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A LATE TRIASSIC CYNODONT FROM HOLWELL QUARRIES (SOMERSET, ENGLAND)

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Abstract : The presence of the dromatheriid cynodont *Pseudotriconodon wildi* is reported from the Rhaetian of Great Britain in the fissure deposits at Holwell Quarries. The British Rhaetic cynodont fauna, although consisting only of one dromatheriid tooth, one tooth of *Tricuspes*, and one tritylodontid fragmentary jaw, is similar to that found in the Germanic Realm. It appears to be the remnant of a fauna that covered all of Western Europe before the fragmentation of its habitat due to the Rhaetian transgression.

Keywords : Cynodontia, Triassic, Rhaetian, Great Britain, Europe.

**Un cynodonte dans le Trias supérieur des carrières d'Holwell
(Somerset, Angleterre)**

Résumé : La présence du cynodonte *Pseudotriconodon wildi* est signalée dans des remplissages de fissures rhétiens des carrières d'Holwell, en Angleterre. La faune de cynodontes du Rhétien d'Angleterre, bien que connue uniquement d'après une dent de Dromatheriidés, une dent de *Tricuspes*, et un fragment de mâchoire de Tritylodontidés, est similaire à celle trouvée à la même époque en Europe continentale dans le bassin germanique. Il s'agit probablement des restes d'une faune plus ancienne qui couvrait l'ensemble de l'Europe avant que celle-ci ne soit fragmentée en plusieurs îles par la transgression rhétienne.

Mots clés : Cynodontia, Trias, Rhétien, Europe, Grande-Bretagne.

INTRODUCTION

The fissure fillings at Holwell quarries have yielded one of the most diverse fauna from the British Rhaetian, including hybodont and neoselachian sharks (Duffin, 1998a, b), actinopterygians, placodonts (Moore, 1859, 1861; Kühne, 1946; Duffin, 1978; Storrs, 1999), choristoderes (Storrs *et al.*, 1996, Storrs, 1999), sphenodontians (Benton & Spencer, 1995), trytilodontids (Savage & Waldman, 1966; Savage, 1971), morganucodontids, and haramiyids (Kühne, 1946; Parrington, 1946; Butler & McIntyre, 1994; Storrs, 1994). Victorian geologist Charles Moore (1859, 1861, 1862, 1864, 1867) was the first to study these fissures, set in quarries that are now closed. The Charles Moore collection was deposited at the Bath Royal Literary and Scientific Institution (BRLSI) in 1881 after his death but, unfortunately, it has suffered from neglect following the closure of this institution from 1940 to 1968. In 1998, I had the opportunity to visit the BRSLI and to study the tooth C108 mentioned by Clemens (1980). However, I was unable to locate the tooth of *Tricuspes* from the Rhaetian of Vallis Vale figured by Huene (1933, see also Clemens, 1980).

LOCALITY

The village of Holwell (ST727452) had two large quarries, one to the North and one to the South, working the Clifton Down Limestone Group of Carboniferous Limestones (Viséan, Early Carboniferous) on the southern flank of the Beacon Hill pericline in the Mendip Hills of Somerset. A good description of the geology of these quarries can be found in Savage & Waldman (1966). The limestones are vertically penetrated by fissures, which have yielded many vertebrate remains as well as molluscs and echinoderms (Kühne, 1946). However, the fissures studied by Moore and subsequently by Kühne are no longer exposed. Their vertebrate assemblages are of Rhaetian age (Storrs, 1994; Duffin, 1998a, b) and are massively dominated by fish remains. They have yielded 45,000 teeth of *Lissodus minimus* to compare with 29 mammalian teeth when Charles Moore was searching them (Savage, 1993).

By Triassic times, the Mendip Hills stood out as islands in the Early Mesozoic Sea. The fissures at Holwell correspond to neptunian dykes (Simms, 1994) probably covered by the sea; the sea floor sediment, with its fish remains, get swept into the fissure along with remains of terrestrial animals living close to the nearby shore-line and carried into the sea by flood waters (Savage, 1993). The sediments accumulated slowly over a long time span and there was probably rarely a direct opening to the surface. These sediments and fossil debris filtered down through a capping of rock debris (Simms, 1994). The concentrative mechanism in the Holwell fissures is therefore an abiotic allochthonous one (Simms, 1994).

SYSTEMATIC PALAEONTOLOGY

Order Therapsida Broom, 1905
Infraorder Cynodontia Owen, 1861
Family Dromatheriidae Gill, 1872
Genus *Pseudotriconodon*,
Hahn, Lepage & Wouters, 1984
Pseudotriconodon wildi Hahn,
Lepage & Wouters, 1984

The tooth C 108 is pentacuspid, elongated antero-posteriorly and compressed labio-lingually in apical view (Fig. 1). It is 2.0 mm mesiodistally (*contra* 1.6 mm according to Clemens, 1980) and 0.8 mm labiolingually. The ratio "length/width" is therefore 2.5. In mesial and distal view, the labial and lingual sides of the crown appear nearly straight and almost parallel to each other without any visible constriction at the base of the crown. All the cusps are in line with the antero-posterior axis of the crown and the cutting edge is therefore perfectly straight. The main cusp occupies a median position and has the outline of an isosceles triangle. The accessory cusplets are slightly asymmetric. The first pair is not well individualized from the main cusp. The second pair is very reduced,

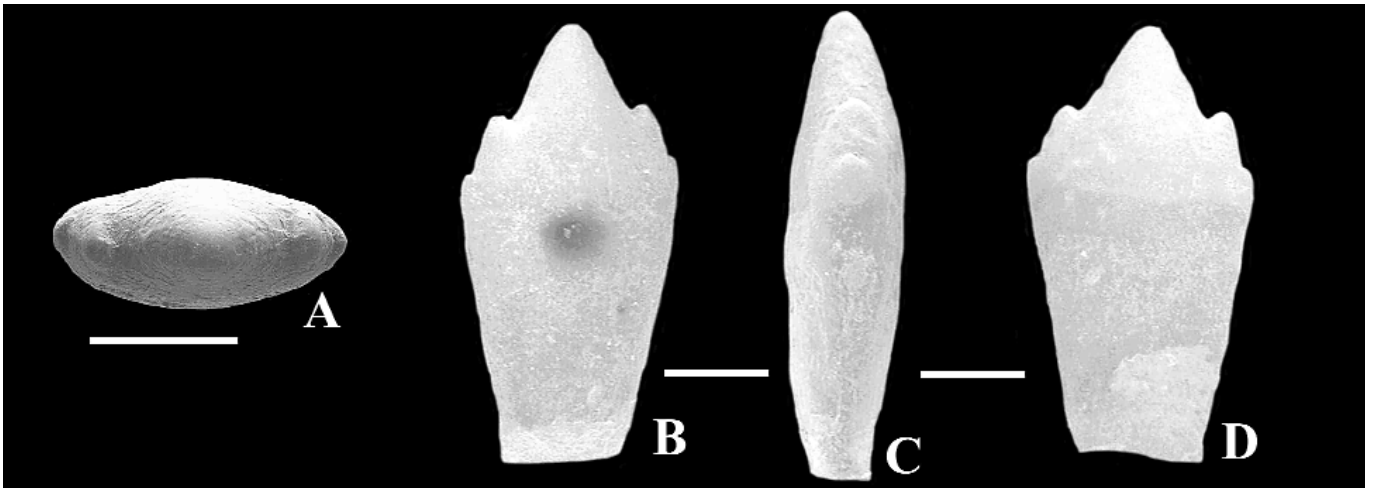

Fig. 1: Tooth (C 108) of *Pseudotriconodon wildi* from Holwell Quarries in A: apical, B: labial or lingual, C: mesial or distal, and D: labial or lingual views. All scale bars represent 1 mm.
Fig. 1: Dent (C 108) de *Pseudotriconodon wildi* des carrières d'Holwell en vues A: apicale, B: labiale ou linguale, C: mésiale ou distale, et D: labiale ou linguale. Toutes les barres d'échelle représentent 1 mm.

set on the labial and lingual edge of the crown. The vertical axes of the accessory cusps diverge slightly from that of the main cusp. The enamel is perfectly smooth.

There is a single root, semielliptical in outline, which is 1.8 mm high while the crown is only 1.3 mm high. The root is therefore 1.4 times as high as the crown. There is no furrow on the labial or lingual side of the root.

DISCUSSION

C 108 differs from the teeth of the pterosaur *Eudimorphodon* by being more compressed labiolingually with nearly parallel labial and lingual sides. The ratio "length/width" range from 1.79 to 2.32 in *Eudimorphodon* (Cuny *et al.,* 1995) while it is 2.5 in C 108. Small, strongly compressed pentacuspid teeth like C 108 are more reminiscent of those of Triassic cynodonts possessing a sectorial dentition. The absence of a constriction at the base of the crown differentiates C 108 from teeth of the genera *Tricuspes, Gaumia,* and *Lepagia* (Sigogneau-Russell & Hahn, 1994; Godefroit & Battail, 1997). Absence of such a constriction is also recorded in *Microconodon* (Osborn, 1886), but in this latter genus the root is apparently divided along its whole height by a slight furrow (Simpson, 1926), completely missing on C 108. Absence of subdivision of the root also separates C 108 from the teeth of *Dromatherium* (Godefroit & Battail, 1997). C 108 also differs from the teeth of *Hahnia obliqua* and *Meurthodon gallicus* by a straight main cusp, not curved toward the lingual or distal side (Godefroit & Battail, 1997), but its shape agrees perfectly with that of the teeth of *Pseudotriconodon wildi* from the Norian of Medernach (Luxembourg, Hahn *et al.,* 1984; Cuny *et al.,* 1995) and from the Norian/Rhaetian of Saint-Nicolas-de-Port (France, Godefroit & Battail, 1997). Its measurements are included in the variation observed in the teeth of *Pseudotriconodon wildi* from Saint-Nicolas-de-Port (Godefroit & Battail, 1997). These teeth are different from those of *Pseudotriconodon chatterjeei,* which possess distinct striations on the labial and lingual faces of the crown (Lucas & Oakes, 1988).

The genus *Pseudotriconodon* was hitherto restricted to Luxembourg (Norian, Medernach, *P. wildi,* Hahn *et al.,* 1984), Belgium (Rhaetian, Habay-la-Vieille, *Pseudotriconodon?* Sp., Hahn *et al.,* 1987), France (Norian/Rhaetian, Saint-Nicolas-de-Port, *P. wildi,* Godefroit & Battail, 1997), and New Mexico (Norian, Bull Canyon, *P. chatterjeei,* Lucas & Oakes, 1988). Its discovery in South West England, located between the Germanic Realm and North America, is therefore not surprising. However, it has to be noted that Sues & Olsen (1990) claimed that *P. chatterjeei* is not referable to this genus, but without argumentation. If these authors are right, then *Pseudotriconodon* is restricted to Western Europe and its record in Holwell is the most western one, which is true for the species *P. wildi* anyway. Its known stratigraphic distribution is restricted to the Norian-Rhaetian interval (Godefroit & Battail, 1997), which is in accordance with the Rhaetian age proposed for the fissure-fillings in Holwell (Storrs, 1994; Duffin, 1998a, b).

The only other cynodont remain from Holwell quarry is a jaw fragment of a Tritylodontidae *incertae sedis* (Savage & Waldman, 1966; Savage, 1971) found in 1961 in the North Quarry. Godefroit & Battail (1997), like Savage (1971) considered this record to be Early Jurassic in age. However, this jaw fragment was found together with a fish fauna not different from that found with the haramiyid teeth from Holwell (Savage & Waldman, 1966), and pointing towards a Rhaetian age (Duffin, 1998a, b; Storrs, 1994). It is unlikely that the tritylodontid jaw fragment from the North quarry came from the same fissure as the one that yielded the tooth of *Pseudotriconodon wildi* because most of the Moore's specimens appear to have been found in the South quarry (Kühne, 1946). The fish fauna associated with the cynodont and mammalian remains is however the same in the fissures from both the North and the South quarries, suggesting that both the Tritylodontidae and *Pseudotriconodon wildi* were leaving near the same time in the Mendip Hills. Tritylodontids were also present in the Germanic realm (Godefroit & Battail, 1997) and one of the three species identified in Germany, *Tritylodon fraasi,* is quite similar to the Holwell specimen (Savage, 1971). In the Rhätsandstein bone bed of Württemberg, Dromatheriidae (*Tricuspes tuebingensis)* were also coexisting with the Tritylodontidae (*Oligokyphus triserialis, Tritylodon fraasi, Chalepotherium plieningeri)* (Godefroid & Battail, 1997) like they did at Holwell.

Godefroit and Battail (1997) considered the Rhätsandstein assemblage as being intermediate between the typical late Norian - Rhaetian assemblages and the Liassic ones, mainly because of the presence of tritylodontids. The absence of *"Hybodus" minor* and the abundance of *Synechodus rhaeticus* (Duffin, 1998b) points towards a late Rhaetian age for the Holwell assemblage as *"Hybodus" minor* seems to be more abundant during the early Rhaetian than during the late Rhaetian, the reverse being true of *Synechodus rhaeticus* (Cuny *et al.,* 2000). Thus, the Holwell record of *Pseudotriconodon wildi*, in addition of being the most western one, may also be the youngest one.

The Rhätsandstein tritylodontids are currently considered the oldest members of this family, their age being probably not older than late Norian and not younger than early Hettangian (Godefroit & Battail, 1997). The presence of a closely related form of a similar age in Holwell leaves us with two possibilities concerning the origin and early history of this family:

1 - The tritylodontids appeared sometimes during the Rhaetian, whether in the Germanic Realm or in the British Isles, and managed to colonize several islands in Europe.

2 - The tritylodontids appeared in Europe prior to the Rhaetian transgression but were very rare, as indicated by their apparent absence from the late Norian - Rhaetian cynodont assemblages in Europe. This absence might be the result of a competition with the Haramiyidae (Godefroit & Battail, 1997). The separation of several populations between different islands during the Rhaetian transgression facilitated their subsequent radiation.

The association of these tritylodontids with Dromatheriids that are known prior to the Rhaetian transgression (*Pseudotriconodon wildi* at Medernach) or just at the beginning of the transgressive process (*Pseudotriconodon wildi, Tricuspes tuebingensis, T. sigogneauae, T. tapeinodon,* and *Meurthodon gallicus* at Saint-Nicolas-de-Port) favours the second hypothesis. The presence in Holwell of the hara-miyids *Thomasia moorei* and *Thomasia anglica*, both known in Saint-Nicolas-de-Port (Butler & MacIntyre, 1994) also reinforce the idea that the cynodont mammalian fauna of Holwell is the remnant of a fauna that once covered all of Western Europe (Sigogneau-Russell & Hahn, 1994). This is a more parcimonious hypothesis than to consider multiple colonization events from the Germanic Realm.

CONCLUSION

The cynodont fauna recovered from Holwell quarries, though currently represented by only two fossils, shows strong affinities with the cynodonts from the Germanic Realm. The Holwell fauna is probably the remnant of a cynodont fauna that lived all over Europe prior to the Rhaetian transgression and went unnoticed because of a lack of interest in Keuper vertebrate microremains (Sigogneau-Russell & Hahn, 1994). The species *Pseudotriconodon wildi* is indeed known in the Germanic Realm prior to the Rhaetian transgression at Medernach (Hahn *et al.,* 1984; Cuny *et al.,* 1995) where it was coexisting with two other genera of cynodont those stratigraphic distribution extends into the Rhaetian: *Gaumia* and *Tricuspes* (Godefroit & Battail, 1997). This supports the assertation made by Godefroit *et al.* (1998) that the European faunas consisting of small animals did not suffer from the Rhaetian transgression-induced diminution of the surface of the emerged land. On the contrary, the separation of several populations between different islands may have facilitated the radiation of a small cynodont and mammalian fauna. The Holwell fauna also indicates that the cynodont fossil record in the Upper Triassic of Great Britain is probably much richer than usually thought.

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