VERTEBRATA

PETROLACOSAURUS KANSENSIS LANE, A PENNSYLVANIAN REPTILE FROM KANSAS

By FRANK E. PEABODY

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ILLUSTRATIONS

1. Assistant Professor of Zoology, University of Kansas.

ABSTRACT

The osteology, relationships and environment of *Petrolacosaurus kansensis* Lane, a primitive reptile from the Late Pennsylvanian strata of Kansas, is described and discussed. Heretofore, topotypic individuals of the species have been described briefly as representing two genera, *Petrolacosaurus* and *Podargosaurus*—a pelycosaur and an araeoscelid, respectively. The latter genus is here placed in synonymy with the former.

It is concluded that *Petrolacosaurus kansensis* represents a new family of primitive reptiles showing relationships which place it at the base of the Eosuchia while also evidencing strong relationships with primitive cotylosaurs. *P. kansensis* is a purely terrestrial reptile, an inhabitant of a conifer-pteridosperm environment, but preserved by rafting in lagoonal deposits in association with land plants, and land and marine invertebrates.

INTRODUCTION

In 1945 Professor H. H. Lane, of the University of Kansas, published a short description of two new reptiles from Pennsylvanian strata of Kansas. This report followed others by R. C. Moore, N. D. Newell, M. K. Elias, F. M. Carpenter and C. W. Hibbard on the geology, invertebrate and fish fauna, and terrestrial flora of the locality producing the reptilian remains. The geological report (Moore *et al.*, 1936) is of particular importance because the age of the fossil-bearing beds is clearly demonstrated to be Pennsylvanian, rather than Permian, as first indicated by the land plants.

On joining the staff of the University of Kansas in 1948, I became interested in the reptilian remains because of their age and rich faunal and floral associations. Discovery of important additional material in the University of Kansas Museum of Natural History whetted interest, and Professor Lane, now emeritus, graciously allowed me to take over and enlarge upon his original study of the reptiles.

Rarity of Pennsylvanian reptiles justifies full illustration of skeletal parts. Thus, much time has been spent on careful preparation of specimens under the microscope, and drawings are presented for most of the specimens, including new drawings of specimens figured by Lane (1945). Photographs prove

unsatisfactory, since the delicate bone and matrix are nearly the same color. Immersion in ethyl acetate was tried in order to heighten photographic contrast, but did not solve the problem. Use of this wetting agent enhances visual study considerably, however.

For comparative material I am indebted to Drs. Everett C. Olson and Rainier Zangerl, who made available to me the original specimens of *Araeoscelis* and *Mycterosaurus* in the Chicago Natural History Museum. Dr. Willis J. Stovall, of the University of Oklahoma, kindly gave permission to collect amphibian and reptilian material from one of his localities, the rich Permian fissure deposits near Fort Sill in western Oklahoma. The reptiles in particular have been of the utmost value as comparative material. Dr. Robert W. Wilson, curator of fossil vertebrates in the University of Kansas Museum of Natural History, has contributed much in thoughtful co-operation and in critical reading of the manuscript. Mr. Victor Hogg, a talented student in Fine Arts at the University, has ably assisted me with illustrations. Original drawings made by me are greatly enhanced by his inking technique, and Figures 10, 11 and Plate 3 are his own, made under my supervision.

GEOLOGICAL OCCURRENCE

Few fossiliferous rocks rival the rich diversity of the shales containing *Petrolacosaurus*. Associated with this Pennsylvanian reptile are the remains of approximately 20 genera of land plants, 5 genera of land-dwelling arthropods, 10^2 genera of marine invertebrates, a genus of coelacanth fish, and possibly tetrapod footprints.

N. D. Newell discovered the fossiliferous shales in the course of geological mapping in 1931. They are exposed in a roadcut near the north bank of Pottawatomie Creek, 6 miles northwest of Garnett, Kansas (Section 32, T. 19 S., R. 19 E.). The shales dip gently westward, as do the underlying and overlying strata. According to Newell's map and section (Moore *et al.*, 1936), the shales form a thin lens having only local outcrop and a maximum thickness of 10 feet. A disconformity delimits the shales below and above.

Fossil plants from the Garnett locality aroused immediate interest, for they exhibit a decided Permian aspect not expected in strata considered to be deep in the Pennsylvanian section. Subsequent geological and paleontological investigation by Moore, Elias & Newell (1936) demonstrated clearly that the land plants from Garnett represent a "Permian" facies in the Pennsylvanian of Kansas.

At the time of the first reports, the Missourian Series, which includes the strata of the Garnett locality in its upper part, was considered Middle Pennsylvanian in age. Later, Moore (1944, 1949) placed the Missourian Series with the Virgilian Series in the Upper Pennsylvanian. Thus at present, the age of the Garnett fossils may be considered as middle Upper Pennsylvanian, approximately upper Conemaugh (middle Stephanian on the European scale).

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2. Including fossils in the overlying South Bend limestone, the fauna contains 23 genera of invertebrates.

The shales of the Garnett locality are correlated with the Rock Lake shale of the Platte Valley in southeastern Nebraska, the type locality. The Stanton formation which includes the Rock Lake shale member is more extensive; it or its correlatives extend southward from Nebraska, Missouri, and Iowa, across Kansas and into northern Oklahoma (MOORE et al., 1944). The Shumway limestone of central Illinois and Ames limestone of the Ohio Valley are less certain correlatives. On this regional basis the fossiliferous shales at the Garnett locality seem to be definitely younger than the Danville locality of Illinois (lower Conemaugh), the Mazon Creek locality of Illinois (Allegheny), and the Linton locality of Ohio (upper Allegheny), but definitely older than any of the reptile-bearing redbeds of the southwestern United States.

Interest in the land plants from Garnett resulted in the discovery of *Petrolacosaurus*, which is preserved within a narrow zone on plant-bearing surfaces of the laminated shale. However, there are no available field notes documenting the discovery. All the reptile remains described by LANE (1945) were found in 1931 and 1932, in the latter year by a field party from the Museum of Natural History consisting of HENRY H. LANE, CLAUDE HIBBARD, DAVID DUNKLE, WALLACE LANE, LOUIS COGHILL and CURTIS HESSE. Other specimens not described by LANE but obviously from the Garnett locality, in all probability were found at the same time. To my knowledge the only specimen of *Petrolacosaurus* not obtained in 1931 and 1932 is a series of three vertebrae kindly loaned to me by Dr. MAXIM ELIAS, now of the Nebraska Geological Survey. The vertebrae were found by him at the type locality on October 23, 1948.

SYSTEMATIC DESCRIPTION

CLASS **REPTILIA**, ORDER **EOSUCHIA**

FAMILY **PETROLACOSAURIDAE** PEABODY, n. fam.

Type.—*Petrolacosaurus* LANE, 1945.

Diagnosis.—Late Pennsylvanian reptiles with persistent rachitomous features of approximately seymourian grade in the vertebral column and limb girdles, but possessing progressive features appearing for the first time in reptilian history, cervical vertebrae moderately elongate, neural arches excavated for lightness, limbs with elongate distal segments, general adaptation for purely terrestrial mode of life. Family is intermediate between primitive cotylosaurs, on one hand, and eosuchians and possibly pelycosaurs, on the other.

Tentatively the family is placed at the base of the Order Eosuchia.

GENUS **PETROLACOSAURUS** LANE, 1945

Type species.—*P. kansensis* LANE, 1945, p. 381.
Synonym.—*Podargosaurus* LANE, 1945.
Occurrence.—Upper Pennsylvanian, Kansas.

Diagnosis.—A small, slender, terrestrial reptile with well-developed limbs and long tail; palate primitive, resembling *Youngoides* closely; skull fenestrate, probably a lateral temporal opening at least; cervical vertebrae showing seymourian stage of rachitomy, moderately elongate with atlas centrum excluded from ventral surface of column; neural arches and centra excavated laterally, intercentra large and persist into caudals; iliac blade expanded anteriorly and has ligamentous lap-joint with fan-shaped, principal sacral rib; zeugopodium definitely longer than stylopodium in anterior and posterior limb; carpus and tarsus fully ossified in adult, of cotylosaur design but with enlarged discoid ulnare and calcaneum, long-necked astragalus with buttressed, oblique platform providing a concave, relatively inflexible articulation with tibia; a single tarsal centrale, first distal tarsal lost; ribs dichocephalous with tuberculum and capitulum connected by web; capitulum articulates with intercentrum in cervical and anterior dorsal vertebrae; gastralia well-developed but delicate; long bones of the limbs, metapodials and ribs hollow; dentition probably insectivorous.

Petrolacosaurus kansensis LANE, 1945

Plates 1-3, Figures 1-9, 11

Synonym.—*Podargosaurus hibbardi* LANE, 1945.

Holotype.—KUMNH (Kansas University Museum of Natural History) no. 1424 (specimens preserved on apposed plates of shale) Figs. 8-9; adult right hind limb consisting of most of the femur, and the distal one-fourth of the tibia and fibula in articulation with a complete foot. Specimen was split from shale with some loss of bone and is preserved on apposed halves of the shale slab. A missing piece of shale carrying the proximal tibia and fibula makes it impossible to associate the femur without question with the lower limb, but both are of the right side, and are of the proper comparable size as indicated by other specimens. Furthermore, LANE reports (oral communication) that the femur lay in the rock in a position indicative of, though not actually in, articulation.

Topotypes.—KUMNH no. 1425 (on apposed plates of shale), Fig. 5; a nearly complete left half of the adult pelvic girdle, lacking a small anterior portion of the pubis, and having a small opening broken through the plate of the ischium in such a way as to suggest a natural foramen. Dimensions of the specimen suggest that it may belong with the holotype, certainly not with specimens listed below.

KUMNH no. 1423 (on apposed plates of shale), Fig. 6, *C*; a complete right front limb with all bones in position except the humerus which is rotated approximately 90° on its long axis with respect to the radius and ulna. This specimen is the type of *Podargosaurus hibbardi*, here placed in synonymy. It cannot be associated with "the other parts of the skeleton" (LANE, 1945, p. 385) for the "other parts" refer to a skeleton, no. 1427, possessing duplicate parts of both forelimbs. This limb is designated as left by LANE, but contours of the phalanges and the overlap of the proximal ends of metacarpals upon each other indicate that the limb is the right one.

KUMNH no. 1426 (on apposed plates of shale), Fig. 6, *A*; an immature right hind limb lacking the femur but with the tibia and fibula in position. The tarsus is incompletely ossified so presumably this limb is from an immature individual. The limb is described by LANE (1945, p. 388) under "associated remains" and the inference is that it belongs to the same individual as represented by no. 1423 and is therefore a part of the skeleton no. 1427, but the skeleton has parts of both hind limbs. This immature hind limb is possibly associated with the following specimen, to which it corresponds in proper relative size and stage of mesopodial ossification.

KUMNH no. 1429 (on apposed plates of shale), Fig. 6, *B*; an immature, left front limb complete except for distal phalanges of digits III and IV which have been broken off and lost. The bones are lying in position except for digit V which is rotated 180° with respect to the other digits and lies obliquely across their palmar surfaces. The carpus is incompletely ossified and the elements are jumbled. Proportions and ossification of this limb are such that it could belong to the individual represented by no. 1426. This specimen is not mentioned in LANE's account.

KUMNH no. 1428, Fig. 4; a sub-adult skeleton originally more or less complete but partly destroyed by weathering. Friable nature of the enclosing matrix resulted in the loss of parts of all four limbs and unfortunately most of a crushed and fragile skull. This specimen is described by LANE (1945, p. 389, paragraphs 3 and 4) as the associated parts of the individual represented by the forelimb no. 1423. As shown in the figure, the distinguishable elements indicate a single skeleton somewhat disarticulated but with the various regions of the vertebral column, the pelvic girdles and front and hind limbs close to their natural positions. The pectoral girdle and cervical region, in addition to most of the skull, have been lost. The long tail extends away from the pelvis to a sharp break, from which point it loops gracefully to one side. The two hind limbs parallel each other, and their proximal ends are close to the disarticulated pelvis. The forelimbs extend backward, overlying the

pelvic region, and their proximal ends were undoubtedly close to the pectoral girdle. The skull is represented only by a tantalizing fragment of the postorbital region and by an isolated maxillary. The skull lies near its natural position, judging from the position of the other skeletal elements. Some parts of the skeleton must have been contained in the overlying shale which was split off to expose the specimen, but none of this shale was saved.

KUMNH no. 1427, Fig. 2; postcranial skeleton of a young adult originally complete, with the vertebral column coiled in a figure 8 and twisted 180° in the middle of the dorsal series. The limbs lie close to their natural position. The skeleton is exposed as it lay in place; the overlying shale which contained parts of the skeleton was not saved except for several small bits. Also, portions of the imbedding layer are missing, as indicated in the figure. Judging from the complete preservation of the atlas complex and by the presence of a splenial near the scapulo-coracoid, the skull may have been nearby.

The specimen was not seen by LANE. However, there is no doubt that it came from the Garnett locality and was probably obtained by the field party of which Professor LANE was a member.

KUMNH no. 8351, Pls. 1, 2, Fig. 1; an immature skull with lower jaws and a series of 5 cervical vertebrae in position, preserved palate down in a thin slab of shale. Unfortunately, most of the roof of the skull and the maxillaries drifted away before burial probably as the result of immature sutures between bones. Also lost were the centra of the 4th and 5th cervical vertebrae. Several investing bones of the posterior left cheek and the two premaxillaries remain probably because they were held down by the more deeply imbedded lower jaws. The whole specimen shows the effects of a gentle oblique crushing from right to left; any displacement of bones is related to this crushing. This hitherto undescribed specimen was found among others obtained from the Garnett locality. The skull and vertebrae were almost completely imbedded in the matrix and had escaped notice.

KUMNH no. 8355, Pl. 1, Fig. 7; isolated carpus, well ossified and in nearly perfect articulation except that distal carpalia 1-2 are jumbled in position. The proximal part of metacarpals 3, 4 and 5 are preserved while metacarpal 1 and its phalanges lie nearly hidden beneath metacarpals 3-5. This hitherto undescribed specimen and a fragment of ilium (not described here) possibly belong with the young adult skeleton numbered 1427.

Nebraska Geological Survey (no number), Pl. 1, Fig. 3, *B*; series of 3 dorsal vertebrae kindly loaned for preparation and study by MAXIM ELIAS (see p. 5). These vertebrae are more or less articulated and preserved with them are well-formed intercentra.

Horizon.—Rock Lake shale member of the Stanton formation, Lansing group, Missourian Series,

Pennsylvanian System. KUMNH Paleo. Loc.—Kansas: Anderson County no. 1.

Diagnosis of species.—As for the genus.

Discussion.—LANE (1945) described *Petrolacosaurus kansensis* from an isolated hind limb and pelvis, and referred the genus to the Pelycosauria (in 1946, to the Sphenacodontidae) mainly on tarsal characteristics. Another isolated front limb with associated skeletal parts thought to belong with the limb was described as *Podargosaurus hibbardi* and referred to the Protorosauria (in 1946, to the Araeoscelidae) because of "long slender limbs, the very long tail, almost threadlike at its termination, the single-headed ribs, the humerus with an epicondylar foramen." None of these characters are entirely protorosaurian, and the ribs prove to be dichocephalous when prepared further. The pelycosaurian rather than araeoscelid design of the carpus is not mentioned. Further preparation of the described material and of newly discovered specimens demonstrates that all of the reptilian remains from the Garnett locality pertain to a single species.

Support for the above conclusion lies in the following facts. Two similar skeletons (nos. 1427-28), with parts of all four limbs in position, demonstrate clearly the architecture of the elongate limbs, including excellent details of carpus and tarsus. The front and hind limb ascribed to separate genera by LANE compare closely with front and hind limbs found together on the skeletons. Also, a perfect sacral rib preserved with one skeleton (no. 1427)

has a markedly expanded tip which could be applied only to an expanded iliac blade like that of the isolated pelvis referred by LANE to *Petrolacosaurus*.

There remains the problem of relating the newly discovered skull to the other skeletal material, but this is solved by discovery that, except for size, the cervical vertebrae articulated with it match closely the corresponding cervical vertebrae of the headless skeleton (no. 1427). Also, the teeth of the lower jaw and premaxillary of the skull are similar in structure to those of the maxillary belonging with the other skeleton (no. 1428).

A series of measurements of length (table below) lends final support to the conclusion that we are dealing with at least 7 individuals of one species, perhaps of one population, which show variation in size and stage of ossification, owing to differences in age. The smaller specimens lack full ossification in the skull, vertebrae, and especially in the mesopodials (nos. 1426, 1429); individuals of intermediate size have nearly complete ossification of mesopodials but lack complete ossification of pelvic elements (no. 1428), whereas the largest individuals show complete ossification of mesopodials and also of the pelvis.

Under the circumstances, either of the two species erected by LANE could be retained as the valid one. However, since *Petrolacosaurus kansensis* has page priority, it is thought best to retain this name as valid, even though "*Podargosaurus*" may be more descriptive for the small, agile reptile from the Rock Lake shale.

TABLE 1.—*Comparative Length of Elements in Millimeters*

Elements	Individuals (Index Numbers Defined Below *)							
	1	2	3	4	5	6a	6b	7
humerus	....	35 + [b]	....	....	35	26	....	....
radius	....	42	....	36[b]	37	27	....	....
ulna	....	42 +	....	37	38	28 +	....	....
ulnare	....	7	....	5	6	....	....	....
metacarpal IV	....	16[b]	....	....	15	11	....	....
phalanges	....	14	....	....	14	10	....	....
(II) 1-3 manus over-all	....	60[b]	....	....	55	40[b]	....	....
femur	57 ±	39[b]	....	34	....	....	....	....
tibia	....	47[b]	....	40	....	....	31	....
fibula	....	....	....	35[b]	....	....	29	....
calcaneum	16	14[b]	....	....	....	....	5 +	....
astragalus	16	....	....	9	....	....	6	....
metatarsal IV	23	21	....	17	....	....	14	....
phalanx (IV) 1	15	13	....	12	....	....	9	....
phal. (II) 1-3	20	16	....	14	....	....	11	....
pes over-all	85	75[b]	....	70[b]	....	....	53	....
centrum (dorsal)	....	6.5	7	6	....	....	....	....
spine of axis	....	15	....	....	....	....	....	7
axis centrum	....	10	....	....	....	....	....	4.5
centra 2 + 3	....	21	....	....	....	....	....	10
skull: pmx. to bo	....	64[b]	....	....	....	....	....	33
maxillary	....	....	....	25	....	....	....	18[b]

a. Individuals—(1) KUMNH 1424, type, hind limb. (2) KUMNH 1427, skeleton with parts of four limbs. (3) Nebraska specimen. (4) KUMNH 1428, skeleton with parts of four limbs. (5) KUMNH 1423, front limb. (6a) KUMNH 1429, front limb; (6b) KUMNH 1426, hind limb. (7) KUMNH 8351, skull with cervicals.

b. Estimated.

OSTEOLOGY

Although more remains of *Petrolacosaurus* may be obtained from the Garnett locality, the available material warrants a detailed description. Except for the skull roof, the skeleton is well represented, indeed far better than for any other Pennsylvanian reptile; and the exceptional preservation of the carpus and tarsus present in so many specimens of *Petrolacosaurus* is all too rare for reptiles of any geological age.

SKULL

Description of the skull must be based on an immature specimen (Fig. 1), which unfortunately lacks most of the roof in the critical area of the postorbital fenestrae. This deficiency is partly offset by fragments preserved in another specimen (Fig. 4). However, the lost roof of the skull exposes an excellent dorsal view of the palate and basicranial axis. With few exceptions, the bones are extremely thin and fragile, the thinnest portions being little more than a colored film in the matrix. The following description pertains to the immature skull and jaws unless otherwise indicated.

The skull is moderately elongate and high, much in the proportions of *Youngoides*. Over-all dimensions from premaxillary to basioccipital and from articular to articular are 33 and 15 mm., respectively. Whether or not the skull possessed one, two, or no temporal openings cannot be demonstrated conclusively at present; however, several observations point to the existence of at least one opening which is a lateral one. A delicate fenestrated roof is indirectly suggested by the curious circumstances of preservation seen in the immature skull. The complete head with cervical vertebrae attached evidently came to rest palate down in soft mud and then most of the roofing bones drifted away, leaving both rami of the lower jaw, the complete palate, basicranial axis and vertebrae almost undisturbed.

Dentition

Marginal teeth are sub-isodont, and rounded in cross section (avg. diam. 1 mm.), with no lateral compression evident. Anterior teeth are slightly recurved and have the tips pointed, but not acutely; posteriormost teeth are short, straight, and bluntly rounded at the tip. The pulp cavity is prominent, extending nearly to the tip of the crown; in most specimens it is filled with a transparent mineral. There is no indication of labyrinthine structure.

The teeth are set close together in a groove having the labial rim somewhat higher than the lingual rim, at least in the dentary. There is little or no development of bone separating the close-set teeth. In anterior teeth where several pulp cavities are exposed, the implantation appears relatively deep, but the posterior two or three teeth are shallowly im-

planted. There is no swelling at the base of the individual tooth, such as is evident in *Araeoscelis*. The general style of implantation is undoubtedly primitive, like that of small var anosaurs, and *Youngina* as described by Broom (1924).

There are 29 teeth in the dentary, probably a like number in the upper jaw, with four certainly contained in the premaxillary. Irregularities in length of teeth indicate active tooth replacement by the primitive method described by Romer (1949) whereby an "odd and even" replacement is complicated by a "wave" replacement running posteriorly. Irregularities due to age of individual teeth do not obscure the fact that the first two teeth in the premaxillary are enlarged, fanglike (1.25 mm. max. diam.), and oppose much smaller and shorter teeth in the lower jaw. The fragment of maxillary (Fig. 4) lacks the anterior half; so the size of teeth cannot be determined in the region where pelycosaurian teeth show enlargement. Probably there was no marked enlargement here; the maxillary is certainly deep, however, not shallow, as in captorhinids.

Palatal teeth are well developed on the pterygoids and parasphenoid. On the pterygoid, the teeth are arranged in triradiate fashion—in longitudinal, diagonal and transverse rows. The longitudinal series extends from the basisphenoid process forward along the median ventral margin as a single row of approximately 24 small teeth; the diagonal series extends from near the basisphenoid process probably on to the palatine, but this cannot be determined certainly. These teeth are arranged in an elongate patch rather than in single file. The transverse row lies along the posterior border of the pterygoid flange; the teeth tend toward alignment in a single row. The flange teeth form a prominent triturating ridge, surprisingly robust in view of the otherwise rather fragile nature of the skull. Although variable in size, the largest teeth are 0.75 mm. in maximum diameter. Anterior teeth of the diagonal series are strongly developed also, while the teeth of the longitudinal series are uniformly small. The pulp cavity of a pterygoid tooth is relatively large, as in the marginal dentition.

The parasphenoid is noteworthy for the small patches of small denticles which it bears posterior to the basisphenoid processes. In addition, the narrow anterior spine of the parasphenoid bears a single row of small, sharp denticles, as in *Millerosaurus*, a cotylosaur.

Whether or not the vomer bears teeth cannot be determined, for the left ramus of the lower jaw covers the critical area. In the lower jaw, no evidence of teeth is seen on bones other than the dentary.

DERMAL BONES OF THE SKULL ROOF

Premaxillary. — This element has the three-pronged structure of primitive reptiles, such as *Captorhinus*. It is lightly built, however, and high enough to indicate a large external naris, opening laterally from a narrow high snout. By contrast, *Araeoscelis* has a small premaxillary and a small external naris. The palatine process is hidden from view in the specimen; apparently it fitted into a wedgelike slot in the vomer (in the immature skull the right premaxillary is pushed over and disengaged from the vomer). In pelycosaurs, the palatine process is quite short and abuts against the
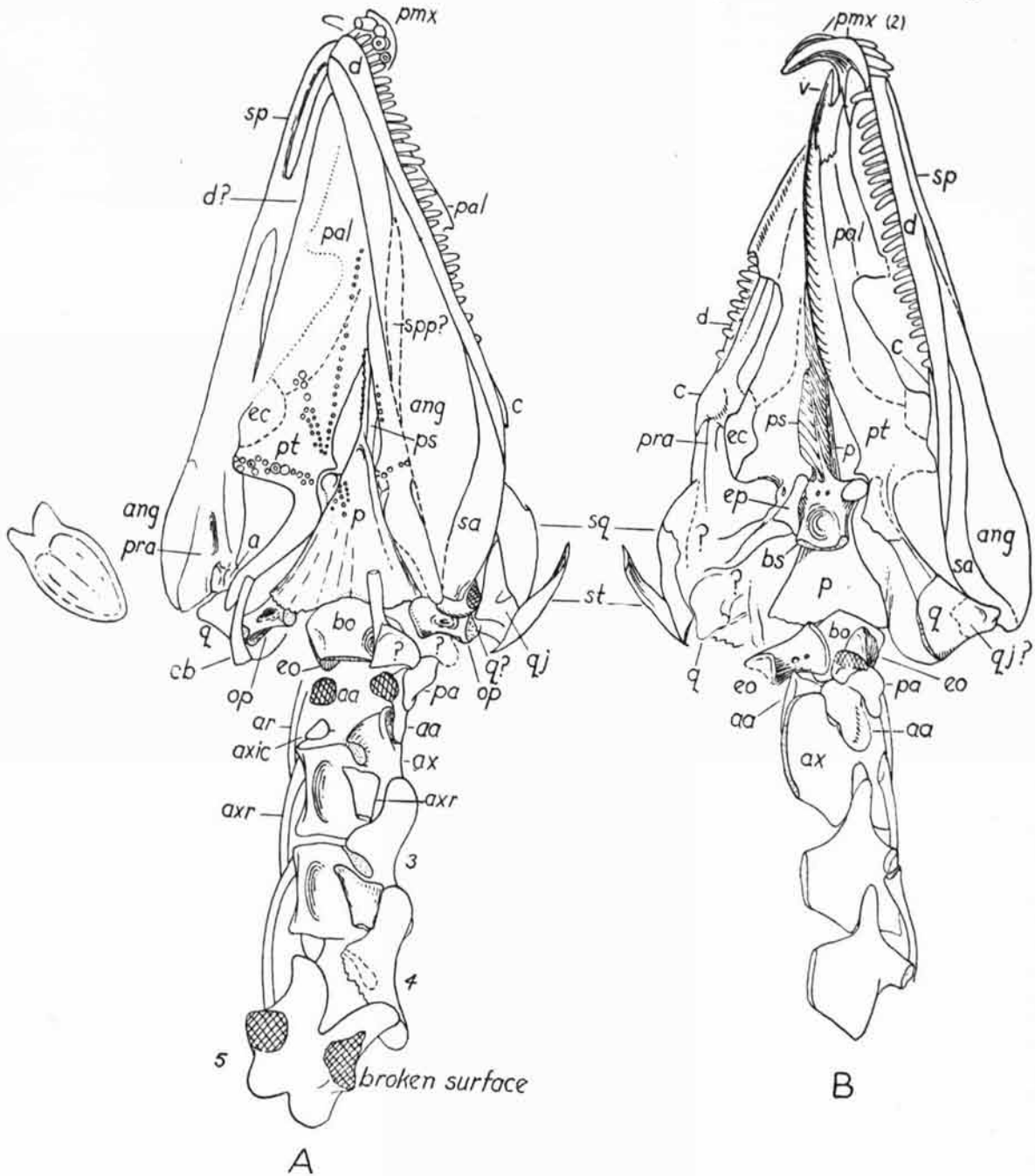

FIGURE 1.—*Petrolacosaurus kansensis* LANE. Immature skull and lower jaws, with articulated cervical vertebrae, KUMNH no. 8351, × 3. (A) Ventral view of palate, oblique view of vertebrae and lower jaws; note cupule of pteridosperm. (B) Dorsal view showing palate exposed by loss of skull roof; note effects of slight crushing from right to left.

vomer. The short process in *Dimetrodon*, however, dorsally has a small wedge fitting into a shallow slot in the vomer.

The nasal process is of moderate length and does not extend posterior to the external naris. The first three premaxillary teeth are enlarged, as in captorhinomorphs. An articulatory surface for the maxillary is plainly evident on the latero-dorsal aspect of the maxillary process of the premaxillary.

Maxillary.—The isolated maxillary (Fig. 4) belonging to skeleton no. 1428 is incomplete, but the preserved posterior half indicates an extensive lateral surface, one which probably restricted the breadth of the lacrymal at least to the extent seen in *Varanops*. Unfortunately, the damaged impression of the lost anterior half lacks that part which might indicate a restricted lacrymal as in *Mycterosaurus* or *Youngina*. Contours of the dorsal posterior border indicate an extensive jugal suture. The alveolar margin has a slightly convex outline.

Jugal.—Interpretation of the fragmentary skull of skeleton no. 1428 (Fig. 4) is extremely difficult, even as to correct orientation. An orbit is suggested by a circular impression of thin, fragile plates of bone. What seems to be the posterior border shows a diagonal division, suggesting the postorbital-jugal suture. Buried deeply (carefully prepared from the under side) is a bone tentatively identified as the right jugal. Its postorbital process is a robust bar, indicating that a lateral temporal opening lay behind it.

?Quadratojugal and ?squamosal.—At the left postero-lateral angle of the immature skull are two, or perhaps three thin investing bones applied closely to the quadrate region. The bones were extremely thin membranous plates originally and are preserved now mainly as film-covered impressions. There has been some crumpling also to complicate the structure. A satisfactory interpretation of this region must await discovery of better specimens. Nevertheless, one important condition is indicated, namely, that the plate of bone, seen in ventral view to extend forward and under the lower jaw, bordered a lateral opening in the skull. Indication of this lies in the apparently free, concave border, which delimits the bone anteriorly (Fig. 1); judging by its position, this bone must be either the squamosal or quadratojugal. If it is the latter, it is extraordinarily large and has a posterior part broken away, which lies alongside the articular region. If it is the squamosal, then the small posterior portion is a small quadratojugal in position, and the squamosal formed most of the posterior border of a lateral fenestra, as in *Mycterosaurus* and *Sphenodon*. If the anterior element is considered to be the squamosal, the postero-lateral element is probably an elongate supratemporal. The evidence for a lateral opening remains, and when taken with the shred of evidence from the fragmentary skull

no. 1428, indicates more definitely a skull having at least a lateral fenestra behind the orbit. There is little indication one way or another that the skull of *Petrolacosaurus* had a dorsal fenestra also, and therefore a diapsid plan.

PALATE AND BASICRANIAL AXIS

Nearly every feature of the palate and basicranial axis recalls the pattern described for *Youngoides* by OLSON (1936). As will be shown, some features which differ may reflect age differences, whereas others merely may comprise data provided by a dorsal view, not seen in the several skulls of younginids.

Vomer.—The right vomer, as exposed in dorsal view (Fig. 1, *B*), is relatively broad, concave longitudinally, and bifurcate unequally at either end. The anterior bifurcation probably engaged the palatine process of the premaxillary. The posterior bifurcation is irregular and forms an indistinct suture with the pterygoid and palatine. Laterally, the vomer is apparently bordered throughout most of its length by a robust narial process of the palatine, a condition (to my knowledge) known only in *Youngoides*[3] (OLSON, 1936). The upturned median border of the vomer is applied to the median vertical plate of the pterygoid. The internal naris must have been, as in *Youngoides*, between the narial process of the palatine and the maxillary. Possibly there was a narrow vacuity developed between the two vomers but not to the extent seen in *Youngoides*. In general proportions, the vomer is similar to that of *Sphenodon*.

As noted above, the ventral surface of the right vomer cannot be seen; and since the left one appears to have been lost, the dentition, if any, must remain undescribed.

Palatine.—This long element is so very delicate and thin that its lateral margins are indistinct. However, its anterior process definitely has an extensive suture with the vomer (see above). Medially, a long curving suture with the pterygoid runs posteriorly and then sharply sideward to an indistinct suture with the ectopterygoid. The anterior lateral margin is thickened, suggesting that the internal naris was long and slitlike, with its posterior border formed by a narrow palatine-maxillary bridge. Posterior to the bridge, the lateral margin of the palatine is deeply excavated, indicating a large infraorbital vacuity bordered by palatine, maxillary, and ectopterygoid. The vacuity is relatively anterior in position and indicates a short-faced skull. The dorsal surface of the palatine has a distinct ridge running diagonally from the anterior edge of the vacuity to the postero-lateral tip of the vomer.

3. CAMP (1945, p. 88) questions the presence of this peculiar feature in *Youngoides*.

The shape of the palatine and its relations with surrounding bones and openings nearly duplicates the condition seen in the palate of *Youngoides* as described by OLSON (1936).

Ectopterygoid.—The individuality of this element is not clearly shown, but in the dorsal view of the left side, an angulate line may be the suture between it and the pterygoid. If this is so, then the ectopterygoid must be relatively large. The bone is thick and bosslike. Whether or not it articulated with the maxillary or jugal cannot be determined.

Pterygoid.—Dorsal and ventral views of the pterygoid indicate clearly that this bone has extraordinary length. The horizontal anterior process is narrow, extending forward nearly to, if not actually articulating with, the vomer. The median vertical plate of the pterygoid displaces the interorbital septum of the sphenethmoid and extends (in dorsal view) forward to lie between the vomers. This anterior relation is not exposed in *Youngoides* but could have been present. Between the two pterygoid bones is a definite vacuity of about the width and length seen in *Captorhinus*.

Laterally, the pterygoid forms a heavy flange which bears robust teeth, as indicated earlier. Medial and slightly anterior to the row of flange teeth is a well-defined process, which articulates loosely with the basipterygoid process of the basisphenoid.

The basipterygoid process is well behind the transverse row of flange teeth in such forms as *Dimetrodon* and *Captorhinus*. It has an anterior position in *Youngoides* and *Ophiacodon*, and possibly this is the primitive position with respect to the flange teeth.

The long quadrate process of the pterygoid extends diagonally to an extensive contact with the median surface of the triangular quadrate. The process is angulate in cross section, being formed by two flanges. One, seen in dorsal view, is nearly vertical being inclined dorso-medially (inclination lessened in the specimen by crushing). The other flange, seen in ventral view, is essentially horizontal. This curving narrow flange extends medially, thus forming a space between it and the vertical flange, which ROMER & PRICE (1940, p. 60) state "presumably was occupied by the eustachian tube and middle ear cavity." The horizontal flange of our specimen has almost the same shape and relationships as in *Youngoides*.

Interpretation of the vertical flange is less satisfactory than for the horizontal flange, because in dorsal view, careful preparation outlined what appears to be a long narrow shaft of bone, closely applied to the vertical flange. At the posterior end, it seems to pass under the quadrate and imperceptibly into the surface of the vertical flange. Anteriorly, the shaft assumes a shape suggesting an epipterygoid more or less in the usual position. So delicate is the preservation that I cannot distinguish a definite break between the "epipterygoid" part of the shaft and the posterior part. At first it was thought that the shaft was part of a squamosal-postorbital arch, but as indicated by its position under the quadrate and continuity with it, this cannot be so. Another possibility is that the extremely thin vertical flange of the pterygoid is buckled in a longitudinal direction. Certainly the left quadrate ramus has undergone considerable buckling.

Epipterygoid.—Identification of this element in the immature skull is uncertain. On the right side it seems to be missing, although its presence is suggested by a curious break in the right pterygoid (see above); on the left side, a small object of the expected shape is applied closely to the crumpled quadrate process of the left pterygoid. The object has the correct size, narrow ascending process, and expanded ventral blade of a primitive epipterygoid. If this is a correct identification, the element has fallen forward so that the blade is still near its original articulation. Dorsally on the pterygoid and lateral to its basipterygoid articulation is a broad longitudinal depression, which may have received the epipterygoid blade. Nothing in our specimen supports OLSON's (1936) suggestion that the "block" of bone in *Youngoides* is the basal process of the epipterygoid. As noted above, the basipterygoid processes in our specimen appear in ventral view to be isolated "blocks" although the dorsal view does not bear this out.

Quadrate.—The right quadrate is clearly exposed by the loss of investing bones which once covered it laterally. It is platelike, fan shaped in lateral view, and has a transversely elongate process at the ventral apex for articulation with the lower jaw. The articulatory process is rather narrow transversely and simply constructed, having none of the expansiveness seen in *Captorhinus*. The posterior border is rounded and gently concave longitudinally. A small oblique surface, for articulation of the squamosal perhaps, appears at the posterodorsal extremity of the quadrate blade. A quadrate foramen cannot be located along the exposed posterior area of the blade. The quadrate has nearly its original position, except that it has been tilted medially. In the original position, it probably was oriented with the blade directed antero-medially following the plane of the pterygoid flange. The blade was inclined forward, so that its posterior border was more or less vertical in lateral view.

In lateral view, at least, the quadrate shows a design and relationship with surrounding bones to be expected in a small primitive reptile. The median surface of the left quadrate may be exposed in the dorsal view but I cannot delimit it surely among elements involved in crumpling of the left posterior corner of the skull.

Parasphenoid.—The individuality of this element

is excellently outlined in the immature skull. The anterior process is a narrow, straight spine, armed with a single row of teeth ventrally, and it extends to a point approximately at the anterior limit of the interpterygoid vacuity. The spine underlies two plates of bone and has a distinct linear suture with them (see below). The parasphenoid expands posteriorly as a thin triangular plate which passes between the basipterygoid processes and becomes extremely broad (7 mm., which is half the distance from articular to articular, outside dimensions). The plate is slightly concave ventrally, more so between the basipterygoid processes. Lateral margins are rounded in ventral view and are of thicker bone. The posterior border of the plate is ragged, suggesting a growing margin, and it meets the basioccipital in slight overlap ventrally. Fine striations on the ventral surface of the plate converge anteriorly. Dorsally, the parasphenoid plate is applied to the short basisphenoid in such a way as to suggest that the two elements are separate entities in this immature skull.

As noted previously, the parasphenoid plate bears a patch of small teeth posterior to the basisphenoid processes.

Basisphenoid.—In dorsal view, the basisphenoid is clearly outlined as an element of primitive reptilian design. There is a hemispherical depression for the pituitary, somewhat truncated by the posterior border of the basisphenoid. The border suggests a continuation in cartilage which was not preserved. The lateral wall of the pituitary pit, rounded on the dorsal border, rises posteriorly, suggesting a posterior suture with a cartilagenous dorsum sella, and perhaps a proötic. Laterally, the basisphenoid carries a strong basipterygoid process, the right one being clearly seen in dorsal view. The articulatory surface is directed antero-laterally and appears rather large for the thin engaging process of the pterygoid. The articulation at this point seems to have been a loose one. In ventral view, the basipterygoid process gives the appearance of a "nearly unossified block which lies between the two bones" (pt. and bs.) as described from *Youngoides* by OLSON (1936, p. 527).

Dorsally, in front of the pituitary pit and between the basipterygoid processes, are small paired foramina, presumably for the internal carotid artery. At this level in *Captorhinus* and in *Dimetrodon*, the basisphenoid-parasphenoid c o m p l e x turns abruptly antero-dorsally. There is no flexure whatsoever at this point in *Petrolacosaurus*. Neither is there more than slight lateral compression of the basisphenoid-parasphenoid complex.

Anteriorly, the basisphenoid is continuous with paired vertical plates of thin bone which diverge dorsally. At least on the right side, there seems to be no suture between the plate and the basisphenoid. On the left plate a small area is broken

out, giving the appearance of a suture with the basisphenoid. These plates can be seen in ventral and lateral view, where they meet the spine of the parasphenoid in a straight longitudinal suture. However, they do not extend postero-ventrally between the basipterygoid process and the parasphenoid, as the presumably homologous elements do in *Youngoides* (OLSON, 1936).

Near the anterior limit of the interpterygoid vacuity, the paired plates join and continue forward as a single median plate. Anteriorly, the single plate narrows dorso-ventrally, as the median vertical plates of the pterygoid rise at a low angle to form the anterior portion of a median septum (Fig. 1, *B*).

The paired plates represent the sphenethmoid element of primitive reptiles. ROMER (1946) describes a similar structure in the cotylosaur, *Limnoscelis*. However, the dorsal view of this element in *Limnoscelis* is not available, and ROMER says of the ventral view afforded (p. 161), "the sphenethmoid appears to present a definite posterior margin, as expected, some distance in front of the region of the basal articulation." In *Petrolacosaurus*, the comparable element definitely extends to a strong union with the basisphenoid.

Basioccipital and exoccipital.—In ventral view, the basioccipital appears as a spade-shaped, heptagonal plate of thickened bone. The posterior limit is truncate transversely and was probably finished off by a single cartilaginous condyle. A single condyle is indicated indirectly by the structure of the atlas (see below). The breadth of the condylar surface and position of the exoccipitals indicate that the condyle was formed mainly or completely from the basioccipital.

Position of the condyle with respect to the points of jaw articulation is of special interest. In all pelycosaurs with comparable or longer skulls, the basioccipital condyle lies well forward of a line connecting the jaw articulation. In our specimen the condyle has a position posterior to this line a feature approached by *Youngoides* and *Araeoscelis*.

Anteriorly, the basioccipital terminates in a manner suggesting continuity with areas of cartilage. The relatively large gap between basisphenoid and basioccipital must have been filled with cartilage of the basal plate. As indicated above, the expanded plate of the parasphenoid sheaths the basicranial axis ventrally.

In dorsal view, the left exoccipital appears in position. It forms the lateral wall of the foramen magnum, and because of its large ventro-median process resting on the basioccipital, much of the ventral wall as well. The footplate is not fused with the basioccipital; rather, it seems to be merely applied to it. The right exoccipital seems to be pushed out of position slightly, so that in ventral view the foot plate appears slightly displaced pos-

teriorly. The dorsal end of this element is covered by another element, which I identify as the right proatlas. The supraoccipital seemingly was lost, along with the roofing bones.

Lack of a complete occiput and displacement or loss of roofing bones preclude any attempt to reconstruct precisely the height of the skull. However, the high premaxillary, maxillary with its high facial process, moderately long epipterygoid, and moderately high axial spine certainly indicate a skull at least as high as in *Youngina* and *Prolacerta*.

In the concave median wall of the exoccipital, there is one large foramen and possibly a second smaller one ventro-medially, both for the exit of the 12th cranial nerve from the braincase. Dorsally, the exoccipital has a triangular surface, which articulated with the missing supraoccipital.

Otic region.—As might be expected in a fragile and incompletely ossified skull, the otic region is difficult to interpret. The difficulty is heightened by circumstances of preservation that have crumpled together the elements at the left posterior end of the skull. Nevertheless, on the right side in ventral view, a thick, elongate element lies in approximately the position of an opisthotic. The expanded proximal end lies immediately dorsal to the postero-lateral extension of the parasphenoid and lateral to the anterior half of the basioccipital but does not make contact with it. The obtuse distal end makes contact with the quadrate and quadrate process of the pterygoid (seen in dorsal view). Probably the right quadrate has been pushed medially; if so, the distal end of the opisthotic probably did not have the exact relative position originally that it now has. The ventral surface has a deep longitudinal pit which probably housed a slender stapes.

If the element described above is an opisthotic, *Petrolacosaurus* resembles *Youngoides*, *Sphenodon*, and *Iguana*, in each of which size and relationship of the opisthotic and stapes are essentially the same. Yet there is possibility that the element in question is a large stapes, such as characterizes the pelycosaurs. It seems too large for this skull, however, and the ventral longitudinal pit has neither the shape nor position of a stapedial foramen.

A slender, flat bar somewhat expanded posteriorly lies beneath the end of the right opisthotic. This bar is probably not a stapes but a fragment of the hyoid apparatus, perhaps ceratobranchial I. It and the left counterpart, which lies ventrally along the left border of the basioccipital, have the proper position displaced to the left, to be expected as a result of oblique crushing.

Identification of the two longitudinal bars as hyoid elements leaves the specimen without a recognizable stapes. If this interpretation is correct, then the stapes must have been small, slender, and unossified.

There is no evidence of a proötic. Its absence, coupled with the wide separation of basisphenoid and basioccipital, indicates that the otic region was incompletely ossified.

LOWER JAW

Both rami of the lower jaw are clearly preserved in approximately their original position, except that oblique crushing from right to left has rotated the rami on the long axis. Thus, the lateral surface of the left ramus is seen in ventral view (Fig. 1, A) lying horizontally, and the lateral surface of the right ramus is seen in dorsal view (Fig. 1, B) tilted approximately 45 degrees from the horizontal. When in natural position, the rami were tilted medio-ventrally, as in *Captorhinus*. The outer surface of the ramus is smooth rather than sculptured.

In lateral outline, the alveolar margin of the dentary is nearly straight. Posterior to the slight prominence of the coronoid, the surangular border curves strongly downward to the articular, which thus lies well below the alveolar line. The ventral border of the ramus is nearly straight. In dorsal outline, the ramus is nearly straight, except for a slight median curvature in the articular region. Anteriorly, the slender rami meet with little medial curvature, indicating indirectly a pointed snout on the skull. In cross section anteriorly, the rami appear somewhat rounded; posteriorly, the section is elongate mainly because of the large, deep angular.

The long, straight rami, lying more or less in position, outline a moderately long skull, already suggested by the shape of the palate. In dorsal outline, the skull must have resembled generally that of *Youngoides;* in lateral outline, the skull must have been comparable also, but higher at the level of the nares.

Despite good exposures of jaw surfaces, it is extremely difficult to delineate completely sutures between the thin and fragile elements. Thus, areas of a dentary, angular, surangular, prearticular, articular and at least one splenial and one coronoid are definitely recognizable, but the exact limits of each are not everywhere clear. The most definite sutures are those between the dentary and adjoining elements.

Dentary.—On both rami, the dentary definitely extends narrowly backward, lateral to and beyond the coronoid. In contrast with its considerable length, the dentary is restricted ventro-laterally by a large splenial, or splenials, and a large angular. Thus, a lateral view of a ramus in position would appear as in Figure 1, B, in which the dentary is long, narrow, and widely separated from the ventral border of the ramus.

Splenial.—In lateral view, a large splenial forms the ventro-anterior area of the ramus and enters strongly in the symphysis, along with the dentary. On the left ramus, there is the faint suggestion of

a small and narrow postsplenial. The splenial, as exposed medially in the right ramus, is connected by a bridge with a dorsal element, which is either the medio-dorsal flange of the long dentary or an elongate coronoid complex. Thus, two elongate fenestrae characterize the median surface of the ramus. Incomplete ossification undoubtedly complicates the interpretation here.

Coronoid.—Both right and left coronoids are partly exposed in the immature mandible, so that details of structure are fairly evident. The element is confined to the median surface, except for a small area of the broad dorsal process, which can be seen in direct lateral view extending slightly above the level of the dentary. A long and strong anterior process buttresses the median alveolar border at least as far forward as the sixth-from-last tooth in the dentary. The process bears no teeth. Existence of a separate anterior coronoid, if present, cannot be determined. A narrow posterior process extends along the median surface of the dentary and surangular, and a broad descending process adjoins a long prearticular. The coronoid seems to be similar generally to that of *Captorhinus*.

Angular.—This element has the large size and relationships in lateral view that are seen in *Captorhinus*. Posteriorly, the angular is broad dorso-ventrally and overlaps the dorso-medial surangular in a long curving suture. Anteriorly, the angular narrows but continues strongly forward below the tooth row of the dentary. In median view, the angular forms a broad area below the prearticular, with the result that the depth of the petrolacosaurid jaw posteriorly is mainly due to the expansive angular. There is no evidence of a posterior notch, as in sphenacodonts.

Surangular.—The elongate dentary and large angular limit the surangular to a narrow, strongly curved outline in lateral view. Its actual extent medially cannot be determined. Posteriorly, the surangular is applied to the articular, the exact area being marked by a slightly everted dorsal border.

Prearticular.—This element is confined to the median surface; it buttresses broadly the ventro-median aspect of the articular and then narrows anteriorly, forming the median border of the adductor fossa and seems to pass under (lateral to) the coronoid. There is a longitudinal depression, presumably for muscle attachment in the prearticular immediately below the articular.

Articular.—Details of this element are indistinct, although both right and left bones seem to be in position. The right articular can be identified more definitely, and it is well ossified. A retro-articular process, if developed at all, slanted steeply downward between posterior ends of the investing prearticular and surangular. Certainly there was no

strong posterior extension of the articular, as seen in *Captorhinus*.

The skull of *Petrolacosaurus*, though represented by incomplete and immature specimens, is clearly that of a primitive reptile. Such amphibian characteristics as the separate parasphenoid and exoccipitals and the unossified gap between basioccipital and basisphenoid may well be the result of immaturity. The palate, with its well-developed toothed flanges on the pterygoids, the parasphenoid slightly compressed transversely, and the single basioccipital condyle, are reptilian. Furthermore, the palate is of the rhynchocephalian type, with long pterygoids touching the vomers and with wide-set, narrow internal nares. Except for the infra-orbital fenestra and the peculiar relationship of palatine to vomer, the palate is pelycosaurian. However, these two characteristics are found in the diapsid, *Youngoides*, although not in pelycosaurs. There may be a question concerning the extension forward of the palatine lateral to the vomer, but the large infraorbital fenestrae are definitely present. They are absent in pelycosaurs, well developed in *Youngoides*, *Sphenodon* and *Iguana*, and in many archosaurs. Certainly the palate of *Petrolacosaurus* resembles more closely in shape and structure the palate of *Youngoides*, as described by OLSON (1936), than any other known reptile. Insofar as the evidence goes, the skull is definitely fenestrate. A lateral temporal opening, largely bounded behind by a large squamosal and in front by a jugal bar, is indicated. Evidence for or against the presence of an upper opening is lacking.

The lower jaw of *Petrolacosaurus* cannot be understood fully in the immature specimen, but there is little doubt of its primitive nature. The degree of latero-ventral limitation of the dentary is an amphibian characteristic generally, for example, as in *Seymouria*. *Cotylorhynchus*, among pelycosaurs, retains a splenial prominently displayed in lateral view, but primitive reptiles usually show a progressive limitation of the splenial, or splenials, to the ventral and median surface of the ramus.

In conclusion, the skull and lower jaws of *Petrolacosaurus* suggest, independently of the postcranial skeleton, a primitive fenestrate reptile having an admixture of some amphibian with strong cotylosaurian characteristics, but also evidencing potential development in the direction of diapsids.

AXIAL SKELETON

GENERAL FEATURES OF VERTEBRAE

A fairly accurate count of vertebrae is possible because the two skeletons (Figs. 2, 4) supplement each other in this respect. Description of the vertebral column is based on skeleton no. 1427, unless otherwise noted. Position of the anterior or principal sacral vertebra can be located reasonably in skeleton no. 1427, opposite the fan-shaped first

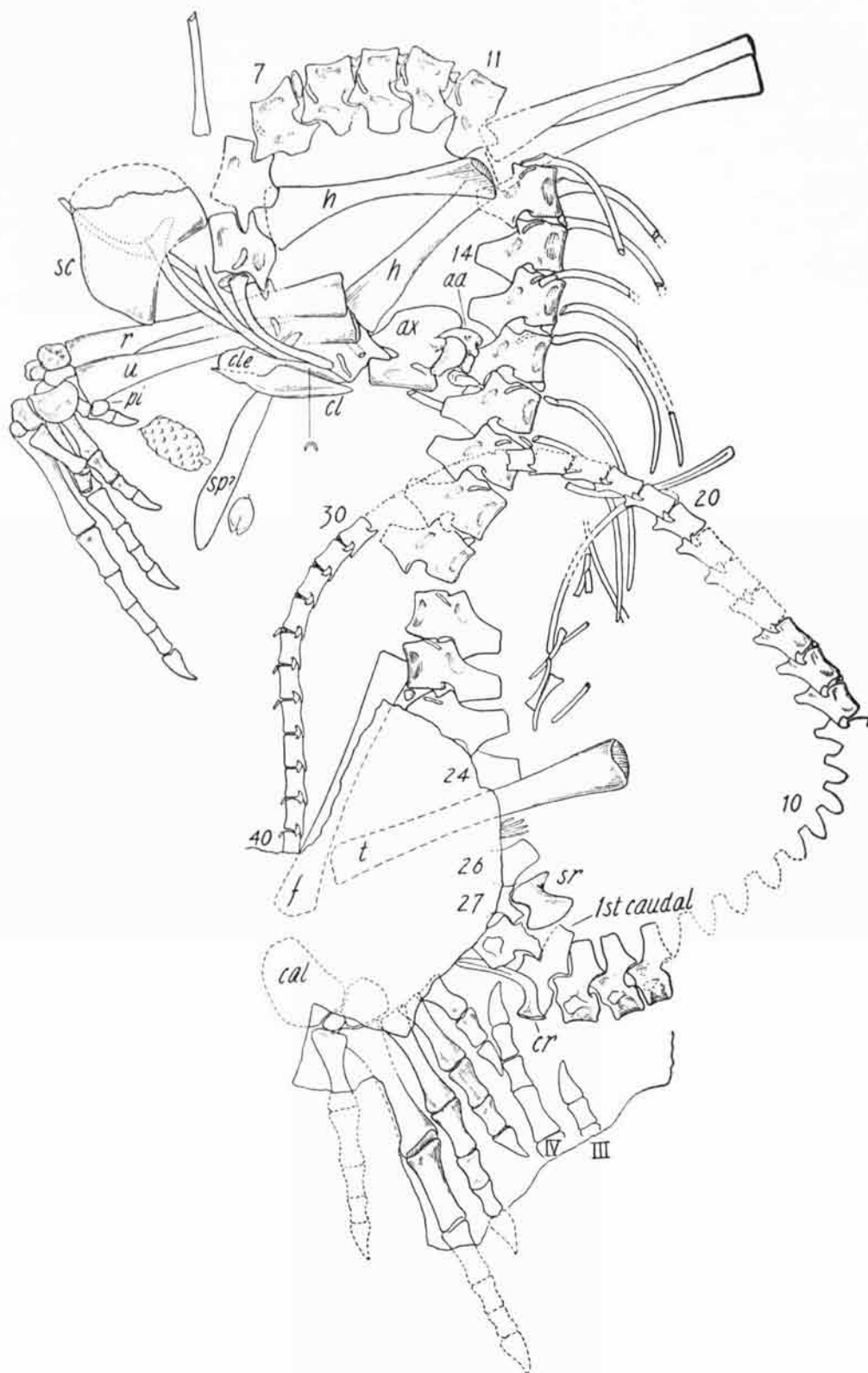FIGURE 2.—*Petrolacosaurus kansensis* LANE. Post-cranial skeleton of young adult, KUMNH no. 1427, × 1; left manus flexed showing plantar view of digits, left pes exposed in plantar view. Note cone of conifer and cupule of pteridosperm near the manus.

sacral rib, even though a piece of shale bearing the centrum has been lost. Two gaps occur in the presacral series[4] where the left tibia and right forelimb lie across the column. Although not shown in the drawing (Fig. 2), there is slight evidence in the specimen that one vertebra occupied each gap. This gives a presacral count of 26 vertebrae; in any other interpretation, the count cannot be less than 24 or more than 26. Of sacrals, there are probably two (see below), the first being the principal one and the second contributing but little to the iliac connection.

The vertebra lying opposite the head of a large caudal rib is chosen as the first caudal (depending on the interpretation of sacral vertebrae, the choice could be the next vertebra forward). In spite of the gaps in the caudal series, a count of 40 caudals can be made confidently in skeleton no. 1427. The 40th caudal has a neural arch and a relative size indicating numerous distal vertebrae. Skeleton no. 1428 corroborates this, for the distal tail is composed of at least 12 spool-shaped centra without neural arches. Though the bone is lost proximally, impressions permit estimation of total length of the tail and therefore additional comparison with skeleton no. 1427. A minimum count of caudal vertebrae for *Petrolacosaurus* is reasonably given as 60; a maximum count is 65. Total length of the caudal series well exceeds that of the precaudal series, because the caudal length from 1 to 40, as measured from skeleton no. 1427, nearly equals the precaudal series. Proportionate length of the tail is about that reconstructed for *Varanosaurus* by Romer & Price (1940, fig. 42). Considerable flexibility of the neck and tail is suggested by the death pose of both skeletons. Skeleton no. 1427 provides the following measurements taken on a line through the center of the centra.

Measurements of Petrolacosaurus Vertebrae

Cervical region (1-7)............................. 74 mm.
Dorsal and sacral region (8 to first caudal)...... 169
Caudal region (1-40) 229
           (41-60 est.) .... 100 +
Total length of column........................ 572 mm.

CENTRUM

The centra are amphicoelous, with notochordal pits developed to the extent seen in pelycosaurs. There is no evidence of a canal joining the pits, except in the atlantal centrum. Ventrally and ventro-laterally at either end, the margin of the face of the centrum is broadly excavated to accommodate a relatively large intercentrum. The latter is present between all except distal caudal vertebrae and reaches maximum size in the cervical series. Centra of the dorsal, sacral, and anterior caudal series have an elongate excavation or depression

ventro-laterally. In the mid-dorsals, the depression is so deep as to suggest a device for lightening the mass of the centrum, just as a more dorsal excavation undoubtedly lightens the massive neural arch (see below). The depression in the centrum becomes shallow in the anterior dorsals and disappears in the cervicals; it becomes shallow posterior to the rib-bearing caudals and disappears posterior to the 16th caudal. The paired excavations, where well developed, constrict the ventral border but not enough to form a sharp keel. However, in the elongate cervicals, where the sides of the centra are only broadly excavated, a sharp longitudinal keel is developed; this detail is exposed in the im-

TABLE 2. *Proportions of Centra; Length, Transverse Diameter, and Vertical Diameter*

Specimen		Length	Transv. diam.	Vert. diam.
Nebraska vertebra, dorsal[a]....		7.0	5.0[b]	5.5 mm.
1428 prox. caudal				
(or ?sacral)[a]		4.0	2.5	....
caudal, 10th from last...		3.0	1.5	....
dorsal		6.0	....	4.5
1427	presacral 2...........	10.0	....	....
	3...........	10.0	....	....
	4...........	10.0	....	....
	5...........	9.0	....	5.5
	6...........	10.0	....	....
	7...........	6.5[b]	....	....
	8...........	6.5	....	5.5
	9...........	6.5	....	....
	10...........	....	....	....
	11...........	....	....	....
	12...........	....	....	....
	13...........	6.0	....	5.5
	14...........	6.0	....	....
	15...........	6.5	....	6.0
	16...........	7.0	....	....
	17...........	6.5	....	....
	18...........	6.5	....	....
	19...........	....	....	....
	20...........	....	....	5.0
	21...........	....	....	....
	22...........	6.0	....	6.0
	23...........	....	....	....
	24...........	....	....	....
	25...........	....	....	....
	26...........	....	....	....
	caudal 14...........	5.5	2.0[b]	3.0
	39...........	4.5	1.5[b]	2.0
8351	cervical 2...........	4.5	....	2.5
	3...........	4.5	....	2.5

a. Ratio of length to transverse diameter is 1.4 to 1.
b. Estimated.

mature specimen no. 8351 (Fig. 1, A), in which crushing may be responsible in part.

In the dorsal series of skeleton no. 1427, the face of the centrum is higher than wide by a ratio[5] of

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4. Although the presacral series has an incipient lumbar region, lack of good preservation justifies the use of "dorsal" for the post cervical-presacral vertebrae.

5. Romer's linear unit (Romer & Price, 1940) is impractical for general use with our small specimens; the centra offer few faces that can be measured accurately for the transverse diameter. A more suitable reference here is the *vertical* diameter of the posterior face of the centrum. As Romer (1947) has employed the average length of dorsals as a useful point or unit of reference, I shall use it here to facilitate the comparisons. Where the vertebral column is incomplete, the ratio of length to height (vertical diameter) is fairly adequate for description.

approximately 1.15 to 1; and the centrum is longer than the vertical diameter (height) by a ratio of 1.2 to 1. Thus, the dorsal centrum is relatively longer and its face higher than in cotylosaurs.

In the caudal series, the centra become relatively long and laterally compressed. At the 14th caudal, the length-vertical diameter ratio is 1.8 to 1; at the 39th caudal, 2.2 to 1, while the length relative to the average length of a dorsal vertebra is 1:1.2 and 1:1.4, respectively.

In the cervical region, an abrupt elongation of centra starts with the 6th vertebra and continues to the axis (no. 2). Although the 7th centrum is not elongate, its neural arch has elongate prezygapophyses and a short spine, suggesting that the cervical series consists of 7 vertebrae. The 5 elongate centra are of equal length; each is 1.5 times longer than the average dorsal centrum. Faces of the elongate centra have the same vertical diameter as the dorsals. Transverse diameter cannot be measured but seems to be no greater than the vertical.

Ratio of length to vertical diameter is 1.9:1, compared to 1.2:1 in the dorsals, and this can be considered to be the adult ratio. Cervical centra of the immature specimen (no. 8351) are slightly less elongate, the length-vertical diameter ratio being 1.8:1. Because the cervical centra were separated by a distinct gap (Fig. 3), the real length of the neck is appreciably greater than indicated by the total length of cervical centra. Thus, *Petrolacosaurus* is a long-necked reptile, resembling *Araeoscelis* and *Prolacerta* in this respect.

TABLE 3. *Ratio of Length of Cervical Centra to Length of Dorsal Centra in Various Reptiles.*

Petrolacosaurus	1.5+	Araeoscelidia	
Eosuchia		*Araeoscelis*	1.8
Youngina	no data	*Macrocnemus*	2.1
Prolacerta	(2.0)	*Trachelosaurus*	1.8
Palaeogama	0.8	*Tanystropheus*	3.3
Tangasaurus	?1.0	*Trilophosaurus*	1.1
Heleosaurus	1.1	*Coelurosauravus*	1.6
Saurosternon	1.1	Protorosauria	
Lacertilia		*Protorosaurus*	2.2
Varanus salvator	1.3		
Iguana sp.	.7	( ) estimated	
Gerrhonotus coeruleus	.8	* after Romer, 1947	

INTERCENTRUM

This element is best described later in connection with the different regions of the column, but a few general observations are given here. Intercentra are definitely present from the atlas to the anterior caudal vertebrae and reach maximum size in the neck; in the anterior caudals, the element forms a pair of demi-intercentra, as described below. Importance of the intercentra as structural units in the small reptile, *Petrolacosaurus*, is indicated by the usual presence of the bony element in place, even in an isolated series of three mid-dorsal vertebrae (Fig. 3, B). Here, the external surface of the intercentrum is broadly lanceolate in ventral view but not strongly arcuate in transverse section. The medio-ventral surface is flat antero-posteriorly, delimited by a ridge of bone before and behind, and is one-fourth the length of the ventro-median surface of the neighboring centrum. When two mid-dorsal vertebrae are articulated, a narrow space remains
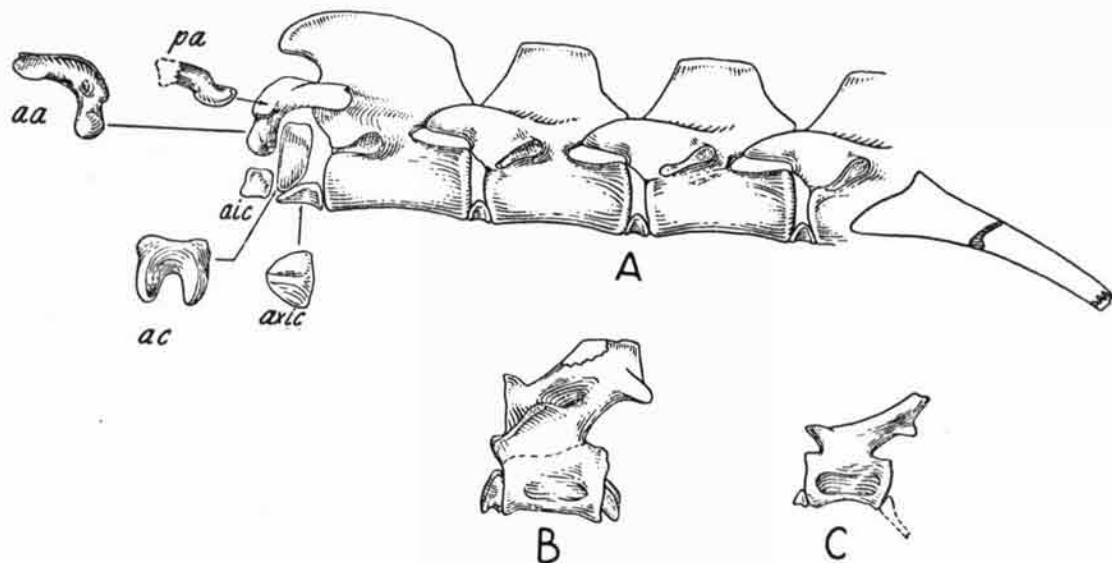

FIGURE 3.—*Petrolacosaurus kansensis* LANE. (A) Cervical vertebrae of KUMNH no. 1427 (Fig. 2) drawn from undamaged underside, and shown here in normal position with added median view of atlantal arch, posterior view of atlantal centrum, and ventral view of axial intercentrum. (B) One of three anterior dorsal vertebrae loaned from Nebraska Geological Survey (no number); view from slightly below horizontal. (C) Caudal vertebra (15th) of KUMNH no. 1427. All figures × 2. (Detail of proatlas from KUMNH no. 8351.)

above the intercentrum and between the centra which was filled probably with non-osseous tissue.

Neural Arch

The neural arch generally is fused solidly to the centrum and sutures are obliterated. In an immature specimen (no. 8351), however, the arches of two cervical vertebrae have lost their centra, indicating a sutural joint rather than fusion in the young of *Petrolacosaurus;* and in cervical vertebrae 2, 3 and 4 of a young adult (no. 1427), a definite suture is visible between centrum and neural arch (Fig. 3). An arch of a typical dorsal vertebra is massive, suggesting the heavy build of cotylosaurs, but relieved by a narrow, deep excavation coursing obliquely between pre- and postzygapophyses. This feature nearly duplicates the condition seen in *Araeoscelis,* except that the excavation is narrower. It is best developed in the mid-dorsals, and becomes shallow in anterior dorsals and post-sacrals. Thus, a dorsal vertebra has two pairs of deep excavations, one in the arch, and one in the centrum, which seem to be adaptations for weight economy in an otherwise cotylosaurian structure.

Zygapophyses are wide set and sturdily built except where attenuated on distal caudals; the plane of articulation is only slightly tilted medio-ventrally from the horizontal and is thus cotylosaurian, rather than pelycosaurian. In the post cervical vertebrae, the postzygapophysis extends backward over a pillar-like prezygapophysis, but in the cervical series the prezygapophysis is especially massive, extending well in front of the anterior face of the centrum so as to interlock with a strongly built postzygapophysis. Articular faces are large and meet in a plane oriented as in the dorsals (excepting the atlas-axis articulation; see below). In these features, the cervicals resemble those of *Prolacerta,* described by Camp (1945), more than those of *Araeoscelis.* Zygapophyses persist beyond the 40th caudal vertebra, probably to about the 50th (Figs. 2, 4).

An important feature of the cervical neural arch is a definite extension forward of the antero-ventral part of the pedicel beyond the face of the centrum (Fig. 3). This overhang, although slight in the dorsal vertebrae, is definite, and it is strongly developed in the cervicals. Here the space below the overhang is occupied mainly by a relatively large intercentrum, but apparently it contained also cartilage or other non-osseous tissue. Thus, the vertebral column of *Petrolacosaurus* seems to be extremely primitive in the cervical region, in spite of elongate centra. The intercentral structure approaches the rachitomous plan seen in *Seymouria* (White, 1939).

Spines of the neural arches of mid-dorsals are well developed, thin transversely, and broad antero-posteriorly; but the distance from zygapophysial plane to dorsal border is invariably somewhat less than the distance from that plane to the ventral border of the centrum. Anteriorly, the spines shorten so that from the 10th vertebra forward, they are low and broad, becoming more so on the elongate cervicals. Posteriorly, the spines become narrower antero-posteriorly in the proximal caudals, diminishing thereafter and disappearing on the 23rd or 24th caudal. There is no suggestion in the caudal arches of enlargement to form a sculling surface.

A diapophysis of primitive design is developed on the antero-lateral aspect of the vertebra. On a mid-dorsal vertebra, the diapophysis has the form of a low crescentic ridge curving antero-ventrally toward the face of the centrum and the lateral tip of the intercentrum. The triangular head of the rib (see below) articulated with the ridge and abutted against the intercentrum. This condition is seen in cotylosaurs such as the captorhinids. In mid-dorsals of a *Captorhinus* individual at hand, the diapophysis is not as extensive antero-ventrally, and the capitulum of the rib does not reach the intercentrum.

In the cervicals, the diapophysis is more massive and protruding but the narrow articulatory surface ends just short of the face of the centrum. The cervical rib articulated with the diapophysis and with the large intercentrum, thus forming a definite vertebra-arterial foramen. The diapophysis on the posterior dorsals is shorter, the rib head smaller; consequently no contact with the intercentrum was effected.

Atlas-axis Complex

In the headless skeleton, no. 1427, all the elements of the complex, excepting proatlantal, are preserved nearly in position, despite loss of the skull. The immature skull, no. 8351, is clearly associated with proatlantal and atlantal arch elements in position, but the remaining elements are poorly preserved and difficult to interpret. Preparation from above and below affords maximum detail in both specimens (Figs. 1, 3). In general, the atlas-axis complex is comparable to that described for pelycosaurs by Romer & Price (1940). There are paired proatlantal arches, unfused atlantal arch elements, and a separate atlantal intercentrum, centrum, and axial intercentrum. However, the latter three elements do not appear to be so fully ossified as in adult pelycosaurs.

The proatlas is a robust, paired element, relatively large when compared with other reptiles. The main body is bladelike and curves dorso-anteriorly in a nearly vertical plane from a strong, transversely developed post-zygapophysis applied to the atlantal arch. The point of articulation with the occiput may have been above the exoccipital; there is no configuration of this element that suggests a condylar surface. As preserved in the immature specimen, the proatlas is directed toward a point well above the plane of the atlantal arch. The cranial tip of the proatlas is hidden on the left side and damaged on the right so that its contours are in doubt.

The halves of the atlantal arch are somewhat comparable to those of *Dimetrodon limbatus* (ROMER & PRICE, 1940, pl. 23), except that there is no lateral spine directed posteriorly alongside the axial blade. A longitudinal ridge occurs on the demi-arch, however, which suggests incipient development of such a spine. The main body of the demi-arch is essentially an elongate plate, concave beneath, and forming a strong medially directed postzygapophysis at the posterior end, a lesser but definite prezygapophysis directed dorso-laterally for the proatlas at the anterior end. Medially, the plate thins over the neural canal. Ventro-anteriorly, there is a stout, elongate foot, sculptured medially to receive the condyle, and a strong lateral process for the tuberculum of the atlantal rib. A large foramen pierces the element medially at the juncture of the foot with the plate. The latter is relatively long, but appears short in comparison with the elongate axis.

In general features, the atlantal arch resembles pelycosaurs, and both types differ clearly from the captorhinid element, of which a number of perfect examples are at hand (Fig. 10). In *Captorhinus*, the neural plate is relatively short, the foot process relatively large and bulky, and with a constricted neck separating the facet-bearing foot from the neural plate. Articulation with the atlantal rib is provided for by a small latero-ventral tubercle on the ventro-lateral tip of the foot, rather than by the large, separate and elongate process of petrolacosaurs, which springs more directly from the base of the neural plate. Thus in several obvious features the atlantal arch of petrolacosaurs is more like pelycosaurs than captorhinids.

The short atlantal centrum has the shape of an inverted U that wedges ventrally between the atlantal intercentrum and a large axial intercentrum but does not reach the ventral surface of the column. This relationship might be regarded as advanced, since ROMER & PRICE (1940, p. 107) state on reasonable grounds that exclusion of the atlantal centrum from the ventral surface is an advanced characteristic in pelycosaurs; participation in the ventral surface is a primitive characteristic of sphenacodonts, edaphosaurs and advanced cotylosaurs (Fig. 10, A). However, the primitive intercentral structure noted earlier in the cervical vertebrae of *Petrolacosaurus* suggests that perhaps its wedge-shaped atlantal centrum is not advanced. In *Seymouria*, admittedly a transitional form between amphibians and reptiles, the atlantal centrum is also excluded from the ventral border, and thus retains a "persistent rachitomous structure" (ROMER, 1947, p. 285). There is possibility that in phylogeny of the amniote atlas, the atlantal centrum has gained and then lost participation in the ventral border of the column. Thus, the wedge shape of the atlantal centrum in *Petrolacosaurus* might be

seymourian in character, rather than truly advanced, as in certain pelycosaurs.

The dorso-lateral aspect of the atlantal centrum is thickened for support of the neural arch, and the posterior face is deeply excavated by the dorsal half of a large notochordal pit. In skeleton no. 1427, the anterior face is covered by the right atlantal demi-arch and cannot be seen.

The atlantal intercentrum is oblong transversely, in lateral view quadrangular, and furnished with a bosslike lateral process, presumably for the capitulum of the atlantal rib. Anteriorly, the element is partly hidden, but the fact that there is a finished surface for the condyle is not obscured. Judging from shape and relationships, there can be little doubt that the atlas complex articulated with a single occipital condyle.

The axial intercentrum is large, as may be expected, and exceeds in length, if not in bulk, all other intercentra. Excessive length is correlated with ventral restriction of the atlantal centrum. The intercentrum is platelike, rather than crescentic, and lacks a well-defined longitudinal keel. No facet for the axial rib occurs at the lateral tip, but there is room for one on the cartilage which undoubtedly extended the dorso-lateral border.

In skeleton no. 1427, a typical mid-dorsal intercentrum wedges in between elements clearly recognized as atlantal and axial intercentra. This extra intercentrum is interpreted as a dorsal element out of position. The "extra" intercentrum apparently belongs with the dorsal vertebrae which lie across the front end of the atlas.

The axis displays a high, prominent hatchet-shaped spine, which extends well forward over the atlantal arch in a confining position. The dorsal border is broadly convex posteriorly to a point over the postzygapophyses. From here, the border slopes gently down in concave outline. In the immature specimen, the dorsal border appears to have been finished off in cartilage. The prezygapophysis is a strongly built ovoid platform, which extends forward beyond the centrum and apart from the more median and forward extension of the pedicel noted earlier. The size and shape of the axial centrum closely resembles that of the following cervicals.

Despite the fact that the various elements of the atlas-axis complex are clearly delimited in skeleton no. 1427, the task of placing them in correct position (Fig. 3) is difficult. Apparently there was much cartilage in the complex. Certainly, the atlantal centrum seems too thin antero-posteriorly for the relatively long neural arch, and the arrangement shown may not be exactly correct. Lack of full ossification here, as well as between the following cervicals, contrasts markedly with the fullness of ossification in the carpus of the same specimen.

RIBS

Each vertebra, from the atlas to at least the 4th caudal, bore ribs, with possible exception of a posteriormost dorsal. If skeleton no. 1427 be accepted as adult, it can be said that nowhere in the column is there any complete fusion of rib to vertebra. Even the posterior dorsals, the principal sacral, and the caudal ribs all lie disarticulated in the matrix.

With possible exception of the principal sacral, all ribs have a large internal cavity. Where not filled in with transparent mineral, the hollow ribs are crushed flat in such manner that a median furrow gives the shaft a bipartite appearance (Fig. 4). The head of a cervical and dorsal rib is an enlarged, generally triangular plate, representing tuberculum and capitulum joined by a web of thin bone, hence actually dichocephalic. In the cervicals, where separate processes are to be expected, the connecting web is also strongly developed. Measurements of capitular-tubercular separation, when compared with the articulatory ridge on the vertebra, indicate that the capitulum of all precaudal ribs, except the posterior dorsals, articulated with the intercentrum or close to it. A small posterior dorsal rib (Fig. 2) has a head too small, though obviously still triangular, to extend beyond the diapophyseal ridge.

An anterior dorsal or posterior cervical rib lying under the scapulocoracoid of specimen no. 1427 (prepared from below) has a remarkably robust head, showing tuberculum and capitulum widely separated but connected by a full web (Fig. 3). The resulting articulatory surface was certainly applied to centrum and intercentrum. The neck of this rib is excavated posteriorly. Ribs in this position are moderately spatulate distally.

LANE (1945) justifiably described the dorsal ribs of skeleton no. 1428 as having single heads, in the sense that lizard ribs are single headed. Weathering had damaged the specimen and coated the fragile remains with a thin calcareous scum. Further preparation reveals several undamaged rib heads, which exhibit the triangular plate, well shown in specimen no. 1427. Articulation of rib with vertebra in *Petrolacosaurus* is quite clearly primitive and cotylosaurian. However, even the captorhinid shows more restriction of rib head to neural arch.

The main body of the cervical and dorsal rib is circular in cross section, becoming flattened distally so that the rib end, especially on the anterior dorsals, appears moderately spatulate. Anterior cervical ribs are preserved nearly in position on the immature specimen (Fig. 1). On the left side, the atlantal rib and the distal part of the axial and third cervical ribs are missing. The right atlantal rib is well developed and nearly hidden but is certainly expanded, and judging from the structure of the atlas complex, dichocephalous. The axial rib is definitely longer than an elongate cervical centrum, and the third rib is approximately as long as two elongate cervical centra. Skeleton no. 1427 shows that rib length increases rapidly to a maximum in the mid-dorsal region and drops off again rapidly in the posterior dorsals. A perfectly preserved posterior dorsal rib (Fig. 2) approximately equals the length of an elongate cervical centrum.

Truncate distal ends of mid-dorsal ribs indicate attachment to costal cartilages, but the short posterior dorsals have a more pointed tip, suggesting no such attachment.

A description of the principal sacral rib is included with that of the pelvic girdle (see below).

Caudal ribs are represented well enough in the two skeletons (Figs. 2, 4) to make their nature and articulation clear. A proximal caudal is acutely L-shaped and articulates firmly with a large diamond-shaped area on the vertebra. The rib when in position, extended directly sideward, then curved abruptly backward in a horizontal plane to parallel the column. A succeeding rib lay median and parallel to the one in front. The caudal rib shown in Figure 2 extended posteriorly 14.5 mm. so that its tip was opposite the head of the third succeeding rib. There were at least 4 pairs of well-developed caudal ribs; our specimens do not show the posterior region of rib-bearing caudals but this undoubtedly was like that of pelycosaurs. Certainly the caudal ribs, or the transverse processes that may represent them posteriorly, have disappeared on the 14th caudal. In structure and arrangement of caudal ribs, *Petrolacosaurus* agrees closely with pelycosaurs, as described by ROMER & PRICE (1940, p. 112) and WILLISTON (1925, fig. 84).

Chevron bones undoubtedly were well developed in the tail of *Petrolacosaurus*, but only a small series is preserved intact on the middle caudals of skeleton no. 1427 (Fig. 2). Here the chevrons are short and extremely delicate; their position is intervertebral. Serial diminution indicates longer spines anteriorly and loss of spines posteriorly before the 50th vertebra. There is no evidence in the chevrons or associated neural arches of an enlarged tail surface adapted for lateral, sculling motion.

Intercentral gaps seem unduly large in the proximal caudals of skeleton no. 1427 (Fig. 2). Associated with caudal ribs of skeleton no. 1428 are three similar and peculiarly shaped bones (Fig. 4, in circle), which appear to be asymmetrical and therefore not median elements. Each bone has a shape something like a tiny Dutch wooden shoe. A pair of these elements fitted together, with long axes parallel and concavities approximated (or directed posteriorly?), probably represents separate halves of an anterior caudal intercentrum. It follows that they represent incipient development of stout anterior chevrons. Such structures could fill the large intercentral gaps seen in skeleton no. 1427. If this interpretation is correct, and there is nothing else in the skeleton which could be con-

fused with these "demi-intercentra" (hypocentra pleuralia of GOODRICH, 1930, p. 48), *Petrolacosaurus* possesses a primitive characteristic known, according to GOODRICH, only in eryopsoid labyrinthodonts and in the diadectid, *Sphenosaurus*. Of course, the skeleton showing separate hypocentra pleuralia is a sub-adult, judging from gross size and incomplete ossification of the pelvis, as mentioned earlier.
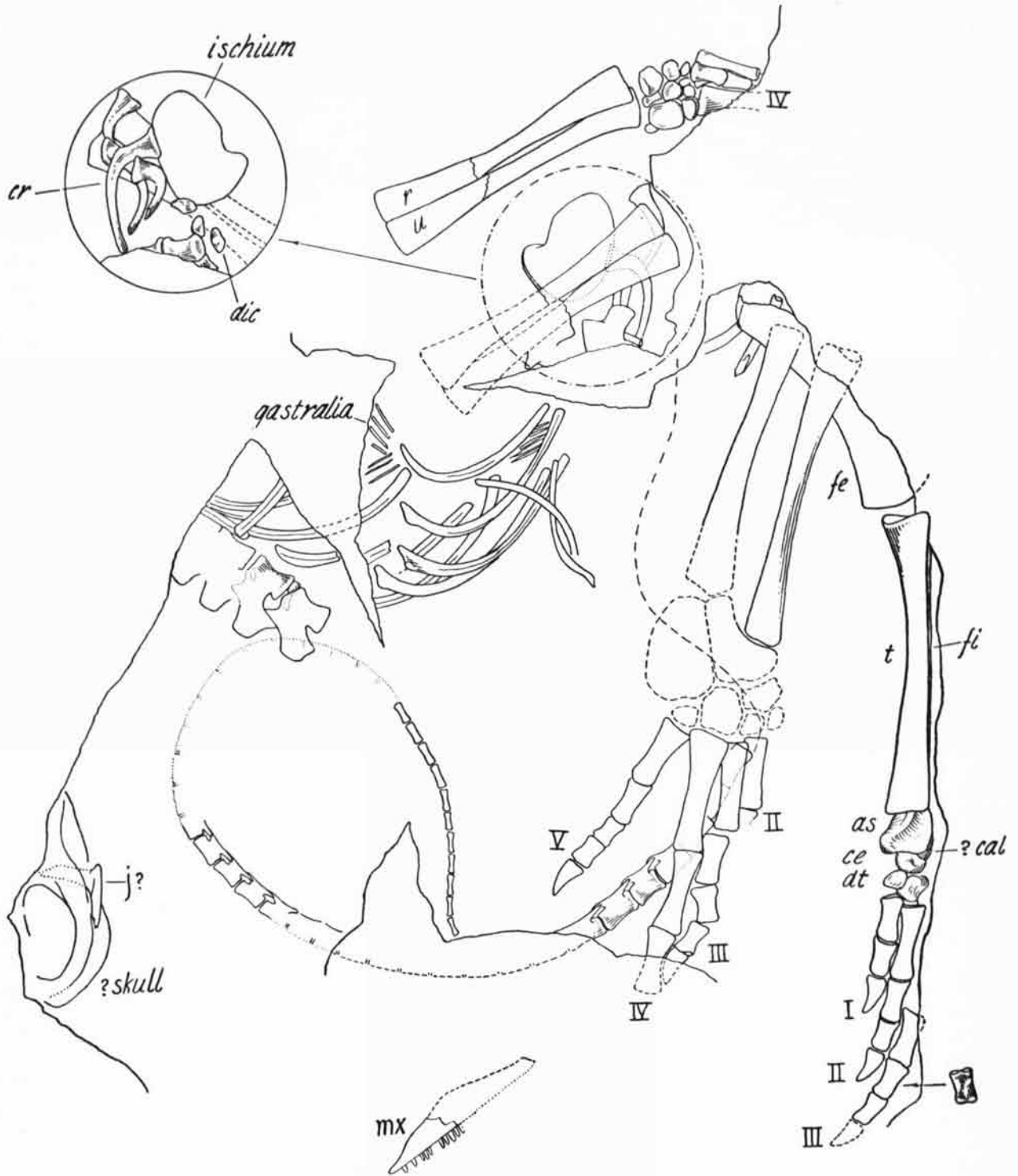

FIGURE 4.—*Petrolacosaurus kansensis* LANE. Skeleton of subadult with fragments of skull associated, KUMNH no. 1428, × 1.25; left circle shows underside of elements in right circle.

GASTRALIA

Associated with the dorsal ribs of skeletons nos. 1427 and 1428 are patches of delicate splints arranged close together in more or less parallel fashion. Little more of a pattern can be made out (their total extent is not shown in the drawings). Despite the presence of fin rays of coelacanth fish occurring in the same stratum, it seems reasonable to regard the delicate splints associated with the dorsal ribs and in the original postion of the belly as gastralia of *Petrolacosaurus.* Perhaps the delicate nature of the gastralia is a small but significant indication of land, rather than aquatic or semi-aquatic habits.

PECTORAL GIRDLE

Elements of the pectoral girdle are preserved only in skeleton no. 1427 (Fig. 2). The left scapulocoracoid, lying lateral side up near the left radius, and the right clavicle, lying median side up near the third cervical vertebra, are identified with reasonable certainty. A third element, lying parallel to and slightly overlapped by the clavicle, is probably a relatively large cleithrum. All these elements lack parts, which fell away when the specimen was split out originally; and the overlying shale presumably bearing impressions was not saved. Probably in this manner, the interclavicle was lost.

SCAPULOCORACOID

This element is an expansive, rather simple plate of bone showing no suture which might distinguish coracoid or coracoids from the scapular portion. Unfortunately, the glenoid region has been broken away with loss of the articulatory surface and any associated foramen, if present. Anteriorly, the element thins to a delicate film of bone, partly damaged, but by its extended position indicating a broad scapular ramus. Ventrally, the thickened coracoid border is perfectly preserved, and obviously was continued medially in cartilage. The scapulocoracoid is thickly rounded along its concave posterior border, especially the ascending scapular ramus. Probably the scapular ramus was extended dorsally (beyond limits shown by its impression) by a suprascapular cartilage. The position of the glenoid must have been at the apex of the angle formed by posterior scapular and posterior coracoid borders, rather than at a lower and posterior position. A "high" glenoid is indicated indirectly by the extensive flat contour of the posterior coracoid area, which extends from below nearly to the angle. It is assumed that the glenoid would be supported by a thickened subglenoid swelling as in any primitive girdle. The inferred high position of the glenoid, together with other features described, suggests a scapulocoracoid resembling the lacertilian element, minus the characteristic an-

terior emarginations or fenestrations. Damaged as it is, there yet appears to be no basic similarity to the pelycosaur element, in which the medial coracoid border is straighter and the glenoid low and posterior in position; and there is no indication of two coracoid elements, so characteristic of synapsid reptiles.

General contours of the scapulocoracoid resemble those of *Araeoscelis,* but the peculiar posterior position of glenoid condyles [6] in this form could not have been present in *Petrolacosaurus,* else some evidence of them would be seen in the impression even though the bone at the critical point has been lost.

The size of the scapulocoracoid seems small, relative to the forelimb, an indication probably, that considerable areas of cartilage extended the coracoid and scapular borders. Thus, cartilage seems to have been extensive in the pectoral girdle of skeleton no. 1427, even though the carpus and tarsus were completely ossified.

CLAVICLE

The clavicle consists of an expanded ventral blade, 13 mm. long, narrowly trangular in outline, with a short ascending process. The blade is noteworthy for a thick, upturned anterior border, a feature more amphibian than reptilian. The ridge thus formed extends nearly to the tip of the blade. In cotylosaurs and pelycosaurs, the ridge, which is a continuation of the ascending process, fades out quickly on the blade. The blade thins to an even border posteriorly; where pieces of the blade are missing, the impression shows a slight development of ventral grooves diverging from a point at the juncture of the blade with the ascending process. Dorsally the surface of the blade is smooth and slightly concave.

Although damaged and somewhat crushed down to the plane of the blade, the ascending process terminates in the matrix in a manner suggesting that its total length is represented. As such, it is considerably shorter than in a captorhinid or pelycosaur.

CLEITHRUM

Partly damaged and lying parallel to the clavicle is a thin, elongate element, which can be doubtfully interpreted at best. The possibility that it is a detached jaw element (prearticular?) cannot be dismissed entirely, because what appears to be a detached splenial lies nearby. However, the element seems to be expanded at one end (damaged) and extended at the other into a long stem of thin bone. Identification as an interclavicle is questionable, because the element does not appear bilaterally symmetrical, the expanded tip is relatively

6. Personal study of *Araeoscelis* raises a doubt concerning the peculiar "triple" condyle of the glenoid (WILLISTON, 1914, fig. D). The dorsalmost condyle may well be a fragment from another element.
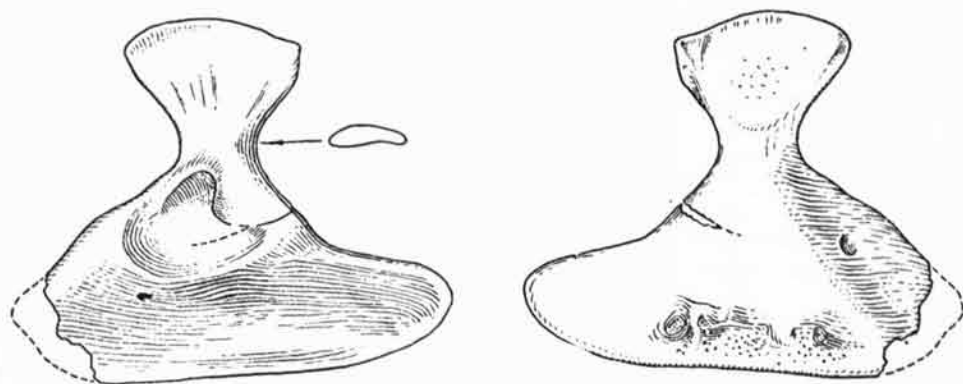
FIGURE 5.—*Petrolacosaurus kansensis* LANE. Left half of adult pelvis, KUMNH no. 1425, × 1.5; external view on left, median view on right.

small, and the stem is markedly U-shaped in cross section. The same three characteristics suggest that the element is a relatively large cleithrum of the eryopsoid and diadectid type, a view not incompatible with the observation that the clavicle has a flanged blade and a seemingly short ascending process. The possibility that the element in question is a relatively large cleithrum is strengthened by comparison with an excellent specimen of *Diadectes* (Harvard Mus. Comp. Zool. no. 1786). The cleithrum, which is in position on the scapulocoracoid, is similar in relative size and shape to the petrolacosaur element. Thus, it seems probable that *Petrolacosaurus* possessed a large spatulate cleithrum of primitive cotylosaur stage generally, and one definitely less reduced than in pelycosaurs and captorhinids. Nevertheless, the pectoral girdle of *Petrolacosaurus* is lightly built as in lizards, and shows little of the massiveness of pelycosaur or captorhinid.

PELVIC GIRDLE AND SACRUM

LANE (1945) has described the external surface of the adult pelvis, no. 1425. But the preparation of the inner surface exposes more detail of importance, including the obturator foramen, thought by LANE to be absent. Accordingly, the specimen is refigured here (Fig. 5).

PELVIS

The adult pelvis has a well-ossified pubo-ischiac plate, perforated only by a small obturator foramen. Pubis and ischium are solidly fused, so that not even a notch remains in the symphysial border. However, union of the plate with the ilium is less solid, for in medial view the ilio-ischiac suture is clearly broken apart. The ilio-pubic suture is fused indistinguishably. In the subadult skeleton no. 1428 (Fig. 4), the ischium is discoid; the anterior, posterior, and ventral borders probably were extended by cartilage, and the acetabular portion, too, was mainly cartilage.

In external view, the pubo-ischiac plate is concave longitudinally below the acetabulum. The newly exposed inner surface is of particular interest, for it clearly suggests the pelycosaur, rather than captorhinomorph. A modestly developed ridge descends from the ilio-pubic suture obliquely forward to the median symphysis. A triangular area is thus formed, pierced by the obturator foramen, and representing the area of attachment for the pubo-ischio-femoralis internus muscle. While the area is more definite than in most pelycosaurs, it is not the precisely defined area characteristic of captorhinomorphs (CASE, 1911, pl. 8, fig. 5). In the latter, the descending ridge becomes markedly prominent and keel-like, and at the symphysis, a characteristic buttress is formed, which meets a corresponding buttress on the opposite side. Such a structure is scarcely suggested in the petrolacosaur pelvis. But there are definite structures present designed to strengthen the median symphysis. Along the pubic and anterior ischial symphysis is a relatively wide, rugose area, as in *Dimetrodon*. Rugosities here appear to be secondary formations developed dorsal to the symphysis proper. The plane of this area indicates clearly that the two halves of the plate met at an acute angle, as in pelycosaurs. Details of the rugose surface are somewhat different from those of pelycosaurs, however. The surface is interrupted by two vertical notches lined with smooth bone; when the two halves of the plate were in place, opposed notches formed symphysial pits. Significance of these pits or gaps may simply be that the rugose area is in the process of forming a more complete surface, such as seen in *Dimetrodon*.

Features of the adult acetabulum are slightly damaged, but its general contour is clear and is as shown in Figure 5. The iliac condyle of the acetabulum is situated well forward near the anterior border, as in some primitive pelycosaurs, for example, *Clepsydrops*.

Above the acetabulum, the ilium expands anteroposteriorly to form a wide blade, nearly symmetri-

cal, but slightly more expanded anteriorly. The iliac neck, thus formed, is flattened in cross section. Superficially, the blade resembles that found in edaphosaurid pelycosaurs, but there are two important points of difference. First, there is no defined area for attachment of epaxial musculature on either medial or lateral surface. If there is such an area, it is ill defined by smooth bone along the dorsal third of the lateral surface. ROMER & PRICE (1940, p. 126) state that in pelycosaurs this area is invariably well defined and generally median or dorsal. Secondly, the medial surface of the iliac blade, perfectly preserved, shows a large semicircular area which can be only the articulating surface of a relatively large sacral rib, like that of skeleton no. 1427. The surface of the semicircular area is characterized by minute and irregular hummocks. Low ridges anteriorly and posteriorly and fine vertical striations ventrally demarcate the area. Although one principal sacral rib is indicated, evidence for a second small sacral rib is seen in configuration of the posterior median blade of the ilium, as in *Seymouria*. Although none has been identified in our specimens, it probably was small and slender and contributed but little to sacral strength. At best, the ilium and ilio-sacral articulation seem to have been like those of primitive pelycosaurs, but there is no insertion of rib end into well-defined groove or cavity. Rather, the articulation seems to have been a simple lap-joint held in place by ligaments, as described for *Eryops* by OLSON (1936a); and the iliac blade is more comparable to that of *Seymouria* or *Eryops* than to that of edaphosaurid pelycosaurs.

SACRUM

Loss and damage to this structure is fortunately offset by the presence of a nearly perfect sacral rib (Fig. 2), preserved approximately in position in skeleton no. 1427. Its presence is critical, for it provides the only good evidence for associating the isolated adult pelvis described above with the skeletons. The rib is short, powerfully expanded proximally and distally, and thus has a constricted neck. Proximally, the expansion forms a narrow tuberculocapitular plate, more massive, but otherwise not unlike the head of the mid-dorsal ribs. The plane of the tuberculo-capitular plate is oblique, rather than vertical, with respect to the plane of the expanded distal end, indicating that articulation with the vertebra was oblique and essentially the same as between mid-dorsal rib and vertebra. The length of articulatory surface is 6 mm., nearly as long as a mid-dorsal centrum at 6.5 mm., and when in position, the capitulum surely extended antero-ventrally, with the result that it touched the intercentrum. The tuberculum is large and partly demarcated from the more narrow capitulum by a ventral groove.

Distally, the sacral rib expands into a nearly symmetrical fan with a maximum width (anteroposterior) of 8.5 mm. It is bent down on the neck and presents a smooth, slightly concave surface to the iliac blade. Thus, a lap-joint held together by ligaments is indicated by the sacral rib, as well as by the iliac blade described above. In median view, the sacral rib blade shows a slight irregularity on the posterior border, suggesting, as does the ilium, an articulation with a second but small and slender sacral rib.

In every respect except relative size, the principal sacral rib of skeleton no. 1427 (Fig. 2) correlates well with the expanded ilium of the isolated pelvis (Fig. 5). The latter belongs to a larger individual, possibly the same one represented by the type specimen.

It can be said with reasonable assurance that the sacrum of *Petrolacosaurus* consists of a principal sacral vertebra with its pair of powerfully expanded ribs. The anteriormost caudal vertebra, with its pair of slender ribs, probably contributed slightly to the ilio-sacral joint. The main support was supplied by one pair of ribs, which for the purpose have expanded tips wider than the mid-dorsal centrum is long.

The pelvic girdle and sacrum of *Petrolacosaurus* is obviously built on a primitive tetrapod plan, recalling that of primitive pelycosaurs among reptiles, but actually of no more than seymourian grade. The principal sacral rib, with its narrow dichocephalous head and decurved distal fan, is more like that of the rachitome, *Eryops*, than of a reptile, and especially so with respect to the lapjoint of sacral rib with iliac blade. In most pelycosaurs, *Araeoscelis*, and even *Captorhinus*, the principal sacral rib tends to lose the oblique, narrow dichocephalous head; and the distal end develops an obtuse surface which abuts, rather than laps against, the ilium. The distal fan of the principal sacral rib is relatively wide in *Petrolacosaurus;* it is 1.3 times wider than the average dorsal centrum is long, and the dorsal centrum itself is relatively long. This excessive width may be correlated with terrestrial habits which demanded a strong sacro-iliac joint, produced from a primitive plan consisting of one principal sacral vertebra.

LIMBS

Thirteen limbs, seven of them forelimbs, are represented. Most of these were originally complete as they lay in the matrix. Five of the thirteen were isolated from the body, yet remained more or less intact. Of the eight limbs actually associated with the two skeletons, all were more or less intact but none was articulated with its girdle. Thus, the mode of preservation seems independently to suggest that the limbs of *Petrolacosaurus* were exceedingly well-knit structures.
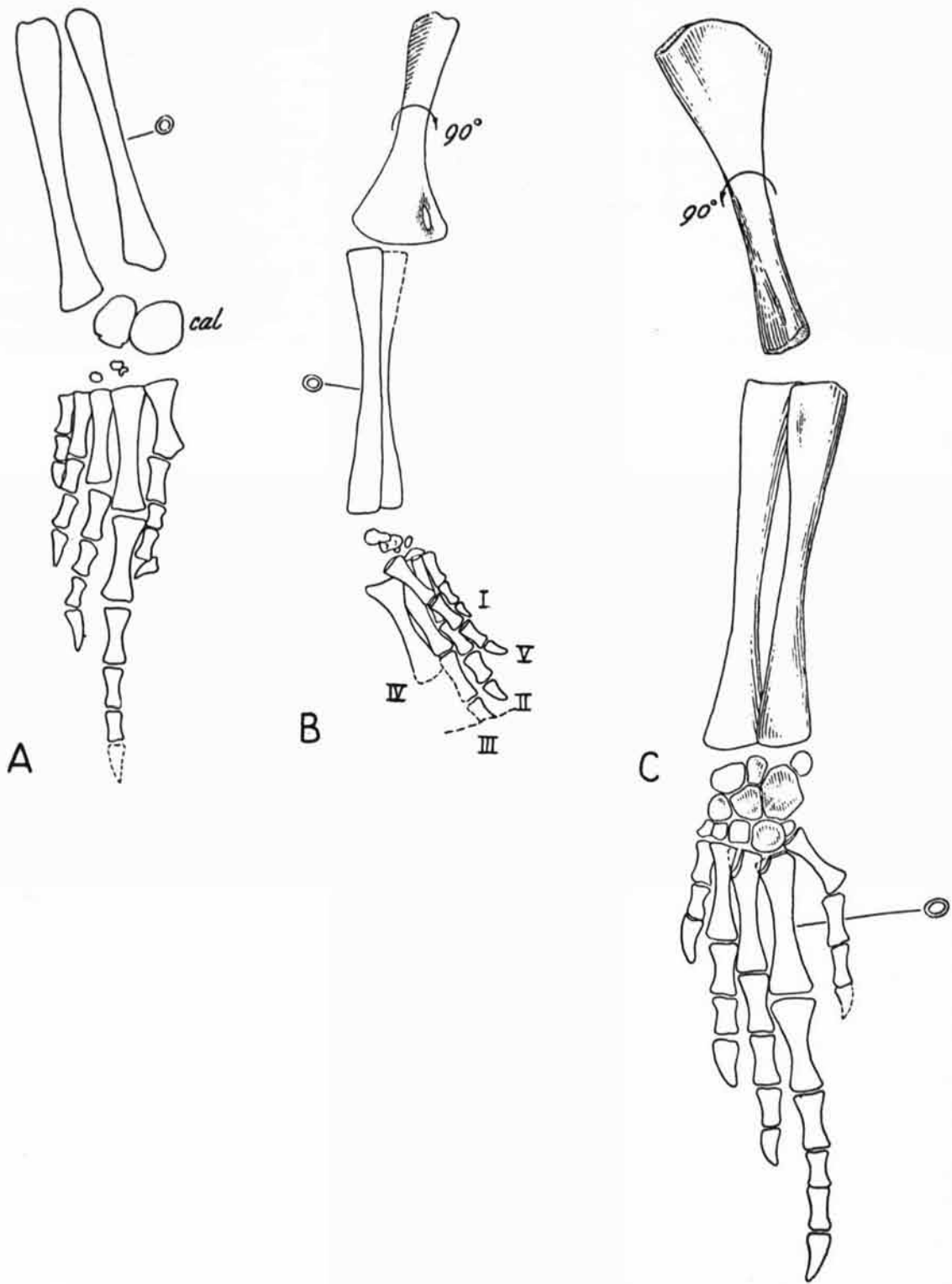
FIGURE 6.—*Petrolacosaurus kansensis* LANE. (A) Immature right hind limb lacking femur, KUMNH no. 1426. (B) Immature left forelimb, KUMNH no. 1429. (C) Subadult right forelimb, KUMNH no. 1423. All figures × 1.5, plantar view; note rotation of proximal segment in B and C.

Skeleton no. 1427 is complete enough to show approximately the length of limbs relative to the length of the body. Over-all length of the front and the hind limb is conservatively estimated at 135 and 165 mm., respectively. The dorsal and sacral regions together measure 169 mm. Thus, the front limb is 0.8 times, the hind limb nearly 1.0 times as long as the dorsal-sacral region. By contrast, the front and hind limb of *Varanus salvator* are, respectively, 0.65 [7] and 0.75 times the length of the dorsal-sacral region.

Despite the large number of limbs represented, their present condition prevents many direct comparisons of length. Nevertheless, several important facts emerge. When the length of long bones is compared to average length of dorsal centra, it is found that, proportionately, the limbs are not so long as those of *Araeoscelis*, although they are relatively slender. However, by the same values, it is apparent that the zeugopodium of the front and hind limb is longer relative to the stylopodium than in any known Paleozoic reptile, including *Araeoscelis*. There are few reptiles, exclusive of archosaurs and their derivitives, which have zeugopo-

TABLE 4. *Length of Limb Bones Relative to Length of Average Dorsal Centrum*

	Humerus	Radius	Femur	Tibia
Petrolacosaurus no. 1427...	5.4	6.5	...	...
1428...	...	6.0	5.7	6.6
Dimetrodon [*]	6.6	5.3	6.8	5.2
Araeoscelis [*]	6.6	...	7.7	8.0
Macrocnemius [*]	5.7	5.0	7.4	7.6
Palaeagama [*]	5.6	4.0	6.7	6.7
Varanus salvator [**]	4.6	3.7	5.6	4.0

[*] From Romer, 1947.
[**] Average length of dorsal vertebra disregards procoelous condition.

dium longer than stylopodium, and even in them the elongation is confined to the hind limb, and is correlated with rapid bipedal locomotion. In aquatic reptiles—mesosaurs, ichthyosaurs, plesiosaurs and mosasaurs—there is a tendency toward marked reduction in length of zeugopodium relative to stylopodium. All pelycosaurs have a longer stylopodium (ROMER & PRICE, 1940, p. 136), although near equality is attained in the hind limb of *Mycterosaurus*. ROMER's figures (Table 4) for the humero-radial proportion of *Dimetrodon* are almost exactly reversed in *Petrolacosaurus*. By contrast, *Araeoscelis* shows a slightly longer zeugopodium, at least in the hind limb; length of the front limb is unknown. According to ROMER (1947), other araeoscelids, and eosuchians as well, show equality of stylo- and zeugopodium in the hind limb, but in the front limb the zeugopodium is short. Thus, in *Petrolacosaurus* the definite elongation of the zeugopodium in both

7. Measurement of over-all length of the forelimb includes a correction to compensate for the relatively short length of manus digit IV in *Varanus*.

the front and hind limb is unique among reptiles having a sprawled posture, except possibly *Araeoscelis*. This characteristic taken alone, or along with such others as the perfect ossification in the adult carpus and tarsus, strongly indicates that *Petrolacosaurus* was terrestrial, fully quadrupedal in gait, perhaps arboreal, and that it was capable of rapid locomotion.

Bones of the limbs are slender and lightly constructed. Broken ends reveal that the shaft region of the long bones (metapodials and longer phalanges) is hollow; commonly the cavity is filled secondarily with transparent calcite. As shown in the illustrations, the shaft is round, the cavity is large, and the perichondral bone is thin; these are characteristics also of the long bones of *Araeoscelis* and *Mycterosaurus*. Crushing is apparent in a number of specimens, but generally the mineral fill seems to have been deposited before pressure was great enough to collapse the fragile bones. Nevertheless, the ends of the radius and ulna are flattened, and at least part of this flattening is considered original.

Although bones of the manus and pes are well ossified and present definitive surfaces to each other even in subadults, the articulatory surfaces between long bones and between limbs and girdle were obviously cartilaginous. More complete ossification is indicated in the adult femur (Fig. 8) than in that of subadults, but the ends remain relatively simple and unfinished, even in adults.

FORELIMB

The humerus is primitively constructed; the proximal and distal ends are expanded plates, twisted approximately 90 degrees with respect to each other. Immature humeri are constructed simply and lack any pronounced processes or definitive articulatory surfaces. The head of the humerus has a narrow, convex surface which was capped by cartilage; a lateral (deltoid) process is only slightly developed and is delineated from the convex surface by a slight convexity (Fig. 6, *C*). Distally, an elongate entepicondylar foramen pierces the entepicondyle, which is somewhat larger than the ectepicondyle. The distal articulatory surface is simple and lacks definitive radial and ulnar surfaces.

The radius and ulna are elongate and of nearly equal length; they are of almost the same shape, even in the adult skeleton (Fig. 2). The ulna lacks an olecranon process, and characteristically, the flattened proximal ends of the radius and ulna present a nearly linear surface to the humerus. Similarly, the distal surfaces present a nearly linear articulation to the carpus (Figs. 2, 4, 6). The distal ends of the radius and ulna are flattened and there is some overlapping of one on the other, as can be seen in superior view. A like amount of flattening is not present in the tibia and femur of the same

individual. Possibly the present shape of the radius and ulna is natural and not the result of crushing. Yet the short transverse width of the proximal part of the carpus strongly suggests that at least some posthumous flattening of the radius and ulna has taken place. Characteristically, the radius and ulna have cylindrical mid-shafts, which are well separated from each other (Figs. 2, 4, 6). The ulna is not curved preaxially, and accordingly the middle part of the shaft does not fit snugly against the radius, as reported by LANE (1945, p. 386).

The carpus is excellently represented by four specimens in nearly perfect articulation (Figs. 2, 4, 6-7). One in particular (Fig. 7) shows how perfectly ossified was the adult mesopodium of *Petrolacosaurus,* and it may be regarded as typical in this respect. All the carpal elements present definitive surfaces to each other and obviously fitted neatly and compactly together with a minimum of cartilage between surfaces. In general pattern, the carpus is pelycosaurian, there being eleven elements—radiale, intermedium, ulnare, pisiform, 2 centralia, and 5 distal carpals — arranged and shaped approximately as in *Ophiacodon* and *Varanosaurus.* LANE (1945) did not recognize a pisiform in his description of the carpus; he described the two centralia as one, distal carpals 1 and 2 as one, and numbered distal carpals 3, 4, 5 as 2, 3, 4, respectively. However, LANE saw only the one carpus (type of his *Podargosaurus*) and one less ossified and most difficult to interpret. Discovery of the piece of shale split off from this specimen, carrying bone and impression, adds details which make a new figure desirable (Fig. 6, *C*). As restudied, LANE's specimen is in essential agreement with the other and more complete carpi.

Although the carpus of *Petrolacosaurus* agrees fairly well with that of primitive pelycosaurs, there are a number of distinctive features of importance. The radiale, well shown in two specimens (Figs. 2, 7), has a prominent ridge on the dorsal surface, as in pelycosaurs, but is more oblique to the long axis. The radial surface is completely transverse to the long axis, rather than tilted dorso-distally as in pelycosaurs. Apparently distinctive is a small knob on the distal articulatory surface, which may represent a small fused centrale. It fits partly into the angle formed by the proximal surfaces of the median and lateral centrale and partly into the proximal surface of the former.

The intermedium is rather slender and somewhat cylindrical proximo-distally, and together with the ulnare, extends characteristically farther proximally than the radiale, but not nearly to the degree seen in pelycosaurs. This feature explains why the radius and ulna, which lie in place in several specimens, appear to have nearly the same length, that is to say, the radius extends distally only slightly beyond the ulna, so that the zeugopodial-autopodial
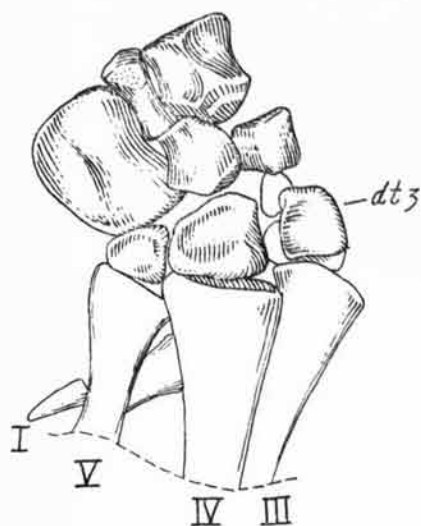

FIGURE 7. — *Petrolacosaurus kansensis* LANE. Right carpus of young adult, KUMNH no. 8355, × 3, showing completely ossified elements; dorsal view.

joint is more nearly transverse than usual for a primitive forelimb.

A peculiar feature of the adult carpus is a large and discoid ulnare, which, if found isolated, might well be mistaken for a fibulare. The ulnare articulates with the lateral centrale, and distal carpals 4 and 5 in almost exactly the same manner as the fibulare articulates with the enlarged distal tarsals 4 and 5. Although the ulnare is expanded laterally more than in pelycosaurs generally, its relations with the other carpals is comparable.

A small, discoid pisiform, closely applied to the proximo-lateral surface of the ulnare, is clearly seen in three of four specimens and in the fourth (Fig. 7) probably was lost with the radius and ulna, which originally lay in articulating position in the matrix.

The lateral surface of the median centrale bears a proximo-distal groove into which the lateral centrale fits snugly. This feature, in addition to the knob on the distal radiale, makes of the three elements — radiale, median and lateral centrale — a close-fitting, interlocking unit. The lateral centrale differs from that of pelycosaurs only in that the surface presented to the radiale is tilted approximately 45 degrees to the long axis. ROMER & PRICE (1940, p. 159) state that the corresponding surface of the radiale tends to face strongly the lateral side, and thus nearly vertical to the long axis in ophiacodonts and sphenacodonts.

Five distal carpals are clearly represented in only one specimen, but combinations of lateral and medial elements in other specimens clearly indicate that five are characteristic and arranged as in pelycosaurs. The fourth element has a strong contact with the lateral centrale and ulnare, while the third

adjoins the lateral and median centrale. The second distal carpal is in contact with most of the remaining distal surface of the median centrale, leaving but little surface for the first distal carpal. The fifth distal carpal, triangular in shape, tends to be wedged in between the ulnare and the fourth distal carpal, precisely as the fifth distal tarsal is wedged between the fibulare and fourth distal tarsal.

In general proportions, the carpus is about as long as broad, in spite of the lateral extension of the discoid ulnare. In pelycosaurs, and captorhinids also, the carpus is generally broader than long. Thus, the petrolacosaur carpus seems to show elongation, probably correlated with the more obvious elongation of radius and ulna. A definitive joint plane is apparently lacking within the carpal mass, and even between carpus and zeugopodium, mobility of radius on radiale must have been slight. As pointed out earlier, the entire line of articulation here is nearly transverse to the long axis, the radius and ulna being approximately equal in length. Movement in the wrist region was obviously of the unspecialized type, best seen in amphibians where there is no localization of joints between elements. However, a definitive joint plane between carpus and metacarpals is suggested by the right manus of specimen no. 1427 (Fig. 2). The manus has been flexed in such a way as to suggest that the easiest plane of flexure, if present at all, was between carpus and metacarpals—certainly not between carpus and zeugopodium.

Metacarpals are elongate and they graduate in length from I to IV. Metacarpal V is not distinctive in shape, but is noticeably divergent to the degree seen in pelycosaurs. The marked degree of divergence shown by specimen no. 1423 (Fig. 6, C) is considered accidental. Some expression of digit length relative to the other limb segments may be obtained by comparing the length of metacarpal IV with that of the elongate carpus (taking the distance from proximal ulnare to distal tip of the distal fourth carpal). Metacarpal IV is 1.5 times as long as the carpus, instead of approximately the same length, as in pelycosaurs except for *Varanops*, in which the metacarpals are also attenuate.

Metacarpals (and metatarsals as well) have a cylindrical shaft and are flattened and expanded at either end, so that the total width proximally of the five elements exceeds the width of the carpus. Thus, in order to articulate with the carpus, the metacarpals overlap each other proximally in a specific manner. The lateral border of metacarpal I overlaps (in dorsal view) the median border of metacarpal II, and so on. This relation is found also in the pes; consequently, the ventral or dorsal aspect of autopodium is easily recognized when elements are in position. ROMER & PRICE (1940, p. 167) note that an overlap such as that described above is characteristic of manus and pes in pelycosaurs; and it is present in the primitive archosaur *Yaleosaurus*, in crocodiles, rhynchocephalians, and others. However, in certain reptiles, the system of overlap seems to be reversed, as in the pseudosuchian *Prestosuchus*. WILLISTON (1914) reconstructs the feet of *Araeoscelis* with the reversed overlap of proximal metapodials. An overlap is never found among amphibians and is not well developed in cotylosaurs. It is lacking in reptiles highly adapted to aquatic life.

Metacarpals and metatarsals show a marked and even increase in over-all proportions from I through IV; the result is that the 4th element is extremely robust and long. The increase is somewhat more accentuated than in most pelycosaurs and markedly more so than in post-Paleozoic reptiles. The tendency in many diverse lines of reptiles has been to shorten the 4th metapodial, particularly the 4th metacarpal. This reduction is apparent even in lizards with extremely attenuate digits. Thus, *Petrolacosaurus* is primitive with respect to the relatively large size of the 4th metatarsal, and particularly of the 4th metacarpal.

Phalanges of the manus and pes are clearly illustrated; consequently little need be said concerning their general character. It seems curious that so many specimens of *Petrolacosaurus* should have the feet preserved in undistorted condition, the digits regularly disposed in divergent pose. Possibly the digits were webbed, and thus were regularly held in position in death. However, the fine matrix which has preserved delicate details of many land plants and fragile insects, as well as small patches of what appear to represent skin around the neck (noted during preparation of the immature skull), surely would have preserved some indication of webbing between the digits, had it been present.

In all specimens, the phalangeal formula for the manus is 2-3-4-5-3 and for the pes is 2-3-4-5-4. Length measurements of the many articulated digits bring out several interesting facts (Table 5). The progressive increase in length of digits from I to IV is relatively marked in adult specimens, even more so in young specimens, and is about that found in long-footed pelycosaurs, for example, *Varanops*. Counting the length of digit I as unity, digits II-IV increase in proportion approximately 1.75, 2.5, 3.5 times the length of digit I in the manus, and approximately 1.5, 2.1, 3.5 in the pes. Living lizards, such as *Varanus* and *Gerrhonotus*, show considerably less proportional lengthening. Steady increase in length from I to IV in *Petrolacosaurus* results in digit IV being extremely attenuate in both the manus and pes. The tip of digit III regularly lies near the distal end of the second phalanx of digit IV when the two digits are near apposition.

As with the metapodials, a tendency in many

lines of post-Paleozoic reptiles has been to reduce the relative length of digit IV, especially in the manus. *Petrolacosaurus* is primitive in the robust development of digit IV of the manus, as well as of the pes.

ROMER & PRICE have remarked (1940, p. 166) that within a group, small pelycosaurs probably have more attenuate feet than large pelycosaurs, but supporting data are lacking. A natural corollary may be that younger individuals of a species have more attenuate digits than older individuals, and measurements of immature specimens of *Petrolacosaurus* (Table 5) indicate that such is the case. The progressive increase seen in the two small and poorly ossified specimens (Figs. 6, A, B) is definitely greater than in the adult, digit IV being more than 4.5 times the length of digit I, at least in the pes.

In adults, the distal tips of subterminal phalanges have well-developed lateral tuberosities, more pronounced in the pes than in the manus, for the attachment of strong collateral ligaments. This indicates that the digits of this small reptile were strong. Terminal phalanges have moderately decurved points and are moderately compressed transversely, indicating the presence in life of sharp claws, but not claws markedly decurved, as in *Varanus salvator*. Independently, claws are suggested by a faint impression in the shale matrix of specimen no. 1427 in the correct position on digit II of the left manus.

HIND LIMB

The hind limb is less well represented than the forelimb, although until they were damaged, skeletons nos. 1427 and 1428 (Figs. 2, 4) possessed right and left hind limbs in nearly perfect articulation. Thus, the isolated right limb, which is the type of *Petrolacosaurus kansensis*, remains the most informative of available specimens. This has been carefully restudied and new drawings have been made (Figs. 8, 9) which point up interpretations differing
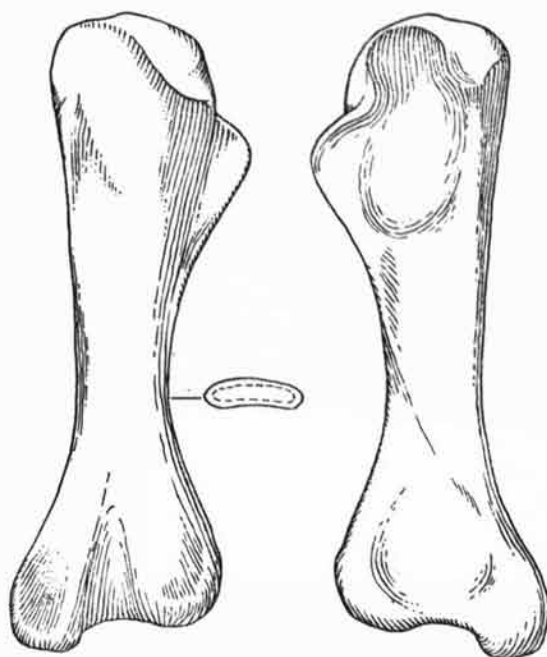

FIGURE 8.— *Petrolacosaurus kansensis* LANE. Right femur of adult, KUMNH no. 1424 (type), × 1.5, associated with lower limb (Fig. 9); dorsal view on left, ventral view on right. Drawn from cast made from impressions in apposed plates of shale; specimen somewhat flattened.

somewhat from those of LANE (1945), who concluded that the limb is pelycosaurian.

The femur of the type is reconstructed from the natural mold remaining in the shale after removal of bone fragments. Plaster casts of the mold afford the detail seen in Figure 8. Allowing for crushing, which has flattened the element somewhat and bent preaxially the internal trochanter, the femur is closely comparable in detail to that of the cotylosaur, *Captorhinus*, and of pelycosaurs generally. LANE's original figure of the limb (1945, fig. 1) is

TABLE 5. *Proportional Length of Digits II-V Relative to Digit I (Value 1.0)*

| | | | Manus | | | | | Pes | | |
	I	II	III	IV	V	I	II	III	IV	V
Petrolacosaurus										
1427	1.0	1.7	2.5	3.6	...	1.0	1.6	2.3	3.5	2.1
1423	1.0	1.8	2.4	3.5	1.5	...	...	...	...	...
1428	...	...	...	...	...	1.0	1.5	2.1	3.5[a]	2.4
1424	...	...	...	...	...	1.0	1.5	2.0	3.2	1.9
immat. 1429	1.0	2.3	...	...	2.1	...	...	...	...	...
1426	...	...	...	...	...	1.0	1.9	2.9	4.6	2.3
Varanops										
brevirostris [b]	1.0	1.6	2.9	4.1	2.0	1.0	1.6	2.4	3.2	1.4
Varanus salvator	1.0	1.4	1.7	1.7	1.4	1.0	1.2	1.5	1.8	1.5
Gerrhonotus										
coeruleus	1.0	1.7	2.0	2.0	1.5	1.0	1.6	2.1	2.2	1.7

a. Estimated.

b. ROMER & PRICE, 1940, figs. 40E, 41D.

confusing in that the femur is shown in ventral view, and the articulating lower leg and pes are shown in dorsal view. The distal postaxial (fibular) condyle is thus placed preaxially in contact with the tibia. Also, the proximal part of the femur is incompletely drawn, for it lacks most of the head and the flared internal trochanter.

Proximally, the head of the femur bears a well-developed internal (lesser) trochanter, beginning at the ventro-preaxial border of the head and passing obliquely distad, to become a poorly defined adductor ridge. On the dorsal surface near the head, a prominent process is developed, probably for attachment of the pubo-ischio-femoralis internus muscle, the principal short abductor of the femur. The head itself is terminal, with a convex and narrow articular surface. The structure of the femur definitely indicates a sprawled posture, in which the thigh moves in a more or less horizontal plane. Distally, the impression is damaged but in dorsal aspect, it clearly outlines the prominent postaxial condyle, separated from the preaxial condyle by a deep intercondylar fossa. Allowing for individual variation in *Captorhinus*, there is little to distinguish the femur of *Petrolacosaurus* from this cotylosaur. It is significant that the femur of our specimen lacks the attenuation seen in *Mycterosaurus* and *Araeoscelis*, reptiles of comparable size. Thus, while showing elongation of the lower leg, the femur of *Petrolacosaurus* appears relatively unaffected by this specialization.

Little can be said concerning the tibia and fibula except that they are long and slender relative to the femur, and in the one specimen (Fig. 4) where the femur and tibia are articulated, the tibia is clearly longer than the femur. Also, in the immature limb (Fig. 6, A) which lacks the femur, the tibia and fibula appear long and slender, and actually prove to be so when a comparison is made with the pes (taking the length of the 4th metatarsal as a reference and checking against the most complete specimen). The length ratio of the 4th metatarsal to the tibia in the above specimens, when applied to the type specimen (Fig. 9), indicates that LANE's (1945, fig. 1) reconstruction of the length of tibia and fibula is far short, approximately three-fourths, of the actual length.

Both the tibia and fibula articulate firmly with the tarsus, leaving a wide space between their distal portions, as in the limbs of most primitive reptiles. Unlike the radius and ulna, which are of nearly equal length, the tibia substantially exceeds the fibula in length, because of its more distal articulation with the astragalus. Inequality of length is further enhanced in *Petrolacosaurus* because of the apparent elongation of the astragalus proximal to the tibial facet. Of particular interest is the positive manner in which the tibia articulates with the astragalus. There is considerable freedom of movement at this joint in pelycosaurs and cotylosaurs,
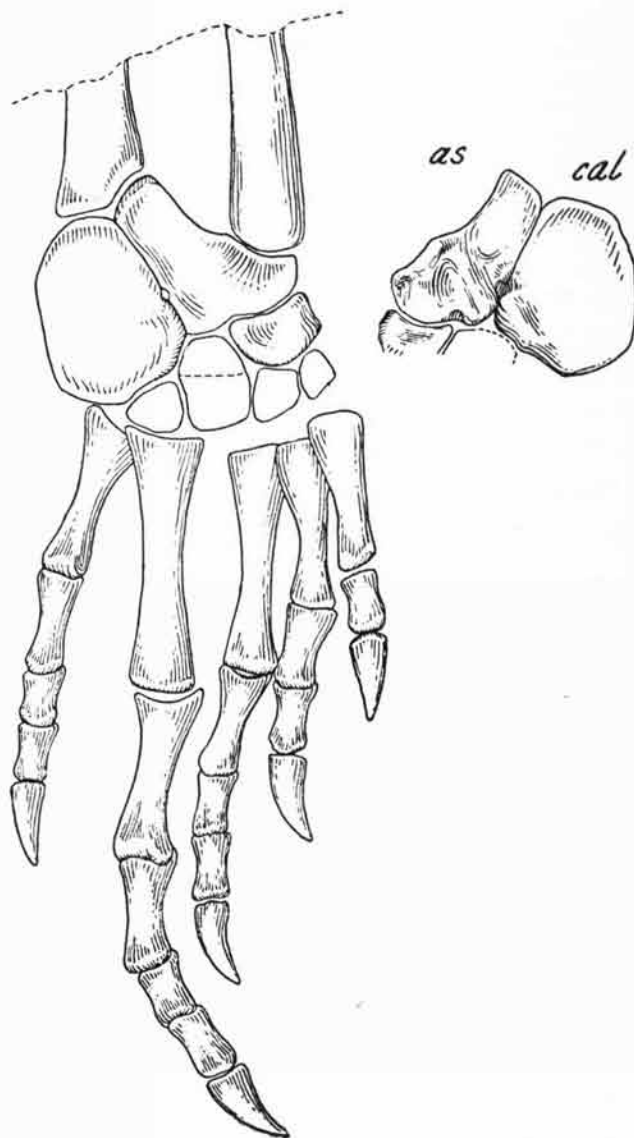

FIGURE 9.—*Petrolacosaurus kansensis* LANE. Right pes of adult, KUMNH no. 1424 (type), × 1.5, associated with femur (Fig. 8); dorsal view of pes, plantar view of astragalus and calcaneum to right. Tarsus drawn from casts made from impressions in apposed plates of shale.

and when a limb of these reptiles is found articulated, the tibia is usually displaced from its contact with the astragalus. However, in the several limbs of *Petrolacosaurus*, the tibia shows no displacement, not even in an immature specimen (Fig. 6, A) where the carpus was largely cartilaginous. Thus, the mode of preservation indicates that the tibia of *Petrolacosaurus* had more positive, less free articulation than seen in pelycosaurs generally. Observations of the tarsus support this conclusion.

The tarsus is best represented in the type specimen, where it must be studied from impressions of dorsal and ventral surfaces in the matrix. Most of the bone has been lost and fragments remaining

have been partly removed in preparation. Unfortunately, right and left tarsi of both skeletons, originally complete, have been lost almost completely by weathering or through exigencies of collection. But where parts are preserved, they agree with the type specimen. Also, the immature tarsus, though incompletely ossified, agrees with the type specimen insofar as bone is present.

The interpretation of the tarsus given here differs from that of LANE (1945) mainly in the delineation and naming of central and distal tarsal elements. Restudy shows that these elements are larger than shown in LANE's original figure and fit together compactly, as in the mature carpus. Also, LANE's distal tarsal 1 is either 2 alone or 2 is fused with 1, his distal tarsal 2 is the third, his distal tarsal 3 and centrale 2 (lateral) are probably one unit and represent the typically large distal tarsal 4, his distal tarsal 4 is the typically small and triangular 5th, and lastly his distal tarsal 5 is the broken proximal end of metatarsal V. The only deformation noticeable in the pes consists of a slight lateral displacement of the proximal ends of metatarsals IV and V and a slight distal displacement of digits I-III. Normally IV articulates mainly with distal tarsal 4 and with a median portion of 5, and V articulates with the remainder of distal tarsal 5.

No single element in *Petrolacosaurus* is more distinctive than the long-necked astragalus. Fundamentally it is constructed on the L-shaped plan of primitive reptiles. Proximally, the vertical arm of the L, dorso-ventrally compressed, has a strong fibular facet, sharing equally the articulatory surface of the fibula with the adjoining calcaneum. Medially, the vertical arm has a free surface extending obliquely to the tibular facet; laterally, the vertical arm has a long straight border articulating with the medial aspect of the calcaneum—an articulation interrupted distally by opposed grooves in both elements forming the perforating foramen. The horizontal arm of the L has a strong latero-distal contact with the 4th distal tarsal and a remaining and major distal articulation with a single centrale. Medially, the horizontal arm is thicker, more massive, in support of the platform for articulation with the tibia.

The dorsal surface of the astragalus is gently concave, and the concavity is accentuated distally by a buttressing of the tibial facet. Ventrally, the surface is divisible into ridges and valleys of characteristic development which give it a roughened appearance. Prominent among the irregularities is a conspicuous notch in the distal border, which does not carry through to the dorsal surface but is expressed there by a broad reëntrant angle in its distal border. This notch is not well developed in pelycosaurs (ROMER & PRICE do not mention it, and their excellent figures do not show it), but it is found in comparable development in *Captorhinus*, where it receives the latero-proximal end of the

centrale. Two diverging, rounded ridges extend distally from the border of the tibial facet; a narrower one extends to the latero-distal corner, and a broader one extends distally toward the centrale. The former is comparably developed in *Captorhinus* but the latter seems to be unique in its development, and to constitute a ventral buttressing of the peculiar tibial facet, a feature certainly not characteristic of pelycosaurs.

Whereas the tibial facet of pelycosaurs appears as a broad hemispherical surface directed medially, dorsally, and proximally, this surface in *Petrolacosaurus* forms a broad platform that is slightly concave in dorsal outline. The platform is not directed medially at its distal border, and the disto-median border of the astragalus does not enter into the tibial surface. In both the type specimen and a subadult (Figs. 9, 4), the astragali are essentially alike in this respect. The tibia thus has a positive articulation on the astragalus, and one which lacks the freedom of movement characteristic of pelycosaurs. As noted above, the finding of so many hind limbs with the tibia squarely in place independently suggests a positive articulation of tibia with astragalus.

Comparison of the tibial facet with that of *Captorhinus* (of which several isolated and three articulated astragali are at hand, Fig. 10, *C*) and with SCHAEFFER's (1941) description of *Labidosaurus* shows that the structure is more nearly cotylosaurian than pelycosaurian. SCHAEFFER has pointed out that the labidosaur tarsus is a nearly ideal primitive plan from which to derive all the reptiles. In this form, the tibial facet is nearly flat and is tilted dorsally and proximo-medially. Also the facet does not involve the medianmost area of the astragalus, a condition seen clearly in *Petrolacosaurus*. *Captorhinus* is intermediate between *Labidosaurus* and *Petrolacosaurus* on one hand, and pelycosaurs on the other in this respect. The tibia-astragalus articulation of *Petrolacosaurus* suggests the condition seen in *Varanus* and other diapsid reptiles in which, as SCHAEFFER (1941) has pointed out, a meso-tarsal joint developed in sharp contrast to the cruro-tarsal joint of the synapsidans.

Even with the flattened tibial facet and a relatively restricted movement of the tibia on astragalus, it must be noted that the increased length of the tibia and fibula in *Petrolacosaurus* would make possible a greater degree of twisting of one bone on the other than if these elements were shorter. Thus, in walking movement, with the femur operating essentially in a horizontal plane, there would be in the extra length of tibia and fibula something of the flexibility seen in the shorter pelycosaurian tibia, which articulates with a hemispherical surface on the astragalus.

The immature pes (Fig. 6, A) throws some light on the evolution of the reptilian astragalus. The partly ossified astragalus of this specimen, broken
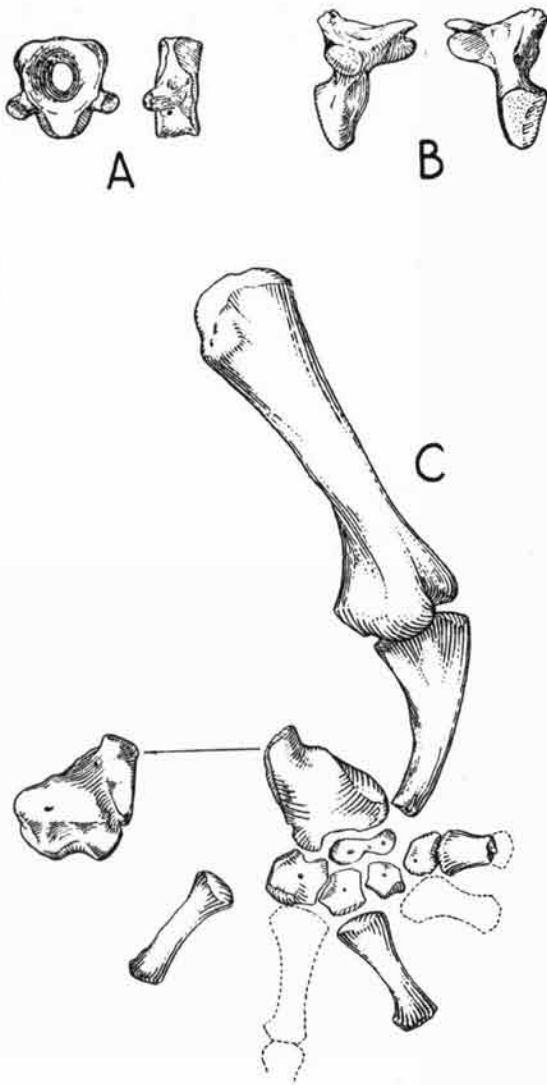
FIGURE 10.—Selected specimens of *Captorhinus* sp. for comparison with *Petrolacosaurus kansensis* LANE. (A) Atlantal centrum, KUMNH no. 9610, × 2, posterior view and lateral view of right side. (B) Atlantal arch, KUMNH no. 9609, × 2, lateral (left) and median (right) views. (C) Partial right hind limb, KUMNH no. 8694, × 2.5; dorsal view of tarsus with plantar view of isolated astragalus, KUMNH no. 9608. Note dumbbell-shape of centrale and apposing deep notch in astragalus.

cleanly in a plane parallel to the dorsal surface, shows two distal emarginations which suggest a separate centrale in the process of fusing with the intermedium. There is no clear evidence suggesting a tripartite astragalus composed of intermedium, centrale and tibiale, as in *Captorhinus* (Peabody, 1951).
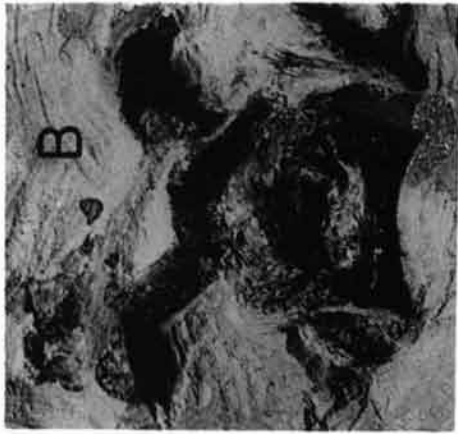
Elongation is the most obvious pelycosaurian characteristic in the astragalus of *Petrolacosaurus*. In over-all dimensions the astragalus is 1.5 times as long as broad, a proportion also found in species of *Dimetrodon* and *Edaphosaurus*. The proportion is much lower, only 1.1 to 1, in *Ophiacodon* and *Labidosaurus*. *Captorhinus* is intermediate but closer to *Petrolacosaurus* (1.4 to 1). Some species of pelycosaurs probably exceed 1.5 to 1. The astragalus of *Petrolacosaurus* appears longer than it actually is, because of the long, free border on the median edge. This feature gives the astragalus a proportionately longer neck than in other astragali having similar length-breadth proportions. Probably the lengthened neck is but another expression of the elongation seen in the zeugopodium and digits of *Petrolacosaurus*. It need not be regarded as indicating definite pelycosaurian affinities, but rather as a peculiarity of this long-limbed reptile, probably developed from a captorhinomorph pattern.

The calcaneum is a large discoid plate meeting the astragalus in a long, straight articulation. Dorsal and ventral surfaces are gently concave; the distal border is thick and shallowly emarginated to receive the proximo-lateral facet of the large 4th distal tarsal and the proximal facet of the triangular 5th distal tarsal (Fig. 9). Except for elongation which matches that of the astragalus, there is nothing to distinguish the calcaneum from that of *Captorhinus*. The pelycosaurian calcaneum may be equally discoid and elongate but commonly it has a straighter distal surface, lacking the double emargination for the 4th and 5th distal tarsals.

A single large centrale underlies the buttressed, medial part of the astragalus in a position corresponding to the lateral centrale of pelycosaurs. There is no evidence of a median centrale and if present originally, it is improbable that this element became detached and was carried away. Both dorsal and ventral surfaces of the centrale show a

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broad central furrow running proximo-distally. Articulation with the astragalus resembles that seen in *Captorhinus*.

ROMER & PRICE (1940) have shown that pelycosaurs regularly possess a median and lateral centrale and that the latter tends to enlarge and take over the function of both, thereby relegating the former to a relatively unimportant median position. The centrale of *Labidosaurus* is much compressed proximo-distally and has been considered to be the lateral element of the primitive two in reptiles. This is apparently the view taken by SCHAEFFER (1941, p. 430) who states "there is but a single centrale or navicular that is very much compressed proximodistally." Thus, it appears that pelycosaurs retain a condition more primitive than that of *Labidosaurus*, a cotylosaur. However, in excellent specimens of *Captorhinus* at hand, the centrale is compressed less than in *Labidosaurus* and has a dumbbell shape suggesting a fusion of two elements (Fig. 10, *C*). Microscopic examination of the dorsal surface indicates two centers of ossification, and centrally reveals a proximo-distal zone of different texture suggestive of the line of fusion. Thus, the lateral centrale of pelycosaurs and the transversely elongate centrale of *Captorhinus* and *Labidosaurus* may not be exact equivalents. It follows that the single centrale of *Petrolacosaurus*, though broader proximo-distally than in cotylosaurs, may represent both median and lateral elements fused together. In any event, the occurrence of a single centrale, as in *Petrolacosaurus*, is not characteristic of pelycosaurs, and we have another instance in which the "pelycosaurian" design attributed to the petrolacosaur tarsus by LANE, is more apparent than real.

Distal tarsals are in position except for the first, which is probably lost in *Petrolacosaurus*. Correlated with this loss is a bunching of metatarsals by overlapping of their proximal ends, so that the first metatarsal articulates with the 2nd distal tarsal. The 4th distal tarsal is shown in Figure 9 as a large element typical of many tetrapods other than cotylosaurs and pelycosaurs. LANE (1945, fig. 1) has shown this element as double, consisting of a proximal centrale and a distal tarsal. This region is unsatisfactorily preserved in the type and not represented in other specimens. LANE's interpretation is based on the presence of two pits in the broken bone remaining on one slab of matrix. Bone and impression have been lost completely on the apposing slab. The common boundary of the pits is represented in my Figure 9 by dashed line. I have not ventured to remove the bone and expose the underlying impression of the ventral surface, which presumably should show whether or not there are two elements. If LANE's interpretation is correct, then the tarsus of *Petrolacosaurus* contains a distal centrale, found only in amphibians, for example,

Trematops. I have taken the seemingly more conservative view that the two pits observed by LANE are accidental and the 4th distal tarsal has the large shape and position normally found in cotylosaurs and pelycosaurs. Unfortunately, the originally complete tarsus of skeleton no. 1427 (Fig. 2) shows the impression of only the latero-distal tip of the 4th distal tarsal; the critical part is lost. It may be noted that in at least one pelycosaur, the large distal 4th tarsal appears to be a combination of two elements. The hind foot of *Casea broilii* (Walker Museum no. 657) seems to possess a relatively small distal 4th tarsal, quite separate from a large proximal element, which, in position at least, corresponds to a distal centrale. The 5th distal tarsal is triangular and articulates proximally with an emargination in the calcaneum, medially with the 4th distal tarsal and distally with the 5th metatarsal and part of the 4th. This relation is clearly shown in skeleton no. 1427.

Metatarsals and phalanges are discussed in the previous section; a few remarks on the 5th metatarsal are warranted here. This element is clearly shown in two specimens and there is no proximo-lateral enlargement which can be regarded as the prototype of the robust hook seen in rhynchocephalians and chelonians. Proximal ends of the metatarsals engage each other in characteristic overlap, as pointed out in the discussion of the manus. The overlap of the proximo-lateral metatarsal upon proximo-distal metatarsal is more accentuated in the pes than in the manus; probably this is correlated with the loss of the 1st distal tarsal.

The hind limb of *Petrolacosaurus* is distinctly reptilian and primitive in structure, bearing marked resemblance to the hind limb of captorhinomorphs and pelycosaurs. Pelycosaurian resemblances are probably reflections of the fact that pelycosaurs themselves are primitive reptiles, and certainly in their foot structure, nearly as close to the basic reptilian stem as the captorhinomorphs. Characteristics of the astragalus and calcaneum point to a cotylosaurian stage of development, albeit with a superimposed elongation correlated with lengthened zeugopodium, and thus not pelycosaurian, in which elongation of astragalus is associated with a short zeugopodium. Presence of a single centrale also suggests the cotylosaur, rather than the pelycosaur, and lack of a first distal tarsal represents a specialization peculiar to *Petrolacosaurus*.

A further conclusion is that *Petrolacosaurus* has metapodials and digits showing primitive proportions but with superposed attenuation, definitely correlated with the elongation already noted in zeugopodium and basipodium. The elongate structure of the limbs is probably due to a real elongation of distal segments, rather than to a shortening of the proximal segment.

Elongation of distal segments of the limbs is a

FIGURE 11.—Reconstruction of skeleton of *Petrolacosaurus kansensis* LANE, based mainly on specimen KUMNH no. 1427 (Fig. 2), approximately × 0.5.
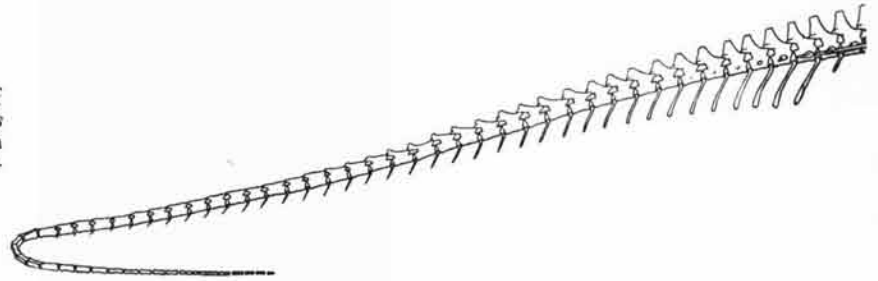
characteristic foreign to most aquatic tetrapods, since the act of propulsion in water demands strengthening and elongation of the proximal segment of limbs in accordance with demands of powerful muscles which attach to it. Rapid motion on land is generally enhanced by elongation of distal segments. Since *Petrolacosaurus* shows this latter characteristic and moreover lacks a sculling tail, the conclusion is reasonably made that this reptile, despite its interment in marine sediments, was an inhabitant of the land in situations where rapid locomotion was practical.

RELATIONSHIPS OF PETROLACOSAURUS

Perhaps it is prophetic that Professor LANE saw both pelycosaurian and araeoscelid characteristics in the remains of *Petrolacosaurus*. Certainly the suite of characters developed in the present study suggests several of the important reptilian phyla which were in existence before the end of the Permian Period. The Pennsylvanian age and relatively xerophytic environment of *Petrolacosaurus* afford the time and place which may well have been critical in the rise of progressive reptiles. Thus, it is not unexpected to find that *Petrolacosaurus* possesses a combination of characteristics suggesting early beginnings of radiation from the cotylosaur line. Certainly, from the standpoint of geologic time, *Petrolacosaurus* is the first reptile known to have 'developed such specializations as elongate cervical vertebrae, weight-decreasing excavations in the vertebrae, and elongate distal segments of the limbs. Such specializations emphasize forcibly the relict nature of Permian cotylosaurs upon which most of our ideas of reptilian origin are based. The fortunate circumstance allowing us a brief appraisal of Pennsylvanian reptile life away from the coal swamps also emphasizes the void yet to be bridged in the history of the first radiation of reptilian life.

As pointed out earlier, there is little doubt that the specimens described here belong to a single genus and species, rather than to two separate genera representing two major reptilian groups as originally described. Under the present interpretation, the various specimens are individuals of one species but of different stages of growth. Thus, the way is clear for an evaluation of *Petrolacosaurus kansensis* in terms of early tetrapod phylogeny.

Numerous characteristics indicate clearly that we are dealing with a reptile, not with an amphibian. The palate with flanged pterygoids, the progressive atlas-axis complex, a single occipital condyle, a pisiform, and the tarsus with evolved astragalus all point definitely to the reptilian status of *Petrolacosaurus*.[8]

Evaluation of *Petrolacosaurus* as a reptile is difficult, for it is obviously as close to the primary dichotomy of reptiles as are primitive pelycosaurs and cotylosaurs. This relationship is apparent in such characteristics as the modified cotylosaurian vertebrae with large intercentra, the primitive nature of the rib head and its articulation, the primitive sacrum, the humerus with a 90-degree twist, and the relatively large cleithrum—to mention a few. On the other hand, the skull appears to be fenestrate, the atlantal centrum is excluded from the ventral border of the column, the cervical vertebrae are elongate, and the limbs are decidedly elongate in the distal segments. These are a few of a number of specializations not seen in cotylosaurs, and for the most part, not in pelycosaurs. We are thus confronted with a palimpsest which is difficult to interpret in terms of early reptilian phylogeny.

Lack of a complete skull of *Petrolacosaurus* showing clearly the characteristics of suspected fenestra is a handicap, to be sure, in assessing relationships. But it must be granted that the evolution of post-orbital fenestrae in reptiles passed through a stage or stages, possibly in the Pennsylvanian, when "extra openings" were of questionable taxonomic value. The Pennsylvanian age of *Petrolacosaurus* is therefore a deterrent in assigning undue importance to the nature of suspected fenestra, especially in view of the many characteristics available for comparison from other skeletal parts.

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8. In 1949, *Petrolacosaurus* was reported by me (PEABODY, 1949) as a pelycosaur, with the qualification that it is most closely related to primitive pelycosaurs but seems to be even more primitive in a number of characters.
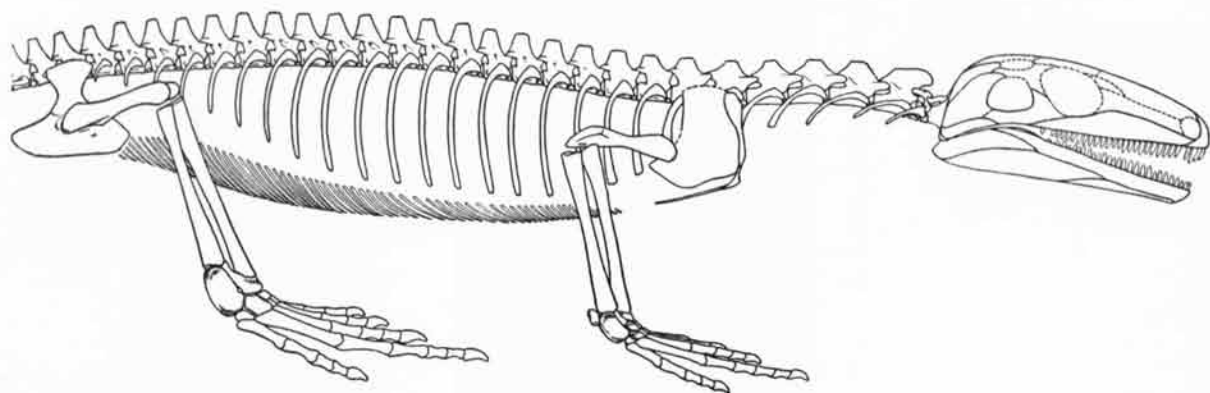
Phyletic relationships of the several styles of fenestration established in Permian reptiles is still in doubt, and although CAMP (1945) has tentatively derived the Diapsida from the Anapsida via the Parapsida, there is no conclusive proof of this derivation. Also, ROMER (1946, p. 172) questions the derivation of the diapsid archosaurs from the diapsid eosuchians, because of significant differences in skull structure. A study of reptilian tarsi by SCHAEFFER (1941) leads indirectly to the conservative, probably correct view that the various known patterns of fenestration developed independently from the Anapsida. After a broad survey of the evidence, ROMER (1945a, p. 193) states that the diapsids appear to be of independent origin insofar as relationships with araeoscelids are concerned. Also it should be pointed out that the Anapsida, usually considered a natural category, masks a diversity that belies its seeming cohesion (OLSON, 1947). An incipient transition from non-fenestrate to fenestrate skull within the Anapsida is indicated by BROOM (1938, 1948), who describes two South African cotylosaurs possessing irregular post-temporal openings of synapsid style. Thus, it seems best to evaluate *Petrolacosaurus* at first without regard for the exact character of its post-temporal fenestrae, if they actually existed. As pointed out earlier, the weight of direct evidence from the skull roof indicates at least one temporal fenestra, and that a lateral one. Evidence of eosuchian characteristics in other parts of the skeleton suggests indirectly that there may be two pairs of temporal fenestrae, a diapsid condition.

Disregarding the fenestrae, other characteristics of *Petrolacosaurus* show that it lies somewhere between cotylosaurs on one hand, and eosuchians and pelycosaurs on the other. Araeoscelid [9] relationships are distant, in spite of the fact that por-

tions of the petrolacosaur skeleton were referred here originally. The only important characteristics held in common are elongate cervical vertebrae, excavated neural arches and elongate zeugopodia. Cervicals of comparable length are found in the eosuchian *Prolacerta;* excavation of neural arches is probably a parallel development in lightly built reptiles; an elongate zeugopodium is also found in eosuchians. Also a temporal fenestra, insofar as it is indicated in *Petrolacosaurus,* is latero-temporal rather than supra-temporal, as in *Araeoscelis.* Of great importance are the carpi and tarsi. They are well represented in both genera, and have few features which evidence any but a distant relationship between araeoscelids and *Petrolacosaurus.*

Comparison of *Petrolacosaurus* with various other primitive tetrapods offers more positive evidence of probable relationships. Several skeletal features that appear to be little advanced, if any, over the seymouriamorph amphibians are as follows:

(1) Lower jaw with dentary sharing much of lateral surface with large splenial.

(2) Cervical vertebra has relatively large intercentrum associated with pronounced extension of neural arch anterior to its pleurocentrum — a close approach to seymouriamorph structure.

(3) Sacrum eryopsoid, with unfused, principal sacral rib bearing distinct capitulum and tuberculum; simple lap-joint with iliac blade; latter expanded as in pelycosaurs but more simply constructed, lacking a definite surface for attachment of epaxial musculature.

(4) Clavicular blade with stout flange on anterior border and with a seemingly short ascending process; cleithrum relatively large and long (also comparable to diadectid cotylosaurs).

(5) Parasphenoid large, and, at least in juveniles, separate from basisphenoid; also exoccipitals not ankylosed with basioccipital.

(6) Paired intercentra in anterior caudal vertebrae (also found in certain diadectids).

9. Concerning the relationships of araeoscelids, protorosaurs and eosuchians, a view is taken here which is a compromise on the views of CAMP (1945) and ROMER (1945). The category "Araeoscelidia" replaces "Protorosauria," and includes *Araeoscelis* and its close relatives exclusive of *Protorosaurus.* The latter is placed with primitive diapsids (CAMP, 1945), but "Protorosauria" is rejected as a substitute for "Eosuchia" (ROMER, 1947).

The basic structure of *Petrolacosaurus,* although masked by a number of progressive features, suggests the basic structure of captorhinomorph cotylosaurs in the following features:

(1) Teeth on anterior spine and posterior fan of parasphenoid; slight lateral compression of parasphenoid, no vertical flexure of anterior spine, which is parallel to and but little dorsal to plane of pterygoids. Premaxillary teeth enlarged.

(2) Occipital condyle posterior to line joining quadrate condyles.

(3) Sphenethmoid comparable to that of *Limnoscelis* (also to the diapsid, *Youngoides*).

(4) Vertebrae amphicoelous, notochordal, with persistent and large intercentra; proatlas large; neural arches stout (but excavated); zygapophysial plane nearly horizontal; diapophyses as in *Captorhinus.*

(5) Ribs dichocephalous but tuberculum and capitulum joined by web, as in *Captorhinus.*

(6) Scapula broad and without definite anterior border; cleithrum large, as in a diadectid.

(7) Tarsus cotylosaurian but general elongation gives pelycosaurian appearance; tibial facet of astragalus restricted, not hemispherical; only one centrale present as in *Labidosaurus* and *Captorhinus.*

In the following characteristics *Petrolacosaurus* suggests a "post-cotylosaur" stage, but these characteristics are those shown also by a number of progressive reptiles developed from stem reptiles:

(1) Fenestrate skull, possibly synapsid or diapsid.
(2) Maxillary expanded dorsally.
(3) Jaw-articulation well below tooth-row.
(4) Elongate cervical centra.
(5) Centrum of atlas excluded from ventral border of column (may be primitive rather than advanced).
(6) Pronounced overlap of proximal ends of metapodials.
(7) Light, hollow ribs; hollow long bones and metapodials.

Eosuchian relationship is most strongly suggested in the structure of the palate although a number of post-cranial features add emphasis:

(1) Palate with markedly elongate pterygoids, separated vomers; infraorbital fenestra; palatine extended forward lateral to vomers. Structure generally close to that of *Youngoides.*

(2) Parasphenoid greatly expanded posteriorly as in *Youngoides.*

(3) Opisthotic and probably a slender stapes as in *Sphenodon.*

(4) Scapulocoracoid lacertilian except for lack of fenestrae; no evidence of more than one coracoid.

(5) Elongate cervical vertebrae (definitely non-pelycosaurian in character but may be araeoscelid); shape of axis spine and massive, extended prezygapophyses much as in *Prolacerta;* dorsal vertebrae comparable with *Youngina* (cf. HUENE, 1944, fig. 6).

(6) Concave tibial facet on astragalus.

If it were possible to demonstrate clearly a single, latero-temporal fenestra in *Petrolacosaurus,* reference to synapsids would seem obligatory according to present concepts. However, it is just possible that diapsids may have developed first a lateral opening, then the superior opening. With the nature of the fenestrae not surely known, there is little to suggest the synapsid pelycosaur except for characteristics which, on the whole, seem to be pre-pelycosaurian, or at best primitive pelycosaurian. The elongate cervicals and elongate distal segments of the limbs are the strongest bar to pelycosaur relationship. Characteristics favoring relationship to pelycosaurs are:

(1) Ilium expanded as in caseid pelycosaurs but relation with epaxial muscles and with principal sacral rib in pre-pelycosaur stage.

(2) Carpal structure close to that of the primitive pelycosaur; tarsal structure superficially pelycosaurian owing to elongation.

(3) Caudal ribs similar to those of ophiacodonts.

A few, but nevertheless important, characteristics of *Petrolacosaurus* appear to be special adaptations, in part, to its environment and are unique for Pennsylvanian reptiles.

(1) Deep excavation in neural arch of dorsal vertebrae, somewhat as in *Araeoscelis* but narrower; also excavation in side of centrum.

(2) Elongate cervical centra, which may be considered as independently acquired, since lengthening of the neck in this fashion is met with in a number of distantly related reptiles, for example, *Araeoscelis, Tanystropheus, Prolacerta,* and *Varanus.* Unique combination of elongate cervicals with seymouriamorph overhang of neural arches.

(3) Elongation of distal segments of the limbs; correlative features are large discoid ulnare and long-necked astragalus.

(4) First distal tarsal apparently lost from the tarsus.

EXPLANATION OF PLATE 2

FIGURE　　　　　　　　　　　　　　　　　　PAGE

A—*Petrolacosaurus kansensis* LANE. Immature skull and cervical vertebrae, KUMNH no. 8351 (Fig. 1, *B*); dorsal view showing exposed dorsal surface of palate, × 4. Darkened holes are "windows" in thin, shale matrix 6

B—*Petrolacosaurus kansensis* LANE. Forelimb of KUMNH no. 1427 (Fig. 2) associated with cone of *Walchia;* × 3 . . 39

Interment of *Petrolacosaurus* in marine deposits immediately brings to mind the aquatic mesosaurs and the possibility of close relationship. Since both are fundamentally primitive and appear early in reptilian history, they probably are close to the primary branching of progressive reptiles from stem reptiles. However, aquatic specializations of mesosaurs are so pronounced, for example, backward displacement of nostrils with elongation of the snout, elongation of the proximal segment of the limb, elongation of the neck by "adding" short vertebrae, pachyostial ribs, sculling tail, and so on, that there is small chance for extended comparison with *Petrolacosaurus*. And in the few specializations of the latter, a fundamentally opposite trend is evident, for example, elongation of the neck by lengthening individual vertebrae, and lengthening of distal rather than proximal limb segments.

A final conclusion concerning the exact relationship of *Petrolacosaurus* must be made with the fact in mind that this reptile is remarkably primitive and generalized. Excepting a few specializations, it could serve as the prototype of most later reptiles; it is close to the hypothetical "pre-ophiacodont" anapsid postulated by ROMER (1948). And there is yet the fact that well-differentiated pelycosaurs were contemporaries of *Petrolacosaurus*. As ROMER & PRICE state (1940, p. 34), "The discovery of these two widely divergent genera [*Edaphosaurus* and *Clepsydrops*] well down in the Stephanian indicates that the pelycosaurs must have originated at least as early as the . . . Middle Pennsylvanian."

Consideration of all the osteological facts, particularly the above census of characteristics, leads me to conclude that *Petrolacosaurus* represents a group of progressive Pennsylvanian reptiles heretofore unknown. As a group, here given family rank, these reptiles stand so close to the primary dichotomy of reptilian radiation that they retain the basic plan of the primitive cotylosaur, but masked by progressive features. Some of these are specializations appearing for the first time in tetrapod history. The combination of characteristics, particularly a younginid palate and elongate cervical vertebrae, together with elongate distal segments of the limbs and the concave tibial facet on the astragalus, suggest a position at or near the base of the eosuchian dichotomy. While these characteristics are not entirely definitive, they do suggest that the potentials of the petrolacosaurid lay more nearly in the direction of eosuchians than in that of pelycosaurs.

As a phylogenetic consequence of this conclusion, eosuchians seem to be independently derived from basal anapsid stock at a level close to the origin of synapsids. There follows the implication that eosuchians arose in the Northern Hemisphere, although typical eosuchians appear first in the Upper Permian of South Africa. Perhaps because of their development during Pennsylvanian time in a "Permian" environment, the early eosuchians have remained largely unchronicled in the rocks. Only the special circumstances represented in the rare occurrence of *Petrolacosaurus* have combined to bring us this brief glimpse of an early radiation of progressive reptiles from the basal stock.

ENVIRONMENT

The unusual association of marine and terrestrial organisms at the type locality of *Petrolacosaurus* is worthy of close study for several reasons. Of most importance is the possibility that *Petrolacosaurus*, though buried in marine deposits, actually lived in the terrestrial environment indicated by associated land plants. Since these plants represent a relatively rare xerophytic assemblage among Pennsylvanian floras, the association of the reptile with it constitutes a unique record for Pennsylvanian tetrapods. Also, the marine deposit itself is of particular interest, for it displays some of the features of sediments deposited in a marginal embayment or lagoon—a rare geological occurrence, according to TWENHOFEL (1950, p. 121) who states, "The extensive shallow epicontinental seas of the Paleozoic and Cretaceous of North America presented ideal conditions for the development of

marginal lagoons and barriers, and the frequent rising of sea level should have made their preservation possible. No really proved example has been found. This may rest upon misinterpretation."

As a preliminary to a discussion of the environment of *Petrolacosaurus*, a faunal and floral list on the generic level has been compiled from the scattered papers of several authors. Some of these accounts are in the nature of preliminary descriptions; two major biologic groups are represented by undescribed material (noted in list). Thus, the generic list given below is not a final one but is accurate as of 1950. Eighteen genera (NEWELL, in MOORE *et al.*, 1936) of marine invertebrates occurring in the South Bend limestone, immediately overlying the Rock Lake shale, are not included here. Plants are listed according to identifications by ELIAS (in MOORE *et al.*, 1936).

Fauna and Flora of the Rock Lake Shale Member of the Stanton Formation, Upper Pennsylvanian, Near Garnett, Kansas

COELENTERATA
  Cup coral (noted by author, not identified in previous works)
ECHINODERMATA
  Crinoid stem segments (not identified in previous works)
BRACHIOPODA
  Composita
BRYOZOA
  Rhombopora
  Fenestella
  Polypora
PELECYPODA
  Myalina
  Lingula
  Yoldia
  Sedgwickia
ARTHROPODA
  Scorpionida (ELIAS, 1937)
    ?Mazonia
  Blattoidea
    Phyloblatta (CARPENTER, identification of specimen no. I-252 in Univ. Kansas Dept. Entomology)
    Mylacris (ELIAS identification, personally communicated)
  Megasecoptera (CARPENTER, 1933).
    Euchoroptera
    Parabrodia
VERTEBRATA
  Choanichthyes (HIBBARD, 1933)
    Coelacanthus
  Amphibia
    Nectridian vertebrae reportedly found, but now lost.
    Footprints reported but occurrence questionable.
  Reptilia (LANE, 1945)
    Petrolacosaurus
FLORA *
  Palaeophycus (2)
  Annularia
  Sphenopteris (3)
  Pecopteris
  Neuropteris (2)
  Odontopteris (2)
  Callipteridium
  Alethopteris (2)
  Desmopteris (2)
  Taeniopteris (4)
  Pteridospermostrobus
  ?Lepidophyllum
  Cordaites (2)
  Samaropsis (4)
  ?Dicranophyllum
  Walchia (4)
  Voltzia
  ?Ulmania
  ?Lecrosia
  Dichophyllum (2)

a. Numbers in parentheses indicate species.

The most important conclusions drawn by previous workers are: (1) The reptile-bearing shales near Garnett represent a member in the Stanton formation of Missourian age (MOORE *et al.*, 1936).

(2) "The species of *Lingula, Sedgwickia,* and *Myalina* are relatively abundant and suggest brackish water or otherwise abnormal [marine] environment" (NEWELL, in MOORE *et al.*, 1936, p. 28). (3) The land plants represent a "Permian" facies in the Pennsylvanian because of the "predominance of *Walchia pinniformis,* with addition of other conifer-like remains and of *Taeniopteris*" (ELIAS, in MOORE *et al.*, 1936, p. 12). *Callipteris* is the only typically Permian genus absent from the flora.

The possibility that the fossiliferous shales represent the site of an embayment or lagoon is not mentioned by previous workers, except indirectly in references to "abnormal" deposition, to brackish water mollusks, and to the quantities of obviously terrestrial plants. Synthesis of all the facts now available point to the following interpretation.

Terrestrial and fluviatile organisms were rafted by a slow-running river into a marginal embayment or lagoon protected by a barrier sand bar. Calcareous mud, mainly transported by the river, was deposited in thin, possibly cyclic layers on the eroded surface of a marine limestone. The lagoon was deep enough so that waves did not disturb the bottom and the barrier bar was complete enough to exclude strong marine currents. Under these conditions, thin-bedded mud devoid of ripple marks or scour marks accumulated and formed what is now approximately 10 feet of fossiliferous shale. Deposition of mud served to impoverish the marine invertebrate fauna and exclude scavenging forms, while simultaneously preserving the remains of indigenous marine invertebrates and rafted terrestrial organisms. Rafted material became waterlogged, probably during transport, and some maceration occurred, for quantities of detached needles of conifers literally blacken some of the bedding planes. Corpses of reptiles came to rest on the mud bottom and became partly imbedded. Before complete burial, differential decay weakened exposed parts. For example, the immature skull rested thus dorsal side up. Most of the roof of the delicate skull then became detached and drifted away probably with the strengthened current which deposited the next layer of mud. Parts of the roof remained, because they were locked in place by the deeply imbedded lower jaws and palate. (Recognition of top and bottom of the specimen in such occurrences has a practical advantage for the preparator, because the under side of the bone is usually more firm than the upper side. Top and bottom are easily determined from the matrix by noting that the bedding planes immediately below

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EXPLANATION OF PLATE 3
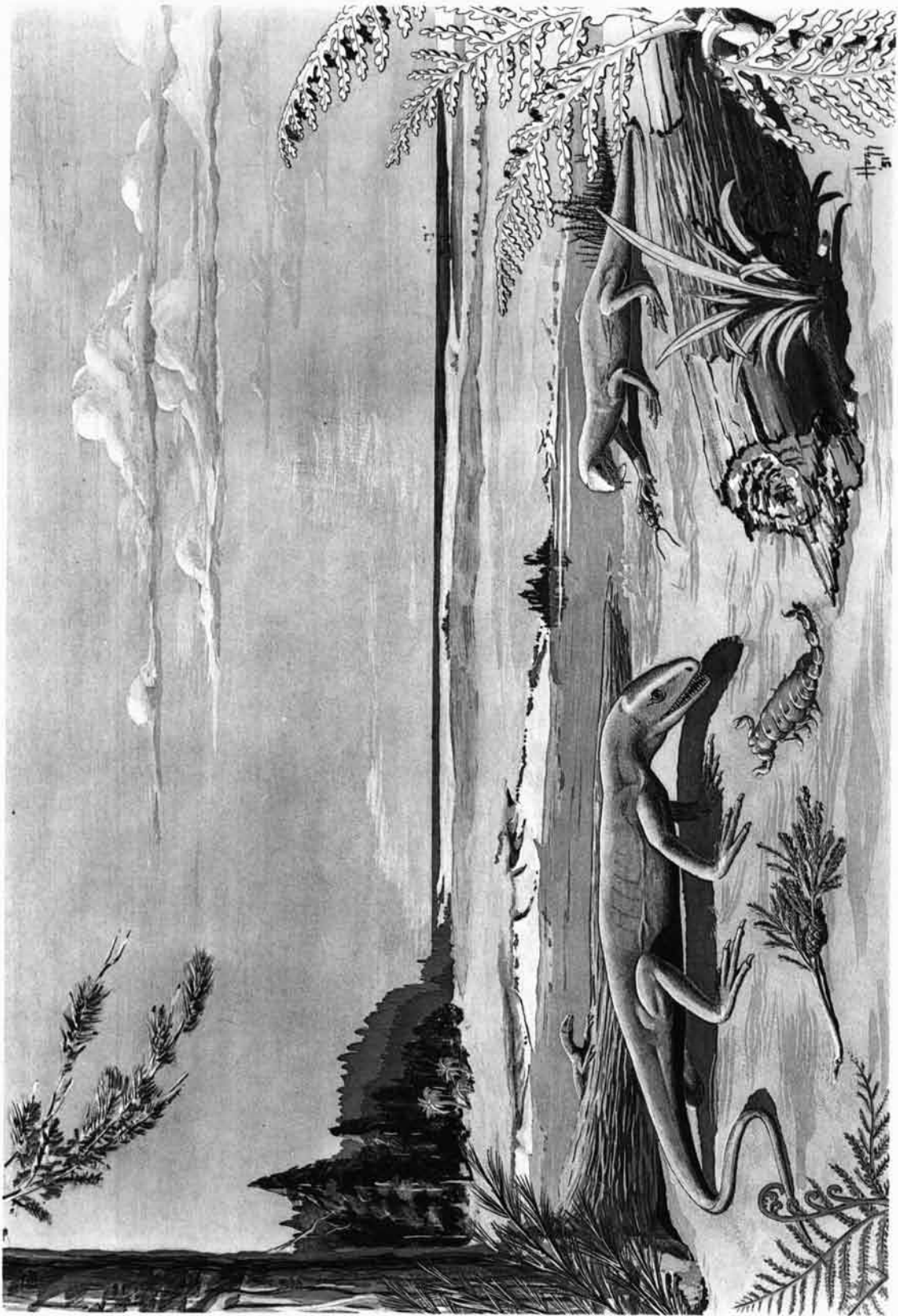
PEABODY—Pennsylvanian Reptile

the bone are strongly depressed whereas the planes in the covering layers intersect the bone.)

NEWELL's (in MOORE *et al.*, 1936) geologic section indicates that deposition of mud in the lagoon was finally interrupted by shoreward advance of the barrier bar, which is represented by "highly lenticular," "quite thin," and "locally absent" sandstone. Planation by an encroaching sea normally would have destroyed the lagoonal deposits, but after a short period of erosion, subsidence caused the site of the Pennsylvanian lagoon to become once more the floor of a shallow sea.

It should be emphasized that the association of *Petrolacosaurus* with most of the listed genera is exact; the original mud surfaces on which the reptilian corpses came to rest also bear well-preserved remains of other organisms. However, the latter are not confined to the reptile-bearing planes.

Skeleton no. 1427 (Pl. 2, Fig. 2) is exactly associated with a cone of *Walchia* and a cupule of a pteridosperm; skull no. 8351 is likewise associated with a cupule of a pteridosperm (Pl. 1, Fig. 1); and skeleton no. 1428 is associated with bryozoans, a segment of crinoid stem, and pelecypods. Also *Coelacanthus* is found pressed against large branches of *Walchia* and on the same surface with the insect *Parabrodia*. The scorpion occurs on the same surface with bryozoans (MOORE *et al.*, 1936, fig. 6:12). Thus, for practical purposes, absolute contemporaneity of *Petrolacosaurus* with the other organisms is indicated positively.

Other considerations being equal, it is reasonable to assume that the plants, arthropods and reptiles may have been transported from one and the same terrestrial environment and at the same time by relatively quiescent but perhaps flooding waters of a Pennsylvanian river. Presence of coelacanth fish could be expected under these conditions. Lack of any but dubious evidence of amphibians could also be expected, assuming that the river flowed through a relatively dry landscape dominated by conifers.

Completeness of the reptilian skeletons and isolated limbs, the presence of delicate winged insects, and of fruits of conifer and pteridosperm suggest a common place of origin and one that was not far away. As ELIAS (1932) has remarked, there cannot be question of a "highland" origin, for our knowledge of the regional deposition precludes such a view. Rather, the conifer-fern assemblage probably grew fairly close to the coast under dryer conditions than those prevailing in the coal swamps.

Alternate assumptions are: *Petrolacosaurus* may have been an aquatic form, such as *Mesosaurus*, living in the marine embayment or lagoon and may have become accidentally associated with the land flora, as is obviously the case with the marine invertebrates. Or, *Petrolacosaurus* may have been an aquatic river dweller and thus accidentally associated with the land flora.

A critical consideration at this point is the osteology of *Petrolacosaurus*: Is it an aquatic reptile somewhat comparable to the more obviously aquatic *Mesosaurus*, or is it a purely terrestrial form that one might reasonably expect to have inhabited a conifer-fern forest? The foregoing study of *Petrolacosaurus* strongly supports the second view.

Well-knit limbs, with elongation of distal segments and perfect ossification of the adult carpus and tarsus are characteristics especially suggestive of terrestrial life. Length of the limbs relative to the length of dorsal and sacral series of vertebrae is definitely greater than in a lizard such as *Varanus salvator* (p. 26). Also, the long bones, metapodials and ribs are lightly constructed, with large central cavities. There is no hint of the pachyostosis of the aquatic mesosaur. Although small patches of skin (and delicate plants) are preserved with the skeletons, there is no evidence of a skin web between the naturally disposed digits. The terminal phalanges indicate the presence of sharp, moderately compressed claws which may be considered a terrestrial adaptation. Locomotion on land demands a firm sacral connection of pelvis with vertebral column, and certainly the sacrum of *Petrolacosaurus*, though primitive, is strongly developed.

If *Petrolacosaurus* was definitely aquatic, its long tail would be expected to show in the structure of neural and haemal spines modifications for sculling locomotion, as in *Mesosaurus*. But the neural spines rapidly decline and disappear on the 24th or 25th caudal vertebra and the haemal spines, already short and delicate at the 30th caudal, diminish and disappear at the 50th caudal. The last 12 to 15 caudals are simple spools devoid of spines. Caudal ribs and transverse processes, which might possibly expand a tail surface horizontally, are nonexistent after the 10th caudal. Serial diminution of neural and haemal spines is about that seen in primitive pelycosaurs as figured by ROMER & PRICE (1940) and definitely more abrupt than in the water monitor, *Varanus salvator*. In the latter, the serial diminution is constant but neural spines are carried on to the 97th caudal (total 97), the haemal spines at least to the 80th caudal. It should be pointed out that although V. *salvator* is a rapid and efficient swimmer, there is no evidence of the habit in the limb structure. *Petrolacosaurus* shows no obvious modification of the caudal vertebrae that suggests aquatic adaptation of the tail as a sculling mechanism. Had this reptile been more than a casual swimmer, the neural and haemal spines should reflect the habit to some extent, and had it been as aquatic as a crocodile or as a mesosaur, the caudal spines should show enlarge-

ment, rather than serial diminution in the middle region of the tail. Combination of limb characteristics, cited above, with characteristics of the tail, offers strong indication of a purely terrestrial mode of life for *Petrolacosaurus*.

Association of *Petrolacosaurus* with conifers raises the possibility of arboreal habits; elongate digits and lightened structure of the bones are suggestive of climbing ability. MERTENS (1942, p. 71) has concluded from a monographic study of varanid lizards that arboreal forms have long digits and strongly decurved claws, whereas purely terrestrial forms have short digits and only slightly decurved claws. But *Petrolacosaurus* combines long digits with only slightly decurved claws. Since the long digits are apparently related to a general lengthening of the distal segment of the limb— an adaptation for speed on the ground—it seems likely that *Petrolacosaurus* was a casual climber, if at all.

There is nothing in the dentition of *Petrolacosaurus* which points to a fish or plankton diet. Marginal teeth of this little reptile are only weakly recurved and not laterally compressed. Although moderately long, the teeth are obviously set too close to each other and are not inclined outward to allow for an interlocking occlusion in the fashion of a mesosaur or plesiosaur. However, teeth on the pterygoid flanges are surprisingly large and long for a small reptile, and together with the marginal and parasphenoid dentition, would have functioned well in the capture of contemporaneous cockroaches, scorpions and megasecopterans.

A moderately long and flexible neck, with approximately the proportions seen in *Varanus*, is one characteristic of *Petrolacosaurus* that may indicate aquatic habits. However, some species of *Varanus* are not aquatic in habits, but insofar as can be determined from MERTENS' (1942) exhaustive description, these have a neck equally as long as aquatic species. Although MERTENS notes that some species are long-necked, others short-necked, he omits from his discussion of adaptive features any consideration of neck length relative to terrestrial or aquatic habits. Certainly among the obviously aquatic mosasaurs, relatives of the varanids, there is no elongation of neck vertebrae.

From all observable facts, and admittedly using some negative evidence, it seems reasonable to conclude that *Petrolacosaurus* was an agile, terrestrial reptile that lived among conifers and ferns of a Pennsylvanian landscape. Accidental deaths in or near a river resulted in rafting of numerous carcasses of the reptile, as well as local arthropods and plants, downstream to the brackish waters of a quiet marine embayment or lagoon. Here the fine sediments, transported at least in part by the river, fouled the lagoon, impoverished the indigenous fauna of marine invertebrates, but simultaneously excluded scavengers, and preserved both indigenous and introduced organisms. Thus, the brackish water deposits represented by the Rock Lake shale member of the Stanton limestone unexpectedly supply an important and unique chapter in the history of the early terrestrial reptiles.

ABBREVIATIONS USED IN THE ILLUSTRATIONS

SKULL

a	articular	pal	palatine
ang	angular	pmx	premaxillary
bo	basioccipital	pra	prearticular
bs	basisphenoid	ps	presphenoid
c	coronoid		(sphenethmoid)
cb	ceratobranchial	pt	pterygoid
d	dentary	q	quadrate
ec	ectopterygoid	qj	quadratojugal
eo	exoccipital	sa	surangular
ep	epipterygoid	sp	splenial
in	internal naris	spp	postsplenial
j	jugal	sq	squamosal
mx	maxillary	st	supratemporal
op	opisthotic	v	vomer
p	parasphenoid		

POSTCRANIAL SKELETON

aa	atlantal arch	dt	distal tarsal
ac	atlantal centrum	fe	femur
aic	atlantal	fi	fibula
	intercentrum	h	humerus
ar	atlantal rib	ic	intercentrum
as	astragalus	pi	pisiform
ax	axis	pa	proatlas
axic	axial intercentrum	r	radius
axr	axial rib	re	radiale
cal	calcaneum	sc	scapulocoracoid
ce	centrale	sr	sacral rib
cr	caudal rib	t	tibia
dc	distal carpal	u	ulna
dic	demi-intercentrum	ue	ulnare

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