

New information on the pectoral girdle and vertebral column in *Lupeosaurus* (Reptilia, Pelycosauria)

STUART S. SUMIDA¹

Department of Biology, University of California, Los Angeles, Los Angeles, CA 90024, U.S.A.

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UCLA VP 1651, a new specimen from the Lower Permian Admiral Formation of Archer County, Texas, provides information on heretofore unknown portions of the postcranial skeleton of the large pelycosaur *Lupeosaurus*. Presacral neural spines are elongate and have a subcircular cross section. Laterally directed tubercles are not present on any of the neural spines. Cervical vertebrae appear to have elongate neural spines and sharply keeled centra. Transverse processes are positioned relatively high above the bases of the centra through the length of axial column. The pattern of tilting of the neural spines is similar to that in the primitive edaphosaur *Ianthasaurus hardesii*. The proximal end of the first sacral rib contributes significantly to the intervertebral articular facet usually formed by the centra. The sacral ribs do not appear to fuse with one another distally. The ventral clavicular plate is greatly expanded anteriorly. The posterior edge of the subcoracoscapular fossa is very well defined. The available morphological information does not warrant a separate familial designation for the genus *Lupeosaurus*. Despite the lack of laterally directed tubercles of the neural spines, *Lupeosaurus* appears to be referable to the Edaphosauridae. However, in the absence of cranial materials, this association must remain tentative. Although this description adds new information for only a restricted portion of the skeleton, it does appear to confirm the existence of a distinct, albeit rare, pelycosaur from the extensively studied fauna of the Lower Permian.

Un spécimen nouveau, UCLA VP 1651, récupéré dans la Formation d'Admiral du Permien inférieur, dans le comté d'Archer, Texas, fournit des enseignements sur des parties, inconnues jusqu'à présent, du squelette procrânien du grand pélycosaure *Lupeosaurus*. Les neurépinés présacrals sont allongés et sont subcirculaires en coupe transversale. Aucune des neurépinés ne porte des tubercules dirigées latéralement. Les vertèbres cervicales sont munies de neurépinés allongés avec centre à crêtes aiguës. Des excroissances transversales sont localisées en position relativement élevée au-dessus des bases des centres, tout le long de la colonne axiale. Le mode d'inclinaison des neurépinés est analogue à celui observé chez l'édaphosaure *Ianthasaurus hardesii*. La terminaison proximale de la première côte sacrale contribue significativement à la facette articulaire intervertébrale formée habituellement par le centre. Les côtes sacrales ne semblent pas se fusionner l'une à l'autre dans leur prolongement. La plaque claviculaire ventrale antérieure est grandement développée. L'arête postérieure de la fosse subcoracoscapulaire est très bien définie. Les connaissances morphologiques actuelles ne justifient pas une désignation familiale distincte pour le genre *Lupeosaurus*. En dépit de l'absence de tubercules dirigées latéralement sur les neurépinés, l'espèce *Lupeosaurus* est tout de même considérée ici comme appartenant aux Edaphosauridés. Cependant, à cause du manque de matériaux crâniens, cette association pourrait bien être révisée ultérieurement. Quoique les nouveaux enseignements fournis par cette description soient limités à une portion restreinte du squelette, ils supportent l'existence d'un pélycosaure distinct, cependant rare, dans la faune très étudiée du Permien inférieur.

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Introduction

The relationships of primitive reptiles, particularly the most primitive of the mammal-like reptiles, or Pelycosauria, have been the subject of considerable attention recently (Reisz 1980; Brinkman and Eberth 1983; Carroll 1986). Most of the recent work on pelycosaurs takes as its departure point the work of Romer and Price (1940), a work that still provides much of the framework for the accepted relationships of the group. Despite the fact that more recent studies have refined (and in some cases redefined) many of the phylogenetic conclusions of Romer and Price, certain taxa remain poorly characterized. Among the more enigmatic of pelycosaurs is the large Early Permian form *Lupeosaurus*.

Romer (1936) erected the genus *Luperosaurus* based on what was supposed to have been the type specimen of "*Dimetrodon gigas*." He noted that it appeared to be intermediate between the genera *Dimetrodon* and *Edaphosaurus*. However, it was actually a referred specimen. Further, it was referred to what is probably a synonym for the labyrinthodont

amphibian *Eryops*. Subsequently, Romer (1937) presented a revised preliminary description of this large Early Permian pelycosaur, renaming it *Lupeosaurus kayi* and describing it as very similar to *Edaphosaurus* but lacking the characteristic, laterally directed tubercular cross bars on the neural spines (Fig. 1). Later, in a more detailed account, Romer and Price (1940) erected the family Lupeosauridae for reception of the genus. Although Romer and Price (1940) considered the genus deserving of familial distinction, they noted that it might be referable to the Edaphosauridae, possibly even antecedent to it.

The above descriptions of *Lupeosaurus kayi* were based on incomplete, postcranial materials. These included portions of the presacral, sacral, and anterior caudal regions of the vertebral column, the endochondral shoulder girdle, most of the pelvic girdle, humerus, femur, parts of the radius and tibia, and other scattered elements. Romer and Price (1940) noted that, although the exact locality was lacking, most of the materials assignable to *Lupeosaurus* had been recovered from what they termed "the lower part" of the Lower Permian Wichita deposits of north-central Texas. Included in this designation were remains (from oldest to youngest) from the

¹Present address: Department of Anatomy, University of Chicago, 1025 East 57th St., Chicago, IL 60637, U.S.A.

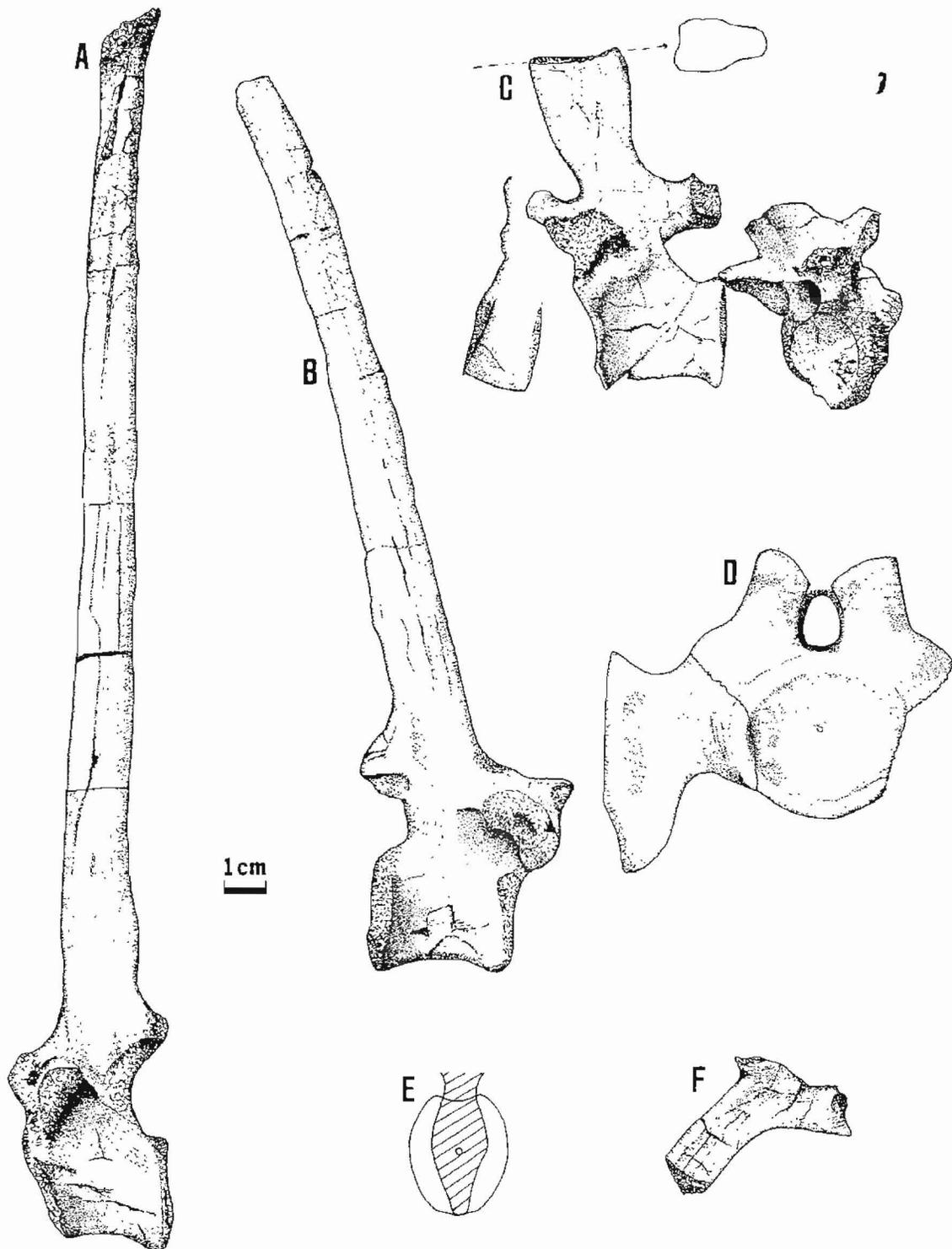


FIG. 1. UCLA VP 1651, axial structures in *Lupeosaurus* cf. *L. kayi*. (A) Mid-dorsal vertebra, left lateral aspect; dorsal end of the neural spine is missing. (B) Posterior dorsal vertebra, right lateral aspect; dorsal end of the neural spine is missing. (C) Portions of three posterior cervical vertebrae. Anteriormost of the series is only partially preserved. Middle member of the series is seen in left lateral aspect. Arrow is directed to outline representation of the neural spine cross section. Posteriormost member of the series is seen in anterolateral (left) aspect. Neural spines are missing in all three. (D) Partial reconstruction of first sacral vertebra and associated right rib, anterior aspect. Neural spine is not restored. (E) Transverse section (crosshatched) through the centrum of a cervical vertebra to demonstrate the extent of the ventral keel. The outline of the posterior end of the centrum is superimposed. (F) Left dorsal rib head, posterior aspect. Dotted lines indicate approximate extent of capitular head and direction of costal shaft.

Moran, Putnam, and Admiral formations (see also Heaton (1979) and Romer (1958, 1974) for chronostratigraphic comparisons).

No new information regarding this large and enigmatic pelycosaur has been published since its familial description (Romer and Price 1940). In 1963, W. Dalquest collected a small quantity of bone from a surface exposure in the Lower Permian Admiral Formation near Lake Kickapoo, Archer County, Texas. He sent the specimen to the vertebrate paleontology collections of the University of California at Los Angeles (UCLA VP), where P. Vaughn identified it as *Lupeosaurus* cf. *Lupeosaurus kayi*. This identification was later confirmed by A. S. Romer. The specimen (UCLA VP 1651) was found within the previously established stratigraphic range attributed to *Lupeosaurus* and based on this and the morphological information presented below appears to be clearly assignable to the genus *Lupeosaurus*. The specimen, a single individual, provides new information concerning the dermal shoulder girdle, the presacral, and the sacral regions of the vertebral column, including the structure of the curiously elongate neural spines. It also includes part of the scapulocoracoid, a badly weathered femur, and a tentatively associated phalangeal element.

Morphological description

To compare the relative sizes of structures in closely related groups of mature organisms (especially pelycosaurs), the linear measures have been divided by the orthometric linear unit (referred to here simply as "unit" or OLU of Romer and Price 1940) (Romer 1948; Currie 1978; Berman 1979). It takes as a standard of comparison the average measure of the radii of mid-dorsal and posterior dorsal vertebrae raised to the two-thirds power. Its use is based on the assumptions that the vertebrae act as a series of weight-bearing devices and that the cross-sectional area of vertebral centra, proportional to the measure of the radius squared, would be a function of that weight. Further, the volume of the body varies as the cube of radial measure; thus the cube root would be a reasonable reflection of that measure in linear terms. In the case of UCLA VP 1651, the OLU is 5.6 mm^{-1} . Reference to this measure will be made through the course of the following description.

Axial skeleton

Cervical vertebrae in *Lupeosaurus* are only poorly known, and no neural spines from this region were available to Romer and Price (1940). A series of three vertebrae from UCLA VP 1651 appears to represent the posteriormost cervical vertebrae (Fig. 1C). Only the middle member of the series is well preserved. Its centrum is approximately 30 mm long (5.3 units) and is comparable to the dorsal vertebrae in width. However, the width of the centrum anterior to it is only about 85% that of the dorsal centra. The cervical centra have a distinct mid-ventral keel; transverse sections through the middle of the centra are almost diamond-shaped in outline (Fig. 1E). The anterior and posterior lips of the cervical centra are sharper than those of the dorsal vertebrae. As indicated by Romer and Price (1940), the transverse processes are located relatively high above the ventral margin of the centrum, 7.5 units in the case of UCLA VP 1651. As in the type specimen and other materials assigned to *Lupeosaurus* (Romer and Price 1940), this relatively high position of the transverse processes

appears to be conspicuous in the cervical region as well as in other parts of the column.

The proximal portions of the cervical neural spines are broadly oval and just slightly constricted anteroposteriorly at their base. As in *Edaphosaurus*, the bases of the neural spines tilt forward relative to the centra and neural arches — at an angle of 20° in UCLA VP 1651. Portions of at least eight different neural spines are preserved with the scapulocoracoid in UCLA VP 1651 (Fig. 3A). The association suggests that at least some of the spines are probably cervical neural spines. The spines cannot be removed from their association with the scapulocoracoid because of the particularly recalcitrant matrix. Despite this, they do indicate that the anterior and posterior furrows typically found in more posterior neural spines are either absent or only weakly developed. The lengths of the fragments suggest that the posterior cervical neural spines may have been 31 or more units in length. Closer to their bases, the spines take on a more triangular outline in cross section (Fig. 1C).

UCLA VP 1651 includes two well-preserved dorsal vertebrae, each missing only the distal end of the neural spine (Figs. 1A, 1B), and another more fragmentary dorsal vertebra. Both of the better preserved vertebrae appear to be from the mid-dorsal region of the vertebral column. The centra are 26 mm (specimen in Fig. 1A) and 27 mm (specimen in Fig. 1B) in width, measured at the posterior articular surfaces. The anterior and posterior lips of the centra are chipped, but the greatest lengths of the centra appear to have been 37 and 35 mm (approximately 6.6 and 6.3 units), respectively. These measures are closely comparable to those reported by Romer and Price (1940) for anterior dorsal and mid-dorsal vertebrae of a specimen that they interpreted as a female of *L. kayi*. The centra are deeply amphicoelous, and although worn, their anterior and posterior articular faces appear to have had heavy lips. The pedicels are located over the anterior portion of the centra in a manner similar to that in *Edaphosaurus* and most other pelycosaurs. The transverse processes are essentially like those in *Edaphosaurus*. The neural arches are tall and narrow and show no evidence of neuro-central sutures or lateral excavations.

The most conspicuous feature of the dorsal vertebrae in *Lupeosaurus* is the elongate nature of the neural spines. They are not complete in either of the vertebrae illustrated in Fig. 1, but they were obviously quite long. Mid-dorsal neural spines appear to have been at least 55 units in length. Portions of at least a dozen other neural spines are preserved in UCLA VP 1651. In addition to *Lupeosaurus*, a number of pelycosaurian genera exhibit elongate neural spines. Included among them are *Dimetrodon*, *Secodontosaurus*, *Edaphosaurus*, *Ianthasaurus*, and *Ctenospondylus*. Because there are a variety of long-spined pelycosaurs, an understanding of the differences in neural spine morphology would facilitate interpretation of the condition in *Lupeosaurus*. Its neural spines lack laterally directed tubercles, thus differing markedly from those in *Edaphosaurus* and *Ianthasaurus*. In *Lupeosaurus*, furrows run the length of the anterior and posterior aspects of the spines and are more deeply developed in the vertebrae from the mid-dorsal region of the axial column. However, the furrows are not as deep as those of most species of *Dimetrodon* (an exception is *Dimetrodon milleri*, Romer and Price 1940); the neural spines in *Lupeosaurus* are essentially subcircular in cross sec-

tion, and they do not take the shape of a "figure 8" as in *Dimetrodon*. The tail neural spines in *Ctenospondylus* are more laterally compressed and blade-like than those in *Lupeosaurus* or other long-spined pelycosaurs (Vaughn 1964; Berman 1978). The elongate neural spines in *Secoگونotosaurus* were only tentatively referred to that form (Romer and Price 1940), and a definitive statement about their structure awaits a more detailed reexamination of the genus.

The relative postures of the neural spines in *Lupeosaurus* are similar to those reported for the primitive edaphosaur *Ianthasaurus hardestii* by Reisz and Berman (1986). Cervical neural spines appear to project forward at an angle of about 20° relative to the vertical axis of the vertebra (Fig. 1C), the mid-dorsal spine extends directly dorsally (Fig. 1A), and the posterior vertebra angles caudally (Fig. 1B) (Romer and Price 1940, Fig. 69). The sail connecting the elongate neural spines appear to have been strong enough to support spines even when broken. At least one of the isolated neural spine fragments possesses a healing callus that could only have developed if the two portions of the spine had remained in contact.

The number of sacral vertebrae in *Lupeosaurus* is not known. UCLA VP 1651 includes the first and second sacral vertebrae, but the possible presence of a third cannot be determined with certainty. As expected, the first sacral (Fig. 1D) is quite robust. The centrum is short in comparison with those of the presacrals but is much wider. Posterior to the articulation of the sacral ribs, the sacral centrum is laterally constricted, its mid-ventral surface forming a longitudinally oriented strut. The pedicel and anterolateral surface of the sacral centrum are dominated by the articulation of the large sacral rib. Posterodorsally, the articulation is heavily buttressed. The anterior zygapophyses are supported by thick, dorsomedially tilted, bony columns. The configuration of the second sacral vertebra is like that of the first, with a few proportional differences: the anterior zygapophyses are set closer to the sagittal plane, the costal articulations are smaller, and the sides of the centra are not so deeply constricted. Neural spines are not preserved in either of the sacral vertebrae.

The first pair of sacral ribs are typically stout and extend almost directly laterad. The costal shaft is quite short, yet it is constricted between its articular heads (Fig. 1D). Anteriorly, the proximal end of the first sacral rib contributes substantially to the intervertebral articular facet usually formed by the centrum (Fig. 1D). The attachment of the rib to the sacral centrum appears to have been a firm ankylosis, as evidenced by the fact that the left sacral rib was broken at mid-shaft and not at the articulation. The iliac articulation is a broad, flat face directed almost exclusively laterally. It is subcircular in outline. As in *Edaphosaurus* and caseids (Romer and Price 1940; Stovall *et al.* 1966), the sacral ribs do not appear to fuse distally. The synapophysis for the second sacral rib is only about 40% the size of the first.

The neural spines of the anterior caudal vertebrae are somewhat triangular at their bases. Otherwise, the caudal vertebrae preserved with UCLA VP 1651 add little information to that already evident in the illustrations provided by Romer and Price (1940, Pl. 43, figs. A-C).

A single dorsal rib head is preserved in UCLA VP 1651 (Fig. 1F). It is similar in general proportions to those in *Edaphosaurus*; however, a small tubercular articulation may be distinguished from the costal shaft. The costal shaft does not curve as distinctly dorsad as do those in *Edaphosaurus*. As

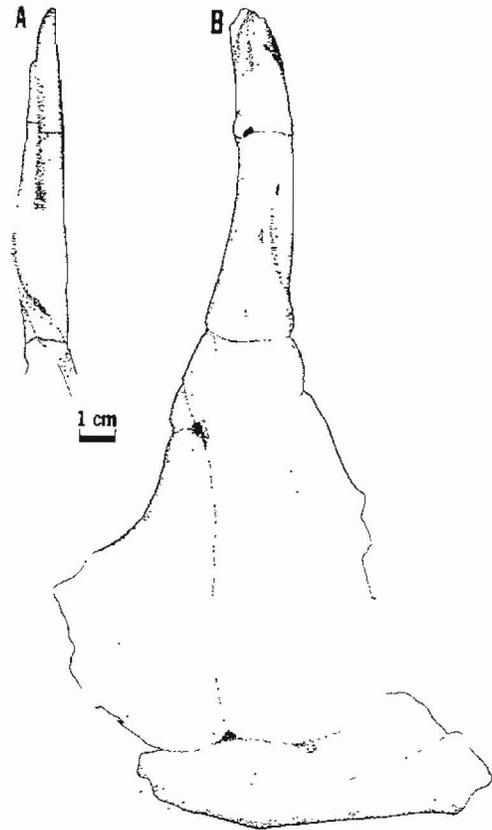


FIG. 2. UCLA VP 1651, *Lupeosaurus* cf. *L. kayi*. (A) Left clavicle, posterior aspect of dorsal clavicular stalk. (B) Left clavicle, lateral (outer) aspect. Dotted lines indicate presumed extent of the clavicle in life.

only a small portion of one rib is preserved, and assignment to a specific region of the column is difficult, the significance of these differences cannot be determined with confidence.

Appendicular skeleton

UCLA VP 1651 includes most of the left clavicle with little postmortem distortion (Fig. 2), the majority of the left scapular blade, a very small portion of the coracoid plate, and the anterior half of the glenoid articular fossa (Fig. 3). Except for a fragment of a cleithrum that may be referable to the genus (Romer and Price 1940), elements of the dermal shoulder girdle had been previously unknown for *Lupeosaurus*, and a more complete picture of the pectoral girdle may now be presented.

In a manner conspicuously like that in edaphosaurs, the clavicle is widely expanded ventrally. If only the preserved portion of the clavicle is considered, it measures almost 17 units across the ventral plate. This figure falls toward the upper limit of the range for edaphosaurs and is much larger than in sphenacodonts. Additionally, the broken anteromedial edge of the ventral clavicular plate is extremely thick and robust, and the anterodorsal edge is thickened and directed almost directly medially, indicating that it extended even farther forward. If the missing portions of the specimen were restored, the measure across the ventral clavicular plate would be even greater (Fig. 2). The width of the ventral clavicular plate is one of the more obvious characters that tends to ally *Lupeosaurus* with edaphosaurs.

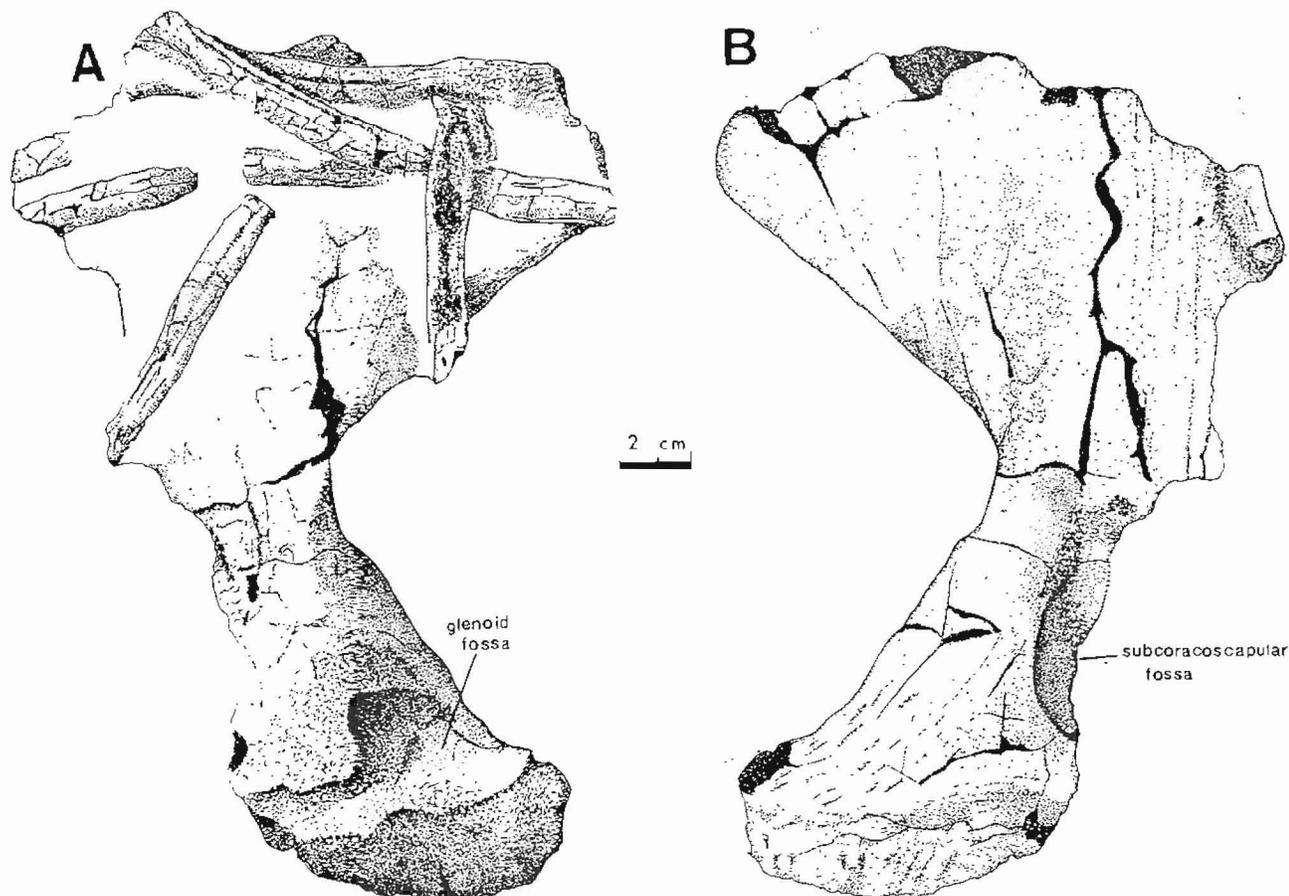


FIG. 3. UCLA VP 1651, *Lupeosaurus* cf. *L. kayi*, partial left scapulocoracoid. (A) Lateral (outer) aspect. Portions of neural spines and matrix (represented by white unshaded area) obscure most of the upper portion of the blade. (B) Medial (inner) aspect. Dotted lines indicate presumed extent of scapula in life. Estimation of scapular extent based in part on Romer and Price (1940).

Ventrally, the edge of the clavicle diminishes in thickness to what was probably a broadly overlapping joint with the interclavicle. The posterior edge is chipped but appears to have been fairly thin. The dorsal stalk of the clavicle is a laterally compressed extension above the ventral clavicular plate. It is stout, its posterior aspect providing a sturdy tongue-and-groove articulation for the dorsal scapular blade (Fig. 2). Anteriorly, no distinct marks for attachment of the cleithrum are preserved.

Almost the entire dorsal edge of the scapular blade is preserved. If postmortem breakage and separation are taken into account, it is approximately 22 units long. This is slightly larger than even in those specimens of *Lupeosaurus* described by Romer and Price (1940) and, as is characteristic of *Lupeosaurus*, relatively longer than in most other pelycosaurs. The lateral face of the scapula in UCLA VP 1651 is obscured by the neural spines preserved with it; however, there is no reason to doubt that it was probably a fairly smooth surface, as reconstructed by Romer and Price (1940). The medial surface of the scapula is completely free of matrix. It clearly demon-

strates the broadly flared nature of the blade (Fig. 3B) and the acute caudal angulation of the posterior margin (Romer and Price 1940, Pl. 44). The posterior half of the medial surface is characteristic by a broad, gently convex fossa, at least some of which may have provided a portion of the origin for the subcoracoscapularis muscle.

The supraglenoid foramen is not preserved in UCLA VP 1651, an indication of its placement anterior to the supraglenoid buttress. The supraglenoid buttress is a thick pillar of bone, almost six units in medio-lateral measure. The bone of the lateral surface is poorly preserved and does not allow further description. The medial aspect of the buttress is characterized by coarse striations, a marked contrast to the smooth internal surface of the dorsal scapular blade. The striations run dorsoventrally, turning caudally after passing posterior to the subcoracoscapular fossa. The posteriormost edge of the fossa is preserved. It is clearly defined by a lip of uniformly finished bone and is lunate in shape.

Only the anterodorsal portion of the glenoid articulation is available for study in UCLA VP 1651, and the surface is of

marginal preservation (Fig. 3A). The anterior glenoid convexity (terminology of Jenkins 1971) appears to be similar to that in *Dimetrodon* (Romer and Price 1940; Jenkins 1971). Although the poor preservation makes interpretation difficult, a narrow depression appears to border the glenoid convexity ventrally. This depression is continuous with the more concave, posterior portion of the glenoid articulation. Romer and Price (1940) noted that the glenoid was a relatively long structure in *Lupeosaurus*; however, not enough is preserved in UCLA VP 1651 to allow further comment or comparison. Deep to the glenoid articulation, the scapulocoracoid bulges conspicuously in the medial direction, giving the pectoral girdle a sigmoid outline in posterior view.

Included in UCLA VP 1651 is a very poorly preserved left femur. It compares in general proportions with the femur illustrated for *Lupeosaurus* by Romer and Price (1940). Its incomplete nature and weathered surface do not allow a detailed treatment of its structure, but its general shape and proportions do not preclude assignment of the specimen to *Lupeosaurus*. One questionably associated distal phalangeal element is also included with UCLA VP 1651. It is broad, flat, and very short. Distally, it has the shape of a splayed wedge and is not claw-like.

Although this description adds new information for only a restricted portion of the skeleton, it does appear to confirm the existence of a distinct, albeit rare, pelycosaur from the extensively studied fauna of the Early Permian.

Summary and discussion

Recently, Reisz (1980) questioned the validity of the *Lupeosauridae*, relegating *Lupeosaurus* to a position of incertae sedis within the Pelycosauria. However, its marked similarity to *Edaphosaurus* remains striking. Thus, their potential relationships must be considered. *Lupeosaurus* and *Edaphosaurus* share a conspicuous expansion of the ventral plate of the clavicle. The clavicles of edaphosaurs are among the largest of those in pelycosauria, and the clavicle in *Lupeosaurus* ranks among the largest of those forms displaying such an expansion. In both genera, this expansion is achieved by a high degree of development of the anteromedial portion of the ventral clavicular plate. No other pelycosaurian genera approach edaphosaurs or *Lupeosaurus* in their degree of development of this portion of the dermal shoulder girdle. Some caseids also have a relatively large ventral clavicular plate, but they are not as large as those in *Lupeosaurus* or *Edaphosaurus*; further, caseids do not possess the extremely elongate neural spines found in either of these genera.

The structure of the subscapulocoracoid fossa in *Lupeosaurus* is more similar to that in edaphosaurs than that in other pelycosauria. However, it is deeper and has a more sharply defined lunate posterior margin. The broadly flared dorsal margin of the scapular blade in UCLA VP 1651 is a condition that tends to separate it from *Edaphosaurus* while being conspicuously similar to the condition in the type of *Lupeosaurus*.

Structures of the vertebral column also bear mention in a consideration of the relationships of *Lupeosaurus*. Dorsal neural spines and the distal portions of cervical neural spines are subcircular in cross section. This condition is not unique to *Lupeosaurus*, nor is the possession of ventral keels on the vertebrae. Subcircular neural spines are found in a variety of reptiles and advanced anthracosaurian amphibians, as are keeled centra. The limitation of ventral keels to the cervical

region in *Lupeosaurus* is a primitive condition that it shares with *Edaphosaurus* and other pelycosauria.

The orientations of the neural spines in the cervical, mid-dorsal, and posterior dorsal regions of the presacral column are similar to those found in the primitive edaphosaur *Ianthasaurus* (Reisz and Berman 1986). The cervical spines are tilted forward about 20° relative to the vertical axis of the centrum, those of mid-dorsal vertebrae project almost directly upward, and the posterior neural spines angle caudally. Although previously unknown, the cervical neural spines apparently were quite elongate. Further, the shortening of cervical centra relative to those of the more posterior dorsal series parallels that pattern seen in *Edaphosaurus*. As in *Euphrosaurus*, the anterior zygapophyses are located at a level relatively high above the ventral margin of the centra — approximately seven to eight units. The sacral ribs in *Lupeosaurus* remain unfused distally, a similarity to the condition in caseids and apparently *Edaphosaurus* (Romer and Price 1940).

Although *Lupeosaurus* shares a number of traits with *Edaphosaurus* and *Ianthasaurus*, certain differences remain. The most striking is its lack of laterally projecting tubercles of the neural spines. The Edaphosauridae is currently defined by, among other things, these lateral tubercles. However, Reisz and Berman (1986) observed that such tubercles are absent on the posterior neural spines of the primitive edaphosaur *Ianthasaurus*. They further speculated that the primitive condition for the vertebral column in edaphosaurs might be a complete lack of such tubercles. Additionally, the tubercular process of the rib is more strongly developed in *Lupeosaurus* than in *Edaphosaurus*. Reisz and Berman considered the lack of a tubercular process a derived feature of *Edaphosaurus* relative to the more primitive *Ianthasaurus*.

Lupeosaurus combines a mosaic of derived and primitive features. Although it may be closely related to *Edaphosaurus* and *Ianthasaurus*, it is clearly more primitive, especially in its lack of laterally projecting tubercles of the presacral neural spines. Because of the absence of diagnostic cranial materials, suggestions of phylogenetic relationship may only be tentative; however, the following evaluations are offered. It appears that Reisz (1980) was correct in pointing out that a familial distinction for *Lupeosaurus* relative to other pelycosaurian genera is not justified. With the addition of new information from the dermal shoulder girdle and the vertebral column, *Lupeosaurus* appears to be more closely related to members of the Edaphosauridae. Of the characteristics observable in UCLA VP 1651, similarities include (i) elongate neural spines, (ii) a similar angulation of the neural spines relative to the vertebral bodies, (iii) the relatively high position of the transverse processes relative to the vertebral bodies, (iv) relatively small size of the cervical centra compared with the rest of the centra, and (v) the expanded ventral clavicular plate. *Lupeosaurus* shares the last characteristic with some caseids as well, but no caseids possess both the large ventral clavicular plate and elongate neural spines. Conversely, many pelycosaurian genera exhibit elongate neural spines, but none have the expanded ventral clavicular plate. As presently defined (Reisz and Berman 1986), *Lupeosaurus* would be excluded from the Edaphosauridae because of the lack of lateral tubercles of the neural spines; however, as noted by Berman and Reisz (1986), this character might not apply to the most primitive members of the family. In light of these conditions and the inappropriateness of maintaining a separate family for the reception of *Lupeosaurus*, it is tenta-

tively referred to the Edaphosauridae here, presumably as a very primitive member of that grouping. Although similar to *Edaphosaurus* in many ways, *Lupeosaurus* appears to be generically distinct by virtue of its possession of a widely flared dorsal scapular blade, the lack of laterally projecting tubercles of the neural spines, and what is apparently the most exaggerated expression of the large ventral clavicular plate among the edaphosaurs.

Because of the lack of diagnostic cranial material in *Lupeosaurus* and the incomplete nature of the preservation of the shoulder girdle in *Ianthasaurus*, the referral of *Lupeosaurus* to the Edaphosauridae remains tentative, and a new familial definition is not offered at this time. A better understanding of the most primitive members of the Edaphosauridae has been provided by Berman and Reisz (1986), but a clear picture of how *Lupeosaurus* is related to other edaphosaurs awaits the discovery of cranial materials referable to this genus, as well as more complete specimens of the small, primitive edaphosaur *Ianthasaurus*. *Ianthasaurus* still appears to provide the best model for primitive edaphosaurs, whereas *Lupeosaurus* probably represents the end point of an early offshoot from some primitive type of "edaphosaurid" stock.

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