

# A NEW GENUS OF RHYNCHOSAUR FROM THE MIDDLE TRIASSIC OF SOUTH-WEST ENGLAND

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Typescript received 16 October 2006; accepted in revised form 15 January 2007

**Abstract:** We present a description of new cranial and postcranial material representing a new genus of rhynchosaur (Diapsida, Archosauromorpha) from the Otter Sandstone Formation (Mid Triassic) of Devon, south-west England. The taxon had been named *Rhynchosaurus spenceri* Benton, 1990, but cladistic analysis of the clade, and one autapomorphy, show that it does not belong to *Rhynchosaurus*, and a new generic name is required. We propose the name *Fodonyx* for this genus. A cladistic analysis of the Rhynchosauria confirms the main discoveries of previous analyses, and that *Fodonyx* is sister group to the Hyper-

odapedontinae, the clade of Late Triassic rhynchosaurs. The new cladistic analysis, for which many more characters were coded for *Fodonyx* than before (a rise from 39 to 75 per cent), counter-intuitively produced less well-resolved results: the new codings of previously uncoded characters introduced conflict so that *Fodonyx* turns out to be less like the Late Triassic rhynchosaur clade than had been assumed before.

**Key words:** Rhynchosaur, Triassic, Otter Sandstone Formation, Devon, Archosauromorpha.

RHYNCHOSAURS were terrestrial, herbivorous basal archosauromorphs of the Early–Late Triassic. Large claws on the hind feet suggest the ability to dig well and the heavy jaws and interlocking tooth-plates imply a diet of tough vegetation and tubers (Benton 1983). Rhynchosaurs enjoyed a near-global distribution, having been found in Great Britain (Benton 1983, 1990), South Africa (Dilkes 1998), Zimbabwe (Raath *et al.* 1992), Tanzania, Madagascar (Buffetaut 1983), India (Chatterjee 1974), Brazil (Langer and Schultz 2000), Argentina, Canada and the United States (Lucas *et al.*, 2002; Nesbitt and Whatley 2004). There are currently some 15 valid species of rhynchosaur, recognised after recent revision and recognition of synonymies, as well as a further five unnamed, or tentatively named, taxa based on incomplete remains from other locations (Benton 1983, 1990; Hunt and Lucas 1991; Langer and Schultz 2000).

Cladistic analyses of the phylogeny of rhynchosaurs (Benton 1983, 1985, 1990; Evans 1988; Dilkes 1995, 1998; Wilkinson and Benton 1995; Langer *et al.* 2000a; Langer and Schultz 2000) have revealed a common pattern: two basal forms, *Mesosuchus* and *Howesia* from the Lower Triassic of South Africa, then a number of Mid Triassic forms, principally *Rhynchosaurus* and *Stenaulorhynchus*, and a crown clade of Late Triassic forms, species of *Hyperodapedon* and *Scaphonyx*.

The Devon rhynchosaur was named *Rhynchosaurus spenceri* by Benton (1990), a new species assigned to

the existing genus *Rhynchosaurus* Owen, 1842. The new specific name was established since *R. spenceri* differed from all other then-known rhynchosaurs, but the remains were too incomplete to determine whether it belonged to a distinct genus or not. Indeed, *R. spenceri* was excluded from the cladistic analysis by Benton (1990) because so many parts of the skeleton were unknown, and hence uncoded in the character matrix. This approach was criticized by Wilkinson and Benton (1995): excluding a taxon from cladistic analysis simply because it is incompletely coded is inappropriate. On including *R. spenceri* in a repeat of Benton's (1990) cladistic analysis, they found that it fell between the other two species of *Rhynchosaurus*, *R. articeps* and *R. brodiei*, on the one hand, and the Late Triassic clade on the other. Langer and Schultz (2000) found the same thing, and indicated that *R. spenceri* was definitively not a member of the genus *Rhynchosaurus*.

The aims of this paper are to present new material of the Devon rhynchosaur, concentrating in particular on a new partial skeleton and a new skull, and to place this in the context of a thorough phylogenetic analysis of rhynchosaur relationships. Our conclusion is that the Devon rhynchosaur cannot remain a species of *Rhynchosaurus* and has to be assigned to a new genus.

*Institutional abbreviations.* BRSUG, Bristol University, Department of Geology; EXEMS, Royal Albert Museum, Exeter.

## SYSTEMATIC PALAEOLOGY

Subclass DIAPSIDA Osborn, 1903  
 Infraclass ARCHOSAURIFORMES Huene, 1946  
 Order RHYNCHOSAURIA Osborn, 1903  
 Family RHYNCHOSAURIDAE Huxley, 1859

Genus FODONYX gen. nov.

*Fodonyx spenceri* (Benton, 1990)  
 Text-figures 1–7

[Full synonymy list to 1990 in Benton 1990]

- 1993 *Rhynchosaurus spenceri* Benton, 1990; Benton *et al.*, pp. 167–170.  
 1994 *Rhynchosaurus spenceri* Benton, 1990; Benton *et al.*, pp. 145–146.  
 1995 *Rhynchosaurus spenceri* Benton, 1990; Wilkinson and Benton, pp. 141–147.  
 1997 *Rhynchosaurus spenceri* Benton, 1990; Benton, pp. 145–147.  
 2000 ‘*Rhynchosaurus*’ *spenceri* Benton, 1990; Langer and Schultz, pp. 647–648.  
 2000 ‘*Rhynchosaurus*’ *spenceri* Benton, 1990; Langer *et al.*, pp. 120, 123–127.

*Derivation of name.* The new generic name *Fodonyx* is modelled on the name *Scaphonyx*, given to the Brazilian rhynchosaur by Woodward (1907), and meaning ‘spade claw’: Latin, *fodere*, to dig, and Greek, *onyx*, claw, hence meaning ‘digging claw’, in reference to the large unguals present on the foot.

*Holotype.* EXEMS 60/1985.292, a partial skull and mandible, including the floor of the orbit and the palate of the right side, a partial palate of the left side, the posterior right-hand angle of the skull, and both mandibles (Benton 1990, figs 28–29, 31, 36i–j, 37f–g).

*Referred material.* Material listed by Benton (1990, pp. 221–222) as well as EXEMS 79/1992 (a partial postcranial skeleton; Benton *et al.* 1993), BRSUG 27200 (a nearly complete skull), EXEMS 60/1985.20 (isolated right jugal); EXEMS 60/1985.48 and BRSUG 26874 (two isolated parietals); BRSUG 26875 (partial dorsal vertebra); EXEMS 60/1985.324 (partial toe with ungual).

*Locality and horizon.* Various sites along the South Devon coast from Ladram Bay to Port Royal, Sidmouth (maps and map references in Benton 1990, 1997; Benton *et al.* 1993, 1994), all in the upper half of the Otter Sandstone Formation (Sherwood Sandstone Group). The unit is dated as Anisian on the basis of faunal comparisons and matching with palynologically dated units in the English Midlands (Benton *et al.* 1994). This has since been confirmed by magnetostratigraphy (Hounslow and McIntosh 2003), who found that the lower parts of the Otter Sandstone Formation correspond to the early and mid Anisian, and the upper parts, which contain the majority of the macro-

fossils, correlate with late Anisian and latest Anisian magnetozones on the marine standard.

*Revised diagnosis.* *Fodonyx* has a single apomorphy that distinguishes it from other rhynchosaurs: the paraoccipital processes, when seen in posterior view, angle ventrally. In all other rhynchosaurs, these processes are either horizontal or are raised dorsally. The cladistic analysis also confirms that *Fodonyx* is distinct from any other known rhynchosaur. *Fodonyx* differs from *Rhynchosaurus* (as represented by *R. articeps* and *R. brodiei*) in having the orbits orientated more dorsally than laterally, a major diagonal crest on the jugal that reaches the anterior portion of the orbit, and ornamentation on the external surface of the jugal with crests and bosses dorsal to this diagonal crest, in having the frontal longitudinal groove almost the same depth throughout, a basiptyergoid process that is broader than long, and chevron bones that taper distally. *Fodonyx* lacks the characters of the Late Triassic Hyperodapedontinae (see below).

## MORPHOLOGY OF THE SKULL

*Introduction*

A new rhynchosaur skull was found in spring 1999 by Mark Hounslow at Pennington Point, about 20 m east of the River Sid outfall (National Grid reference SY 130873). It was *in situ* (many fossils have come previously from fallen blocks) at the base of the cliff, and found at a time when much of the beach gravel had been swept away. Stratigraphically, the skull was found about 3 m below the top of Andy Newell’s Unit C, the Pennington Point Member of Gallois, and layer 21 of Hounslow and McIntosh (2003). According to the magnetostratigraphy of these authors, the age of this horizon is within the late Illyrian (latest Anisian), equivalent to the lower part of the Tethyan *P. trammeri* (conodont) Zone.

This skull (BRSUG 27200) was prepared by Remmert Schouten in the Bristol Palaeontology Laboratories in 2004 and 2005. The sandstone was removed from the dorsal and right-hand sides and the whole of the palate was exposed. The orbital and temporal regions on the right-hand side were prepared deep into the specimen. Sandstone was left in parts of the left-hand side in order to keep the specimen stable.

The skull is typically rhynchosaurian, triangular in shape in dorsal view, with large subcircular temporal fenestrae and orbits, a large midline naris, hooked ‘tusk’-like premaxillae, and broad maxillary tooth plates. The skull was probably rather lower than assumed by Benton (1990), whose reconstruction was based on materials that lacked the skull roof. It is nearly complete and has the

lower jaws in place (Text-figs 1–2). The posterior ventral corners of the skull, including both quadrates, the quadratojugals and parts of the jugals are missing. The skull roof has been depressed slightly, causing movement between skull roof bones at suture lines. The braincase is intact but has been disarticulated and moved slightly forward within the cranium. The base of the lower jaw has been eroded, probably before preservation, and is also missing parts of the angular and surangular.

*Skull roof* (Text-figs 1A, C, E, 2A, C, E)

The premaxilla is long and runs up over the snout to contact the prefrontal, close to the orbit. At its tip, the premaxilla is small and triangular in cross-section. The two premaxillae do not quite contact at their anterior tips, probably as a result of the post-mortem crushing. As a pair they form the classic rhynchosaurian ‘beak’. The premaxillae separate from one another rapidly backwards to provide space for the nasal bones and the boundaries of the heart-shaped single naris. Towards the distal end, there is a deep facet posterolaterally worn out by the anterior tip of the dentary when the jaws are closed. Just above this is a change in angle and texture in the premaxilla, with more marked longitudinal striations in the dorsal half of the element. This presumably marks where skin covered the dorsal half, and perhaps a keratinous sheath covered the distal, smoother half of the premaxilla.

The maxilla is broad and plate-like, forming much of the anterior side of the snout, as well as carrying the massive tooth plate. It contacts the premaxilla for three-quarters of the length of the latter. Posteriorly, the maxilla contacts the prefrontal, lacrimal and jugal, and it runs back to terminate below the posterior portion of the orbit. A number of foramina are visible, both for nerves and capillaries, in a row about 10 mm above the curved ventral tooth-bearing margin, and possibly indicating the limit of gum tissue. On the ventral edge, a number of unworn posterior teeth are visible in lateral view. The ventral view is obstructed by the mandibles, but the maxillary tooth plate was clearly an elongate triangle, divided by a midline groove, as seen in numerous isolated maxillae (Benton 1990, pp. 274–276). The occlusal surface of the maxillary tooth plate shows an anterior part, where bone and teeth are worn smooth by use, and a posterior part where up to five lateral teeth remain unworn and bear their enamel caps (stained black in preservation). Hidden from view are the medial tooth rows, and the subsidiary medial groove, seen in isolated maxillary tooth plates.

The nasal bones are large and paired, with a zigzag suture line down the midline of the skull. As with most rhynchosaurs, the nasals are shorter than the frontals, but they are similar in width. The nasals form the curved posterior border of the naris, and they extend back with the lateral margin in contact fleetingly with the premaxilla, and mainly with the prefrontal. The posterior margin is pointed, forming a firm zigzag suture with the narrow anterior margin of the frontal.

The lacrimal is small and placed on the anterior edge of the orbit. The lacrimal ducts are clearly visible along the inner edge of the orbital opening.

The prefrontal is large and borders the anterodorsal margin of the orbit, forming a thick, angular ‘eyebrow ridge’. Medially, the prefrontal is bounded by the nasals and frontals, but it does not meet the postfrontal.

The jugal is a complex four-branched element forming the ventral margin of the orbit and the anterior and ventral margins of the lower temporal fenestra. The anterior branch is bounded ventrally by the maxilla, and contacts the lacrimal anterodorsally. There is a deep, smooth depression in this branch beneath the orbit, and the jugal expands laterally to swing into the posterior process beneath the lower temporal fenestra. This portion is missing on both sides, something seen in many incomplete rhynchosaur skulls. Based on the distribution of this character in all other derived rhynchosaurs, the posterior branch of the jugal met the quadratojugal at the back of the lower temporal opening. The dorsal branch of the jugal forms the thin anterior margin of the lower temporal fenestra, and underlies the ventral branch of the postorbital, forming a strong pillar behind the orbit. The crest along the anterior margin of this pillar is more pronounced than seen in other rhynchosaurs. The medial branch of the jugal, which lies above and behind the maxillary tooth plate in the palate, is incompletely preserved. The jugal carries some small vessel openings and rugosities along the sloping ventral margin of the anterior process where it lies above the maxilla, but this rugose ridge is much less pronounced than in other large rhynchosaurs, such as *Hyperodapedon* (Benton 1983).

The frontals are long and together form an extended diamond-shaped portion of the skull roof. They are joined to each other firmly down the midline along a suture line that is straight posteriorly, and has small zigzags anteriorly. The frontals contact the nasals in front, the prefrontal and postfrontal laterally, with a short exposure in the dorsal orbital margin, and it tapers back to connect with the parietals nearly at a point. The anterior portion of the frontals is roughly horizontal, but they are dished posteriorly, and rise to a low, smooth ridge along the line of the frontal/postfrontal suture.

The postfrontal is roughly triangular, forming the posterodorsal margin of the orbit. There is a long, straight, posteromedial contact with the frontal, and posteriorly with the parietal. This posterior parietal contact dips ventrally, and is overlain by the pointed medial branch of the postorbital, which sits in a deep ‘socket’ of the postfrontal.

The parietals are fused, and together form a T-shaped element running from the frontals and postfrontals back to the occiput, and laterally to the squamosals. They form the medial borders of the upper temporal fenestrae. The midline portion of the parietals is triangular in cross-section, with a high, narrow ridge dorsally. The posterior margin of the parietals is slightly concave in dorsal view, and quite deep and flat in occipital view, where the lateral wings extend for virtually the width of the upper temporal fenestrae, lying beneath the medial branches of the supratemporals and squamosals.

The postorbitals are roughly T-shaped, with medial, posterior and ventral branches. The medial branch runs to a point that sits in a deep ‘socket’ formed by the underlying postfrontal. The medial and posterior branches form the anterior and lateral margins of the upper temporal fenestra and the dorsal margin of the lower temporal fenestra. This branch sends a long, broad,

but thin, tongue back over the main body of the squamosal, and terminates in line with the posterior margins of the temporal fenestrae. The ventral branch is triangular in cross-section, forms a deep posterior margin of the orbit, and sits on a broad attachment with the jugal.

The presence or absence of the supratemporal has long been debated in *Rhynchosaurus* and other rhynchososaurs (Benton 1990, p. 228). Here it is clearly present and well defined, a slender element lying in a gully along the posterior margin of the squamosal and contacting the parietal medially. The supratemporal is present in other Early and Mid Triassic rhynchososaurs, but is clearly absent in Late Triassic forms such as *Hyperodapedon* and *Scaphonyx*.

Only the right squamosal is preserved, and that only in part. It is a three-branched element that forms much of the posterior margin of the skull, as well as the posterior margins of both temporal fenestrae. The medial and ventral branches outline the bulk of the dorsolateral and lateral margins of the occiput. The medial branch lies over the lateral branch of the parietal, and forms a concavity for the supratemporal. The ventral branch descends along the posterior margin of the lower temporal fenestra, and its posterior margin curves forwards around the conch-like depression over the quadrate and quadratojugal, which it overlies. This detail is not seen in the present specimen, but was described in EXEMS 60-1/985.292 (Benton 1990, fig. 28c–d). In BRSUG 27200 the medial branch of the squamosal extends forwards at least half-way between the temporal fenestrae, beneath the postorbital.

The quadratojugal and quadrate are largely missing on both sides, with only a small part of the dorsal portion of the quadrate adhering beneath the squamosal. An isolated right quadrate/quadratojugal unit is present in the holotype skull of *F. spenceri* (EXEMS 60/1985.292; Benton 1990, fig. 28). The separation might be because, although the quadratojugal and quadrate form a massive column in the posterior corner of the skull, their connection to the rest of the skull, through the posterior branch of the jugal, the ventral branch of the squamosal, and the quadrate wing of the pterygoid, is weak and is likely to break in a defleshed specimen.

#### *Palate and hyoids* (Text-figs 1B, 2B)

Much of the palate is intact, though parts have fragmented, probably before preservation, and some is preserved with calcitic matrix that could not be prepared away without risk to the underlying material. The palate is sharply triangular, bounded by the massive maxillary tooth plates on either side in the anterior half, and with the pterygoids swinging posterolaterally from the midline to the quadrates in the posterior half. The anterior lateral parts of the palate are partly obscured by the mandibles.

The paired vomers are relatively long with a simple suture between them. They are composed of very thin bone that has degraded somewhat. Anteriorly, they meet at a point just behind the premaxillae, and laterally fuse with the maxillae. Posteriorly, they narrow to enclose the anterior part of the choana.

The paired palatines meet the vomers anteriorly in the midline, and they contact each other along a straight midline suture.

The palatine forms most of the medial, posterior and lateral borders of the choana and part of the infraorbital foramen. Posterolaterally the palatine sits below the lateral wing of the pterygoid, and meets the ectopterygoid.

The pterygoids are the largest elements in the palate, and they have three main processes. The anterior processes meet each other with a short midline suture in a V-shape just behind the palatines, but the pterygoids then open up for most of the midline, forming a clear interpterygoid space. The lateral process of the pterygoid is broad and plate-like, meeting the jugal above and each palatine anterolaterally, and lying above the ectopterygoid. The lateral process sweeps in a broad, partial spiral into the deep, plate-like posterolateral, or pterygoid, process that traverses the posterior portion of the palatal view of the skull to meet the quadrate in the posterolateral corner of the skull. This contact is partially preserved here, but the rest is seen in EXEMS 60/1985.282 (Benton 1990, fig. 28d). Medially, the pterygoids form shallow pockets for the basiptyergoid processes of the braincase.

The ectopterygoid is small and spans behind the maxillary tooth plate and sits behind the lateral wing of the pterygoid, meeting the jugal laterally. The ectopterygoids cannot be seen in palatal view (Text-fig. 1B) as they are covered by matrix and hyoid elements.

Hyoids have been reported before in *Hyperodapedon* and *Scaphonyx* (Benton 1983, pp. 637–638), but understandably they are rarely seen. In the current specimen, anterior portions of a right and left hyoid element (hy, Text-fig. 2B) are preserved below the ectopterygoids, in contact with the splenial on either side, and running posteromedially for 15 mm or so. Each element is circular in cross-section, about 4 mm across, and longitudinally striated.

#### *Braincase* (Text-figs 1B, D, 2B, D)

The endocranium is largely intact and *in situ*. It has slightly dissociated from the skull and moved down and to the right, but maintains its orientation. The left-hand side is eroded, but the centre and right are complete. Calcitic matrix has made some areas impossible to prepare fully. Overall, it is typical of rhynchososaurs in size and shape (cf. Benton 1983).

The basioccipital is short, carrying the hemispherical occipital condyle. It meets the basisphenoid on a straight suture across the tubera sphenooccipitales. The basisphenoid narrows dramatically in front of the tubera, with a deep depression in the ventral middle portion, before expanding anterolaterally into the basiptyergoid processes. These extend ventrally as somewhat trumpet-shaped processes, and have been rammed deep into the receiving pits in the pterygoids, presumably by taphonomic dislocation. Although the end has slightly eroded, the rather more complete right basiptyergoid process is 62 mm in length, and therefore *c.* 50 per cent longer relative to skull length than in *Rhynchosaurus* and 100 per cent larger in absolute size.

The paroccipital process on the right side shows the typical exoccipital and opisthotic. The cranial nerve foramina, metotic foramen, fenestra ovale and exoccipital-opisthotic suture cannot be distinguished because of the difficulties of preparation. The

paroccipital process runs slightly ventrally, and its distal end expands to form a deep, dorsoventrally orientated distal portion where it contacts the squamosal and quadrate (Text-fig. 1D).

The prootic is hard to make out because of adhering calcitic matrix. The supraoccipital can be determined in rough outline: it is a roof-like element, forming the dorsal margin of the foramen magnum, and extending up to meet the underside of the parietal in a point in the midline.

#### *Lower jaw* (Text-figs 1B–C, E, 2B–C, E)

Only the anterior portions of both lower jaws are preserved, the posterior elements having been largely removed; the ventral margins of both mandibles have also been eroded, since they stuck out of the block in which the skull was found. Enough of the lower jaw is preserved to show its typical rhynchosaur shape, and the complete mandibles in the holotype (EXEMS 60/1985.282; Benton 1990, figs 28, 31) allow a full reconstruction (Text-fig. 2C).

The dentary forms more than the anterior half of the mandible. It carries teeth on its expanded dorsal face, but these are largely obscured, except for four or five unworn posterior jaw-crest teeth on the left mandible, because the jaws are tight shut. The dorsal margin of the dentary curves up to an anterodorsally extended, rounded anterior tip. This anterior tip fits neatly in a facet of the premaxilla when the jaws are closed. The dentary extends from a thick tooth-bearing dorsal portion downwards as a thin plate around the cavity occupied in life by Meckel's cartilage. The lateral plate meets the splenial ventrally, and the angular and surangular behind. The dentary bears a 4-mm-deep 'smooth' zone below the tooth row, and below that are major vessel openings, especially towards the front of the jaw.

The splenial is complete on both sides (except for the skimmed-off ventral portion of the mandibles). It forms the medial wall of the channel for Meckel's cartilage, and the ventral part of the anterior mandible. It is seen in lateral view only towards the front of the jaw, where it expands to support the strong symphyseal plates.

A portion of the right surangular is preserved, attached to the posterior dorsal margin of the dentary. Only the anterior part of the angular may be seen on the eroded ventral face of the mandible where it extends between dentary and splenial in the floor of the cavity for Meckel's cartilage. The prearticular and articular are absent.

## MORPHOLOGY OF THE POSTCRANIAL SKELETON

The description of the postcranial skeleton that follows is based on the partial skeleton EXEMS 79/1992, found in Ladram Bay (National Grid reference SY 098852) in 1992, and described briefly by Benton *et al.* (1993). Further preparation since then has revealed more detail, and the following elements may now be identified: portion of the mandible (ventral portion of angular?), 17 dorsal and

anterior caudal vertebrae, nearly all separated into centra and neural arches, three chevrons, numerous ribs, including a nearly complete anterior dorsal rib, much of the anterior gastral basket, left scapula, left humerus, left ilium, ?both ischia, and partial left hindlimb (tibia, fibula, ankle and foot elements). The specimen is seen in ventral view (Text-fig. 3), as shown by the gastralia and ventral views of the dorsal centra. This is the original orientation of the specimen in the rock (Benton *et al.* 1993), so the carcass must have flipped over, belly uppermost (perhaps floating in the river that deposited it, the belly inflated with digestive gases). Most of the elements to the right of the main blocks with the backbone and ribs are then from the left side of the animal. The hindlimb is bent back, and seen in ventral view, with the foot trailing behind the carcass.

Most of the remains (vertebrae, ribs, gastralia, chevrons, left ilium) sit in three sandstone blocks that overlap and fit together firmly. The left hindlimb and foot is in three blocks that may be linked to the main blocks via some rib ends. The small blocks with the left scapula, left humerus and mandible probably lie in front. A further eight small blocks with isolated vertebrae, ribs, the ?ischia, and other remains have lost their association, but are part of the specimen.

#### *Vertebrae and chevrons*

In total 17 vertebrae are present and appear to be all dorsal and caudal, with no cervical or sacral vertebrae present, even in the pelvic area. They are all disarticulated and lie scattered between the shoulder and hip regions, surrounded by ribs; in most cases, the centra and neural arches lie separated. For this reason, the centra and neural arches are described separately.

The preserved dorsal centra are uniform in size and shape and are roughly equal in height and diameter (Text-fig. 3). They range in length from 16 or 17 mm for anterior dorsal centra to 14 or 15 mm for posterior dorsals. They are deeply amphicoelous and spindle-shaped with a pronounced narrowing towards the centre. The centra are deep and lack a ventral keel. The articular ends are roughly circular in anterior and posterior views, and each articular end is surrounded by a pronounced lip that curves over and forms a major projection from the lateral and ventral sides of the centrum. The dorsal surface of the centrum is exposed in many cases (Text-fig. 4A–C) and shows a deep midline excavation in the floor of the neural canal, sometimes with narrow, sharp-crested, longitudinal ridges in the base. The neural arch facets are broad and flat, and run down each side of the dorsal surface of the centrum. Generally, these longitudinal facets are traversed by shallow transverse ridges and grooves that match grooves and ridges on the base of the neural arches.

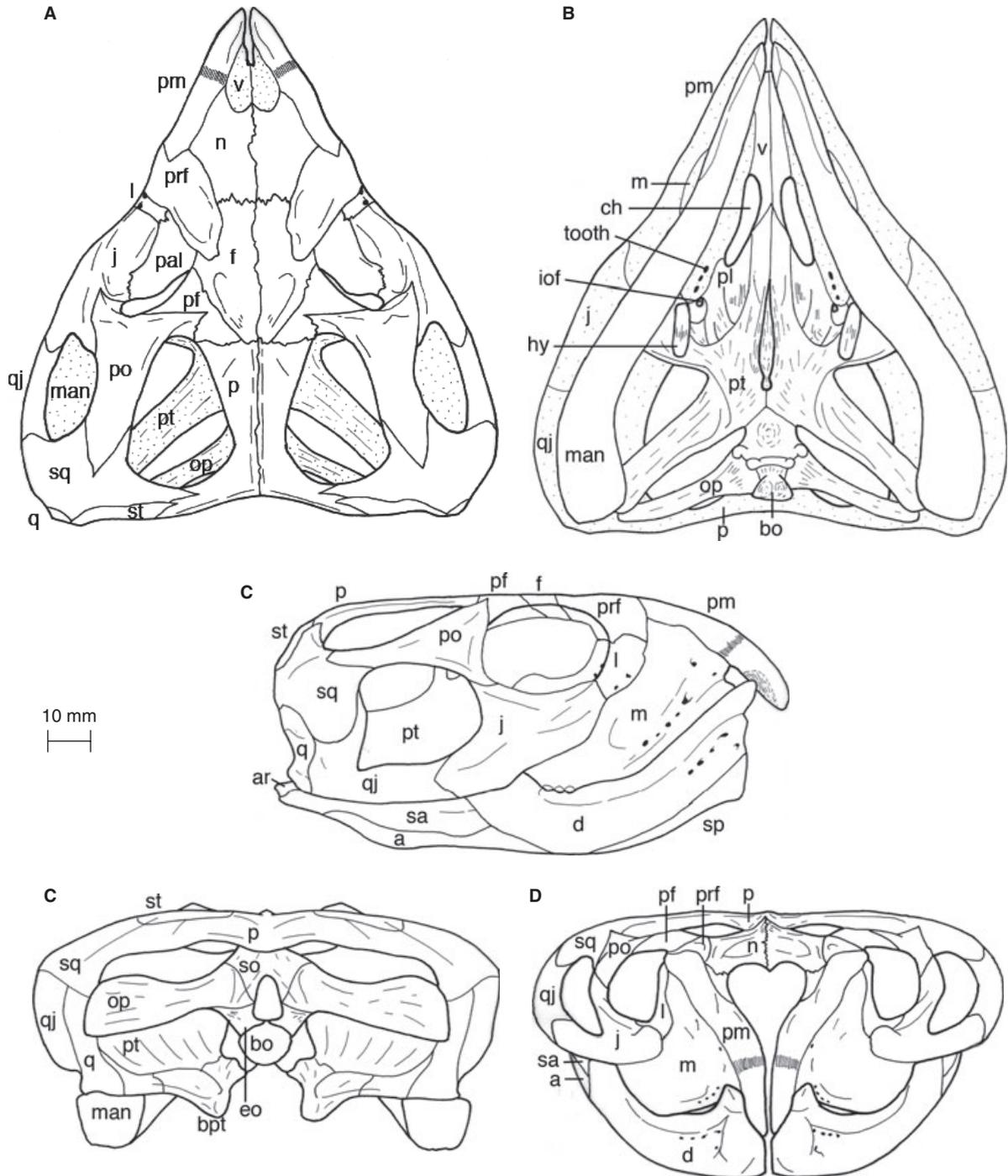
Several disarticulated neural arches provide information from dorsal, ventral and lateral views. The neural arch of dorsals



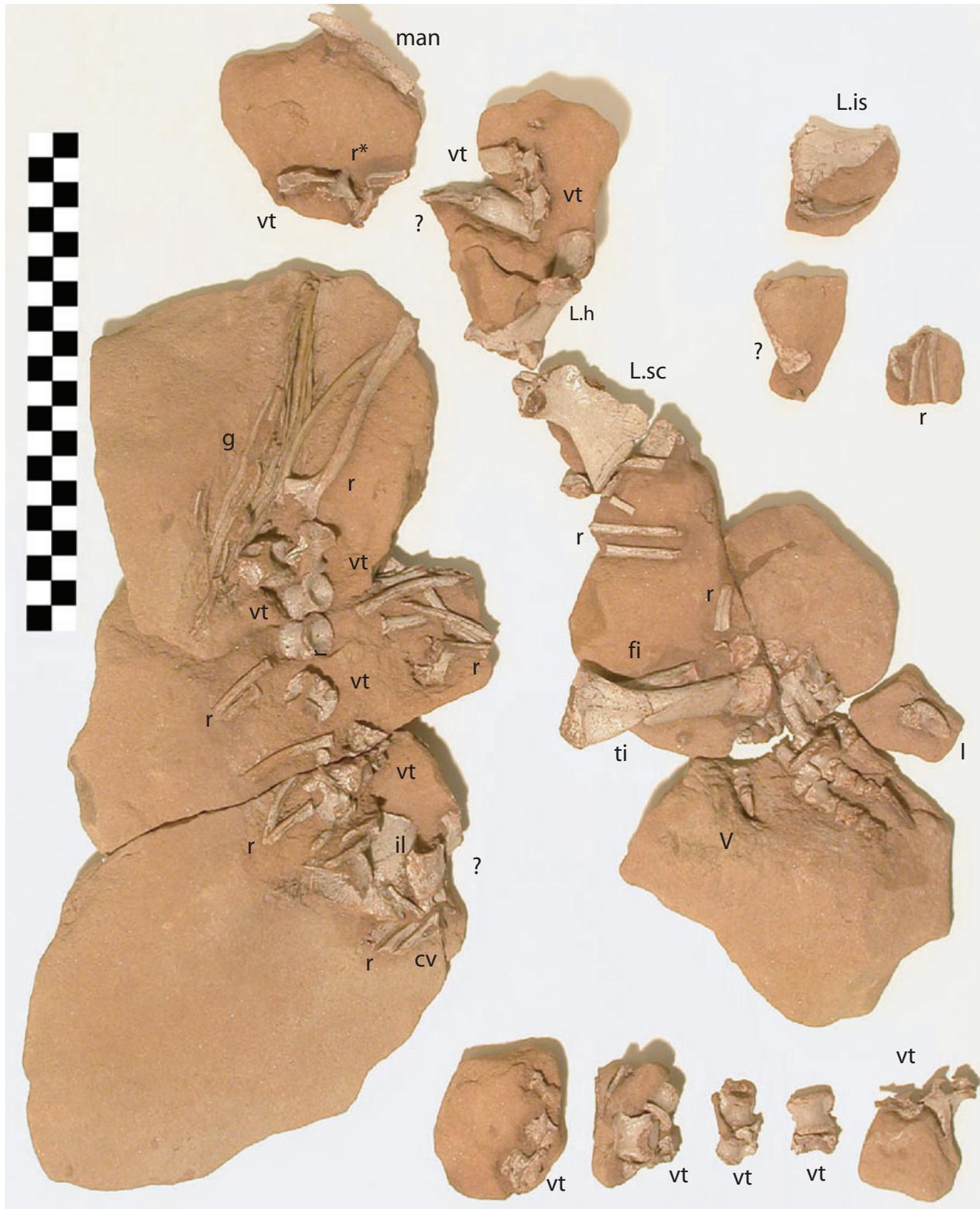
**TEXT-FIG. 1.** *Fodonyx spenceri* (Benton, 1990) from the Otter Sandstone Formation (Middle Triassic, Anisian) of Devon, south-west England. Skull (BRSUG 27200) in A, dorsal, B, ventral (excludes separate right squamosal), C, right lateral, D, posterior, and E, anterior views.

(Text-figs 3, 4A–B) is broad, as in most larger rhynchosaurs (Benton 1983, 1990), supporting the zygophyses, transverse processes and the dorsal spine. The neural canal is roughly cir-

cular in cross-section. In anterior view, the neural arch sits with broadly expanded facets on top of the centrum, and these facets nearly meet in the midline above the centrum. They extend



**TEXT-FIG. 2.** Reconstruction of *Fodonyx spenceri* (Benton, 1990) from the Otter Sandstone Formation (Middle Triassic, Anisian) of Devon, south-west England, based on skull BRSUG 27200, and with additional information from the holotype, EXEMS 60/1985.282, in A, dorsal, B, ventral, C, right lateral, D, posterior, and E, anterior views. For explanation of abbreviations, see Appendix. Some sutures cannot be determined from the new skull and are highly variable in other rhynchosaurs, and thus cannot be estimated with confidence and are not included. The posterior part of the lower jaw and parts of the squamosal and quadratojugal are restored based on existing material of *F. spenceri* (compare with Text-fig. 1).



**TEXT-FIG. 3.** *Fodonyx spenceri* (Benton, 1990) from the Otter Sandstone Formation (Middle Triassic, Anisian) of Devon, south-west England. Partial postcranial skeleton (EXEMS 79/1992). Scale bar represents 200 mm split into divisions of 10 mm. For explanation of abbreviations, see Appendix.

upwards into narrow pillars on either side of the neural canal that support the broad prezygapophyses. The postzygapophyses extend ventrolaterally from the posterior margin of the neural spine, and support the articular faces. The articular faces of pre- and postzygapophyses are broad and nearly circular. In many cases, they appear to be orientated sub-horizontally, tilted up by only 10–20 degrees laterally: this would allow considerable lateral bending of the vertebral column, but very little dorsoventral flexion. The transverse processes are anteroposteriorly broad, and located anteriorly, just behind, and partly below, the prezygapophyses. They project at right angles to the midline of the vertebra, and are broad and oval, with smooth edges. The base of the neural spine is broad and occupies the posterior half of the neural arch. The spine itself is not preserved in many vertebrae. In an anterior dorsal, near the humerus, the spine is 17 mm high, measured from the postzygapophyseal facet, and it narrows from 12 mm in anteroposterior length at the base, to 10 mm distally. There is no spine table.

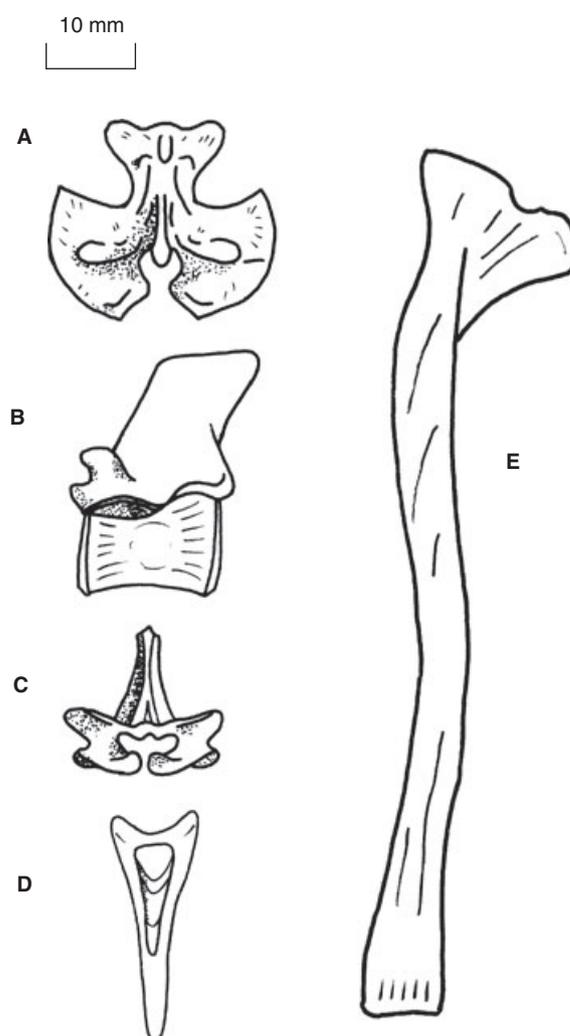
A series of three chevrons is preserved, only the anterior of which may be seen in anterior and lateral views (Text-fig. 4D), the other two being partially concealed behind it and in the matrix. The anterior chevron is 24 mm long, but its distal end is missing. The chevron is the usual Y shape, but the dorsal facets are fused into a single element, 9 mm across, bridging over a triangular-shaped opening. The ventral projections of the chevron outline the triangular opening, and come together as a keel that expands distally to be 5 mm deep anteroposteriorly, but the distal termination is unknown.

#### Ribs and gastralia

Numerous ribs are present, though most are fragments of the main shaft, and these show little more than that the ribs were robust and deep, and bore a longitudinal groove on the broader lateral face. One or two posterior dorsal ribs appear to show their proximal end, a single capitulum 5 or 6 mm wide.

One moderately complete anterior dorsal rib, lacking only the distal tip, is preserved (Text-fig. 3 (r), 4E), probably from one of the first three or four vertebrae of the trunk. It is some 98 mm long, and 22 mm wide anteriorly, narrowing to 8 mm in the middle, and 10 mm distally. The broad capitulum has an oval articular facet *c.* 12 mm wide that attached to the transverse process. A narrower tuberculum, *c.* 7 mm wide, is found on a ventral process attached to the side of the centrum. This rib is remarkably straight, and lacks the normal curvature one might expect to encompass the rather curved flanks of a bulky herbivore; in life, it probably angled backwards from an anterior dorsal vertebra, rather as seen in the better articulated specimens of *Hyperodapedon gordonii* figured by Benton (1983, fig. 27).

An isolated rib head close to the mandibular fragment (r\*, Text-fig. 3) is probably also an anterior rib, but the shaft is much more curved, and this might come from behind the anterior 'straight' ribs. The shaft, some 20 mm from the head, is 5 mm wide, and it narrows distally to 4 mm, but the whole specimen is no more than 30 mm long. The dichoccephalous head is beautifully shown, spanning 19 mm. The articular face



**TEXT-FIG. 4.** Reconstruction of axial material of *Fodonyx spenceri* based on EXEMS 79/1992. A, dorsal view of a single vertebra. B, left lateral view of a single vertebra. C, anterior view of a partial vertebra (centrum not shown). D, chevron. E, dorsal rib.

of the capitulum is oval in outline, with a posterior twist, terminating the oval with a tail shaped like the number 6. The face measures 4 × 10 mm in maximum dimensions. The tuberculum articular face is more circular in outline, with a diameter of 4 mm. The capitulum and tuberculum heads are separated by a deep, V-shaped lamina of bone, and the tuberculum extends 5 mm, and the capitulum 3 mm, from the base of the V.

Some 15–20 anterior gastralia (g, Text-fig. 3) are seen in a bunch below the anteriormost dorsal vertebrae and the anterior 'straight' dorsal rib. The gastralia appear to be in three segments, the long, narrow lateral elements overlapping a middle segment, some 25 mm long. Lateral gastralia are 60–70-mm-long, thin, strap-like elements, some 2 mm wide and 0.1 mm deep. The complete gastral basket is rather disarticulated, but the orientation of the elements is roughly straight from side to side, with little evidence of a forward or backward V-shape.

*Shoulder girdle and forelimb*

Both scapulae are present. The left scapula (L.sc., Text-fig. 3) is incomplete around all but the anterior margin. The blade broadens dorsally from a narrow point of 20 mm at the base of the blade to at least 40 mm wide measured anteroposteriorly at the distal margin. The anterior margin has a prominent boss (partially missing), against which the clavicle may have attached (cf. Benton 1990, fig. 17c). The ventral part of the scapula, with the facet for attachment to the coracoid, and the glenoid facet, is incomplete. The right scapula is beneath the main blocks, behind the mid-dorsal ribs, and shows a medial view of the blade.

The left humerus (L.h., Text-fig. 3) is incomplete at both proximal and distal ends, but it is similar in size and shape to the left humerus described by Benton (1990, fig. 33). The bone is some 65 mm long, as preserved, 35 mm across the proximal end, and 33 mm across the distal end, although these measurements are probably rather less than for the complete bone. The posterior wing of the proximal end is broad and thin, while the deltopectoral crest, largely missing, has a broad base. The shaft of the humerus is oval in cross-section, and 7 mm across at its narrowest point. The distal end, set at some 90 degrees to the proximal end, shows the ventral depression seen by Benton (1990), but the supinator crest and articular margins are incomplete.

*Pelvis and right hindlimb*

The pelvis is represented by incomplete remains of the ilium and ischium, which are identified by their overall shape, in comparison with these elements in other rhynchosaurs, and their

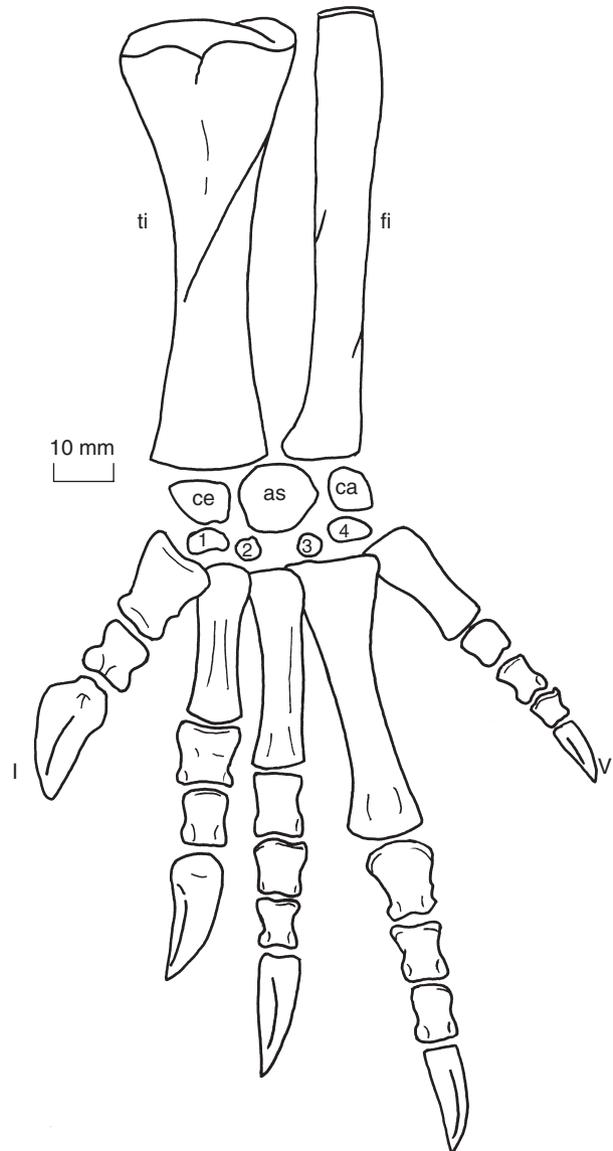


**TEXT-FIG. 5.** Detail of lower left hindlimb, in ventral view, of *Fodonyx spenceri* from EXEMS 79/1992. For explanation of abbreviations, see Appendix.

location relative to the posterior dorsal vertebrae, and the partial right hindlimb. Two parts of the ilium are present, both showing the medial surfaces. Deep growth lines in a radiating pattern from the centre are clearly visible in both. The left ilium (il., Text-fig. 3) lies behind some posterior dorsal vertebrae and ribs, and shows a medial view of the dorsal blade, but it is difficult to orientate.

Putative remains of both ischia are in a small block. The left ischium (L.is., Text-fig. 3) is most complete, showing its dorsal thickened and rounded margin, the buttress behind the major facet for attachment to the ilium, and most of the curved, rounded blade. The right ischium is more embedded in the matrix and is harder to describe.

The preserved left hindlimb lacks only a femur (Text-figs 3, 5–6). It consists of almost all the bones of the leg and foot



**TEXT-FIG. 6.** Reconstruction of lower left hindlimb, in dorsal view, of *Fodonyx spenceri* based on EXEMS 79/1992. For explanation of abbreviations, see Appendix.

except the femur. The foot is split across two overlapping blocks and the break-line runs across the tarsals and metatarsals. All five digits are present. The tibia is broken but largely intact, though the dorsal surface is eroded. The fibula is missing its distal end and is mostly hidden behind the tibia. Almost all of the ankle bones and distal tarsals appear to be present but are partially concealed by other bones and the matrix; they are also somewhat worn and so difficult to identify. At least four metatarsals are present, but they are broken, and parts of the foot are lost across the break between the blocks. The tarsals and unguals are almost all present, though some are reduced to fragments or impressions in the matrix.

The tibia (Text-figs 5–7) is largely complete; it is 84 mm long, and anteroposteriorly quite thin, with a broad-faced head and shaft but with a relatively narrow base. The cross-section is a compressed oval measuring  $13 \times 6$  mm at the narrowest point. The shaft shows a distinct twist, highlighted by a diagonal ridge that probably lay behind the fibula in life. The proximal end is 34 mm across; the articular surface shows heavy wear, and no fine detail is preserved. The distal end is 21 mm across.

The fibula (Text-figs 5–7) is obscured by both the tibia and matrix and the distal end is missing, though an impression of the end is present in the matrix (with some bone fragments). It appears to be similar in length to that of the tibia and relatively robust, although more slender than the tibia, with an oval cross-section measuring  $8 \times 5$  mm at the distal end. Both the tibia and fibula have been rotated prior to preservation so that they lie in a position that is the reverse of what would normally be expected.

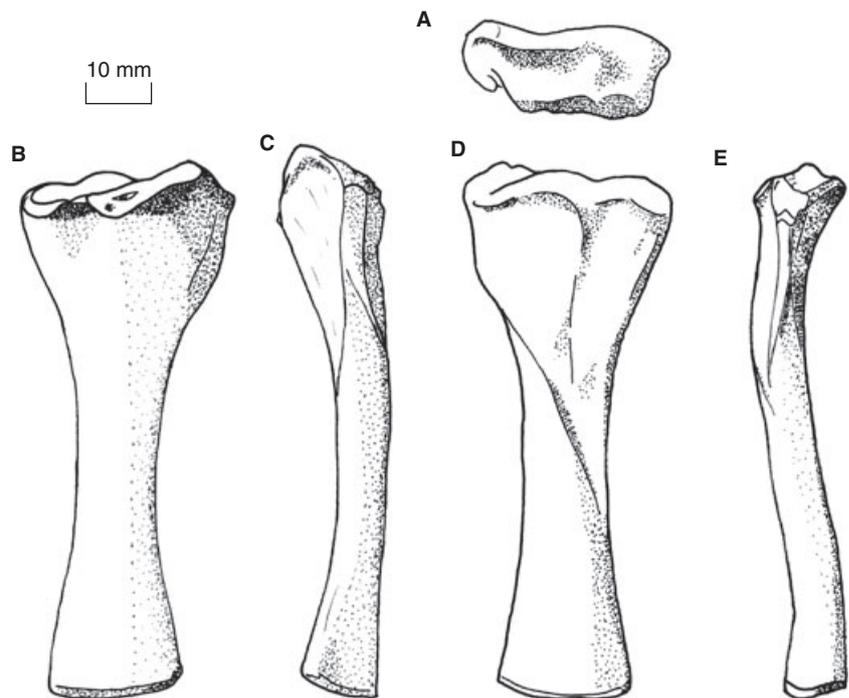
The proximal tarsals (Text-figs 5–7) are difficult to identify, partly because of the rotation of the limb, but mainly because they are of similar size and shape. All three are present, but are heavily worn, rounded and distorted. One is located beneath the

fibula and is probably the centrale. Another lies immediately below, and a third is present behind the tibia on the underside of the matrix, presumably the astragalus and calcaneum respectively. Three distal tarsals are identified, DI, DII and DIII (Text-fig. 6). DIII is only visible on the underside of the matrix. Again, these are worn and/or broken.

The metatarsals have all been broken across their width, and the proximal ends of metatarsals (mt) III–V are partly hidden beneath the tibia. Mt I is short and broad, 13 mm wide at the proximal end and 15 mm long. Mt II, III and IV are long and flat; the breakages mean that their true lengths are hard to determine, but they measure between 32 and c. 50 mm long. Mt V is badly broken, but the 18-mm-wide proximal end is seen well under the slab. The broad proximal end of mt III heavily overlaps II and IV.

The phalanges are largely intact and show the expected number of elements per digit: 2, 3, 4, 5, 4. Most phalanges retain their articulation, although some have rotated within their digits. All are broader at the proximal end than the distal; they become narrower and taller distally, partly so that the penultimate phalanx in each digit supports the high ungual. Four unguals are present (that from digit IV is missing, but an impression is left in the matrix). Ungual I is displaced, being on a separate block, but there is a clear mark on the first tarsal where it would attach. The unguals are large, ranging in length from 20–23 mm in digits 1 and 2 to 10 mm in digit 5. The unguals are at most 4 mm broad proximally at the base, the ventral line is curved slightly downwards, and the dorsal margin much more so. Overall, the ungual shape is a rather rounded-ended structure without major recurvature, as seen in other rhynchosaurs. Each ungual bears a shallow groove along the sides distally, presumably for locking of the keratin sheath, and the ungual bone is pitted in the dorsal area.

**TEXT-FIG. 7.** Reconstruction of left tibia of *Fodonyx spenceri* based on EXEMS 79/1992, in A, proximal, B, anterior, C, left lateral, D, posterior, and E, right lateral views.



## CLADISTIC ANALYSIS OF THE RHYNCHOSAURIA

### Taxa

In attempting to re-analyse the relationships of rhynchosaurs with data from the new material of *Fodonyx spenceri*, we produced a data matrix as comprehensive as possible, including all rhynchosaur taxa and all available phylogenetically informative characters. We excluded *Scaphonyx fischeri* Woodward, 1907 because the taxon is ill defined, a probable *nomen dubium* (Langer and Schultz 2000).

Taxa were coded as follows: *Mesosuchus* (Dilkes 1998), *Howesia* (Dilkes 1995), *Rhynchosaurus articeps*, *R. brodiei*, and *Fodonyx spenceri* (Benton 1990 and pers. obs.), *Otischalkia* (Hunt and Lucas 1991), *Ammorhynchus* (Nesbitt and Whatley 2004), *Stenaulorhynchus* (Huene 1938 and pers. obs.), *Mesodapedon* (Chatterjee 1980), *Hyperodapedon* (*Isalorhynchus*) *genovefae* (Buffetaut 1983; Langer *et al.* 2000a), '*Scaphonyx*' *sulcognathus* (Azevedo 1982; Schultz 1986; Azevedo and Schultz 1987), *Hyperodapedon gordonii* (Benton 1983 and pers. obs.), *H. huxleyi* (Chatterjee 1974), *H. huenei* (Langer and Schultz 2000), *H. mariensis* Tupi-Caldas, 1933 (Langer and Schultz 2000), 'Mariante rhynchosaur' (Schultz and Azevedo 1990), Zimbabwe *Hyperodapedon* (Raath *et al.* 1992), Wyoming *Hyperodapedon* (Lucas *et al.* 2002), *H. sanjuanensis* (Huene 1929; Sill 1970; Azevedo 1984; Benton and Kirkpatrick 1989; Langer *et al.* 2000b), *Supradapedon* (Chatterjee 1980), and the Nova Scotia rhynchosaur (Chatterjee 1980; Benton 1990; pers. obs.).

As outgroup we selected three other archosauromorphs, *Proterosuchus* (coded from Cruickshank 1972, ankle from Carroll 1976, and braincase from Clark *et al.* 1993), *Prolacerta* (coded from Gow 1975, with braincase from Evans 1986, and skull from Modesto and Sues 2004), and *Trilophosaurus* (coded from Gregory 1945). These three represent the clades Archosauria (= Archosauriformes), Prolacertiformes and Trilophosauridae respectively, three major clades within Archosauromorpha that are close relatives of Rhynchosauria (Benton 1985; Evans 1988; Dilkes 1998).

We retained all taxa in the analysis initially, and did not delete any simply because they were coded for only a small proportion of the possible characters. Then, following the principles of safe taxonomic deletion (Wilkinson and Benton, 1995), we excluded eight taxa that were coded identically to more fully coded taxa: *Mesodapedon* (= *Stenaulorhynchus* and others); *Otischalkia* (= *Rhynchosaurus articeps*); *Hyperodapedon genovefae*, Zimbabwe *Hyperodapedon*, and *Supradapedon* (= *Hyperodapedon gordonii* and others); Wyoming *Hyperodapedon* and Nova Scotia rhynchosaur (= *Hyperodapedon sanjuanensis*).

### Characters

Numerous characters of potential significance in determining the phylogeny of rhynchosaurs have been proposed and debated (Chatterjee 1974, 1980; Benton 1983, 1985, 1990; Dilkes 1995, 1998; Langer and Schultz 2000; Langer *et al.* 2000a, b). We carried out a review of all characters proposed hitherto and sought further characters. Our procedure was to: list all characters and variants in classic anatomical order from the tip of the snout to the last toe bone; combine synonymous characters used by different authors, and retain the clearest character definition in each case; consider the wording of each character definition carefully, and to revise and reword where necessary for clarity; code every character in the revised list for all 20 taxa; further revise the character definitions in the light of uncertainties in coding from specimens and from the literature; weed out characters that are ambiguous and/or uncodable.

In the end, 75 characters were retained that are codable (Appendix, first section). Of these, characters 13 and 52 are currently phylogenetically uninformative, so they were excluded from the cladistic analyses. They remain in the list though, since they cannot be coded for each rhynchosaur taxon and might in the end show variations in state.

The characters weeded from the master list include some that were used by previous authors. For example, the following six characters from Benton (1983, p. 709) were excluded because they could not be defined and coded in any meaningful way, or were invariant across all taxa: 'dorsum sellae high', 'exoccipitals take part in occipital condyle', 'spheno-occipital tubera bifurcate ventrally', 'reduced presacral vertebrae 8 and 9', 'compressed scapula', and 'large lateral glenoid fossa'. Two further characters were excluded because they are redundant with others: 'pterygoids directed mainly posteriorly' (= character 29); adductor fossa extends more than halfway along jaw (= character 36).

Dilkes (1995, pp. 683–694) accepted 12 of Benton's (1990) 26 characters, modified six, and excluded eight. We accept five of Dilkes' (1995) modifications; the sixth was a concern about an unquantified definition of the relative sizes of the jugal and maxilla. This character (9 here) has been reworded for clarity. All of the eight characters excluded by Dilkes (1995) are retained:

1. Character 13, a frontal that is broader than long, is autapomorphic in *Stenaulorhynchus*; we argue that autapomorphies should be retained in character lists, and excluded at the analytical stage because future finds may confirm them in other taxa.
2. Ch. 22, absence of the parietal foramen, was said to be autapomorphic in *Mesosuchus*, but that is retention of a primitive state seen in the outgroup; Dilkes (1995, p. 684) argued that absence of the parietal foramen was plesiomorphic for rhynchosaurs,

but its absence in archosaurs, *Trilophosaurus*, and from some specimens of *Prolacerta* is more likely a parallelism of the apomorphic state (basal amniotes all have the foramen).

3. Ch. 23, absence of the supratemporal, was excluded because of uncertainties in the literature, but these are somewhat clearer now (Dilkes 1998; this study).
4. Ch. 24, the shape of the ventral process of the squamosal, was indeed poorly expressed, but the character is quantified here.
5. Ch. 29, the occipital condyle lying roughly in line with the quadrates, was seen to be variable in the outgroup, but, with redefinition (Dilkes 1998; this study), this character can be retained.
6. Ch. 44, the relative widths of the medial and lateral portions of the maxillary tooth plate, is indeed an inapplicable character for the outgroups and for *Mesosuchus* and *Howesia* since they lack a tooth plate with a major groove; this character is retained here, however, since it may help sort out the derived rhynchosaurs.
7. Ch. 64, the relative lengths of the humerus and femur was said to be an autapomorphy of *Hyperodapedon*; we find a wider distribution of the derived state and so retain this character.
8. Ch. 70, relative size of the centrale, was a poorly defined character, but it has been redefined and distinguished from ch. 66.

The final tally of 75 characters (Appendix, first section) includes characters introduced by Chatterjee (1980), Benton (1985, 1990), Dilkes (1995, 1998) and Langer and Schultz (2000), although the wording is occasionally modified (see Table 1 for details of sources and modifications). One new character, 34, the shape of the supraoccipital, was mentioned by Dilkes (1995), but has not been used hitherto in phylogenetic analysis.

Codings for a number of characters have been changed from codings in previous analyses:

1. Ch. 3, the open lower temporal bar, was coded confidently as '1' for *Rhynchosaurus articeps* and *Stenaulorhynchus* by Benton (1990), even though that area of the skull is not preserved in any specimens, as indeed noted by Benton (1990, p. 231) and Dilkes (1995) in *R. articeps* and Huene (1938, p. 88) in *Stenaulorhynchus*; re-coded as '0'.
2. Ch. 4, the presence of a single median naris in *Howesia*, was coded as '?' by Benton (1990), although its presence is indicated by Dilkes (1995, p. 668); re-coded as '1'.
3. Ch. 6, the premaxillary beak in the Nova Scotia rhynchosaur, was coded as '?1' by Benton (1990), but there is no evidence for this; re-coded as '?'.
4. Ch. 9, the enlarged jugal in *Scaphonyx sanjuanensis*, was reported as '?0' by Benton (1990), but this taxon shows the derived state (Sill 1970); re-coded as '1'.
5. Ch. 19, the relative length of the parietal and frontal in *Howesia*, was coded as '?1' by Benton (1990), but '0' by Dilkes (1998); the latter view is accepted.
6. Ch. 20, fusion of the parietals in *Mesosuchus*, was coded as '0' by Benton (1990), and '1' by Dilkes (1998); the latter view is accepted.
7. Ch. 23, absence of the supratemporal, was coded in *Howesia* as '?' by Benton (1990) and '0' by Dilkes (1998), in *Stenaulorhynchus* as '1' by Benton (1990) and '?' by Dilkes (1998), and in *Scaphonyx fischeri* as '1' by Benton (1990)

**TABLE 1.** Outline classification of the rhynchosaurs, based on the cladistic analysis (Text-fig. 8B), and including the deleted taxa that, so far as codable, match more fully coded taxa. These are indicated with an asterisk (\*) and placed immediately below one of the taxa with which their coded characters are identical.

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Order Rhynchosauria Osborn, 1903
<i>Mesosuchus browni</i> Watson, 1912
<i>Howesia browni</i> Broom, 1905
Family Rhynchosauridae Huxley, 1859
<i>Stenaulorhynchus stockleyi</i> Houghton, 1932
* <i>Mesodapedon kuttyi</i> Chatterjee, 1980
<i>Rhynchosaurus articeps</i> Owen, 1842
<i>Rhynchosaurus brodiei</i> Benton, 1990
* <i>Otischalkia elderae</i> Hunt and Lucas, 1991
* <i>Ammorhynchus navajoi</i> Nesbitt and Whatley, 2004
<i>Fodonyx spenceri</i> (Benton, 1990)
Subfamily Hyperodapedontinae Chatterjee, 1969
'Scaphonyx' <i>sulcognathus</i> Azevedo and Schultz, 1987
<i>Hyperodapedon huenei</i> Langer and Schultz, 2000
<i>Hyperodapedon gordonii</i> Huxley, 1859
* <i>Hyperodapedon genovefae</i> (Buffetaut, 1983)
<i>Hyperodapedon huxleyi</i> Lydekker, 1881
*Zimbabwe <i>Hyperodapedon</i> (Raath <i>et al.</i> 1992)
* <i>Supradapedon stockleyi</i> (Boonstra, 1953)
<i>Hyperodapedon mariensis</i> (Tupi-Caldas, 1933)
'Mariante rhynchosaur' (Schultz and Azevedo 1990)
*Nova Scotia rhynchosaur
<i>Hyperodapedon sanjuanensis</i> Sill, 1970
*Wyoming <i>Hyperodapedon</i> (Lucas <i>et al.</i> 2002)

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and '?' by Dilkes (1998); the view of Dilkes (1998) is accepted for the first two, but not for the third, based on Huene (1929, p. 10).

8. Ch. 24, a broad ventral process of the squamosal, was coded as '?' by Benton (1990) and '1' by Dilkes (1998) in *Howesia*; the latter view is accepted. It was also coded as '0' by Benton (1990) in *F. spenceri*, but is actually broad (pers. obs.); re-coded as '1'.
9. Ch. 29, the occipital condyle in line with the quadrates in *F. spenceri*, was coded as '?0' by Benton (1990), but '1' by Dilkes (1998); the latter view is accepted.
10. Ch. 35, the deep mandible in *Howesia*, was coded as '0' by Benton (1990) and '?' by Dilkes (1998); the dentary is indeed incomplete (Dilkes 1995), so Dilkes' (1998) coding is accepted.
11. Ch. 36, the elongate dentary in *Mesosuchus*, was coded as '?0' by Benton (1990), but is clearly '0' (Dilkes 1998).
12. Ch. 39, ankylothecondont teeth, had been suggested in *Trilophosaurus* (Gregory 1945; Dilkes 1995, p. 673) but not in other members of the outgroup until Modesto and Sues (2004, pp. 347–348) argued strongly for ankylothecondont implantation in *Prolacerta*; both re-coded as '1'.
13. Ch. 40, absence of premaxillary teeth, was assumed to be the case in the Nova Scotia rhynchosaur by Benton (1990), but cannot be determined for *Fodonyx*, so it is re-coded as '?' in both *Hyperodapedon genovefae* and *Otischalkia*; Benton (1990) recorded '?1' for this character; it is confirmed by

- Buffetaut (1983) and Hunt and Lucas (1991) and so is recoded as '1' for both.
14. Ch. 45, lingual teeth on maxilla in *Mesosuchus*, coded as '?0' by Benton (1990) and '0' by Dilkes (1998); the latter is accepted.
  15. Ch. 46, numbers of dentary tooth rows, coded in *Mesosuchus* as '0' by Benton (1990) but '2' by Dilkes (1998), and in *Scaphonyx sanjuanensis* coded as '?0' by Benton (1990), and confirmed as '0' by Langer *et al.* (2000b); the latter coding accepted in both cases.
  16. Ch. 49, vomerine teeth absent in *Rhynchosaurus articeps*, coded as '1' by Dilkes (1998), but cannot be determined for *Fodonyx*, so is coded '0', as in Benton (1990).
  17. Ch. 50, palatine teeth absent in *Rhynchosaurus articeps*, coded as '1' by Dilkes (1998), but cannot be determined for *Fodonyx*, so is coded '0', as in Benton (1990).
  18. Ch. 51, pterygoid teeth absent, coded in *Howesia* as '0' by Benton (1990), '1' by Dilkes (1998), and in *R. articeps* as '?1' by Benton (1990), '1' by Dilkes (1998); in both cases, Dilkes' (1998) codings are accepted; this character was coded as '?1' by Benton (1990) in *R. spenceri*, but cannot be determined for *Fodonyx*, so is coded '?' here.
  19. Ch. 52, postaxial intercentra absent in *Stenaulorhynchus*, coded as '0' by Langer and Schultz (2000), and '1' by Dilkes (1998); retained as '1'.
  20. Ch. 57, tapering chevrons in *Scaphonyx fischeri*, is coded as '?' by Dilkes (1998), but is retained as '1' here, based on Huene (1942).
  21. Ch. 60, the proximal anchor-like shape of interclavicle in *Howesia*, coded as '1' here, as indicated by Broom (1906, p. 595), although Dilkes (1995, p. 676) noted that the shoulder girdle region is now lost, and Dilkes (1998) coded as '?'.
  22. Ch. 61, expansion of the posterior branch of the interclavicle in *H. gordonii*, coded as '0' by Dilkes (1998) but it is clearly '1' (Benton 1983, fig. 29d).
  23. Ch. 64, the humerus longer than the femur, coded in *Howesia* as '0' by Benton (1990) and '?' by Dilkes (1998), but data in Broom (1906) and Dilkes (1995) indicate quite clearly that the femur is longer than the humerus, and so it is coded '0' here.
  24. Ch. 65, a femur with a wide distal end, coded in *Howesia* as '1' by Dilkes (1998), but data in Broom (1906) and Dilkes (1995) suggest that the ratio of distal femur width to length is 0.31 (17/55), and should then be coded as '1'; it is coded '0' for *Otschalkia*, but this is true only if the ascribed femur (Hunt and Lucas 1991) really is from this rhynchosaur.
  25. Ch. 66, the presence of three proximal tarsals in *Mesosuchus* and *Howesia*, was coded as '1' by Benton (1990), and '0' by Dilkes (1998), based on the reinterpretation of the rhynchosaur ankle by Dilkes (1995); the latter view is accepted here.
  26. Ch. 70, the presence of a large centrale in *Mesosuchus* and *Howesia*, was coded as '0' by Benton (1990), and '1' by Dilkes (1998), based on the reinterpretation of the rhynchosaur ankle by Dilkes (1995); the latter view is accepted here.
  27. Ch. 71, absence of a contact between the centrale and distal tarsal 4 in *Mesosuchus*, was coded as '1' by Dilkes (1998), even though the contact can be seen in Dilkes (1998, fig. 22), so it is coded as '0' here.

28. Ch. 72, a small distal tarsal 4 in *R. articeps*, was coded as '0' by Langer and Schultz (2000), although distal 4 is similar in size to distals 1–3 (Benton 1990, fig. 20), so it is coded as '1' here.

### Phylogenetic results

The phylogenetic analysis yielded 36 most parsimonious trees (MPTs), with a length of 114, consistency index (CI) of 0.68, retention index (RI) of 0.85, and rescaled consistency index (RC) of 0.58. The majority-rule consensus tree (Text-fig. 8A) shows reasonable evidence for the stem positions of *Mesosuchus* and *Howesia* respectively. *Stenaulorhynchus* is then the basalmost member of core Rhynchosauridae, followed by the two species of *Rhynchosaurus*, *R. articeps* and *R. brodiei*. Next comes *Fodonyx*, with some confidence, followed by a clade of species of *Hyperodapedon* and 'Scaphonyx'. 'Scaphonyx' *sulcognathus* and *Hyperodapedon huenei* appear to be basal taxa to a crown unresolved group of several *Hyperodapedon* species, with *H. gordonii* and *H. huxleyi* possibly paired.

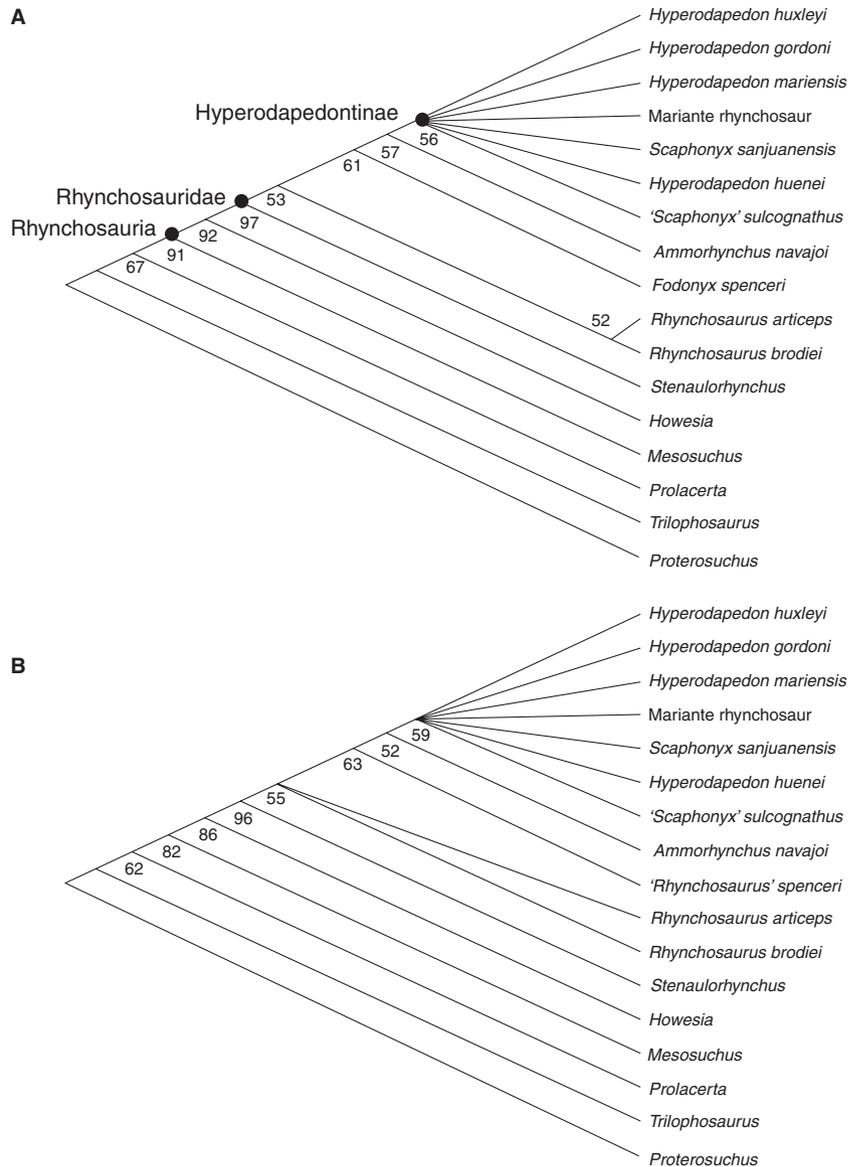
Bootstrapping of the majority rule consensus (Text-fig. 8B) gave a less-resolved tree, with strong support for all clades indicated before, except the pairing of the two species of *Rhynchosaurus* (this clade is found in only 53 per cent of bootstrap replicates), the position of *Rhynchosaurus* between *Stenaulorhynchus* and *Fodonyx* (found in only 55 per cent of bootstrap replicates), and the crown clade of six species of *Hyperodapedon* (found in only 51 per cent of bootstrap replicates). The position of *Fodonyx*, between *Rhynchosaurus* and the Hyperodapedontinae, as defined by Langer and Schultz (2000), is reasonably secure (found in 88 per cent of bootstrap replicates).

One of the aims of this project had been to see whether fuller coding of the characters of *Fodonyx* would improve our understanding of its phylogenetic position, and of the Rhynchosauridae as a whole. Whereas only 29 out of the 75 characters (39 per cent) were coded for 'Rhynchosaurus' *spenceri* by Benton (1990), the new material allowed us to code 56 of the 75 characters (75 per cent) as well as to correct three of the previously published codings. Removing *Fodonyx* from the analysis and replacing it with 'Rhynchosaurus' *spenceri*, coded as by Benton (1990), and without the benefit of the new skull and postcranial material, gave rise to a similar cladogram. Fewer MPTs were generated (11), tree length is shorter (L = 110), and the consistency index and other tree statistics are better (CI = 0.70; RI = 0.87; RC = 0.61).

## DISCUSSION

More complete, and corrected coding, of characters might be expected to improve the cladistic result: there should

**TEXT-FIG. 8.** Cladistic analysis of the relationships within Rhynchosauria. A, majority rule consensus tree of 36 MPTs. Figures indicate the proportions of source trees that include the node above. B, phylogeny of the Rhynchosauria, with names of major clades indicated. Bootstrap percentages (based on 1000 replicates) are indicated for each node. This tree (showing only nodes supported by more than 50% of bootstrap replications) is identical to the strict consensus tree of all 36 source trees, except that for ‘*Scaphonyx*’ *sulcognathus*.



perhaps be fewer MPTs (the data matrix is the same size both before and after), these ought perhaps to be shorter, and the consensus tree might be expected to show higher bootstrap values at relevant nodes. Our observation is that none of these occurred. Fuller, and corrected, codings for *Fodonyx* made the tree weaker in all those measures.

Evidently, the improved data recording for *Fodonyx* has increased incongruence. In the ‘old’ analysis, ‘*Rhynchosaurus*’ *spenceri* is linked to Hyperodapedontinae in 99 per cent of bootstrap replicates, whereas this falls to 88 per cent in the ‘new’ analysis. This suggests that the algorithm substituted hyperodapedontine-like values for some of the missing 61 per cent of data in the 1990 analysis. Even though *Fodonyx* shares its overall size and its skull shape with the hyperodapedontines, it retains plesiomorphic

features that have been revealed by the new material and draw it down the cladogram, away from the crown Hyperodapedontinae.

Both analyses confirm that the Devon rhynchosaur is not a species of *Rhynchosaurus*, as had been assumed by Benton (1990), but that it represents a separate taxon, as suggested by Benton *et al.* (1993), Wilkinson and Benton (1995), and Langer and Schultz (2000). The bootstrap value of 88 per cent (Text-fig. 8B) is not overwhelmingly strong, but perhaps sufficient to justify its placement in the phylogeny. Furthermore, the Devon taxon cannot be hoisted into the crown clade, Hyperodapedontinae (*Hyperodapedon* + ‘*Scaphonyx*’), and the new analysis shows that it is in many regards more primitive than had been thought, based on less complete material. The cladistic analysis (Text-fig 8A–B) provides weak support for the pairing of *R. articeps*

and *R. brodiei* as species of one genus, *Rhynchosaurus*, although the second species is so incompletely known that there are serious problems of missing data.

Within Hyperodapedontinae, as defined by Langer and Schultz (2000), the species of *Hyperodapedon* are hard to resolve. They found that the species of *Hyperodapedon* and 'Scaphonyx' formed a polytomy, and that 'Scaphonyx' *sanjuanensis* should be regarded as a species of *Hyperodapedon*. They found a pairing of the type species of *Hyperodapedon*, *H. gordonii* and *H. huxleyi*, and that *H. huenei* was a basal species. We also find a tentative pairing of *H. gordonii* with *H. huxleyi*, and *H. huenei* basal (Text-fig. 8A), but these divisions are not robust and not supported by bootstrap analysis, nor do they appear in the strict consensus tree (Text-fig. 8B). We find, as did Langer and Schultz (2000), that 'Scaphonyx' *sulcognathus* is the basal hyperodapedontine and, because the type species of the genus 'Scaphonyx' *fischeri* Woodward, 1907 is perhaps a *nomen dubium* (Langer and Schultz 2000), 'S.' *sulcognathus* requires a new generic name.

#### Classification

Taken conservatively, and including the previously excluded taxa, a complete classification of rhynchosaurs is indi-

cated in Table 1. Character transformations at each node in the cladogram (Text-fig. 8B) are indicated in the Appendix.

## CONCLUSIONS

As long suspected, the 'Devon rhynchosaur', called *Rhynchosaurus spenceri* by Benton (1990), belongs to a new genus, placed midway between other species of *Rhynchosaurus* and the Late Triassic hyperodapedontines *Hyperodapedon* and 'Scaphonyx'. New materials of the Devon rhynchosaur, assigned to the new genus *Fodonyx* here, have yielded a great deal more information about the skull and skeleton. They confirm what had been determined before but add anatomical detail of the skull roof, snout, occiput, braincase, vertebral column, ribs, limb girdles, and hindlimb (Text-fig. 9).

There is a time difference of perhaps 5–8 myr between the species of *Rhynchosaurus* and *Fodonyx*. The Helsby Sandstone Formation/Tarporley Siltstone Formation boundary of the Cheshire Basin, source of *Rhynchosaurus articeps*, is early Anisian in age, based on biostratigraphic and mapping evidence (Benton *et al.* 1994), whereas the Otter Sandstone Formation of Devon, source of *Fodonyx spenceri*, has been dated as latest Anisian on the basis of biostratigraphy (Benton *et al.* 1994) and magnetostratigraphy



**TEXT-FIG. 9.** Life restoration of *Fodonyx spenceri*, based on the skeletal material described here, depicted among the low plants that may have formed its diet. Drawing by Andrea Cobbett.

(Hounslow and McIntosh 2003). This age difference might explain why *Fodonyx* is more derived than *Rhynchosaurus*.

*Acknowledgements.* We thank Malcolm Hart and Mark Hounslow, discoverers of the new skeleton and skull of *Fodonyx* respectively. We also thank David Hill (then Bristol City Museum) and Remmert Schouten (Department of Earth Sciences, University of Bristol) for preparing the skeleton and skull so skilfully. The partial skeleton has formed the centrepiece of exhibitions in museums in Plymouth, Exeter, and Sidmouth, and the skull is on show in the Department of Earth Sciences, University of Bristol: thanks to curators in all of these institutions for varied help.

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## APPENDIX

### Characters used in phylogenetic analysis

The characters are listed in standard anatomical order. The plesiomorphic state for each character is coded as ‘0’, and derived states as ‘1’ and ‘2’, as appropriate.

#### Skull shape (5)

1. Maximum skull width relative to midline skull length: longer than broad (0), broader than long (1). [Benton 1983, p. 709; 1985, p. 133; 1990, character 1]
2. Skull height (maximum, measured in lateral view) relative to midline skull length: <50% (0), >50% (1).
3. Lower temporal fenestra: closed ventrally (0), open ventrally (1). [Dilkes 1998, ch. 4]
4. External nares: separate (0), single medial naris (1). [Benton 1985, p. 131; 1990, ch. 4, reworded]
5. Orientation of orbits – maximum area when seen in lateral or dorsal views: mainly lateral (0), mainly dorsal (1). [Langer and Schultz 2000, ch. 3] Possible linkage to ch. 1.

#### Dermal skull elements (23)

6. Premaxilla ventral margin: horizontal (0), down-turned and forming (1). [Benton 1985, p. 132; 1990 ch. 3, modified according to Dilkes 1995]

7. Premaxilla and prefrontal contact: absent (0), present (1). [Dilkes 1998, character 7]
8. Maxilla ventral margin: horizontal (0), convex (1). [Dilkes 1998, ch. 16]
9. Jugal area in lateral view: smaller than maxilla (0), larger than maxilla (1). [Benton 1983, p. 709; 1985, p. 133; 1990, ch. 5, reworded]
10. External surface of jugal: not ornamented (0), ornamented with crests and bosses dorsal to major diagonal crest (1). [Langer and Schultz 2000, ch. 5]
11. Major diagonal crest on jugal: short, and does not reach anterior portion of orbit (0), long, and reaches anterior portion of orbit (1). [Benton 1983, p. 709; Langer and Schultz 2000, ch. 4]
12. Width of jugal/postorbital bar: less than 40% (0) or more than 40% (1) of maximum orbital diameter. [Langer and Schultz 2000, ch. 6, reworded]
13. Frontal shape: longer than broad (0), broader than long (1). [Benton 1983, p. 709; 1990, ch. 6]
14. Frontal longitudinal groove: much deeper posteriorly than anteriorly (0), almost the same depth throughout (1). [Langer and Schultz 2000, ch. 2]
15. Shape of dorsal surface of frontal next to sutures with post-frontal and parietal: flat to slightly concave (0), depressed with deep pits (1). [Dilkes 1998, ch. 20]
16. Shape of dorsal surface of postfrontal: flat to slightly concave (0), depressed with deep pits (1). [Dilkes 1998, ch. 21]
17. Postfrontal enters border of upper temporal fenestra: no (0), yes (1). [Benton 1983, p. 709]

18. Length of anteroventral process of postorbital relative to posterodorsal process: longer (0), shorter (1). [Dilkes 1998, ch. 23, reworded]
19. Midline length of parietal relative to frontal: shorter (0), longer (1). [Benton 1983, p. 709; 1990, ch. 7, reworded]
20. Parietals: separate (0), fused (1). [Benton 1985, p. 131; 1990, ch. 8]
21. Parietal table: broad (0), constricted and with sagittal crest (1). [Dilkes 1998, ch. 26]
22. Parietal foramen: always, or sometimes, present (0), always absent (1). [Benton 1985, p. 132; 1990, ch. 9]
23. Supratemporal: present (0), absent (1). [Benton 1985, p. 133; 1990, ch. 10]
24. Breadth of ventral process of squamosal at mid-height, relative to breadth of lower temporal fenestra: <50% (0), >50% (1). [Benton 1990, ch. 11, reworded]
25. Quadratojugal anterior process: present (0), absent (1). [Dilkes 1998, ch. 35, reworded]
26. Ectopterygoid and palatine contribute to lateral border of suborbital fenestra: with maxilla (0), maxilla excluded (1). [Dilkes 1998, ch. 41]
27. Suture between ectopterygoid and pterygoids: complex overlap (0), simple overlap (1). [Dilkes 1998, ch. 142, polarity reversed]
28. Ectopterygoid reaches lateral corner of transverse flange of pterygoid: no (0), yes (1). [Dilkes 1998, ch. 42, reworded]

#### *Braincase (6)*

29. Relative position of occipital condyle: approximately in line with quadrates (0), markedly anterior to quadrates (1). [Benton 1983, p. 709; 1985, p. 133; 1990, ch. 12]
30. Relative midline length of basioccipital and basisphenoid: basisphenoid longer (0), basioccipital longer (1). [Benton 1983, p. 709; Langer and Schultz 2000, ch. 10, reworded]
31. Basipterygoid process: longer than broad (0), broader than long (1). [Benton 1983, p. 709; Langer and Schultz 2000, ch. 9]
32. Orientation of basipterygoid processes: anterolateral (0), lateral (1). [Dilkes 1998, ch. 43]
33. Club-shaped ventral ramus of opisthotic: present (0), absent (1). [Dilkes 1998, ch. 46, polarity reversed]
34. Supraoccipital shape: plate-like (0), inverted V-shape (1). [Dilkes 1995 1998]

#### *Mandible (4)*

35. Maximum depth of mandible relative to length: less than one-quarter (0), from one-quarter to one-third (1). [Benton 1983, p. 709; 1985, p. 133; 1990, ch. 13, reworded]
36. Length of dentary relative to length of mandible: half, or less than half (0), over half (1). [Benton 1990, ch. 14, reworded and polarity reversed, as in Dilkes 1995]
37. Jaw symphysis: formed largely by dentary (0), formed only by splenial (1). [Dilkes 1998, ch. 71]
38. Divergence of dentaries in front of symphysis: absent (0), present (1). [Dilkes 1998, ch. 72]

#### *Teeth (13)*

39. Tooth implantation: subthecondont or thecodont (0), ankylothecondont (1). [Benton 1985, p. 132; 1990, ch. 15]
40. Premaxillary teeth: present (0), absent (1). [Benton 1985, p. 131; 1990, ch. 2, modified]
41. Number of rows of teeth on maxilla: single row (0), multiple rows (batteries) of teeth (1). [Benton 1985, p. 132; 1990, ch. 16, modified]
42. Tooth occlusion: single sided overlap (0), flat occlusion (1), blade and groove jaw apparatus, where dentary blade(s) fit precisely into maxillary groove(s) (2). [Benton 1985, p. 133; 1990, ch. 17, modified according to Dilkes 1995]
43. Number of grooves on maxilla: none (0), one (1), two (2). [Benton 1983, p. 709; 1985, p. 133; 1990, ch. 18]
44. Relative width of tooth-bearing areas lateral and medial to maxillary groove: medial wider than lateral (0), lateral wider than medial (1). [Chatterjee 1980; Benton 1983, p. 709; 1990, ch. 19, reworded]
45. Lingual teeth on medial face of maxilla: absent (0), present (1). [Benton 1983, p. 709; 1985, p. 133; 1990, ch. 20, reworded]
46. Number of rows of teeth on dentary: one (0), two (1), more than two full rows (2). [Benton 1983, p. 709; 1985, p. 133; 1990, ch. 21, modified]
47. Lingual teeth on medial face of dentary: absent (0), present (1). [Langer and Schultz 2000, ch. 20, reworded]
48. Numbers of dentary teeth in tooth row: more in anterior half (0), more in posterior half (1). [Langer and Schultz 2000, ch. 18, reworded]
49. Vomerine teeth: present (0), absent (1). [Dilkes 1998, ch. 66]
50. Palatine teeth: present (0), absent (1). [Dilkes 1998, ch. 67]
51. Pterygoid teeth: present (0), absent (1). [Benton 1983, p. 709; 1985, p. 133; 1990, ch. 22]

#### *Postcranial (24)*

52. Postaxial intercentra: present (0), absent (1). [Langer and Schultz 2000, ch. 22]
53. Slender and tapering cervical ribs: present (0), absent (1). [Benton 1985, pp. 116–117; Dilkes 1998, ch. 77, polarity reversed]
54. Cervical rib accessory process: present (0), absent (1). [Dilkes 1998, ch. 78, polarity reversed]
55. Neural arches of mid-dorsals: deeply excavated (0), shallowly excavated (1). [Dilkes 1998, ch. 84, polarity reversed]
56. Ratio of lengths of caudal transverse processes to centra: >1.0 (0), <1.0 (1). [Dilkes 1998, ch. 89, polarity reversed]
57. Distal width of chevron bones relative to width of proximal area: same width or wider (0), narrower/tapering (1). [Langer and Schultz 2000, ch. 23]
58. Posterior process on coracoid: present (0), absent (1). [Benton 1983, p. 709; 1985, p. 133; 1990, ch. 23]
59. Coracoid foramen: restricted to coracoid (0), shared between coracoid and scapula (1). [Langer and Schultz 2000, ch. 24]
60. Shape of proximal end of interclavicle: broad diamond (0), gracile anchor (1). [Dilkes 1998, ch. 96]

- 61. Posterior stem of interclavicle: little change in width along entire length (0), expands distally (1). [Dilkes 1998, ch. 98, reworded]
- 62. Relative lengths of anterior and posterior blades of ilium: posterior blade longer (0), anterior blade longer (1). [Benton 1983, p. 709; 1985, p. 128; Langer and Schultz 2000, ch. 27]
- 63. Anterior apron of pubis: absent (0), present (1). [Dilkes 1998, ch. 104]
- 64. Relative length of femur and humerus: femur longer than humerus (0), humerus same length, or longer than, femur (1). [Benton 1983, p. 709; 1985, p. 133; 1990, ch. 24, modified]
- 65. Relative proportions of femur; distal width/total length: <0.3 (0), >0.3 (1). [Dilkes 1998, ch. 111]
- 66. Number of proximal tarsals: two (0), three, by incorporation of centrale (1). [Benton 1985, p. 131; 1990, ch. 25]
- 67. Perforating foramen: between astragalus and calcaneum (0), between distal ends of tibiale and fibula (1). [Dilkes 1998, ch. 115]
- 68. Relative length of astragalar facets for tibia and centrale: tibial facet longer (0), centrale facet longer (1). [Langer and Schultz 2000, ch. 28]
- 69. Lateral tuber of calcaneum: present (0), absent (1). [Benton 1985, p. 115; Dilkes 1998, ch. 116, polarity reversed]
- 70. Size of centrale relative to width of calcaneum: smaller (0), similar size (1). [Benton 1985, p. 131; 1990, ch. 26]
- 71. Contact between centrale and distal tarsal 4: present (0), absent (1). [Dilkes 1998, ch. 118, reworded]
- 72. Size of fourth distal tarsal relative to other distal tarsals: twice as large (0), approximately same size (1). [Langer and Schultz 2000, ch. 29]
- 73. Ratio of lengths of metatarsals I and IV: >0.4 (0), <0.4 and >0.3 (1), <0.3 (2). [Dilkes 1998, ch. 123; see also Modesto and Sues 2004, p. 348]
- 74. Ratio of lengths of digits 3 and 4: <0.81 (0), >0.81. [Dilkes 1998, ch. 124; recoded according to Modesto and Sues 2004, p. 348]
- 75. Length of metatarsal I relative to first phalanx: longer (0), same length (1). [Benton 1983, p. 709, reworded]

*Matrix of characters used in phylogenetic analysis*

Characters are present in states 0 and 1, with some in state 2, as defined in the descriptions of characters above. A question mark (?) indicates that the character cannot be coded in existing material, and ‘N’ indicates that the character is non-applicable and so cannot be coded. Non-applicable characters were treated as uncertain (?) for the cladistic analyses.

	10	20	30	40	50	60	70
<i>Proterosuchus</i>	00000	00000	00000	00000	00000	00000	00000
<i>Prolacerta</i>	00100	10000	00000	00000	00001	00000	00000
<i>Trilophosaurus</i>	01000	0?0?0	00000	0?200	11???	N??01	00?00
<i>Mesosuchus</i>	00110	11000	00001	11001	10001	00000	00000
<i>Howesia</i>	00110	?1100	00001	11001	1100?	00000	00?0?
<i>Rhynchosaurus articeps</i>	00?10	11100	00001	10111	11000	11100	00110
<i>Rhynchosaurus brodiei</i>	00?10	11110	00001	101??	?????	1?1??	?????
<i>Stenaulorhynchus</i>	00?10	11100	00101	10111	11?00	1?100	00110
<i>Mesodapedon</i>	?????	?21??	?????	?????	?????	?????	?????
<i>Fodonyx spenceri</i>	00111	11101	10011	01101	1100?	11100	10010
<i>Rhynchosaurus spenceri</i>	11?1?	1?111	1???	?????	?????	1110?	?????
<i>Otischalkia</i>	?????	11???	?????	?????	?????	?????	?????
<i>Ammorhynchus</i>	?????	?21??	?????	?????	?????	?????	?????
<i>Hyperodapedon genovefae</i>	?????	1?1??	?????	?????	?????	?????	?????
<i>Scaphonyx sulcognathus</i>	11011	11111	11001	11111	11110	11111	11111
<i>Hyperodapedon huenei</i>	11011	11111	11011	11111	11110	11111	11111
<i>Hyperodapedon gordonii</i>	11011	11111	11011	11111	11110	11111	11111
<i>Hyperodapedon huxleyi</i>	11011	11111	11011	11111	11110	11111	11111
<i>Hyperodapedon mariensis</i>	1?2?1	?????	11?1?	?????	??11?	??211	1???
<i>Mariante rhynchosaur</i>	11011	11111	11011	11111	11110	11111	11111
<i>Zimbabwe Hyperodapedon</i>	?????	1?1??	?????	?????	?????	?????	?????
<i>Wyoming Hyperodapedon</i>	?????	1?1??	?????	?????	?????	?????	?????
<i>Scaphonyx fischeri</i>	11011	11111	11011	11111	11110	11111	11111
<i>Scaphonyx sanjuanensis</i>	11011	11111	11?1?	?????	11?10	??211	1?210
<i>Supradapedon</i>	?????	?21??	?????	?????	?????	?????	?????
<i>Nova Scotia rhynchosaur</i>	?????	?21??	?????	?????	?????	?????	?????

*Character transformations*

In this list, unequivocal characters are not annotated, convergences are marked with an asterisk (\*), reversals with a negative sign (-), and characters that may be placed at different nodes, depending on whether accelerated transformation (A) or delayed transformation (D) is assumed. Derived states for multistate characters are indicated in parentheses after the character number. Nodes are indicated in Text-figure 9.

Node 1. Rhynchosauria (= *Mesosuchus* + all taxa above)

4, 6, 7, 8, 15, 16, 17\*, 20, 21, 42(1), 46(2)\*, 55, 61, 70, 73(1)

Node 2. *Howesia* + all taxa above

22, 33<sup>A</sup>, 37<sup>A</sup>, 38<sup>A</sup>, 39, 40<sup>A</sup>, 41, 45, 47, 49<sup>A</sup>, 51, 53<sup>A</sup>, 54<sup>A</sup>, 60, 65, 73(2)<sup>A</sup>, 74<sup>A</sup>

Node 3. Rhynchosauridae (= *Stenaulorhynchus* + all taxa above)

-17, 18, 19, 26, 27<sup>A</sup>, 28, 33<sup>D</sup>, 34, 37<sup>D</sup>, 38<sup>D</sup>, 40<sup>D</sup>, 42(2), 43(2), 49<sup>D</sup>, 50, 53<sup>D</sup>, 54<sup>D</sup>, 63, 66, 67, 71, 73(2)<sup>D</sup>, 74<sup>D</sup>, 75

Node 4. *Rhynchosaurus* + all taxa above

27<sup>D</sup>, 36, 56, 69\*, 72

Node 5. *Rhynchosaurus*

-55, -65, -73(2->1)\*, -75

Node 6. *Fodonyx* + all taxa above

5, 10, 11, 14, 17\*, 31, 57, 58<sup>A</sup>, 68<sup>A</sup>

Node 7. Hyperodapedontinae (= '*Scaphonyx*' *sulcognathus* + all taxa above)

1, 2, -3, 9\*, 12, 23, 24, 29, 30, 32, 35, -45, 48, 58<sup>D</sup>, 68<sup>D</sup>

Node 8. *Hyperodapedon huenei* + all taxa above

-46(2->1)

Node 9. Other species of *Hyperodapedon* and '*Scaphonyx*'

43(1), 44, 59

*Mesosuchus*: 25, 69\*

*Rhynchosaurus brodiei*: 9\*

*Fodonyx*: -16, -19, -33

'*Scaphonyx*' *sulcognathus*: -14

*Hyperodapedon mariensis*: 46(2)\*, -59\*

*Hyperodapedon huxleyi*: -59\*

*Hyperodapedon gordonii*: -44

*H. huxleyi* + *H. gordonii*: 46(1), 62, 64

*Scaphonyx sanjuanensis*: -35, -66, -70

*Anatomical abbreviations*

a, angular; ar, articular; as, astragalus; bo, basioccipital; bpt, basipterygoid process; ca, calcaneum; ce, centrale; ch, choana; cv, chevron; d, dentary; ec, ectopterygoid; eo, exoccipital; f, frontal; fi, fibula; g, gastralia; h, humerus; hy, hyoid; I, digit one; il, ilium; is, ischium; iof, infraorbital fenestra; j, jugal; l, lacrimal; L, left; m, maxilla; man, mandible; n, nasal; op, opisthotic; p, parietal; pf, postfrontal; pl, palatal; pm, premaxilla; po, postorbital; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; r, rib; R, right; sa, surangular; sc, scapula; so, supraoccipital; sp, splenial; sq, squamosal; st, supratemporal; ti, tibia; v, vomer; vt, vertebra; V, digit five; ?, unidentified bone; 1, 2, 3, 4, distal tarsals 1, 2, 3, 4.