Coten (Aka Coton) End Quarry, Warwick, Warwickshire

[SP 2900 6550]

Highlights

Coten End Quarry has produced the most diverse assemblages of fossil amphibians and reptiles in the English Midlands, including more than eight species. The reptiles range from lizard-sized plant-and insect-eaters to large carnivorous forms.

Introduction

This site consists of a small quarry within the town of Warwick which is currently used as a small-bore rifle range. It displays a section in the upper part of the Bromsgrove Sandstone Formation. The list of reptiles and amphibians from Coten End is large, and the site is the most productive for Mid Triassic tetrapods in the Midlands. It is the type locality for various species of temnospondyl amphibians as well as the reptiles *Bromsgroveia walkeri* Galton, 1985 and *Rhynchosaurus brodiei* Benton, 1990. Further quarrying would doubtless produce more reptile remains from the 'dirt bed', but the site is now surrounded by housing.

Coten End Quarry was worked in the early 19th century for building stone, and Murchison and Strickland (1840, p. 343) stated that it 'has been most productive in the remains of vertebrata'. Howell (1859, p. 40) described the Warwick Triassic in general terms, and Hull (1869, pp. 88–9) distinguished the Building Stones (Lower Keuper Sandstone) overlain by Waterstones containing the amphibians.

Murchison and Strickland (1840, pl. 28, figs 6–10) were the first to figure bones from Coten End which they identified as teeth of '*Megalosaurus',* and of a 'Saurian', as well as an unidentified vertebra. Owen (1841b) named one of the 'teeth' *Anisodon gracilis,* and later (Owen, 1842a, p. 535) he reinterpreted this specimen as the ungual phalanx (claw) of the temnospondyl amphibian *Labyrinthodon (Mastodonsaurus) pachygnathus.* He also examined the vertebra described by Murchison and Strickland, assigning it to the temnospondyl amphibian *L. leptognathus* (Owen, 1842a, pp. 523–4, pl. 45, figs 5–8). Both specimens have since been reidentified as rhynchosaur remains: a premaxilla (the 'tooth') and a dorsal vertebra (Benton, 1990c). Owen (1842c) described further jaw, skull and postcranial fragments from Coten End as pertaining to *L. leptognathus* and *L. pachygnathus* (now assigned to the genera *Stenotosaurus* and *?Cyclotosaurus* respectively; Milner *et al.,* 1990), and also gave an account of the microscopic anatomy of the teeth of *Mastodonsaurus* from Coten End and compared it with that of German Keuper forms. Later (1842d), he described skull fragments of various temnospondyls, including *M leptognathus* and *M. pachygnathus.* All of Owen's descriptions were based on the extensive collections by Dr Lloyd of Leamington.

In the 1840s and 1850s the Reverend P.B. Brodie and Dr Lloyd collected jaw bones of *Rhynchosaurus* from Coten End and these were described by Huxley (1869), who mistakenly ascribed them to the related form *Hyperodapedon* from Elgin. Huxley (1870a) also described supposed dinosaur remains from Coten End and redescribed many of Owen's Mastodonsaurus bones as probably dinosaurian. L.C. Miall (1874) agreed with these reassignments and described further remains of *Mastodonsaurus.* Huene (1908b) redescribed most of the supposed dinosaur material.

More recently, in a new phase of research on British Triassic vertebrates, Walker (1969) provided reidentifications of many of the archosaurs and other reptiles from Coten End (Figure 4.6) and Paton (1974a) revised the temnospondyls. Gallon (1985a) reviewed the archosaur material and named a new rauisuchian, *Bromsgroveia walkeri,* Benton (1990c) established the new species *Rhynchosaurus brodiei,* and Benton and Walker (in prep.) revised the prolacertiform *Rhombopholis,* the type specimens of all three of which came from the site.

Rhynchosauroid footprints have also been recorded (e.g., Beasley, 1906); some of these appear to be associated with large groove marks produced by the flow of water. Further details of these, and of the skeletal faunas are given in Benton *et al.* (1994).

Description

The Bromsgrove Sandstone Formation (upper part of the Sherwood Sandstone Group) is from 20–35 m thick in Warwickshire (Warrington *et al.,* 1980, pp. 38–9, table 4; Old *et al.,* 1987, p. 20), and the middle to upper portions of this formation are exposed at Coten End. These units equate with the former Waterstones' and 'Building Stones' (Warrington *et al.,* 1980, p. 39). Murchison and Strickland (1840, p. 344) gave a section in the quarry:

	Thickness (ft)
a. Soft, white sandstone and thin beds of marl	8
b. Whitish sandstone, thick bedded	12
c. Very soft sandstone, coloured brown by manganese, called 'Dirt-bed' by the workmen	1
d. Hard sandstone, called 'Rag'	c. 2
Total	23

This section was confirmed by Hull (1869, pp. 88–9). Old *et al.* (1987, p. 23) documented 7 m of massive sandstone and flat-bedded sandstone grading up into 4 m of cross-bedded sandstone and mudstone in the quarry. This section was interpreted as lying near the middle of the thin Bromsgrove Sandstone Formation of the Warwick district and hence may lie within 10 m of the base of the overlying Mercia Mudstone Group. There are still good exposures in the quarry which show channelled and cross-bedded, water-laid, buff and red sandstone units varying in thickness from one to three metres. Laterally discontinuous marl and clay bands, 0.1–0.5 m thick, probably correspond to the fossiliferous Dirt bed.

According to Murchison and Strickland (1840, p. 344), the fossil bones were found principally in the Dirt-bed. Hull (1869, pp. 88–9) stated that the amphibian fossils occurred in the Waterstones', but Walker (1969, 1970a) noted that the reptiles came from the upper part of the Building Stones, a fine-grained, brown-coloured sandstone which forms a bed essentially equivalent to the 'Dirt-bed' of Murchison and Strickland.

The specimens of *Rhynchosaurus brodiei* from Coten End are preserved in a disarticulated state as far as can be determined, and no groups of elements were ever found in even moderately close association. Murchison and Strickland (1840, p. 344) described the bones as 'rolled and fragmentary', but subsequent studies have shown that they are not abraded, nor are they distorted, as Miall (1874, p. 417) noted (Benton, 1990c; Benton *et al.,* 1994).

The bone is preserved as hard, white to buff-coloured material, apparently with all of the original internal structure intact. However, Murchison and Strickland (1840, p. 344) noted that the bones were in a decomposed condition when they were freshly collected and suggested treatment with gum arabic as a useful method of curation. This description is hard to equate with the present hard and well-preserved condition of the fossil bone in the museum collections.

Fauna

The faunal list of fishes, amphibians and reptiles is derived from Huene (1908b), Allen (1908), Horwood (1909), Wills (1910), Walker (1969), Paton (1974a), Galton (1985a), Benton (1990c) and Benton *et al.* (1994).

Osteichthyes: Dipnoi: Ceratodontidae

Ceratodus laevissimus (Miall, 1874)

Tooth of a ceratodontid lungfish (WARMS)

'Temnospondyli': Capitosauridae

Stenotosaurus leptognathus (Owen,1842a)

Jaws and other skull fragments (WARMS)

Cyclotosaurus pachygnathus (Owen,1842a)

Jaws and other skull fragments (WARMS)

'Temnospondyli': Mastodonsauridae.

Mastodonsaurus sp. indet. (Owen, 1842a) Jaw and skull fragments (WARMS)

Diapsida: Archosauromorpha: Prolacertiformes: Macrocnemidae

Rhombopholis scutulata (Owen, 1842a) Ilium, femur (WARMS)

Diapsida: Archosauromorpha: Rhynchosauridae

Rhynchosaurus brodiei Benton, 1990 About 7 jaw and skull fragments and 3 skeletal elements (WARMS), 3 skull remains (BMNH), 2 maxillary tooth-plates (BGS(GSM)).

Archosauria: Crurotarsi: Pseudosuchia:

?Poposauridae

Bromsgroveia walkeri Galton, 1985 Vertebrae, sacrum, ilium, ischium, ?femur (WARMS)

Archosauria: Crurotarsi: indet.

'Large thecodontian' ilium (WARMS)

Cladeiodon lloydi Owen, 1841 About ten isolated teeth (WARMS, BMNH, BGS(GSM))

'Prosauropod dinosaur' cervical vertebra (BMNH)

Interpretation

Murchison and Strickland (1840, p. 342) correlated the 'sandstones of Warwick' with those of Ombersley and Bromsgrove, which they had correlated with the Buntsandstein of Germany since they were separated from 'true Keuper sandstone' by a vast thickness of red and green marl. On the other hand, Owen (1842c, 1842d) agreed with the view of Buckland, that the Warwick sandstone was Keuper in age on the basis of identity of the temnospondyls with those of the German Keuper. The discontinuous fine-grained bands, including the bone-bearing horizon, probably represent overbank pools subsequently broken up by flood waters. The middle to upper portions of this formation, as seen at Coten End, have been interpreted as deposits of mature, meandering river channel and floodplain complexes (Warrington, 1970b).

The mistaken identification of *Hyperodapedon* from Coten End by Huxley (1869) led to correlation of the Lossiemouth Sandstone of Elgin with that termed Lower Keuper Sandstone at Warwick (e.g. Huene, 1908c). Later, Huene (1908c, 1908d) correlated the Warwick sandstone with the German Lettenkohle, of Ladinian age, on the basis of the occurrence of the temnospondyl *Mastodonsaurus giganteus* and the plant *Equisetum arenaceum* from Bromsgrove.

Walker (1969) suggested an Early to Mid Ladinian age for the upper part of the Building Stones or 'Lower Keuper Sandstone' on the basis of *Rhynchosaurus* and *Macrocnemus.* Paton (1974a) gave an Early Ladinian age and Warrington *et al.* (1980 pp. 39–40, table 4), on the basis of palynological work by Warrington, gave the age of the Bromsgrove Sandstone Formation (formerly 'Building Stones') as Late Scythian to Early Ladinian, with the reptiles occurring in the upper part. Warrington (in Benton *et al.,* 1994) reviews evidence from miospores which places the Bromsgrove Sandstone Formation in the Anisian. Indeed, north of the Warwick–Leamington area, miospores indicate an Anisian age for the lower part of the overlying Mercia Mudstone Group, hence clearly constraining the age of the Coten End site as Anisian (Figure 4.2).

The Coten End fauna (Figure 4.6) consists of fishes, up to four species of aquatic carnivorous or piscivorous temnospondyl amphibians, a moderately sized insectivore or carnivore (macrocnemid), two herbivores (*Rhynchosaurus brodiei,* ?'prosauropod dinosaur'), and two or more terrestrial carnivores ('thecodontian', *Bromsgroveia, Cladeiodon*) which may have fed on the herbivores. The numbers of specimens of all taxa are small, but *Rhynchosaurus, Bromsgroveia* and two species of *Cyclotosaurus seem* to be represented by more than five specimens each (Benton *et al.,* 1994).

The capitosaur temnospondyls, well represented here by *Mastodonsaurus, Stenotosaurus* and *Cyclotosaurus,* were heavily built moderate-sized aquatic amphibians, with heads about 200 mm long. The skull is vaguely crocodile-like, flattened, with long jaws closely lined with teeth. There were other series of teeth on the palate to assist in gripping prey and the skull was heavily ornamented and bore lateral line canals which were sensory systems for use under water. Their diet included fishes and probably small tetrapods. The deposits in which the fossils are found indicate the presence of large rivers, a probable habitat for the temnospondyls, and some fishes have been found which may have featured in their diet. Several temnospondyl species have been described from Coten End, most of which have been synonymized with the named taxa: *Mastodonsaurus jaegeri* Owen, 1842, *M. lavisi* Seeley, 1876, *M. ventricosus* Owen (1842), *M. giganteus* Owen (1842) and *Diadetognathus varvicencis* Miall (1874). Milner *et al.* (1990) noted that the amphibians compare broadly with material from central Europe and North America. *Mastodonsaurus* is known from Anisian to Carnian units in Germany (mainly the Keuper).

The prolacertiform *Rhombopholis* turns out to be rather like *Macrocnemus,* a slender lizard-like animal, 500–800 mm long. It had large eyes and many small teeth and may have been a carnivore or piscivore. *Macrocnemus* is well known from the marine Grenzbitumenzone (Anisian/Ladinian boundary) at Tessin, in the Swiss Alps, and in neighbouring deposits in North Italy. Other species come from the Upper Buntsandstein in Germany (Scythian/Anisian) and from the Upper Muschelkalk (?Ladinian) of Catalonia, Spain. It is a prolacertiform, a largely Triassic group of reptiles closely related to archosaurs (Benton, 1985).

Rhynchosaurus brodiei was a moderate-sized rhynchosaur with a skull 90–140 mm long (estimated body length, 0.5–1.0 m) and a herbivorous diet (Benton, 1990c). It differs from *R. articeps* from Grinshill (skull length 60–85 mm) in being considerably larger and in having a broader skull. The jugal in *R. brodiei* is much deeper than that of *R. articeps,* being the largest bone in the side of the skull, the orbit in *R. brodiei* is placed relatively further forward, and the maxilla is relatively smaller than in *R. articeps.* The characteristic 'tusks', slicing dentition and tooth plate, and large eyes, are shown by these specimens.

Bromsgroveia walkeri was a moderate- to large-sized carnivorous quadruped (rauisuchid) or biped (poposaurid) (Galton, 1985a), based on an isolated ilium. It probably preyed on small terrestrial and semi-aquatic reptiles *Rhynchosaurus* and *Macrocnemus.* Other archosaurs are represented by teeth called *Cladeiodon lloydi.* These range in length from 10 to 50 mm and could belong to *Bromsgroveia,* or to some other carnivorous archosaur. The so-called 'prosauropod dinosaur' could be the oldest in the world, if it really is correctly identified, but that is uncertain.

Comparison with other localities

The nearest analogues of the Coten End fauna come from the Bromsgrove Sandstone Formation of Guy's Cliffe (see below) and Bromsgrove (see above), and the Otter Sandstone Formation of Sidmouth and Budleigh Salterton (see below).

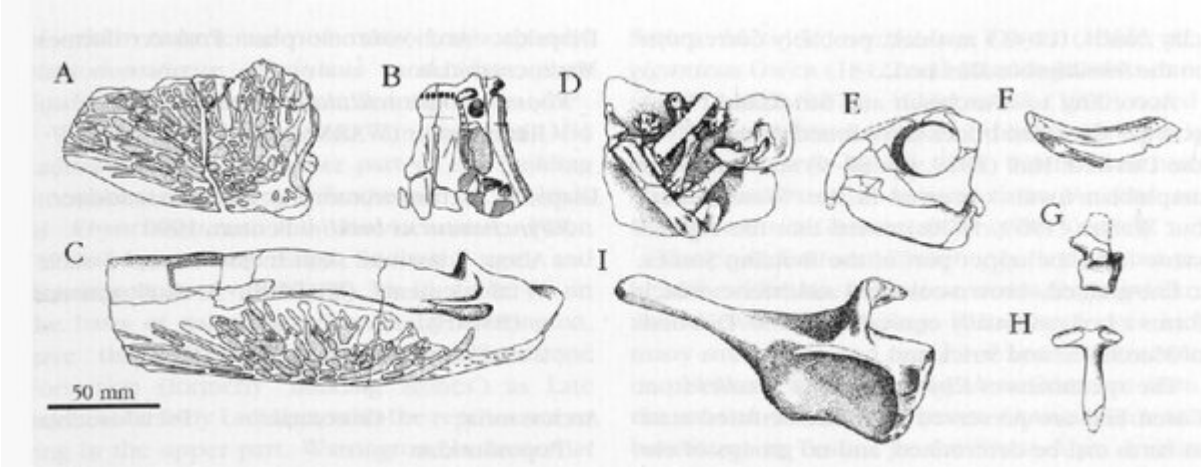
Outside the British Isles, the fauna compares with Early to Mid Triassic faunas from France (Grès à Voltzia) and Germany (Buntsandstein) and Mid to Late Triassic faunas from Germany (Lettenkeuper).

Conclusions

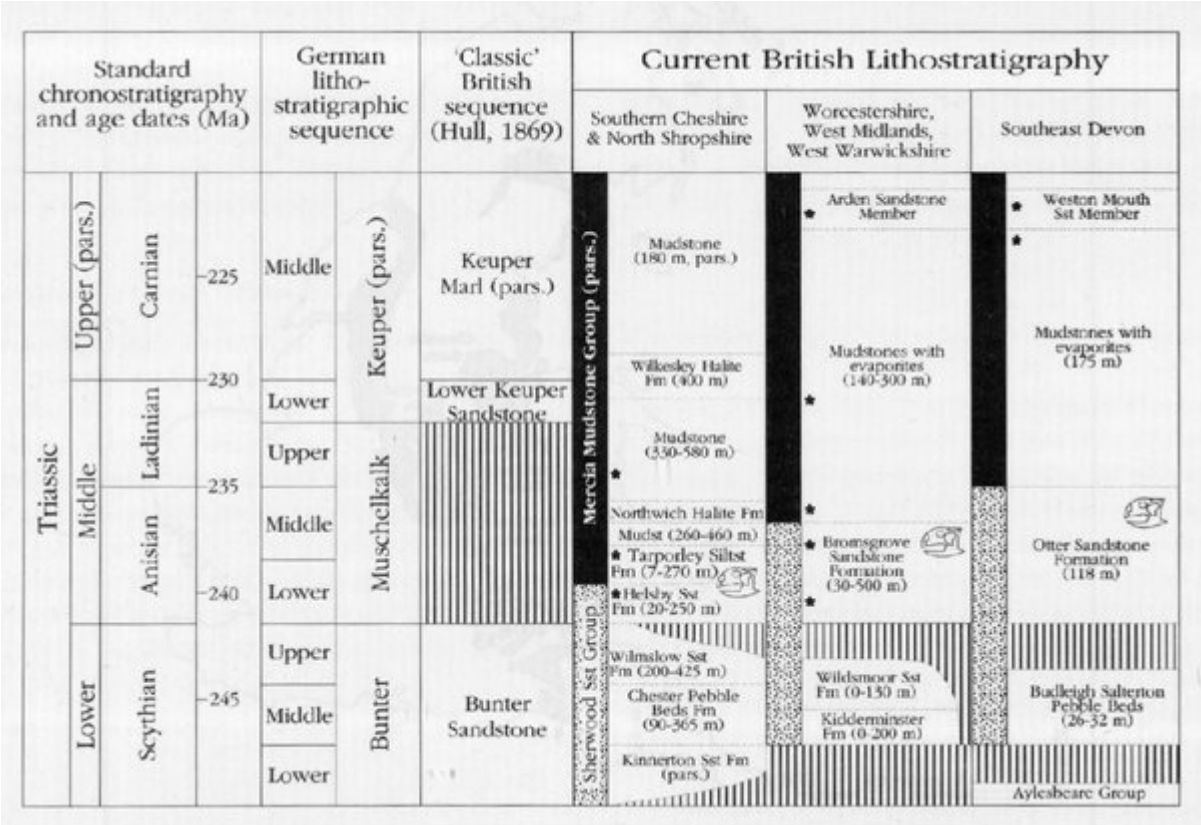
The value of the Coten End fauna, and the other British examples of similar age, is linked to the difficulty in correlation. There are no mainland European terrestrial faunas of the same age, since the Muschelkalk marine transgression occupies that interval of time. Coten End preserves the richest Mid Triassic continental tetrapod fauna in Britain and

probably in Western Europe. Although the potential for re-excavation is now restricted it is still possible, hence the conservation value of the site.

References



(Figure 4.6) Typical elements of the Warwick fauna. (A) Left postero-external angle of the skull of 'Cyclotosaurus pachygnathus' (Cyclotosaurinae incertae sedis) in lateral view (WARMS Gz13); (B) part of the snout of 'Stenotosaurus leptognathus' (Stenotosaurinae incertae sedis) in palatal view (WARMS Gz38); (C) posterior portion of a left lower jaw of 'Stenotosaurus leptognathus' in lateral view (WARMS Gz35); (D) scattered bones of cf. Macrocnemus (Rhombopholis scutulata) (WARMS Gz10); (E)–(H), assorted remains of Rhynchosaurus brodiei: (E) anterior part of the skull in lateral view (WARMS Gz6097/ BMNH R8495), (F) anterior part of a dentary in medial view (WARMS Gz950), (G) mid-dorsal vertebra in right lateral view (WARMS Gz17), and (H) interclavicle in ventral view (WARMS Gz34); (1) right ilium of Bromsgroveia walkeri in lateral view (WARMS Gz3). After various sources; from Benton et al. (1994).



(Figure 4.2) The stratigraphy of the British Triassic reptile faunas. Correlations of the standard Triassic divisions and the German Triassic sequence with the British Triassic, as proposed by Hull (1869) for the 'classical' British succession, and by Warrington et al. (1980) for currently recognized lithostratigraphical units. Skull symbols indicate the levels of the main tetrapod faunas, and asterisks denote palynological evidence of relative age. Age dates (Ma ± 5) after Forster and

Warrington (1985). From Benton et al. (1994).