

THE SPECIES OF *RHYNCHOSAURUS*, A
RHYNCHOSAUR (REPTILIA, DIAPSIDA) FROM THE
MIDDLE TRIASSIC OF ENGLAND

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The rhynchosaur *Rhynchosaurus articeps* Owen, 1842, from the Middle Triassic of Grinshill, northern Shropshire, England, was a small reptile, about 0.5 m long. About 17 individual animals are represented by skulls, complete skeletons and partial skeletons, and these have permitted detailed restorations. The skull (60–80 mm long) is low and broad at the back, and it shows all of the typical rhynchosaur features of beak-like premaxillae, single median naris, fused parietal, broad maxillary tooth plate and dentary, both with multiple rows of teeth, and a deep lower jaw. The skeleton shows adaptations for fast terrestrial locomotion with a semi-erect hindlimb posture and for scratch-digging with the hind-foot. The skeleton is relatively more slender than that of most other middle and late Triassic rhynchosaurs, but this is probably an allometric effect of its much smaller size (they are typically 1–2 m long).

A further species of *Rhynchosaurus* from Warwick, named here *R. brodiei*, is represented by 15 specimens of partial skulls, tooth-bearing elements, and isolated postcranial bones. It was slightly larger than *R. articeps*, with a typical skull length of 90 mm, and estimated body length of 0.6 m, but the skull length ranged up to 140 mm. It differs from *R. articeps* in having a much larger jugal in the cheek area, and in the greater height and breadth of the skull. The isolated maxillary fragments from Bromsgrove probably also belong to *R. brodiei*.

The third species of *Rhynchosaurus* from Devon, named here *R. spenceri*, is now known from numerous specimens of at least 25 individuals, most of which were collected recently. These show a range in estimated skull length from 40 to 170 mm, but most specimens are at the upper end of that range, with an average skull length of 140 mm, and an estimated total body length of 0.9–1.0 m. *R. spenceri* differs from *R. articeps* and *R. brodiei* in having a skull that is broader than it is long (otherwise a

character of late Triassic rhynchosaurs), and it shares the large jugal character with *R. brodiei*.

Teeth are not well preserved in *R. articeps*, but several specimens of *R. brodiei* and *R. spenceri* give detailed information. The pattern of wear, and the nature of the jaw joint, suggest that *Rhynchosaurus* had a precision-shear bite, as in other rhynchosaurs, with no back and forwards motion. The maxilla had two grooves, a major and a minor one, which received two matching ridges of the dentary on occlusion. The multiple rows of teeth on maxilla and dentary, and the surrounding bone, wore down as uniform units. The diet was probably tough vegetation, which was dug up by scratch-digging, raked together with the hands or the premaxillary beak, and manipulated in the mouth by a strong tongue.

Rhynchosaurus is found variously in fluvial-intertidal deposits with evidence of desiccation (Grinshill, Warwick, Bromsgrove), and fluvial-aeolian deposits laid down in arid conditions with occasional flash floods (Devon). The bones have generally been transported (Warwick, Bromsgrove, Devon), but the Grinshill specimens are largely complete and undisturbed. The associated floras and faunas at Warwick, Bromsgrove, and Devon include pteridophytes, gymnospermopsids, bivalves, scorpions, freshwater fish, temnospondyl amphibians and reptiles (macrocnemids, thecodontians, ?procolophonids).

Rhynchosaurs are archosauromorph diapsids, possibly related to the enigmatic *Trilophosaurus*, and a sister group to Prolacertiformes + Archosauria. A cladistic analysis of Rhynchosauria reveals one major subgroup, the Hyperodapedontinae (*Hyperodapedon* and *Scaphonyx*), which is late Triassic in age. The earlier rhynchosaurs, including the middle Triassic *Stenaulorhynchus* and *Rhynchosaurus*, appear to form successively closer outgroups to the Hyperodapedontinae. The three species of *Rhynchosaurus* share only one possible synapomorphy in comparison with *Stenaulorhynchus*: The dentary is well over half the length of the lower jaw. The 'Rhynchosaurinae' (*Stenaulorhynchus* and *Rhynchosaurus*) was not established as a monophyletic group in the present analysis. These two genera share two postulated synapomorphies: the occipital condyle lies well in front of the quadrates, and there are two grooves on the maxilla and two ridges on the dentary. A third postulated synapomorphy, the presence of a single row of teeth on the pterygoid, has not been confirmed in this study for either *Rhynchosaurus* or *Stenaulorhynchus*. However, these postulated synapomorphies are outweighed by the synapomorphies that *Rhynchosaurus* shares with the Hyperodapedontinae.

The specimens of *Rhynchosaurus* have been used as biostratigraphic indicators for the English middle Triassic, indicating Anisian to early Ladinian ages. The three species can be arranged in a sequence from 'most primitive' to 'most advanced', but this cannot be used confidently to give a stratigraphic sequence.

1. INTRODUCTION

Rhynchosaurus articeps was named in 1842 as a new monospecific genus (Owen 1842 *b, c*), the first rhynchosaur to be described. Since then, many specimens have been collected from several localities in the middle Triassic of England, and descriptions of some of these have been published. There has been some confusion over the nomenclature of these specimens – some have been referred to *Rhynchosaurus* and some to the late Triassic genus *Hyperodapedon* – and many of the specimens have never been described.

Two specimens of *Rhynchosaurus* were in fact figured and described before 1842 (Murchison & Strickland 1840, p. 344, pl. 28, fig. 9, 10), although they were not correctly recognized at that time. The first specimen, from the middle Triassic of Leamington, Warwickshire, was identified as 'a smooth curved tooth' and Owen (1841 *b*, pl. 62A, fig. 3) named it *Anisodon*

gracilis, but later (Owen 1842*a*, p. 535) suggested that it was an ungual phalanx of *Labyrinthodon pachygnathus*. Owen (1842*a*, pp. 52–53) identified the second specimen as a vertebra of *Labyrinthodon leptognathus*. During 1840–1 Owen received collections of middle Triassic reptiles from two areas: quarries in and around Warwick (from Dr Lloyd) and from the quarries on Grinshill, north of Shrewsbury (from the Reverend T. Ogier Ward). In a paper presented to the Geological Society of London on 24 February 1841 he clearly viewed most of the Warwick and Grinshill material as belonging to various species of *Labyrinthodon* (i.e. *Mastodonsaurus*, which had been described by Jaeger from the German late Triassic in 1828). In an abstract of the paper (Owen 1841*a*) he clearly included a great range of different amphibian and reptile bones (and, tentatively, also the producer of the footprint *Cheirotherium*) in *Labyrinthodon*. By the time this paper was published (Owen 1842*a*), and by the time of the British Association meeting in August 1841, Owen (1842*b*) had separated the Grinshill animal from *Labyrinthodon* and described it as a reptile, erecting the new genus and species *Rhynchosaurus articeps* (Owen 1842*b,c*). He regarded it as a ‘lacertian’ (i.e. a lizard), but did not make the link with the Warwick material of *Rhynchosaurus*, which was still included in *Labyrinthodon* (Owen 1842*a*).

Owen (1845, 1859) later argued that *Rhynchosaurus* was related to *Dicynodon*, in part because of the pair of ‘tusks’ and its apparent toothlessness. He made it clear a little later (Owen 1863), in describing a new specimen of *R. articeps* from Grinshill, that he saw the premaxillary beak as a means of piercing its prey. In addition, he noted the similarities between *Rhynchosaurus* and *Sphenodon* (termed by him *Rhynchocephalus*), a concept that was later to become standardized in the ‘Rhynchocephalia’ (see, for example, Romer (1966)).

Meanwhile, Huxley (1859*a*) described the second rhynchosaur, *Hyperodapedon gordonii* from the late Triassic of Elgin in northeast Scotland, and clearly noted its relationship to *Rhynchosaurus*. Later (Huxley 1869), he directly linked the Elgin rhynchosaur with the finds from Warwick, and some new fossils from Devon, in calling all of them *Hyperodapedon*. The new specimens included tooth-bearing maxillae from Coton End Quarry in Warwick, sent to him by Dr Lloyd (who formerly supplied Owen) and the Reverend P. B. Brodie, and a similar specimen from the coast near Budleigh Salterton in Devon, sent to him by Mr W. Whitaker. Huxley noted that *Hyperodapedon* was closely related to *Rhynchosaurus* (and to the living *Sphenodon*), but he did not consider that the Warwick or Devon material might in fact be *Rhynchosaurus* as the latter ‘has shown no trace of teeth in either upper or under jaw’ (Huxley 1869, p. 147), an incorrect assertion (see below, §3.4). Huxley (1869) also noted new rhynchosaur material from the Triassic of India, which was later described (Lydekker 1885) as *Hyperodapedon huxleyi*.

Further rhynchosaur fossils were collected in the middle Triassic of Devon, and noted by Seeley (1876, p. 282), Metcalfe (1884), Carter (1884), and Lydekker (1888, p. 299) as *Hyperodapedon*. Burckhardt (1900) named a Warwick mandible and partial skull as the new species *Hyperodapedon minor*.

Further material of the Grinshill *Rhynchosaurus* was described by Huxley (1887), Woodward (1907), Watson (1910), Huene (1929), and Hughes (1968). New material, referred to *Hyperodapedon gordonii*, was also described from the Middle Triassic of Bromsgrove, near Birmingham (Wills 1907, 1910). Huene (1929, 1938, 1939*b*, 1956), and others (see, for example, Romer 1960), continued to regard the Warwick and Devon rhynchosaurs as being identical with *Hyperodapedon gordonii* from Elgin. Walker (1969, 1970) noted, however, that all

of the rhynchosaur material from the English Midlands and from Devon is *Rhynchosaurus*, although the Warwick–Bromsgrove and the Devon animals could be different species. The common occurrence of *Rhynchosaurus* in four different sedimentary basins within the English Triassic has been used to correlate these units stratigraphically (Warrington *et al.* 1980).

The aims of this study have been to:

(i) describe the osteology of the English rhynchosaurs on the basis of material that has been previously described, as well as many specimens that have not hitherto been described, including the recent major collections from the Triassic of Devon;

(ii) reconstruct the English rhynchosaurs and assess their functional morphology and palaeoecology;

(iii) assess the relationships of the English rhynchosaurs from the various localities, and determine whether they are all *Rhynchosaurus articeps*, whether some belong to new species of *Rhynchosaurus*, or even to new rhynchosaur genera;

(iv) assess the relationships of the English rhynchosaurs to other rhynchosaurs;

(v) assess the use of the English rhynchosaurs in stratigraphy.

Repository abbreviations are: BATGM, Bath Geology Museum; BGS, British Geological Survey, Keyworth, Nottingham; BMNH, British Museum (Natural History), London; CAMMZ, Cambridge University, Museum of Zoology; CAMSM, Sedgwick Museum, Cambridge; EXEMS, Exeter Museum; GPIT, Institut und Museum für Geologie und Paläontologie, Tübingen; MANCH, Manchester Museum; RSM, Royal Museum of Scotland; SHRBM, Shrewsbury Borough Museum; SHRCM, Shropshire County Museum, Ludlow, WARMS, Warwickshire Museum, Warwick.

2. MATERIALS AND METHODS

2.1. Preparation

Most of the rhynchosaur specimens were prepared by mechanical means at the time of their discovery in the mid-19th century. Dr A. D. Walker (Newcastle Upon Tyne) prepared several of the Warwick and Shrewsbury rhynchosaur specimens and the Bromsgrove specimens in 1967, 1968 and 1971, and he and Dr R. L. Paton (Edinburgh) prepared BATGM M20a, b in 1969–70. In the course of the present work, limited mechanical preparation was done by the author in 1984–6 on SHRBM G132/1982, '3'; BMNH R1236, R1237 and MANCH L7642 from Grinshill to expose parts of the braincase and palate, and on WARMS Gz34, the interclavicle from Warwick. Most of the specimens in the new collections from Devon (EXEMS, various numbers) were prepared mechanically by Mr P. Spencer, Dr M. A. Taylor, and by the author in 1983–7. Particular attention was paid to EXEMS 60/1985.292, a partial skull, which was prepared mechanically by the author over several months in 1986–7.

2.2 English rhynchosaur localities

English rhynchosaurs have been collected from at least five localities (figure 1). The type specimen, and later material of *Rhynchosaurus articeps*, were collected from the various Grinshill quarries, located on a hill between the villages of Grinshill and Clive. The dates of discovery range from 1840 to 1985. There are presently four main quarries on the crest of the hill (National Grid References SJ 5205 2392, SJ 5238 2387, SJ 5249 2384, SJ 5264 2380), one of which (the last) is still operational. The specimens of *R. articeps* appear to have come from more

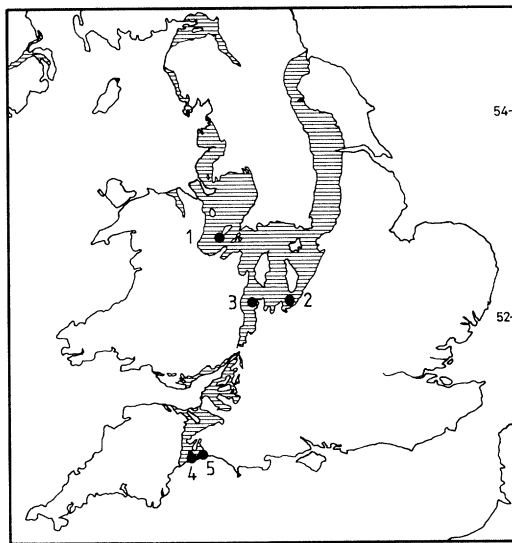


FIGURE 1. Map of England showing the distribution of Triassic rocks (shaded), and the localities that have yielded remains of *Rhynchosaurus*: 1, Grinshill, Shropshire; 2, Warwick, Warwickshire; 3, Bromsgrove, West Midlands; 4, Budleigh Salterton, Devon; 5, Sidmouth, Devon.

than one of the quarries (D. B. Thompson, personal communication, 1984), from the siltstones and fine sandstones of the Tarporley Siltstone Formation (formerly the 'Waterstones') and possibly also from the sandstones immediately below, the top of the Grinshill Sandstone Formation (formerly the 'Ruyton and Grinshill Sandstones' or the 'Building Stones'). These units have been dated as middle Triassic (close to the Anisian–Ladinian boundary) by Walker (1969) or older (Scythian–Anisian) by Warrington *et al.* (1980, p. 33, table 4).

The 'Warwick rhynchosaur' is represented by specimens from two of several quarries in Triassic sandstones in and around the town of Warwick. The main locality is Coton End Quarry, a small quarry within Warwick, beside a railway line and with access to Wharf Street (SP 2900 6550) which produced several rhynchosaur specimens in the 19th century, including those described by Owen and Huxley, as well as bones of labyrinthodont amphibians. The bones came from the 'Dirt bed', a fine-grained brown-coloured sandstone, a horizon within the Bromsgrove Sandstone Formation (formerly the 'Building Stones'). This has been dated as early- to mid-Ladinian by Walker (1969), early Ladinian by Paton (1974), or late Scythian to early Ladinian by Warrington *et al.* (1980, pp. 39–40, table 4), with the reptiles occurring in the upper part. At least one rhynchosaur specimen, the first-figured premaxilla (Murchison & Strickland 1840, p. 344, pl. 28, fig. 9), was collected at Leamington, together with other reptile and amphibian remains. These may be from quarries within Leamington (Murchison & Strickland 1840, p. 343; e.g. SP 325666), or from nearby Cubbington Heath (Hull 1869, p. 89; SP 332694).

A few rhynchosaur remains were also found early this century in quarries near Hilltop Hospital, on Breakback or Rock Hill, in Bromsgrove, near Birmingham (SO 948698). The specimens are labelled as having come from 'Wilcox S. Quarry'. These quarries (Wills 1907, 1910, pp. 254–256) formerly showed sections in the Bromsgrove Sandstone Formation, and this has been dated as the equivalent of the fossiliferous horizons at Warwick and Leamington (Walker 1969; Paton 1974; Warrington *et al.* 1980, pp. 38–39, table 4).

The 'Devon rhynchosaur' has been found at several localities along the coast between Budleigh Salterton and Sidmouth. Several specimens collected in the 19th century came from below High Peak (SY 144858), 2 km west of Sidmouth, and from the mouth of the Otter River, on its left bank (SY 077820), just east of Budleigh Salterton. Extensive collections of rhynchosaur specimens have been made more recently (1982–5) from 15 or more localities between Budleigh Salterton and Sidmouth (SY 0807 8212 to SY 1066 8639), and just east of Sidmouth (SY 1297 8730). The specimens have been collected partly from fallen blocks of red sandstone and from horizons at the base of the cliff and on the foreshore (Spencer & Isaac 1983). The fossiliferous horizons in Devon, parts of the Otter Sandstone Formation, have been dated as Anisian by Walker (1969), a view accepted by Paton (1974) and Warrington (1980, pp. 43–44, table 4).

Further details of the sedimentology, taphonomy and palaeoecology of the English rhynchosaur localities are given below (see §§8.4–8.7).

2.3. *Number of individuals*

The specimens of English rhynchosaur are listed below by localities, with brief details of the portions preserved. Specimens are listed in sequence by repository. Full details of collecting data and former descriptions and illustrations are available from the author. In estimating the number of individuals present, collecting data were taken into account, and attempts were made to fit pieces together. There is no evidence that specimens in different collections were broken up from single specimens, unless otherwise stated.

Rhynchosaurus articeps, the 'Shrewsbury rhynchosaur'

About 17 individuals of *R. articeps* have been collected from Grinshill, but some specimens have been missing since the 19th century, and the total could be greater. The minimum number of individuals (MNI), estimated on the basis of the number of skulls, is 7.

- (i) SHRBM G132/1982 (formerly 'ShM 1'). Nearly complete skull and mandible.
- (ii) SHRBM G134/1982 (formerly 'ShM 2'). Vertebrae, ribs, right scapula, coracoid and humerus.
- (iii) SHRBM 3. Nearly complete skull and mandible, cervical and dorsal vertebrae, ribs, left coracoid, left arm, partial left hindlimb in ventral view.
- (iv) SHRBM G133/1982 + G151/1982 (formerly 'ShM 4'). Part and counterpart of a skeleton with cervical and dorsal vertebrae, ribs, gastralia, right scapula and forearm, parts of pelvis and both hindlimbs (but not feet).
- (v) SHRBM 5. Partial skeleton in ventral view: gastralia, pelvis, parts of both hindlimbs. Missing in 1983.
- (vi) SHRBM 6. Partial skeleton in ventral view, jumbled dorsal vertebrae, ribs, and right forelimb.
- (vii) SHRBM 7. Caudal vertebrae, part of the right ischium and head of right femur.
- (viii) BMNH R1236. Nearly complete skull and mandible, slightly flattened.
- (ix (a)) BMNH R1237. Badly crushed skull and mandible. Goes with skeleton BMNH R1238 (not R1239, as Lydekker (1888, p. 297) said).
- (ix (b)) BMNH R1238. Partial skeleton in ventral view, showing some vertebrae, ribs, gastralia, right forelimb and partial right hindlimb.

(x) BMNH R1239. Part and counterpart, showing impressions of the left mandible, gastralium, pectoral girdle, partial right forelimb, pelvis, and left hindlimb.

(xi) BMNH R1240 (caudal vertebrae in two blocks) and R1241 (partial hindlimb), all three of which fit together.

(xii) BATGM M20a,b. Two blocks with dorsal and caudal vertebrae, ribs, gastralium, various pelvic bones, and the right hindlimb.

(xiii) MANCH L7642 (skull and cervical vertebrae) and L7643 (ribs).

(xiv) SHRCM G07537–8. Two blocks containing 11–12 posterior dorsal, sacral and anterior caudal vertebrae.

(xv) SHRCM G3851. Series of 12–13 caudal vertebrae.

(xvi) Keele University, unnumbered. Skull and partial skeleton embedded within three blocks. Unprepared.

(xvii) Keele University, unnumbered. Indeterminate bone fragment.

The 'Warwick rhynchosaur'

About 15 individual specimens of the Warwick rhynchosaur have been collected from Coton End Quarry in Warwick, and from Leamington Old Quarry. The *MNI*, estimated on the basis of left dentaries, right maxillae and left maxillae is four. All specimens are from Coton End Quarry unless otherwise stated.

(i) WARMS Gz17. Dorsal vertebra.

(ii) WARMS Gz19. Left ischium.

(iii) WARMS Gz34. Interclavicle.

(iv) WARMS Gz950/1 and 2. Right dentary and (?) fragment of splenial.

(v) WARMS Gz955. Small right maxilla.

(vi) WARMS Gz959. Posterior part of a right dentary.

(vii) WARMS Gz960. Right maxilla.

(viii) WARMS Gz1046. Small right premaxilla. From Leamington, according to most sources, although Murchison and Strickland (1840, p. 344) imply it is from Coton End.

(ix) WARMS Gz4712. Anterior end of left dentary and splenial.

(x) WARMS Gz4715. Snout region of skull: both premaxillae, parts of maxillae and vomers, and tip of left dentary.

(xi) (a) WARMS Gz6097 (renumbered from Gz1275). Partial skull (left side), including snout, maxilla and orbital area back to the anterior areas of the temporal fenestrae. Fits on to BMNH R8495.

(xi) (b) BMNH R8495 (renumbered from R2623A). Mandible and ventral parts of skull (left side) in two pieces, including dentary, splenial, maxilla and fragments of palate. Fits on to WARMS Gz6097.

(xii) BMNH R2623 (renumbered from R2623C). Fragment of a left dentary.

(xiii) BMNH R8494 (renumbered from R2623B). Right maxilla, posterior portion, with parts of palatine, ectopterygoid and jugal.

(xiv) BGS GSM 59745. Left maxilla.

(xv) BGS GSM 90493. Left maxilla.

The 'Bromsgrove rhynchosaur'

Two specimens of the Bromsgrove rhynchosaur have been recorded. Since both maxillae are of different sizes, they must have come from two individuals, although the MNI is one.

- (i) CAMSM G336. Small right maxilla.
- (ii) CAMSM G337. Posterior portion of a small left maxilla.

The 'Devon rhynchosaur'

Five or more specimens of the Devon rhynchosaur were found in the late nineteenth century; 27 specimens were collected from 1982 to 1985. At least 24 individual animals may be represented, based on dates of collection and localities. Rhynchosaur remains have been found at numerous localities between Budleigh Salterton and Sidmouth. The older specimens are localized to the nearest cliff or bay, and the newer collections are localized more precisely by their National Grid reference (the 8-figure map references define a 10 m × 10 m square on the ground). Specimens from the same location are listed together; these could belong to single individuals, but probably do not, as the bones are disarticulated and generally found in fallen blocks. Only specimens (xv), (xvi), (xviii) and (xxi) were found *in situ* (P. Spencer, personal communication, 1988). Specimens (v)–(xxiv) were collected by Mr P. S. Spencer between 1982 and 1985 (Spencer & Issac 1983).

- (i (a)) BMNH R330. Left premaxilla. High Peak, near Sidmouth.
- (i (b)) BMNH R330. At least one thousand largely unidentifiable bone fragments. High Peak, near Sidmouth, and River Otter, Budleigh Salterton.
- (ii) BMNH R9190 (renumbered from R4215). Anterior part of a right dentary. Picket Rock Cove, Sidmouth.
- (iii) BGS GSM 90494. Right maxilla, anterior portion. Left bank of the River Otter, close to its mouth.
- (iv) EXEMS 65/1984. Partial skull and mandible in five pieces, consisting of anterior palate, two maxillae, right pterygoid, and right mandible back to the adductor fossa. Locality: Smallstones Point, between Ladram Bay and Chiselbury Bay (SY 096847).
- (v) EXEMS 60/1985.11. Partial right premaxilla. Locality: Sandy Cove (SY 0987 8545).
- (vi) EXEMS 60/1985.12. Partial right dentary. 60/1985.15. Two mid-dorsal vertebrae. 60/1985.23. Broken piece of mandible (?). Locality: SY 1010 8555.
- (vii) EXEMS 60/1985.13. Small left maxilla. Locality: SY 1010 8555.
- (viii) EXEMS 60/1985.37–45. Nine pieces of anterior skull and mandible, consisting of both premaxillae, the anterior end of the left maxilla, the anterior ends of both dentaries and splenials, the posterior toothed part of the right dentary, and two unidentified pieces. Locality: SY 1022 8567.
- (ix) EXEMS 60/1985.46. Left ectopterygoid of a large rhynchosaur. Locality: SY 1022 8567.
- (x) EXEMS 60/1985.56. Partial right dentary. 60/1985.57. Three mid-dorsal vertebrae. 60/1985.282. Left humerus, radius and ulna. Locality: SY 1032 8587.
- (xi) EXEMS 60/1985.66. Skull element: jugal or surangular (?). 60/1985.67. Anterior portion of left splenial. Locality: SY 1044 8589.
- (xii) EXEMS 60/1985.74. Impression in the matrix of a small right maxilla. Locality: SY 1044 8587.

- (xiii) EXEMS 60/1985.91. Tiny right premaxilla. Locality: Green Point (SY 1053 8598). Cited by Spencer & Isaac (1983, p. 269) as an 'ungual phalange' of a possible 'thecodontid'.
- (xiv) EXEMS 60/1985.92. Left premaxilla. Locality: SY 1297 8731.
- (xv) EXEMS 60/1985.284. Lateral portion of a large left maxilla in three pieces. Locality: Windgate (SY 1066 8639).
- (xvi) EXEMS 60/1985.285. Anterior portion of a left maxilla. Locality: SY 1067 8640.
- (xvii) EXEMS 60/1985.290. Small right maxilla. Locality: SY 0957 8495.
- (xviii) EXEMS 60/1985.292. Partial skull and mandible, in 14 pieces. Floor of orbit and palate of right side (maxilla, jugal, palatine, pterygoid, ectopterygoid), partial palate of left side (palatine, pterygoid), posterior right-hand angle of skull (quadrate, quadratojugal, squamosal), and both mandibles, the right more complete than the left. Locality: SY 1060 8639.
- (xix) EXEMS 60/1985.312. Posterior portion of a large left (?) maxilla. Locality: SY 1054 8626.
- (xx) EXEMS 60/1985.313. Posterior portion of a right dentary. Locality: ?
- (xxi) EXEMS 7/1986.3. Small left maxilla, damaged at back, with part of orbital floor. Locality: SY 1057 8641.
- (xxii) EXEMS 7/1986.4. Posterior portion of a large right maxilla, with parts of the jugal and palatine around the infraorbital foramen. Locality: SY 1052 8598.
- (xxiii) EXEMS 7/1986.5. Damaged posterior portion of a right mandible (surangular, articular, ?prearticular). Locality: SY 1051 8598.
- (xxiv) EXEMS 7/1986.6. Large right premaxilla. Locality: SY 1053 8608.

TAXONOMY

Class Reptilia Laurenti, 1769
 Subclass Diapsida Osborn, 1903
 Order Rhynchosauria (Gervais, 1859) Osborn, 1903
 Family Rhynchosauridae Huxley, 1859
Rhynchosaurus Owen, 1842

3. *RHYNCHOSAURUS ARTICEPS* OWEN, 1842

(*Figures 2–20; figures 44 and 45, plates 1 and 2*)

- 1841a 'batrachian' Owen, p. 582.
 1842b *Rhynchosaurus* Owen, pp. 145–153.
 1842c *Rhynchosaurus articeps* Owen, pp. 355–369, pl. 5, 6.
 1859 *Rhynchosaurus* Owen; Owen, pp. 237–238.
 1863 *Rhynchosaurus articeps* Owen; Owen, pp. 466–467, pl. 25.
 1869 *Rhynchosaurus* Owen; Huxley, pp. 143, 147.
 1884 *Rhynchosaurus* Owen; Touche, p. 54, figs 723, 766.
 1887 *Rhynchosaurus articeps* Owen; Huxley, pp. 689–692, figs 2, 5, pl. 27.
 1888 *Rhynchosaurus articeps* Owen; Lydekker, pp. 296–297.
 1900 *Rhynchosaurus articeps* Owen; Burckhardt, p. 532, fig. 3.

Figures 44–50 appear on plates 1–7.

- 1902 *Rhynchosaurus* Owen; Beasley, pp. 13–14, pl. 1, fig. 2.
1904 *Rhynchosaurus articeps* Owen; Woodward, p. 286.
1906 *Rhynchosaurus articeps* Owen; Winwood, p. 161.
1907 *Rhynchosaurus articeps* Owen; Woodward, pp. 293–299, fig., pl. 2.
1910 *Rhynchosaurus articeps* Owen; Watson, pp. 155–158, pl. 4.
1929 *Rhynchosaurus articeps* Owen; Huene, pp. 37, 40–41, pl. 6, 7.
1929 *Rhynchosaurus* sp.; Huene, p. 37.
1938 *Rhynchosaurus articeps* Owen; Huene, pp. 110–111, fig. 10.
1939b *Rhynchosaurus articeps* Owen; Huene, pp. 499, 502–504, fig. 3.
1968 *Rhynchosaurus articeps* Owen; Hughes, pp. 469–470.
1969 *Rhynchosaurus articeps* Owen; Walker, pp. 470–71, 473.
1970 *Rhynchosaurus articeps* Owen; Walker, in Warrington, p. 217.
1980 *Rhynchosaurus articeps* Owen; Chatterjee, p. 64.
1983 *Rhynchosaurus articeps* Owen; Benton, p. 693, figs 50, 52.
1984b *Rhynchosaurus*; Benton, p. 772.

Diagnosis: Consistently smaller than other English rhynchosaurs (figure 27); jugal shallower than in other taxa, smaller than the maxilla in lateral view, the opposite of the case in the Warwick and Devon forms. Skull primitively narrower than its length, unlike the Devon *Rhynchosaurus* at least.

Lectotype (designated here). SHRBM G132/1982 (formerly ShM 1; figure 44a, b). A nearly complete skull and mandible. Triassic, Grinshill, near Shrewsbury.

Paralectotype (designated here). SHRBM G134/1982 (formerly ShM 2; two blocks stuck together; figure 45a). Anterior part of a skeleton (vertebrae, ribs, scapula, coracoid and humerus). Triassic, Grinshill, near Shrewsbury.

3.1. *The holotype of Rhynchosaurus articeps*

In the first descriptions of *Rhynchosaurus articeps* (Owen 1842b, c) no holotype was designated, nor has one been subsequently. The two papers were published at about the same time, and the descriptions are very similar, although only Owen (1842c) was illustrated. The type series includes a fairly complete skull (SHRBM G132/1982: Owen 1842c, pl. 5), a partial skull (now lost: Owen 1842c, pl. 6, fig. 6), some dorsal vertebrae and ribs (SHRBM G134/1982: Owen 1842c, pl. 6, figs 1, 3, 4; counterpart (fig. 2) now lost), some caudal vertebrae (now lost: Owen 1842c, pl. 6, fig. 5), a scapula, coracoid and humerus (SHRBM G134/1982: Owen 1842c, pl. 6, figs 8, 9), some dorsal vertebrae, ribs and limb bones (now lost: Owen 1842c, pl. 6, fig. 7), and a partial ilium and two limb bones (now lost: Owen 1842b, pl. 6, fig. 10).

The specimens had been found some years earlier by John Carline, quarrymaster, and Dr T. Ogier Ward, a naturalist from Shrewsbury, and given to the museum of the Shropshire and North Wales Natural History Society (Page 1979). Ward had previously described footprints, ripple marks and 'rain-mark' impressions [*sic*] from Grinshill (Ward 1840; noted in Murchison (1839, appendix, p. 734)). These footprints were later identified as of 'rhynchosauroid' type (Beasley (1906) and §8.4 herein). Ward then obtained several bones from Grinshill over a year (August 1840 to November 1841) from various quarrymen,

TABLE 1. MAIN MEASUREMENTS (IN MILLIMETRES) OF *RHYNCHOSAURUS ARTICEPS*

(Estimates are marked with an asterisk.)

	SHRBM G132/ 1982	SHRBM G134/ 1982	SHRBM 4	BMNH R1239	BMNH R1237/ R1238
skull length in midline (premaxilla – quadrate level)	82	—	—	—	70*
skull width across quadratojugals	65*	—	—	—	52
maximum width of maxillary tooth plate	8*	—	—	—	—
mandible length	91	—	—	—	73
presacral column length	—	—	190*	230*	240*
scapulocoracoid height	—	56*	—	—	—
scapula height	—	41	—	—	—
scapula length	—	21	19	—	—
coracoid length	—	29*	—	35	—
coracoid breadth	—	20*	—	27	—
interclavicle length	—	42*	—	38	42
humerus length	—	45	28	42	41
humerus, proximal breadth	—	21	15	22	18
humerus, least diameter of shaft	—	6	4	5	5
humerus, distal breadth	—	20*	12*	21*	—
radius length	—	—	22	31*	32
radius, proximal breadth	—	—	2	—	—
ulna length	—	—	24	31	33
ulna, proximal breadth	—	—	6	—	8
metacarpal II length	—	—	8	—	8
manus length including carpus	—	—	30*	30*	35*
ilium, crest length	—	—	—	—	25*
ilium, breadth of neck	—	—	—	—	10*
ilium height	—	—	—	—	15*
pubis length	—	—	—	14	—
pubis, maximum breadth	—	—	—	27	—
ischium length	—	—	—	25	—
ischium breadth	—	—	—	20	—
femur length	—	—	50*	52*	—
femur, least diameter of shaft	—	—	4	6	—
tibia length	—	—	40*	38	—
tibia, proximal breadth	—	—	6	—	—
tibia, distal breadth	—	—	—	—	8
fibula length	—	—	—	51	—
metatarsal IV length	—	—	—	25	25
pes length including tarsus	—	—	—	70*	80
estimated length of presacral and sacral vertebral column	—	—	205*	250*	260*
estimated length of tail (0.7 times presacral and sacral length)	—	—	145*	175*	182*
estimated total length of vertebral column	—	—	350*	425*	442*

although he later (Ward 1874) stated that *Rhynchosaurus* was ‘first discovered by myself in 1838–39’. He sent the bones to Owen at the Royal College of Surgeons in several parcels (Owen correspondence, Coll. Sherborn, BMNH letters 110, 103, 118, 105, 109, 107, 114, 116); a few details from these letters help to determine which specimens were found together, and the order of discovery, details not made clear in Owen (1842*b,c*).

In his first letter to Owen, dated ‘Aug. 6’ (? 1840) (BMNH 110), Ward noted that the bones were found in the same beds as the footprints and probably belonged to the same animal. These

first specimens included 'vertebrae' and 'a number of other bones that are much broken, some of which are hollow like the long bones of mammalia or birds, but I have offended the quarryman, so now he will not part with any of them, or I should have been enabled to send almost an entire skeleton except the head'. Owen (1842*c*, p. 356) also distinguished these specimens as being among the first to be found. The vertebrae are now numbered SHRBM G134/1982 (described by Owen 1842*b*, pp. 146–148; 1842*c*, pp. 356–358, pl. 6, figs 1–4). Ward also enclosed a partial skull, stating 'those that I have marked as jaw bones were not found in the same quarry as the vertebrae, but I believe in nearly the same bed'. These are probably the lower jaws described by Owen (1842*b*, p. 150; 1842*c*, pp. 363–364, pl. 6, fig. 6) and now lost.

Ward apparently managed to obtain the other bones that formed part of the 'entire skeleton', and he describes them in some detail in his letters to Owen dated 'Nov. 23' and 'Nov. 27' (? 1840) (BMNH 103, 118). He mentions 'two hollow bones (of the extremities), a portion of scapula and vertebrae and ribs'. These are most likely the specimens described by Owen (1842*b*, pp. 151–153; 1842*c*, pp. 364–367, pl. 6, figs 7–10). Most of these are now lost, although the 'scapula' is on a block that is part of SHRBM G134/1982.

Ward (letter dated 'June 20' (? 1841); BMNH 109) then sent Owen a key specimen, a good skull 'belonging to the bones I sent you'. Ward's description in the letter, and his warning to Owen to 'take care not to wet the nasal end which is glued only' strongly indicate that this is the skull SHRBM G132/1982 described by Owen (1842*b*, pp. 147–150; 1842*c*, pp. 358–363, pl. 4). Ward clearly implies that this skull belongs with the postcranial elements that he sent earlier. He reiterated this in a letter dated 'October 26' (? 1841) (BMNH 114), stating that 'the bones I sent you viz, ribs, vertebrae and pelvis, belong to the head of the *Rhynchosaurus* sent afterwards'.

A third important consignment of bones was then sent to Owen (Ward letter dated 'Nov. 3' (? 1841); BMNH 116). These consisted of nine pieces: five in fine sandstone and four in a coarse 'burr' (coarse-grained sandstone). The first five pieces fitted together, and they contained vertebrae, ribs, pelvic bones and 'broken extremities'. These correspond to SHRBM G133/1982 and SHRBM G151/1982 (one individual). The bones in the 'burr' are not described in the letter.

The matrix of the *Rhynchosaurus* bones confirms the various specimen assignments given above. Owen (1842*b*, p. 146) summarized as follows: 'They occur at the Grinsill [*sic*] quarries, in a fine-grained sandstone, and also in a coarse burr-stone; in the latter are imbedded some vertebrae, portions of the lower jaw, a nearly entire skull, fragments of the pelvis and of two femora: in the fine-grained sandstone, vertebrae, ribs, and some bones of the scapular and pelvic arches are imbedded.' The specimens in the fine-grained sandstone were figured by Owen (1842*c*, pl. 6, figs 1–4, 8, 9; see also p. 364), and those in the coarse-grained sandstone were also figured by him (Owen 1842*c*, pl. 5, pl. 6, figs 6, 7, 10; see also pp. 356, 367). Among those specimens that still exist, SHRBM G132/1982 is indeed preserved in a coarse pinkish-grey sandstone, whereas SHRBM G134/1982, G133/1982 and G151/1982 are in a fine-grained grey sandstone.

The fine skull of *R. articeps* (SHRBM G132/1982), the first figured specimen (Owen 1842*c*, pl. 5) is designated as lectotype. It was possibly associated with the postcranial elements figured at the same time (Owen 1842*c*, pl. 6, figs 7, 10), but which are now lost. The only surviving postcranial elements (SHRBM G134/1982), described and figured in the first papers (Owen

1842 *b, c*, pl. 6, figs 1, 3, 4, 8, 9), are in a fine-grained matrix, and thus cannot belong with the skull. These latter associated postcranial elements are designated as paralectotype. The specimen SHRBM G133/1982 (plus G151/1982), although found at the same time as the others, was not described by Owen, having come to his attention after he had read his 1842 *b* paper, and it is not included in the type series.

3.2. Skull

General

The skull description and restoration (figure 2*a-d*) is based on specimens SHRBM G132/1982, 3; BMNH R1236, R1237; and MANCH L7642. The proportions of the posterior parts of the skull were hard to ascertain as the available specimens are either incomplete in this region, or distorted by some compression. The restorations of the palate, occiput and braincase (figures 2*c, d* and 6*e-g*) are based on particularly patchy information. *R. articeps* appears to have a broader and relatively lower skull than in the restoration by Huene (1938, p. 110; 1939 *b*, p. 503). The restoration by Woodward (1907) seems to be much more accurate.

The skull shape is typical of all other rhynchosaurs, especially those of the middle Triassic, such as *Stenaulorhynchus*. In ventral view (figure 2*a*), the braincase is set forward of the posterior margin of the parietal, but not so far forward as in *Stenaulorhynchus* (Huene 1938), or as Benton (1983, fig. 44*b*) suggested for *Rhynchosaurus*. Most of the *R. articeps* skull remains indicate an animal with a skull length of 60–85 mm (table 2). The type specimen (SHRBM G132/1982) has a skull length apparently somewhat greater than the other four skulls, but the latter are all much more distorted and should probably have longer skulls if restored.

TABLE 2. ESTIMATED SKULL LENGTHS OF SPECIMENS OF *RHYNCHOSAURUS ARTICEPS*

(Measurements are of the midline skull length, from the anterior end of the premaxilla to the back of the parietal, as seen in dorsal view (figure 2).)

SHRBM G132/1982	82 mm
SHRBM '3'	70 mm ?
BMNH R1236	75 mm ?
BMNH R1237	70 mm ?
MANCH L7642	60 mm ?

Throughout the description, comparisons with other rhynchosaurs are given, and these are based on published descriptions as follows: *Stenaulorhynchus* (Huene 1938), *Scaphonyx* (Huene 1929, 1942; Sill 1970); *Hyperodapedon gordonii* (Benton 1983), and *H. huxleyi* (Chatterjee 1974).

Dermal bones of the skull roof (figures 2–5 and 44)

The paired *premaxillae* are heavy bones which form a curved 'beak' that descends below the maxilla. They diverge dorsally, and form the boundaries of a droplet-shaped median narial opening (figures 2*b, 3c, 5b* and 44*a*). The *maxillae* will be described as part of the palate.

The paired *nasals* meet along an irregular suture in the midline (figures 2*b, 3c, 4b, 5b* and 44*a, c*). They are about the same length as the frontals, or slightly shorter, as in other rhynchosaurs. This is hard to determine in *R. articeps*, however, as the anterior margin of the nasals is damaged in most specimens.

The paired *frontals* meet medially (figures 2*b, 3c, 4b, 5b* and 44*a, c*), and they border the orbits for a short distance, contrary to Huene's (1929, p. 40) view.

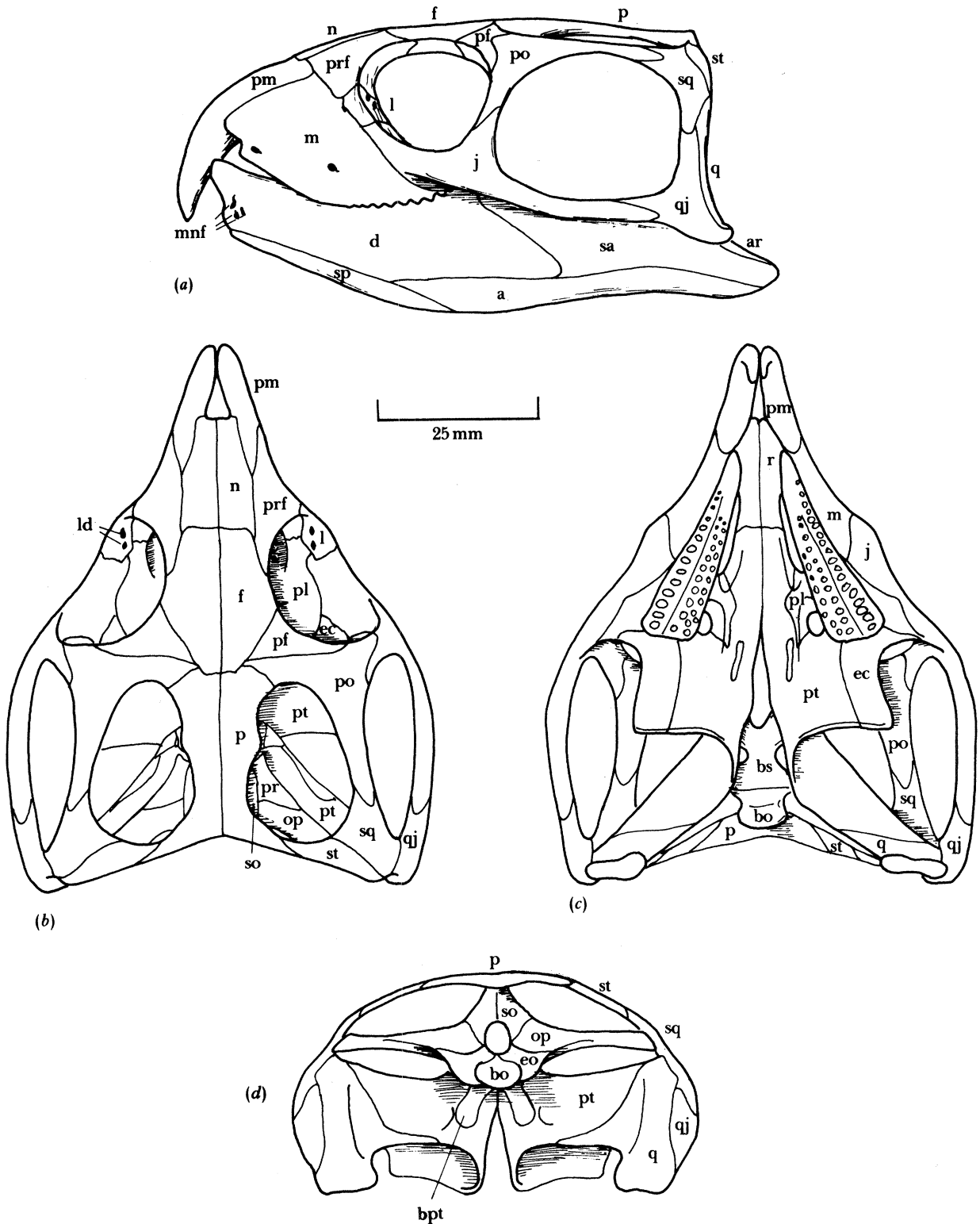


FIGURE 2. Restoration of the skull of *Rhynchosaurus articeps* in (a) left lateral, (b) dorsal, (c) palatal and (d) occipital views. Based on SHRBM G132/1982, with the front of the snout and back of the mandible from SHRBM 3, posterior parts of the skull roof from BMNH R1236, and palate and braincase from BMNH R1236 and MANCH L7642. The posterior regions of the skull, and the occipital view, are the most restored. The jaws are shown slightly open. (Abbreviations used in figures are listed on p. 306.)

The fused T-shaped *parietal* element (figures 2*b*, 3*c*, 4*b*, 5*b* and 44*a, c, d*) contacts the frontal, the postorbital, and possibly also the postfrontal in front, although the latter two contacts are not clear. The narrow posterior wings contact the supratemporals, but only lightly as this contact is broken in many specimens (figures 5*b* and 44*c*). The 'interparietal' identified by Huene (1929, p. 40, pl. 6, fig. 1*a, c*) in SHRBM G132/1982 is the displaced posterior part of the parietal.

The *supratemporals* are narrow elongate elements that form part of the posterior margin of the upper temporal fenestra. In most specimens they are preserved out of articulation (figures 3*b-d*, 4*b*, plate 1*a-d*), but their shape, and that of the neighbouring elements, suggests that they ran diagonally between the posterior wing of the parietal and the dorsal process of the squamosal (figure 2*b, d*). Watson (1910, p. 155) named these elements epiotics, and Huene (1929, p. 40) identified them as tabulars.

Supratemporals were not expected in *R. articeps*, and A. D. Walker (personal communication; 1987) doubted their presence after preparing the relevant specimens. However, further preparation by the author has tended to confirm their presence in all appropriate specimens (SHRBM G132/1982, 3; BMNH R1237; MANCH L7642). The fact that these specimens show similar isolated narrow tongues of bone on both sides located in front of the lateral wing of the parietal, and behind the medial wing of the squamosal, suggests that these are truly separate elements. The alternative view, that these are broken-off lateral parietal processes, is hard to sustain, as the 'break' has occurred in exactly the same way on both sides in each specimen. Further, the shape and size of the supratemporal is the same in each specimen, even though the apparent width of the parietal lateral processes seems to vary, presumably owing to the nature of the preservation (absent in SHRBM G132/1982, concealed in SHRBM 3 and MANCH L7642, long and tapering in BMNH R1237).

The supratemporal is present, and very similar in shape, in the early rhynchosaurs *Mesosuchus* (Haughton 1924, p. 19; Broom 1925, pp. 6-7 as 'tabulars') and *Howesia* (Haughton 1924, p. 24). It had been assumed (Benton 1983, p. 694, 1984*a*, p. 579, 1984, p. 133) that all the later rhynchosaurs had lost this element. There may be a supratemporal in *Stenaulorhynchus*. Huene (1938, p. 88, pl. 1, fig. 1, pl. 2, fig. 1) shows that this genus has a bifurcating dorsal squamosal process that met the parietal (? squamosal + supratemporal). The posterior portion of the dorsal process has been interpreted by Chatterjee (1970) as a supratemporal; while A. D. Walker (personal communication, 1987) regards it as a broken piece of the lateral process of the parietal. The specimen (GPIT 317*a*; figure 44*e*) is hard to interpret, but it seems unlikely that the parietal would have had such long lateral processes which would have broken off cleanly and symmetrically on both sides. They are interpreted tentatively here as supratemporals.

The *lacrima* appears to lie lower down and to extend further back in lateral view (figures 2*a, b*, 3*a, b*, 5*a, b*, 44*b*) than in other rhynchosaurs. The lacrimal appears partially to cover a large vessel opening in its anterodorsal corner, where it meets the maxilla and the prefrontal (figures 2*a, 3a*). Inside the orbit the lacrimal is roughly square in shape, and it surrounds two openings for the lacrimal duct (ld, figures 2*b, 5b*), just as in *Hyperodapedon*. Medially, the lacrimal meets an ascending process of the palatine (figures 2*b, 5b*).

The *prefrontal* (figures 2*a, b, 3a-c, 44a, b*) has a thickened orbital margin, but it is not rugose as in *Hyperodapedon*. Medially, the prefrontal apparently meets an ascending process of the palatine (figures 2*b, 5b*).

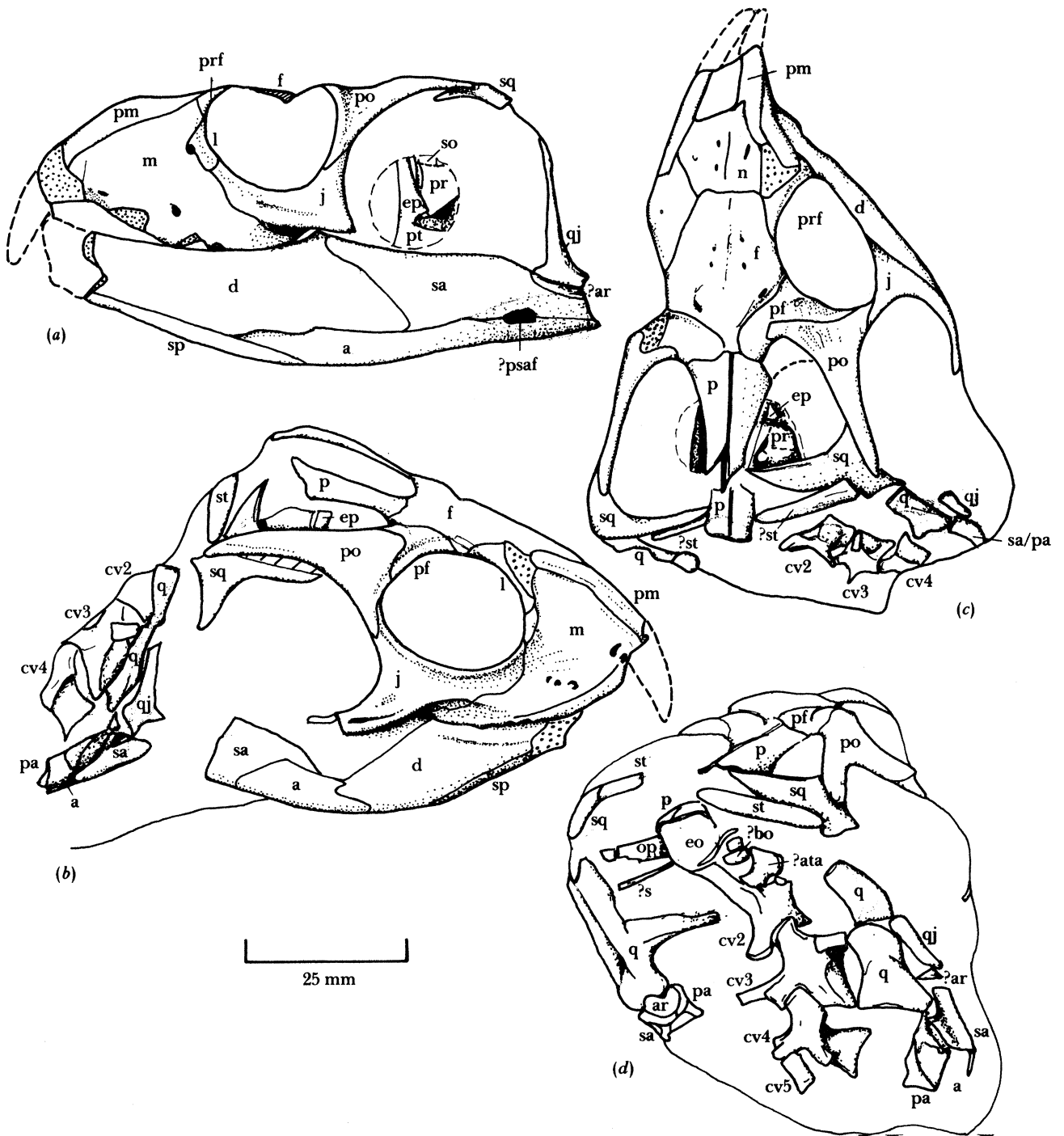


FIGURE 3. *Rhynchosaurus articeps*. The lectotype specimen, SHRBM G132/1982 in (a) left lateral, (b) right anterolateral and dorsal (c) dorsal and (d) occipital views.

The sturdy *postfrontal* (figures 2a, b, 3b, c, 4b, 5b, 44a-c) may meet the parietal, but that contact is not clear in all specimens. Likewise, the *postorbital* (figures 2a, b, 3a-c, 4a, b, 5a, b, 44a-d) probably met the parietal behind. It descends very low in the posterior border of the orbit.

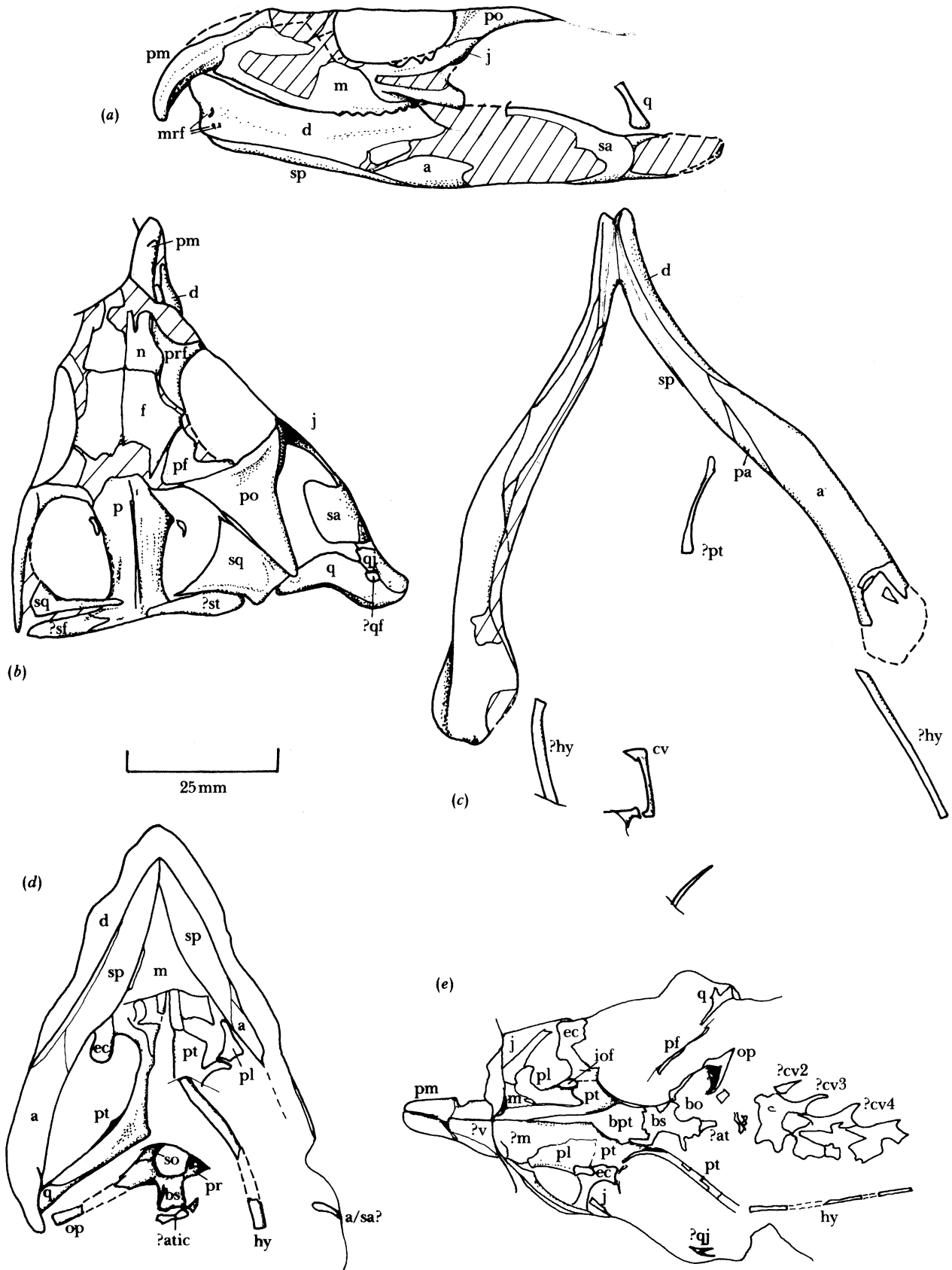


FIGURE 4. *Rhynchosaurus articeps*. (a-c) SHRBM in (a) left lateral, (b) dorsal and (c) ventral views. (d) BMNH R1237 in ventral view. (e) MANCH L7642 in ventral view; the bone is missing in many places.

The *jugal*, as in other rhynchosaurs, is a three-pronged element (figures 2*a-c*, 3*a-c*, 4*a*, 5*a-c*, 44*a, b*) and it is all well preserved except for the posterior process, which presumably ran back to meet the quadratojugal. The jugal is a low element, as in *Stenaulorhynchus*, and does not form a deep cheek area as in the late Triassic forms. The lateral ridge and cheek rugosity seen in *Hyperodapedon* and *Scaphonyx* are not so clearly developed in *R. articeps*.

The *quadratojugal* is known only from fragments (figures 3*a, b*, 44*b, d*) which suggest that it was a narrow element rather than the broad plate seen in late Triassic forms. Likewise, the descending process of the *squamosal* appears to be much narrower than in *Hyperodapedon* and *Scaphonyx*, where it is a broad plate-like element.

Dermal bones of the palate (figures 2, 4*c, e*, 5, 44, 45)

The tooth-plate of the maxilla is curved in side view (figures 2*a*, 3*a, b*, 4*a*, 5*a*, 44*b*), although Huene (1939, p. 502) said that it was 'beinahe gerade' (nearly straight). There are several large blood vessel or nerve canals (lateral alveolar foramina) in lateral view (figures 2*a*, 3*a, b*, 44*b*). The tooth-plate of the maxilla is seen in ventral view only in BMNH R1236, where a few teeth may be seen on either side of the dentary (figures 5*c*, 45*d*). In the restoration (figure 2*c*) it is assumed that the maxilla of *R. articeps* was like that of the Warwick rhynchosaur.

The paired *vomers* are restored (figure 2*c*) as in other rhynchosaurs, although only the posterior contact with the pterygoid is seen (figures 4*e*, 5*c*). In BMNH R1236 there appears to be a midline gap between the posterior parts of the vomers, whereas in other rhynchosaurs these two elements remain in contact along their entire length. However, in MANCH L7642 the gap does not extend so far forward, and it is assumed that BMNH R1236 is distorted.

The complex five-pronged *Palatine* is seen in ventral and dorsal views (figures 2*b, c*, 4*e*, 5*b, c*, 45*d*). The ventral view seen in MANCH L7642 (figure 4*e*) is hard to make out because of poor preservation, and because the specimen appears to be broken through just above the plane of the palate.

The *ectopterygoid* is not clearly seen in any specimens (figures 4*d, e*, 5*b, c*), but it appears to be typical of other rhynchosaurs (figure 2*b, c*). The *pterygoids* are long elements that meet in the midline (figures 2*c, d*, 4*e*, 5*d*, 44*g*), although they may have pulled apart in some specimens (figures 4*d, 5c*, 45*d*). The deep contact with the epipterygoid seems to be typical (figure 3*a*) as are the deep pits for the basiptyergoid processes (figures 2*c, d*, 5*d*, 44*g*), and the other pits and ridges seen in occipital view (figures 2*d*, 5*d*, 44*g*). Several authors (Woodward 1907; Huene 1929, 1938, 1939*b*; Chatterjee 1980) have noted 6–7 teeth on a short ridge on the pterygoid. This ridge is seen only in BMNH R1236 (?ptt, figure 5*c*), located near the midline, but individual teeth cannot be made out. It is not clear whether *R. articeps* had pterygoidal teeth or not (see below, §7).

Quadrate and epipterygoid (figures 2–5, 44)

The *quadrate* is a strong vertical element with a broad articular condyle (figures 2*a, c, d*, 3*a-d*, 44*a, b*), as in other rhynchosaurs. It is uncertain whether *R. articeps* had a quadrate foramen. Watson (1910, p. 156) states that, during preparation of MANCH L7642, he observed that there was no quadrate foramen. However, a quadrate foramen appears to be present in SHRBM 3 (?qf, figure 4*c*), and the Devon *Rhynchosaurus* has one.

The *epipterygoid* (figures 3*a-c*, 5*b*, 44*a, b*) has a typical broad flat base and a vertical rod-like

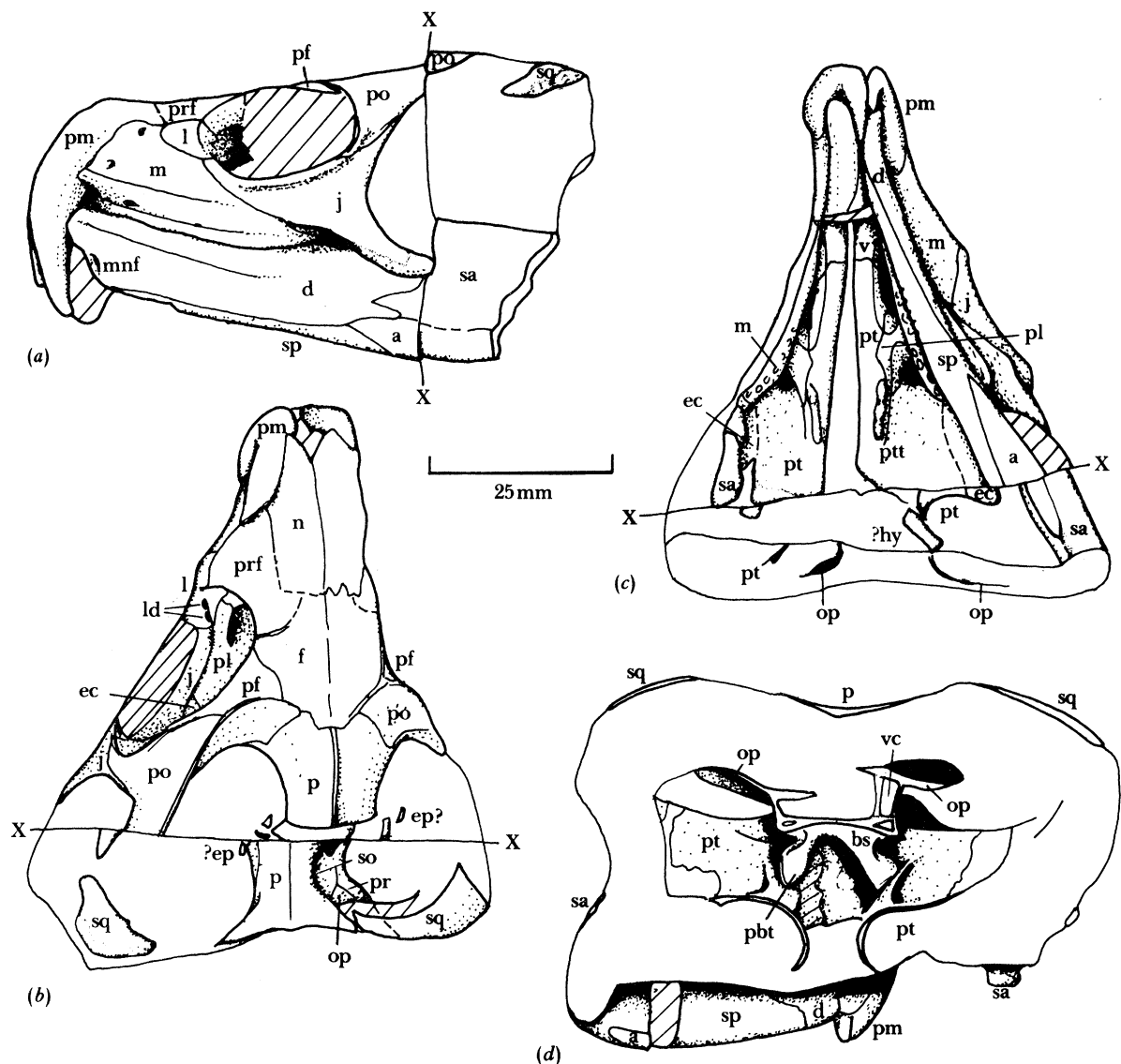


FIGURE 5. *Rhynchosaurus articeps*. BMNH R1236 in (a) left lateral, (b) dorsal, (c) palatal and (d) posterior views. Note that view (a) is a true lateral view and hence is foreshortened.

portion that is flattened and narrows rapidly as it rises to a possible loose contact with the side of the parietal.

Endocranium (figures 2–6, 44)

The ossified elements of the endocranium are not well preserved, but portions may be seen in SHRBM G132/1982; BMNH R1236, R1237; and MANCH L7642, and these have allowed tentative composite restorations (figure 6*e–g*). It is hard to illustrate the braincase of specimens (figures 3*a, d, 4d, e, 5d, 6a–d, 44b, c, f, g*) because only limited views are available, and most of these are rather incomplete or are located awkwardly.

The *basioccipital* seems to be typically rhynchosaurian, as does the *basisphenoid*. The latter has long basipterygoid processes (bpt, figures 2*d, 5d, 6b–g, 44g*) with paired carotid foramina (cf,

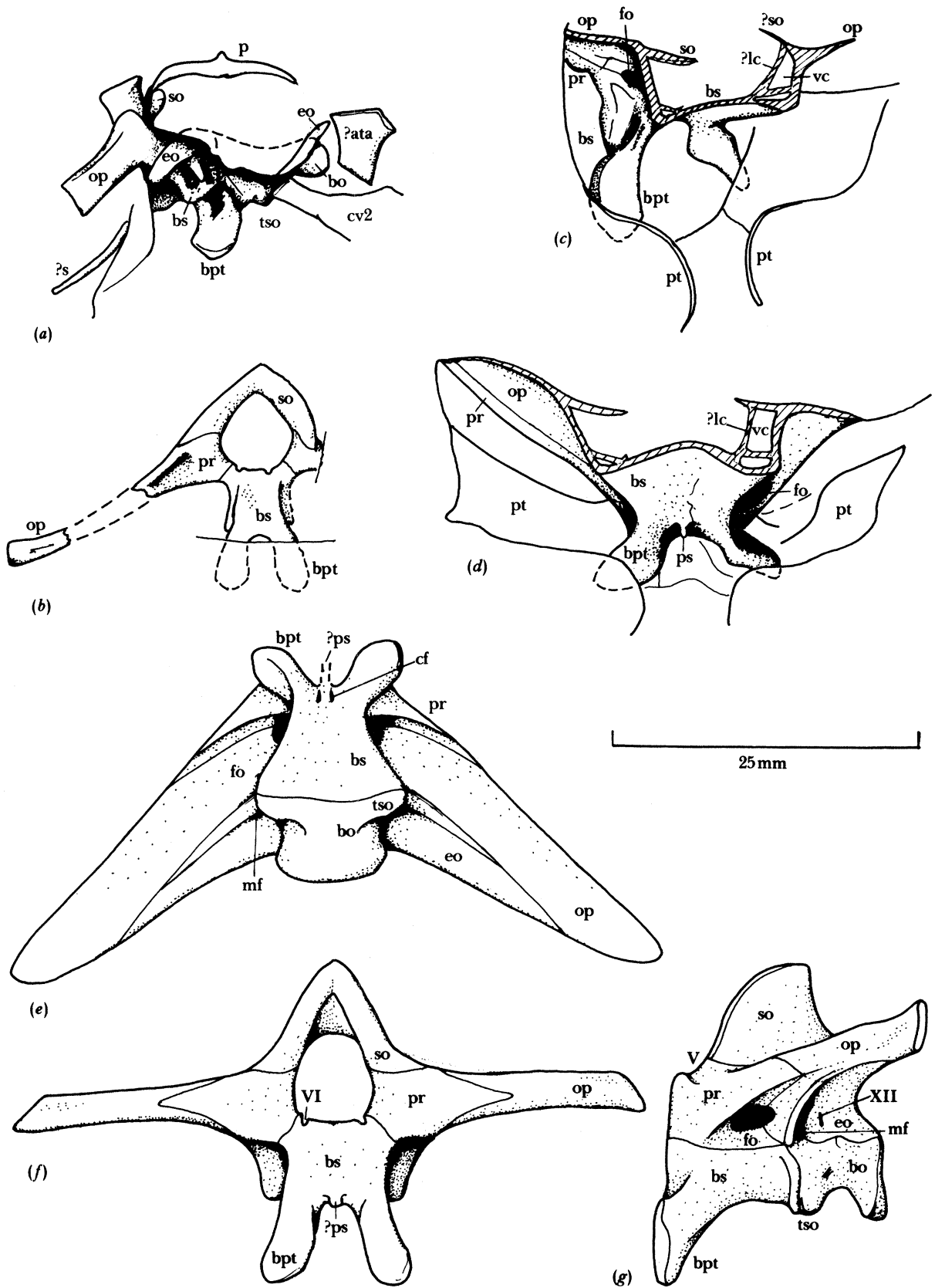


FIGURE 6. *Rhynchosaurus articeps*. The brain case, as seen in (a) posterior view of SHRBM G132/1982, (b) anteroventral view of BMNH R1237, (c) posterolateral and (d) posterior views of BMNH R1236. Restorations of the brain case in (e), ventral (f) anterior and (g) left lateral views.

figure 6*e*) between their proximal ends. The base of a long cultriform process (ps?, figure 6*d-f*) may have been associated with retractor fossae for the retractor bulbi eye muscles on the dorsum sellae, as in *Hyperodapedon* (Chatterjee 1974; Benton 1983), but these are not preserved here. At the top of the dorsum sellae are indications of lateral notches for the abducens nerve (VI, figure 6*b, f*), as in *Hyperodapedon* (Benton 1983, fig. 10*d*).

The paired *exoccipitals* (figures 2*d, 6a, e, g*) appear to be perforated laterally by one or two hypoglossal foramina (XII), and they form the posterior margin of the metotic foramen (mf). The full extent of the contact between the exoccipital and the opisthotic in the paroccipital process is not clear.

The *opisthotics* meet the basioccipital by a narrow pillar which forms the anterior margin of the metotic foramen (figure 6*e, g*). In a cross section through the braincase, the vestibular cavity (vc, figures 5*d, 6c, d, 44g*) is a rectangular space bounded laterally, and possibly also medially, by the opisthotic. If the medial 'pillar' is opisthotic, it would be the lagenar crest (?lc, figure 6*c*). It could alternatively be the prootic which bounds the anterior area of the otic capsule, but the cross section is probably placed too far back for that.

The *prootics* bear anterior incisures for the trigeminal nerve (V, figures 3*a, 6b-g, 44g*) and, like the *supraoccipital* (figures 2*d, 4d, 6b, f, g*), is typical of other rhynchosaurs.

A *stapes* may be present in SHRBM G132/1982, on the left-hand side (figures 3*d, 6a*). A long slender rod-like element is preserved beneath the opisthotic, running between the otic region of the braincase and the dorsal end of the quadrate. Unfortunately, the ends of this possible stapes are not preserved.

Hyoid apparatus (figures 4*c-e, 5c, 16, 44f, 45d*)

A number of specimens of *R. articeps* are preserved with strap-like pieces of bone lying between the mandibles in the throat region. These elements are 1–3 mm wide, up to 30 mm long, and fairly straight (hy?, figures 4*c-e, 5c, 16, 44f*). By analogy with *Scaphonyx* and *Hyperodapedon* (Benton 1983, pp. 637–638), these are interpreted as hyoid elements, as suggested by Owen (1863, p. 467). It cannot be said whether the present specimens represent ossified ventrally placed ceratobranchials, or ossified epiphyal portions of the ceratohyal, as is probably the case in *Scaphonyx* and *Hyperodapedon*. In the latter cases, however, the hyoid elements are more clearly in association with the posterior portion of the mandible, and could be interpreted as having once been in contact with the extracolumella (extrastapes). In *R. articeps*, three of the putative hyoid elements are straight and located behind the mandible (figures 4*c, e, 16*; ceratobranchials?) and two are located further forward, just beneath the pterygoid and posterior mandibular region (figures 4*d, 5c*; ceratohyals?).

3.3. *Mandible* (figures 2–5, 7, 15*b, 16, 44, 45*)

The mandibles of *R. articeps* are fairly well preserved in a number of specimens: SHRBM G132/1982, 3; BMNH R1236, R1237; an impression of a mandible is seen in BMNH R1239. Some aspects of the medial view of the mandible are seen in BMNH R1236. The lower jaw is a boat-shaped element that rises to a point in front, which contacts the premaxilla and extends into a relatively long retroarticular process behind the glenoid fossa (figures 2*a, 4a*).

The *dentary* forms the anterior two thirds of the mandible in lateral view (figures 2*a, 3a*). This is similar to the proportion in *Hyperodapedon* and *Scaphonyx*, but differs from *Stenaulorhynchus*, in which the proportion is about one half. Laterally, there are several large mandibular foramina

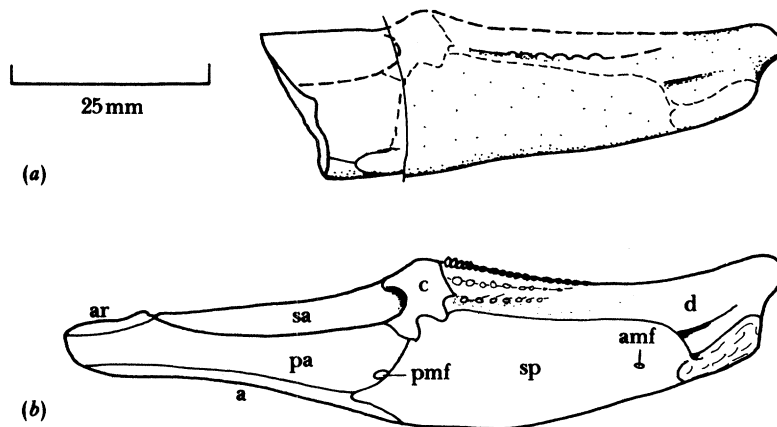


FIGURE 7. *Rhynchosaurus articeps*. Left mandible, in medial view, (a) of BMNH R1236 and (b) restored from that specimen, and from others.

for blood vessels and nerves (mnf, figures 2a, 4a, 5a), in very much the same arrangement as in other rhynchosaurians. In medial view (figure 7), the dentary bears two or more rows of teeth, but details of the teeth are better seen in the Warwick rhynchosaur (see §§4.3 and 7).

The *splenial* (figures 2a, 3a, b, 4a, c, 5a, c, 7, 44b) is typical of other rhynchosaurians. The *coronoid* is seen only in BMNH R1237, where the anterior tip is just exposed on the right-hand side.

The *angular* and *surangular* (figures 2a, 3a-d, 4a, d, 5a, c, 7, 44a, b, f) are typically rhynchosaurian, even in details such as the thin vertical sheet within the adductor fossa formed at the contact of the surangular and the prearticular (figures 3b, 44b), as in *Hyperodapedon*. It is uncertain whether the damaged area near the back in SHRBM G132/1982 is equivalent to the posterior supra-angular foramen (?psaf, figure 3a).

The anterior tip of the prearticular, where it meets the splenial and angular, is seen in SHRBM 3 (figure 4c). The posterior region is seen in a disarticulated state in SHRBM G132/1982 (figure 3b, d), with a long midline facet for contact with the surangular, and a flat-faced posterior termination. The *articular* is also seen unclearly (figures 2a, 3a-d, 15b, 16, 44a, b), and it appears to be bounded ventrally by the surangular (and the prearticular?).

3.4. Axial skeleton

Vertebral column (figures 3, 4, 8-17, 44, 45)

Several series of vertebrae of *R. articeps* are preserved, but none is complete. Partial series of presacral vertebrae are seen in a number of specimens (SHRBM 1-6; BMNH R1237/R1238, R1239, SHRCM G3851, G07537-8; BATGM M20a/b); sacrals in SHRBM 5, 7; BMNH R1239; SHRCM G07537-8, and BATGM M20a/b; and caudals in SHRBM 7; BMNH R1240; SHRCM G07537, and BATGM M20a/b. These indicate that *R. articeps* had 25 presacral vertebrae, as Huene (1929, p. 41) suggested (8 cervicals, 17 dorsals), 2 sacral vertebrae, and more than 9 caudal vertebrae (probably 25 to 30). The vertebrae of *R. articeps* are hard to study in detail because they are usually broken through at random, they are small, and they are soft in relation to the sediment, so that they cannot be prepared out very successfully.

The *atlas* is not well represented. A probable atlas centrum is seen just below the braincase in BMNH R1237 (figures 4d, 8b, 44f). It is as broad as the base of the braincase and

rectangular in cross section. Directly above this element, on the other side of the block, are the two atlantal arches, apparently in about the correct position in relation to the skull roof (figure 44c), and the atlas intercentrum and axis (figure 8b). A possible atlantal arch is also seen in SHRBM G132/1982 (?ata, figures 3d, 6a, 8a). The exact shape of these tiny atlantal arches cannot be made out, but they appear to resemble those of *Stenaulorhynchus* (Huene 1938, pl. 3, fig. 1) and *Hyperodapedon* (Chatterjee 1974, fig. 15b; Benton 1983, fig 19g). Poor remains of probable atlantal elements (intercentrum, centrum?) are preserved in ventral view behind the basioccipital in MANCH L7642 (figure 4e).

The *axis* (figures 3d, 4e, 8a, b, 44c) has a nearly circular centrum in cross section, and there is a long prezygapophyseal, and a curved postzygapophyseal, process. These were probably united to form a broad fan-like neural spine, as in other rhynchosaurs, but it is not clear whether this spine was formed largely from bone or cartilage. Rib attachments, and facets for the axis intercentrum cannot be seen in the present material. However, there is a small facet on the prezygapophyseal region for the atlas arch (ata, figure 8a), and another facet on the anterior lateral margin of the centrum, probably for the atlas centrum (atce, figure 8a), as in *Hyperodapedon* (Benton 1983, fig. 19a-c).

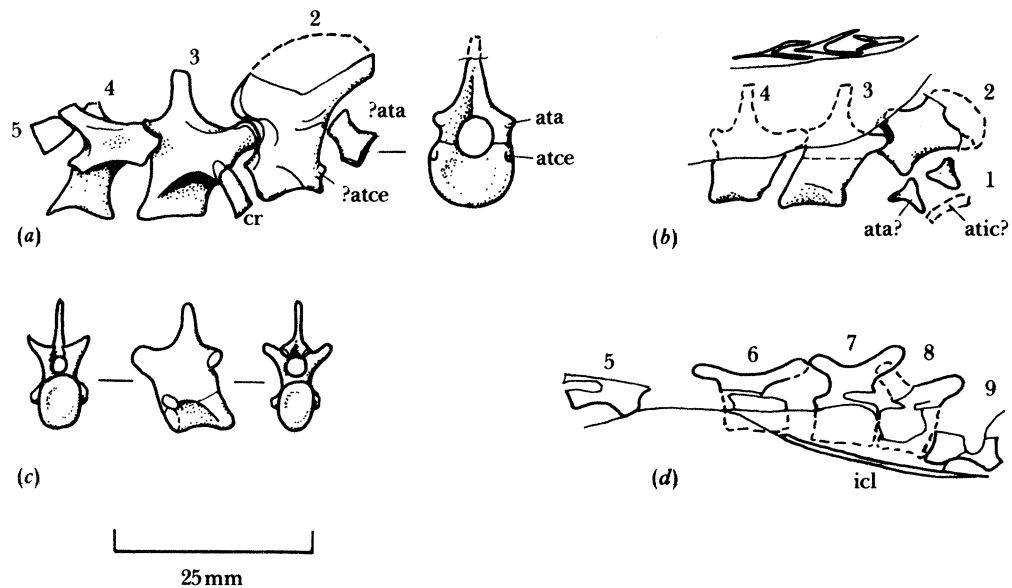


FIGURE 8. *Rhynchosaurus articeps*. Cervical vertebrae. (a) SHRBM G132/1982 (nos. 2-5) in right lateral view; (b) BMNH R1237 (nos. 1-4), in right lateral view; (c) restoration of cervical vertebra 3, based on the last two specimens, in anterior, left lateral and posterior views; and (d) BMNH R1238 (nos. 5-9), in left lateral view.

The other *cervical vertebrae* (figures 3d, 4e, 8a, b, d, 10a, 14, 15a, 16, 44c) are also poorly represented. Cervical vertebra 3 (figure 8c) has a deep centrum, relatively short zygapophyses which stand at an angle of 40-60° above the horizontal, and a short peg-like neural spine. A partial cervical rib is apparently present (figures 3d, 8a); this indicates the location of a large diapophysis near the anterior edge of the vertebra. The parapophysis cannot be seen, but it probably lay below, on the anterior margin of the centrum (figure 8c), as in other rhynchosaurs. The neural spine is lost in cervicals 4(?) and 6-8 at least, and these vertebrae

have broad pre- and postzygapophyses that appear to be orientated nearly vertically, as in *Hyperodapedon*. The centra of the cervical vertebrae are relatively longer than those of the larger *Stenaulorhynchus*, *Scaphonyx*, and *Hyperodapedon* (ratio of length:height is 1.0–1.5, compared with 0.7–1.0 in the large forms).

The *dorsal vertebrae* are present in a number of specimens, but generally in poor condition (figures 10*a–c*, 11*a, d*, 14, 15*b*, 16, 17*a*). The centrum is roughly circular in end view, and it seems to have a slight ventral keel (figure 16). As in other rhynchosaurs, the breadth of the dorsal centra is roughly constant, but the length increases in the mid-trunk region, while those in the shoulder and sacral regions are shorter (figure 9). The rib articulations are not well preserved, but probably both parapophysis and diapophysis were just distinguishable in the

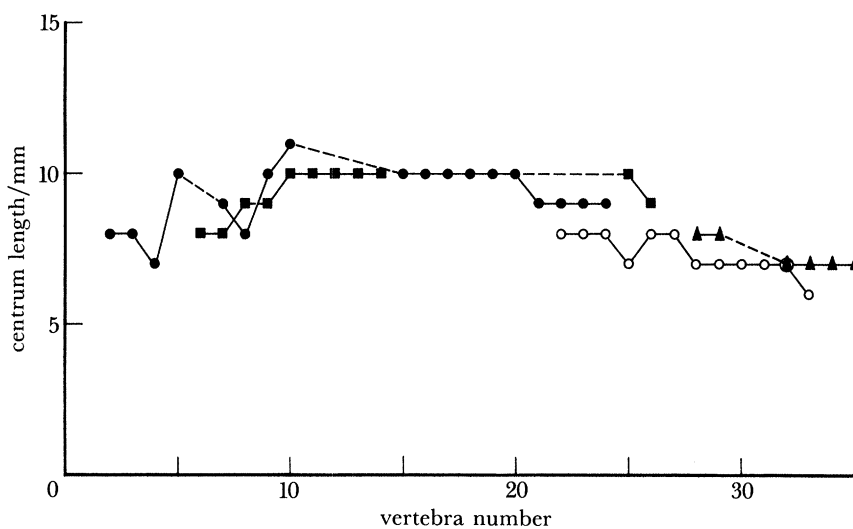


Figure 9. *Rhynchosaurus articeps*. Centrum lengths of vertebrae (measured in the midline, in millimetres) of BMNH R1237–R1238 (solid circles), SHRBM 4 (squares), BATGM M20a/b (open circles) and SHRBM 7 (triangles).

anteriormost two or three dorsals, as in *Stenaulorhynchus*. The oval diapophysis is apparently projected horizontally on a broad flattened transverse process in mid and posterior dorsals at least (figure 10*b, c*). The zygapophyses are broad and rounded in dorsal view, but they cannot be studied in detail. The neural spines seem to be about the same height throughout the dorsal series (7 mm in BMNH R1239) (figure 10*a*), but they seem to be broader in the middle of the trunk than in front or behind (3 mm in presacral 9, 6 mm in presacral 20 in BMNH R1239; ?3 mm in presacral 25 in BATGM M20a/b) (figure 10*a, c*).

The two *sacral vertebrae* are seen in partial preservation in two specimens (figures 11, 45*b, c*). Both vertebrae appear to have centra of approximately the same length. The zygapophyses are large, and are placed at a high angle (*ca.* 60°) above the horizontal. The neural spines are similar to those of the last presacrals and the first caudals, and they are set well back over the postzygapophyses. The second sacral vertebra has a longer neural spine, in an anteroposterior direction, than the first.

The sacral ribs are probably separate from the vertebrae, as in other rhynchosaurs, but they appear to be firmly fused to the transverse processes. The ribs of the first sacral vertebra are longer than those of the second (figure 11). The dorsal part of the rib is broad (figures 11*a–c*, 12*a, 45b, c*), but in a horizontal cross section (figure 11*d*) it can be seen that the rib is greatly

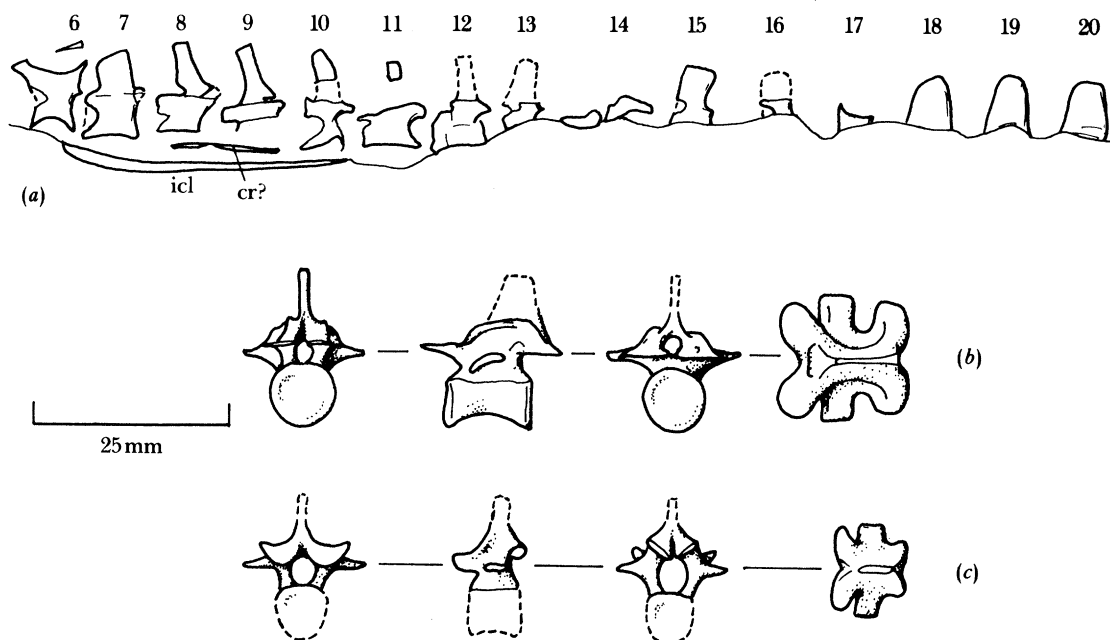


FIGURE 10. *Rhynchosaurus articeps*. Dorsal vertebrae. (a) BMNH R1239 (presacrals 6–20), in left lateral view; (b) restoration of presacral vertebra 15 (anterior dorsal), based on SHRBM 2; and (c) restoration of presacral vertebra 25 (posterior dorsal), based on BATGM M20a.

constricted in the middle, as in *Hyperodapedon* (Benton 1983, p. 655, fig. 24e). The second sacral rib, like that of the late Triassic rhynchosaur, does not appear to have the backwards-pointing spine seen in *Stenaulorhynchus* (Huene 1938, pl. 4, fig. I–II).

The *caudal vertebrae* (figures 11a, b, d, 12, 45b, c) are incompletely known. By comparison with other rhynchosaur, it is assumed that *R. articeps* had 25–30 caudals. The centra of the first five or so caudal vertebrae seem to be about the same size as the sacrals, but the centra become lower, while maintaining a similar length, in more posterior caudals (figure 12c, g). In ventral view (figures 11d, 12e), the centra of anterior caudal vertebrae at least are laterally constricted, giving rise to a ventral ‘keel’. The neural spine is narrow and tall, and it increases in height from the first to the sixth caudal (5–12 mm) (figures 11a, 12a, d, f), then remains the same for the next seven or so caudals, before decreasing to a 3 mm ‘spike’ in the mid caudals (figure 12c, g). The caudals of *R. articeps* resemble those of *Stenaulorhynchus*, but differ from those of *Hyperodapedon* and *Scaphonyx*, which have low neural spines. The forwards ‘slope’ of the caudal vertebrae (figure 12d), with a long prezygapophysis and a short postzygapophysis, and the long transverse processes in anterior caudals are typical of rhynchosaur.

Ribs (figures 3d, 8a, 10a, 13–16, 17a)

Ribs are preserved in a number of specimens, of which SHRBM 3, 4; BMNH R1238 and R1239 were most useful for restoration of the overall form. Ribs are present on all presacral vertebrae, except probably the atlas and axis, and on the anterior caudal vertebrae. The cervical and anteriormost dorsal ribs were probably double-headed, and all others single-headed, as in other rhynchosaur, but the articular heads are not well preserved in any specimens.

Cervical ribs are represented only by fragments (figures 3d, 8a, 10a), none of which is good

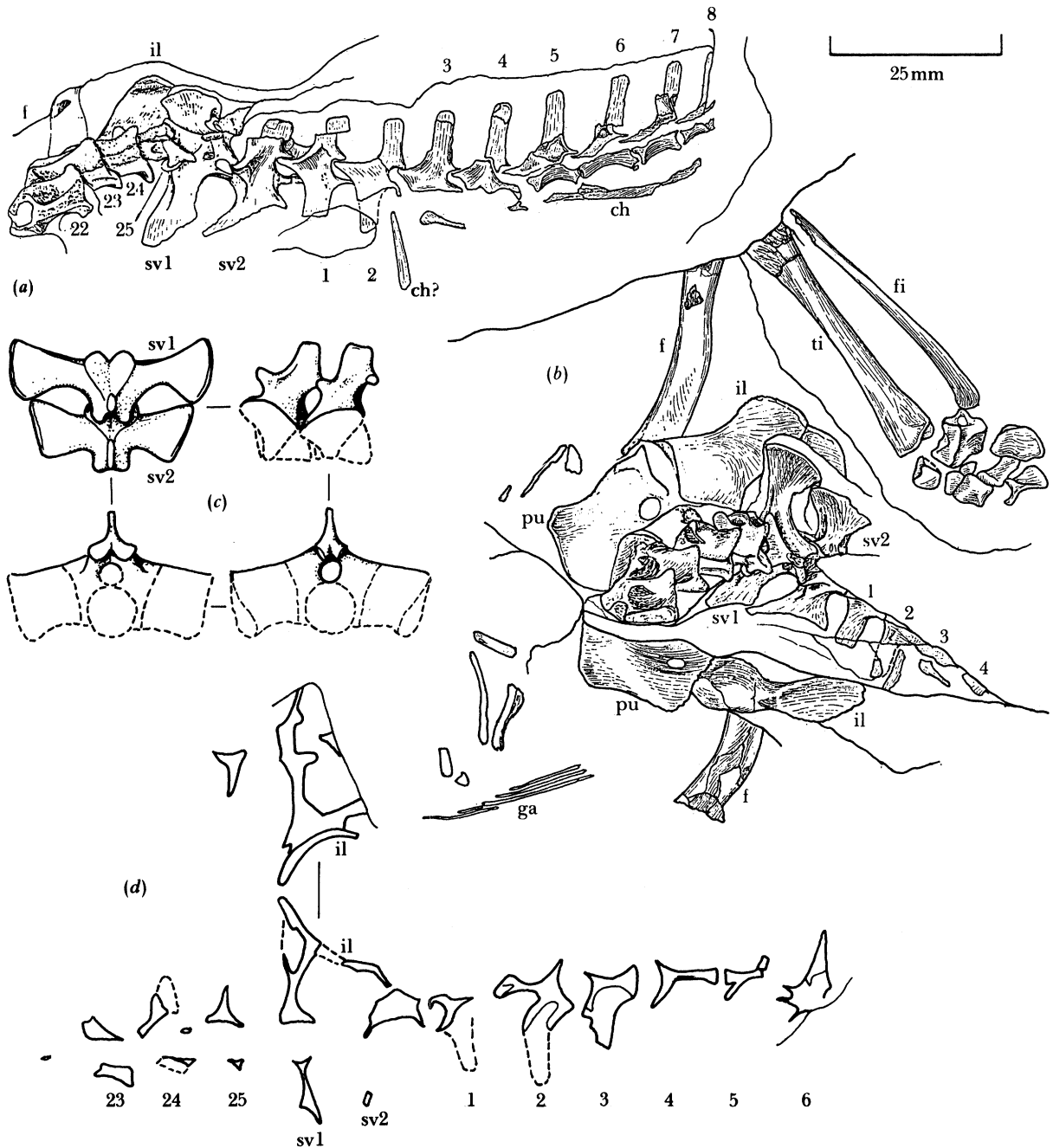


FIGURE 11. *Rhynchosaurus articeps*. Sacral vertebrae. (a, b) BATGM M20a/b, in (a) left dorsolateral and (b) dorsal views, showing dorsal vertebrae (presacrals 22–25), sacral vertebrae 1 and 2, and caudal vertebrae 1–8; (c) restoration of sacral vertebrae 1 and 2, in dorsal, lateral, anterior, posterior views, based on BATGM M20a/b, and SHRCM 7 (for the posterior view); (d) SHRCM G07357–8, showing dorsal vertebrae (presacrals 23–25), sacral vertebrae 1 and 2, and caudal vertebrae 1–6, in ventral view. (Parts (a) and (b) were drawn by A. D. Walker.)

enough for restoration. The dorsal ribs vary considerably in length (figure 13). The anterior two ribs at least are broad and long, and they run back in close proximity to each other, and overlap the more typical ribs behind (figures 15, 16). They are known otherwise only in *Hyperodapedon gordonii* (Benton 1983, figs 27, 40). The remaining dorsal ribs increase in length

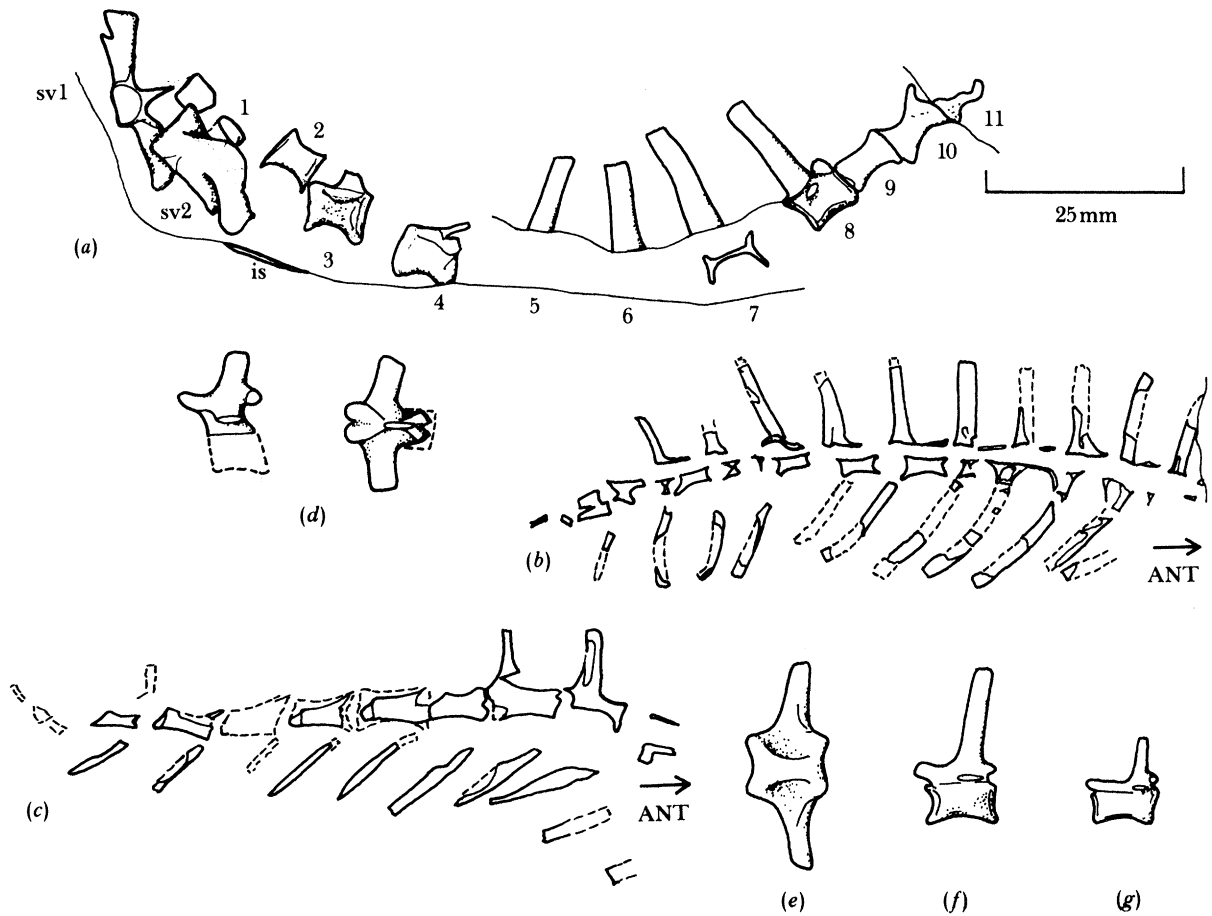


FIGURE 12. *Rhynchosaurus articeps*. Caudal vertebrae. (a) SHRBM 7, showing sacral vertebrae 1 and 2, and caudal vertebrae 1-11, mostly in left lateral view; (b) SHRCM G3851, showing 12 or 13 anterior and mid-tail caudal vertebrae, in right lateral view; (c) BMNH R1240, showing 8 or 10 mid-tail caudal vertebrae in right lateral view; (d) restoration of caudal vertebra 1, in left lateral and dorsal views, based on BATGM M20a/b; (e) restoration of caudal vertebra 2 in ventral view, based on SHRCM G07357; (f) restoration of caudal vertebra 6 in left lateral view, based on SHRBM 7 and BATGM M20a; and (g) restoration of a mid-caudal vertebra, about number 15-20, based on BMNH R1240.

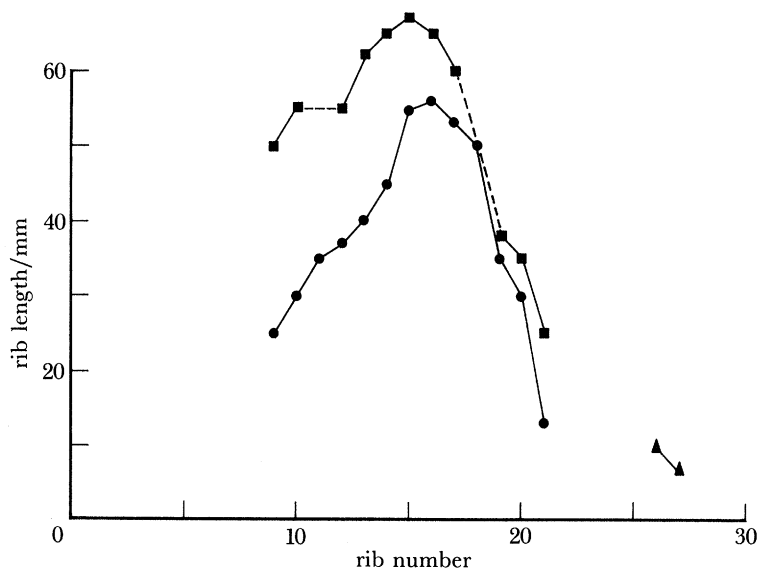


FIGURE 13. *Rhynchosaurus articeps*. Lengths of the ribs, measured in millimetres and averaged for left and right, where possible, of SHRBM 4 (circles), BMNH R1239 (squares) and BATGM M20a/b (triangles).



FIGURE 14. *Rhynchosaurus articeps*. SHRBM 4, a partial skeleton, lacking the skull, the tail, and the limbs of the left side, in dorsal view of the ventral slab.

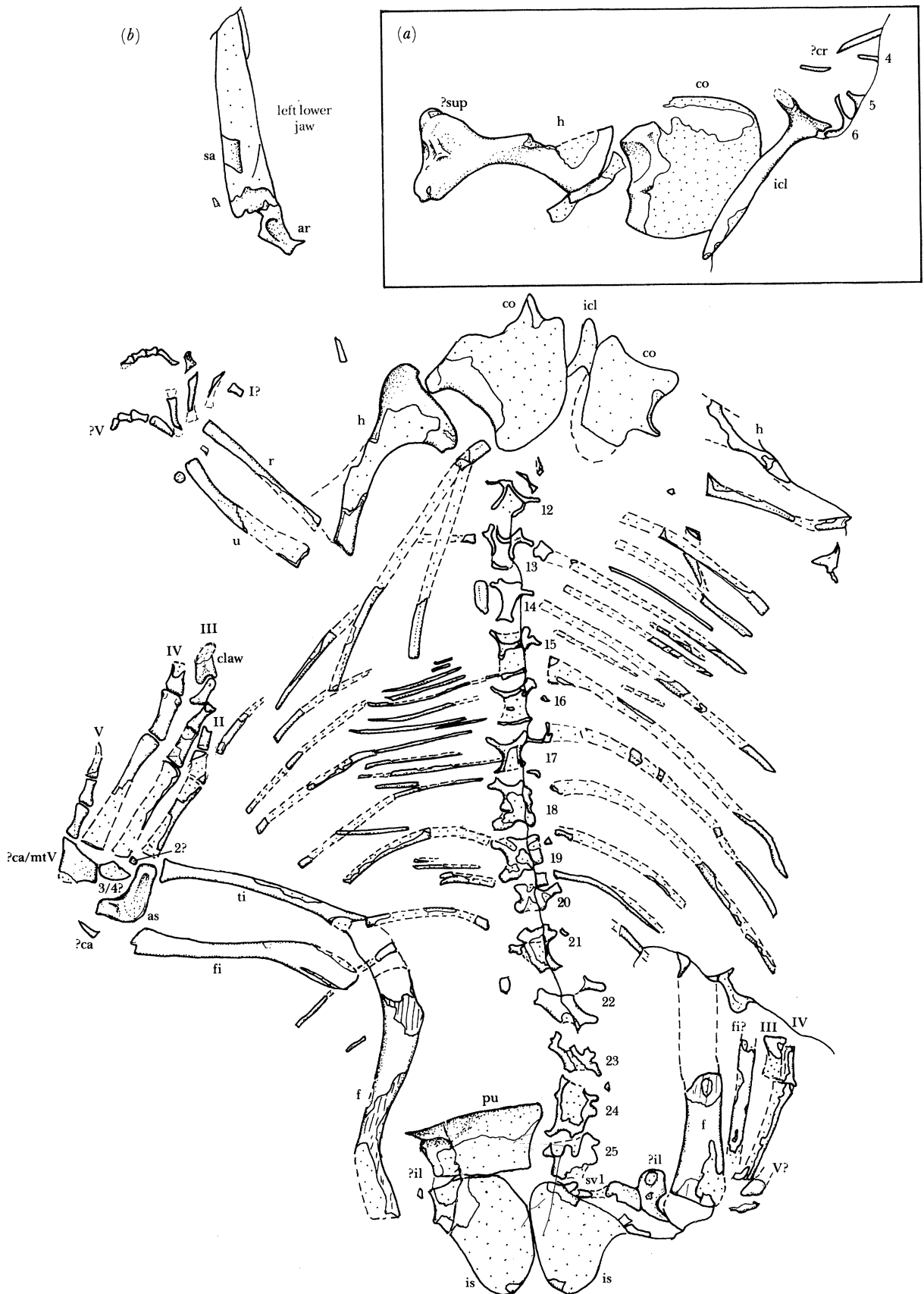


FIG. 15. *Rhynchosaurus articeps*. BMNH R1239, a partial skeleton, lacking the skull, the tail, and parts of the limbs, in ventral view of the anterior part of the dorsal slab (a) and dorsal view of the ventral slab (b).

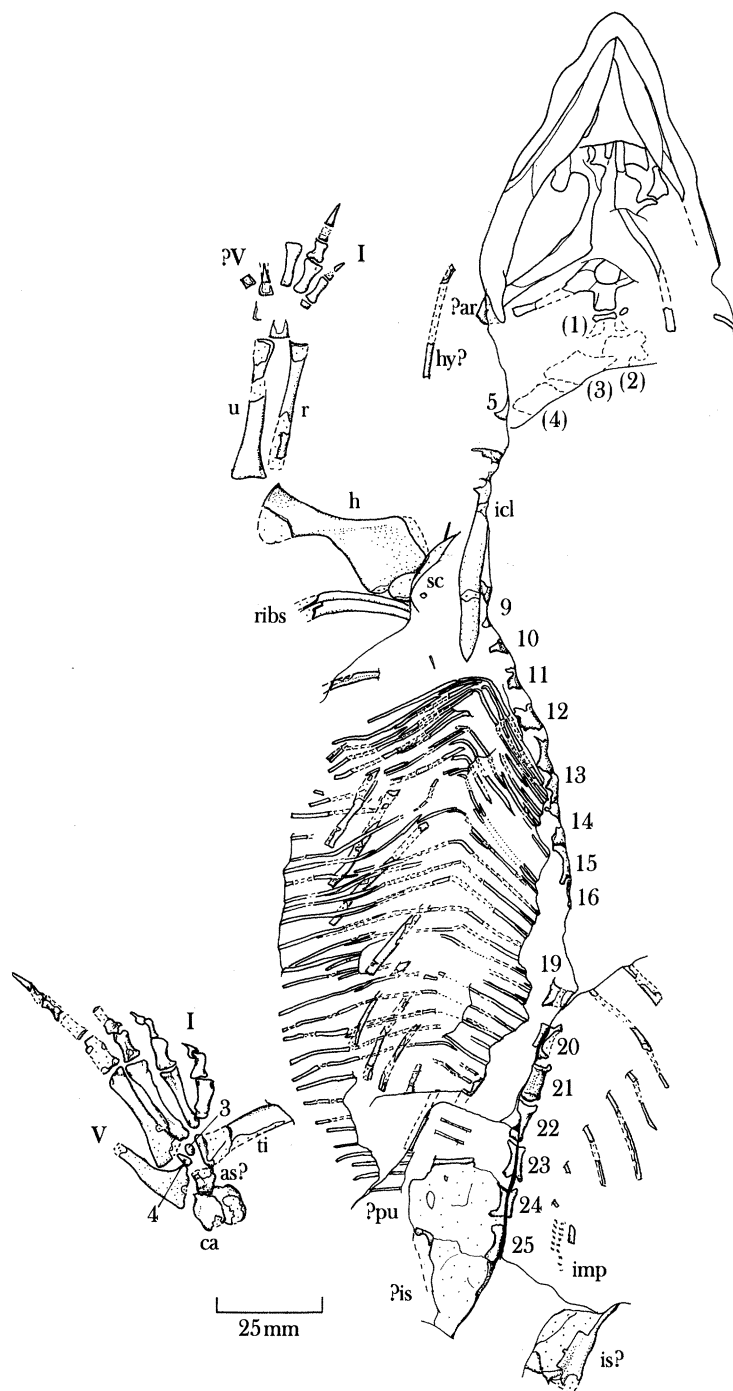


FIGURE 16. *Rhynchosaurus articeps*. BMNH R1238, and R1237 (skull), a partial skeleton lacking the tail and the limbs of the left side, in ventral view.

to the 15th or 16th, and then decrease backwards (figure 13). In all dorsal ribs the shaft is flattened, and it is marked by a midline longitudinal groove along the ventromedial face (figure 17 *a*), as Owen (1842 *c*, p. 364; 1863, p. 467) noted, and a corresponding elevated ridge along the dorsolateral face (figures 15, 17). The articular head of mid and posterior dorsal ribs is up to twice as broad as the shaft, when it is preserved, and the distal ends are also expanded, but not to the same extent (figures 14–16).

Chevron bones (figures 11 a, 12 b, c, 45 c)

Long chevron bones, associated with caudal vertebrae, are 13–14 mm long and *ca.* 2 mm wide, with squared distal ends. One apparently longer chevron (figures 11 a, 45 c) may consist of two overlapping elements. The articular ends are less clearly seen, but they were probably bifurcated to form a Y-shape, as in other rhynchosaurs, which attached at the base of the centra between caudal vertebrae. In life, the chevrons probably run back beneath one or two vertebrae, as in *Stenaulorhynchus* and *Scaphonyx*, but not three or four, as in *Hyperodapedon*.

Gastralia (figures 14–16)

In the most complete example (figure 16) there are 35 or more rod-like gastralia (not 23–24, as Huene (1929, p. 41) suggested) that form a continuous abdominal armour from the posterior tip of the interclavicle to the anterior tip of the pubis. The anterior gastralia form a distinct V-shape with the apex pointing forwards. The angle declines backwards, and the gastralia 20+ are nearly straight. The most posterior gastralia are not clear, but they might form a slight backwards-pointing V-shape, as in *Hyperodapedon*. Each gastralium has a central element, and lateral portions that overlap well towards the midline, as is clearly seen in BMNH R1238 (figure 16) and SHRBM 5. The central element does not appear to be divided in the midline, but the preservation is not good enough to be sure throughout the series. The gastralia are of approximately uniform width throughout, and they are closely spaced, with about three for every vertebra and rib. The gastralia do not contact the ribs, and there is no evidence of an ossified sternum. Gastralia are poorly known in most rhynchosaurs, but *H. gordonii* has a similar arrangement of *ca.* 50 gastralia spaced at three per vertebra.

3.5. *Appendicular skeleton**Shoulder girdle (figures 14–18, 45 a)*

Parts of the shoulder girdle are preserved in SHRBM 2, 3, 4, 6; BMNH R1238 and R1239, but in all cases the separate elements are disarticulated and usually poorly preserved.

The *scapula* as typically rhynchosaurian (figures 14, 17 a, c, 45 a). The anterior margin is thickened, possibly as a small acromion process against which the clavicle rested. Owen (1842 c, pp. 364–5, pl. 6, fig. 8) mistakenly showed a long anterior spine on the lower margin of the scapula in SHRBM 2.

The *coracoid* (figures 15, 17 b, c) is also typical, and both elements nearly meet in the midline on either side of the interclavicle (figure 15 b). There is a sizeable coracoid foramen in front of the glenoid facet as in most rhynchosaurs, although *Hyperodapedon* and *Scaphonyx* have a coracoid incisure that reaches the dorsal margin.

The *interclavicle* (figures 8 d, 10 a, 14, 15 a, 16, 17 b–d) has a pocket on either side of the anterior cross-bar into which the clavicles would have inserted, but the latter elements are not clearly preserved in any specimen, except for a possible fragment (?cl, figures 17 a, 45 a). Huxley (1887, pl. 27, fig. 3) labelled a narrow strip of bone in front of the coracoid in BMNH R1239 as 'cl', but this is probably part of the coracoid (co, figure 15 a). Huene (1929, p. 41) also tentatively identified a clavicle in BMNH R1238, but he suggested a different bone: 'the long curved element which...lies behind the right humerus'. This is probably the pair of bones identified here as anterior dorsal ribs (ribs, figure 16).

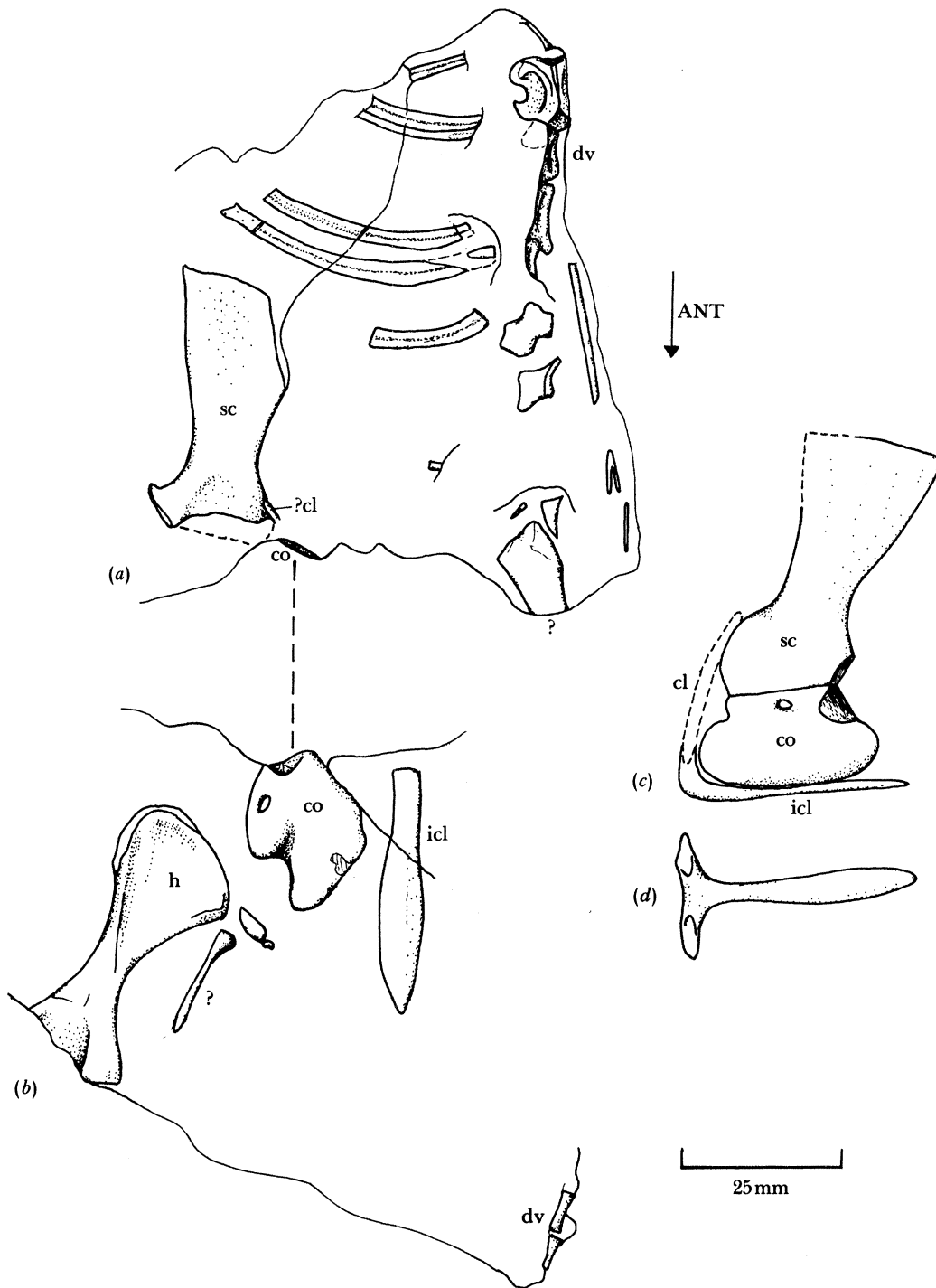


FIGURE 17. *Rhynchosaurus articeps*. The shoulder girdle. (a, b) SHRBM G134/1982 (paralectotype) in dorsal and ventral views, showing dorsal vertebrae, ribs, and elements of the shoulder girdle and forelimb; (c) restoration of the shoulder girdle in left lateral view, based on SHRBM G134/1982 and 4; (d) restoration of the interclavicle in ventral view, based on BMNH R1239.

Forelimb (figures 14–18)

The forelimb is preserved fairly completely in a number of specimens: SHRBM 2, 3, 4, 6; BMNH R1238 and R1239, and these have allowed a generalized reconstruction (figure 18*b, c*).

The *humerus* (figures 14–16, 17*b*, 18) has the typical broad ends and narrow shaft seen in all rhynchosaurs. The deltopectoral crest is a narrow anteroventral plate at right angles to the proximal end (dpc, figures 17*b*, 18*b*). The shaft is elliptical in cross section, and the long axis of the ellipse changes its orientation as the shaft twists along its length. The thin supinator crest (sup, figures 15*a*, 18*b, c*) on the anterior margin of the ectepicondyle is like that of *Hyperodapedon*.

The *radius* (figures 14, 15*b*, 16, 18*a, c*) seems to be the same length as the ulna in some specimens (BMNH R1239), in others shorter (SHRBM 4), or even longer (SHRBM 6; BMNH R1238). There is no regular pattern in other rhynchosaurs: in *Hyperodapedon* the radius is slightly shorter than the ulna, in *Stenaulorhynchus* both elements are about equal in length, and in *Mesosuchus* the radius is slightly longer than the ulna. As preserved, the radius seems to be flat or elliptical in cross-section.

The *ulna* (figures 14, 15*b*, 16, 18*a, c*) is heavier than the radius, and it has a curved medial edge and a straight lateral one. Owen (1842*b*, p. 152; 1842*c*, pp. 366–7, pl. 6, fig. 7) described a radius and ulna in a specimen that is now lost.

The *wrist* region is poorly known: a few carpals are preserved (figures 14, 15*b*, 16, 18*a*), but their identification is uncertain. The three elements preserved in SHRBM 6 (figure 18*a*) are identified tentatively as ulnare, intermedium, and distal carpal 4, as noted by Woodward (1907). The wrist is restored (figure 18*c*) with three proximal carpals and four distal carpals (1–4). The wrist of other rhynchosaurs is also poorly known, and only of limited help in restoration, but *Rhynchosaurus* probably had a radiale that attached firmly to the distal end of the radius, as in *Hyperodapedon* (Benton 1983, fig. 31*f*) and *Mesosuchus* (Haughton 1921, pl. 3, fig. 5). Rhynchosaurs seem to have retained three proximal carpals, but they may have lost the fifth distal carpal.

The five *metacarpals* are present in several specimens (figures 14, 15*b*, 16, 18*a, c*), and they vary in length, metacarpals II–IV being at least twice as long as I and V. Metacarpal V is not as short as I, although Huene (1929, p. 41) stated the opposite. The *phalangeal series* may be reconstructed as 2.3.4.5.3, as Woodward (1907) noted (figure 18*c*), and this differs from the pattern of 2.3.4.5.4 in *Hyperodapedon* and *Scaphonyx*, the only other rhynchosaurs in which these values can be established. In all digits the distal phalanges are shorter than the proximal ones, and the claws are narrow and high-sided. Claws I and V seem to be shorter than the others. The digits are relatively long when compared with other rhynchosaurs, but this is probably a scale effect that reflects the small body size of *R. articeps* compared with most of its relatives.

*Pelvic girdle (figures 11, 12*c*, 14–16, 19, 45*b, c*)*

Elements of the pelvis are preserved in SHRBM 4, 5, 7; BMNH R1238, R1239, R1241; SHRCM G07357–8; and BATGM M20a/b. Restorations were attempted (figure 19*d, e*) on the basis of BATGM M20a/b and BMNH R1239 (ischia) in particular, but these may be inaccurate as most of the material is incomplete and not preserved in three dimensions.

The *ilium* (figures 11*b, d*, 15*b*, 19*b–e*, 45*b*) appears to have a nearly straight dorsal margin,

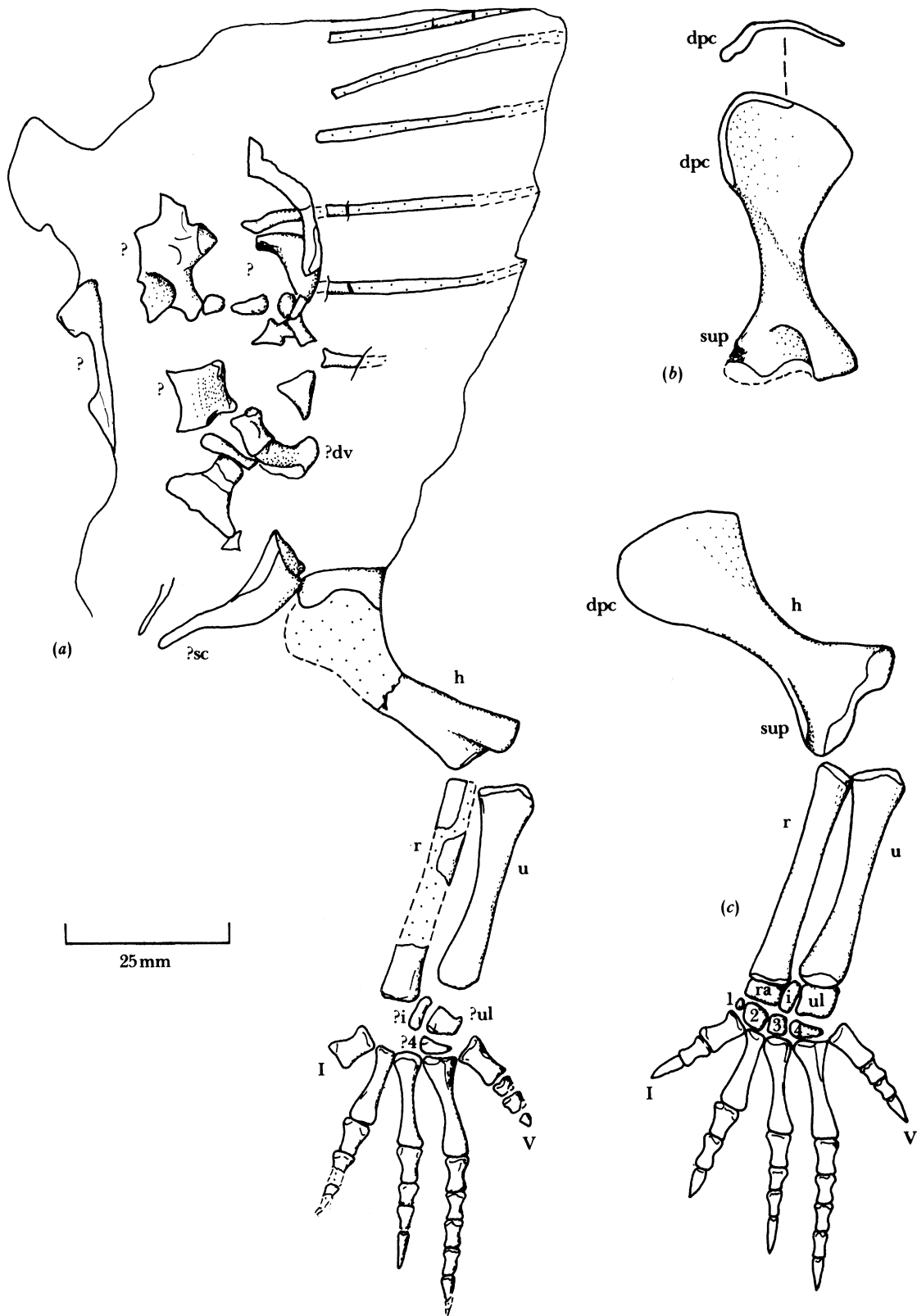


FIGURE 18. *Rhynchosaurus articeps*. The forelimb. (a) SHRBM 6, showing dorsal vertebrae, ribs, and right forelimb in posteroventral view; (b) restoration of the right humerus in posteroventral and proximal views, based on SHRBM G134/1982 and BMNH R1239; (c) restoration of the right forelimb in anterodorsal view.

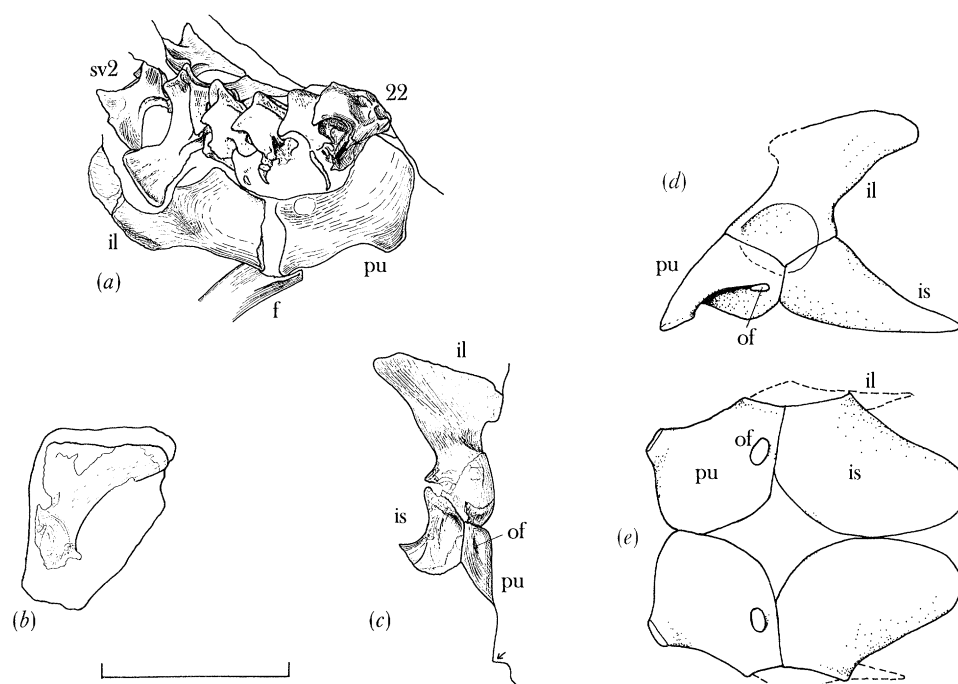


FIGURE 19. *Rhynchosaurus articeps*. The pelvic girdle. (a) BATGM M20a in dorsal view, showing the right pubis and ilium; (b, c) BATGM M20a/b, showing the left ilium in lateral view (b), and the left ilium, ischium and pubis in medial view (c); (d, e) restorations of the pelvis in left lateral (d), and ventral (e) views, based on BATGM M20a/b. In (c), the small arrow marks the limit of the pubis. The ventral view (e) shows the pubes and ischia rather flattened out, as in the specimen. (Parts (a-c) were drawn by A. D. Walker.)

a long posterior process, and probably a short anterior process, as in other rhynchosaur. In medial view (figure 19a, c), there appear to be facets for the sacral ribs. Owen (1842b, p. 152; 1842c, p. 367, pl. 6, fig. 10) described a supposed ilium in a specimen that is now lost. It could equally well be a partial pubis with its processus lateralis, but the figure is hard to interpret.

The *pubis* (figures 11a, b, 14, 16, 19a, c-e, 45b, c) seems to be as long as it is broad, on the basis of BATGM M20a/b, whereas in other rhynchosaur it is broader than long. The medial and posterior edges of the pubes bound a diamond-shaped space, as in *Hyperodapedon*, and there are large obturator foramina close to the posterior margins. The size of the foramen is hard to assess since the bone is thin in that area, and it might in fact have been smaller than is shown.

The *ischium* (figures 15b, 16, 19c-e) is a short rounded element as in other rhynchosaur.

Hindlimb (figures 11b, 14-16, 20, 45b)

The hindlimb is preserved in several specimens of *R. articeps*: SHRBM 3, 4, 5, 7; BMNH R1238, R1239, R1240/R1241; and BATGM M20a/b. The most useful specimens for reconstruction were BMNH R1238 and R1239, and BATGM M20a/b, but even in these cases the bones are incomplete and offer a largely two-dimensional appearance.

The *femur* (figures 11b, 14, 15b, 20a, 45b) is a sigmoidally curved bone, but its articular ends are unknown. There is a clear twist in the shaft, which is oval in cross section proximally, but more nearly circular towards the distal part of the shaft. The slight process on the medial margin of the femur (?pife, figure 20a) is probably the structure in *Stenaulorhynchus*, interpreted by Huene (1938, p. 104, pl. 10, fig. 1a) as the site of insertion of part of the M.

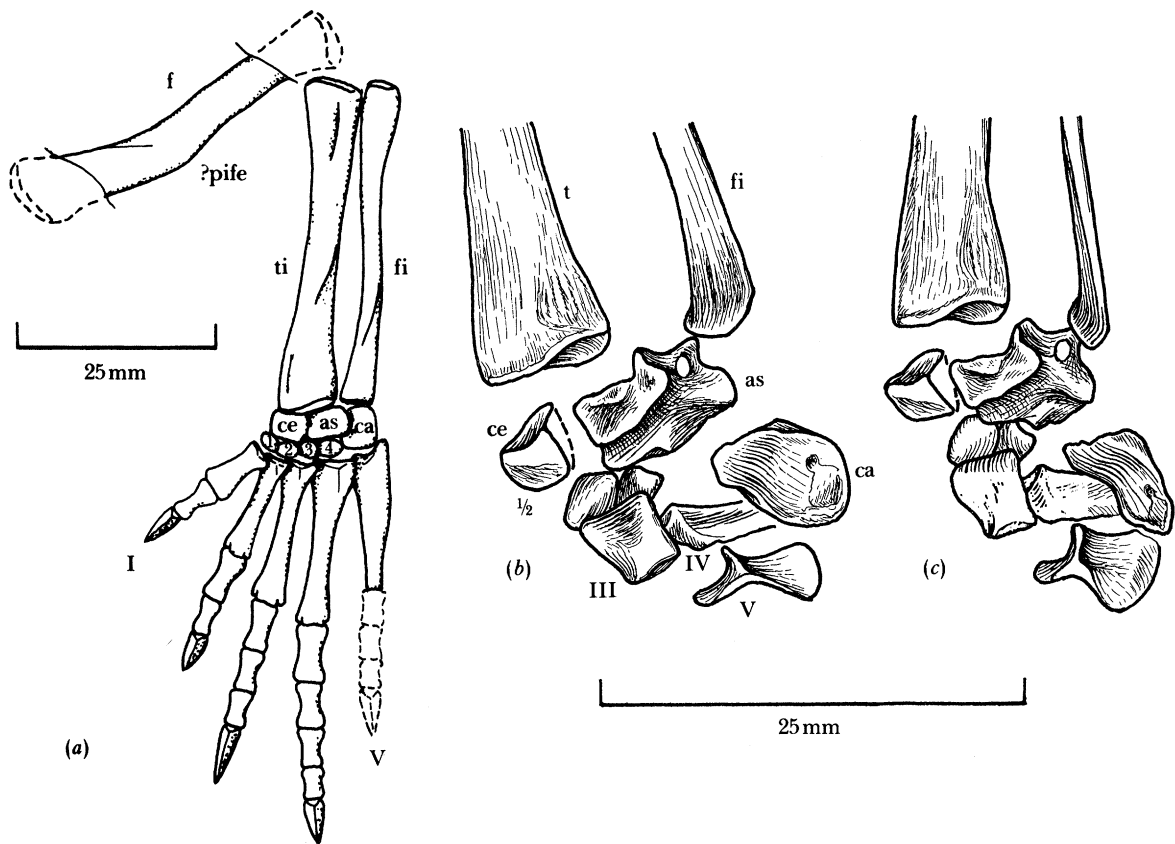


FIGURE 20. *Rhynchosaurus articeps*. The hindlimb. (a) restoration of the left hindlimb in anterodorsal view, based on BATGM M20a, BMNH R1238 and R1239; (b, c) 'exploded' views of the ankle region of BATGM M20a, in posterior and posterolateral views, showing proximal ends of metatarsals III-V.

puboischiofemorales externus group, powerful retractors of the hindlimb. The femur of *R. articeps* seems to be less massive than that of the larger rhynchosaur. Owen (1842*b*, pp. 152-153; 1842*c*, p. 367, pl. 6, fig. 10) described two supposed femora in a specimen that is now lost. These could equally well represent a tibia and a fibula, but the preservation was apparently poor.

The tibia and fibula (figures 11*b*, 14, 15*b*, 16, 20, 45*b*) are equal in length, but shorter and rather narrower than the femur. Both elements are flattened and divided clearly into an anterior (extensor) and posterior (flexor) face, as in other rhynchosaur. Both show a twist in the shaft in both posterior and anterior views. The distal ends are broad, and that of the tibia has two faces for articulation with the centrale and the medial part of the astragalus. The latter part of the articular surface slopes up, forming a concave facet (figures 1*b*, 45*b*).

Elements of the tarsus are present in several specimens (figures 15, 16); they are particularly well preserved in posterior view in BATGM M20a/b (figures 11*b*, 20*b*, *c*, 45*b*). The reconstruction (figure 20*a*) shows three proximal tarsals: the centrale, astragalus, and calcaneum, the terms applied by Carroll (1976) who argued that these elements of the rhynchosaur tarsus are equivalent to those of primitive reptiles. Hughes (1968) and Chatterjee (1974) called these three proximal tarsals the tibiale, intermedium, and fibulare respectively.

The centrale is a pyramidal or quadrangular element that has short flat surfaces for

articulation with the tibia proximally, the astragalus laterally, and distal tarsal 1 (? and 2) distally. The *astragalus* may be the largest tarsal element, as in other rhynchosaurs. In posterior view (figure 20*b, c*), it has a square face, and broad concave faces for articulation with the calcaneum laterally, and distal tarsals 2 and 3 distally. The proximal articular surface of the astragalus is roughly L-shaped, as in *Stenaulorhynchus* (Huene 1938, pl. 11, fig. 1*c*) and *Scaphonyx* (Hughes 1968, fig. 5), with a long oval-shaped slightly concave facet for articulation with the tibia, and a smaller concave facet for articulation with the fibula. These two facets are separated by a low ridge. The *calcaneum* is a smaller ovoid element (figures 15*b, 16, 20*) with narrow surfaces for contact with the fibula proximally and the astragalus medially. The astragalar facet is on a small convex process that fits into the lateral pit on the astragalus. The calcaneum has a curved lateral edge, and it descends distally below the line of proximal tarsals, presumably just contacting the fifth metatarsal, as in other rhynchosaurs.

It is assumed that *R. articeps* had four *distal tarsals* in a row above metatarsals I–IV (figure 20*a*), as in other rhynchosaurs, but they are incompletely known (figures 15*b, 16, 20b, c*). Distal tarsals 2 and 3 probably fitted into the concave pits on the distal face of the astragalus; tarsals 1 and 4 presumably contacted the centrale and calcaneum respectively.

The *metatarsals* vary greatly in shape and size (figures 15*b, 16, 20a*). The first is the shortest, but it is not such a broad stumpy element as in *Stenaulorhynchus*, *Hyperodapedon* and *Scaphonyx*. The metatarsals increase in length from II to IV, and V is rather shorter again and L-shaped. Metatarsal V is not such a tiny element in *R. articeps* as in some of the larger rhynchosaurs, although Woodward (1907, p. 294) restored it as such. The proximal ends of the metatarsals are broad, and the articular surface of metatarsal III at least seems to be roughly square (figure 20*b, c*).

The *phalanges* are all short and have expanded ends, and the phalangeal formula is 2.3.4.5.3/4, as in other rhynchosaurs where the formula can be established. In each digit the phalanges reduce in length distally, except for the unguals (figures 15*b, 16, 20a*). In dorsal view the ungual phalanges are narrow and pointed, and in lateral view they were probably high, blunt-ended and bilaterally compressed, with a sharp dorsal peak (claw, figure 15*b*). The ungual phalanx is attached to a roller-like distal articular facet of the preceding phalanx, and a high degree of rotation was probably possible, as in *Hyperodapedon* (Benton 1983, fig. 35*e*).

3.6. *Skin* (figure 16)

Burckhardt (1900, p. 532) figured an example of 'skin' with scales in the abdominal region of BMNH R1238. He showed small rounded scales between the ribs, and larger scales on each side of the vertebral column. Careful examination of the specimen shows only a small number of impressions in the sandstone in that region (imp, figure 16). Each impression is rhomboidal in shape and about 1 mm in maximum diameter. There are twenty or so such impressions running in two parallel longitudinal rows of about ten each. Burckhardt (1900) also mentions skin in BMNH R1240, and Woodward (1907, p. 298, pl. 2, fig. 2) notices a similar phenomenon in SHRBM 6 in the region of the forelimb. In these specimens there are faint 'pock marks' in the sandstone around the skeleton. However, the arrangement of marks is irregular, and there does not appear to be any associated organic matter.

In the specimens just cited, and in a number of others, the sandstone around the skeleton, often between the ribs, appears to be generally smoother, or different in texture, from the rest of the matrix. It is not clear whether this phenomenon, and the 'pock marks', are impressions

of skin and dermal scutes, or whether the decaying soft parts of the carcass caused minute differences in the texture of the enclosing unconsolidated sand, which became a recognizable sedimentary lamina or parting surface in the solid rock. This 'smoothing' phenomenon, in different sedimentary circumstances, is well known in vertebrate fossils in fine sediment (e.g. *Archaeopteryx* (Charig *et al.* 1986)).

4. *RHYNCHOSAURUS BRODIEI*, NEW SPECIES, FROM WARWICK

(figures 21–27, 46–47)

- 1840 'a smooth curved tooth', Murchison & Strickland, p. 344, pl. 28, fig. 9.
 1840 'a vertebra'; Murchison & Strickland, p. 344, pl. 28, fig. 10.
 1841 *b Anisodon gracilis* Owen, pl. 62A, fig. 3 (*nomen dubium*)
 1842 *a Labyrinthodon leptognathus* Owen, pp. 523–524, pl. 45, figs 5–10.
 1842 *a Labyrinthodon pachygnathus* Owen, p. 535.
 1869 *Hyperodapedon* Huxley; Huxley, pp. 144–146, fig. 1.
 1871 *Hyperodapedon* Huxley; Lyell, fig. 391.
 1893 *Hyperodapedon* Huxley; Brodie, p. 173.
 1900 *Hyperodapedon minor* Burckhardt, pp. 492, 530 (*nomen dubium*).
 1905 *Hyperodapedon gordonii* Huxley; Newton, p. 284.
 1908 *Hyperodapedon gordonii* Huxley; Allen, p. 276.
 1908 'tooth of a saurian'; Allen, p. 277.
 1929 *Rhynchosaurus* sp.; Huene, p. 37.
 1929 *Hyperodapedon gordonii* Huxley; Huene, p. 37.
 1969 *Rhynchosaurus* sp.; Walker, pp. 470, 471, 473.
 1970 *Rhynchosaurus articeps* Owen; Walker, p. 217.
 1980 *Rhynchosaurus articeps* Owen; Chatterjee, p. 64.
 1983 *Rhynchosaurus* sp.; Benton, pp. 693, 706–708, figs 53*d*, 54*d*.
 1984 *b Rhynchosaurus*; Benton, p. 773, fig. 17.

Diagnosis. Differs from *R. articeps* in being considerably larger (skull length 90–140 mm, compared with 60–85 mm), and in having a broader skull. Jugal in *R. brodiei* much deeper than that of *R. articeps*, being the largest bone in the side of the skull. Orbit in *R. brodiei* placed relatively further forward, and maxilla relatively smaller than in *R. articeps*.

Derivation of name. The specific name *brodiei* for the Warwick rhynchosaur is selected to honour the Reverend P. B. Brodie, who collected the holotype specimen as well as many other fossil reptiles from Warwick.

Holotype. WARMS Gz6097 + BMNH R8495 (figure 46*a–c*). A partial skull and mandible (left side), including the snout, maxilla, orbital area and lower jaw, back to the temporal region. Triassic, Coton End Quarry, Warwick. Noted by Huxley (1869), Burckhardt (1900) and Huene (1929), but described and figured here for the first time. These two parts were fitted together and photographed for the first time by A. D. Walker in 1967.

4.1. *The holotype of Rhynchosaurus brodiei*

The holotype of *R. brodiei*, now unfortunately curated in two separate institutions (WARMS Gz6097 + BMNH R8495), was apparently first cited in 1869. Huxley (1869, p. 146, footnote)

stated: 'I am indebted to my friends the Rev. P. B. Brodie and Mr Kershaw for drawing my attention to some additional examples of the Warwickshire *Hyperodapedon*. Two of them are fragmentary palato-maxillary bones. The third has very much the appearance of two crushed palato-maxillary bones, with one ramus of the mandible of a small specimen; but I have not been able to work it out fully.' Huxley's 'third specimen' is most probably WARMS Gz6097/BMNH R8495, as most other Warwick specimens are single elements. At that time, it was presumably still enclosed in matrix, which would have made it harder to interpret: much of the matrix was removed only in 1968 by A. D. Walker.

Two other names have apparently been given to the Warwick rhynchosaur in the past, *Anisodon gracilis* Owen 1841 and *Hyperodapedon minor* Burckhardt 1900, but they are designated as *nomina dubia* here because they were inadequately characterized. Owen's name was applied to the partial premaxilla WARMS Gz1046, but no description was given and this specimen lacks any diagnostic characters of *Rhynchosaurus*, or of any particular rhynchosaur species.

Burckhardt (1900, p. 492) described some features that were to be seen in *H. minor*, namely the angular, 'a portion of the coronoid', and the 'opercular' (i.e. splenial). Later, Burckhardt (1900, p. 530) referred to 'a fragment of *H. minor*, containing the germs of the teeth, which have as yet not cut through the bone', and he also noted 'the principal row of mandibular teeth'. The holotype of *H. minor* was said (Burckhardt 1900, p. 492, footnote) to be 'a fragment mentioned by Huxley, Q. J. G. S., 1859 [*sic* = 1869], p. 146'. Burckhardt was studying in the British Museum (Natural History) at the time, and his descriptions seem to refer to the specimen BMNH R8495 ('R2623' at that time, which included two other specimens; see §2.3 above), which shows all of the features he noted. However, in view of the uncertainty, Burckhardt's name is also designated *nomen dubium*. Neither name, *Anisodon gracilis* or *Hyperodapedon minor*, has been used to my knowledge other than in the original publications.

4.2. Skull

General

The skull of *R. brodiei* is known principally from the type specimen (WARMS Gz6097/BMNH R8495), which represents the anterior two thirds of the skull and mandible. Additional information on the premaxillae and anterior palate comes from WARMS Gz4715, and on the posterior part of the maxilla and the lateral part of the palate from BMNH R8494. Several isolated maxillae (GSM 59745, 90493; WARMS Gz955, Gz960) were also used. The posterior part of the skull – the region of the temporal fenestrae, braincase and occiput – is unknown. It has been restored tentatively (figure 21) on the basis of *R. articeps*.

The skull of *R. brodiei* (figure 21a) is higher than that of *R. articeps* (figure 2a), and the orbit is placed relatively further forward. The maxilla is relatively smaller, and the jugal is relatively larger than in *R. articeps*. In dorsal view (figure 21b), the posterior region of the skull appears to be broader than in *R. articeps* (figure 3b), but this is not certain because of incomplete preservation. The posterior part of the partial skull WARMS Gz6097/BMNH R8495 is more expanded than in *R. articeps*, and the natural curve of the jugals and postorbitals, if continued, gives the skull shape in figure 21.

The best remains from Warwick indicate an animal with a skull length of 90–94 mm (figure 21). However, some jaw elements appear to come from larger individuals. The fragment of anterior mandible (WARMS Gz4712; figure 24e,f) is about one and two thirds as large as the reconstructed skull (? skull length 150–160 mm), and four isolated maxillae and two dentaries

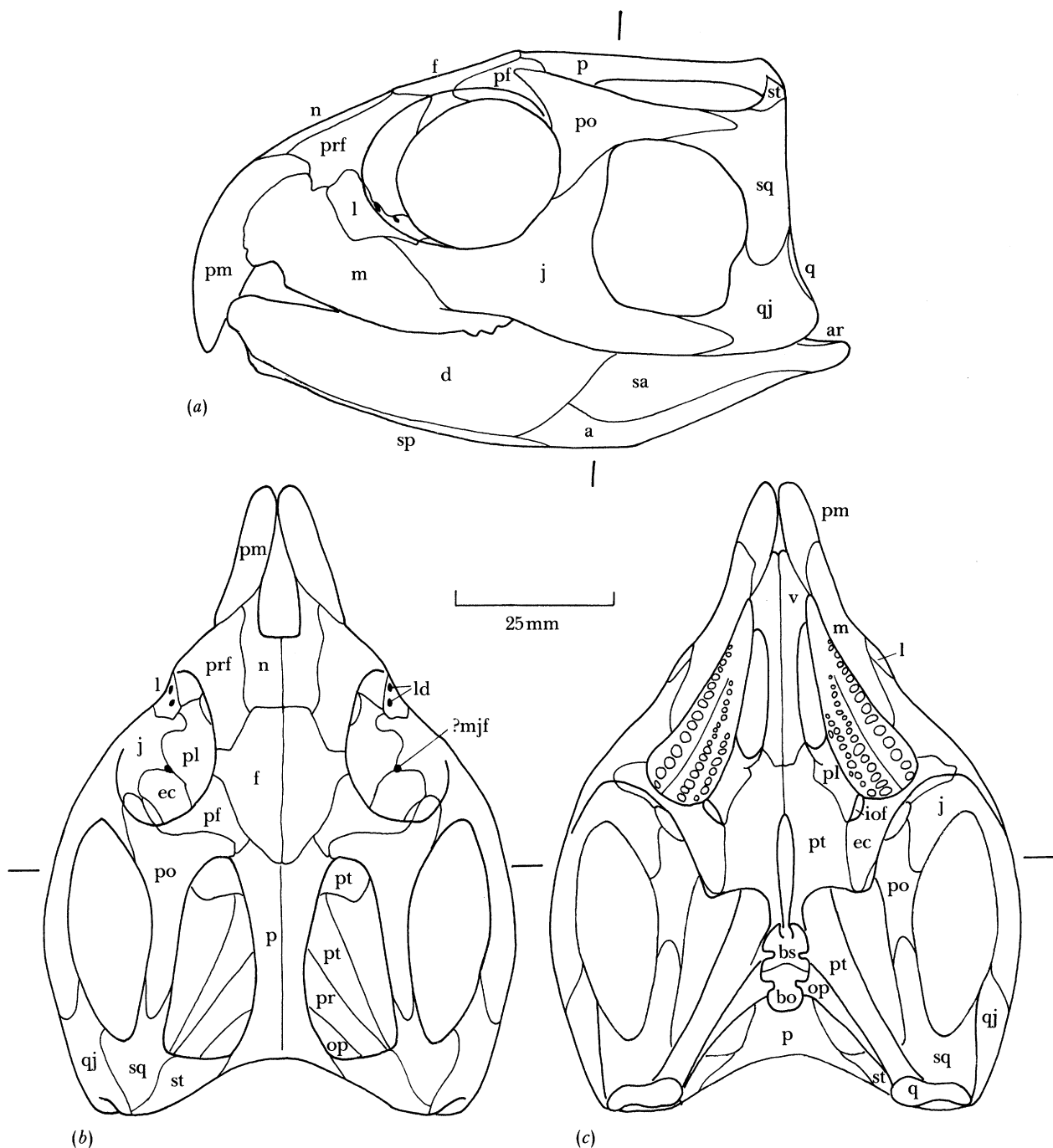


FIGURE 21. *Rhynchosaurus brodiei*. Restorations of the skull in (a) left lateral, (b) dorsal and (c) palatal views, based on the holotype specimen, WARMS Gz6097/BMNH R8495, with additional information from other specimens. The posterior portions of the skull, behind the marker lines, are based on *R. articeps*.

also suggest larger-sized skulls (table 3). These skull sizes are clearly greater than the known range of *R. articeps* (60–85 mm), and they seem to indicate that larger specimens of *R. brodiei* were up to twice as long as *R. articeps*, and were thus considerably heavier animals.

In the following skull descriptions, general points are not repeated from the description of

TABLE 3. ESTIMATED SKULL LENGTHS OF SPECIMENS OF *RHYNCHOSAURUS BRODIEI*

(Skull lengths are estimated from measurements of the maximum width of the tooth-bearing portions of the maxilla and the dentary, and they are shown with question marks (?). These estimated measures are probably subject to an error of plus or minus 5–10 mm.)

	maximum dentary width	maximum maxilla width	estimated midline skull length
WARMS Gz4715	—	—	? 85 mm
WARMS Gz955	—	11 mm	? 90 mm
WARMS Gz6097/BMNH R8495	—	12 mm	93 mm
BMNH R8494	—	13 mm	? 110 mm
BGS GSM 59745	—	13 mm	? 110 mm
WARMS Gz950	8 mm	—	? 120 mm
WARMS Gz960	—	14 mm	? 120 mm
WARMS Gz959	9 mm	—	? 130 mm
BGS GSM 90493	—	17 mm	? 140 mm

R. articeps. Important differences from that species, and features in which the specimens of *R. brodiei* offer additional information are noted.

Dermal bones of the skull roof (figures 21–23, 46)

The distal tips of the *premaxillae* are not known, but they were probably rounded as in *R. articeps*. They are rounded to triangular in cross section distally, and more oval-shaped proximally (figures 22*a*, 46*d*). The distal portion of the premaxilla may have been covered with a horny sheath in life, and there is a slight facet near the lower end where the dentary rostrum lay when the jaws were closed (figures 21*a*, 22*c*, 23, 46*a*, *b*, *e*).

The premaxilla WARMS Gz1046 (figures 22*a*, 46*d*) is historically interesting since it is the remains of the so-called 'smooth curved tooth, flattened on one side' figured by Murchison & Strickland (1840, pl. 29, fig. 9). This is the first published figure of a rhynchosaur. Owen (1841*b*, pl. 62A, fig. 3; 1842*a*, p. 535) later sectioned this specimen at both ends (as is seen in the specimen now), and determined that it was bone and not tooth, although he identified it as an unguis phalanx of *Labyrinthodon*. In the 1841*b* volume, Owen named this specimen *Anisodon gracilis*.

The *maxillae* will be described as part of the palate. The *nasals* are represented only by a fragment adhering to the right premaxilla (figure 22*b*), and they are restored (figure 21*a*, *b*) on the assumption that their lateral and posterior boundaries are marked along the broken prefrontal and frontal edges in the holotype (figure 23*c*).

The suturing relationships of the *frontals* may be seen better in *R. brodiei* than in *R. articeps*. The frontal underlies the nasal, prefrontal, postfrontal, and parietal. The extensive suture plane for the parietal is seen in dorsal view (figure 23*c*). Ventrally (figure 23*d*), the frontals are sculpted as in *Hyperodapedon gordonii*: a longitudinal ridge runs forwards and downwards from the middle of the bone, into the internal 'septum' formed by the prefrontal in front of the orbit (figures 23*b*, 46*b*). In front of this ridge, in the ventral view of the frontal is a rounded depression (?ob, figure 23*d*) for the olfactory bulb of the brain.

The *parietals* are not present, and it is not clear from the suture surfaces at the back of the preserved part of the skull (figure 23*c*) whether they contacted the postorbital as well as the frontal and postfrontal.

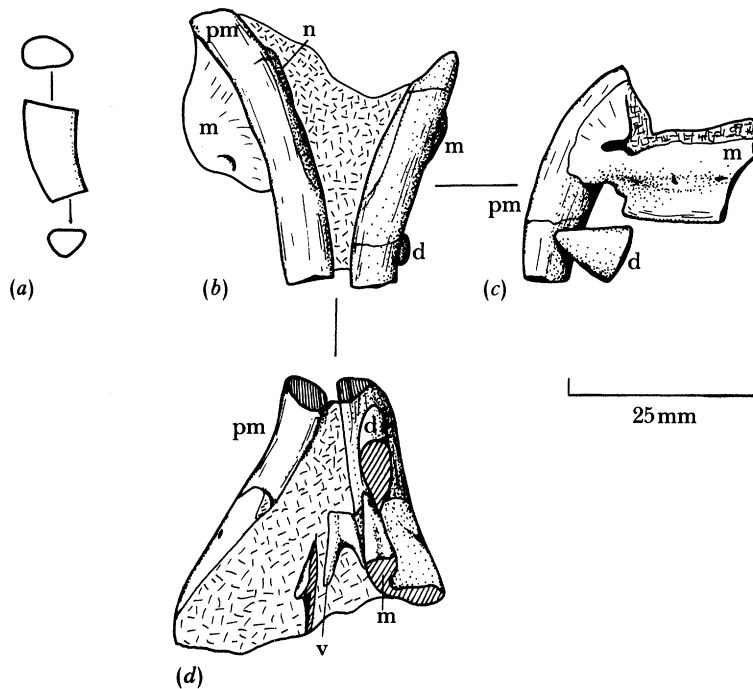


FIGURE 22. *Rhynchosaurus brodiei*. Isolated skull elements. (a) Partial left premaxilla, WARMS Gz1046, in left lateral view, with outlines of the two cut ends; (b) partial snout, WARMS Gz4715, in anterior, left lateral, and ventral views. The matrix is shaded with irregular dashes.

The *lacrimal* is seen in both lateral and medial views (figures 23 *a, b*, 46 *a, b*), and there is an indication of the half-spiral or S-shaped ridge that lies above the medial exit of the lacrimal duct, as in *Hyperodapedon* (Benton 1983, figs. 5 *b*, 9 *d*). The *prefrontal* is also seen in both lateral and medial views (figure 23 *a, b*, 46 *a, b*), and in the latter, it descends much lower on the medial ridge than in *Hyperodapedon*.

The *postfrontal* is a small triangular element (figures 21 *a, b*, 23, 46 *a, b*), as in *R. articeps*. The *postorbital* is incompletely preserved, but internally the ventral process nearly touched the ectopterygoid (figures 23 *b, c*, 46 *b*). In most other rhynchosaur, the postorbital did not descend as low as this, barely below the level of the top of the lower temporal fenestra in *Hyperodapedon* and *Stenaulorhynchus*.

The *jugal* is the largest element in the side view of the skull (figures 21 *a*, 23 *a*, 46 *a*), which is not the case in *R. articeps*. Medially, the jugal forms a broad horizontal shelf within the orbit, and borders the lacrimal, palatine, and ectopterygoid (figures 21 *b*, 23 *b, c*, 46 *b*). It is not clear whether there was a median jugal foramen lying between the jugal, ectopterygoid, and palatine (?mjf, figure 21 *c*), as in *Hyperodapedon* (Benton 1983, p. 620). The *quadratojugal*, *squamosal*, *quadrate*, and *epipterygoid* are not preserved; they are restored (figure 21) as typical rhynchosaur elements, with information from *R. articeps*.

Dermal bones of the palate (figures 21–23, 46)

The tooth-plate of the *maxilla* is a curved tapering triangular element in ventral view (figures 21 *c*, 23 *d*), bearing three longitudinal rows of large teeth, arranged on either side of a midline groove: one lateral and two medial rows. There are also small teeth on the medial surface of

the maxillary tooth-plate (figures 23 *b*, 46 *b*). The dentition is described in §7. In other views (figures 21–23), the maxilla is also typically rhynchosaurian.

The paired *vomers* are represented only by their anterior tips (figure 22 *d*). The anterior border of the left-hand choana may just be seen (cf. figure 21 *c*). Only the posterior part of the *palatine* is preserved, where it contacts the ectopterygoid, pterygoid, and maxilla behind the choana (figures 21 *c*, 23 *d*). In dorsal view (figures 21 *c*, 23 *c*, 46 *c*), this process is seen, as well as portions that meet the jugal in the floor of the orbit and the lacrimal and prefrontal in front.

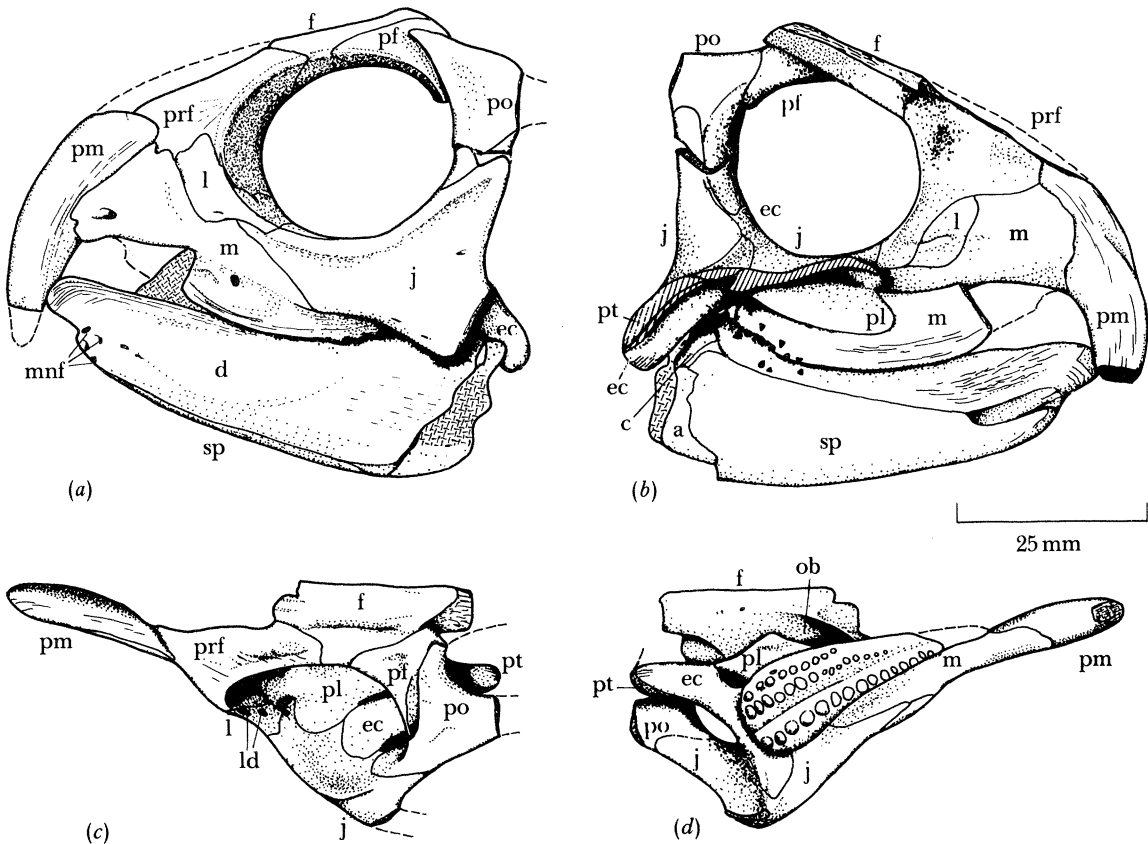


FIGURE 23. *Rhynchosaurus brodiei*. The type skull and mandible, WARMS Gz6097/BMNH R8495, in (a) left lateral, (b) medial, (c) dorsal and (d) palatal views.

The *ectopterygoid*, as in other rhynchosaurs, is a complex little bone that contacts the maxilla, jugal, palatine, and pterygoid (figures 21 *b*, *c*, 23 *b–d*, 46 *a–c*). The *pterygoid* is represented only by the lateral portion that lies above the ectopterygoid (figures 23 *b*, *c*, 46 *b*), and it is reconstructed (figure 21 *b*, *c*) according to the pattern seen in *R. articeps* and other rhynchosaurs.

The *braincase* is not preserved in any of the Warwick material, and it is restored in general outline on the basis of information from *R. articeps* and *Stenaulorhynchus* (Huene 1938; Benton 1983, pp. 699–700).

4.3. Mandible (figures 21–24, 46)

The best preserved mandible is BMNH R8495, which shows the anterior two-thirds, and additional information on the tooth-bearing portion of the dentary was obtained from BMNH

R2623, WARMS Gz950/1 and Gz959. One specimen (WARMS Gz4712) also preserves the anterior part of the dentary and splenial.

As restored, the *dentary* forms the anterior three fifths of the mandible, compared with two thirds in *R. articeps*. There is a flattened facet on the medial side of the anterior tip of the dentary (figures 23*b*, 24*a*, *b*, 46*b*, *f*) where it meets the premaxilla. The tooth-bearing portion overlies the broad meckelian canal which passes into a groove anteriorly just above the symphyseal portion of the splenial. The splenial overlaps much of the dentary medially, and when it is removed, a clear ridge can be seen marking its upper extent (figures 24*a*, 46*f*). There are two main longitudinal rows of teeth on the dorsal surface of the dentary. The lateral row of teeth is elevated slightly above the others and, at the back, the most posterior five or six teeth are very high (figure 24*c*). There are several rows of lingual teeth running up the medial face of the dentary, and these teeth are unworn at the back (figures 23*b*, 24*a*, *c*, *g*, 46*j*, *k*).

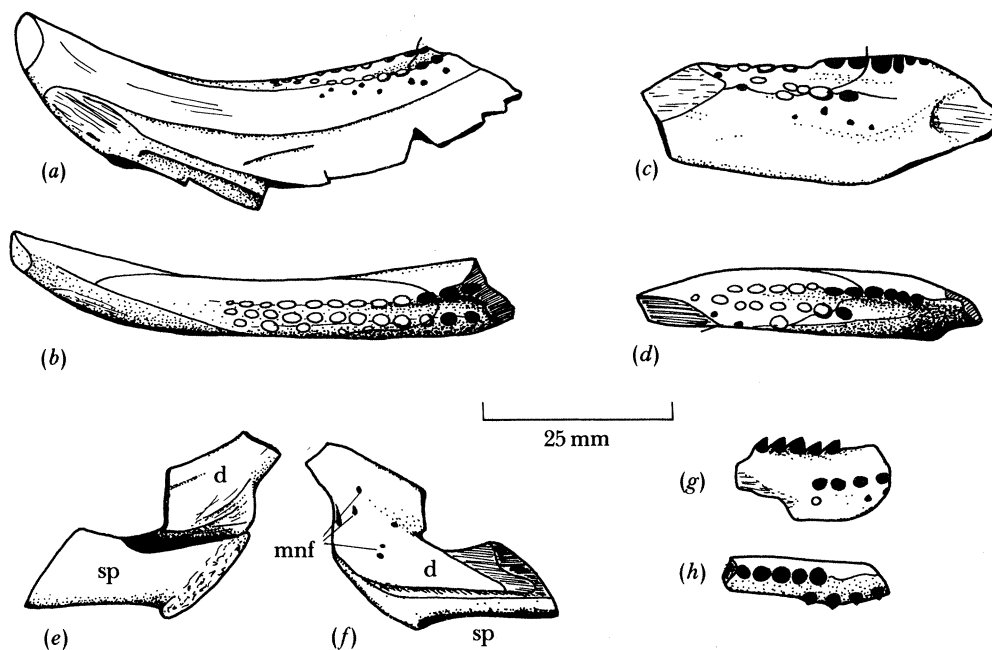


FIGURE 24. *Rhynchosaurus brodiei*. Mandibular remains. (*a*, *b*), Right dentary, WARMS Gz950, in medial and dorsal views; (*c*, *d*) posterior part of a right dentary, WARMS Gz959, in medial dorsal views; (*e*, *f*) anterior tip of a left dentary and splenial, WARMS Gz4712, in medial and lateral views; and (*g*, *h*) fragment of a left dentary, BMNH R2623, in medial and dorsal views.

The *splenial* covers the medial face of the dentary, and it is contacted behind by the *coronoid*, represented only by a fragment (figures 23*b*, 46*b*). Only the anterior tip of the *angular* is to be seen in lateral and medial views (figures 23*a*, *b*, 46*a*, *b*), where it inserts well forward between the dentary and splenial. The *surangular*, *prearticular*, and *articular* are not preserved, and the posterior part of the lower jaw is reconstructed (figure 21*a*) as in other rhynchosaurians.

4.4. Postcranial skeleton (figure 25)

Postcranial remains of *R. brodiei* are limited to a dorsal vertebra, an interclavicle, and a left ischium, which were first recognized as rhynchosaurian by A. D. Walker in 1967.

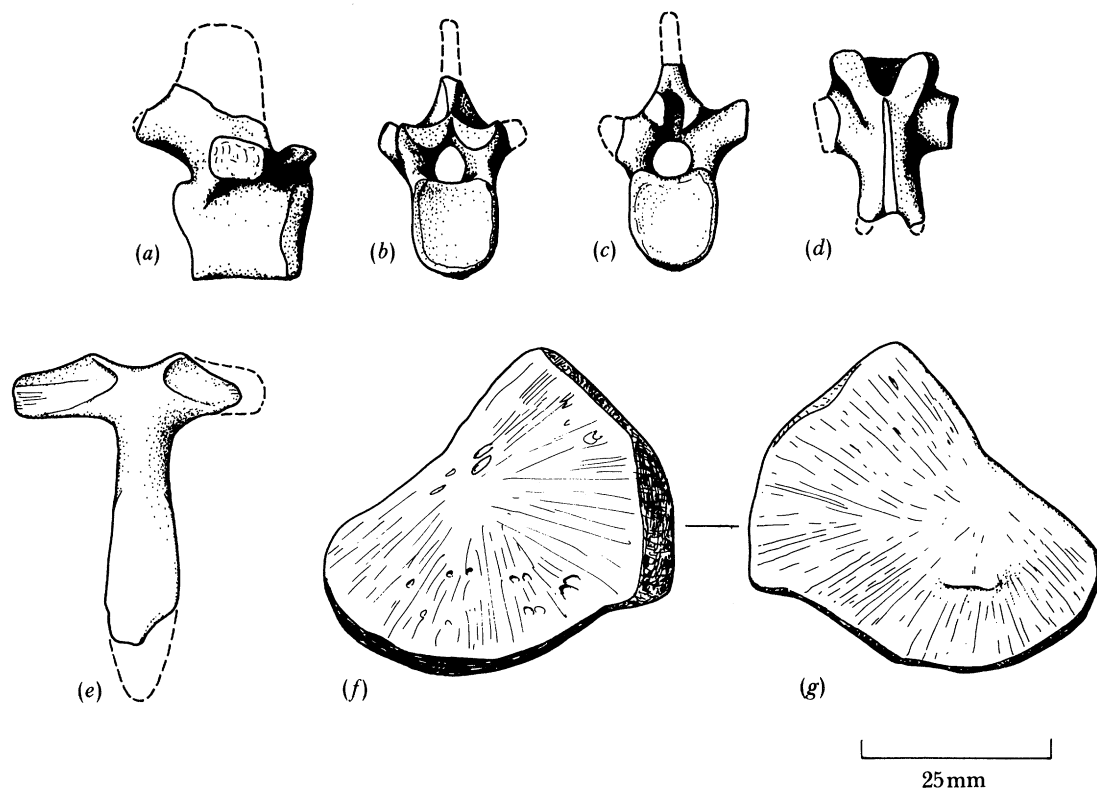


FIGURE 25. *Rhynchosaurus brodiei*. Postcranial elements. (a–d) Mid-dorsal vertebra, WARMS Gz17, in (a) right lateral, (b) anterior, (c) posterior and (d) dorsal views. (e) Interclavicle, WARMS Gz34, in ventral view. (f, g) Left ischium, WARMS Gz19, in dorsal and ventral views.

Dorsal vertebra

The dorsal vertebra (figure 25 a–d) is rather well preserved, showing a short amphicoelous centrum, and most of the neural arch. There are rugose areas around the anterior face and most of the posterior face of the centrum, as well as at the end of the rib facet, which may show that these areas were finished in cartilage in life.

This vertebra is probably a mid to posterior dorsal: the centrum is relatively short and the zygapophyses are at fairly high angles (about 60°) as in posterior dorsals of *R. articeps*. However, the vertebrae of *R. articeps* are not well enough preserved to allow a detailed comparison. In other rhynchosaur, fusion of the parapophysis and diapophysis, as here, occurs behind the first few dorsals. The overall shape of the vertebra is rather like dorsals 15–21 in *Stenaulorhynchus* (Huene 1938, pl. 4). This specimen differs from posterior dorsals of *Hyperodapedon*, and possibly *R. articeps*, in that the transverse processes are relatively short. Further, in *H. huxleyi*, the centra seem to remain higher than their length throughout the back (Chatterjee 1974, p. 236). The *R. brodiei* vertebra is rather similar in size and shape to some rhynchosaur vertebrae from the middle Triassic of Madagascar, named *Isalorhynchus* (Buffetaut 1983, fig. 3).

This vertebra was originally interpreted (Owen 1842a, pp. 52–53, pl. 45, figs 5–8) as that of a labyrinthodont amphibian, but Miall (1874, p. 431) noted that it was wrongly identified.

Shoulder girdle

The *interclavicle* (figure 25*e*) is nearly complete, and shows the typical rhynchosaurian dagger shape, with a horizontal posterior process, and a vertically placed cross-bar. There are clearly marked pockets on the lateral processes of the cross-bar for the clavicles (cl, figure 25*e*). The interclavicle of *R. brodiei* is similar to that of *R. articeps*, although it was possibly relatively shorter.

This bone was originally described (Owen 1842*a*, pp. 53–54, pl. 45, figs 9, 10) as the interclavicle of a labyrinthodont. Owen's figures did not show the true shape of the bone since it had not been fully prepared then: he did not show the true anterior margin of the lateral wings. Miall (1874, p. 431) recognized that this element was not from a labyrinthodont.

Pelvic girdle

The *ischium* (figure 25*f, g*) is a thick element, ranging from 11 mm at the anterolateral edge to 1–2 mm at the posterodorsal edge. The anterior margin is divided into two massive facets, one for the ilium, and one for the pubis. There is a slight boss on the ventrolateral face (figure 25*g*); this may have been associated with the origin of the puboischiofemoralis externus muscle. The ischium is apparently like that of *R. articeps* and most other rhynchosaurs, although it seems different from that of *Stenaulorhynchus* (Huene 1938, pl. 16, fig. 1), in which the ischium appears to fan out backwards.

Ischia are often not clearly identifiable, and the present specimen is of an appropriate size to be ascribed tentatively to other taxa such as the Warwick poposaurid or the 'macrocnemid' (Walker 1969), or to the trilophosaurid (represented by an ilium, WARMS Gz4714). However, the present ischium is quite different in shape from the rectangular and slender elements of most thecodontians, and of poposaurids in particular (Chatterjee 1985), and also from the L-shaped element of *Macrocnemus* (Peyer 1937) and of *Trilophosaurus* (Gregory 1945).

5. *RHYNCHOSAURUS BRODIEI* (?), FROM BROMSGROVE(figures 26, 47*j–l*)

- 1907 *Hyperodapedon gordonii* Huxley; Wills, p. 32.
- 1910 *Hyperodapedon gordonii* Huxley; Wills, p. 264.
- 1929 *Hyperodapedon gordonii* Huxley; Huene, p. 37.
- 1969 *Rhynchosaurus* sp.; Walker, pp. 470, 471, 473.
- 1970 *Rhynchosaurus articeps* Owen; Walker, p. 217.
- 1983 *Rhynchosaurus* sp.; Benton, p. 693.

The only fossils from Bromsgrove that are identifiable as those of a rhynchosaur are two small maxillae (figures 26, 47*j–l*). Many other fossils from Bromsgrove in the Sedgwick Museum were labelled as rhynchosaurs, but these pertain to thecodontians, prolacertiforms, trilophosaurs, or nothosaurs, or they are unidentifiable (Walker 1969). One 'rhynchosaurian premaxilla' (CAMSM R341) is actually a coprolite!

The Bromsgrove maxillae (figure 26) are virtually indistinguishable from the Warwick ones (figure 35). The rows of occlusal and lingual teeth, the two longitudinal grooves, and the patterns of tooth wear seem to be identical. The two Bromsgrove maxillae probably came from

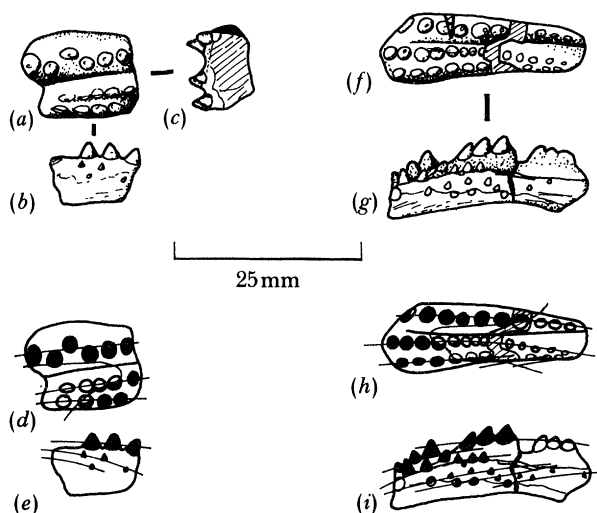


FIGURE 26. *Rhynchosaurus brodiei* from Bromsgrove. Maxillae. (a–e) Right maxilla, CAMSM G337, in ventral (a, d), lateral (b, e) and posterior (c) views, with the nature of the teeth, ‘Zahnreihen’ and the area of occlusion marked (d, e); (f–i) left maxilla, CAMSM G336, in ventral (f, h) and medial (g, i) views, with the nature of the teeth, ‘Zahnreihen’ and the area of occlusion marked (h, i).

DESCRIPTION OF PLATE 1.

FIGURE 44. (a–d, f, g) *Rhynchosaurus articeps* and (e) *Stenaulorhynchus stockleyi* skulls. (a, b) The lectotype specimen, SHRBM G132/1982, in dorsal (a) and left lateral (b) views. (c) BMNH R1237 in dorsal view. (d) MM L7642 in dorsal view. (e) GPIT 317a, posterior part of the skull in dorsal view, showing the postulated supratemporal (st). (f) BMNH R1237 in ventral view. (g) BMNH R1236 in posterior view. Magnifications: (a–d, f, g) $\times 1$; (e) $\times 0.5$. (Photograph (e) by A. D. Walker.)

FIGURE 44. For description see opposite.

DESCRIPTION OF PLATE 2.

FIGURE 45. (a–d) *Rhynchosaurus articeps* and (e) *Stenaulorhynchus stockleyi*. (a) The paralectotype specimen, SHRBM G134/1982, showing the scapula (top), ribs (right), and dorsal vertebrae (bottom). (b, c) BATGM M20a/b, showing dorsal, sacral, and caudal vertebrae, pelvis, and right hindlimb in dorsal (b) and left lateral (c) views. (d) BMNH R1236, skull in ventral view, showing the supposed pterygoidal teeth (arrow). (e) GPIT 317a, middle part of the skull in ventral view, showing the supposed pterygoidal teeth (arrow). Magnifications: (a–c) $\times 1$; (d) $\times 1.4$; (e) $\times 0.7$. (Photograph (d) by A. D. Walker; (e) by W. Wetzel (GPIT).)

DESCRIPTION OF PLATE 3

FIGURE 46. *Rhynchosaurus brodiei* from Warwick, skull and mandibles. (a–c) The holotype specimen, WARMS Gz6097/BMNH R8495, in lateral (a), medial (b), and medioventral (c) views. Part (c) shows some of the maxillary and dentary teeth (BMNH R8495). (d) WARMS Gz1046, a partial right premaxilla, cut at both ends, the first-figured rhynchosaur specimen. (e) WARMS Gz4715, a partial snout, in left-lateral view. (f–h) WARMS Gz950, a partial right dentary, in medial (f), lateral (g), and occlusal (h) views. (i) WARMS Gz959, a partial right dentary, in occlusal view. (j, k) BMNH R2623, a partial left dentary, in medial (j) and occlusal (k) views. Magnifications: (a, b) $\times 1$; (c) $\times 1.6$; (d, e) $\times 2$; (f–h) $\times 1.5$; (i) $\times 2.3$; (j, k) $\times 2.1$. (Photographs (c–k) by A. D. Walker.)

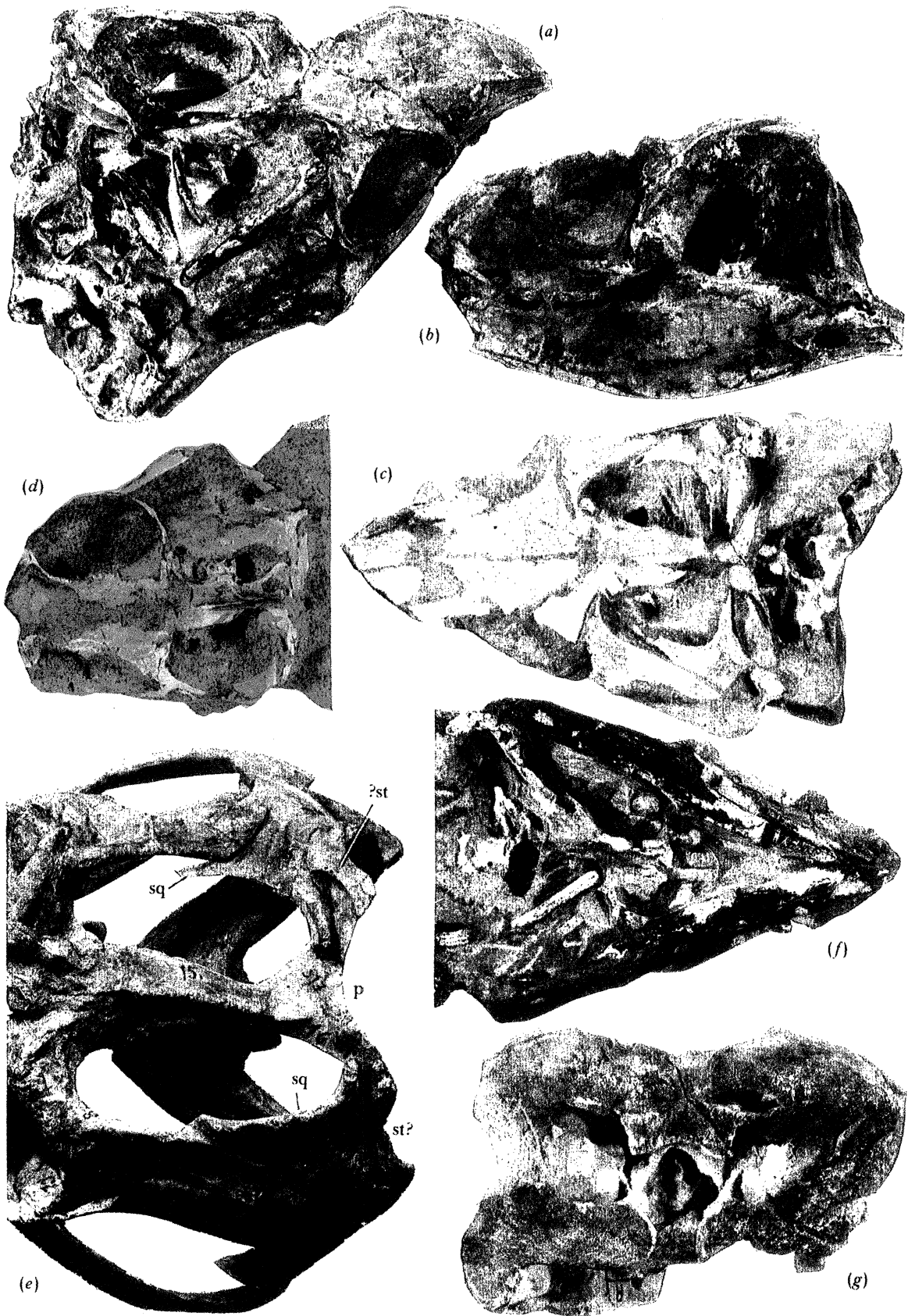


FIGURE 44. For description see opposite.

(Facing p. 260)



FIGURE 45. For description see p. 260.

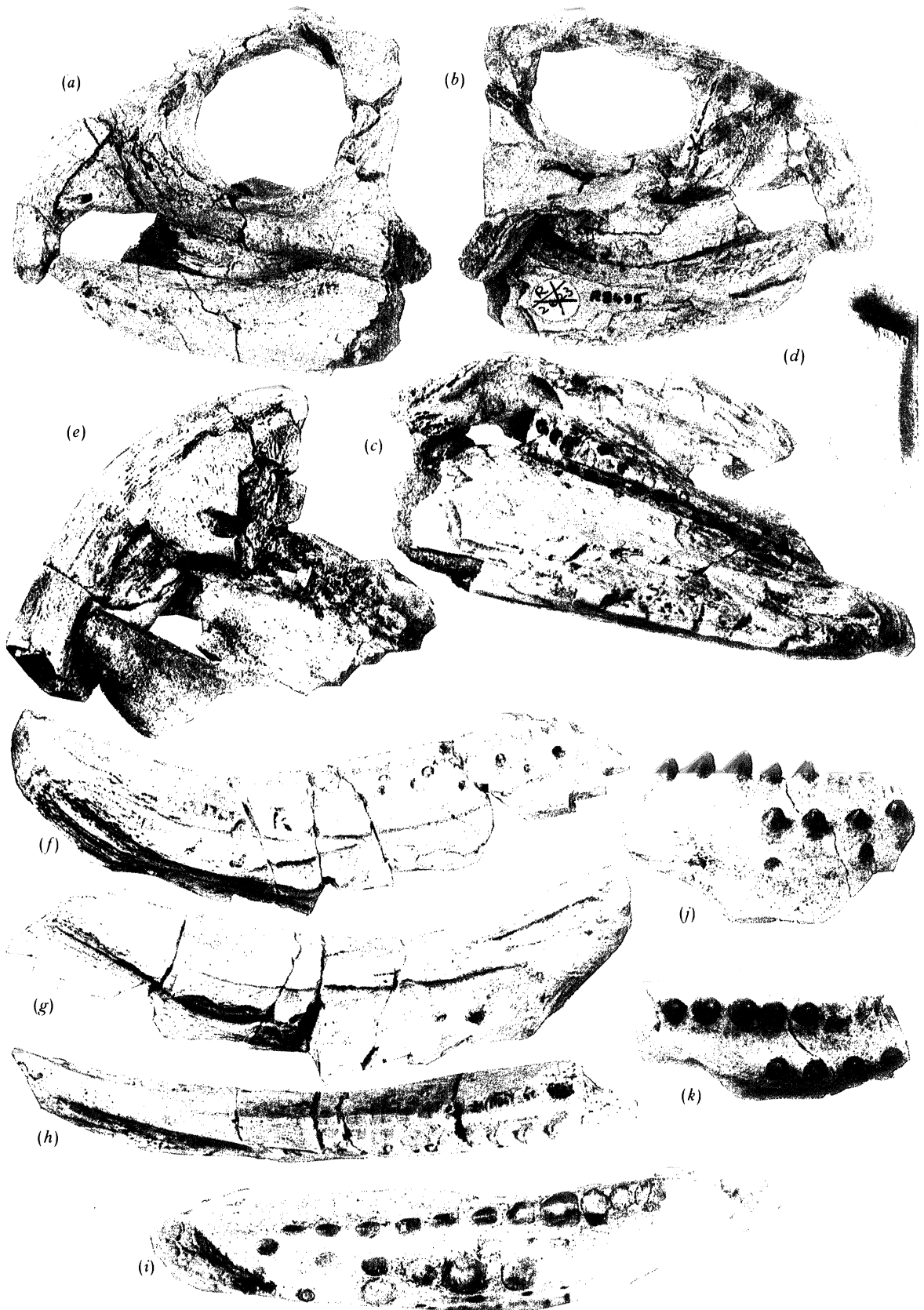


FIGURE 46. For description see p. 260.

DESCRIPTION OF PLATE 4

FIGURE 47. *Rhynchosaurus brodiei* from Warwick (*a-i*) and Bromsgrove (*j-l*); maxillary tooth-plates. (*a*) WARMS Gz955, right maxilla, in occlusal view; (*b*) WARMS Gz960, right maxilla, in occlusal view; (*c*) BGS GSM 90493, left maxilla, in occlusal view; (*d-h*) GBS GSM 59745, left maxilla, in occlusal (*d*), medial (*e*), lateral (*f*), dorsal (*g*) and posterior (*h*) views; (*i*) BMNH R8494, right maxilla, in occlusal view; (*j, k*) CAMSM G336, right maxilla, in occlusal (*j*) and medial (*k*) views; (*l*) CAMSM G337, left maxilla, in occlusal view. Magnifications: (*a*) $\times 2.8$; (*b*) $\times 1.8$; (*c*) $\times 2.3$; (*d-h, j-l*) $\times 2.5$; (*i*) $\times 2.2$. (All photographs by A. D. Walker.)



FIGURE 47. For description see opposite.

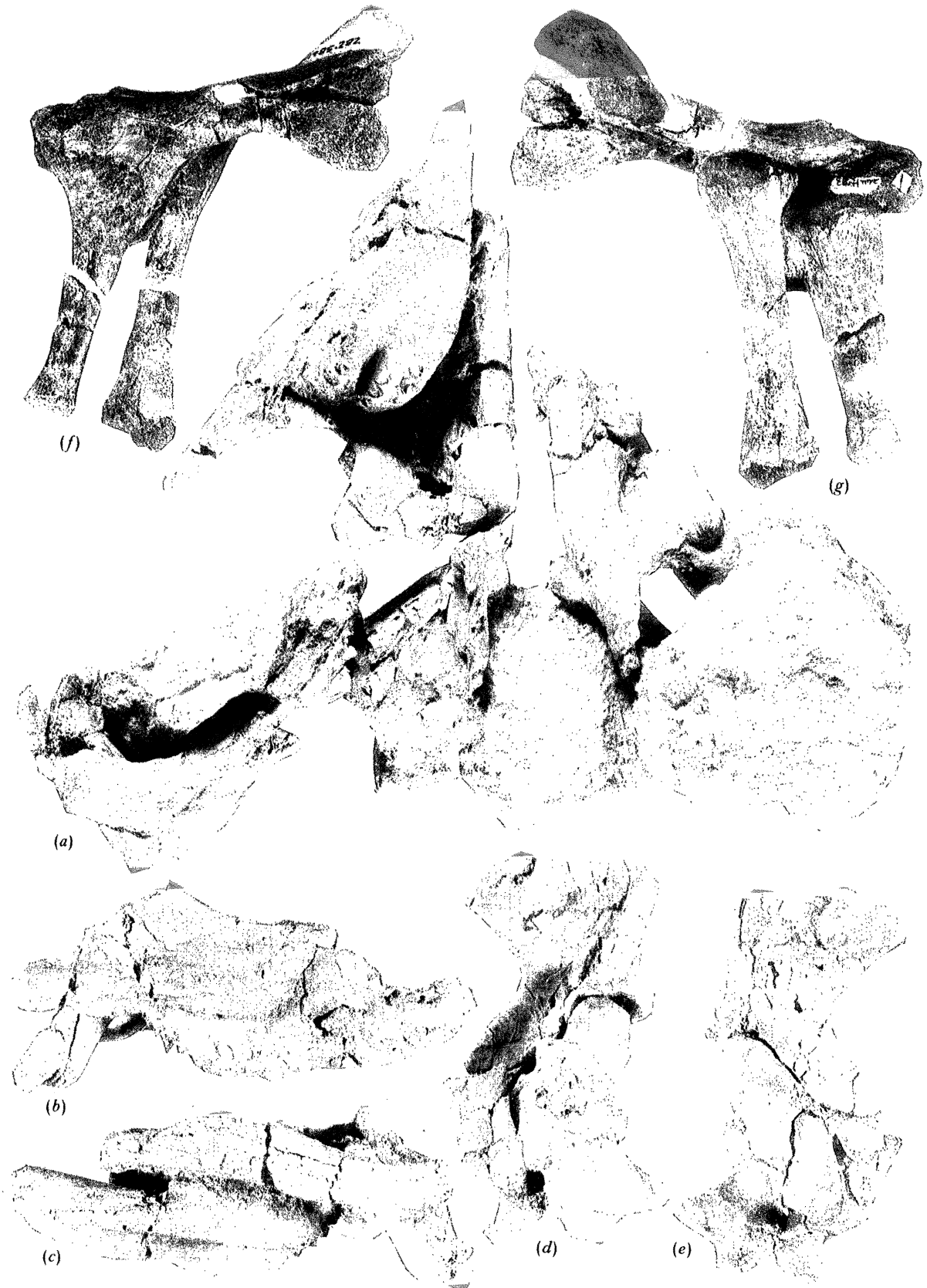


FIGURE 48. For description see p. 261.



FIGURE 49. For description see p. 261.



FIGURE 50. For description see opposite.

animals with total skull lengths of 85–95 mm, by comparison with the Warwick specimens. This is at the lower end of the size range of *R. brodiei*.

6. *RHYNCHOSAURUS SPENCERI*, NEW SPECIES, FROM DEVON

(figures 28–34, 36, 37, 48–50)

- 1869 *Hyperodapedon*; Huxley, p. 146.
 1869 *Hyperodapedon*; Whitaker, pp. 152, 156.
 1876 *Hyperodapedon*; Lavis, p. 277.
 1876 *Hyperodapedon*; Seeley, p. 282.
 1884 'curved spine'; Metcalfe, p. 260, fig. 2.
 1892 *Hyperodapedon*; Irving, p. 69.
 1893 *Hyperodapedon*; Irving, p. 82.
 1905 *Hyperodapedon gordonii* Huxley; Newton, p. 285.
 1911 *Hyperodapedon*; Woodward & Ussher, p. 11.
 1929 *Hyperodapedon gordonii* Huxley; Huene, p. 37.
 1969 *Rhynchosaurus*; Walker, p. 471.
 1970 *Rhynchosaurus*; Walker, p. 217.
 1973 *Rhynchosaurus*; Pattison *et al.*, p. 247.
 1980 *Rhynchosaurus*; Warrington *et al.*, p. 44.
 1982 *Rhynchosaurus (Hyperodapedon)*; Laming, p. 151.
 1983 *Rhynchosaurus*; Spencer & Isaac, pp. 267, 268.
 1983 *Rhynchosaurus* sp.; Benton, p. 693.
 1984 *b Rhynchosaurus*; Benton, p. 772.

DESCRIPTION OF PLATE 5

FIGURE 48. *Rhynchosaurus spenceri*, the holotype specimen, EXEMS 60/1985.292 (*a–e*). (*a*) Ventral view of the skull; (*b, c*) right palatal portion in lateral (*b*) and medial (*c*) views; (*d, e*) right quadrate, quadratojugal, and squamosal in posteromedial (*d*) and lateral (*e*) views. (*f, g*) Forelimb (humerus, radius, ulna), EXEMS 60/1985.282, in ventral–posterior (*f*) and dorsal–anterior (*g*) views. All magnifications $\times 1$.

DESCRIPTION OF PLATE 6

FIGURE 49. *Rhynchosaurus spenceri*, right mandibles. (*a, b*) EXEMS 60/1985.292 in occlusal (*a*) and medial (*b*) views; (*c*) EXEMS 60/1985.56 in occlusal views; (*d–f*) BMNH R9190 in occlusal (*d*), medial (*e*) and lateral (*f*) views; (*g, h*) EXEMS 60/1985.313 in occlusal (*g*) and medial (*h*) views. Magnification: (*a, b*) $\times 1$; (*c, g, h*) $\times 2$; (*d–f*) $\times 1.6$. (Photograph (*d*) by A. D. Walker.)

DESCRIPTION OF PLATE 7

FIGURE 50. *Rhynchosaurus spenceri*, maxillary tooth-plate from the right side (*a, b, f–i*) and from the left side (*c–e*), and premaxillae (*j–n*). (*a, b*) EXEMS 7/1986.3 in lateral (*a*) and occlusal (*b*) views; (*c*) EXEMS 60/1985.13 in occlusal view; (*d, e*) BGS GSM 90494 in occlusal (*d*) and medial (*e*) views; (*f*) EXEMS 65/1984 in occlusal view; (*g*) EXEMS 60/1985.312 in occlusal view; (*h, i*) EXEMS 7/1986.4 in posterior cross section (*h*) and occlusal (*i*) views; (*j, k*) EXEMS 60/1985.37, both premaxillae, in anterior (*j*) and posterior (*k*) views; (*l*) EXEMS 7/1986.6, a right premaxilla, in medial view; (*m, n*) EXEMS 60/1985.92, a left premaxilla, in lateral (*m*) and medial (*n*) views. Magnifications: (*a–i*), $\times 2$; (*j–n*), $\times 1$.

Diagnosis. Differs from *R. articeps* in being generally much larger (estimated skull length 40–175 mm (mean 115 mm), compared with 60–85 mm) (figure 27) and probably in having a higher and broader skull. Large jugal and relatively small maxilla. Differs from *R. brodiei* in having a relatively much wider skull. Teeth in lateral row on the maxilla much larger than other maxillary teeth, and with rather oval cross section (whereas in *R. brodiei* they are circular in cross section) and about the same size as, or only slightly larger than, medial teeth. Secondary maxillary groove present even in young animals, whereas less clearly developed in *R. brodiei*. Tooth rows on maxilla of *R. spenceri* less regular than in *R. brodiei*, and they frequently ‘meander’.

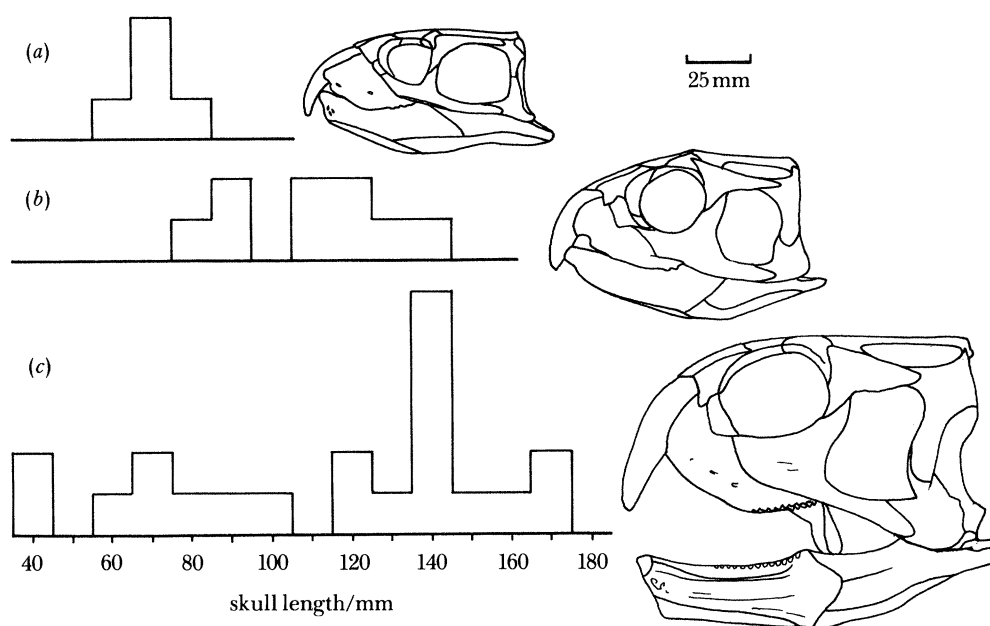


FIGURE 27. Histograms of the midline skull lengths of the three species of *Rhynchosaurus*. (a) *R. articeps*, five specimens, table 2; (b) *R. brodiei*, nine specimens, table 3; (c) *R. spenceri*, 21 specimens, table 4.

Derivation of name. The specific name *spenceri* is given in honour of Mr Patrick Spencer, formerly of Sidmouth, who collected the holotype and most of the known material of this species.

Holotype. EXEMS 60/1985.292 (figure 48). A partial skull and mandible, including the floor of the orbit and the palate of the right side, a partial plate of the left side, the posterior right-hand angle of the skull, and both mandibles.

6.1. Skull

General

The skull description is mainly based on the specimen EXEMS 60/1985.292, with additional information from EXEMS 60/1985.37–45 and the isolated premaxillae, maxillae and dentaries listed in §2.3. It has been hard to reconstruct the skull because nothing is known of the dorsal or lateral skull roof, apart from the premaxilla, maxilla, jugal, and squamosal, nor of the braincase. The palatal and occipital views are also incomplete. The missing regions have

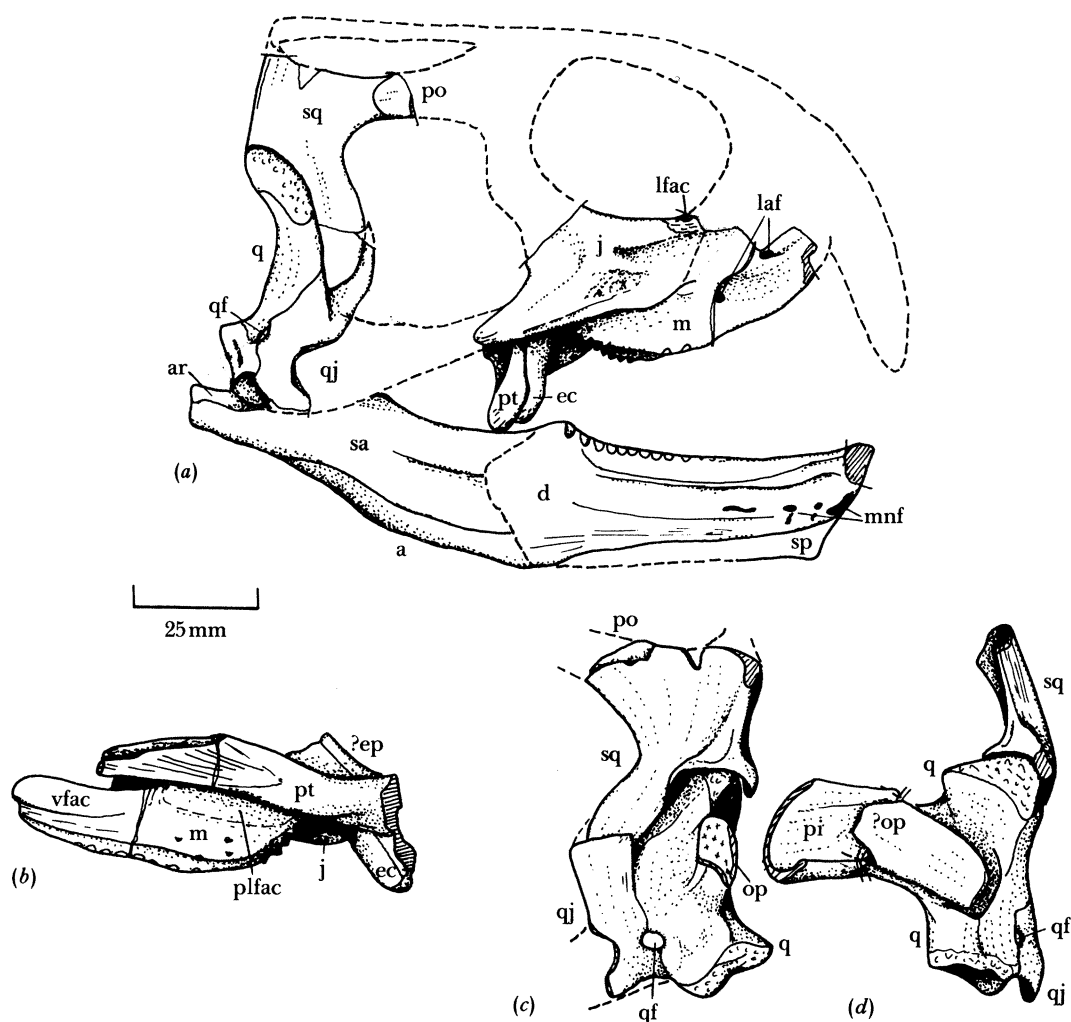


FIGURE 28. *Rhynchosaurus spenceri*. The holotype skull, EXEMS 60/1985.292, in (a) right lateral view, with restored areas indicated by dashed lines; (b) medial view of the palatal portion; and (c, d) medial and posterior views of the quadrate, quadratojugal, squamosal, and opisthotic.

been restored tentatively in the side view of the skull (figure 28), and only partly in the dorsal and ventral views (figure 29), on the basis of *R. articeps* and other rhynchosaur.

In side view, *R. spenceri* has the broad jugal and reduced maxilla of *R. brodiei*, unlike *R. articeps* (figure 28). In dorsal and ventral views (figure 29), the skull is very much wider than those of *R. articeps* or *R. brodiei*. The ratio of maximum width:midline length of the skull is 1.29 in the type specimen of *R. spenceri*, and 0.83 (estimate) in the type specimen of *R. brodiei*. The breadth of the posterior portion of the skull of *R. spenceri* is confirmed by the length of the pterygoid, and by fitting the several portions of the palate and quadrate region together, as well as by the broad posterior splay of the mandibles (figure 31 a).

The skull remains of *R. spenceri* indicate a large range of skull sizes, but most of them seem to be as large as the illustrated skull, EXEMS 60/1985.292, and some are even larger. Midline skull lengths are estimated (table 4) from restored specimens, where possible, but more generally from the maxillary tooth-plates and the dentaries, as for *R. brodiei* (§4.2, table 3) as

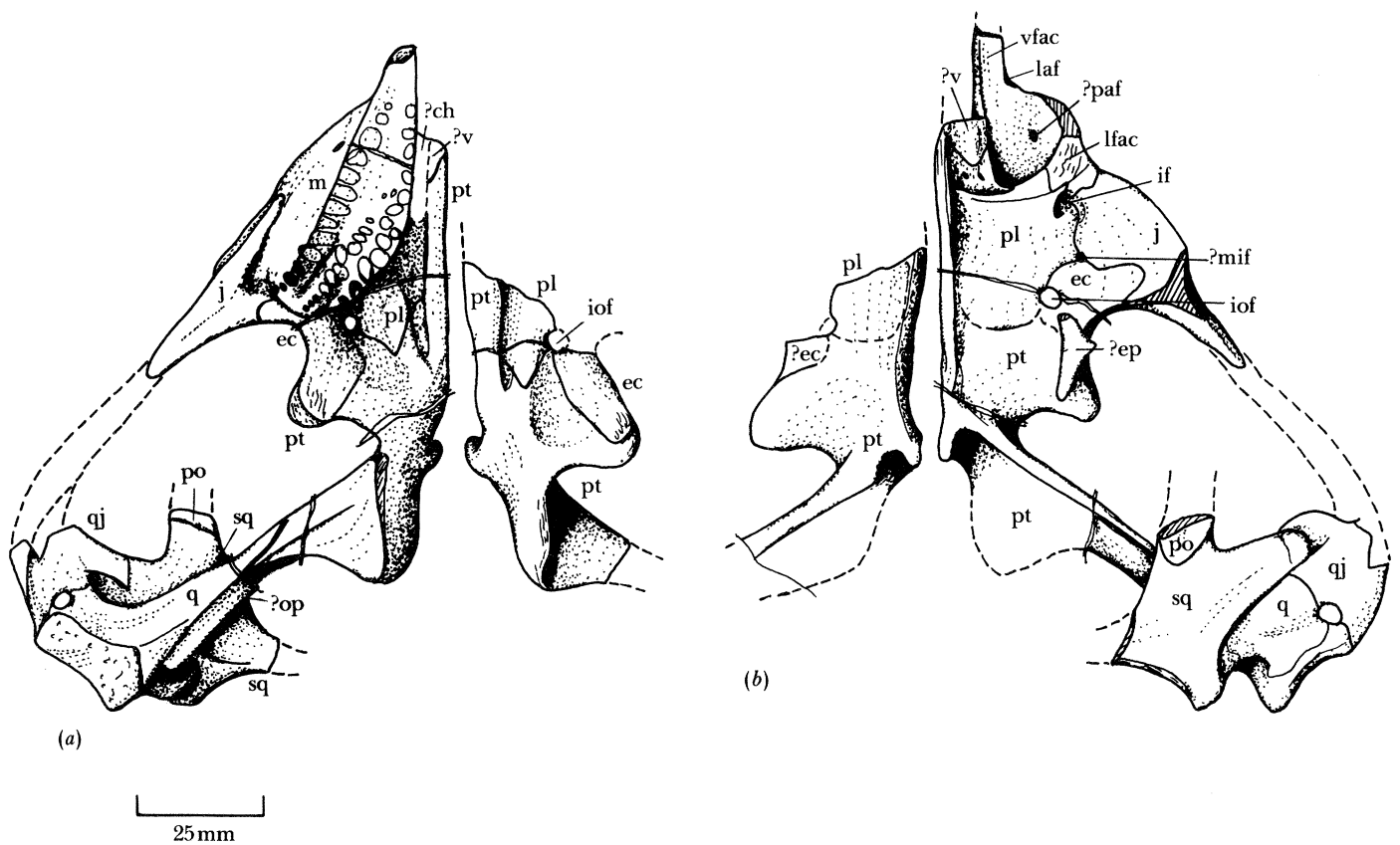


FIGURE 29. *Rhynchosaurus spenceri*. The holotype skull, EXEMS 60/1985.292, in (a) palatal and (b) dorsal views. Restored portions are outlined with dashed lines.

TABLE 4. ESTIMATED SKULL LENGTHS OF SPECIMENS OF *RHYNCHOSAURUS SPENCERI*

(The estimates, and magnitudes of possible errors, are as in table 3.)

	maximum dentary width	maximum premaxilla depth	maximum maxilla width	estimated midline skull length
EXEMS 60/1985.91	—	4.5 mm	—	? 40 mm
EXEMS 60/1985.74	—	—	5 mm	? 40 mm
EXEMS 60/1985.290	—	—	8 mm +	? 65 mm +
EXEMS 60/1985.11	—	7 mm	—	? 70 mm
EXEMS 60/1986.3	—	—	9 mm	? 75 mm
EXEMS 60/1985.13	—	—	10 mm	? 80 mm
BGS GSM 90494	—	—	11 mm +	? 90 mm
EXEMS 60/1985.92	—	10 mm	—	? 100 mm
EXEMS 60/1985.285	—	—	14 mm	? 120 mm
EXEMS 60/1985.56	8 mm +	—	—	? 120 mm +
BMNH R9190	9 mm	—	—	? 130 mm
EXEMS 60/1985.292	10 mm	—	17 mm	140 mm
EXEMS 60/1985.313	10 mm	—	—	? 140 mm
BMNH R330	—	14 mm	—	? 140 mm
EXEMS 60/1985.37-45	—	14 mm	—	? 140 mm
EXEMS 7/1986.6	—	14 mm	—	? 140 mm
EXEMS 65/1984	—	—	18 mm	? 145 mm
EXEMS 60/1985.312	—	—	19 mm	? 150 mm
EXEMS 7/1986.4	—	—	21 mm	? 160 mm
EXEMS 60/1985.46	—	—	—	? 170 mm
EXEMS 60/1985.284	—	—	—	? 175 mm

well as from the premaxillae. Two very large specimens, consisting of an ectopterygoid (EXEMS 60/1985.46) and a partial maxilla (EXEMS 60/1985.284), have been included, with skull lengths estimated from their general proportions.

The range in estimated skull lengths for *R. spenceri* (40–175 mm) is greater than those for *R. articeps* (60–82 mm) or *R. brodiei* (93–140 mm). Although there are relatively few specimens of the two latter species, histograms of the estimated skull lengths (figure 27) show different size distributions, with *R. articeps* being smaller than *R. brodiei*. The size range of *R. spenceri* overlaps that of both of these species, which is probably a function of the considerably larger sample size.

The means of the size ranges of the three rhynchosaurs appear to show a separation into two forms. The mean skull length for *R. articeps* is 71.4 mm, for *R. brodiei* 110.9 mm, and for *R. spenceri* 115.7 mm, the means of the latter two being statistically very similar. The histograms do hint at a separation of *R. brodiei* and *R. spenceri* in terms of the modes of size classes. The specimens of *R. brodiei* fall into two broad ‘classes’ with modes at 90 mm and 110–120 mm. The specimens of *R. spenceri* fall into at least three ‘classes’ with modes at 40 mm, 70 mm and 140 mm. The 140 mm mode is probably further enhanced by three other specimens of *R. spenceri* that could not be tabulated: EXEMS 60/1985.12, 60/1985.67, and 7/1986.5 are portions of lower jaw that match the type specimen in size.

In the following skull description, general points are not repeated from the description of *R. articeps*. Important differences from that species, and from *R. brodiei*, and features in which the specimens of *R. spenceri* offer additional information, are noted.

Dermal bones of the skull roof (figures 28, 29, 30 a–n, 48, 50)

The *premaxillae* (figure 30 a–n, 50 j–n) are known from a sequence of animals of very different sizes, the maximum width in lateral view varying from 4.5 to 14 mm. Their cross section ranges from broadly triangular or rectangular near the distal tip, to droplet-shaped halfway up, to flattened proximally. Several specimens show flattened facets at the proximal end for contact with the maxilla and nasal (fnm, figure 30 d, k–n). There is a facet on the lateral face at the distal end for the tip of the dentary (nd, figure 30 a, e, k, m, 50 l). The premaxilla BMNH R330 (figure 30 f) was figured by Metcalfe (1884, fig. 2) when it was rather more complete. It included the distal tip then, and an additional proximal portion. The specimen was stated to have been ‘ $3\frac{1}{2}$ inches in the arc, by $\frac{13}{25}$ inch in greater diameter when entire’ (that is, about 89 mm long by about 13 mm across, although Metcalfe’s published illustration suggests measurements of 70 mm and 16 mm respectively). His illustration may have been reduced in the press, as a manuscript drawing by him in BMNH matches his quoted measurements. The present measurements are 35 mm long by 14 mm wide.

The *maxilla* is very like that of *R. brodiei*, especially in ventral view (figures 29 a, 48 a). In lateral view there are several clearly developed lateral alveolar foramina (laf, figure 28 a). Dorsally, there are indications of the superior alveolar canal (?paf, figure 29 b), and this is shown in several of the isolated maxillae, just as in *Hyperodapedon* (Benton 1983, figs 6 b, 8).

The *nasals*, *frontals*, *parietals*, *supratemporals*, *lacrimal*, *prefrontal*, and *postfrontal* are not present, and the *postorbital* is represented only by a posterior fragment (figures 28 a, c, 29 b, 48 b, d). The *jugal* is the largest element in the side view of the skull. There is a facet at the front where it probably contacted the lacrimal (lfac, figures 28 a, 29 b). The lateral face of the bone is sculpted with coarse rounded bumps and troughs, as seen in *Hyperodapedon gordonii*, but not in *R. articeps* or *R. brodiei*. In dorsal view, the jugal enters the floor of the orbit, and it is not clear, as also in *R. brodiei*, whether *R. spenceri* had a median jugal foramen or not (?mjf, figure 29 b).

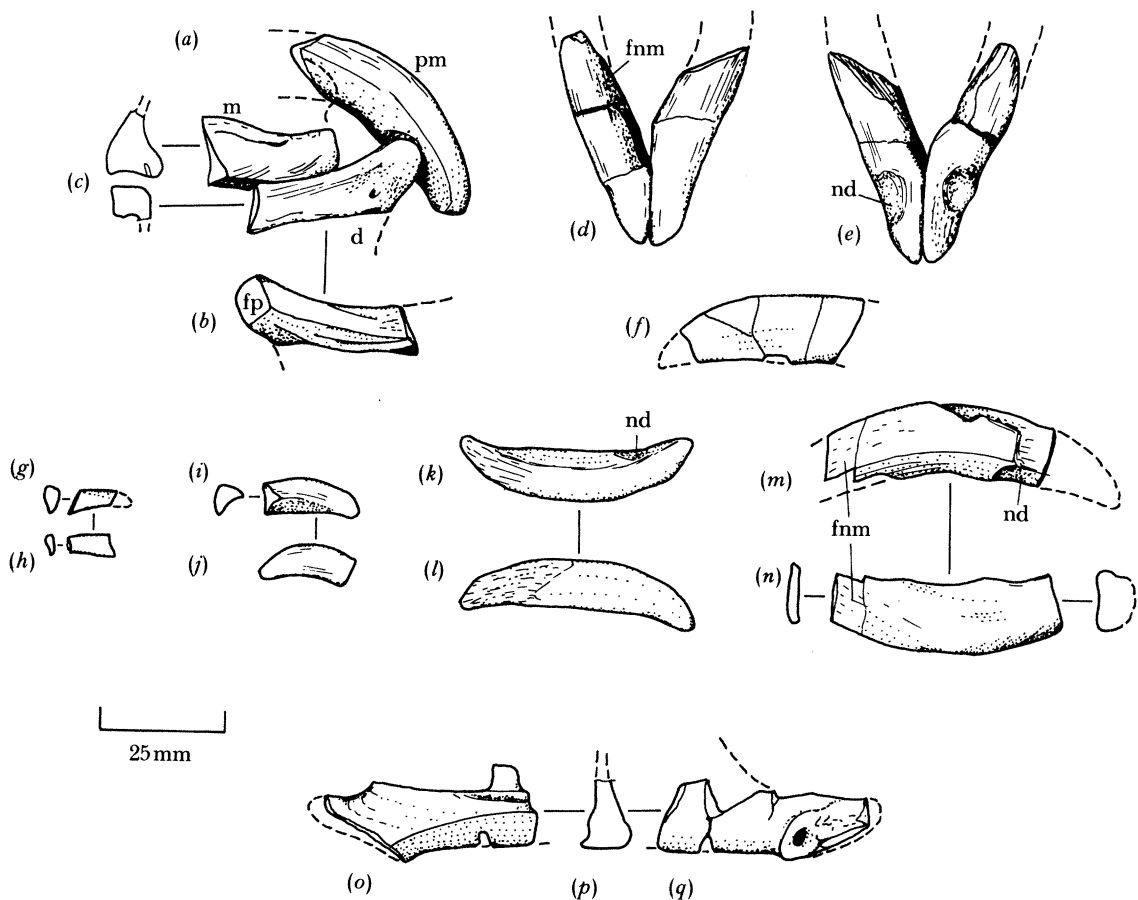


FIGURE 30. *Rhynchosaurus spenceri*. Isolated skull and mandible remains. (a-e) Partial snout, EXEMS 60/1985.37-45, with premaxillae, anterior maxilla, and anterior dentary, in right lateral (a), medial (b), and cross section (c) views, and in anterior (d) and posterior (e) views of the premaxillae; (f) left premaxilla, BMNH R330, in lateral view; (g-n) isolated premaxillae of the right (g-i, m, n) and left (k, l) sides, in lateral (g, i, k, m) and medial (h, j, l, n) views, EXEMS 60/1985.91 (g, h), EXEMS 60/1985.11 (i, j), EXEMS 60/1985.92 (k, l), EXEMS 7/1986.6 (m, n); and (o-q), anterior portion of left splenial, EXEMS 60/1985.67, in lateral (o), cross section (p), and medial (q) views, showing the symphysis.

The *quadrotojugal* is preserved only in part, lacking the anterior process that met the jugal (figures 28a, c, d, 48b, d). The quadrotojugal has a long contact with the quadrate, and there is a large circular quadrate foramen. In lateral view (figures 28a, c, 48b, d) the quadrotojugal forms a slit-like pocket to receive the ventral branch of the squamosal, and a rectangular sheet of the quadrotojugal lies behind that branch and forms the lower part of the margin of the lower temporal fenestra. The quadrotojugal seems to have been a broad element, as in most larger rhynchosaur, and unlike the apparently narrow bone seen poorly preserved in *R. articeps*.

The *squamosal* is preserved nearly complete (figures 28, 29, 48b, d) except for the medial branch that would have contacted the supratemporal and parietal. In posterior view (figures 28c, d, 48d) a broad subvertical thickened pillar of the squamosal runs down to a broad triangular end which supports a deep recess into which the massive dorsal head of the quadrate fits. This process was also probably involved in the lateral attachment of the paroccipital process and extracolumella, as in *Hyperodapedon*.

Dermal bones of the palate (figures 28 a, b, 29, 48)

The *vomers* may be represented by short fragments, but their sutures with the pterygoids cannot be made out (figures 29, 48*a*) and a broad facet on the maxilla may mark a posterior contact (vfac, figures 28*b*, 29*b*). The *palatine* is fairly completely preserved, although the medial and anterior contacts are not clear in ventral view (figures 29*a*, 48*a*). A facet on the medial face of the maxilla shows the broad palatine contact (plfac, figure 28*b*). In dorsal view the palatine forms much of the floor of the orbit, and it surrounds an inferior orbital foramen (iof, figure 29*a*, *b*) as well as an infraorbital foramen (if, figure 29*b*), as in *Hyperodapedon*.

The *ectopterygoid* (figures 29, 48*a*) is very like that of *R. brodiei*, forming contacts with lateral palatal elements, and having a striated posterior margin. The right *pterygoid* is fairly completely preserved (figures 28*b*, *d*, 29, 48*a*, *c*), the left less so. The anterior branches are vertically placed and they have a striated contact surface in the midline (figures 28*b*, 48*c*), as in *Hyperodapedon*. The lateral branch that contacts the palatine and ectopterygoid has a striated posterior margin. This branch swings up and back to provide contact for the epipterygoid above and the basiptyergoid processes of the braincase below, but these parts are not clearly exposed. This part turns and runs back as a thin sheet to contact the quadrate, which sends out a long medial process beneath it (figures 28*d*, 29*a*, 48*a*). There is a clear diagonal ridge on the anterior face, running ventrolaterally towards the quadrate, as in *Hyperodapedon*.

Quadrate and epipterygoid (figures 28, 29, 48)

The *quadrate* is well preserved. It consists of a vertical pillar-like portion which fits into a deep socket beneath the squamosal, and is roughly triangular in cross-section. It supports the articular condyle, which is roughly rectangular, being broadest medially and constricted in the middle (figures 29*a*, 48*a*), with a marked twist. The various contacts of the quadrate, with the quadratojugal, squamosal, and pterygoid, have been noted above.

The *epipterygoid* is represented by a possible displaced fragment resting on the dorsal surface of the palate (figures 28*b*, 29*b*, 48*c*). This fragment consists of a broadly triangular bone, which could be part of the ventral portion that contacts the pterygoid, and this passes into a narrow strap-like process which has a flattened oval cross section, just as in *R. articeps* and *Hyperodapedon*.

Endocranium (figures 28 d, 29 a, 48 a)

The braincase is not preserved complete, but its general shape may be inferred from the position of the pterygoids. The only possible braincase element preserved is a rectangular rod of bone that lies just behind the quadrate, and separated from it by 4–8 mm of matrix (?op, figures 28*d*, 29*a*, 48*a*). This could be the lateral end of the paroccipital process, made from the *opisthotic*, by comparison with other rhynchosaurs, although the element has been displaced downwards from its true location at the contact of the squamosal and the quadrate.

6.2. Mandible (figures 28 a, 30 a–c, o–q, 31, 49)

The best-preserved mandibles are those of EXEMS 60/1985.292, the type specimen. Additional information on the dentary and splenial was obtained from EXEMS 60/1985.37–45 and 60/1985.65; several other specimens showed further details of the tooth-bearing portions of the dentary.

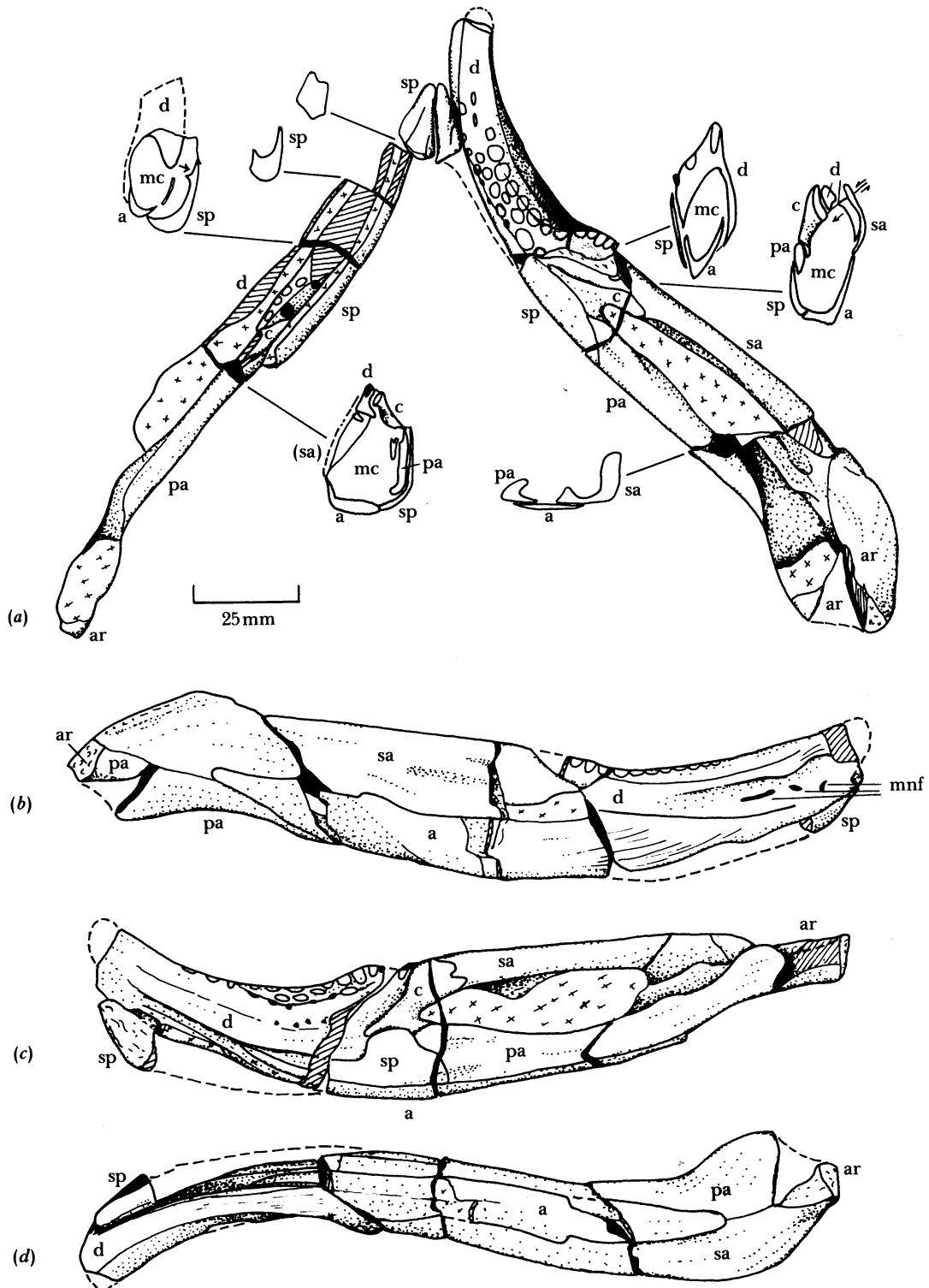


FIGURE 31. *Rhynchosaurus spenceri*. Mandibles of the holotype specimen, EXEMS 60/1985.292 in (a) dorsal, (b) right lateral, (c) right medial and (d) right ventral views. Cross sections of the mandibles are shown in (a), with the outlines traced from broken surfaces.

The full extent of the *dentary* is not certain, but it probably formed just over half of the total length of the mandible, which is more like the condition in *R. brodiei* (estimated as three fifths) than in *R. articeps* (two thirds). The anterior tip of the dentary bears a curved rectangular facet where it rubs against the premaxilla (fp, figure 30*b*). In lateral view, a number of large mandibular foramina can be seen (mnf, figures 30*a*, 31*b*), as in other rhynchosaur. The shape of the dentary and the teeth (see §7) are generally as in *R. brodiei*. Cross sections of the mandible (figure 31*a*) show similar internal arrangements to those seen in other rhynchosaur (Benton 1983, 1984*b*).

The *splénial* is preserved only incompletely. There is a large rugose symphyseal portion at the anterior end (figures 30*q*, 31) which intermeshes with the symphysis on the other side, but this intramandibular joint must have been rather flexible in life as the two elements separate readily before fossilization. The contacts of the splénial with the dentary, angular, prearticular, and coronoid may be seen in medial view, and in the cross sections (figure 31).

The *coronoid* is better represented than in either *R. articeps* or *R. brodiei*, and it shows exactly the same complex shape as in *Hyperodapedon*, containing the prearticular, dentary and surangular (figures 31*a*, *c*, 49*a*, *b*). Likewise, the posterior jaw elements, the *angular*, *surangular*, *prearticular* and *articular*, are well represented, and appear to show the same features as in other rhynchosaur (figures 31, 49*a*, *b*). The cross sections (figure 31*a*) show, for example, how the angular is V-shaped anteriorly, and becomes L-shaped further back, and finally flat where it lies beneath the adductor fossa. The surangular starts anteriorly as a vertical sheet high on the side of the jaw, and descends to the floor near the back of the adductor fossa where it forms a clear midline vertical sheet, as in other rhynchosaur. The articular is a thick element that lies on the sheet-like prearticular and surangular. The glenoid fossa appears to be roughly transverse in orientation, and behind it, the articular forms a short retroarticular process. This seems to bear a vertical slit-like opening near the midline, as in *Hyperodapedon* (Benton 1983, fig. 13*a*), but this is obscured by a missing fragment (figures 31*b*, *c*, 49*a*, *b*).

6.3. Postcranial skeleton (figures 32–34, 48*f*, *g*)

Postcranial remains of *R. spenceri* include only two short series of dorsal vertebrae and a partial left forelimb (humerus, radius, ulna). No other rhynchosaurian vertebrae, ribs, or appendicular remains have been identified.

Dorsal vertebrae (figure 32)

Dorsal vertebrae are represented by specimens EXEMS 60/1985.15 (two vertebrae) and 60/1985.57 (three vertebrae). The centra are roughly circular in cross section, and they are strongly constricted in the middle, which produces a slight ventral crest (figure 32*d*, *i*). The amphicoelous terminal facets are surrounded by rugose areas, which may suggest that the centrum was finished in cartilage. There is a deep curved excavation on the upper posterior margin of one of the larger vertebrae between centrum and neural arch (figure 32*e*), which is not known in other rhynchosaur. The suture between the centrum and the low laterally compressed neural arch is clearly visible in larger specimens (figure 32*e*). The rib articulations are projected on short transverse processes, and the diapophysis is rounded in lateral view (figure 32*a*, *e*), as in *R. brodiei* and most larger rhynchosaur except *Hyperodapedon gordonii*, which has flatter diapophyses.

The five vertebrae are probably anterior to mid-dorsals in the range of presacrals 10–20. The

centra are longer than those of the anteriormost dorsals, the neural spine is lower than in anterior or posterior dorsals, and the zygapophyseal angle of 30° matches that of dorsals 10–20 in *Hyperodapedon*. The two larger vertebrae may be anterior dorsals (presacrals 10–15) because of the slightly vertically oriented pear-shaped rib facet (figure 32*e*), in which the parapophysis and diapophysis were close to each other, but not quite fused. The three smaller vertebrae may be in the region of presacrals 15–20 because the neural spine base is relatively shorter, and the rib facet seems to show parapophysis and diapophysis fully fused. The vertebrae are like those of *R. brodiei* and other rhynchosaurs (see §4.5).

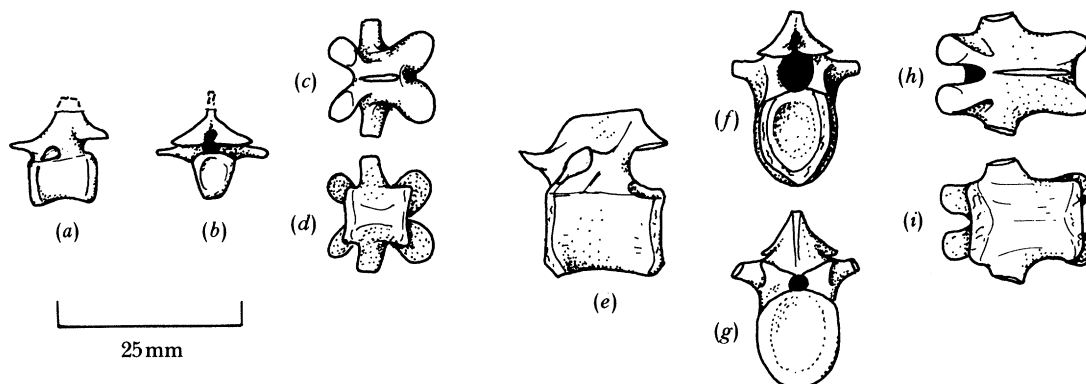


FIGURE 32. *Rhynchosaurus spenceri*. Dorsal vertebrae. (a–d) EXEMS 60/1985.57, in lateral, posterior, dorsal, and ventral views; (e–i) EXEMS 60/1985.15, in lateral, posterior, anterior, dorsal, and ventral views. The centrum in (a–d) and the anterior view (g) are largely restored.

Forelimb (figures 33, 48*f, g*)

A left forelimb (humerus, radius, ulna) is preserved (EXEMS 60/1986.282).

The humerus (figures 33*a–e*, 48*f, g*) has the expanded ends and narrow shaft of all rhynchosaur humeri. The proximal end bears a narrow posterior articular surface and a heavy deltopectoral crest. The shaft is ovoid to triangular in cross section, and it twists so that the proximal and distal articular ends are set at an angle of 45° to each other. The broad flat distal end bears a deep depression on the ventral side, which is much more sharply bounded than in *Hyperodapedon* or *Stenaulorhynchus*. The ectepicondyle, with its supinator crest, and the distal articular surface are incomplete. The distal end (maximum estimated width 35 mm) is narrower than the proximal end (maximum width 45 mm), a similar relation to that seen in other rhynchosaurs.

The radius (figures 33*f–k*, 48*f, g*) is a flattened element, slightly concave on the anterior face. It expands proximally, with a well-defined curved hollow area on the posterior face (figure 33*i*) as in *Stenaulorhynchus* (Huene 1938, pl. 7, fig. 4), and more clearly developed than in *Hyperodapedon*. The proximal articular surface is divided into two facets (figure 33*j*), a short lateral one that faces dorsolaterally at an angle of 45° , a facet for articulation with the medial edge of the ulna (uf, figure 33*f, i, j*), and a longer curved medial facet for articulation with the humerus. The distal articular face is more triangular in shape (figure 33*k*), with a curved anterior edge, and a pointed posterior edge that matches a slight midline ridge near the distal end (figure 33*i*).

The ulna (figure 33*l–p*) may have been slightly longer than the radius, but it is incomplete distally. The cross-sectional dimensions of the shaft are similar to those of the radius (in most

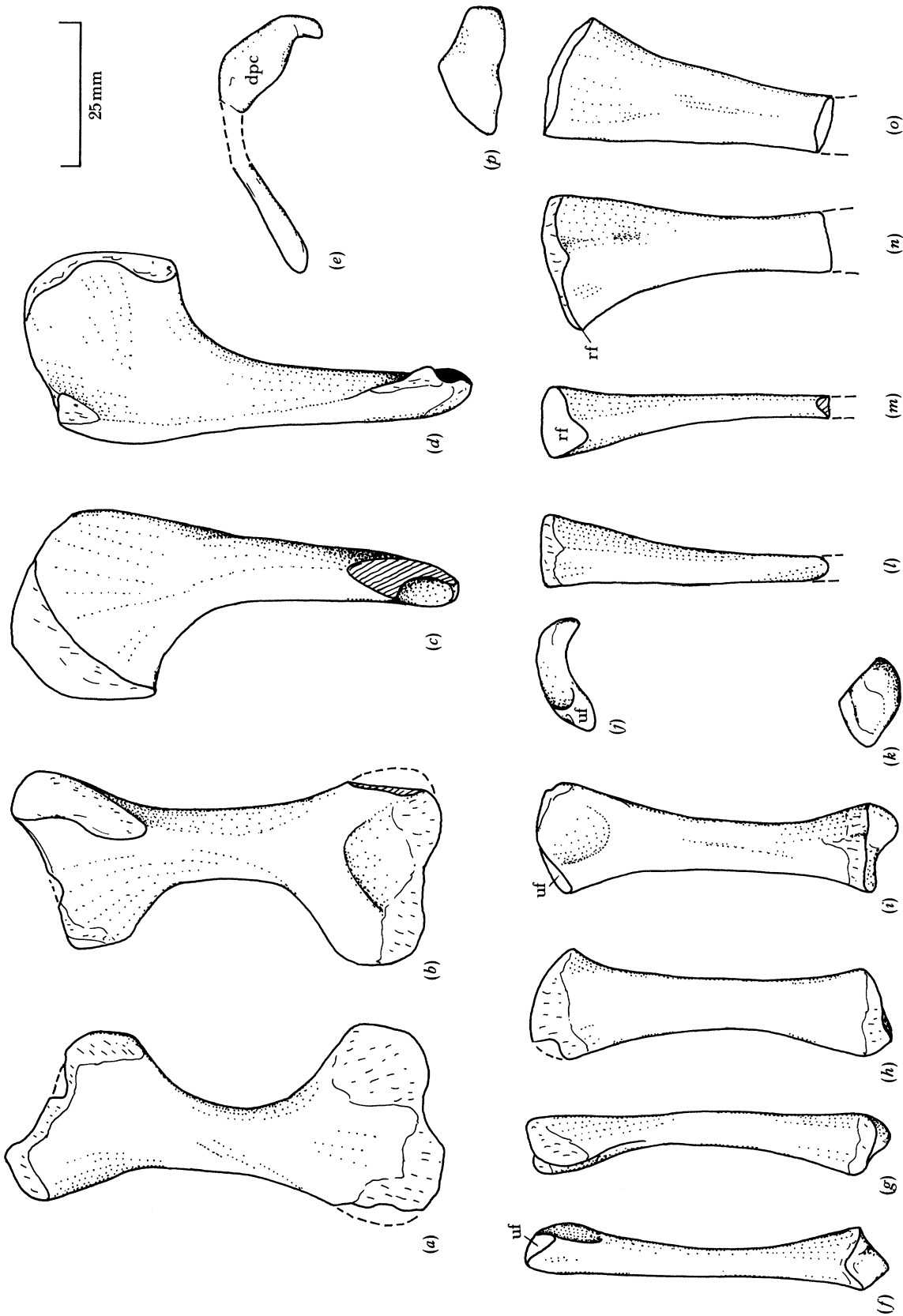


FIGURE 33. *Rhynchosaurus spenceri*. Elements of the left forelimb EXEMS 60/1985.282. (a-e) The humerus in (a) dorsal, (b) ventral, (c) anterior, (d) posterior and (e) proximal views. (f-k) The radius in (f) lateral views, (g) medial, (h) anterior, (i) posterior, (j) proximal and (k) distal views. (l-p) The ulna in (l) lateral, (m) medial, (n) anterior, (o) posterior and (p) proximal views. The distal end of the humerus is damaged, and the distal end of the ulna is missing.

other rhynchosaurs the radius is distinctly more slender than the ulna). In anterior and posterior views (figure 33*n, o*), the lateral margin of the shaft is much straighter than the medial margin, a feature of most rhynchosaurs. The broad proximal end bears a convex cordate articular surface (figure 33*p*), as in other rhynchosaurs, and the point in the outline is matched by a clear midline ridge on the anterior face (figure 33*n*). The straight medial edge of the articular surface contacts the radius, and lies above the area of the ulna that articulates with the ulnar facet of the radius (rf, figure 33*m, n*).

Function of the forelimb (figure 34)

It is clearly not possible to study joint mobility and musculature of the forelimb in any detail because the shoulder girdle, wrist, and hand are unknown, and the distal end of the humerus (elbow joint) is also damaged. What is known fits the model described for *Hyperodapedon* (Benton 1983, pp. 677–680). The fact that the radius, and probably the ulna, are shorter than the humerus, points to a sprawling or semi-erect forelimb gait (criteria of Bakker 1971). The great breadth of the proximal end of the humerus, and its L-shape, suggest a long subhorizontal sweep of the upper arm during a forelimb stride, over an arc of about 100°, as in *Hyperodapedon*.

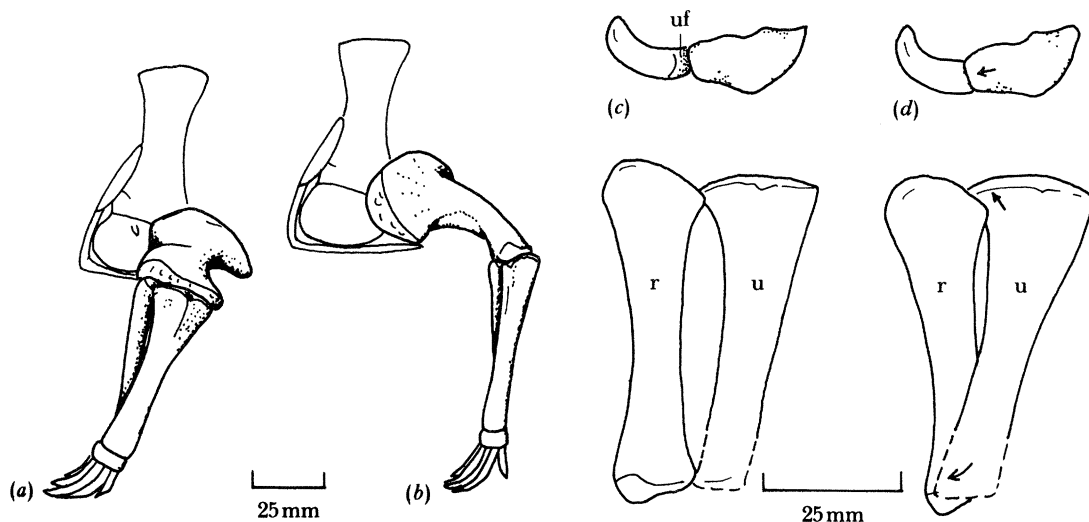


FIGURE 34. *Rhynchosaurus spenceri*. (a, b) The restored forelimb gait, based on EXEMS 60/1985.282, with the foot and shoulder girdle from *Hyperodapedon*, shown in left lateral view. The limb is shown at the most anterior position, at the beginning of a stride (a), and at the posterior extent of the back-swing (b). During the stride, the radius and ulna twist, and the ulna slips up onto a facet on the radius (c, d).

During the power stroke, the radius and ulna probably rotated with respect to each other and with respect to the distal end of the humerus (figure 34). At the beginning of the power stroke, with the humerus swung well forward, the radius was probably elevated slightly. As the humerus swung back through a lateral orientation to the posterolateral extreme, the ulna rose considerably during the stride on to the ulnar facet of the radius (uf, figure 34*c, d*). The twist of the forearm during the backwards swing of the humerus would have allowed the hand to maintain its orientation on the ground. The power stroke elevated the body (figure 34*a, b*) and moved it forward.

7. DENTITION OF *RHYNCHOSAURUS*(figures 2–5, 7, 23, 24, 31, 35–37, 45*d*, 46, 47, 49, 50)

The rhynchosaur dentition is unusual in several respects (Chatterjee 1974; Benton 1984*b*). There are multiple rows of teeth; the teeth have ankylothecondont implantation (that is, the deeply rooted teeth are fused to the bone of attachment, but there is no socket); and there is no typical reptilian tooth replacement from below. New teeth are added at the back and medially, and they are progressively worn from front to back of the jaw. The teeth are arranged in longitudinal 'Zahnreihen', each of which shows an ontogenetic series of teeth, ranging from newly ankylosed teeth at the back to fully worn and largely resorbed teeth at the front of the jaw.

The dentition of all three species of *Rhynchosaurus* is described in this section. The teeth are best seen in *R. brodiei*, but additional points may be observed in *R. spenceri* from Devon. *R. articeps* is important for historical reasons, which are considered first.

7.1. History of research

Owen (1842*b, c*) noted 'the apparent absence of teeth' in the original specimens of *R. articeps*, although he observed that the lateral edge of the maxilla was 'slightly dentated'. The jaws were firmly closed, and Owen was clearly not sure about the 'edentulous character of this very singular Saurian'. However, later (Owen 1863) he referred to *R. articeps* as being toothless, like the mammal-like reptile *Dicynodon* with which he sought to ally the rhynchosaurs. Owen (1859) also noted 'traces of dental structure' in the premaxillae, which he went on to describe in more detail (Owen 1863, p. 466): 'the bony tissue of the produced tips [of the premaxillae] acquiring the hardness and almost the texture of dentine'. Huxley (1869, 1887) and Lydekker (1885, 1888) repeated Owen's view that *R. articeps* had no teeth on its upper or lower jaws, which was presumably the reason why the rhynchosaur specimens from Warwick, Bromsgrove and Devon had to be placed in the genus *Hyperodapedon*. The specimens of *H. gordonii* from Elgin, known since 1859, clearly had several rows of teeth on the maxilla and at least one on the dentaries, and toothlessness was cited as a diagnostic character of *Rhynchosaurus* (i.e. *R. articeps*).

Several authors have reported palatal teeth in *R. articeps*. Huxley (1887, p. 690) noted evidence of teeth on 'palatal bones' (i.e. the palatine) arranged in one or two longitudinal rows. This row, or rows, clearly visible in BMNH R1236 (figures 5*c*, 45*d*) (Huxley 1887, pl. 27, fig. 1) is actually the medial row on the maxillary tooth-plate. Woodward (1907, p. 296, pl. 2, fig. 1) stated that he observed 'stumpy teeth' on a pair of longitudinal ridges on the pterygoid. He also repeated Huxley's observation of a row of teeth on the 'palatine' (i.e. maxilla). He clearly indicated that the dentary also bore 'a single row of stumpy teeth', as seen in BMNH R1236. Huene (1929, p. 40; 1938, p. 111; 1939*b*, p. 50) recognized rows of teeth on the maxilla and dentary, and also described six or seven teeth placed medially in a longitudinal row on the pterygoid.

7.2. Pterygoidal teeth?

The question of pterygoidal teeth is important. Primitive rhynchosaurs, such as *Howesia* and *Mesosuchus*, had multiple rows of palatal teeth (Broom 1906; Haughton 1924; Malan 1963; Chatterjee 1969, 1974, 1980; Benton 1983). Chatterjee (1969, 1974, 1980) discovered a single medial row of about five teeth on the pterygoid of *Stenaulorhynchus*, a discovery that apparently

accorded with Woodward's (1907) and Huene's (1929, 1938, 1939*b*) observations on *R. articeps*. This primitive character (possession of palatal teeth) was used by Chatterjee (1969, 1974) and Benton (1983) as part of a diagnosis of the Rhynchosaurinae (i.e. the Middle Triassic forms *Stenaulorhynchus* and *Rhynchosaurus*). Benton (1984*a*, 1985) used the synapomorphy 'single row of teeth on pterygoid' (as compared with the primitive state, 'multiple rows') as part of the definition of the Rhynchosaurinae.

The single rows of pterygoidal teeth in *Stenaulorhynchus* and *Rhynchosaurus* have not been adequately illustrated, and their presence is not yet clearly demonstrated. The specimen of *Stenaulorhynchus* figured by Chatterjee (GPIT 317*a*) does not show pterygoidal teeth (figure 45*e*), nor does an extremely well preserved pair of pterygoids of another specimen of that genus (BMNH, unnumb.). These latter show small (10–15 mm long) ridges on the medial portion of the pterygoid, as in *R. articeps*, but no teeth. Further, close examination of the relevant specimens of *R. articeps* (SHRBM G132/1982; BMNH R1236, R1237; MANCH L7642) has not confirmed the presence of pterygoidal teeth, although it must be noted that the specimens BMNH R1237 and MANCH L7642 are not well enough preserved for any clear determination to be made. In BMNH R1236, there are indeed longitudinal ridges on the medial portion of the pterygoids (figures 5*c*, 45*d*), but there is no unequivocal evidence for teeth on these ridges. The relevant portions of the pterygoid are not preserved in *R. brodiei*, but the Devon *Rhynchosaurus* clearly lacks pterygoidal teeth (figure 29*a*).

7.3. Maxillary teeth

The maxillary tooth-plates are divided by a main central longitudinal groove, which is seen in adults and juveniles (figures 23*d*, 35, 36*a, b, d, i, k*, 47, 50*b, c, f*). There is a subsidiary groove,

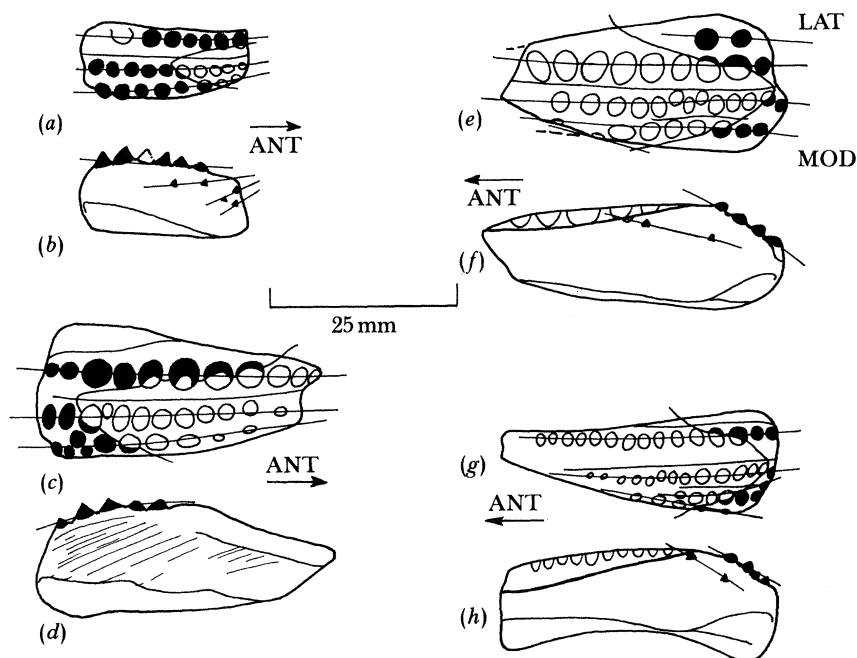


FIGURE 35. *Rhynchosaurus brodiei*. Outlines of maxillary tooth-plates, showing unworn teeth (shaded black), worn teeth (unshaded), suggested 'Zahnreihen' (thin lines), and areas of occlusion. (a–d) Right maxillae; (e–h) left maxillae; all in ventral and medial views. (a, b) WARMS Gz955; (c, d) WARMS Gz960; (e, f) BGS GSM 90493; (g, h) GBS 59745.

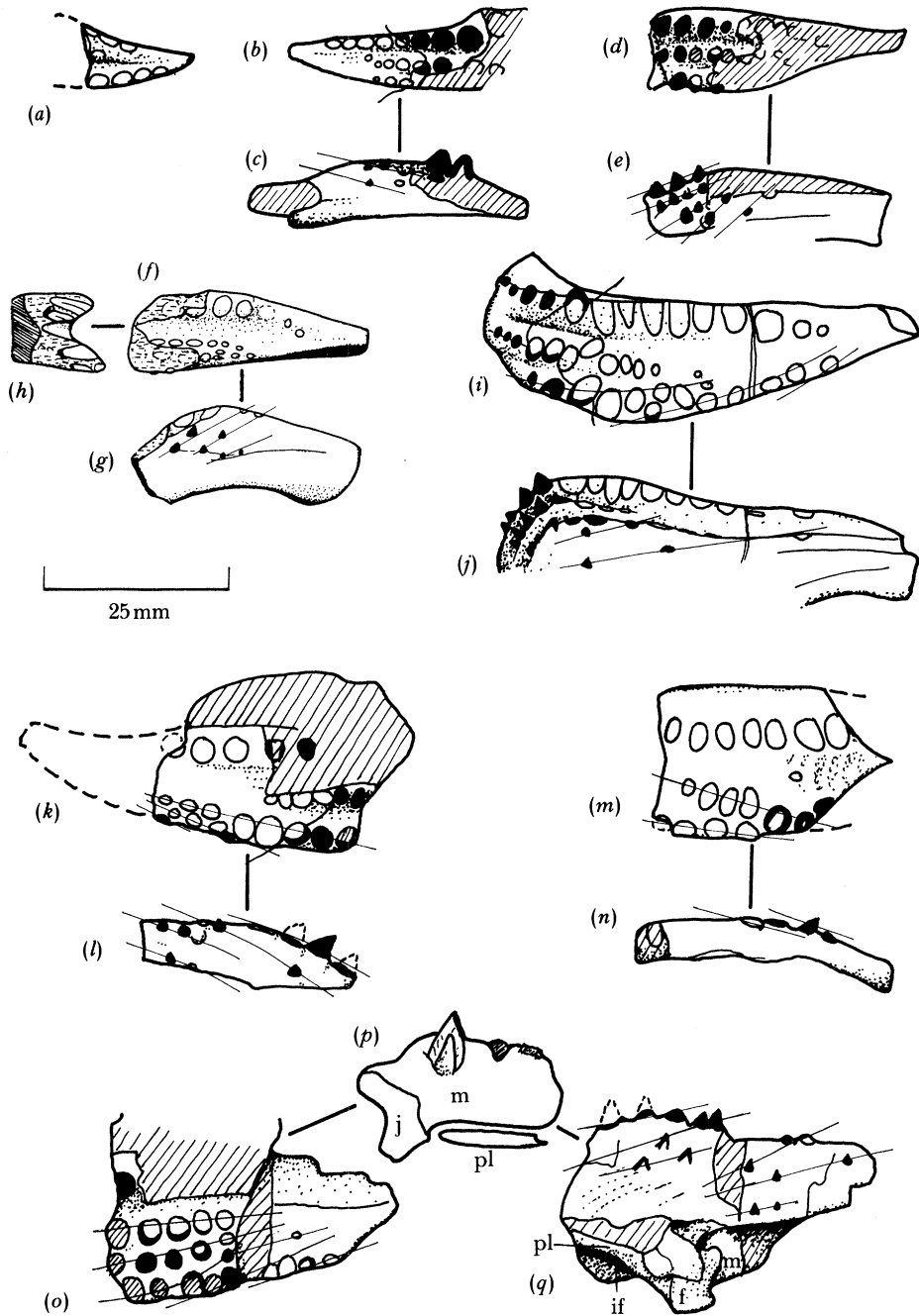


FIGURE 36. *Rhynchosaurus spenceri*. Maxillae of the right (a, d-j, o-q) and left (b, c, k-n) sides of (a) EXEMS 60/1985.290; (b, c) EXEMS 7/1986.3; (d, e) EXEMS 60/1985.13; (f-h) BGS GSM 90494; (i, j) EXEMS 60/1985.292; (k, l) EXEMS 65/1984; (m, n) EXEMS 60/1985.312; and (o-q) EXEMS 7/1986.4. Unworn teeth are shaded solid, worn teeth, and worn areas of teeth, are shown blank, and 'Zahnreihen' are shown by thin lines. Specimens are shown in occlusal (a, b, d, f, i, k, m, o) and medial (c, e, g, j, l, n, q) views, with cross sections as seen on broken surfaces in (h) and (p).

near the back, on the medial side of the main groove, seen only in older specimens. In ventral view, there are generally three longitudinal rows of teeth (four in larger animals), one (or two) lying laterally to the main groove, and two lying medially. The subsidiary groove lies between these two medial rows. The longitudinal 'Zahnreihen' are not so simple, however. There are newly ankylosed teeth on the medial side, and these run down and forwards to the occlusal edge, where they pass over on to the ventral surface of the tooth-plate (figures 35, 36, 47, 50).

The teeth from juvenile and adult *R. brodiei* and *R. spenceri* show clear patterns of wear. A juvenile maxilla (figures 35*a, b*, 47*a*) shows nearly all the teeth unworn, and the second groove hardly developed. A slightly larger specimen (figures 35*g, h*, 47*d-h*) shows extensive tooth wear, and only a few unworn teeth at the back. There is a small subsidiary groove on the medial side. Two larger specimens (figures 35*c-f*, 47*b, c*) also show extensive areas of wear, and some unworn teeth at the back. The teeth in occlusion are large. In one of these specimens (figures 35*e, f*, 47*c, i*) an additional tooth row has started on the lateral side of the main groove.

As far as can be seen, all maxillary teeth have deep roots and conical pointed crowns. The teeth on the lateral side of the main groove are always larger (2–4 mm diameter) than the medial ones (1–2.5 mm diameter). The teeth are circular in cross section, with no subtriangular ones, as seen in *Hyperodapedon*. However, angled wear planes often give to the teeth an apparently elliptical cross section (figures 36*i, m*, 50*g*); the worn root portions may have a slightly square shape in some cases, possibly as a result of their close packing in the bone of the maxilla. It has not been possible to section any of the tooth-bearing elements, but the evidence from broken surfaces suggests that *Rhynchosaurus* had deep-rooted teeth as in *Stenaulorhynchus*. A section across a maxillary tooth-plate, seen in BMNH R8494, shows that the root of a lateral tooth was straight-sided, solid, and at least 5 mm long. The dentine is preserved with an orange colour, as in specimens of *Stenaulorhynchus* and *Hyperodapedon* (Benton 1984*b*).

Broken specimens of *R. spenceri* show details of the shape of maxillary teeth (figures 36*h, k, l, p*, 50*f, h*). Newly ankylosed teeth are circular to elliptical in cross section and have a large hollow pulp chamber. They are closely packed, and the packing seems to account for the 'squashed' elliptical shape of some. The tooth has a pointed thimble-like shape, and thin dentine walls. Older anterior teeth have thicker walls.

7.4. Dentary teeth

The teeth of the dentary are arranged in several longitudinal rows (figures 24, 37, 46, 49). The lateral row is elevated on a sharp crest that rises posteriorly well above the occlusal surface (figures 24*c, g*, 37*g, i*, 49*g*). In this posterior region, the teeth are generally unworn, as they have not yet come into occlusion. *R. brodiei* has one main medial row of teeth and a scattering of small lingual teeth (figure 24); *R. spenceri* has two to four medial tooth rows, lying both on the occlusal surface of the dentary and on the medial side. Most of the teeth are worn flat by contact with the maxilla, but the most posterior ones, and those on the medial face, are unworn. In large specimens of *R. spenceri*, there is a clear groove on the occlusal surface just medial to the rising lateral tooth row (gr, figure 37*f, h, i*).

The teeth are conical and deep-rooted. A broken newly ankylosed tooth (figures 24*g, h*, 46*j, k*) is hollow and thimble-shaped: the pulp chamber has not yet started to fill with dentine. In older worn teeth, the pulp chamber fills, and tooth becomes solid dentine from top to bottom. The dentary teeth are generally circular or subrectangular in cross section and deeply rooted,

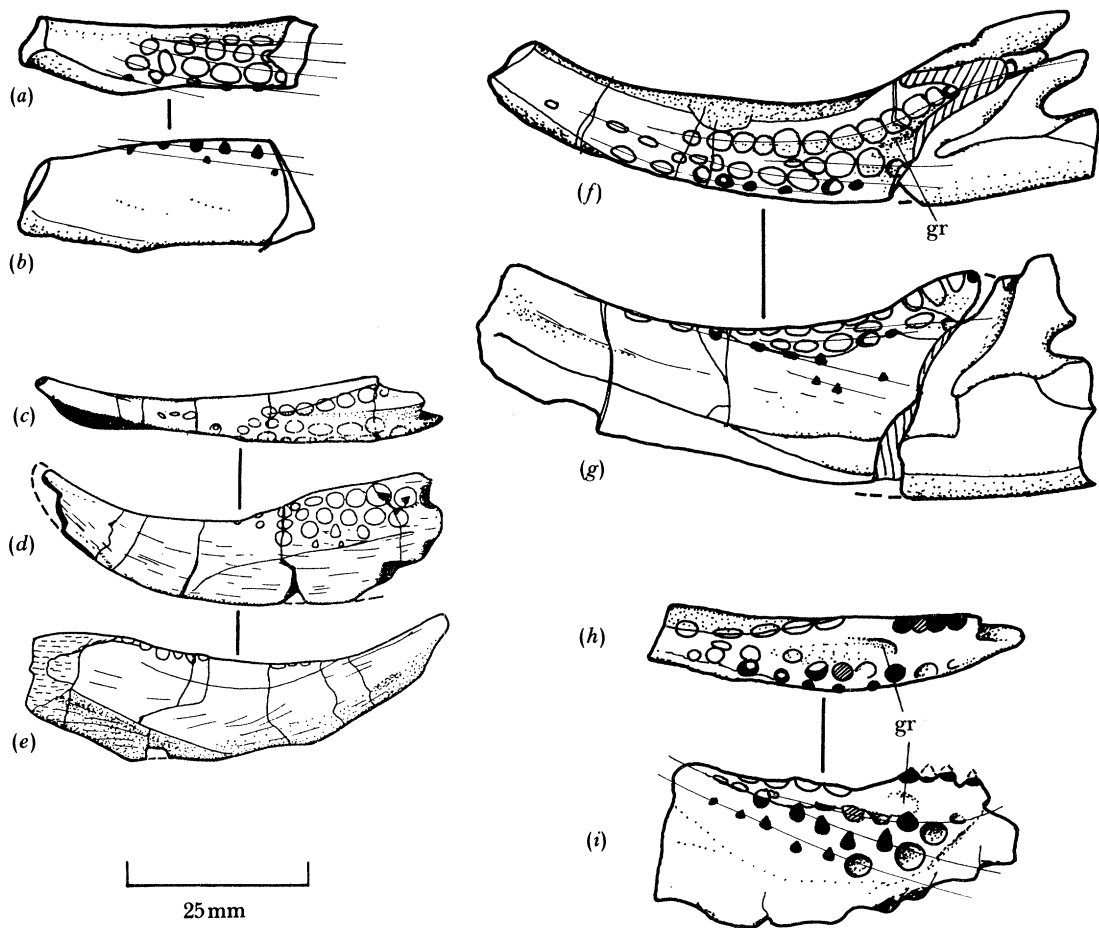


FIGURE 37. *Rhynchosaurus spenceri*. Dentaries of the right side of (a, b) EXEMS 60/1985.56; (c-e) BMNH R9190; (f, g) EXEMS 60/1985.292; (h, i) EXEMS 60/1985.313. Conventions are as in figure 33. Specimens are shown in occlusal (a, c, f, h), medial (b, d, g, i) and lateral (e) views. Note the unankylosed tooth pits in (i).

as is seen on broken surfaces (figures 31, 49a-c). Those in the lateral row have the deepest roots, whereas the medial teeth are generally smaller and often not deeply rooted. Unworn tooth crowns are conical and pointed.

7.5. Tooth wear and jaw occlusion

The longitudinal groove is clearly an inherent part of the rhynchosaur maxilla, and it has not been produced solely by wear, because the groove is present in the unworn posterior region (Chatterjee 1974). Nevertheless, the main groove is deepened by wear from the crest of the dentary, and the occlusal surface of the maxilla is further modified by the action of the jaws. In the specimens of *Rhynchosaurus*, it is easy to see which teeth have been worn, and which have not. Firstly, newly erupted rhynchosaur teeth have a coating of dark-brown or black enamel on their crowns. This is removed with wear, and the yellowish or pink-stained dentine is exposed. Secondly, the wear flattens the teeth until the crowns are removed to the level of the surrounding bone. In figures 24 and 35-37 the areas of wear on the maxillae and dentaries are marked out. These areas are semi-elliptical in plan, and they start near the back of each tooth-plate and expand sideways to encompass the entire width of the tooth-plate in the middle and

anterior regions. Additionally, a subsidiary groove may be worn in the medial tooth field of the maxilla by the medial ridge near the top of the dentary.

In the material of *R. brodiei*, there is no pair of tooth-bearing elements that may be examined for the precise fit of maxilla and dentary, but the type specimen of *R. spenceri* offered just this information. The two elements were separated in preparation, and their fit appears to be perfect. The bone of the occlusal surface of the maxilla and dentary wears flat only slightly faster than the teeth. The worn teeth are nearly flush with the bone, but project by a tiny amount, which suggests that the enamel and dentine of the teeth controls the overall rate of wear. As in other rhynchosaurs, tooth and bone occlude and wear each other indiscriminately; there is rarely tooth-tooth occlusion. The elliptical areas of wear on the maxilla and dentary match each other precisely. The grooves on each element are also exactly matched by teeth on the other element (figures 36*i*, 37*f*, 48*a*, 49*a*).

It is not possible to see pits that precisely mirror individual teeth, as in *Hyperodapedon gordonii* (Benton 1983, fig. 16*c-f*), but the irregular topography of both occlusal surfaces is the same. This confirms the interpretation of the rhynchosaur jaw action as a precision-shear type (Benton 1983) and not a propalinal type (back and forwards slicing), as suggested by Sill (1971*a*). Part of this evidence for a propalinal jaw action was his observation of possible longitudinal scratches on tooth-bearing elements of *Scaphonyx*, but such features have not been seen in *Rhynchosaurus*, nor in *Hyperodapedon*.

The articulation between the quadrate and the articular in *R. spenceri* (figures 28, 48) confirms the precision-shear jaw action, as also in *H. gordonii* (Benton 1983, pp. 646–647). The joint permits only a simple hinge-like rocking between both elements, with no possibility of back and forwards sliding, as would be necessary to permit a propalinal action. *Rhynchosaurus*, like *Hyperodapedon*, appears to have had a precision-shear bite on the basis of four pieces of evidence: the absence of longitudinal scratches, the precise fit of maxilla and dentary, matching elevations and depressions in the occlusal topography, and a constrained quadrate-articular joint.

7.6. *Tooth replacement and function of the dentition*

Rhynchosaurs did not have typical reptilian tooth replacement. Teeth became ankylosed at the back of the jaw, or the posteromedial region, as deep-rooted cylinders with a large pulp chamber. As the animal grew in size, new bone was also added at the back and posteromedial regions of the tooth-bearing elements, and new areas of the jaws swung into occlusion. The overall effect was to move newly ankylosed teeth into the field of occlusion from the back. These teeth became more solid with the deposition of secondary dentine in the pulp chamber, and the tooth crowns were worn away to the level of the bone of the jaw. As the occlusal field moved back, the individual teeth moved forwards passively relative to that field, until they passed out at the front. These old worn teeth were much reduced, and they also became resorbed from the base (Benton 1984*b*).

Rhynchosaurus shows all of the features that point to this mode of tooth replacement. The longitudinal 'Zahnreihen' are ontogenetic series of teeth, with newly ankylosed ones lying at the back, or posteromedially, and progressively older ones towards the front (figures 24, 35). In chance broken sections, the tooth shape is seen to be very much like that of *Stenaulorhynchus*, and some maxillae show clear growth lines in side view (figure 35*d*), as in *Hyperodapedon huxleyi* (Chatterjee 1974) and other rhynchosaurs.

Teeth were generated in a dental lamina that probably ran along the posteromedial and

posterior parts of both tooth-bearing elements, as in *Stenaulorhynchus* and *Hyperodapedon* (Benton 1984*b*). In the maxilla, there is a clearly flattened area above the smallest lingual teeth (figures 36) which probably marks the location of the dental lamina. It then ran round the back of the maxilla in a deep V-shaped groove between maxilla and ectopterygoid (figures 23*d*, 29*a*, 47*i*, 48*a*). In the dentary, the dental lamina ran below the smallest lingual teeth and up behind a slight posterodorsally-trending groove (figures 24*c*, 37*i*, 49*h*) to lie in a channel between the dentary and the anterior margin of the coracoid (figures 31*a, c*, 37*g*, 49*a, b*).

In some specimens there is clear evidence of unankylosed teeth. Once a tooth has been generated in the dental lamina, it moves towards the medial face of the tooth-bearing bone, and erodes a pit into which it becomes ankylosed. Empty pits may be seen at the beginnings of several 'Zahnreihen' (figures 37*i*, 49*h*). These are larger than the recently ankylosed teeth just in front, which suggests that once that young tooth has been moved into place, bone grows back around it to hold the tooth firmly. The teeth on the lingual surface of maxilla or dentary generally appear to be small, but this is probably because only the tip of the conical crown is exposed. The more anterior teeth of a series which have come into occlusion are worn flush with the bone, and their full cross-sectional area is seen. As the teeth are worn down, the pulp chamber fills with dentine. Fully worn teeth, at the anterior end of a series, are often little more than short stumps, and they may then cease to be worn as the occlusal area moves backwards with jaw growth.

Rhynchosaurus had powerful jaw muscles accommodated in the expanded temporal area, as in other rhynchosaurs (Sill 1971*a*; Chatterjee 1974; Benton 1983). Further, a case has been made (Romer 1963; Sill 1971*a*; Benton 1983, 1984*b*) that rhynchosaurs, including *Rhynchosaurus*, were specialized for eating tough vegetation such as seed ferns, the rhizomes of cycads, the 'fruit' of lycopsids, sphenopsids, ferns and bennettitaleans. The Bromsgrove Sandstone formation and the Otter Sandstone Formation, both of which have yielded bones of *Rhynchosaurus*, have also produced plant remains such as pteridophytes and coniferophytes in the former, and horsetails in the latter, possible elements in their diet.

7.7. Comparison of the dentition

The dentition of *Rhynchosaurus*, as seen in *R. brodiei* and *R. spenceri*, is most like that of *Stenaulorhynchus* from the Middle Triassic of Tanzania (Benton 1984*b*) and *Mesodapedon* from the Middle Triassic of India (Chatterjee 1980). *Rhynchosaurus* shows the distinguishing features of the Middle Triassic forms, when compared with those of the Late Triassic: there are two grooves on the maxilla (although the subsidiary medial one is less clearly marked in *Rhynchosaurus* than in *Stenaulorhynchus* and *Mesodapedon*), there are teeth on the lingual face of the maxilla, and the dentary has tooth rows elevated on two ridges that fit into the maxillary grooves.

The teeth of *Rhynchosaurus* differ from those of *Stenaulorhynchus* in being relatively larger in comparison to the size of the tooth-plate. For example, a juvenile maxilla of *R. brodiei* (figures 35*a*, 47*a*), which is the same width as one of *Stenaulorhynchus* (Benton 1984*b*, fig. 14*b*), has an average of four teeth in 10 mm of the tooth row, compared with an average of five in the latter. In a larger specimen of *R. spenceri* (figure 36*e*), which is the same width as a specimen of *Stenaulorhynchus* (Benton 1984*b*, fig. 14*c*), there are several rows of closely packed teeth up to 4 mm in diameter, whereas the teeth of the latter reach only 3 mm. The tooth rows in this specimen of *Stenaulorhynchus* have a gap of 4–6 mm between them, whereas the tooth rows of

R. spenceri have a spacing of only 1–4 mm. Finally, a very large maxilla of *R. spenceri* (figure 36*h*) has gaps of 1–3 mm between tooth rows (tooth diameter 1–4 mm) whereas a *Stenaulorhynchus* maxilla of similar size (Benton 1984*b*, fig. 14*g*) has gaps of 2–8 mm (tooth diameter 0.5–2 mm).

8. PALAEOBIOLOGY AND TAPHONOMY

8.1. Restoration of the skeleton of *Rhynchosaurus articeps* (figure 38)

In the restoration of the skeleton (figure 38), the skull is based on SHRBM G132/1982, and the postcranial skeleton on SHRBM 4, BMNH R1238, and R1239. Overall length is based on an animal with a skull length of 80 mm, presacral length of 253 mm, sacrum length of 17 mm, and tail length of 190 mm (total length 540 mm, the larger size represented by specimens such as SHRBM G132/1982 and G134/1982).

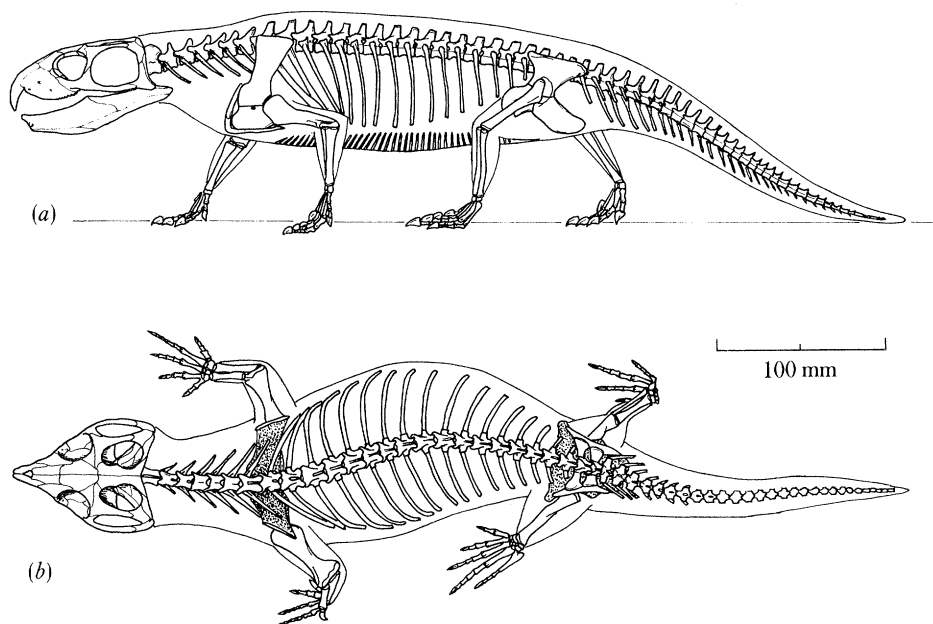


FIGURE 38. *Rhynchosaurus articeps*. Restoration of the skeleton of an individual with 80 mm skull length in (a) left lateral and (b) dorsal views. Based on specimens, as described in the text.

The head is tilted slightly downwards, as in other rhynchosaurs (Chatterjee 1974; Benton 1983), which is the best position for forward vision during locomotion. The backbone is reconstructed from the available partial series of vertebrae (figures 10–18), with general information from other rhynchosaurs. The vertical and lateral curvature of the backbone (figure 38*a, b*) is added for realism, by reference to living reptiles. The distribution and arrangement of ribs, gastralia and chevrons is only partly restored from specimens, with information from other better-preserved rhynchosaurs.

R. articeps is shown (figure 38*a, b*) in a 'fast-walking' pose, with the body hoisted well clear of the ground. The pose of the limbs shows a partly sprawling forelimb and a semi-erect hindlimb, as restored in *Hyperodapedon* (Benton 1983). The shapes of the girdles and limbs of *R. articeps* are relatively well known (figures 14–20), but the nature of the joints is less certain.

The pelvis (figure 19*d, e*) is enlarged for the skeletal restoration (figure 38), although its relative width in dorsal view is reduced as the restoration (figure 19*e*) was made largely from flattened specimens.

8.2. Restoration of the skeleton of *R. brodiei* and *R. spenceri* (figure 39)

In figure 39 outline restorations of *R. brodiei* and *R. spenceri* are compared with the restoration of *R. articeps*. *R. brodiei* is shown as a member of the smaller size class with a skull length of about 90 mm (figures 21, 28). The preserved postcranial remains are few (shaded black in figure 39*b*) and the skeleton is assumed to be identical to that of *R. articeps*, and enlarged in proportion to the skull size, giving an estimated total body length of 610 mm for the type specimen of *R. brodiei*.

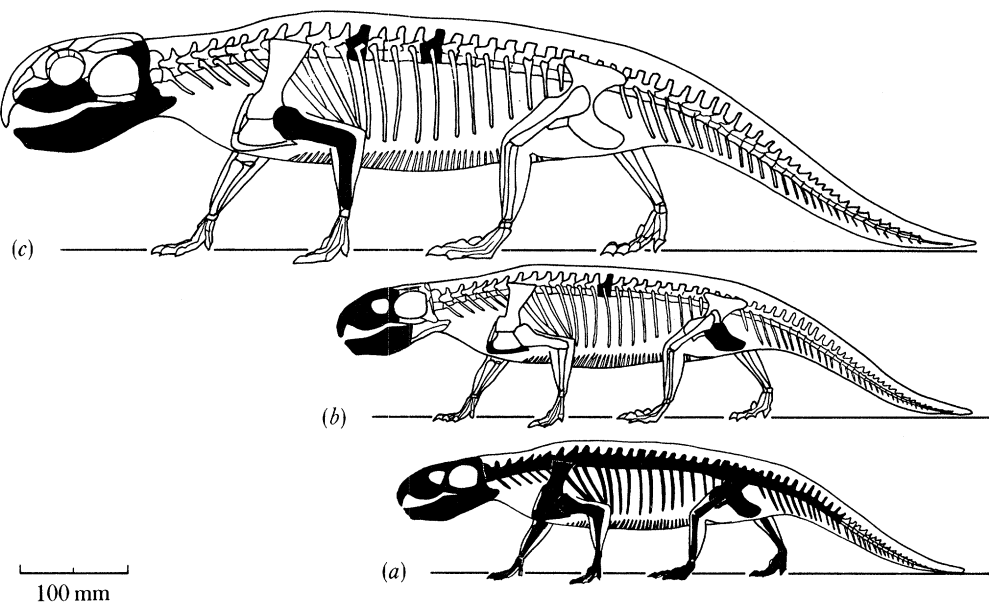


FIGURE 39. Restorations of the skeletons of the three species of *Rhynchosaurus*, drawn to the same scale. (a) *R. articeps*; (b) *R. brodiei*; (c) *R. spenceri*. Part (a) is based on figure 38; (b) and (c) are enlarged from that, with modifications as described in the text. Known elements for each species are shaded black, unknown elements being left blank.

The restoration of *R. spenceri* (figure 39*c*) is based on only slightly more complete material, and it shows an animal of the typical larger size class (midline skull length 140 mm). The skull, forelimb and dorsal vertebrae are based on specimens; the rest of the skeleton is scaled up, in proportion with the skull length, from the restored skeleton of *R. articeps*, but with the overall proportions slightly altered. It is assumed that *R. spenceri*, having a skull about twice as long as that of *R. articeps*, approached the proportions of the larger rhynchosaurus such as *Hyperodapedon*, which had a midline skull length of about 180 mm (Benton 1983). The body and tail are made relatively a little shorter than in *R. articeps*, and the limbs relatively heavier. This gives an estimated total body length of 945 mm (skull length 140 mm, presacral length 443 mm, sacral length 30 mm, tail length 332 mm).

8.3. Functional morphology of *Rhynchosaurus*

These comments are brief because the specimens of *R. articeps* are preserved in such a way that muscle attachments may not be reconstructed from bone surface features, and the limb

bones cannot be manipulated. Further, the material of the other two species is incomplete. Comparisons are made with the species of *Hyperodapedon* that have been the subject of more detailed functional analyses (Chatterjee 1974; Benton 1983).

The sensory systems of *Rhynchosaurus* were probably similar to those of *H. gordonii* (Benton 1983). There is a large anterior space in the skull of all three species, surrounded by nasals, maxillae and vomers, which suggests a large nasal capsule and a good sense of smell. The orbit is large, and this points to a large eye, and probably a good sense of sight. Finally, there is no sign of a tympanic crest in the quadrate–squamosal area, and thus *Rhynchosaurus* may have lacked a tympanum. Hearing may have been mediated by specialized skin membranes behind the quadrate for airborne sounds, and by the throat and extensive hyoid apparatus for ground-borne sounds.

Rhynchosaurus appears to have been a typical rhynchosaur in its feeding adaptations (Benton 1983, 1984*b*). There is an extensive hyoid apparatus in *R. articeps*, which suggests a large powerful tongue that may have been used in manipulating food items. The maxillary and dentary dentition, and the jaw joint, of *R. brodiei* and *R. spenceri* (§7) suggest that these species had a precision-shear bite, as in other rhynchosaurs. The diet was probably tough vegetation. No plant remains have been found with *R. articeps*, but plant fossils have been found in association with *R. spenceri* (horsetails) and with *R. brodiei* (sphenopsids and pteropsids, and miospores of lycopsids, coniferopsids, and cycadopsids) (Warrington *et al.* 1980, p. 39).

The long beak-like premaxillae may have functioned in digging, or in raking together food materials. The hindlimb of *R. articeps* appears to have been capable of strong backwards motions, and the claws of the pes are narrow and high, presumably well adapted for scratch digging by backwards kicks of the leg, as in *Stenaulorhynchus* (Huene 1938, 1939*a*) and *Hyperodapedon* (Benton 1983).

The joint morphology could not be studied in detail in *R. articeps*, and only in very general terms in *R. spenceri* (§6.3); the pose (figure 38) is an assumption. The stride length appears to have been 75–95 mm in *R. articeps*.

8.4. *Environment and taphonomy of R. articeps from Grinshill (figure 40)*

Sedimentology

The remains of *R. articeps* have been found in the Tarporley Siltstone Formation, and possibly the Grinshill Sandstone Formation, of a number of quarries on Grinshill (§2.2). The sandstones were quarried in the 18th and 19th centuries for building stone for much of Shrewsbury and northern Shropshire, and sections were described by Murchison (1839, pp. 37–41), Hull (1869, pp. 64, 73), and Pocock & Wray (1925, pp. 39–40).

The Tarporley Siltstone Formation, typically ranging from 20 to 250 m in thickness (Warrington *et al.* 1980, table 4), is only about 7 m thick at Grinshill. Two facies, A and B, have been identified by Thompson (1985, pp. 119–121). Facies A consists of trough-shaped erosion channels filled with beds of ripple cross-laminated fine- to medium-grained sandstone, which bear on their bedding surfaces ripple marks, rhynchosauroid footprints (see below), trace fossils formed by invertebrates (?), and supposed raindrop impressions, which were reported for the first time from Grinshill (Buckland 1839; Ward 1839). Facies B consists of thin to medium interbedded fine sandstones, siltstones, and mudstones, each about 10–20 mm thick (muds and silts) or 100 mm thick (sands). Many horizons show ripple marks, load casting, flute marks and

prod marks. Mudcracks and halite pseudomorphs have been observed, as well as rhynchosauroid footprints and poor invertebrate trace fossils.

Thompson (1985) interprets the overall sedimentary regime of these two facies as 'tropical arid belt fluvial and marine marginal hypersaline lagoon (salina) deposits'. Facies A is interpreted by him as deposited by low-energy rivers, which occasionally dried up, and which suffered intermittent rain showers. Facies B appears to represent similar quiet and hot conditions, with evidence for current activity (? rivers) and wave activity (? lagoons). Seawater pools occasionally dried out, leaving salt crystals, and muddy surfaces were desiccated, producing mud cracks. Rhynchosaurs and other reptiles (see below) walked across the muds. 'The environment was probably fluvial-intertidal rather than lake marginal.'

The underlying Grinshill Sandstone Formation (approximately equivalent to the Helsby Sandstone Formation of the northern and central portions of the Cheshire Basin) (Warrington *et al.* 1980, p. 31) consists of about 30 m of buff and yellow, medium-grained, well-sorted sandstones. These are well cemented, and contain many small flakes of manganese. Large-scale cross-beds are visible in vertical quarry faces, which suggest aeolian conditions of deposition (Thompson 1985). The Grinshill Sandstone Formation appears to grade into the Tarporley Siltstone Formation through a bed of loose sand, about 300 mm thick, termed the Esk Bed (Pocock & Wray 1925, pp. 39-40; Thompson 1985, p. 119).

Vertebrate footprints have been reported from Grinshill by several authors (e.g. Ward 1840; Beasley 1902). They were found on ripple-marked surfaces in a finely laminated buff-coloured sandstone, beneath the rubbly red-coloured sandstone called 'Fee', presumably equivalent to part of Thompson's (1985) Facies B. The commonest tracks are of the rhynchosauroid type, termed rhynchosauroid D1 by Beasley (1902); rarer finds include *Cheirotherium* prints.

Occurrence of the reptiles

The *R. articeps* specimens occur in two major sediment types, as noted by Owen (1842*b*, p. 146): a fine-grained grey sandstone (e.g. SHRBM 2, 3, G133/1982, G151/1982) and a coarser pinkish-grey sandstone termed by him 'burr-stone' (e.g. SHRBM G132/1982, 6, 7; MANCH L7642). The fine sandstone is grey to beige in colour and has subrounded sand grains with greenish mud flakes and specks of mica and manganese. The slabs show fine parallel lamination and the horizontal surfaces may show evidence of ripple marks as well as irregular lumps up to 10 mm in diameter.

Walker (1969, p. 470) observed that the specimens of *R. articeps* came from the Tarporley Siltstone Formation (the fine-grained grey sandstone), and from the top of the Grinshill Sandstone Formation (the coarser sandstone). This was implied also in Pocock & Wray's (1925, pp. 39-40) section, in which the top of the Grinshill Sandstone is described as 'Hard Burr: Hard yellowish-white sandstone, 2 ft. 6 in.'. However, Thompson (1985, p. 118) doubts whether any bones have been found in the Grinshill Sandstone Formation, noting (D. B. Thompson, personal communication) specimens only from his facies A of the Tarporley Siltstone Formation in the operating quarry (SJ 526238).

Taphonomy

There is no detailed field information at present about the relations of the remains of *R. articeps* to the sediments because the museum slabs are generally too small to indicate a great

deal about the sedimentology. It cannot be said, for example, whether the specimens lay in channels or on dried-up sand-flats.

Outline sketches of the more complete specimens of *R. articeps* (figure 40) show that they were fossilized flattened in a horizontal plane, although it cannot be said whether they were lying on their bellies or on their backs, as was also the case with *Hyperodapedon* from Elgin (Benton

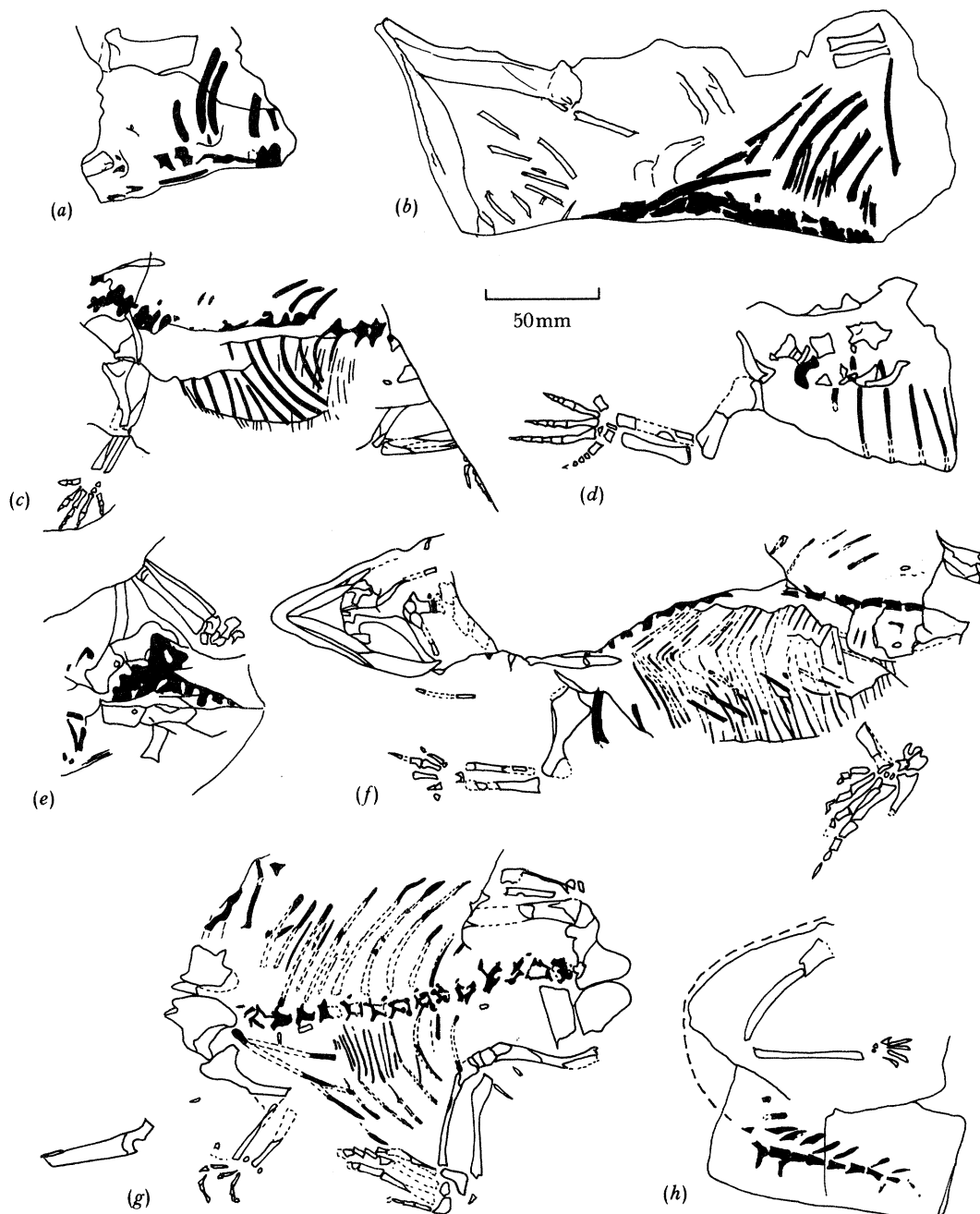


FIGURE 40. *Rhynchosaurus articeps*. Outline sketches of specimens as preserved in the rock, to illustrate the pose of the carcasses. Vertebrae and ribs are shaded black; all other elements are shown in outline. (a) SHRBM G134/1982; (b) SHRBM 3; (c) SHRBM 4; (d) SHRBM 6; (e) BATGM M20a/b; (f) BMNH R1237 (skull), R1238 (skeleton); (g) BMNH R1239; and (h) BMNH R1240 (vertebrae), R1241 (hindlimb), with the reconstructed course of the tail shown by a dashed line.

1983; Benton & Walker 1985). The vertebral column appears to be unbroken, and the ribs are still in articulation. The gastralia often appear to be shifted to the right or the left (figure 40*c, f*), presumably as a result of the collapse of the body cavity to a flat plane. The limbs are in a natural resting pose, with the forelimbs flexed and pointing forwards or sideways, and the hindlimbs pointing backwards or sideways. The shoulder girdle and pelvis usually retain their correct positions, with the coracoids, pubes and ischia remaining essentially in contact ventrally, and the ilia touching the sacral vertebrae (figure 40*c, e-g*), but the scapulae, being less firmly attached, may be displaced over the vertebral column, or laterally. The skull is occasionally present undamaged and in close articulation with the vertebral column, but more often it is found separately, or attached to a few cervical vertebrae. However, this form of incompleteness, and others in which only the anterior or posterior postcranial remains are present (e.g. figure 40*a, b, d, e, h*), is probably the result of incomplete collection rather than incomplete preservation of the skeleton.

In the specimens of *R. articeps* there is no evidence of disarticulation by water currents, wind, or moving sand. The animals generally appear to have dried naturally and to have been covered by sand fairly rapidly. Further, there is no evidence of scavenging of the skeletons by carnivores, although there was evidently some form of rauisuchian in the fauna, as suggested by the *Cheirotherium* footprints (see above).

The bone is preserved intact as a soft white, only partly mineralized, substance. This has often been damaged by handling, and positive preparation was difficult. Watson (1910, p. 155) describes how soft the bone was in a freshly collected specimen. Bones found in the finer sediment show signs of compression; those in the coarser sandstone were less affected during fossilization. Specimens in the coarser 'burr' sandstone have poorer preservation of bone material (e.g. SHRBM 6 and 7) and there are often iron-oxide-filled hollows visible within bones. In some specimens the long bones appear to have been hollow, as noted by Ward in letters to Owen (BMNH, Owen correspondence 110, 118), and by Owen (1842*b*, p. 153; 1842*c*, p. 367, pl. 6, figs 7, 10). These specimens are now lost, but they are reported by Owen to have occurred in the coarse 'burr' stone.

The only signs of disarticulation are in skull specimens. For example, SHRBM G132/1982 (figure 3) shows some of the posterior skull elements (left squamosal, supratemporal, quadrate and quadratojugal) pushed down and back, and the cervical vertebrae run down and to the side, instead of straight back. The posterior view of this skull (figure 3*d*) shows that the top portion has been pushed over to the left, thus making both quadrates lean to the left. The skull SHRBM 3 has also apparently been displaced in the same way, so that the posterior right-hand lower angle is seen spread out to the side in dorsal view (figure 4*b*). However, the overall distortion has not affected the mandibles, which are in natural connection (figure 4*c*), suggesting that the distortion was probably caused by the collapse of the skull rather than by a unidirectional tectonic force.

Two of the skull specimens (BMNH R1237; MANCH L7642; figure 4*d, e*) seem to be extensively disarticulated, with most of the skull elements separated by bands of matrix, as if the skull has been 'exploded'. However, this is probably largely the result of post-collection damage to the soft bone, as the overall proportions of these skulls are maintained. The braincase of BMNH R1237 is swivelled out of place so that its anterior face points ventrally (figure 4*d*) and the squamosal and supratemporal have been displaced in both cases, as has happened in other specimens. These sutural unions must have been weaker than the others.

The only clear evidence of tectonic damage is in BMNH R1236, where a small fault runs vertically across the posterior region of the skull, offsetting the posterior parts of the parietal, braincase, squamosal, and mandible by about 5 mm to the left (figure 5*b*). The fracture is simple, representing a sharp break of the affected bones, with only a few displaced flakes of the parietal and (?) epipterygoid in a zone about 2 mm in front of the fault.

8.5. *Environment and taphonomy of R. brodiei from Warwick*

Sedimentology

The remains of *R. brodiei* have been found in the Bromsgrove Sandstone Formation of Coton End Quarry (spelt 'Coten End' by some authors), Warwick, and one specimen has come from a quarry at Leamington, as noted above (§2.2).

Coton End quarry was operational in the early 19th century for building stones. There are still good exposures in the quarry, which show channelled and cross-bedded water-laid buff and red sandstone units varying in thickness from 1 to 3 m. Laterally discontinuous marl and clay bands, from 100 to 500 mm thick, probably correspond to the fossiliferous 'Dirt bed'. Murchison & Strickland (1840, p. 344) gave a section in this quarry:

a. Soft, white sandstone and thin beds of marl	8 feet
b. Whitish sandstone, thick-bedded	12
c. Very soft sandstone, coloured brown by manganese; called "Dirt-bed" by the workmen	1
d. Hard sandstone, called "Rag", about	2
	<hr style="width: 50%; margin-left: auto; margin-right: 0;"/> 23 feet.

This was confirmed by Hull (1869, pp. 88–89). Old *et al.* (1987, p. 23) document 7 m of massive sandstone and flat-bedded sandstone grading up into 4 m of cross-bedded sandstone and mudstone in Coton End Quarry.

The Bromsgrove Sandstone Formation is from 30 to 500 m thick in Warwickshire (Warrington *et al.* 1980, pp. 38–39, table 4; Old *et al.* 1987, p. 20); the middle to upper portions of this Formation, as seen at Coton End, have been interpreted as deposits of mature meandering river channel and floodplain complexes (Warrington 1970*b*). The quarry is close to the junction of the Bromsgrove Sandstone Formation with the overlying mudstones of the Mercia Mudstone Group (unnamed formation).

Rhynchosauroid footprints have been recorded from Coton End quarry (see, for example, Beasley 1906); some appear to be associated with large groove marks produced by the flow of water.

Occurrence of the reptiles

The fossil bones were found principally in the 'Dirt bed', according to Murchison & Strickland (1840, p. 344). Hull (1869, pp. 88–89) stated that the amphibian fossils occurred in the 'Waterstones'; Walker (1969, 1970) noted that the reptiles came from the upper part of the 'Building Stones'. These two units are equated with the upper parts of the Bromsgrove Sandstone Formation (Warrington *et al.* 1980, p. 39).

Most of the rhynchosaur bones from Warwick have been entirely freed of matrix, but WARMS Gz34 is in a hard fine-grained laminated grey sandstone, which does not clearly

match Murchison & Strickland's (1840) description of the 'Dirt bed'. Other specimens are in yellow or greenish-coloured fine- to medium-grained sandstone with coarse patches, which might accord better with the description of the 'Dirt bed'.

Taphonomy

The Warwick specimens of *R. brodiei* are preserved in a disarticulated state; as far as can be determined, no groups of elements were ever found in even moderately close association. The majority of the 15 specimens are isolated maxillae (5) or tooth-bearing portions of the dentary (4), with a few single postcranial elements (3) and an isolated premaxilla. However, the partial skull and mandible (figure 23) and the 'snout' (figure 22) show that more complete material might be expected. This is confirmed by the specimen of cf. *Macrocnemus* from Leamington (WARMS Gz10: type of *Rhombopholis scutulata* Owen 1842), which consists of several limb bones and vertebrae on a single slab, and the archosaur sacrum (WARMS Gz1 and 2), consisting of three partial vertebrae.

The specimens show little sign of sedimentary wear: indeed, the surface of the bone is very well preserved, showing fine details of striations and blood vessel openings. The ends of broken elements are not worn. It is hard to assess how much of the damage was produced before deposition, and how much during collection, as most specimens have been partly or completely prepared out of the matrix. However, the isolated interclavicle (WARMS Gz34) and the isolated dorsal vertebra (WARMS Gz17) are entirely surrounded by matrix and had presumably been removed from the carcass before deposition. The damaged posterior end of the interclavicle (figure 25*e*) was damaged before burial, as shown by preparation by the author. Murchison & Strickland (1840, p. 344) described the bones as 'rolled and fragmentary', but subsequent studies have shown that they are not abraded, nor are they distorted, as Miall (1874, p. 417) noted.

The bone is preserved as hard white to buff-coloured material, apparently with all of the original internal structure intact. In broken sections, the dentine of the teeth is yellow, and the enamel is dark brown. However, Murchison & Strickland (1840, p. 344) noted that the bones were in a decomposed condition when they were collected, resembling 'stiff jelly, with singular hues of blue and red. It is necessary to remove them with great care from the quarry, and when dry, to saturate them with a solution of gum arabic, as the best means of preserving them.' This description is hard to tally with the present hard and well-preserved condition of the fossil bone in museum collections.

The Warwick bones seem to have been derived from nearby and washed along for some distance in the streams or rivers that deposited the sediment, but not far enough to cause significant abrasion. This had the effect of breaking up the carcasses, although skulls seem to have remained intact. Unfortunately, it is not known how the bones relate to the channels and other sedimentary structures, because specimens have not been collected recently.

The Warwick fauna

Coton End quarry has been the main source of fossils in the Warwick area, but a number of other quarries nearby produced similar faunas. Already in the 1830s, Murchison & Strickland (1840, p. 343) stated that it 'has been most productive in the remains of *Vertebrata*'. Murchison & Strickland (1840, pl. 28, figs 6–10) figured bones which they identified as teeth of '*Megalosaurus*', and of 'a Saurian', as well as an unidentified vertebra.

Owen (1841*b*) named one of the 'teeth' *Anisodon gracilis* (see §4.1); later (Owen 1842*a*, p. 535) he identified this specimen as an ungual phalanx of *Labyrinthodon pachygnathus*. He also interpreted the vertebra as that of *L. leptognathus* (Owen 1842*a*, pp. 523–524, pl. 45, figs 5–8). Both specimens have been reinterpreted as rhynchosaur remains: a premaxilla (the 'tooth') and a dorsal vertebra (see §§4.2, 4.5). In the same paper, Owen (1842*a*) described other jaw, skull, and postcranial fragments from Coton End as pertaining to *L. leptognathus* and *L. pachygnathus* (both assigned to the genus *Mastodonsaurus*), and also (1842*d*) gave an account of the microscopic anatomy of teeth of *Mastodonsaurus* from the same quarry. Owen's descriptions were based on the extensive collections by Dr Lloyd of Leamington.

In the 1840s and 1850s the Reverend P. B. Brodie and Dr Lloyd collected jaw bones of *Rhynchosaurus* from Coton End, and these were described by Huxley (1869) as *Hyperodapedon*. Huxley (1870) described supposed dinosaur remains from Coton End and redescribed many of Owen's *Mastodonsaurus* bones as probably dinosaurian. Miall (1874) agreed with these reassignments and described further remains of *Mastodonsaurus*. Huene (1908) redescribed most of the supposed dinosaur material, Walker (1969) provided reidentifications of many of the archosaurs and other reptiles from Coton End, and Paton (1974) revised the labyrinthodonts.

The Coton End fauna consists of the following taxa (data from Allen 1908; Huene 1908; Horwood 1909; Wills 1910; Walker 1969; Paton 1974; Galton 1985):

1. *Ceratodus laevisimus* Miall, a tooth of a ceratodontid lungfish.
2. *Cyclotosaurus leptognathus* (Owen 1842), jaws and other skull fragments (WARMS: Owen 1842*a*, pp. 516–525; Miall 1874, p. 425; Wills 1916, pp. 7–9, figs 5, 6; Paton 1974, pp. 255–265, 280–282), a small capitosaur labyrinthodont with a flattened crocodile-shaped skull, 210 mm long. Diet: fish and ? small tetrapods.
3. *Cyclotosaurus pachygnathus* (Owen 1842), jaws and other skull fragments (WARMS: Owen 1842*a*, pp. 526–537; Miall 1874, pp. 418–424; Wills 1916, pp. 9–11, figs 7–9; Paton 1974, pp. 265, 280), a moderate-sized capitosaurid labyrinthodont with a lower skull than *C. leptognathus*. Diet: fish and ? small tetrapods.
4. *Mastodonsaurus jaegeri* (Owen 1842), jaw (BGS: Owen 1842*a*, pp. 537–538).
5. *Mastodonsaurus lavisi* (Seeley 1876), skull fragments (WARMS: Miall 1874, pl. 26, figs 1A, 3A, B; Paton 1974, pp. 265–266, 281–282), a large mastodonsaurid labyrinthodont with an estimated skull length of 500–600 mm. Diet: fish and ? small tetrapods. [The species *M. giganteus* (Owen 1842), *M. ventricosus* (Owen 1842) and *Diadetognathus varvicensis* Miall 1874 from Coton End have been synonymized with the four labyrinthodonts above.]
6. cf. *Macrocnemus*, ilium and femur (WARMS: Owen 1842*a*, pl. 45, figs 11–15; Walker 1969, p. 472), a slender lizard-like insectivore, carnivore or piscivore, 50–80 mm long. A prolacertiform.
7. *Rhynchosaurus brodiei* n. sp., skull and mandible remains, isolated postcranial elements (WARMS, BMNH, BGS: Huxley 1869), a moderate-sized rhynchosaur with a skull 90–140 mm long (estimated body length, 0.5–1.0 m), with herbivorous diet.
8. Large thecodontian, ilium (WARMS: Walker 1969, p. 473), presumably a large carnivore.
9. *Bromsgroveia walkeri* Galton 1985, vertebrae, sacrum, ilium, ischium, and (?) femur (WARMS: Owen 1842*b*, pl. 45, figs 1–8, 16, 17; Huxley 1870, pl. 3, figs 9, 10; Huene 1908, pp. 200–201, figs 214, 228, 233; Walker 1969, p. 471 ('poposaurid'); Chatterjee 1985,

pp. 445, 447, 448; Galton 1985, pp. 11–12, figs 2E–I, 4H, I; Benton 1986*a*, p. 298), a moderate- to large-sized carnivorous quadruped (rauisuchid) or biped (poposaurid).

10 Archosaur indet. (*Cladeiodon lloydi* Owen 1841), about ten isolated teeth (WARMS, BMNH, BGS: Murchison & Strickland 1840, pl. 28, figs 6*a*, *b*, 7; Owen 1841*b*, pl. 62A, fig. 4; Huxley 1870, pl. 3, figs. 4, 11; Huene 1908, figs 267, 269–272; Walker 1969, p. 471). These could belong to the rauisuchian (no. 9), the large thecodontian (no. 8), or to some other carnivorous archosaur.

11. ‘Prosauropod dinosaur’, a cervical vertebra (BMNH: Walker 1969, p. 473). If this were truly a dinosaur, it could be the oldest in the world (cf. Benton 1986*a*).

The Coton End fauna has been supplemented by finds from other neighbouring quarries which show similar lithologies, such as Guy’s Cliff, Leek Wootton, Cubbington Heath, and Leamington. Old Leamington Quarry (? SP 325666) has produced remains of the fish *Gyrolepis* (Walker 1969, p. 472), *Mastodonsaurus jaegeri*, *Cyclotosaurus pachygnathus*, *C. leptognathus*, cf. *Macrocnemus* (type specimen of Owen’s *Rhombopholis scutulata* (Owen 1842*b*, pp. 538–541, pl. 46, figs 1–5; smaller than the Coton End macrocnemid), *Rhynchosaurus*, and a ‘prosauropod’ tooth (BGS: Murchison & Strickland 1840, pl. 28, fig. 7*a*; Huene 1908, fig. 265). Cubbington Heath quarry (SP 332694) has yielded *M. jaegeri*, *C. pachygnathus*, and *C. leptognathus* (Huxley 1859*b*; Woodward 1908; Wills 1916, pp. 9–11, pl. 3). Guy’s Cliffe (SP 293667) produced remains of the jaws of *M. jaegeri* (Owen 1842*b*, pp. 537–538, pl. 44, figs 4–6, pl. 37, figs 1–3; Miall 1874, p. 433), probably the first find of a tetrapod in the area, having been collected in 1823 (Buckland 1837). This last specimen is now lost.

The fauna, then, consists of fishes, four species of aquatic carnivorous or piscivorous temnospondyl, a moderately sized insectivore or carnivore (macrocnemid), two herbivores (*Rhynchosaurus*, ? ‘prosauropod dinosaur’), and two or more terrestrial carnivores (‘thecodontian’, *Bromsgroveia*, *Cladeiodon*) which may have fed on the herbivores. Numbers of specimens of all taxa are small, but *Rhynchosaurus*, *Bromsgroveia*, and the two species of *Cyclotosaurus* seem to be represented by more than five specimens each.

8.6. *Environment and taphonomy of R. brodiei from Bromsgrove*

Sedimentology

The quarries near Hilltop Hospital in Bromsgrove (SO 948698) formerly showed sections in the Bromsgrove Sandstone Formation (‘Building Stones’ and ‘Waterstones’). Wills (1907, 1908, pp. 29–32, 1910, pp. 254–256) described the succession as 15–20 m of alternating sandstones and shales, and a band of ‘marl conglomerate’. The units are lens-shaped, and the sandstones appear to show cross-bedding (Wills 1907, fig. 1). Some of the lenticular beds are ‘true marls, others sandy shales, green, brown, or red in colour’.

Wills (1950, pp. 84–85) 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. He interpreted (Wills 1970, pp. 263–266) the fossiliferous lenticular beds as deposits in channels, pools, or lakes on the floodplain. Warrington (1970*b*, pp. 204–205), on the other hand, interpreted the Bromsgrove Sandstone Formation as high-sinuosity stream deposits passing diachronously into the marine-influenced ‘Waterstones’. The sum of floral and faunal evidence points to freshwater or brackish conditions at the time of deposition of the fossiliferous units (Wills 1910, p. 263; Ball 1980).

Occurrence of the fossils

Wills (1907, pp. 30–31; 1908, p. 15) 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 these contained abundant fragmentary arachnid remains. The red marl and red sandstone were barren of fossils, and plants occurred in the grey sandstone. He identified these fossiliferous units as ‘the Waterstones and upper part of the Building Stone’, equivalent to the upper portion of the Bromsgrove Sandstone Formation (Warrington *et al.* 1980, p. 39), as at Warwick (see above).

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 grey in colour, 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 colour is in parts ochreous and others brown, instead of the usual green...’ (Wills 1910, pp. 260–261).

Taphonomy

The bones from the Bromsgrove quarries are all isolated pieces: jaw fragments of labyrinthodonts, 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 vertebra. Fine details on the bones are often preserved, such as the sculpture on the labyrinthodont bones (Wills 1916; Paton 1974), and sharp posterior teeth in the *Rhynchosaurus* maxillae (figure 26). However, the specimens are all single elements, and some transport by water seems evident. Most of the specimens have been prepared out of the matrix, and it cannot be said how much of the incompleteness of each specimen is the result of damage before burial, and how much the result of collection failure. Wills (1910, pp. 260–261) implied that the bones were found in a fragmentary condition, and that the damage was predepositional.

The bone is now in a hard and apparently well-preserved state, with all internal structure of bone and tooth intact. Wills (1910, p. 261) noted that the bones suffered some damage when they came from parts of the marl conglomerate that had decayed: ‘we find bones in the 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 & Strickland (1838, p. 344) of the initial state of bones from the Warwick ‘Dirt bed’ (see above).

The Bromsgrove flora and fauna

Wills (1907, 1908, 1910, pp. 264–265) listed the following plants and animals from the Bromsgrove quarries (with modifications from Walker 1969; Paton 1974; Warrington *et al.* 1980, p. 39) (horizons: S, sandstones; M, mudstones):

- Sphenopsids (horsetails and relatives): *Equisetites* (S, M), *Schizoneura* (M)
 Gymnospermopsids (cycads, cycadeoids, conifers): *Voltzia* (S, M), *Pterophyllum* (M), *Yuccites* (M)
 Annelids: *Spirorbis* (Ball 1980)
 Bivalves: *Mytilus* (M)
 Arthropods: conchostracan *Euestheria* (M), scorpionid arachnids *Mesophonus* and *Spongiophonus* (M)
 Fish: shark *Acrodus* (S), perleidid *Dipteronotus* (M), lungfish *Ceratodus* (S), coprolites (S), scales (M)
 Amphibians: *Mastodonsaurus* (S), *Cyclotosaurus* (S)
 Reptiles: *Rhynchosaurus* (S), rauisuchian (? including 'Teratosaurus' and 'Cladeiodon') (S), cf. *Macrocnemus* (S), nothosaur (S).

The tetrapod remains from Bromsgrove are sparse, but they appear to indicate a fauna that is essentially the same as that from Warwick. The association with remains of plants, invertebrates, and fishes provides additional useful palaeocological information not available elsewhere in the British Triassic.

8.7. *Environment and taphonomy of R. spenceri from Devon (figure 41)*

Sedimentology

The remains of *R. spenceri* have come from the Otter Sandstone Formation, a unit 118 m thick deposited in fluvial ephemeral braided stream environments, and forming part of a sequence 1 km thick of continental red beds of Late Carboniferous to late Triassic age (Laming 1982). The sequence was described at High Peak (SY 144858) by Whitaker (1869), Ussher (1876), and Irving (1888). The succession is summarized below, with measurements estimated from Lavis (1876, fig. 1), on the assumption that High Peak is 155 m high (contour on 6 in topographic map) (figure 41).

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

The base of the Otter Sandstone Formation, exposed to the west of Budleigh Salterton, is unconformable on the Budleigh Salterton Pebble Bed. Ventifacts and other aeolian indicators have been noted (Henson 1970). At Otterton Point there are irregular calcretes; the *Rhynchosaurus* jaw found there was associated with cross beds, calcite-cemented nodules, and a breccia consisting of poorly rounded pebbles, mostly less than 10 mm in maximum diameter (Lavis 1876; Ussher 1876; Metcalfe 1884). Eastwards, in Ladram Bay and towards Sidmouth, these calcretes become less common, and the formation is dominated with sandstones in large and small channels with occasional siltstone lenses.

Henson (1970), Laming (1982), and Mader & Laming (1985) interpreted the Otter Sandstone Formation as representing a mixture of fluvial and aeolian deposition, with aeolian sediments concentrated at the base. The middle and upper fluvial portions were deposited by braided rivers flowing from the west and south west, interspersed with temporary lakes in the

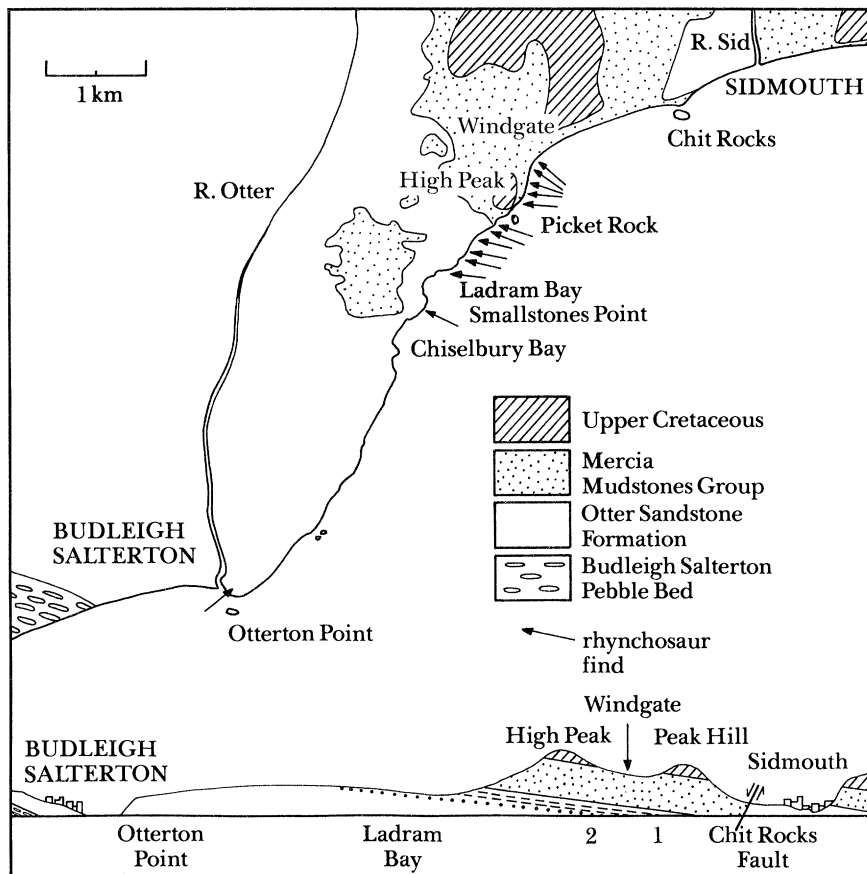


FIGURE 41. The occurrence of rhynchosaur fossils in the Otter Sandstone Formation. A geological map of the coastal section between Budleigh Salterton and Sidmouth, showing the major rock outcrops and the rhynchosaur localities. The vertical section of the same coast line (below) shows the major topographic features and the geological units. The 'white bands' (1) and the 'saurian or batrachian band' (2) are indicated. After Ussher (1876) and Hutchinson (1906), with field observations by the author.

flood plain which produced the mud and silt horizons. The numerous calcrete horizons indicate subaerial soil formation in semi-arid conditions (Mader & Laming 1985). The climate was semi-arid with rather little rainfall and long dry periods when river beds dried out, but with seasonal or occasional rains leading to flash floods. However, there is no evidence for outright aridity; salt pseudomorphs and desiccation cracks are known, but not particularly common, in the Otter Sandstone Formation (Lavis 1876; Woodward & Ussher 1911; Henson 1970).

Occurrence of the fossils

The recent collections have come from blocks from the top 20 m or so of the Otter Sandstone Formation, most commonly in the intraformational conglomerates and breccias, but also in all other lithologies (Spencer & Isaac 1983). The tetrapod bones are generally in a fine to medium-grained reddish sandstone that often contains larger clasts (pebbles, mudflakes) up to 20 mm in diameter, which may have a pinkish, greenish, or ochreous colour. The more complete fish, on the other hand, are preserved in a dark red siltstone, and may be associated with plants. Spencer & Isaac (1983, p. 268) reported only 'indeterminate bone fragments' found *in situ* in an intraformational conglomerate horizon', but since then P. Spencer (personal

communication) has found four rhynchosaur specimens (EXEMS 60/1985.284, 285, 292, and 7/1986.3) in a single horizon at beach level. Spencer & Isaac (1983) noted that the whole formation is probably 'sparsely fossiliferous', but the main problem is that the cliffs are so steep and high, and most fossils have been found in fallen blocks on the shore.

The most clearly localized of the older finds were made at Otterton Point (SY 078820): Whitaker (1860) reported that his *Rhynchosaurus* jaw came from a large block fallen from the low cliff on the left bank of the Otter River just above its mouth, 'where the sandstone is somewhat brecciform', and Metcalfe (1884) reported supposed bone fragments from 'numerous points near Budleigh Salterton and Otterton Point'.

The early authors believed that there was one or more bone beds at the eastern end of the exposure. Lavis (1876) and Metcalfe (1884) placed it 'about 10 feet from the top of the sandstone'; Hutchinson (1906) and Woodward & Ussher (1911) placed it 'about 50 feet below the base of the Keuper Marls', a difference of some 40 feet (13 m) (figure 41). Hutchinson (1879, p. 2) gave the most detailed account of these horizons. He had found horsetail stems in a bed at the top of the sandstone, 'about eight or ten feet above' a group of two or three 'White bands' which appeared as clear horizons on 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 the under cliff has concealed the stratification at this place; but it may be fifty feet below, and amongst the beds of red rock'. Hutchinson described how this bone-bearing horizon began at beach level 'somewhere under Windgate', indeed close to many of Spencer's recent finds, and rose in the cliff westwards for 'about half-a-mile' where it reached a height of about 20 m above sea level. Fallen blocks from this point provided Lavis' (1876) find.

Taphonomy

The tetrapod fossils are generally isolated elements: jaws, teeth, partial skulls, or single postcranial bones. However, some bones occur in articulation, such as the type skull and jaw of *R. spenceri* (EXEMS 60/1985.292), the associated humerus, radius and ulna (EXEMS 60/1985.282), and the two sets of vertebrae (EXEMS 60/1985.15 (two), 60/1985.57 (three)).

The commonest individual finds are isolated maxillae (9), premaxillae (5), partial dentaries (5), and other isolated skull and mandible fragments (5), with partial skulls and mandibles in association (3), sets of vertebrae (2), and associated limb bones (1) being less common. The rarity of postcranial remains, compared with the relative abundance of parts of the skull and mandible of *R. spenceri*, seems to be genuine. There are not large collections of unidentifiable ribs, fragments of vertebrae, or shafts of long bones. The rarity could be the result of selective collecting or, more probably, selective preservation: the bulk of skull remains are tooth-bearing elements, which are nearly always heavily represented in rhynchosaur-bearing deposits in all parts of the world.

The incompleteness of most specimens of *R. spenceri* is largely the result of predepositional disarticulation and breakage, as is shown by their context in the sediment, although there has doubtless been an element of collection failure. 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), but others show detailed preservation of surface features and delicate sharp teeth. The remains of the two skulls of *R. spenceri* (EXEMS 65/1984, 60.1985.292) were largely

undistorted, although the squamosal in EXEMS 60/1985.292 had fallen down a little relative to its original position, presumably as a result of slight collapse of the skull.

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 rhynchosaurs (§§8.5, 8.6) and in rhynchosaurs from elsewhere in the world (Benton 1984*b*).

The Otter Sandstone flora and fauna

The only plants yet found in the Otter Sandstone Formation are stems and leaves of large horsetails (Hutchinson 1879; and more recent finds).

The vertebrate fossils were found from 1868 onwards. Huxley (1869) and Whitaker (1869) described a tooth-plate of *Hyperodapedon* (i.e. *Rhynchosaurus*) from Otterton Point. Seeley (1876) reported a fine lower jaw and other bones of *Mastodonsaurus lavisi* and a possible *Hyperodapedon* (i.e. *Rhynchosaurus*) tooth-plate which Lavis (1876) had collected in Picket Rock Cove, to the west of High Peak. Metcalfe (1884) figured remains of *Hyperodapedon* (i.e. *Rhynchosaurus*), *Mastodonsaurus* jaws, and other bones collected by H. J. Carter, and the latter (Carter 1888) described further remains, including fish scales. There were no further reports of vertebrate finds until Spencer & Isaac (1983) and Milner *et al.* (1990) described new collections that greatly enlarged the faunal list. The fauna contains the following taxa.

1. Deep-bodied perleidid fish, *Dipteronotus*, about 60–70 mm long, as also known from Bromsgrove.
2. Scales of a variety of palaeoniscoid fish, *Gyrolepis* (?), and the lungfish *Lepidosteus* (Carter 1888).
3. *Mastodonsaurus lavisi* (Seeley 1876), skull fragments and part of a lower jaw (BMNH, EXEMS: Seeley 1876; Wills 1916, p. 11; Paton 1974, pp. 273–279, 282, figs 14B, 16B), a large capitosaurid labyrinthodont, with an estimated skull length of 500–600 mm. Diet: fish and animals at the waterside. Also known from Warwick and Bromsgrove (see §§8.5, 8.6).
4. *Eocyclotosaurus* sp., remains of a skull, about 150 mm long, and other fragments (EXEMS: Spencer & Isaac 1983, p. 268).
5. Capitosaurid *inc. sed.*, posterior part of a mandible (EXEMS: Milner *et al.* 1990).
6. *Rhynchosaurus spenceri* n.sp., skull and mandible remains, isolated maxillae, and postcranial elements (BMNH, GSM, RSM, EXEMS: Huxley 1869, pp. 141, 146; Whitaker 1869, p. 156; Seeley 1876, p. 283; Metcalfe 1884, p. 260, fig. 2; Woodward (in Irving 1888, p. 163; in Carter 1883, p. 319); Spencer & Isaac 1983, p. 268), a moderate-sized rhynchosaur with a skull length of 40–175 mm (mean, 116 mm; estimated mean body length 0.8 m; range 0.4–1.3 m), herbivorous.
7. *Tanystropheus* sp., small tooth (EXEMS), a small insectivore.
8. Procolophonid *inc. sed.*, three small dentaries, a maxilla, and an interclavicle (EXEMS: Spencer & Isaac 1983, p. 268; Milner *et al.* 1990), a small herbivore.
9. Thecodontians – rauisuchians and others (?) – numerous teeth (EXEMS: Spencer & Isaac 1983, p. 269), a jaw (BMNH: Metcalfe 1884, p. 261, fig. 3) and postcranial elements, including (?) a long neural spine (EXEMS) from small to medium-sized carnivores (teeth range in length from 2 to 20 mm).

9. RELATIONSHIPS OF THE RHYNCHOSAURS

9.1. *The place of the Rhynchosauria within the Diapsida (figure 42)*

Until recently, most authors classed the rhynchosaur with the sphenodontids in the Rhynchocephalia (see, for example, Romer 1966). This viewpoint was questioned by a number of authors more recently (reviewed by Carroll 1977; Brinkman 1981), and several independent cladistic analyses now place the rhynchosaur in an archosauromorph branch of the Diapsida, in association with prolacertiforms and archosaurs (see, for example, Benton 1983, 1984*a*, 1985; Evans 1984, 1986, 1988; Gauthier 1984; Chatterjee 1986).

Within the Archosauromorpha, the Rhynchosauria have been placed in three positions (figure 42), either as more derived than *Trilophosaurus* (Benton 1984*a*, 1985), as less derived than *Trilophosaurus* (Evans 1988), or as the sister-group of *Trilophosaurus* alone (Chatterjee 1986). All three authors agree in pairing Prolacertiformes with Archosauria.

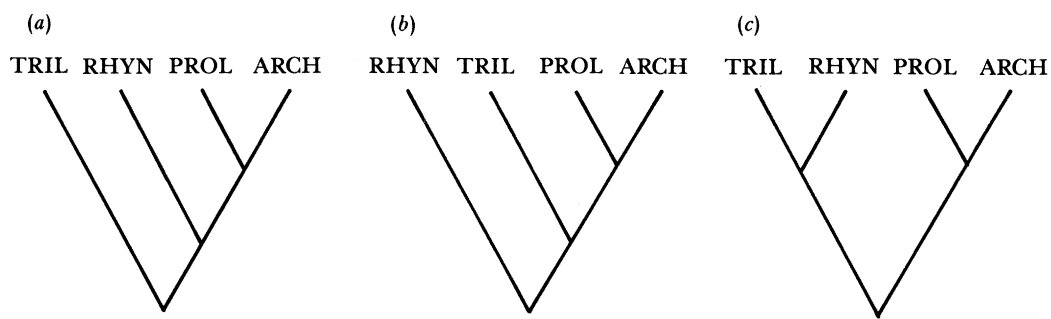


FIGURE 42. Three views of the cladistic relationships of Rhynchosauria (RHYN) to *Trilophosaurus* (TRIL), Prolacertiformes (PROL), and Archosauria (ARCH). (a) After Benton (1984*a*, 1985); (b) after Evans (1988); (c) after Chatterjee (1986).

Benton (1984*a*, 1985) argued that *Trilophosaurus* lacked the following postulated synapomorphies of the other three (figure 42*a*).

- (1) Premaxilla extends up behind naris.
- (2) Nares are elongate and lie close to the midline. (The nares fuse into a single median naris in Rhynchosauria.)

(3) Quadratojugal (if present) is located mainly behind the lower temporal fenestra, instead of below it. If a lower temporal bar is present, it is formed largely by the jugal, and the squamosal has a short ventral process. (The state of this character is questionable in *Trilophosaurus* as it has no lower temporal fenestra, and the posterior region of the side of the skull is poorly preserved (Gregory 1945).)

Evans (1988) based her cladogram (figure 42*b*) on the absence in rhynchosaur of these postulated synapomorphies of the other three:

- (1) Ribs run back parallel to the cervical vertebral column.
- (2) Cervical ribs have an anterior process.
- (3) Nasals are longer than the frontals.

Chatterjee (1986) argued that the rhynchosaur and *Trilophosaurus* share (figure 42*c*) the following postulated synapomorphies:

- (1) Ankylothecondont tooth implantation.
- (2) Premaxilla and anterior part of dentary are edentulous.

(3) Parietal has a strong median crest.

Each cladogram (figure 42) is supported by three postulated synapomorphies, and they cannot therefore be separated on grounds of parsimony. However, if *Mesosuchus* is a rhynchosaur (see below), the third hypothesis (figure 42c) is weakened, as this animal lacks Chatterjee's (1986) characters (1) and (2), and (3) is not clear.

9.2. Relationships within the Rhynchosauria (figure 43)

There are currently about 12 genera and 16 species of rhynchosaur listed by various authorities (e.g. Chatterjee 1980; Benton 1983; Buffetaut 1983) (table 5). Many of these taxa are represented by only fragmentary remains. The early 'rhynchosaur' *Noteosuchus* lacks many diagnostic parts, and it is not considered here (Benton 1985).

TABLE 5. THE TAXA OF RHYNCHOSAURS

(The species are arranged in approximate stratigraphic order. Data from Dutuit (1976), Chatterjee (1980), Benton (1983), Buffetaut (1983), and Murry (1986).)

Early Triassic
<i>Mesosuchus browni</i> , Cynognathus Zone, South Africa
<i>Howesia browni</i> , Cynognathus Zone, South Africa
Middle Triassic
<i>Stenaulorhynchus stockleyi</i> , Manda Formation, Tanzania
<i>Mesodapedon kuttyi</i> , Yerrapalli Formation, India
<i>Rhynchosaurus articeps</i> , Tarporley Siltstone Formation, England
<i>Rhynchosaurus brodiei</i> , Bromsgrove Sandstone Formation, England
<i>Rhynchosaurus spenceri</i> , Otter Sandstone Formation, England
Late Triassic
? <i>Acrodonta irerhi</i> , Argana Formation, Morocco
<i>Isalorhynchus genovefae</i> , Isalo II Formation, Madagascar
<i>Scaphonyx fischeri</i> , Santa Maria Formation, Brazil
<i>Scaphonyx sanjuanensis</i> , Ischigualasto Formation, Argentina
'Texas rhynchosaur', Dockum Group, U.S.A.
'Nova Scotia rhynchosaur', Wolfville Formation, Canada
<i>Hyperodapedon gordonii</i> , Lossiemouth Sandstone Formation, Scotland
<i>Hyperodapedon huxleyi</i> , Maleri Formation, India
<i>Supradapedon stockleyi</i> , ?Upper Triassic, Tanzania

In constructing a cladogram of rhynchosaur relationships, 26 characters were assessed from specimens and from the literature (table 6). Polarity was determined by comparison with an outgroup of 'other early diapsids' (*Claudiosaurus*, *Petrolacosaurus*, *Prolacerta*, *Thadeosaurus*, *Youngina*). The characters are listed below, with the primitive (0) and derived (1, 2, 3) conditions noted. Where more than one derived state exists, the sequence of codes (1, 2, 3) does not imply an evolutionary sequence. [Note that, with reference to character (19), *H. gordonii* generally has a wider medial than lateral tooth field, as stated by Benton (1983, p. 43), although one figured specimen (Benton 1983, figs 15, 53g; 1984b, figs 15a, 17) is exceptional in showing the opposite state.]

A data matrix was established for all 16 rhynchosaurian taxa (table 7), but only nine were well enough known to be used in the cladistic analysis: the early forms *Mesosuchus* and *Howesia*, and *Stenaulorhynchus*, *Rhynchosaurus articeps*, *R. brodiei*, *Hyperodapedon gordonii*, *H. huxleyi*, *Scaphonyx fischeri*, and *S. sanjuanensis*. The other eight (including *R. spenceri*) are incomplete in that less than 67% of the potential synapomorphies could be assessed, and they were excluded from the analysis. This data matrix was analysed by the PAUP (phylogenetic analysis using parsimony)

package (version 2.4) developed by David L. Swofford (1985) on an IBM-PC. The trees were rooted with a cross-section of other diapsids defined as the ancestor. The GLOBAL branch-swapping, FARRIS optimization, MULPARS, and UNORDERED options were invoked. The analysis of relationships of the nine well-represented taxa gave rise to three equally parsimonious cladograms (length 35 steps, consistency index (CI) 0.857); the differences occurred in the relative placements of *R. articeps* and *R. brodiei*, whether as sister-groups of each other, or as successive outgroups of the late Triassic forms (figure 43). Other permutations of the taxa were tried, but all yielded essentially the same pattern of relationships.

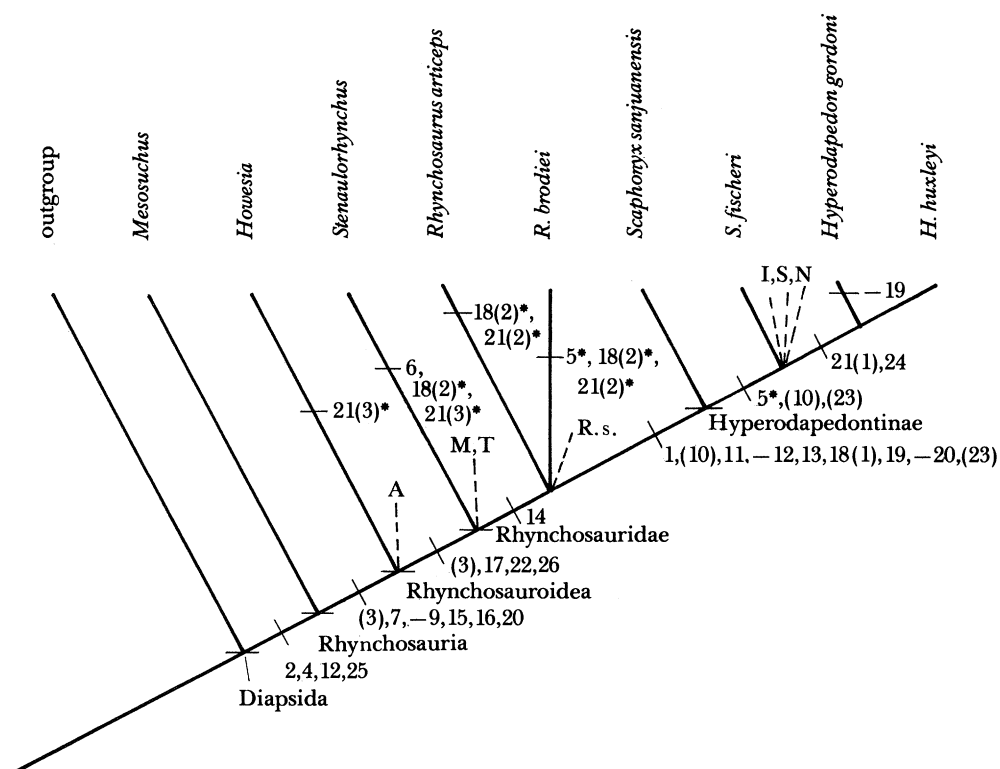


FIGURE 43. The most parsimonious cladogram showing the relationships of the nine best-known taxa of rhynchosauria, based on a cladistic analysis by the PAUP program of 26 characters (see text and table 7). The length of the tree is 35 steps; CI is 0.857. Postulated parallelisms are indicated by an asterisk, postulated reversals by a negative sign, uncertainly placed characters by parentheses, and derived character states by (1), (2) or (3). Seven less-well-known taxa have been added to the core cladogram (see text). Abbreviations: A, *Acrodonta*; I, *Isalorhynchus*; M, *Mesodapedon*; N, Nova Scotia rhynchosaur; R. s., *Rhynchosaurus spenceri*; S, *Supradapedon*; T, Texas rhynchosaur.

The major conclusions from the cladistic analysis are:

(1) *Mesosuchus* and *Howesia* are the most primitive rhynchosauria, being successive outgroups to the remainder, the view of Benton (1983, 1985). They do not appear to share synapomorphies with each other.

(2) *Stenaulorhynchus* and *Rhynchosaurus* form successive outgroups to the remaining rhynchosauria. The present analysis did not confirm the commonly held view (see, for example, Chatterjee 1974, 1980; Benton 1983, 1985) that these two genera form a subfamily Rhynchosaurinae.

(3) The three species of *Rhynchosaurus* do not always form a clade. *R. spenceri* is too

incompletely known to be included in the analysis. *R. brodiei* and *R. articeps* may be sister taxa, but they could equally parsimoniously be successive outgroups to the Late Triassic taxa, according to this analysis.

(4) The Late Triassic taxa form a unique clade in all analyses, clearly distinguished from the taxa already noted by several synapomorphies. This group is equivalent to the Subfamily Hyperodapedontinae of Chatterjee (1974) and Benton (1983, 1985).

(5) The genus *Scaphonyx* appears to be paraphyletic as '*S. sanjuanensis*' is the outgroup to the remaining hyperodapedontines in all analyses, as far as the brief published description indicates (Sill 1970). However, C. L. Schultz (personal communication, 1988) expresses doubt about the validity of this species.

(6) The genus *Hyperodapedon* is monophyletic.

The remaining seven taxa were assessed for synapomorphies, as far as possible, and added to the core cladogram (figure 43, dashed lines). *Acrodenta* could not be placed; *Mesodapedon* and the Texas rhynchosaur fall simply within the Rhynchosauridae, and the other three in the hyperodapedontine group. However, several of these taxa (*Mesodapedon*, *Acrodenta*, *Isalorhynchus*, *Supradapedon*) appear to lack diagnostic characters, and others (Texas, Nova Scotia rhynchosaur) have yet to be described. Data on the two North America forms have been gleaned from published sources (Chatterjee 1980; Murry 1986).

9.3. The 'Rhynchosaurinae'

The three species of *Rhynchosaurus* were hitherto assumed to fall in a clade with *Stenaulorhynchus*, termed the Subfamily Rhynchosaurinae (Chatterjee 1969, 1974; Benton 1983, 1984a, b, 1985). The diagnostic characters of this group were:

- (1) Occipital condyle lies well in front of the quadrates (character 12).
- (2) Presence of two grooves on the maxilla (character 18).

Unfortunately, the occipital condyle character is unknown in *R. brodiei* and *R. spenceri*, and it is apparently shared with *Mesosuchus*. The nature of the grooves is unique to *Rhynchosaurus* and *Stenaulorhynchus*, but it is outweighed in the analysis by other postulated synapomorphies. A third postulated synapomorphy, the presence of a single row of teeth on the pterygoid (Chatterjee 1969, 1974, 1980; Benton 1985), is no longer held to be valid (see §7).

The three species of *Rhynchosaurus* share only one possible synapomorphy: the dentary is well over half the length of the lower jaw (character 14), a parallelism with Hyperodapedontinae (although this is not known in *R. brodiei*). *R. brodiei* and *R. spenceri* appear to be advanced over *R. articeps* in that the jugal occupies a larger area of the cheek than the maxilla (character 5), a parallelism with most Hyperodapedontinae. *R. spenceri* is advanced over the other two in the fact that the greatest breadth of its skull is greater than the midline length (character 1), a parallelism with Hyperodapedontinae. *R. articeps* and *R. brodiei* share the apparently advanced possession of two major tooth rows on the dentary (character 21) compared with the large number of dentary tooth rows in *R. spenceri*. Note that the three characters shared by species of *Rhynchosaurus* and Hyperodapedontinae are interpreted as parallelisms because they are greatly outweighed by the seven or more synapomorphies of Hyperodapedontinae that are absent in the species of *Rhynchosaurus*.

Stenaulorhynchus differs from the species of *Rhynchosaurus* in a number of features, only one of which can be shown to be an autapomorphy:

- (1) Frontal is broader than long (character 6).

(2) Very anterior position of the occipital condyle relative to the quadrates, especially when compared with *R. spenceri* (the posterior position of the occipital condyle in this species is suggested by the location of the basiptyergoid pits on the pterygoid), the largest species of *Rhynchosaurus*.

(3) Teeth on the maxilla are relatively smaller than in *Rhynchosaurus* (see §7).

(4) Presence of a backwards-pointing spine on the second sacral rib (Huene 1938, pl. 4, fig. II).

In addition, *Stenaulorhynchus* is much larger than *Rhynchosaurus*, with a skull length of 240 mm and a total body length of 1.83 m (Huene 1938, 1939a), compared with 80–140 mm and 0.54–0.95 m in the three species of *Rhynchosaurus*. Huene (1938) shows no supratemporal in *Stenaulorhynchus*, possibly a parallelism with the Hyperodapedontinae (character 10), but this element could be present in the strange split medial process of the squamosal shown by Huene (1938, pl. 1, figs 1, 2, pl. 2, fig. 1) (see §3.2).

In the absence of characters 1, 5 and 14, and parallelisms between species of *Rhynchosaurus* and Hyperodapedontinae, *Stenaulorhynchus* would seem to be more 'primitive' than *Rhynchosaurus*, the view that has generally been taken (Walker 1969 (tentatively), 1970; Sill 1971b; Chatterjee 1974, 1980, p. 62; Benton 1984b).

10. *RHYNCHOSAURUS* AND THE STRATIGRAPHY OF THE ENGLISH MIDDLE TRIASSIC

The species of *Rhynchosaurus*, occurring as they do in four separate Middle Triassic basins, have figured strongly in the dating of their respective formations. Walker (1969, 1970) argued that all relevant horizons were certainly Middle Triassic in age because of the resemblance between *Rhynchosaurus* and *Stenaulorhynchus*, and because of the intermediate evolutionary position of *Rhynchosaurus* between the Early Triassic *Howesia* and *Mesosuchus*, and the late Middle Triassic or Late Triassic *Hyperodapedon* and *Scaphonyx*. At that time, the only other vertebrate evidence for age came from Warwick and Bromsgrove, where an extensive associated tetrapod fauna (§§8.5, 8.6) confirmed this view. In particular, the macrocnemid, the poposaurid, the nothosaur, and the amphibians pointed to an age between Anisian and earliest Carnian, by comparison with independently dated horizons in Germany and North America. The absence of phytosaurs at either Warwick or Bromsgrove tended to rule out a Late Triassic age, and Walker settled for early to mid-Ladinian. By implication, the Devon reptiles were regarded as rather older.

Paton (1974) surveyed the evidence from the labyrinthodont amphibians, and stated that the Warwick–Bromsgrove horizons were of the same age as the Otter Sandstone because of the near identity of the species. The two labyrinthodont genera *Mastodonsaurus* and *Cyclotosaurus* are known from well-dated horizons in Germany, the former spanning from Scythian to Ladinian, and the latter from Ladinian to Carnian. Paton (1974) concurred with Walker's suggestion of an early to mid-Ladinian age.

Evidence for stratigraphic age from macrofossils other than the tetrapods is available only from Bromsgrove and Devon. Wills (1910) suggested correlation of the Bromsgrove Sandstone Formation with the German Lettenkohle, generally regarded as late Ladinian in age, on the basis of the plants and invertebrates. He later (Wills 1948) allowed the possibility of an alternative correlation with the Voltziensandstein of Germany or Grès à *Voltzia* of Alsace, now

dated as Anisian. Wills (1970, pp. 260–261) noted that the Bromsgrove plants indicated late Scythian to late Ladinian ages, by comparison with German material, the scorpions and the fish *Dipteronotus* and *Ceratodus* suggested an Anisian or Ladinian age, and the conchostracan *Euestheria* a late Ladinian to Norian age. Warrington *et al.* (1980, pp. 39–40) concurred, and dated the Bromsgrove Sandstone Formation as ?late Scythian – early Ladinian, with the reptiles and amphibians occurring in the upper part. The Otter Sandstone fauna and flora is generally comparable to that from Bromsgrove, but Milner *et al.* (1990) are unable to determine whether the age is Anisian or Ladinian, based on the new vertebrate specimens.

The four English rhynchosaur localities have not yielded fossil pollen and spores which could be dated, but palynomorphs from elsewhere in the reptile-bearing formations of the English Midlands have given additional independent evidence of age. Warrington (1967, 1970*b*) dated the ‘Waterstones’ and the underlying ‘Keuper Sandstone’ (now, the Bromsgrove Sandstone Formation) in a borehole at Bromsgrove as late Scythian to early Ladinian, on the basis of miospores. The boundary between the sandstone and the Waterstones is interpreted as diachronous, and it is dated as Anisian. The age of the *Rhynchosaurus* specimens at Bromsgrove, which came from the top of the Keuper Sandstone and from the Waterstones (§8.6), would then be early Anisian to early Ladinian. Warrington (1970*a, b*) later argued that the Waterstones unit was strongly time-transgressive, and that in Cheshire it was late Scythian in age, on the basis of palynological evidence. This would imply a mid to late Scythian age for *R. articeps*, which came from the Waterstones, and also possibly from the underlying sandstones. Fisher (1972), on the other hand, argued that palynological evidence could date the Waterstones of Merseyside equally as late Scythian or as early Anisian.

Pattison *et al.* (1973) surveyed palynological and macrofossil biostratigraphic data, and their dates for the three species of *Rhynchosaurus* were: *R. articeps* (late Scythian), *R. brodiei* (early to mid-Anisian), and *R. spenceri* (early to late Anisian). Warrington *et al.* (1980) provided these dates: *R. articeps* (early Anisian), *R. brodiei* (late Anisian to early Ladinian), and *R. spenceri* (early to late Anisian). The upwards revision of the first two dates was based on the biostratigraphic evidence from the reptiles (Warrington *et al.* 1980, pp. 33, 39–40). The date of the Otter Sandstone Formation (Anisian) was based solely on Walker’s (1969, 1970) statement that the Devon *Rhynchosaurus* was more primitive than that from Warwick–Bromsgrove (?early Ladinian).

The problems in dating these Middle Triassic formations are typical of much of the British Triassic, which lacks the ammonoids necessary for correlation with the standard marine stages in the Alps and Canada. Any standardized biostratigraphical zonal scheme for Britain would have to be based on palynomorphs (Warrington *et al.* 1980, p. 11), but pollen and spores are absent from many critical geological formations, as has already been noted.

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KEY TO ABBREVIATIONS USED IN FIGURES

Skull and mandible

a	angular	n	nasal
amf	anterior meckelian foramen	ob	olfactory bulb cavity
ar	articular	op	opisthotic
bo	basioccipital	p	parietal
bpt	basipterygoid process	pa	prearticular
bs	basisphenoid	paf	posterior alveolar foramen
c	coronoid	pf	postfrontal
cf	carotid foramen	pl	palatine
ch	choana	plfac	facet for palatine
d	dentary	pm	premaxilla
ec	ectopterygoid	pmf	posterior meckelian foramen
eo	exoccipital	po	postorbital
ep	epipterygoid	pr	prootic
f	frontal	prf	prefrontal
fnm	facet for nasal and maxilla	ps	parasphenoid
fo	fenestra ovalis	psaf	posterior supra-angular foramen
fp	facet for premaxilla	pt	pterygoid
gr	groove	ptt	supposed pterygoid teeth
hy	hyoid element	q	quadrate
if	infraorbital foramen	qf	quadrate foramen
iof	inferior orbital foramen	qj	quadratojugal
j	jugal	s	stapes
l	lacrimal	sa	surangular
laf	lateral alveolar foramina	so	supraoccipital
lc	lagenar crest	sp	splenic
ld	lacrimal duct	sq	squamosal
lfac	facet for lacrimal	st	supratemporal
m	maxilla	tso	tubera sphenio-occipitale
mc	meckelian canal	v	vomer
mf	metotic foramen	vc	vestibular cavity
mjf	medial jugal foramen	vfac	facet for vomer
mnf	mandibular foramen		

Postcranial skeleton

1, 2, 3, 4	numbers of vertebrae, or of distal tarsals	I, II, III, IV, V	digit numbers I-V
ANT	anterior	h	humerus
ast	astragalus	i	intermedium
at	atlas	icl	interclavicle
ata	atlas arch	il	ilium
atce	atlas centrum (facet for)	imp	impression
atic	atlas intercentrum	mt	metatarsal
ca	calcaneum	of	obturator foramen
ce	centrale	pife	puboischiofemoralis externus process
ch	chevron	pu	pubis
cl	clavicle	r	radius
co	coracoid	ra	radiale
cr	cervical rib	rf	radial facet
cv	cervical vertebra	s	scapula
dpc	deltopectoral crest	sup	supinator crest
dv	dorsal vertebra	sv	sacral vertebra
f	femur	ti	tibia
fi	fibula	u	ulna
ga	gastralia	uf	ulnar facet
		ul	ulnare