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FUNCTIONAL AND EVOLUTIONARY ASPECTS OF THE POSTCRANIAL ANATOMY OF DICYNODONTS (SYNAPSIDA, THERAPSIDA)

by SANGHAMITRA RAY

Department of Geology and Geophysics, Indian Institute of Technology, Kharagpur 721302, India; e-mail: sray@gg.iitkgp.ernet.in

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Abstract: Restoration of the major skeletal muscles and functional morphological analysis of the postcranium were carried out on two Triassic dicynodont genera, *Wadiasaurus* and *Lystrosaurus*. A phylogenetic analysis of 12 selected Permian and Triassic dicynodont taxa was conducted and the postcranial character states were then mapped onto the most parsimonious tree. The analysis revealed changes in pectoral girdle and forelimb morphology, which included reduction of the coracoid plate, increasing robustness of the deltopectoral crest, change in humeral orientation from lateral to caudolateral, increasing prominence of the humeral head, and increasing robustness of the radius. Such changes can be associated with a functional tendency to reduce the lateral component of the propulsive force while still in an abducted mode. On the other hand, changes associated with the pelvic girdle included expansion of the preacetabular iliac process, reduction of the postacetabular iliac process, craniocaudal expansion of the iliac blade, change in the shape of the pubis from flat and plate-like to small and rod-like with a cranial process, and change in acetabular orientation from lateral to caudolateral. The femoral head, starting from a cranioproximal position, progressively became dorsally pronounced and offset from the body. Other features/changes associated with the femur included increasing robustness of the trochanter major, and increasing flattening of the femoral midshaft. Changes in the axial skeleton included increasing stiffening of the trunk to reduce lateral undulations, increasing dorsoventral flexion, and increasing sacral vertebral count, which can be correlated with the preacetabular iliac expansion. These findings suggest that the dicynodont postcranial skeleton evolved towards more upright hindlimb morphology with the body held well off the ground.

Key words: Dicynodont, evolution, postcranial anatomy, phylogeny.

DICYNODONTIA, an extinct group of non-mammalian therapsids, diversified into numerous genera and species during the Middle and Late Permian (Lucas 2002) to become the dominant terrestrial herbivores of that time. Apart from Russia, Scotland and China, Middle–Late Permian dicynodonts are known from the Gondwanan countries such as South Africa, Tanzania, Zambia, Mozambique, Madagascar, Brazil and India. During the Triassic, dicynodonts had an almost world-wide distribution but their generic and specific diversity decreased markedly at the onset of the Triassic. They eventually became extinct by end of the Late Triassic.

Following the initial work by Owen (1845, 1859), Seeley (1889) and Broom (1901, 1932), dicynodonts have been studied extensively (e.g. Camp and Welles 1956; Watson 1960; Crompton and Hotton 1967; Cluver 1971, 1978; Cluver and Hotton 1981; King 1981*a*, *b*, 1988, 1993; Cluver and King 1983; Ray 2000, 2001). Most of these studies dealt with taxonomy and emphasized the cranial peculiarities of the dicynodonts. These cranial features included the masticatory region, which was essentially covered by keratinized epithelium, a flared zygomatic arch, and a W-shaped quadrate-articular jaw joint that facilitated a propalinal masticatory action. The dicynodonts were primary consumers (Hotton 1986). They had various roles as herbivores (i.e. browsers and foragers) and consumed a variety of food such as leaves, stems, roots, fleshy parts of plants and even small invertebrates (King 1993). Most dicynodonts exhibited a postural dichotomy, which consisted of abducted forelimbs and nearly adducted hindlimbs as revealed from earlier work on few genera such as *Cistecephalus* (Cluver 1978), *Kawingasaurus* (Cox 1972), *Dicynodon* (King 1981*b*) and *Diictodon* (Ray and Chinsamy 2003).

Although numerous well-preserved dicynodont postcrania have been collected, very few papers describe and evaluate functional aspects of dicynodont postcranial anatomy in detail (e.g. Huene 1935; Camp and Welles 1956; Cox 1959, 1972; Cluver 1978; King 1981*a*, *b*, 1985; Walter 1986; Bandyopadhyay 1988; Rubidge *et al.* 1994; Ray and

Chinsamy 2003; Vega-Dias *et al.* 2004; Surkov *et al.* 2005). In addition, previous attempts at determining the relationships among dicynodonts were mostly based on cranial features (e.g. Keyser and Cruickshank 1979; Cluver and King 1983; King 1988; Angielczyk 2001; Surkov and Benton 2004). Thus, comparative functional anatomical descriptions were almost absent and this disparity resulted in phylogenetic studies being overly reliant on cranial features.

This paper addresses these gaps in our knowledge. It presents the first detailed comparative study of the postcranial anatomy of a wide sample of Permian and Triassic dicynodonts, including soft tissue reconstruction based on two Triassic taxa: *Wadiasaurus*, an endemic form from India, and *Lystrosaurus*, which was nearly Pangaean in distribution. The postcranial functional morphology of some selected dicynodont genera was evaluated in order to construct a phylogenetic tree showing their interrelationships and to assess the evolutionary signatures within these skeletons.

Institutional abbreviations. ISI, Indian Statistical Institute, Kolkata, India (ISIR, prefix to specimen number indicating reptile collection); GSI, Geological Survey of India, Kolkata, India; GS, Council for Geosciences, Pretoria, South Africa; SAM, Iziko: South African Museum, Cape Town, South Africa, TSK, University Museum, Oxford, UK.

Abbreviations used in text-figures. ac pr, acromion process; acet, acetabulum; add, M. adductor femoris; amb, M. ambiens; bi, M. biceps; br, M. brachialis; cb, M. coracobrachialis; cbl, M. coracobrachialis longus; cf, M. coccygeo-femoris; cn cr, cnemial crest; cor, coracoid; del, M. deltoideus; dpc, deltopectoral crest; ect, ectepicondyle; ent, entepicondyle; ent. f, entepicondylar foramen; ext it, M. extensor ilio-tibialis; fcu, M. flexor carpi ulnaris; fdl, M. flexor digitorium longus; fl f, flexor fossa; ft, M. femoro-tibialis; fte + fti, M. flexores tibiales; gl, glenoid fossa; gst, M. gastrocnemius; i fem, M. ilio-femoralis; i fem 1, i fem 2, i fem 3, three subdivisions of M. ilio-femoralis; i fib, M. ilio-fibularis; i tib, M. ilio-tibialis; isch, ischium; ist, M. ischio-trochantericus; ld, M. latissimus dorsi; ls, M. levator scapulae; obt f, obturator foramen; ol pr, olecranon process; pco, procoracoid, pec, M. pectoralis; per, M. peroneus longus and brevis; pife, M. pubo-ischio-femoralis externus; pifi, M. pubo-ischio-femoralis internus; pit, M. puboischiotibialis; pr qu, M. pronator quadratus; pu, pubis; r con, radial condyle; sa f, facets for the sacral ribs; sas, M. serratus anterior superficialis; scs, M. subcoracoscapularis; sha, M. scapulohumeralis anterior; sig n, sigmoidal notch; sol, M. soleus; spc, M. supracoracoideus; sup, supinator; thl, M. triceps humeralis lateralis; thm, M. triceps humeralis medialis; tib ant, M. tibialis anterior; tm, trochanter major; tr, trochlea; tri, M. triceps.

MATERIAL AND METHODS

The seven Permian genera considered in this study are *Eodicynodon*, *Robertia*, *Diictodon*, *Pristerodon*, *Kingoria*, *Cistecephalus* and '*Dicynodon*' (a paraphyletic taxon: Angielczyk and Kurkin 2003*a*, *b*), whereas the five Triassic forms are *Lystrosaurus*, *Kannemeyeria*, *Wadiasaurus*, *Stahleckeria* and *Placerias*. The adult skull size of the genera examined ranged from *c.* 50 to 600 mm, and the specimens were collected from different stratigraphic horizons and geographical regions. The material included partial and complete, articulated and/or disarticulated skeletons housed in the SAM, GS, ISI and GSI. Specimens with the same catalogue number but differentiated by 'a', 'b' or 'c' are separate skeletons associated within a single block. Most of the postcranial skeletons examined were associated with skulls, except for that of *Wadiasaurus*. *Wadiasaurus* material amounting to about 700 skeletal elements was collected from a monospecific locality of the Yerrapalli Formation, Pranhita-Godavari Basin, India (Bandyopadhyay 1988). The details of the specimens examined are given in the appendix.

Information on *Eodicynodon*, *Kingoria*, *Stahleckeria* and *Placerias* was drawn from Cox (1959), King (1985), Walter (1986), Camp and Welles (1956) and Rubidge *et al.* (1994). Additional sources of information on other dicynodonts are Pearson (1924*a*, *b*), Romer and Price (1944), Camp and Welles (1956), Watson (1960), Roy Chowdhury (1970), Cluver (1978), King (1981*a*, *b*), Walter (1986), Bandyopadhyay (1988), Ray (2001), Maisch (2001) and Ray and Chinsamy (2003). In addition, photographs of TSK 14 (*Dicynodon trigonocephalus*), which was described by King (1981*b*), and photographs of a mounted skeleton of *Stahleckeria*, housed in the Institut und Museum für Geologie and Paläontologie der Universität Tübingen, Germany, were also studied.

Analyses of skeletal articulations and biomechanics were performed using isolated skeletal elements and plasticine models. Because soft tissues and their osteological correlates do not always follow a one-to-one relationship (Bryant and Seymour 1990), soft anatomy reconstruction is limited only to those muscles with unequivocal osteological correlates in the form of rugosities, pits and surface markings that indicate sites of muscle origin and insertion (Ray and Chinsamy 2003). Precise assessments of muscle size are not possible in fossils, so only qualitative evaluations of these features were made. Muscle names follow the terminology of Romer (1922, 1923).

Skeletal measurements were carried out using Mitutuyo digimatic calipers with a precision of 0·01 mm. Measurements were mostly taken from the undistorted skeletal elements, but where distortion had occurred (i.e. where the elements had suffered uniform shear only) the same measurement was performed on both left and right elements and the average was taken. The result was also averaged wherever multiple adult specimens of the same taxon are measured. In the descriptions of the skeleton restorations, the propodials (humerus and femur) were considered as orientated laterally at a right angle to the sagittal plane, whereas the antebrachium (radius and ulna) and crus (tibia and fibula) were considered as vertically orientated and perpendicular to the propodials. Extensor surfaces of the antebrachium and crus were considered to face cranially. The skeletal reconstructions of *Pristerodon*, *Diictodon* and *Lystrosaurus* are based on several articulated skeletons. Even though *Wadiasaurus* is known from disarticulated skeletal elements, it is reconstructed based on the skeletal proportions of *Kannemeyeria* because the two genera are sister taxa (Bandyopadhyay 1988; Maisch 2001). The dicynodont *Stahleckeria* is restored from the photograph of a mounted skeleton housed at Tübingen, with additional information from Camp and Welles (1956). The computer programmes PAST (Hammer *et al.* 2001) and PAUP 4.0b10 (Swofford 2000) were used for computing the phylogenetic tree for mapping of the character-state distributions.

POSTCRANIAL FUNCTIONAL MORPHOLOGY

Muscle restoration in Wadiasaurus *and* Lystrosaurus

Wadiasaurus was a large [skull length along dorsal midline (SL) *c.* 400 mm] generalized dicynodont that lived in herds (Bandyopadhyay 1988). Roy Chowdhury (1970) and Bandyopadhyay (1988) described *Wadiasaurus* in considerable detail. *Lystrosaurus*, by contrast, was a medium-sized form (SL *c.* 110 mm) and was traditionally considered to be semi-aquatic/amphibious (Watson 1912; Cluver 1971; Retallack *et al.* 2003). An alternative lifestyle comprising a fully terrestrial with a probable burrowing habit was proposed by King and Cluver (1991). Recent study on the bone histology of *Lystrosaurus* suggests a lifestyle that combined digging and swimming (Ray *et al.* 2005). The anatomy of *Lystrosaurus* has long drawn the attention of various workers (e.g. Watson 1912; Broom 1932; Cluver 1971; King 1991; King and Cluver 1991; Surkov *et al.* 2005) because of its inferred lifestyle. Nevertheless, certain salient features in the postcrania of *Wadiasaurus* and *Lystrosaurus* are restated below in order to evaluate functional aspects of the postcranial anatomy of the two dicynodonts.

Pectoral girdle and forelimb. The scapular blade of *Wadiasaurus* is long, narrow, and slender [scapular length (ScL)/scapular width at the dorsal margin (ScW) is 6·21; Pl. 1, fig. 1). In contrast, the scapular blade of *Lystrosaurus* is broad, and has a craniocaudally flaring dorsal border (ScL/ScW is 3·5; Pl. 1, fig. 5) and a thick, rod-like caudal edge (Text-figs 1–2). This ratio differs considerably from that of the other dicynodonts examined such as *Diictodon*, *Pristerodon*, and *Cistecephalus* (*c.* 5–5·3), and *Kannemeyeriia*, *Stahleckeria*, and *Placerias* (4·5–5·73). Because the lateral surface of the scapular blade represented the site of origin of M. deltoideus and M. serratus anterior superficialis, such distinct variation in the proportions of the scapula of *Wadiasaurus* and *Lystrosaurus* suggested differing physiological cross-sectional areas for the muscles. The origination sites for M. scapulohumeralis anterior and M. supracoracoideus remained as inferred for other dicynodonts. Medially, the scapular blade of both *Wadiasaurus* and *Lystrosaurus* has a shallow but distinct depression, which was the origination site of M. subcoracoscapularis.

The scapula and the coracoid plate form an outward, open-notched glenoid fossa in the two dicynodonts. This fossa faces caudolaterally with sharply defined upper and lower lips. The scapular part of the glenoid fossa is slightly concave whereas the coracoid part is slightly convex. Although the procoracoid is not preserved in *Wadiasaurus*, it is small and subtriangular in *Lystrosaurus*. Relative to the scapula the coracoid is also small and subtriangular. Its lateral surface is concave and its ventral margin has an unfinished and wavy appearance that suggests a cartilaginous extension of the coracoid to the interclavicle. The ventrolateral surface of the coracoid was the site of origination of M. coracobrachialis and M. biceps. Medially, the cranial edge of the coracoid was the origination site of M. triceps.

The degree of expansion of the proximal end of the humerus (HPW) relative to the distal end (HDW) differs considerably in *Wadiasaurus* and *Lystrosaurus* (Pl. 1, figs 2, 6). In the former, HPW/HDW > 1 whereas in the latter, HPW/HDW < 1, although both of them are less than the humeral length (HL). Muscle restoration on the humeri of the two dicynodonts showed that it conforms to the patterns inferred for other dicynodonts such as *Diictodon* (Ray and Chinsamy 2003), *Cistecephalus* (Cluver 1978), and *Dicynodon trigonocephalus* (King 1981*b*). A widely flaring and robust deltopectoral crest (dpc is 50 per cent of HL in *Wadiasaurus* and 39 per cent in *Lystrosaurus*) with prominent longitudinal striations on its thick caudal edge may have provided insertion sites for M. deltoideus and M. pectoralis on the dorsal and ventral surfaces, respectively. The origination area of M. triceps humeralis lateralis is marked by a shallow depression on the proximodorsal surface whereas M. triceps humeralis medialis may have originated from the deep triangular depression surrounding the trochlea on the dorsal surface of the humerus (Text-figs 1–2).

A prominent tubercle on the caudal edge for insertion of M. latissimus dorsi characterizes the humeri of the two dicynodonts (Text-figs 1C–D, 2B–C). Other features of the humerus include a large entepicondylar foramen that obliquely pierced the ventral surface of the humeral shaft, and a large, raised, asymmetric area on the ventral humeral surface for articulation with the ulna and radius. In *Wadiasaurus* a triangular, highly raised trochlea continues on the dorsal surface and possibly suggested greater ulnar extension than was possible in *Lystrosaurus*. Well-developed and robust ectepicondylar and entepicondylar regions in the two dicynodonts suggested considerable origination sites for the extensors and flexors, respectively.

Although the radius and the ulna are much shorter than the humerus [radial length (RL)/HL is 0·6] in the two dicynodonts, their morphologies are distinctly different. In *Wadiasaurus*, the radius is rod-like and stout with expanded proximal and distal ends and a narrow midshaft region (Text-fig. 1E–F; Pl. 1, fig. 3). The expansions at the two ends are nearly equal (RPW ≈ RDW). The proximal articular surface is concave and elliptical whereas the distal articular surface is oval and convex (ratio between the two axes is 1·4 : 1). In contrast, the distal end of the radius of *Lystrosaurus* is extended lateromedially (Text-fig. 2E; Pl. 1, fig. 7) and strongly elliptical in cross-section. The ratio between the long and short axes is about 4 : 1, resulting in a flattened distal end of the radius (e.g. SAM-PK-K1415).

The ulna of *Wadiasaurus* (Text-fig. 1G–I; Pl. 1, fig. 4) is stout but craniocaudally compressed. It is characterized by a prominent, high, and thick wedge-shaped olecranon process (ISIR41/51; ol pr *c.* 29 per cent of UL), whose cranial face represents the site of insertion of M. triceps. In *Wadiasaurus* the olecranon is completely ossified and fused with the ulna in contrast to that of *Stahleckeria* and other Triassic dicynodonts, in which the olecranon process remained as a separate ossification from the ulna. Cranially, the olecranon process and the shaft of the ulna together form a continuous shallow depression that probably was the site of origin of M. flexor digitorium longus and M. flexor carpi ulnaris. On the caudal surface is a deep elongate depression that served as the site of insertion of triceps muscles. Just below the sigmoid notch is a deep groove for the radius. Distally, the medial edge is striated, indicating the origination site for M. pronator quadratus.

On the other hand, a high olecranon process is absent in *Lystrosaurus* (Text-fig. 2D; Pl. 1, fig. 8). The distal end of the ulna is flattened and subelliptical in cross-section. It is positioned in the same plane as the distal end of the radius and together these bones form a flattened, lateromedially extended articular surface for the manus. The manus has been well described in both *Lystrosaurus* (Text-fig. 2F) and *Wadiasaurus* (Bandyopadhyay 1988, p. 220, fig. 24). In both it is broad, robust and short with blunt and stout claws, and exhibits a phalangeal formula of 2-3-3-3-3. The phalanges of *Wadiasaurus* are short and broad compared with those of *Diictodon* (Ray and Chinsamy 2003) and *Lystrosaurus*. The proximal and penultimate phalanges have basal tuberosities at the corners in plantar view. The terminal phalanx is a short but broad claw with a ventral curvature and a boss on its plantar side.

Pelvic girdle and hindlimb. The iliac blade of *Wadiasaurus* is wide (IL/IH *c.* 2), subtriangular and concave laterally (Text-fig. 3A–B; Pl. 1, fig. 9). The dorsal edge of the iliac blade is highly convex, smooth, and asymmetric from cranial to caudal, and its caudal end is almost at a 45-degree angle to the horizontal plane. In contrast, the ilium of *Lystrosaurus* is fan-shaped, and inclined *c.* 20 degrees relative to the horizontal plane. An interesting feature in *Lystrosaurus* is the presence of two prominent, U-shaped, deep notches on the dorsal iliac border (Text-fig. 4; Pl. 1, fig. 13). This feature has not been observed in any other dicynodont. Although King (1981*b*) noted shallow notches in *Dicynodon trigonocephalus*, a possibility that these notches are due to damage cannot be ruled out (K. Angielczyk, pers. comm. 2005). The preacetabular iliac process (IA) is larger than the postacetabular process (IP) and the ratio between IA and total iliac blade length (IL) of *Wadiasaurus* and *Lystrosaurus* is more or less similar, being 0·52 ($n = 3$) in *Wadiasaurus* and 0·5 ($n = 5$) in *Lystrosaurus*. However, the postacetabular iliac process is much shorter in *Wadiasaurus* than that in *Lystrosaurus* (Text-figs 3–4). The IP/IL ratio is 0·19 ($n = 3$) in the former and 0·3 ($n = 6$) in the latter. The ilium has a short, constricted neck above the acetabulum. The medial iliac surface has facets for the expanded distal ends of the sacral ribs. At least five facets (Text-fig. 3B) are distinctly visible in *Wadiasaurus* (ISIR175/27).

The small, robust and twisted pubis (ISIR175/161) of *Wadiasaurus* (Text-fig. 3A–B) is similar to that of *Stahleckeria*. Its craniolateral end is everted and has an unfinished, roughened appearance suggesting probable attachment for abdominal fascia (Camp and Welles 1956) or a cartilaginous epipubis (Bandyopadhyay 1988), or it may have been the cartilaginous extension of the pubis itself. Caudally the pubis meets the much larger ischium in a straight suture, which is interrupted dorsally by a median, large, circular obturator foramen. In *Lystrosaurus*, on the other hand, the pubis is flat and plate-like (Text-fig. 4B). In both dicynodonts, the acetabulum, formed by the ilium and the pubo-ischiadic plate, is deep, large, concave, subcircular, and somewhat obliquely elongated. It has a somewhat caudolateral orientation in *Wadiasaurus*, but in *Lystrosaurus* the acetabulum is more laterally orientated. The iliac face of the acetabulum is concave and medially has a circular depression. It corresponds to a similar depression on the pubo-ischiadic surface of the acetabulum. The ischium is broad and caudoventrally expanded in

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EXPLANATION OF PLATE 1

Figs 1–8. Pectoral girdle and forelimb elements of the two dicynodonts.

Figs 1–4. *Wadiasaurus indicus* Roy Chowdhury, 1970. 1, ISIR 175/169, right scapular blade in lateral view; × 0·13. 2, ISIR 175/1, left humerus in dorsal view; × 0·2. 3, ISIR 175/120, left radius in cranial view; × 0·4. 4, ISIR 41/51, left ulna in cranial view; × 0·3.

Figs 5–8. *Lystrosaurus murrayi* (Huxley, 1859). 5, SAM-PK-K8, right scapular blade in lateral view; × 0·5. 6, SAM-PK-1340, right humerus in dorsal view; × 0·5. 7–8, SAM-PK-K1165. 7, left radius in cranial view; × 0·3. 8, left ulna in cranial view; × 0·2.

Figs 9–16. Pelvic girdle and hindlimb elements of the two dicynodonts.

Figs 9–12. *Wadiasaurus indicus* Roy Chowdhury, 1970. 9, ISIR175/69, right ilium in lateral view; × 0·2. 10, ISIR 174/1, left femur in dorsal view; × 0·2. 11, ISIR175/421, right tibia in cranial view; × 0·2. 12, ISIR 175/184, right fibula in cranial view; × 0·3.

Figs 13–16. *Lystrosaurus murrayi* (Huxley, 1859). 13, SAM-PK-K1415, sacrum in dorsal view showing U-shaped notches on the dorsal iliac border (arrows); × 0·4. 14, SAM-PK-K8038, right femur in dorsal view; × 0·3. 15–16, SAM-PK-K1165, left tibia and left fibula in craniolateral views, respectively; × 0·7.

All elements apart from 9 and 13 are reproduced at the same absolute length for comparative purposes.

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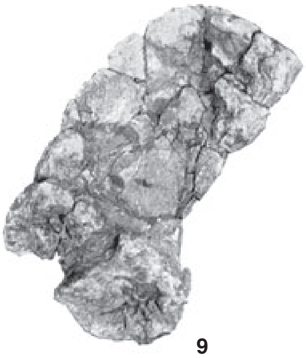

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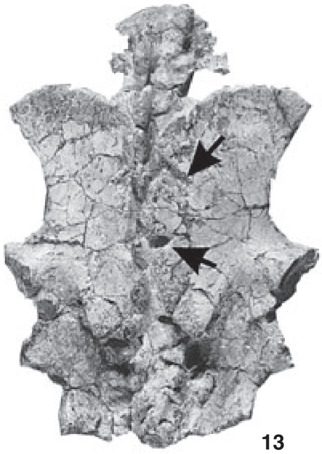

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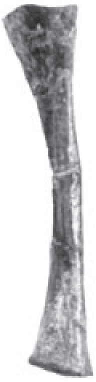

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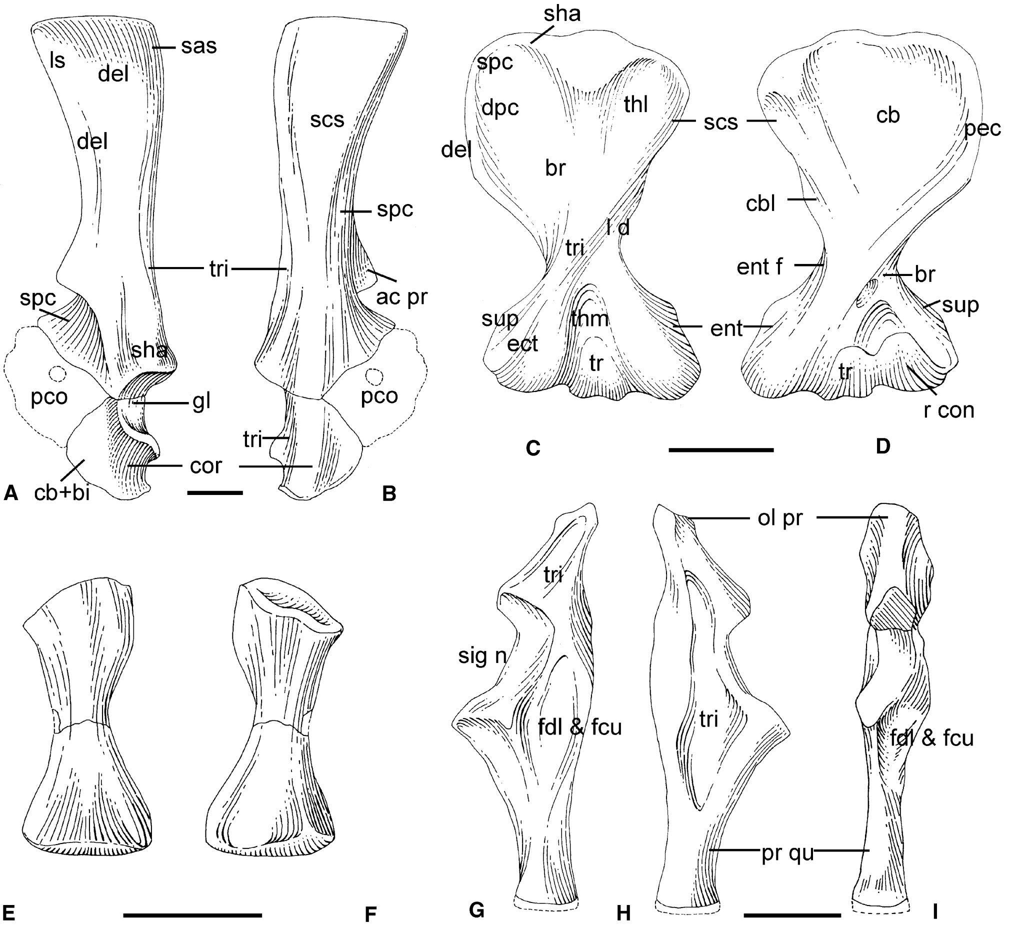
RAY, *Lystrosaurus*, *Wadiasaurus*

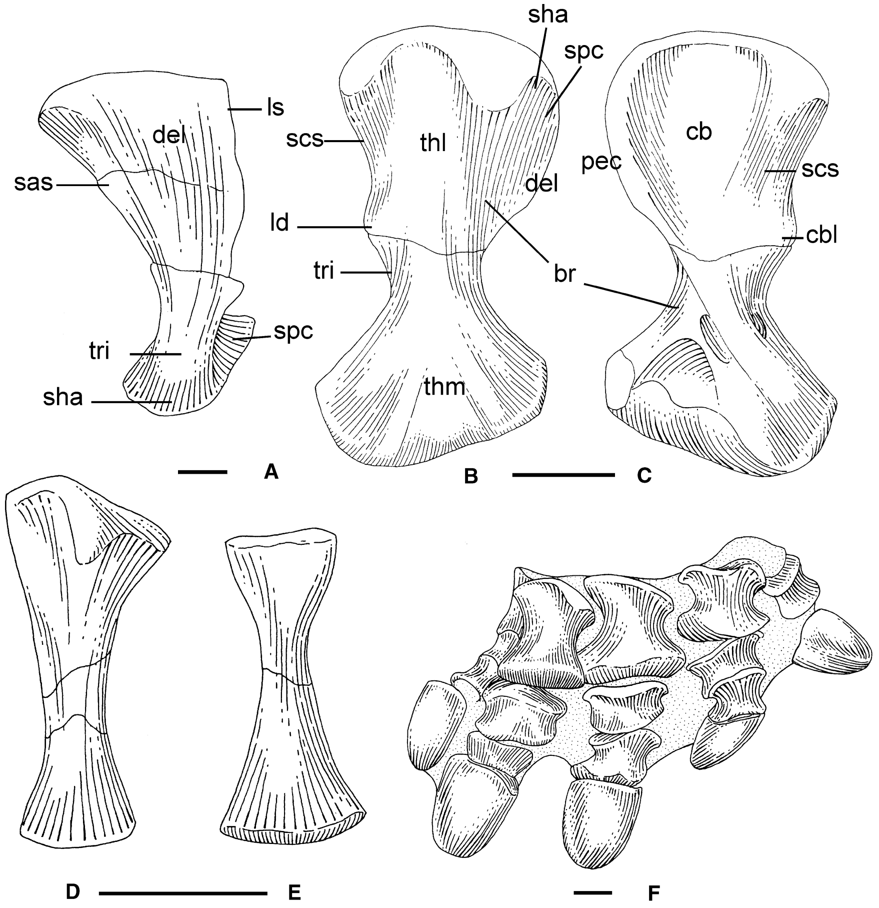


TEXT-FIG. 1. *Wadiasaurus indicus* Roy Chowdhury, 1970. Reconstruction of the sites of muscle origin and insertion on pectoral elements. A–B, ISIR175/169, ISIR41/294, restored left scapulocoracoid in A, lateral and B, medial views. C–D, ISIR175/16 left humerus, in C, dorsal and D, ventral views. E–F, ISIR175/178 left radius in E, cranial and F, caudal views. G–I, ISIR41/51 left ulna in G, cranial, H, caudal and I, medial views. Scale bars represent 60 mm.

the two dicynodonts. However, in *Wadiasaurus*, the ischium can be subdivided into lateral and medial flanges that meet at about 60 degrees. A prominent median ridge occurs on the lateral ischial surface at the line of union of these two flanges, which ends distally in a tuberosity (Text-fig. 3A). In contrast, the ischium of *Lystrosaurus* is flat and plate-like (Text-fig. 4B).

In general, a well-developed head at the cranioproximal extremity, which is more pronounced dorsally, characterizes the femur in the two dicynodonts (Text-figs 3C–D, 5A–B; Pl. 1, figs 10, 14). Other features include greater proximal expansion in comparison with the distal expansion (FPW/FDW > 1), and a distinct trochanter major [tm is 30 per cent of femoral length (FL) in *Lystrosaurus* and *c.* 40 per cent of FL in *Wadiasaurus*]. The femoral midshaft of *Wadiasaurus* is much more dorsoventrally flattened than that of *Lystrosaurus*, as suggested by the ratio between the long (FMW-L) and short (FMW-S) axes. In the former FMW-L : FMW-S is 1 : 2·21 ($n = 6$) whereas in the latter it is 1 : 1·35 ($n = 5$). The distal articular surface consisting of two convex areas/condyles is inclined somewhat ventrally, forming an angle of about 30–40 degrees with the longitudinal femoral axis. Another feature distinguishing between the femora of the two dicynodonts is the presence of an elongated but shallow popliteal area (flexor fossa) in *Wadiasaurus* and a deep, subrounded flexor fossa in *Lystrosaurus*.

Muscle restoration on the pelvic girdle and hindlimb (Text-figs 3–5) follows the pattern inferred for other dicynodonts such as *Diictodon* (Ray and Chinsamy 2003). However, in *Lystrosaurus*, the notched dorsal border resulted in three possible origination sites on the ilium for M. ilio-femoralis, which may therefore have been subdivided into cranial, medial, and caudal segments (Text-fig. 5A). Although M. ilio-femoralis was inserted into the caudal edge of the trochanter major in *Lystrosaurus*, prominent striations and shallow depressions in the femora of SAM-PK-K8038 and SAM-PK-K1415 suggested that the attachment of M. ilio-femoralis was more pronounced on the ventral surface and subdivided into three specific sites (Text-fig. 5B). M. flexores tibiales originated from the distal ischial tuberosity in *Wadiasaurus* and *Lystrosaurus*, and M. ischio-trochantericus originated from the lateral and medial surfaces of the medial flange of the ischium in both dicynodonts. M. pubo-ischio-femoralis externus probably originated from the ventrolateral surface of the puboischiadic plate just below the



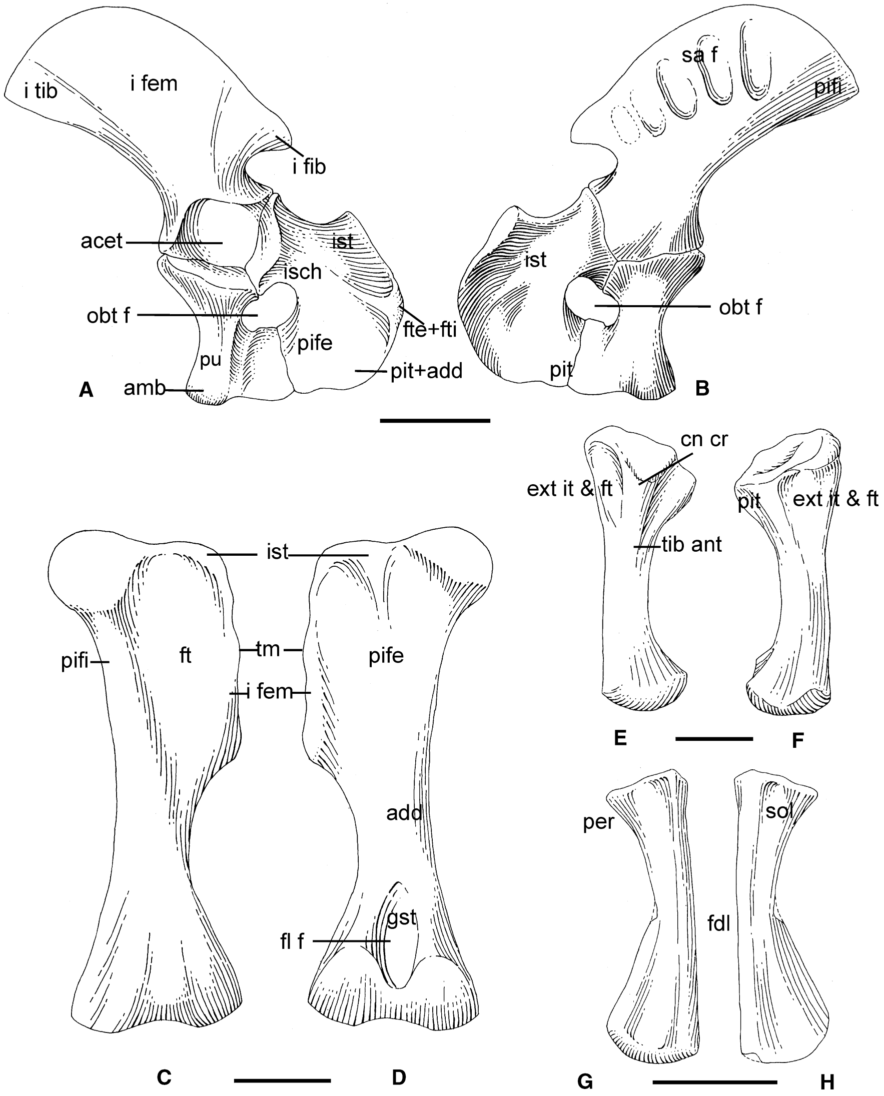
TEXT-FIG. 2. *Lystrosaurus murrayi* (Huxley, 1859). Reconstruction of the sites of muscle origin and insertion on pectoral elements. A, SAM-PK-K8, right scapula in lateral view. B–C, SAM-PK-1340, right humerus in B, dorsal and C, ventral views. D–E, SAM-PK-K1415, D, left ulna and E, radius in cranial views. F, SAM-PK-K8038, manus in dorsal view. Scale bars represent 30 mm.

obturator foramen, as suggested by strong muscle scars in that region. In *Wadiasaurus*, this muscle was possibly subdivided into cranial and caudal segments, as discussed below. Other sites of origin included the cranial end of the iliac medial surface for M. pubo-ischio-femoralis internus and the cranial end of the lateral iliac surface for M. ilio-tibialis, as suggested by strong oblique striations.

On the proximodorsal surface of the femur, a shallow depression marked the site of origination of M. femoro-tibialis. The thick edge of the trochanter major (on both dorsal and ventral surfaces) formed the insertion site of M. ilio-femoralis. A broad, flat area just distal to the femoral head, on the proximocranial edge, formed the site of insertion of M. pubo-ischio-femoralis internus, whereas M. ischio-trochantericus was inserted on a raised triangular area on the proximoventral femoral surface. This raised area probably subdivided the site of insertion of M. pubo-ischio-femoralis externus into cranial and caudal parts in *Wadiasaurus*, whereas no subdivisions are apparent where this muscle takes origin from the pubo-ischiadic plate. Other muscles such as adductors, M. gastrocnemius, flexors and extensors were restored in conformity with other dicynodonts.

The general morphology of the tibia and the fibula of *Wadiasaurus* and *Lystrosaurus* is more or less similar (Text-figs 3E–H, 5C–F; Pl. 1, figs 11–12, 15–16). The tibia is rod-like and robust with expanded proximal and distal ends (TiPW/TiDW > 1) and a prominent cnemial crest. Although the mid shaft region is elliptical in cross-section, the tibia of *Wadiasaurus* is more flattened [TiMW-L:TiMW-S is 1 : 1·54 ($n = 9$)] than that of *Lystrosaurus* [TiMW-L:TiMW-S is 1 : 1·27 ($n = 5$)]. As in other dicynodonts, the proximal tibial surface for articulation with the femur was composed of two oval and concave sulci separated by a low ridge, whereas the distal surface was circular and convex for articulation with the astragalus. A shallow depression on the cranioproximal edge of the cnemial crest was the site of insertion of M. extensor ilio-tibialis and M. femoro-tibialis, whereas M. pubo-ischio-tibialis was probably inserted on the proximocaudal surface of the tibia, as suggested by prominent muscle scars and a shallow depression. The site of origin of M. tibialis anterior was a flat area on the cranial surface of the tibia.

On the other hand, the fibula is slender, flattened craniocaudally and has an expanded distal end in comparison with the proximal end (FiPW/FiDW < 1). As in the case of the femur and tibia, the midshaft region is more flattened in *Wadiasaurus* [FiMW-L:FiMW-S is 1 : 1·53 ($n = 8$)] than that in *Lystrosaurus* [FiMW-L:FiMW-S is 1 : 1·26 ($n = 5$)]. The proximal articular surface is crescentic with a shallow depression whereas the distal

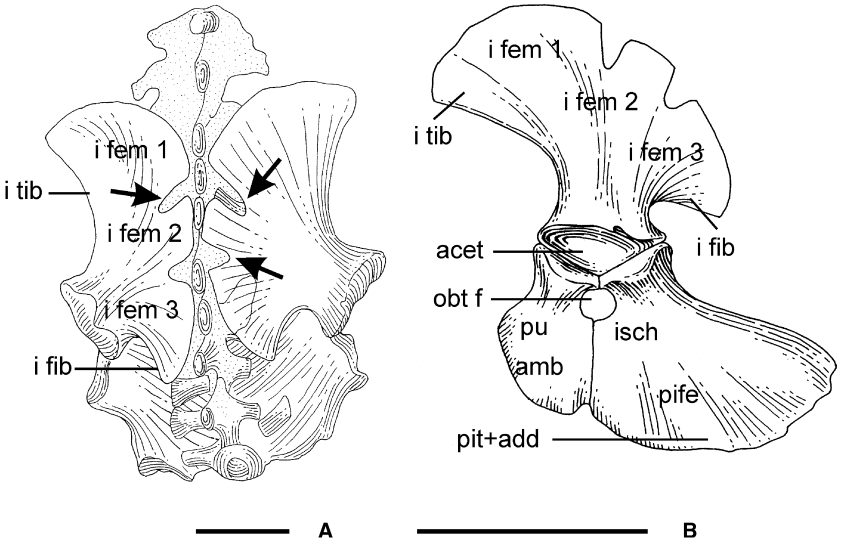


TEXT-FIG. 3. *Wadiasaurus indicus* Roy Chowdhury, 1970. Reconstruction of the sites of muscle origin and insertion on pelvic elements. A–B, restored left ilium and pubo-ischiadic plate in A, lateral and B, medial views, based on specimens ISIR175/27, 175/61, 175/143, and 175/161. C–D, ISIR174/1 left femur in C, dorsal and D, ventral views. E–F, ISIR41/67, right tibia in E, cranial and F, caudal views. G–H, ISIR175/185 right fibula in G, cranial and H, caudal views. Scale bars represent 60 mm.

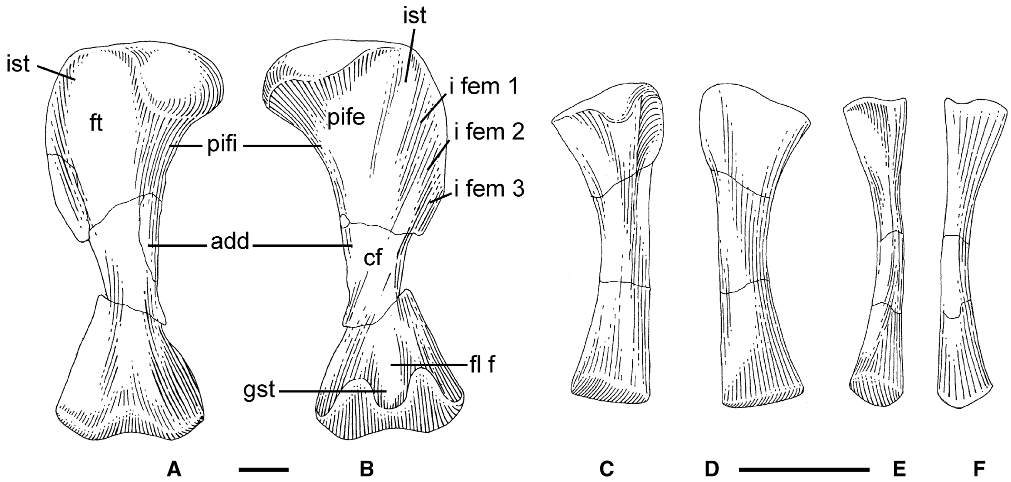
articular surface is teardrop shaped and slightly convex. Certain muscles were inserted on the fibula, such as M. ilio-fibularis on the proximocranial surface at the midshaft region, and M. soleus on the flat, slightly concave area of the proximocaudal surface. M. flexor digitorium longus and M. peroneus longus and brevis probably originated along the raised lateral edge and proximomedial edge of the fibula, respectively.

The pes in both *Wadiasaurus* (Bandyopadhyay 1988, p. 221, fig. 25) and *Lystrosaurus* is similar to but smaller than the manus. A similar size discrepancy is also found in the Permian dicynodont *Diictodon* (Ray and Chinsamy 2003) and seems to be a characteristic feature for the dicynodonts. The pedal formula is 2-3-3-3-3. The pedal phalanges are short and broad, and similar in morphology to the manual phalanges. The terminal phalanges are drawn into short, blunt claws with plantar bosses for the attachment of flexor muscles.

Vertebral column. As shown by Bandyopadhyay (1988), there were probably 25 presacral vertebrae in *Wadiasaurus* of which about seven were cervicals, 18 dorsals, and about five sacral vertebrae. The number of caudal vertebrae is indeterminate. In *Lystrosaurus*, however, there were about six cervicals, 20 dorsals, six sacrals, and ten caudal vertebrae. The cervical prezygapophyses of the two dicynodonts are slightly concave and form an angle of about 10–20 degrees to the horizontal plane. On other hand, the dorsal prezygapohyses are concave, dish-like, and form an angle of about 50–60 degrees to the horizontal. The angle increases towards the sacrum, suggesting that lateral undulation became constrained towards the sacrum, where dorsoventral flexion was mainly prevalent. This differs from the condition seen in the Permian digging dicynodonts such as *Diictodon* and *Cistecephalus*, which have wide, flat zygapophyses of the presacral vertebrae, indicating their ability to undulate laterally (Ray and Chinsamy 2003).



TEXT-FIG. 4. *Lystrosaurus murrayi* (Huxley, 1859). Reconstruction of the sites of origin and insertion of muscles on pelvic elements. A, SAM-PK-K1165, sacrum in dorsal view (arrows indicate notched dorsal iliac border). B, restored left ilium and puboischiadic plate in lateral view. Based on specimens SAM-PK-K1165, SAM-PK-1371, and SAM-PK-1415. Scale bars represent 30 mm.

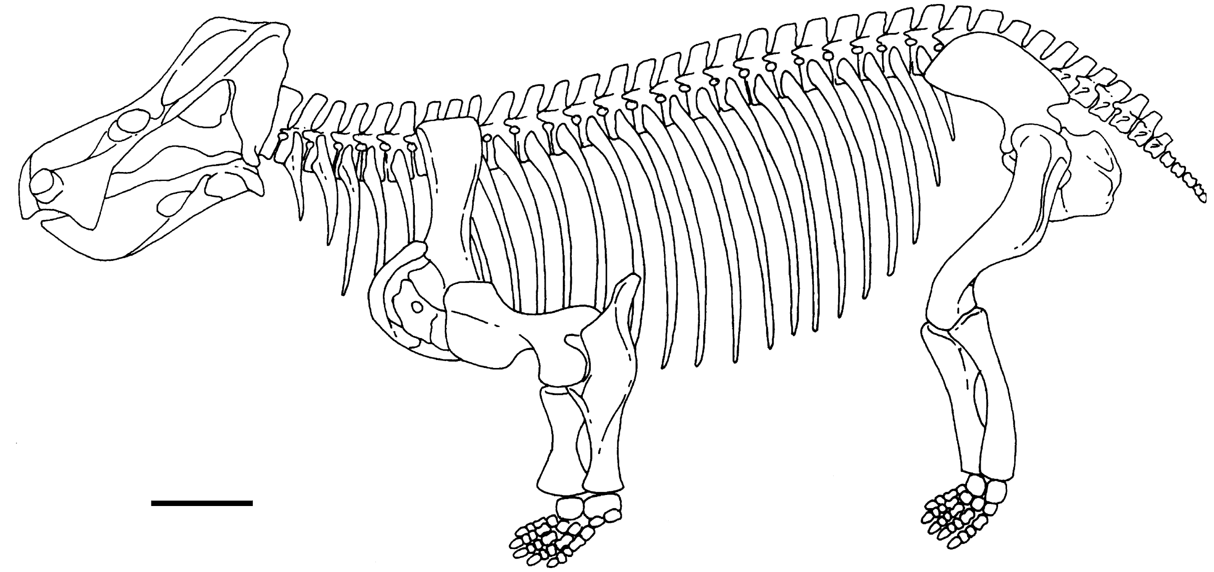


TEXT-FIG. 5. *Lystrosaurus murrayi* (Huxley, 1859). A–B, SAM-PK-K8038, right femur in A, dorsal and B, ventral views showing the reconstruction of the sites of origin and insertion of muscles. C–D, SAM-PK-K1165, left tibia in C, cranial and D, caudal views. E–F, SAM-PK-K1165, left fibula in E, cranial and F, caudal views. Scale bars represent 30 mm.

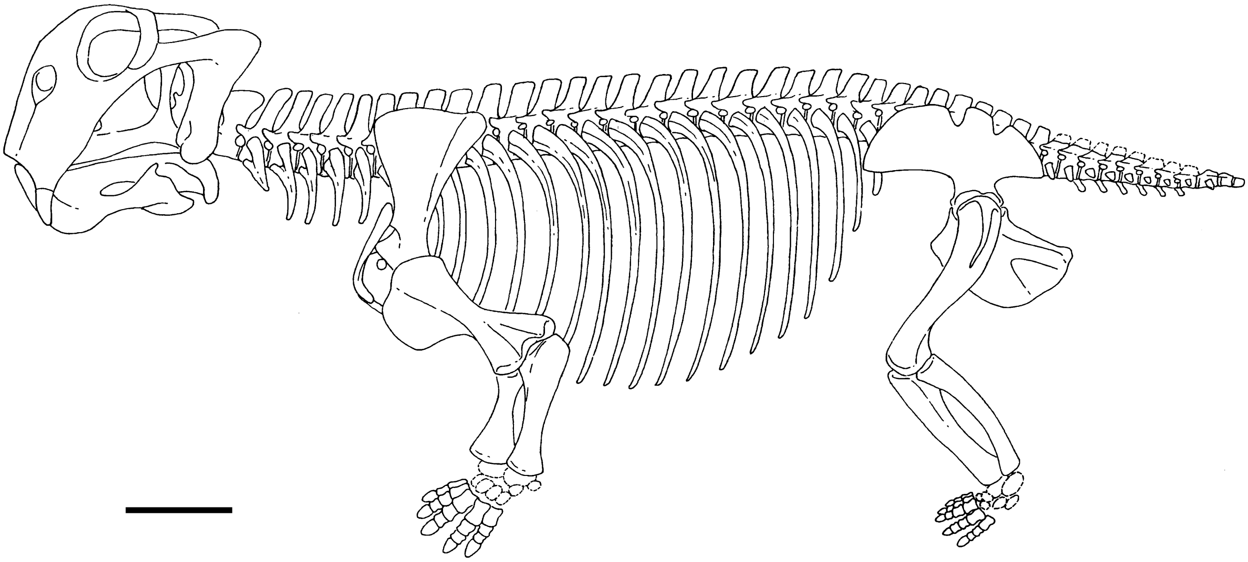
Functional anatomy of Wadiasaurus *and* Lystrosaurus

The long cervical neural spines of *Wadiasaurus* and *Lystrosaurus* provided extensive anchorage for the ligamentum nuchae and neck muscles as in extant hoofed mammals (Alexander 1989). These muscles were used in supporting, elevating, and moving the large head, which constituted about 20 per cent of the total body length in *Wadiasaurus* and *Lystrosaurus* (Text-figs 6–7). The angle of the scapular blade and curvature of the complete and undistorted dorsal ribs that have been recovered suggest that the overall body-shape of *Wadiasaurus* and *Lystrosaurus* was barrel-like or cylindrical. Although, pronounced lateral undulation and dorsoventral flexion of the neck region, including the required rotation of the head, was permitted, lateral undulation became constrained towards the sacrum, as suggested by the high angle of the pre- and post-zygapophyses with the horizontal plane. In *Wadiasaurus*, the caudoventral inclination of the midcaudal centra and the caudal slope of the neural spines (Bandyopadhyay 1988), the high convexity of the dorsal edge of the iliac blade, especially the 45 degree angulation of its caudal end relative to the horizontal, and the orientation of the sacral rib facets suggest an abrupt downturning of the tail in contrast to that of *Lystrosaurus*.

As is typical of advanced dicynodonts, *Wadiasaurus* and *Lystrosaurus* showed a postural dichotomy with the forelimb in an abducted position and the hindlimbs in a nearly adducted stance, resulting in the pelvic girdle being held higher above the ground than the pectoral girdle. In *Wadiasaurus*, the caudolaterally placed open-notched glenoid fossa resulted in the articulation of the humerus in a near-sagittal plane but still in an abducted position,



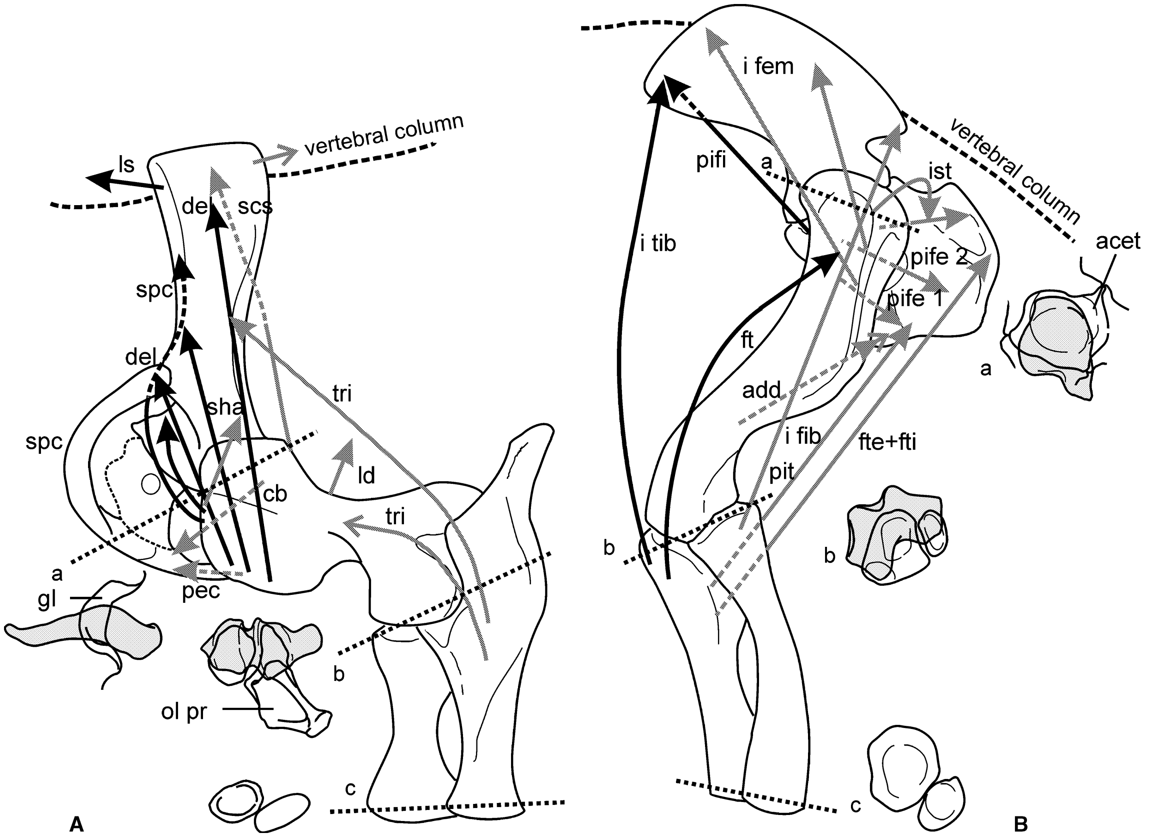
TEXT-FIG. 6. *Wadiasaurus indicus* Roy Chowdhury, 1970. Reconstruction of the skeleton, based on ISIR38, 175/348, 175/281, 175/222, 175/350, 175/236, 175/256, 175/16, 41/51, 174/1, 41/67 and 175/185. Skeletal proportions estimated from the closely related *Kannemeyeria* (Pearson 1924*b*; Cruickshank 1975). Scale bar represents 50 mm.



TEXT-FIG. 7. *Lystrosaurus murrayi* (Huxley, 1859). Reconstruction of the skeleton, based on SAM-PK-K1165, SAM-PK-1415, SAM-PK-K8038 and SAM-PK-K8. Scale bar represents 50 mm.

and was quite similar to that found in other Triassic dicynodonts (Walter 1986) and cynodonts (Jenkins 1971). However, the humeral articulation was more laterally placed in *Lystrosaurus*. In the two dicynodonts, humeral elevation and protraction were performed by M. supracoracoideus and M. deltoideus. The sites of origin and insertion showed that M. latissimus dorsi and M. subcoracoscapularis functioned as the main forelimb retractor (Text-fig. 8A). Simultaneously the humerus was rotated about its longitudinal axis by all the muscles.

The humeral movement involved mainly rolling of the humeral surface over the coracoid part of the glenoid fossa, as suggested by the concave ventral surface of the proximal humerus. This caused protraction-retraction in a horizontal plane involving elevation and depression, respectively, and simultaneous rotation of the humerus. This movement was similar to the forelimb movement of the cynodont *Luangwa* (Kemp 1980). As mentioned above, the two dicynodonts differ in the proportions of the scapular blades. In the case of *Wadiasaurus*, the scap-



TEXT-FIG. 8. Lines of action of the main limb muscles of *Wadiasaurus* are shown with the A, forelimb and B, hindlimb at rest. The positions of the proximal and distal articular surfaces are shown by a, b and c, for the forelimb and d, e and f, for the hindlimb. Lines of action are shown by heavy arrows that run approximately between the origination and insertion sites, with the arrowhead directed towards the origin. The black and grey arrows indicate, respectively, major elevators and depressors in A and major protractors and retractors in B. The grey contoured areas indicate the proximal and distal articular surfaces of the A, humerus and B, femur of *Wadiasaurus*.

ular blade was exceptionally long, suggesting a large area of origination of M. deltoideus, which in turn resulted in increased humeral elevation and helped in keeping the body well above the ground. In *Lystrosaurus* the wide and broad scapular blade with a thick rod-like caudal edge suggested substantial development of M. deltoideus and M. serratus anterior superficialis that probably resulted in enhanced humeral excursion relative to other studied genera. Such a humerus-dominated approach towards digging or swimming activity by *Lystrosaurus* is similar to the digging activity of *Diictodon*, as noted by Ray and Chinsamy (2003).

Large and prominent sites of insertion and origin, as indicated by the high olecranon process and well-developed humeral ectepicondyle and entepicondyle, suggest stronger extensors and flexors in *Wadiasaurus* than in *Lystrosaurus*. This, in turn, suggests that efficient forearm movement (extension and flexion) was biomechanically important in *Wadiasaurus*. An asymmetric, elongate sigmoid notch at the medial margin of the ulna (Text-fig. 1G) corresponded to the triangular and prominent trochlea. In contrast, a high olecranon process was absent in *Lystrosaurus* (Text-fig. 2D), which suggests that humeral extension and not forearm extension constituted the main propulsive forelimb movement. The flattened and lateromedially expanded radius and ulna of *Lystrosaurus* aligned with a broad and robust manus to produce a paddle-like distal forelimb that probably helped in swimming and/or digging.

In *Lystrosaurus* and *Wadiasaurus*, the femur was rotated medially about its longitudinal axis so that the head lay in the acetabulum with the trochanter major more laterally placed, as is evident from the femoral morphology and shape of the acetabulum. In this fairly adducted position the femur could move in a wide protraction-retraction arc. M. ilio-femoralis originating on the lateral surface of the ilium and inserted on the trochanter major acted as a powerful long axis rotator and elevator. However, as the femur swung progressively backwards the cranially originating M. ilio-femoralis would have had a retractive function. This is especially evident in the parasagittal stance of the hindlimb (such as the therocephalians and non-mammalian cynodonts), where M. ilio-femoralis was responsible for increasing the caudal/posterior extent to which the femur could retract (Kemp 1978, 1980). This is further corroborated by the fact that M. ilio-femoralis had a more pronounced insertion on the ventral femoral surface than on the dorsal in the two dicynodonts. The other retractors were M. ilio-fibularis, M. flexores tibiales and M. ischio-trochantericus, as suggested by their caudoventrally directed lines of force (Text-fig. 8B). Protraction was performed mainly by M. pubo-ischio-femoralis internus. This protraction-retraction of the femur provided the main propulsive force for the dicynodonts. Extension and flexion of the crus was brought about by M. ilio-tibialis, M. ilio-fibularis, M. ambiens, M. femoro-tibialis, and a complex of muscles from the pelvis to the tibia and fibula. Thus, *Wadiasaurus* held its hindquarters high up from the ground.

Bandyopadhyay (1988) has shown conclusively from taphonomic study that *Wadiasaurus* was a generalized herbivore that lived in herds. Although *Lystrosaurus* conforms to the usual dicynodont skeletal structure, there were certain distinctive features in its gross postcranial anatomy. These included a wide scapular blade, a wide, paddle-like distal forelimb, and possible subdivision of M. ilio-femoralis with pronounced sites of insertion on the ventral femoral surface, suggesting that the hindlimb could have been held close to the body. Additional information from bone microstructure revealed very thick cortices of the dorsal ribs, extensive secondary reconstruction, and trabecular infilling of the medullary region, suggesting a semi-aquatic lifestyle for *Lystrosaurus* (Ray *et al.* 2005). However, most dicynodonts appear to have had the ability to dig (Hotton 1986; Ray and Chinsamy 2003), and this possibility is not excluded for *Lystrosaurus*, because articulated skeletons have been found in burrow casts (Retallack *et al.* 2003). Like many extant semi-aquatic animals, *Lystrosaurus* probably had a combined semi-aquatic and digging habit.

Functional anatomy of other dicynodonts examined

Similar study of the postcranial anatomy of the Permian forms (*Eodicynodon*, *Robertia*, *Diictodon*, *Pristerodon*, *Cistecephalus* and *Dicynodon*) showed that except for *Eodicynodon* and *Robertia*, dicynodonts exhibited a postural dichotomy with the forelimbs and the hindlimbs in abducted and semi-adducted positions, respectively. In *Eodicynodon* (SL *c.* 100 mm) and *Robertia* (SL *c.* 50 mm, SAM-PK-11885, King 1981*a*), which are the basal dicynodonts (King 1988), the femur and the humerus both had an abducted/sprawling position (King 1981*a*; Rubidge *et al.* 1994). Other features of *Robertia* included extensive postural musculature, a laterally facing gleno-humeral articulation, a moderate trochanter major (30 per cent of FL), a high iliac blade (IL/IH is 1) with a small preacetabular iliac process (IA/IL is 0·35), a well-developed postacetabular iliac process (IP/IL is 0·43) and only two sacral vertebrae (Tables 1–2).

The humerus of *Diictodon* (SL *c.* 100 mm) was articulated in a near horizontal plane. However, its caudolateral orientation resulted in a reduced transverse component of propulsive thrust during locomotion (Ray and Chinsamy 2003). The hindlimb gait of *Diictodon* was similar to the high walk of the crocodilians. Other distinctive features of *Diictodon* included a large iliac blade (IL/IH *c.* 1·25), a slightly caudolaterally orientated acetabular articulation, a trochanter major relatively larger than that of *Robertia* (tm is 35 per cent FL) and three or four sacral vertebrae (Table 2). *Diictodon* was a relatively slow walker and had a fossorial life habit (Ray and Chinsamy 2003). It used a rotation-thrust method of digging in which humeral excursion (rather than forearm extension) played a dominant role. The short limbs, with well-developed forelimb elevators and depressors, and long wide manus, with long blunt claws, facilitated digging. The hindlimbs with well-developed retractors and short, blunt claws, helped in soil removal.

On the other hand, the humerus of *Pristerodon* (SL *c.* 50 mm) was more laterally orientated than that of *Diictodon* and held in an abducted position, whereas the acetabular-femoral articulation was similar to that of *Diictodon*, suggesting a similar hindlimb gait (Ray and Chinsamy 2003). Other characteristic postcranial features of *Pristerodon* include a distinctly asymmetric radio-ulnar facet, a moderate olecranon process (Table 1), a significant expansion of the preacetabular iliac process (IA/IL is 0·4), a moderate trochanter major (tm is 30 per cent FL) and four sacral vertebrae. In all of the three genera discussed so far, lateral undulation of the vertebral column helped considerably in locomotion.

Cluver (1978) considered *Cistecephalus*, a small (SL *c.* 50 mm) Late Permian form, as a highly specialized dicynodont that 'shows a number of fundamental departures from the usual dicynodont condition' (p. 213). Its cranial characteristics include a broad intertemporal region and a rounded occiput, suggesting an increased attachment area for neck and shoulder musculature, and the absence of an interpterygoid vacuity, resulting in a strengthened basicranial region. In addition, notable postcranial features of *Cistecephalus* include a robust humerus with greatly expanded proximal and distal ends, the width of which was equal to the humeral length (Table 1), a strong olecranon process (ol pr is 30·2 per cent UL), a radius almost as long as the humerus (RL $\sim$ HL), a large

TABLE 1. Characteristic features in the pectoral girdle and forelimb of the dicynodont genera examined. Asterisk (*) indicates presence of a cleithrum.

	SL (mm)	Scapular blade morphology and angle to the vertical plane	ScL/ ScW	HL/HPW or HDW	HPW/ HDW	dpc = % HL	Inferred humeral orientation	Olecranon process (ol pr = % UL)
Eodicynodon	*c.* 100	Broad, not constricted above acromion process	–	> 1	*c.* 1	40	Lateral	Moderate (18)
*Robertia**	*c.* 50	Sloping cranially, *c.* 30°	–	> 1	*c.* 1	40	Lateral	Weak
*Diictodon**	100	*c.* 20°	*c.* 5	> 1	*c.* 1	40	Near-sagittal plane	Weak
Pristerodon	*c.* 50	Low angle to the vertical plane, cranial edge ridge-like	5·33	> 1	> 1	45	More laterally placed than *Diictodon*	Moderate
*Cistecephalus**	*c.* 50	Nearly vertical	5·33	1	1	37	Lateral	High (30)
Kingoria	114	*c.* 20°	*c.* 4	–	–	–	Lateral	–
Dicynodon	*c.* 100–400	Fan-shaped, distally a raised, knob-like structure; *c.* 20°	*c.* 4	> 1	*c.* 1	60	Lateral	Moderate
Lystrosaurus	110	Widely flaring, almost vertical blade with thick caudal edge	3·5	> 1	< 1	39	Lateral	Moderate
Kannemeyeria	*c.* 450	Slender, *c.* 10°	4·5	> 1	*c.* 1	45	Caudolateral	Moderate
Wadiasaurus	400	Slender, thick caudal edge, *c.* 35°	6·21	> 1	> 1	*c.* 50	Caudolateral	High (29)
Stahleckeria	*c.* 600	Flaring, robust, *c.* 20°	5·33	> 1	*c.* 1	50	Caudolateral	High (34)
Placerias	*c.* 600	Slender, narrow, *c.* 15°	5·73	> 1	> 1	48	Caudolateral	High (40)

iliac blade [total iliac length (IL)/iliac height (IH) = 1·33–1·5], considerable expansion of the preacetabular iliac process (IA/IL is 0·5, Table 2), and a wide manus with fused phalanges. The usual postural dichotomy was present in *Cistecephalus*, with the humerus in a lateral and abducted position, and the femur adducted with the knee close to the body (Cluver 1978). However, a distinctive feature of the vertebrae is the high angles of the zygapophyses throughout the vertebral column. This suggests a much reduced or nearly absent lateral undulation, though dorsoventral flexion and axial rotation were both possible. All the cranial and postcranial characteristics provided strong evidence for digging and burrowing activities (Cluver 1978).

Another aberrant Late Permian form was *Kingoria* (SL is 114 mm; Cox 1959). The most distinctive feature of *Kingoria* is its pelvic girdle and the hindlimb (King 1985). The iliac blade is almost triangular (IL/IH is 2·6) with a considerable preacetabular iliac process (IA/IL is 0·5) and a very small postacetabular iliac process (IP/IL is 0·05). The ischium is stout, plate-like, and caudoventrally extended. The femoral head occupies the cranioproximal corner and is offset from the main body of the bone. Acetabular-femoral articulation and muscle restoration suggested that in *Kingoria*, the hindlimb was adducted with the femur turned in towards the body (King 1985). The latter feature allowed the hindlimb to be retracted by simple rotation of the femoral head, so that the retraction component of the gait was more significant than in other dicynodonts, such as *Robertia* and *Dicynodon* (King 1985). Although not much of the forelimb was known, the gleno-humeral articulation suggested that the humerus was still in an abducted/sprawling position.

King (1981*b*) studied the functional anatomy of *Dicynodon* (*D. trigonocephalus*, SL *c.* 160 mm) in considerable detail. The forelimb was in an abducted position and provided postural support and locomotion through protraction-retraction and rotation of the humerus. The hindlimb was in a semi-erect or parasagittal position through most of the stride, and could produce powerful but slow locomotory force. Lateral undulation of the vertebral column was much reduced whereas long axis rotation of the proximal limb bones was pronounced in *Dicynodon*. Other distinctive features of *Dicynodon* include a massive deltopectoral crest (dpc is 60 per cent of HL), which contrasted with that of other Permian dicynodonts (where dpc is ≤45 per cent HL, Table 1), considerable expansion of the iliac blade (IL/IH is 2·61) with a large preacetabular iliac process (IA/IL is 0·5) and a small postacetabular iliac process (IP/IL is 0·2), a robust trochanter major (tm is 37 per cent of FL), and five sacral vertebrae (Table 2).

The five Triassic forms examined were large dicynodonts ranging in adult SL from 110 to 600 mm. As

TABLE 2. Characteristic features in the pelvic girdle and hindlimb of the dicynodont genera examined. Asterisk (*) indicates that the dicynodonts were foragers or browsers, or digging for roots, stems and rhizomes.

	SVC	IA/IL	IP/IL	IL/IH	Iliac features	Acetabular orientation	Trochanter major (tm = % FL)	FMW-L/ FMW-S	Inferred life habits
Eodicynodon	3	0·11	0·4	0·82	Small, long neck	Craniolateral	Moderate (*c.* 30)	1·01	?Diggers
Robertia	2 or 3	0·35	0·43	1	High	Craniolateral	Moderate (30)	–	–
Diictodon	3 or 4	0·4	0·23	1·24	Wide, concave laterally	Slightly caudolateral	Distally extended (*c.* 35)	1·31	Burrower
Pristerodon	4	0·4	0·2	1·24	Wide	Slightly caudolateral	Moderate (30)	*c.* 1·21	–
Cistecephalus	3	0·5	0·25	1·42	–	Craniolateral	Confined to the cranioproximal corner	*c.* 1·31	Fossorial
Kingoria	4 or 5	0·5	0·05	2·6	Triangular	Craniodorsally extended; lateral	Robust (36)	–	–
Dicynodon	5	0·5	0·21	2·61	?Notch on dorsal border	Open dorsally, lateral	Robust (37)	1·42	Generalized
Lystrosaurus	6	0·5	0·3	1·83	Notched dorsal border	Lateral	Moderate (30)	1·35	Semi-aquatic and diggers
Kannemeyeria	6	*c.* 0·5	0·15	2	Expanded, plate-like	Lateral	Robust (37)	2·08	Generalized*
Wadiasaurus	5 or 6	0·52	0·19	*c.* 2	Subtriangular	Caudolateral	Robust (39)	2·04	Generalized*
Stahleckeria	6	0·5	0·18	1·7	Preacetabular region bent outwards	Caudolateral	Robust (38)	*c.* 2	Generalized*
Placerias	7+	*c.* 0·44	0·11	1·2	Extreme vertical expansion	Caudolateral	Robust (37)	*c.* 2	Generalized*

shown above, *Lystrosaurus* was quite distinctive and probably had a combined semi-aquatic and digging habit. The other Triassic dicynodonts such as *Kannemeyeria*, *Wadiasaurus*, *Stahleckeria*, and *Placerias* were large, robust animals with SL ≥ 400 mm, and exhibited somewhat similar postcranial anatomy, as evidenced in Tables 1–2. The humerus is robust with a large proximal expansion (HPW/HDW ≥ 1) and a massive deltopectoral crest (dpc is *c.* 45 per cent HL for *Kannemeyeria* and *c.* 50 per cent HL for the rest). The ulna has a high olecranon process (ol pr ≥ 30 per cent UL), except in *Kannemeyeria*, which has a weak to moderate olecranon process. However, the radius is massive in all the genera examined. The humerus was still in an abducted position orientated caudolaterally. As in *Diictodon*, the caudolateral orientation of the humerus in the Triassic forms reduced the transverse component of the propulsive thrust. The presence of a high olecranon process suggests that forearm extension and flexion played an important role in locomotion.

The degree of expansion of the preacetabular iliac process is more or less similar (IA/IL is 0·5), except for *Placerias* (IA/IL *c.* 0·44). In contrast, there is considerably less expansion of the postacetabular ilium (Table 2). The ischium in the Middle Triassic genera forms a triangular flange, which is bent inwards (suggesting a large origination site for M. ischio-trochantericus) and has a prominent median ridge on the lateral surface for attachment of M. flexores tibiales. The femur is characterized by a dorsoventrally flattened midshaft (FMW-L/FMW-S ≥ 2), and a robust trochanter major (tm = 35 per cent FL, except for *Lystrosaurus*, in which it is 30 per cent FL). Similar flattening is also observed in the tibia of the Triassic dicynodonts. Muscle restoration and osteological evidence suggest that the hindlimb was almost fully adducted and that locomotion involved a wide protraction-retraction arc.

PHYLOGENETIC PERSPECTIVES

Phylogenetic analyses

A matrix consisting of 12 dicynodont taxa and 27 morphological characters was constructed (Table 3) and subjected to a maximum parsimony analysis using PAUP 4.0b10 (Swofford 2000) and PAST (Hammer *et al.* 2001). Multistate characters were treated as unordered and all characters were weighted equally. Unknown/missing characters were coded as '?'. The branch and bound search algorithm was used, and 1000 random addition sequence

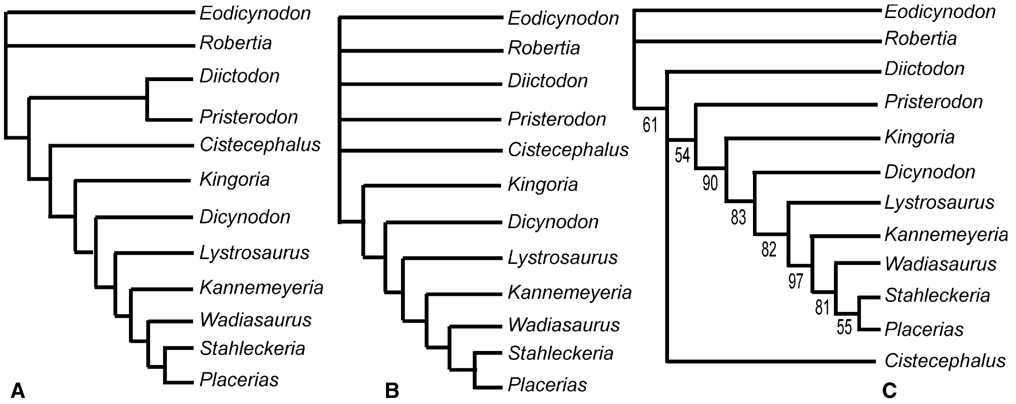
TABLE 3. Data matrix used in the phylogenetic analysis. The characters are discussed in the Appendix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Eodicynodon	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Robertia	1	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0
Diictodon	1	0	1	0	2	1	1	1	1	0	1	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	2
Pristerodon	1	1	1	0	1	0	0	1	2	0	1	0	1	0	1	1	1	0	1	0	1	1	1	0	0	1	2
Cistecephalus	1	2	1	0	2	0	0	0	3	0	0	0	0	1	0	0	2	0	2	1	0	1	1	0	0	0	0
Kingoria	1	2	1	0	2	0	0	1	1	0	1	1	1	1	?	0	1	?	?	1	2	2	1	2	?	1	1
Dicynodon	1	2	1	1	2	2	1	1	2	0	2	1	1	1	2	0	1	1	1	1	1	2	1	2	0	2	1
Lystrosaurus	1	2	1	1	2	2	1	1	2	0	2	1	1	1	0	0	2	1	1	1	1	1	2	0	0	3	1
Kannemeyeria	1	2	1	2	2	2	1	1	2	1	3	2	1	1	1	1	2	1	1	1	2	2	2	2	1	3	1
Wadiasaurus	1	2	1	2	2	2	1	1	2	1	3	2	1	1	1	1	2	1	2	1	2	2	2	2	1	2	2
Stahleckeria	1	2	1	2	2	2	1	1	2	1	3	2	1	1	1	1	2	1	2	1	2	1	2	2	1	3	2
Placerias	1	2	1	2	2	2	1	1	2	1	3	1	1	1	1	1	2	1	2	0	2	1	2	2	1	4	2

replicates were run to prevent the search becoming trapped in a local tree-length minimum. Although cranial features such as suture pattern, presence or absence of certain bones, features of mandible and palate were the primary foci of previous phylogenetic analysis (King 1988; Angielczyk 2001; Maisch 2001; Surkov and Benton 2004), the present analysis includes both cranial and postcranial characters. Many of the postcranial characters have not been used in previous studies, and the basal dicynodont *Eodicynodon* (Rubidge *et al.* 1994) was used as the outgroup. The accelerated transformation (ACCTRAN) option was used for character-state optimization.

The analysis recovered three most parsimonious trees (MPTs), each with a length of 69 steps, a consistency index (CI) of 0·68, a homoplasy index (HI) of 0·32, and a retention index (RI) of 0·76. The MPT that best matches the stratigraphical ranges of the taxa, with minimum inference about unrecorded stratigraphical distributions (Skelton and Smith 2002), is shown in Text-figure 9A. A strict consensus of the three MPTs is shown in Text-figure 9B, revealing that there is no agreement on the positions of *Robertia*, *Diictodon*, *Pristerodon* and *Cistecephalus*. A bootstrap analysis (1000 replicates) shows moderate to strong support (Text-fig. 9C) for the fully resolved clades seen in the strict consensus (Text-fig. 9B). The topological result is generally compatible with those of previous workers such as King (1988), Angielczyk (2001), Maisch (2001), and Surkov and Benton (2004), but there are some important differences.

Although *Robertia* and *Diictodon* have been considered closely related taxa based on cranial characters (King 1988; Angielczyk 2001), Ray and Chinsamy (2003) noted considerable differences between their postcrania. These differences lie in the gleno-humeral articulation, iliac proportions, sacral vertebral count (SVC), and the degree of femoral adduction (Tables 1–2). In the present analysis,



TEXT-FIG. 9. Cladograms showing interrelationships of selected Late Permian and Triassic dicynodonts, based on cranial and postcranial characters (Table 3; Appendix). A, one of three most parsimonious trees. B, strict consensus tree. C, bootstrap tree with bootstrap values > 50 per cent shown.

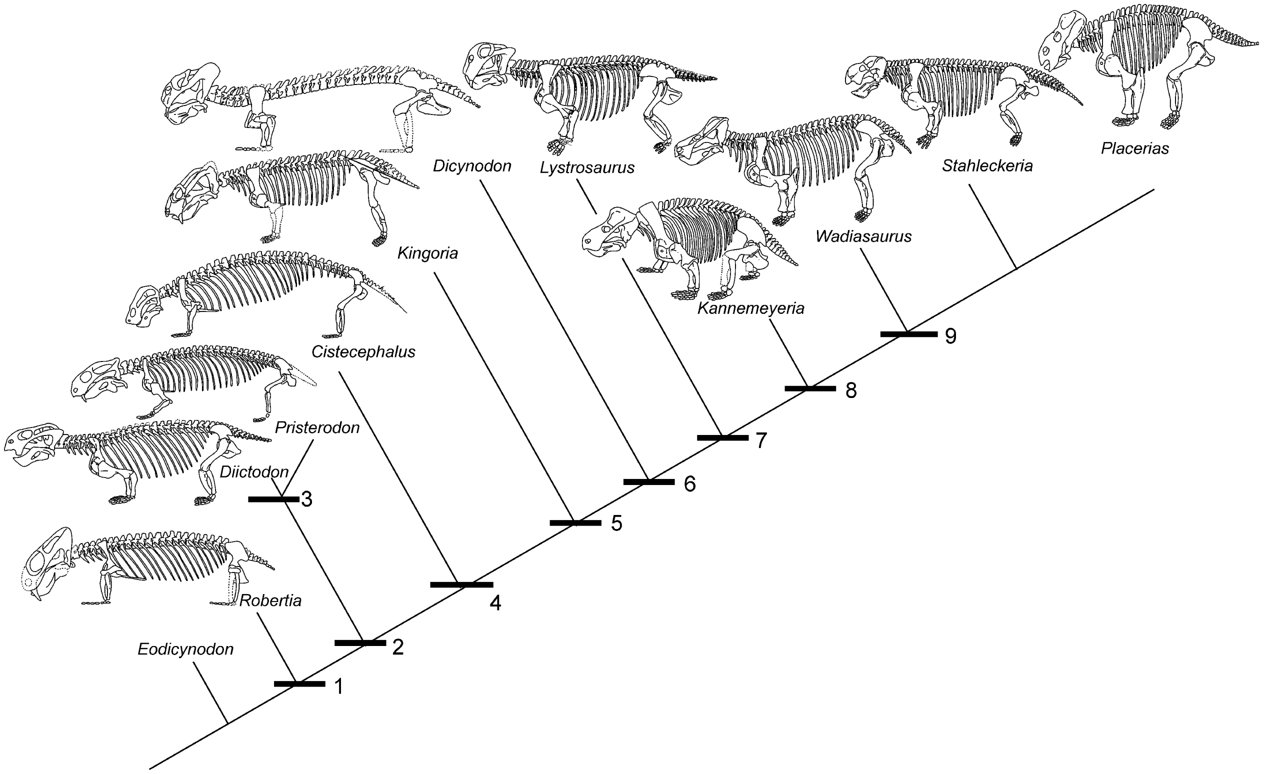
Robertia is considered more basal than *Diictodon*. *Diictodon* and *Pristerodon* grouped together on the basis of certain postcranial characters such as the caudolaterally orientated gleno-humeral and acetabular articulations (Text-fig. 10). Thus, the traditional monophyly of *Diictodon* and *Robertia* is questioned here, echoing the suggestion of Surkov and Benton (2004). In addition, *Kingoria* and *Cistecephalus* do not group together. The former is more advanced than the latter, a position supported by character states such as absence of the cleithrum, tm > 35 per cent of FL, and the lateral orientation of the acetabulum. Surkov *et al.* (2005) also noted a basal position for *Cistecephalus* with respect to *Kingoria*.

The monophyly of all Middle Triassic Kannemeyeriiformes is apparent from the cladograms (Text-fig. 9) and is characterized by a dpc of 41–50 per cent of HL, a caudolateral gleno-humeral orientation, $\mathrm{IP/IL} \leq 0{\cdot}2$, and a flattened femoral midshaft. *Kannemeyeria* is considered here to be more basal than *Wadiasaurus*. The latter taxon shares with the stahleckeriids (*sensu* Maisch 2001) a strongly developed or high olecranon process and a caudolaterally orientated acetabular articulation.

Evolutionary trends

Mapping of the postcranial character-state distributions onto the computed phylogenetic framework of the selected dicynodonts (Text-fig. 10) revealed certain important evolutionary trends in the dicynodont postcranial skeleton. These included changes in the forelimb and hindlimb articulations, the positions of muscular origins and insertions, the proportions of various bones, and the structure of the axial skeletons.

The most informative characters in terms of low homoplasy level (i.e. CI and RI are 1·00 and $\geq 0{\cdot}67$, respectively) are cranial characters 4, 6, 8 and 10–12, and postcranial characters 14, 15, 17, 18, 23–25 and 27. These



TEXT-FIG. 10. This cladogram shows the evolution of postcranial skeleton. The synapomorphies are as follows: 1, premaxilla fused, vomer fused, stapedial foramen absent (1, 3, 8); 2, moderately developed humeral head, $0{\cdot}4 < \mathrm{IP/IL} > 0{\cdot}2$ (17, 21); 3, gleno-humeral and acetabular articulations caudolaterally orientated (16, 27); 4, coracoid plate reduced, $\mathrm{IA/IL} \geq 0{\cdot}5$ (14, 20); 5, cleithrum absent, tm > 35 per cent, and acetabulum laterally orientated (13, 24, 27); 6, massive radius (RMW/RL = high), moderate olecranon process (18, 19); 7, strongly developed humeral and femoral heads, and SVC = 6 (17, 23, 26); 8, dpc = 41–50 per cent of HL, $\mathrm{IP/IL} \leq 0{\cdot}2$, gleno-humeral orientation caudolateral, and $\mathrm{FMW\text{-}L/FMW\text{-}S} \geq 0{\cdot}2$ (15, 16, 21, 25); 9, high olecranon process, acetabular articulation caudolaterally orientated (19, 27). Sources for skeletal reconstructions of *Robertia*, *Cistecephalus*, *Dicynodon*, *Kannemeyeria* and *Placerias* are Pearson (1924*a*, *b*), Camp and Welles (1956), Cluver (1978), and King (1981*a*, *b*). The skeletal reconstruction of *Kingoria* is based on King (1985). A reconstruction of *Eodicynodon* is not offered because of insufficient published material. The number of each character in the data matrix is given in parentheses.

characters document major patterns of skeletal evolution in the dicynodonts. The cranial characters suggest an increase in the cross-sectional area of the jaw muscles through enlargement of the temporal fenestra, as well as strengthening of the symphyseal region of the mandible to produce a more efficient masticatory system. The postcranial characters, on the other hand, include reduction of the coracoid plate, robustness of the deltopectoral crest, a strongly developed proximal humeral surface, robustness of the radius, a strongly developed femoral head, robustness of the trochanter major, flattening of the femoral midshaft, and a caudolateral acetabular orientation.

The ancestral condition in the dicynodont pectoral girdle and forelimb articulation includes the presence of a cleithrum and a deltopectoral crest that constituted about 40 per cent of HL in the Permian forms, and a laterally orientated humerus suggestive of an abducted forelimb posture. On the line to *Placerias*, changes in the pectoral girdle and forelimb included loss of the cleithrum in the later forms, increasing robustness of the deltopectoral crest, which changed to *c.* 50 per cent HL in the Triassic forms (Text-fig. 11), a change in humeral orientation from lateral to caudolateral, increasing prominence and asymmetry of the radioulnar facet, and increasing robustness of the radius and the ulna.

On the other hand, the ancestral condition of the dicynodont pelvic girdle and hindlimb involved an unexpanded ilium with two or three sacral vertebrae, small sites of origin for M. ilio-femoralis and M. ilio-tibialis, and a pubo-ischiadic plate lacking a well-developed origination site for M. ischio-trochantericus. The most obvious change in the dicynodont ilium was shape change in the form of expansion of the preacetabular process (IA/IL *c.* 0·3–0·5) and craniocaudal expansion (with certain exceptions) such that IL/IH changes from *c.* 1 to 2 in the later dicynodonts (Text-fig. 11). Preacetabular expansion of the ilium resulted in the cranial expansion of the origination sites of M. ilio-femoralis and M. ilio-tibialis, presumably correlated with enlargement of these protractor muscles. Similar increase in the physiological cross-sectional areas, increase in the moment arm and force-generating capability of the protractor muscles was also noted in the theropod dinosaurs (Hutchinson 2001). Other evolutionary changes in the pelvic girdle included decrease of the postacetabular iliac process (IP/IL *c.* 0·4–0·11), reduction of the flat, plate-like pubis to form a small pubis with a rod-like cranial process, and a change in acetabular orientation from lateral to caudolateral.

On the line to *Placerias*, hindlimb evolution involved a change in femoral head position from cranioproximal to dorsally pronounced head that was offset from the shaft, enlargement of the trochanter major from about 30 per cent of FL in basal forms to nearly 40 per cent (Text-fig. 11), and flattening of the femoral midshaft (FMW-L/FMW-S changed from *c.* 1·2 to 2). The pronounced femoral head and trochanter major of later dicynodonts suggested the presence of powerful retractors and protractors in comparison with the Permian forms.

Changes associated with the axial skeleton included a reduction in lateral undulation and an increase in dorsoventral flexion of the dorsal vertebrae, especially near the sacral region. SVC also increased from two or three in *Eodicynodon* to more than seven in *Placerias* (Table 2).

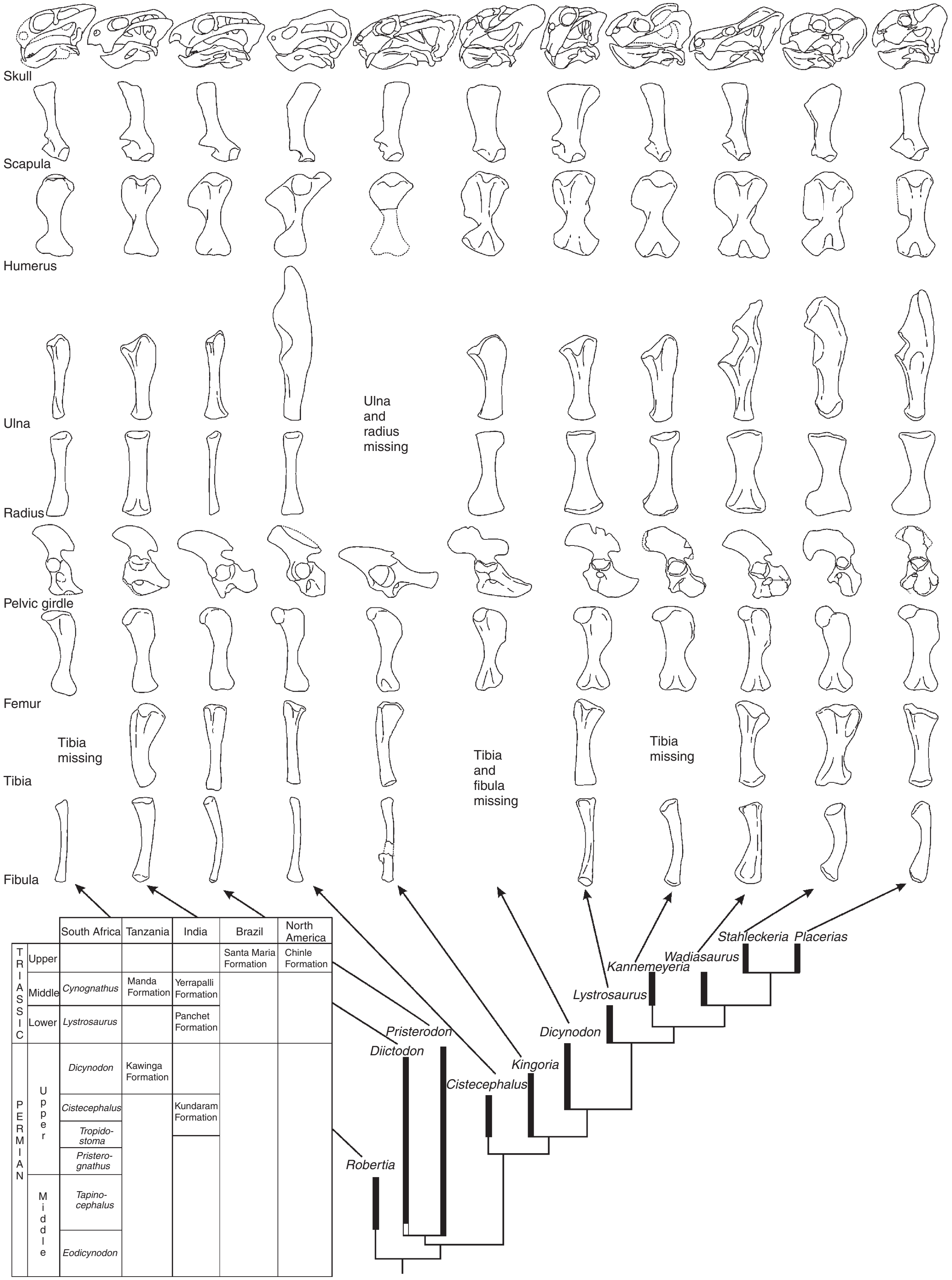
Discussion

The ancestral condition of the postcranial skeleton as seen in *Eodicynodon* and *Robertia* constituted a sprawling posture with the fore- and hindlimbs in an abducted position, which in advanced Permian and Triassic forms gave way to a postural dichotomy in which the forelimbs were still in an abducted position, but the hindlimbs had attained a semi-erect or adducted stance.

Although movement in general was related to depression and elevation of the forelimb, extension and flexion of the crus, and protraction-retraction of the hindlimb, evolution of the postcranial skeleton of the dicynodonts involved a change towards a more upright hindlimb posture with the body held well off the ground. The expansion of the sacrum, suggested by the increasing sacral vertebral count, together with the more steeply inclined pre- and postzygapophyses, suggested stiffening of the trunk in the later dicynodonts, especially in the Triassic taxa. Pronounced lateral undulation was probably replaced by pronounced dorsoventral flexion. Such reduction in the lateral movement of the vertebral column in the later dicynodonts may have been associated with the nearly erect, adducted hindlimb posture (Carrier 1987) in dicynodonts.

The dorsoventral flattening of the femora and the tibiae in the plane of knee extension and flexion, as evident from the elliptical cross-section of these bones in the Triassic dicynodonts, suggests enhanced resistance to mediolateral bending (Blob 2001). This could be correlated with the change from sprawling to a more upright, parasagittal stance, in which the loading regime on the limb bones changed from essentially torsion to bending (Blob 2000). The posture of the later dicynodonts was probably similar to the ‘high walk’ of crocodilians (Gatesy 1991) and showed varying degrees of femoral adduction.

To complement the nearly adducted hindlimb posture, the forelimb took on a more parasagittal orientation, as evidenced by the caudolateral orientation of the glenoid fossa, which reduced the lateral component of the propulsive force, though still maintaining the sprawling posture. This type of gleno-humeral articulation, with limited


Skull
Scapula
Humerus
Ulna
Ulna and radius missing
Radius
Pelvic girdle
Femur
Tibia
Tibia missing
Tibia and fibula missing
Tibia missing
Fibula
South Africa
Tanzania
India
Brazil
North America
TRIASSIC
Upper
Middle
Lower
PERMIAN
Upper
Middle
Santa Maria Formation
Chinle Formation
Cynognathus
Manda Formation
Yerrapalli Formation
Lystrosaurus
Panchet Formation
Dicynodon
Kawinga Formation
Cistecephalus
Kundaram Formation
Tropidostoma
Pristerognathus
Tapinocephalus
Eodicynodon
Robertia
Diictodon
Pristerodon
Cistecephalus
Kingoria
Dicynodon
Lystrosaurus
Kannemeyeria
Wadiasaurus
Stahleckeria
Placerias

contact between the glenoid and the humerus, probably did not generate much locomotory force (Kemp 1980, 1982; King 1988) and in basal Permian forms was augmented by pectoral girdle movement and lateral undulation of the vertebral column. Even in the later Permian taxa, the ventral curvature of the proximodorsal axis of the humerus, ventrolateral positioning of the distal humeral facets for radial and ulnar articulation, and extension of the trochlea onto the dorsal humeral surface suggested that the humerus was depressed below the level of the glenoid fossa and the body was held relatively well off the ground, especially in comparison with earlier forms such as *Eodicynodon* and *Robertia*.

However, the fore- and hindlimb kinematics varied among the dicynodonts, as suggested by variations in the scapular blade, gleno-humeral and acetabular articulations, and the inferred muscle restorations. In addition, certain specialized life habits can be inferred from the postcranial features. For example, the robust humerus and the strong olecranon process of *Cistecephalus* are suggestive of digging activites. Except for *Eodicynodon* and *Robertia*, all dicynodonts had acquired a nearly adducted hindlimb stance, and the variations noted in their pelvic and hindlimb morphology were the result of diversification within this mechanical context, as suggested by Ray and Chinsamy (2003).

In summary, dicynodont posture in general and hindlimb stance in particular may be regarded as forming a wide spectrum ranging from substantial limb abduction in the basal, Permian forms to almost total limb adduction in the later Triassic forms. As is evident from the cladogram (Text-fig. 10), several significant anatomical and functional transitions on line to the Triassic forms were distributed across many nodes rather than being concentrated in only one or two nodes. The changes occurred in an incremental fashion and although the present study is in no way exhaustive, inclusion of all valid dicynodont genera would be expected to reveal an even more gradual transformation.

CONCLUSIONS

Inferred muscle reconstruction and functional morphology of the dicynodonts were drawn from two Triassic dicynodont genera: *Wadiasaurus* and *Lystrosaurus*. *Wadiasaurus* had a near sagittal articulation of the humerus, an efficient forearm movement (extension and flexion), a reduced/restricted lateral undulation of the vertebral column, and a semi-erect, adducted stance of the hindlimbs. Certain postcranial features of *Lystrosaurus* are distinctive, including a wide scapular blade, a lateromedially broadened antebrachium forming a paddle-like structure, and segmentation of M. ilio-femoralis with pronounced sites of insertion on the ventral femoral surface. The paddle-like distal forelimb of *Lystrosaurus* is suggestive of a specialized lifestyle, possibly a combination of digging and swimming habits.

The relationships among 12 dicynodont genera were analysed, yielding three most parsimonious trees, which are used as a framework to examine the evolution of posture in Triassic dicynodonts. Evolutionary changes in the pectoral girdle and forelimb morphology of the dicynodonts included increasing robustness of the deltopectoral crest, a change in humeral orientation from lateral to caudolateral, increasing prominence and asymmetry of the radio-ulnar facet, and increasing robustness of the radius and the ulna. Changes in the pelvic girdle and hindlimb structure included preacetabular iliac expansion resulting in increased cross-sectional area for M. ilio-femoralis and M. ilio-tibialis, a decrease in postacetabular iliac expansion, increased dorsoventral iliac expansion, a change in the shape of the pubis from flat and plate-like to small and rod-like with a cranial process, a change in acetabular orientation from lateral to caudolateral, a shift of the femoral head from cranioproximally positioned to dorsally pronounced and offset from the body, increasing robustness of the trochanter major, and increasing flattening of the femoral midshaft. Changes in the axial skeleton included stiffening of the trunk to reduce lateral undulation, increasing dorsoventral flexion, and increasing sacral vertebral count, which can be correlated with the expansion of the preacetabular iliac process.

The evolution of the dicynodont postcranial skeleton involved a shift towards more upright hindlimb morphology with the body held well off the ground. Although a postural dichotomy with the forelimbs in an abducted posture still existed, the lateral component of the propulsive force and the degree of lateral undulation of the vertebral column were reduced to complement the upright or nearly adducted hindlimb stance.

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TEXT-FIG. 11. An overview of the variations in the scapula, humerus, ulna, radius, pelvic girdle, femur, tibia, and fibula of the dicynodonts examined (except *Eodicynodon*) from left to right: *Robertia* (King 1981*a*), *Diictodon* (Ray and Chinsamy 2003), *Pristerodon*, *Cistecephalus* (Cluver 1978), *Kingoria* (King 1985), *Dicynodon* (*D. trigonocephalus*: King 1981*b*), *Lystrosaurus*, *Kannemeyeria*, *Wadiasaurus*, *Stahleckeria*, and *Placerias* (Camp and Welles 1956); the skeletal elements are reproduced at the same absolute length and mapped onto a stratigraphically calibrated cladogram for comparative purposes. Solid black bars indicate known stratigraphic ranges of the dicynodont genera, whereas the white bar indicates a ghost lineage.

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APPENDIX

Dicynodont material studied

Robertia: SAM-PK-11885, 11782, cast of nearly complete skeletons from the *Tropidostoma* Assemblage Zone, Beaufort Group, South Africa; Late Permian.

Diictodon: SAM-PK-K1633a, K7725, K6716a, 10166, K5477a, b, GS-RMS214, collected from the *Tropidostoma* and *Cistecephalus* assemblage zones, Beaufort Group, South Africa; Late Permian.

Pristerodon: SAM-PK-10161, 10141, K9997, from the *Cistecephalus* Assemblage Zone, South Africa; ISIR 209, complete skull from the Kundaram Formation, Pranhita-Godavari basin, India; Late Permian.

Cistecephalus: GS K224, SAM-PK-10665, K5513, K6814, from the *Cistecephalus* Assemblage Zone, South Africa; Late Permian.

Dicynodon: SAM-PK-K6580, 12002, K138, K1687, K2680, from the *Dicynodon* Assemblage Zone, Beaufort Group, South Africa; Late Permian.

Lystrosaurus: SAM-PK-K8083, K1371, K1165, 1415, from the *Lystrosaurus* Assemblage Zone, South Africa; GSI types 17863, 17860, 17864, 17846, 17847, ISIR 766, 767 from the Panchet Formation, India; Early Triassic.

Kannemeyeria: SAM-PK-K4826, 11269, 2771, from the *Cynognathus* Assemblage Zone, Beaufort Group, South Africa; Middle Triassic.

Wadiasaurus: ISIR41/41–42, 171, 172/0–15, 173/0–5, 174/0–1, 175/0–417, from the Yerrapalli Formation, Pranhita-Godavari Basin, India; Middle Triassic.

Characters used in phylogenetic analysis

1. Premaxillae (unfused = 0, fused = 1). Except in *Eodicynodon*, the premaxillae were indistinguishably fused in all the dicynodont taxa examined. In *Eodicynodon* the premaxillae are unfused and separated by a suture (King 1988; Rubidge 1990).

2. Maxillary postcanine teeth (laterally placed = 0, medially deflected = 1, absent = 2). In *Eodicynodon* (*E. oosthuizeni*) the maxillary postcanine teeth were more laterally placed than in any other dicynodont (Rubidge 1990). In *Robertia* and *Pristerodon* the maxillary teeth are obliquely arranged, in which the mesial end was more medially placed and the distal end was positioned laterally. In all other dicynodonts examined, postcanine teeth are absent.

3. Vomers (unfused = 0, fused = 1). Most basal synapsids, including *Eodicynodon*, possess an unfused pair of vomers with a midline suture. In all other dicynodonts the vomer is completely fused.

4. Sagittal crest (absent = 0, low = 1, high = 2). In lateral profile of the crania a distinct sagittal crest, measured above the dorsal orbital margin (*sensu* Vega-Dias *et al.* 2004) and formed by the postorbital and parietal, is found in the Triassic dicynodonts examined such as *Wadiasaurus*, *Kannemeyeria*, *Placerias*, and *Stahleckeria* (coded as 2). This feature is absent in *Eodicynodon*, *Robertia*, *Diictodon*, *Pristerodon*, *Cistecephalus*, and *Kingoria* (coded as 0) and very weakly developed in *Dicynodon* and *Lystrosaurus* (coded as 1).

5. Mandibular teeth (present on the dorsal surface of the dentary = 0, on medial swelling = 1, absent = 2). In basal synapsids and *Eodicynodon*, teeth are present on the dorsal surface of the dentary (Rubidge 1984, 1990), whereas in *Robertia* and *Pristerodon*, a short tooth row is present on the medial swelling of the dentary. In all other dicynodonts, mandibular teeth are absent (coded as 2).

6. Mandibular symphyseal region in dorsal view (small with short dentary tables = 0, slightly upturned, elongate and dentary table with groove-like morphology = 1, well developed, elongate with grooved dentary tables bounded by low ridges = 2). The anterior/cranial dorsal surface of the dentary where the two mandibular rami meet constitutes a small, rounded depression bounded on either side by a short 'dentary table' (*sensu* Crompton and Hotton 1967) in *Eodicynodon* (Rubidge 1990), *Cistecephalus*, and *Kingoria* (coded as 0). Although *Pristerodon* has relatively expanded dentary tables, the dorsal symphyseal area is small (coded as 0). In *Robertia* and *Diictodon*, this area is slightly upturned and elongate and the dentary table has a groove-like morphology (coded as 1) whereas in all other dicynodonts, it is well developed and elongate with the dentary table having a groove bounded by low ridges.

7. Labial fossa (absent = 0, present = 1). The labial fossa bounded by the palatine, the jugal and the maxilla served as a passage for a blood vessel (Cluver 1971) and is absent in most of the Permian forms other than *Diictodon* and *Dicynodon*. In the former the labial fossa is not strongly developed (Sullivan and Reisz 2005). It is, however, well developed in *Dicynodon* and other Triassic forms examined in this study.

8. Stapedial foramen (present = 0, absent = 1). Although the form of the stapes is variable in the various skulls of *Eodicynodon*, the stapes is pierced by a large and nearly complete stapedial foramen (Cluver and King 1983; Rubidge 1990). A fully enclosed stapedial foramen is also present in *Cistecephalus*, *Kawingasaurus* (Cox 1972) and *Endothiodon* (Ray 2000). However, the last two genera are not included in this analysis. The presence of a stapedial foramen (coded as 0) is considered to be the basal condition in dicynodonts (King 1988).

9. Interpterygoidal vacuity (short = 0, long = 1, long and reached palatal exposure of palatines = 2, absent = 3). The interpterygoid vacuity is short in proportion to the basicranial axis in *Eodicynodon* (Rubidge 1990), whereas it is relatively long in *Robertia*, *Diictodon*, and *Dicynodon*, and reaches the palatal exposure of the palatines in other dicynodonts examined. However, in *Cistecephalus* this vacuity is absent, a condition attributed to strengthening of the skull (Cluver 1978).

10. Postfrontal (present = 0, absent = 1). Although the size of the postfrontal may vary, this bone is present in all the Permian forms examined. A narrow and elongated postfrontal is also present in the Early Triassic *Lystrosaurus*, but the postfrontal is absent in all other Triassic genera examined.

11. Parietal (widely exposed = 0, partially overlapped by postorbital = 1, nearly completely overlapped but not crest-like = 2, completely overlapped and crest-like = 3). Dorsal surface exposure of the parietals, bounded on either side by the postorbitals, varies in dicynodonts. In *Eodicynodon* (Rubidge 1990) and *Cistecephalus*, they are widely exposed (coded as 0), whereas in *Robertia*, *Diictodon*, *Pristerodon* and *Kingoria* the postorbital partially

overlaps the parietals. In *Dicynodon* and *Lystrosaurus* the parietal is almost completely overlapped by the postorbitals but is not crest-like, in contrast to other Triassic forms examined.

12. Ratio between interorbital (IO) and intertemporal (IT) widths [very low (*c.* 1) = 0, moderate (*c.* 2) = 1, high (*c.* 3) = 2]. The IO/IT ratio is *c.* 1 in all Permian forms except *Kingoria* (1·7) and *Dicynodon* (*c.* 1·5), indicating that in these taxa the width of the interorbital region is either equal or slightly more than that of the intertemporal region. In *Kingoria*, *Dicynodon*, and *Lystrosaurus*, this ratio is higher (1·5–2) than that of the Permian forms. In the Triassic forms IO/IT is high (= 3), except that of *Placerias* (1·6).

13. Cleithrum (present = 0, absent = 1). Presence of a cleithrum is the basal condition in dicynodonts (Cluver and King 1983; King 1988) and was probably present in the common ancestor of all anomodonts (Angielczyk 2001). Presence of a cleithrum is uncertain in *Eodicynodon* (Rubidge *et al.* 1994) and is coded as '?'. However, it is present in *Robertia*, *Diictodon*, and *Cistecephalus* but is absent in all other dicynodont genera examined.

14. Coracoid plate (flaring = 0, reduced = 1). A craniocaudally flaring coracoid plate is noted in *Eodicynodon* (Rubidge *et al.* 1994), *Robertia* (King 1981*a*), *Diictodon* (Ray and Chinsamy 2003), and *Pristerodon* (pers. obs.). By comparison, the coracoid plate is much reduced in all other dicynodonts.

15. Deltopectoral crest (dpc ≤ 40 per cent of HL = 0, 41–50 per cent = 1, > 50 per cent = 2). The deltopectoral crest, which was the site of insertion of the glenoid rotating muscles such as M. pectoralis and M. deltoideus, extends a variable distance from the humerus in dicynodonts. In *Eodicynodon*, *Robertia*, *Diictodon*, *Cistecephalus*, and *Lystrosaurus* it constitutes ≤ 40 per cent of HL (coded as 0). No complete humerus of *Kingoria* is known (King 1985), so this character was coded as '?'. Except in *Dicynodon*, the deltopectoral crest ranges from 40 to 50 per cent of HL. In *Dicynodon*, the deltopectoral crest is particularly robust and massive (King 1981*a*; pers. obs.), and constitutes about 60 per cent of HL.

16. Gleno-humeral orientation (lateral = 0, caudolateral = 1). The gleno-humeral articulation in some Permian forms, such as *Eodicynodon* (Rubidge *et al.* 1994), *Robertia* (King 1985), and *Cistecephalus* (Cluver 1978) is more laterally orientated than in other dicynodonts, in which the humerus is more caudolaterally orientated.

17. Proximal humeral articular surface/head (slightly convex = 0, expanded and more dorsally placed = 1, strongly developed = 2). The proximal humeral articular surface in Permian dicynodonts such as *Eodicynodon* and *Robertia* is a slightly convex area that rolled over the coracoid surface of the glenoid fossa during forelimb movement. This articular surface is more expanded and dorsally placed in *Diictodon*, *Pristerodon*, *Kingoria*, and *Dicynodon*, and forms a distinct head in *Cistecephalus* and in all Triassic dicynodonts.

18. Radius [slender (RMW/RL *c.* 0·1) = 0, massive (RMW/RL = 0·2) = 1]. A re-examination of the radii of all taxa showed that in *Eodicynodon*, *Robertia*, *Diictodon*, *Pristerodon*, and *Cistecephalus* the ratio between the midshaft width and length of the radius (RMW/RL) is about 0·1 and the radius is slender. This is particularly evident when the radii are shown scaled to the same length (Text-fig. 10). However, the radius of *Kingoria* is unknown and this character was coded as '?'. On the other hand, the radii of *Dicynodon*, *Lystrosaurus*, *Kannemeyeria*, *Wadiasaurus*, *Stahleckeria*, and *Placerias* have RMW/RL ≥ 0·2 and are relatively massive.

19. Olecranon process (poorly developed = 0, moderately developed = 1, strongly developed/high = 2). The olecranon process, constituting the site of attachment for the triceps, M. flexor digitorium longus and M. flexor carpi ulnaris, is poorly developed in *Robertia* and *Diictodon*, but moderately developed (*c.* 18 per cent of UL) in *Pristerodon*, *Dicynodon*, *Lystrosaurus*, and *Kannemeyeria*. A strong and high olecranon process constituting *c.* 30 per cent of UL is present in *Cistecephalus*, *Wadiasaurus*, *Stahleckeria*, and *Placerias*.

20. Ratio between length of the preacetabular iliac process and total iliac length (IA/IL < 0·5 = 0, ≥ 0·5 = 1). The ratio IA/IL is less than 0·5 in *Eodicynodon*, *Robertia*, *Diictodon*, *Pristerodon*, and *Placerias* (Table 2). In all other taxa, this ratio is either equal to or greater than 0·5, suggesting enhanced sites of insertion of M. ilio-femoralis, one of the main hindlimb retractors.

21. Ratio between length of the postacetabular iliac process and total iliac length (IP/IL ≥ 0·4 = 0, 0·4 < > 0·2 = 1, ≤ 0·2 = 2). The IP/IL ratio is equal to 0·4 in *Eodicynodon* and greater than 0·4 in *Robertia*, whereas it is much lower in *Kingoria* (0·05, Table 2). In all other Permian forms and in *Lystrosaurus*, the IP/IL ratio varies between 0·4 and 0·2, but in all other Triassic forms it is less than 0·2.

22. Ratio between the length and height of the iliac blade (IL/IH ≤ 1 = 0, 1–2 = 1, ≥ 2 = 2). In *Eodicynodon* and *Robertia*, the IL/IH ratio is equal to or less than 1, whereas in *Diictodon*, *Pristerodon*, *Cistecephalus*, *Lystrosaurus*, *Stahleckeria*, and *Placerias* the ratio varies from 1 to 2. In *Kingoria*, *Dicynodon*, *Kannemeyeria* and *Wadiasaurus* the iliac blade is long in comparison with its height (IL/IH = 2, Table 2) and was coded as '2'.

23. Femoral head (weakly developed = 0, cranioproximal swelling = 1, strongly developed = 2). The femoral head is weakly developed in *Eodicynodon* and *Robertia* (coded as '0'). It forms a slight but distinct cranioproximal swelling in *Diictodon*, *Pristerodon*, *Cistecephalus*, *Kingoria*, *Dicynodon*, and *Lystrosaurus*, and is strongly developed in other dicynodonts examined.

24. Trochanter major (tm ≤ 30 per cent FL = 0, 30–35 per cent = 1, > 35 per cent = 2). The trochanter major, which was the site of insertion of M. ilio-femoralis, is moderately developed (*c.* 30 per cent FL) in *Eodicynodon*, *Robertia*, *Cistecephalus*, *Pristerodon*, and *Lystrosaurus*. However, morphological variations in the trochanter major, such as its confinement to the cranioproximal corner of the femur (*Cistecephalus*) or its distal extension (*Diictodon*), were not considered. A robust trochanter major constituting > 35 per cent FL is present in *Kingoria*, *Dicynodon* and other Middle and Upper Triassic forms.

25. Femoral midshaft cross-section/femoral asymmetry (FMW L/FMW-S < 1·5 = 0, ≥ 2 = 1). Femoral midshaft cross-section or femoral asymmetry (Blob 2001) was defined as the ratio between the two perpendicular axes of maximum and minimum diameter. In the Permian forms and in *Lystrosaurus*, the femoral cross-section is either circular or oval (FMW-L/FMW-S varying from 1·01 to 1·42), but in other Triassic forms the femoral

cross-section is distinctly elliptical and dorsoventrally flattened (FMW-L/FMW-S varying from 2 to 2·08).

26. Sacral vertebral count (SVC ≤ 3 = 0, 4 = 1, 5 = 2, 6 = 3, ≥ 7 = 4). The sacral vertebral count (SVC) is probably 3 in *Eodicynodon* (Rubidge *et al.* 1994). In some dicynodonts the number is uncertain. For example, SVC may be either 2 or 3 in *Robertia* (King 1981*a*), 3 or 4 in *Diictodon*, and 4 or 5 in *Kingoria* (King 1985). In such cases the lower number is accepted. In *Pristerodon* SVC is 4, whereas it is 5 in *Dicynodon* (Table 2). SVC is 6 in the Triassic dicynodonts other than *Wadiasaurus* (SVC = 5) and *Placerias* (SVC = 7+).

27. Acetabular orientation (craniolateral = 0, lateral = 1, caudolateral = 2). In general, the acetabulum is deep, concave and hemispherical, though its orientation is found to differ among dicynodonts and could be related to the degree of adduction of the hindlimbs. Skeletal reconstruction of the studied taxa shows that the acetabulum had a craniolateral orientation in *Eodicynodon* and *Robertia* (King 1981*a*, p. 217, fig. 9B) and *Cistecephalus* (coded as '0'). It had a lateral orientation in *Kingoria*, *Dicynodon*, *Lystrosaurus*, and *Kannemeyeria*, whereas the acetabular orientation was more caudolaterally positioned in other taxa.