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## Late Triassic dinosaur teeth from southern Belgium Dents de dinosaures du Trias supérieur de Lorraine belge

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### Abstract

Isolated Dinosaur teeth have been discovered in the Upper Triassic locality of Habay-la-Vieille, in southern Belgium. Ornithischia are represented by three dental morphotypes; two of them closely resemble isolated teeth from the Middle or Upper Jurassic of Portugal and England. The presence of sauropods in the Upper Triassic of Europe is confirmed. Sauropods already had a wide geographical distribution during the Latest Triassic, as fossils have been discovered in South Africa, Thailand and western Europe. At Habay-la-Vieille, sauropods and prosauropods co-existed at the end of the Triassic. Two dental morphotypes may tentatively be referred to as theropod dinosaurs. The study of isolated teeth indicates that dinosaurs were already well diversified in the Latest Triassic of western Europe. **To cite this article: P. Godefroit, F. Knoll, C. R. Palevol 2 (2003) 3–11.** © 2003 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

### Résumé

Des dents isolées de dinosaures ont été découvertes dans les Trias supérieur d'Habay-la-Vieille, en Lorraine belge. Les Ornithischia sont représentés par trois morphotypes, dont deux semblent très proches de dents isolées découvertes dans le Jurassique moyen à supérieur du Portugal et d'Angleterre. La présence de sauropodes dans le Trias supérieur d'Europe est confirmée. Les sauropodes occupaient déjà une aire de répartition géographique étendue au cours du Trias terminal, puisque des ossements ont été découverts en Afrique du Sud, en Thaïlande et en Europe occidentale. Des sauropodes et des prosauropodes ont coexisté à Habay-la-Vieille à la fin du Trias. Deux morphotypes dentaires peuvent prudemment être attribués à des dinosaures théropodes. L'étude des dents isolées montre que les dinosaures étaient déjà bien diversifiés en Europe occidentale à la fin du Trias. **Pour citer cet article : P. Godefroit, F. Knoll, C. R. Palevol 2 (2003) 3–11.**

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## Version abrégée

### Introduction

Depuis la découverte, en 1878, des célèbres *Iguanodons* de Bernissart, très peu de fossiles de dinosaures ont été mis au jour sur le territoire belge. Plusieurs dents isolées de dinosaures du Trias supérieur, découvertes dans le gisement d'Habay-la-Vieille en Lorraine belge, sont décrites dans cet article. Ce gisement est bien connu, parce qu'il a déjà fourni des dents isolées de cynodontes [19,22,23] et de mammaliaformes primitifs [12,21,48]. L'âge rhétien des sédiments est confirmé par des analyses palynologiques [33].

### Paléontologie

#### *Ornithischia*

Trois morphotypes dentaires peuvent prudemment être rapprochés des dinosaures ornithischiens sur la base de la combinaison de plusieurs caractères, tels que la couronne basse et triangulaire, la présence d'une constriction bien marquée entre la racine et la couronne, la présence de gros denticules formant un angle de 45° avec le bord de la couronne, ou encore l'asymétrie de la couronne en vue mésiale ou distale [26,37,38].

Le premier morphotype dentaire (Fig. 1) ressemble beaucoup aux spécimens décrits comme des dents pré-maxillaires distales d'*Alocodon kuehnei* [40]. Le second morphotype dentaire présent à Habay-la-Vieille (Fig. 2) ressemble quant à lui aux spécimens décrits comme des dents maxillaires postérieures de ce même taxon [40]. *Alocodon kuehnei* a été décrit à l'origine dans le Callovien ou l'Oxfordien du Portugal [40], mais également dans le Bathonien d'Angleterre [15]. S'il est loin d'être sûr que toutes les dents rapportées à *Alocodon kuehnei* appartiennent bien au même taxon, il est toutefois surprenant de constater que des morphotypes dentaires semblables sont connus depuis le Trias supérieur jusqu'au Jurassique moyen à supérieur. Le troisième morphotype dentaire présent à Habay-la-Vieille (Fig. 3) ressemble beaucoup à une dent décrite dans le Trias supérieur de Saint-Nicolas-de-Port, dans le Nord-Est de la France.

#### *Sauropodomorpha*

IRSNB R211 (Fig. 4) présente une série de caractères habituellement considérés comme synapo-

morphiques pour les Eusauropoda : couronne de forme spatulée, émail dentaire finement plissé et facettes occlusales bien développées [42,47]. La présence probable de denticules le long des bords de la couronne indique que cette dent n'appartient pas à un Neosauropoda. IRSNB R212 (Fig. 5) peut, quant à elle, être rapportée à un Prosauropoda : la couronne est haute et symétriquement comprimée labio-lingualement, ses carènes portent une quinzaine de grands denticules formant un angle d'environ 45° avec le bord de la couronne, couronne et racine ne sont pas séparés par une constriction bien marquée. Des dents similaires ont été décrites dans le Trias supérieur de Saint-Nicolas-de-Port [5,11,20]. Elles ressemblent beaucoup à celles du prosauropode *Plateosaurus* [16,36].

#### *Theropoda*

Certaines dents trouvées à Saint-Nicolas-de-Port rappellent celles des dinosaures théropodes : elles sont caniniformes et leurs carènes portent des crénelures bien marquées. Cependant, de tels types de dents peuvent également, au Trias supérieur, être observés dans d'autres lignées indépendantes d'Archosauriformes [20]. C'est pourquoi elles sont ici identifiées comme Theropoda indet.

Les dents les plus courantes (Fig. 6) ressemblent beaucoup à celles rapportées à *Liliensternus liliensterni*, du Norien supérieur d'Allemagne, par leur taille et leur forme générale, mais également par la distribution asymétrique des crénelures le long des carènes mésiale et distale [25,36]. Ce type dentaire peut cependant également être observé chez d'autres cératosaures [7,34,46]. D'autres dents se distinguent de ce morphotype par leur forme générale plus élancée, moins recourbée, et par la présence de minuscules crénelures, uniquement le long de la carène distale (Fig. 7).

#### Discussion

Bien que leurs fossiles soient relativement rares à Habay-la-Vieille, les dinosaures apparaissent bien diversifiés, indiquant que les principaux groupes de dinosaures étaient déjà bien implantés en Europe occidentale à la fin du Trias. C'est particulièrement le cas pour les petits ornithischiens, également connus dans plusieurs localités d'Allemagne, de France et du grand-duché de Luxembourg [10,20,24]. C'est la première fois qu'un fossile indubitable de sauropode est décrit dans le Trias supérieur d'Europe. Sauropodes

et prosauropodes se côtoyaient à Habay-la-Vieille parce qu'ils occupaient des niches écologiques différentes : les dents de sauropodes sont adaptées à un régime alimentaire herbivore [42], tandis que celles des prosauropodes reflètent plutôt un régime de type omnivore [1]. Les sauropodes avaient déjà une aire de répartition géographique très étendue au Trias terminal, puisqu'en dehors de l'Europe occidentale, on en a également découvert des fossiles au Lésoto [43] et en Thaïlande [4].

Si l'étude des dents isolées de dinosaures est souvent frustrante, à cause de l'impossibilité d'établir des identifications précises, particulièrement dans des sédiments datés du Trias supérieur, elle apporte cependant de précieuses informations sur la biodiversité réelle de ces animaux à une période donnée. Il est regrettable que de telles recherches sur les microrestes de dinosaures du Trias supérieur n'aient pas encore été tentées systématiquement en dehors de l'Europe occidentale et de l'Amérique du Nord.

## 1. Introduction

In March 1878, coal miners uncovered pieces of dinosaur bones deep in an underground mine called the Sainte-Barbe pit, near Bernissart in western Belgium. It was the beginning of one of the greatest dinosaur discoveries of all times: more than 30 complete, articulated skeletons of the Early Cretaceous ornithomimid *Iguanodon*. Most of the specimens belong to *Iguanodon bernissartensis* [31], whereas one smaller individual belongs to *Iguanodon atherfieldensis* [32]. These were the first complete skeletons of large dinosaurs ever found and still remain one of the greatest accumulations of a single dinosaur taxon. One theropod phalanx was also found at Bernissart. But apart from this spectacular discovery, dinosaur remains are very rare and fragmentary in Mesozoic strata from Belgium. An isolated, still unpublished iguanodontid metatarsal was found in the 1950s by a quarryman in Wealdian clays at Baudour, about 12 km west of Bernissart. The ornithomimid *Craspedodon lonzeensis* is based on three teeth discovered in the Santonian to Lower Campanian [6] Glauconie de Loncée, in the Namur Province, together with the ungual phalanx of some theropod dinosaur [13]. A handful of hadrosaurid and theropod bones was also collected in shallow marine strata from various localities in the type area of the

Maastrichtian stage (western Netherlands and eastern Belgium) [3,29,30,44].

Herein we describe some isolated dinosaur teeth recently found in the Late Triassic of Habay-la-Vieille, southern Belgium. Since the early 1980s, sediments from this locality have been intensively screen-washed and have provided numerous vertebrate micro-remains [14]. This locality has particularly drawn the attention of palaeontologists because of the presence of cynodonts [19,22,23] and early mammaliaformes [12,21,48] isolated teeth. Four sedimentological sequences may be recognised in the section exposed at Habay-la-Vieille: the basal one is regressive, whereas the three others are transgressive [2]. Three main bonebeds have been described throughout the sequence. The lithofacies observed at Habay-la-Vieille represent subtidal and littoral deposits. The Rhaetian age of the sediments has been confirmed by palynological analyses [33].

All specimens described herein are housed in the palaeontological collections of the 'Institut royal des Sciences naturelles de Belgique' (IRSNB).

## 2. Palaeontology

### 2.1. *Ornithischia*

The following teeth are tentatively referred to the ornithischian dinosaurs, because they present a combination of the following characters [26,37,38]: (1) low, triangular crown in labial or lingual view; (2) well-developed neck between crown and root; (3) prominent large denticles arranged at 45° or more to the mesial and distal edges; (4) maxillary and dentary teeth asymmetrical in mesial and distal views. The combination of these characters has long been considered a good identification key of a generalised ornithischian tooth. However, this has been dismissed [28], and, therefore, the ornithischian identification of the following specimens must be considered tentative.

#### 2.1.1. *Ornithischia* indet. morphotype 1 (Fig. 1)

IRSNB R208 closely resembles specimens described as distal premaxillary teeth of *Alocodon kuehnei* [40]. The crown is leaf-shaped in labial or lingual view and somewhat higher than long. Its labial side is regularly convex and smooth, whereas its lingual side is less convex and ornamented, with strong vertical

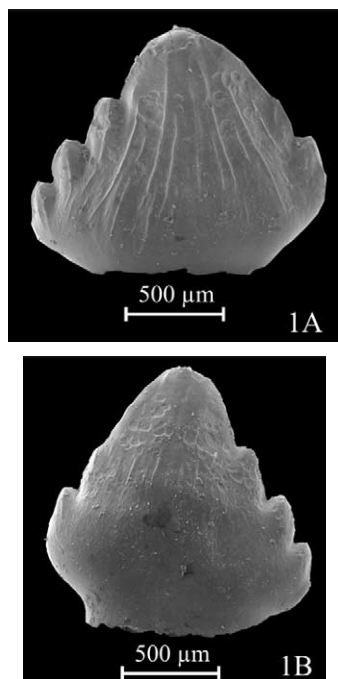


Fig. 1. Dinosaur teeth from the Upper Triassic of Habay-la-Vieille (southern Belgium). **1**, *Ornithischia* indet. morphotype 1 (IRSNB R208), **A**: lingual view, **B**: labial view.

Fig. 1. Dents de dinosaures du Trias supérieur d'Habay-la-Vieille (Sud de la Belgique). **1**, *Ornithischia* indet. morphotype 1 (IRSNB R208), **A** : vue linguale, **B** : vue labiale.

ridges. It is slightly curved backward and inward. Its convex mesial edge bears two denticles, whereas its concave distal edge bears three denticles.

#### 2.1.2. *Ornithischia* indet. morphotype 2 (Fig. 2)

IRSNB R209 resembles specimens described as caudal cheek teeth of *Alocodon kuehnei* [40]. The crown is much mesio-distally longer than high and rather labio-lingually thick. The main central cusp is symmetrically flanked by four well-individualised denticles along the mesial and distal edges of the crown. Its regularly convex labial side bears a large elliptical occlusion facet. A few vertical ridges ornament the base of its concave lingual side.

*Alocodon kuehnei* was originally described from the Jurassic (Upper Callovian-Middle Oxfordian; [35]) of western Portugal [40]. Similar teeth were also described from the Upper Bathonian Forest Marble Formation of southern England [15]. *Alocodon* was previously referred to as different kinds of ornithischian dinosaurs, e.g., fabrosaurids [15,40]. The holotype of

*Alocodon kuehnei* resembles a maxillary tooth of the possible hypsilophodontid *Zephyrosaurus schaffi*, but it is in fact not diagnostic at a specific level. Consequently, *Alocodon kuehnei* should be regarded as a *nomen dubium* [28,45]. Moreover, it is not certain at all that all the isolated teeth originally described as *Alocodon kuehnei* really belong to a single taxon. Nevertheless, it is remarkable that such typical dental morphotypes have a large stratigraphic range, from the Upper Triassic till the Middle or Upper Jurassic.

#### 2.1.3. *Ornithischia* indet. morphotype 3 (Fig. 3)

IRSNB R210 is triangular in outline, slightly higher than long and very narrow. The crown is slightly curved backward and inward. The labial side is more convex than the lingual one. Both mesial and distal

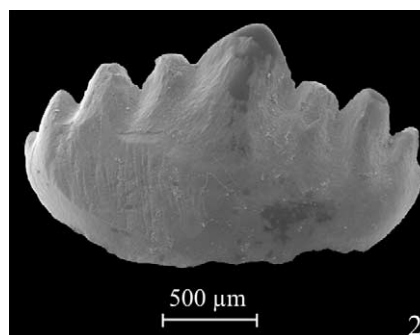


Fig. 2. *Ornithischia* indet. morphotype 2 (IRSNB R209), labial view.  
Fig. 2. *Ornithischia* indet. morphotype 2 (IRSNB R209), vue labiale.

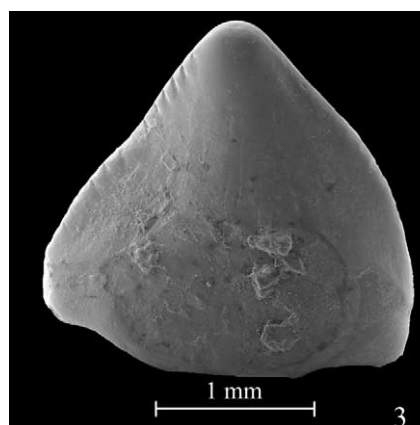


Fig. 3. *Ornithischia* indet. morphotype 3 (IRSNB R210), lingual view.  
Fig. 3. *Ornithischia* indet. morphotype 3 (IRSNB R210), vue linguale.

edges bear a dozen very small denticles, arranged at about 45° to the edges of the crown. Because they are so worn, it is not possible to know whether or not these denticles reached the base of the crown. Several delicate ridges ornament the lingual side of the crown.

A very similar tooth was described from the Late Triassic of Saint-Nicolas-de-Port, northeastern France [20]. If such dental morphotype possibly belongs to ornithischian dinosaurs, thorough comparisons with known taxa do not allow a more precise identification [20].

## 2.2. Sauropodomorpha

### 2.2.1. Eusauropoda indet. (Fig. 4)

The root of IRSNB R211 is broken off; it is rounded in cross-section and separated from the crown by a slight constriction. The crown is typically spatulate. It is rather mesio-distally expanded, with a convex labial side and a slightly concave lingual side. The distal part of the crown therefore has a D-shaped cross-section. The surface texture of the enamel is wrinkled. The labial side of the crown bears one shallow vertical groove along its mesial margin. This character indicates an imbricate arrangement of adjacent teeth: this gentle groove accommodated the lingual aspect of the distal margin of the next anteriormost tooth. An extended V-shaped wear facet is developed along the mesial and distal edges of the crown. Such a wear facet suggests precise interlocking occlusion. Although they are extremely eroded because of wear, denticles were apparently developed along both margins of the crown.

This tooth displays a number of characters usually regarded as synapomorphic for Eusauropoda [42,47]: tooth crown mesio-distally enlarged and D-shaped in cross-section (spatulate tooth crowns), tooth enamel with wrinkled texture, and precise interlocking occlusion. However, the distribution of these characters may be misleading, because reliable *Vulcanodon* tooth material is not available. Consequently, it cannot be excluded that at least some of these characters are in fact synapomorphic for Sauropoda. The probable presence of denticles along the margins of the crown suggests that IRSNB R211 does not belong to the Neosauropoda. Tooth crown overlap (vertical groove on labial side of the crown) is sometimes regarded as also synapomorphic for Eusauropoda [47]. However, this character is unreliable, because it is also present in the

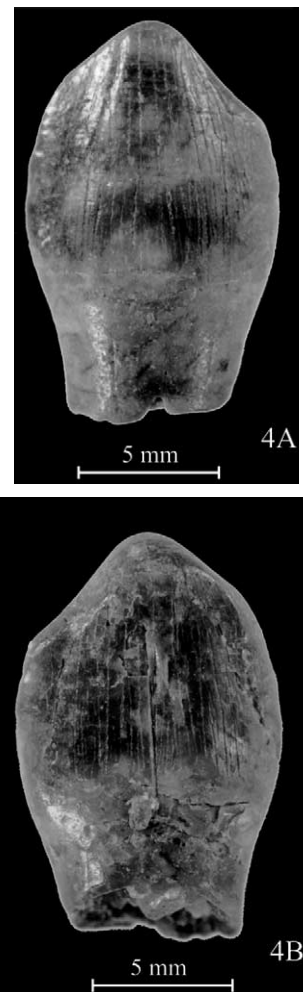


Fig. 4. Eusauropoda indet. (IRSNB R211), A: labial view; B: lingual view.

Fig. 4. Eusauropoda indet. (IRSNB R211), A : vue labiale ; B : vue linguale.

prosauropod *Massospondylus* [8], to cite just one example amongst sauropodomorphs. Teeth tentatively referred to the prosauropod *Yunnanosaurus*, from the Early-Jurassic Lower Lufeng Formation of Yunnan (China), also present large wear facets along their mesial and distal edges [17,39]. However, referral of these teeth to *Yunnanosaurus* is very doubtful and they are best identified as Sauropoda as well [1].

### 2.2.2. Prosauropoda indet. (Fig. 5)

The crown of IRSNB R212 is labio-lingually compressed, higher than long, and slightly recurved back-



Fig. 5. Prosauropoda indet. (IRSNB R212), lingual view.

Fig. 5. Prosauropoda indet. (IRSNB R212), vue linguale.

wards and inwards. Both carinae bear about 15 coarse denticles, set at about  $45^\circ$  to the edges. The labial side of the crown is smoothly convex mesio-distally, whereas depressed areas separate the carinae from the middle part of the crown on the lingual side of the crown. The enamel is wrinkled on both sides. The tip of the crown bears a small rounded abrasion facet. Crown and root are not separated by a marked constriction. The root is elliptical in cross-section.

Similar teeth have been described in the Upper Triassic of Saint-Nicolas-de-Port, in northeastern France [5,11,20]. They closely resemble the teeth of a number of prosauropods, such as *Plateosaurus*, which is common in the Late Triassic of Germany, Switzerland, France and Greenland [16,18,27,36]. The recurvature observed in IRSNB R212 indicates that it is probably a premaxillary tooth [1]. The enamel of prosauropod teeth is usually smooth and a wrinkled texture, as observed on IRSNB R212, is regarded as synapomorphic for Eusauropoda [47]. However, it is very unlikely that IRSNB R212 is a eusauropod premaxillary tooth, because it has a very typical prosauropod general morphology [1,17]. It is therefore tentatively referred to Prosauropoda indet., pending further evidence.

### 2.3. Theropoda

The following teeth closely resemble those of theropod dinosaurs: they are caniniform, recurved backwards and their carinae bear serrations. However, it must be noted that, in Late Triassic times, such a dental morphology can also be observed in several independent lineages of Late Triassic Archosauriformes [20]. For that reason, they are herein referred to as Theropoda indet.

#### 2.3.1. Theropoda indet. morphotype 1 (Fig. 6)

Several shed teeth of this morphotype have been found at Habay-la-Vielle. IRSNB R213 is by far the largest and best preserved of the series. The crown is caniniform, curved backwards and strongly compressed labio-lingually. The lingual side is slightly more convex than the labial one. The distal carina bears well-developed rectangular serrations (around 5 per millimetre) all along the height of the crown. The serrations are perpendicular to the carina. The mesial carina forms a cutting edge near the apex of the crown and gradually becomes rounded towards the root. Serrations are present along the apical two thirds of the mesial edge; they are slightly smaller than the distal serrations. The enamel is not smooth, but gently wrinkled on both sides of the crown.

Such teeth closely resemble those of the ceratosaur *Liliensternus liliensterni* [25], from the Late Norian of Germany, by their size and shape, but also by the density and distribution of the serrations [36]. A tooth

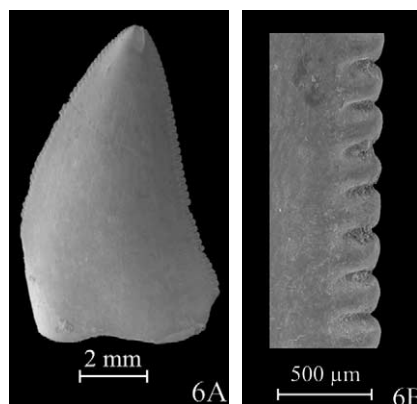


Fig. 6. Theropoda indet. morphotype 1 (IRSNB R213), A: lateral view, B: detail of distal serrations.

Fig. 6. Theropoda indet. morphotype 1 (IRSNB R213), A: vue latérale, B: détail des crénelures distales.



Fig. 7. Theropoda indet. morphotype 2 (IRSNB R214), **A**: detail of distal serrations, **B**: lateral view.

Fig. 7. Theropoda indet. morphotype 2 (IRSNB R214), **A** : détail des crénelures distales, **B** : vue latérale.

referred to as *Liliensternus airelensis* from the Hettangian of Normandy (France) differs from the Habay-la-Vieille specimens by its smooth enamel [9]. Very similar teeth, with wrinkled enamel, were also discovered in the Late Triassic of Saint-Nicolas-de-Port [5,11,20]. Definitive attribution of such isolated material to *Liliensternus* would be very hazardous, because similar tooth morphology may be observed in other ceratosaurids [7,34,46], as well as in other Late Triassic Archosauriformes [20].

### 2.3.2. *Theropoda indet. morphotype 2* (Fig. 7)

Two specimens significantly differ from the typical *Liliensternus* morphotype teeth described above. They are more slender, less compressed labio-lingually and less recurved backwards. The serrations on the distal carina are minute (12–15 serrations per millimetre). There is no trace of serrations on the well-developed mesial carina.

## 3. Discussion

Although dinosaur remains are rare at Habay-la-Vieille, they appear well diversified, suggesting that the major dinosaur groups were well established in Europe since the end of the Triassic. The small size of the dinosaur fossils collected at Habay-la-Vieille prob-

ably has a taphonomic rather than an ecologic explanation. The vertebrate assemblage from this locality is a mixture of terrestrial and marine forms. The marine vertebrates are by far dominant within the Habay-la-Vieille bonebeds, represented to date by several thousands fossils of all sizes. Although very diversified, the terrestrial component of the bonebeds represents only a few percents of the recovered specimens. All the fossils of terrestrial vertebrates are of small size. Such vertebrate assemblage is characteristic for littoral or subtidal deposits, as also suggested by sedimentological studies of the locality [2,33]. The bones and teeth of terrestrial animals were probably transported over a relatively long distance, leading to a preferential grading of the smaller elements.

Small ornithischian dinosaurs are known from Carnian and Norian deposits in North and South America [26]. In Europe, isolated ornithischian teeth are known from several other Late Norian-Rhaetian localities in Württemberg (Germany: '*Plateosaurus ornatus*' [24]), eastern France [20] and Luxembourg [10]. It has been supposed that the diversifications of the ornithischians were related to the extinction of other low-browsing herbivores, such as aetosaurs, at the end of the Triassic [26]. However, ornithischians, although already diversified from the Latest Triassic, remain rare till the Middle Jurassic, so that the extinction of primitive low-browsing herbivorous archosaurs and the rise of the ornithischians are not really synchronous.

The study of isolated sauropodomorph teeth from Habay-la-Vieille substantiates that sauropods were already present in Western Europe at the end of the Triassic. They co-existed with prosauropods, but occupied different ecological niches. Whereas sauropod teeth are adapted for an herbivorous diet [42], the morphology of prosauropod teeth rather indicates an omnivorous diet [1]. A tooth with two well-defined wear facets was previously described in the Upper Norian or Rhaetian of Saint-Nicolas-de-Port (Lorraine, France), suggesting the presence of a sauropod besides typical prosauropod remains [18]. *Blikanasaurus cromptoni*, from the Upper Norian or Rhaetian of South Africa, is now regarded as the most plesiomorphic sauropod dinosaur [43]. *Isanosaurus attavipachi* is a Late Norian or Rhaetian sauropod from Thailand [4]. This indicates that sauropods already had a wide geographic distribution by Latest-Triassic times (western Europe, South Africa and Thailand) and that they

must have had a relatively long, although nearly completely unknown, evolutionary history during the Late Triassic, as previously suggested by calibrated phylogenies of Sauropoda [41,43,47].

The study of Late Triassic dinosaur teeth is especially frustrating because of the impossibility for detailed determinations based on such an incomplete material. However, it produces accurate information about the real dinosaur biodiversity during this period. For that reason, it is disappointing that the search for dinosaur and other vertebrate micro-remains has not been systematically attempted to date in Late Triassic terrestrial deposits outside western Europe and North America. This would be particularly welcome in Gondwana, where small Mesozoic tetrapods are under-represented in fossil collections.

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