THE UPPER PERMIAN REPTILE *ADELOSAURUS* FROM DURHAM

by SUSAN E. EVANS

ABSTRACT. The Upper Permian reptile *Adelosaurus* from the Marl Slate of Durham, England, is redescribed and compared with contemporary genera. The study confirms Watson's (1914) conclusion that *Adelosaurus* is generically distinct from *Protorosaurus* to which it was originally referred. The skeleton seems immature, and shows a combination of primitive and derived character states. Amongst the latter, are the possession of a strong humerus with little proximal or distal expansion, and of a slender sigmoidal femur and triangular ilium, character states shared with diapsids. In the absence of the skull and ankle, however, this classification remains tentative. *Adelosaurus* adds a fifth, probably terrestrial, component to the Kupferschiefer/Marl Slate reptilian assemblage which currently includes a glider, *Coelurosauravus*, the long-necked, perhaps semi-aquatic, *Protorosaurus* and, from German deposits only, a parieasaur, and the enigmatic *Nothosauravus*.

IN the last decade, there has been a resurgence of interest in early diapsid reptiles, particularly with respect to their phylogenetic relationships. The earliest known diapsid, *Petrolacosaurus* has been shown to have affinities both to protorothyrid captorhinomorphs (Reisz 1981; Heaton and Reisz 1986) and to the enigmatic *Araeoscelis* (Reisz *et al.* 1984). Together, *Petrolacosaurus* and *Araeoscelis* form the diapsid group Araeoscelidia. Most of our information about these diapsids comes from Upper Carboniferous and Lower Permian deposits in northern Pangaea, while the bulk of our knowledge of Upper Permian diapsids, amongst which the ancestors of Mesozoic and Cenozoic groups are usually sought, is from southern Pangaea—most notably from deposits in Madagascar and South Africa. Relatively little is known of contemporary diapsid faunas in northern Pangaea. However, the Kupferschiefer/Marl Slate deposits of northern Germany and Britain provide at least a weak link between the northern and southern faunas. The deposits have yielded a number of specimens of *Protorosaurus*, a long-necked reptile related to *Prolacerta* (Lower Triassic, South Africa and Antarctica), and of the glider *Coelurosauravus* (= *Weigeltisaurus* = *Gracilisaurus*, Evans and Haubold 1987) which has also been found in Madagascar (Carroll 1978). Haubold and Schaumberg (1985), reviewing the Kupferschiefer fauna, also note the presence of a pareiasaur, *Parasaurus*, and *Nothosauravus* which they tentatively link to the aquatic diapsid *Claudiosaurus* (Upper Permian, Madagascar).

In 1870, Hancock and Howse described a small skeleton from the Marl Slate of Middridge, Durham. They compared it with known examples of *Protorosaurus speneri* and concluded that the new find was congeneric with *Protorosaurus*. The small size of the specimen, in addition to differences in rib structure and limb proportions, led Hancock and Howse to erect a new species, *P. huxleyi*. Watson (1914), however, noted differences between *P. huxleyi* and other specimens of *Protorosaurus*. Most notable were the proportions of the cervical vertebrae—short in *P. huxleyi* and elongate in *P. speneri*. On this basis, he created a new genus, *Adelosaurus*, for the *P. huxleyi* specimen, but left its taxonomic position unresolved. Huene (1956) and Kuhn (1969*b*) referred *Adelosaurus* to Broomiidae, and Romer (1966) to either Younginiformes or Protorosauridae; Vaughn (1955) left it *incertae sedis*. Haubold and Schaumberg (1985) list *P. huxleyi* as a junior synonym of *P. speneri* and omit any mention of *Adelosaurus*.

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SYSTEMATIC PALAEONTOLOGY

Class REPTILIA
?Subclass DIAPSIDA
Genus ADELOSAURUS Watson 1914

Type species. Adelosaurus huxleyi (Hancock and Howse 1870).

Holotype. G.26.49, The Hancock Museum, Newcastle upon Tyne.

Type locality. Railway cutting, 1 km south-south-west of Middridge, Durham, England (NZ 2455 2535).

Type horizon. Marl Slate (Upper Permian).

Diagnosis. A small, probably terrestrial, reptile showing the following combination of character states: amphicoelous, notochordal vertebrae with broad neural arches and low spines; no development of cervical or dorsal transverse processes; an estimated sixteen to eighteen dorsal vertebrae; gastralia present; preserved ribs single-headed; scapula and coracoid fused; scapular blade low; cleithrum probably retained; no trace of sternum; short rhomboid interclavicle with broad clavicular facets; long, almost horizontal glenoid; humerus with broad shaft but little expansion of proximal and distal ends; entepicondylar foramen present, but no trace of ectepicondylar foramen; radius and ulna of equal length; radius 64 % of humeral length; ulna lacks olecranon and sigmoid notch; ulnare and intermedium notched for perforating artery; medial and lateral centralia retained; medial centrale fails to contact distal carpals 3 or 4; metacarpals and digits short; phalangeal formula 2:3:4:(3+):3; ilium with triangular blade; long slender sigmoidal femur; tibia almost 90 % of femoral length; fibula very slender; metatarsals long.

DESCRIPTION

The reptile lies on its back (not on its belly, as described by Hancock and Howse 1870). The skull has been lost. The skull fragment mentioned in the original description is part of the pectoral girdle. A mass of bone fragments below the right arm may be part of the occiput and/or atlas-axis complex (text-fig. 1).

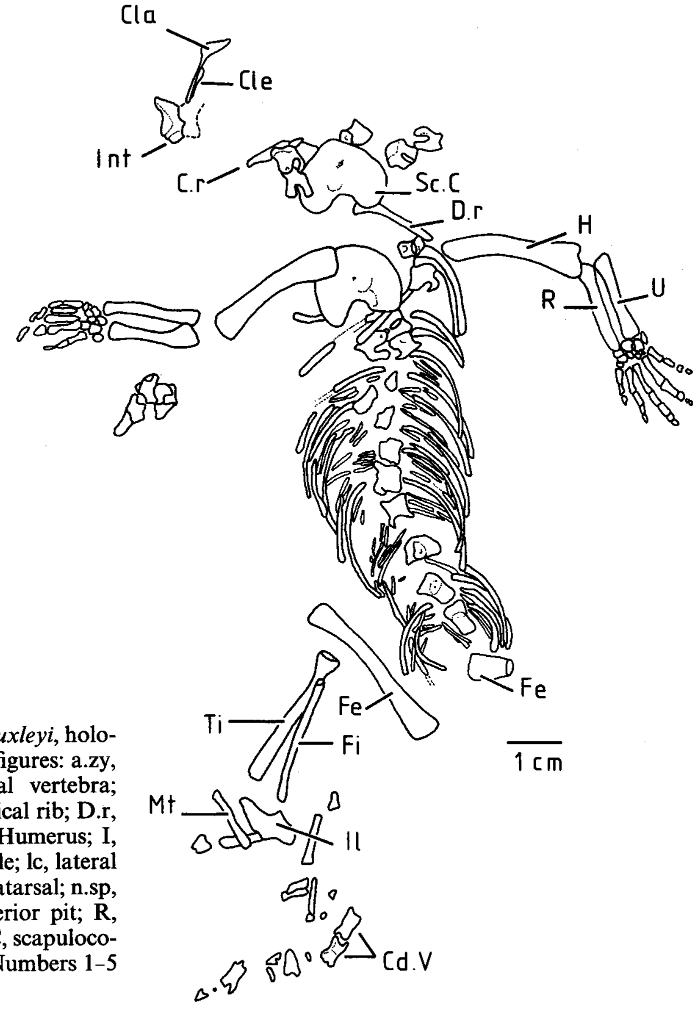
The axial skeleton. Hancock and Howse (1870) made a count of fourteen or fifteen dorsal rib pairs; there are fifteen pairs preserved. One anterior vertebra has shorter ribs associated with it and is probably a cervical (see below).

Each dorsal rib has a small single head. The proximal shaft is flattened and slightly expanded; distally it becomes more circular in cross-section. The longest ribs are in the mid-dorsal region, but towards the rear of the body they become shorter and the enclosed body cavity narrows. Between consecutive ribs, there are slender gastralia, apparently three pairs per vertebral segment. These are clearest on the left side of the body where they appear to begin between the sixth and seventh rib pair.

Because of the position of the animal at death, many of the vertebrae are seen in ventral or ventrolateral view, with the neural spines obscured by ribs and gastralia. A total of nineteen presacrals and six fragmentary caudals is preserved.

The vertebral centra are of roughly equal length. On vertebral morphology alone, it would be difficult to distinguish dorsals from cervicals, but the ribs provide a key. Each of the fourteen vertebrae at or behind the level of the proximal humeral heads is associated with a pair of long dorsal ribs. An additional five vertebrae lie clustered around the most anterior (left) scapulocoracoid. Of these, at least one may be a dorsal (the most anterior rib pair); the other four are probably cervicals. This confirms Watson's (1914) conclusion that the cervical vertebrae of *Adelosaurus* are short, in contrast to those of *Protorosaurus*. Unfortunately, these anterior vertebrae are poorly preserved. They are similar to the dorsals except that the rib facet lies slightly further back (text-fig. 2A). Hancock and Howse (1870) give a count of seven cervicals, but this was, presumably, an estimate. There are at least fifteen dorsals, one for each rib pair. The femoral heads lie just behind the last preserved presacral. The sacrum is missing, but from the diameter of the body at the end of the vertebral series, it seems unlikely that there are many missing presacrals. If the first rib preserved is that of the first dorsal, then an estimate of sixteen to eighteen dorsals seems reasonable.

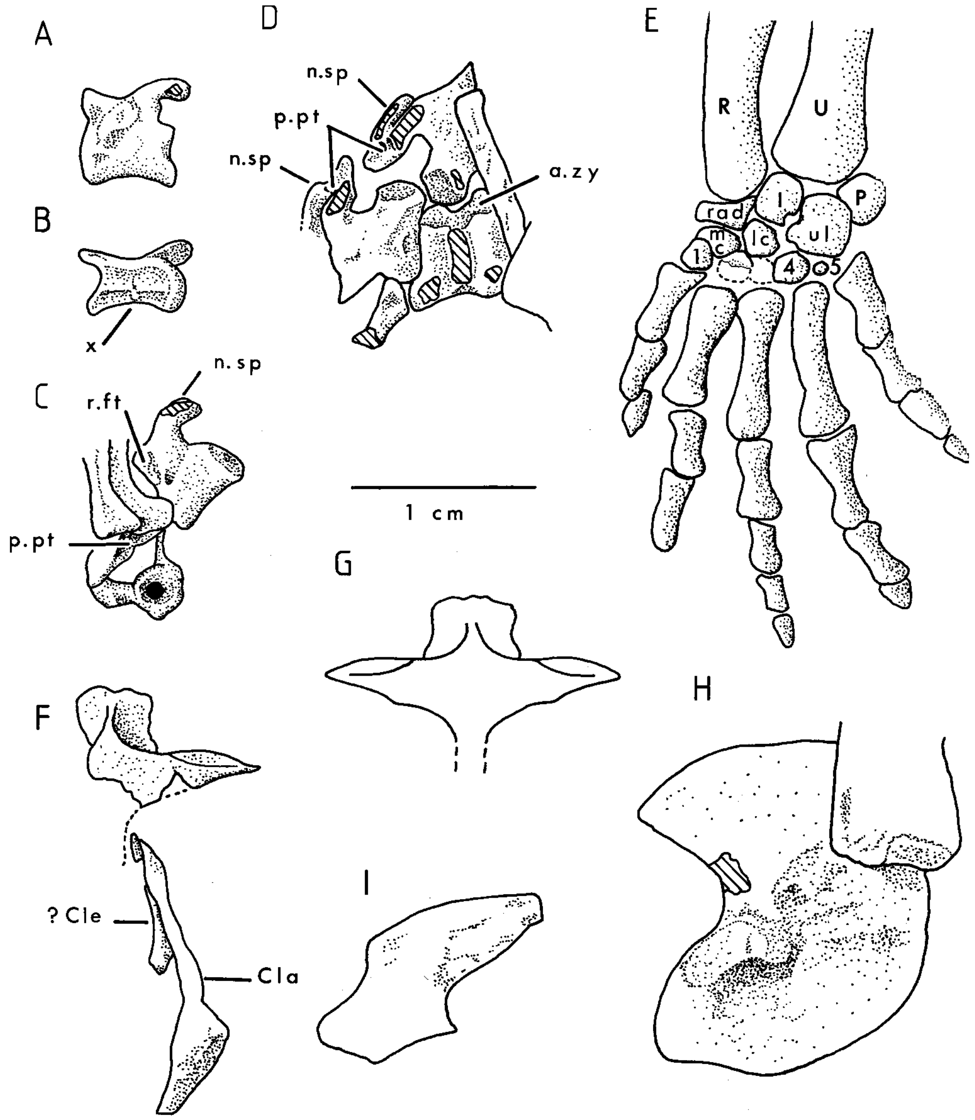
The dorsal centra (text-fig. 2C, D) are relatively short (compared, for example, with those of the contemporary



TEXT-FIG. 1. Skeleton of *Adelosaurus huxleyi*, holotype, G.26.49. Abbreviations used in figures: a.zy, anterior zygapophysis; Cd.V, caudal vertebra; Cla, clavicle; Cle, cleithrum; C.r, cervical rib; D.r, dorsal rib; Fe, femur; Fi, fibula; H, Humerus; I, intermedium; Il, ilium; Int, interclavicle; lc, lateral centrale; mc, medial centrale; Mt, metatarsal; n.sp, neural spine; P, pisiform; p.pt, posterior pit; R, radius; rad, radiale; r.ft, rib facet; Sc.C, scapulocoracoid; Ti, tibia; U, ulna; ul, ulnare. Numbers 1–5 refer to distal carpals.

glider *Coelurosauravus* (Evans 1982; Evans and Haubold 1987)). They are rounded, lack a ventral keel, and are amphicoelous—probably notochordal (text-fig. 2C). The neural arch is much wider than the centrum, so that, even allowing for some compression, the arch pedicels diverge upward in end view. There is a short low neural spine (again in sharp contrast to *Protorosaurus*), above the broad, flattened arch. The zygapophyses are almost horizontal. The posterior zygapophyses are swollen; between them, at the base of the neural spine, there is a deep pit—probably for the insertion of intervertebral ligaments. This does not, however, show the pit and tubercle arrangement found in the intervertebral facets of younginiforms (Currie 1981). The anterior zygapophyses are broad and flat. For the most part, they lie anterior to the neural spine. There are no transverse processes and the rib facet lies at the anterior edge of the arch pedicel.

Only a few caudal vertebrae are preserved, separated from the last dorsal by a gap of about 50 mm (text-fig. 1). They match the mid to posterior caudals of other genera in being cylindrical with small zygapophyses and no neural spines (text-fig. 2B). Ventrally, there is a deep groove for the caudal blood vessels. A weak line of discontinuity runs down the centrum at the mid-point of the vertebra passing on to the ventral surface and obstructing the caudal groove. This may be a developmental feature rather than a functional autotomy plane.



TEXT-FIG. 2. *Adelosaurus huxleyi*, holotype, G.26.49. A, cervical vertebra, left lateral view. B, caudal vertebra, ventrolateral view, x marks the line of discontinuity (see text). C, D, associated dorsal vertebrae. E, Left hand, dorsal view. F, interclavicle, clavicle, and possible cleithrum, ventral view. G, restoration of interclavicle, ventral view. H, right scapulocoracoid, lateral view. I, right ilium, medial view.

Most of the vertebrae are disarticulated, but in a few places there are bone fragments between adjacent centra. Watson (1914) interpreted these as tiny intercentra but they could also be fragments of ribs or gastralia.

The appendicular skeleton. The preserved parts of the pectoral girdle include the two scapulocoracoids, the interclavicle, a clavicle, and a possible cleithrum.

The interclavicle is exposed in ventral view (text-fig. 2F). The left crus is almost complete, but the right crus and the interclavicular stem are damaged leaving a few bone fragments and an incomplete impression. None the less, the bone can be partially reconstructed (text-fig. 2G). The shape is that of a short rhomboid, almost

T-shaped, with wide clavicular facets that taper laterally. Anteriorly, the clavicles are separated by a narrow spur of bone.

In association with the interclavicle, there are two slender bones (text-fig. 2F). The larger, probably the left clavicle, has a long, narrow shaft expanding into a broad terminal plate. Adjacent to its shaft, there is a fragment of a more slender bone which may be a cleithrum.

Both scapulocoracoids are preserved in lateral view (text-fig. 2H). The scapula and coracoid are fused without trace of a suture. The two parts are of roughly equal size, with a low scapular blade and a relatively short coracoid portion. This suggests that only one coracoid ossification was involved—a conclusion reached by Watson (1914) and Kuhn (1969*b*). The glenoid cavity lies at the junction of the scapula and coracoid. It is long and almost horizontal in orientation, ending anteriorly in a well-developed boss. In front of this is the coracoid foramen. There is no supraglenoid buttress.

The forelimbs are well preserved. The right arm described Hancock and Howse (1870), and figured by Kuhn (1969*b*, p. 31, fig. 14.2) is, in fact, the left. The humerus is strong with a relatively thick shaft and little proximal or distal expansion. A depressed area at the distal end of the left humerus may be a small entepicondylar foramen but there is no visible ectepicondylar groove. The joint surfaces are unfinished. Taking the length of an average dorsal vertebra as the standard, x (see Currie 1981), the length of the humerus is 5·1x.

The radius and ulna are strong and rather short (radius, 3·4x). The radius is 64 % of the humeral length. It is slightly twisted and of similar width throughout. The ulna is expanded at both ends, with the greatest width proximally but there is no sigmoid notch or olecranon (*contra* Huene 1956 and Kuhn 1969*b*).

The left hand is preserved in dorsal (extensor) view; the right in plantar (flexor) position. This accounts for small differences in detail between the two. The left hand is the more complete (text-fig. 2*e*). As in all primitive reptiles, there are three rows of carpals—proximal, central, and distal. The proximal carpal row of *Adelosaurus* contains four bones—radiale, intermedium, ulnare, and pisiform. Of these, the radiale is the smallest, with the ulnare roughly twice its size. The pisiform is nearly as large as the intermedium. Both ulnare and intermedium are notched for the passage of a perforating artery. The central carpal row contains medial and lateral centralia of roughly equal size. The medial centrale contributes to the radial border of the carpus but does not contact distal carpals (DC) 3 or 4 (*contra* Tangasauridae, see Currie 1981). There are slight differences between the two hands with respect to the distal carpal row. Distal carpals 1 and 4 are clearly preserved but rounded impressions mark the positions of 2 and 3. While it is conceivable that these carpals were simply lost, their absence in both hands when the remaining carpals are relatively undisturbed, renders this improbable. It is more likely that DCs 2 and 3 were incompletely ossified at the time of death. In the left hand, DC4 is smaller relative to DC1 than on the right, but there is a small lateral bone which may be an unfused DC5. The five metacarpals (MC) are short and stout (longest, 1·3x), with expanded ends. MC1 and 5 are of roughly equal length, followed in increasing order of size by MCs 2, 3, and 4. The proximal phalanges are even shorter. Ungual phalanges are poorly preserved on both hands, but they seem short and triangular. The phalangeal formula is 2:3:4:(3+):3.

Our knowledge of the pelvic girdle is restricted to the ilium, although, surprisingly, Kuhn (1969*b*) describes the pubis and ischium as plate-like. The ilium is, unfortunately, preserved in medial view (text-fig. 2I), its ventral border angled by facets for the pubis and ischium. The blade is directed posterodorsally and is triangular with a blunt tip. This may indicate incomplete ossification (Currie 1981). The surface is roughened for the attachment of sacral ribs. Compared to those of contemporary genera, the ilium of *Adelosaurus* is small (length 2·4x as compared to 3·5x in Younginiformes and Millerettidae).

Except for a fragment of the left femoral head, only the right hindlimb is preserved (text-fig. 1). The femur is long and slender (6·3x), with a gently sigmoid shaft. Proximal and distal ends are of nearly equal width. The femur is longer than the humerus, but is a more gracile bone. The tibia (5·4x) is nearly 90 % of the femoral length. Its proximal end is wider than the distal end, but there is no crest. The fibula, by comparison, is very slender. The foot is represented by isolated metatarsals and phalanges but there is no trace of the tarsus. The longest metatarsals (2·4x) are almost twice the length of the longest metacarpal. As a whole, the forelimb (humerus + radius) is 75 % of the length of the hindlimb (femur + tibia) but the proportions of the pro- and epipodials are different, such that while the humerus is 86 % of the femoral length, the radius is only 62 % of the tibial length.

Life stage and habit. Although the scapulocoracoid and vertebral centres are fully co-ossified, the specimen shows signs of incomplete ossification: absence of joint surfaces on the long bones; non-ossification of DCs 2 and 3; the differences in the ossification of DCs 4 and 5 in the two hands; and the blunt-ended iliac blade. This could be taken as evidence of either immaturity or an aquatic lifestyle.

In the terrestrial younginiform *Thadeosaurus* (Currie and Carroll 1984) the ossification centres of the carpals appear before the scapulocoracoid suture closes. In this respect, *Adelosaurus* more closely resembles the aquatic younginiform *Hovasaurus* (Currie 1981), where the scapula and coracoid fuse before some of the carpal centres appear. However, in *Hovasaurus*, as is common in aquatic animals, the neurocentral sutures remain open until late in life. In *Adelosaurus* and *Tangasaurus* (Currie 1981), they are closed.

On balance, it seems more likely that the skeleton of *Adelosaurus* described here is that of an immature, rather than juvenile, animal in which the body proportions are unlikely to be significantly different from those of the adult. The long, rather slender, hindlimbs suggest an agile terrestrial form. The Marl Slate and Kupferschiefer are thought to have been laid down in the relatively shallow coastal waters of the Late Permian Zechstein Sea (Smith 1970; Pettigrew 1980). In addition to fish, the deposits yield abundant plant remains suggestive of coastal forest or woodland (Pettigrew 1980; Haubold and Schaumberg 1985) which would have been home to the glider *Coelurosauravus* and some, at least, of the remaining reptiles, including *Adelosaurus*.

DISCUSSION

Adelosaurus differs from *Protorosaurus*, to which it was originally referred (Hancock and Howse 1870), in several respects, most notably the proportions of the humerus and cervical vertebrae, and the length of the dorsal neural spines. None of the known specimens of *Protorosaurus* shows a clear series of cervical and dorsal vertebrae and estimates of vertebral numbers vary. Huene (1926) and Seeley (1888) count seven cervical vertebrae, but Huene's reconstruction shows a long eighth vertebra which may also be a cervical. Similarly, estimates of dorsal numbers vary from sixteen to eighteen, although there seems to be a general agreement on sixteen dorsal ribs (Huene 1926; Seeley 1888; Haubold and Schaumberg 1985; pers. obs.). If *Adelosaurus* were a juvenile *Protorosaurus*, then we would expect elongated vertebrae in front of the first long rib. This is not the case.

The pareiasaur *Parasaurus* is known from three fragmentary specimens. It shares with *Adelosaurus* the primitive captorhinomorph condition of the vertebrae but the proportions of the two animals are quite different, even allowing for the immaturity of *Adelosaurus*. *Parasaurus* is stoutly built, with four to six sacral ribs meeting a broad iliac blade. The vertebrae are short and very wide, and there are no gastralia (Kuhn 1969*a*). *Coelurosauravus* is a highly specialized glider (Carroll 1978; Evans 1982; Evans and Haubold 1987) with long ribs and elongated cervical and dorsal vertebrae. *Nothosauravus* is represented by a single notochordal vertebra with either long transverse processes or fused ribs. Neither genus bears any resemblance to *Adelosaurus*.

Adelosaurus therefore represents a fifth member of the Kupferschiefer/Marl Slate reptilian assemblage. In the absence of the skull and ankle, however, its phylogenetic position remains equivocal. The general structure of the vertebrae, shoulder girdle, and carpus are primitive. The low neural spines, broad neural arches, short rib pedicels, notochordal centra, and barely inclined zygapophyses are primitive amniote character states (Heaton and Reisz 1986) but the slender sigmoidal femur, triangular iliac blade, and unexpanded humerus are derived states.

The Upper Permian millerettids have been linked to captorhinomorph reptiles by Gow (1972) and Heaton (1980), and it is generally agreed that they represent either modified or juvenile (incompletely ossified) anapsids (Gauthier 1984; Benton 1985; Evans 1988), although their precise relationships are still debated. *Adelosaurus* shares several character states with millerettids, including a single coracoid, loss of the supraglenoid buttress and short rhomboid interclavicle, but these states are found in other genera. *Adelosaurus* differs from millerettids in the shape of the iliac blade, the sigmoid femur, the probable retention of a cleithrum, and the proportions of the radius and humerus.

Huene (1956) and Kuhn (1969*b*) link *Adelosaurus* with *Broomia* (Middle Permian, South Africa). *Broomia* has recently been redescribed by Thommasen and Carroll (1981), who classify it as a millerettid on the basis of the anterior position of the quadrate condyles and the structure of the foot. *Adelosaurus* is more gracile than *Broomia*, and has broader clavicles. Both have a sigmoid femur. In the carpus, the ulnare of *Broomia* is long and narrow while that of *Adelosaurus* is short and broad. The perforating foramen in *Adelosaurus* passes between intermedium and ulnare, but in *Broomia* the foramen is larger and includes the lateral centrale in its borders. In both carpal characters, *Broomia* shows the more primitive condition. There is little to support a relationship between *Adelosaurus* and *Broomia*.

Broad neural arches with low neural spines are also found in pareiasaurs (discussed above) and procolophonids. Procolophonids are known from Permian and Triassic deposits world-wide. They combine primitive vertebrae with a dorsoventrally compressed body, short tail, and very short epipodials. The iliac blade has an anterior process which meets an additional sacral rib. These derived character states are not shared by *Adelosaurus*.

One feature of the *Adelosaurus* skeleton which differentiates it from the majority of primitive reptiles, including those discussed above, is the short, triangular iliac blade. With the exception of some pelycosaurs, such as *Ophiacodon* and *Dimetrodon* (in which the proportions of the humerus, neural spines and scapula blade, and the structure of the rib facets preclude relationship), this type of blade is usually found in diapsids. The Diapsida are diagnosed largely on the basis of cranial characters, most notably the possession of an upper temporal fenestra. In the absence of a skull, confirmation of diapsid status is difficult unless the specimen clearly shows the derived character states of one of the diapsid subgroups. Recent reviews of the Diapsida (Gauthier 1984, 1986; Benton 1985; Evans 1988) recognize a primary dichotomy which produced an early radiation of essentially primitive, but gracile, genera—the Araeoscelidia—on the one hand, and the majority of typical diapsids (including archosaurs, rhynchosaurs, prolacertiforms, lepidosaurs, and younginiforms) on the other. This second group has been alternatively named Sauria (Gauthier 1984, 1986) and Neodiapsida (Benton 1985). The latter term is used here.

Adelosaurus lacks the majority of diagnostic araeoscelid character states for which it could be coded: elongated cervical vertebrae; ventral keels on cervical and dorsal vertebrae; neural arches with deep lateral excavations; elongated coracoid process for triceps; radius nearly equal in length to the humerus (Reisz *et al.* 1984). Of fourteen neodiapsid character states (Evans 1988), *Adelosaurus* can be coded for only four: single coracoid, loss of the supraglenoid buttress, slender sigmoidal femur, and absence of an ossified olecranon and sigmoid notch, although the last could reflect immaturity. *Adelosaurus* stands in much the same position as the contemporary South African genera *Galesphyrus* and *Heleosaurus* whose diapsid status is equally tenuous. These genera are provisionally classified as early offshoots from the diapsid stem (Benton 1985; Evans 1988) since they lack the diagnostic character states of any major diapsid group. Placed with them is *Claudiosaurus* from the Upper Permian of Madagascar. This genus has been described as a sauropterygian ancestor allied to younginiforms (Carroll 1981). It is a diapsid, but it lacks the derived character states of the Younginiformes, as diagnosed by Currie (1982). *Claudiosaurus*, like *Adelosaurus*, *Galesphyrus*, and *Heleosaurus*, has broad vertebrae with low neural spines—confirming that this primitive condition can be found in early diapsids. It differs from *Adelosaurus* in the elongation of the cervical and dorsal vertebrae, the less expanded clavicles, and the greater width of the distal humeral head. *Adelosaurus* resembles tangasaurid younginiforms in the general proportions of the scapulocoracoid and limbs, and in the possession of short cervical vertebrae, but it lacks younginiform character states (Currie 1982; Evans 1988) including the specialized intervertebral joints, long radius, contact between medial centrale and DC4, and the presence of an ossified sternum.

Adelosaurus clearly lies at a similar evolutionary level to primitive diapsids, but it lacks the diagnostic character states of any known genus or group and its inclusion within the Diapsida remains provisional until further material is recovered.

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