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THE FIRST SPHENODONTIAN REMAINS (LEPIDOSAUROMORPHA, REPTILIA) FROM THE LATE TRIASSIC OF THE GAUME (SOUTHERN BELGIUM)

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ABSTRACT. Two small dentary fragments from bone beds HLV2 and HLV3 (Sables de Mortinsart, Rhaetian, Late Triassic) are described and identified as cf. *Diphydontosaurus* sp. and *Clevosaurus* sp. These are the first records of sphenodontian reptiles from the Belgian Triassic.

KEYWORDS: Sphenodontia, Rhaetian, Belgian Lorraine.

RESUME. Deux petits fragments de dentaires provenant d'Habay-la-Vieille (bone-beds HLV2 et HLV3, Sables de Mortinsart, Rhétien, Trias supérieur) sont décrits et identifiés comme *Diphydontosaurus* sp. et *Clevosaurus* sp. C'est la première fois que des reptiles sphénodontes sont mentionnés dans le Trias belge.

MOTS-CLES: Sphenodontia, Rhétien, Lorraine belge.

1. INTRODUCTION

The sphenodontians are a group of diapsid reptiles which were particularly diverse in the Late Triassic. The earliest representative is possibly *Palacrodon* Broom from the Early Triassic of South Africa, and the latest is *Sphenodon*, the living Tuatara, now extant on a few small islands off New Zealand. Many gaps exist in the fossil record; none have been recorded from Tertiary rocks, and records in the Jurassic and Cretaceous are relatively sparse. It is believed that the decline in sphenodontian diversity is probably due to competition with lizards (Evans & Fraser, 1990).

Occasional highly fossiliferous sediments infilling fissures in British Late Triassic palaeokarst have provided large quantities of disarticulated sphenodontians (Evans, 1980, 1981 ; Fraser, 1986, 1988 ; Whiteside, 1986 ; Fraser & Duffin, in preparation). Indeed, the bulk of our knowledge of the group has issued from the study of these faunas. Such concentration lagerstätten have generally proved very difficult to date (see Fraser, 1986 for an outline discussion of the problems involved).

The Late Triassic and Early Jurassic record of the group is summarised in Table 1 for ease of reference (named material only).

2. GEOLOGICAL BACKGROUND

Habay-la-Vieille is a small village 7.5 km WNW of Arlon in the Gaume region of south east Belgium. In this area, Mesozoic rocks are banked up against the Paleozoic strata which form the Ardennes. The Triassic rocks of the area were mapped for the Belgian Geological Survey by Jérome (1910) following earlier work by Dumont (1849) and Dormal (1894). Maubeuge (1954) gave a valuable summary, noting an «excellent section» in the railway cutting at Habay-la-Vieille in which variegated Keuper marls with dolomitic nodules pass through a complete arenaceous «Rhaetic» succession (almost 9 m thick) to Hettangian limestones (see also Joly, 1908 ; Maubeuge, 1955 ; Keppens, 1972).

The construction of the E25/E411 motorway from Liège to Arlon necessitated new cuttings in Triassic

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Taxon	Formation	Age	Locality	Material
un-named	Dockum	Late Triassic	USA	dentary + maxilla
Gephyrosaurus bridensis	fissure infill	?Late Hettangian - Early Sinemurian	South Wales	Disassociated skull and postcranial remains
Brachyrhinodon taylori	Lossiemouth Sandstone	?Norian	Elgin, Scotland	Skulls and postcranial material
Polysphenodon mulleri	borehole	Carnian - Lower Norian	Hannover, N. Germany	Skull, limbs and vertebrae (casts)
Diphydontosaurus avonis	fissure infill	Penarth Group, Rhaetian	West of England, Belgium	Disassociated skull and postcranial remains
Planocephalosaurus robinsonae	fissure infill	Late Triassic	Cromhall, West of England	Disassociated skull and postcranial remains
Sigmala sigmala	fissure infill	Late Triassic	Cromhall	jaws
Pelecymala robusta	fissure infill	Late Triassic	Cromhall	maxillae
Pelecymala?	fissure infill	Late Triassic	Cromhall	dentary + ?palatine
Clevosaurus hudsoni	fissure infill	Late Triassic	Cromhall	complete skeletons
Clevosaurus minor	fissure infill	Late Triassic	Cromhall	palatine + maxilla

Table 1. Summary of the Late Triassic and Early Jurassic record of fossil sphenodontian reptiles.

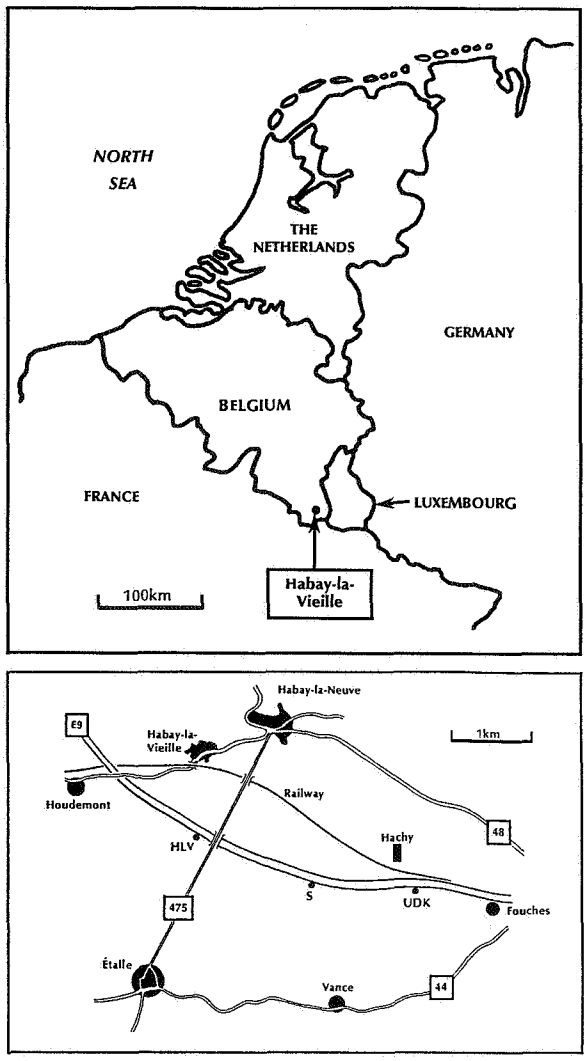

Figure 1. Sketch map to show the location of localities cited in the text.

strata adjacent to Hachy and 750 m south of the Habay-la-Vieille railway cutting in the early 1980's. The sequence comprises 10 to 11 m of sands and intercalated clays showing a variety of bedding features. A detailed stratigraphic log with facies analysis and granulometric study has been compiled by Bock (1980). A section collated from data recorded by Bock, and incorporating measurements made by Jean-Claude Lepage (†) and the present author at different stages in the excavation of the cutting is given in Text-figure 2.

The Sables de Mortinsart contain *Rhaetavicula contorta* (Portlock) which has been (wrongly) taken as an indicator of Rhaetian age (see Pearson, 1970)(Wouters, Sigogneau-Russell & Lepage, 1984). Samples collected by the present author from the clays 2 m above the topmost dolomitic horizon of the Marnes à Marnolites (? Steinmergel, Norian) were processed and examined for palynomorphs. The assemblage confirms a Rhaetian age (Warrington, written communication) as currently defined, and suggests an horizon roughly equivalent to the Westbury Formation or low down in the Cotham Member (Lilstock Formation) of the Penarth Group (British «Rhaetic»).

The littoral character of the Belgian «Rhaetic» is clear (Maubeuge, 1954) and Joly (1907) has given a faunal analysis, which must not be considered exhaustive (Maubeuge, 1954:394).

Georges Wouters (†), Jean-Claude Lepage (†), Paul Coupatez and Dominique Delsate, with others

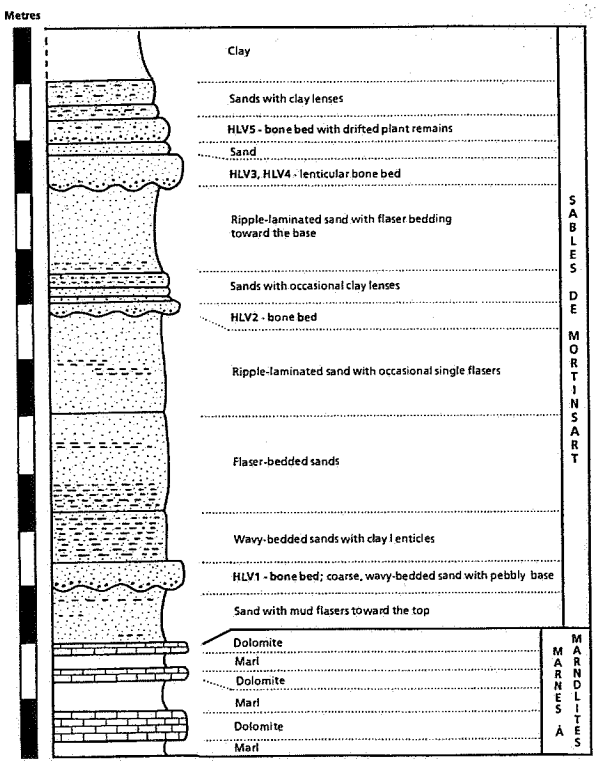

Figure 2. Stratigraphic log of the «Rhaetic» section at Habay-la-Vieille, Belgium.

(including the present author), sampled bone beds throughout the sequence at three main sites (Text figure 1):

1. HLV - 875 m south of Habay-la-Vieille.
2. S - 100 m north of Sagnette and 1.6 km WSW of HLV.
3. UDK - 100 m SW of Unter der Kirche, Hachy and 1 km west of S.

The locations are identified by letters, as above, and this notation has been employed in earlier papers on the haramiyids, cynodonts and multituberculates from the section (see literature listed below). The section is no longer available.

The sediments were washed and screened, the vertebrate remains concentrated by the interfacial method of Freeman (1982) and the residue picked using a binocular microscope.

Preliminary faunal lists for these samples were given by Duffin *et al.* (1983), and some specimens were figured by Delsate & Lepage (1991). Detailed description of the fish remains is in preparation. The vertebrate faunal assemblage is closely similar to that obtained from Attert (see discussion in Duffin & Delsate, 1993) and confirms a Rhaetian age for the deposit.

The presence of drifted plant remains in the higher parts of the sequence testifies to the proximity of upland areas, making the localities possible candidates for Mesozoic mammals and terrestrial reptiles. Careful searching, largely by Jean-Claude Lepage (†), has yielded teeth of the haramiyids *Haramiya fissurae* (Simpson) (Wouters, Sigogneau-Russell & Lepage, 1984), the cynodonts *Lepagia gaumensis* Hahn, Wild & Wouters (1987), *Gaumia longiradicata* Hahn, Wild & Wouters (1987), *Gaumia* ? *incisa* Hahn, Wild & Wouters (1987), *Microscalenodon nanus* Hahn, Lepage & Wouters (1988) and *Pseudotriconodon* sp., plus the multituberculate *Mojo usuratus* Hahn, Lepage & Wouters (1987).

The purpose of this paper is to report 2 sphenodontian dentary fragments from Habay-la-Vieille.

3. SYSTEMATIC PALAEONTOLOGY

Class Reptilia Laurenti, 1768
Subclass Diapsida Osborn, 1903
Infraclass Lepidosauromorpha Benton, 1983
Order Sphenodontia Lydekker, 1888
Family Sphenodontidae Cope, 1869
Genus *Diphydontosaurus* Whiteside, 1986

Type species : *Diphydontosaurus avonis* Whiteside (1986).
Genoholotype : BU 23760, an isolated right dentary (Bristol University).
Diagnosis : (after Whiteside 1986:383-4). Small sphenodontian with a partially pleurodont marginal dentition, teeth present on palatine, pterygoid and vomer. Enlarged lateral tooth row on vomer. Teeth on the anterior half of the maxillary tooth row pleurodont. Teeth on the posterior half of the maxilla acrodont, the anterior of these showing an alternation in size. Premaxilla with pleurodont teeth. Articular, prearticular, surangular and possibly angular form fused unit. Dentary with long posterior process. Meckelian fossa narrowed in mid-region by dentary. Teeth on the anterior and mid-region of the dentary tooth row pleurodont. Posterior teeth of dentary tooth row acrodont with the anterior of these alternating in size.

cf. *Diphydontosaurus* sp.
Text-figures 3a-d

Material : 1 specimen ; BM(NH) R 12711, an isolated fragment from the posterior region of the left dentary.

Locality : Road cutting (E25/E411; Liège-Luxembourg), 1.6 km south of Habay-la-Vieille, Province of Luxembourg, southern Belgium.

Topographic map : Arlon 68. Grid reference 890 096. Longitude 5°37'E, latitude 49°44'N. See Text-figure 1.

Horizon : HLV2, 6 m above the base of the Sables de Mortinsart. See Text-figure 2.

Age : «Rhaetic», Late Triassic.

Lithology : conglomeratic bone bed.

Description of R 12711

The specimen is a partial left dentary bearing one complete tooth. The total length of the fragment is 4.64 mm, the total height measured at the tooth is 1.8 mm, and the maximum labiolingual width is 0.68 mm. The lack of foramina for the cutaneous branches of the alveolar nerve on the outer face of the bone suggests that it originates from a mid or posterior part of the jaw. In occlusal view, the specimen is slightly arcuate.

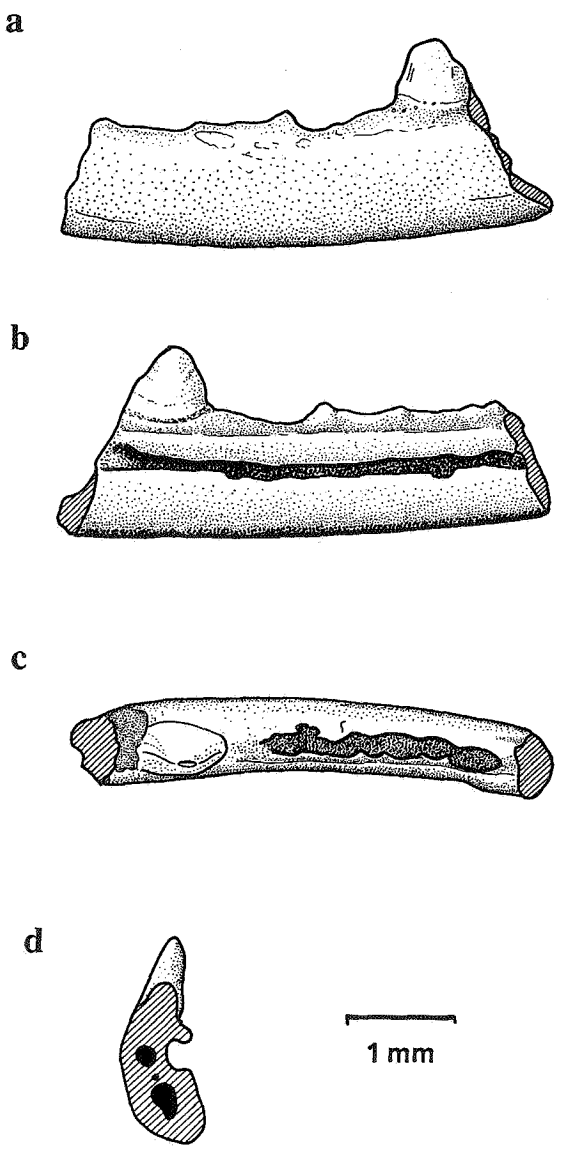

Figure 3. BM(NH) R 12711, a fragmentary dentary of ? *Diphydontosaurus* sp. from HLV2, Sables de Mortinsart (Late Triassic) of Habay-la-Vieille, Belgium.
a, labial view ; b, lingual view ; c, occlusal view ; d, transverse section.

The tooth is upright with a fairly narrow base (0.8 mm) and ankylosed to the labial crest of the jaw. Very small anterior and posterior flanges are developed, each bearing a small wear facet. The tooth is laterally compressed and has no ridge or shoulder basally. The tooth axis slightly inclined anteriorly. A few small vertical ridges are present on the labial face of the tooth.

There is space for a further four teeth on the dentary fragment anterior to the tooth described above. The elliptical bases of at least two such teeth, each of which would have been acrodont, can be seen in occlusal view (text-figure 3c). By comparison with Whiteside (1986), such acrodont teeth are further evidence of the posterior position of the jaw fragment. There is no sign of replacement pits on any of the tooth bases.

Irregularities in the upper marginal region of the outer face of the bone probably represent abraded wear marks produced by contact by the maxillary teeth during occlusion (Text-figure 3a). The Meckelian groove is open for the entirety of its preserved length, but becomes slightly shallower anteriorly (Text-figure 3b). The inferior alveolar canal, which would have carried the chorda tympani nerve, internal mandibular nerve, mandibular artery, and (anteriorly) the mandibular vein, can be clearly seen in the broken surface caudad (Text-figure 3d).

Discussion of affinities

The Belgian dentary is unlike those of *Planocephalosaurus*, *Sigmala* and *Clevosaurus* in both proportions and characters of the dentition. The specimen from Habay-la-Vieille is quite shallow, while dentaries of *Planocephalosaurus*, *Sigmala* and *Clevosaurus* are relatively deep. Furthermore, these genera show closure of the Meckelian groove anteriorly, and possess acrodont teeth ankylosed to the crest of the dentary both labially and lingually. This contrasts with the condition in the British material of *Diphydontosaurus* in which the teeth are ankylosed to the jaw only on the labial side, and an open Meckelian groove for the full length of the dentary.

The shallow groove running ventral to the teeth on the Belgian specimen is present to some extent in both

Planocephalosaurus and *Diphydontosaurus*, and probably marks the remains of the anterior shelf which supported anterior pleurodont teeth. Anterior teeth in *Planocephalosaurus* are semi-acrodont with a deeply recessed lingual base sitting on a reduced anterior shelf, while posterior teeth are located on the mandibular crest. The lingual base of the tooth is lower than that of the labial base in R 12711, indicating affinity with posterior teeth of *Diphydontosaurus*, in which the anterior 17 teeth are pleurodont and the posterior 8 are acrodont. *Gephyrosaurus* has a fully pleurodont dentition (Evans, 1980).

The tooth on the Belgian specimen is much more laterally compressed than those of *Sigmala* or *Pelecymala*, as is the dentary as a whole. In occlusal view, R 12711 describes a gentle arc (Text-figure 3c). This contrasts with the robust, straight central section of an overall sinusoidal mandibular flexure *Sigmala sigmala* (Fraser, 1986). Furthermore, the upright nature of the Belgian tooth contrasts with the recurved teeth with expanded bases in *Pelecymala robustus* (Fraser, 1986).

The dentary is therefore provisionally identified as cf. *Diphydontosaurus* sp.

Genus *Clevosaurus* Swinton, 1939

Type species : *Clevosaurus hudsoni* Swinton (1939).

Diagnosis : (teeth and jaws only, summarised from Robinson, 1973). Dentition acrodont. Small teeth in rows on vomer and pterygoid ; on palatine a single row of 4 to 6 large teeth, parallel to maxillary teeth, flanked by a single tooth mesial to the most anterior member of the palatine row. Premaxillary teeth variable ; 3 in smaller individuals, chisel-shaped and slightly bicuspate in larger individuals. Up to 10 smaller, slightly obtuse conical teeth on the maxilla, followed by 4 larger obtusely conical teeth with a prominent flange on the posterior face of the crown. Dentary bears up to 11 small anterior teeth, all but the anterior 4 showing alternating size ; these are followed by 4 large obtusely conical teeth, the first 3 of which have a large anterolabial and a small posterior flange, the fourth having a single anterior flange.

Clevosaurus sp.
Text-figures 4a-e

Material : 1 specimen; BM(NH) R 12712, an isolated , heavily worn dentary fragment.

Locality : Road cutting (E25/E411; Liège-Luxembourg), 1.6 km south of Habay-la-Vieille, Province of Luxembourg, southern Belgium. Topographic map : Arlon 68. Grid reference 890 096.

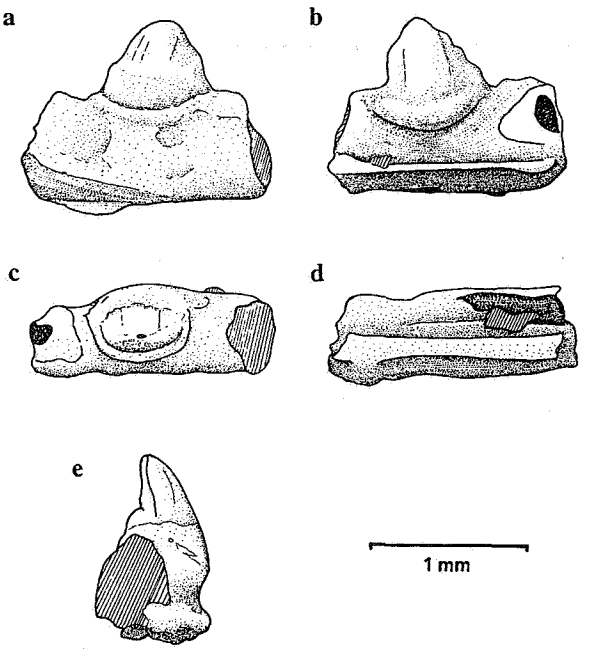

Figure 4. BM(NH) R 12712, a fragmentary dentary of *Clevosaurus* sp. from HLV3, Sables de Mortinsart, Late Triassic of Habay-la-Vieille, Belgium.
a, labial view ; b, lingual view ; c, occlusal view ; d, inferior (basal) view ; e, posterior view.

Longitude 5°37'E, latitude 49°44'N. See Text-figure 1.

Horizon : HLV3, 8.1 m above the base of the Sables de Mortinsart. See Text-figure 2.

Age : «Rhaetic», Late Triassic.

Lithology : lenticular bone bed.

Description of R 12712

This specimen (Text-figure 4) is an isolated dentary fragment with one complete tooth and one tooth base situated on the dorso-medial border. It is believed to be derived from the posterior to mid-region of the dentary because of the absence of foramina for the cutaneous branches of the alveolar nerve on the outer face of the bone, and because of its moderate depth. The total length of the fragment is 1.57 mm, the total height measured at the tooth is 1.15mm and the maximum labiolingual width is 1.80 mm. The fragment is considerably rolled and abraded with some evidence of pressure solution over the bone surface. The lingual shelf which overlies the Meckelian groove remains, but the lower part of the bone has been lost ; only the roof of the Meckelian groove remains.

The tooth is fairly upright, but has slight medial inclination in (presumed) posterior view (Text-figure 4e), and the tooth axis is slightly angled posteriorly. The tooth is 0.58 mm high and has quite a long base (0.69 mm). The cusp is not sharply pointed and has

been subject to a certain amount of wear. Wear facets from occlusal contact with the corresponding maxillary teeth are developed on the anterior and posterior parts of the labial face of the tooth, forming two small flanges. The tooth base is slightly expanded labially and surmounted by a low horizontal ridge.

The tooth is acrodont, sitting on top of the labial wall of the dentary, to which it is ankylosed Text-figure 4a). Lingually, the base of the tooth sits on a poorly developed lingual shelf (Text-figure 4b).

Discussion of R 12711

The presence of an acrodont tooth distinguishes this specimen from *Gephyrosaurus*. Having lost the ventral part by breakage, the dentary must have been fairly deep when complete, contrasting with the more shallow condition typical of *Diphydontosaurus*. This suggests that the affinities of the specimen are more likely to lie with *Clevosaurus*, *Pelecymala* or *Sigmala*. This is further confirmed by the presence of wear facets on the tooth indicating precise occlusal relations with opposing maxillary teeth. Mature sphenodontians often show deep occlusal grooves penetrating the labial surface of the dentary itself and indicative of a precise shearing action with no propalinal jaw movement.

R12712 cannot belong to *Pelecymala* which has much more labiolingually expanded tooth bases (Fraser, 1986). Anterior and posterior flanges are only weakly developed in the Belgian specimen. This recalls the condition in *Sigmala*. However, juvenile and hatchling teeth in *Clevosaurus* lose their flanges by wear. The absence of secondary bone and the development of only weak wear facets suggests that the Belgian specimen is from a juvenile. The presence of the ridge or shoulder toward the base of the tooth is typical of *Clevosaurus*.

Two species of *Clevosaurus* have been described : *C. hudsoni* Swinton and *C. minor* Fraser. Fraser (1988:161) comments that the dentaries of these 2 species are indistinguishable except on the basis of size and that, at localities where they occur together, «an exceptionally large individual of *C. minor* could be mistakenly assumed to be *C. hudsoni*». Owing to the small size and incomplete nature of the specimen, plus the fact that it comes from a juvenile, it is impossible to make a confident assignation to species level.

4. CONCLUSIONS

The specimens described above are the first records of Belgian Late Triassic lepidosauromorph reptiles.

Sphenodontian remains are relatively common in Late Triassic karstic fissure infills from the West of England and South Wales. They inhabited an archipelago of small islands made up of Palaeozoic rocks. *Diphydontosaurus* is known from 2 fissure deposits at Tytherington Quarry (Avon) and Cromhall Quarry (also known as Slickstones Quarry) in Gloucestershire (Whiteside, 1986). Non-reworked palynomorphs and occasional fish remains in the sediment surrounding sphenodontian remains from Tytherington suggest a late Westbury Formation age (Lower Rhaetian) (Whiteside, 1983, 1986).

The record of *Diphydontosaurus* from Cromhall Quarry has been taken by Fraser & Walkden (1983, 1984) to be Late Norian on the basis of lithological similarity with the Mercia Mudstone Group (Red Keuper Marls and Tea Green Marls) and in the absence of palynomorphs. Whiteside (1986) has argued that the Cromhall record is also more likely to be equivalent to the Westbury Formation on the basis of accompanying specimens of *Pholidophorus*, known only from the «Rhaetic» and younger deposits in Britain.

Clevosaurus accompanies *Diphydontosaurus* in fissure faunas at Tytherington and Cromhall and is also present in the collection of vertebrates made from the Holwell fissure filling in the Mendips by the Victorian collector Charles Moore (Fraser & Duffin, in preparation). At Holwell, the accompanying fauna is strongly in favour of a Penarth Group age for the sediments.

The records of ? *Diphydontosaurus* and *Clevosaurus* sp. from the Belgian «Rhaetic» provides useful confirmatory evidence in favour of a «Rhaetic» rather than Norian date for the British fissure faunas.

Sphenodontian bones are quite fragile and easily broken during transportation. Post-mortem damage to the Belgian specimens testifies to this fact and the presence of pressure solution features on R 12712 suggests that they may have lain within unconsolidated sediment for some time.

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