Bridgend Quarries, Glamorgan

[SS 895 760], [SS 899 765], [SS 902 768], [SS 906 757]

Introduction

The Glamorgan area has a selection of early Jurassic fissure infills preserved in Triassic karstic features in Carboniferous limestones (Figure 2.7). The fissure sediments have preserved a range of taxa, including sphenodonts and mammals (Benton and Spencer, 1995). Four quarries — Ewenny Quarry [SS 902 768], Duchy Quarry [SS 906 757], Pont Alun (or Pontalun or Lithalun) Quarry [SS 899 765] and Pant Quarry [SS 895 760] — have produced four mammalian genera (Kermack *et al.*, 1973; Clemens, 1986).

The first record of Welsh mammal fossils from cave fissure deposits was made in the late 1940s by Walter Kuhne (Robinson, 1957). The first description (Kuhn, 1949b) was of the type specimen of *Morganucodon watsoni*, based on a single lower molar (Kermack *et al.*, 1973). Since then many more specimens have been recovered, thanks to extensive collecting in the 1950s, 1960s and 1970s by Kenneth Kermack, Frances Mussett and Pat Lees.

The Bridgend Quarries GCR site comprises four localities that expose fissure infill sediments (Kermack *et al.*, 1981; Clemens, 1986) preserved in Carboniferous Limestone (Kermack *et al.*, 1973). The importance of these sites was first realized during the 1950s, when the low degree of mechanization ensured that removal of the fissure-fill sediments was by hand. The increasing use of heavy machinery in the exploitation of the limestones has meant that it is becoming increasingly difficult to excavate the fissure fills by hand (Kermack *et al.*, 1973), although new fissures yielding bone occasionally come to light (P.G. Gill, pers. comm., 2004).

Description

The cave fissures are developed in Carboniferous Limestone. The fissures take the form of narrow slots that follow the joint planes and are thought to represent immature solution features (Robinson, 1971). These slots are up to 1.0 m wide but are generally somewhat narrower (Kermack *et al.*, 1973; Evans and Kermack, 1994).

The sediments infilling the caverns and fissures range in composition from soft plastic clays to hard marls. A variety of sediment colours also have been recorded from the sites, including red, green, yellow and dark grey. Haematite grains and pebbles and plant (*Hirmeriella muensteri*) remains are common (Robinson, 1971; Kermack *et al.*, 1973; Evans and Kermack, 1994). The bone material ranges in colour from white to dark grey and brown, although white bone in a red matrix is most common. There is no evidence to suggest that the bones were reworked (Evans and Kermack, 1994).

Unlike many fissure-fill sites, the Bridgend Quarries sediments have been dated — on the basis of *Hirmeriella* (*Cheirolepis*) spores at Duchy, Pont Alun and Pant quarries — as Hettangian–Sinemurian in age (Evans and Kermack, 1994).

Fauna

The majority of the specimens preserved in the Bridgend Quarries fissures are attributable to the lepidosaur *Gephyrosaurus bridensis*. described by Evans (1980, 1981), and the remainder are mammalian. Fraser (1985) also noted 'unidentified archosaurs' from Pont Alun Quarry. *Oligokyphus, Thomasia,* archosaurs and sphenodontians have also been recorded from Pant quarry (Evans and Kermack, 1994).

MAMMALIA

Morganucodontidae

Morganucodon watsoni Kuhne, 1949b

?Morganucodon sp.
Kuehneotheriidae
Kuehneotherium praecursoris Kermack,
Kermack, and Mussett, 1968
?Kuehneotheriidae
"Kuhneon duchyense Kretzoi, 1960"
'Haramiyida'
Haramiyidae

Thomasia sp.

The dominant mammal is *Morganucodon watsoni* (Evans and Kermack, 1994), a shrew-sized insectivore with a skull 26 mm long (Figure 2.8). *Morganucodon* has a lower jaw composed mainly of the dentary bone; however, the jaw joint comprises contacts of both the dentary with the squamosal and the articular with the quadrate, the latter also functioning as a 'middle' ear. It also retained several remnants of other reptilian jaw bones, and in these respects it is more primitive than any modern mammal (Kermack *et al.*, 1973, 1981). The cheek teeth are divided into molars and premolars, a fully mammalian character, and tooth replacement appears to have been fully mammalian also, with a milk set and an adult set (reptiles replace their teeth many more times). The cheek teeth of *Morganucodon* occlude, and jaw movement was more complex than in advanced cynodont reptiles: it was rather triangular, with a certain amount of back-and-forwards movement, but a sideways component also. The skeleton of *Morganucodon* is incompletely known, but details of this portion of the anatomy are complemented by its relative *Megazostrodon* from Lesotho (Jenkins and Parrington, 1976). (Figure 2.8) The skull of the basal mammal *Morganucodon in lateral(a)* and dorsal (b) views. (After Kermack *et al.*, 1981.)

There has been some confusion concerning the use of the names *Morganucodon* 1949b, established for material from the Bridgend Quarries, and *Eozostrodon* Parrington, 1941, established for material from Hoiwell Quarries (see GCR site report). The former name was championed by Kermack and the latter by Parrington. Clemens (1979), in an attempt to attain nomenclatural stability, showed that the two were different at least at species level. He recommended that the name *Eozostrodon parvus* should be used only for the poorly known morganucodontid material from Holwell Quarries, and the name *Morganucodon* should be used for the more complete material from South Wales.

Kuehneotherium praecursoris is represented by isolated teeth and rare jaw fragments (Kermack *et al.*, 1968; Gill, 1974). Kuehneotherium was also a small insectivore, equipped with delicate three-cusped teeth. The occurrence of isolated teeth is explained by the fragile bones and tapering roots: the teeth fall out of the jaws easily, and once the teeth have been lost the jaw quickly fragments (Evans and Kermack, 1994). It is possible that the specimens of *Kuehneotherium* from Pant Quarry and Pont Alun Quarry are specifically different (Evans and Kermack, 1994).

The first tooth of a new group was noted by Kühne (1950) from Duchy Quarry as 'Duchy 33', identified at the time as a symmetrodont, (Cassiliano and Clemens, 1979). It was named *Kubneon duchyense* by Kretzoi (1960). Kermack *et al.* (1968), in describing *Kuehneotherium*, noted that their new genus was distinct from *Kuhneon* but that the original tooth on which the latter had been based was probably an upper not a lower molar and had since been lost. Their recommendation that *Kuhneon duchyense* be considered a *nomen vanum* is adopted here (P.G. Gill pers. comm., 2004).

The record of *Thomasia* is based on one tooth fragment from Pant (Kermack et al., 1981, p. 135).

Interpretation

Before the transgression of the Rhaetic Sea, the Vale of Glamorgan was an area of low-lying land with ephemeral freshwater playas. The Carboniferous Limestone formed low hills. The Rhaetic transgression flooded this low-lying plain, leaving the hills as small islands, including St Bride's Island south of Bridgend Quarries (Robinson, 1971; Kermack *et al.*, 1973; Simms, 1990). St Bride's Island was relatively small, with a maximum area of 20 km², and may have formed part of an archipelago. The palaeoclimate has been reconstructed as tropical/sub-tropical with heavy seasonal rains; the island lay at approximately 15°N latitude (Evans and Kermack, 1994). Continued subsidence eventually resulted in the complete submergence of the islands during the Sinemurian Stage (Kermack *et al.*, 1973).

Several theories have been put forward in order to account for the preservation of the vertebrate fossils in the Welsh fissures. The first suggests that the creatures were washed into the caves during periods of heavy rain. However, it is unlikely that this would so effectively concentrate the vertebrate remains. An alternative is that forest fires or flash floods killed large numbers of animals, which were washed into the fissures. These theories fail to account for the absence of invertebrates. Finally, the fossil assemblage may represent a predator accumulation. This hypothesis is supported by the patterns of bone damage and modification (for example, the tooth marks on the surfaces of some of the bones), the relative proportions of the bones preserved and the general small body size of the taxa represented (Evans and Kermack, 1994).

The two main mammal groups represented at Bridgend Quarries were once thought to document a major split in mammalian evolution, with the morganucodontids documenting the first prototherians, a group represented today by the monotremes. *Kuehneotherium*, by contrast, has three-cusped teeth that have an offset central cusp, allowing uppers and lowers to interlock because of their 'reversed triangle' pattern in crown view. This cusp pattern was considered to represent the first stage in evolution of complex occlusion, such as is found in typical therians. Thus, *Kuehneotherium* was seen as the first therian mammal, that is, a distant ancestor of marsupials and placentals.

More recent work, however, using only derived characters and studying more of the anatomy than just teeth, has produced a more complex phylogeny (reviewed by Benton, 2005). Indeed, current cladograms (e.g. Rowe, 1988, 1993; Wible *et al.*, 1995; Luo *et al.*, 2001, 2002) place the morganucodontids as second-most basal mammal group, with *Kuehneotherium* as third most basal (see Chapter 1). The sym-metrodonts, now recognized as polyphyletic occur scattered through the phylogenetic tree (Kielan-Jaworowska *et al.*, 2004)

Comparison with other localities

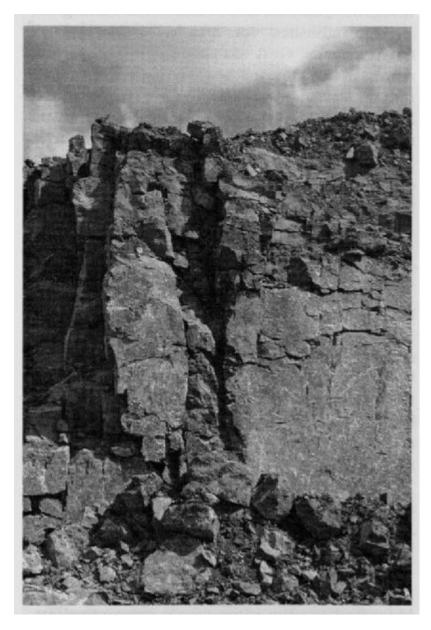
The faunas from the Bridgend Quarries are comparable in age to those preserved at Holwell Quarries and Windsor Hill Quarry. However, more taxa are represented, although there is little overlap between the faunas. This possibly reflects the increased opportunities for collecting provided by four quarries all within a small geographical area.

Morganucodon has also been described from the Rhaetic bone beds at Hallau, Kanton Schaffhausen, in Switzerland (Clemens, 1980). *Kuehneotherium* is known from Late Triassic sites at Emborough, Saint-Nicholas-de-Port, France (Godefroit and Sigogneau-Russell, 1999), Syren, Luxembourg (Godefroit *et al.*, 1998) and Jameson Land, East Greenland (Jenkins *et al.*, 1994).

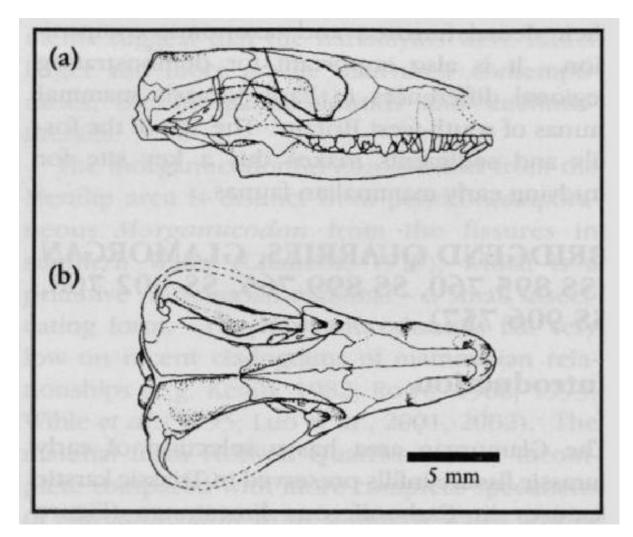
Conclusions

The Late Triassic–Early Jurassic Welsh fissure-fill sediments provide incomparable evidence about early mammal evolution. *Morganucodon watsoni* and *Kuehneotherium praecursoris* are unique basal mammals (Clemens *et al.*, 1979). The good degree of preservation and relative abundance of the mammalian remains has allowed detailed reconstructions of significant parts of the anatomy of these Early Jurassic mammals, and *Morganucodon*, together with the African *Megazostrodon*, are the most completely known early mammal fossils in the world. This is a key site of undisputed international Importance.

References



(Figure 2.7) Bridgend Quarries GCR site, Glamorgan. Example of an Early Jurassic fissure fill in the Carboniferous Limestone. (Photo: W.A. Wimbledon.) genera (Kermack et al., 1973; Clemens, 1986).



(Figure 2.8) The skull of the basal mammal Morganucodon in lateral (a) and dorsal (b) views. (After Kermack et al., 1981.)