et al*. 1973, 1981; Young 1978; Luo & Wu 1994) and Arizona (Jenkins *et al*. 1983). *Megazostrodon* Crompton & Jenkins, 1968 is known from a nearly complete skeleton from the Early Jurassic of Lesotho (Crompton 1974; Jenkins & Parrington 1976) and one nearly complete skull with atlas and axis from the Early Jurassic of South Africa (Gow 1986). *Erythrotherium* Crompton, 1964 is known from a nearly complete skeleton from the Early Jurassic of Lesotho (Crompton 1974; Jenkins & Parrington 1976), while *Dinnetherium* Jenkins, Crompton & Downs, 1983 is only known from jaws and cranial elements from the Early Jurassic of Arizona (Jenkins *et al*. 1983; Crompton & Luo 1993). Other genera are only known from isolated or even single teeth (Supplemental Table 2).

The Late Triassic locality of Saint-Nicolas-de-Port, north-eastern France, has yielded an abundant microfauna including numerous morganucodont teeth which have not been studied extensively (Sigogneau-Russell & Hahn 1994; Sigogneau-Russell pers. comm. 2011). The fossil richness of the 'Grès infraliasiques' Formation in the vicinity of Saint-Nicolas-de-Port has been known for a long time (Levallois 1851, 1862). However, the locality of Saint-Nicolas-de-Port became famous for its fossil mammals only in 1975 when Georges Wouters found the first Late Triassic mammal-like tooth from France in a sand quarry (Russell *et al*. 1976). Soon after this initial discovery, screenwashing operations were organized on a large scale in Saint-Nicolas-de-Port (Sigogneau-Russell 1978). Over one thousand mammalian isolated teeth were recovered, representing more than three times the quantity of mammal teeth from all other European Late Triassic sites together (Sigogneau-Russell & Hahn 1994; Kielan-Jaworowska *et al*. 2004). Denise Sigogneau-Russell conducted the study of this material, publishing 14 papers between 1976 and 1999. Concerning Morganucodonta, the genus *Brachyzostrodon* was erected on the basis of lower molars, with the type species *B. coupatezi* Sigogneau-Russell, 1983. Subsequently, Hahn *et al.* (1991) described a second species, *B. maior*, and two sets of upper molars referred to the same genus (*B*. sp. 1 and *B*. sp. 2). Finally, Sigogneau-Russell & Hahn (1994) suggested the presence of the genus *Morganucodon* and another genus of Morganucodontidae Kühne, 1958.

The purpose of the current study is to describe the taxonomic and morphological diversity of morganucodonts from the Saint-Nicolas-de-Port quarry and to document their fossil record across the Triassic/Jurassic transition.

Geological framework

Saint-Nicolas-de-Port is located in the eastern part of the Paris Basin, close to the city of Nancy (Lorraine Region) (Fig. 1A). The deposits yielding the material described here are part of the 'Grès infraliasiques' Formation (Fig. 1B) and consist of a succession of sand, sandstone and clay beds. Al Khatib (1976) described its depositional environment as a shallow marine platform very close to the continent. The site consists of a superposition of four sedimentary cycles. Each cycle begins with coarse sand with a bone-bed, followed by more-or-less ferruginous or clayey sands and sandstones and finally green clay (Fig. 2) (Laugier 1971). However, the structure of the formation is much more complicated. Most of the layers are lenticular and, therefore, the outcrops show great lateral variation (Fig. 2) (Godefroit & Battail 1997). For this reason, the precise level from which the mammalian teeth described by Sigogneau-Russell were collected remains uncertain; nevertheless, it seems that most specimens came from only one bone-bed (Fig. 2) (Godefroit & Battail 1997).

In the Lorraine and Vosges area, the base of the 'Grès infraliasiques' Formation rests on the green marls which characterize the top of the Norian 'Marnes irisées' Formation (Fig. 1B) and is often made up by a conglomerate which indicates the beginning of the Rhaetian transgression (Laugier 1971; Al Khatib 1976). Because of the ambiguity of the status of the Rhaetian in Europe, by the second half of the twentieth century Buffetaut & Wouters (1986) and Cuny (1995) had ascribed a latest Norian age to the Saint-Nicolas-de-Port outcrop. Since 1991, the Rhaetian has been recognized as a standard stratigraphical unit by the Subcommission on Triassic Stratigraphy and no longer as a local lithostratigraphical stage (Ogg 2012). Because the

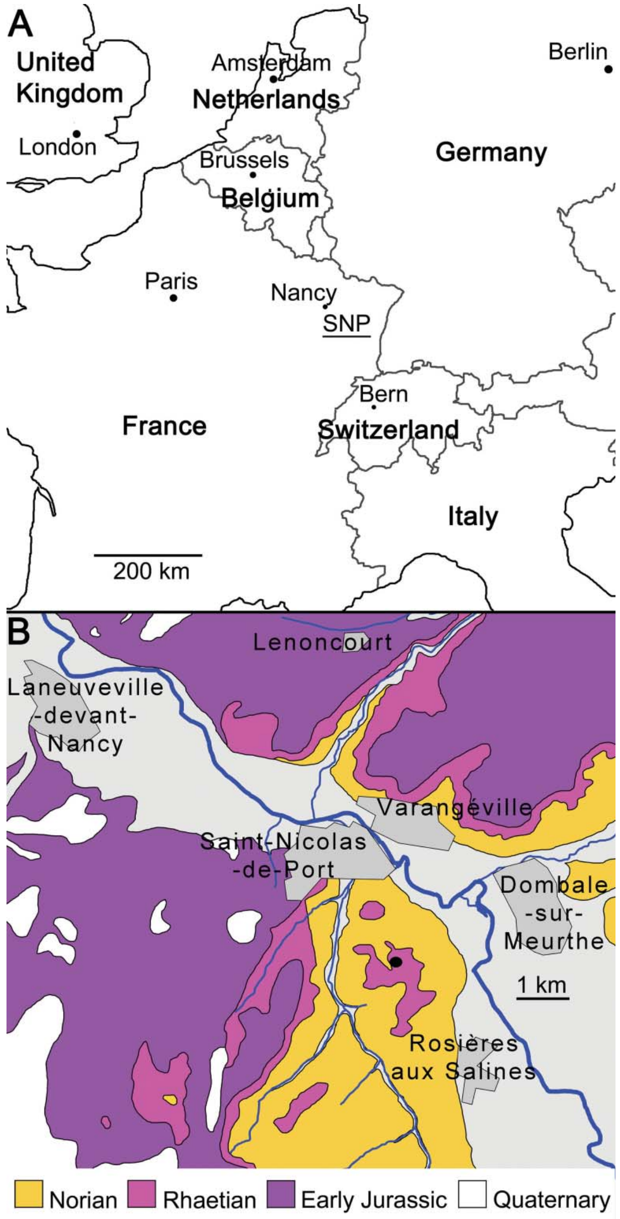

Figure 1. A, location of Saint-Nicolas-de-Port; scale bar = 200 km. **B,** geological map of the Saint-Nicolas-de-Port area (from Hilly *et al*. 1977; Vincent *et al*. 1978); black dot: fossil site of SNP.

'Grès infraliasiques' Formation is younger than the transgression and can be correlated with Rhaetian strata in Germany (Deutsche Stratigraphische Kommission 2005; Sues & Fraser 2010), we consider here that the microfauna from Saint-Nicolas-de-Port is Rhaetian in age, as already suggested by previous studies (Laugier 1971; Al Khatib 1976; Sigogneau-Russell & Hahn 1994).

There are some doubts about the ages of many sites that we have compared with Saint-Nicolas-de-Port below: their Rhaetian age is generally accepted but Norian or Hettangian alternatives cannot be excluded (see Supplemental Table 2 for references). These discussions were developed before the recognition of the Rhaetian by the International Commission on Stratigraphy, and few sites have been studied again since 1991. Because of these stratigraphical debates, we need to be cautious in our discussion and to keep in mind that a reinterpretation of site ages can lead to different conclusions.

Associated fauna

Saint-Nicolas-de-Port has yielded the most diverse mammalian fauna hitherto recorded from the Late Triassic (Sigogneau-Russell & Hahn 1994, 1995; Sigogneau-Russell & Godefroit 1997; Godefroit & Sigogneau-Russell 1999; Kielan-Jaworowska *et al*. 2004), as well as numerous fossils of other taxa. The non-tetrapod fauna is represented by four species of shark, two species of dipnoans and three indeterminate genera of actinopterygians (Cuny 1995). There are also three families of temnospondyls (Cuny 1993b). Among Sauropsida, there are several examples of Lepidosauromorpha, including a possible sphenodontid and some archosaurs, such as one species of phytosaur, one pterosaur, a possible ornithischian and one prosauropod (Godefroit & Cuny 1997). Finally, 10 species of non-mammalian cynodonts are present, plus one unidentified genus (Godefroit & Battail 1997).

Material and methods

Institutional and other abbreviations

GIT: Geologisches Institut Tübingen (now Institut für Geowissenschaften, Eberhard Karls Universität), Tübingen, Germany; **IRSNB**: Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; **KM**: Kota Mammals; **MNHN**: Muséum National d'Histoire Naturelle, Paris, France; **NHMUK**: Natural History Museum, London, UK; **PIMUZ**: Paläontologisches Institut und Museum der Universität Zurich, Zurich, Switzerland; **RAS**: Rosières-aux-Salines, another name for the study site; **SNP**: Saint-Nicolas-de-Port; **VPL/JU**: Vertebrate Palaeontology Laboratory, Jammu University, Jammu, India.

Material

This study focuses on the collections of isolated teeth of morganucodonts collected from Saint-Nicolas-de-Port. Five collections have been studied. The first one was made by Dr D. Sigogneau-Russell's team and is housed in the MNHN, Paris. It is identified with numbers bearing the acronym 'SNP'. The second collection includes a set of casts of specimens, prefixed 'RAS', housed in the IRSNB, Brussels, found at the same time as the Sigogneau-Russell team collection. Both collections come from the same stratigraphical level (see above). The other three

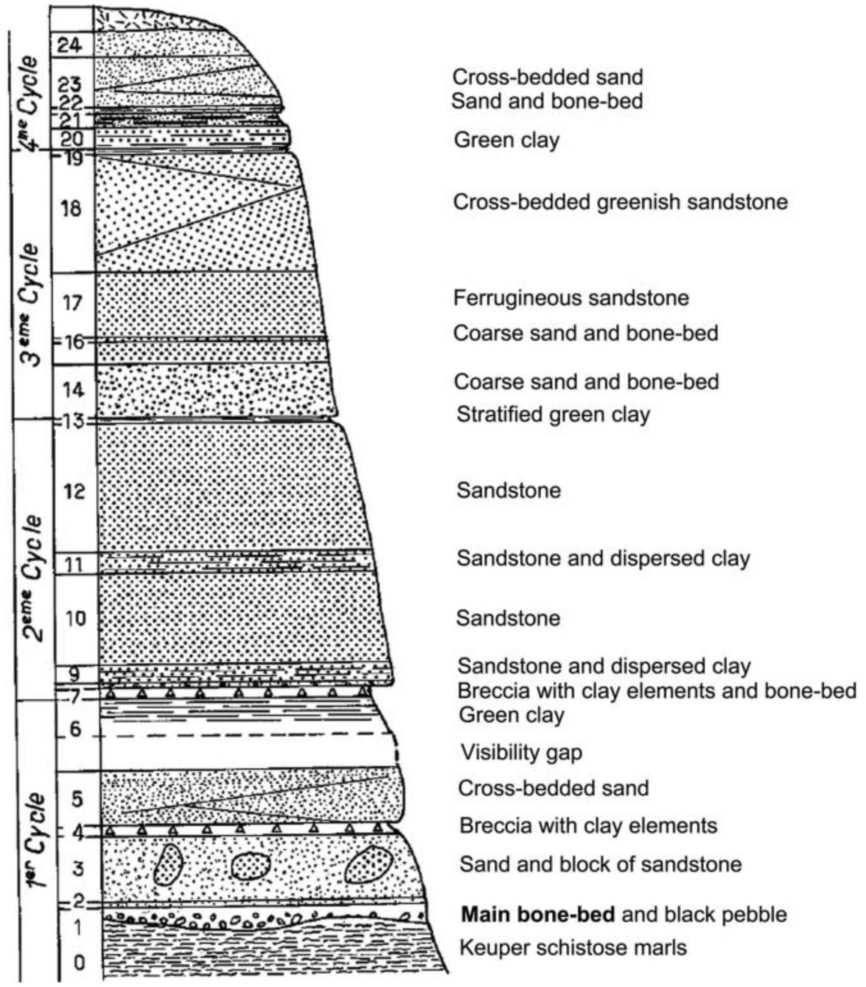

Figure 2. Stratigraphical section of the 'Grès infraliasiques' Formation at Saint-Nicolas-de-Port quarry (Godefroit & Battail 1997).

collections were made by amateur palaeontologists. The G. Wouters Collection, kept at the MNHN and the IRSNB, is identified by the suffix 'W' or 'FW'. The collection of J.-C. Lepage is housed in the MNHN under identification numbers with the name 'Lepage' or the letter 'L'. These collections include original specimens and casts. The Dr D. Delsate Collection is housed in the MNHN with identification number bearing the acronym 'DD'. Problematic specimens are the numbers '10 Ph' and '202', which bear no indication of the collection. They all come from the sand quarry of Saint-Nicolas-de-Port but their exact stratigraphical provenance within the quarry is unknown.

Observations, drawings and measurements

All teeth described here were observed under a binocular microscope (CETI) at a magnification of 36×. Drawings were made by the first author with a camera lucida. Biometric measurements were made with a digital readout (Heidenhain ND 1200, Traunreut, Germany). These measurements were used to make boxplots and statistical tests with the R statistical environment (R Development Core team 2013). Wilcoxon tests were used to compare samples because they are too small (<30 specimens) for the Student t-test (Poinsot 2005). Three-dimensional images of studied teeth were obtained by X-ray computed tomographic (CT) scans at the AST-RX platform of the MNHN using a phoenix|x-ray|v|tome|x L 240-180 CT scanner. All scans were computed with an isotropic voxel size of 3.43179 μm, a high-voltage of 60 kV and a current of 200 μA, except SNP 2001 with an isotropic voxel size of 3.46665 μm and a current of 280 μA. Images were processed with VGStudio Max 2.2 (Volume Graphics, Heidelberg, Germany).

Dental nomenclature

The dental nomenclature used is essentially that of Crompton & Jenkins (1968, text-fig. 2) which defines cusps *a* to *g* with a drawing. Cusp *i* was first used by Pacey (1978) (see also Clemens 2011). The first author has added cusps e' and *i*′ in order to clarify some descriptions. Cusp definitions are: *a*, high central cusp in the main row; *b*, mesial cusp in relation to *a* in the main row; *c*, distal cusp in relation to *a* in the main row; *d*, distal cingular cusp in relation to *c*; *e*, the most mesial cusp on the lingual cingulum; *e*′, (disto)lingual cingular cusp in relation to *e*; *f*, the most mesial cusp on the labial cingulum; *g*, lingual cingular cusp between apices *a* and *c* (also known as the 'kühnecone', Parrington 1967); *i*, (mesio)lingual cingular cusp in relation to *d*; *i*′, (mesio)lingual cingular cusp in relation to *i*. This nomenclature has a descriptive purpose and does not necessarily imply homology. Capital letters are used for upper teeth and lower case letters for lower teeth.

The descriptions of the wear facets are based on the nomenclature of von Koenigswald *et al*. (2012, p. 146) for jaw movements. This nomenclature is used to define the direction and the angle of the slope of the wear facets (see Supplemental Appendix 1). The process and the pattern of occlusion are beyond the scope of this article and will be dealt with in detail elsewhere.

Methodology for characterizing the Saint-Nicolas-de-Port material

This study only focuses on molariform teeth of morganucodonts, because it is difficult to distinguish their premolariform teeth from those of their mammalian and cynodontan relatives (Godefroit & Battail 1997). Morganucodont molariform teeth have at least three cusps in the main row. Nevertheless, the distalmost premolars of several morganucodonts are quite molariform in aspect (e.g. Mills 1971; Parrington 1971), and we are unable to distinguish such 'molariform premolars' from the true molars. The identification of specimens as Morganucodonta is based on the following features: (1) a main row of three cusps, usually with (2) a supplementary fourth lesser distal cingular cusp and (3) cingular elements on at least one side (e.g. Kermack *et al.* 1973; Kielan-Jaworowska *et al.* 2004).

Descriptions and identifications of the isolated teeth from Saint-Nicolas-de-Port are based on tooth orientation, reconstruction of dental series, and to association of lower and upper molariforms.

The anatomical orientation of specimens is necessary to locate them in the tooth row and to name the cusps for descriptions and comparisons. In Morganucodonta, upper molariforms have both lingual and labial cingular elements (Kermack *et al.* 1973; Kielan-Jaworowska *et al.* 2004), and in lower molariforms, the central cusp is much higher (Jenkins & Crompton 1979). The labiolingual axis is quite easy to define because the cingulum of the lower teeth is always lingual, whereas the lingual cingulum of the upper teeth is almost always uninterrupted and less developed than the occasionally interrupted labial cingulum (Kielan-Jaworowska *et al.* 2004). The distal cusp *d*/*D* is usually aligned mesiodistally with the main row while the mesial cusps *e*/*E* and *f*/*F* are seldom aligned (Kielan-Jaworowska *et al.* 2004).

Three trends are evident in the tooth rows of Morganucodonta: (1) the cingular elements grow posteriorly; (2) the largest molariform tooth is generally the first molar (e.g. *Megazostrodon*) or the second molar (e.g. *Morganucodon*), rarely the third molar (sometimes in *Morganucodon*); and (3) size differences between main cusps decrease posteriorly (Mills 1971; Parrington 1971; Kermack *et al.* 1973; Crompton 1974; Clemens 2011).

Occlusal relations of upper and lower molariforms are inferred on the basis of size similarity, morphological concordance and wear facets. The wear facets are related to the three occlusion patterns in Morganucodonta. The first one is the 'offset shearing' described in *Morganucodon*, with the shearing of the lingual side of cusp *A* along the labial side of the notch between cusps *a* and *c* (Fig. 3A) (Crompton & Jenkins 1968). The second is the 'embrasure shearing' described in *Megazostrodon*, with the shearing of the lingual side of cusp *A* along the labial side of the space between the cusp *c* of the anterior tooth and the

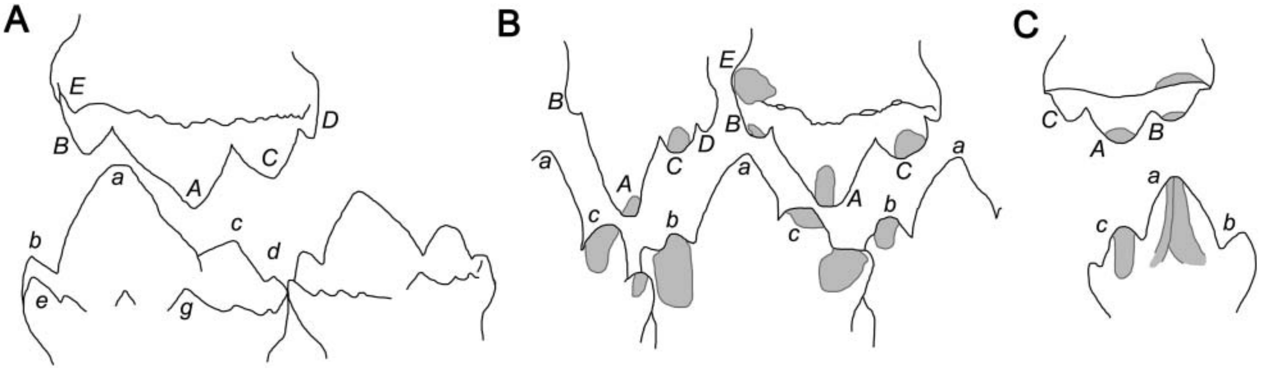

Figure 3. Reconstruction of occlusal relationships and wear facets of molariform teeth. **A,** *Morganucodon*, upper and lower teeth in lingual view. **B,** *Megazostrodon*, wear facets in grey, upper in lingual view and lower in labial view. **C,** *Bridetherium*, wear facets in grey, upper in lingual view and lower in labial view (from Crompton & Jenkins 1968; Crompton 1974; Clemens 2011).

cusp *b* of the posterior tooth (Fig. 3B) (Crompton & Jenkins 1968). The third was described in *Bridetherium*, with the shearing of the lingual side of cusp *A* along the labial side of cusp *c* (Fig. 3C) (Clemens 2011).

Special attention must be paid to the great variability of some of the characters, especially the cingular features as shown, for example, by specimens of *Megazostrodon* (Gow 1986). Moreover, this variability can affect details anywhere in the crown, as shown in extant seals (Jernvall 2000; Salazar-Ciudad & Jernvall 2010). Alongside variations linked to tooth rank position or individual variations, this variability can be caused by minor changes at the population level and consequently might be unusable in taxonomic and phylogenetic analyses (Jernvall 2000; Salazar-Ciudad & Jernvall 2010).

Systematic palaeontology

Mammaliaformes Rowe, 1988
Order **Morganucodonta** Kermack, Musset & Rigney, 1973
Family **Morganucodontidae** Kühne, 1958
Genus ***Morganucodon*** Kühne, 1949

Type species. *Morganucodon watsoni* Kühne, 1949.

Additional species. *Morganucodon heikuopengensis* Young, 1978; *Morganucodon oehleri* Rigney, 1963; *Morganucodon peyeri* Clemens, 1980; unnamed species (Jenkins *et al*. 1983).

Diagnosis. (Kühne 1958, translated from German) "*M. watsoni* is a Rhaetic triconodont with at least 14 postcanines, of which the main cusp is always bent backwards. From the unicuspid first postcanine there is a gradual transition to two-, three-, four-, and finally five-cusped posterior postcanines. The posterior accessorial cusp is always larger than the anterior accessorial cusp, if both are present. Upper posterior postcanines have a continuous cingulum, lower posterior postcanines only have a lingual cingulum, in which the largest cingulum-cuspule is recognizable as an orimentary ['orimentär', probably meaning incipient] metaconid and the posterior cingulum-cuspule as an orimentary talonid."

Distribution. Upper Triassic (Rhaetian): Saint-Nicolas-de-Port ('Grès infraliasiques' Formation), Lorraine, France; and Hallau, Kanton Schaffhausen, Switzerland. Lower Jurassic: fissure fillings of Saint Bride's Island, Wales, UK; Yunnan (Lower Lufeng Formation), China and Arizona (Kayenta Formation), USA.

Morganucodon peyeri Clemens, 1980
(Figs 4A, 5)

Diagnosis. (Clemens 1980) "A small morganucodontid with molariform teeth smaller than those of *Morganucodon oehleri* but approximately the same size as those of *M. watsoni*, however, their crowns appear to be relatively narrower than those of the latter species. Buccal and lingual cingula of upper molariforms tend to be more weakly developed than those of *M. watsoni* and *M. oehleri* and the buccal more frequently interrupted across the base of the principal cusp. Resembling *M. watsoni*, but not *M. oehleri*, the lingual cingulum of the lower molars of *M. peyeri* is relatively well developed. Possibly the presence of a large, anterolingual cingular cusp, almost as large as the anterior accessory cusp, might separate *M. peyeri* from the other species. No evidence of buccal cingula, present on a very few lower molars of *M. watsoni* (Parrington, 1971) and on some of the few described molars of *M. oehleri* (Mills, 1971), has been found in the small sample of *M. peyeri*."

Holotype. PIMUZ AIII-329, left lower molar in a fragment of dentary, from Hallau (Upper Triassic, Switzerland).

Referred material from Saint-Nicolas-de-Port. Lower molariforms: 10 Ph (left) (Fig. 5B), SNP 33 (right), SNP 99 W (left) (Figs 4A, 5A), SNP 171 W (right). SNP 253 W (right), SNP 527 W (left), SNP 2003 (left). SNP 99 W and 10 Ph are the sole complete teeth in this set. All other teeth are broken at the level of the junction between cusps *a* and *c*, except for SNP 33 in which part of cusp *c* is preserved.

Measurements. See Table 1.

Description. The three cusps of the main row are aligned along the mesiodistal axis of the tooth, although the apex of cusp *b* can be slightly labial to cusp *a*. Cusp *a* is the largest cusp and is slightly recurved distally. Cusp *c* is the second cusp in length, and cusp *b* is the smallest in length and width (about half the width of cusp *a*). Cusps *b* and *c* are at the same level, similar in height and degree of separation from cusp *a*. In lateral view, the mesial crest of cusp *a* can be either concave (SNP 99 W, SNP 253 W, SNP 2003) or straight, with a short vertical section at its lower end (10 Ph, SNP 33, SNP 171 W, SNP 525 W). In the same view, the distal crest of cusp *a* is generally straight, with a vertical section at its lower end. The vertical part of the distal crest is longer than that of the mesial crest. SNP 33 is the sole tooth with an entirely straight distal crest. The crest joining cusp *b* to cusp *e* forms an obtuse angle with the crest joining *a* to *b*.

There is no labial cingular element. The lingual cingulum is divided into two parts. Cusp *e* forms alone the mesial cingulum. This cusp is slightly smaller than *b*, but located much lower on the crown. It is projected slightly more mesially than *b* and is extended by a distal crest which extends down to the base of *a*. The distal cingulum is preserved only

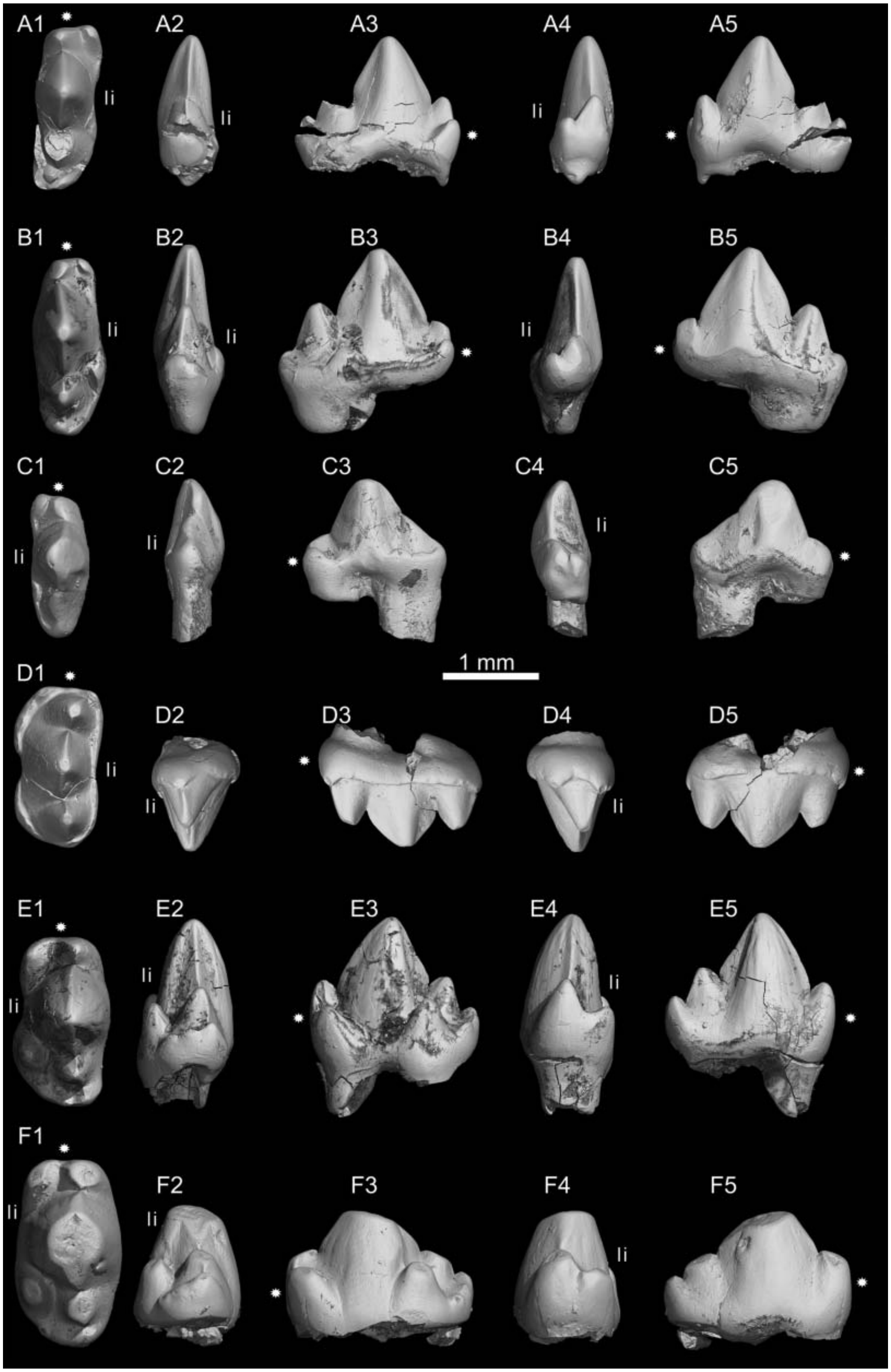

Figure 4. Views of CT-scan reconstructions of morganucodont molariforms. **A,** *Morganucodon peyeri*, SNP 99 W, left lower. **B–D,** *Megazostrodon chenali*; **B,** SNP 28 W, left lower; **C,** SNP 725, right lower, holotype; **D,** SNP 324 W, right upper. **E, F,** *Brachyzostrodon coupatezi*; **E,** SNP 500 W, right lower; **F,** SNP 68 W, right lower. Abbreviations and symbol: 1, occlusal view; 2, distal view; 3, lingual view; 4, mesial view; 5, labial view; 'li', lingual face; white star, mesial extremity.

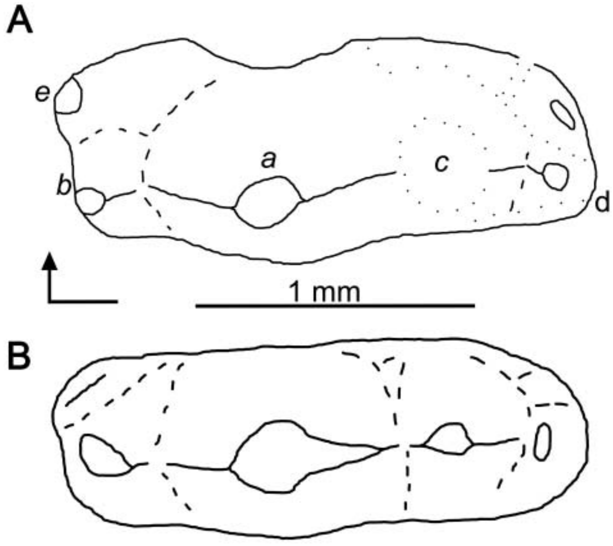

Figure 5. Sketch drawings of lower molariforms of *Morganucodon peyeri* in occlusal view. **A,** SNP 99 W (left); **B,** 10 Ph (left). Right-angled arrow indicates mesial extremity and lingual face. Letters in italics correspond to cusp nomenclature.

in SNP 99 W and 10 Ph, and is weakly developed bearing a single cusp, *d*, and a minute cuspule that is lingual to cusp *d* (except in 10 Ph). The cingulum extends from cusp *d* to the base of cusp *a*. Cusp *d* is the smallest cusp of the tooth and is located labially relative to *c*.

Wear. None of the Saint-Nicolas-de-Port specimens show traces of wear.

Remarks. According to Clemens (1980), the main and almost unique diagnostic character of *Morganucodon peyeri* is biometrical. The holotype of *M. peyeri* AIII-329 is as long as the largest tooth of *M. watsoni* but much shorter than the smallest molar of *M. oehleri* (Table 2). The width of AIII-329 is less than the mean width of *M. watsoni* and the width of the smallest molar of *M. oehleri* (Table 2) (Mills 1971; Kermack *et al*. 1973; Clemens 1980). The exception is the fourth molar of the holotype of *M. oehleri*, which is as small as some teeth of *M. watsoni* (Table 2) (Kermack *et al*. 1973). As a result, the length to width ratio is greater in *M. peyeri* than in *M. watsoni* ($W = 33$, $p = 0.005495$) and *M. oehleri* ($W = 12$, $p = 0.05714$) (Table 2; Fig. 6). SNP 99 W and 10 Ph perfectly match the relative size proportion of AIII-329. The Saint-Nicolas-de-Port specimens are longer than AIII-329 and as narrow as (10 Ph) or narrower than (SNP 99 W) AIII-329 (Tables 1, 2). Morphological comparison shows that the distal lingual cingulum of SNP 99 W is less developed than that of *M. oehleri* and lacks cusp *g*, which is typical of the latter. However, the mesial lingual cingulum of all specimens from Saint-Nicolas-de-Port is equivalent to this part in *M. watsoni* and *M. peyeri* (Kühne 1958; Mills 1971; Clemens 1980).

Family **Megazostrodontidae** Gow, 1986
Genus ***Megazostrodon*** Crompton & Jenkins, 1968

Type species. *Megazostrodon rudnerae* Crompton & Jenkins, 1968.

Additional species. *Megazostrodon chenali* sp. nov.

Emended diagnosis. *Megazostrodon* differs from all other morganucodontans by three main characters: (1) the labial cingulum of upper molars is well developed, with robust cusps, and divided into mesial and distal lobes (also present in *Brachyzostrodon*, *Dinnetherium* and some specimens of *Morganucodon*); (2) cusp *A* occludes between cusp *c* of the opposite molar and cusp *b* of the succeeding molar (‘embrasure shearing’ occlusion; also possibly present in *Erythrotherium* and *Purbeckodon*); and (3) the bottom of the notch between cusps *a* and *c* is clearly higher than that between cusps *a* and *b* (also present in *Bridetherium*, *Erythrotherium*, *Hallautherium* and *Paceyodon*).

Distribution. Upper Triassic (Rhaetian): Saint-Nicolas-de-Port (“Grès infraliasiques” Formation), Lorraine, France. Lower Jurassic: ‘Lesotho (Upper Elliot Formation)’ and ‘Orange Free State (Upper Elliot Formation)’, South Africa.

Megazostrodon chenali sp. nov.
(Figs 4B–D, 7, 8)

Diagnosis. This new species differs from *M. rudnerae* by the smaller cusps on the labial cingulum of the upper molariforms. Its lower molariforms differ by having less developed lingual cingular elements, with a cusp *g* reduced or absent and the absence of additional lingual cuspules to cusps *e* and *g*.

Etymology. In recognition of the great contribution of the amateur palaeontologist Emmanuel Chenal to the study of the microvertebrates from the Late Triassic of Lorraine and Vosges, France.

Holotype. MNHN SNP 725, right lower molariform (m2?), from Saint-Nicolas-de-Port (Upper Triassic, France) (Fig. 4C).

Referred material. Upper molariforms: RAS 5 FW (mesial right), SNP 27 (mesial left), SNP 324 W (distal right) (Figs 4D, 8), SNP 2006 (mesial left). Lower molariforms: RAS 37 FW (left m3?) (Fig. 7), RAS 72 G (left mesial?), RAS 90 FW (left m2?), RAS 94 G (left m2?), RAS 98 FW (left m3?), RAS 100 FW (right m4?), RAS 923 W (left m1?), RAS 933 W (right m4?) (Fig. 7), SNP 28 W (left m2?) (Figs 4B, 7), SNP 65 W (left m1?) (Fig. 7), SNP 152 W (right mesial?), ?SNP 225 W (left

Table 1. Dental measurements (in mm) of morganucodont molariforms from Saint-Nicolas-de-Port (Upper Triassic, France).

Taxon	Specimen	L	W	R
Morganucodon peyeri	10-Ph	1.73	0.62	2.79
	SNP 99 W	1.67	0.59	2.83
Megazostrodon chenali	RAS 37 FW	1.68	0.72	2.33
	RAS 90 FW	1.67	0.65	2.57
	RAS 94 G	1.79	0.68	2.63
	RAS 98 FW	1.68	0.72	2.33
	RAS 100 FW	1.69	0.75	2.25
	RAS 923 W	1.59	0.49	3.25
	RAS 933 W	1.79	0.86	2.08
	SNP 28 W	1.82	0.69	2.64
	SNP 65 W	1.99	0.47	4.23
	SNP 324 W	1.78	0.94	1.89
	SNP 725	1.52	0.63	2.41
	SNP Lepage 134	1.59	0.66	2.41
Brachyzostrodon coupatezi	SNP 68 W	1.94	1.07	1.81
	SNP 100	1.87	1.15	1.63
	SNP 500 W	1.73	0.96	1.80
	SNP 737	2.16	1.06	2.04
Brachyzostrodon cf. *coupatezi*	37 L	1.59	0.64	2.48
	85 L	1.10	0.52	2.12
	RAS 47	1.14	0.56	2.02
	RAS 717	1.73	0.78	2.22
	SNP 29 W	1.80	0.94	1.91
	SNP 81	1.43	0.70	2.04
Brachyzostrodon maior	RAS 1020	2.67	1.21	2.21
	RAS 785	1.87	1.15	1.63
Brachyzostrodon cf. *maior*	RAS 45 FW	2.00	1.19	1.68
Paceyodon davidi	SNP 2001	2.42	0.78	3.10
Rosierodon anceps	62 L	1.21	0.49	2.47
	89 L	0.94	0.50	1.88
	202	1.21	0.58	2.01
	SNP 22	0.80	0.43	1.84
	SNP 79 L	1.21	0.50	2.42
	SNP 739	1.24	0.68	1.81
Paikasigudodon cf. *yadagirii*	SNP 736	1.34	0.67	2.00
Morganucodonta indet. 1	RAS 39 FW	1.39	0.67	2.07
Morganucodonta indet. 2	SNP 523 W	1.52	0.86	1.77

Note: L: length; W: width; R: ratio of length to width.

distal?), SNP 491 W (right distal?), SNP Lepage 134 (left m3?).

Measurements. See Table 1.

Description

Lower molariforms. The main cusps, *a*, *b* and *c*, are aligned mesiodistally (general case) or form an obtuse angle (average 150–160°) open towards the labial side (RAS 72 G, RAS 933 W, SNP Lepage 134 and SNP 491 W). Cusp *a* is heavily compressed transversely and very slightly recurved distally. Cusps *b* and *c* are more conical in shape than cusp a. Cusp *b* is more or less oblique relative to the mesiodistal axis. In width and height, cusp *a* is the largest and cusp *b* the smallest cusp. Cusp *c* is closer to cusp *a* in height but closer to cusp *b* in width. Notch *a*–*c* is deeper than notch *a*–*b*, but the apex of *b* is never higher than the base of the notch *a*–*c*. In lateral view, the crest joining cusp *a* to cusp *b* is rather convex except in RAS 72 G and RAS 923 W, where this crest is nearly straight. In the same view, the crest joining cusp *a*

Table 2. Dental measurements (in mm) of morganucodont molariforms taken from the literature.

Taxon	Specimen	L	W	R	Reference
Morganucodon peyeri	AIII-329	1.65	0.62	2.66	Clemens (1980)
Morganucodon watsoni					
Lower molars	M24560				Mills (1971)
	M1	1.28	0.54	2.37	
	M2	1.44	0.70	2.06	
	M3	1.20	0.62	1.94	
	M4	0.82	0.56	1.46	
	M24590				Mills (1971)
	M1	1.16	0.46	2.52	
	M2	1.40	0.70	2.00	
	M3	1.30	0.64	2.03	
	M22679				Mills (1971)
	M1	1.10	0.44	2.50	
	M2	1.50	0.70	2.14	
	M22768				Mills (1971)
	M1	1.10	0.46	2.39	
	M2	1.38	0.66	2.09	
Morganucodon oehleri					
Lower molars	CUP 2320				Kermack *et al*. (1973)
	M1	1.90	0.76	2.50	
	M2	2.30	0.98	2.35	
	M3	1.89	0.83	1.07	
	M4	1.06	0.45	2.36	
Megazostrodon rudnerae					
	M26407				Original observation
Lower molars	M1	1.77	0.57	3.11	
	M2	1.67	0.77	2.17	
	M3	1.27	0.73	1.74	
?*Brachyzostrodon*					Clemens & Martin (in press)
	GIT 1561/14	2.28	1.48	1.54	
Paceyodon davidi	M45920	3.30	1.60	2.06	Clemens (2011)
Paikasigudodon yadagirii	KM/10	1.88	1.06	1.77	Prasad & Manhas (2002)

Note: L: length, W: width, R: ratio of length to width.

to cusp *c* is straight in its upper part and becomes nearly vertical under the level of the tip of cusp *c*, with some exceptions. In SNP 65 W, the change of slope is above the apex of *c*. In RAS 72 G, RAS 98 FW, RAS 923 W, RAS 933 W and SNP Lepage 134, the upper part of the crest is rather concave, the change of slope is either at the level of the apex of cusp *c*, or just above, and its lower part is far from vertical. In RAS 90 FW and RAS 100 FW, the crest *a*–*c* is truncated by wear (see below). The crest joining cusp *b* to cusp *e* forms a slightly obtuse angle with the main row, except when the main row is an obtuse angle in which case the angle formed by crests is clearly acute. The crest joining cusp *c* to cusp *d* is entirely straight.

There is no labial cingular element. The lingual cingulum is divided into mesial and distal parts. The mesial part is mostly made up by cusp *e*. This cusp forms the mesiolingual corner of the tooth and is the largest cingular cusp. It is placed lower than cusp *b*. Cusp *e* is often followed by *e*′, a minute cusp in the continuation of cusp *e* and that is slightly more lingual and lower than the latter. The distal part of the lingual cingulum extends from cusp *d* to beneath the notch *a*–*c*, except in RAS 90 FW where cusp *g* is mesial to the notch *a*–*c*. Its distal end is higher than the mesial one. Cusp *d* forms this distal end. It is slightly smaller than cusp *e* and placed directly distal or slightly labial to cusp *c*. When cusp *d* is labial to cusp *c*, it corresponds to an obtuse-angled main row, except in RAS 37 FW where the main row is straight and *d* labial. The mesial end is formed by *g*, a cusp smaller than cusp *d*, with two sets of exceptions: in RAS 72 G, RAS 933 W and SNP 65 W where cusp *g* is absent (but in RAS 72 G, the area where cusp *g* would have been expected from

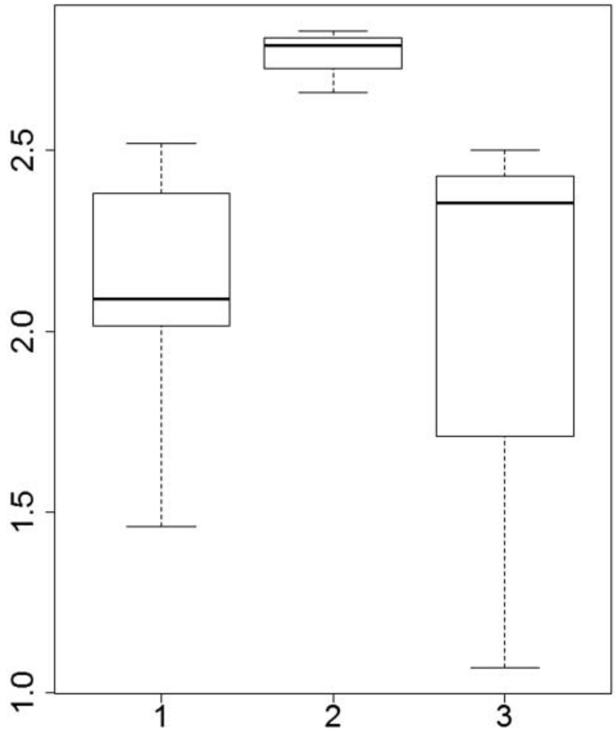

Figure 6. Boxplot for length to width ratio of some molariform teeth of *Morganucodon* based on measurements in Tables 1 and 2. 1, *M. watsoni*; 2, *M. peyeri*; 3, *M. oehleri*. Bold line inside box represents the median; lower and upper borders of box represent respectively the first and third quartiles; and the lower and upper extremities of the 'whisker' represent respectively the minimum and maximum values.

other, intact specimens is missing); in SNP 152 W and ?SNP 225 W, cusp *g* is larger than cusp *d*. RAS 90 FW, RAS 933 W and SNP 28 W bear a cusp *i* directly lingual to cusp *d*. SNP 65 W displays an additional cusp *i*′ that is mesiolingual to *i*. RAS 37 FW, RAS 98 FW, SNP Lepage 134 and SNP 491 W shows an additional cuspule joining cusps *i*′ and *g*.

Identification of tooth position in the postcanine row. In *Megazostrodon rudnerae*, the length of the lower molars decreases posteriorly, whereas their width increases posteriorly in the type species (Table 2). In other words, there is a decrease of the length to width ratio posteriorly (Table 2). Cusp *c* is much reduced in the distal molars. The mesial and distal cingula and their cusps grow to form a continuous chain in some teeth. However, the cingular elements are not helpful for identifying the rank position in this new species. Indeed, they are weakly developed, very sensitive to wear and show much individual variation. There is no more reduction of cusp *c* in the hypodigm. The length to width ratio is used as a proxy for determining the position of specimens in the tooth row (Table 1). Identification of tooth position in the series remains tentative in the Saint-Nicolas-de-Port material. RAS 72 G, SNP 152 W, SNP 225 W and SNP 491 W were not measured because of their poor preservational states, and tentative tooth rank identification is based on either their slender or stout appearance.

Remarks on SNP 225 W. The interpretation of this specimen is difficult because the anterior half and the base of the crown are missing. It shows no diagnostic character of *Megazostrodon*, and the cingular elements are very different from those of other specimens in their relative development. SNP 225 W is tentatively referred to *Megazostrodon chenali*, pending additional data.

Upper molariforms. The main cusps, *A*, *B* and *C*, form a lingually opened obtuse angle (average 160°). The apex of each main cusp is situated closer to the lingual border than to the labial border. Their labial side is strongly convex, whereas their lingual side is rather flattened and almost vertical. Cusp *A* is larger and higher than the other two cusps. Cusp *B* is a little smaller than cusp *C*, but they are subequal in height. Cusp *A* is very slightly recurved distally. The notches between these cusps are similar in depth but notch *A*−*C* is a little lower. In lateral view, the crests going from the tip of cusp *A* are straight in their upper part, and under the level of the tips of cusps *B* and *C* they bow to become almost vertical. The crests coming from cusps *B* and *C* towards cusp *A* or, respectively, cusps *E* and *F*, are entirely straight in occlusal and lateral views. The cingular cusps are much smaller than the main cusps.

The lingual cingulum extends from cusp *D* to the mesial extremity of the tooth with cusp *E*. It is smooth, thin and subhorizontal. Only SNP 324 W shows a very

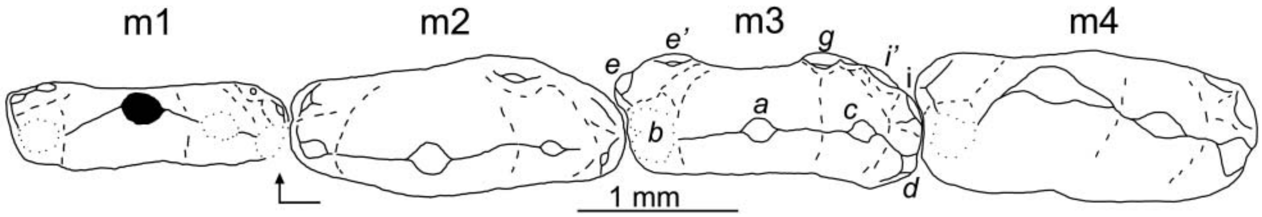

Figure 7. Hypothetical composite reconstruction of the left lower jaw of *Megazostrodon chenali* in occlusal view; m1, SNP 65 W; m2, SNP 28 W; m3, RAS 37 FW; m4, RAS 933 W (drawing reversed to appear as a left tooth). Right-angled arrow indicates mesial extremity and lingual face. Letters in italics correspond to cusp nomenclature.

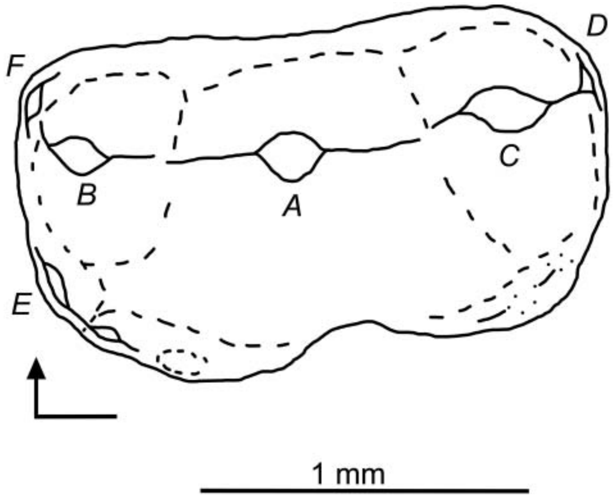

Figure 8. Sketch drawing of upper molariform of *Megazostrodon chenali* (SNP 324 W, right) in occlusal view. Right-angled arrow indicates mesial extremity and lingual face. Letters in italics correspond to cusp nomenclature.

slight elevation beneath the apex of cusp *A* and a very slight hollow in occlusal view. Cusp *E* forms the mesiolingual corner of the tooth and is among the largest three cingular cusps. Cusp *E* is always in the continuation of the angle outlined by the main cusps. The labial cingulum is much more developed than the lingual cingulum and is divided into mesial and distal lobes. The lobes are more or less crenulated by cuspules. Each lobe begins medially at the lowest level of the crown, extends horizontally under the apex of an accessory cusp (*B* or *C*), and then rises to the extremity of the tooth. The mesial lobe is the most crenulated lobe. It bears the mesiolabial cusp *F*, which forms the mesiolabial corner of the tooth, and is a little lower than *E* but similar in size. The mesial lobe either joins the lingual cingulum on the mesial side of the tooth (SNP 2006), or ends just before it (SNP 324 W). In both cases, a groove is outlined between *E* and *F*, possibly for the insertion of cusp *D* of the preceding molar. The distal lobe joins cusp *D*, which is smaller than *E* and *F*. It is either in the continuation of the angle (SNP 324 W), or directly distal to *C* (RAS 5 FW, SNP 27).

Identification of tooth position in the postcanine row. In *Megazostrodon rudnerae*, molar shape changes posteriorly showing reduction in length, increase in width, and enlargement of the cingular elements. SNP 324 W exhibits a more developed labial cingulum and a stouter outline. RAS 5 FW, SNP 2006 and SNP 27 are more slender and similar in size; however, their broken state makes this uncertain. These specimens are thus considered as mesial molariforms (closer to M1 or M2 of *M. rudnerae*), and SNP 324 W is considered as a distal molariform (closer to M3 or M4 of *M. rudnerae*).

Wear. Upper molariforms in the Saint-Nicolas-de-Port material lack heavy wear. Only two teeth are worn. Cusp *A* of SNP 324 W is slightly worn with a faint, shallow lingual facet. Cusp *B* bears a steep mesiolingual wear facet, cusp *E* a very steep, similarly oriented wear facet, while cusp *C* has a shallow distal or disto-distolingual wear facet. Cusp *D* bears a very steep disto-distolingual wear facet, possibly an interdental wear facet. The lingual cingulum bears two, very slight, vertical lingual wear facets just beneath the apex of *B* and *C*. The labial cingulum and its cusps show several traces of wear, but these are not related to the contact with the lower molars. In RAS 5 FW, wear facets are present only on the apices of cusps *B* and *C*. These facets have the same orientation as those of SNP 324 W and both are steep.

In the lower molariforms, SNP 28 W shows a vertical mesio-mesiolabial facet on the labial side of cusp *b*. RAS 94 G bears the same facet as SNP 28 W, a shallow distal facet on the apex of cusp *a*, a shallow disto-distolabial facet on the apex of cusp *c*, and a shallow distolabial facet on the distal side of cusp *d*. Each facet is more inclined than the more mesial facet. RAS 923 W shows the same facets as RAS 94 G, but also bears a very steep labial facet on the side of cusp *a*, from the apex to half-height. SNP 725 is so heavily worn that the labial side is almost completely truncated. The entire labial side of cusp *b* is occupied by a very steep mesiolabial facet. A very steep labial (slightly mesial) facet extends along the upper half of the labial side of cusp *a*. The labial side of cusp *c* is entirely truncated by a very steep labio-distolabial facet. Cusp *d* is almost completely worn out by a very steep labio-mesiolabial facet. The latter two facets form a large, shallow, U-shaped valley. RAS 90 FW and RAS 100 FW show slightly different patterns. In RAS 90 FW, the distal crest of cusp *a* is truncated by a notch halfway between the apex of cusp *a* and the apex of cusp *c*. This notch is composed by a distal vertical facet and a steep distal facet, the two facets forming an obtuse angle. In RAS 100 FW, the distal crest of cusp *a* is truncated by a wide hollow which joins the apex of cusp *a* and almost joins the level of the apex of cusp *c*. No facets can be distinguished within the hollow but its extremities show a gentler slope than in RAS 90 FW. Moreover, cusp *b* is truncated by a mesiolabial steep facet which extends from the apex to the base of the cusp. Cusp *c* shows a shallow distal facet on its apex and a very steep labial facet on the upper part of its labial side.

The wear facets described in the *Megazostrodon chenali* hypodigm are consistent with the descriptions of the material of *Megazostrodon* by Crompton (1974), although the wear of crest $a-c$ was neither described nor depicted by Crompton (1974).The wear is concentrated mesially to cusps *b*/*B*, distally to cusps *c*/*C* and transversely to cusps *a*/*A*. As in *M. rudnerae*, *M. chenali* shows an 'embrasure shearing' occlusion pattern with cusp *a* shearing between cusp *C* of the anterior molar and cusp *B* of the posterior molar.

Remarks. Characters of the lower molars distinguishing the new species from *Megazostrodon rudnerae* also resemble those of *Morganucodon* (weak development of cingular elements). On the other hand, the characters of the main cusp row and the occlusal pattern relate this species to *Megazostrodon rudnerae* (e.g. relations between notches, wear pattern). The latter differences are here considered most consistently significant of the occurrence of a new species of *Megazostrodon*, *M. chenali* sp. nov., at Saint-Nicolas-de-Port.

In their review of synapsids from Germany, Clemens & Martin (in press, fig. 7a–c, e, f) described an incomplete tooth from Olgahain (GIT 1561/15) as a morganucodontid indet. By comparison with the Saint-Nicolas-de-Port material described here, GIT 1561/15 shows a great resemblance with SNP 725 (Fig. 4C), the holotype of *Megazostrodon chenali*. GIT 1561/15 especially matches two diagnostic features included in the emended diagnosis of *Megazostrodon* and one diagnostic features of *M. chenali*. The bottom of the notch between cusps *a* and *c* is higher than that between cusps *a* and *b* (Clemens & Martin in press, fig. 7b, c), although the difference is weak in comparison with SNP 725 and rather close to the difference in SNP 28 W (Fig. 4B). The planar surface described by Clemens & Martin (in press, fig. 7a, c) on the labial side of cusp *c* in GIT 1561/15 fits the very steep labio-distolabial facet on cusp *c* of SNP 725. GIT 1561/15 shows a slightly flattened surface on the top of the labial side of cusp *a* (Clemens & Martin in press, fig. 7a, c), which can be considered as the beginning of the very steep labial facet on cusp *a* of SNP 725, and RAS 923 W. GIT 1561/15 shows a slight notch on the distal crest of cusp *a* which fits the notch described in RAS 90 FW and RAS 100 FW. GIT 1561/15 displays the same dental wear pattern as *Megazostrodon*. This specimen shares with the SNP specimens smaller lingual cingular elements by comparison with *M. rudnerae*. As a consequence, we tentatively refer GIT 1561/15 to *M. chenali*.

Family ***incertae sedis***

Genus ***Brachyzostrodon*** Sigogneau-Russell, 1983

Emended diagnosis. *Brachyzostrodon* is characterized by lower molariforms with sub-equal cusps *b*, *c*, the cusp directly lingual to *b* and *g*. Cusps *b* and *c* are not connected to a cingulum or rarely so for *g*. The enamel surface is often wrinkled (as in *Wareolestes*). Upper molariforms are characterized by: (1) a well-developed labial cingulum with robust cusps and divided into mesial and distal lobes (also present in *Dinnetherium*, *Megazostrodon* and some specimens of *Morganucodon*); (2) a distolabial cingulum rising from the base of cusp *A* to cusp *D* (also present in *Dinnetherium*); and (3) an uninterrupted lingual cingulum with a strong downslope between cusps *A* and *E* (also present in *Bridetherium*).

Type species. *Brachyzostrodon coupatezi* Sigogneau-Russell, 1983.

Additional species. *Brachyzostrodon maior* Hahn, Sigogneau-Russell & Godefroit, 1991; *Brachyzostrodon* cf. *coupatezi* and *Brachyzostrodon* cf. *maior* (see below).

Distribution. Upper Triassic (Rhaetian): Saint-Nicolas-de-Port ('Grès infraliasiques' Formation), Lorraine, France; and possibly Upper Triassic (Norian): Jameson Land (Fleming Fjord Formation), Greenland.

Brachyzostrodon coupatezi Sigogneau-Russell, 1983
(Figs 4E, F, 9, 15)

Emended diagnosis. In *B. coupatezi*, the cusp directly lingual to cusp *b* is *e*, by contrast with *B. maior* where it is *e*′ (Figs 9, 13). The lower molariforms of *B. coupatezi* are slightly smaller than *B. maior* (Table 1; Fig. 10).

Remarks. The biometric criterion for species identification deserves caution for two reasons. Firstly, the difference in size is slight. There is overlap of dental dimensions in the two species: RAS 785 (*B. maior*) and SNP 100 (*B. coupatezi*) have the same length and width (Table 1). Secondly, the number of measurements (2 in *B. maior* and 4 in *B. coupatezi*) is too low to be considered

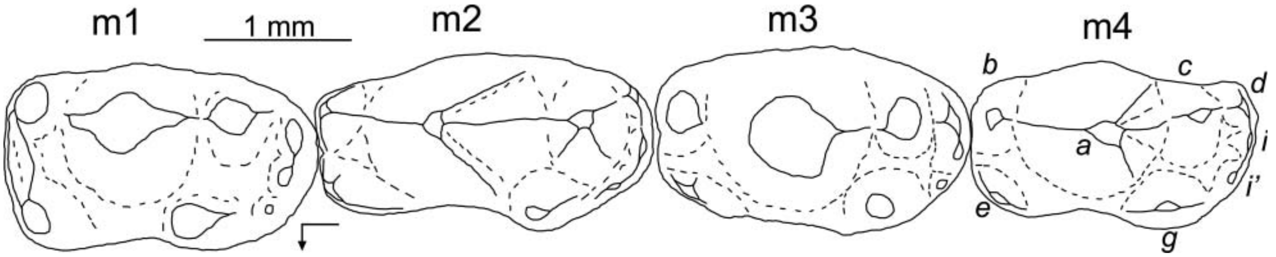

Figure 9. Hypothetical composite reconstruction of the right lower jaw of *Brachyzostrodon coupatezi* in occlusal view; m1, SNP 100; m2, SNP 737; m3, SNP 68 W; m4, SNP 500 W. Right-angled arrow indicates mesial extremity and lingual face. Letters in italics correspond to cusp nomenclature. Scale bar = 1 mm.

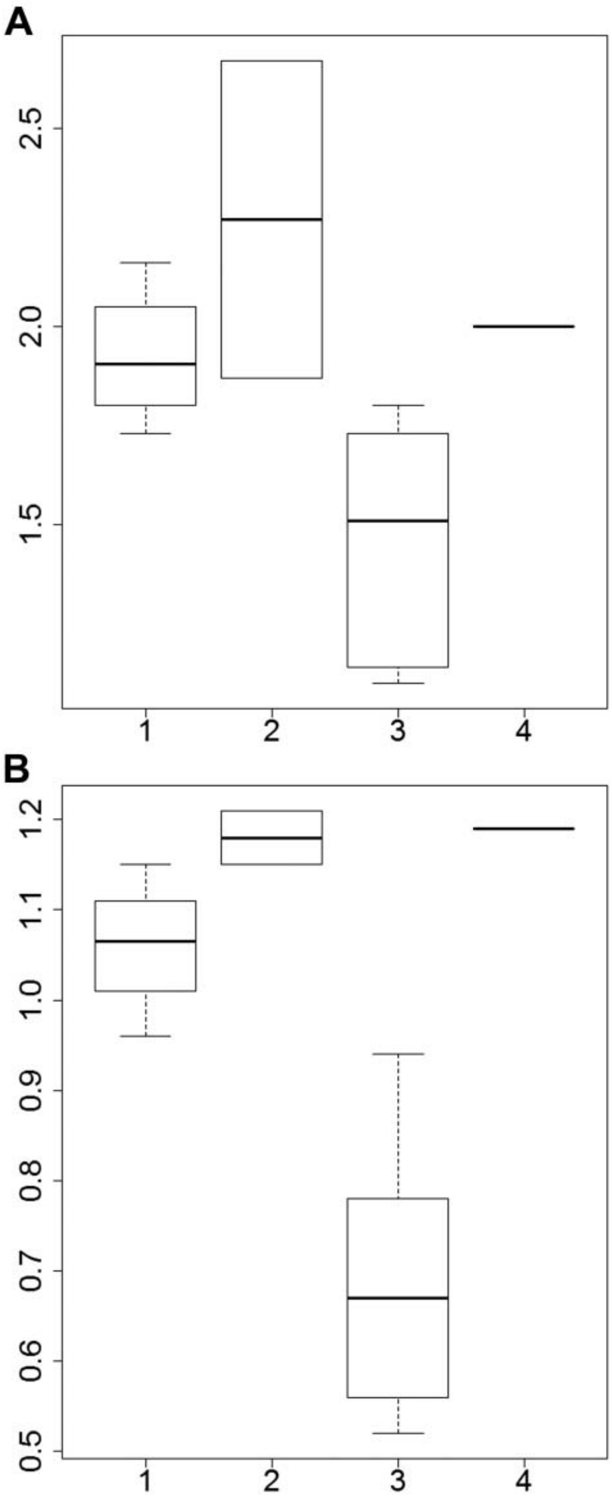

Figure 10. Boxplots of some molariform teeth of *Brachyzostrodon* based on measurements in Tables 1 and 2. **A,** length; **B,** width. 1, *B. coupatezi*; 2, *B. maior*; 3, *B.* cf. *coupatezi*; 4, *B.* cf. *maior*. Bold line inside box represents median; lower and upper borders of box represent respectively the first and third quartiles; and lower and upper extremities of the 'whisker' represent respectively the minimum and maximum values.

as representative and precludes use of the Wilcoxon test (Poinsot 2005).

Holotype. MNHN SNP 100, left lower molariform (m1?), from Saint-Nicolas-de-Port (Upper Triassic, France) (Fig. 9).

Referred material. Lower molariforms: RAS 875 (right), SNP 68 W (right m3?) (Figs 4F, 9), SNP 108 W (right m1?), SNP 500 W (right m3 or m4?) (Figs 4E, 9, 15), SNP 737 (right m2?) (Fig. 9).

Measurements. See Table 1.

Description. The enamel of the tooth is more or less wrinkled. The main cusps are aligned mesiodistally. However, even in the general case where the apex is centred on the base, the apices of cusps *b* and *c* are slightly labial to the apex of cusp *a*. Sometimes the apex of cusp *b* is projected mesiolabially (SNP 737), or the apex of cusp *c* is projected labially (SNP 108 W). Cusps *b* and *c* are subequal in length, width and height, even though the base of cusp *c* is slightly wider than the base of cusp *b*. Their bases are slightly compressed mesiodistally. Cusp *b* forms the mesiolabial corner of the tooth. Cusp *a* is the largest, two or three times larger than any other cusp, and is curved distally. The base of cusp *a* is either almost circular (general case), or rather elliptical (SNP 737). The mesial crest of cusp *a* is always convex. Its distal crest is either entirely straight (SNP 500 W), or with a more vertical section at its lower end (SNP 108 W, SNP 737).

There is no labial cingular element. Cusp *e* forms the mesiolingual corner of the tooth. It is sub-equal in size to cusp *b*, but clearly situated lower on the crown. Cusps *b* and *e* are connected by a transverse crest which forms the mesial side of the tooth. The base of cusp *e* ends in the flank of cusp *a*, after the notch *a*–*b*. It is followed by a minute cuspule *e*′ in SNP 108 W. Cusp *g* is always situated in front of the notch *a*–*c*, except in SNP 68 W and SNP 108 W where its apex is slightly distal. This cusp is sub-equal in size to cusp *c* and situated at the same level as cusp *e*. It is never connected with another cingular element, except in SNP 500 W where it is connected with the distal crest. The distal crest forms the distal border of the tooth from the labial corner to the lingual corner. It always bears three distinct cusps *d*, *i* and *i*′ (except in SNP 108 W where *i*′ is not shown). Cusp *d* is the most labial and largest one. Cusp *i* is directly lingual to cusp *d* and smaller, and cusp *i*′ is mesiolingual to cusp *i* and the smallest of the crests. Cusp *d* is labial (SNP 500 W, SNP 737), directly distal (SNP 68 W) or lingual (SNP 100, SNP 108 W) to the apex of cusp *c*. A crest always connects cusps *c* and *d*. The distal crest is the most distant from cusp *g* in SNP 100 and SNP 108 W. In SNP 68 W, the crest is clearly closer to cusp *g*. There is connection between the distal crest and the cusp *g* in SNP

500 W, whereas the crest extends lingually to cusp *g* in SNP 737.

Identification of tooth position in the postcanine row. The main variation within the material of *B. coupatezi* is the mesiodistal length of cusp *a*. There is also some variation of the occlusal outline of this cusp, which is circular (e.g. SNP 100, m1 in Fig. 9) to elliptical in shape (e.g. SNP 737, m2 in Fig. 9). We thus infer that the largest tooth of the series has the most elliptical cusp *a*, and that the teeth at each end of the series have the most circular cusp a. Differences in the distal crest have been used to distinguish mesial and distal teeth.

Wear. SNP 100 and SNP 68 W are heavily worn. Unfortunately, post-mortem alteration precludes the interpretation of the wear pattern on cusps *c*, *g* and *a* in SNP 100. Cusp *a* retains part of the wear facets but their pattern is not clear, cusp *e* is worn by a horizontal surface, and cusp *b* bears a shallow mesiolabial facet. Cusps *d* and *i* show faint, steep distal wear facets. There is also a vertical labial facet on the side of cusp *c*, particularly marked on the base of the cusp. Specimen SNP 68 W shows no trace of post-mortem alteration. Cusp *b* bears a steep mesiolabial facet. The apex of cusps *a* and *c* are removed by a steep distolabial facet. Cusp *g* shows a steep linguo-distolingual facet, whereas cusp *e* shows a steep mesiolingual facet.

Brachyzostrodon cf. *coupatezi* Sigogneau-Russell, 1983
(Figs 11A, 12, 15)

Remarks. Comprising material previously described as *Brachyzostrodon* sp. 1 by Hahn *et al.* (1991, p. 240, text-fig. 3, pl. 2, figs 1, 2).

Diagnostic characters. This material differs from *B.* cf. *maior* by: (1) a smooth lingual cingulum, the highest point of which is situated below the apex of cusp *A*; (2) well-defined cusps on the labial cingulum; (3) a cusp *D* clearly distinct from *C* (Figs 12, 14); and (4) a slightly smaller size (Table 1; Fig. 10).

Referred material. Upper molariforms: 37 L (right) (Fig. 12B), 85 L (left), RAS 47 (left), RAS 717 (right), SNP 18 L (right), SNP 29 W (left) (Figs 11A, 12A, 15), SNP 55 L (right), SNP 73 (right), SNP 81 (left), SNP 84 (right).

Measurements. See Table 1.

Description. The main cusp row is straight. The mesial part of the crown is lower than the distal part. As a consequence, cusp *B* is much lower than cusp *C*, although the cusps are sub-equal in size. Cusp *A* is the largest, not more than twice the size of cusp *C*. The crests joining the cusps are straight in lateral view. The enamel surface is wrinkled in SNP 18 L, SNP 29 W and SNP 73 (surface preservation of SNP 55 L is too poor for this observation).

The lingual cingulum is smooth and generally continuous from cusp *D* to the mesial end of the tooth (disrupted beneath the apices of cusps *B* and *C* in RAS 717). The highest point of the cingulum is situated beneath the apex of cusp *A*. The distal part is almost horizontal, whereas the mesial part extends down to a minimum just before cusp *E*. The latter forms the mesiolingual corner of the tooth; it is the second largest cingular cusp in size (smaller than cusp *D*, but larger than cusp *F*), except in 85 L where this relationship is reversed. The lingual cingulum ends on the mesial side, either in contact with the labial cingulum (37 L, RAS 717), or just before it (85 L, RAS 47, SNP 29 W, SNP 81). The cingula are not developed on the mesial side of 55 L. The labial cingulum is divided into more or less separated mesial and distal parts. The two parts almost join in front of the apex of cusp *A*. The mesiolabial cingulum is horizontal and extends from the mesial end of the crown to a point at least distal to the notch *A*−*B*. This cingulum can only bear the cusp *F*, forming the mesiolabial corner; cusp *F* is a little farther from the main row than cusp *E* (37 L, 85 L, SNP 29 W). This cingulum can also bear the cusp *F*, plus 2 or 3 cuspules distal to cusp *F* (RAS 47, RAS 717). In SNP 81 there is a cusp, sub-equal in size to cusp *F*, in front of the notch *A*−*C*. The distolabial cingulum extends down from cusp *D* to a point either in front of the notch *A*−*C* (37 L, SNP 18 L, SNP 29 W), or mesial to this notch (RAS 47, RAS 717, SNP 81). Cusp *D* is the most distal cusp. It is slightly labial to cusp *C* in 37 L, SNP 18 L and SNP 29 W. The next cusps decrease in size. In SNP 29 W, RAS 717 and 37 L, there are two cusps: cusp *I* is directly labial to cusp *D*, and cusp *I*′ is mesiolabial to cusp *I* and is situated in front of the apex of cusp *C*. In SNP 18 L and SNP 81, another cusp is added and stands in front of the apex of cusp *C*. In RAS 47, there is a chain of cuspules all along the distal cingulum.

Wear. Specimen SNP 29 W shows a weak very steep lingual wear facet, which spreads from beneath the apex of cusp *B* to a point halfway between the notch *A*−*B* and the apex of cusp *A*. The part mesial to the notch is orientated slightly distally, and the part distal to the notch slightly mesially. RAS 47 is much more heavily worn. A very steep distolingual facet extends on the entire lingual face of cusp *B*. It is connected with a very steep mesiolingual facet on the lingual cingulum between the notch *A*−*B* and the apex of cusp *A*. The apex of cusp *A* and the upper part of its lingual side are truncated by a steep mesiolingual facet. The lingual side of cusp *C* is entirely worn by a very steep distolingual facet that is connected with a very steep disto-distolingual facet on the side of cusp *D*.

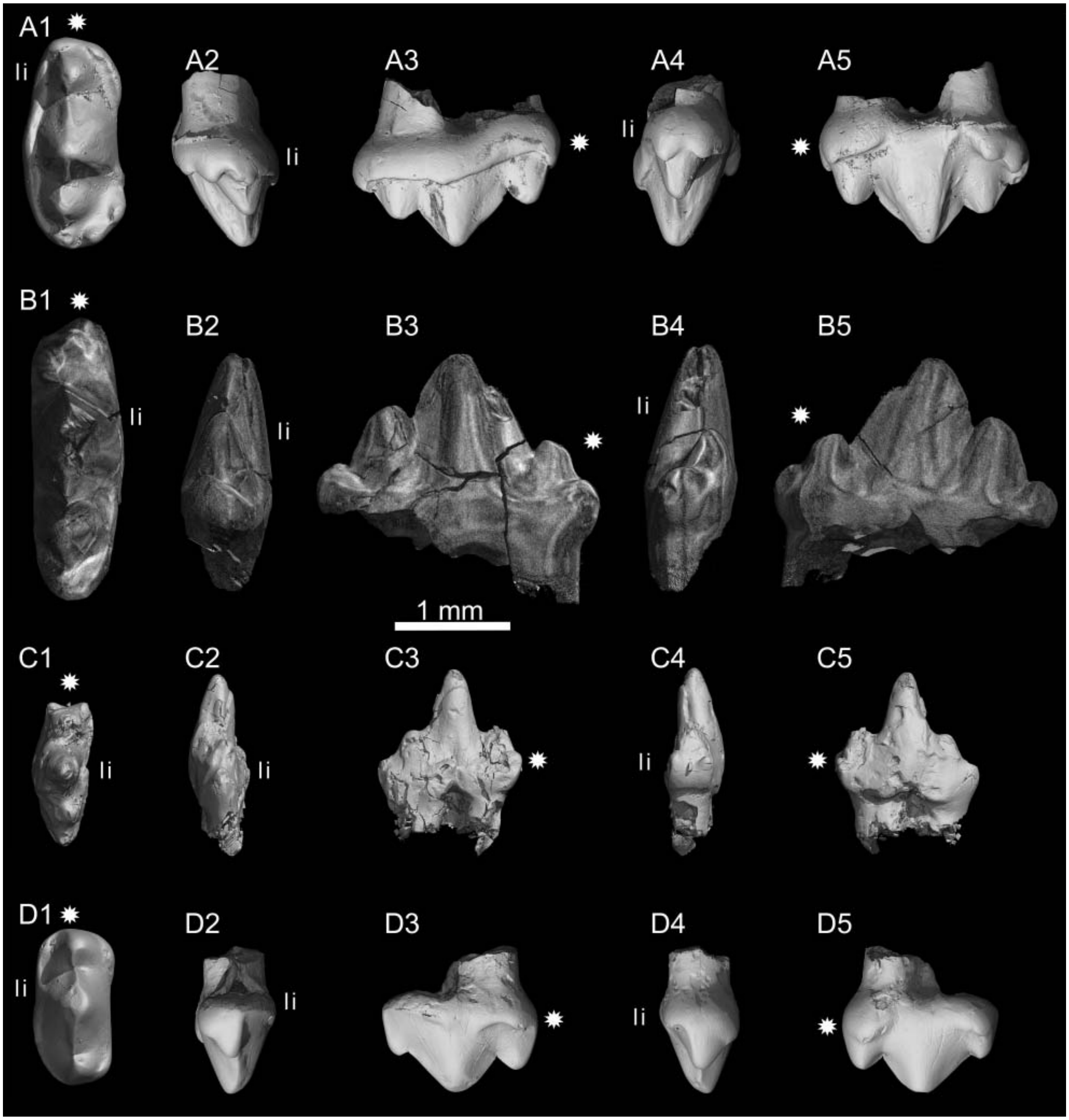

Figure 11. Views of CT-scan reconstructions of morganucodont molariforms. **A**, *Brachyzostrodon* cf. *coupatezi* (SNP 29 W, left upper); **B**, *Paceyodon davidi* (SNP 2001, left lower); **C**, *Rosierodon anceps* (SNP 62 L, left lower, holotype); **D**, *Paikasigudodon* cf. *yadagirii* (SNP 736, left upper). 1, occlusal view; 2, distal view; 3, lingual view; 4, mesial view; 5, labial view. White star shows mesial extremity and 'li' shows the lingual face.

Brachyzostrodon maior Hahn, Sigogneau-Russell & Godefroit, 1991 (Fig. 13)

Emended diagnosis. In *B. maior*, the cusp directly lingual to *b* is *e′*, by contrast to *B. coupatezi* where it is *e*. Cusp *e* is mesial to the space between cusps *b* and *e′* (Figs 9, 13). The teeth of *B. maior* are slightly larger than those of *B. coupatezi* (see comments on the biometry above) (Table 1; Fig. 10).

Holotype. IRSNB RAS 1020, right lower molariform (m2?), from Saint-Nicolas-de-Port (Upper Triassic, France) (Fig. 13).

Referred material. Lower molariforms: RAS 785 (left, m3?) (Fig. 13), SNP DD 44 (left).

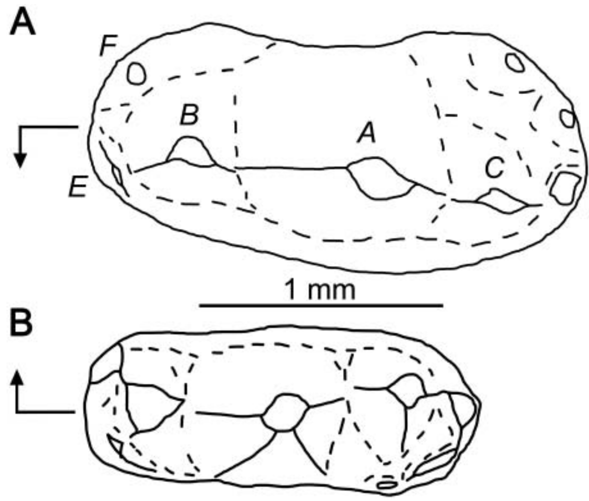

Figure 12. Sketch drawings of upper molariforms of *Brachyzostrodon* cf. *coupatezi* in occlusal view. **A,** SNP 29 W (left); **B,** 37 L (right). Right-angled arrows indicate mesial extremity and lingual face; letters in italics correspond to cusp nomenclature.

Measurements. See Table 1.

Description. The enamel surface is more or less wrinkled on cusp *a* of RAS 1020 and RAS 785. The main cusps are aligned along the mesiodistal axis, although the apex of cusp *b* is projected rather labially. Cusp *b* is either subequal in size to cusp *c* (RAS 1020), or larger than cusp *c* (RAS 785). Cusp *a* is the largest cusp of the tooth, being two or three times larger than any other cusp. The mesial and distal crests of cusp *a*, preserved only in RAS 1020, are convex in lateral view.

There is no labial cingular element. In RAS 1020, cusp *e′* is directly lingual to cusp *b*, sub-equal in size and located at the same level. Cusp *e* is mesial to the space between cusps *b* and *e′* and is smaller than cusps *e′* and *g*. In RAS 785, the topography is the same but cusp *e* is larger and in a more distolingual position. Cusp *e′* is slightly larger than cusp *b*. As a consequence, *e′* is more distal, not directly lingual to *b*, but in front of the notch *a*−*b*. Cusp *g* is always in front of the notch *a*−*c* and not connected with another cingular element. It is slightly smaller than cusp *e′*. The distal crest is very variable with three observed morphologies: (1) labially decreasing series *d*−*i*−*i′* (RAS 1020); (2) series with d and *i′* sub-equal in size and *i* much reduced (RAS 785); and (3) series with *d* and *i* (instead of *i′*) well developed at each extremity (SNP DD 44).

Identification of tooth position in the postcanine row. This is based on the morphological characters and size proportions seen in *B. coupatezi*.

Wear. SNP DD 44 and RAS 785 show wear on all cusp apices. In SNP DD 44, the apex of cusp *c* is worn by a steep labio-mesiolabial facet. Cusp *d* bears a very steep disto-distolabial facet. Cusp *i* is marked by a shallow distolingual facet. Finally, cusp *g* shows a steep linguo-distolingual facet. The apex of cusp *a* in RAS 785 is truncated by a set of four wear facets. The largest facet is a shallow labial surface seen in the centre and the labial side of the apex. The lingual side shows a shallow lingual facet. The mesial and distal crest respectively bears shallow mesial and distal facets. A steep labio-mesiolabial facet spreads over the apex and the labial side of cusp *b*. Cusp *e* is worn by a shallow lingual facet and cusp *e′* by a steep facet of similar orientation. There is a steep labial facet on the entire side of cusp *c*, which is extended by a shallow facet of similar orientation on the base of cusp *a*. Cusp *i′* bears a steep distolingual facet. Cusp *g* shows a steep lingual facet.

***Brachyzostrodon* cf. *maior* Hahn, Sigogneau-Russell & Godefroit, 1991**
(Fig. 14)

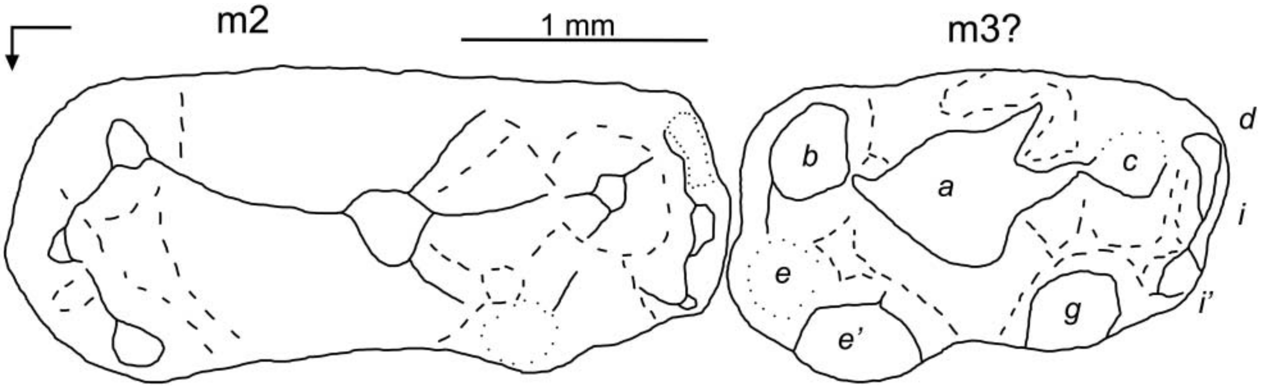

Figure 13. Hypothetical composite reconstruction of the right lower jaw of *Brachyzostrodon maior* in occlusal view; m2, RAS 1020; m3, RAS 785. Right-angled arrow indicates mesial extremity and lingual face; letters in italics correspond to cusp nomenclature.

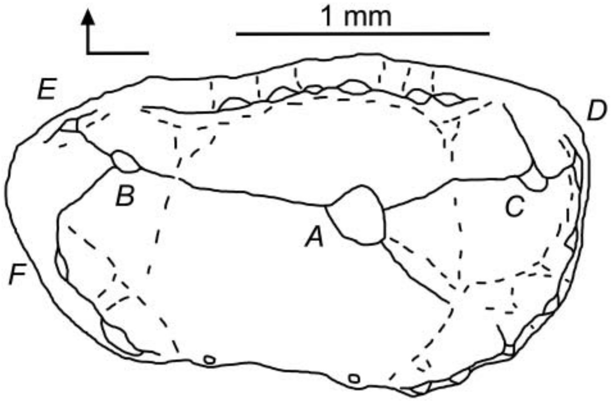

Figure 14. Sketch drawing of upper molariform of *Brachyzostrodon* cf. *maior* in occlusal view (RAS 45 FW, right). Right-angled arrow indicates mesial extremity and lingual face; letters in italics correspond to cusp nomenclature.

Remarks. Material previously described as *Brachyzostrodon* sp. 2 by Hahn *et al.* (1991, p. 241, text-fig. 4, pl. 2, fig. 3).

Diagnostic characters. This material differs from *B.* cf. *coupatezi* by: (1) a more or less crenulated lingual cingulum; (2) a distolabial cingulum with a chain of cuspules, the most lingual of which, recognized as cusp *D*, is little differentiated from cusp *C* (Figs 12, 14); and (3) a slightly larger size (Table 1; Fig. 10).

Material. Upper molariforms: RAS 45 FW (right) (Fig. 14), SNP 5 Ph (left), SNP 292 W (right).

Measurements. See Table 1.

Description. The enamel surface is wrinkled on all main cusps. These cusps are more or less conical in shape and aligned mesiodistally, but the apex of cusp *B* is projected slightly lingually. Cusp *A* is the largest cusp of the tooth. Cusp *B* is a little smaller than cusp *C* and stands at a lower level. The crests joining these cusps are straight in occlusal and lateral views.

The lingual cingulum is continuous and entirely crenulated from cusp *D* to the mesial face of the tooth, except in RAS 45 FW where it is disrupted beneath the apex of cusps *B* and *C*. This cingulum is faintly inclined downward from cusp *D* to a point halfway between the apex of cusp *A* and the notch *A*–*B*. The remaining part tilts more strongly to cusp *E*. There is no mesial connection between the lingual and labial cingula. The labial cingulum is divided into mesial and distal parts. The mesial part terminates distally to the notch *A*–*B*. It bears two distinct cusps in RAS 45 FW. The largest cusp, *F*, is as mesial as cusp *E* and has the same size as the latter. The smallest cusp is situated in front of the notch *A*–*B*. The distal part extends from cusp *D* to a point mesial to the notch *A*–*C* and bears at least four weakly developed cusps (more than six in RAS 45 FW). Cusp *D* is poorly distinct from the other; it is recognized by its position immediately distal to cusp *C*.

Wear. There is no trace of wear on these specimens.

Remarks on the upper molariforms of *Brachyzostrodon*. Hahn *et al*. (1991) defined two sets of upper molariforms identified as *Brachyzostrodon*, but did not investigate their relationships with the two species based on lower molariforms. In this study, we establish an association between lower molariforms and upper molariforms using morphometric data. The size difference between the two sets of upper teeth is greater than the difference between the lower teeth, although the former difference is based on a smaller number of measurements (Table 1; Fig. 10). Thus, no statistical test is possible (Poinsot 2005). Biometry is not a clear-cut criterion but is relevant for taxonomic referral. Another argument is the relative abundance of lower and upper sets. The difference in abundance between the two sets of upper teeth is equivalent to the difference between the two sets of lower teeth. As a consequence, upper molars identified as *B.* sp. 1 by Hahn *et al.* (1991) are identified here as *B.* cf. *coupatezi*, and upper molars identified as *B.* sp. 2 by Hahn *et al.* (1991) are identified here as *B.* cf. *maior*.

Another incomplete tooth from Olgahain, GIT 1561/14, has been described by Clemens & Martin (in press, fig. 7d, g–j) as a morganucodontid indet. They compared this tooth with *Brachyzostrodon* and *Helvetiodon* Clemens, 1980, but did not refer it formally to either of these taxa. We consider that GIT 1561/14 differs from *Helvetiodon* because a mesial accessory cusp is present in the tooth from Olgahain. This specimen matches the three diagnostic features of *Brachyzostrodon* relative to the upper molariforms. The smooth enamel of GIT 1561/14 is not problematical because several teeth of *Brachyzostrodon* do not display wrinkled enamel (e.g. RAS 47, SNP 29 W, SNP 55 L). This specimen seems closer to *B.* cf. *coupatezi* for two reasons: (1) the labial cingulum bears well-defined cusps; and (2) the lingual cingulum is smooth. On the other hand, however, GIT 1561/14 seems closer to *B.* cf. *maior* for three reasons: (1) the lingual cingulum shows some irregularities, which suggest the presence of cusps prior to abrasion; (2) the state of preservation precludes assessment of the degree of separation between cusp *C* and cusp *D*, but Clemens & Martin (in press) suppose that cusp D ‘was probably relatively small’, which is likely in view of their figure 7a; and (3) GIT 1561/14 is a little shorter than RAS 1020, the longest tooth of *Brachyzostrodon* from SNP (Tables 1, 2). In its morphological features, the tooth from Olgahain shows characteristics of both sets of upper molars of *Brachyzostrodon*. However, we consider its size as significant enough to tentatively refer GIT 1561/14 to *Brachyzostrodon* cf. *maior*.

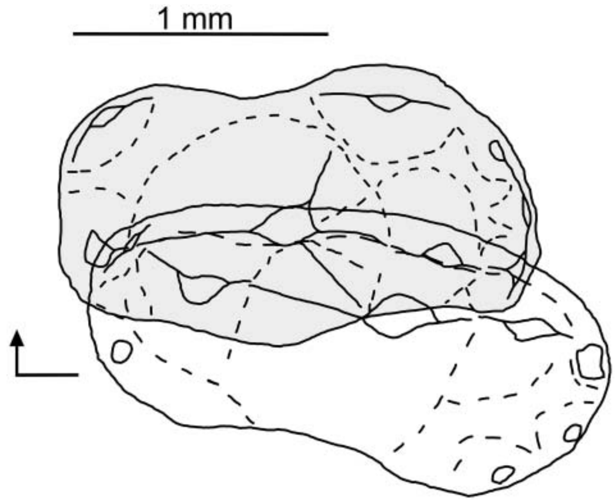

Figure 15. Reconstruction of occlusal relationships between a lower molariform of *Brachyzostrodon coupatezi* (SNP 500 W, in light grey) and an upper molariform of *B.* cf. *coupatezi* (SNP 29 W, transparent). Right-angled arrow indicates mesial extremity and lingual face.

Occlusion in *Brachyzostrodon*. Hahn *et al.* (1991) have already pointed out the peculiar wear pattern of *Brachyzostrodon*, with the development of the wear facets on the apex of the lower cusps. Heavy abrasion of the cusps is also characteristic. The alternate pattern of occlusion seems to be the same in *Morganucodon*, according to the distribution of wear facets (Sigogneau-Russell 1983; Hahn *et al.* 1991). Another clue for this interpretation is the close match of the crests of the main row in lower molariforms with the groove delimited by the lingual cingulum in the upper molariforms (Fig. 15). The difference in wear patterns between *Brachyzostrodon* and *Morganucodon* can be explained by the masticatory process and/or the diet (Hahn *et al*. 1991).

Genus ***Paceyodon*** Clemens, 2011

Type species. *Paceyodon davidi* Clemens, 2011.

Diagnosis. As for the species.

Distribution. Upper Triassic (Rhaetian): Saint-Nicolas-de-Port (“Grès infraliasiques” Formation), Lorraine, France; Lower Jurassic: Pant 4, fissure-fillings of Saint Bride’s Island, Wales, UK.

Paceyodon davidi Clemens, 2011
(Figs 11B, 16)

Diagnosis. (Clemens 2011) “The crown of the type and only specimen, interpreted to be a right lower molariform, is larger than lower molariforms of all currently known morganucodontans (*sensu* Kielan-Jaworowska *et al.* 2004) and most other Late Triassic or Early Jurassic mammaliaforms. Principal cusps are aligned along either side of an axis that diverges mesiobuccally from the mesiodistal axis of the crown. The mesiolingual shelf, which presumably carried cusp e, is exceptionally large and salient mesially, but lacks a notch to form an interlock with the preceding postcanine. If present, cusp g was relatively small. At the level of cusp c, the crown is narrower than its mesial end and then tapers distally. The two roots are large and not widely separated.”

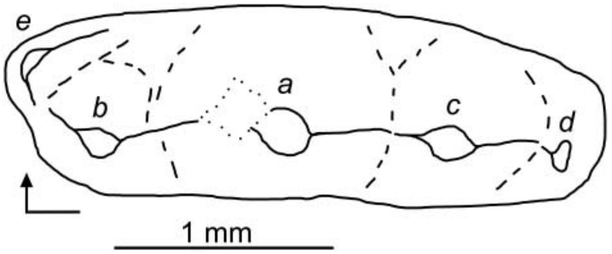

Figure 16. Sketch drawing of lower molariform of *Paceyodon davidi* in occlusal view (SNP 2001, left). Right-angled arrow indicates mesial extremity and lingual face; letters in italics correspond to cusp nomenclature.

Holotype. NHMUK M45920, right lower molariform; Pant Quarry (Lower Jurassic, UK).

Referred material from Saint-Nicolas-de-Port. Lower molariform: SNP 2001 (left) (Figs 11B, 16).

Measurements. See Table 1.

Description. The main cusps are aligned along the same axis, although cusp *b* is positioned more labially from the alignment. Cusp *a* is the largest and cusp *b* the smallest cusp. The differences between cusps *a* and *c* are similar to the differences between cusps *c* and *b*. The apex of cusp *b* lies below the bottom of the notch *a*−*c*. Cusps *a* and *c* are slightly projected distally. The distal crest of cusp *a* is convex in lateral view; the other crests are straight.

There is no labial cingular element. Cusp *e* alone forms the mesial lingual cingulum and the mesiolingual corner of the tooth. It is sub-equal to cusp *b* in size, but stands much lower and much more mesial. The distal crest of *e* ends in front of the notch *a*−*b*. Cusp *d* is directly distal to cusp *c*. Cusp *d* is less developed than cusp *e*, but distinct enough from cusp *c*. Cusp *d* has a very short labial extension. The distal lingual cingulum is a weak bulge, which extends to the base of cusp *a* in front of the notch *a*−*c*.

Wear. There is no trace of wear on this specimen.

Remarks. There are four differences between the holotype of *Paceyodon davidi* and SNP 2001: (1) the holotype is much larger (almost 1 mm difference) (Tables 1, 2); (2) in SNP 2001 the distal crest of cusp *a* is more convex in lateral view; (3) cusp *b* is more distinct from cusp *a*; and (4) the lingual cingulum is less developed.

Differences 2–4 can be explained by individual variations or by the position in the dental series; they are not diagnostic characters. Difference (1) is more remarkable because 1 mm is approximately the mean size of molars in Morganucodonta, except in *Brachyzostrodon*, *Wareolestes* and *Paceyodon* (Kielan-Jaworowska *et al.* 2004; Clemens 2011). However, this difference in size corresponds to a length ratio of 1.3, which is a range of size observed in morganucodonts, such as *Morganucodon* (Table 2) (Mills 1971; Clemens 1980). Actually, the size difference seen here is difficult to interpret, because the real range of variations is unknown in *Paceyodon*. As a consequence, the Saint-Nicolas-de-Port specimen described here is conservatively referred to the type species, *P. davidi*.

Genus ***Rosierodon*** gen. nov.

Type species. *Rosierodon anceps* sp. nov.

Diagnosis. As for the species-type.

Etymology. Rosier-: after Rosières-aux-Salines, a city close to the type locality; -odon: from the Greek οδους, meaning tooth.

Distribution. Upper Triassic (Rhaetian): Saint-Nicolas-de-Port ('Grès infraliasiques' Formation), Lorraine, France.

Rosierodon anceps sp. nov.
(Figs 11C, 17)

Etymology. From the Latin 'anceps', ambiguous, because the referred specimens show a mixture of features seen in morganucodonts and kuehneotheriids.

Diagnosis. This new taxon is known only by lower molariforms distinguished by: (1) an occlusal outline in half-circle with a straight lingual face and a strongly convex labial face; (2) a very tall cusp *a*, symmetrical in lateral view; and (3) a circumference of the cusp *b* larger than the circumference of the cusp *c*.

Holotype. MNHN 62 L, lower left molariform (Figs 11C, 17A); from Saint-Nicolas-de-Port (Upper Triassic, France).

Referred material. Lower molariforms: 89 L (right), 202 (right), RAS 796 (left) (Fig. 17B), SNP 11 (right), SNP 22 (right), SNP 79 L (left), SNP 414 W (right), SNP 739 (left).

Measurements. See Table 1.

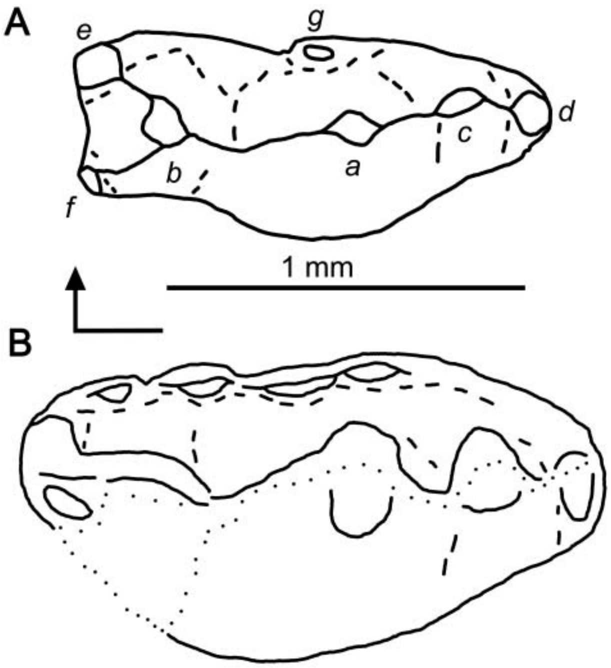

Figure 17. Sketch drawings of lower molariforms of *Rosierodon anceps* in occlusal view. **A,** SNP 62 L (left, holotype); **B,** RAS 796 (left). Right-angled arrow indicates mesial extremity and lingual face; letters in italics correspond to cusp nomenclature.

Description. The occlusal outline of the crown forms a half-circle. The lingual side is straight, whereas the labial side is strongly convex. The distal extremity is rather pointed. The mesial extremity is either also rather pointed (SNP 11, SNP 79 L and RAS 796), or flatter with a concavity delimited by two cingular cusps, the lingual cusp being slightly more distal than the lingual cusp (62 L, 89 L, 202 and SNP 414 W). The main cusps are aligned mesiodistally. Cusp *b* projects slightly mesially. Cusps *a* and *c* are strictly vertical (except for cusp *c* in 202 and SNP 11, which is faintly projected distally). Cusp *a* is by far the highest cusp of the tooth, but is not much larger than the other cusps in circumference. Cusps *b* and *c* are sub-equal in height but cusp *b* is larger in circumference. Both notches *a*–*b* and *a*–*c* are very shallow and have the same width. Cusps *b* and *c* are not well separated from cusp *a*. There are crests joining cusp *a* to cusps b and *c*, cusp *c* to cusps *a* and *d*, and cusp *b* to cusps *a*, *e* and *f* (when present). All of these crests are straight in occlusal and lateral views.

Cusp *d* forms the distal extremity of the tooth. It is in the same alignment as the main cusps. It is less detached from cusp *c* than cusps *b* and *c* are from cusp *a*. Cusp *d* is the second cingular cusp in size (smaller than cusp *e*, larger than cusp *g*). From this cusp, the lingual cingulum extends to the mesial extremity. This cingulum, as a whole, is straight in lateral view, except for a slight rise between the apex of cusp *a* and the notch *a*–*c* in some specimens (89 L, SNP 22, SNP 79 L and SNP 414 W), which can become a cusp *g* in other specimens (62 L, 202, RAS 796, SNP 11 and SNP 739). The lingual cingulum is smooth, except in RAS 796 where it is crenulated between cusp *d* and the notch *a–b*. SNP 11 also shows a little cuspule just distal to cusp *e*. Cusp *e* forms the mesiolingual corner of the tooth. In SNP 11, 202 and 89 L, the lingual cingulum continues beyond cusp *e* and bypasses the cusp *b* to the labial side of the tooth. This extension is absent in SNP 22, seems absent in SNP 79 L, and this part is not preserved in RAS 796. In 62 L, SNP 414 W and SNP 739, the labial extension carries a more or less developed cusp *f*. If cusp *f* is present, there is a notch in the cingulum between the cusps *e* and *f*.

Wear. Wear facets are not preserved, except in 89 L where there is a steep disto-distolabial wear facet on the apex of cusp *a* and a very steep distolabial wear facet on the upper part of the labial side of cusp *c*.

Remarks. This new taxon perfectly matches the three main features of Morganucodonta: (1) a main row of three cusps, usually with (2) a supplementary fourth lesser distal cingular cusp, and (3) cingular elements on at least one side (e.g. Kermack *et al.* 1973; Kielan-Jaworowska *et al.* 2004). However, it does not resemble any of the known genera of Morganucodonta. The most similar genus is *Purbeckodon* (see Butler *et al*. 2012) but this does not show any of the diagnostic characters of the Saint-Nicolas-de-Port material. Besides those morganucodont features, the Saint-Nicolas-de-Port teeth are rather similar to *Kuehneotherium* Kermack, Kermack & Musset, 1968: the development of the cingular elements, and the shape and proportions of main cusps are very similar in these two taxa. The possibility that these teeth are either anterior postcanines of *Kuehneotherium*, or a closely related form, has been considered. Some symmetrodont forms can show great variation in the triangulation of the main cusps of molars along the tooth row. In *Tinodon* Marsh, 1879, the main cusps are almost aligned on the first molar, but are more triangulated in the more posterior molars (Crompton & Jenkins 1967). However, the specimens described here are very different from the premolars known for early 'symmetrodonts' (Godefroit & Battail 1997; Gill 2004). Their variability is too important to represent only one or two loci of anterior molars. Consequently, the Saint-Nicolas-de-Port material is tentatively considered as representing a new genus of Morganucodonta, *Rosierodon*.

Genus ***Paikasigudodon*** Prasad & Manhas, 2002

Type species. *Kotatherium yadagirii* Prasad & Manhas, 1997.

Diagnosis. (Prasad & Manhas 2002) "Upper molar crown bearing a high central cusp with a flat labial face and convex lingual face; cusp *B* higher than *C*; presence of a large anterolabial cusp connected to *B* by a sharp crest; presence of an anterior and a posterior small lingual cingular cuspule; rudimentary lingual cingulum between *A* and *B*. Differs from *Morganucodon* in the presence of a high central cusp *A* and large anterolabial cusp *F*; differs from *Morganucodon*, *Jeholodens*, *Austrotriconodon*, and all triconodontids in the non-linear arrangement of cusps; differs from *Morganucodon*, *Megazostrodon*, and *Gobiconodon* in the absence of a well-defined lingual cingulum and the presence of cusp *B* larger than cusp *C*; differs from *Gobiconodon* and *Megazostrodon* in the presence of asymmetrically placed *B* and *C*; differs from *Brachyzostrodon* Sigogneau-Russell, 1983 in the non-linear arrangement of cusps and non-wrinkled enamel on the crown."

Distribution. Upper Triassic (Rhaetian): Saint-Nicolas-de-Port ('Grès infraliasiques' Formation), Lorraine, France; Early? Jurassic: Paikasigudem (Kota Formation), Andhra Pradesh, India.

Paikasigudodon* cf. *yadagirii (Prasad & Manhas, 1997; Prasad & Manhas, 2002) (Figs 11D, 18)

1997 *Kotatherium yadagirii* Prasad & Manhas: 565, figs 2, 3.

2002 *Paikasigudodon yadagirii* Prasad & Manhas: 453, figs 4, 5.

Diagnosis. As for the genus.

Holotype. KM/10 (VPL/JU), left upper molariform; from Paikasigudem (Lower? Jurassic, India).

Material from Saint-Nicolas-de-Port. Upper molariform: SNP 736 (left) (Figs 11D, 18).

Measurements. See Table 1.

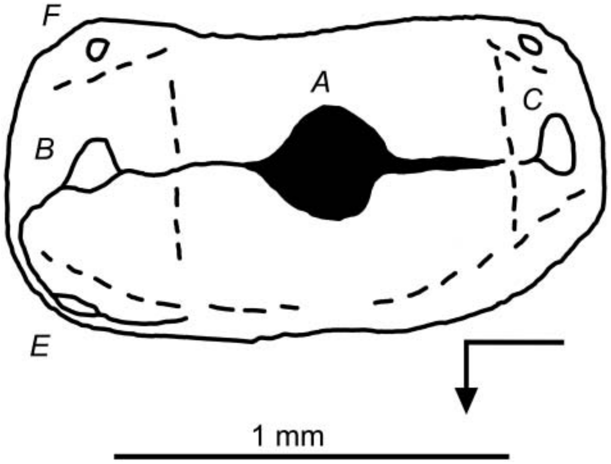

Figure 18. Sketch drawing of upper molariform of *Paikasigudodon* cf. *yadagirii* in occlusal view (SNP 736, left). Right-angled arrow indicates mesial extremity and lingual face; letters in italics correspond to cusp nomenclature.

Description. The main cusps are more or less aligned mesiodistally, but cusps *B* and *C* are a little more labial than cusp *A*. The outline of the tooth reflects this topography, with a concave labial side and a convex lingual side. Cusp *A* is the largest cusp and cusp *C* the smallest. Cusp *B* is closer to *C* than to *A* in size. The crests joining these cusps are straight in occlusal and lateral views.

Cusp *F* is directly mesial to cusp *B* and the largest cingular cusp, but barely distinct from cusp *B*. It is not extended by a cingulum. On the labial side, there is also a short and faint cingulum in front of the apex of cusp *C* and the notch *A*–*C*. Cusp *E* is directly mesial to cusp *B*, smaller than cusp *F*, but more distinct from cusp *B*. A crest extends from the apex of cusp *B* on the mesiolingual side of the cusp for joining the mesial extremity of the lingual cingulum. The cingulum extends distally from cusp *E* to a point beneath the apex of cusp *A*. There is also a faint cingulum from the distal part of cusp *C* to a point beneath the apex of cusp *A*. The two lingual cingula are close to each other.

Wear. There is a shallow lingual wear facet on the apex of cusp *A* associated with two smaller wear facets just below on the lingual side of cusp *A*. One is distolingual and the other is mesiolingual. These facets are steep, and extend from the respective crest of cusp *A* to join the other facet medially.

Remarks. SNP 736 clearly matches the diagnosis of *Paikasigudodon*, except for the following differences: (1) the cusps are less developed than those in the holotype; (2) there is neither a sharp crest joining *B* and *F*, nor labial cingular cuspules; and (3) the Saint-Nicolas-de-Port specimen is smaller than the specimen from India. These differences can be explained as individual variations, variations linked to the tooth rank position, or can be used as diagnostic differences of a new species. The specimens differ most noticeably in their geological age. As a consequence, the Saint-Nicolas-de-Port material is referred in open nomenclature to *P.* cf. *yadagirii*.

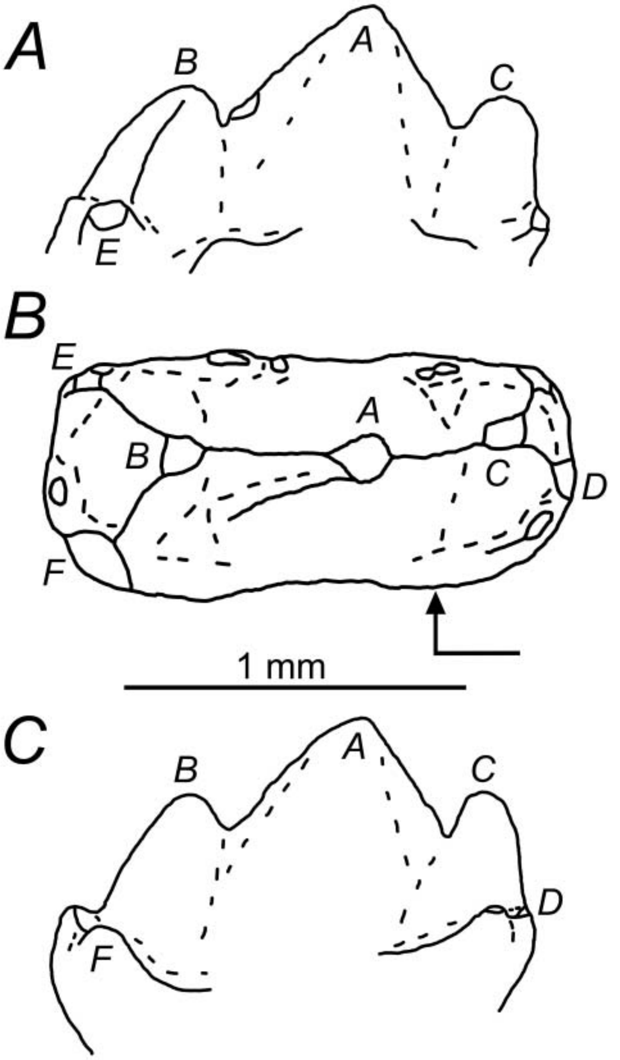

Figure 19. Sketch drawing of upper molariform of Morganucodonta indet. 1 in **A,** lingual, **B,** occlusal and **C,** labial views; RAS 39 FW, right. Right-angled arrow indicates mesial extremity and lingual face; letters in italics correspond to cusp nomenclature.

Morganucodonta indet. 1

(Fig. 19)

Material. Upper molariform: RAS 39 FW (right) (Fig. 19).

Measurements. See Table 1.

Description. The main cusps are aligned mesiodistally, but the apex of cusp *A* is slightly more labial than the apex of cusps *B* and *C*. Cusp *A* is the largest cusp. Cusp *B* is slightly longer than cusp *C*; both have the same height. All are conical in shape and bent distally. The apex of *A* is slightly recurved distally. Notches *A*–*B* and *A*–*C* have the same depth. The base of cusp *B* is more detached from the base of cusp *A* than the base of cusp *C*. All crests joining the cusps are straight in occlusal and lateral views, except for an irregularity in the mesial crest of cusp *A* at the level of the apex of *B*. There are slight sulci along the labial and lingual sides of both crests of cusp *A*. The mesial part of the crown is at a lower level than the distal part.

The lingual and labial cingula are divided into mesial and distal parts by the cusp *A*. In the lingual cingulum, the disruption is situated just beneath the apex of cusp *A*. The distolingual cingulum is horizontal and extends from cusp *D* to the base of cusp *A*. The cingulum bears a cusp that is larger than *D* and forms the distolingual corner of the tooth. This cusp is connected to the apex of cusp *C* by a straight crest. The distolingual cingulum is slightly crenulated in front of the notch *A*–*C*. The mesiolingual cingulum extends from the base of cusp *A* to the mesial face of cusp *B*. It tilts from its beginning towards cusp *E* and bears a small cusp in front of the notch *A*−*B*. Cusp *E* forms the mesiolingual corner of the tooth and is larger than cusps *D* and *F*. The mesiolingual cingulum does not join the mesiolabial cingulum. The hollow between them is lingual to the axis of the main cusps. The mesiolabial cingulum extends downwards from cusp *F* to the base of cusp *A* below the notch *A*−*B*. Cusp *F* is the most mesial cingular cusp. A second cusp, distolabial to *F* and sub-equal in size, forms the mesiolabial corner of the tooth. The distolabial cingulum extends downwards from cusp *D* to the base of cusp *A*, below the apex of *A*. Cusp *D* is small and barely distinct from cusp *C*. It is labial to the apex of *C*. A second cusp, larger than *D*, forms the distolabial corner of the tooth.

Wear. There is no trace of wear.

Remarks. This specimen is similar to the upper molariforms of *Brachyzostrodon*. However, there are several important differences: the tilt of the main cusps, the disruption of the lingual cingulum, and the size relations between the labial cingular cusps and cusps *B* and *C*. RAS 39 FW can be seen as either an outlier specimen of *Brachyzostrodon*, or a representative of the upper dentition of a new genus. With so little information, it is more appropriate to refer it in open nomenclature to Morganucodonta indet. 1.

Morganucodonta indet. 2
(Fig. 20)

Material. Upper? molariforms: SNP 523 W (left?) (Fig. 20), SNP 2004 (left?).

Measurements. See Table 1.

Description. The main cusps are aligned along an axis that is slightly shifted from the mesiodistal axis of the tooth, with cusp *B* being more lingual than the cusp *C*. Cusp *A* is by far the largest cusp. Cusps *B* and *C* are sub-equal in size. The enamel surface of cusp *A* is wrinkled. Cusps *B* and *C* are conical in shape and cusp *A* is elliptical. The labial sides of the cusps are much more convex than the lingual side. The sole well-preserved crest is the mesial crest of cusp *A*, which is straight in occlusal and lateral views. Notches *A*−*B* and *A*−*C* are shallow.

On the lingual side of the tooth, there is a cingulum (crenulated in SNP 2004) in front of notch *A*−*B*. This cingulum extends downwards from the base of cusp *A* to the base of cusp *B*. It either terminates near the mesiolingual corner of the tooth (SNP 523 W), or reaches it (SNP 2004). On the same side, there is also a cingulum in front of notch *A*−*C*. It extends horizontally from the base of cusp *A* and bypasses cusp *C* to join the labial cingulum. On the labial side, there are two cingular cusps, sub-equal in size with cusps *B* and *C*, in front of notches *A*−*B* and *A*−*C*. The mesiolabial cingular cusp is slightly larger than the distolabial cingular cusp. The mesiolabial cusp extends from a point labial to cusp *B*, where its apex is, to a point close to the median plane of the tooth. It is extended by a faint cingulum ending at the mesial extremity of the tooth. The distolabial cusp is poorly preserved, but the cingulum on which it stands extends from a point close to the median plane of the tooth to a point labial to cusp *C* close to the distal extremity of the tooth and joins the lingual cingulum.

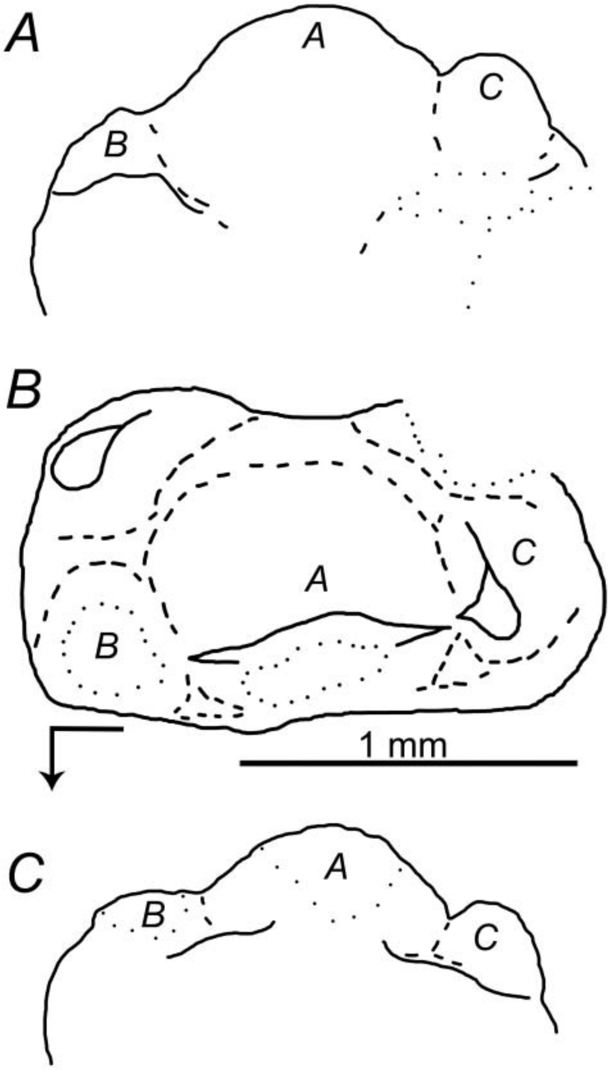

Figure 20. Sketch drawing of upper? molariform of Morganucodonta indet. 2 in **A,** lingual, **B,** occlusal and **C,** labial views; SNP 523 W, left?. Right-angled arrow indicates mesial extremity and lingual face; letters in italics correspond to cusp nomenclature.

Wear. SNP 523 W is too poorly preserved for the interpretation of wear facets. However, it seems that the lingual side of cusp *A* carried a large, very steep lingual wear facet. SNP 2004 shows no trace of wear.

Remarks. These specimens are rather similar to the upper molariforms of *Brachyzostrodon* in the outline of the cingular elements. However, the cingular elements differ in the interruption of the lingual cingulum and the development of two large labial cusps. SNP 523 W and SNP 2004 recalls lower molariforms of *Brachyzostrodon* because of the relationships of the main cusps between them and the presence of two large cingular cusps. However, the development of labial and lingual cingula is diagnostic of the upper molars in Morganucodonta. It also lacks the distal crest seen in a lower molariforms of *Brachyzostrodon*. The wrinkled enamel is shared with *Brachyzostrodon* and *Wareolestes*. The latter genus is morphologically more distant from SNP 523 W and SNP 2004 than *Brachyzostrodon*. Pending more data, these Saint-Nicolas-de-Port specimens are referred in open nomenclature to Morganucodonta indet. 2.

Discussion

Systematics

Within the Saint-Nicolas-de-Port fauna, *Megazostrodon* and *Brachyzostrodon* are the most abundant morganucodont genera. Together, they represent about two-thirds of the morganucodont material, whereas *Morganucodon* and *Rosierodon* represent about one-quarter of the material, and *Paceyodon*, *Paikasigudodon* and indeterminate morganucodonts are only about one-tenth of the material (Supplemental Table 1).

With the exception of *Morganucodon* and *Megazostrodon*, which are the type genera of their respective families, all other genera identified at Saint-Nicolas-de-Port are considered here as family *incertae sedis*. The family Morganucodontidae, defined by Kühne (1958), was elevated to the suborder Morganucodonta by Kermack *et al.* (1973). This shows that Morganucodontidae, as a family, has been given different definitions and contents. However, the most recent diagnosis of Morganucodontidae by Kielan-Jaworowska *et al.* (2004) is the same as that of *Morganucodon*, because it is the best-known genus. This latter diagnosis is far less inclusive than the diagnosis proposed by Kühne (1958). The diagnosis of the family Megazostrodontidae, erected to include *Megazostrodon* and *Dinnetherium*, is based on two characters related to the lower jaw, and one character related to the upper molars (Gow 1986). The two families Megazostrodontidae and Morganucodontidae are based on three genera represented by mandibles; but mandibular diagnostic features are not applicable in more than 15 genera of morganucodonts that are currently known, for the most part, exclusively on the basis of their teeth. A revision of the family diagnoses of the morganucodonts is necessary to account for their currently admitted generic diversity. This needs a phylogenetic analysis of all morganucodonts, which is beyond the scope of this paper. It will be developed after the completion of the taxonomic study of the entire mammalian fauna from Saint-Nicolas-de-Port, which is in progress.

Depositional environments and fossil record

Comparison of Rhaetian and Jurassic mammal faunas in relative abundance and taxonomic diversity must take into account the notable taphonomic differences between these faunas. This complicates the investigation and understanding of mammal macroevolution around the Triassic/Jurassic (TJ) boundary. All European Rhaetian mammal localities are considered as corresponding to marine deposits (Fig. 21) (e.g. Clemens 1980; Sigogneau-Russell & Hahn 1994). Mammal remains have been hydrodynamically transported, causing breakage and sorting of skeletal elements before fossilization. Rhaetian morganucodonts were very small animals, probably weighing less than 100 g (Kielan-Jaworowska *et al.* 2004), and between 27 and 89 g for *Morganucodon* (Luo *et al.* 2001). Their delicate bones were easily broken during taphonomic processes (e.g. by predators, transportation and diagenesis). Hydrodynamic transportation and sorting explains the concentration of isolated, millimetric teeth in European sites, but these sites are improperly referred to locally as 'bone-beds'. In this regard, the Rhaetian European fossil record cannot be considered as representative of the original morganucodont diversity. However, Saint-Nicolas-de-Port represents an exception. The remarkable diversity and abundance of fossil mammals in this site can be explained either by an exceptionally rich original faunal assemblage, or by better conditions of post-mortem concentration. Field data support favourable taphonomic conditions rather than an exceptionally rich original biocoenosis. The coeval locality of Varangéville, 10 km north of Saint-Nicolas-de-Port, does not exhibit similar mammalian abundance or diversity (Godefroit 1997). According to fieldworkers at the Saint-Nicolas-de-Port quarry, most mammal fossils came from a single sand lens (Godefroit & Battail 1997; Godefroit pers. comm. 2013). The Saint-Nicolas-de-Port deposits represent better conditions for concentration than other European Rhaetian sites, and the fossiliferous sand lens was a kind of metrical 'Konzentrat-Lagerstätte'. The Saint-Nicolas-de-Port mammal fauna is indeed the richest known mammal fauna in the Rhaetian. Even if it is clearly biased taphonomically, it still represents the best reference site for the beginning of the early evolutionary history of mammals.

Early Jurassic mammal localities show differences between one another and with the Rhaetian localities with respect to their depositional environments. The localities of Wales are similar to the Rhaetian localities of England, both being deposits filling fissures (e.g. Robinson 1971; Evans & Kermack 1994), but have yielded teeth, cranial and postcranial material without evidence of reworking (see

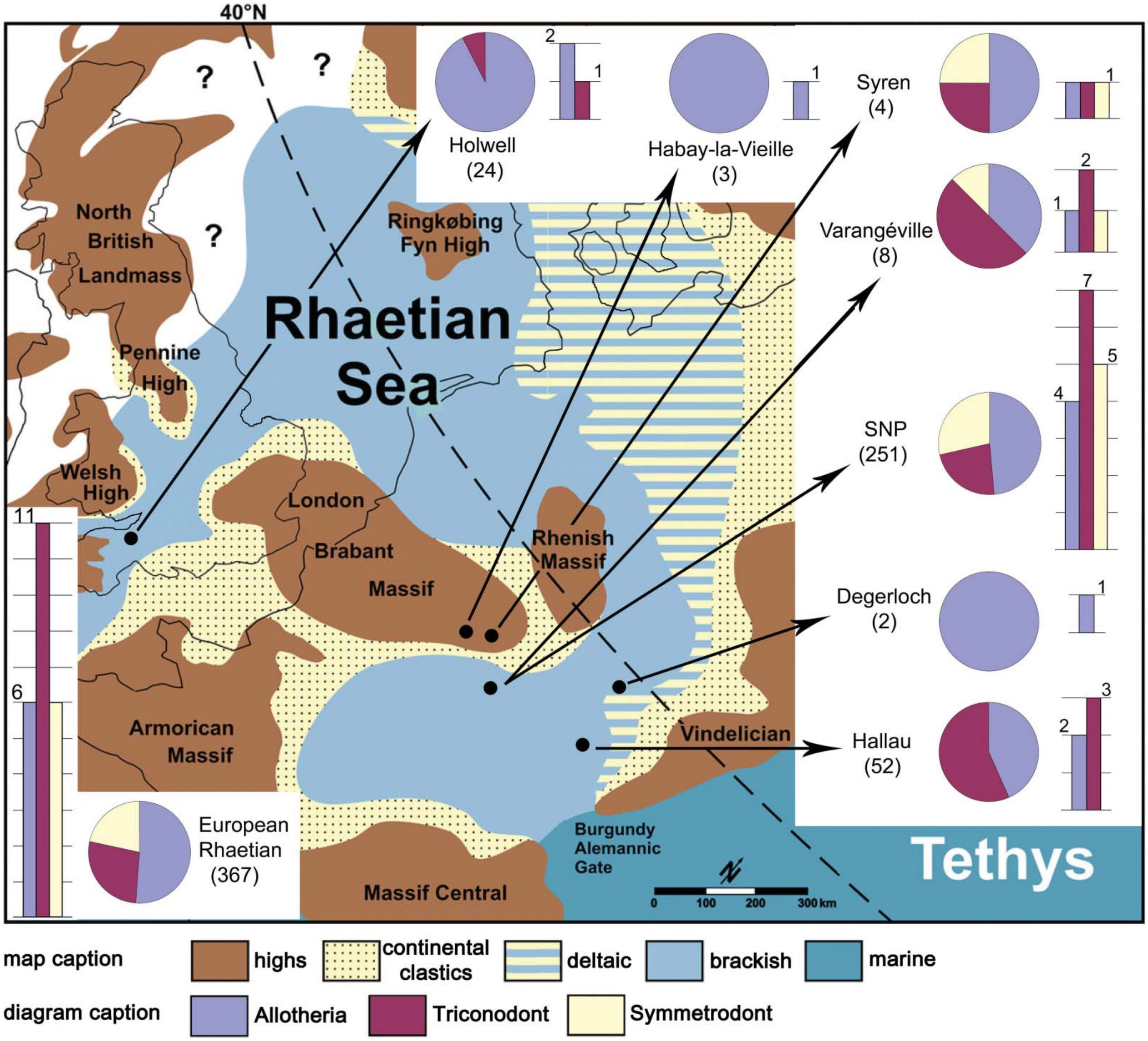

Figure 21. Palaeogeographical map showing some Rhaetian localities which have yielded mammalian remains (localities follow coastline; Habay-la-Vieille and Syren are located in the continental domain of the London Brabant Massif, although these sites are described as marine, because the palaeogeographical map has been reproduced without modification). Numbers between brackets are the total number of molariform teeth in the locality. Pie charts represent relative abundances of morphological groups (Allotheria, 'Symmetrodont', 'Triconodont'). Bar charts represent the specific diversity of morphological groups (map from Fischer *et al*. 2012; see Supplemental Table 1 for details).

Supplemental Table 2 for references). Early Jurassic localities in India are considered as lacustrine deposits (Prasad & Manhas 2002). Only isolated teeth have been described from these localities (see Supplemental Table 2 for references), but cranial and postcranial elements are reported to be present (Datta *et al*. 1978). Early Jurassic localities of southern Africa, North America and China most strongly differ from Rhaetian localities by their condition of preservation. They have yielded isolated skulls and more or less complete mammal skeletons (see Supplemental Table 2 for references) and are linked to flood plain deposits (Luttrell 1993; Bordy *et al*. 2004) or to a mosaic of lacustrine and fluvial deposits (Luo & Wu 1994). In these low energy environments, cranial and post-cranial remains are often associated and well preserved, but biases in preservation of biodiversity remain important.

Diversity and abundance of morganucodonts at Saint-Nicolas-de-Port

This study highlights again the exceptional importance of the Saint-Nicolas-de-Port site for the understanding of the evolution of early mammals. Six morganucodont genera are described here, plus two un-named taxa represented by two sets of indeterminate specimens. Consequently, Morganucodonta is now the most diverse order at Saint-Nicolas-de-Port, with seven identified species, along with four species of Haramiyida and five species of 'symmetrodonts' (Kuehneotheriidae) Kermack, Kermack & Musset, 1968, Woutersiidae Sigogneau-Russell & Hahn, 1995 and *Delsatia* Sigogneau-Russell & Godefroit, 1997 (Supplemental Table 1; Fig. 21).

A summary of the relative abundance of the main groups, based on published data and only for molariform teeth, is presented in Supplemental Table 1. It shows that, even though morganucodonts are diverse, they are rare in the Saint-Nicolas-de-Port fauna, as well as the 'symmetrodonts'. The morganucodonts are largely outnumbered by haramiyids, as previously pointed out by Sigogneau-Russell (1983).

Diversity and abundance of morganucodonts within Late Triassic and Early Jurassic faunas

Rhaetian mammals are only known in Europe, and only as isolated teeth (Supplemental Table 1). With the exception of Hallau (Switzerland), Holwell (England), Saint-Nicolas-de-Port and Olgahain (Germany), each of the other Rhaetian localities has yielded no more than 10 mammal teeth (Supplemental Table 1; Fig. 21). Haramiyids are more abundant than morganucodonts (Fig. 21), and are known from all localities. Morganucodonts are absent in Habay-la-Vieille (Belgium) and are more numerous than haramiyids in Hallau and Varangéville (France) (Fig. 21). 'Symmetrodonts' are present only in France and in Luxembourg and are, at the most, as numerous as morganucodonts (Fig. 21). As in Saint-Nicolas-de-Port, morganucodonts are more diverse than other mammalian groups in Hallau, Varangéville (Fig. 21) and possibly in Olgahain (see above). Each group is represented by one species in Syren (Luxembourg) (Fig. 21). In Holwell, haramiyids are the most diverse, with two species against one species of morganucodont (Fig. 21). As a whole in the Rhaetian of Europe, morganucodonts are twice as diverse as haramiyids, which are in turn as diverse as the 'symmetrodonts' (Fig. 21).

Our discussions about relative abundances of mammals are based on isolated teeth. However, the number of teeth by individual varies according to taxon, sometimes markedly. The minimal number of individuals (MNI) is generally more significant, but this can be applied only in mammal taxa in which the dental formula is known and for teeth with well-established positions in the tooth series, which is not the case for Rhaetian mammals. Correcting the number of specimens identified for each species by the average number of teeth by dental row in each main taxon allows estimation of the MNI (Supplemental Table 3). There are three, four or five molars in morganucodonts (e.g. Mills 1971; Kermack *et al*. 1973; Crompton 1974), six molars in early 'symmetrodonts' (Gill 2004), and two or three molars in haramiyids (Jenkins *et al*. 1997; Zheng *et al*. 2013; Zhou *et al*. 2013). Correction by dental row requires knowledge of tooth position (upper/lower, left/right) for all specimens; however, left/right information is not available for each specimen discussed here. Supplemental Table 3 shows corrections by number of molariforms in the same jaw, but only for Saint-Nicolas-de-Port, Hallau, Holwell and Olgahain because the other sites have yielded so few specimens that correction results in only one individual per species. As a result, their corrected relative abundance corresponds to the diversity diagram (Fig. 21). For localities presented in Supplemental Table 3, the pattern of relative abundance shows variation linked to the specific diversity of each main taxon. In Holwell, the correction moderates haramiyid overabundance (Supplemental Table 3). In Hallau, the ratio is reversed: haramiyids are slightly more numerous than morganucodonts (Supplemental Table 3). In Saint-Nicolas-de-Port, ratios change in an important way. Morganucodonts are almost twice as numerous as 'symmetrodonts' but, because of uncertainty in correction, they are either as numerous as haramiyids, or two times less numerous (Supplemental Table 3). Following taxonomic interpretation at Olgahain, the relative abundance of morganucodonts and haramiyids is either the same as in Holwell, or the same as in Saint-Nicolas-de-Port (Supplemental Table 3). Therefore, correction by approximation of MNI strongly changes our view of Rhaetian European mammalian fauna. Discussion based on isolated teeth gives contrasting patterns of relative abundance for the four main localities (Hallau, Holwell, Olgahain and Saint-Nicolas-de-Port), and correction results in a unique pattern for each of these localities. Haramiyids are more numerous than morganucodonts, and 'symmetrodonts' are the least numerous, although uncertainty in dental formulae obscures the importance of these differences.

At the beginning of the Early Jurassic, mammals attained a Pangean distribution (Supplemental Table 2; Fig. 22). Morganucodonts are present in all known Early Jurassic mammal localities with a specific diversity (12 species) comparable to that of Rhaetian localities (11 species) (Supplemental Table 2). However, the diversity of the Early Jurassic localities is more uniform, with usually one or two species, than the Rhaetian localities that can contain up to seven species (Supplemental Table 2). The general mammal assemblage known in the Rhaetian (morganucodonts, haramiyids and 'symmetrodonts') is only found in Welsh localities (e.g. Pacey 1978; Evans & Kermack 1994; Clemens 2007). In contrast to Rhaetian localities, there is no dominant taxon in the Early Jurassic localities (see Kielan-Jaworowska *et al*. 2004 for review).

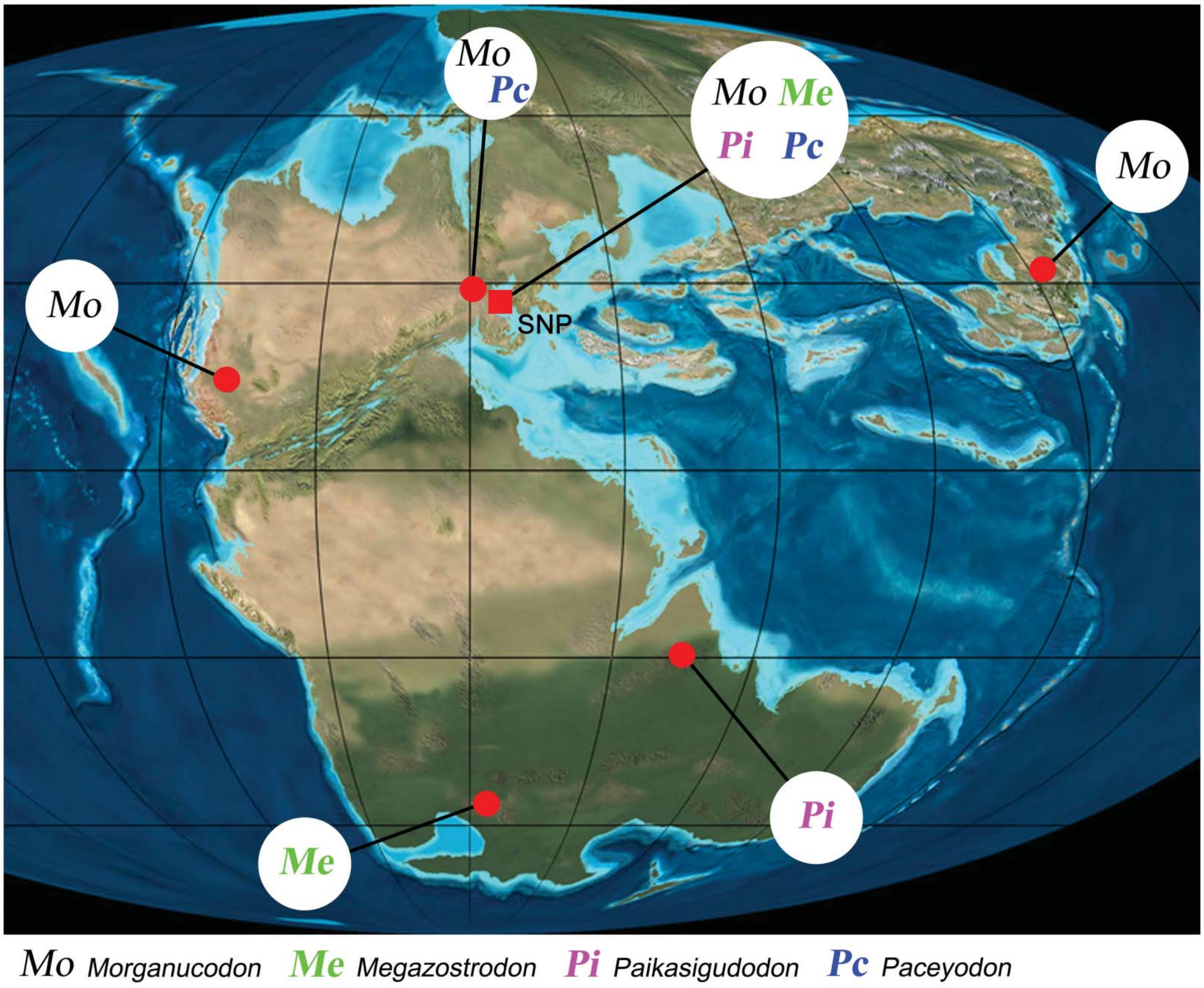

Figure 22. Palaeogeographical map showing Rhaetian (square) and Early Jurassic (circles) localities that have yielded morganucodonts (map from Blakey 2013; see Supplemental Table 2 for details).

Saint-Nicolas-de-Port contains the most diverse morganucodonts assemblage in the world, and also the richest one for the Rhaetian.

Distribution of morganucodonts in time and space

Although fossil data are far from being complete, current data show a major contrast in distribution between the morganucodont genera. Whereas most of the genera are only known from a single locality, four genera (*Morganucodon*, *Megazostrodon*, *Paceyodon* and *Paikasigudodon*) are known from several localities and show significant geographical distributions and stratigraphical ranges (Supplemental Table 2; Fig. 22).

Late Triassic morganucodonts are only known in Europe, with one possible exception, whereas Early Jurassic morganucodonts are distributed worldwide (Supplemental Table 2; Fig. 22). Even though the possible morganucodont *Gondwanadon* is known from India (Datta & Das 1996), fossil data suggest that the Late Triassic Europe was the centre of initial diversification of morganucodonts from where they spread out widely in the Early Jurassic (Supplemental Table 2; Fig. 22). *Morganucodon* is the most widespread morganucodont with a Laurasian distribution in the Early Jurassic (Supplemental Table 2; Fig. 22). By contrast to the east−west distribution of *Morganucodon*, *Megazostrodon* and *Paikasigudodon* have a north−south continental distribution (Supplemental Table 2; Fig. 22). Taking into account sampling biases, this suggests a possible worldwide distribution of most of the Early Jurassic morganucodont genera.

Excepting the possible presence of morganucodonts in the Carnian and Norian (Supplemental Table 2), our knowledge of morganucodonts begins in the Rhaetian, with the first occurrence of eight genera representing more than half of the known morganucodont genera

(Supplemental Table 2). This great diversity suggests an initial morganucodont diversification as early as the Norian. The evolution of morganucodont faunas across the Triassic–Jurassic boundary is more difficult to assess. Current fossil data show extinction of 50% of the genera and appearance of 55% of the genera at this boundary (Supplemental Table 2). However, actual extinction and appearance rates cannot be assessed at the Triassic–Jurassic transition because of problems of stratigraphical resolution and taphonomy. Nevertheless, *Morganucodon* has long been known to cross the Triassic–Jurassic boundary (see Supplemental Table 2 for references), and this study shows that three other genera did likewise (Supplemental Table 2; Fig. 22). Indeed, all well-known morganucodont genera cross this boundary. The Triassic/Jurassic extinction event seems not to have impacted morganucodonts, even though this event remains poorly known, including for morganucodonts and other early mammals.

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Supplemental material

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Supplemental Table 1. Abundance and diversity of Rhaetian mammal localities. ‘Morphological group’ is used for the clarity of Figure 21.

Morphological group	Taxon	Number of molariform	References
Saint-Nicolas-de-Port (France)			
Triconodont		62	
	Morganucodonta		This publication
	Morganucodon peyeri	7	
	Megazostrodon chenali sp. nov.	19	
	Brachyzsotrodon coupatezi	16	
	Brachyzostrodon maior	6	
	Rosierodon anceps gen. et sp. nov.	9	
	Paceyodon davidi	1	
	Paikasigudodon cf. *yadagirii*	1	
	Morganucodonta indet. 1	1	
	Morganucodonta indet 2	2	
Symmetrodont		71	
	Kuehneotheriidae	55	Godefroit & Sigogneau-Russell 1999
	Kuehneotherium praecursoris		
	Kuehneotherium sp.		
	Woutersiidae		Sigogneau-Russell & Hahn 1995
	Woutersia mirabilis	8	
	Woutersia butleri	5	
	Incertae sedis		Sigogneau-Russell & Godefroit 1997
	Delsatia rhupotopi	3	
Allotheria		118	
	Haramiyida		
	Haramiyidae	106	Sigogneau-Russell 1989
	Thomasia antiqua		
	Thomasia moorei		
	Theroteinidae		Hahn *et al*. 1989
	Theroteinus nikolai	8	
	Theroteinus sp.	4	
Varangéville (France)			Godefroit 1997
Triconodont		4	
	Morganucodonta		
	Morganucodon sp.	1	
	aff. *Morganucodon*	1	
	Morganucodont indet.	1	
	Sinoconodontidae		
	aff. *Sinconodon*	1	
Symmetrodont		1	
	Woutersiidae		
	Woutersia mirabilis	1	
Allotheria		3	
	Haramiyida		
	Haramiyidae		
	Thomasia antiqua	1	
	Thomasia cf. *antiqua*	2	
Boisset (France)			Cuny 1993a
Allotheria		1	
	Haramiyida		
	Haramiyidae		
	Thomasia sp.	1	
Symmetrodont		1	
	Kuehneotheriidae	1	
Hallau (Switzerland)			Clemens 1980
Triconodont		30	

	Morganucodonta		
	Morganucodon peyeri	18	
	?*Morganucodon* sp.	3	
	?Morganucodonta		
	Helvetiodon schutzi	7	
	Hallautherium schalchi	2	
Allotheria		22	
	Haramiyida		
	Haramiyidae		
	cf. *Thomasia antiqua*	4	
	Thomasia moorei	2	
	Thomasia sp.	2	
	Haramiyidae?	14	
Degerloch (Germany)			Clemens 1980; Clemens & Martin in press
Allotheria		2	
	Haramiyida		
	Haramiyidae		
	Thomasia antiqua	2	
Gaisbrunnen (Germany)			Clemens 1980; Clemens & Martin in press
Allotheria		1	
	Haramiyida		
	Haramiyidae		
	?*Thomasia* sp.	1	
Olgahain (Germany)			
Triconodont		2	Clemens & Martin in press
	Morganucodonta		
	Morganucodont indet.	2	
Allotheria		14	Clemens 1980; Clemens & Martin in press
	Haramiyida		
	Haramiyidae		
	Thomasia antiqua	7	
	?*Thomasia antiqua*	7	
Lisowice (Poland) (Late Norian or Rhaetian)			Świło *et al.* in press
Triconodont		1	
	Morganucodonta		
	Hallautherium sp.	1	
Syren (Luxembourg)			Godefroit *et al*. 1998
Triconodont		1	
	Morganucodonta		
	Morganucodonta indet.	1	
Symmetrodont		1	
	Kuehneotheriidae		
	Kuehneotherium sp. nov.	1	
Allotheria		2	
	Haramiyida		
	Haramiyidae		
	Thomasia antiqua	2	
Habay-la-Vieille (Belgium)			
Allotheria		3	
	Haramiyida		Delsate 1996
	Haramiyidae		
	Thomasia woutersi	2	
	Multituberculata?		Hahn *et al*. 1987
	Mojo usuratus	1	
Attert (Belgium)			Delsate 1994
Allotheria		1	
	Haramiyida		

	Haramiyidae		
	Thomasia woutersi	1	
Holwell (Great Britain)			
Triconodont		2	
	Morganucodonta		Parrington 1941
	Eozostrodon parvus	2	
Allotheria		22	
	Haramiyida		
	Haramiyidae	22	Butler & Macintyre 1994
	Thomasia antiqua		
	Thomasia moorei		
Emborough (Great Britain) (Norian for Fraser *et al*. 1985 but Rhaetian for Whiteside & Marshall 2008)			
Symmetrodont		2	
	Kuehneotheriidae		Fraser *et al.* 1985
	Kuehneotherium praecursoris	2	

Supplemental Table 2. Summary of described morganucodonts with indication of ages and localities. '?' in taxon column means 'morganucodont identification questionable'; '?' in age columns means 'age of locality questionable'; '?' in area column means 'presence of genus in locality questionable'.

Taxa	Ages						Area	References
	Carnian	Norian	Rhaetian	Early J.	Middle J.	Early C.		
Gondwanadon tapani?	+						India	Datta & Das 1996
Brachyzostrodon sp.		+					Greenland?	Jenkins *et al.* 1994
Brachyzostrodon coupatezi			+				France	Sigogneau-Russell 1983
Brachyzostrodon maior			+				France	Hahn *et al.* 1991
Eozostrodon parvus			+				Great Britain	Parrington 1941
Helvetiodon schutzi?			+				Switzerland	Clemens 1980
Hallautherium schalchi?			+				Switzerland	Clemens 1980
Hallautherium sp.		+?	+?				Poland	Swilo *et al.* in press
Rosierodon anceps gen. et. sp. nov.			+				France	this publication
Paceyodon davidi			+	+			France, Great Britain	Clemens 2011; this publication
Paikasigudodon cf. *yadagirii*			+				France	this publication
Paikasigudodon yadagirii				+?	+?		India	Prasad & Manhas 2002
Megazostrodon chenali sp. nov.			+				France, Germany	Clemens & Martin in press; this publication
Megazostrodon rudnerae				+			Lesotho, South Africa	Crompton 1974, Gow 1986
Morganucodon peyeri			+				France, Switzerland	this publication; Clemens 1980
Morganucodon watsoni				+			Great Britain	Kühne 1949
Morganucodon oehleri				+			China	Rigney 1963
Morganucodon heikuopengensis				+			China	Young 1978
Morganucodon sp. nov.				+			Great Britain	Smith *et al.* 2010
Morganucodon sp.			+	+			Arizona, France	Jenkins et al. 1983; Godefroit 1997
Bridetherium dorisae				+			Great Britain	Clemens 2011
Indotherium pranhitai				+			India	Yadagiri 1984
Indozostrodon simpsoni				+			India	Datta & Das 2001
Erythrotherium parringtoni				+			Lesotho	Crompton 1964

Dinnetherium nezorum	+			Arizona	Jenkins *et al*. 1983
Wareolestes rex		+		Great Britain	Freeman 1979
Purbeckodon batei?			+	Great Britain	Butler *et al*. 2012

Supplemental Table 3. Correction of abundance in Rhaetian mammal localities by number of molariforms teeth by jaw (morganucodont: 6, 8 or 10, symmetrodont: 12, haramiyid: 4 or 6). Abbreviations: L: number of lower molariforms; MNI: minimal number of individual; U: number of upper molariforms; '?' in L and U columns means allocation questionable. See Supplemental Table 1 for references.

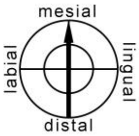
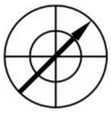
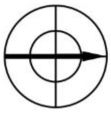
Morphological group	Taxa	U	L	MNI
Saint-Nicolas-de-Port (France)				
Triconodont				10-14
	Morganucodonta			
	Morganucodon peyeri	0	7	1-2
	Megazostrodon chenali sp. nov.	4	15	2-3
	Brachyzostrodon coupatezi	10	6	1-2
	Brachyzostrodon maior	3	3	1
	Rosierodon anceps gen. et sp. nov.	0	9	1-2
	Paceyodon davidi	0	1	1
	Paikasigudodon cf. *yadagirii*	1	0	1
	Morganucodonta indet. 1	1	0	1
	Morganucodonta indet. 2	2?		1
Symmetrodont				6
	Kuehneotheriidae	22	33	3
	Kuehneotherium praecursoris			
	Kuehneotherium sp.			
	Woutersiidae			
	Woutersia mirabilis	5	3	1
	Woutersia butleri	3	2	1
	Incertae sedies			
	Delsatia rhupotopi	0	3	1
Allotheria				13-19
	Haramiyida			
	Haramiyidae	61	45	11-16
	Thomasia antiqua			
	Thomasia moorei			
	Theroteinidae			
	Theroteinus nikolai	5	3	1-2
	Theroteinus sp.	0	4	1
Hallau (Switzerland)				
Triconodont				4-5
	Morganucodonta			
	Morganucodon peyeri	9	9	1-2
	?*Morganucodon* sp.	2	1	1
	?Morganucodonta			
	Helvetiodon schutzi	6	1?	1
	Hallautherium schalchi	0	2	1
Allotheria				6-7

	Haramiyida			
	Haramiyidae			
	cf. *Thomasia antiqua*	0	4	1
	Thomasia moorei	2	0	1
	Thomasia sp.	0	2	1
	Haramiyidae?	14?		3-4
Holwell (Great Britain)				
Triconodont				1
	Morganucodonta			
	Eozostrodon parvus	0	2	1
Allotheria				3-4
	Haramiyida			
	Haramiyidae	9	13	3-4
	Thomasia antiqua			
	Thomasia moorei			
Olgahain (Germany)				
Triconodont				1-2
	Morganucodonta			
	Morganucodont indet.	1	1	1-2
Allotheria				2-3
	Haramiyida			
	Haramiyidae			
	Thomasia antiqua	3	4	1
	?*Thomasia antiqua*	7?		2

Appendix

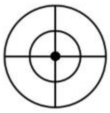
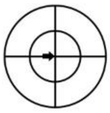
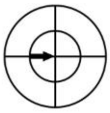
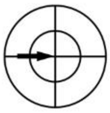
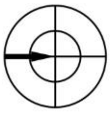
Tables of illustrations and definitions for descriptors of wear facets (From von Koenigswald *et al*. 2013).

Definitions of directional descriptors, with their related angle values, and associated symbols (From von Koenigswald *et al*. 2013).

Direction	Angle	Symbols
Mesial	About 0° ± 12°	
Mesio-mesiolingual	About 22°± 12°	
Mesiolingual	About 45°± 12°	
Linguo-mesiolingual	About 68°± 12°	
Lingual	About 90°± 12°	
Linguo-distolingual	About 112°± 12°	

Distolingual	About 135°± 12°	
Disto-distolingual	About 158°± 12°	
Distal	About 180°± 12°	

Definitions of descriptors for the inclination, with related angle values, and associated symbols (From von Koenigswald *et al*. 2013).

Inclination	Angle	Symbols
Vertical	About 90°±12°	
Very steep	About 68°±12°	
Steep	About 45°±12°	
Shallow	About 22°±12°	
Horizontal	About 0°±12°	

Reference

Koenigswald, W., Anders, U., Engels, S., Schultz, J. A. & **Kullmer, O.** 2013. Jaw movement in fossil mammals: analysis, description and visualization. *Paläontologische Zeitschrift*, **87**, 141–159.