

LYSTROSAURUS GEORGI, A DICYNODONT FROM THE LOWER TRIASSIC OF RUSSIA

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ABSTRACT—The postcranial skeleton of *Lystrosaurus georgi* from the lowermost Triassic of the Moscow Basin, Russia, is described for the first time. This species retains contact between the premaxillae and palatine and is characterized by a narrow and elongated ischium, an autapomorphy for this species. Phylogenetic analysis of 27 Permian and Triassic dicynodont taxa using 18 postcranial characters confirms other recent hypotheses, but does not support a close relationship between *Cistecephalus* and *Kingoria*. The low homoplasy level among characters of the pelvis and femur, compared with the shoulder girdle and forelimbs, suggests that the former region documents the pattern of anomodont evolution better than the latter. Analysis of character changes revealed that a general evolutionary trend in the dicynodont postcranium relates to acquisition of semisprawling locomotion.

INTRODUCTION

Lystrosaurus was a famous survivor of the end-Permian mass extinction, and it became widespread in the Early Triassic, when representatives of this genus were the dominant component in tetrapod assemblages worldwide. *Lystrosaurus* remains are abundant in South Africa, and are known from Antarctica, India, and China, with peripheral finds from the European part of Russia (Kalandadze, 1975) and Mongolia (Surkov, 1999). Unfortunately, most descriptions so far have focused only on cranial remains, even though these are generally associated with more or less complete skeletons (Rubidge, 1995; Smith, 1995). Until recently, descriptions of *Lystrosaurus* postcranial material and reconstructions (Young, 1939; Li, 1983; Broom, 1903a; Watson, 1913) were either based on skeletal parts that usually did not relate to the cranial material, or there was no broad comparison with other Permian and Triassic dicynodonts (Watson, 1912; DeFauw, 1986). Here we attempt to remedy this deficiency by presenting a thorough description of the postcranial skeleton of *Lystrosaurus georgi* from Russia, with a consideration of synapomorphic and autapomorphic features among the Permian and Triassic forms.

Institutional abbreviations—**AMNH**, American Museum of Natural History, New York, USA; **BMNH**, Natural History Museum, London, England; **KPM**, Kotelnich Paleontology Museum, Russia; **PIN**, Paleontological Institute, Moscow, Russia; **PMHN**, Muséum National d'Histoire Naturelle, Paris, France; **SAM**, South African Museum, Cape Town, South Africa; **SGU**, collection of Saratov University, Russia; **UT**, Universität Tübingen, Museum und Institut für Geologie und Paläontologie, Tübingen, Germany.

MATERIAL STUDIED

During this research we investigated the following postcranial material from South Africa: *Lystrosaurus* sp. (BMNH R3591), *Lystrosaurus murrayi* (PMNH 1937-13), *Lystrosaurus mccaigi* (SAM-PK-K9958), and *Lystrosaurus* sp. (SAM-PK-K8038), all *Lystrosaurus* Assemblage Zone, Lower Triassic; as well as *Tropidostoma* sp. (SAM-PK-K9960); *Diictodon* sp. (SAM-PK-K1633); *Pelanomodon halli* (BMNH 4067). Material from Russia included: *Dicynodon*(?) sp. (SGU 104/3884), Sokolki Faunal Complex, Upper Permian; *Tropidostoma*(?) sp. (KPM, 20/92), *Deltavjatia vjatkensis* Assemblage Zone, Upper Permian; *Rhinodicynodon gracile* (PIN 1579/50), Donguz Gorizont, Middle

Triassic; and from South America: *Stahleckeria potens* (UT n2), Santa Maria Formation, Middle Triassic; *Kannemeyeria semicephalus* (BMNH 3740). We also referred for comparison to descriptions of postcranial skeletons by Camp and Welles (1956), Cox (1959, 1965; 1972), Watson (1960), Ewer (1961), Cruickshank (1967), Cluver (1978), King (1981a, b; 1985), DeFauw (1986), Rubidge et al. (1994), Bandyopadhyay (1988), and Ray and Chinsamy (2003).

We referred the specimen KPM 20/92 to *Tropidostoma*(?) sp. This postcranium was associated with skull fragments that were tentatively referred to *Tropidostoma*, and the identification of the Russian specimen with this South African genus was retained here.

SYSTEMATIC PALEONTOLOGY

Suborder THERAPSIDA Broom, 1905

Order DICYNODONTIA Owen, 1856

Suborder PRISTERODONTIA Cluver and King, 1983

Family LYSTROSAURIDAE Broom, 1903b

Definition—A monophyletic taxon including the genera *Lystrosaurus* and *Kwazulusaurus*.

Diagnosis—Medium to large dicynodonts with snout strongly extended ventrally; anterolateral corner of snout angular; temporal bar wide; ectopterygoids absent; rugose portion of palatine narrow and small; choana only slightly constricted.

Genus *LYSTROSAURUS* Cope, 1870

LYSTROSAURUS GEORGI Kalandadze, 1975

Diagnosis—Medium-sized lystrosaur with contact between premaxillae and palatine retained; ischiadic plate narrow and elongate, extended posteriorly.

Material—PIN 3447/1, anterior part of the skull and incomplete postcranial skeleton. The postcranial remains consist of 18 vertebrae (axis, two cervicals, ten dorsals, two sacrals, four caudals), nine proximal and some distal fragments of dorsal ribs, the most proximal part of the right scapula, a small fragment of the left coracoid, right humerus and ulna, most of the right ilium and all of the left, and the proximal part of the right ischium, right and left femora, both tibiae, the complete left fibula and distal part of the right fibula, and several scattered bones of the foot—

one astragalus, four metapodials (two of them partly destroyed), one phalanx, three pre-ungular phalanges, and five ungular phalanges.

Geographic Location and Stratigraphy—The specimen was found at the Astashikhinskoye-1 locality which is situated on the eastern part of the Moscow syncline (Fig. 1), on the right bank of the Vetluga River, 0.6 km north of Astashikha village, and 10.5 km north-west of Voskresenskoye village, Nizhny Novgorod region (Tverdokhlebov et al., 2003). The geological section exhibits the lowermost part of the Triassic, the Vokhmian Gorizont, corresponding to the Induan stage (Shishkin et al., 2000), including the Astashikhian and Ryabinskian members.

The rocks of the Astashikhian Member are slightly organic, brown-red clays and contain nodules of light pink marl. There are some horizontal beds of bluish-gray silt and a bed, which is of uniform thickness, of rust-coloured, fine-grained sand. The Ryabinskian Member is represented by sandy-conglomeratic deposits, which transgressively overlie the Astashikhian clays. They consist of greenish-gray, brownish-red, cross-bedded sand layers with conglomeratic and sandstone lenses, which are more frequent in the lower part. The whole section is 18.5 m thick (Fig. 1; Lozovskiy, 1983).

The skeleton of *Lystroraptor georgi* was found by G. I. Blom in 1958 in the brown-red clays at the base of the Astashikhian section and it was initially referred to the genus *Dicynodon* (Blom, 1968) until Kalandadze's (1975) re-evaluation. Later, Lozovskiy (1983) proved the age of this section by discovery of

Early Triassic ostracods, conchostracans, and indeterminate bivalves in the *Lystroraptor*-bearing beds. From the base of the overlying Ryabinskian Member, Ochev (1992) discovered the distal part of a (?) *Lystroraptor* femur together with *Tupilakosaurus* vertebrae.

DESCRIPTION

Skull—The anterior part of the skull remains (Fig. 2) suggest a total length of about 180 mm. Remains of the skull suggest that it was generally similar to other *Lystroraptor* specimens. The snout is short, wide, slightly convex, and with a small midline ridge on the dorsal surface of the premaxillae. The angle between the dorsal surface of the snout and the temporal part of the skull is about 120°. The orbits are large, and rise somewhat above the skull roof. There is a prominent thickening on the anterodorsal edge of the orbits, evidence of lateral projection of the prefrontals. The tusks are rather large, their maximum diameter being 11 mm. The palatine contacts the premaxillae, pterygoid, and maxilla.

Vertebral column—The vertebral column is disarticulated, and most of the vertebrae have lost their neural arches.

The axis is very robust and has a massive dens (Fig. 3A–C; d), which is 26 mm wide and inclined at an angle of 18° to the longitudinal axis of the centrum. The dens is semicircular in dorsal view. It is not separated from the centrum by a distinct suture as in *Lystroraptor murrayi* (Cluver, 1971). The lateral surfaces of the centrum are concave. Two small parapophyses (Fig. 3A–C; par) project ventrolaterally for 5 mm at the level of the base of the dens. They are triangular in cross section and oriented posteriorly. There is a midline ridge along the ventral surface of the centrum. The neural canal is widest (14 mm) at the middle of the odontoid process. The posterior surface of the centrum is deeply amphicoelous.

The cervical vertebrae (Fig. 3D, E) have centra that are almost circular in cross section, but slightly flattened dorsoventrally and deeply amphicoelous. The lateral surfaces of the centra are deeply concave. The oval, vertically-oriented parapophyses (Fig. 3E; par) are rather massive projections, 7 × 4 mm across and 4 mm high. The diapophyses (Fig. 2E; dp) are slightly concave rounded facets at the base of the neural arch. The neural arches are partly preserved with only parts of their lateral walls remaining.

The anterior dorsal vertebrae (Fig. 3F–I) are deeply amphicoelous, circular in cross section and, like the cervicals, slightly flattened dorsoventrally. The parapophyses are united with the diapophyses to form wide and posteriorly bent synapophyses (Fig. 3F; syn) with distinctive slightly concave facets for the capitulum (Fig. 3G; fcap) at the boundary between neural arch and centrum. The neural arches are massive and fused to the centra

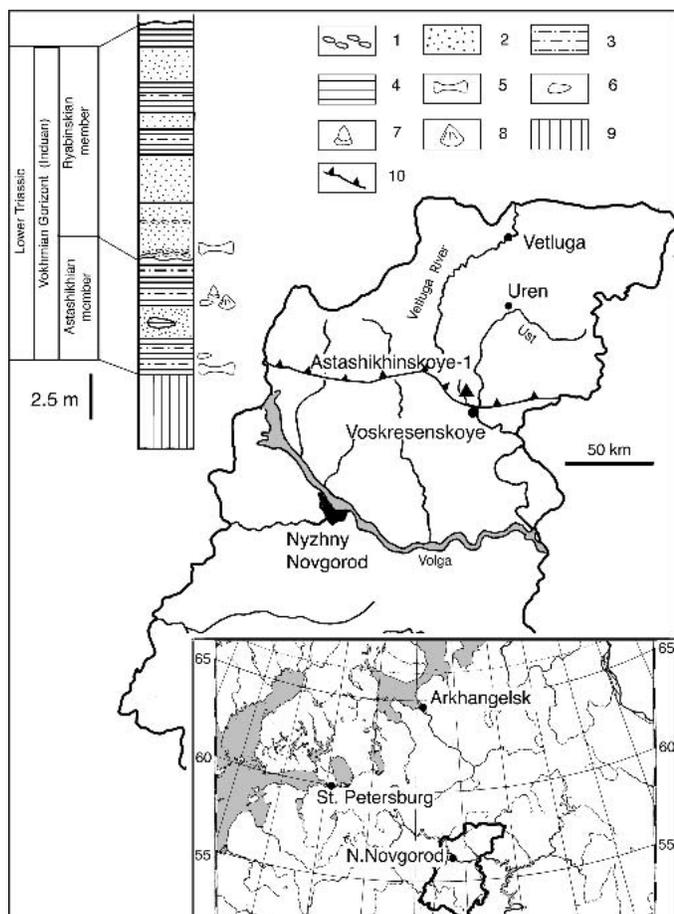


FIGURE 1. Location of the Astashikhinskoye-1 site and its geological section (after Lozovskiy, 1983). 1, conglomerate; 2, sand; 3, silt; 4, clay; 5, tetrapod remains; 6, ostracods; 7, conchostracans; 8, bivalves; 9, section obscured by grass; 10, schematic boundary of the Lower Triassic deposits.

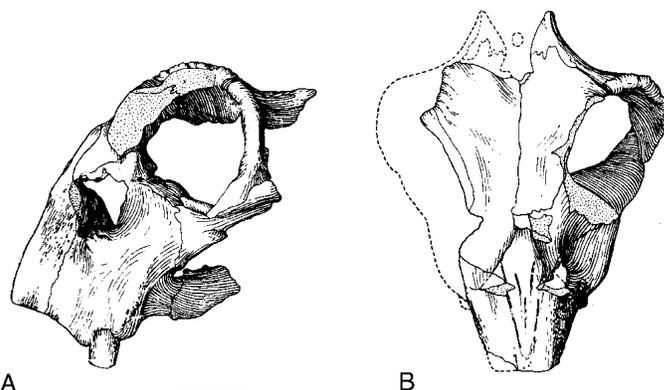
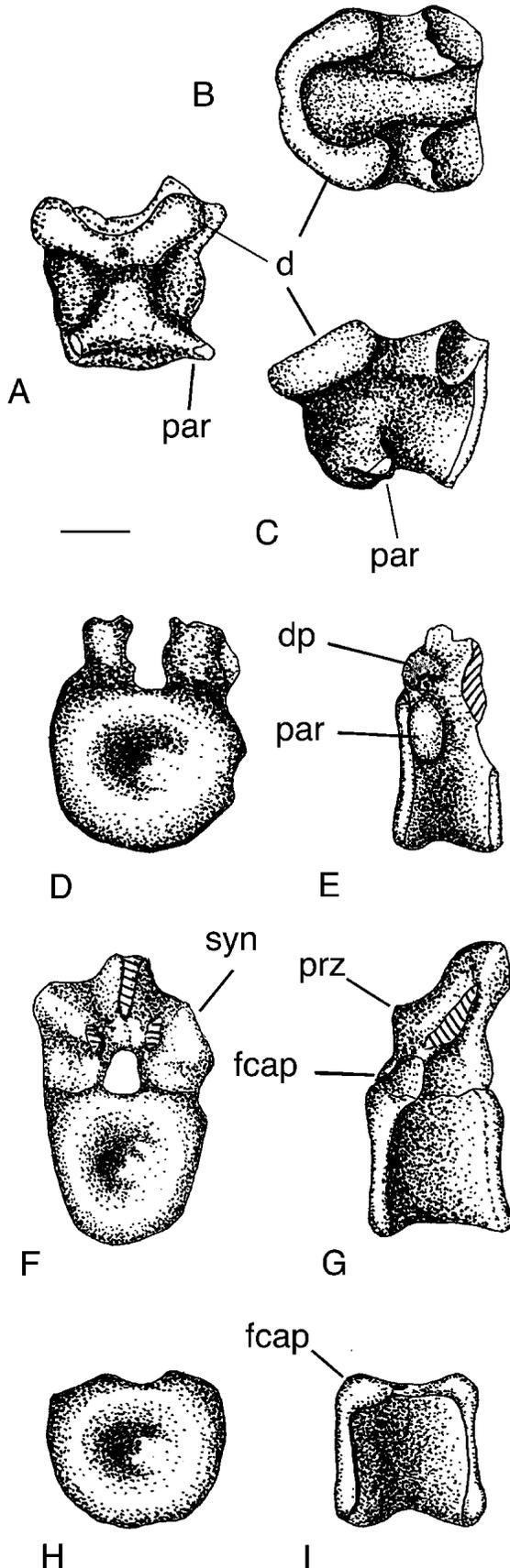


FIGURE 2. Skull of *Lystroraptor georgi* Kalandadze, 1975 (PIN 3447/1) in (A) left lateral and (B) dorsal views. Scale bar equals 30 mm.



along a clear suture. None of the neural spines of the dorsal vertebrae is fully preserved, but judging by their remains, they were probably about 10 mm wide and 15 mm high. The prezygapophyses (Fig. 3G; *prz*) are partly broken away, and are small anterior projections at the base of the neural spines. They are oriented at an angle of 40–45° to the parasagittal plane of the vertebrae. The minimum angle is in the first dorsal vertebra, which has a remarkably massive synapophysis (10 mm high and 10 mm wide). The latter is inclined at 68° to the longitudinal axis of the centrum.

The posterior dorsal vertebrae (Fig. 3H, I) are deeply amphicoelous, and are more elongated and dorsoventrally flattened than the anterior dorsals. The lateral surfaces are strongly concave, and anterodorsally they bear a small triangular facet (Fig. 3I; *fcap*) for the capitular part of the rib. The neural canal is narrowest at the midpoint.

The sacral vertebrae (Fig. 4A, B) are massive and slightly amphicoelous. They were not fused together. As with the posterior dorsals, they are dorsoventrally flattened, but more elongated. Oval and deeply concave parapophyseal facets (Fig. 4A, B; *par*) are present along the anterior part of the vertebra side. They are 8 × 12 mm across and positioned just below the base of the neural arch. The parapophyseal facet of the first sacral vertebra is oval and posterolaterally oriented at an angle of 45–50° to the longitudinal axis of the vertebra. The parapophyseal facet of the next vertebra is round. The neural arches are not preserved, but presumably they were fused with the centra. Dorsal damage of the iliac blade prevented reconstruction of the number of sacral vertebrae from imprints of the facets. Judging from the length of the anterior iliac process, however, it is unlikely that there were more than six. Watson (1912) and DeFauw (1986) reported six vertebrae in the sacrum of *Lystrosaurus*, and study of *L. murrayi* (PMNH 1937-13) also revealed about six vertebrae in the sacrum.

The centra of the anterior caudal vertebrae (Fig. 4C, D) are amphicoelous and triangular in cross section. Their lateral surfaces are slightly concave. There are no traces of parapophyses on the lateral sides. The posterior caudal vertebrae (Fig. 4E, F) are deeply amphicoelous and subrectangular in cross section. The two projecting hemapophyses (Fig. 4E; *hp*) are placed at the anterior edge of the ventral surface. The neural arches are massive, with low spines and strong plate-like, laterally-oriented synapophyses (Fig. 4E; *syn*). The prezygapophyses (Fig. 4E; *prz*) are wide, expanded dorso-ventrally, and almost vertically oriented.

The dorsal ribs are completely preserved and include nine proximal and some distal fragments. The proximal end of the dorsal rib (Fig. 4G, H) is dorsoventrally elongated in cross section with no strong separation of the capitulum and tuberculum, but corresponding facets are recognisable (Fig. 4G, H; *cap*, *tb*). They are vertically oval and proximally convex, and the capitulum is larger than the tuberculum. The rib neck is not pronounced. The ribs are oval in cross section (7 × 4 mm). Narrow, and shallow grooves extend along the anterior and posterior sides of the ribs, near their head.

Pectoral Girdle—The scapular fragment is 90 mm high (Fig. 5A, B). The acromion is not preserved, so it is impossible to

FIGURE 3. Cervical and dorsal vertebrae of *Lystrosaurus georgi* Kalandadze, 1975 (PIN 3447/1). A–C, axis in anterior (A), dorsal (B), and lateral (C) views; D, E, cervical vertebra in anterior (D) and lateral (E) views; F, G, anterior dorsal vertebra in anterior (F) and lateral (G) views; H, I, posterior dorsal vertebra in anterior (H) and lateral (I) views. Scale bar equals 10 mm. **Abbreviations:** *d*, dens; *dp*, diapophysis; *fcap*, facet for capitulum articulation; *par*, parapophysis; *prz*, prezygapophysis; *syn*, synapophysis.

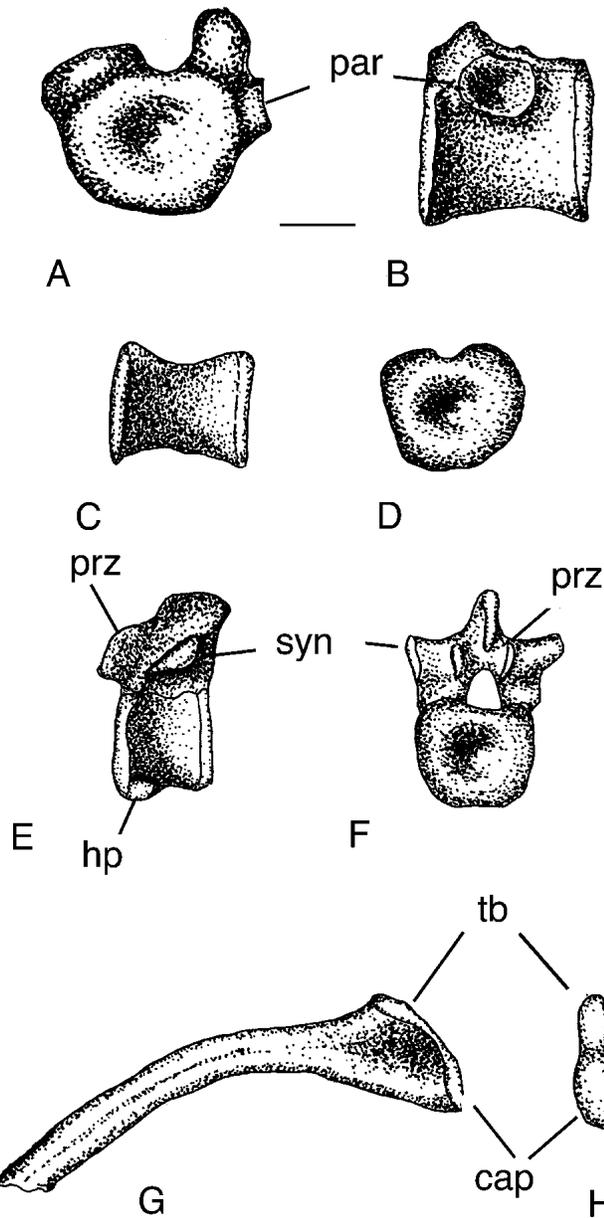


FIGURE 4. Sacral and caudal vertebrae and dorsal rib of *Lystrosaurus georgi* Kalandadze, 1975 (PIN 3447/1). **A, B**, sacral vertebra in anterior (**A**) and lateral (**B**) views; **C, D**, anterior caudal vertebra in anterior (**C**) and lateral (**D**) views; **E, F**, posterior caudal vertebra in anterior (**E**) and lateral (**F**) views; **G**, dorsal rib in lateral view; **H**, rib head in medial view. Scale bar equals 10 mm. **Abbreviations:** *cap*, capitulum; *hp*, hemapophysis; *par*, parapophysis; *prz*, prezygapophysis; *syn*, synapophysis; *tb*, tuberculum.

estimate precisely the degree of lateral deflection, although remains of the anterior edge of the scapular blade do not suggest that it was pronounced. The procoracoid projection (Fig. 5A; *prc*) is partly broken off, but judging from its remains, it was oriented at an angle of about 45° to the parasagittal plane. A similar orientation of the procoracoid projection has also been noted in other specimens of *Lystrosaurus*. This is much more lateral than in *D. trigonocephalus* (King, 1981a) and (?) *Dicynodon* (Surkov, 1996) where the angle is 90°. The scapular blade is slightly concave from the lateral side. As the acromion is not preserved, it is not possible to reconstruct the insertion of the *m. supracoracoideus*, but judging from more complete remains of

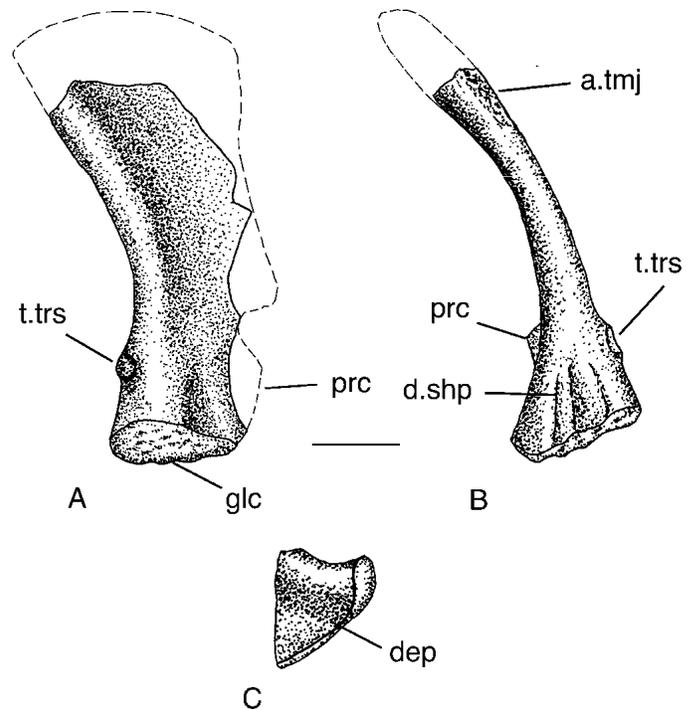


FIGURE 5. Scapular and coracoid fragments of *Lystrosaurus georgi* Kalandadze, 1975 (PIN 3447/1). **A, B**, fragment of the right scapula in lateral (**A**) and posterior (**B**) views; **C**, coracoid fragment in ventral view. Scale bar equals 20 mm. **Abbreviations:** *a.tmj*, area for attachment of *m. teres*; *dep*, depression; *d.shp*, area for *m. scapulohumeralis*; *glc*, glenoid cavity; *prc*, procoracoid projection; *t.trs*, tuber for *m. triceps scapula*.

Lystrosaurus in the South African Museum, and descriptions by Colbert (1974) and DeFauw (1986), the laterally deflected procoracoid projection probably did not permit broad attachment of this muscle to the inner surface of the scapula, as in *D. trigonocephalus* (King, 1981a). Therefore, insertion of this muscle on the lateral surface of the scapulacoracoid, as reconstructed for *Thrinaxodon* (Jenkins, 1971) and *Lystrosaurus curvatus* (DeFauw, 1986), seems more probable for *L. georgi*. The insertion of the *m. deltoideus* was not very different from the condition in *D. trigonocephalus* (King, 1981a) or in cynodonts (Jenkins, 1971; Kemp, 1980), being attached to the clavicles and the anterior edge of the scapula. However, the absence of reliable evidence makes it difficult to differentiate the insertions of the *m. supracoracoideus* and *m. deltoideus* on the lateral face of the scapula.

The posterior edge of the scapular blade is thicker than the anterior, and the *m. subcoracoscapularis* was probably attached to the medial surface along almost all of this edge. The upper quarter of the edge is thickened (Fig. 5B; *a.tmj*) with a rough surface for the muscle attachment. A similar area for muscle attachment on the posterior edge of the scapula in *Thrinaxodon* was interpreted as the site for the *m. teres major* (Jenkins, 1971). Since it is unlikely that the insertions of the *m. serratus* and *m. subcoracoscapularis* were both in this rather small area, we also identify this structure as the site of the initially separated *m. teres major*. A similar conclusion on the initial separation of the *m. teres major* in *Lystrosaurus* was also made previously by DeFauw (1986), who noted the "bevelled caudal margin near the vertebral border; with muscle scars on both faces." The initial differentiation of the *m. teres major* probably occurred at least in some species of *Lystrosaurus*, although we have not observed such roughened surfaces for muscle attachment on the posterior edge of the scapula in Permian or Triassic dicynodonts other than *L. georgi*. The *m. serratus* and *m. levator scapulae* presum-

ably shared the inner surface of the scapula along its dorsal edge, as in most other taxa.

The proximal end of the scapula is massive, and the glenoid cavity (Fig. 5A; glc) is slightly concave, and measures 20 × 25 mm. This region was poorly ossified, so it is quite difficult to distinguish the margin between the procoracoid and coracoid articular facets. A prominent tubercle (10 × 6 mm) with a rough surface (Fig. 5A, B; t.trs) is situated on the posterolateral edge of the distal end of the scapula, 15 mm above the glenoid cavity. This is quite normal for dicynodonts, and it was probably the attachment site for the scapular head of the m. triceps (Cruickshank, 1967; King, 1981a; DeFauw, 1986). Another muscle attachment was in the triangular depression (Fig. 5B; d.shp), which is 10 mm ventromedially from the triceps tubercle (see also DeFauw, 1986). The sharp ridge divides this depression into two asymmetrical parts, a lateral and a narrower medial one. The proximal position of this depression and its location medially to the triceps tubercle suggests that it is the insertion site of the m. scapulohumeralis posterior. Even though the additional depressed and ridged area on the posteromedial surface of the scapula has been observed only in *L. georgi*, this feature may characterize at least some *Lystrosaurus* species, because DeFauw (1986) observed tubercle grooves for the triceps in *L. curvatus* and *L. declivis*.

Only a fragment of the posterolateral part of the left coracoid is preserved (Fig. 5C). This bone had a concave posterolateral edge and convex medial edge. The posterolateral edge is thickened and rounded. There is a depression (Fig. 5C; dep) on the ventral side along the lateral edge, probably for the m. coracobrachialis (King, 1981a).

Forelimb—The humerus is 125 mm long (Fig. 6A, B); its distal end is greatly expanded to 73 mm, whereas the proximal end is only 47 mm wide. The proximal shaft is massive, and the proximal joint surface is rounded. The deltopectoral crest (Fig. 6A; dc) is 60 mm long and oriented at about 90° to the plane of the proximal shaft. It is up to 27 mm wide near the middle part of the bone, and descends abruptly, continuing on to the ventral surface as a low ridge. The ridge is penetrated by a large oval entepicondylar foramen (Fig. 6A; fent), located 12 mm below the distal end of the deltopectoral crest, with its entrance 10 mm above its exit. The posterodorsal side of the proximal shaft bears a pronounced short ridge (Fig. 6B; r.sbsc) probably for the m. subcoracoscapularis insertion (King, 1981a; DeFauw, 1986).

Another sharp ridge, 15 mm long, is located 10 mm distally of the last mentioned (Fig. 6A, B; a.trh). A similar ridge is known in humeri of other *Lystrosaurus* species (DeFauw, 1986), the Permian genera *Dicynodon*, *Oudenodon*, and *Rhachiocephalus* (King, 1981a; DeFauw, 1986; Surkov, 1996) and the Triassic *Tetragonias* (Cruickshank, 1967) and *Rhinodicyonodon* (Surkov, 1998), but that of *L. georgi* is longer and runs more proximally. This ridge is usually considered as the insertion for the m. triceps (e.g., King, 1981a; DeFauw, 1986).

The articular end is thin and elongated, and triangular in cross section. The distal condyles are expanded, and the anterior (entepicondyle) is more massive than the posterior and bears the radial facet (capitulum) on its ventral side. The capitulum (Fig. 6A; cp) is oval (16 × 12 mm) and concave. The trochlea (Fig. 6A, tr) is placed posterior to the capitulum at the level of the bone axis and approximately in the middle of the distal shaft. Even though the capitulum and trochlea facets are continuous, the latter is more pronounced, with a block-shaped convex surface (25 × 15 mm). The triangular depression (Fig. 6B; dep) corresponds to the facet on the dorsal surface of the bone.

The ulna is a rather massive bone, 87 mm long (Text-fig. 6C–F). The proximal shaft is much wider than the distal, their widths being 37 mm and 26 mm respectively (Fig. 6E, F). The sigmoid cavity (Text-fig. 6D; scav) is concave and hemispherical. Its length is 20 mm and width 15 mm. The dorsal edge of the ulna is

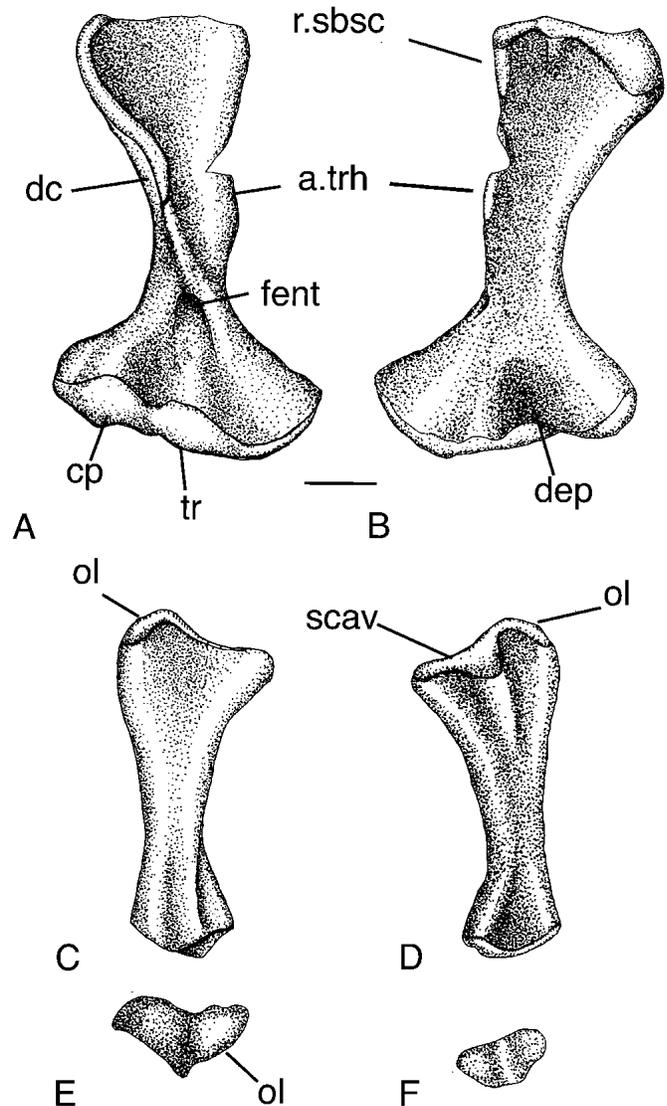


FIGURE 6. Forelimb elements of *Lystrosaurus georgi* Kalandadze, 1975 (PIN 3447/1). **A, B**, right humerus in ventral (**A**) and dorsal (**B**) views; **C, D**, right ulna in lateral (**C**) and medial (**D**) views; **E**, proximal shaft of the ulna in dorsal view; **F**, distal shaft of the ulna in ventral view. Scale bar equals 20 mm. **Abbreviations:** a.trh, area for attachment of m. triceps; cp, capitulum; dc, deltopectoral crest; dep, depression; fent, foramen entepicondylar; ol, olecranon; r.sbsc, ridge for attachment of m. subcoracoscapularis; scav, sigmoid cavity.

smooth and was not fully ossified, and the massive olecranon (Fig. 6C–D; ol) is rounded and low, suggesting that it was finished with cartilage in life. The lateral side of the proximal shaft is deeply concave. The proximal end is oval in cross section, and narrowest in the lower third. In life, the proximal end of the radius would have been positioned in the depression on the medial side of the ulnar proximal shaft, while the distal end of the radius fitted the depression on the anteromedial side of the distal shaft of the ulna. The distal shaft of the ulna is irregularly oval in cross section and convex.

Pelvic girdle—The ilium has an elongated preacetabular process (Fig. 7A, B pac), 50 mm along its lower edge, and slightly thickened ventrally. It is strongly damaged dorsally; the posterior process is missing, so it has been reconstructed (dashed lines) from the ilium of *L. murrayi* (PMNH 1937-13) and *Lystrosaurus* sp. (SAM-PK-K8038). Watson (1912) suggested that the notched

dorsal edge of the ilium is an autapomorphy of *Lystrosaurus*, but King (1991) noted the presence of such notches on the dorsal edge of the ilium in *D. trigonocephalus*. King's (1981a) figure of the ilium of *D. trigonocephalus* does not, however, show well-pronounced lystrosaur-like notches, and we have not seen this feature in the ilia of non-lystrosaur dicynodonts, nor is it reported in other dicynodonts, so we prefer to follow Watson's (1912) proposal. The proximal part of the ilium is not as stout as in (?) *Dicynodon* (Surkov, 1996) and *D. trigonocephalus* (King, 1981a), but it is much thinner transversely. The acetabulum (Fig. 7A; ac) is large and quadrangular. It is concave and oriented ventrolaterally and slightly anteriorly. The supraacetabular buttress (Fig. 7B; sb) is wide and strongly expanded laterally, forming the thickest part of the ilium base. A deep and wide groove, the postacetabular notch, leads to the acetabulum at an angle of 45° posteriorly to the buttress (Fig. 7A, B; n). Tendons of the m. ilio-femoralis, which was presumably attached to the lateral surface of the ilium blade (Kemp, 1982), most probably passed through this notch. The facet for articulation of the ischium (Fig. 7A; fisch) is long and narrow (12 × 32 mm). The pubic facet (Fig. 7A; fpub) is small and slightly concave (10 × 12 mm).

The ischium is nearly complete, with some damage along the posterodorsal edge. The blade is unusually narrowed dorso-ventrally (Fig. 7C) and concave along the dorsal edge, which is slightly deflected laterally. The external surface of the ischium possibly served as origin of the m. pubo-ischio-femoralis externus, as in other therapsids (Kemp, 1982). The m. ischio-trochantericus was probably attached to the low, sharp ridge

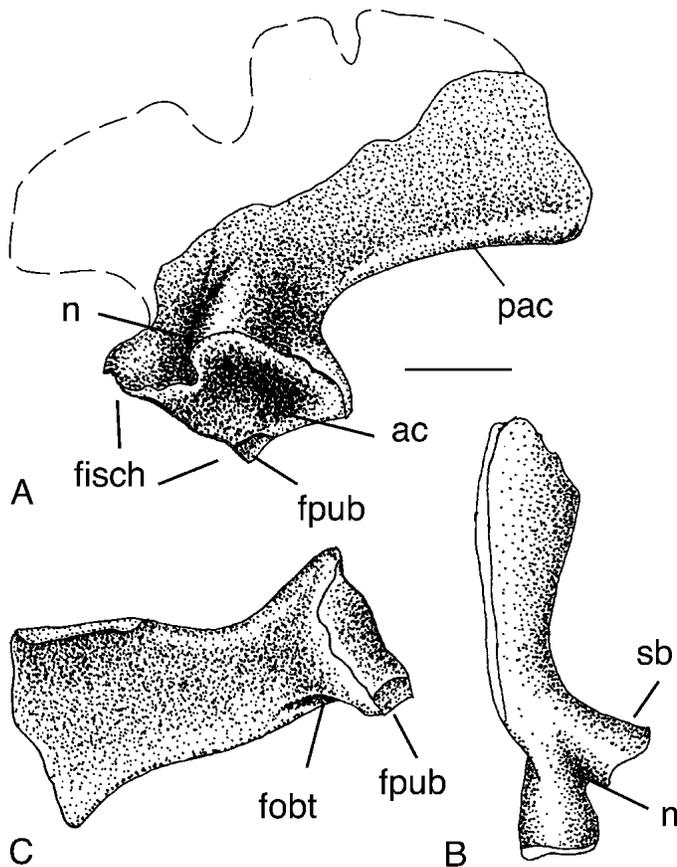


FIGURE 7. Pelvic girdle of *Lystrosaurus georgi* Kalandadze, 1975 (PIN 3447/1). **A, B**, right ilium in lateral (**A**) and posterodorsal (**B**) views; **C**, right ischium in ventrolateral view. Scale bar represents 20 mm. **Abbreviations:** ac, acetabulum; fisch, facet for the ischium attachment; fobt, foramen obturatorium; fpub, facet for pubis attachment; pac, preacetabular process; sb, supraacetabular buttress.

along the dorsal edge of ischium on its medial side. The proximal end is massive and rectangular in cross section with an elongate and slightly concave acetabular surface. There are two elongate and narrow facets for ilium and pubis attachments, measuring 12 × 32 mm and 7 × 10 mm respectively. The notch of the obturator foramen (Fig. 7C; fobt) is situated on the ventromedial edge of the proximal part of the ischium just below the acetabulum. This foramen was about 10 mm across and placed on the border between the ischium and pubis.

Even though no remains of the pubis have been found, judging from facets on the ilium and ischium of *L. georgi*, it was much thinner and more slender than in *Dicynodon* (?) sp. (SGU 104/3884) and *Rhinodicynodon* (PIN 1579/50), and was perhaps comparable to the pubis of *Lystrosaurus* sp. (AMNH 9349; Colbert, 1974).

Hindlimbs—The femur is a stout bone, 136 mm long (Fig. 8A, B). The proximal shaft is rounded, but not circular, and its axis is oriented at an angle of 36° to the shaft. A small, shallow depression (Fig. 8A; dep) is present on the anterodorsal side of the proximal shaft, beneath the joint surface. This depression might represent the minor trochanter for the m. puboischiofemoralis. The lateral part of the proximal shaft forms a well-developed trochanter major (Fig. 8A–B; tmj), which extends distally for about a third of the bone length. Its lateral edge is thickened and rough. A slightly concave wide depression is present on the posterodorsal surface of the proximal shaft. No traces of the fourth trochanter, which DeFauw (1986) reported for *Lystrosaurus*, have been noticed. The end is oval in cross section (19 × 16 mm). The distal end of the femur is massive and rectangular in cross section, the internal condyle being bigger than the external. The condyles are divided by a wide and rather deep depression, the flexor fossa (Fig. 8B; ff), on the ventral side of the bone. Another shallow depression divides the condyles on the dorsal side. There are two ridges (Fig. 8B; r), 20 mm long, on the ventrolateral side of the external condyle. Since the lateral portion of the m. gastrocnemius is attached to the lateral condyle of

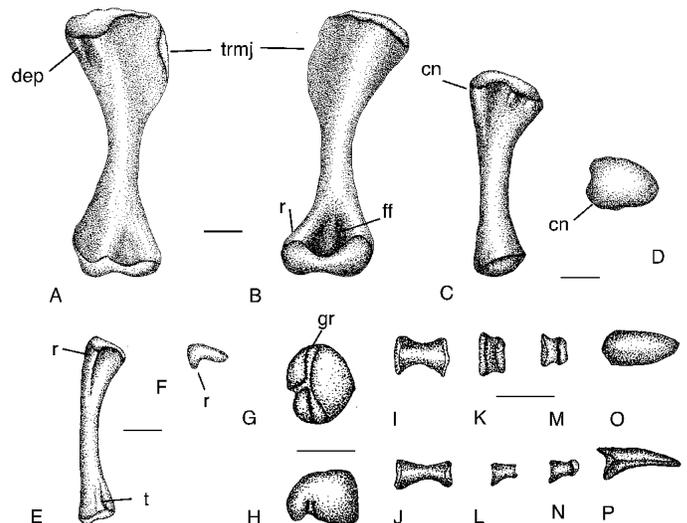


FIGURE 8. Hindlimb elements of *Lystrosaurus georgi* Kalandadze, 1975 (PIN 3447/1). **A, B**, left femur in dorsal (**A**) and ventral (**B**) views; **C**, left tibia in lateral view; **D**, proximal shaft of tibia in dorsal view; **E**, right fibula in lateral view; **F**, proximal shaft of fibula in dorsal view; **G, H**, astragalus in ventral (**G**) and lateral (**H**) views; **I, J**, distal element of metapodium in ventral (**I**) and lateral (**J**) views; **K, L**, phalanx in ventral (**K**) and lateral (**L**) views; **M, N**, preungular phalanx in ventral (**M**) and lateral (**N**) views; **O, P**, ungular phalanx in dorsal (**O**) and lateral (**P**) views. Scale bar equals 20 mm. **Abbreviations:** cn, crista nemialis; dep, depression; ff, flexor fossa; gr, groove; r, ridge; t, torus; trmj, trochanter major.

the femur in recent tetrapods (Romer, 1956; Gurtovoy et al., 1992), these ridges on the *Lystroraptor* femur might be interpreted as the site of insertion of the same muscle.

The tibia is a relatively stout bone, with a length of 105 mm (Fig. 8C, D). The proximal shaft is more massive than the distal, being triangular in cross section, and narrowing posteriorly. The cnemial crest (Fig. 8C, D; cn) is unpronounced. A shallow groove runs 25 mm long medial to the crest (Fig. 8C, D; gr). The distal end is oval in cross section (13 × 15 mm), and bears another groove, 30 mm long, with a rough surface along its posterior side. The distal shaft is almost round in cross section, with a diameter of 28 mm. The articulating surface is slightly convex and oriented slightly ventrolaterally.

The fibula (Fig. 8E, F) is a slender bone, 98 mm long. It is bowed slightly posteriorly, and has wide and parasagittally elongate ends. The proximal shaft is thin (22 × 7 mm) with a pronounced sharp ridge on the lateral side (Fig. 8C, D; r), which runs distally for a third of the length of the bone. The distal shaft is more massive, and elliptical in cross section (14 × 18 mm). There is a small depression on the anterolateral side, whose medial edge is formed by a sharp torus, 17 mm long (Fig. 8C; t). The distal end is thin and oval in cross section, and measures 7 × 9 mm.

Ankle and Foot—The astragalus (Fig. 8G) is a massive bone that is slightly oval in dorsal view. Its dorsal surface is convex and hemispherical. The ventromedial face bears three grooves (Fig. 8G; gr) which run radially from the centre.

The metapodials (Fig. 8I, J) are spool-shaped bones, 16–21 mm long. Their ventral surfaces are more concave than their dorsals. The articular facets are oval, the proximal ones being slightly larger than the distals. The dimensions of the facet of the largest metapodial are 12 × 18 and 9 × 18 mm respectively.

There are several phalanges (Fig. 8K–P). One (Fig. 8K–L) is short and wide, measuring 9 × 14 mm; it is slightly narrowed in the middle part. The ventral surface is more concave than the dorsal. The proximal articular surface is concave, whereas the distal is convex. The pre-ungular phalanges (Fig. 8M, N) are slightly longer than wide, measuring 16 × 15 mm. They are narrow in the middle part, and the proximal articular surface is flat or concave, the distal spool-shaped. The lower surfaces are more concave than the dorsal. The unguals are flat and wide (Fig. 8O, P), narrow distally, and thin in cross section. The proximal articular surface is concave, but this edge is convex and round in dorsal view. The largest one is 31 mm long and 17 mm wide.

PHYLOGENETIC ANALYSIS

Despite many descriptions of postcranial remains of *Lystroraptor* (Broom, 1903a; Watson, 1912, 1913; Young, 1939; Colbert, 1974; Li, 1983), no detailed comparison with other dicyodont postcranial material has been attempted. Therefore we summarised data from personal observations and available literature on the dicyodont postcranium and used these in a phylogenetic analysis. Twenty-seven taxa were included: *Angonisaurus*, *Aulacephalodon* (DeFauw, 1986), *Cistecephalus* (Cluver, 1978), *Dicynodon* (?) sp., *D. trigonocephalus* (King, 1981a), *Diictodon* (Ray and Chinsamy, 2003), *Dinodontosaurus* (Cox, 1965), *Eodicynodon* (Rubidge et al., 1994), *Ischigualastia* (Cox, 1965), *Kingoria* (Cox, 1959; DeFauw, 1986), *Kannemeyeria*, *Kawingasaurus* (Cox, 1972), *Lystroraptor georgi*, *L. curvatus* (DeFauw, 1986), *L. murrayi*, *L. mccaigi*, *Oudenodon* (DeFauw, 1986), *Pelanomodon halli*, *Placerias* (Camp and Welles, 1956), *Pristerodon* (Watson, 1960; Ray and Chinsamy, 2003), *Wadisasaurus* (Bandyopadhyay, 1988), *Rhinodicynodon*, *Robertia* (King, 1981b), *Stahleckeria*, *Tropidostoma*, *Tetragonias* (Cruickshank, 1967), and *Zambiasaurus* (Cox, 1969). We distinguished 18 informative and 5 uninformative postcranial characters.

Informative characters

1. 'Massiveness' of Axis—Ratio of height of axis to its full length (including odontoid process), 0.55–0.65 = 0; 0.69–0.75 = 1; >0.9 = 2. The measurements on different dicyodonts (Table 1) revealed three distinct groups of values, as noted.

2. Angle between Odontoid and Longitudinal Axis of Centrum—20–25° = 0; 40–45° = 1. Variations in the odontoid angle may reflect the angle at which the head was held (Table 1).

3. Number of Sacral Vertebrae—Two = 0; three = 1; four = 2; five = 3; more than five = 4. The general trend is for increase in the number of sacral vertebrae (DeFauw, 1986; Angielczyk, 2001; Maisch, 2001, 2002), so we considered this character as ordered. Increasing number of sacral vertebrae above five probably corresponded to the acquisition of semi-sprawling locomotion. Increase in sacrum length occurred by incorporation of the last dorsal vertebrae (Surkov, 1999). Involvement of the posterior dorsal vertebrae in the sacrum apparently reduced lateral flexibility of the vertebral column and prevented collapse of the body during non-sprawling movements (Kemp, 1982). Possible semi-sprawlers include *D. trigonocephalus*, *Kingoria* (King, 1981a, 1985), *Dicynodon* (SGU 104/3884), *Lystroraptor*, *Rhinodicynodon* and other Middle-Late Triassic dicyodonts (Surkov, 1999). All these forms have a sacrum consisting of 5+ vertebrae and corresponding development of additional features in the pelvis, such as a supraacetabular buttress and a laterally expanded trochanter major. *Kingoria*, with four vertebrae in the sacrum and an undeveloped supraacetabular buttress, is excluded from the list of long-sacrum semi-sprawlers because of complete reduction of the ilium posterior process. From our point of view, this and some other features in the skeleton of *Kingoria* that are unusual for dicyodonts (see characters 7, 10, 12, 16, 17 in Appendix 1) may reflect a quite specific mode of life for this creature, even the ability to climb (DeFauw, 1986), that require additional investigation.

TABLE 1. Measurements of the axis and humerus of selected dicyodonts used in the analysis

Taxa	Angle of odontoid to longitudinal axis of centrum	Ratio of height to length of the axis	Ratio of deltopectoral crest length to humerus length
<i>Eodicynodon</i>	?	?	0.46
<i>Robertia</i>	?	?	0.43
<i>Diictodon</i>	?	?	0.43
<i>Pristerodon</i>	?	?	0.41?
<i>Cistecephalus</i>	?	0.52	0.34
<i>Kawingasaurus</i>	?	?	0.45
<i>Tropidostoma</i>	24	0.75	0.5
<i>Kingoria</i>	25	0.6	0.44
<i>Oudenodon</i>	?	?	0.50
<i>Pelanomodon</i>	44	0.74	0.53
' <i>Dicynodon</i> (?) sp.'	?	?	0.55
<i>D. trigonocephalus</i>	45	0.55	0.62
<i>Lystroraptor georgi</i>	18	0.69	0.45
<i>L. murrayi</i>	?	?	0.45
<i>L. mccaigi</i>	?	1.1	0.45
<i>L. curvatus</i>	?	?	0.35
<i>Kannemeyeria</i>	20	0.94	0.54
<i>Rhinodicynodon</i>	25	0.74	0.57
<i>Tetragonias</i>	?	?	0.5
<i>Angonisaurus</i>	23	0.72	?
<i>Dinodontosaurus</i>	?	?	0.48
<i>Wadisasaurus</i>	40	0.92	0.52
<i>Stahleckeria</i>	20	0.96	0.57
<i>Placerias</i>	?	?	0.48
<i>Ischigualastia</i>	?	?	0.63
<i>Zambiasaurus</i> (juvenile)	?	?	0.48

4. Relative Expansion of Upper Two-thirds of Scapular Blade—Narrow = 0; wide = 1. The width of the scapular blade reflects the development of the dorsal pectoral muscles such as the *m. deltoideus* (King, 1981a). The general trend for this feature is expansion of the scapular blade in advanced Permian, and many Triassic, forms such as *Oudenodon*, *Aulacephalodon*, *Dicynodon*, *Lystrosaurus*, *Rhinodicynodon*, *Stahleckeria*, *Dinodontosaurus*, and *Ischigualastia*. The wide scapula of *Eodicynodon* is probably an autapomorphy, because the scapula of more basal anomodonts (Brinkman, 1981; Ivakhnenko, 1994) is narrow and slender. A reversal of this character appeared in some Middle-Late Triassic dicynodonts: *Kannemeyeria*, *Wadiasaurus*, and *Placerias*.

5. Ossification of Postero-dorsal Corner of Scapular Blade—Poor = 0; good = 1. We considered this character (Fig. 9A) as ordered. This feature might relate to the separation of the *m. teres major* and/or greater development and more posterior placement of the *m. serrati*, both of which attached to the upper part of the scapular blade and worked as suspensors, thereby involving the scapula in the stride to increase its length (Jenkins and Gaslow, 1983; Kuznetsov, 1999). Poor ossification of the posterodorsal corner of the scapula can be seen in all primitive dicynodonts. Further development and ossification of this corner occurred in the most advanced toothless forms and may indicate greater involvement of the scapula in the stride as a part of the acquisition of the semi-sprawling gait and reduction in lateral flexibility of the vertebral column.

6. Participation of Procoracoid in Glenoid Cavity—Excluded = 0; involved = 1. Exclusion of the procoracoid from the glenoid is probably the common state in dicynodonts, although the procoracoid in *Pelanomodon*, *Dicynodon* (?) sp., *D. trigonocephalus* (King, 1981a), and *Lystrosaurus* (see also DeFauw, 1986) was partly involved in the glenoid.

7. Deep Groove Along Anterior Edge of Scapula—Absent = 0; present = 1. This groove makes the cross section of the scapula above the acromion Y-shaped. The feature has been

reported by Cox (1965, 1969) for *Ischigualastia* and *Zambiasaurus* respectively. Probably the groove reflects the placement of the *m. supracoracoidalis* along the anterior edge of the scapula. This groove is seen, among dicynodonts, only in *Kingoria* and *Stahleckeria*.

8. Appearance of Posteroventral Area of Scapula—Additional ridges for *m. scapulothoracalis posterior*, absent = 0; present = 1. The posteroventral region of the scapula usually bears a single tubercle or groove (Cruikshank 1967; King, 1981a; DeFauw, 1986) for the *m. triceps*. Additional grooves and ridges probably reflect strengthening of the *m. scapulothoracalis posterior* which attaches in this area. The character has been mentioned here for *L. georgi* and reported by DeFauw (1986) for *L. curvatus* and *L. declivis*.

9. Appearance of Sternum—Egg-shaped and with 2–3 pairs of rib facets = 0; rhomboidal and with single pair of rib facets = 1.

10. Deltopectoral Crest—Extended = 0; shortened = 1. The development and distal extent of the deltopectoral crest corresponds to the strength of the *m. pectoralis*. The latter kept the body above the ground in the sprawling posture, and its strength was proportional to body weight (Rubidge et al., 1994). This is clearly seen in different-sized dicynodonts, such as *Eodicynodon* versus *Dicynodon* (Table 1). In relatively small dicynodonts, *Eodicynodon*, *Diictodon*, *Robertia*, *Pristerodon*, *Cistecephalus*, and *Kawingasaurus*, the distal expansion of the deltopectoral crest is 0.34–0.46. In larger forms, such as *Tropidostoma*, *Dicynodon*, *Oudenodon*, *Pelanomodon*, and the Middle-Late Triassic taxa, the distal expansion is 0.5–0.7. *Lystrosaurus* and *Kingoria* (DeFauw, 1986), however, have short deltopectoral crests (about 0.45), despite being similar in size to *Dicynodon* or *Tropidostoma*.

11. Olecranon Process—High and well ossified = 0; poorly ossified and presumably cartilaginous = 1; well ossified but formed by secondary ossification = 2. Since there is no visible suture dividing the high olecranon from the shaft of the ulna in *Eodicynodon*, *Cistecephalus*, and *Kawingasaurus*, the develop-

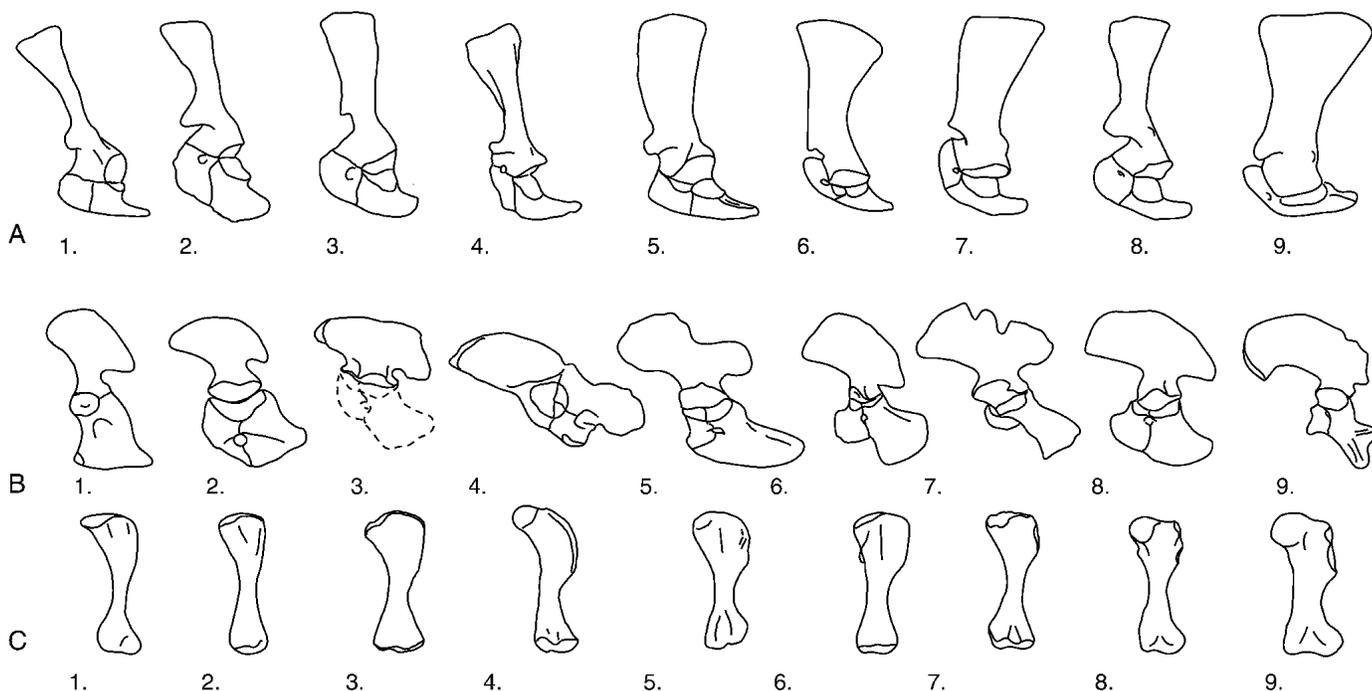


FIGURE 9. Shoulder girdles (A), pelvic girdles (B) and femora (C) of the Late Permian and Triassic dicynodonts; not to scale. 1, *Robertia* (after King, 1981b); 2, *Diictodon* (SAM-PK-K1633); 3, *Kingoria* (Cox, 1959; DeFauw, 1986); 4, *Tropidostoma* (shoulder girdle SAM-PK-K9960), *Tropidostoma* (?) sp., (ilium and femur KPM, 20/92); 5, *Dicynodon trigonocephalus* (after King, 1981a); 6, *Dicynodon* sp. (SGU 104/3884); 7, *Lystrosaurus georgi* (shoulder girdle reconstructed from studied material and literature data); 8, *Rhinodicynodon* (after Surkov, 1998); 9, *Stahleckeria* (UT 2).

ment of secondary ossified skeletal elements among dicynodonts (Walter, 1985) presumably appeared only in the Middle-Late Triassic, although this requires further study.

12. Ossification of Humerus Capitellum and Tuberculum—Well ossified and separate capitellum and tuberculum = 0; capitellum and tuberculum continuous = 1. Fully ossified and separate capitellum and tuberculum appeared only in *Eodicynodon* (Rubidge et al., 1994), *Cistecephalus* (Cluver, 1978), *Kawingasaurus* (Cox, 1972), and probably *Kingoria* (DeFauw, 1986). The normal condition in dicynodonts is to retain continuous, poorly separated facets.

13. Supraacetabular Buttress—Undeveloped = 0; poorly developed = 1; well developed = 2. The supraacetabular buttress is well developed in advanced dicynodonts (sensu King, 1988), where it is accompanied by a postero-acetabular notch/depression that probably accommodated tendons of the m. iliofemoralis. It presumably prevented dislocation of the femur during the stride in the semi-sprawling type of locomotion. We consider this character as ordered.

14. Ventral Expansion of Pubic Plate—Significantly expanded = 0; reduced and without noticeable ventral expansion = 1. This character (Fig. 9B) is considered as ordered, since the expansion is seen in primitive forms, such as *Eodicynodon* (Rubidge et al., 1994) and *Robertia* (King, 1981b) and the derived state is seen in *Dicynodon* (King, 1981a; Surkov, 1996) and *Rhynodicynodon* (Surkov, 1998).

15. Pubic Tubercle—Absent = 0; present = 1. This tubercle was probably involved in strengthening the m. pubo-ischiofemoralis, which was attached to it. The tubercle is absent in *Lystrosaurus* (see also Colbert, 1974; DeFauw, 1986) and present in *Stahleckeria* (Fig. 9B).

16. Posteroventral Expansion of Ischium—Widened = 0; narrow and posteriorly oriented = 1. The first state (Fig. 9B) occurred in most dicynodont taxa, the second in *Kingoria* and *L.georgi*. According to DeFauw (1986), a narrow, ventrally-oriented ischiadic plate is seen in the pelvis of *Dicynodon* cf. *leoniceps*, but we did not find sufficient data on its postcranium to include this taxon in the analysis.

17. Proximal End of Femur—Articulation surface not well defined = 0; well defined = 1; forming semispherical, antero-medially-oriented head = 2; hemispherical and medially oriented = 4. A well-defined proximal articulation surface (Fig. 9C) and then a hemispherical, anteromedially-oriented head is a feature that relates to long-axis rotation of the femur in semi-sprawling locomotion (King, 1981a). Acquisition of an antero-medial hemispherical femur head may be a general trend among dicynodonts (Surkov, 1999), and some taxa, such as *Cistecephalus* (Cluver, 1978) and *Kingoria* (King, 1985; DeFauw, 1986) have a well-formed hemispherical femur head that is medially oriented.

18. Lateral Expansion of Trochanter Major—None = 0; poorly expanded = 1; well expanded = 2; divided and with a third trochanter = 3. Gradual lateral expansion of the trochanter major among dicynodonts has been linked to the development of the m. iliofemoralis by King, (1981a, b). These states are clearly seen in *Robertia*, *Tropidostoma*, *Dicynodon*, and *Rhynodicynodon* (Fig. 9C). The character is considered as ordered.

Uninformative Characters

A. Dorsal Arching of Vertebral Column—A tentative investigation of flexibility in the vertebral column has been made in *Tropidostoma* (?) sp. (KPM 20/92), *Dicynodon* (?) sp. (SGU 104/3884), and *L. georgi* (Surkov, 1999). Using Slijper's (1946) formula, the load on centra along the vertebral column of *Dicynodon* (?) sp. (SGU 104/3884) and *L. georgi* was similar to values for mammals, suggesting possible arching of the spines in these taxa. The vertebral column of *Tropidostoma* (?) sp. (KPM 20/92)

revealed no possible arching—the characteristic condition for sprawling reptiles. However, this character had to be omitted because of a lack of similar data for most taxa.

B. Fusion of Sacral Vertebrae—This feature has been seen in the large Triassic dicynodonts *Rhadiodromus*, *Stahleckeria*, and possibly also in *L. mccaigi*. The last four vertebrae were fused in *Stahleckeria*, but the exact condition in other taxa is unclear. Since this feature is undoubtedly ontogenetic and related to the size of the animal, it is also excluded.

C. Projection on Anterior Margin of Procoracoid—This character has been described for *Kawingasaurus* (Cox, 1972) and *Cistecephalus* (Cluver, 1978), but it is autapomorphic for those genera and so has not been included in the analysis.

D. Reduction of Posterior Process of Ilium—This has been observed only in *Kingoria* and has not been included in the analysis. This feature is autapomorphic.

E. Notched Dorsal Border of Ilium Blade—This is confidently known only for *Lystrosaurus*. King (1981a) mentioned notches along the dorsal edge in *D. trigonocephalus*, but, as noted above, no lystrosaur-like notches could be seen in her paper. This feature is probably an autapomorphy of *Lystrosaurus* and so has not been included in the analysis.

Cladistic Analysis

A data matrix for the 27 taxa and 18 characters discussed above is shown in Appendix 1. *Eodicynodon* is treated as the outgroup. The permutation probability (PTP) test (Faith and Cranston, 1991) was applied using PAUP (version 4.0b.10, Swoford 1998) on a Macintosh iMAC computer. Characters 3, 5, 13, 14, 18 were ordered, the rest equally weighted, and 99 random data sets were generated. The result was PTP = 0.01, whether or not *Eodicynodon* was included, indicating that the data set contains hierarchical structure.

Parsimony analysis of the data set was also carried out using PAUP (branch and bound search, characters equally weighted and unordered, trees rooted with the outgroup *Eodicynodon*). The search yielded 9342 equally most parsimonious trees (MPTs), with length (L) = 53; consistency index (CI) = 0.528; retention index (RI) = 0.790. Reduction in the level of homoplasy and in the number of MPTs was achieved by the successive approximation approach (Carpenter, 1988) to character weighting. The characters were re-weighted according to the rescaled consistency index and an iterative branch and bound search yielded 192 MPTs (L = 21,14; CI = 0.687; RI = 0.889) (Fig. 10A). Bremer support for each node was estimated using the TreeRot v2b software (Sorenson, 1999).

Lack of resolution is predictable from examination of the data matrix (Appendix 1) because the genus *Oudenodon* shares the same features as *Dicynodon* (?) sp. and *D. trigonocephalus*, with the exception of missing values. A similar situation can be observed for *Kawingasaurus*, *Tetragonias*, and *Angonisauros*. According to Wilkinson's (1995) strategy of safe taxonomic reduction, these taxa may be removed from the analysis without affecting the result. Branch and bound analysis of the reduced data matrix yielded 12 MPTs (L = 21,14; CI = 0.687; RI = 0.882; Fig. 10B). The character compatibility permutation test of the data set (Appendix 1) without *Angonisauros*, *Kawingasaurus*, *Oudenodon*, or *Tetragonias* yielded PTP = 0.01, indicating significant phylogenetic structure, for all taxa and for the ingroup (based on 99 random permutations).

Comparison

Phylogenetic analysis based only on postcranial characters yielded trees that are similar to the phylogenetic studies of King (1988), Maisch (2001, 2002), Angielczyk (2001), and Angielczyk and Kurkin (2003), but the current hypothesis contradicts the

position of *Cistecephalus* as a close relative of *Kingoria* (King, 1988; Angielczyk, 2001; Angielczyk and Kurkin, 2003), the pairing of *Diictodon* and *Robertia* (Angielczyk, 2001; Angielczyk and Kurkin, 2003), and the clades (*Robertia* + *Diictodon* + *Kingoria* + *Cistecephalus*) (King, 1988) and (*Stahleckeria* + *Placerias* + *Ischigualastia*) (Maisch, 2001, 2002). Topological constraints were employed to investigate the robustness of the relationships represented in Figure 10B in comparison with previous phylogenetic hypotheses. The tree with monophyletic (*Diictodon* + *Robertia*) yielded an MPT of nearly the same length ($L = 20.99$, $CI = 0.684$, $RI = 0.884$), a slightly longer tree was produced with constrained monophyletic (*Stahleckeria* + *Placerias* + *Ischigualastia*; $L = 21.33134$; $CI = 0.681$; $RI = 0.879$), but constrained monophyly of (*Kingoria* + *Cistecephalus*) and (*Robertia* + *Diictodon* + *Kingoria* + *Cistecephalus*) yielded a much longer MPT ($L = 22.798$, $CI = 0.630$, $RI = 0.852$; $L = 23.404$, $CI = 0.614$, $RI = 0.842$).

These results are important as an assessment of the value of dicynodont postcranial characters in phylogenetic analysis. Consideration of topological constraints indicates that the relationships among anomodonts achieved on postcranial characters is not very different from the hypotheses of Angielczyk (2001), Angielczyk and Kurkin (2003), or Maisch (2001, 2002) of a polyphyletic (*Robertia* + *Diictodon*), *Kingoria*, and *Cistecephalus*, but this study rejects the postulated monophyly of (*Robertia* + *Diictodon* + *Kingoria* + *Cistecephalus*), which was also not supported by Angielczyk (2001), and it also rejects a closer relationship of *Kingoria* and *Cistecephalus*.

The current study confirms results of an analysis of Triassic dicynodont relationships based on basicranial characters (Surkov and Benton, 2004). The selection of taxa is different in part, but

clades based on braincase characters that are confirmed here include: the Mid-Late Triassic clade (*Kannemeyeria*, *Placerias*, *Ischigualastia*) with *Angonisauros* and *Tetragonias* paired as sister group; then *Lystrosaurus* and *Dicynodon* as next outgroups, followed by *Aulacephalodon*, and with *Robertia*, *Diictodon*, *Pristerodon*, and *Eodicynodon* as successive outgroups to the bottom of the tree. Only *Kingoria* appears in different locations, above *Pristerodon* here, but at the base of the cladogram with *Eodicynodon* on the basis of basicranial characters.

Character and Postural Evolution

Analysis of homoplasy levels indicated that there were more synapomorphies associated with the pelvis (characters 3, 13, 14, $RI = 1$) and proximal part of the femur (character 17, $RI = 0.909$; 18, $RI = 0.818$), than with the shoulder girdle and forelimbs (characters 8, 11, $RI = 1$). Such a distribution of phylogenetic structure suggests that the main changes in the anomodont postcranium concerned the construction of the pelvis and femur rather than the shoulder girdle and forelimbs. This is also clearly seen from tracing of changes in the main branching points of the estimated tree (Fig. 10A). Analysis of the cladogram (Fig. 10A) also shows that the most significant synapomorphies (highest Bremer support values) occurred at the node subtending *Aulacephalodon* and the Triassic taxa. Changes at this node correspond to the increase in the number of sacral vertebrae to five, and development of the supraacetabular buttress. These changes also probably related to the development of a well-expanded trochanter major, seen in all taxa in this clade except *Aulacephalodon* and *Angonisauros*, whose femurs are unknown. Since all of these synapomorphic characters relate to semi-sprawling lo-

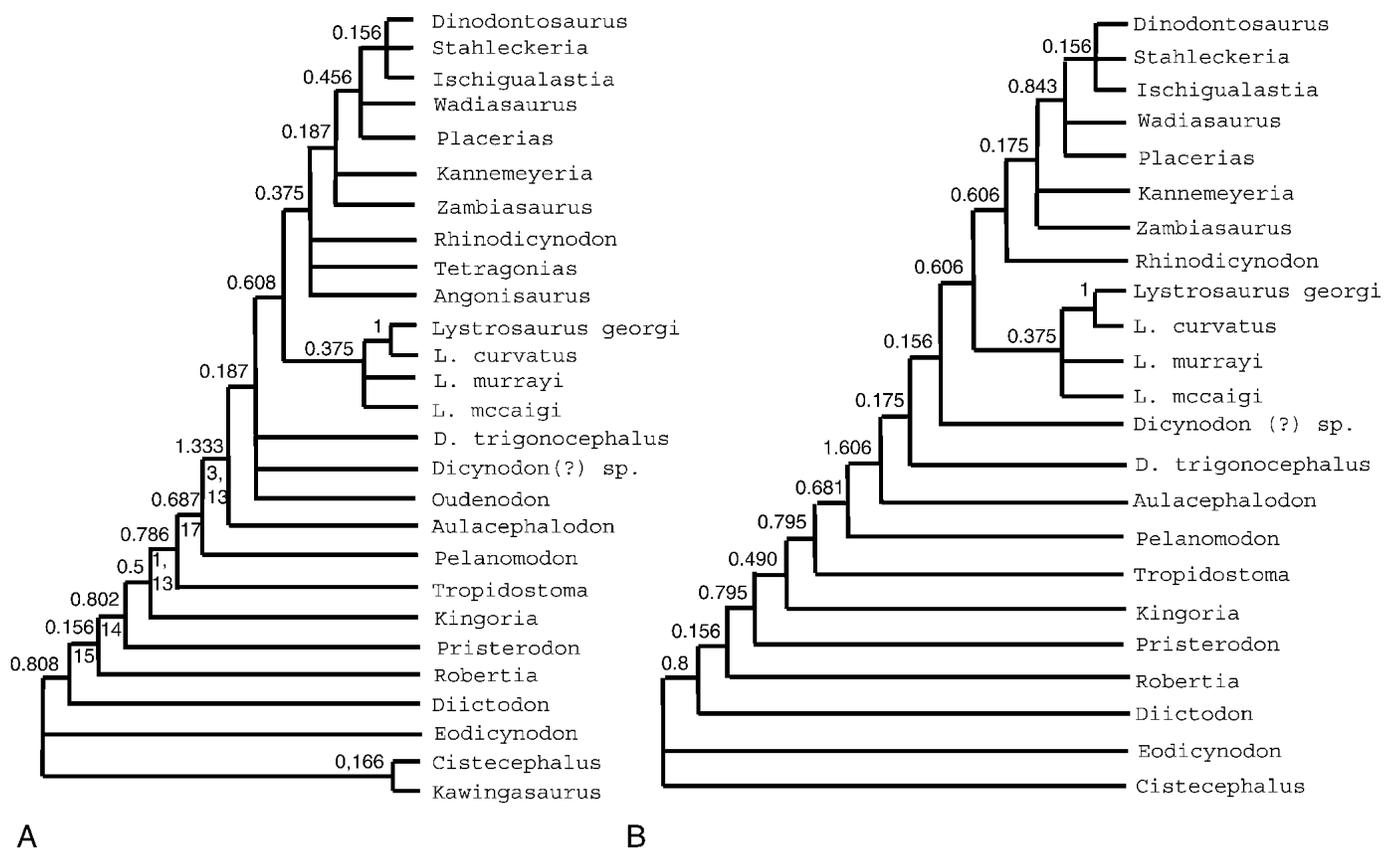


FIGURE 10. Most-parsimonious hypotheses of the relationships of selected Late Permian and Triassic dicynodonts (Table 1) based only on data on postcranial morphology. **A**, Strict consensus of the 192 most-parsimonious trees after a successive approximations approach to character weighting (changed characters are shown below nodes); **B**, the most-parsimonious tree after safe reduction (deletion of *Kawingasaurus*, *Oudenodon*, *Angonisauros*, *Tetragonias*). Bremer support values are shown above nodes.

comotion, we may presume this for all taxa in this clade. Therefore, this analysis of synapomorphies, and changes in the dicynodont postcranium, have revealed that there was a general trend in dicynodont evolution to acquisition of a semi sprawling posture, which occurred in advanced Late Permian forms. Since dicynodonts were herbivorous, a more erect orientation of the femur allowed them to reduce the load of the large abdomen and therefore an increase in body size became possible without significant loss of energy to keep the body above the ground; this was fully seen in Middle-Late Triassic forms.

SUMMARY AND CONCLUSION

Phylogenetic analysis based only on dicynodont postcranial characters yielded generally similar results to those obtained by King (1988), Maisch (2001, 2002), and Angielczyk (2001), based on cranial and postcranial characters. The topological position of the genus *Lystrosaurus* remained unaltered, a genus that is well defined by the relative shortness of the deltopectoral crest and increased length of the sacrum. *Lystrosaurus georgi* is characterized by the narrow and posteriorly oriented ischium and it still retains a contact between the premaxillae and palatine. The appearance of the posteroventral part of the scapula suggests a close relationship to *L. curvatus*.

The phylogeny indicates a close relationship of the Middle-Late Triassic taxa from South America (*Dinodontosaurus*, *Stahlackeria*, *Ischigualastia*). Our investigation also supported Angielczyk's (2001) hypothesis of polyphyly of the Late Permian (*Robertia* + *Duictodon*), *Kingoria*, and *Cistecephalus* (contra King, 1988), but strongly opposes a close relationship between *Cistecephalus* and *Kingoria*, as suggested by King (1988) and Angielczyk (2001).

The low homoplasy level among characters in the pelvis and femur compared to the shoulder girdle and forelimbs suggests that the former region documents the pattern of anomodont evolution better than the latter.

Analysis of character changes revealed that the general evolutionary trend in the dicynodont postcranium relates to acquisition of semisprawling locomotion, and first appeared in advanced toothless forms such as *Aulacephalodon*. This shift to a more erect posture in dicynodonts occurred in parallel with cynodonts, but in a different way (Kemp, 1982), and it reflects a common strategy to gain maximum efficiency in locomotion.

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APPENDIX 1

Data matrix of selected Late Permian—Triassic dicynodonts. Characters are listed and described in the text.

	1	
	1234567890	12345678
<i>Eodicynodon</i>	??010?00?0	00?00000
<i>Robertia</i>	??00000000	11001000
<i>Diictodon</i>	???1000000	11000000
<i>Priesterodon</i>	??200?0000	11011000
<i>Cistecephalus</i>	0?101?0000	00000030
<i>Kawingasaurus</i>	???01?00?0	00??????
<i>Tropidostoma</i>	10100?0000	111???01
<i>Kingoria</i>	0020101011	10011132
<i>Oudenodon</i>	??311?00?0	?12???12
<i>Aulacephalodon</i>	??301?00??	??2?????
<i>Pelanomodon</i>	11201100?0	11111011
<i>'Dicynodon(?) sp.'</i>	??31110010	11210012
<i>D. trigonocephalus</i>	01311100?0	11211012
<i>Lystrosaurus georgi</i>	10411?01?1	11210112
<i>L. murrayi</i>	??41110011	11210012
<i>L. mccaigi</i>	2?411?00?1	11210?12
<i>L. curvatus</i>	??411101?1	11210012
<i>Kannemeyeria</i>	20401000?0	11211022
<i>Rhinodicyonodon</i>	1041100010	11210023
<i>Tetragonias</i>	??411000?0	11210023
<i>Angonisaurus</i>	10411000??	??2100??
<i>Dinodontosaurus</i>	??4110?0?0	21211022
<i>Rechnisaurus</i>	2140100010	21211023
<i>Stahleckeria</i>	2041101000	21211022
<i>Placerias</i>	??40100010	21210022
<i>Ischigualastia</i>	??41101000	212????2
<i>Zambiasaurus</i>	??40101010	11210022