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Fossil Reptiles of Great Britain

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Chapter 4

British Triassic fossil reptile sites

INTRODUCTION: TRIASSIC STRATIGRAPHY AND SEDIMENTARY SETTING

The British Triassic deposits have a broad U-shaped outcrop in the English Midlands, with a continuation south-westwards to south Wales and Devon (Figure 4.1). Smaller outcrops occur in northwest England, in Northern Ireland and in Scotland (Warrington *et al.*, 1980, figs 2 and 3). The sediments are almost wholly continental terrestrial red-beds deposited in fault-bounded basins in southern and western Britain and on the more regionally subsiding Eastern England Shelf, which formed the onshore marginal part of the Southern North Sea Basin (Audley-Charles, 1970; Holloway, 1985). In the Late Permian and Early Triassic, renewed and extensional subsidence in the Wessex Basin, Worcester Graben and the Needwood and Cheshire basins, resulted in the establishment of an axial drainage system which

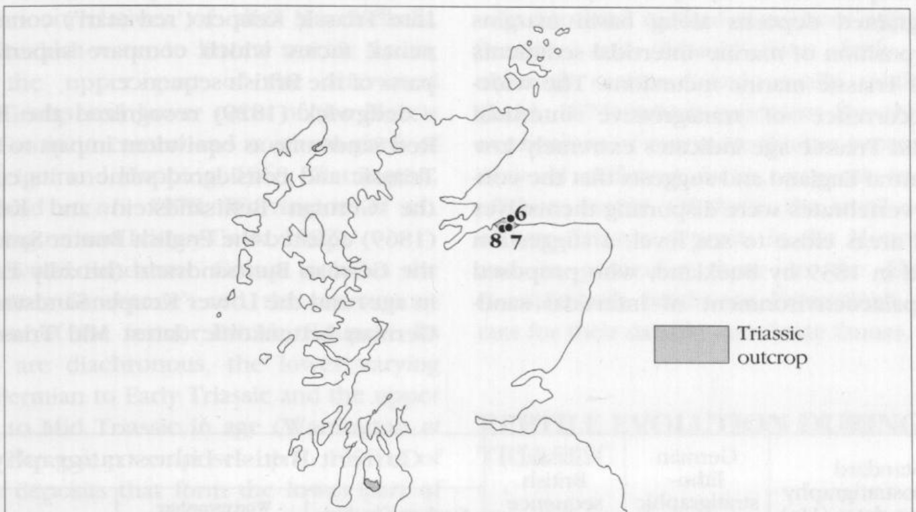

Figure 4.1 Map showing the distribution of Triassic rocks in Great Britain. GCR Triassic reptile sites: (1) Grinshill Quarries; (2) Coten End Quarry; (3) Guy's Cliffe; (4) Sidmouth coast section; (5) Otterton Point; (6) Lossiemouth East Quarry; (7) Spynie; (8) Findrassie; (9) Bendrick Rock; (10) Aust Cliff; (11) Slickstones (Cromhall) Quarry; (12) Durdham Down; (13) Emborough Quarry; (14) Tytherington Quarry.

flowed northwards from the Variscan Highlands (Holloway, 1985). The south-to-north regional palaeoslope, and the proximal to distal depositional pattern which developed, is reflected in the diachronous nature of the Sherwood Sandstone–Mercia Mudstone Group boundary (Figure 4.2), with coarse clastics being deposited in the south, while mudstones and evaporites accumulated farther north (Warrington, 1970a, 1970b; Warrington *et al.*, 1980; Warrington and Ivimey-Cook, 1992). This general sedimentary pattern was complicated locally by the introduction of coarse-grained deposits along basin margins and the deposition of marine–intertidal sediments during Mid Triassic marine incursions. The widespread occurrence of transgressive intertidal facies of Mid Triassic age indicates extremely low relief in central England and suggests that the contemporary vertebrates were disporting themselves in lowland areas close to sea level, a suggestion first offered in 1839 by Buckland, who proposed (1844) a palaeoenvironment of intertidal sandbanks.

In the British Triassic there is a general dearth of biostratigraphically useful fossils (Figure 4.2). This, combined with rather limited vertical facies variations throughout the sequence, has led to problems of correlation across Britain and between the British Isles and abroad. The standard stages of the Triassic were defined using ammonoids in the marine sequences of southern Europe, and it has been hard to correlate the continental Triassic of Britain with these type successions. In Germany the Early to Mid Triassic Buntsandstein ('mottled sandstone') and Mid to Late Triassic Keuper ('red marl') consist of continental facies which compare superficially with parts of the British sequence.

Sedgwick (1829) recognized the British New Red Sandstone as equivalent in part to the German Triassic and considered some units equivalent to the German Buntsandstein and Keuper. Hull (1869) equated the English Bunter Sandstone with the German Buntsandstein (broadly Early Triassic in age) and the Lower Keuper Sandstone with the German Lettenkohle (latest Mid Triassic to early

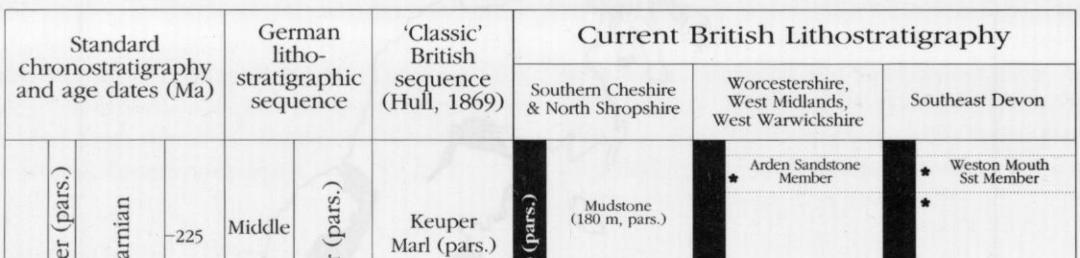

Figure 4.2 The stratigraphy of the British Triassic reptile faunas. Correlations of the standard Triassic divisions and the German Triassic sequence with the British Triassic, as proposed by Hull (1869) for the 'classical' British succession, and by Warrington *et al.* (1980) for currently recognized 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).

Late Triassic in age). He argued that a major unconformity in the British sequence corresponded to most of the Mid Triassic and represented the Muschelkalk. Warrington *et al.* (1980) advocated the abandonment of the terms 'Bunter' and 'Keuper' as applied in Britain, and established a lithostratigraphic nomenclature with correlations based on palynomorphs and other fossils where possible (Figure 4.2).

Palynological work (Warrington, 1967, 1970b; Geiger and Hopping, 1968) showed that deposits of Mid Triassic age are present in Britain (Figure 4.2), where correlatives of the Muschelkalk, including brackish-water to littoral marine facies, occur in the upper part of the Sherwood Sandstone Group and lower parts of the Mercia Mudstone Group in central and northern parts of England (Geiger and Hopping, 1968; Warrington, 1974a; Ireland *et al.*, 1978; Warrington *et al.*, 1980; Warrington and Ivimey-Cook, 1992).

The Sherwood Sandstone Group includes the former 'Bunter Sandstone' and the arenaceous (lower) parts of the former British 'Keuper'. Its boundaries are diachronous, the lower varying from Late Permian to Early Triassic and the upper from Early to Mid Triassic in age (Warrington *et al.*, 1980). The group comprises up to 1500 m of arenaceous deposits that form the lower part of British Triassic successions. The sandstones are red, yellow or brown in colour, and pebbly units occur, especially in the Midlands. Most of the deposits are of fluvial origin, but there are many aeolian units (Thompson, 1969, 1970a, 1970b).

The Mercia Mudstone Group corresponds broadly with the former 'Keuper Marl', and encompasses the dominantly argillaceous and evaporitic units that overlie the Sherwood Sandstone Group throughout much of Britain. Its lower boundary may be sharp, but there is commonly a passage upwards from predominantly sandy to predominantly silty and muddy facies at a diachronous interface that varies regionally from Early to Mid Triassic in age. The upper boundary, associated with a marine transgression which apparently occurred approximately contemporaneously throughout much of Europe, lies within the Rhaetian Stage. The group comprises dominantly red mudstones with subordinate siltstones. Extensive developments of halite and of sulphate evaporite minerals suggest deposition in hypersaline epeiric seas, connected to marine environments in associated sabkhas, and in playas (Warrington, 1974b).

The Penarth Group, which overlies the Mercia Mudstone Group, consists of argillaceous, calcareous and locally arenaceous formations, predominantly of marine and lagoonal origin. The topmost beds of the Penarth Group (Lilstock Formation, Langport Member), pass up into grey bituminous shales and limestones, which are lithologically indistinguishable from and continuous with the beds of the overlying Jurassic. The top of the British Triassic is placed above the Penarth Group within the Blue Lias, at the point of appearance of the first ammonite, *Psiloceras* (Cope *et al.*, 1980a; Warrington *et al.*, 1980).

In Scotland red-bed sequences assigned to the Permian and Triassic form fairly numerous, although scattered and usually small, outcrops (Judd, 1873) which represent the thin marginal expressions of extensive thicker successions, possibly of different facies, present in important offshore basins. Of these, the small occurrences of Late Triassic deposits in the Moray Firth area and in particular those in the Elgin district (Lossiemouth Sandstone Formation), are important for their datable vertebrate faunas.

REPTILE EVOLUTION DURING THE TRIASSIC

The Triassic Period was a time of major flux among tetrapods. The earliest Triassic faunas were of low diversity by comparison with the Late Permian faunas, a consequence of the end-Permian mass extinction event. The ecological niches left vacant by removal of the old faunas were soon filled in the Early Triassic by several new tetrapod groups and by re-radiation of surviving groups from the Permian. In several parts of Gondwanaland, Early Triassic faunas were uniquely dominated by the dicynodont *Lystrosaurus*, which often comprised 95% or more of the individuals in a fauna. The remainder of these faunas consisted of small plant- and insect-eating therapsids, and some archosaurs. The archosaurs (Triassic forms are often termed 'thecodontians'), new groups of therapsids, particularly cynodonts, and the rhynchosaurs (archosauromorphs) rose to prominence during the Early and Mid Triassic.

Mid Triassic tetrapod faunas worldwide were strikingly similar (Benton, 1983a, 1983b) being dominated by rhynchosaurs or by dicynodonts as herbivores, and with associated fish-eating temnospondyl amphibians and a variety of prolacertiforms, small- to medium-sized insectivores, and procolophonids, modest-sized plant-and insect-eaters. These animals were preyed on by a range of cynodonts and thecodontians, some of the latter, the rauisuchians, achieving large size (up to 5 m long). These faunas continued into the early part of the Late Triassic, but were apparently decimated at the end of the Carnian (Benton, 1983a, 1983b, 1986a, 1986b, 1991, 1994a, 1994b): the rhynchosaurs and larger therapsids all died out, as well as some smaller groups.

Following this extinction event, the dinosaurs, pterosaurs, crocodilomorphs, sphenodontians (lizard relatives), and other groups radiated during the last 15–20 Ma of the Triassic, the Norian. The thecodontians, particularly the rauisuchians, ornithosuchids, fish-eating phytosaurs, and herbivorous aetosaurs dwindled during this time, and finally died out near the Triassic/Jurassic boundary, an extinction event that was also marked by major effects on marine life.

BRITISH TRIASSIC REPTILE SITES

The British Triassic is for the most part unfossiliferous, and tetrapod faunas occur only sporadically. However, some of these faunas are locally rich. The principal reptiliferous horizons lie within three rock units: the uppermost portion of the Sherwood Sandstone Group of south-west England and the Midlands (Anisian), the Lossiemouth Sandstone Formation (Carnian) of north-east Scotland, and the Penarth Group (Rhaetian), of central and south-west England. These provide excellent information on Mid Triassic terrestrial reptiles, rare elsewhere in the world, on Late Carnian pre-extinction faunas, and on terminal Triassic forms. Virtually all the Mid Triassic bone-bearing sites are selected as GCR sites, as are all the Carnian localities around Elgin, and most of the fissure localities. Aust Cliff is selected as the sole Rhaetian GCR site out of dozens of other candidates, since it has yielded most specimens in the past.

Some of the most unusual British Triassic reptile faunas are the insular assemblages from fissure-fill deposits within fossilized cave systems developed in the Carboniferous Limestone of south-west England and South Wales. The deposits range in age at least from the Late Norian, possibly the Late Carnian, to the Early Jurassic and some have been correlated lithostratigraphically and biostratigraphically with the local marginal Trias (formerly the 'Dolomitic Conglomerate'). The best examples of these fissure sites, as well as sites in the Mid Triassic of the English Midlands and Devon, the Carnian of north-east Scotland and the Penarth Group of south-west England, have been selected as GCR sites.

Reptile bones have not been reported from the British Early Triassic, but Wills and Sarjeant (1970) noted a variety of small reptilian footprints from the Bunter (=Kidderminster and Wildmoor Sandstone Formations) of a borehole at Bellington, Worcestershire. *Cheirotherium* footprints have been observed in the Wilmslow Sandstone Formation in the Wilmslow Waterworks Borehole (Thompson, pers. comm., 1993). The British record of fossil reptiles is also sporadic during Mercia Mudstone Group times: reptiles are represented by undiagnostic dissociated bones from the conglomeratic marginal Triassic of the Bristol district, and rarely from the Arden Sandstone Member of the Midlands and the Weston Mouth Sandstone Member of south-east Devon, both of which are Carnian in age. Some of the fissure deposits around Bristol and in South Wales may date from Late Carnian and Norian times, as might the footprints from Barry, South Wales (see below).

MID TRIASSIC OF THE ENGLISH MIDLANDS

Numerous localities in the English Midlands have yielded fossil reptiles of Mid Triassic age, from the upper part of the Sherwood Sandstone Group (Bromsgrove Sandstone Formation, Helsby Sandstone Formation; Figure 4.2) and the lower part of the Mercia Mudstone Group (Tarporley Siltstone Formation). These, and other neighbouring units, have also yielded significant ichnofaunas (see below).

In the Warwick area, old quarries at Guy's Cliffe, Leek Wooton, Cubbington Heath, Coten End and Leamington have yielded many fragmentary fossil reptiles, but only Guy's Cliffe and Coten End are extant. A number of localities in Leamington and Warwick (e.g. Coten End, SP 29006550; Leamington Old Quarry, SP 325666) have produced remains of the reptiles *Macrocnemus* (type specimen of Owen's *Rhombopholis scutulata* (Owen, 1842a, pp. 538–41, pl. 46, figs 1–5), *Rhynchosaurus brodiei* (Benton, 1990c), *Cladeiodon lloydi* (Owen, 1841b), *Bromsgroveia walkeri* (Galton, 1985a), a possible prosauropod tooth (Murchison and Strickland, 1840, pl. 28, fig. 7a; Huene, 1908b, figs 210–11, 265), the temnospondyls *Mastodonsaurus*, *Cyclotosaurus pachygnathus*, *C. leptognathus* and the fish *Gyrolepis* (Walker, 1969, p. 472). Cubbington Heath Quarry (SP 335694) has yielded *M. jaegeri*, *C. pachygnathus* and *C. leptognathus* (Huxley, 1859c; Woodward, 1908a; Wills, 1916, pp. 9–11, pl. 3). Guy's Cliffe (SP 293667) has produced remains of the jaws of *Mastodonsaurus* sp. (=*M. jaegeri*) (Owen, 1842a, pp. 537–8, pl. 44, figs 4–6; pl. 37, figs 1–3; Miall, 1874, p. 433), probably the first find of a tetrapod to be made in the area, having been collected in 1823 (Buckland, 1837). A ?prosauropod femur and tooth have been recorded from Leek Wooton (SP 289689), but the site of the quarry from which this specimen was collected is uncertain. Elsewhere in the Midlands good remains of *Rhynchosaurus articeps* have been obtained from a series of quarries at Grinshill, Shropshire (SJ 520237), and a fine skull of *C. leptognathus* was collected from Stanton, near Uttoxeter, Staffs (SK 126462) (Woodward, 1904).

Many localities in the Early and Mid Triassic of the English Midlands, especially in Cheshire, have yielded rhynchosauroid and *Cheirotherium* footprints (Tresise, 1993). The richest of these footprint localities is Storeton Quarry, Higher Bebington (SJ 303838), source of hundreds of slabs, but now filled in (Tresise, 1989, 1991). Other localities in Cheshire and Merseyside include Rathbone Street, Liverpool; Delamere Forest; 'Mr Leach's quarry', Runcorn; Beetle Rock Quarry, Runcorn; Overhill, Iveston and Weston Point, all near Runcorn; Runcorn Hill; Flaybrick Hill, Birkenhead; Daresbury; Oxton Heath; Moorhey, near Great Crosby; Eddisbury; Warrington; Five Crosses Quarry, Frodsham; Potbrook, Mottram St Andrews; Wazards Well, Alderley Edge; Haymans Farm Borehole, Nether Alderley, all in the Helsby Sandstone Formation and Tarporley and Lymm in the Tarporley Siltstone Formation. The only Cheshire site that has recently produced footprints is Red Brow Quarry, Daresbury (SJ 567834) and scattered occurrences in boreholes and in field walls (Thompson, 1970a; Ireland *et al*., 1978; Sarjeant, 1974, pp. 312–13). Localities in Shropshire include Grinshill (site of reptile finds as well – see below) and Oaken Park Farm, Albrighton (Sarjeant, 1974, pp. 316–17). Localities in Derbyshire are Weston Cliff on the River Trent and Dale Abbey, Stanton-by-Dale (Sarjeant, 1974, p. 321) and in Staffordshire, Stanton; Coven, near Brewood; Burton Bridge, Burton-on-Trent; Ashby Road, Burton-on-Trent; Hollington; Townhead Quarry, Alton; Chillington; Great Chatwell (Sarjeant, 1974, pp. 319–21; Delair and Sarjeant, 1985, pp. 131–2). Localities in Warwickshire are Birkbeck; Shrewley Common; Witley Green, near Preston Baggot; Coten End Quarry, Warwick; Rowington (Sarjeant, 1974, pp. 314–16; 1985), and in Worcestershire: Barrow Churz, Malvern (Sarjeant, 1974, p. 324). Localities in Leicestershire are Shoulder-of-Mutton Hill, Leicester; Castle Donington; and Derby Road, Kegworth, although the first two are rather uncertain (Sarjeant, 1974, pp. 317–19), and in Nottinghamshire: Colwick, Nottingham; Ollerton; Sherwood district or Mapperley Park, Nottingham (Sarjeant, 1974, pp. 321–3). Unfortunately, most of these localities, listed largely from 19th century reports, are either lost or untraceable. A strong case could not be made for listing any Mid Triassic footprint locality or localities as a GCR site. A complete overview of these sites is urgently required (King, M.J. in prep.).

At Bromsgrove, near Birmingham, three quarries near Hilltop Hospital, on Breakback or Rock Hill (SO 948698) are also known for their Middle Triassic tetrapods. These quarries (Wills, 1907, 1910, pp. 254–6) formerly showed good sections in the Finstall Member of the Bromsgrove Sandstone Formation (the former Building Stones and Waterstones). Wills (1907; 1908, pp. 29–32; 1910, pp. 254–6) described the succession as 15–20 m of alternating sandstone and shales, and a band of 'marl conglomerate'. Some lenticular beds are 'true marls', others are sandy shales, green, brown or red in colour. Individual units are lens-shaped, and the sandstones appear to show cross-bedding (Wills, 1907, fig. 1). The present sections are very limited, and the sites could not be recommended as GCR sites.

The Bromsgrove Sandstones at Bromsgrove (Figure 4.2) are approximately equivalent in age to the fossiliferous horizons at Warwick and Leamington (Walker, 1969; Paton, 1974a; Warrington *et al*., 1980, pp. 38–9, table 4). The flora and fauna from Bromsgrove is similar to those from Warwick, and from the Otter Sandstone Formation of Devon, and they assist our understanding of these GCR sites. The fauna comprises arthropods: conchostracans (*Euestheria*), scorpionid arachnids (*Mesophonus, Spongiophonus, Bromsgroviscorpio and Willsiscorpio*), annelids (*Spirorbis*), and a bivalve (*?Mytilus*). The vertebrates include the shark *Acrodus*, the perleidid *Dipteronotus* and the lungfish *Ceratodus*, as well the capitosaurid amphibians *Cyclotosaurus pachygnathus* and *Mastodonsaurus* (Wills, 1916, pp. 2–7, figs 2–4, pl. 2; Paton, 1974a), and reptiles cf. *Macrocnemus*, *Rhynchosaurus brodiei*, rauisuchian remains (?including '*Teratosaurus*', '*Cladeiodon*'), *Bromsgroveia walkeri*, a ?prosauropod tooth (Huene, 1908b, p. 242, figs 273a, b; Galton, 1985a; Benton, 1990c), a trilophosaur, a nothosaur (Walker, 1969) and other, undiagnostic, remains. The remains of *R. brodiei* from Bromsgrove are labelled as having come from 'Wilcox S. Quarry'. The Bromsgrove fauna is associated with a rich flora that includes sphenopsids (horsetails and relatives) and gymnosperms (cycads, cycadeoids, conifers).

The following Midlands Mid Triassic localities are selected as GCR sites:

1. Grinshill Quarries, Shropshire (SJ 520237). Middle Triassic (Anisian), Helsby Sandstone and Tarporley Siltstone Formations.
2. Coten End Quarry, Warwick, Warwickshire (SP 290655). Middle Triassic (Anisian), Bromsgrove Sandstone Formation.
3. Guy's Cliffe, Warwick, Warwickshire (SP 293667). Middle Triassic (Anisian), Bromsgrove Sandstone Formation.

GRINSHILL QUARRIES, SHROPSHIRE (SJ 520237)

Highlights

Grinshill Quarries have had a long history of producing skeletons and footprints of fossil reptiles. The quarries have yielded many skeletons of the small plant-eater *Rhynchosaurus*, and they are the richest site for such material in the British Isles.

Introduction

Grinshill Hill, and the adjoining Clive Hill, 300–500 m north of Grinshill village, are marked by numerous quarries, of which four large ones lie along the crest of the hill (SJ 5205 2392, SJ 5238 2387, SJ 5249 2384, SJ 5264 2380). The last of these is still operational (Figure 4.3). The quarries, exposing sections in the Tarporley Siltstone Formation and the Helsby Sandstone Formation, have yielded specimens of the reptile *Rhynchosaurus* and associated rhynchosauroid footprints. All the old quarries on Grinshill Hill are

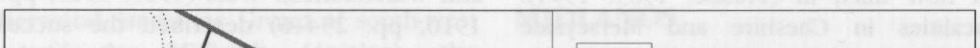

Figure 4.3 The Grinshill localities. The map is based on published maps of the British Geological Survey (BGS 1:63, 360 scale Geological Sheet 138, Wem) and on field observations by M.J.B. I. Bridge Quarries; II. working quarry (ECC Quarries Ltd).

still accessible and the currently operating quarry provides good exposure. Although excavation is slow, fresh finds of bones and footprints occur from time to time.

The buff-coloured sandstone of Grinshill was quarried in the 18th and 19th centuries and provided much of Shrewsbury and northern Shropshire with building stone. Murchison (1839, pp. 37–41) described a section taken in one of the Grinshill quarries and the Reverend Dr T. Ogier Ward of the Shrewsbury Natural History Society described (1840) vertebrate footprints, rain mark impressions and ripple marks taken from the Waterstones of Grinshill (Ward, 1840; noted in Murchison, 1839, appendix, p. 734). More footprints were reported from Grinshill by Beasley (1896, 1898, 1902, 1904, 1905, 1906), who identified most of them as of 'rhynchosauroid' type. Thompson (1985) and Benton *et al.* (1994) note also the occurrence of some cheirotherioid tracks at Grinshill.

The first bones from Grinshill, discovered during the 1840s, were noted by Ward (1840). The specimens had been found some years earlier by John Carline, quarrymaster at Grinshill, and were given to the museum of the Shropshire and North Wales Natural History Society. Between August 1840 and November 1841, Ward obtained several more bones belonging to *Rhynchosaurus* from various quarrymen, although he later claimed that these specimens were 'first discovered by myself in 1837–1838' (Ward, 1874). These he sent to Richard Owen at the Royal College of Surgeons in several packages (Owen correspondence, Coll. Sherborn, BMNH letters 110, 103, 118, 105, 109, 107, 114, 116; D.B. Thompson, pers. comm., 1988).

In a paper to the Geological Society of London on 24th February 1841, Owen referred most of the Grinshill material to a species of *Labyrinthodon* (i.e. *Mastodonsaurus*), an amphibian which Jaeger (1828) had described from the Late Triassic of Germany. Owen (1842b, 1842c) later recognized the reptilian affinities of the material and named it *Rhynchosaurus articeps*. Further specimens of *Rhynchosaurus* provided more detail for the description of the skull (Owen, 1859a, 1863a). *Rhynchosaurus* was later redescribed from Owen's specimens and from newer material by Huxley (1887), Woodward (1907a), Watson (1910a), Huene (1929a, 1938, 1939), Hughes (1968) and Benton (1990c). More details of the history may be found in Benton (1990c) and Benton *et al.* (1994).

Some *Rhynchosaurus* remains have been recovered recently from Grinshill, as well as 11 slabs bearing good vertebrate trackways, collected by Dr J. Stanley and Dr D.B. Thompson (Keele University) between 1968 and 1982. All of this material came from the single operational quarry.

Description

Grinshill Hill consists of Triassic sediments dipping north and north-west. It is bounded to the east and west by NE–SW trending faults and these are linked by two WNW–ESE trending faults.

Murchison (1839, pp. 37–41) gave a section in 'Grinshill Stone Quarries', a locality no longer identifiable exactly – it may have been generalized from several quarries (Pocock and Wray, 1925, p. 39). Hull (1869, p. 64), in his revision of the Triassic rocks of the Midlands, showed the presence of Upper Mottled Sandstone, Lower Keuper Sandstone and Waterstones at Grinshill (although he could not identify the boundary between the last two), and reproduced Murchison's section in simplified form:

	Thickness Ft in
Lower Keuper Sandstone	
1. Fee and jay (rubbly thin bedded rock)	13 0
2. Flag rock, yellowish or light brown in colour	19 0
3. Sand bed called Esk	0 9
4. Hard burr	2 6
5. Coarse freestone, mottled, of yellowish and reddish colours, best building stone	9 6
6. Grey freestone	7 6
7. Good light yellow freestone underlain by a seam of clay	11 0
8. Good white freestone	2 0
9. Strong white freestone	8 0
Upper Mottled Sandstone (Bunter)	
10. Sandy and bad freestone	2 0
11. Bad stone, sometimes used for walls, &c	9 0
12. Soft yellow sandstone, the grains of sand cemented by decomposed feldspar	4 6
13. Sandstone of deep red colour sunk through for water	222 0
TOTAL	311 7

Pocock and Wray (1925, pp. 15–16) established the 'Ruyton and Grinshill Sandstones' to include 'a group of red and yellow freestone, forming a passage-bed between the Bunter and Keuper and including at its base a small thickness of the Upper Mottled Sandstone and limited upward by the base of the Waterstones'. For the 'main Grinshill quarries, 550 yards N20 degrees E of the Elephant and Castle Hotel', Pocock and Wray (1925, pp. 39–40) offer the section:

		Thickness **Ft in**
Keuper Marl: Red marl	seen to	2 0
Waterstones:		
Flag rock: grey and light-yellow sandstone, evenly bedded, with thin reddish seams; ripple marks		20 0
Esk bed: incoherent grey sandstone and sand, with harder patches; full of specks of manganese dioxide		0 9
Grinshill Sandstone:		
Hard burr: hard yellowish-white sandstone (coarse-grained sandstone)		2 6
Hard yellowish freestone		2 6
Soft yellow sand		0 2
White and pale-yellow freestone, with iron-stained patches towards the base		33 0
White freestone with iron-stained and speckled patches	seen to	5 6

Pocock and Wray (1925, p. 40) gave another section taken in the only quarry then working (650 yards N45 degrees E of the hotel) which shows a similar succession. The Upper Mottled Sandstone of these authors (f3) has been renamed the Wilmslow Sandstone Formation, the Ruyton and Grinshill Sandstones (or the Building Stones; f4) the Helsby Sandstone Formation, and the Waterstones the Tarporley Siltstone Formation (Warrington *et al.*, 1980).

The Tarporley Siltstone Formation, typically ranging from 20 m to 250 m in thickness (Warrington *et al.*, 1980, table 4), is only about 6–10 m thick at Grinshill. The sediments are well-bedded, white, pale-green or reddish fine-grained sandstones and marls. Two facies, A and B, have been identified by Thompson (1985, pp. 119–21). Facies A, fluvial and tidal, is characterized by trough-shaped erosion channels filled with beds of ripple cross-laminated, fine- to medium-grained sandstone, which bear on their bedding surfaces ripple marks, rhynchosauroid footprints (see below), trace fossils formed by invertebrates(?), and supposed raindrop impressions, which were reported for the first time from Grinshill by Ward (1840) and Buckland (1844). Facies B, largely intertidal and rarely hypersaline, consists of interbedded fine sandstones, siltstones and mudstones. The mud and silt horizons are generally 10–20 mm thick; the sand beds are thicker at about 100 mm. Many of these horizons show current and wave ripple marks, load casting, flute marks and prod marks. A few show adhesion ripple marks, indicating half wet, half dry conditions. Mudcracks and halite pseudomorphs have been observed occasionally, as well as rhynchosauroid footprints and poorly preserved invertebrate trace fossils.

The underlying exposure of Helsby Sandstone consists of about 30 m of buff and yellow, medium-grained, well-sorted sandstones. These are well cemented, and contain numerous small spots of manganese hydroxide. Large-scale cross-beds are sometimes visible in vertical quarry faces, bearing lamination structures which imply aeolian conditions of deposition (Thompson, 1985), relating to large transverse barchanoid dune ridges. At Grinshill, the Helsby Sandstone Formation appears to grade up into the Tarporley Siltstone Formation through a bed of loose sand, about 0.3 m thick, termed the Esk Bed (Pocock and Wray, 1925, pp. 39–40; Thompson, 1985, p. 119), of indeterminate environmental origin (Figure 4.4).

Most of the reptile specimens appear to have come from the debris associated with quarrying, but were probably derived from horizons within a thickness of about 2 m. The *R. articeps* specimens occur in two main lithologies, as noted by Owen (1842b, p. 146); a fine-grained grey sandstone and a coarser pinkish-grey sandstone (his coarse 'burr-stone').

The remains of *R. articeps* and the tetrapod trackways appear to have come from a number of quarries on Grinshill (D.B. Thompson, pers. comm., 1984). The footprints described by Ward (1840) were found on ripple-marked surfaces in a finely laminated buff-coloured sandstone beneath the rubbly red-coloured sandstone called 'Fee', presumably equivalent to part of Thompson's (1985) largely intertidal Facies B. Walker (1969, p. 470) observed that the specimens of *R. articeps* came from the siltstones and fine sandstones of the Tarporley Siltstone Formation, and possibly from the immediately underlying beds at the top of the Grinshill Sandstones (the coarser sandstone) (Walker, 1969). This was implied also in Pocock and Wray's (1925, pp. 39–40) section, in which the top of the Grinshill Sandstone is

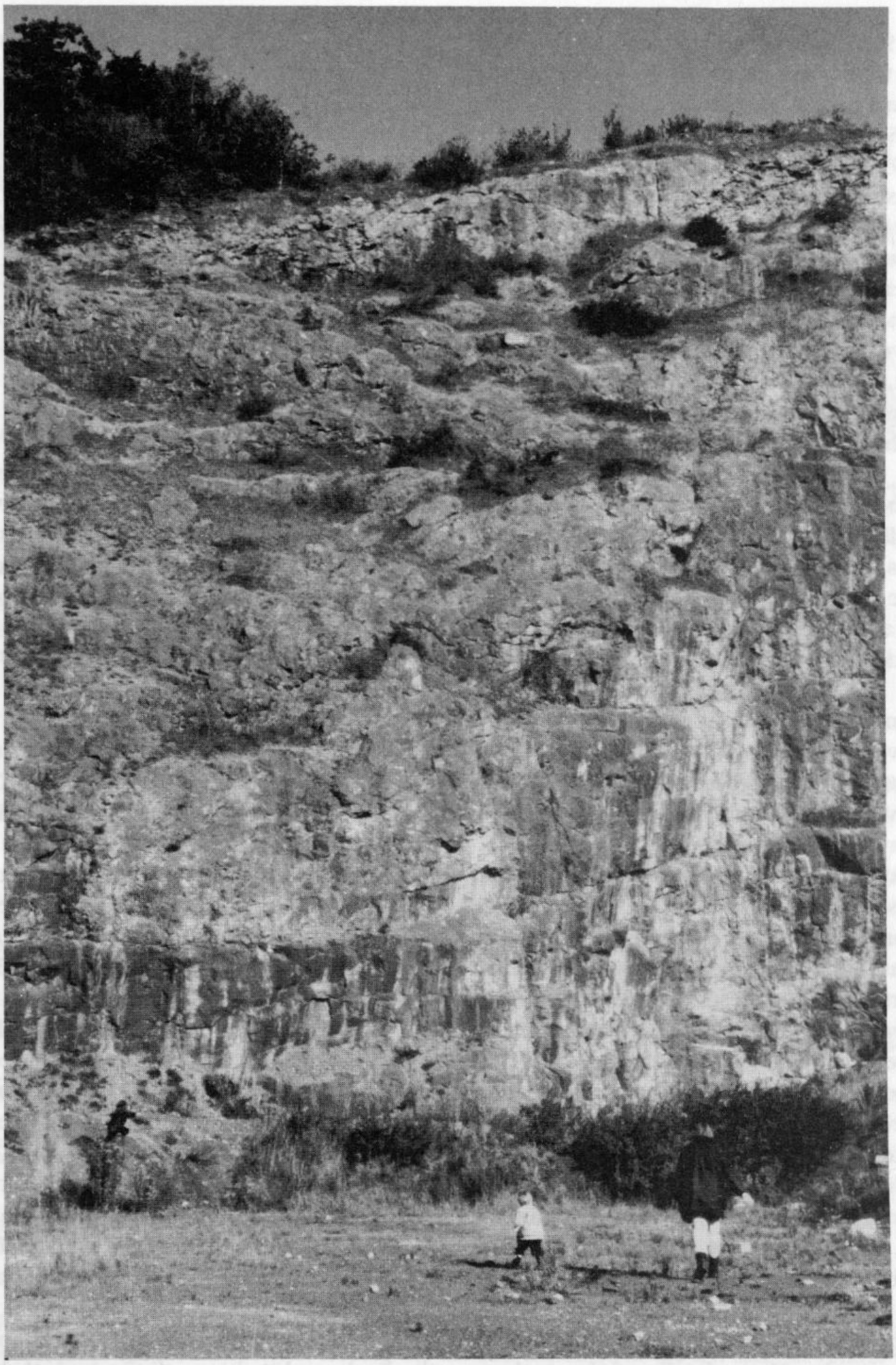

Figure 4.4 The operational quarry on Grinshill: view of the north face, showing the massive cross-bedded Helsby Sandstone Formation at the bottom, and the softer, more thin-bedded Tarporley Siltstone Formation above. (Photo: M.J. Benton.)

described as 'Hard Burr: Hard yellowish-white sandstone, 2ft 6in'. However, Thompson (1985, p. 118) was doubtful whether any bones had been found in the aeolian Grinshill Sandstone Formation, noting (D.B. Thompson, pers. comm.) specimens only from his largely fluvial Facies A of the Tarporley Siltstone Formation, in the operating quarry (SR 526 238).

Mr John O'Hare, the former quarry owner, is certain that the Keele University (1984) *Rhynchosaurus* specimen came from the lowest 0.2 m of the Tarporley Siltstone Formation. The

1986 and 1991 finds are in large blocks of coarse sandstone, which are most likely to have come from the hard burr stones at the top of the aeolian Grinshill Sandstone (D.B. Thompson, pers. comm., 1993).

The Grinshill specimens of *Rhynchosaurus* are largely complete (Figure 4.5) and undisturbed, but the bone material is soft and friable. The skeletons tend to lie flat in the dorso-ventral plane with the limbs stretched out to the sides: this suggests relatively rapid burial with little scavenging or transport.

The commonest tetrapod tracks at Grinshill are of the 'rhynchosauroid' type termed rhynchosauroid D1 by Beasley (1902); rarer finds include *Cheirotherium* prints, all from the Tarporley Siltstone Formation. The remainder are small prints, possibly of a different vertebrate type. These include small arcs of claw marks ('type C') and more or less complete 'hand'-shaped marks which could be of the same foot type ('type B'). The rhynchosauroid prints are generally small (15–20 mm across) and, when well preserved, they show clawed digits with an opposing associated impression. Single slabs may preserve a variety of impressions belonging to a number of overlapping trackways.

The tracks are most frequently preserved in sandstone as negative moulds on the undersurface of current and wave ripple-marked horizons. The ripples are asymmetrical and, because they are on an undersurface, their crests are well preserved. The preservation of these trackways is excellent. One slab preserves 11 distinct sets of claw prints, and in some specimens there is clear indication that the claws were twisted sideways (revealing their arcuate shape) as the foot was impressed into the sediment. Another specimen (JSW GH 3) exhibits a more or less circular area of sediment disturbance, which appears to suggest that the animal had been engaged in some activity such as eating from the ground. Other specimens exhibit regular series of impressions which appear to be teeth or jaw marks. More details of the taphonomy of the skeletons and footprints are given in Benton *et al.* (1994).

Fauna

Diapsida: Archosauromorpha: Rhynchosauridae

Rhynchosaurus articeps Owen, 1842

About 17 individuals: SHRBM, SHRCM, BMNH, MANCH, BATGM, Keele Univ; some specimens have been missing since the 19th century and the total could be greater

Footprints

Rhynchosauroides sp.

23 slabs: SHRBM, MANCH, WARMS, BGS(GSM), BUGD, others in private hands

Cheirotherium sp.

Two slabs: SHRBM, SHRCM.

Interpretation

On the basis of palynological evidence Warrington (1970b) dated the basal Helsby Sandstone Formation as Scythian, a view followed by Pattison *et al.* (1973), and by Warrington *et al.* (1980, p. 33, table 4) who placed the overlying Tarporley Siltstone Formation in the Anisian. However, a more recent assessment of the palynological data (Warrington, *in* Benton *et al.*, 1994) confirms an Anisian age for both formations (Figure 4.2).

The ages have also been debated on the basis of the reptiles. Walker (1969, 1970a) argued that all relevant horizons were of Mid Triassic age because of the resemblance between *Rhynchosaurus* and *Stenaulorhynchus*, and because of the purported intermediate evolutionary position of *Rhynchosaurus* between Early and Late Triassic rhynchosaurs. Its closest relative seems to be *Stenaulorhynchus* from the Manda Beds (?Anisian), of Tanzania, although it seems slightly more advanced in some respects according to Walker (1969). *Stenaulorhynchus* and *Rhynchosaurus* were grouped in the subfamily 'Rhynchosaurinae' (Chatterjee, 1974, 1980; Benton, 1983d), but this view has not been supported in more recent analyses (Benton, 1990c).

Rhynchosaurus articeps was a relatively small reptile, about 0.5 m long, and probably like a large lizard in appearance (Figure 4.5). The triangular skull (60–80 mm long) is low and broad at the back, and it shows all the typical rhynchosaur features of beak-like premaxillae, a single median naris and fused parietal. The dentition was specialized, as in other rhynchosaurs, consisting of a grooved maxillary tooth plate with several rows of teeth and a lower jaw (that slots into the groove) with teeth on the upper edge and down the inside surface. The pattern of wear, and the nature of the jaw joint, suggest that *Rhynchosaurus* had a precision shear bite, as in other rhynchosaurs, with no back and forwards

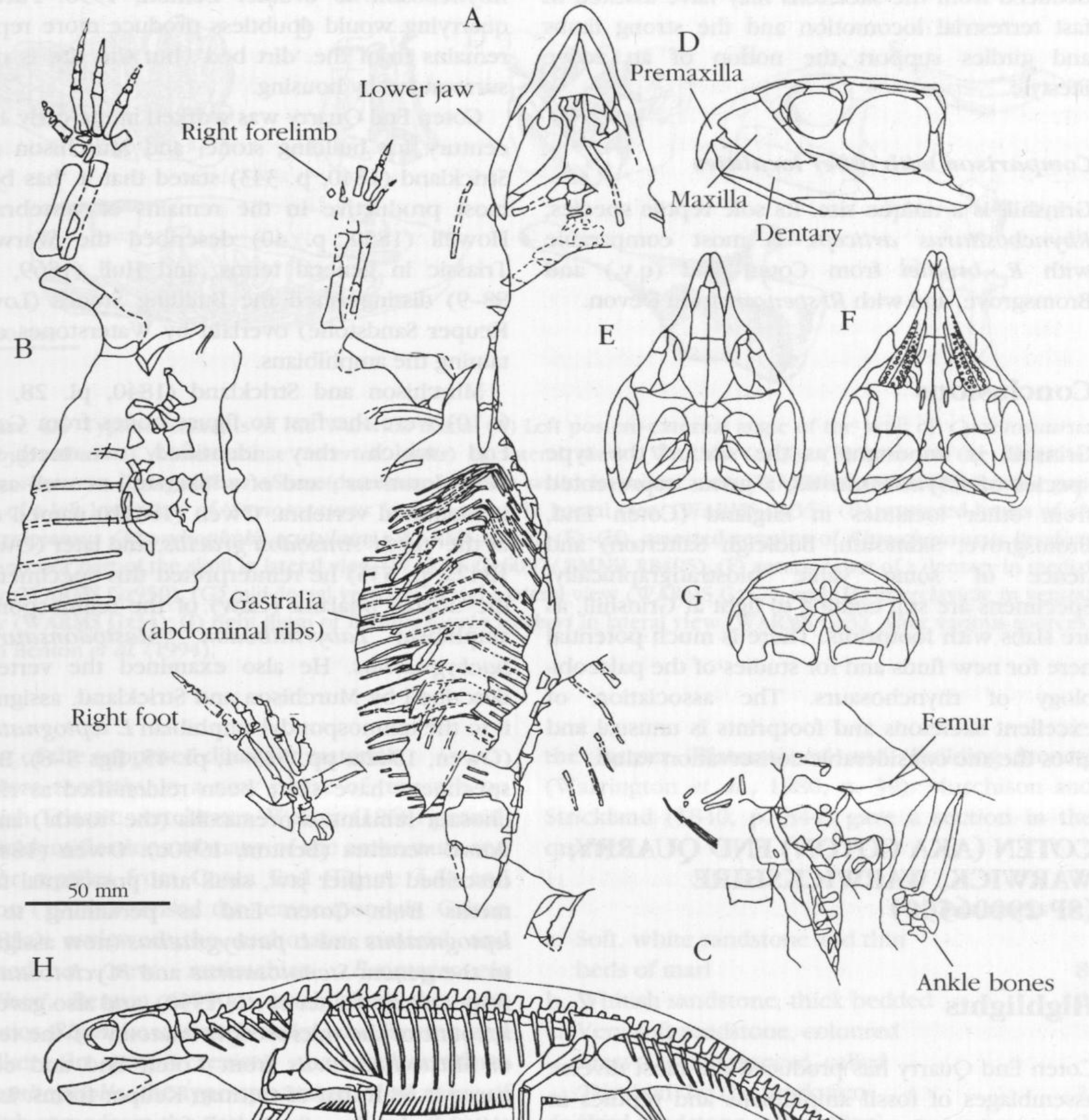

Figure 4.5 *Rhynchosaurus articeps*, the only member of the Grinshill skeletal fauna: typical fossil remains (A–C) and restorations (D–H). (A) Partial skeleton lacking the tail and the limbs of the left side, in ventral view (BMNH R1237, R1238); (B) dorsal vertebrae, ribs, and right forelimb in posteroventral view (SHRBM 6); (C) pelvic region, right leg with ankle bones, presacral vertebrae 22–25, sacral vertebrae 1 and 2, and caudal vertebrae 1–8 (BATGM M20a/b); (D)–(G) restoration of the skull, based on SHRBM G132/1982 and 3 and BMNH R1236, in lateral (D), dorsal (E), ventral (F), and occipital (G) views; (H) restoration of the skeleton in lateral view in walking pose. All based on Benton (1990a).

motion. The diet was probably tough vegetation, which was dug up by scratch digging, raked together with the fore feet or the premaxillary beak, and manipulated in the mouth by a large, fleshy tongue (Benton, 1990c).

The skeleton of *R. articeps* is relatively more slender than that of most other Mid and Late Triassic rhynchosaurs. This is probably an allometric effect resulting from its relatively smaller size. The slim body and the semi-erect limb posture deduced from the skeletons may have assisted in fast terrestrial locomotion and the strong limbs and girdles support the notion of an active lifestyle.

Comparison with other localities

Grinshill is a unique site. Its sole reptile species, *Rhynchosaurus articeps,* is most comparable with *R. brodiei* from Coten End (q.v.) and Bromsgrove, and with *R. spenceri* from Devon.

Conclusions

Grinshill is important as the site of the type species of *Rhynchosaurus*, a genus represented from other localities in England (Coten End, Bromsgrove, Sidmouth, Budleigh Salterton) and hence of some value biostratigraphically. Specimens are still coming to light at Grinshill, as are slabs with footprints. There is much potential here for new finds and for studies of the palaeobiology of rhynchosaurs. The association of excellent skeletons and footprints is unusual and gives the site considerable conservation value.

COTEN (AKA COTON) END QUARRY, WARWICK, WARWICKSHIRE (SP 29006550)

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

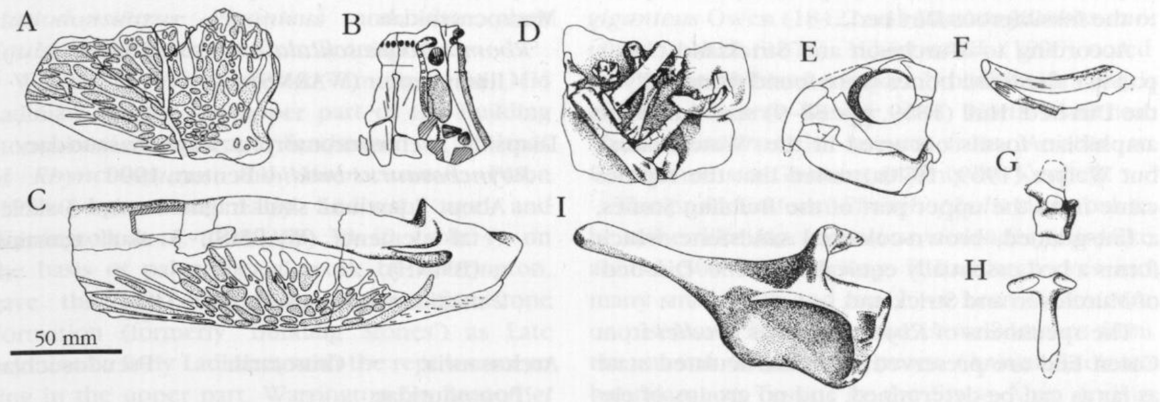

Figure 4.6 Typical elements of the Warwick fauna. (A) Left postero-external angle of the skull of '*Cyclotosaurus pachygnathus*' (Cyclotosaurinae *incertae sedis*) in lateral view (WARMS Gz13); (B) part of the snout of '*Stenotosaurus leptognathus*' (Stenotosaurinae *incertae sedis*) in palatal view (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); (I) right ilium of *Bromsgroveia walkeri* in lateral view (WARMS Gz3). After various sources; from Benton *et al.* (1994).

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. Galton (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.

GUY'S CLIFFE, WARWICK, WARWICKSHIRE (SP 293667)

Highlights

Guy's Cliffe is the site of a superb specimen of a large fish-eating amphibian, *Mastodonsaurus jaegeri*, one of the best-preserved examples of this group.

Introduction

The exposures in the grounds of Guy's Cliffe House and on the banks of the River Avon below which comprise Guy's Cliffe, display good sections in the Bromsgrove Sandstone Formation which yielded a fine specimen of *Mastodonsaurus* early in the 19th century. Although not a reptile but an amphibian tetrapod, this specimen is important in correlating the Triassic Warwick sandstones with those of Bromsgrove and Devon. Guy's Cliffe House is owned by freemasons; the property is fenced off and access is difficult, but re-excavation could produce further finds.

Buckland (1837) described the 'excellent section' at Guy's Cliffe as exposing Keuper sandstone. This age assignment was based on a find made in 1823 of 'part of the jaw and other bones of a saurian . . . presented to the Oxford Museum by the late Butic Greathead, Esq.' This was probably the first find of a tetrapod to be made in the area. Buckland (1837) identified the bones as those of *Phytosaurus*, a German form. The original specimen, although now lost, is well represented by casts.

Owen (1842a, pp. 537–8, pl. 44, figs 4–6, pl. 37, figs 1–3) and Miall (1874, p. 433) described Buckland's 'saurian'; in reality fine specimens of the lower jaw of the temnospondyl *Mastodonsaurus jaegeri*. Milner *et al*. (1990, p. 878) suggest that the Warwickshire material of *Mastodonsaurus*, including *M. jaegeri*, should properly be given *nomen dubium* status and redefined as *Mastodonsaurus* sp.

Howell (1859, p. 40) and Hull (1869, pp. 88–9) reviewed the lower Keuper Sandstone at Guy's Cliffe and elsewhere, and Huene (1908c) described sections at Guy's Cliffe and proposed that the outcrops provided evidence of subaerial dunes as well as water-laid deposits.

Description

Murchison and Strickland (1840, p. 344) published the following section from a quarry in the grounds of Guy's Cliffe House:

	Thickness (ft)
Sandstone and beds of marl	8
Solid sandstone, whitish or grey, occasionally of a reddish tint	12
Red, micaceous marl, with wedges of sandstone	8
Solid, light-coloured, reddish tinted sandstone,	*c.* 20
Total	48

Huene (1908c) showed cross-bedded sandstone units that had been eroded into a channel and covered by a discontinuous breccia layer in a section at Guy's Cliffe 'below the house of Lord Algernon Percy, on the bank of the Avon'. He noted that the bedding was very irregular and that ripple marks occurred over some beds. Another section figured by Huene 'on the rocky cliff opposite Guy's Cliffe House shows contorted sandstones with laterally discontinuous marl and breccia bands'. These features he attributed to the action of moving dunes 'near the border of the sea'.

Good sections of 7–10 m of cross-bedded, buff-coloured sandstone with irregular shale lenses are still exposed in the grounds of Guy's Cliffe House.

Behind the house is a yard which is bounded to the west by the house, to the north by a chapel and to east and south by rock. The outcrop has been chiselled vertical, and stables and hermit's holes are built into the rock on the south side. On the east is the historic Guy's Cave cut into the rock.

Fauna

'Temnospondyli': Mastodonsauridae.

Mastodonsaurus sp. (=*Mastodonsaurus jaegeri* Owen, 1842)
Remains of lower jaw – casts only

Interpretation

Buckland (1837) placed the Guy's Cliffe sandstone in the Keuper on the basis of the bones collected in 1823, misidentified by him as *Phytosaurus*, a form common in the German Keuper. However, Murchison and Strickland (1840, p. 346) assigned a Bunter age to the 'sandstone of Warwick, Bromsgrove and Ombersley', but were troubled by Buckland's 'saurian' which they attempted to explain away as a Bunter form.

Owen's (1842c, 1842d) recognition of the identity of the Warwick *Mastodonsaurus* with those of the German Keuper confirmed Buckland's view. Howell (1859, p. 40) and Hull (1869, pp. 88–9) confirmed the age of the sandstones of Guy's Cliffe and other Warwick localities as 'Lower Keuper'. Huene (1908c, 1908d) and Wills (1910) repeated the correlation of the Warwick and Bromsgrove sandstones and suggested their equivalence to the German Lettenkohle (Ladinian). Walker (1969) and Paton (1974a) suggested an Early Ladinian assignment on the basis of reptiles and amphibians respectively. Warrington (*in* Benton *et al.*, 1994) gave palynological evidence for an Anisian age, as at Coten End (see above), the most comparable locality.

Conclusions

Guy's Cliffe has produced a good specimen of *Mastodonsaurus jaegeri* (*Mastodonsaurus* sp.), a heavily built, fish-eating, crocodile-like amphibian (over 2 m long), the best British example of this species. The conservation value of the site relates largely to the importance of this fossil amphibian for correlating the Warwick sandstones and the potential for future finds.

MID TRIASSIC OF DEVON

The Mid Triassic of Devon is represented by the Otter Sandstone Formation. Inland, the formation has a poorly exposed outcrop in east Devon around the districts of Budleigh Salterton and Sidmouth and further inland beyond Honiton, but on the coast, between Sidmouth and Budleigh Salterton, it is exposed in a series of fine sea cliffs and the fossil vertebrate specimens come from these coast sections (Figure 4.7). The recent discovery of a rich vertebrate fauna from several localities between Budleigh Salterton and Sidmouth has provoked interest in the Otter Sandstone as a productive source of Middle Triassic vertebrates. The locality was known to the late Victorians, who had collected among the first known remains of *Rhynchosaurus* and good material of the amphibian *Mastodonsaurus* from the same localities, but their finds were rather sparse.

Two sites, one at Otterton Point, near Budleigh Salterton, and the other covering the cliffs nearer to Sidmouth, are selected. The former is primarily of historic interest as the locality at which the remains of Triassic vertebrates were first recognized from Devon.

4. Sidmouth coast section (SY 092838–SY 131873). Middle Triassic (Anisian), Otter Sandstone Formation.
5. Otterton Point, near Budleigh Salterton (SY 07758196). Middle Triassic (Anisian), Otter Sandstone Formation.

HIGH PEAK (SIDMOUTH), EAST DEVON (SY 092838–SY 131873)

Highlights

The Otter Sandstone Formation at Sidmouth is the richest active Mid Triassic reptile site in Britain. Ten or more species of amphibians and reptiles have been found here, most of them recently, and the site represents one of the most promising terrestrial reptile localities of its age anywhere in the world.

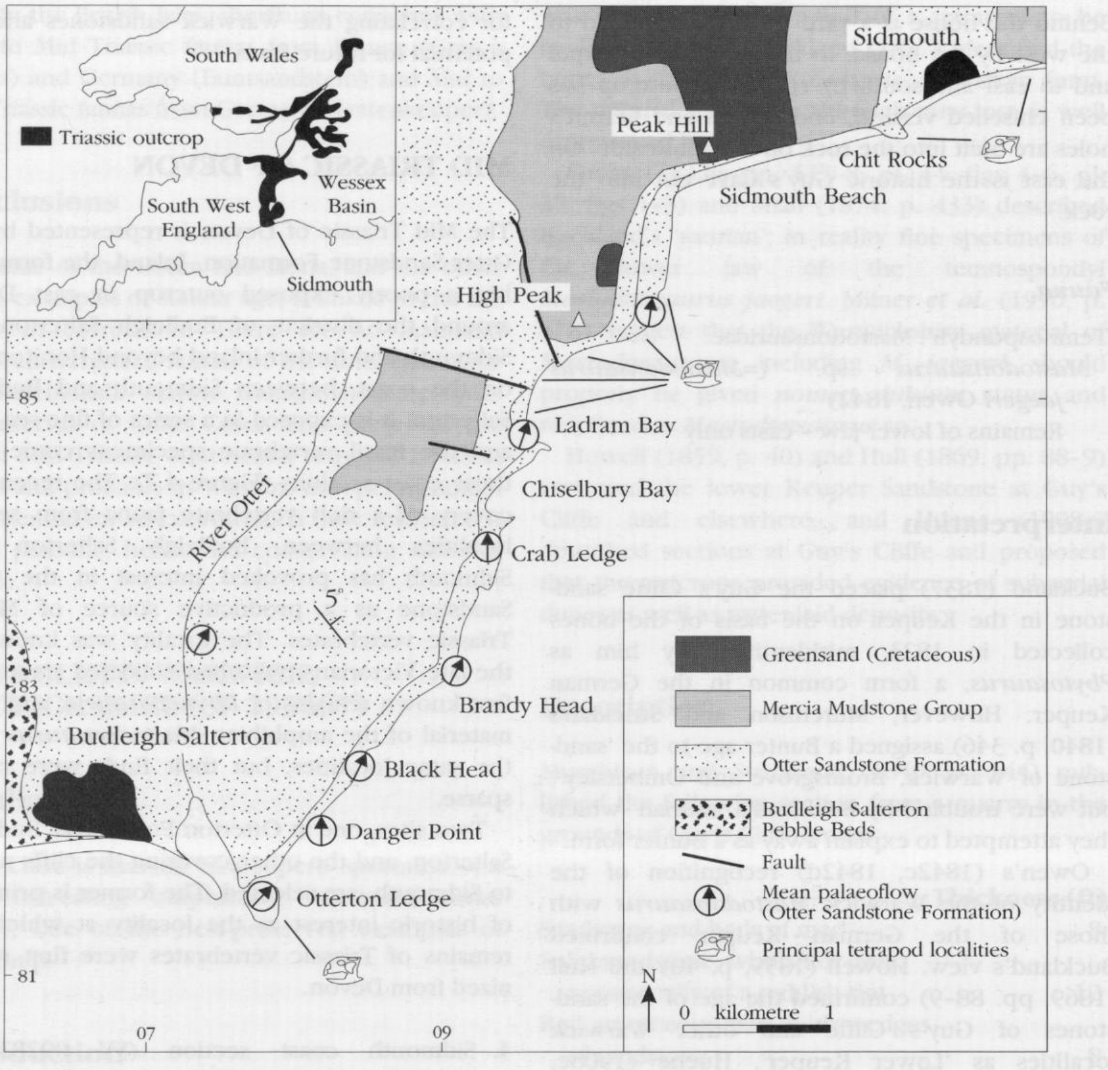

Figure 4.7 Map of the coastal outcrop of the Otter Sandstone Formation between Sidmouth and Budleigh Salterton, Devon. The major Triassic formations are indicated, together with mean fluvial palaeoflow directions, and principal tetrapod localities. From Benton *et al.* (1993).

Introduction

The fossiliferous beds are developed in the series of high cliffs to the west of Sidmouth between Chiselbury Bay (SY 092838) and Chit Rocks (SY 121869), and at Port Royal, just east of Sidmouth (SY 12978730). The whole locality (Figure 4.7) is important as one of the most productive sources of tetrapods of Mid Triassic age in Britain and fresh finds are made every year (1980–94) after cliff falls. However, it is difficult and dangerous to collect from the cliff face and most of the fossils have come from fallen blocks on the foreshore, or *in situ* from ledges at beach level (Figure 4.8).

Whitaker (1869) distinguished 'red sandstone' overlain by 'red marl' in the New Red Sandstone at High Peak (SY 144858), which is in turn overlain by Cretaceous Upper Greensand, and he reported the first finds of vertebrates from the Otter Sandstone Formation. Lavis (1876) reviewed the Sidmouth coast in more detail, and Seeley (1876a) described a fine lower jaw and other bones of *Mastodonsaurus lavisi* and a possible *Hyperodapedon* (=*Rhynchosaurus*) tooth plate which Lavis had collected. Hutchinson (1879) further reported fossil plant remains that he identified as stems of an equisete or calamite. Ussher (1876), Metcalfe (1884), Carter (1888), Irving (1888, 1892, 1893), Hull (1892) and

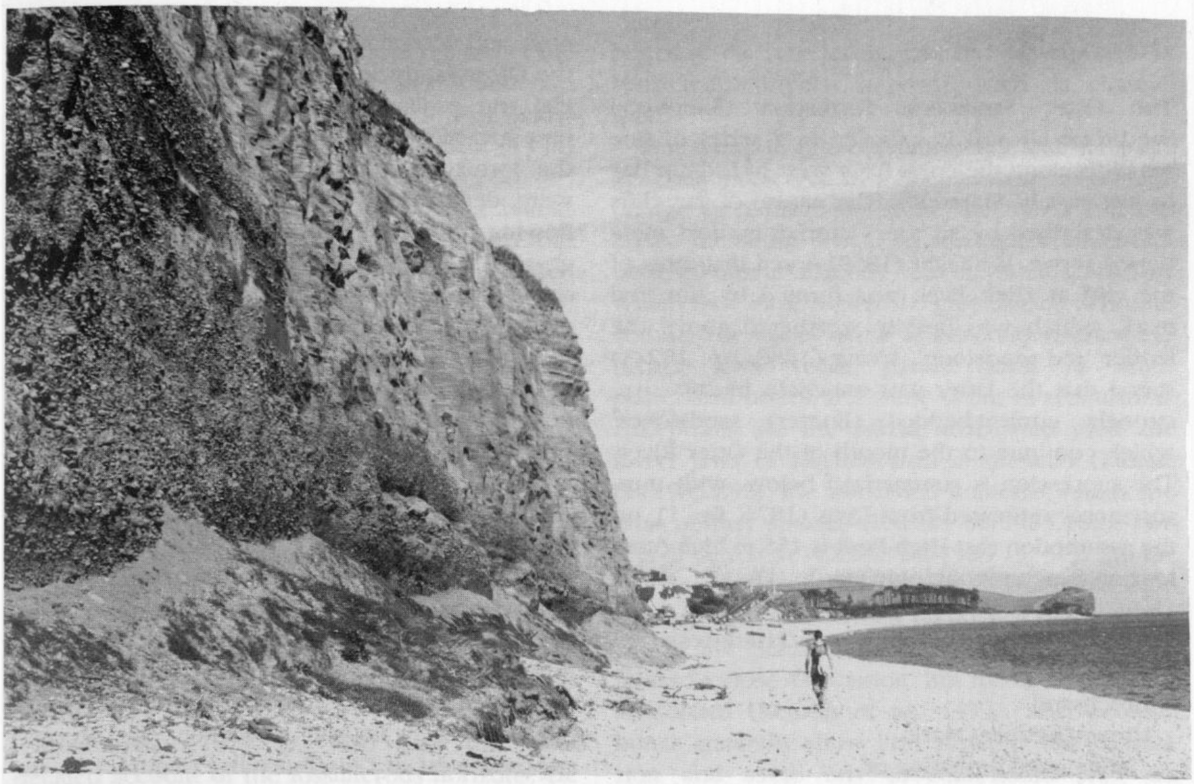

Figure 4.8 The Otter Sandstone Formation exposed in the cliffs west of Sidmouth, view looking east. Fish and reptile remains have been found at various horizons. (Photo: M.J. Benton.)

Woodward and Ussher (1911) discussed the stratigraphy and dating of the coastal section near Sidmouth, with particular attention to occurrences of fossil vertebrate material. Metcalfe (1884) figured remains of *Rhynchosaurus*, *Mastodonsaurus* jaws, and other bones collected from fallen blocks near High Peak, while Carter (1888) described further remains, including fish scales and coprolites.

A second phase of work on the Otter Sandstone Formation coast section began in the 1960s. Laming (1966, 1968) and Henson (1970) provided further information on the sedimentology and stratigraphy of the formation. Warrington *et al.* (1980), Laming (1982) and Warrington and Scrivener (1990) discussed the problems of correlating the Otter Sandstone with other Triassic sequences. Leonard *et al.* (1982), Selwood *et al.* (1984), Mader and Laming (1985), Lorsong *et al.* (1990), Mader (1990), Smith (1990), Purvis and Wright (1991), Smith and Edwards (1991) and Wright *et al.* (1991) carried out studies on the sedimentology of the Otter Sandstone Formation, focusing on the palaeosols and other climatic indicators. Spencer and Isaac (1983), Milner *et al.* (1990), Benton (1990c) and Benton *et al.* (1994) described collections of fishes and tetrapods made between 1982 and 1994 by P.S.S. that greatly enlarged the faunal list.

The Otter Sandstone Formation has been regarded as 'sparsely fossiliferous' (Spencer and Isaac, 1983). This mistaken impression may be the result of the steepness and height of the cliffs and the fact that most fossils so far collected have come from fallen blocks on the shore. The Sidmouth to Budleigh Salterton section has yielded the largest number of remains of fossil reptiles and amphibians from the New Red Sandstone of Devon, and one of the widest ranges of fossil amphibians and reptiles from the British Middle Triassic, and it continues to produce new finds. Type specimens of *Mastodonsaurus lavisi* and *Rhynchosaurus spenceri* come from High Peak, and other unusual finds include the ?ctenosauriscid neural spine, the tanystropheid tooth and the exquisite small procolophonids. These small fossils may be of biostratigraphic value.

Description

The Otter Sandstone Formation (Sherwood Sandstone Group) is exposed in a series of fine sea cliffs along the coast from west of Ladram Bay to just east of Sidmouth. The nature of the cliffs was described by all the Victorian authors mentioned above. Whitaker (1869) noted that most of the cliff at High Peak was formed by the 'red marl', which was heavily weathered above the harder 'red sandstone'. Irving (1888, pp. 152–3) stated that the latter was underlain by 'massive, strongly current-bedded (Bunter) sandstones' which continue to the mouth of the Otter River. The succession is summarized below, with measurements estimated from Lavis (1876, fig. 1), on the assumption that High Peak is 155 m high (contour on 6-inch topographic map).

	Thickness (m)
Chalk gravel	5
Greensand	30
Upper (Keuper) Marls (unnamed formation of Mercia Mudstone Group)	60
Otter Sandstone Formation	*c.* 60

The Otter Sandstone Formation (the 'red sandstone') comprises *c.* 118 m of medium- to fine-grained red sandstones which dip gently eastwards in the coast section. The formation continues northwards to Somerset and eastwards as far as Hampshire and the Isle of Wight beneath younger Triassic sediments (Holloway *et al.*, 1989). It rests unconformably on the Budleigh Salterton Pebble Beds, a 20–30 m thick unit of fluvial conglomerates (Henson, 1970; Smith, 1990; Smith and Edwards, 1991). The contact is marked by an extensive ventifact horizon (Leonard *et al.*, 1982) that represents a non-sequence of unknown duration and is interpreted by Wright *et al.* (1991) as a desert pavement associated with a shift from a semi-arid to an arid climate.

Calcretes occur abundantly at Otterton Point, Budleigh Salterton (see below), but farther east they are rarer and the formation is dominated by sandstones in large and small channels, with occasional siltstone lenses. The sandstones occur in cycles, often with conglomeratic bases, and fine upwards through cross-bedded sandstones to ripple-marked sandstones. The Otter Sandstone Formation is capped by water-laid siltstones and mudstones of the Mercia Mudstone Group.

Henson (1970), Laming (1982, pp. 165, 167, 169) and Mader and Laming (1985) interpreted the Otter Sandstone Formation as comprising fluvial and aeolian deposits. Sandstones near the base are aeolian, and middle and upper parts of the formation are of fluvial origin; sandstones were deposited by ephemeral braided streams flowing from the south and south-west (Selwood *et al.*, 1984). The comparatively thin mudstones are interpreted as the deposits of temporary lakes on the floodplain. The calcretes indicate subaerial soil and subsurface calcrete formation in semi-arid conditions (Mader and Laming, 1985; Lorsong *et al.*, 1990; Mader, 1990; Purvis and Wright, 1991). The climate was semi-arid, with long dry periods when river beds dried out, and seasonal or occasional rains leading to violent river action and flash floods.

Recent collections of amphibian and reptile bones have come from the top 40 m or so of the Otter Sandstone Formation and occur in all lithologies, but most commonly in intraformational conglomerates and breccias (Spencer and Isaac, 1983). Lower in the sequence, in breccias exposed west of Chiselbury Bay (Figure 4.7), the abundance of tetrapod finds declines significantly. The bones are generally in a fine- to medium-grained reddish sandstone that often contains clasts of pinkish, greenish or ochreous calcrete and mudflakes up to 20 mm in diameter. The more complete fish specimens are, however, preserved in dark red siltstone, sometimes in association with plants and conchostracan crustaceans. Plant remains are preserved in iron oxide in all the lower-energy deposits, and their occurrence appears to be controlled by the sedimentology.

The only specimens found *in situ* by Spencer and Isaac (1983, p. 268) came from 'the lowest of three intraformational conglomerates', but these were 'indeterminate bone fragments'. Since 1983, four rhynchosaur specimens (EXEMS 60/1985.284, 285, 292, and 7/1986.3) have been collected *in situ* from a single horizon at beach level, and a partial rhynchosaur skeleton was found at the top of the foreshore exposures in Ladram Bay in 1990 (EXEMS 79/1992). It is likely that fossils occur at numerous levels throughout the Otter Sandstone Formation, but most have been found in fallen blocks on the shore and locating the original horizons in the cliffs is difficult.

The Victorian authors believed that one or more discrete bone beds occurred at the eastern end of the outcrop. Lavis (1876) and Metcalfe

(1884) placed it 'about 10 feet from the top of the sandstone'; Hutchinson (1906) and Woodward and Ussher (1911) placed it 'about 50 feet below the base of the Keuper Marls', some 40 ft (13 m) lower in the section.

Lavis (1876) made his finds in fallen blocks from a 'fossiferous zone' consisting of up to four beds and 'characterized by lithological differences, in as much as the matrix is composed of much coarser sandstone, containing here and there masses of marl varying in size from that of a pea to that of a hen's egg. In these beds ripple-marks are very plentiful. The fragments of bone which are found in this zone seem to be very slightly water-worn'. Metcalfe (1884) gave further details of this locality at High Peak, stating that bones were found in fallen blocks of sandstone from a light-coloured band in the cliff close below the base of the 'Upper Marls' (Mercia Mudstone Group). Carter (1888) recovered bone material and coprolites from this locality.

Hutchinson (1879, p. 384) gave the most detailed account of the fossiliferous horizons. He found equisetalean plant stems in a bed at the top of the sandstone and 'about eight or ten feet above' two or three 'white bands' which appear as clear horizons in the cliff face. Then, 'one or two steps below' the White bands 'is what I venture to call the Saurian or Batrachian band, in which Mr Lavis found his Labyrinthodon; but I cannot exactly say how many feet this band is below the white bands, because the fall down of the under cliff has concealed the stratification at this place; but it may be fifty feet below and amongst the beds of red rock. Be that as it may, the Saurian band rises out of the beach somewhere under Windgate, as the hollow between the two hills is called, and ascends westwards into High Peak Hill, and having proceeded for about half-a-mile, and having attained a height of sixty or seventy feet above the sea, a fall of the cliff enabled Mr Lavis to find his specimens on the beach, and I was so fortunate as to see them soon afterwards.'

Woodward and Ussher (1911, pp. 12–13) summarized an unpublished section drawn up by Hutchinson in 1878 in which he located the bone bed '100 feet above the talus on the beach, and about 50 feet below the base of the Keuper Marls'. No trace of any tetrapod-bearing horizon in the form of a bone bed can be seen today, and there is no evidence that one existed. The Victorian geologists evidently expected to find bones at discrete levels, and had no concept of restricted lenticular deposits, such as channel lags.

The tetrapod fossils (Figures 4.9 and 4.10) are generally preserved in a fine- to medium-grained, orange to reddish sandstone that often contains clasts, including reworked rhizolith concretions, up to 20 mm in diameter, and claystone intraclasts which may have a pinkish, greenish or ochreous colour. The bones occur as generally isolated elements: jaws, teeth, partial skulls or single postcranial bones, but some occur in articulation. Exceptions are the partial articulated skull and lower jaws of *Rhynchosaurus spenceri* (EXEMS 60/1985.292), the associated humerus, radius and ulna of that species (EXEMS 60/1985.282), two sets of vertebrae (EXEMS 60/1985.15, 57), and the recently collected partial rhynchosaur skeleton (EXEMS 79/1992), which comprises much of the trunk, the pelvis and the hindlimbs, with the bones in close association, but mostly slightly disarticulated (Benton *et al.*, 1993). The tetrapod bones generally show little obvious sign of abrasion and some tiny procolophonid jaws are exquisitely well preserved. More details of taphonomy are given by Benton *et al.* (1994).

About half of the identifiable tetrapod bones found are rhynchosaur remains, and most of these are parts of the skull, especially the jaw elements, which have a high preservation potential. The amphibians are represented mainly by skull and pectoral girdle elements, all relatively dense and with characteristic sculpture. The small reptiles are represented by limited postcranial elements, a partial skull (with lower jaws articulated), teeth and small segments of jaw, and the larger archosaur(s) by teeth and vertebrae. Specimens of the fish *Dipteronotus* and fossil invertebrates (Figures 4.9J, 4.10H–J) obtained from a claystone lens, east of Windgate, are extremely well articulated and occur in association with a 'still water' fauna of branchiopod crustaceans.

Fauna

The faunal list of invertebrates, fishes, temnospondyl amphibians and reptiles is compiled from Benton (1990c), Milner *et al.* (1990) and Benton *et al.* (1994).

Arthropoda: Crustacea: Branchiopoda
Lioestheria
Carapaces of adults and juveniles (BRSUG)

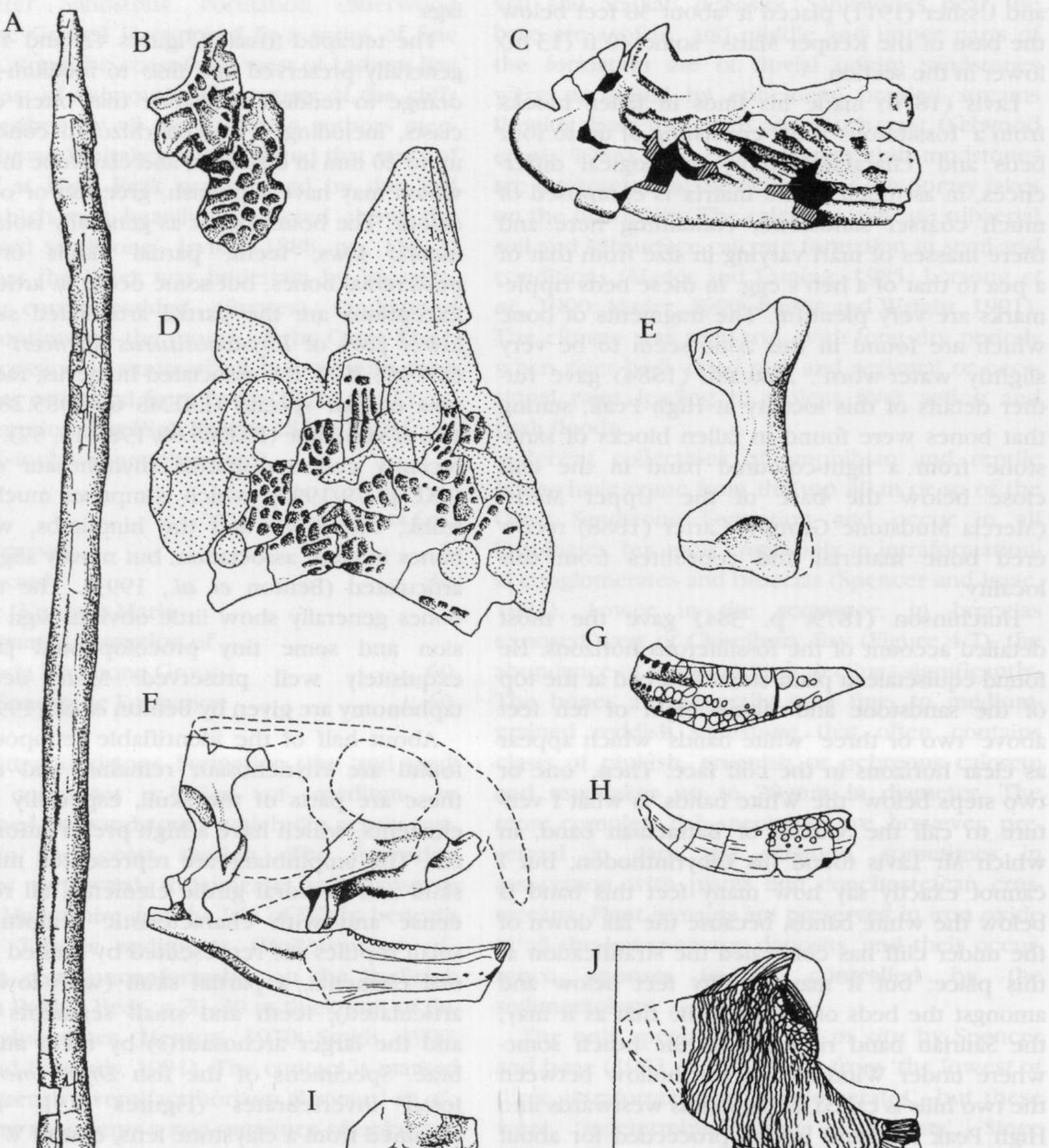

Figure 4.9 Larger elements of the Otter Sandstone Formation fauna of Devon. (A) Spine of an unknown vertebrate, possibly a dorsal neural spine of a ctenosauriscid archosaur (EXEMS 60/1985.88); (B) fragment of the skull roof of *Mastodonsaurus lavisi* in dorsal view (EXEMS 60/1985.287); (C) posterior portion of a right mandible of an unknown capitosaurid, in lateral view (EXEMS 60/1985.78); (D) incomplete skull roof of *Eocyclotosaurus* sp., in dorsal view (EXEMS 60/1985.72); (E)–(I) remains of *Rhynchosaurus spenceri*: (E) left humerus in ventral view (EXEMS 60/1985.282), (F) restored skull in right lateral view (EXEMS 60/1985.292), (G) right maxilla in ventral view (EXEMS 60/1985.292), and (H) right dentary in lingual view (BMNH R9190). (I) Vertebra of an archosaur (Bristol Univ. unnumb.); (J) the neopterygian ('palaeonisciform') fish *Dipteronotus cyphus* (EXEMS 60/1985.293). After various sources; from Benton *et al.* (1994).

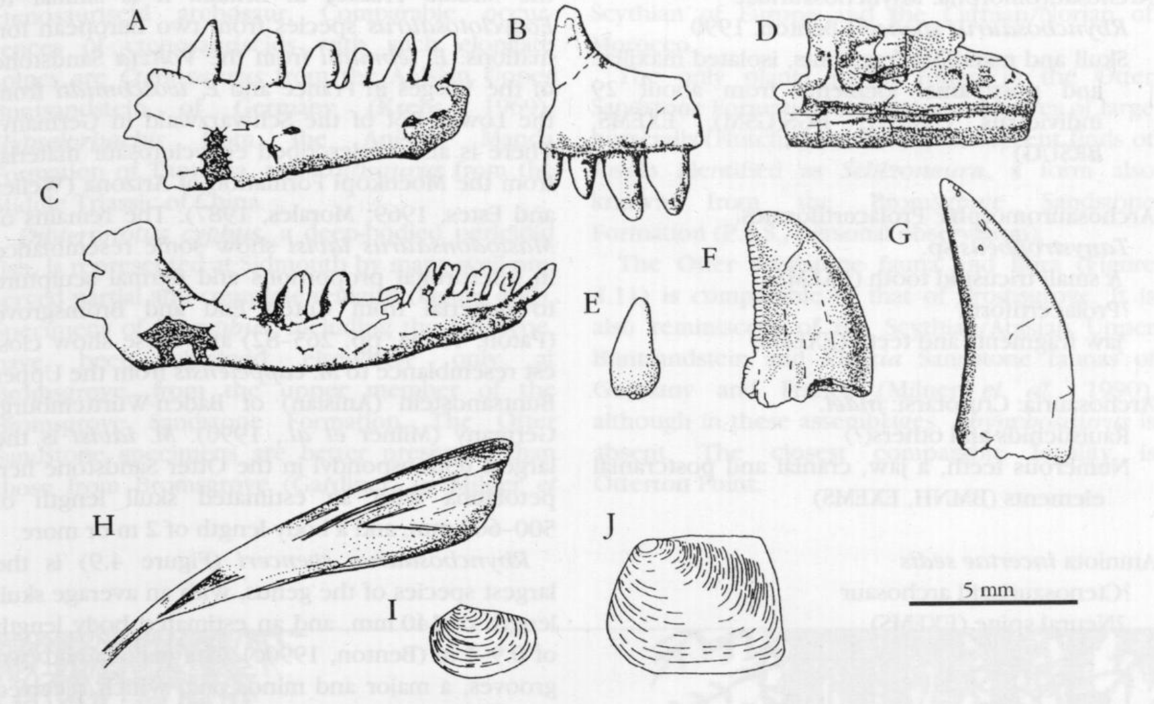

Figure 4.10 Smaller elements of the Otter Sandstone Formation fauna of Devon. Right dentaries (A, C) and a left maxilla (B) of a procolophonid, all in lateral view (EXEMS 60/1985.311, 3, and 154); (D) dentary fragment of an unknown small pleurodont reptile, showing pits for teeth, in lingual view; (E) tooth of ?*Tanystropheus*, showing small accessory cusps (EXEMS 60/1985.143); (F), (G) recurved teeth of two kinds of unknown archosaurs (BRSUG unnumb.); (H) unidentified insect wing (BRSUG unnumb.); (I), (J) carapaces of the conchostracan *Euestheria* (BRSUG unnumb.). After various sources; from Benton *et al.* (1993).

Euestheria
Carapaces of adults and juveniles (BRSUG)

Arthropoda: Crustacea: Ostracoda
Two carapaces, apparently representing separate taxa (BRSUG)

Arthropoda: Insecta
Insect wing (BRSUG)

Mollusca: Bivalvia
Taxon unidentified; single valve (BRSUG)

Osteichthyes: Actinopterygii: Neopterygii: Cleithrolepididae
Dipteronotus cyphus Egerton, 1854
Complete specimens, pieces of flank, individual scales and spines (EXEMS)

Osteichthyes: Actinopterygii: 'Palaeonisciformes'
Gyrolepis(?) and others
Scales

Sarcopterygii: Dipnoi: Lepisosteidae
Lepisosteus sp.
Scales in coprolites

'Temnospondyli': Mastodonsauridae
Mastodonsaurus lavisi (Seeley, 1876), *nomen dubium*
Skull fragments and part of a lower jaw (BMNH, EXEMS)

'Temnospondyli': Benthosuchidae
Eocyclotosaurus sp
Remains of a skull and other fragments (EXEMS)

'Temnospondyli': Capitosauridae
Capitosauridae *incertae sedi*
Posterior part of mandible (EXEMS)

Anapsida: Procolophonidae
Procolophonid *incertae sedis*
Three small dentaries, a maxilla and an interclavicle (EXEMS, BRSUG)

Archosauromorpha: Rhynchosauridae
Rhynchosaurus spenceri Benton, 1990
Skull and mandible fragments, isolated maxillae and postcranial elements from about 29 individuals (BMNH, BGS(GSM), EXEMS, BRSUG)

Archosauromorpha: Prolacertiformes
Tanystropheus sp.
A small tricuspid tooth (EXEMS)
?Prolacertiform
jaw fragments and teeth (EXEMS)

Archosauria: Crurotarsi: *indet.*
Rauisuchids and others(?)
Numerous teeth, a jaw, cranial and postcranial elements (BMNH, EXEMS)

Amniota *incertae sedis*
?Ctenosauriscid archosaur
?Neural spine (EXEMS)

Interpretation

Attempts to recover palynomorphs from the Otter Sandstone Formation have so far not been successful (Warrington, 1971, and pers. comm. to P.S.S., 1983). Its age is poorly constrained by occurrences of Late Permian miospores in the lower part of the Permo-Triassic succession near Exeter (Warrington and Scrivener, 1988, 1990) and Carnian taxa in the Mercia Mudstone Group, 135 m above the Otter Sandstone Formation. The only other biostratigraphic indicator, the vertebrate fauna itself, is all that is available for consideration. Walker (1969, 1970a), Paton (1974a) and Benton (1990c) favoured a Ladinian age for the fauna, but Milner *et al.* (1990) argued that an Anisian age was most likely. The association of the perleidid fish *Dipteronotus cyphus* (Anisian–earliest Ladinian), *Eocyclotosaurus* (Late Scythian–Anisian), procolophonids (Scythian–Anisian), ?ctenosauriscid (Anisian–Carnian) and ?tanystropheid (Anisian–Ladinian) identifies the Anisian as the only shared date (Figure 4.2).

The remains of three forms of temnospondyl amphibian (*M. lavisi*, *Eocylotosaurus*, sp., capitosaur *incertae sedis*) are abundant in the Otter Sandstone Formation (Figure 4.9). These were all aquatic, superficially crocodile-like forms, and were probably carnivores or piscivores which fed at the waterside. The new eocyclotosaur material represents the first find of a benthosuchid from the Middle Triassic in Britain. It is similar to *Eocyclotosaurus* species from two European formations: *E. lehmani* from the *Voltzia* Sandstone of the Vosges in France and *E. woschmidti* from the Lower Röt of the Schwarzwald in Germany. There is also undescribed eocyclotosaur material from the Moenkopi Formation of Arizona (Welles and Estes, 1969; Morales, 1987). The remains of *Mastodonsaurus lavisi* show some resemblance in interorbital proportions and dermal sculpture to material from Coten End and Bromsgrove (Paton, 1974a, pp. 265–82) and these show closest resemblance to *M. cappelensis* from the Upper Buntsandstein (Anisian) of Baden-Württemburg, Germany (Milner *et al.*, 1990). *M. lavisi* is the largest temnospondyl in the Otter Sandstone herpetofauna with an estimated skull length of 500–600 mm, and a body length of 2 m or more.

Rhynchosaurus spenceri (Figure 4.9) is the largest species of the genus, with an average skull length of 140 mm, and an estimated body length of 0.9–1 m (Benton, 1990c). The maxilla had two grooves, a major and minor one, which received two matching ridges on the dentary when the lower jaw was in full occlusion. The genus *Rhynchosaurus* is also recorded from the Bromsgrove Sandstone Formation of the Midlands (*R. brodiei* at Coten End Quarry, Leamington, and Bromsgrove) and from Grinshill Quarry, Shropshire *(R. articeps)* (see above). *R. spenceri* is distinguished from these forms in having a larger skull length (140 mm), a skull that is broader than it is long (otherwise a character of Late Triassic rhynchosaurs) and a tendency for the tooth rows on the maxilla to 'meander'.

Some recently collected procolophonid remains (Figure 4.10A–C) appear to belong to a primitive form, and Fraser (in Milner *et al.*, 1990) suggested that they most closely resembled the Mid Triassic (Anisian) form *Anisodontosaurus greeri* from the Holbrook Member of the Moenkopi Formation of Northern Arizona, USA. Re-examination of the material by P.S.S. indicates that there may be up to three taxa, and the most closely related forms appear to be *Kapes*, *Tichvinskia* and *Phaanthosaurus* from the Lower and lower Middle Triassic Vetluga series of the Russian Platform.

A tricuspid tooth (Figure 4.10E), the sole specimen ascribed to the Tanystropheidae, is reminiscent of the teeth of *Tanystropheus* from the Anisian and Ladinian of Central Europe (Wild, 1980a).

An elongate element from the Otter Sandstone

(Figure 4.9A) may provisionally be assigned to a ctenosauriscid archosaur. Comparable occurrences of ctenosauriscids with such elongate spines are *Ctenosaurus* from the Anisian Upper Buntsandstein of Germany (Krebs, 1969), *Hypselorhachis* from the Anisian Manda Formation of Tanzania, and *Lotosaurus* from the Middle Triassic of China.

Dipteronotus cyphus, a deep-bodied perleidid fish, is represented at Sidmouth by many well-preserved partial and complete remains (Figure 4.9J). Specimens of *D. cyphus*, including the holotype, have been obtained elsewhere only at Bromsgrove, from the upper member of the Bromsgrove Sandstone Formation. The Otter Sandstone specimens are better preserved than those from Bromsgrove (Gardiner, *in* Milner *et al.*, 1990). *Dipteronotus* is known also from the Scythian of Europe and the Carnian/Norian of Morocco.

The only plants so far found in the Otter Sandstone Formation are stems and leaves of large horsetails (Hutchinson, 1879), and recent finds of fossils identified as *Schizoneura*, a form also known from the Bromsgrove Sandstone Formation (P.S.S., personal observation).

The Otter Sandstone fauna and flora (Figure 4.11) is comparable to that of Bromsgrove. It is also reminiscent of the Scythian/Anisian Upper Buntsandstein and *Voltzia* Sandstone faunas of Germany and France (Milner *et al.*, 1990), although in these assemblages, *Rhynchosaurus* is absent. The closest comparable locality is Otterton Point.

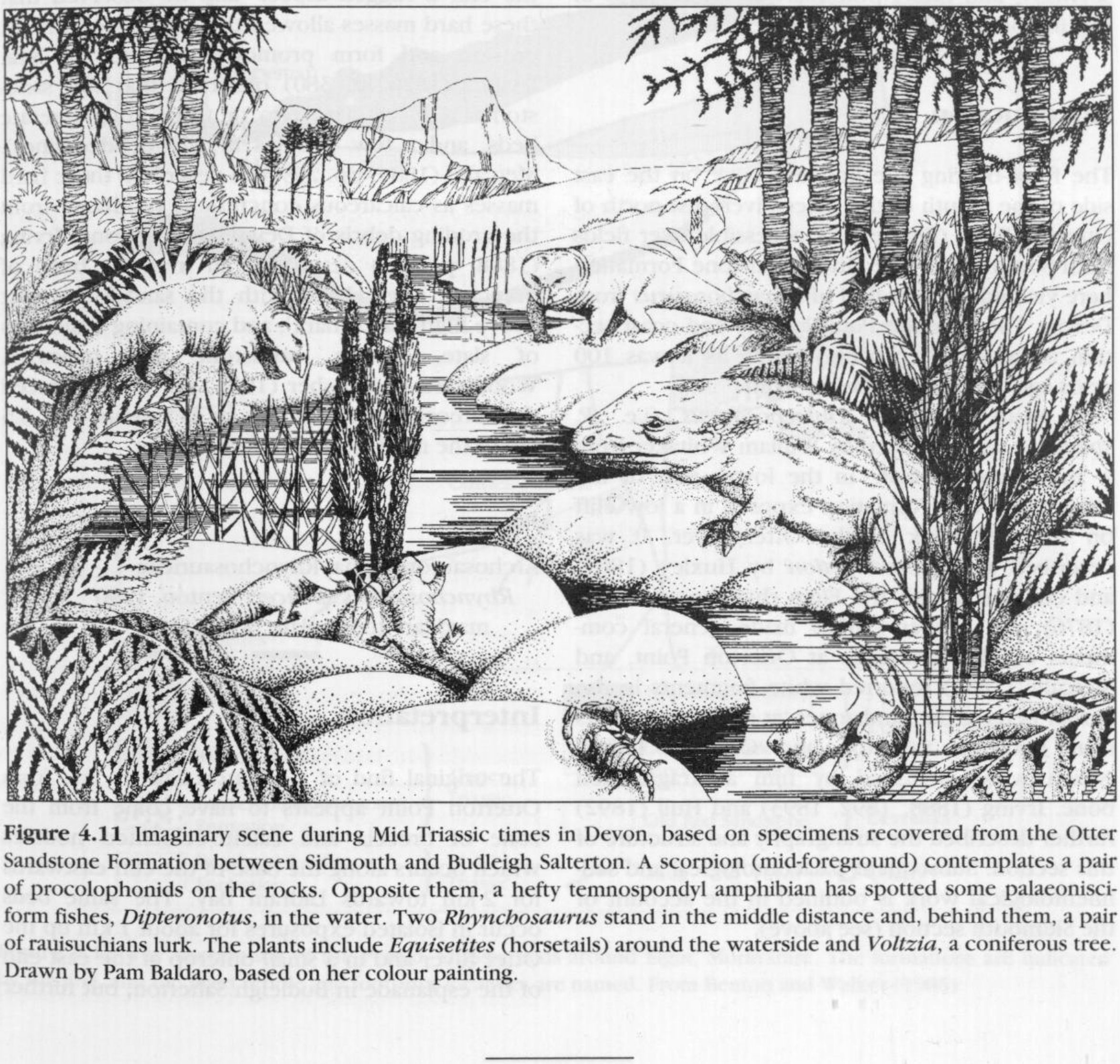

Figure 4.11 Imaginary scene during Mid Triassic times in Devon, based on specimens recovered from the Otter Sandstone Formation between Sidmouth and Budleigh Salterton. A scorpion (mid-foreground) contemplates a pair of procolophonids on the rocks. Opposite them, a hefty temnospondyl amphibian has spotted some palaeonisciform fishes, *Dipteronotus*, in the water. Two *Rhynchosaurus* stand in the middle distance and, behind them, a pair of rauisuchians lurk. The plants include *Equisetites* (horsetails) around the waterside and *Voltzia*, a coniferous tree. Drawn by Pam Baldaro, based on her colour painting.

Conclusions

The coast at Sidmouth offers vast potential for study of Mid Triassic reptiles. New finds are made all the time *in situ* and in fallen blocks, with erosion constantly supplying new specimens. This potential and the importance of past finds give the site its conservation value.

OTTERTON POINT (BUDLEIGH SALTERTON), EAST DEVON (SY 07758196)

Highlights

The Otter Sandstone Formation at Otterton Point is the source of a specimen of *Rhynchosaurus spenceri*, and offers potential for future finds of this important Mid Triassic reptile.

Introduction

The fossil-bearing site lies in a cove on the east side of the mouth of the Otter River, just north of Otterton Point (Figure 4.7), accessible over fields from South Farm. The Otter Sandstone Formation here yielded the first find of *Rhynchosaurus* from Devon. The Otterton Point locality and coast section in general is probably much as it was 100 years ago, and fresh finds are likely.

A tooth plate of *Rhynchosaurus* (i.e. *R. spenceri*) was collected by William Whitaker from a 'brecciated horizon' in the lower part of the Otter Sandstone Formation exposed in a low cliff on the east bank of the Otter River. It was described as *Hyperodapedon* by Huxley (1869) and compared with the Elgin rhynchosaur. Lavis (1876) and Ussher (1876) made general comments on the sandstone at Otterton Point, and Metcalfe (1884) reported white fragments in the harder beds of the sandstones 'at numerous points near Budleigh Salterton and Otterton Point', which were identified by him as fragmented bone. Irving (1888, 1892, 1893) and Hull (1892) further described the stratigraphy and structure of this section. Subsequent palaeontological and sedimentological work is outlined in the account of the Sidmouth section (see above).

Description

At Otterton Point hard, calcite-cemented, cross-bedded sandstone units (less than 0.5 m thick) in the Otter Sandstone Formation contain calcite-cemented rhizoliths, up to 1 m deep, and other calcrete formations (Mader, 1990; Purvis and Wright, 1991). Purvis and Wright (1991) attributed the large vertical rhizoliths to deep-rooted phreatophytic plants which colonized bars and abandoned channels on a large braidplain. The sedimentology of the Otter Sandstone Formation is more fully described in the Sidmouth account (see above).

These phenomena were noted by earlier authors. Whitaker (1869) commented that 'on the left bank of the Otter [the sandstone] has, in parts a brecciated character'. Lavis (1876) noted that the sandstones at Otterton Point 'contain curious irregular branching-shaped masses of harder texture, which withstand the weathering and give the cliff a rugged aspect' and he observed that these hard masses allowed the sandstone to resist erosion and form promontories into the sea. Ussher (1876, p. 380) observed that the sandstones here 'contain two or three conglomerate beds, and a few pebbles in false-bedded lines'. Metcalfe (1884, pp. 259–60) described these hard masses as calcareous concretions produced from the eroding debris of Devonian limestone. Irving (1888, p. 153) described 'an irregular band of breccia... intercalated with the sandstones, just above high-water mark', and containing fragments of slate, granite, sandstone and quartzite. Woodward and Ussher (1911, pp. 10–11) traced this 'brecciated horizon' as far as Ladram Bay, 3.5 km to the north-east of Otterton Point.

Fauna

Archosauromorpha: Rhynchosauridae
Rhynchosaurus spenceri Benton, 1990
maxillary tooth-plate BGS(GSM)

Interpretation

The original find of a *Rhynchosaurus* jaw from Otterton Point appears to have come from the zone of breccia and calcite-cemented nodules which occurs along the base of the cliff eastwards for 2 km towards Ladram Bay. The same beds occur in isolated exposures for about 1 km up the Otter River and in a small outcrop at the east end of the esplanade in Budleigh Salterton, but further remains of *R. spenceri* have not been recovered from any of these localities. Professor R.J.G. Savage of Bristol University washed and sieved loose matrix from some of these exposures along the Otter River and obtained numerous remains of fish, including isolated teeth, scales and spines, and a thecodont tooth fragment (pers. comm. to P.S.S., 1983).

Comparison with other localities (see the account of the Sidmouth site)

Conclusions

Otterton Point yielded the first evidence of Mid Triassic reptiles from Devon, and formed a useful point of comparison with localities elsewhere in England, especially with the larger Sidmouth section. The importance of past finds and the potential for new ones gives the site its conservation value.

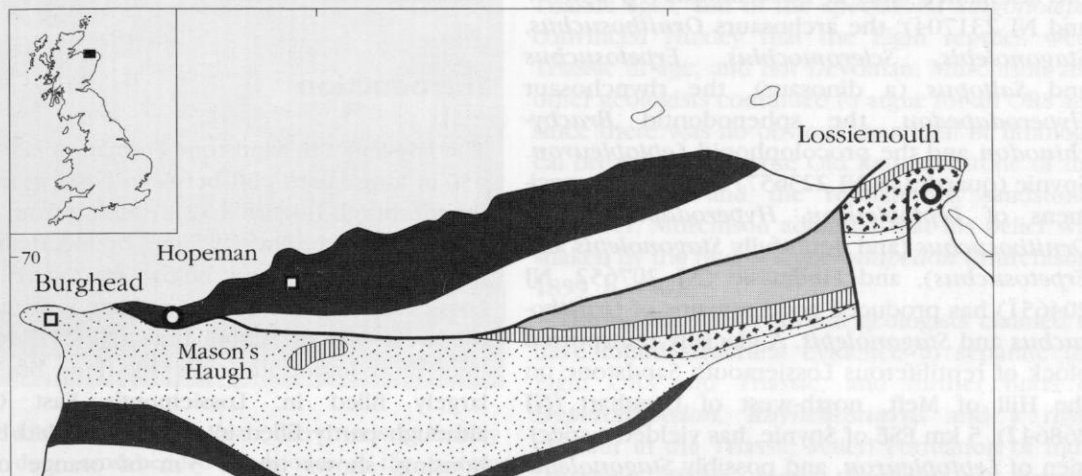

Figure 4.12 The distribution of the Permo–Triassic beds around Elgin, Morayshire. The formations are indicated by shading, and the main reptile and footprint localities are named. From Benton and Walker (1985).

LATE TRIASSIC OF SCOTLAND

The Lossiemouth Sandstone Formation (Late Carnian) of Grampian, Scotland is famous for its reptile fauna. The outcrop is distributed in three fault-bounded blocks at Lossiemouth, Findrassie and Spynie, and in an east–west strip about 2 km south-west of Lossiemouth (Figure 4.12). Finds of reptiles are restricted to several small quarry workings at Spynie and Findrassie and the coast section at Lossiemouth, where finds came from excavations at Lossiemouth East and West Quarries. The largest fauna has been obtained from the last-named sites at Lossiemouth (NJ 236707 and NJ 231704): the archosaurs *Ornithosuchus, Stagonolepis, Scleromochlus, Erpetosuchus* and *Saltopus* (a dinosaur), the rhynchosaur *Hyperodapedon*, the sphenodontid *Brachyrhinodon* and the procolophonid *Leptopleuron*. Spynie (quarries at NJ 223657) has yielded specimens of *Leptopleuron, Hyperodapedon* and *Ornithosuchus* (and doubtfully *Stagonolepis* and *Erpetosuchus*), and Findrassie (NJ 207652, NJ 204651) has produced good remains of *Ornithosuchus* and *Stagonolepis*. A glacially transported block of reptiliferous Lossiemouth Sandstone on the Hill of Meft, north-west of Urquhart (NJ 268642), 5 km ESE of Spynie, has yielded a specimen of *Leptopleuron*, and possibly *Stagonolepis* scutes (Taylor, 1920). All the reptile-bearing localities can be correlated on the basis of identical reptile assemblages and on lithology, and it is likely that the Lossiemouth Sandstone Formation at Lossiemouth East and West Quarries is the same as that at Spynie and Findrassie. Three locations are selected as GCR sites:

1. Lossiemouth East Quarry (NJ 236707), Upper Triassic (upper Carnian), Lossiemouth Sandstone Formation.
2. Spynie (NJ 223657). Upper Triassic (upper Carnian), Lossiemouth Sandstone Formation.
3. Findrassie (NJ 207652, NJ 204651). Upper Triassic (upper Carnian), Lossiemouth Sandstone Formation.

LOSSIEMOUTH EAST QUARRY (NJ 236707)

Highlights

Lossiemouth East Quarry is one of the richest Late Triassic reptile sites in Britain, the source of superb specimens of six species of archosaur, one procolophonid and a sphenodontid. Four of the reptiles have been found nowhere else. The reptiles from this site are important in making palaeobiogeographical interpretations for the Late Triassic: the most similar faunas elsewhere are in India and South America.

Introduction

The Lossiemouth Sandstone Formation is seen in a 450 m long raised cliff between Lossiemouth and Branderburgh (Figure 4.12), running from School Brae to the old railway station, bounded above by Prospect Terrace and below by Quarry Road. Lossiemouth West Quarry, which is located on the west side of School Brae (NJ 231704), was once more important for reptile finds, but is now largely filled in. Lossiemouth East Quarry, although partly filled in and surrounded by new housing, shows up to 3 m of orange or grey weathering, jointed sandstone in its eastern part (Figure 4.13) and partially to the west. Fossils could still probably be collected at the lower level of the East Quarry, which seems to have been the location of the reptile band. Neville Hollingworth obtained pieces of bone and a good skull of *Leptopleuron*, from the nearby beach in 1979.

Building stone was quarried in Lossiemouth as early as 1790, where two hills 'abound with excellent quarries in white and yellow free-stone, which is not to be found anywhere else in the Moray Firth. About 20 masons, including apprentices, and nearly double that number of labourers, are constantly employed in quarrying and dressing stones, to supply the demand for that article from this and neighbouring counties' (Lewis Gordon in Sinclair, 1793, vol. 4, p. 78). The West Quarry had ceased to work by 1912, but the larger East Quarry continued in operation until 1936 or later (according to County valuation rolls).

In 1844 a workman named Anderson collected a slab bearing casts of 31 scales, or scutes, at Lossiemouth. These he passed to the Elgin town clerk and geologist, Patrick Duff, who tried with-

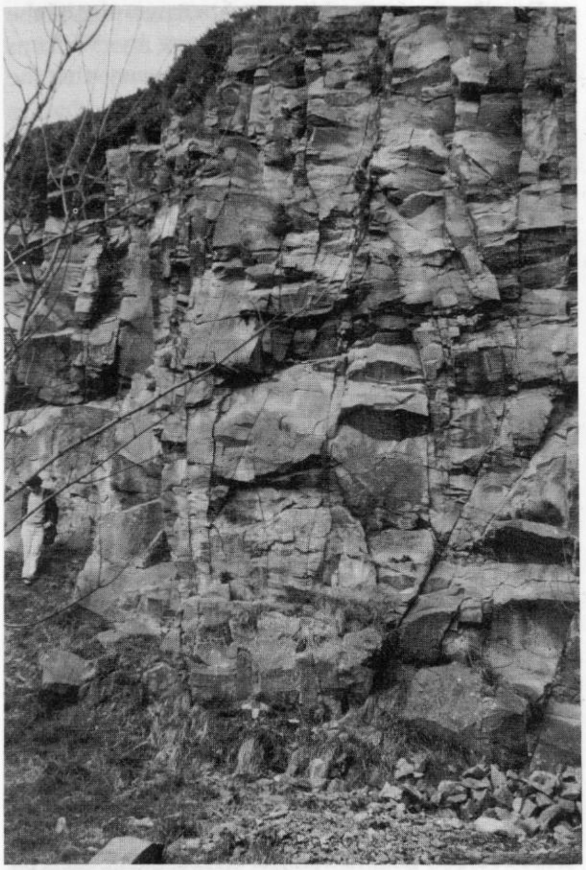

Figure 4.13 Lossiemouth East Quarry: view of heavily jointed dune cross-bedded sandstones at the eastern end of the site. Reptile skeletons were found at the base of the quarry. (Photo: M.J. Benton.)

out success to have them identified in Edinburgh. Eventually, he sent drawings to the Swiss palaeontologist, Louis Agassiz, who identified them as belonging to an Old Red Sandstone (ORS) fish related to the large ganoid *Gyrolepis*. He named it *Stagonolepis robertsoni* after Alex Robertson, a local geologist (Agassiz, 1844, p. 139, pl. 31, figs 13 and 14). On the basis of this find, it seemed clear to Agassiz that the age of the Lossiemouth beds was Devonian, as had been previously assumed largely on the basis of lithological similarity with neighbouring sediments of undoubted Old Red Sandstone age.

In 1858 Mr Martin, schoolmaster in Elgin, 'detected . . . a bone, possibly the scapula of a reptile . . . It was near the same place that Mr Duff's specimen . . . of *Stagonolepis robertsoni* was found' (Gordon, 1859, p. 46). This bone was collected in sandstone beds behind the houses of Lossiemouth (Murchison, 1859, pp. 427–8), thus the East Quarry. Murchison collected further remains of limb bones in September, 1858, in company with George Gordon, minister of Birnie and naturalist. These remains were shown (Huxley, 1859a, 1859b) to be associated with the scutes of *Stagonolepis robertsoni* and proved that it was a reptile and, in particular, an ancestral crocodile according to Huxley (1875, 1877).

Some poorly preserved remains of another reptile were found at Lossiemouth by Gordon in April and May, 1859. These were interpreted as a rhynchosaur (Huxley, 1869) and named *Hyperodapedon gordoni* (Huxley, 1859a). The presence of an animal clearly closely related to the English *Rhynchosaurus* (from rocks of known Triassic age), and of the specialized *Stagonolepis* convinced Huxley that the Elgin reptiles were Triassic in age, and not Devonian. Murchison and other geologists continued to argue for an ORS age since there was no obvious structural or lithological break between true Old Red Sandstone of the Elgin district and the reptiliferous sandstone. However, Murchison admitted that his belief was shaken by the find of *Hyperodapedon* (Murchison, 1859, p. 436).

During the 1860s several geologists claimed to have found structural evidence to separate the Elgin ORS and Triassic, and further finds of *Hyperodapedon*, *Rhynchosaurus* and a rhynchosaur in the Triassic Maleri Formation of India (Huxley, 1869) were enough to convert Murchison and with him most other geologists: 'To such fossil evidence as this the field geologist must bow, I willingly adopt the view established by fossil evidence, and consider that these overlying sandstones and limestones are of Upper Triassic age' (Murchison, 1867, p. 267).

Further material of *Hyperodapedon* was described by Huxley (1887), Burckhardt (1900), Boulenger (1903) and Huene (1929a, 1938, 1939). Boulenger (1903) erected a new genus, *Stenometopon*, based on a specimen that supposedly differed from *Hyperodapedon*, but which is merely a distorted example (Benton, 1983d).

A well-preserved skeleton of *Leptopleuron lacertinum* (*Telerpeton elginense*) was collected by James Grant, a Lossiemouth schoolmaster, in 1866 and described by Huxley (1867a). This was the second specimen collected, the first having been found at Spynie in 1851 (see below). Further bones of *Stagonolepis* were also collected in the 1860s (Anon., 1864) which provided materials for detailed monographs by Huxley (1875, 1877).

In the early 1890s Grant discovered a small skull and partial skeleton built into a breakwater at Lossiemouth, probably originating from one of the Lossiemouth quarries; it was named *Erpetosuchus granti* by Newton (1894b). Between 1895 and 1920 William Taylor, a retired chemist and naturalist, collected extensively in both East and West Quarries at Lossiemouth. He supplied materials for further descriptions of *Hyperodapedon* (Boulenger, 1903), *Ornithosuchus* (originally collected at Spynie; Boulenger, 1903; Watson, 1909a; Huene, 1914), *Leptopleuron* (Boulenger, 1904a; Huene, 1912a, 1920), and type specimens of the new genera and species *Scleromochlus taylori* (Woodward, 1907b; Huene, 1914), *Saltopus elginensis* (Huene, 1910a) and *Brachyrhinodon taylori* (Huene, 1910b, 1912b). Recent redescriptions of much of this material have been published (Walker, 1961, 1964; Benton, 1983d; Benton and Walker, 1985; Fraser and Benton, 1989; Figure 4.14) and others are in preparation by M.J.B. and P.S.S.

Description

Lossiemouth West Quarry showed '30 ft of hard, white, fine-grained, laminated and even-grained sandstone . . . with about 5 ft of till on top. The rock is close jointed with a dominant west-north-west-trending set and a subordinate north-north-east set, both sets dipping nearly vertically. The former is composite (i.e. two joint directions with an angle of about 20 degrees between them) and the joints often carry fillings of barytes and brown fluorspar, such fillings being filled over an inch across in some places' (Peacock *et al.*, 1968, p. 67). There is probably a small NE–SW trending fault below School Brae since the floor of the East Quarry is rather higher than that of the West.

Lossiemouth East Quarry is located in a sea cliff which was extensively quarried, and still exposes sections showing up to 20 m of hard to friable, yellow and grey sandstone, weathering orange, and jointed in the eastern part. The sandstones may be finely laminated, but more usually they show large-scale cross-beds on well-weathered surfaces. An isolated 3 m high sea stack at the eastern end shows white dune-bedded sandstone. Further west in the quarry, near a footpath up the slope, various sections show purple ORS and mudstone at the base, surmounted by yellow or white, soft, thinly-bedded Triassic sandstone. A block of 'cherty rock' that overlies the reptile beds at Spynie and north of Lossiemouth is also seen here.

Details of cross-bedding and petrography of the Lossiemouth sandstones are given by Williams (1973). The section in the East Quarry that he gives is:

	Depositional environment	Thickness (m)
(Cherty Rock)	altered caliche	
Sago Pudding Sandstone	water-lain, reworked aeolian	1-2
Lossiemouth Sandstone Formation	aeolian	18
Burghead Sandstone Formation	fluviatile	*c.* 4
Upper Old Red Sandstone		

Most of the reptiles were apparently collected in the West Quarry, but only the East Quarry is now exposed to any extent. Murchison (1859, p. 428) stated that the bones found then were collected 'in the lowest part' of the freestones being quarried at Lossiemouth which were 'underlain by red strata' (?ORS). Gordon (1859, p. 46) confirmed this, stating that the lowest beds at Lossiemouth were red clay (i.e. within the ORS?), succeeded by yellowish soft sandstone and then harder sandstone. The red clay may be equivalent to that reported by Peacock *et al.* (1968, p. 65) as 'micaceous siltstone', the yellowish soft sandstone may be the 'Burghead beds equivalent', and the harder sandstone is probably the Lossiemouth Sandstone. The bones were found 'immediately under this hard siliceous sandstone, in a quarry half-way to the new harbour from Rockhouse, and in the face of the wall of rock that overhangs the houses fronting the old harbour.' This probably refers to the east end of Lossiemouth East Quarry (NJ 237707). Judd (1873, p. 137) stated that the reptiles were found '100 ft below the top of the sandstones', which would imply at about the base of the Lossiemouth Sandstone Formation, if its complete thickness is taken into account. Judd (1886a, pp. 397, 403) added that the reptile remains all came from 'a single band of soft rock'. Further, Gordon (1892, p. 245) states that most of the fossils were found at the level of the platform made by the quarrymen in the base of the quarry where the sandstone became 'softish and rubbly'. Williams (1973, p. 130) notes that 'the quarry floor approximates to the contact of the aeolian sandstones with the floodplain deposits' (the water-laid Burghead Beds), and the reptiles seem to have been found near to this transition.

The remains of reptiles are normally well preserved in articulation and only a few show disturbance, possibly through scavenging. Individual bones, particularly the smaller ones, show few signs of crushing or compression. The larger limb bones, however, appear to have been more susceptible to crushing and distortion and may show damage even when in association with other unaffected elements. The bone material is usually in a corroded state and may be partly leached out, but in a few specimens where the original material is present, internal structure may be clear, with cavities marked by replacement minerals. These minerals, which include iron oxide (goethite) and fluorite, sometimes overgrow bone margins adhering with the surrounding matrix, and in such cases are hard to remove. Most commonly, however, the Lossiemouth reptiles are preserved as external moulds in very well cemented sandstone, and details of bone form are best obtained from casts taken from the cleared natural rock moulds. Various methods that involve use of flexible synthetic 'rubbers' (e.g. RTV silicone rubber, PVC) have been employed in order to preserve the rock moulds and produce highly detailed copies of the bone (Walker, 1961, 1964, 1973; Benton and Walker, 1981).

Fauna

Anapsida: Procolophonidae
Leptopleuron lacertinum Owen, 1851 (=*Telerpeton elginense* Mantell, 1852)
c. 26 individuals: BMNH, NMS, EGNM

Lepidosauria: Sphenodontida
Brachyrhinodon taylori Huene, 1910
c. 10 individuals: BMNH, NMS, ELGNM

Archosauromorpha: Rhynchosauridae
Hyperodapedon gordoni Huxley, 1859
c. 29 individuals: BMNH, BGS(GSM), NMS, MANCH

Archosauria: Crurotarsi: Pseudosuchia: Stagonolepididae
Stagonolepis robertsoni Agassiz, 1844
6 large individuals: BMNH, AUZD, ELGNM, BGS(GSM)
11 small individuals: BMNH, AUZD, AUGD, NMS, ELGNM, BGS(GSM)

Archosauria: Crurotarsi: Ornithosuchidae
Ornithosuchus longidens (Huxley, 1877)
7 individuals: BMNH

Archosauria: Crurotarsi: *incertae sedis*
Erpetosuchus granti Newton, 1894
1 individual: BMNH
Scleromochlus taylori Woodward, 1907
5 individuals: BMNH
'Thecodontian'
1 individual: MANCH

Archosauria: Dinosauria: *incertae sedis*
Saltopus elginensis Huene, 1910
1 individual: BMNH

Interpretation

The Lossiemouth Sandstone Formation at Lossiemouth, Spynie and Findrassie is of the same age since it contains the same reptiles and is lithologically similar. It is placed in the Late Triassic on the basis of its varied reptile fauna (Walker, 1961; Benton, 1983d, 1986b, 1991, 1994a, 1994b). *Hyperodapedon* is represented in the Maleri Formation of central India and *Stagonolepis* (= *Calyptosuchus*) is reported in the lower part of the Petrified Forest Member of the Chinle Formation of Arizona (Hunt and Lucas, 1991b). The latter unit is dated palynologically as uppermost Carnian and the shared phytosaur *Paleorhinus* ties the lower part of the Petrified Forest Member to the Maleri Formation, and also to the Blasensandstein in Germany, and the marine Opponitzer Schichten of Austria, which are dated by ammonoids (Hunt and Lucas, 1991a, 1991b). On the evidence of these two reptile genera, the Lossiemouth Sandstone Formation is dated firmly as latest Carnian (Late Tuvalian palynological zone; *macrolobatus* ammonoid zone).

Lossiemouth has yielded specimens of all eight Late Triassic Elgin reptiles (Figures 4.14 and 4.15), so they will be discussed here. Each of the eight reptiles is unique to the Elgin area and some, in fact, have been placed in separate monogeneric families. Some of the reptiles (rhynchosaur, ornithosuchid) compare best with Gondwanaland faunas of similar age, such as those of the Maleri Formation in India, the Santa Maria Formation of Brazil and the Ischigualasto Formation of Argentina. Other elements (aetosaur, procolophonid, sphenodontid) are shared with the lower units in the North American Chinle Formation and

Dockum Group, and with some parts of the Keuper of Germany. However, the links with these northern faunas are surprisingly weak, despite their close proximity to Elgin in the Late Triassic: Elgin lacks the temnospondyl amphibians and phytosaurs which are so important in North America and Germany.

Leptopleuron lacertinum was a specialized procolophonid, about 175 mm in length, and may have resembled the present-day North American desert horned lizard (*Phrynosoma*). It had a triangular skull, when viewed from above, which bore spines, and the eye sockets were exceptionally elongated. *Leptopleuron* may have been a herbivore, but more probably it was an omnivore capable of feeding on a variety of food items; its deep jaws and row of transversely broadened molariform teeth would have made an efficient grinding mechanism. *Leptopleuron* was identified as a lizard by Owen (1851a), a batrachian (amphibian) by Mantell (1852) and a lacertilian (lizard) by Huxley (1867a). However, Boulenger (1904a) noted the affinities of *Leptopleuron* with *Procolophon* from South Africa, and reclassified these as Procolophonia in the Order Cotylosauria, the so-called 'stem reptiles'. *Leptopleuron* is most similar to an undescribed procolophonid from Fraser's (1985, 1988b) 'Site 1', a productive fissure fill locality at Slickstones Quarry (Cromhall Quarry), Avon, and both of these forms share affinities with the larger *Hypsognathus* from the Upper Triassic Newark Group of New Jersey, USA (Upper Triassic to Lower Jurassic: Olsen and Galton, 1977) and *Paotedon*, from Triassic rocks in Lin-Che-Yu, Pao-Te, north-western Shansi, China. P.S.S. is currently redescribing *Leptopleuron*.

The tiny sphenodontid *Brachyrhinodon* has acrodont teeth on the jaw margins and on the palate, and a very short snout (hence the name). The narial region is unusual as it overrides the premaxillary teeth. It probably lived a cryptic existence feeding on insects or fruit (Fraser and Benton, 1989). Walker (1966) suggested that *Brachyrhinodon* may be congeneric with *Polysphenodon* from the Middle Keuper of Hanover, but Fraser and Benton (1989) found that, in a cladistic analysis of sphenodontid rela-

Figure 4.14 The reptiles of the Late Triassic Lossiemouth Sandstone Formation, near Elgin, Morayshire. Skulls of (A) *Stagonolepis*; (B) *Hyperodapedon*; (C) *Ornithosuchus*; (D) *Erpetosuchus*; (E) *Leptopleuron*; (F) *Brachyrhinodon*; (G) *Scleromochlus*. From Benton and Walker (1985).

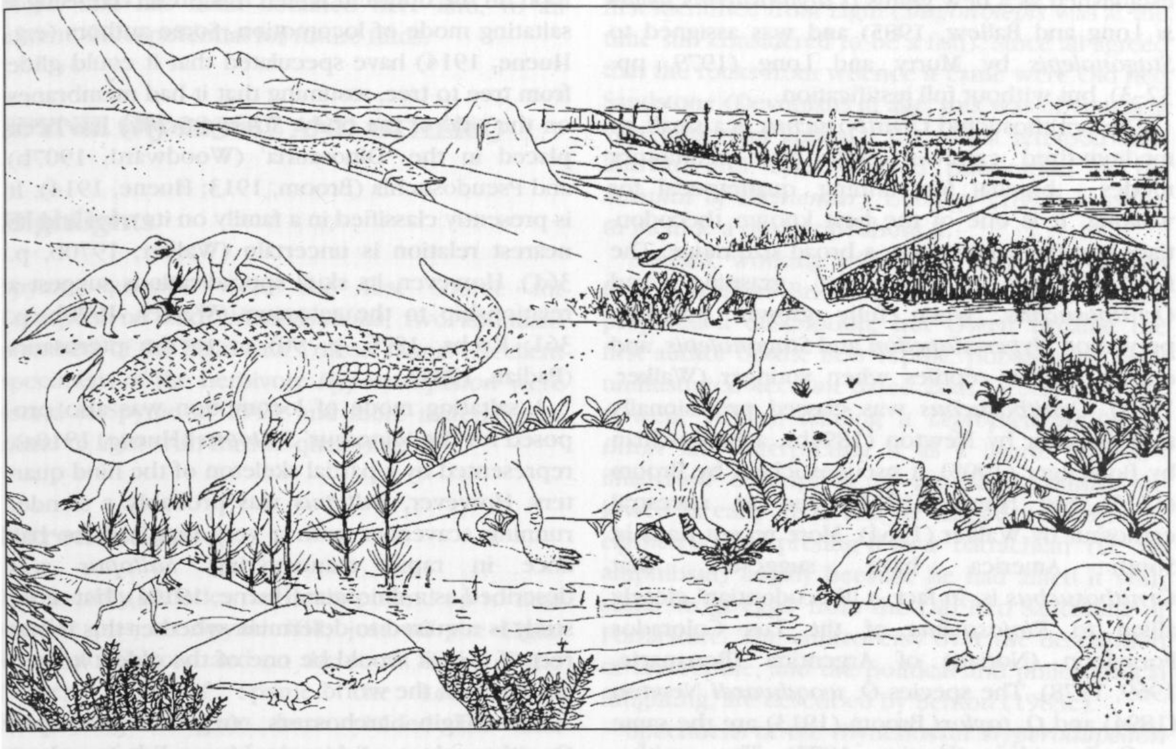

Figure 4.15 Imaginary scene at Elgin, Morayshire, in Late Triassic times, showing reconstructions of reptiles with typical Late Triassic plants. Three *Hyperodapedon* feed on seed-ferns in the foreground. Behind them, an *Ornithosuchus* runs towards the armoured *Stagonolepis* which is looking over its shoulder. Behind *Stagonolepis*, two *Erpetosuchus* feed on a small carcass. On the rocks in the left foreground are two *Leptopleuron*, a tiny *Brachyrhinodon* and a small bipedal dinosaur, *Saltopus*. To the right of the rocks is the tiny *Scleromochlus* at the side of the pond. In and around the pond there are horsetails, cycads and ferns, and there are tall lycopods in the distance. Based on a colour painting by Jenny Halstead. From Benton and Walker (1985).

tionships, the two were rather different.

Hyperodapedon was a bulky, 1.3 m long, terrestrial quadruped with strong limbs. The 100–200 mm long skull was very broad at the back – there was an anterior premaxillary 'beak' and the teeth were arranged in multiple rows on the maxilla. The dentary had a sharp edge and it cut into a groove on the maxillary tooth-plate. *Hyperodapedon* probably cut up tough plant material with a powerful precision shear bite. The massive, laterally flattened claws of the foot and the construction of the hind limb strongly suggest their use for scratch digging (Benton, 1983b, 1983d, 1984). *Hyperodapedon* was classified from the start with the English *Rhynchosaurus* and they were regarded as relatives of the living tuatara, *Sphenodon* (Huxley, 1869, 1887; Burckhardt, 1900; Boulenger, 1903; Huene, 1929a). *Hyperodapedon* is a typical Upper Triassic rhynchosaur, its closest relatives being *Hyperodapedon (Paradapedon) huxleyi* from the Maleri Formation of India, and *Scaphonyx* from the Santa Maria Formation of Brazil and Ischigualasto Formation of Argentina, all Late Carnian in age (Benton, 1983d, 1990c).

The aetosaur *Stagonolepis* has a roughly crocodile-like skull and peg-like teeth. The snout had a curious blunt end, probably for digging. Its body was well armoured with large scutes and it had powerful digging limbs (Walker, 1961). *Stagonolepis* was thought of as a 'ganoid' fish by Agassiz (1844) and as a crocodile by Huxley (1859b, 1875, 1877). Huene (1942) classed the genus as a pseudosuchian thecodontian, and Walker (1961) recognized its close affinities with *Aetosaurus* from the Stubensandstein (middle Norian: Anderson and Cruickshank, 1978; Tucker and Benton, 1982; Benton, 1986b, 1994a, 1994b) of Germany. Murry and Long (1989) and Hunt and Lucas (1991b) report *Stagonolepis wellesi* from the lower part of the Petrified Forest Member of the Chinle Formation of Arizona. This taxon was established as a new genus (*Calyptosuchus wellesi* Long and Ballew, 1985) and was assigned to *Stagonolepis* by Murry and Long (1979, pp. 32–3), but without full justification.

The ornithosuchid *Ornithosuchus* is a small- to medium-sized carnivore with two locomotory modes – bipedal for running, quadrapedal for walking. It is one of the best known thecodontians and the fossils show a broad size range. The forelimb was adapted for grasping, and *Ornithosuchus*, when fully grown, probably preyed on *Hyperodapedon* and *Stagonolepis*, and on the smaller reptiles when younger (Walker, 1964). *Ornithosuchus* was classed provisionally as a dinosaur by Newton (1894b), a parasuchian by Boulenger (1903), a pseudosuchian by Broom (1913) and Huene (1914), and an ancestral carnosaur by Walker (1964). More recent finds in South America have suggested that *Ornithosuchus* is, in fact, a 'thecodontian' closely allied to *Riojasuchus* of the Los Colorados Formation (Norian) of Argentina (Bonaparte, 1969, 1978). The species *O. woodwardi* Newton (1894) and *O. taylori* Broom (1913) are the same as *O. longidens* (Huxley, 1877). The ornithosuchids were placed on the dinosaur/pterosaur branch of archosaur evolution by Gauthier (1986), Benton and Clark (1988) and others, but Sereno and Arcucci (1990) and Sereno (1991b) argue that they fall on the crocodilian side of the Crurotarsi.

Erpetosuchus, another crurotarsal archosaur, has a narrow 75 mm long skull with a huge antorbital fenestra and a broad 'square' posterior skull roof. The carnivorous and/or insectivorous dentition is peculiar, with long sharp recurved teeth at the front of the jaws and toothless longtitudinal ridges behind which may have been used for crushing prey or for masticating the food to an extent prior to swallowing. The need to masticate food may also connect with the presence of an incipient secondary palate. *Erpetosuchus* was classed as a parasuchian by Newton (1894b) and as a pseudosuchian by Broom (1913), Huene (1914) and Walker (1970b). The nearest relations of *Erpetosuchus* are probably *Parringtonia* from the Manda Formation (Mid Triassic) of Tanzania, and possibly *Dyoplax* from the Upper Schilfsandstein (Late Carnian) of Baden-Württemberg.

Scleromochlus, represented by five specimens, has a relatively huge skull, nearly as long as the trunk, short forelimbs, but long hindlimbs and a long tail. The long hindlimbs have been interpreted (Woodward, 1907b; Huene, 1914) as adaptations for jumping and it may have sought food on the dunes in which it is preserved using a saltating mode of locomotion. Some authors (e.g. Huene, 1914) have speculated that it could glide from tree to tree, assuming that it had membranes on the side of the body. *Scleromochlus* has been placed in the 'Dinosauria' (Woodward, 1907b) and Pseudosuchia (Broom, 1913; Huene, 1914). It is presently classified in a family on its own and its nearest relation is uncertain (Walker, 1970b, p. 361). However, its skull specializations suggest a relationship to the aetosaurs (Walker, 1970b, p. 361; Krebs, 1976, p. 90) or to the pterosaurs (Padian, 1984).

A saltating mode of locomotion was also proposed for the 'dinosaur' *Saltopus* (Huene, 1910a), represented by a partial skeleton of the hind quarters. However, *Saltopus* was probably a slender running scavenger with a very long tail for balance in rapid manoeuvring. *Saltopus* was described as a dinosaur (Huene, 1910a), but more study is required to determine whether this is correct: if it is, it would be one of the oldest known dinosaurs in the world.

The Elgin archosaurs (e.g. *Stagonolepis, Ornithosuchus, Scleromochlus, Erpetosuchus*) have forced major changes in the classification of the order (e.g. Broom, 1913; Huene, 1914; Bonaparte, 1969; Krebs, 1976; Gauthier, 1986; Benton and Clark, 1988; Sereno and Arcucci, 1990; Sereno, 1991b). The very difficulty experienced in classifying many of these reptiles has demanded detailed redefinitions of the various families and, in particular, reappraisal of their relations to the dinosaurs and crocodiles.

Conclusions

The site is important for its distinctive reptiles of Late Carnian age, which include four genera of archosaurs, a sphenodontid and a procolophonid; four of the genera occur nowhere else. The fauna is unusual in showing close affinities with those of southern continents (India, South America), as well as with those of the rest of western Europe and North America and, in that the remains are preserved in aeolian deposits, clearly not the natural habitat of the majority of the animals. In evolutionary terms, many of the genera are unique, or belong to rare groups (e.g. *Scleromochlus, Erpetosuchus, Brachyrhinodon*).

The conservation value of the site lies mainly in the richness and uniqueness of the fossil reptile fauna that has been obtained here and, to an extent, in its potential for future finds.

SPYNIE (NJ 223657 AND OTHERS)

Highlights

Spynie quarries were the first source for *Leptopleuron* and *Ornithosuchus*, two abundant members of the Elgin Late Triassic fauna. Excellent specimens of the herbivore *Hyperodapedon* were found at Spynie in 1947, and more material may come to light with further quarrying.

Introduction

The locality includes one main pit and up to nine smaller pits on Spynie Hill, just off the Elgin-Lossiemouth road and on the south shore of the former Loch of Spynie. The Lossiemouth Sandstone Formation here yielded the first remains of the procolophonid *Leptopleuron* and of the ornithosuchid *Ornithosuchus*, and some good material of *Hyperodapedon*. Most of the Spynie quarries are overgrown and/or filled with debris. One large pit is still clear, however (Peacock *et al.*, 1968, Quarry no. 4), and has been worked a little recently. Fossils could be found in the lower beds with further working. Neville Hollingworth collected odd bone pieces from quarry refuse in about 1980.

Spynie Hill was worked before 1790: 'Under a thin stratum of marsh soil, the whole of this ridge seems to be a mass of excellent hard free-stone; of which there is a quarry, near the summit of the hill, that supplies a large extent of the country with mill-stones, and the town of Elgin and the neighbourhood with stones for building' (A. Gordon, *in* Sinclair, 1794, vol. 10, p. 629). The various pits were worked until the 1880s and do not appear to have operated again until recently. Moray Stone Cutters lease the main pit (to the east of the others) and have blasted in the 1980s (Figure 4.16).

In October 1851 William Young, a quarryman at Spynie, showed a small reptile, preserved as part and counter-part, to Patrick Duff (Anon., 1851). This was sent to London where various people examined it, including Charles Lyell, Gideon Mantell and Richard Owen. It was immediately recognized as a tetrapod, and was thus the first identified from Elgin (*Stagonolepis* was at the time still considered to be a fish). Since all agreed that the rocks from whence it came were Old Red Sandstone (Devonian) in age, this was obviously a very important animal – the oldest tetrapod then known, and Lyell delayed publication of his *Manual of Elementary Geology* (1852) in order to include a postscript about it.

Mantell, working with Lyell, and with his old friend Lambart Brickenden, who lived in Elgin, prepared a description, but Owen became the first author on the new reptile, publishing a brief unillustrated account dated 20th December 1851 (Owen, 1851a), naming it *Leptopleuron lacertinum* and interpreting it as a lizard. Mantell's illustrated description of the same animal followed in early 1852 and he named it *Telerpeton elginense*, interpreting it as a 'batrachian' (i.e. an amphibian) largely because he had allied it with some 'frogs eggs' from the Old Red Sandstone of Forfarshire. The controversy over the description of this reptile, and the political and philosophical infighting, are described by Benton (1983c).

Specimens of the rhynchosaur *Hyperodapedon*

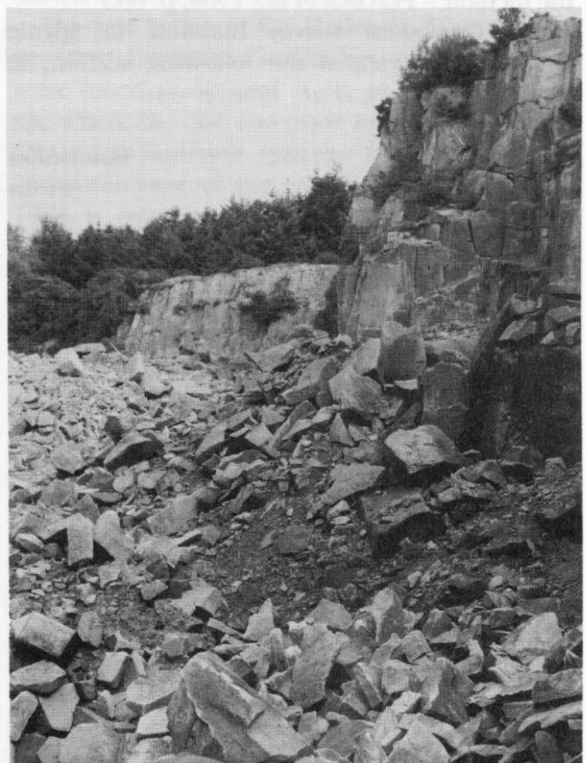

Figure 4.16 The main quarry at Spynie, looking northwards along the east face. Blasting has just taken place, leaving broken blocks that have, from time to time, yielded fossil reptile remains. (Photo: M.J. Benton.)

were collected at Spynie in the 1870s, and in 1891 (Anon., 1891) the first *Ornithosuchus* was discovered by George Gordon, clergyman and naturalist. This fossil, consisting of a partial skeleton and skull was described by Newton (1894b) as the new genus and species, *Ornithosuchus woodwardi*. Taylor (1920) mentions *Stagonolepis* and *Erpetosuchus* from Spynie, but there seems to be no evidence for these. Two fine skulls of *Hyperodapedon* were collected at Spynie in 1947 by Professor T.S. Westoll and are now in the NMS.

Description

In the main quarry (NJ 22256565), 20 m faces may be seen displaying grey jointed sandstone, highly siliceous at the top and more calcareous lower down, weathering orange. The joints may be filled with fluorspar, galena or sphalerite. The transition to the Cherty Rock (a sandy limestone and chert) is also exposed at the top. A 10 m deep pit, worked recently, exposes softer greyish-yellow calcareous sandstone. (This is quarry no. 4 of the memoir – Peacock *et al.*, 1968, p. 68.)

The Geological Survey borehole in Spynie Quarry no. 4 yielded the following section, in summary (Peacock *et al.*, 1968, p. 68):

	Thickness Ft	in
Lossiemouth Sandstone Formation:		
Cherty Rock	5	0+
Sandstone, hard and siliceous at top, softer below	76	6
Yellowish calcareous siltstone with thin beds of gritty sandstone	26	10
Presumed Old Red Sandstone:		
Siltstone and sandstone with galls of green clay. Some reddish brown colouration	4	0

Early writers did not specify precisely which of the pits yielded the specimens of *Leptopleuron, Hyperodapedon* or *Ornithosuchus*, but the reptiles at Spynie appear to have been found low in the Lossiemouth Sandstone Formation, as at Lossiemouth East Quarry (see above). Peacock *et al.* (1968, p. 68) identify the two westernmost quarries as those that yielded the reptiles. Quarry no. 1 (NJ 21926555), now filled in, lay outside the Hill of Spynie and exposed 5 m of fine- to coarse-grained sandstone overlain by a few feet of broken rock. Large-scale dune-bedding occurred in the top of the face. This quarry is supposed to have yielded *Hyperodapedon* (Gordon in Huxley, 1877; Linn, 1886; Peacock *et al.*, 1968, p. 68).

Quarry no. 2 (NJ 22066557) is small, but deep (12–15 m), and lies in the Spynie Hill wood. This is supposed to have been 'a much larger quarry in which specimens of *Leptopleuron (Telerpeton)* were found' (Peacock *et al.*, 1968, p. 68). It should be noted that this quarry (no. 2, Peacock *et al.*, 1968) presently contains very large trees, probably over 100 years old. The type specimen of *Leptopleuron lacertinum* 'was found at the bottom of a shaft which had been sunk through 51 feet of sandstone down to a soft rubbly bed' (Duff in Murchison, 1859, p. 435). Gordon (1859, pp. 45–6), added that the type specimen of *Leptopleuron lacertinum* was found *in situ*: 'it was extracted from the living rock, deep in a quarry opened on the west end of the hill', and Martin (*c*.1860) stated that the specimen was 'found low down, in the bottom of the quarry'.

The specimens of *Ornithosuchus* collected by quarrymen in 1891 may have come from the large quarry still in operation (NJ 22256565), this being quarry no. 3 of Peacock *et al.* (1968, p. 68). This was also the site of the two skulls of *Hyperodapedon* collected in 1947.

The bone material is often powdery, or replaced by iron oxide, and casting is the best method of study, as for the material from Lossiemouth East Quarry (see above).

Fauna

Anapsida: Procolophonidae
Leptopleuron lacertinum Owen, 1851
(=*Telerpeton elginense* Mantell,1852)
2 individuals: NMS, BGS(GSM)

Archosauromorpha: Rhynchosauridae
Hyperodapedon gordoni Huxley, 1859
3 individuals: BGS(GSM), NMS

Archosauria: Crurotarsi: Ornithosuchidae
Ornithosuchus woodwardi Newton, 1894
3 individuals: BGS(GSM), BMNH

Interpretation

Descriptions of the reptiles *Leptopleuron, Hyperodapedon* and *Ornithosuchus* are given in the Lossiemouth East Quarry report (see above).

Conclusions

Spynie is important as the first recorded source of *Leptopleuron* and of *Ornithosuchus*, and the site has the best potential for future finds thereby giving it considerable conservation value. Specifically, the specimens of both *Leptopleuron lacertinum* are some of the best, and two of the best preserved skulls of *Hyperodapedon* yet known were collected in 1947, the last substantial find of reptiles from any of the Lossiemouth Sandstone Formation sites.

FINDRASSIE (NJ 207652, NJ 204651)

Highlights

Findrassie quarries produced some of the first of the Elgin reptiles to be recorded. The site is important because of the high quality of preservation of the specimens.

Introduction

The site includes a series of largely overgrown pits in a wooded area about 1 km due east of Findrassie House. The Lossiemouth sandstones here have produced good remains of *Ornithosuchus* and *Stagonolepis*. The excellent quality of preservation of fossil remains makes Findrassie worth conserving in the hope of future quarrying operations.

The Findrassie quarries were worked on a small scale in the mid 19th century: Martin (*c.* 1860) wrote that 'the quarry is now seldom worked, except occasionally for the purpose of obtaining material for road-metal'. The Findrassie quarries do not appear to have been worked after the 1860s.

The first bones of *Stagonolepis robertsoni*, which Agassiz (1844) had previously described as a fish on the basis of some scales found at Lossiemouth, were collected at Findrassie around 1857 (Gordon, 1859, p. 44; also Murchison, 1859, p. 435). At the same time a fragment of jaw with long dagger-like teeth was also collected, and ascribed tentatively to *Stagonolepis* by Huxley (1859a, pp. 434–5). He later (Huxley, 1877, pp. 43–5, pl. 4, fig. 1) described it as the new genus and species *Dasygnathus longidens*. This has since been shown to belong to *Ornithosuchus* (Walker, 1964, p. 66).

Description

The first quarry mentioned by Peacock *et al.* (1968, p. 69) (NJ 20726524) lies concealed in the southern part of Findrassie woods just beside a field. It is shallow and largely overgrown but exposes patches of hard siliceous sandstone, with occasional cavities produced by weathering.

A second set of pits (Peacock *et al.*, 1968, p. 69) (NJ 20456510) consists of three quarries, the middle one of which exposes a 7 m face of massive, hard, fine-grained sandstone, the top part being hard and siliceous and pinkish in colour with scattered larger quartz grains, and the bottom yellow to yellow-brown with rusty spots. There are several other small pits in the Findrassie woods and on the moor to the west of the wood, a large shallow quarry (NJ 20176496) shows massive, pinkish-brown sandstone with pebbles.

The East Lodge of the Findrassie Estate, where the first Findrassie specimens of *Stagonolepis* were found, is situated at NJ 20746545, and the site where the find was made might be one of the remaining Findrassie quarries lying to the south and south-west of the entrance (Peacock *et al.*, 1968, p. 69), but it could now be filled (Walker, 1961, p. 106). Linn (1886) recorded that *Stagonolepis* was found 'in the more westerly' of a line of three quarries (?NJ 20156495), but Peacock *et al.* (1968, p. 137) suggest a more easterly pit at NJ 205651 as the probable source of the reptiles.

The Findrassie specimens figured by Huxley (1877) are in the form of well-preserved moulds, but specimens in ELGNM labelled 'Findrassie' have bone preserved, which may indicate a different locality. There are occasional pebbles in the matrix of many slabs and the early specimens, at least, must have come from the base of the reptiliferous sandstone, in beds just above the ORS (Gordon, 1859; Walker, 1961).

Fauna

Archosauria: Crurotarsi: Pseudosuchia:
  Stagonolepididae
  Stagonolepis robertsoni Agassiz, 1844
    2 large individuals: NMS, ELGNM, AUGD; 1 small individual: ELGNM

Archosauria: Crurotarsi: Ornithosuchidae
Ornithosuchus longidens Huxley, 1877
1 individual: ELGNM

Interpretation

The cranial remains of *Ornithosuchus* from Findrassie were originally named *Dasygnathus longidens* by Huxley (1877, p. 45): these were shown to belong to a carnivorous 'thecodontian' by Walker (1961, pp. 108–10) and synonymized with *Ornithosuchus* by Walker (1964, pp. 63–6). *O. woodwardi* from Spynie and Lossiemouth is the same as *Dasygnathus longidens*, but the better known name *Ornithosuchus* is used since *Dasygnathus* is preoccupied (a beetle named in 1819). The palaeobiology and relationships of *Stagonolepis* and *Ornithosuchus* are discussed in the Lossiemouth report.

Conclusions

This is the locality of the holotype of *Ornithosuchus longidens*, as well as three individuals of *Stagonolepis* and the first known *Stagonolepis* bones (apart from scutes). Remains are usually excellently preserved moulds that give high-fidelity casts for study, and Findrassie is a better site than Lossiemouth or Spynie in terms of the quality of preservation, which gives it special conservation value.

UPPER TRIASSIC OF SOUTH WALES AND CENTRAL AND SOUTH-WEST ENGLAND

Reptiles of Late Triassic age have been obtained in South Wales and south-west and central England from two main sources: marginal Triassic outcropping in South Glamorgan, where an assemblage of trackways of Norian age has recently been discovered, and from the 'Rhaetic Bone Bed' in the Penarth Group. A third important source of Late Triassic reptiles in Britain is from the cave and fissure fillings in the region of the Severn Estuary: these are treated separately towards the end of this chapter.

The marginal Triassic deposits of South Glamorgan have yielded rare finds of dinosaur footprints from at least two localities. Early finds of isolated dinosaur prints probably came from Scorlon, near Porthcawl. A recent discovery at Bendrick Rock, Barry, comprises numerous trackways assignable to the two dinosaur footprint ichnogenera *Anchisauripus tuberosus* and *Gigandipus*.

The 'Rhaetic Bone Bed', actually comprising several ossiferous horizons, is an unusual sequence at the base of the Westbury Beds, with a wide geographic extent. Typical localities yielding reptiles include the following: Devon: Culverhole Point (SY 275893: archosaurs); Somerset: Chilcompton railway cutting (ST 626509; *Pachystropheus*; Antia, 1979; Duffin, 1980), Hapsford Bridge (ST 755490–ST 756489; prosauropod), Blue Anchor Bay (ST 042432; ?crocodile, *Pachystropheus*; Richardson, 1911b; Huene, 1935; Sykes, 1977; Storrs and Gower, 1993); Avon: Aust Cliff, Severn Estuary (ST 566898; ichthyosaurs, plesiosaurs, dinosaurs, *Pachystropheus*; Storrs, 1994), Garden Cliff, Westbury-on-Severn (SO 718128; ichthyosaurs, plesiosaurs, *Pachystropheus*; Etheridge, 1872; Storrs, 1994), New Clifton, Redland (ST 585735; ?reptile (BMNH)), Carrefour (ST 585815; plesiosaur vertebrae); Glamorgan: Stormy Down (SS 846806; megalosaur dinosaur; Newton, 1899); Leicestershire: Wigston (SK 603991; ?phytosaur; Richardson, 1909), Spinney Hills brickpits (SP 604045; plesiosaur, ichthyosaur; Kent, 1968), Glen Parva brickworks (SP 5689; ichthyosaur, plesiosaur; Browne, 1889, 1894; Fox-Strangways, 1903; Horwood, 1916); Nottinghamshire: Bantycock Pit (SK 811502) and Staple Pit (SK 805499; dinosaurs, *Plateosaurus*, *Pachystropheus*, ichthyosaurs, plesiosaurs, crocodile; Martill and Dawn, 1986), Barnstone (Sykes *et al.*, 1970), Beacon Hill (Johnson, 1950), Stanton-on-the-Wolds (SK 637312).

A fossil reptile is also known from sediments of 'Rhaetian' age at Wedmore, Somerset (ST 4448; prosauropod *Camelotia borealis* ['*Avalonia*', '*Picrodon*'; type specimen: BMNH R2870–4, R2876–8]; Seeley, 1898; Galton, 1985c; Storrs, 1993), and Rhaetian sediments in a large glacial erratic at Linksfield, near Elgin (NJ 223641) have produced remains of fishes and reptiles, including plesiosaurs (Taylor and Cruickshank, 1993; Storrs, 1994).

Of these numerous localities, only two could be selected as GCR sites, since many of the others are no longer accessible, or offer only marginally different faunas:

1. Bendrick Rock, South Glamorgan (ST 131668).

Upper Triassic (Norian), Mercia Mudstone Group.
2. Aust Cliff, Avon (ST 565895–ST 572901). Upper Triassic ('Rhaetian'), 'Rhaetic Bone Bed', Westbury Formation.

BENDRICK ROCK, SOUTH GLAMORGAN (ST 131668)

Highlights

Bendrick Rock, Barry is the source of Britain's best dinosaur trackways. Hundreds of footprints have been recorded and collected there over the years, and the site is still extremely rich.

Introduction

Abundant dinosaur footprints have been found in Late Triassic sediments near Bendrick Rock (Figure 4.17). This is the best site in the British Isles for such early dinosaur trackways, and it may be the best in Europe. Its value is in providing clear evidence for dinosaur ichnofaunas in Europe for comparison with the well-known, and similar, ichnofaunas from the eastern United States (Newark Supergroup) and from southern Africa. Although many slabs have now been collected, natural marine erosion and excavation of the site continues to yield further material.

Three-toed dinosaur-like footprints were found by the artist T.H. Thomas in 1878 in a loose slab, possibly from a quarry at Scorlon, Newton Nottage, near Porthcawl (Thomas, 1879). These came from 'flaggy, calcareous beds with subangular pebbles of limestone' of the marginal Triassic. They were described by Sollas (1879), who named them *Brontozoum thomasi*.

The tracks at Bendrick Rock were found in 1974 on bedding surfaces. At least 450 individual prints were observed (Tucker and Burchette, 1977) and many are still *in situ* (the main slabs then exposed were removed to the NMW, and further specimens were excavated in 1990 for exhibition at the NMW).

Figure 4.17 Aerial view of a bedding plane on the foreshore at Bendrick, covered with three-toed dinosaur footprints, named *Anchisauripus*. Each small depression is a footprint. Width of field of view is about 5m. (Photo: M.J. Benton.)

Description

The sediments in the cliff and on the foreshore at Bendrick Rock form part of the marginal Triassic deposits of South Glamorgan (Marginal Triassic of Tucker, 1977), formerly called the Dolomitic Conglomerate or the Littoral Triassic (Ivimey-Cook, 1974). They include fluviatile sandstones and siltstones, and shore-zone lacustrine sediments (Tucker, 1977). The assemblage is laterally equivalent to playa-lake and aeolian deposits at Lavernock and other localities nearby.

These all form part of the Mercia Mudstone Group (Warrington *et al.*, 1980) which ranges in age from the Mid to the Late Triassic (pre-'Rhaetian'). There is no clear evidence of age, although the dinosaur footprints would strongly suggest Late Triassic and probably Norian.

Palaeogeographically, this was a low lying piedmont area, adjacent to islands or hilly upland of Carboniferous Limestone flanked by alluvial fans and talus slopes, and marginal to an inland (epicontinental) sea. The climate was warm and conditions were desert-like with only intermittent rainfall (evidence of evaporites, calcretes, sheet floods).

The sequence including footprints is logged as follows by Tucker and Burchette (1977):

	Thickness (m)
Marl	3.5+
Conglomerate (erosive base)	*c.* 1
Marl	1–1.5
Sandstone (bedded), containing footprints	*c.* 0.8
Conglomerate (channels)	0–2
Marl, with calcareous nodules	0.5–2
Sandstone, trough cross-bedded	*c.* 2
Marl	1
Sandstone, bedded and cross-bedded	1
Marl, with calcareous nodular horizon	1–4
(Resting unconformably on Carboniferous Limestone)	

The footprints occur on several bedding planes, the best being an 0.08 m thick graded sandstone, overlain by a marl parting, and then another sandstone bed, 0.03 m thick (Figure 4.18). The footprint surface also bears ripple marks. Most of the prints are reasonably clear and many are perfect in their preservation, but others are somewhat deformed or reduced to vague squelch marks, which demonstrates that the muddy sand on which the animals were walking was originally soft and damp. However, the prints appear to have been preserved by a desiccation process caused by subsequent drying out of the surface

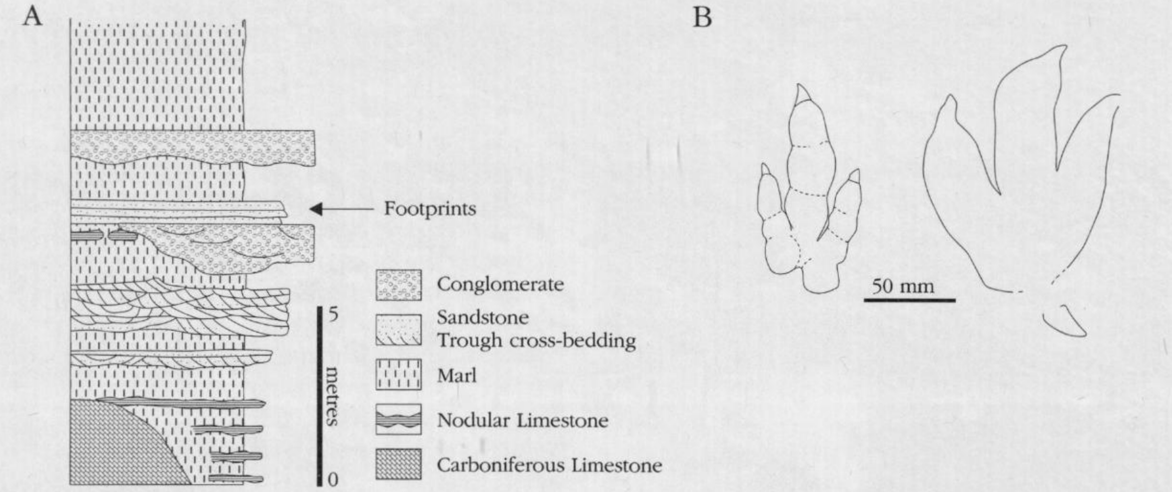

Figure 4.18 The Bendrick Rock footprints. (A) Sedimentary log showing the horizon at which footprints occur; (B) the two footprint types from the locality, each of which is ascribed to ***Anchisauripus***. After Tucker and Burchette (1977).

into which they were impressed. Burial by sediments carried in by thin sheet floods of low turbulence then covered the top of the marked surface.

Fauna

Two types of print occur, a small three-toed variety (105 mm x 70 mm) and a larger four-toed variety, the latter having three toes directed forward and a fourth obliquely backwards (160 mm x 120 mm). Preservation is good, and trackways of many prints may be observed. Tucker and Burchette (1977) attributed the prints to the ichnogenus *Anchisauripus* (Lull) (synonym: *Brontozoum*), but they did not attempt an identification to specific level. Delair and Sarjeant (1985, p. 153) generally compared the smaller Bendrick Rock footprints with *A. thomasi* (Sollas, 1879) and then referred them to *A. tuberosus* (Hitchcock, 1836). They disputed referral of the larger prints to *Anchisaurus* 'since phalangeal pads are not visible' and because of their markedly smaller size, and instead attributed these prints to the ichnogenus *Gigandipus* (Hitchcock), characterizing them as *Gigandipus* sp. nov. The original specimen of *Brontozoum thomasi*, and others collected more recently, are in the NMW (Tucker and Burchette, 1977).

Interpretation

If all the prints are referrable to *Anchisauripus* sp., then it would once have been thought that they had been made by the prosauropod dinosaur *Anchisaurus*, a form known from the Early Jurassic of North America and southern Africa. However, the maker of *Anchisauripus* prints was a small theropod dinosaur (Haubold, 1971), and at least two forms may be implied by the assignment of the prints to two ichnogenera, *A. tuberosus* and *Gigandipus* sp., the latter interpreted by Haubold (1971) as a large form of *Anchisauripus*. However, there are many taxonomic problems with these kinds of trackways: many ichnospecies hitherto assigned to *Anchisauripus* have been reassigned to *Atreipus* and *Grallator* (Olsen and Baird, 1986), and these authors interpret *Atreipus* at least as the footprint of an ornithischian. Hence, these kinds of three-toed footprints have been assigned to all major dinosaur groups: sauropodomorphs, theropods and ornithischians!

Comparison with other localities

There are no other known occurrences of Late Triassic footprints in the British Isles, nor of those of a prosauropod dinosaur. *Anchisauripus* prints have been described from the Late Triassic to Early Jurassic Newark Supergroup of eastern North America (Connecticut, Massachusetts, New Jersey, Pennsylvania, New Mexico) and the Late Triassic of South America (Argentina), as well as possible *Anchisauripus* from the Mid Triassic of France (Haubold, 1971, 1986; Olsen and Baird, 1986). More detailed comparisons and interpretations of the palaeobiology and stratigraphic significance of the Bendrick Rock footprints must await a full review of the relevant ichnotaxa.

Conclusions

Constant erosion by the sea keeps this locality clear of debris, and new footprints are exposed from time to time. Recently excavated footprints from here are currently being studied and have provided material for museum exhibits, e.g. National Museum of Wales in Cardiff. This potential and the importance of the finds from here give the site its conservation value.

AUST CLIFF, AVON (ST 565895-ST 572901)

Highlights

Aust Cliff is world-famous for its superb exposure of Rhaetian marine bone beds. Abundant reptile fossils have been collected, and continue to be collected, representing a mix of mainly marine ichthyosaurs and plesiosaurs, but also rare dinosaur bones.

Introduction

Aust Cliff, at the eastern end of the Severn Road Bridge (Figure 4.19), is Britain's most prolific site for Rhaetian fossil reptiles. The cliff exposes the boundary between the Upper Triassic and Lower Jurassic, and was first described by Buckland and Conybeare (1824), and subsequent accounts have been given by many authors, including Strickland

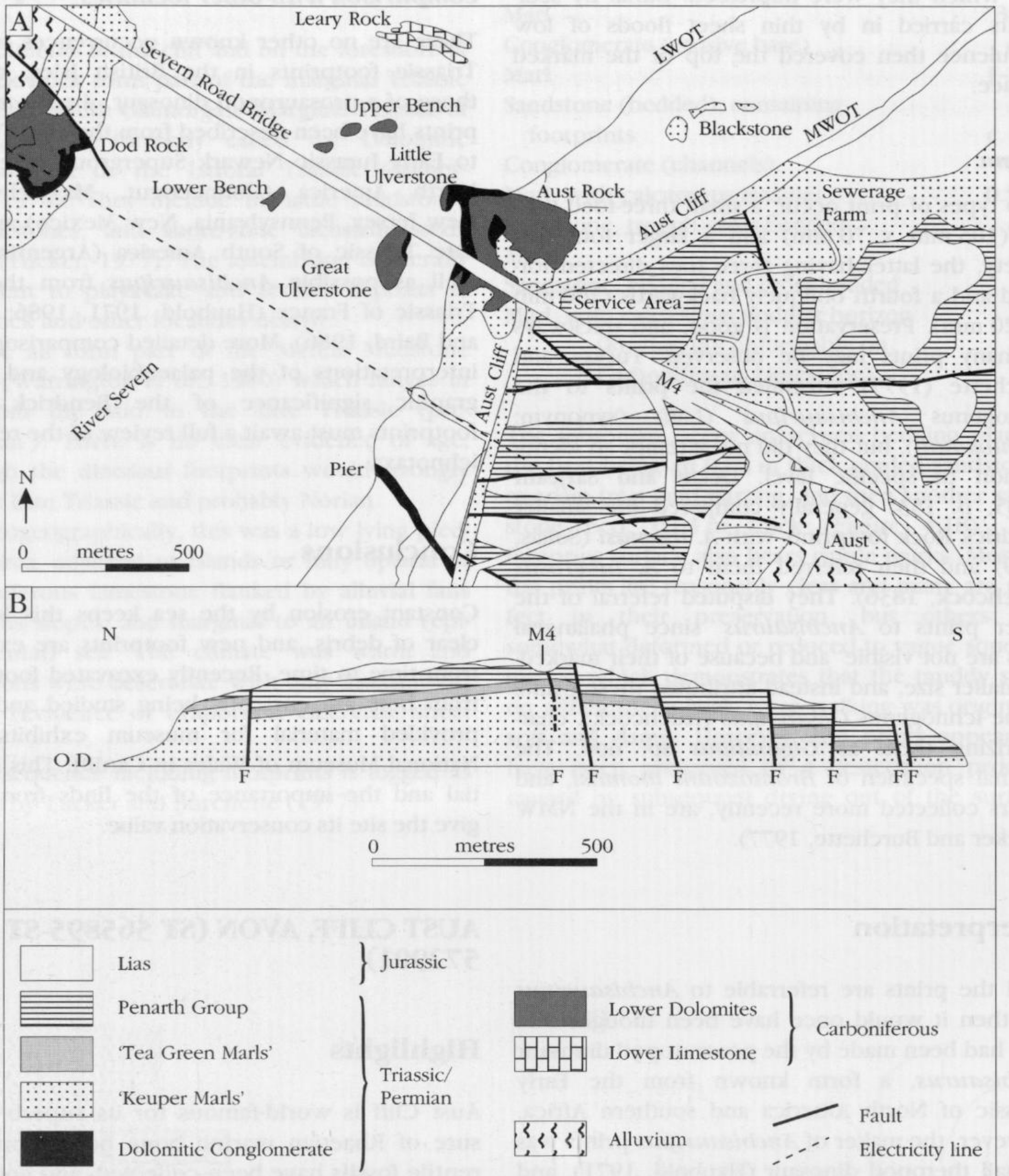

Figure 4.19 The Rhaetian at Aust Cliff. (A) Geological map of the Aust Cliff area; (B) the broad anticlinal structure of Aust Cliff, showing the Lias (1); the Rhaetian (Penarth Group) (2); the 'Tea Green Marls' (3); and the 'Keuper Marls' (4). Both after Hamilton (1977).

(1841), Etheridge (1868), Short (1904), Reynolds (1946), Hamilton (1977) and Storrs (1994). The Aust section has yielded important collections of ichthyosaurs, plesiosaurs and dinosaurs, as well as fishes. The rare dinosaur remains are generally heavily abraded and it is likely that they have been transported for some distance. The site is subject to constant erosion and occasionally produces good new specimens.

Description

Aust Cliff exposes a section through the Upper Triassic and the lower part of the Lower Jurassic (Figure 4.19). It represents the truncated face of a ridge of Triassic and Lower Jurassic rocks surrounded by alluvium. A very gentle anticlinal structure is shown, cut by five small faults with throws to the south ranging from *c.* 1 m to 4.5 m.

Both flexing and faulting have been explained by compaction of the Mercia Mudstone Group sediments. The Mesozoic succession exposed in the cliff is readily subdivided lithologically and biostratigraphically. The lower part of the cliff consists of the Mercia Mudstone Group, including the Blue Anchor Formation ('Tea Green Marls'). Macrofossils are generally absent from these beds, but occur abundantly in the overlying dark and lighter grey sediments of the Penarth Group (including the 'Rhaetic'). Limestones and shales at the top of the cliff form the lowest part of the Lias. This Mesozoic succession rests unconformably on the upturned edges of a Carboniferous Limestone ridge, exposing the Lower Dolomites which dip about 15° south-west. The section (based on Reynolds, 1946, Hamilton, 1977, and Warrington *et al.*, 1980) is:

		Thickness (m)
JURASSIC	Blue Lias (Hettangian)	
	planorbis Beds	(variable)
TRIASSIC	Pre-*planorbis* Beds	(variable)
Penarth Group	Lilstock Formation	*c.* 3.4
	Westbury Formation (bone beds at base)	*c.* 4.3
Mercia Mudstone Group	Blue Anchor Formation	*c.* 7.0
	Red mudstones	*c.* 30.0
CARBONIFEROUS	Carboniferous Limestone	(variable)

The reptile remains are found predominantly in the 'Rhaetic Bone Bed' (Figure 4.20) which occurs in places at the base of the Westbury Formation, the subdivisions of which are (Reynolds, 1946):

Figure 4.20 Aust Cliff: view on the north-eastern side of the Severn Bridge, looking south-east. The red sediments of the Mercia Mudstone Group extend about four-fifths of the way up the cliff, capped by the Penarth Group (latest Triassic). The Blue Lias of the Jurassic lies at the very top, in the vegetation line. Vertebrate remains are found in lenses of 'Rhaetic' Bone Bed, at the base of the Penarth Group. (Photo: G.W. Storrs.)

	Thickness (m)
8. Greenish-black shales	0.3
7. Hard grey limestone ('upper *Pecten* Bed')	0.13
6. Black Shales	2.4
5. Hard pyritous limestone ('lower *Pecten* Bed')	0.18
4. Black shales, hard fissile paper shale above	1.2
3. Bone Bed	0.02–0.15
'Tea-Green Marls'	

The 'Bone Bed' occurs as lenses of grit or intra-formational conglomerate (or breccia) of sedimentary rocks with a calcite-cemented sandy matrix on top of the Blue Anchor Formation, the surface of which may be ripple-marked. The conglomeratic component is made up mainly from clasts of the Blue Anchor Formation sediments, together with quartz pebbles and bone fragments. Many of the fragments of Blue Anchor Formation sediment are squeezed and plastically deformed, which suggests that they were still soft when incorporated into the bone bed. The quartz pebbles are mainly of vein quartz, are mostly well rounded, and are probably derived from older beds (although Wickes, 1904, suggested that they might represent stomach stones, or gastroliths, swallowed by plesiosaurs to aid in the digestion of food).

The vertebrate remains are mainly phosphatized bones, teeth and scales. They are

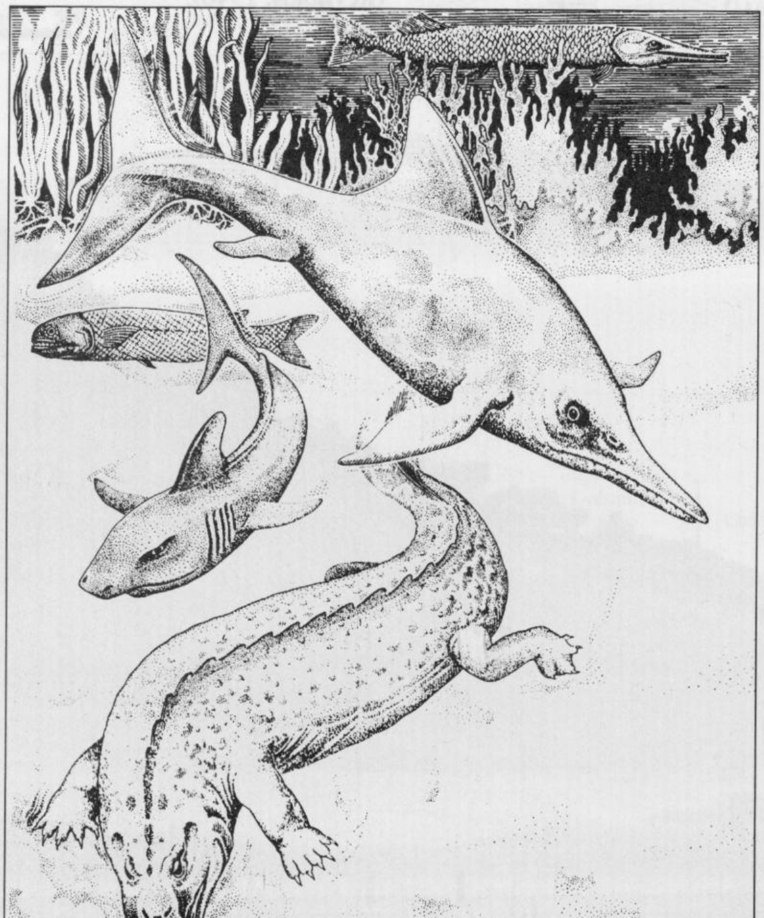

Figure 4.21 Reconstruction of the Rhaetian sea floor, based on fossils from Aust Cliff and neighbouring localities. The fishes are ***Saurichthys***, at top right, ***Birgeria*** at top left, and a hybodont shark in front of it. The marine reptiles include ichthyosaurs (mid-top) and placodonts (lower left). After Duff, McKirdy and Harley (1985).

disarticulated and often rolled and worn, indicating some post-mortem transport. Coprolites (faecal droppings), some possibly of aquatic reptiles, are also abundant: these contain crustacean fragments and abundant fish scales and they are heavily phosphatized, containing 25–50% calcium phosphate. A reconstruction of the Rhaetian sea floor based on fossils from Aust Cliff and neighbouring localities is shown in Figure 4.21.

According to the classification of Sykes (1977), the Bone Bed had a part-primary and part-secondary origin. The indications of primary deposition include the condition and orientation of the fossils, and the poorly sorted nature of the deposit. However, most of the fossils and other clasts show signs of abrasion, which indicates that the deposit is largely reworked. This is borne out by finds of teeth of the Carboniferous fishes *Psephodus magnus*, *Psammodus porosus* and *Helodus* in the bone bed, presumably reworked from the local Carboniferous Limestone or the Coal Measures. Macquaker (1994) and Storrs (1994) conclude that the bed represents a tempestite.

Vertebrate remains are most abundant in the impersistent Bone Bed. A similar fish fauna occurs in the succeeding basal sands of the Westbury Formation and also at the base of the limestone bands and in the shales. Bone-rich debris is also sometimes present in the topmost layers of the green marls at the base of the Rhaetian sequence where the marl is intensely bioturbated. These occurrences of reptile and fish bones in Rhaetian horizons at Aust, other than in the basal bone bed itself, are classified as trace bone beds (Sykes, 1977, p. 220).

Fauna

Dozens of slabs of sediment with fish and reptile bones and teeth are preserved in BRSMG, BRSUG, BMNH, BGS(GSM), CAMSM and in most other British collections. Many of the specimens collected during the last century were identified to species level, and made the types of new species and new genera, but there is no point in listing those since there is rarely enough evidence for such precise determination (see Storrs, 1994, for discussion).

Chondrichthyes: Elasmobranchii
Polyacrodus, Hybodus, Nemacanthus, Palaeospinax, Pseudodalatias, Lissodus

Osteichthyes: Actinopterygii: 'Palaeonisciformes'
'Birgeria', Gyrolepis

Osteichthyes: Actinopterygii: 'Semionotiformes'
Sargodon, Colobodus

Osteichthyes: Sarcopterygii: Dipnoi
Ceratodus

Ichthyopterygia: Ichthyosauridae
'Ichthyosaurus'

Sauropterygia: Plesiosauria: ?Plesiosauridae
'Plesiosaurus'

Archosauromorpha: Choristodera: Pachystropheidae
Pachystropheus rhaeticus (=Rysosteus)

Archosauria: Dinosauria
? Camelotia, megalosaur

Interpretation

The Bone Bed is assumed to have been deposited under marine coastal conditions. The conglomerate shows signs of rapid deposition and winnowing by wave action and shore-line currents. It has been suggested (Macquaker, 1994; Storrs, 1994) that the Aust bone bed represents a storm deposit: a mass of rocks and fossils picked off the shore-line and carried back down into deeper water by the ebb current of a storm sturge, or exhumed and redeposited from penecontemporaneous shallow-water sediments. Other authors suggest that reworking of strandline deposits produced by the Rhaetian transgression might equally have produced the bone bed. This occurred with overstep across the former playa-type sediments of the Mercia Mudstone Group, a palaeoenvironment of intrinsically low relief. Although the palaeontological evidence does not give precise dating, it is probable that the marine flooding phase occurred very rapidly and would have had a strong erosive force. Kent (1970), for example, suggested that the whole of the Midlands was submerged by the transgression almost simultaneously.

Fish remains are common in the Bone Bed at Aust. These include the teeth and fin spines of sharks, teeth and scales of primitive, heavily-scaled, bony fish (*'Birgeria'*, *Sargodon, Gyrolepis*). The most characteristic remains, however, are palatal tooth-plates of the lung fish

Ceratodus, a form close to the extant *Neoceratodus* from Australia.

Temnospondyl amphibians have been reported from Aust, based on mandibles referred to *Metopias diagnosticus* (e.g. Reynolds, 1946), but these have turned out to be the teeth and jaws of a palaeonisciform fish (identified as '*Birgeria*' *acuminata* Agassiz by Savage and Large, 1966, but probably representing a new genus; Storrs, 1994).

The most common reptile remains are ichthyosaurs and plesiosaurs, with a few possible dinosaurs. Ichthyosaurs are represented at Aust by their vertebrae, which are flat circular biconcave elements. One in the BRSUG measures 180 mm across. Other ichthyosaur remains include a humerus (BRSMG), a large lower jaw (Huene, 1912c) and numerous isolated teeth.

The vertebrae and teeth of *Plesiosaurus* are the commonest reptile remains from Aust. The vertebrae are distinguished from those of ichthyosaurs by, among other features, being thicker and having two planar surfaces on the centra. Three species have been named: *P. rugosus, P. costatus* and *P. rostratus*. *P. rugosus* was erected by Owen (1840a) for some vertebrae (BRSMG) which were regarded as sufficiently distinct by Seeley (1874b) to be named as a new genus, *Eretmosaurus*, together with some limbs, limb girdles and apparently similar vertebrae from Granby. Swinton (1930) doubted the validity of the genus, but Persson (1963) retained it, and classified it as a rhomaleosaurid. *P. costatus* was also erected by Owen (1840a) for certain cervical vertebrae, which Swinton (1930) regarded as a possible new genus. Other plesiosaurs reported from Aust include *P. hawkinsi* and *P. rostratus* (Reynolds, 1946). Most plesiosaur specimens from Aust are non-diagnostic teeth, vertebrae, ribs and paddle bones, which Storrs (1994) regarded as Plesiosauria *incertae sedis*. Unfortunately, most of the specimens were destroyed in the BRSMG during the Second World War.

Owen (1842b) named a small reptile vertebra, with a partial humerus and femur from Aust as *Rysosteus*. This was interpreted as a dinosaur by Reynolds (1946), but recent studies by Storrs and Gower (1993), based on material from Aust and from other British Westbury Formation localities, suggests that most *Rysosteus* specimens are the same as *Pachystropheus rhaeticus* Huene, 1935. Storrs and Gower (1993) reinterpret *Pachystropheus (Rysosteus)* as a choristodere, a superficially crocodile-like diapsid of uncertain affinities, and a group that is best known from the Late Cretaceous and Palaeogene, but does have British Mid Jurassic representatives (*Cteniogenys*; see Bathonian site reports below).

Some very large bones, possibly dinosaurian (Reynolds, 1946), lack their articular ends, so that identification is difficult. Three large specimens, found in 1844 (370 mm long, 420 mm in circumference), 1846 (600 mm long, 125 mm in diameter at one end), and between 1846 and 1875 (200 mm long, 370 mm in circumference), were described by Stutchbury (1850) and Sanders (1876).

Some smaller bones (a vertebra, four ends of phalanges, a small rib) in the BMNH and LEICS (Reynolds, 1946) have been identified as *Zanclodon* (Lydekker, 1888a). That attribution is incorrect (*Zanclodon* is an indeterminate archosaur), but they may be termed 'megalosaur *incertae sedis*' for the present. Occasional megalosaur teeth have also been found at Aust (Reynolds, 1946), and three phalanges (BRSUG and in private collections) may also be attributed to a megalosaur. The present whereabouts of these so-called dinosaurs from Aust are uncertain.

Conclusions

Aust Cliff exposes the best section of the Rhaetian beds with the 'Rhaetic Bone Bed' in Britain thus giving the site considerable conservation value. This bone bed occurs in many other localities in England and South Wales, but it is probably best developed at Aust and here contains the most diverse fauna of reptiles. The bone beds of the Westbury Formation have been of considerable importance in Triassic vertebrate palaeontology (Storrs, in press), and have played an important role in the discussion of bone bed formation and diagenesis (e.g. Antia, 1979).

VERTEBRATE-BEARING FISSURE DEPOSITS OF SOUTH-WEST ENGLAND AND SOUTH WALES

Cave and fissure systems developed in the Carboniferous Limestones of the Mendips and Glamorgan (Figure 4.22) during the Late Triassic and earliest Jurassic contain abundant reptilian and other vertebrate remains. The Mendips and parts of South Wales appear to have comprised an archipelago of low limestone islands, and the fissures developed in these limestones preserve a detailed record of the diverse and often insular herpetofaunas of the time (Robinson, 1957a; Tarlo, 1962; Halstead and Nicoll, 1971; Kermack *et al.*, 1973; Fraser, 1986, 1988b, 1994; Savage, 1993). The nature of the palaeokarst and the geology of the caves is reviewed by Simms (1990). The fossil bones, although isolated and disarticulated, are often well preserved and lend themselves to detailed anatomical studies involving a large number of individuals, for example Whiteside (1986) on *Diphydontosaurus avonis* and Fraser (1988c) on *Clevosaurus*. The main Late Triassic (1–8) and Early Jurassic (9–13) fissures of south-west England and Wales (Figure 4.22), and their reptile faunas (see Figure 4.24), are listed below:

1. Slickstones (Cromhall) Quarry, Avon (ST 704916). Seven species of sphenodontid, including the types of *Clevosaurus hudsoni* Swinton, 1935, *C. minor* Fraser (1988c), *Planocephalosaurus robinsonae* Fraser (1982), *Sigmala sigmala* Fraser (1986) and *Pelecymala robustus* Fraser (1986), as well as two unnamed sphenodontids, a procolophonid, the gliding diapsid *Kuehneosaurus*, an ?aetosaur, a ?scleromochlid, a terrestrial crocodilomorph, a ?sphenosuchid, a rhamphorhynchoid pterosaur, the dinosaur *Thecodontosaurus*, the enigmatic diapsid/procolophonid *Variodens* and various unidentified diapsids.
2. Tytherington Quarry, Avon (ST 660890). Type of the sphenodontid *Diphydontosaurus avonis* Whiteside (1986), as well as the sphenodontids *Clevosaurus, Planocephalosaurus*, a crocodilomorph, the dinosaur *Thecodontosaurus*, a 'coelurosaur' dinosaur, and unidentified sphenodontids and archosaurs.
3. Durdham Down, Avon (ST 572747). Types of the prosauropod dinosaur *Thecodontosaurus antiquus* Morris (1843) and the (?) phytosaur *Rileya platyodon* (Riley and Stutchbury, 1840). Also *Diphydontosaurus*.
4. Batscombe Quarry, Somerset (ST 460550). Type of the gliding diapsid *Kuehneosuchus (?= Kuehneosaurus) latissimus* (Robinson, 1962).
5. Emborough Quarry, Somerset (ST 623505). Types of the gliding diapsid *Kuehneosaurus latus* Robinson (1962) and the enigmatic diapsid *Variodens inopinatus* Robinson (1957b), as well as an archosaur, a sphenodontid and the mammal *Kuehneotherium* sp.
6. Highcroft Quarry, near Gurney Slade, Somerset (ST 623499). A reptile jaw (Robinson, 1957a), *?Clevosaurus* (Fraser, 1994).
7. Pant-y-ffynon Quarry, South Glamorgan (ST 047741). Type of the terrestrial crocodilomorph *Terrestrisuchus gracilis* Crush (1984),

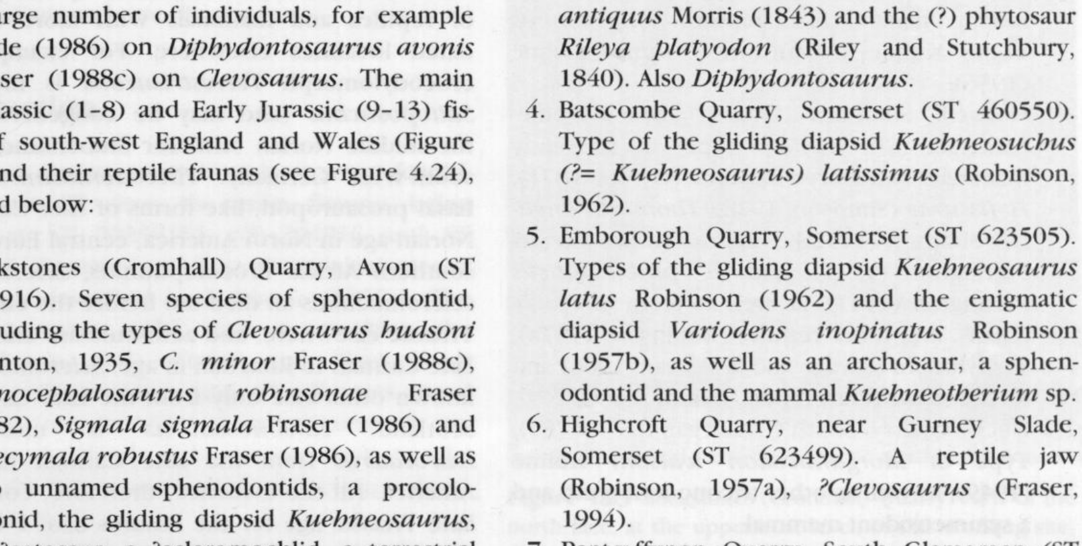

Figure 4.22 Map showing the distribution of Carboniferous Limestone and of tetrapod-bearing GCR fissure sites in south-west England. After Fraser (1985).

as well as the gliding diapsid *Kuehneosaurus*, the sphenodontid *Clevosaurus*, a scleromochlid, the dinosaurs *Thecodontosaurus* cf. *antiquus* (Kermack, 1984) and *Syntarsus*, and lepidosaurs.

8. Ruthin Quarry, South Glamorgan (SS 975796). Type of *Tricuspisaurus thomasi* Robinson (1957), as well as pleurodont reptiles, the sphenodontids *Clevosaurus* and *Planocephalosaurus* and archosaurs (Fraser, 1986, 1994).
9. Windsor Hill Quarry, near Shepton Mallet, Somerset (ST 615452). Types of the tritylodont mammal-like reptiles *Oligokyphus major* Kühne (1956) and *O. minor* Kühne (1956).
10. Holwell Southern Quarry, near Frome, Somerset (ST 727452). Types of the early mammals *Haramiya moorei* (Owen, 1871), *H. fissurae* (Simpson, 1928), *Thomasia anglica* Simpson (1928), *Eozostrodon parvus* Parrington (1941) and *E. problematicus* Parrington (1941), as well as teeth of crocodilians, and other reptiles (Robinson, 1957a), a tritylodont (Savage and Waldman, 1966) and *Clevosaurus* (Fraser, pers. comm., 1993).
11. Duchy Quarry, South Glamorgan (SS 906757). Type of *Morganucodon watsoni* Kühne (1949), as well as other triconodont teeth and a symmetrodont mammal.
12. Pont Alun Quarry, South Glamorgan (SS 899765). Types of the sphenodontian *Gephyrosaurus bridensis* (Evans, 1980, 1981) and *Kuhneosaurus praecursori* Kermack *et al.* (1968), as well as *Morganucodon/Eozostrodon.*
13. Pant Quarry, South Glamorgan (SS 896760). The sphenodontian *Gephyrosaurus*, three sphenodontids, one or more archosaurs, the tritylodont *Oligokyphus* and the mammals *Thomasia, Kuehneotherium* and *Morganucodon watsoni.*

The dating of the fissures is difficult. Robinson (1957a) regarded all the reptile-dominated ('sauropsid') faunas as being Norian in age, and those dominated by tritylodonts and mammals ('theropsid' faunas) as Rhaetian or Early Jurassic. Fraser (1986, 1994) argued that the sauropsid/theropsid, Norian/Rhaeto-Jurassic correlation was not clear-cut: it could just as readily be a taphonomic division of faunas. Independent palynological evidence has established a Rhaetian age for some Tytherington fissures (Marshall and Whiteside, 1980) and a Hettangian–Sinemurian age for Duchy, Pant and Pont Alun Quarries, based on the occurrence of *Hirmerella (Cheirolepis)* spores in the last three sites. The division into sauropsid/theropsid assemblages was further challenged by the discovery of a mammal tooth, *Kuehneotherium* sp., at Emborough Quarry in a fissure otherwise clearly placed in the 'sauropsid' Triassic group (Fraser *et al.*, 1985).

In the absence of further palynological evidence, some indication of the ages of individual fissure faunas may be obtained by comparisons of reptiles and mammals with more securely dated localities elsewhere. For example, the crocodylomorph *Terrestrisuchus* is most like *Saltoposuchus* (and may be congeneric) from the middle Norian Mittlerer Stubensandstein of south-west Germany. *Thecodontosaurus* is a basal prosauropod, like forms of Late Carnian to Norian age in North America, central Europe and southern Africa. Procolophonids, aetosaurs and scleromochlids all died out before the end of the Triassic elsewhere, and aetosaurs are exclusively Late Carnian to Rhaetian in age. *Scleromochlus* is known otherwise only from the Late Carnian of Scotland. *Kuehneosaurus* is most like *Icarosaurus* from the Late Carnian of North America. All the evidence, therefore, confirms a Late Triassic age for the fissures nos. 1–8 in the above list, and probably a range of ages from Late Carnian to Rhaetian. There is no reason why all should be regarded as contemporaneous, but all should postdate the Mid Carnian pluvial episode of Simms and Ruffell (1989, 1990), if those authors are correct that most of the fissures were excavated at that time.

Four fissure localities of scientific and historic importance are selected as GCR sites, while Windsor Hill Quarry has been scheduled for its tritylodont remains as a mammal site (see GCR Fossil Mammals and Birds volume):

1. Slickstones (Cromhall) Quarry, Avon (ST 704916). Late Triassic (Carnian/Norian), fissure fill.
2. Durdham Down, Avon (ST 572747). Late Triassic (Carnian/Norian), fissure fill.
3. Emborough Quarry, Somerset (ST 623505). Late Triassic (Carnian/Norian), fissure fill.
4. Tytherington Quarry, Avon (ST 660890). Late Triassic (Carnian/Norian), fissure fill.

SLICKSTONES (CROMHALL) QUARRY, AVON (ST 704916)

Highlights

Slickstones (Cromhall) Quarry is the site of some of the richest of the fissure deposits in the Bristol–South Wales region. The Late Triassic cave fills have produced excellent specimens of more than 20 species of small reptiles: procolophonids, sphenodontids, gliding kuehneosaurs, problematic archosauromorphs, pterosaurs, crocodilomorphs, thecodontians and rare dinosaurs.

Introduction

Slickstones Quarry contains at least seven fossiliferous cavity-fill sites, the main fissures being located at ST 70359155, ST 704916 and ST 70409165. Fissures 1 and 2 are the original sites of fossil finds described by Robinson (1957a). The quarry company (ARC Ltd) is working the Carboniferous Gully Oolite and Black Rock Limestone (Tournaisian age). The fissures noted are not in areas in which there are currently any quarrying operations; these are not likely to take place in the future, and further collecting is possible (Figure 4.23).

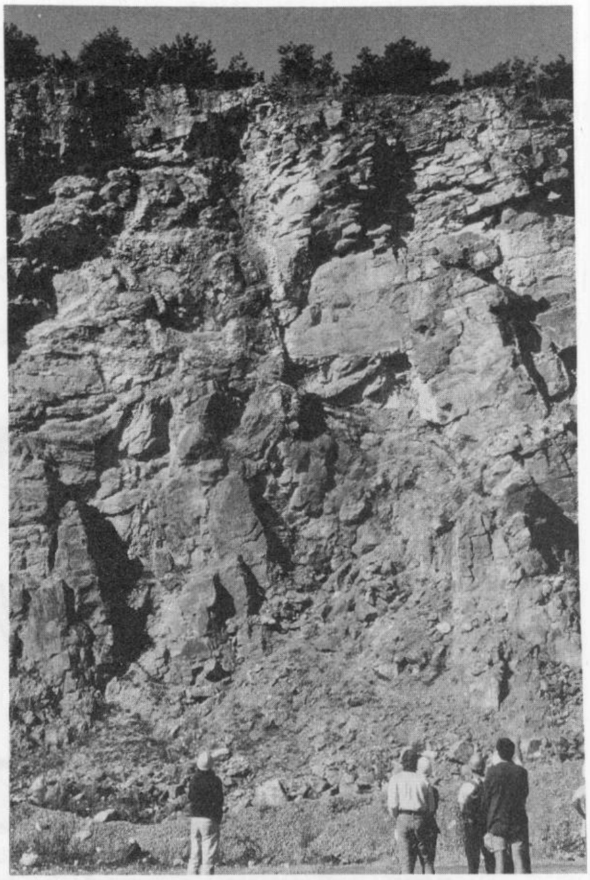

Figure 4.23 Slickstones (Cromhall) Quarry: view of the north face, at the uppermost level, of this working site. A bone-bearing fissure is seen extending down the middle of the photograph. The fissure fills are late Triassic in age, and they occupy caves dissolved into uplifted Carboniferous marine limestones. (Photo: M.J. Benton.)

The vertebrate-bearing fissure deposits in Slickstones Quarry were first exposed during quarrying operations early this century and, having no commercial value, were left *in situ* as a rock promontory. They were later identified by Robinson (1957b) as representing one of the prime examples of a fossilized underground water-course fissure or cave. Robinson (1957b) recorded that F.G. Hudson discovered reptiles in the Slickstones deposits in 1938, this site being the first non-marine fissure discovery. Hudson collected specimens of a sphenodontid which was described and named as the type of *Clevosaurus hudsoni* by Swinton (1939), who did not specify the exact locality. Continued excavation and extensive collecting from the same area revealed the first remains in association, and Robinson *et al.* (1952) and Robinson (1957a) gave further details on the fauna, estimating the total number of reptile species as about nine and listing sphenodontids, squamate lizards and archosaurs. Robinson (1962) mentioned that the gliding 'lizard' *Kuehneosaurus* occurred at Slickstones. Halstead and Nicoll (1971) drew attention to dissociated material within recemented debris in the fissures, which formed the subject of all future work, and noted the occurrence of two further species, a procolophonid and a trilophosaur. Crush (1980) revised the number of species represented at Slickstones Quarry to 10, including *Kuehneosaurus latus*, a prosauropod dinosaur, two ?lizards and *Clevosaurus hudsoni*.

More recently, research by Fraser and Walkden (1983), Fraser (1985, 1994), and Walkden and Fraser (1993) has revealed the presence of six vertebrate-bearing deposits of Triassic age at Slickstones Quarry. Extensive collections were made from all these horizons and they identified six genera of lepidosaurs, including five sphenodontids, and at least four genera of archosaurs, comprising a theropod dinosaur, one or two 'thecodontians' and a possible terrestrial crocodile.

The sphenodontids were most abundant and diverse. Fraser (1982) and Fraser and Walkden (1984) described the dissociated remains of the most abundant form, a new small sphenodontid, *Planocephalosaurus robinsonae*. Specimens of *Clevosaurus* in the AUGD collections were found in five of the fissures and, although they too are mostly dissociated, some articulated remains were collected, including a partial skull and two lower jaws. A third sphenodontid, *Sigmala sigmala* (Fraser and Walkden, 1983; Fraser, 1986), was based on a maxilla, dentary and palatine, and a fourth, *Pelecymala robustus*, was based entirely on isolated jaw elements (Fraser, 1986). Fraser (1988c) described *Clevosaurus* in detail, and formally described the new species *Clevosaurus minor* and a third indeterminate species which he called *Clevosaurus* sp.

Fraser (1988a) described some rare and unusual skeletal elements, including jaw bones and a procoelous vertebra, which he suggested tentatively might represent prolacertiform, thalattosaurian and even pterosaurian remains. The remains of a rhamphorhynchoid pterosaur, the earliest known from Britain, were reported by Fraser and Unwin (1990).

Description

Fraser and Walkden (1983), Fraser *et al.* (1985) and Walkden and Fraser (1993) identified seven fissure and cavity fill sites at Slickstones, six of which yielded vertebrate remains. The seventh, a collapsed cave system, was evidently not fossiliferous and pre-dated the rest on sedimentological grounds. The fissure walls range from subhorizontal to almost vertical in relation to bedding in the Carboniferous Limestone host rock, and the fills are arranged in a linear fashion along a common axis. This alignment of the fissures is not obviously associated with any persistent joint system or with faults; it probably reflects the flow direction of an ancient water course (Fraser, 1985). The fissures have been interpreted as a series of separately filled sink-holes (dolines) and part of a small cave system. Simms (1990), however, disputes this interpretation and regards at least the western fissure as a thermal spring conduit.

The fissure material consists of Triassic landwash laid down in the karstic fissures and cave systems in Carboniferous Limestone. A calcareous, buff-coloured matrix is lodged in Fraser's fissure 1, whereas fissures 3, 4, 5 and 7 contain marls, sandstone, bedded crinoidal limestone and soft, pale green to red mudstones. Most of the fills are nearly horizontally bedded, sometimes with sag-curvature and with some small-scale cross-bedding, and they may contain fragments of stalactites and rare cave pearls. Halstead and Nicoll (1971) mention fluting on the limestone wallrock and laminated red marls (clay grade) in the lower levels, and coarser sandy green marls higher up, the latter formed at a time when the limestone surface had been eroded to approximately the level of the water table.

In fissures 3, 4, 5 and 7 vertebrate remains occur in three principal lithologies: lenses of conglomerate with Carboniferous Limestone clasts in the mudstones enclose reptile bones and remanié fossils, paler sandy mudstones with reptile bones, and hard red calcite-cemented sandstones with the original *Clevosaurus* material and many specimens of the branchiopod crustacean *Euestheria minuta*.

The preservation of the bone is generally excellent, although few bones are complete. Some of the fossils are extremely well preserved and in a fully associated state (i.e. with bones still in position of original articulation), and complete skulls have been found; part of the skin was preserved in one specimen. However, many specimens are broken and show in addition a high degree of rounding and polishing, indicating considerable attrition during transport (Kermack *et al.*, 1973; Fraser and Walkden, 1983).

A certain degree of sedimentary sorting of elements is evident, with coarser sediments tending to contain larger bones in addition to the smallest elements. One lamina was found to contain almost exclusively dentaries of *Clevosaurus* (specimen in BRSUG). Current alignment is not uncommon in some of the beds.

The bone material is preserved as a pale yellow or white substance, but may be dark brown in colour. Unabraded elements often show fine surface detail, preserving tiny foramina and even muscle attachment points.

Fauna

Nearly twenty genera of archosaurs and lepidosaurs (Figure 4.24) have been identified from the six fissure fills, and the variety of assemblages present may represent successional ecosystems. The reptiles are mostly small, the largest, a

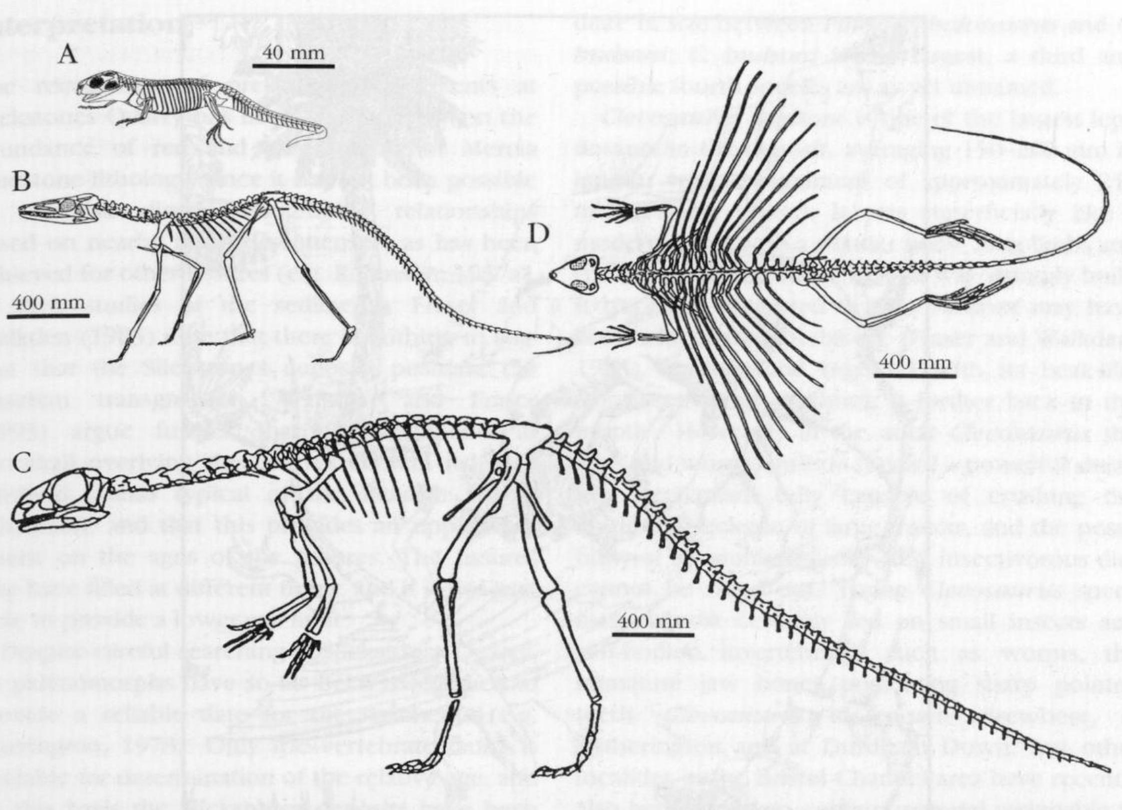

Figure 4.24 Typical reptiles from the Late Triassic fissures in South Wales and around Bristol. Skeletal reconstructions of (A) the sphenodontid *Clevosaurus*; (B) the crocodilomorph *Saltoposuchus*; (C) the prosauropod dinosaur *Thecodontosaurus*; and, (D) the gliding diapsid *Kuehneosaurus*. After various sources; in Fraser (1994).

dinosaur, being no more than one metre long. At least seven species of sphenodontids occur, and for five of these, *Clevosaurus hudsoni, C. minor, Sigmala sigmala, Pelecymala robustus* and *Planocephalosaurus robinsonae*, Slickstones is the type locality. A reconstruction of the faunas of the Bristol region in the Late Triassic, based on fossils found in fisure deposits, is shown in Figure 4.25.

Arthropoda: Crustacea: Branchiopoda
- *Euestheria minuta*
  - Casts of carapaces (AUGD)

Arthropoda: Myriapoda: Diplopoda
- Millipedes
  - Several well-preserved complete and part-enrolled specimens (AUGD)

Arthropoda: Hexapoda: Insecta
- Beetle elytra (AUGD)

Anapsida: Procolophonidae
- Procolophonid
  - Abundant dissociated cranial and postcranial material (AUGD)

Lepidosauria: Sphenodontida
- *Clevosaurus hudsoni* Swinton, 1939
  - Syntypes: BMNH R6100, R9249, R9251, R9252, R9253, R9255–R9260
- *Clevosaurus minor* Fraser, 1988
  - Type specimen: AUGD 11377
- *Clevosaurus* sp.
  - Various specimens (AUGD)
- *Planocephalosaurus robinsonae* Fraser, 1982
  - Type specimen: AUGD 11061
- *Sigmala sigmala* Fraser, 1986
  - Type specimen: AUGD 11083
- *Pelecymala robustus* Fraser, 1986
  - Type specimen: AUGD 11140
- *Diphydontosaurus avonis* Whiteside, 1986
  - Reptile 'B'; AUGD

Archosauromorpha: *inc. sed.*
- *Kuehneosaurus latus* Robinson, 1962
  - Various specimens (AUGD)

Archosauromorpha: Prolacertiformes
- Prolacertiform (?)
  - Premaxilla and maxilla (AUGD)

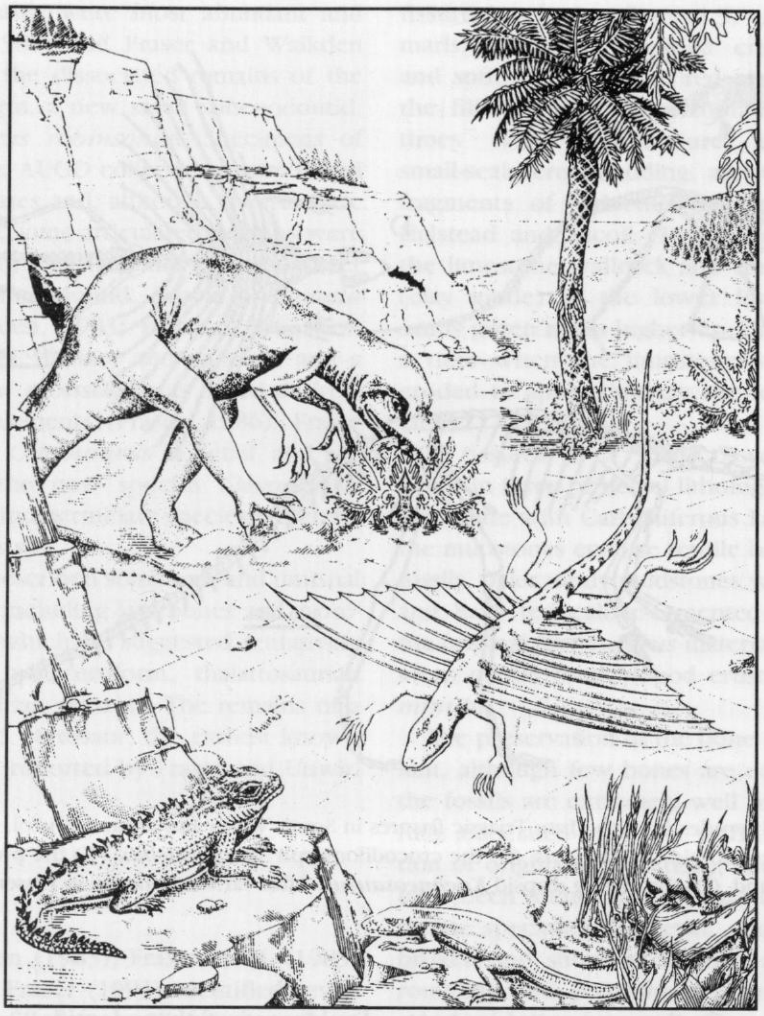

Figure 4.25 Reconstruction of the faunas of the Bristol region in the late Triassic, based on fossil remains found in several fissure deposits. The prosauropod dinosaur *Thecodontosaurus* stands in the background, while the gliding diapsid *Kuehneosaurus* passes over a sphenodontid (bottom left), the possibly lizard-like *Variodens* (bottom middle), and the early mammal *Haramiya* (bottom right). After Duff, McKirdy and Harley (1985).

Archosauromorpha: (?)Trilophosauridae
Variodens sp.
Various (AUGD)
Archosauria indet.
Pterosaur or Thalattosaurian (?)
Fused premaxilla, maxilla and vertebrae (AUGD)
'Thecodontians'
Numerous serrated teeth belonging to two or three genera (AUGD)
Archosaur ('Reptile G')
A single left dentary with three remaining teeth (AUGD)
(?)Scleromochlid
Various (AUGD)
(?)Aetosaur
Various (AUGD)
Archosauria: Crocodylomorpha
Terrestrisuchus sp. and a sphenosuchid
Various (AUGD)
Archosauria: Pterosauria
Rhamphorhynchoid
Metacarpals (AUGD)
Archosauria: Dinosauria: Saurischia: Sauropodomorpha
Thecodontosaurus
Various (AUGD)
Archosauria: Dinosauria: Saurischia: Theropoda
Theropod dinosaur
Various (AUGD)
Unidentified sauropsids

Interpretation

The recognition of pre-Rhaetian sediments at Slickstones Quarry has been based largely on the abundance of red and green marls of Mercia Mudstone lithology, since it has not been possible to establish direct stratigraphic relationships based on nearby bedded sequences, as has been achieved for other fissures (e.g. Robinson, 1957a). In their studies of the sediments, Fraser and Walkden (1983) note that there is nothing to suggest that the Slickstones deposits postdate the Rhaetian transgression. Walkden and Fraser (1993) argue further that the sediments at Cromhall overlying the fissures contain fish and tetrapod faunas typical of the Penarth Group (Rhaetian), and that this provides an upper constraint on the ages of the fissures. The fissures may have filled at different times, and it is not possible to provide a lower age limit.

Despite careful searching at Slickstones Quarry, no palynomorphs have so far been recognized to provide a reliable date for the sediments (e.g. Warrington, 1978). Only the vertebrate fauna is available for determination of the relative age, and on this basis the Slickstones deposits have been assigned a Late Triassic age (Robinson, 1957a) and specifically Late Norian for *Clevosaurus* (Robinson, 1973). Benton (1994a, 1994b) noted that certain elements of the Lossiemouth Sandstone Formation (Late Carnian), such as *Leptopleuron, Brachyrhinodon* and *Scleromochlus*, are very similar to elements of the Cromhall fauna, and *Terrestrisuchus* is very like *Saltoposuchus* from the Mid Norian Stubensandstein of Germany.

Marshall and Whiteside (1980) noted *Clevosaurus* (Figure 4.24A) from fissures at Tytherington, and identified a marine palynomorph assemblage which they regarded as Rhaetian. However, the Slickstone fissures contain faunal elements (e.g. *Kuehneosaurus*) not known from Tytherington, and these indicate a broad age range of Late Carnian to earliest Rhaetian, which accords with similar non-fissure faunas, such as those of the Newark Supergroup of eastern North America.

The most abundant remains at Slickstones Quarry are those of sphenodontids, of which the commonest is *Clevosaurus*. Four species of *Clevosaurus* seem to be present, based on dentitions and distinctive patterns of tooth wear (Fraser and Walkden, 1983; Fraser, 1988c): *C. minor* Fraser, 1988 is the smallest form, intermediate in size between *Planocephalosaurus* and *C. hudsoni*; *C. hudsoni* is the largest; a third and possible fourth species are as yet unnamed.

Clevosaurus hudsoni is one of the largest lepidosaurs in the deposit, averaging 150–200 mm in length, with a maximum of approximately 250 mm (Fraser, 1988c). It was superficially like a modern lizard with a slender body, long limbs and (probably) a long tail. The skull was strongly built. It has been suggested that *C. hudsoni* may have been a facultative herbivore (Fraser and Walkden, 1983), 'raking food together with its beak-like front teeth, and chopping it further back in the mouth'. However, in the adult *Clevosaurus* the jaws and worn dentition formed a powerful shearing mechanism fully capable of crushing the chitin exoskeleton of large insects, and the possibility of an omnivorous or fully insectivorous diet cannot be ruled out. Young *Clevosaurus* specimens almost certainly fed on small insects and soft-bodied invertebrates such as worms, the immature jaw bones possessing sharp pointed teeth. *Clevosaurus* is known elsewhere, at Tytherington and at Durdham Down, but other localities in the Bristol Channel area have recently also been found to contain material assignable to the genus: Pant-y-ffynon (Crush, 1980, fig. 1a), Highcroft (Fraser, 1986), and Holwell (Fraser, pers. comm., 1993).

The remains of *Diphydontosaurus* (Whiteside, 1986), a primitive sphenodontid, best known from Tytherington Quarry, are also present at Slickstones, and at Durdham Down. 'Reptile B' of Tytherington is also present in the Slickstones fauna.

Planocephalosaurus robinsonae (Fraser, 1982) usually exhibits an incomplete lower temporal bar suggesting that this character, formerly thought unique to the squamates, is more widespread in the Lepidosauria as a whole. The genus appears to have close affinities with *Clevosaurus* and *Sphenodon*. The jaw action of *P. robinsonae* is slightly propalinal (back and forth movement), and the dentition (Fraser and Walkden, 1983) indicates that it may have been primarily insectivorous, although possibly capable of taking newly hatched sphenodontids, if the opportunity arose. The genus has been found elsewhere in the fissures at Tytherington and Ruthin Quarry, South Wales, where a sphenodontid maxilla has been found very similar in shape and size to the Slickstones form (Fraser, 1982). Fraser and Walkden (1983) noted subtle differences in the adult *Planocephalosaurus* material obtained from

Tytherington and Slickstones quarries: the Slickstones variety was generally larger in size, exhibiting more robust skull elements. The range of *Planocephalosaurus* from the Norian into the Rhaetian may help explain these slight differences in morphology (Fraser and Walkden, 1983).

The rare sphenodontid *Sigmala sigmala* differs from *Planocephalosaurus* in bearing a high coronoid process and in possessing a somewhat deeper dentary bone. Well-defined facets on the teeth match precisely in opposing jaws and indicate the lack of any propalinal movement for this species. In a review of sphenodontid relationships, Fraser and Benton (1989) found that *Diphydontosaurus* and *Planocephalosaurus* were basal taxa, while *Clevosaurus* fell in a crown group containing mainly Jurassic and Cretaceous forms, as well as the living *Sphenodon*. The other Slickstones taxa are too incompletely known to be used in cladistic analysis.

The procolophonid (Halstead and Nicoll, 1971; Fraser, 1985) shows affinities with *Tricuspisaurus* of Ruthin Quarry, but appears most similar to *Leptopleuron lacertinum*, an advanced form from the Late Carnian Lossiemouth Sandstone Formation of Elgin (Fraser, pers. comm., 1991). The Slickstones procolophonid and *Leptopleuron* share certain affinities with *Hypsognathus* from the Rhaetian of the Newark Supergroup of the eastern USA.

The gliding diapsid reptile *Kuehneosaurus* (Figure 4.24D; Robinson, 1962) is comparable with *Icarosaurus* from the Late Carnian Lockatong Formation of New Jersey, USA. The other discoveries at Slickstones include several archosaurs: an articulated partial skeleton of a terrestrial crocodilomorph, a partial skull of an undescribed thecodontian and other thecodontian remains (a possible scleromochlid and a possible aetosaur) and a procolophonid jaw. Terrestrial crocodilomorphs of comparable age to the Slickstones form include *Terrestrisuchus gracilis* (Figure 4.24B) from fissures in Old Pant-y-ffynon Quarry, South Glamorgan (Crush, 1984). Ruthin Quarry also yielded a terrestrial crocodile (?*Terrestrisuchus*) (Crush, 1984), and other reptiles in the Ruthin sediments include a few jaw fragments of a small archosaur, probably a thecodontian similar to the Slickstones forms (Fraser and Walkden, 1983; Fraser, 1985). Terrestrial crocodilomorphs and aetosaurs are also known from several Late Carnian to Rhaetian localities elsewhere in the world, but scleromochlids hitherto have only been reported from the Lossiemouth Sandstone Formation of Lossiemouth (see above). The trilophosaur/procolophonid specimen figured by Halstead and Nicoll (1971) is closest to *Variodens* from Emborough. The Slickstones fauna shares elements with many of the other fissure sites, but the greatest faunal affinity is with Tytherington, at least six reptiles being common to both localities.

The pterosaurs (Fraser and Unwin, 1990) belong to the Rhamphorhynchoidea and represent the earliest such remains from Britain. The material consists of two specimens of a metacarpal IV (from level K of site 4; Fraser, 1985). Triassic pterosaurs are rare, but well preserved material has been reported from Norian limestones of Cene, near Bergamo, Italy (*Eudimorphodon, Peteinosaurus*) and the Norian of Friuli, Italy (*Preondactylus*) (Wild, 1978a, 1983).

The only invertebrates present in the Slickstones fissures are the crustacean *Euestheria minuta*, and rare diplopod (millepede), and insect remains. An invertebrate fauna is unknown in most of the other fissure fillings of a comparable age, but carapaces of *Euestheria* are recorded from Tytherington.

Conclusions

Slickstones is the richest fissure deposit: nearly twenty reptile taxa have been recognized, and it is the type locality for five species of sphenodontids. The diversity of lepidosaurs at Slickstones is unmatched by any other Triassic locality in the world, and this is the only fissure locality to have produced articulated remains of sphenodontid reptiles. The pterosaur remains are the oldest from Britain, and the only Triassic pterosaurs known outside Italy. This palaeontological importance and the potential for future finds give the site its conservation value.

DURDHAM DOWN, AVON (ST 572747)

Highlights

Durdham Down fissure was the first of the Late Triassic Bristol fissures to be identified. It was the source of the material of the prosauropod dinosaur, *Thecodontosaurus antiquus*, the most primitive member of its group.

Introduction

The fissure at Durdham Down, located in a quarry close to Quarry Steps, is important in being the site of the first discovery of a reptile-bearing fissure in the Bristol region. It was from here that the remains of the prosauropod dinosaur *Thecodontosaurus*, unique to the district around the Severn Estuary, were first described, and the remains of two other prosauropods and a phytosaur recognized. The site also produced a low-diversity fish fauna, represented by spines, scales and teeth, as well as an *Echinus* spine and reworked Carboniferous fossils (Moore, 1881). The fissure cuts through Carboniferous Limestone and was regarded as a true fissure by Tarlo (1959a) and Halstead and Nicoll (1971), in contrast to Robinson (1957a), who viewed the deposit as an infilled depression in the land surface. Although the quarry at Quarry Steps is largely built over today, fissures can be seen on the limestone faces (ST 572747). Careful excavation of the site should produce more finds of *Thecodontosaurus* and establish a detailed stratigraphy for the fissure(s) and the palaeoenvironmental context of the fossils.

The first mentions of the find at Durdham Down seem to be Anon. (1834, 1835). Riley and Stutchbury (1840) described three dinosaurs, of which only two, *Palaeosaurus cylindrodon* and *P. platyodon,* were named as species, *Thecodontosaurus* being referred to only generically. Morris (1843) gave the specific name *T. antiquus*. Seeley (1895) re-examined the material, identifying two, and not three, species of dinosaur, *Thecodontosaurus antiquus* and *Palaeosaurus platyodon*. Huene (1908b) renamed the larger dinosaur *Thecodontosaurus cylindrodon.*

Huene (1902, pp. 62–3) established a new genus and species of phytosaur, *Rileya bristolensis* for a humerus and two vertebrae from Durdham Down. Huene (1908b, p. 240; 1908e) also reclassified the tooth *Palaeosaurus platyodon* as a phytosaur, allied it with the postcranial remains as the species *Rileya platyodon*, and assigned further teeth and postcranial bones to this form.

Halstead and Nicoll (1971) mention a small jaw of the sphenodontid *Clevosaurus*, which has been re-identified as *Diphydontosaurus avonis*, known also from Tytherington and Slickstones (Fraser and Walkden, 1983; Whiteside, 1986), and the articulated skeleton figured (Halstead and Nicoll, 1971, pl. 23B) as a lizard may also belong to this species.

Description

The site of the *Thecodontosaurus* deposit is not known for certain. Pertinent information can be found in the papers of Etheridge (1870), Moore (1881) and Huene (1908a). Etheridge shows two drawings (his figs. 4 and 5) which show the reptile deposit at about 320 ft above mean sea level. Moore (1881, p. 72) mentions specifically a place known as 'The Quarry and The Quarry Steps' and states 'Looking from it [the platform of Quarry Steps], along the Down escarpment to the west, the eye takes in Bellevue Terrace [Belgrave Terrace], on the edge of the Down; and it was between these houses and the quarry, a distance of probably 200 yards, along the same face of limestone . . . that the . . . *Thecodontosaurian* remains were found . . . Unfortunately the precise spot is unknown . . . and built over.' Huene (1908e, 1908f) seemingly misunderstands Moore, naming the site of discovery as Avenue Quarry at the end of Avenue Road, but Moore mentioned this quarry as a location 680 yards away from Quarry Steps and terminating a transect of workings which produced fissures of different ages.

Fauna

Archosauria: Crurotarsi: ?Phytosauria
Rileya platyodon (Riley and Stutchbury, 1840)
Type tooth: BRSMG. Other putative remains: BRSMG, BMNH, YPM
Archosauria: Dinosauria: Saurischia: Sauropodomorpha
Thecodontosaurus antiquus Morris, 1843
Type jaw and other cranial and postcranial material (BRSMG, BMNH, BGS(GSM), YPM)

Interpretation

Moore (1881) regarded the deposit as of 'Rhaetic' age on the basis of a reptile vertebra from Vallis Vale, but later (according to H.H. Winwood) thought it to be 'Upper Keuper' after finding teeth of *Thecodontosaurus* at Ruishton near Somerset. Etheridge (1870) thought the deposit was equivalent to the German Lettenkohle (Ladinian). Conditions at the time of deposition of the Durdham Down fissure system and the dating of the

Tytherington *Clevosaurus* and *Diphydontosaurus* as Rhaetian suggests that the Durdham Down fissure could also be Rhaetian, and the presence of unrolled fish teeth, implying a high water-table, could appear to add support to this notion. Halstead and Nicoll (1971) mention that the matrix is virtually identical to the breccia from the Gliny sea cave; this also implies a marine influence, hence suggesting a Rhaetian age. Moore (1881) describes the fissures very near that of Durdham Down with Rhaetian and Lower Jurassic (Lias) fossils.

On the other hand, *Thecodontosaurus* (Figure 4.24C) is a basal prosauropod in cladistic terms (Gauthier, 1986; Galton, 1990), with relatives from North America and elsewhere that occur in Late Carnian and Norian deposits. *Thecodontosaurus* is known also from fissures in Slickstones, Tytherington, and Pant-y-ffynon quarries, and these are dated, on evidence of their reptile faunas, with a range of Late Carnian to Rhaetian ages, and Pant-y-ffynon even as Late Triassic to Early Jurassic (Kermack, 1984). If *Rileya* is a phytosaur, this would limit the age to Late Triassic only.

Rileya platyodon is an enigmatic form, being regarded by some as a phytosaur and by others as an aetosaur (Westphal, 1976, p. 116). The paucity of the original material (a tooth), and the later assignment of postcranial material to the same species (Huene, 1902; 1908b, p. 240; 1908e) has not helped matters. Restudy of the material is necessary.

The *Thecodontosaurus* bones from Durdham Down show similar size ranges to those from Tytherington, and it would appear that *T. cylindrodon* are adult *T. antiquus*. The new remains of *Thecodontosaurus* sp. from Pant-y-ffynon (Kermack, 1984) may belong to juvenile *T. antiquus*, based on their smaller size and on the incomplete ossification of some bones. The systematic position of *Thecodontosaurus* has been debated recently. Galton and Cluver (1976) referred it to the Anchisauridae, but cladistic analyses (Gauthier, 1986; Galton, 1990), showed that it was a basal sauropodomorph taxon, and it is assigned to its own family, Thecodontosauridae. Galton (1990) also includes *Azendohsaurus* from the Late Carnian Argana Formation of Morocco in this family, but this is based on very limited dental remains and offers little evidence for comparison. The recent analyses of the relationships of *Thecodontosaurus* have been based largely on the ?juvenile Pant-y-ffynon material (Kermack, 1984), and it has yet to be demonstrated that this is the same as the type *T. antiquus* from Durdham Down.

Conclusions

Durdham Down is the type locality of *Thecodontosaurus antiquus* and *T. cylindrodon* (if it is considered a separate species) and of the ?phytosaur *Rileya platyodon*. The only cranial material of *T. antiquus* comes from this site (an occiput held in the YPM). *Thecodontosaurus* is an important basal sauropodomorph dinosaur, seemingly unique to the British fissures.

The historical importance of the fossil finds from this site and its limited potential for re-excavation together give it significant conservation value.

EMBOROUGH QUARRY, SOMERSET (ST 623505)

Highlights

Emborough Quarry is the source of a varied fauna of Late Triassic small reptiles. It is the locality where the best specimens of the extraordinary gliding reptile *Kuehneosaurus* have been found, as well as *Kuehneotherium*, perhaps one of the oldest mammals in the world.

Introduction

Emborough is a disused quarry formerly worked for Hotwells Limestone (Carboniferous: Asbian), which dips to the north-east (Savage, 1977). The reptile-bearing cavity filling is exposed in a promontory in the south-east corner of the eastern quarry. The site is important for yielding numerous remains of the unusual gliding reptile *Kuehneosaurus* and the ?trilophosaur *Variodens*. The fissure site occupies a relatively small proportion of the quarry area, and further collecting is possible.

Reptiles were discovered in fissure sediments at Emborough by Kühne in 1946, but the first discussion on the geology of the deposit and the reptiles was that of Robinson (1957a, 1957b). Robinson (1957b) described a tricuspid reptile, *Variodens inopinatus*, from Emborough on the basis of two dentary fragments and referred it to the Tricuspisauridae. A description of the Emborough gliding diapsid *Kuehneosaurus*, the first known, was made by Robinson (1962). Fraser *et al*. (1985) reported a therian mammal

(*Kuehneotherium*) from Emborough, regarded by them as the oldest therian mammal in the world, and used this as evidence to invalidate earlier claims by Robinson (1957a, 1971) for the existence of a clear-cut distinction between sauropsid-bearing Late Triassic fissure fills and theropsid-bearing Early Jurassic ones (see above).

Description

The sediments may be divided lithostratigraphically into lower and upper units. The lower sediments are unfossiliferous, well-bedded, dark-red clays with green patches. The upper deposit consists of a conglomerate of Carboniferous Limestone clasts, up to boulder-size, set in a matrix of limestone pebbles, pale shale and silts. The silt is finely bedded and free of clasts in some places, usually red, but sometimes pale green. The reptile fossils are found in the higher part of the conglomeratic deposit in the silts. Most of the fossils are dissociated, but some *Kuehneosaurus* material is in articulation.

Fauna

Diapsida: Archosauromorpha: *inc. sed.*
Kuehneosaurus latus Robinson, 1962
Type material: BMNH R8172
Diapsida: Archosauromorpha: ?Trilophosauridae
Variodens inopinatus Robinson, 1957
Type material: BMNH
Diapsida: Archosauria
Archosaur *incertae sedis*
Lepidosauria: Sphenodontida
Planocephalosaurus sp.
Mammalia: 'Symmetrodonta': Kuehneotheriidae
Kuehneotherium sp.
Tooth AUGD 11133

Interpretation

Robinson (1957a) interpreted the sediments as the filling of a collapsed cave, the lower beds being deposited by underground streams and the upper deposit formed by a collapse of the cave roof, with fine silt and the reptile remains brought in by land-wash. Robinson (1957a) and Savage (1977) mention solution features such as water-worn faces and boulders; these and the presence of stalactite fragments in the conglomerate confirm the impression that the void was part of a cave system.

It has been possible to date the sediments filling the Emborough fissure as Late Triassic on the basis of direct stratigraphic evidence using the topographical relationship of the cavity to the local, normally bedded stratigraphy (Robinson, 1957a; Fraser *et al.*, 1985). This age assignment is in accord with the date given to *Icarosaurus* (a close relation of the Emborough diapsid *Kuehneosaurus*) from the Late Carnian (Lockatong Formation) of the Newark Supergroup in New Jersey.

The reptile fauna from Emborough includes the unusual gliding diapsid *Kuehneosaurus latus* (Figure 4.24D; Robinson, 1962, 1967), which is the most abundant animal present (Fraser, 1994), as well as the ?trilophosaur *Variodens inopinatus*, for which Emborough is the type locality. Robinson (1957a) mentions two other reptiles, an archosaur and a sphenodontid, and Fraser *et al.* (1985) reported two teeth of the mammal *Kuehneotherium*.

Kuehneosaurus is represented by dissociated as well as good articulated remains, and the skull including the braincase has been figured by Robinson (1962). The only other kuehneosaurs known are *Kuehneosaurus latissimus* from Batscombe Quarry and *Icarosaurus* from the Lockatong Formation of the eastern USA (Colbert, 1970). The kuehneosaurs, because of the absence of a lower temporal bar, the presence of a streptostylic quadrate and a pleurodont dentition, were formerly considered to represent primitive squamates, the true lizards and snakes. This view has been strongly doubted by Evans (1980, 1988a), Benton (1985), and others, who regard the kuehneosaurs as primitive archosauromorphs, on the basis of numerous characters that place them close to rhynchosaurs and prolacertiforms in the cladogram. *Kuehneosaurus* is a gliding reptile (Figure 4.24D), one of the earliest aerial tetrapods known, which displays a remarkable convergence with the extant gliding lizards of south-east Asia (*Draco*) and also to *Weigeltisaurus*, a gliding form from the Late Permian of Durham (q.v.), Germany and Madagascar. *Kuehneosaurus latus* has also been reported from Slickstones Quarry and the Pant-y-ffynon fissures (Fraser and Walkden, 1983). The numerous Emborough specimens, being mostly dissociated, will allow a complete anatomical study.

The ?trilophosaur *Variodons inopinatus* is known from two dentaries found at Emborough.

The trilophosaurs are a diapsid group, currently placed in the Archosauromorpha (Benton, 1985; Evans, 1988a). Trilophosaurs are known from the Triassic of Russia and North America, but *Variodens* is the only probable representative of the group described from Western Europe. Halstead and Nicoll (1971) have figured a possible trilophosaur from a fissure at Slickstones Quarry. Fraser (1986) and others have hinted that *Variodens* may be a procolophonid.

The *Kuehneotherium* tooth from Emborough was claimed to be the oldest therian mammal fossil in the world, coming as it did from probably pre-Rhaetian sediments (Fraser *et al.*, 1985). The determination of the stratigraphic age of the fissure sediments was disputed, and other equally old mammal remains may be known from France. Lucas and Hunt (1990) reported a supposed mammal skull from the Late Carnian Tecovas Formation of West Texas, USA. Nonetheless, the early record of *Kuehneotherium* points to the possibility of more substantial finds in Emborough.

The fauna is most similar to that of Slickstones (see above), but the dominance of *Kuehneosaurus* at Emborough might suggest a different depositional environment, or a different age. However, the different proportions of taxa could equally well be the result of differential sampling of the fauna, either by the nature of the fissure or of collection error.

Conclusions

Emborough is the type locality of the remarkable gliding reptile *Kuehneosaurus latus*, the only known locality of the trilophosaur/procolophonid *Variodens inopinatus*, and the site for a *Kuehneotherium* tooth, possibly the oldest record of a therian mammal in the world.

This great palaeontological importance, combined with some potential for re-excavation, give the site substantial conservation value.

TYTHERINGTON QUARRY, AVON (ST 660890)

Highlights

Tytherington Quarry has produced abundant and varied Late Triassic reptiles from fissures in the background Carboniferous limestones. This varied fauna includes small lizard-like animals as well as abundant bones of the dinosaur *Thecodontosaurus*.

Introduction

The fissure infillings and their enclosed fauna are found in the new quarry, centred on ST 660890 (Figure 4.26). The quarry company (Amey Roadstone Corporation Ltd) work the Black Rock Limestone and the Black Dolomite of the Carboniferous Limestone which dips in a south-easterly direction at about 20–30°. The fissures in the limestone have yielded a large fauna dominated by lepidosaurs and the dinosaur *Thecodontosaurus* that are dated as Rhaetian on the basis of a contained palynomorph assemblage. Realistically, the only sites that can be preserved are those of fissures which occur at the top level and at the edge of the current quarrying operations, and a palynomorph-bearing fissure on the second level. These fissures are very near the road leading to Tytherington village and it is therefore improbable that any further quarrying will take place on this face. Tytherington is a working quarry and this allows new fissures to be revealed continually, greatly adding to its potential.

The first fossils, discovered in 1975, were the postcranial bones of the prosauropod dinosaur *Thecodontosaurus*. These remains, found by two amateur geologists, Mike Curtis and Tom Ralph, were preserved in a breccia composed of clasts of limestone and dolomitized limestone of Carboniferous age set in a sandy clay matrix. The bulk of the fossil-bearing material (about 10 tonnes) was transported to the University of Bristol, where Whiteside (1983) studied the fauna, and published a description of the cranial skeleton of the most abundant sphenodontid, *Diphydontosaurus avonis* (Whiteside, 1986).

Description

The fissures exhibit a variable morphology; some are aligned vertically on joints, whereas others appear to be true caves which usually follow joints, but also cut unjointed sections of the massive crinoidal limestone and principally follow the dip. The solution fissures can be divided into two types, those formed above (vadose) or below (phreatic) the water table:

Figure 4.26 Tytherington Quarry: view taken in 1981. Fissures containing Triassic sediment occur in the upper levels. (Photo: R.J.G. Savage.)

1. vertical, with sub-parallel walls (vadose);
2. those with a circular cross-section (phreatic).

The sub-parallel fissures probably represent palaeo-dolines (e.g. fissure 1), and are filled with finely laminated calcareous clays and sandstones, some showing cross-bedding and some being ripple-marked, with mud cracks and water droplet impressions. Other doline-like features have an infilling of breccia composed of Carboniferous Limestone clasts in a red sandy matrix and resemble the marginal facies of the local Triassic (the Dolomitic Conglomerate); this can be seen, for example, in fissure 3. Fissure 2 appears to be a phreatic cave formed in times of very high water table, when the sea level was approximately 100 m higher than today. This fissure exhibits long, horizontal solution features and large flute marks formed on the Carboniferous Limestone wallrock. Of the other fissures currently exposed, no. 7 exhibits repeated fining-upward cycles of conglomeratic, sandy Westbury Formation facies with clasts of black shales. This sequence is best exhibited on the southern side; the middle of the fissure is cut by a hydrothermal vein of baryte, galena and sphalerite. The infilling on the northern side of the hydrothermal vein is of contorted Westbury Beds sands and conglomerates which have been deformed, probably as a result of the fall of Carboniferous Limestone blocks into partly consolidated sediment. The hydrothermal vein has also been broken as a result of this fall. Simms (1990) gave further information on the karst aspects of the fissures.

Nine fossil-bearing sites have been identified. The *Thecodontosaurus*-bearing breccia formed the middle section of the infill of a large cavernous fissure (no. 6b; Whiteside, 1983), 4 m in diameter, situated at the third level of the quarry (ST 66188894). Disarticulated isolated bones of a crocodilomorph and two sphenodontids were also found in a fissure (no. 8) lying to the north-west.

A glauconitic clay, a mineral usually associated with marine conditions, recorded from the now destroyed fissure 6b is apparently unique in that it was found in a quartz-rich conglomerate which contains a predominantly terrestrial reptile fauna.

Fauna

Lepidosauria: Sphenodontida
- *Diphydontosaurus avonis* Whiteside, 1986
  - Type specimen: BRSUG 23760 and abundant material in BRSUG
- *Clevosaurus* sp.
  - Varied material (BRSUG)
- *Planocephalosaurus robinsonae* Fraser, 1982
  - Varied material (BRSUG)

Archosauria: Crocodylomorpha
- *Terrestrisuchus* sp.
  - Varied material (BRSUG)

Archosauria: Dinosauria: Saurischia: Sauropodomorpha
- *Thecodontosaurus ?antiquus* Riley and Stutchbury, 1840
  - Varied material (BRSUG).

Interpretation

Marshall and Whiteside (1980) proposed that at least one fissure (no. 2, see below) at Tytherington was infilled in a marginal marine location, on the basis of an assemblage of Rhaetian marine and terrestrial palynomorphs. Whiteside and Robinson (1983) expanded this model, suggesting that the fissure was infilled in a fluctuating freshwater to saline environment, with evidence based upon the occurrence of a glauconitic clay. Whiteside (1983) demonstrated that some fissures were infilled in a freshwater environment, some in brackish conditions, and others in a mixed freshwater and marine regime.

An assemblage of palynomorphs from fissure no. 1 at Tytherington, consisting of 18 elements including the miospore *Rhaetipollis germanicus* and the dinoflagellate cyst *Rhaetogonyaulax rhaetica*, affords unequivocal evidence for a Rhaetian age (Marshall and Whiteside, 1980). The palynomorphs are not reworked, and the enclosing lithology and associated *Euestheria minuta* and *Pholidophorus* indicate equivalence with the Westbury Formation (Rhaetian) (Whiteside, 1983). Fissures 4, 5, 6a and 7 also have Rhaetian palynomorphs indicating equivalence with the Westbury Formation or Cotham Member. All other fissures contain infills interpreted as Rhaetian, except fissure 3, which may be older. The significance of the Tytherington find is that a relatively precise date can be assigned to some of the fissure infillings and the presence of the reptiles *Clevosaurus* and *Diphydontosaurus* in the same matrix is a pointer to the age of the fauna as a whole.

The diversity of sphenodontids from Tytherington is only exceeded by that at Slickstones (Cromhall) Quarry, but at least one species of sphenodontid, here named 'C', is unique to the fissure 1 deposit at Tytherington. The sphenodontids *Clevosaurus* and *Planocephalosaurus* are well represented by isolated material, but *Diphydontosaurus avonis* is the best known form from the site where over 100 individuals have been recovered from fissure 6b. The entire skull (except for the auditory capsule) of this species has been reconstructed (Whiteside, 1986). This form was the smallest member of the Tytherington fauna and its numbers suggest that locally it formed high-density populations. It was probably insectivorous and had a unique dentition among sphenodontids in which pleurodont teeth and acrodont teeth occur together in the same jaws: the pleurodont teeth in the premaxilla and on the anterior margins of the dentary and maxilla, the acrodont teeth behind the pleurodont series on the maxilla and dentary. These alternate in size, an autapomorphic sphenodontid character. All other known sphenodontids have an entirely acrodont dentition, but some have successional anterior teeth as a neotenous feature. *Diphydontosaurus* thus appears to be a primitive form, and Fraser and Benton (1989, p. 440) confirmed this position when, on the basis of computer-based cladistic analyses, *Diphydontosaurus* came out as the most primitive known sphenodontid.

The prosauropod *Thecodontosaurus* is represented at Tytherington by numerous postcranial elements, some of which may be partly articulated. The bones of *Thecodontosaurus* are normally well preserved as a hard white substance with all internal structure intact, but they may be broken and abraded through transport. Such fine preservation of bone assigned to *Thecodontosaurus* is not found at any other fissure locality. See the Durdham Down account for more details of this dinosaur.

Clevosaurus hudsoni, *Planocephalosaurus robinsonae* and sphenodontid 'B' also occur at Slickstones Quarry (Fraser and Walkden, 1983; Fraser, 1988b), and *Clevosaurus* also occurs in the Highcroft Quarry fissure near Gurney Slade and at Pant-y-ffynon Quarries (Crush, 1980). Adult

Planocephalosaurus specimens from the Tytherington fissures appear generally larger than those recovered from Slickstones Quarry, and may represent a more derived later form (Fraser and Walkden, 1983, pp. 359–60, fig. 15). Only one maxillary fragment out of approximately 250 maxillae recovered from Slickstones Quarry is comparable in size to the Tytherington form.

Of the archosaurs, *Thecodontosaurus* has also been recorded from the Durdham Down fissure (Riley and Stutchbury, 1840) and Old Pant-y-ffynon Quarry (Kermack, 1984). The Tytherington material is better preserved than that from Durdham Down, but no cranial elements have so far been identified. The remains of terrestrial crocodilomorphs are better preserved and more numerous at other fissure localities such as Slickstones and Pant-y-ffynon (Crush, 1984).

One important, although rare, member of the Tytherington fauna is a fish whose scales resemble those of *Pholidophorus*, which is found in the Cotham Member (Lilstock Formation, Penarth Group) nearby. The only other non-marine fish found in fissure deposits is *Legnonotus,* a species also recorded from South Wales (M. Howgate, pers. comm.). Tiny reworked teeth and scales of the Rhaetian marine fishes *Gyrolepis*, *Hybodus* and '*Saurichthys*' have been recorded from a number of fissures at Tytherington, and have also been found at Holwell and Windsor Hill (C. Copp, pers. comm.; Savage and Waldman, 1966; Savage, 1977) and in the covering sediments at Cromhall (Walkden and Fraser, 1994). The importance of these fish remains is that they indicate a Rhaetian (probably Westbury Formation time equivalent) age and independently confirm the probability of a saline intrusion into the fissure at the time of infilling.

Contemporaneous invertebrates are rare and, apart from the internal moulds of possible Rhaetian gastropods, the only specimens are a few individuals of the branchiopod *Euestheria minuta* var. *brodeiana* known elsewhere from the Cotham Member.

Conclusions

Tytherington provides many unique finds, particularly *Diphydontosaurus* in fissure 1, an admixture of terrestrial reptiles and non-marine fish in fissure 2, and the palynomorph assemblage of fissure 5. The Tytherington fissures as a whole provide the best evidence of infilling of an ancient subterranean cave complex. The solution-marked surface of fissure 2 is an excellent phreatic cave passage. Moreover, Tytherington is the only quarry in which fissure infillings have been dated independently of the vertebrates.

The considerable conservation value of this quarry lies in the combination of the potential for new finds from continued working and the preservation of some fissures that are marginal to the quarrying.