7

A review of the British Middle Triassic tetrapod assemblages

MICHAEL J. BENTON, GEOFFREY WARRINGTON, ANDREW J. NEWELL, AND PATRICK S. SPENCER

Benton, M. J., Warrington, G., Newell, A. J., and Spencer, P. S. 1994. A review of the British Middle Triassic tetrapod assemblages. In Fraser, N. C. and Sues, H.-D. (eds), In the shadow of the dinosaurs, pp. 131-160. Cambridge University Press, Cambridge, 435 pp.

Introduction

Remains of fossil tetrapods were first recovered from Middle Triassic deposits in England in 1823. Buckland (1837) noted that "part of a jaw and other bones of a Saurian, found in the sandstone at Guy's Cliffe near Warwick, were presented to the Oxford Museum, by the late Butic Greathead, Esq." in 1823. He identified these as the remains of a phytosaur by comparison with specimens in Germany. The original specimen has been lost, but it probably comprised the jaws of the temnospondyl amphibian *Mastodonsaurus*. At about the same time, tracks of then unidentified footprints were exposed at Storeton Hill Quarry, Cheshire, in Middle Triassic rocks (Tresise, 1989). About 1824, footprints were discovered in sandstone near Tarporley, Cheshire, but their significance was not realized immediately (Egerton, 1838).

Further fossil bones, "apparently of Phytosaurus [sic], were found at Warwick by Dr Lloyd of Leamington" in October 1836 (Buckland, 1837), and in June 1838 superbly preserved handlike footprints were identified in the Storeton Quarries near Birkenhead, Merseyside. These immediately attracted wide attention and were recognized as very like footprints from the German Triassic that had been named *Chirotherium* in 1835 (Swinton, 1960; Sarjeant, 1974; Tresise, 1989).

Specimens collected by Dr. Lloyd from Coton End Quarry, Warwick, and from Leamington were identified by Murchison and Strickland (1840, p. 344) as teeth of *Megalosaurus* and of a "Saurian," as well as an unidentified vertebra; these were the first British Middle Triassic skeletal remains to be figured (Murchison and Strickland, 1840, pl. 28, figs. 6–10). Other finds probably had been made at Coton End Quarry, because Murchison and Strickland (1840, p. 343) stated that it "has been most productive of the remains of *Vertebrata*." One of these specimens (Murchison and Strickland, 1840, pl. 28, fig. 9) was reidentified as "a smooth curved tooth" and was named *Anisodon gracilis* by Owen (1841b, pl. 62A, fig. 3). Later, Owen (1842a, p. 535) suggested that this specimen was a terminal claw-bearing phalanx of the amphibian *Labyrinthodon pachygnathus*. Owen (1842a, pp. 523–524) identified a second specimen as a vertebra of *Labyrinthodon leptognathus*, and Owen (1841b) identified some of the teeth as *Cladeiodon lloydi*, which was later regarded as a dinosaur.

Collections of new material not seen by Murchison and Strickland were received by Owen during 1840–1841; these came from quarries in and around Warwick (Figure 7.1), from Dr. Lloyd, and from quarries at Grinshill (Figure 7.1), north of Shrewsbury, from T. Ogier Ward, a Shrewsbury physician. In a paper presented to the Geological Society of London on February 24, 1841, Owen clearly viewed most of this material as representing various species of *Labyrinthodon* [i.e., *Mastodonsaurus*, which had been described by Jaeger (1828) from the German Upper Triassic]. In an abstract of that paper, Owen (1841a) included in *Labyrinthodon* a great range of different amphibian and reptile bones and, tentatively, the producer of the *Chirotherium* footprints. However, before that paper was published in full (Owen, 1842a), and before the British Association meeting in a August 1841 (Owen, 1842b), he had received a new cranium from Dr. Ward, which enabled him to separate the Grinshill animal from *Labyrinthodon*. He described it as *Rhynchosaurus articeps*, a new genus and species of reptile (Owen, 1842b,c). He regarded it as a "lacertian" (i.e., a lizard), but did not connect it with the Warwick material he was studying, which he retained in *Labyrinthodon* (Owen, 1842a). It has subsequently been realized (e.g., Walker, 1969; Benton, 1990) that all the Grinshill material, and much of that from Warwick, pertains to *Rhynchosaurus*. This includes the "tooth"

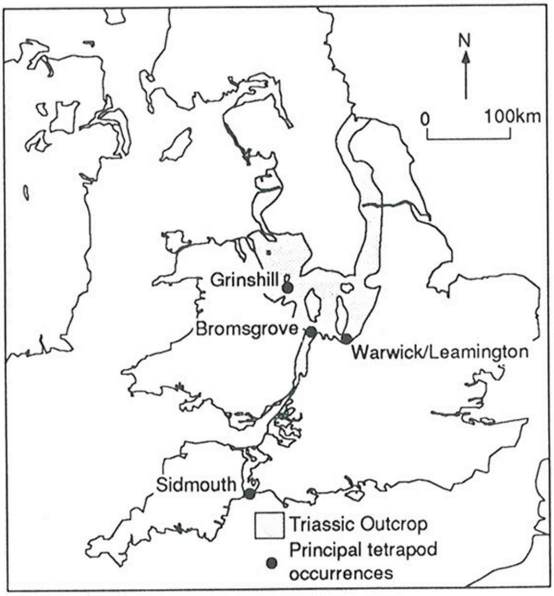

Figure 7.1. The main British Triassic outcrop (stippled), with localities mentioned in the text.

(actually a premaxilla) and the vertebra figured by Murchison and Strickland (1840), which are thus the first figured rhynchosaur fossils. The teeth referred to *Cladeiodon* by Owen (1841b), together with some other fossils from Warwick, were regarded as dinosaurian by Huxley (1870) and ascribed by Huene (1908a) to *Teratosaurus*, a rauisuchian (Galton, 1985; Benton, 1986). However, such generalized archosaur teeth probably are unidentifiable.

Subsequent descriptive work by Owen (1845, 1859, 1863), Huxley (1887), Woodward (1907), Watson (1910), Huene (1929), Hughes (1968), and Benton (1990) has shown that the Grinshill fauna consists exclusively of *Rhynchosaurus articeps*. Further tetrapod fossils, comprising temnospondyl amphibians, a rhynchosaur, a prolacertiform, and various archosaurs, were described from the Warwick area by Huxley (1859, 1869, 1870, 1887), Miall (1874), Burckhardt (1900), Wills (1916), Huene (1908a, 1929), Walker (1969), Paton (1974), Galton (1985), and Benton (1990).

New English sources of Middle Triassic fossil tetrapods were announced after Owen's time. Huxley (1869) described a rhynchosaur jaw bone from the south Devon coast near Sidmouth (Figure 7.1), and subsequent collecting there (Seeley, 1876; Metcalfe, 1884; Carter, 1888; Spencer and Isaac, 1983; Benton, 1990; Milner et al., 1990) has yielded an extensive fauna of temnospondyl amphibians, procolophonids, a rhynchosaur, archosaurs, and other unidentified animals. A solitary, well-preserved temnospondyl skull was discovered at Stanton, Staffordshire (Ward, 1900), and temnospondyl amphibians, a rhynchosaur, archosaurs, a prolacertiform(?), and a nothosaur were recovered from Bromsgrove, Worcestershire (Figure 7.1) (Wills, 1907, 1910, 1916; Walker, 1969; Paton, 1974; Benton, 1990). Footprints, mainly *Chirotherium*, produced by a rauisuchian archosaur, and rhynchosauroid prints were reported from Middle Triassic deposits at numerous localities in the Cheshire basin (Thompson, 1970a, figs. 4 and 5) and the Midlands (Sarjeant, 1974).

The following account of the British Middle Triassic tetrapod faunas is based upon skeletal remains; vertebrate ichnofaunas are noted only where found in association with such remains. The stratigraphy and sedimentology of the host deposits, and the occurrence, composition, taphonomy, and paleoecology of the faunas, have been reviewed by three of us (MJB, AJN, and PSS) and GW has compiled independent evidence of age and has contributed to the assessment of the faunas.

Abbreviations utilized in the text are as follows:

BATGM, Bath Geology Museum
BGS (GSM), British Geological Survey (Geological Survey Museum), Keyworth, Nottingham
BIRUG, Birmingham University, Geology Department collections
BMNH, British Museum (Natural History), London
CAMSM, Cambridge University, Sedgwick Museum
EXEMS, Royal Albert Memorial Museum, Exeter
SHRBM, Shrewsbury Borough Museum
WARMS, Warwickshire Museum, Warwick

Stratigraphic and depositional setting

Terrestrial Middle Triassic tetrapod faunas are less well-known globally than those of Late Triassic age. The best-known European Middle Triassic deposit, the Muschelkalk, extends over parts of Germany, Switzerland, and Poland. This facies is famous for its diverse fauna of nothosaurs, placodonts, and ichthyosaurs and is relatively well dated by ammonoids and other marine fossils, but it does not occur in Britain.

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 Middle Triassic to early Late Triassic in age). He argued that a major unconformity in the British sequence corresponded to most of the Middle Triassic and represented the Muschelkalk (Figure 7.2). Warrington et al. (1980) advocated abandonment of the terms "Bunter" and "Keuper" as applied in Britain and established a lithostratigraphic nomenclature with

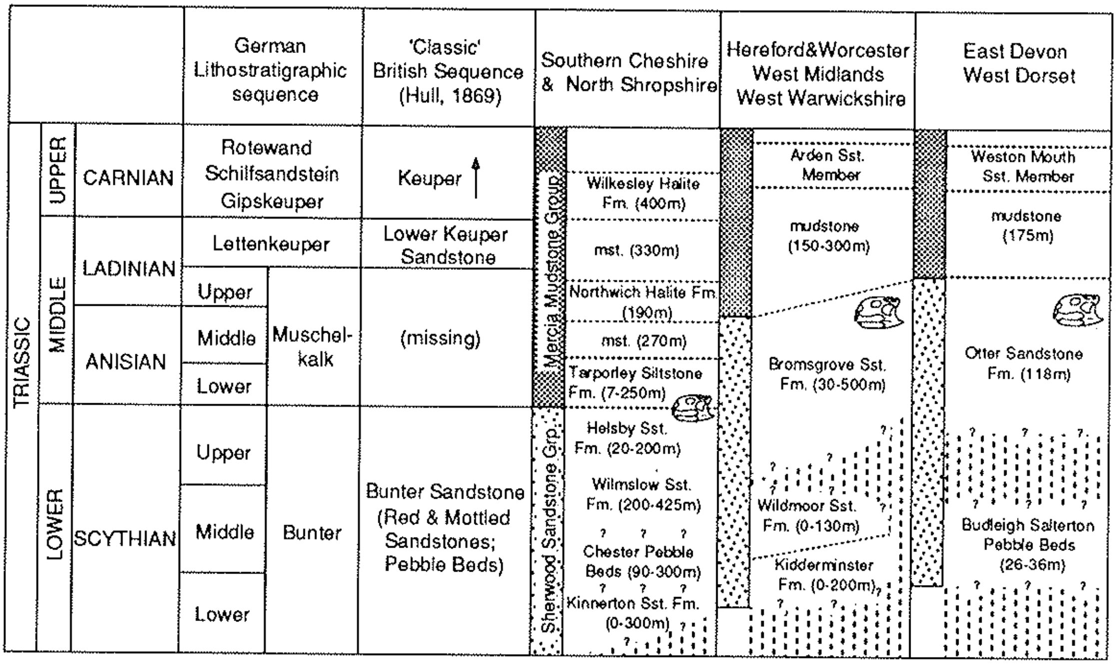

Figure 7.2. Stratigraphic setting of the British Middle Triassic tetrapod faunas. Correlations of the standard Triassic divisions and the German Triassic sequence with the British Triassic, as proposed by Hull (1869) for the "classical" British succession, and by Warrington et al. (1980, modified after the account in this chapter) for currently recognized lithostratigraphic units. Skulls indicate levels of main tetrapod faunas.

correlations based on palynomorphs and other fossils, where possible (Figure 7.2).

Palynological work (Warrington, 1967, 1970b; Geiger and Hopping, 1968) has shown that deposits of Middle Triassic age are present in Britain, 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).

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 ranging from Late Permian to Early Triassic and the upper from Early to Middle Triassic in age (Warrington et al., 1980). The Sherwood Sandstone Group comprises up to 1,500 m of arenaceous deposits that form the lower part of British Triassic successions. The sandstones are red, yellow, or brown in color, and pebbly units occur, especially in the Midlands. Most of the deposits are of fluvial origin, but there are many eolian units (Thompson, 1970a,b), and marine influences are evident toward the top.

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 upward from predominantly sandy to predominantly silty and muddy facies at a diachronous interface that varies regionally from Early to Middle Triassic in age. The upper boundary, associated with a marine transgression that apparently occurred approximately contemporaneously throughout much of Europe, lies within the Rhaetian stage (sensu Richter-Bernburg, 1979). The Mercia Mudstone Group comprises dominantly red mudstones with subordinate siltstones. Extensive developments of halite and of sulfate evaporite minerals suggest deposition in hypersaline epeiric seas, connected to marine environments, in associated sabkhas, and in playas (Warrington, 1974b).

Triassic deposits have a broad U-shaped outcrop in the English Midlands, with a continuation south westward to South Wales and Devon. Smaller outcrops occur in northwest England, in Northern Ireland, and in Scotland (Warrington et al., 1980, figs. 2 and 3). The tectonic and sedimentary regimes established during Permian times continued into the Triassic, with deposition in fault-bounded basins in southern and western Britain and on the more regionally subsiding Eastern England Shelf, which formed the onshore

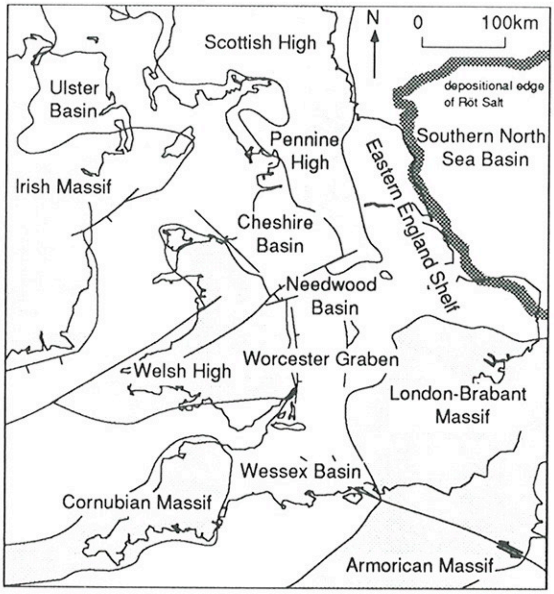

Figure 7.3. Generalized Early Triassic paleotectonic map showing major fault-bounded basins; tetrapod localities correspond with lowland areas in the Wessex basin and the central Midlands (Worcester Graben and adjacent areas).

marginal part of the Southern North Sea basin (Audley-Charles, 1970; Holloway, 1985) (Figure 7.3). In the Late Permian and Early Triassic, renewed and extensional subsidence in the Wessex basin, Worcester graben, and Needwood and Cheshire basins resulted in the establishment of an axial drainage system that flowed northward from the Variscan Highlands (Holloway, 1985). The south-to-north regional paleoslope and the proximal-to-distal depositional pattern that developed are reflected in the diachronous nature of the Sherwood Sandstone–Mercia Mudstone boundary (Figure 7.2), with coarse clastics being deposited in the south, whereas mudstones and evaporites accumulated farther north (Warrington, 1970a,b; 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 Middle Triassic marine incursions. The widespread occurrence of transgressive intertidal facies of Middle 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 paleoenvironment of intertidal sandbanks.

Tetrapod assemblages

Grinshill, Shropshire

Location and fauna. Remains of *Rhynchosaurus articeps* have been found in the Tarporley Siltstone Formation (formerly the "Waterstones"), and possibly immediately below, in the Helsby Sandstone Formation (formerly the "Ruyton and Grinshill Sandstones" or the "Building Stones"), in quarries on Grinshill Hill (variously Grinsill or Grimshill), between the villages of Grinshill and Clive, Shropshire (Figure 7.4). There are many formerly important quarries from which footprints and bones may have been recovered. Of the 40 or so quarries traced by D. B. Thompson (pers. commun. to MJB, 1992), roughly half exposed both the Grinshill Sandstone and the overlying Flagstones. Quarrying for building stone started as early as the fifteenth century and has continued, especially in the eighteenth and nineteenth centuries (Murchison, 1839, pp. 64, 73; Pocock and Wray, 1925, pp. 39–40).

The first finds of footprints and bones appear to have been made in the group of quarries known as the Bridge Quarries, located between SJ 517329 and SJ 519327, the central Bridge Quarry (at about SJ 518328) being the main source, according to manuscript sources (D. B. Thompson, pers. commun. to MJB, 1992). Only one working quarry (Figure 7.5A,B), now owned by English China Clays (ECC) Quarries Division, remains (being centered on SJ 527237). It yields footprints very commonly, but bones are recovered only episodically [e.g., in 1971, 1984 (twice), and 1991].

The only tetrapod species reported thus far is *Rhynchosaurus articeps* Owen, 1842 (Figure 7.6). About 17 individuals have been collected since 1840, at least three of which were found recently in the active quarry. This species, redescribed in detail by Benton (1990), is a small rhynchosaur with a skull length of 60–80 mm (mean: 70 mm) and a total body length of 360–540 mm (mean: 470 mm). It shows the characteristic rhynchosaurian adaptations for feeding on tough vegetation (Benton, 1983, 1984) and differs from its larger relatives mainly in having slender bones, presumably a scaling effect of its small size.

The absence of other tetrapod body fossils from Grinshill is unusual and may be related to environmental or paleogeographic factors, although it is not clear what these may have been. Rauisuchians were also present there, as indicated by rare *Chirotherium* footprints (discussed later), but no bones of these large reptiles have yet come to light.

Host deposits. The Grinshill Sandstone comprises some 20 m of buff and yellow, medium-grained, well-sorted sandstones. These are well cemented and contain many small occurrences of manganese hydroxide. Large-scale cross-beds, at times reactivated, suggesting aeolian deposition, are visible in vertical quarry faces

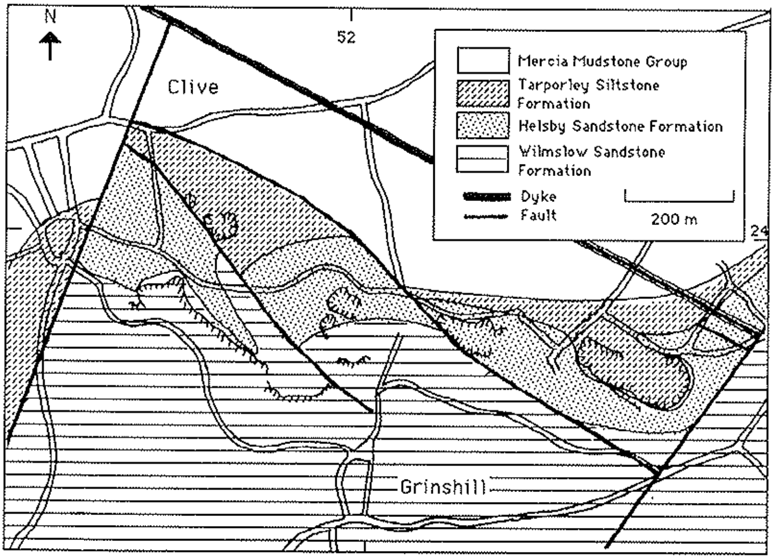

Figure 7.4. Grinshill localities. The map is based on published maps of the British Geological Survey (BGS 1:63360 scale geological sheet 138, Wem) and on field observations by MJB.

(Thompson, 1985). The formation may be equivalent to part of the Helsby Sandstone Formation (Sherwood Sandstone Group) of central and northern parts of the Cheshire basin (Warrington et al., 1980).

The Grinshill Sandstone is separated sharply from the Tarporley Siltstone Formation (Mercia Mudstone Group) by about 0.3 m of loose sand, speckled with manganese oxide flakes and barite nodules, termed the Esk Bed (Pocock and Wray, 1925, pp. 39–40; Thompson, 1985).

The Tarporley Siltstone Formation, which varies from about 10 to 270 m in thickness in the Cheshire basin (Warrington et al. 1980, table 4), is only about 6–10 m thick at Grinshill. Thompson (1985) identified two facies, interpreted by him as "tropical arid belt fluvial and marine-marginal hypersaline lagoon (salina) deposits."

Facies A comprises rippled cross-laminated fine- to medium-grained sandstones that occupy trough-shaped erosion channels. The sandstones bear transverse and linguoid ripples, which reflect northward paleocurrents. They are green-gray in color when freshly exposed. Rippled surfaces bear rhynchosauroid footprints (discussed later), invertebrate trace fossils, and raindrop impressions (Figure 7.5C) that were noted at Grinshill (Ward, 1840; Buckland, 1844) soon after the first-ever report of such structures from the Middle Triassic of Storeton, Cheshire, in 1838 (Tresise, 1991). Rhynchosaur bones were recovered in 1984 from the lowest of these units in the active quarry (D. B. Thompson, pers. commun. to MJB, 1992). This facies is interpreted as representing low-energy fluvial environments with rivers that occasionally dried up; exposed semisolidified muds were pitted during sporadic rain showers (Thompson, 1985). These evidently moist conditions may have supported a seasonal vegetation sought by the herbivorous rhynchosaurs.

Facies B comprises interbedded fine sandstones (to 0.1 m), siltstones, and mudstones (10–20 mm thick), with primary current lineation, asymmetric current and wave ripple marks, and under-surfaces with load casts, flutes, and prod marks. Adhesion ripples have been observed on flat and current ripple surfaces (D. B. Thompson, pers. commun. to MJB, 1992). Mud cracks and pseudomorphs after halite, rhynchosauroid footprints, and invertebrate trace fossils, including a meandering "worm" trail about 15 mm wide, have been observed in situ by MJB. The mudstones and siltstones are stained red in parts, particularly near the base of the Tarporley Siltstone Formation. This facies, with evidence for current activity (?rivers) and wave activity (?lagoons), appears to represent "fluvial-intertidal rather than lake marginal" environments (Thompson, 1985). Brackish pools occasionally dried out, leaving salt crystals and mud-cracked surfaces. Half-damp sand flats developed adhesion ripple features. Rhynchosaurs and other reptiles (discussed later) walked across the muds.

Occurrences of reptiles. As noted by Owen (1842b, p. 146) and by Ward (in litt., BMNH), specimens of *Rhynchosaurus articeps* occur in two sediment types: in a fine-grained sandstone and in a coarser pinkish gray sandstone, termed "burr-stone" by Owen. The fine sandstone is gray to beige in color and has subrounded sand grains, greenish mud flakes, and specks of mica and manganese minerals. Slabs show fine parallel lamination, and some bedding surfaces show ripple marks and irregular clasts up to 10 mm in diameter.

Walker (1969, p. 470) noted that the specimens of

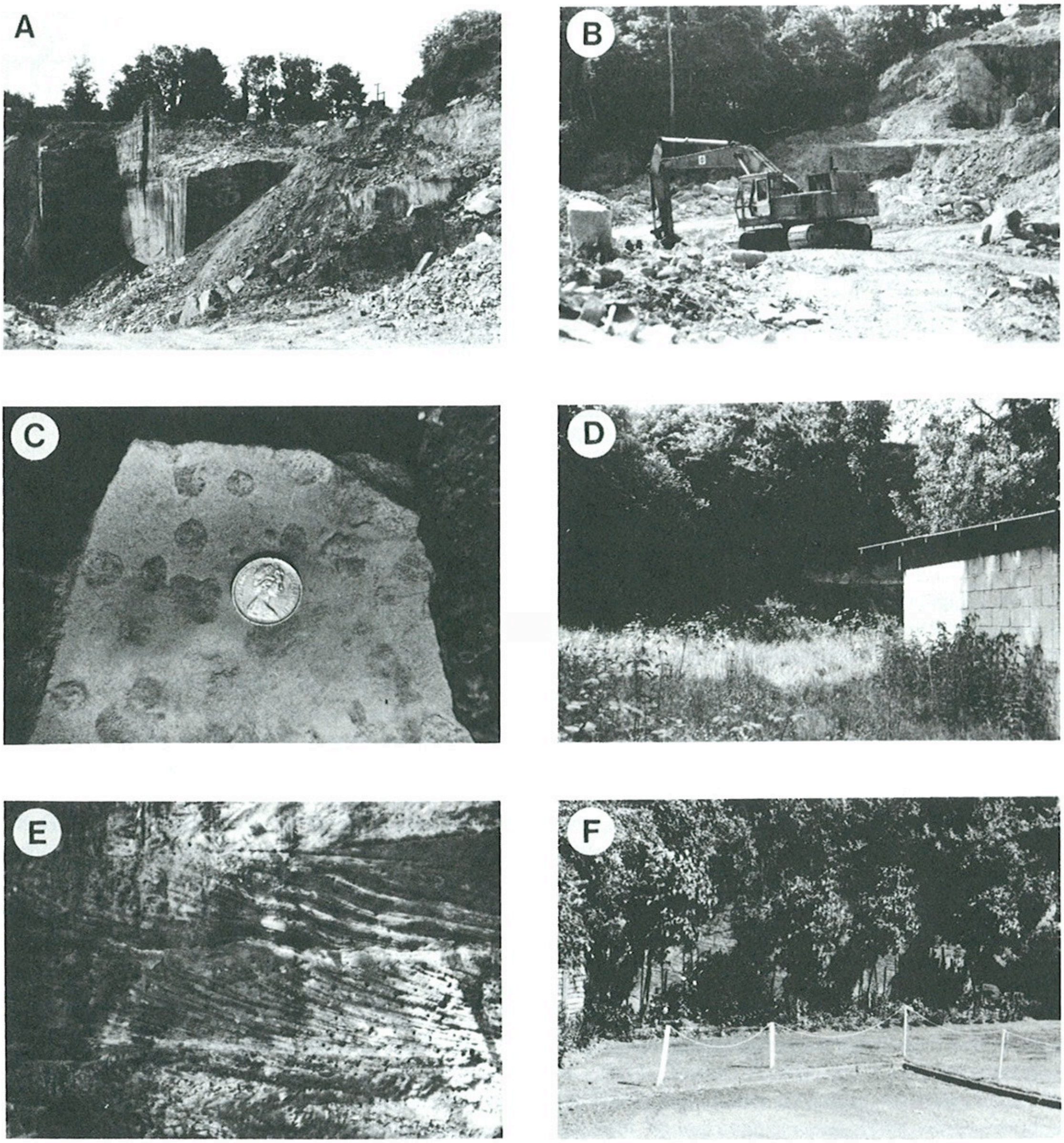

Figure 7.5. Tetrapod-bearing Middle Triassic deposits and localities in central England. Grinshill Stone Quarry prior to becoming owned by ECC Quarries Ltd., looking northward (A) and eastward (B), and a rain-printed slab from that quarry (C) (coin 30 mm in diameter). In the quarry (A, B), the eolian Helsby Sandstone Formation forms clear, manually squared faces, and the overlying Tarporley Siltstone Formation occupies the slope above. (D) Coten End Quarry as it is now, largely overgrown, looking eastward. (E) Section in the banks of the River Avon at Guy's Cliffe, showing the cross-bedding and contorted strata noted by Huene (1908b). (F) Site of the main fossiliferous quarry at Bromsgrove, now filled and forming part of the grounds of a hospital. (All photographs by AJN.)

R. articeps came from the Tarporley Siltstone Formation (the fine-grained gray sandstone) and from the top of the Grinshill Sandstone Formation (the coarser sandstone). This latter rock type was identified in the Building Stones in Aikin and Murchison's succession (Murchison, 1839, p. 40), and both rock types were described in Pocock and Wray's (1925, pp. 39–40) section, in which the top of the Grinshill Sandstone is described as "Hard Burr: Hard yellowish-white sandstone, 2ft. 6in." Thompson (1985) doubted that any bones had been found in the Grinshill Sandstone, but a find in 1991 by Philip Page, a quarryman of ECC Quarries Ltd., appears to confirm the likelihood of the original evaluation.

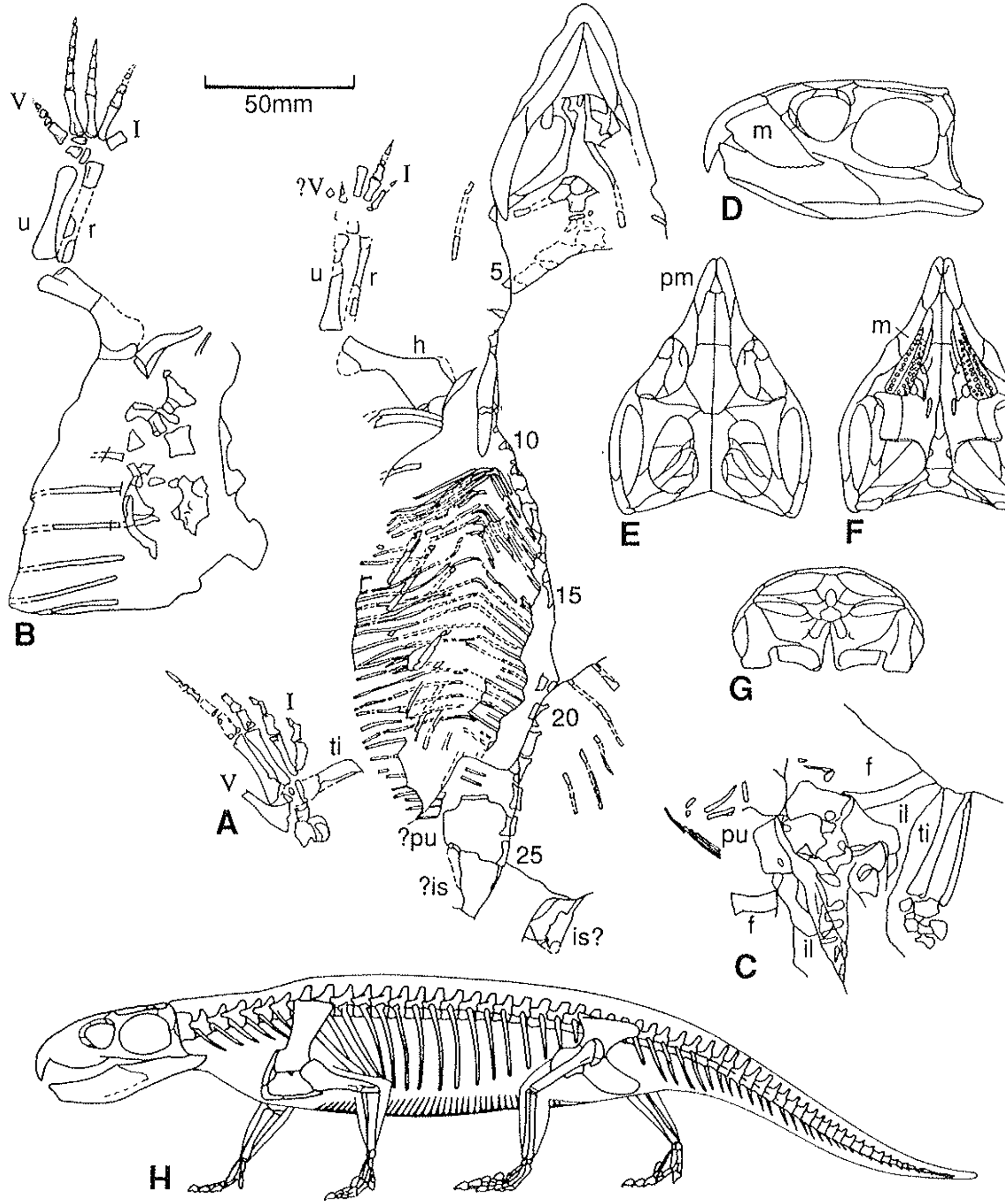

Figure 7.6. *Rhynchosaurus articeps*, the only member of the Grinshill skeletal assemblage: typical fossil remains (A–C) and restorations (D–H). (A) Partial skeleton lacking the tail and the limbs of the left side, in ventral view (BMNH R1237, R1238). (B) Dorsal vertebrae, ribs, and right forelimb in 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). 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. Abbreviations: f, femur; h, humerus; il, ilium; is, ischium; m, maxilla; pm, premaxilla; pu, pubis; r, radius; ti, tibia; u, ulna. Vertebrae and digits are numbered. (All based on Benton, 1990.)

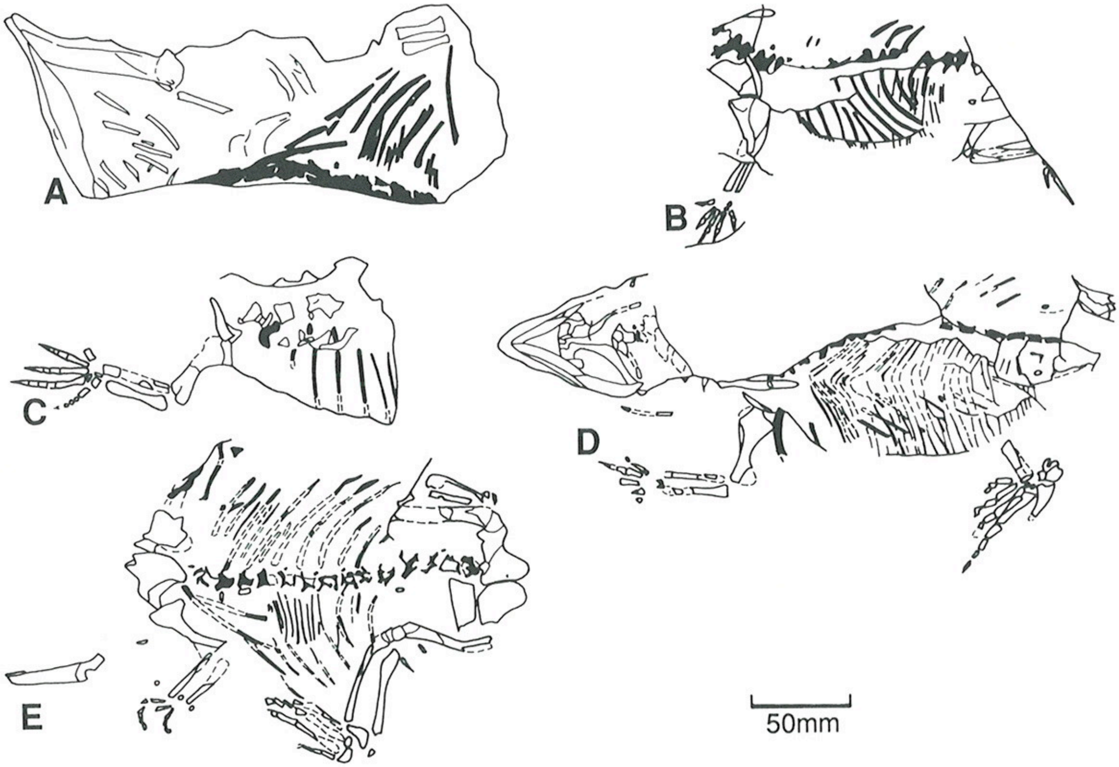

Figure 7.7. Outline sketches of selected specimens of *Rhynchosaurus articeps* from Grinshill as preserved in the rock, to illustrate the pose of the carcasses. Vertebrae and ribs are shaded black, and all other elements are shown in outline. SHRBM 3 (A), SHRBM 4 (B), SHRBM 6 (C), BMNH R1237/R1238 (D), BMNH R1239 (E). (Based on Benton, 1990.)

Taphonomy. There is no detailed field information about the relationships between the remains of *Rhynchosaurus articeps* and the sediments. Museum slabs bearing specimens are mostly too small to offer much sedimentological information, and it cannot be determined whether the extant specimens lay in channels or in pools or at the feet of dunes.

All but one of the reptiles (the 1984 find) were preserved in a horizontal orientation (Figure 7.7), rather than lying on their sides, but it cannot be determined whether they lay belly-up or back-up when they were buried. All postcranial elements appear to be articulated, although loosely attached portions, such as gastralia and scapulae, may have moved slightly out of position. Most skull specimens show slight distortion and disarticulation of loosely sutured elements. This is probably the result of collapse during burial or during postdepositional sediment compaction. The remains evidently were buried rapidly; there is no evidence that parts of the skeleton were removed by water currents, wind, or scavengers before fossilization. One skull (BMNH R1236) shows tectonic damage; a small fault offsets the posterior parts of the parietal, braincase, squamosal, and mandible by about 5 mm.

The bone is preserved as a soft, white, partly mineralized substance. Bones found in the finer sediment often show signs of compression; those in coarser sandstone seem to have been less affected during fossilization. However, bones found in the coarser sediment sometimes have iron-oxide-filled hollows replacing cancellous bone. Further details are given by Benton (1990, pp. 283–286).

Footprints. Rhynchosauroid footprints (Figure 7.8A,B) were found at Grinshill in 1838 and reported by Ward in 1839 (Ward, 1840), the collector of the first specimens of *Rhynchosaurus articeps*. Their first appearance in print was in an addendum by Murchison (1839, p. 734). They were found beneath the rubbly red sandstone called "Fee," on ripple-marked surfaces in a finely laminated, buff-colored sandstone presumably equivalent to part of Facies B of Thompson (1985). Ward (1840, p. 75) described the prints as differing "from those of *Chirotherium* in having only three toes, armed with long nails, directed forwards, not spreading out, and one hind toe on the same side as the longest fore toe, pointing backwards, and having a very long claw. No impression of the ball of the foot

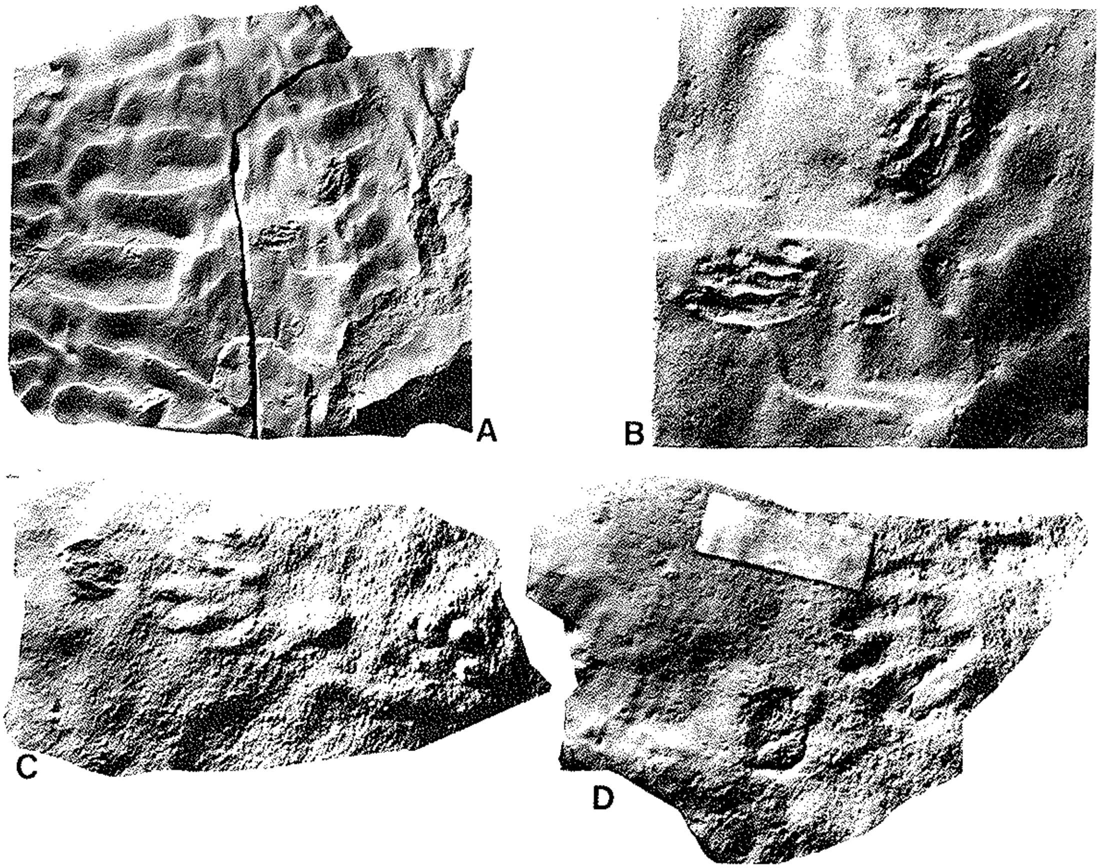

Figure 7.8. Footprints from Grinshill Quarries. *Rhynchosauroides* prints on a ripple-marked surface, SHRBM "2" (A, B), and *Chirotherium*-type prints, SHRBM "1" (C), SHRBM "3" (D). All specimens are from the Tarporley Siltstone Formation of unknown quarries in the Clive-Grinshill area. Magnifications are × 0.2 (A), × 0.6 (B), × 0.27 (C), × 0.22 (D). Photographs by B. Bennission (SHRBM).

in this example; but in another there are three toes and a depression for a ball not unlike that of a dog." He later repeated and stressed the existence of a least one backward-pointing hind toe (Ward, 1874).

Ward (1841) attributed the footprints to the amphibian "*Inosopus scutulatus* [sic] (Owen MS.)," a form of *Labyrinthodon*. The name may be the same as *Labyrinthodon* (*Anisopus*) *scutulatus*, given by Owen (1842a, pp. 538–541, pl. 46, figs. 1–5) to a collection of small bones from Leamington, which he interpreted as amphibian in origin, but which are now regarded as those of a prolacertiform such as *Macrocnemus* (discussed later). Owen (1842b, p. 146; 1842c, pp. 355–356) recognized the footprints as probably those of *Rhynchosaurus articeps*, following a written communication by Ward.

Buckland described these finds graphically: "impressions of small drops of rain and footsteps have . . . been found by Mr Ward. . . . On the same slabs are also very distinct small ripple marks produced by water, the undulations of which shew the direction in which the water ran, while the impressions of the rain, being in an oblique direction, shew in what direction the wind blew at the moment when this shower fell. The footsteps on the same slab shew the direction in which the animal was running" [Buckland, 1840, pp. 246–247; 1844 (for 1839), p. 5].

Beasley (1896, 1898, 1902, 1904, 1905, 1906), described further specimens of footprints from Grinshill and concluded that they probably were varieties of his rhynchosauroid print, type D1. This is a four-toed print, about 30–40 mm in total length, of which often only the three longest digits, presumably representing digits II–IV, are preserved (Figure 7.8A,B). The digit impressions taper from their roots to a pointed tip. The longest digit can reach 35 mm, with a width halfway along of 5 mm. The digits decrease in length from IV to II, and digit I can be very short, often less than a quarter the size of II, but occasionally reaching half its length. An impression of a short digit V is occasionally preserved, but set back from the others, and diverging slightly, but not in the backward-pointing position emphasized by Ward (1840, 1874). The digits often appear to curve to one side, and the claws, in particular, are bent that way. The palm of the print is not preserved. Rhynchosauroid footprints from Grinshill are preserved in the museums in Manchester, Shrewsbury, Ludlow, and Warwick, and in the British Geological Survey collections (Sarjeant, 1983).

Maidwell (1911, p. 142) named Beasley's rhynchosauroid D1 prints *Rhynchosauroides articeps*, but without designating a type specimen. He referred to Beasley's 1896 and 1905 papers, in which a specimen from Weston Quarries, Runcorn, north Cheshire, is illustrated. These authors refer to the original specimens from Grinshill, but these appear never to have been figured, probably because the prints are less well defined than examples from neighboring localities.

Thompson (1985, pp. 119–121) recorded rhynchosauroid footprints in both Facies A and, especially, Facies B at Grinshill. He also noted footprints of *Chirotherium* type (in the museums in Shrewsbury and Ludlow), but could not say whether they came from Facies A or Facies B (Figure 7.8C,D) (Beasley, 1904, p. 225; Sarjeant, 1983, p. 553). Prints collected at Grinshill by J. Stanley have been documented by Delair and Sarjeant (1985).

Warwick and Leamington, Warwickshire

Location and fauna. Fossil amphibian and reptile remains from this area came from the Bromsgrove Sandstone Formation, between about 1840 and 1870, and include the specimens described by Owen (1842a), Huxley (1859, 1869, 1870, 1887), and Miall (1874). The main productive site, Coton End Quarry (SP 289655; Figure 7.5D), Warwick, was worked for building stone in the early nineteenth century, but it was long abandoned when Beasley (1890b, p. 148) reported a visit to the site. The faunal list from the area is based on fossils from this quarry (Figure 7.9). Unless stated otherwise data are from Walker (1969), Paton (1974), Shishkin (1980), Kamphausen (1983), Galton (1985), and Benton (1990).

1. Stenotosaurinae incertae sedis: *Stenotosaurus leptognathus* (Owen, 1842), nomen dubium, jaws and other skull fragments. A small capitosauroid temnospondyl with a flattened crocodile-shaped skull, 210 mm long. The capitosauroids had been assigned to two species of *Cyclotosaurus* by Paton (1974), but Shishkin (1980) assigned *C. leptognathus* to *Stenotosaurus*, and Kamphausen (1983) then argued that the type specimen of this species was indeterminate, thus making the taxon a nomen dubium.
2. Cyclotosaurinae incertae sedis: *Cyclotosaurus pachygnathus* (Owen, 1842), nomen dubium, jaws and other skull fragments. A moderate-sized capitosauroid temnosondyl with a lower skull than *S. leptognathus*.
3. *Mastodonsaurus* sp. [including material referred to as *Mastodonsaurus jaegeri* (Owen, 1842) and *Mastodonsaurus lavisi* (Seeley, 1876)]: a single jaw from Coton End, and one from Guy's Cliffe (the 1823 find), as well as assorted skull fragments. A large mastodonsaurid temnospondyl; estimated skull length 500–600 mm.
4. Cf. *Macrocnemus* (includes *Rhombopholis scutulata* Owen, 1842): partial skeleton (from Old Leamington Quarry) and isolated limb elements. A small lizardlike animal, 50–80 mm long.
5. *Rhynchosaurus brodiei* Benton, 1990: skull and mandible remains and isolated postcranial elements. A moderate-sized rhynchosaur with a skull 90–140 mm long and an estimated body length of 0.5–1.0 m.
6. *Bromsgroveia walkeri* Galton, 1985: vertebrae, sacrum, ilium, ischium, and ?femur. A moderate- to large-sized rauisuchian.
7. "Large thecodontian": an ilium.
8. Archosaur indet. (*Cladeiodon lloydi* Owen, 1841): about ten isolated teeth, which could belong to *Bromsgroveia*, to the "large thecodontian," or to another, as yet unidentified carnivorous archosaur.
9. "Prosauropod dinosaur": a cervical vertebra. If a true dinosaur, this could be the oldest known.

Three other localities in the Warwick-Leamington area also yielded vertebrate remains in the nineteenth century. Old Leamington Quarry (?SP 325666) produced remains of the fish *Gyrolepis* (Walker, 1969, p. 472) and of *Mastodonsaurus*, "*Stenotosaurus*," cf. *Macrocnemus* (type specimen of Owen's *Rhombopholis scutulata*) (Owen, 1842a, pp. 538–541, pl. 46, figs. 1–5), *Rhynchosaurus brodiei*, and a "prosauropod" tooth (Murchison and Strickland, 1840, pl. 28, fig. 7a; Huene, 1908a, fig. 265). Cubbington Heath Quarry (SP 332694) yielded *Mastodonsaurus* and "*Stenotosaurus*" (Huxley, 1859; Woodward, 1908; Wills, 1916, pp. 9–11, pl. 3). Guy's Cliff (SP 294668) (Figure 7.5E) produced remains of the jaws of *Mastodonsaurus* (Owen, 1842a, pp. 537–538, pl. 44, figs. 4–6, pl. 37, figs. 1–3; Miall, 1874, p. 433).

Host deposits. The Bromsgrove Sandstone Formation is 20–35 m thick in the Warwick district (Old, Sumbler, and Ambrose, 1987, p. 20). Coton End Quarry (Figure 7.5D) exposes 10–11 m of channeled and cross-bedded water-laid buff and red sandstone in units 1–3 m thick, with occasional impersistent marl and clay bands 0.1–0.5 m thick.

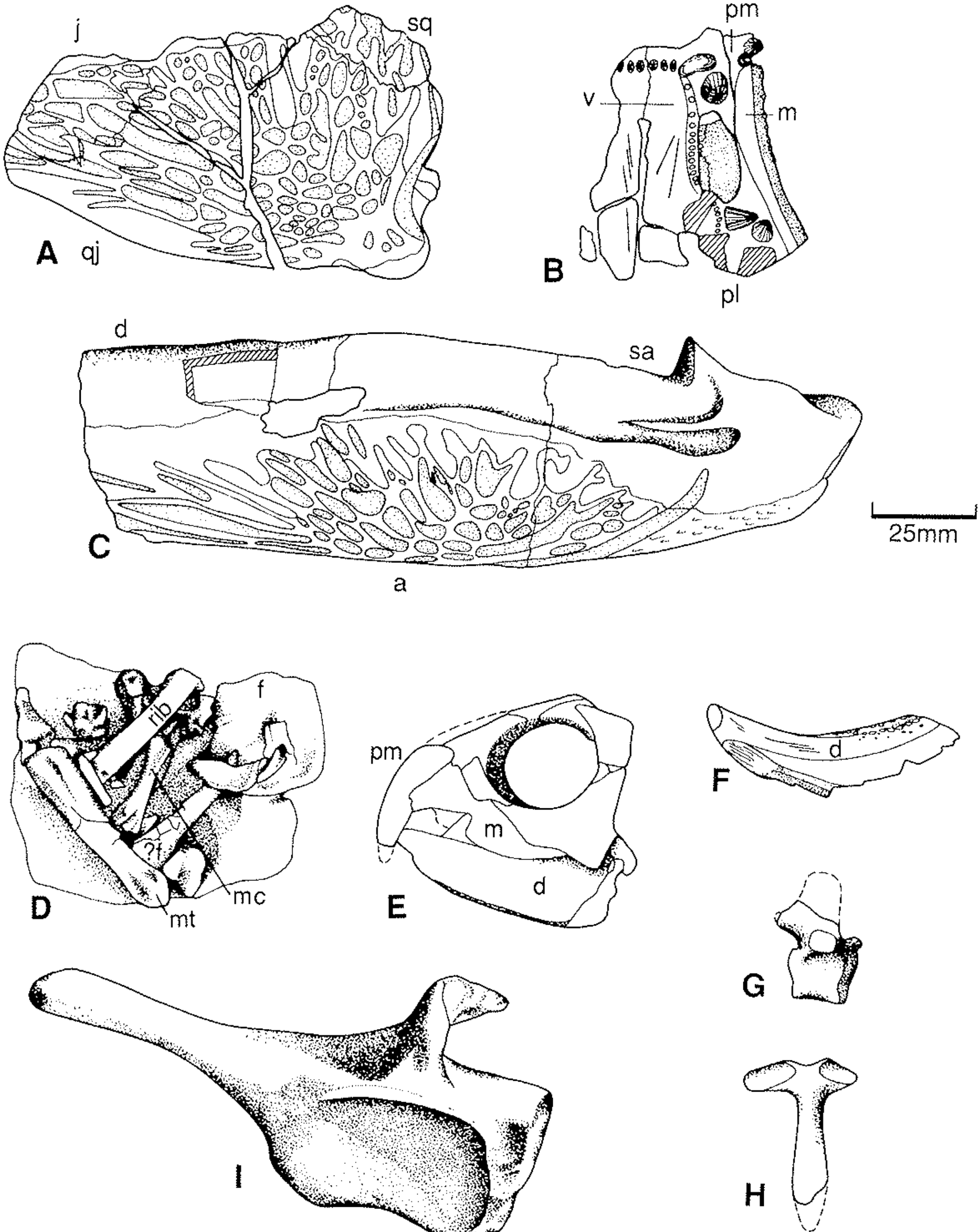

Figure 7.9. Typical elements of the Warwick fauna. (A) Left posteroexternal corner of the skull of "*Cyclotosaurus pachygnathus*" (Cyclotosaurinae incertae sedis) in lateral view (WARMAS Gz 13). (B) part of the snout of "*Stenotosaurus leptognathus*" (Stenotosaurinae incertae sedis) in palatal view (WARMS Gz 38). (C) Posterior portion of a left lower jaw of "*Stenotosaurus leptognathus*" in lateral view (WARMS Gz 35). (D) Scattered bones of cf. *Macrocnemus* (*Rhombopholis scutulata*) (WARMS Gz 10). (E–H) Assorted remains of *Rhynchosaurus brodiei*: anterior part of the skull in lateral view (WARMS Gz 6097/BMNH R8495) (E), anterior part of a dentary in medial view (WARMS Gz 950) (F), middorsal vertebra in right lateral view (WARMS Gz 17) (G), and interclavicle in ventral view (WARMS Gz 34) (H). (I) Right ilium of *Bromsgroveia walkeri* in lateral view (WARMS Gz 3). Abbreviations: a, angular; d, dentary; f, femur; j, jugal; m, maxilla; mt, metatarsal; pl, palatine; pm, premaxilla; qj, quadratojugal; sa, surangular; sq, squamosal. (A–C, after Paton, 1974; D and I after Owen, 1842a; E–H, after Benton, 1990.)

Murchison and Strickland (1840) gave this section for the quarry:

a.	Soft, white sandstone and thin beds of marl	8 feet
b.	Whitish sandstone, thick-bedded	12
c.	Very soft sandstone, colored brown by manganese; called "Dirt-bed" by the workmen	1
d.	Hard sandstone, called "Rag," about	2
		23 feet.

Old et al. (1987, fig. 11) recorded 7 m of massive sandstone and flat-bedded sandstone grading up into 4 m of cross-bedded sandstone and mudstone; this section was interpreted as in the middle of the thin Bromsgrove Sandstone Formation of the Warwick district and thus may be as little as 10 m below the overlying Mercia Mudstone Group.

The only other extant locality that has yielded tetrapod remains is at Guy's Cliffe. Murchison and Strickland (1840, p. 344) gave the following section from a quarry in the grounds of Guy's Cliffe House:

Sandstone and beds of marl	8 feet
Solid sandstone, whitish or grey, occasionally of a reddish tint	12
Red, micaceous marl, with wedges of sandstone	8
Solid, light-colored, reddish tinted sandstone about	20
	48 feet.

Good sections of 7–10 m of cross-bedded buff-colored sandstone with irregular shale lenses are still exposed in an old stable yard of Guy's Cliffe House, near the bank of the River Avon. Huene (1908b) figured a section on the riverbank (SP 29376678) (Figure 7.5E) that showed a large channel covered by a discontinuous breccia layer. He noted that the bedding was very irregular and that ripple marks occurred on some beds. Another section "on the rocky cliff opposite Guy's Cliffe House shows contorted sandstones with laterally discontinuous marl and breccia bands" (Huene, 1908b).

The Bromsgrove Sandstone Formation, as seen at Coton End and Guy's Cliffe (Old et al., 1987), has been interpreted as the deposit of mature complexes of meandering river channels and floodplains (Warrington, 1970b).

Occurrences of tetrapods. According to Murchison and Strickland (1840, p. 344), the fossil amphibian and reptile bones were found principally in the "Dirt-bed" in Coton End Quarry. Hull (1869, pp. 88–89) stated that the amphibian remains occurred in the "Water Stones," but Walker (1969) noted that the reptiles came from the upper part of the "Building Stones" (i.e., the Bromsgrove Sandstone Formation). Most of the Warwick specimens have been cleared of matrix, but some show a yellow or greenish-colored fine- to medium-grained sandstone with coarse patches that might accord with Murchison and Strickland's (1840) description of the "Dirt-bed." In Coton End Quarry, laterally discontinuous marl and clay bands 0.1–0.5 m thick may be observed in the weathered faces, and these probably correspond to the fossiliferous "Dirt-bed." One specimen (WARMS Gz 34) is, however, in a hard, fine-grained, laminated gray sandstone.

Taphonomy. The Warwick amphibians and reptiles are generally preserved in a disarticulated state. The only associated material is the skeleton of cf. *Macrocnemus* from Old Leamington Quarry (WARMS Gz 10), in which a number of limb bones and vertebrae are preserved, still in partial articulation, in a small block. There are also three associated vertebrae from the sacral area of a rauisuchian (WARMS Gz 1, 2) and a partial skull of *Rhynchosaurus brodiei* (WARMS Gz 6097/BMNH R8495), but all other finds from the Warwick area are single postcranial elements, isolated teeth, or jaw elements. The amphibian fossils, comprising parts of the skull roof (WARMS Gz 6, 9, 11, 13, 14, 20, 26, 36, 38, 1057) or partial lower jaws [WARMS Gz 15, 27, 35, 37; BGS(GSM) 27964], are among the largest remains. Unfortunately, none was recovered recently, and there are no records as to whether the bones were found in a disarticulated state or whether their apparent disarticulated state reflects collection methods. We believe that most of the disarticulation is original, because specimens still in the matrix show sandstone surrounding isolated elements.

Contrary to Murchison and Strickland's observation (1840, p. 344) that the bones were "rolled and fragmentary," the specimens show little sign of abrasion; the surface detail is excellent, and broken ends are sharp and unworn. Some, at least, of the breaks appear to have occurred just before deposition, because matrix adheres to the broken surfaces where these are visible. None of the bones shows significant distortion, despite Miall's (1874, p. 417) suggestion to the contrary.

The bone in the Warwick specimens is preserved as hard, white to buff-colored material, apparently with the internal structure intact. In broken sections, the dentine of the rhynchosaur teeth is yellow, and the enamel is stained dark brown. It is difficult to reconcile the current hard, well-preserved condition of the bone with the description given by Murchison and Strickland (1840, p. 344), who noted that the bones were in a decomposed condition when collected and resembled "stiff jelly, with singular hues of blue and red. It is necessary to remove them with a solution of gum arabic, as the best means of preserving them."

Most of the Warwick bones show evidence of transport, but insufficient to cause abrasion. Carcasses, both large and small, were generally broken up (with the exceptions noted earlier), and some bones were broken through sharply. Skulls of amphibians and of the rhynchosaur seem to have survived with less disarticulation. It is not known whether the bones were deposited in channel lag deposits, on cross-bedded point bars, or in finer- grained overbank deposits. The few specimens on which the matrix survives show no sign of clasts indicative of a channel lag.

Footprints. Brodie and Kirshaw (1873) record *Rhynchosaurus* footprints from Warwick, now on display in the Warwick Museum; the locality is not recorded, but Sarjeant (1974, p. 315) suggested that it was Coton End. Beasley (1890a) reported finding "labyrinthodont" and "*Rynchosaurus* [*sic*]" footprints in Coton End Quarry, and later (Beasley; 1898, p. 236; 1906, p. 162) referred to a large slab with footprints from Coton End. He also noted (Beasley, 1906, p. 164) a "slab of Keuper sandstone with Impressions of Plants upon it, from Coton End Quarry, 1872." The "plants" are "longitudinally ribbed" markings that terminate "in narrow rods which look like continuations of the longitudinal ribs" and hence are probably groove marks produced by objects (plant stems, pebbles, bones, etc.) transported by water (Cummins, 1958). This slab lacks "distinct footprints," although a photograph in Beasley's collection shows prints of *Rhynchosauroides* (Sarjeant, 1984, p. 142, no. 46).

Bromsgrove, Worcestershire

Location and fauna. Collections of isolated amphibian and reptile bones were made by L. J. Wills early in this century from the Bromsgrove Sandstone Formation in quarries on Rock Hill (SO 948698), Bromsgrove, near Birmingham; the specimens are labeled as having come from "Wilcox S. Quarry." The Bromsgrove Sandstone Formation (Sherwood Sandstone Group) (Warrington et al., 1980) comprises, in ascending order, the Burcot, Finstall, and Sugarbrook members (Old et al., 1991). The Rock Hill Quarries (Wills, 1907, 1910, pp. 254–256) worked beds in the middle (Finstall) member (formerly the "Building Stones") (Wills, 1970, p. 250; Old et al., 1991), but are now filled in (Figure 7.5F).

The fossil amphibian and reptile remains, together with plants and invertebrates from the Bromsgrove area (Old et al., 1991) (Figure 7.10), were collected almost exclusively by Wills (1907, 1908, 1910). The vertebrate faunal list is based on these publications and on the Wills collections in the CAMSM and BIRUG. Other fossils not listed here include plants, annelids, bivalves, arthropods, and fish (Old et al., 1991).

1. *Mastodonsaurus* sp.: skull plate, ? vertebra, ? tooth. A large mastodonsaurid temnospondyl; estimated skull length 500–600 mm.
2. Cyclotosaurinae incertae sedis: *Cyclotosaurus pachygnathus* (Owen, 1842), nomen dubium, lower jaw piece. A moderately sized capitosauroid temnospondyl; estimated skull length 300 mm.

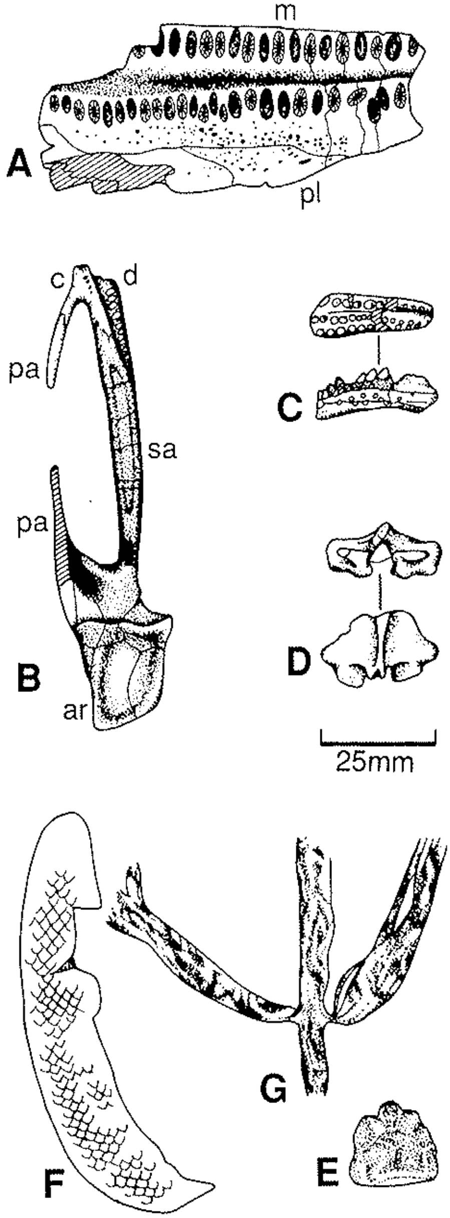

Figure 7.10. Elements of the Bromsgrove fauna and flora. (A) Part of the right upper jaw of *Mastodonsaurus* sp. in ventral view (BIRUG Sp. 1). (B) Posterior end of a right lower jaw of "*Cyclotosaurus pachygnathus*" in dorsal view (BIRUG Sp. 2). (C) Left maxilla of *Rhynchosaurus brodiei* in ventral (top) and lingual (bottom) views (CAMSM G336). (D) Neural arch of a nothosaur dorsal vertebra in anterior (top) and dorsal (bottom) views (CAMSM G351). (E) Headshield of the scorpion *Willsiscorpio bromsgroviensis* (CAMSM G1). (F) Male cone of the conifer *Voltzia heterophylla* showing external surface (CAMSM K1001). (G) Leafy stem of the horsetail *Schizoneura paradoxa* (CAMSM K1079). Abbreviations: ar, articular; c, coronoid; d, dentary; m, maxilla; pa, prearticular; pl, palatine; sa, surangular. (A and B after Paton, 1974; C after Benton, 1990; D after Walker, 1969; E–G after Wills, 1910.)

3. *Rhynchosaurus brodiei* Benton, 1990: small right and left maxilla.
4. Rauisuchian: vertebra and teeth.
5. cf. *Macrocnemus*: a dorsal vertebra (Walker, 1969).
6. Nothosaur vertebra, represented only by the neural arch (Walker, 1969, fig. 1).

Host deposits. Wills (1907, pp. 29–32; 1908; 1910, pp. 257–263) described the succession in the Rock Hill Quarries as 15–20 m of alternating sandstones and shales and a "marl conglomerate" (i.e., intraformational breccia or conglomerate), in lenticular units, with the sandstones apparently cross-bedded.

Wills (1950, p. 85) suggested that the Bromsgrove Sandstone Formation at Bromsgrove formed part of a delta built out into a freshwater, or only slightly saline, lake that was subject to intermittent desiccation. In modern terminology, the intraformational conglomerates would represent torn-up and redeposited overbank deposits or within-river-plain fine deposits. Wills (1970, pp. 263–266; 1976, pp. 107–126) interpreted the fossiliferous lenticular beds as deposits formed in channels, pools, or lakes on the floodplain and envisaged cyclothemic sedimentation from temporary rivers gradually filling the shallow subsiding Midland Cuvette. This basin was separated from the North Sea Basin by the Pennine-Charnwood land barrier, which was breached occasionally so that the Muschelkalk Sea entered briefly from the east, depositing the "Waterstones."

Warrington (1970b, pp. 204–205) considered the Bromsgrove Sandstone Formation as comprising a sequence of low-sinuosity, braided stream deposits, followed by deposits representing higher-sinuosity, meandering rivers; fining-upward fluvial cycles are well developed (Old et al., 1991, fig. 5). The floral and faunal evidence indicates freshwater or brackish conditions at the time of deposition of the fossiliferous units (Wills, 1910; Ball, 1980; Old et al., 1991).

Occurrences of fossils. Wills (1907, pp. 30–31; 1908, p. 312) noted that the majority of the fossils came from "lenticular beds of marl and shale, while some appear in the sandstone." Some horizons were very carbonaceous, and those contained abundant fragmentary arachnid remains. The red marl and red sandstone were barren of fossils, and plants occurred in the gray sandstone.

Wills (1907, p. 33) noted that "the Labyrinthodont remains, next to the plants, are the most abundant fossils, but are apparently confined to the marl conglomerate." This unit was the source of most of the bones. Wills (1907, p. 31) believed that the marl conglomerate formed "a definite horizon in all four quarries." It was known locally as "Cat-brain" and consisted "of small pieces of marl, mostly gray in color, cemented, along with bits of bone or wood and sand, into a compact rock. This hardens to a very tough stone, though one only fit for rough work.... They are associated with one or more laminae, covered with fragments of carbonized wood. Further, it is in, or close to, these marl-conglomerates that most of the teeth and bones of the vertebrates and pieces of stems of plants are found – a significant fact when we consider how many bone-beds are conglomeratic, especially in the Trias...in some cases [the conglomerates] appear to have decayed *in situ*; they are then reduced to a friable and crumbly state, while their color is in parts ochreous and others brown, instead of the usual green" (Wills, 1910, p. 260–261). In a cored borehole at Sugarbrook (SO 9621 6818), some 3 km southeast of Rock Hill, plant remains and crustaceans occurred in similar beds in the upper half of the Finstall Member and at the base of the Sugarbrook Member of the Bromsgrove Sandstone Formation (Old et al., 1991, fig. 5).

Taphonomy. The bones from Bromsgrove are all isolated pieces: jaw fragments of temnospondyl amphibians, vertebrae of a rauisuchian, a tooth of an archosaur, a vertebra of a macrocnemid, partial maxillae of *Rhynchosaurus*, and a damaged neural arch of a nothosaur. Fine details, such as the sculpture on the temnospondyl bones (Paton, 1974) and sharp posterior teeth in maxillae of *Rhynchosaurus*, are often preserved. However, the specimens are all single elements, and some transport by water seems evident, as at Warwick. Most of the specimens have been removed from the matrix, so that little can be determined about their original state. Wills (1910, pp. 260–261) implied that the bones were found in a fragmentary condition and that disarticulation and damage were predepositional.

The bone is now in a hard and well-preserved state, with all internal structure of bone and tooth intact. However, Wills (1910, p. 261) noted that the bones suffered some damage when they were found in parts of the marl conglomerate that had decayed: "we find bones in this decayed rock which are of the consistency of hard soap when first extracted, but quickly harden on exposure to the atmosphere." This is reminiscent of the description given by Murchison and Strickland (1840) of the initial state of the bones from Warwick described earlier.

Sidmouth to Budleigh Salterton, Devon

Location and fauna. Bones of amphibians and reptiles have been found at localities on the coast between Budleigh Salterton and Sidmouth (Figure 7.11). Several specimens collected in the nineteenth century came from below High Peak (SY 104858), 2 km west of Sidmouth, and from the mouth of the River Otter,

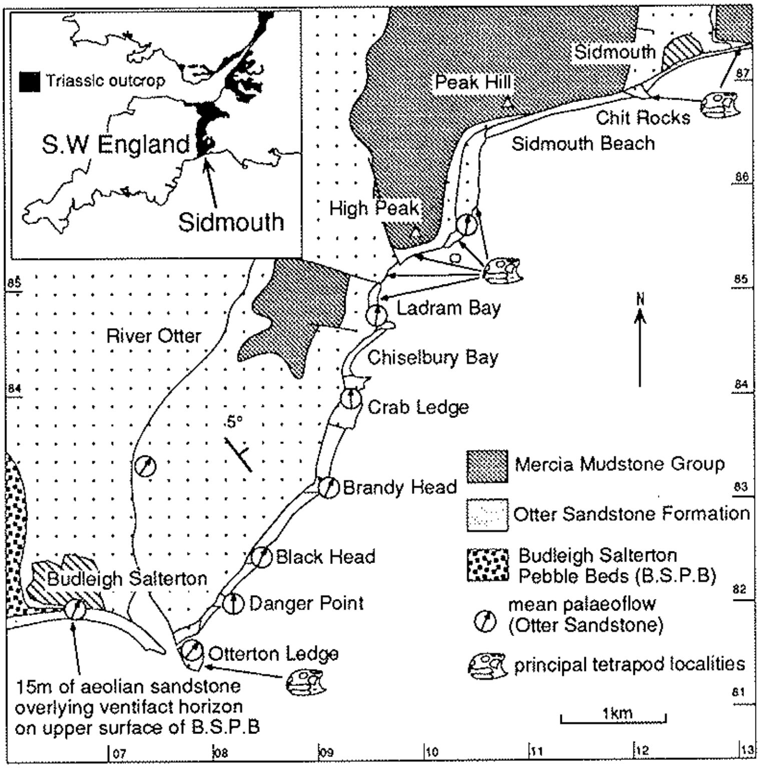

Figure 7.11. Map of the coastal outcrop of the Otter Sandstone Formation between Sidmouth and Budleigh Salterton, Devon. The major Triassic formations are indicated, together with mean fluvial paleoflow directions and principal tetrapod localities. Based on fieldwork by AJN and collecting by PSS.

on its east bank (SY 077820), just east of Budleigh Salterton. Since 1982, extensive collections have been made from at least 15 localities between Budleigh Salterton and Sidmouth (SY 0807 8212 to SY 1066 8639) and just east of Sidmouth (SY 1297 8730), with specimens being collected from fallen blocks of red sandstone and in situ, from horizons at the base of the cliff and on the foreshore (Spencer and Isaac, 1983; Benton, 1990; Milner et al., 1990). Some of the best recent finds of tetrapods have come from Ladram Bay and Chiselbury Bay, parts of the coast not noted as fossiliferous by the Victorian authors.

The fossils all occur in the Otter Sandstone Formation, formerly the "Upper Sandstone" (Ussher, 1876; Woodward and Ussher, 1911). At the western end of the outcrop, at Otterton Point, 12 m of dark red sandstones near the base of the Otter Sandstone Formation are exposed. The cliffs rise to a height of 155 m at High Peak, near the eastern end of the outcrop, where the sequence was described by Whitaker (1869), Lavis (1876), Ussher (1876), and Irving (1888).

The faunal list of amphibians and reptiles is based on Benton (1990), Milner et al. (1990), and more recent unpublished work (MJB and PSS, unpublished data). Other fossils, not listed here, include plants, invertebrates, and fish (Figures 7.12, 7.13, and 7.17).

1. "*Mastodonsaurus lavisi*" (Seeley, 1876), nomen dubium: skull fragments, part of lower jaw, and elements of the pectoral girdle of a large capitosaurid temnospondyl; estimated skull length 500–600 mm. Milner et al. (1990) argued that the type specimen of *M. lavisi* was indeterminate, and the taxon is a nomen dubium.
2. *Eocyclotosaurus* sp.: remains of a skull, about 150 mm long, and other fragments.
3. Capitosauridae inc. sed.: posterior part of a mandible.
4. *Rhynchosaurus spenceri* Benton, 1990: skull and mandible remains, isolated maxillae, and postcranial elements, as well as a partial skeleton collected in 1990. A moderate-sized rhynchosaur with a skull length of 40–175 mm (mean 116 mm) and an estimated mean body length 0.8 m (range 0.4–1.3 m).
5. *Tanystropheus* sp.: a small tooth.
6. Procolophonidae inc. sed.: three small dentaries, a maxilla, and an interclavicle.
7. Rauisuchian: numerous teeth and a few vertebrae.
8. ?Ctenosauriscid archosaur: a long neural spine, possibly part of the dorsal "sail"; this identification is provisional (Milner et al., 1990).

Host deposits. The Otter Sandstone Formation comprises about 118 m of medium- to fine-grained red sandstones. These dip gently eastward in the coast

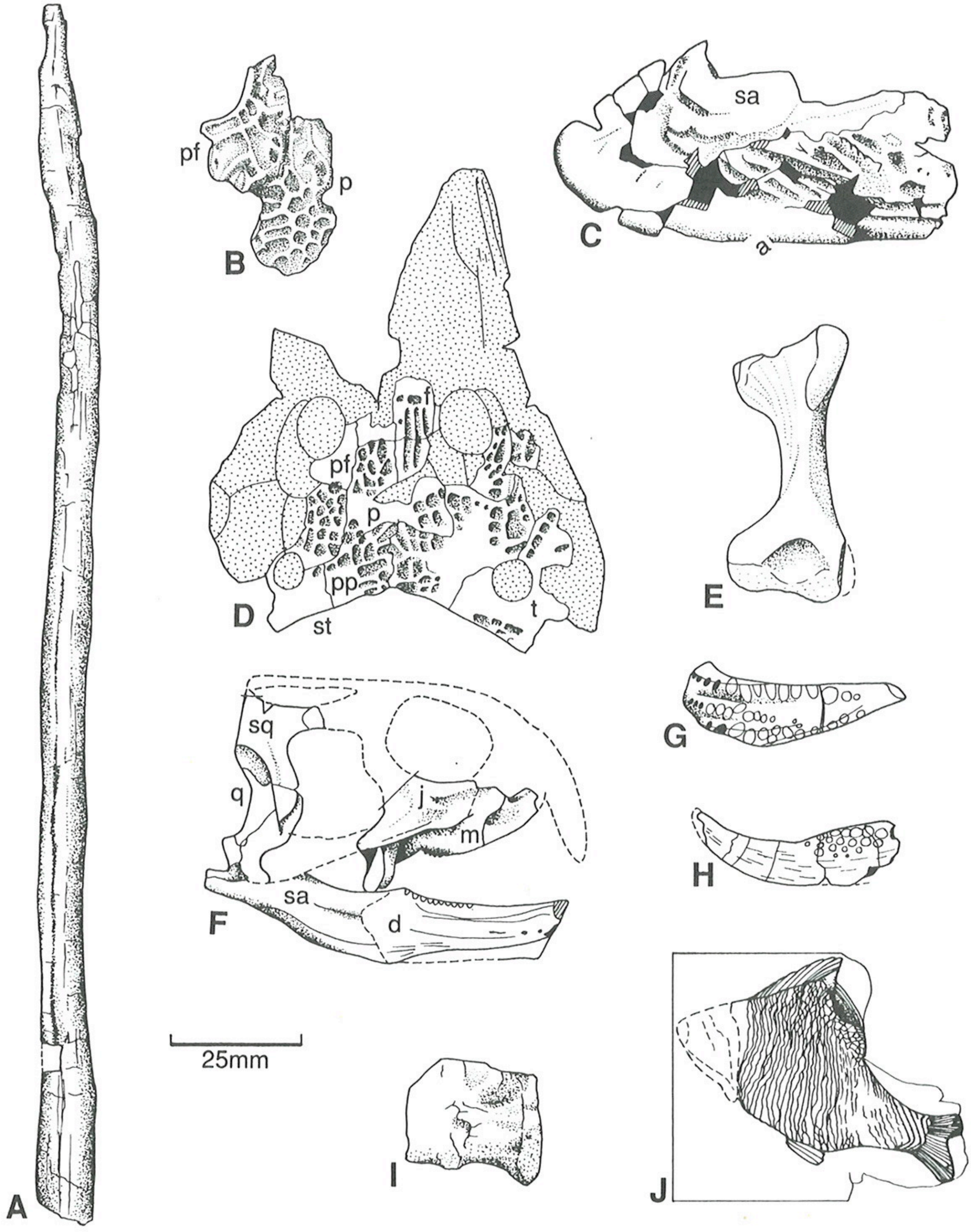

Figure 7.12. Larger elements of the Otter Sandstone Formation fauna from Devon. (A) Spine of an unknown vertebrate, possibly a dorsal neural spine of a ctenosauriscid archosaur (EXEMS 60/1985.88). (B) Fragment of the skull roof of *Mastodonsaurus lavisi* in dorsal view (EXEMS 60/1985.287). (C) Posterior portion of a right mandibular ramus of an unidentified capitosaurid, in lateral view (EXEMS 60/1985.78). (D) Incomplete skull roof of *Eocyclotosaurus* sp., in dorsal view (EXEMS 60/1985.72). (E–H) Remains of *Rhynchosaurus spenceri*: left humerus in ventral view (EXEMS 60/1985.282) (E), restored skull in right lateral view (EXEMS 60/1985.292) (F), right maxilla in ventral view (EXEMS 60/1985.292) (G), and right dentary in lingual view (BMNH R9190) (H). (I) Vertebra of an archosaur (Bristol University, unnumbered). (J) Neopterygian fish *Dipteronotus cyphus* (EXEMS 60/1985.293). Abbreviations: as in Figures 7.6, 7.9, and 7.10, and f, frontal; j, jugal; p, parietal; pf, postfrontal; pp, postparietal; t, tabular. (A and I, original; B–D and J after Milner et al., 1990; E–H after Benton, 1990.)

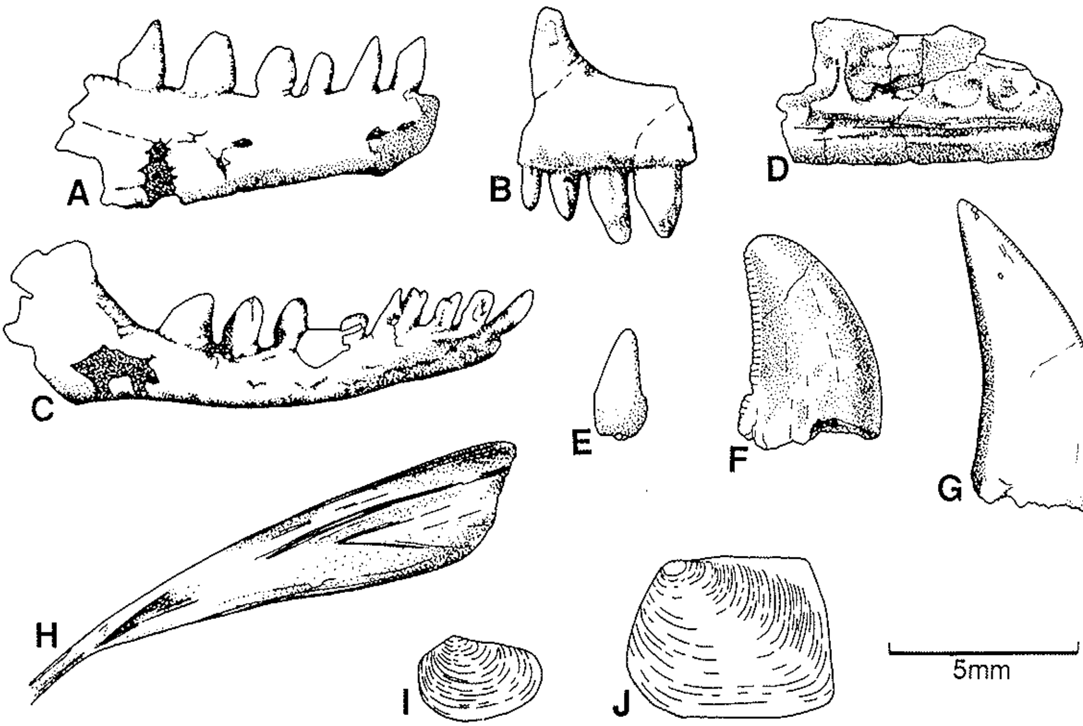

Figure 7.13. Smaller elements of the Otter Sandstone Formation fauna of Devon. Right dentaries (A, C) and a left maxilla (B) of a procolophonid, all in lateral view (EXEMS 60/1985.311, 3, and 154). (D) Dentary fragment of an unknown small pleurodont reptile, showing pits for teeth, in lingual view. (E) Tooth of ?*Tanystropheus*, showing small accessory cusps (EXEMS 60/1985.143). (F, G) Recurved teeth of two kinds of unknown archosaurs (Bristol University, unnumbered). (H) Unidentified insect wing (Bristol University, unnumbered). I, J Carapaces of the conchostracan *Euestheria* (Bristol University, unnumbered). (A–C and E after Milner et al., 1990; D and F–J, original.)

section, and the formation continues northward to Somerset and eastward as far as Hampshire and the Isle of Wight beneath younger Triassic sediments, reducing in thickness to 15 m in the east, and 30–60 m beneath Somerset and eastward as far as Hampshire and the Isle ably on the Budleigh Salterton Pebble Beds, a unit of fluvial conglomerates 20–30 m thick derived from the south and west (Henson, 1970; Smith, 1990; Smith and Edwards, 1991). The contact, visible just west of Budleigh Salterton (Figure 7.14A) (SY 057815), is marked by an extensive ventifact horizon (Leonard, Moore, and Selwood, 1982) that represents a nonsequence of unknown duration and is interpreted by Wright, Marriott, and Vanstone (1991) as a desert pavement associated with a shift from a semiarid to an arid climate. This contact and the layer containing ventifacts have been noted also at inland exposures (Smith and Edwards, 1991, p. 74).

The lowest beds of the Otter Sandstone Formation, exposed west of Budleigh Salterton and in the middle of the foreshore there (SY 064817), are red, rather structureless, well-sorted sandstones (Henson, 1970; Selwood et al., 1984).

At Otterton Point (SY 078819), hard, calcite-cemented, cross-bedded sandstone units (less than 0.5 m thick) contain calcite-cemented rhizoliths, up to 1 m deep, and other calcrete formations (Figure 7.14D) (Mader, 1990; Purvis and Wright, 1991). Purvis and Wright (1991) attributed the large vertical rhizoliths to deep-rooted phreatophytic plants that colonized bars and abandoned channels on a large braidplain. Ussher (1876, p. 380) observed that the sandstones here "contain two or three conglomerate beds, and few pebbles in false-bedded lines." 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 northeast of Otterton Point.

Farther east, calcretes occur more sporadically, and the formation is dominated by sandstones in large and small channels (Figure 7.14C), with occasional siltstone lenses. The sandstones occur in cycles, often with conglomeratic bases, and fine upward through cross-bedded sandstones to ripple-marked sandstones

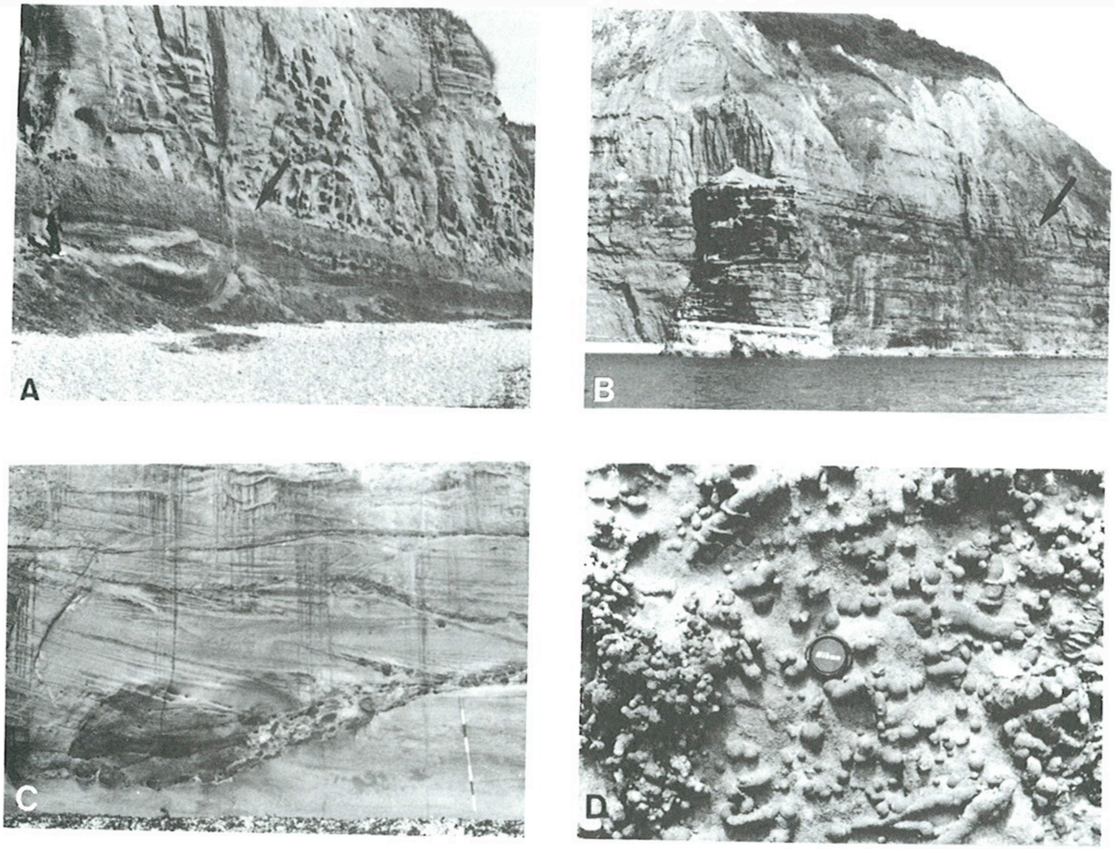

Figure 7.14. Sedimentology and stratigraphy of the Otter Sandstone Formation. (A) The lower contact of the Otter Sandstone Formation with the Budleigh Salterton Pebble Beds (contact marked with an arrow), seen on the coast just west of Budleigh Salterton; note the person for scale. (B) The upper contact of the Otter Sandstone Formation with the Mercia Mudstone Group (contact marked with an arrow), seen below Peak Hill, just west of Sidmouth. (C) Mudclast-lined erosion surface and cross-bedded sandstones in the Otter Sandstone Formation in Chiselbury Bay; note the meter-pole for scale. (D) Calcrete nodules exposed in a vertical cliff section in the Otter Sandstone Formation; the camera lens cap is 50 mm in diameter. (All photographs by AJN.)

(Figure 7.15). The Otter Sandstone Formation is capped by water-laid siltstones and mudstones of the Mercia Mudstone Group (Figure 7.14B).

Henson (1970), Laming (1982, pp. 165, 167, 169), and Mader and Laming (1985) interpreted the Otter Sandstone Formation as comprising fluvial and eolian deposits. Sandstones near the base of the formation are eolian and were accumulated in dunes produced by easterly winds (Henson, 1970), these being transverse barchanoid dune ridges in modern terminology. The middle and upper parts of the formation are of fluvial origin; sandstones were deposited by ephemeral braided streams flowing from the south and southwest (Selwood et al., 1984). The comparatively thin mudstones are interpreted as the deposits of temporary lakes on the floodplain, with impersistent rivers fed from reservoirs in breccia outwash fans elsewhere, in turn recharged by flash floods and episodic rainfall. Numerous calcrete horizons occur and indicate subaerial soil and subsurface calcrete formation in semiarid conditions (Mader and Laming, 1985; Lorsong, Clarey, and Atkinson, 1990; Mader, 1990; Purvis and Wright, 1991).

The climate was semiarid, with long dry periods when riverbeds dried out, and seasonal or occasional rains leading to violent river action and flash floods. However, there is little evidence of complete aridity; desiccation cracks and pseudomorphs after halite are uncommon in the Otter Sandstone Formation (Lavis, 1876; Woodward and Ussher, 1911; Henson, 1970). The relative scarcity of plant fossils may reflect oxidizing conditions in an arid climate (Laming, 1982, p. 170).

Occurrences of fossils. 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,

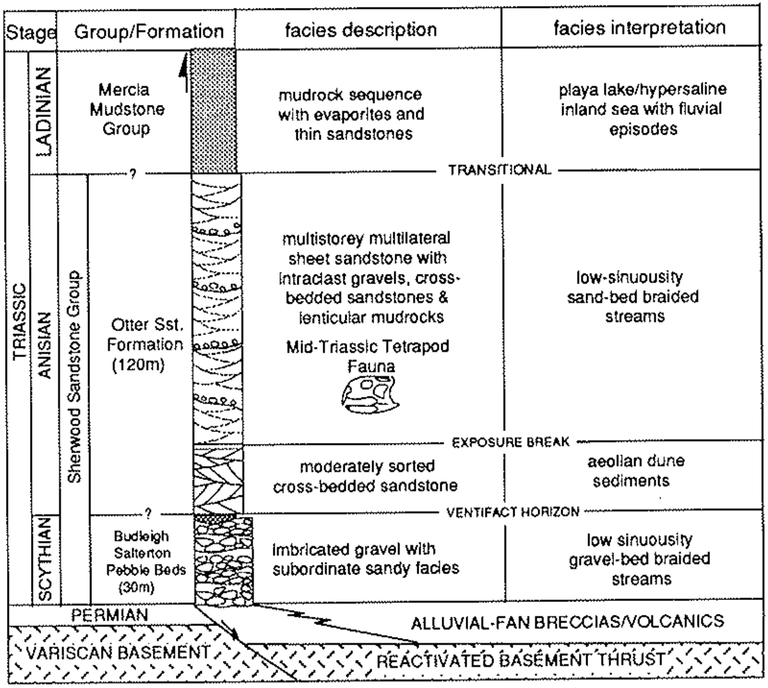

Figure 7.15. Sedimentology and interpreted depositional environments of the Otter Sandstone Formation and adjacent units, based on fieldwork by AJN.

1983). In breccias exposed west of Chiselbury Bay (Figure 7.11), the abundance of tetrapod finds declines significantly lower in the sequence. 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 preservation appears to be controlled by the sedimentation regime.

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. 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 most clearly localized of the older finds is a jaw of *Rhynchosaurus* [BGS(GSM) 90494] recovered from a large displaced block on the east bank of the River Otter (SY 0775 8196) "where the sandstone is somewhat brecciiform" (Whitaker, 1869, p. 156). Metcalfe (1884) reported white fragments, which he identified as bone, in the "harder parts of the sandstones, at numerous points near Budleigh Salterton and Otterton Point."

The Victorian authors believed that one or more discrete bonebeds 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 feet (13 m) lower in the section.

Lavis (1876) made his finds in fallen blocks from an "ossiferous zone" consisting of up to four beds, "characterized by lithological differences, inasmuch 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 waterworn." Metcalfe (1884) gave further details of this locality at High Peak, stating that bones were found in fallen blocks of sandstone from a light-colored 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 stems in a bed at the top of the sandstone and "about eight or ten feet above" two or three "White bands" that appeared 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 bonebed 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.

Taphonomy. The tetrapod fossils are generally isolated elements – jaws, teeth, partial skulls, or single postcranial bones. 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 a recently collected partial rhynchosaur skeleton that comprises much of the trunk region, the pelvis, and the hindlimbs, with the bones in close association, but mostly slightly disarticulated.

About half of the identifiable tetrapod bones found are rhynchosaur remains, and most of these are parts of the skull, especially the jaw elements. This is a phenomenon of preservation, rather than selective collecting, and probably reflects the good preservation potential of teeth and jawbones. This is especially true for rhynchosaurs in which the maxilla and dentary are composed of unusually dense bone, the teeth are firmly ankylosed, and the bone is virtually indestructable. The amphibians are represented mainly by skull and pectoral girdle elements, all relatively dense and with characteristic sculpture. The small reptiles are represented by teeth and small segments of jaw, and the larger archosaur(s) by teeth and vertebrae. These selective features of preservation are comparable with the situation at Warwick.

The incompleteness of most specimens is largely the result of predepositional disarticulation and breakage, as is shown by their context in the sediment. Some specimens show signs of possible abrasion during transport (e.g., EXEMS 60/1985.37–45, 56, 284, 312), as noted also by Lavis (1876, p. 277) on his amphibian bones, but others, especially the jaws of procolophonids, show detailed preservation of surface features and delicate sharp teeth. Most of the fossils are undistorted, although the skull EXEMS 60/1985.292 shows slight displacement of bones at suture lines.

The bone is well preserved as a hard whitish substance (usually stained pink by the matrix), with all internal structure intact. The dentine of the teeth is yellow, and the enamel is stained dark brown, as in the Warwick and Bromsgrove specimens. In an unpublished manuscript (1882, BMNH, Department of Palaeontology), Carter noted that "the smaller fragments are more or less soft and cheesy in consistence, and on drying, become almost powdery so that on being placed in water fall to pieces, while the larger ones are somewhat more competent." This is reminiscent of the previously cited statements by Murchison and Strickland (1840, p. 344) on the Warwick bones, and those by Wills (1910, p. 261) on the bones from Bromsgrove, but it is not borne out by recent observations on freshly exposed bone in the Otter Sandstone Formation. Examination of Carter's collection (BMNH R330) has shown that most of his "bones" are coprolites or calcretes, and indeed Carter (1888) referred to coprolites containing fish scales from the Otter Sandstone Formation.

Other sites

Isolated tetrapod remains have been collected from Middle Triassic deposits at other sites in the English Midlands, but none has shown the potential of the sites discussed here. Those other sites include the following:

1. Hollington, Staffordshire (SK 060388), source of some articulated gastralia of an unknown reptile (BMNH R3227), described by Woodward (1905) as "*Hyperodapedon* sp.," but probably not rhynchosaurian.
2. Stanton, Staffordshire (SK 126462), source of the best-known English Triassic temnospondyl skull (Ward, 1900) (BMNH R3174), the holotype of *Stenotosaurus stantonensis*, described by Woodward (1904) as *Capitosaurus stantonensis*, synonymized with *Cyclotosaurus leptognathus* (Owen, 1842) by Paton (1974), and transferred to *Stenotosaurus* by Shishkin (1980).
3. Emscote, near Warwick (?SP 298658), source of a bone fragment labeled "*Rhombopholis scutulatus*" (WARMS Gz 126), collected by J. W. Kirshaw in 1868.

Paleoecology

It is difficult to determine the ecology of these faunas in detail because of the limited material available. However, it is possible to estimate the relative impor-

Table 7.1. *Numbers of individuals in the Warwick (Wa.), Bromsgrove (Br.), and Devon (De.) assemblages, calculated as minimum number of individuals (MNI) and nonredundant maximum number (NRMAX), and converted to percentages*

	MNI			NRMAX		
Taxon	Wa.	Br.	De.	Wa.	Br.	De.
Amphibians	6 (33%)	2 (25%)	6 (25%)	14 (29%)	7 (41%)	15 (25%)
Rhynchosaurus	4 (22%)	1 (12%)	9 (38%)	15 (31%)	2 (12%)	29 (48%)
Archosaur(s)	5 (28%)	3 (38%)	5 (21%)	15 (31%)	5 (29%)	11 (18%)
Procolophonid	0	0	3 (12%)	0	0	5 (8%)
Nothosaur	0	1 (12%)	0	0	2 (12%)	0
Prolacertiform	3 (17%)	1 (12%)	1 (4%)	5 (10%)	1 (6%)	1 (2%)
Totals	18	8	24	49	17	61

Sources: Data obtained from Paton (1974), Benton (1990), Milner et al. (1990), and from inspection of collections.

tance of the different tetrapod-body fossil types as represented in existing collections and to apply broader knowledge of the habits of the different amphibians and reptiles.

The numbers of individuals of each taxon have been estimated in two ways. The minimum number of individuals (MNI) has been obtained by counting up the most-represented elements in the collections (e.g., complete skulls, right maxillae, left femora) as an unequivocal figure for the absolute minimum number of individuals required to produce all of the known fossils. The second measure, the nonredundant maximum number of individuals (NRMAX), is based on the initial assumption that each bone found separately represents a different individual. This assumed maximum number is reduced by an examination of historical sources and by collecting details that may provide information on original associations of material in the same, or different, repositories. An attempt is made to discover all isolated bones that can be fitted together or that can be associated as being probably the remains of a single individual.

It is likely that the MNI underestimates the number of individuals present in an ancient fauna, and the NRMAX probably overestimates the number. In cases such as the Triassic faunas, where isolated elements dominate, the NRMAX probably gives a better estimate of true numbers, especially where detailed collecting data are available. For example, the Devon tetrapods have been collected from numerous sites along a 7-km coastal section, and site information is taken into account in associating material: A left maxilla and a right maxilla found 4 km apart are unlikely to have come from the same individual, although the MNI figure would imply that! Hence, in the following discussion, the NRMAX figures are used, although MNI figures are also given.

It is not clear, however, which of these measures should give the best *proportional* estimates. There is no reason, for example, that an MNI value based on skulls for one species should be in proportion with that based on right femora for another; indeed, it is more likely that such figures, based of necessity on different skeletal elements, will not be in proportion to true ancient diversities. The NRMAX could be a better proportional estimator for preservation of ancient faunas if all taxa and finds are equally well documented. Of course, both the MNI and NRMAX are influenced by preservation factors, and neither can give a good estimate of the original *living* faunal compositions; both MNI and NRMAX figures are given here (Table 7.1, Figure 7.16, data in Appendix 7.1).

The Grinshill fauna stands out from the others paleoecologically in being monospecific (Figure 7.16). About seventeen individuals of *Rhynchosaurus articeps* have been collected (NRMAX), an MNI of seven, based on skulls, all of which are well preserved. No bones of any other animal have been found in association, though tracks signify the coexistence of rauisuchians.

The Warwick, Bromsgrove, and Devon faunas (Figure 7.16) show similar diversities of taxa (Table 7.1). Comparisons with the Bromsgrove fauna are difficult because fossils are so sparse and so incomplete that many are not clearly identifiable. In both the Warwick and the Devon faunas, the rhynchosaur *Rhynchosaurus* dominates (31% and 48% of all individuals, respectively). Amphibians are more abundant at Warwick (29%) than in Devon (25%), and archosaurs likewise (31% at Warwick, 18% in Devon).

It is possible to infer likely food chains (Figure 7.17). The top carnivores at Warwick and in Devon were archosaurs, probably a rauisuchian (*Bromsgroveia*), and some others, which preyed on the temnospondyl amphibians, rhynchosaurs, and smaller reptiles. The

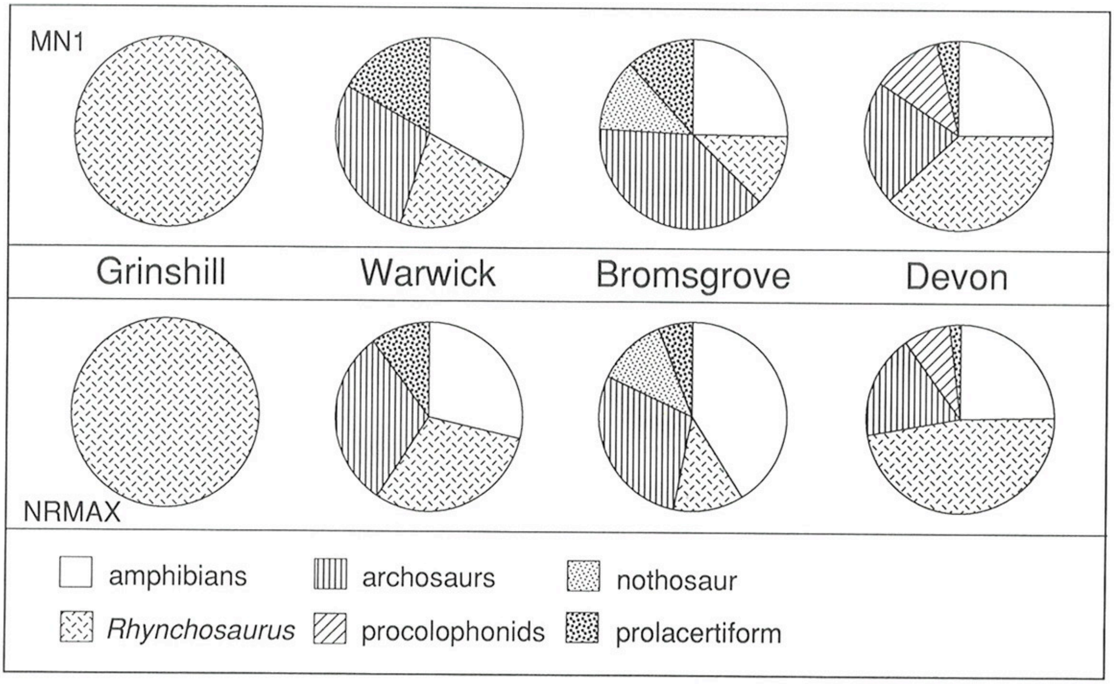

Figure 7.16. Pie charts showing the relative abundances of major tetrapod groups at the four English Middle Triassic localities. The percentages are calculated from the data in Appendix 7.1 and summarized in Table 7.1. MNI figures are minimum numbers of individuals, based on the single maximally represented element; NRMAX figures are based on evidence of localities and dates of finds. MNI figures are minimum estimates and NRMAX figures are maximum estimates of faunal diversity.

amphibians presumably fed almost exclusively on fish. The rhynchosaurs were herbivores, feeding on elements of the equisetalean and coniferalean flora found in association at Bromsgrove. Smaller (100–150 mm long) procolophonid reptiles may also have had herbivorous diets, feeding on low herbaceous plants thus far unrepresented in Middle Triassic collections. The macrocnemid may have fed on arthropods, represented by scorpions from Bromsgrove (Wills, 1910, 1947; Kjellesvig-Waering, 1986), or it may have been a shallow-water predator.

Fish are known from these sites. Only a tooth plate of a ceratodontid lungfish (*Ceratodus laevissimus*) has been found in Coton End Quarry, Warwick (Woodward, 1893), but a more diverse ichthyofauna, comprising the remains of *Acrodus*, a selachian, the dipnoan *Ceratodus*, and the holotype, an almost complete specimen, of the deep-bodied perleidid "palaeonisciform" *Dipteronotus cyphus*, has been found at Bromsgrove (Wills, 1910; Old et al., 1991). The Otter Sandstone of Devon has yielded *Dipteronotus*, about 60–70 mm long, represented by several entire specimens (Milner et al., 1990), and coprolites containing fish scales (Carter, 1888).

Other fossils are represented best at Bromsgrove (Old et al., 1991) and, to a lesser extent, in Devon. Plant remains from the Finstall Member at Bromsgrove comprise *Equisetites arenaceus*(?), *Schizoneura paradoxa* (roots, pith casts, leaves), *Chiropteris digitata*(?), *Yuccites vogesiacus* (leaves and stems), *Voltzia*(?) (pith casts and decorticated stems), *Aethophyllum*, and cones (*Strobilites*, *Willsiostrobus bromsgrovensis*, *W. willsi*). This macrofossil association comprises equisetalean pteridophytes and coniferalean gymnosperms. Microfloras from the Finstall Member reflect a more diverse source flora that included lycopsids, sphenopsids, pteropsids, and gymnosperms; the last, principally conifers, but including cycadalean types, dominated the flora. Invertebrates include the annelid *Spirorbis* (Ball, 1980), a bivalve, *Mytilus*(?) (Wills, 1910), the branchiopod crustacean *Euestheria*, and the scorpions *Bromsgroviscorpio*, *Mesophonus*, *Spongiophonus*, and *Willsiscorpio* (Wills, 1910, 1947; Kjellesvig-Waering, 1986).

A similar, but less diverse, association of plant remains and invertebrates is present in the Otter Sandstone Formation of Devon. Plant remains there comprise rhizomes and stems referable to *Schizoneura*, arthropod cuticle, an insect wing, and branchiopod crustaceans (*Euestheria*, *Lioestheria*) (P. S. Spencer, unpublished data). Rhizoliths indicate the existence of a contemporary indigenous vegetation interpreted as comprising conifers (Mader, 1990) and phreatophytic plants (Purvis and Wright, 1991).

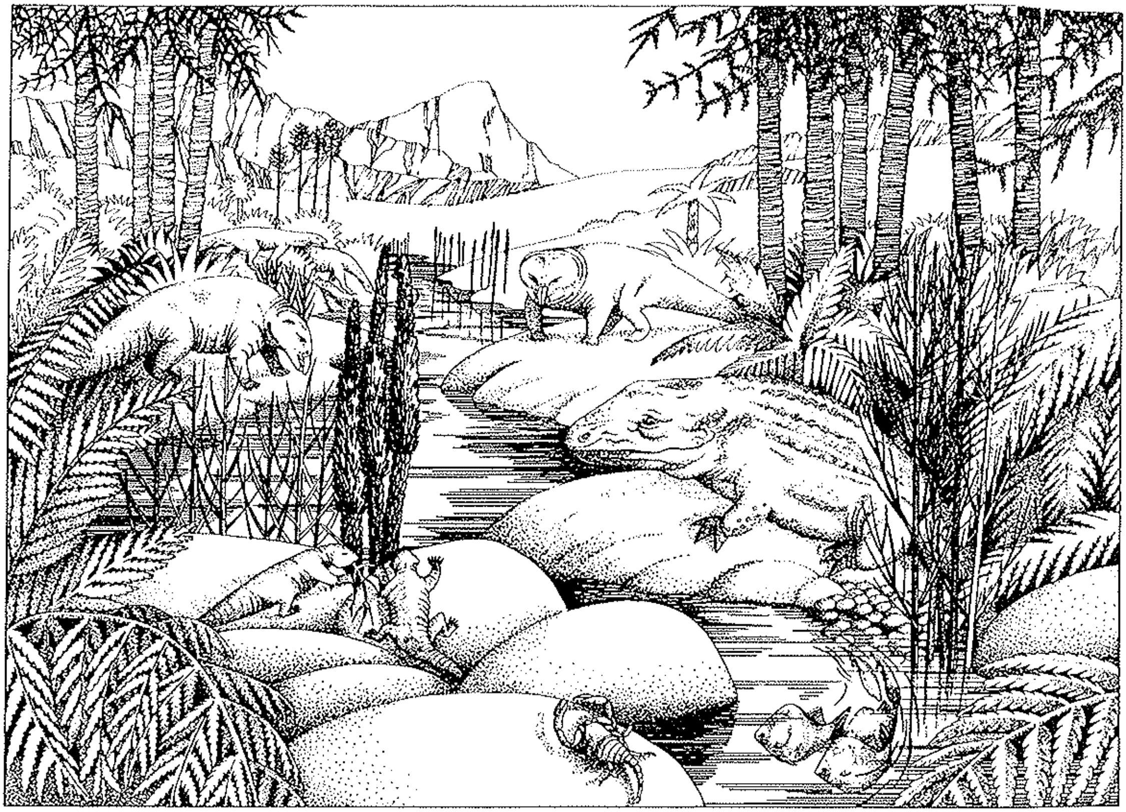

Figure 7.17. Reconstructed scene during the Middle Triassic in Devon, based on specimens from the Otter Sandstone Formation between Sidmouth and Budleigh Salterton. A scorpion (mid-foreground) contemplates a pair of procolophonids on the rocks. Opposite them, a temnospondyl amphibian has spotted some paleonisciform fish, *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 conifer tree. (Drawn by Pam Baldaro, based on her color painting.)

Pteridophytes in the associations from Worcestershire and Devon probably populated damp tracts bordering river channels or in floodplain areas; the gymnosperm components may reflect drier habitats. Scorpions signify dry terrestrial habitats, but the crustaceans indicate the existence of seasonal pools of fresh to brackish water. The records of lungfishes from Worcestershire suggest that rivers there were prone to seasonal drought, but were penetrated intermittently from the north by marine-sourced waters that introduced those and other fish (e.g., a selachian), bivalves, and semi-aquatic reptiles (? prolacertiform and nothosaur) with marine affinity. Temnospondyl amphibians indicate the existence of at least seasonal bodies of fresh water, necessary for breeding, on a floodplain that was inhabited also by herbivorous rhynchosaurs and procolophonids and the carnivorous rauisuchians.

Ages of the tetrapod assemblages

The tetrapod faunas reviewed here have generally been regarded as Middle Triassic, though the views based upon these remains and the associated macrofossils have varied with regard to the assignment of a more precise, Anisian or Ladinian, age. Walker, on the basis of reptiles, favored (1969) an early to middle Ladinian age or (1970) a late Anisian or, preferably, Ladinian age and suggested that the Devon fauna is older than those from the Midlands; this has been construed as indicating an Anisian age for the Devon assemblage. Paton (1974) also proposed an early Ladinian age, on the basis of amphibian remains, but regarded the Devon and Midlands faunas as similar in age. Milner et al. (1990) advocated an Anisian age for the Devon vertebrate fauna.

There is generally no direct independent evidence for the ages of the vertebrate assemblages. Associated footprints, at Grinshill, and macrofossils (plants and invertebrates), known from the Bromsgrove and Devon localities, afford no satisfactory biostratigraphic information. Wills (1970, pp. 260–261), for example, noted that the Bromsgrove plants indicated late Scythian to late Ladinian ages, by comparison with German material; the scorpions suggested an Anisian or Ladinian age; and the conchostracan *Euestheria* suggested a late Ladinian to Norian age. Rhynchosauroid footprints indicate merely a Triassic age, while footprints of *Chirotherium* are usually Early or Middle Triassic in age.

Pollen and spores provide an independent means of correlating British Triassic deposits with the stages based upon marine faunas in the Tethyan realm. They were first recorded from the Bromsgrove Sandstone Formation by Wills (1910), who recovered spores and pollen from plant remains from the vertebrate-bearing locality at Bromsgrove. Within the past three decades, formations in the Sherwood Sandstone Group and Mercia Mudstone Group in many parts of Britain have been assigned ages on the basis of comparison of palynoflorules with those documented from independently dated Triassic sequences elsewhere in Europe.

Palynological information available from northwest and central England indicates that the tetrapod faunas from Grinshill and localities elsewhere in the Midlands are pre-Ladinian, probably Anisian, in age. The Anisian–Ladinian boundary is characterized palynologically by the last occurrence of *Stellapollenites thiergartii* at the boundary (Visscher and Brugman, 1981; van der Eem, 1983) or in the basal Ladinian (Brugman, 1986) and by the appearance of *Ovalipollis pseudoalatus* at the boundary (van der Eem, 1983) or in the basal Ladinian (Visscher and Brugman, 1981). Slightly above the base of the Ladinian, *Camerosporites secatus* and *Duplicisporites* spp. appear, followed by *Echinitosporites iliacoides*, signifying an early Ladinian (Fassan substage) age (Visscher and Brugman, 1981; van der Eem, 1983; Brugman, 1986). The base of the Anisian stage is marked by the lowest occurrences of *Stellapollenites thiergartii* and *Angustisulcites* spp. (Visscher and Brugman, 1981; Brugman, 1986).

Palynoflorules from the Sherwood Sandstone Group and Mercia Mudstone Group in the Cheshire basin and the contiguous West Lancashire–East Irish Sea basin (Warrington, 1970b, 1974c; Fisher, 1972a,b; Warrington, in Earp and Taylor, 1986; Warrington, in Wilson and Evans, 1990) indicate, by reference to the foregoing criteria, that the succession from the basal Helsby Sandstone Formation to a level above the Northwich Halite Formation is of Anisian age. *Angustisulcites klausi* was recorded from the basal Helsby Sandstone in northeast Cheshire (Warrington, 1970b), and assemblages from the Tarporley Siltstone Formation at Liverpool (Fisher, 1972a,b) include *Angustisulcites* spp. together with *Stellapollenites thiergartii* and other taxa, such as *Perotrilites minor*, indicative of an Anisian age; evidence of Anisian age was also obtained from this formation in the Chester district (Warrington, in Earp and Taylor, 1986). Few datable palynoflorules have been recorded from the Mercia Mudstone Group in the Cheshire basin. However, assemblages from mudstones overlying the Northwich Halite Formation indicate a correlation of that unit with the Preesall Salt of west Lancashire, which is assigned a late Anisian age (Warrington, in Wilson and Evans, 1990). Thus, the base of the Ladinian stage in the Cheshire basin is placed within the Mercia Mudstone Group, above the Northwick Halite Formation, and the tetrapod-bearing sequence at Grinshill in the southern part of the basin is therefore pre-Ladinian in age. The reassessment of pollen and spores from the basal Helsby Sandstone Formation as Anisian, rather than late Scythian as previously suggested (Warrington, 1970b), indicates that the Grinshill vertebrates probably are not older than Anisian.

In the central Midlands, palynoflorules recovered from the Bromsgrove Sandstone Formation in the Bromsgrove (Clarke, 1965; Warrington, 1970b), Stratford-upon-Avon (Warrington, in Williams and Whittaker, 1974), and Banbury (Warrington, 1978) areas include *Angustisulcites* spp. and *Stellapollenites thiergartii*, thus indicating an Anisian age. Though the "Waterstones" at Bromsgrove were regarded as early Ladinian (Warrington, 1970b), this is now considered unlikely, as none of the pollen and spore taxa now used to indicate the base of the Ladinian has been recorded in the Bromsgrove succession. Furthermore, the presence of *Tsugaepollenites oriens* in the Bromsgrove Sandstone Formation at Stratford-upon-Avon (Warrington, in Williams and Whittaker, 1974), and possibly near Banbury (Warrington, 1978), implies a correlation with beds in the Kirkham Mudstone Formation (Mercia Mudstone Group) in west Lancashire that are dated as Anisian (Warrington, in Wilson and Evans, 1990). North of the Warwick-Leamington area, the lower part of the Mercia Mudstone Group has yielded *Stellapollenites thiergartii* and is assessed as Anisian; the presence of *Echinitosporites iliacoides* at a higher level in the group there indicates a Ladinian to earliest Carnian age (Warrington in Worssam and Old, 1988). As in the Cheshire basin, therefore, the Anisian–Ladinian boundary in the central Midlands is placed above the stratigraphic level of the tetrapod faunas. Palynoflorules from the Bromsgrove succession afford direct evidence of Anisian age for the tetrapod-bearing sequence there; the lowest pollen and spore assemblages from Bromsgrove were once regarded as late Scythian (Warrington, 1970b), but on the basis of the presence of *Angustisulcites klausi*, they are now reassessed as Anisian.

No pollen and spores have been recovered from the Otter Sandstone Formation in Devon. This formation is poorly constrained palynologically by occurrences of Late Permian palynoflorules in the lower part of the Permo-Triassic succession near Exeter (Warrington and Scrivener, 1988, 1990) and Carnian (Late Triassic) taxa in the Mercia Mudstone Group, 135 m above the Otter Sandstone Formation (Warrington, 1971; Holloway et al., 1989).

The vertebrate evidence can now be reviewed in light of the palynological evidence, which indicates that the tetrapod assemblages in the Midlands are pre-Ladinian, but not older than Anisian; though palynological evidence is lacking in Devon, these findings support the interpretation of the comparable Devon tetrapod assemblage as Anisian in age (Milner et al., 1990).

Gardiner (in Milner et al., 1990) considered that the fish assemblage indicates a Ladinian age for the Bromsgrove and Devon localities, and presumably also Warwick. *Dipteronotus cyphus* is known from Devon and Bromsgrove, indicating that the assemblages are coeval, and the shark *Palaeobates keuperinus* from Bromsgrove is closely similar to *P. angustissimus*, of Ladinian age, from the upper Muschelkalk and Lettenkohle of Germany, Poland, and France. Further, *Gyrolepis albertii* from the Bromsgrove Sandstone Formation is also known from the upper Muschelkalk of various parts of Germany, as well as from younger horizons.

Paton (1974) considered the temnospondyl amphibians from Warwick, Bromsgrove, and Devon to be essentially the same and to indicate a mean age of early Ladinian, based on comparisons with German material. Milner et al. (1990) noted, however, that the British specimens of *Mastodonsaurus* from Warwick, Devon, and Bromsgrove indicate an Anisian to Carnian age, based on comparisons with German material. The other amphibian genus, *Eocyclotosaurus*, is more useful, being known from the *Voltzia* Sandstone of France and the lower Röt of Germany, both dated as latest Scythian or early Anisian in age, and from the Holbrook Member of the Moenkopi Formation of Arizona, dated as early Anisian (Morales, 1983). Hence, the amphibians would appear to indicate an Anisian age for the Warwick, Bromsgrove, and Devon assemblages.

The reptiles generally point to a Middle Triassic, possibly Anisian, age for all the formations (Milner et al., 1990). The procolophonids, macrocnemid, tanystropheid, nothosaur, and rauisuchian archosaurs could all be Anisian or Ladinian in age, although Milner et al. (1990) prefer an Anisian age on the basis of the primitive nature of the Devon procolophonid. The three species of *Rhynchosaurus* fall in the cladogram (Benton, 1990, p. 298) between *Stenaulorhynchus* from the Manda Formation of Tanzania (generally dated as Anisian) and the Hyperodapedontinae (*Hyperodapedon*, *Scaphonyx*), which all are Carnian in age. Hence, the rhynchosaurs, present in all four regions, might indicate a Ladinian age, but the order of branching in a cladogram need not match stratigraphic order.

Part of the problem in dating is, as Milner et al. (1990) noted, the fact that the four English faunal associations may date from the time of the marine Muschelkalk (Anisian/Ladinian) in central Europe. Huene (1908c) and Wills (1910) equated the English faunas with the German Lettenkohle (late Ladinian), which immediately followed the Muschelkalk. Wills (1948) and Milner et al. (1990), on the other hand, recognized more similarities with the Scythian/Anisian late Buntsandstein and *Voltzia* Sandstone faunas of Germany and France, which immediately preceded the Muschelkalk. It is likely, of course, that the English localities fall somewhere between, which may be suggested by the absence of their commonest element, *Rhynchosaurus*, in the central European pre- and post-Muschelkalk terrestrial faunas.

Acknowledgments

We thank Nick Fraser (Virginia Museum of Natural History) and Hans-Dieter Sues (Royal Ontario Museum) for the opportunity to attend the Front Royal meeting and for their encouragement to write this chapter. David Thompson (Keele University) supplied a great deal of sedimentological information and added greatly to the account of Grinshill. We thank Pam Baldaro (Bristol University) for drafting Figures 7.4, 7.6, 7.10, 7.12, 7.13, 7.16, and 7.17, especially for Figure 7.17, which is taken from her original color painting of the Otter Sandstone scene. Bruce Bennisson (Shrewsbury Museum) kindly supplied the photographs in Figure 7.8. We thank Andrew Milner for helpful advice. MJB was funded by the Royal Society, MJB and PSS by NERC grant GR3/7040, and AJN by the Department of Education (Northern Ireland). GW publishes with the approval of the Director, British Geological Survey (N.E.R.C.).

References

Audley-Charles, M. G. 1970. Stratigraphical correlation of the Triassic rocks of the British Isles. *Quarterly Journal of the Geological Society of London* 126: 19–47.

Ball, H. W. 1980. *Spirorbis* from the Triassic Bromsgrove Sandstone Formation (Sherwood Sandstone Group) of Bromsgrove, Warwickshire. *Proceedings of the Geologists' Association* 91: 149–154.

Beasley, H. C. 1890a. A visit to Warwick. *Transactions of the Liverpool Geological Association* 10: 27–30.

1890b. The life of the English Trias. *Proceedings of the Liverpool Geological Society* 6: 145–165.

1896. An attempt to classify the footprints in the New Red Sandstone of this district. *Proceedings of the Liverpool Geological Society* 7: 391–409.

1898. Notes on examples of footprints, &c., from the Trias in some provincial museums. *Proceedings of the Liverpool Geological Society* 8: 233–237.

1902. The fauna indicated in the Lower Keuper Sandstone of the neighbourhood of Liverpool. *Transactions of the Liverpool Biological Society* 16: 3–26.

1904. Report on footprints from the Trias – Part I. *Report of the British Association for the Advancement of Science* 1904(1903): 219–231.

1905. Report on footprints from the Trias – Part II. *Report of the British Association for the Advancement of Science* 1905(1904): 275–282.

1906. Notes on footprints from the Trias in the museum of the Warwickshire Natural History and

Archaeological Society at Warwick. *Report of the British Association for the Advancement of Science* 1906(1905): 162–165.
Benton, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London* B302: 605–720.
1984. Tooth form, growth, and function in Triassic rhynchosaurs (Reptilia, Diapsida). *Palaeontology* 27: 737–776.
1986. The late Triassic reptile *Teratosaurus* – a rauisuchian, not a dinosaur. *Palaeontology* 29: 293–301.
1990. The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. *Philosophical Transactions of the Royal Society of London* B328: 213–306.
Brodie, P. B., and J. W. Kirshaw. 1873. Excursion to Warwickshire, July 10th and 11th, 1871. *Proceedings of the Geologists' Association* 2: 334–387.
Brugman, W. A. 1986. Late Scythian and Middle Triassic palynostratigraphy in the Alpine realm. *Albertiana* 5: 19–20.
Buckland, W. 1837. On the occurrence of Keuper-Sandstone in the upper region of the New Red Sandstone formation or Poikilitic system in England and Wales. *Proceedings of the Geological Society of London* 2: 453–454.
1840. Ichnology. *Proceedings of the Geological Society of London* 3: 245–247.
1844. [President's address, 1839]. *Proceedings of the Ashmolean Society* 16: 5–7.
Burckhardt, R. 1900. On *Hyperodapedon gordoni*. *Geological Magazine* (4) 7: 486–492, 529–535.
Carter, H. J. 1888. On some vertebrate remains in the Triassic strata of the south coast of Devonshire between Budleigh Salterton and Sidmouth. *Quarterly Journal of the Geological Society of London* 44: 318–319.
Clarke, R. F. A. 1965. Keuper miospores from Worcestershire, England. *Palaeontology* 8: 294–321.
Cummins, W. A. 1958. Some sedimentary structures from the Lower Keuper Sandstones. *Liverpool and Manchester Geological Journal* 2: 37–43.
Delair, J. B., and W. A. S. Sarjeant. 1985. History and bibliography of the study of fossil vertebrate footprints in the British Isles: supplement 1973–1983. *Palaeogeography, Palaeoclimatology, Palaeoecology* 49: 123–160.
Earp, J. R., and B. J. Taylor. 1986. Geology of the country around Chester and Winsford. *Memoirs of the British Geological Survey* (sheet 109), London: HMSO.
Egerton, P. G. 1838. On two casts in sandstone of the impressions of the hind foot of a gigantic *Chirotherium*, from the New Red Sandstone of Cheshire. *Proceedings of the Geological Society of London* 3: 14–15.
Fisher, M. J. 1972a. A record of palynomorphs from the Waterstones (Triassic) of Liverpool. *Geological Journal* 8: 17–22.
1972b. The Triassic palynofloral succession in England. *Geoscience and Man* 4: 101–109.
Forster, S. C., and G. Warrington. 1985. Geochronology of the Carboniferous, Permian and Triassic. *Geological Society of London, Memoir* 10: 99–113.
Galton, P. M. 1985. The poposaurid thecodontian *Teratosaurus* v. Meyer, plus referred specimens mostly based on prosauropod specimens from the Middle Stubensandstein (Upper Triassic) of Nordwürttemberg. *Stuttgarter Beiträge zur Naturkunde* B116: 1–29.
Geiger, M. E., and C. A. Hopping. 1968. Triassic stratigraphy of the southern North Sea Basin. *Philosophical Transactions of the Royal Society of London* B254: 1–36.
Henson, M. R. 1970. The Triassic rocks of south Devon. *Proceedings of the Ussher Society* 2: 172–177.
Holloway, S. 1985. Triassic Sherwood Sandstone Group (excluding the Kinnerton Sandstone Formation and the Lenton Sandstone Formation). Pp. 31–34 in A. Whittaker (ed.), *Atlas of Onshore Sedimentary Basins in England and Wales: Post-Carboniferous Tectonics and Stratigraphy*. London: Geological Society.
Holloway, S., A. E. Milodowski, G. E. Strong, and G. Warrington. 1989. The Sherwood Sandstone Group (Triassic) of the Wessex Basin, southern England. *Proceedings of the Geologists' Association* 100: 383–394.
Huene, F. von 1908a. Die Dinosaurier der europäischen Triasformation. *Geologische und Paläontologische Abhandlungen, Supplement-Band* 1: 1–419.
1908b. Note on two sections in the Lower Keuper Sandstone of Guy's Cliff, Warwick. *Geological Magazine* (5) 5: 100–102.
1908c. Eine Zusammenstellung über die englische Trias und das Alter ihrer Fossilien. *Centralblatt für Mineralogie, Geologie, und Paläontologie* 1908: 9–17.
1929. Ueber Rhynchosaurier und andere Reptilien aus den Gondwana-Ablagerungen Südamerikas. *Geologische und Paläontologische Abhandlungen, Neue Folge* 17: 1–62.
Hughes, B. 1968. The tarsus of rhynchocephalian reptiles. *Journal of Zoology (London)* 156: 457–481.
Hull, E. 1869. The Triassic and Permian rocks of the Midland counties of England. *Memoirs of the Geological Survey of the United Kingdom* 1869: 1–127.
Hutchinson, P. O. 1879. Fossil plant, discovered near Sidmouth. *Transactions of the Devonshire Association for the Advancement of Science, Literature, and Art* 11: 383–385.
1906. Geological section of the cliffs to the west and east of Sidmouth, Devon. *Report of the British Association for the Advancement of Science* 1906 (1905): 168–170.
Huxley, T. H. 1859. On a fragment of a lower jaw of a large labyrinthodont from Cubbington. *Memoirs of the Geological Survey of the United Kingdom* 1859: 56–57.
1869. On *Hyperodapedon*. *Quarterly Journal of the Geological Society of London* 25: 138–152.
1870. On the classification of the Dinosauria, with observations on the Dinosauria of the Trias. *Quarterly Journal of the Geological Society of London* 26: 32–50.
1887. Further observations of *Hyperodapedon gordoni*.

Quarterly Journal of the Geological Society of London 43: 675–694.

Ireland, R. J., J. E. Pollard, R. S. Steel, and D. B. Thompson. 1978. Intertidal sediments and trace fossils from the Waterstones (Scythian-Anisian?) at Daresbury, Cheshire. *Proceedings of the Yorkshire Geological Society* 41: 399–436.

Irving, A. 1888. The red-rock series of the Devon coast-section. *Quarterly Journal of the Geological Society of London* 44: 149–163.

Jaeger, G. F. 1828. *Ueber die fossile Reptilien, welche in Württemberg aufgefunden worden sind.* Stuttgart: Metzler.

Kamphausen, D. 1983. *Stenotosaurus gracilis*, ein neuer Capitosauride (Stegocephalia) aus den Unteren Röttonen Oberfrankens. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1983: 119–128.

Kjellesvig-Waering, E. N. 1986. A restudy of the fossil Scorpionida of the world. *Palaeontographica Americana* 55: 1–287.

Laming, D. J. C. 1982. The New Red Sandstone. Pp. 148–178 in E. M. Durrance and D. J. C. Laming (eds.), *The Geology of Devon.* Exeter: Exeter University Press.

Lavis, H. J. 1876. On the Triassic strata exposed in the cliff sections near Sidmouth, and a note on the occurrence of an ossiferous zone containing bones of a *Labyrinthodon. Quarterly Journal of the Geological Society of London* 32: 274–277.

Leonard, A. J., A. G. Moore, and E. B. Selwood. 1982. Ventifacts from a deflation surface marking the top of the Budleigh Salterton Pebble Beds, east Devon. *Proceedings of the Ussher Society* 5: 333–339.

Lorsong, J. A., T. J. Clarey, and C. D. Atkinson. 1990. Lithofacies architecture of sandy braided stream deposits in the Otter Sandstone, U.K. P. 139 in *Sediments 1990, Nottingham, England, Abstracts of Posters.* Utrecht: International Sedimentological Union.

Mader, D. 1990. *Palaeoecology of the Flora in Buntsandstein and Keuper in the Triassic of Middle Europe. Vol. 1. Buntsandstein.* Stuttgart: Gustav Fischer Verlag.

Mader, D., and D. J. C. Laming. 1985. Braidplain and alluvia-fan environmental history and climatological evolution controlling origin and destruction of aeolian dune fields and governing overprinting of sand seas and river plains by calcrete pedogenesis in the Permian and Triassic of south Devon (England). Pp.519–528 in D. Mader (ed.), *Aspects of Fluvial Sedimentation in the Lower Triassic Buntsandstein.* Berlin: Springer-Verlag.

Maidwell, F. T. 1911. Notes on footprints from the Keuper. *Proceedings of the Liverpool Geological Society* 11: 140–152.

Metcalfe, A. T. 1884. On further discoveries of vertebrate remains in the Triassic strata of the south coast of Devon between Budleigh Salterton and Sidmouth. *Quarterly Journal of the Geological Society of London* 40: 257–262.

Miall, L. C. 1874. On the remains of Labyrinthodontia from the Keuper Sandstone of Warwick. *Quarterly Journal of the Geological Society of London* 30: 417–435.

Milner, A. R., B. G. Gardiner, N. C. Fraser, and M. A. Taylor. 1990. Vertebrates from the Middle Triassic Otter Sandstone Formation of Devon. *Palaeontology* 33: 873–892.

Morales, M. 1983. A preliminary report on the terrestrial paleoecology of the Triassic Moenkopi Formation. *Geological Society of America, Abstracts with Programs* (5) 15: 284.

Murchison, R. I. 1839. *The Silurian System.* London: John Murray.

Murchison, R. I., and H. E. Strickland. 1840. On the upper formations of the New Red Sandstone in Gloucestershire, Worcestershire, and Warwickshire; etc. *Transactions of the Geological Society of London* (2) 5: 331–348.

Old, R. A., R. J. O. Hamblin, K. Ambrose, and G. Warrington. 1991. *Geology of the Country around Redditch.* London: HMSO.

Old, R. A., M. G. Sumbler, and K. Ambrose. 1987. *Geology of the Country around Warwick.* London: British Geological Survey.

Owen, R. 1841a. [The skeleton of three species of *Labyrinthodon*]. *Athenaeum* 1841: 581–582.

1841b. *Odontography.* London: Hippolyte Bailliere.

1842a. Description of parts of the skeleton and teeth of five species of the genus *Labyrinthodon* (*Lab. leptognathus, Lab. pachygnathus*, and *Lab. ventricosus*, from the Coton-end and Cubbington Quarries of the Lower Warwick Sandstone; *Lab. Jaegeri*, from Guy's Cliff, Warwick; and *Lab. scutulatus*, from Leamington); with remarks on the probable identity of the *Cheirotherium* with this genus of extinct batrachians. *Transactions of the Geological Society of London* (2) 6: 515–543.

1842b. Report on British fossil reptiles. Part II. *Report of the British Association for the Advancement of Science* 1842(1841): 60–204.

1842c. Description of an extinct lacertian, *Rhynchosaurus articeps*, Owen, of which the bones and foot-prints characterize the upper New Red Sandstone at Grinshill, near Shrewsbury. *Transactions of the Cambridge Philosophical Society* (2) 7: 355–369.

1845. Description of certain fossil crania discovered by A. G. Bain, esq., in the sandstone rocks of the southeastern extremity of Africa, referable to different species of an extinct genus of Reptilia (*Dicynodon*), and indicative of a new tribe or suborder of Sauria. *Transactions of the Geological Society of London* (2) 7: 59–84.

1859. Note on the affinities of *Rhynchosaurus. Annals and Magazine of Natural History* (3) 4: 237–238.

1863. Notice of a skull and parts of the skeleton of *Rhynchosaurus articeps. Philosophical Transactions of the Royal Society of London* 152: 466–467.

Paton, R. 1974. Capitosauroid labyrinthodonts from the Trias of England. *Palaeontology* 17: 253–289.

Pocock, R. W., and D. A. Wray. 1925. *The Geology of the Country around Wem.* London: Geological Survey of England and Wales.

Purvis, K., and V. P. Wright. 1991. Calcretes related to phreatophytic vegetation from the Middle Otter Sandstone of South West England. *Sedimentology* 38: 539–551.

Purvis, K., V. P. Wright and A. Leonard. 1990. Calcretes related to phreatophytic vegetation from the Upper Triassic Otter Sandstone (Sherwood Sandstone Group) of S. W. England. Pp. 441–442 in *Sediments 1990, Nottingham, England, Abstracts of Papers.* Utrecht: International Sedimentological Union.

Richter-Bernburg, G. 1979. Nachwort. Bemerkungen zum Begriff Rhaet. Pp. 151–152 in J. Wiedmann, F. Fabricius, L. Krystyn, J. Reitner, and M. Urlichs, Ueber Umfang und Stellung des Rhaet. *Newsletters in Stratigraphy* 8: 133–152.

Sarjeant, W. A. S. 1974. A history and bibliography of the study of fossil vertebrate footprints in the British Isles. *Palaeogeography, Palaeoclimatology, Palaeoecology* 16: 265–378.

1983. British fossil footprints in the collections of some principal British museums. *Geological Curator* 3: 541–560.

1984. The Beasley collection of photographs and drawings of fossil footprints and bones, and of fossil and recent sedimentary structures. *Geological Curator* 4: 133–163.

Sedgwick, A. 1829. On the geological relations and internal structure of the Magnesian Limestone, and the lower portions of the New Red Sandstone Series in their range through Nottinghamshire, Derbyshire, Yorkshire, and Durham, to the southern extremity of Northumberland. *Transactions of the Geological Society of London* (2) 3: 37–124.

Seeley, H. G. 1876. On the posterior portion of a lower jaw of a *Labyrinthodon* (*L. lavisi*). *Quarterly Journal of the Geological Society of London* 32: 278–284.

Selwood E. B., R. A. Edwards, S. Simpson, J. A. Chesher, R. J. O. Hamblin, M. R. Henson, B. W. Riddolls, and R. A. Waters. 1984. *Geology of the Country around Newton Abbott.* London: British Geological Survey.

Shishkin, M. A. 1980. The Luzocephalidae, a new Triassic labyrinthodont family. *Paleontological Journal* 1980: 88–101.

Smith, S. A. 1990. The sedimentology and accretionary styles of an ancient gravel-bed stream: the Budleigh Salterton Pebble Beds (Lower Triassic), southwest England. *Sedimentary Geology* 67: 199–219.

Smith, S. A., and R. A. Edwards. 1991. Regional sedimentological variations in Lower Triassic fluvial conglomerates (Budleigh Salterton Pebble Beds), southwest England: some implications for palaeogeography and basin evolution. *Geological Journal* 26: 65–83.

Spencer, P. S., and K. P. Isaac. 1983. Triassic vertebrates from the Otter Sandstone Formation of Devon, England. *Proceedings of the Geologists' Association* 94: 267–269.

Swinton, W. E. 1960. The history of *Chirotherium. Liverpool and Manchester Geological Journal* 2: 443–473.

Thompson, D. B. 1970a. The stratigraphy of the so-called Keuper Sandstone Formation (Scythian–?Anisian) in the Permo-Triassic Cheshire Basin. *Quarterly Journal of the Geological Society of London* 126: 151–181.

1970b. Sedimentation of the Triassic (Scythian) Red Pebbly Sandstones in the Cheshire Basin and its margins. *Geological Journal* 7: 183–216.

1985. *Field Excursions to the Cheshire, Irish Sea, Stafford, and Needwood Basins.* Chester: Poroperm Ltd.

Tresise, G. 1989. *The Invisible Dinosaur.* Liverpool: National Museums and Galleries on Merseyside.

1991. The Storeton Quarry discoveries of Triassic vertebrate footprints, 1838: John Cunningham's account. *Geological Curator* 5: 225–229.

Ussher, W. A. E. 1876. On the Triassic rocks of Somerset and Devon. *Quarterly Journal of the Geological Society of London* 32: 367–394.

Van der Eem, J. G. L. A. 1983. Aspects of Middle and Late Triassic palynology. 6. Palynological investigations in the Ladinian and Lower Karnian of the western Dolomites. *Review of Palaeobotany and Palynology* 39: 189–300.

Visscher, H., and W. A. Brugman. 1981. Ranges of selected palynomorphs in the Alpine Triassic of Europe. *Review of Palaeobotany and Palynology* 34: 115–128.

Walker, A. D. 1969. The reptile fauna of the 'Lower Keuper' Sandstone. *Geological Magazine* 10: 470–476.

1970. Discussion contributions. *Journal of the Geological Society of London* 126: 217–218.

Ward, J. 1900. On the occurrence of labyrinthodont remains in the Keuper Sandstone of Stanton. *Transactions of the North Staffordshire Field Club* 34: 108–112.

Ward, T. O. 1840. On the foot-prints and ripple-marks of the New Red Sandstone of Grinshill Hill, Shropshire. *Report of the British Association for the Advancement of Science* 1840 (1839): 75–76.

1841. The *Labyrinthodon. Salopian Journal* 28 April 1841: 2.

1874. Note on the *Rhynchosaurus articeps* Owen. *Nature* (*London*) 11: 8.

Warrington, G. 1967. Correlation of the Keuper Series of the Triassic by miospores. *Nature* (*London*) 214: 1323–1324.

1970a. The 'Keuper' Series of the British Trias in the northern Irish Sea and neighbouring areas. *Nature* (*London*) 226: 254–256.

1970b. The stratigraphy and palaeontology of the 'Keuper' Series of the Central Midlands of England. *Journal of the Geological Society of London* 126: 183–223.

1971. Palynology of the New Red Sandstone of the south Devon coast. *Proceedings of the Ussher Society* 2: 307–314.

1974a. Triassic. Pp. 145–160 in D. H. Rayner and J. E. Hemingway (eds.), *The Geology and Mineral Resources of Yorkshire.* York: Yorkshire Geological Society.

1974b. Les évaporites du Trias britannique. *Bulletin de la Société Géologique de France, Série 7* 16: 708–723.

1974c. Studies in the palynological biostratigraphy of the British Trias. 1. Réference sections in west Lancashire and north Somerset. *Review of Palaeobotany and Palynology* 17: 133–147.

1978. Palynology of the Keuper, Westbury and Cotham beds and the White Lias of the Withycombe Farm Borehole. *Bulletin of the Geological Survey of Great Britain* 68: 22–28.

Warrington, G., M. G. Audley-Charles, R. E. Elliott, W. B. Evans, H. C. Ivimey-Cook, P. E. Kent, P. L. Robinson, F. W. Shotton, and F. M. Taylor. 1980. A correlation of Triassic rocks in the British Isles.

Special Report of the Geological Society of London 13: 1–78.
Warrington, G., and H. C. Ivimey-Cook. 1992. Triassic. *Atlas of Palaeogeography and Lithofacies*. Bath: Geological Society of London.
Warrington, G., and R. C. Scrivener. 1988. Late Permian fossils from Devon: regional geological implications. *Proceedings of the Ussher Society* 7: 95–96.
1990. The Permian of Devon, England. *Review of Palaeobotany and Palynology* 66: 263–272.
Watson, D. M. S. 1910. On a skull of *Rhynchosaurus* in the Manchester Museum. *Report of the British Association for the Advancement of Science* 1910(1909): 155–158.
Whitaker, W. 1869. On the succession of beds in the "New Red" on the south coast of Devon, and on the locality of a new specimen of *Hyperodapedon*. *Quarterly Journal of the Geologial Society of London* 25: 152–158.
Williams, B. J., and A. Whittaker. 1974. Geology of the country around Stratford-upon-Avon and Evesham. *Memoirs of the Geological Survey of Great Britain*. London: HMSO.
Wills, L. J. 1907. On some fossiliferous Keuper rocks at Bromsgrove, Worcestershire. *Geological Magazine* (5) 4: 28–34.
1908. Note on the fossils from the Lower Keuper of Bromsgrove. *Report of the British Association for the Advancement of Science* 1908(1907): 312–313.
1910. On the fossiliferous Lower Keuper rocks of Worcestershire. *Proceedings of the Geologists' Association* 21: 249–331.
1916. The structure of the jaw of Triassic labyrinthodonts. *Proceedings of the Birmingham Natural History Society* 14: 1–16.
1947. British Triassic scorpions. *Monographs of the Palaeontographical Society* 100–101: 1–137.
1948. The *Palaeogeography of the Midlands*. Liverpool University Press.
1950. The *Palaeogeography of the Midlands*, 2nd ed. Liverpool University Press.
1970. The Triassic succession in the central Midlands in its regional setting. *Journal of the Geological Society of London* 126: 225–283.
1976. The Trias of Worcestershire and Warwickshire. *Report of the Institute of Geological Sciences* 76(2): 1–209.
Wilson, A. A., and W. B. Evans. 1990. Geology of the country around Blackpool. *Memoirs of the British Geological Survey*. London: HMSO.
Woodward, A. S. 1893. Palaeoichthyological notes. *Annals and Magazine of Natural History* (6)12: 281–287.
1904. On two new labyrinthodont skulls of the genera *Capitosaurus* and *Aphaneramma*. *Proceedings of the Zoological of London* 1904: 170–176.
1905. On some abdominal ribs of *Hyperodapedon* from the Keuper Sandstone of Hollington. *Report and Transactions of the North Staffordshire Field Club* 34: 115–117.
1907. On *Rhynchosaurus articeps* (Owen). *Report of the British Association for the Advancement of Science* 1907(1906): 293–299.
1908. On a mandible of *Labyrinthodon leptognathus*. *Report of the British Association for the Advancement of Science* 1908(1907): 298–300.
Woodward, H. B., and W. A. E. Ussher. 1911. The geology of the country near Sidmouth and Lyme Regis. *Geological Survey of the United Kingdom*. London: HMSO.
Worssam, B. C., and R. A. Old. 1988. Geology of the country around Coalville. *Memoirs of the British Geological Survey*. London: HMSO.
Wright, V. P., S. B. Marriott, and S. D. Vanstone. 1991. A 'reg' palaeosol from the Lower Triassic of south Devon: stratigraphic and palaeoclimatic implications. *Geological Magazine* 128: 517–523.

Appendix 7.1

Documentation of the identifiable specimens of Middle Triassic tetrapods from England. This list is based on published works, examination of collections in museums, and (for Devon) recent collecting. The MNI estimates, where greater than 1, are justified in terms of the maximally represented skeletal part.

	MNI	NRMAX
Grinshill		
Rhynchosaurus articeps (Benton, 1990, pp. 219–20); also, footprints, *Rhynchosauroides*, *Chirotherium* (i.e., rauisuchian)	7 (skulls)	17
Warwick (all Coton End, unless otherwise stated)		
"*Stenotosaurus leptognathus*" (Paton, 1974; WARMS Gz 6, 11, 35, 38)	2 (left squamosals)	4
"*Cyclotosaurus pachygnathus*" (Paton, 1974; WARMS Gz 13, 14, 26, 36)	2 (right tabulars)	4
Mastodonsaurus sp. (Paton, 1974; WARMS Gz 9, 15, 20, 37, 1075).	2 (posterior right mandibular rami)	5
Amphibian indet. (Paton, 1974; WARMS Gz 27)	0	1
cf. *Macrocnemus* (Walker, 1969; WARMS Gz 19, 21, 3787 [=4714])	1	3
WARMS Gz 10, Leamington	2 (two sizes on slab)	2
Rhynchosaurus brodiei (listed in Benton, 1990, p. 220)	3 (left dentaries)	14
plus one from Leamington	1	1
Bromsgroveia walkeri (Galton, 1975: WARMS Gz 1/2, 3, 5, 121, 128, 970, 1036)	1	7
"Large thecodontian" (Walker, 1969; WARMS Gz 4713)	1	1

"Prosauropod" (Walker, 1969; WARMS Gz 982; BMNH R2628; BGS [GSM] 4873)	1	3
"*Cladeiodon*" (Walker, 1969; WARMS Gz 7, 8, 954, 957, 969)	1	3
WARMS Gz 956, Leek Wootton	1	1

Bromsgrove

"*Cyclotosaurus pachgnathus*" (Paton, 1974; BIRUG Sp. 2)	1	1
Mastodonsaurus sp. (Paton, 1974; BIRUG Sp. 1; CAMSM G369)	1	2
"Amphibian indet." (Paton, 1974; BIRUG Sp. 3; CAMSM G332, 333, 334, 335)	0	4
cf. *Macrocnemus* (Walker, 1969; CAMSM G343)	1	1
Rhynchosaurus brodiei (Benton, 1990, p. 220)	1	2
Bromsgroveia walkeri (Walker, 1969; Galton, 1985; BIRUG 768; CAMSM G353, 357)	1	3
"Large thecodontian" (Walker, 1969; CAMSM G344–349 [= 344a–f]	1	1
"*Cladeiodon*" (Walker, 1969; CAMSM G352, and others)	1	1
Nothosaur (Walker, 1969; CAMSM G351, ? G354)	1	1

Devon

Eocyclotosaurus sp. (Milner et al., 1990; EXEMS 60/1985.72, ? 75, 310)	2 (left tabulars)	3
Mastodonsaurus lavisi (Milner et al., 1990; BMNH R331, R4215; EXEMS 60/1985.287, 309)	2 (right mandibles)	4
Capitosaurid inc. sed. (Milner et al., 1990; EXEMS 60/1985.78)	1	1
Amphibian indet. (Milner et al., 1990; EXEMS 60/1985.2, 4, 79, 96, 148, 183, 308)	1	7
Procolophonids (Milner et al., 1990; EXEMS 60/1985.3, 9, 87, 154, 311)	3 (right dentaries)	5
Rhynchosaurus brodiei (Benton, 1990, pp. 221–2; plus new specimens in Bristol)	9	29
Tanystropheus sp. (Milner et al., 1990; EXEMS 60/1985.143)	1	1
?Ctenosauriscid (Milner et al., 1990; EXEMS 60/1985.88)	1	1
"Thecodontians" (Teeth: EXEMS 60/ 1985.6, 8, 25, 27, 28, 51, 133, 140, 148, 155, 165, 176, 180. Others: EXEMS 60/ 1985.1, 7, 20, 22, 24, 53, 54, 64, 73, 84, 97, 150)	4 (?)	10