The Postcranial Skeleton of the Giant Permian Pelycosaur *Cotylorhynchus romeri*

J. WILLIS STOVALL, LLEWELLYN I. PRICE, AND
ALFRED SHERWOOD ROMER

Museum of Comparative Zoology, Harvard University

THE POSTCRANIAL SKELETON OF THE
GIANT PERMIAN PELYCOSAUR *COTYLORHYNCHUS ROMERI*

J. WILLIS STOVALL, LLEWELLYN I. PRICE, AND ALFRED SHERWOOD ROMER

Introductory note. In 1937 fragmentary remains of a gigantic new pelycosaur from the Oklahoma Permian were brought to the attention of Dr. Stovall of the University of Oklahoma, who shortly after published a preliminary account of the animal, as *Cotylorhynchus romeri*, aided by notes and drawings by Llewellyn I. Price and myself (Stovall, 1937). Subsequently, many additional specimens of this form were found; these were prepared under Dr. Stovall's direction, and studies and drawings were made of much of the material by Mr. Price. It was planned that the material be described in a joint paper by Stovall and Price, but owing to a variety of circumstances, this was never written. Nearly thirty years have passed, and except for a brief notice and figures of the skull in the "Review of the Pelycosauria" (Romer and Price, 1940: 419–421), no further account of *Cotylorhynchus* has appeared. Meanwhile Dr. Stovall has died, and Mr. Price is now resident in Brasil. Adding to the need for description is the fact that Dr. E. C. Olson has found additional remains of *Cotylorhynchus*, and a number of related forms have been discovered in a variety of localities and horizons in Texas and even in Russia (Olson, 1962: 24–47). In this situation, it has been agreed that I should publish a general account of the postcranial anatomy of *Cotylorhynchus*. But although I alone should be held responsible for any inaccuracies or misinterpretations that this

paper may contain, I have felt that the paper should be considered as a joint effort, to give credit to Dr. Stovall for his work in the collection and supervision of preparation of the material, and to Mr. Price for his invaluable notes and drawings of the Oklahoma materials.

—Alfred Sherwood Romer

MATERIALS

Although a broad band of continental Permian beds extends across Oklahoma from the Kansas border to the Red River, relatively few vertebrates have been discovered in the Lower Permian of the state —quite in contrast to the situation to the south, in northern Texas. This relative paucity of finds appears to be due to the generally higher rainfall and consequent better vegetative covering in Oklahoma, and to the more level topography of Oklahoma, in contrast to the Texas area where the presence of a number of limestones and heavy sandstones makes for a more rugged topography and the development of potentially fossiliferous "breaks."

The discovery of abundant remains of a large new type of caseid pelycosaur, *Cotylorhynchus romeri*, was in consequence a major event in the history of paleontological work in Oklahoma. As noted in Stovall's paper (1937: 308), the first find of *Cotylorhynchus* material was made by Dr. W. S. Strain (then a graduate assistant at the

University of Oklahoma). The site lay in the Hennessey shales, 4¾ miles west of Navina, Logan County. The type specimen consisted of an incomplete skull and jaw, a front foot, and interclavicle. Shortly after, a nearly complete postcranial skeleton was found at about the same horizon, in the Hennessey Formation, but close to the city of Norman and hence some 50 miles or so from the region of the first discovery, and during the years 1937–1939 a very considerable number of further *Cotylorhynchus* specimens were collected in the Hennessey shales of the Norman district and prepared by laborers under Works Progress Administration funds. Most of this material is now in the Stovall Museum at Norman, but specimens were also obtained for the museums in Chicago, New York, Washington, and Cambridge. Preparation of the materials at Norman was carried out under the general direction of Dr. Stovall, and notes and figures on much of the material were made by Mr. Price. In the preparation of the present description, Romer has seen all this material, and has utilized Price's notes and figures in addition to his own observations. A word of caution must be given, however. Although preparation was carried out under Dr. Stovall's direction, it is not improbable that, with a considerable number of workers and with a number of specimens undergoing simultaneous preparation, a certain amount of inaccuracy may have occurred in the restoration and association of materials. Further, in the time that has since elapsed, some of the specimens have been moved several times for storage and re-cataloging and further chances of error have crept in.

The reptilian remains from the Hennessey shales of the Norman region appear, curiously, to pertain almost entirely to *Cotylorhynchus*, with very few remains of other reptiles and amphibians—a situation in strong contrast to the usual mixed assemblages generally present in typical Texas redbeds deposits. As far as can be seen, the *Cotylorhynchus* materials from the Nor-

TABLE 1

Specimen No.	Humerus	Radius	Femur	Tibia
4-0-6	352	166+	311	——
4-0-2 (1249)	——	——	312	195
4-0-4	343	188	305	197
CNHM 272	327+	138+	308	127+
AMNH 7517	——	——	——	190
1250 (?)	232+	——	298	170
4-0-16	265	——	285	——
USNM	263	123+	251+	147+
MCZ 3416	246	——	239	135
4-0-13	197	115	——	——
4-0-3	191	110	——	——

man area can be assigned to a single species as far as morphological characters are concerned.[1] There is however, considerable variation in size. In reptiles generally, early growth is rapid, followed by a slower if steady growth; the natural result is that the greater part of specimens recovered in the case of fossil forms should represent relatively young mature animals, with a small percentage of overly large specimens representing individuals which were exceptionally long-lived and consequently exceptionally large, and a small percentage of young and immature individuals. The present materials tend to show a rather greater size range than is common. As a rough index to size, I list the length (in mm) of major limb elements in a number of the better specimens (Table 1).

These specimens are deposited in the following institutions: Chicago Natural History Museum (CNHM); American Museum of Natural History (AMNH); United States National Museum (USNM); Museum of Comparative Zoology, Harvard (MCZ). Other specimens (numbered) are in the University of Oklahoma collection.

As can be seen from this table, the first five specimens listed appear to be of relatively uniform large size. Below this there is a sharp drop to three specimens which are 20 per cent or so smaller than the first

---

[1] Dr. Olson informs me that there is a possible specific difference between the Norman material and the type from Navina.

group but appear to be essentially mature; below, with the MCZ specimen as a transition, there is a drop to small and seemingly immature specimens such as 4-0-3. Possibly there is a specific difference between the first and second groups. Equally possible, however, the contrast is a sexual one; in *Dimetrodon limbatus*, for example, there is a seemingly clear-cut size difference of 10 per cent between the sexes (Romer and Price, 1940: 341–342).

In typical Texas redbeds localities, fossil reptile remains are most commonly found in disarticulated condition, and when found articulated appear to have undergone deposition in a variety of poses. One gets the impression that this is the result of stream action, and that many of the "bone pockets" represent back eddies in streams in which cadavers brought downstream tended to collect (and decompose). But in the Hennessey shales of the Norman region, many of the specimens show clearly that the *Cotylorhynchus* individuals were generally buried in articulated and undisturbed fashion, right side up, with the limbs spread outward at the sides. This strongly suggests that we are here dealing with entombment of quite another sort. South African Permian pareiasaurs, equally large and clumsy herbivores, are typically preserved in similar fashion (Watson, 1913). There are two possible interpretations. Watson, in the case of the pareiasaurs, implies death from starvation, and suggests a covering of the cadavers *in situ* by loess-like materials. I would favor an alternative interpretation in both cases—that the animals were bogged down and entombed in swamps.

Study has been greatly handicapped by the nature of the specimens. Due in part, perhaps, to a rather spongy structure of the skeletal elements, and to the nature of the sediments in which they were embedded, much of the material has been subjected to crushing and distortion, with a consequent limitation of the accuracy with which restoration and illustration can be made. In great measure description and illustration of structures given here are based on a synthesis of a number of specimens. Wherever possible the illustrations are based on specific examples, although frequently with the addition from other individuals of details missing or obscured in the specimen primarily utilized.

It became apparent, even from the material described in Stovall's preliminary paper, that *Cotylorhynchus* was a giant relative of *Casea*, a small Clear Fork Texas pelycosaur described by Williston (Williston, 1910: 590–592; 1911: 111–131, etc.; Romer and Price, 1940: 412–419). Despite cranial differences, *Casea* and a number of other Texas pelycosaurs show such a large number of diagnostic postcranial similarities to *Edaphosaurus* that Romer (Romer and Price, 1940: 21, 366–378) felt justified in including these forms with *Edaphosaurus* in a common suborder Edaphosauria. As in *Casea*, the *Cotylorhynchus* postcranial skeleton agrees in almost every particular with the characteristics assigned to the Edaphosauria as a whole. In consequence, in the description which follows, comparisons are, in general, with *Casea* or other edaphosaurian types.

VERTEBRAL COLUMN

The general characteristics of the *Cotylorhynchus* vertebral column are almost exactly those cited in the "Review of the Pelycosauria" for the suborder Edaphosauria as a whole:

"The number of presacral vertebrae is sometimes reduced. The dorsal vertebrae are moderately to greatly elongated; the cervicals are small in all dimensions. The dorsal centra are spool-shaped, with rounded bottoms, and lack any trace of ventral keel or lip. Intercentra are small. The dorsal transverse processes are moderately elongated and rise from a more antero-dorsal position on the arch than in other pelycosaurs. The zygapophysial surfaces are large, moderately tilted, and extend farther laterally than in sphenacodontids. The neural arches are not excavated above the diapophyses. . . . The atlas centrum reaches the ventral surface of the column."

Only a very few qualifications on this definition need be made to fit *Cotylorhynchus.* (1) It was stated that the presacral count is "sometimes" reduced. At the time this was written, the figure was known only in *Casea* where apparently 24 or 25 presacrals were present (Romer and Price, 1940: 417). It is now known that *Edaphosaurus boanerges* has likewise reduced the primitive pelycosaur number from 27 to 23 presacral vertebrae (Shuler and Witter, 1942). It is thus a reasonable inference that presacral reduction was general in the suborder, and reduction is present in *Cotylorhynchus.* (2) "Intercentra are small." Few are present in any *Edaphosaurus* material; only a single intercentrum was found in the *Casea* material (in the sacral region); none are known in *Cotylorhynchus* except for the atlas-axis. Small gaps between the ventral edges of the centra in all three genera suggest that tiny intercentra were present in cartilaginous form. (3) "The atlas centrum reaches the ventral surface of the column." This appears to be true of *Edaphosaurus,* and Williston (1911: pl. XIV) restores this centrum as reaching the ventral surface in *Casea.* As described below, however, it does not reach this surface in *Cotylorhynchus,* and Williston's material of *Casea* was obviously imperfect and open to misinterpretation.

The *Cotylorhynchus romeri* column includes definitely 25 and probably 26 presacral vertebrae, 3 sacrals, and about 55 caudals. It has proved difficult to determine the presacral count in *Cotylorhynchus.* There are several specimens in which dorsals, lumbars, and sacrals are present in well-connected series; generally, however, the cervicals are poorly preserved or absent. In 4-0-6, however, the cervicals are present. There are definitely 25 well-preserved presacral vertebrae, and apparently one further poorly preserved one. Several specimens show a sacrum of three vertebrae. The tail is preserved in but few cases. In the mounted slab of 4-0-2 (1249), a hind leg and tail, 43 caudals, the last apparently

terminal, are present in seemingly articulated fashion. However, there is a suspiciously sharp drop in the size of centra following element 27, and a photograph of the specimen made during preparation shows that the last 16 vertebrae were not part of the block containing the main part of the material, although they may well pertain to the same individual. Measurements suggest that there is a gap here of about 10 vertebrae, to raise the probable total count to about 53. In the CNHM specimen, 37 caudals are present in articulation with the trunk; following a gap of about 23 cm in the slab there are eight further, much smaller, vertebrae, the last apparently terminal or sub-terminal. The gap is of such length as to suggest that 10 vertebrae are missing here, giving a probable total length of 55 vertebrae. This is a reasonable pelycosaurian number.

Dorsal vertebrae. Such a dorsal vertebra as, for example, vertebra 12 of 4-0-6 (Figs. 1C, 2C), exhibits a typical pelycosaurian and, further, edaphosaurian character. The centra are edaphosauroid—spool-shaped structures without any of the tendency seen in ophiacodontoids and sphenacodontoids for development of a ventral keel. The centrum, as in *Casea,* is relatively short and stout, its length, averaging about 60 mm in large individuals, being but about 1½ times the end height of 38–40 mm. The ventral surface is broad, essentially flattened, but slightly convex; at the margins of this area the sides curve upward sharply and, above this point, are slightly in-pinched. There is no visible suture between arch and centrum. On the sides of the centrum, at about the level where the base of the neural arch pedicel would be expected, there is a low longitudinal ridge, rounded at its summit, running lengthwise from a point well below the upper margin of the centrum anteriorly back to a somewhat higher position posteriorly. Above this point the upper part of the surface of the centrum and the lower lateral surface of the neural arch form a longitudinal depression extending length-
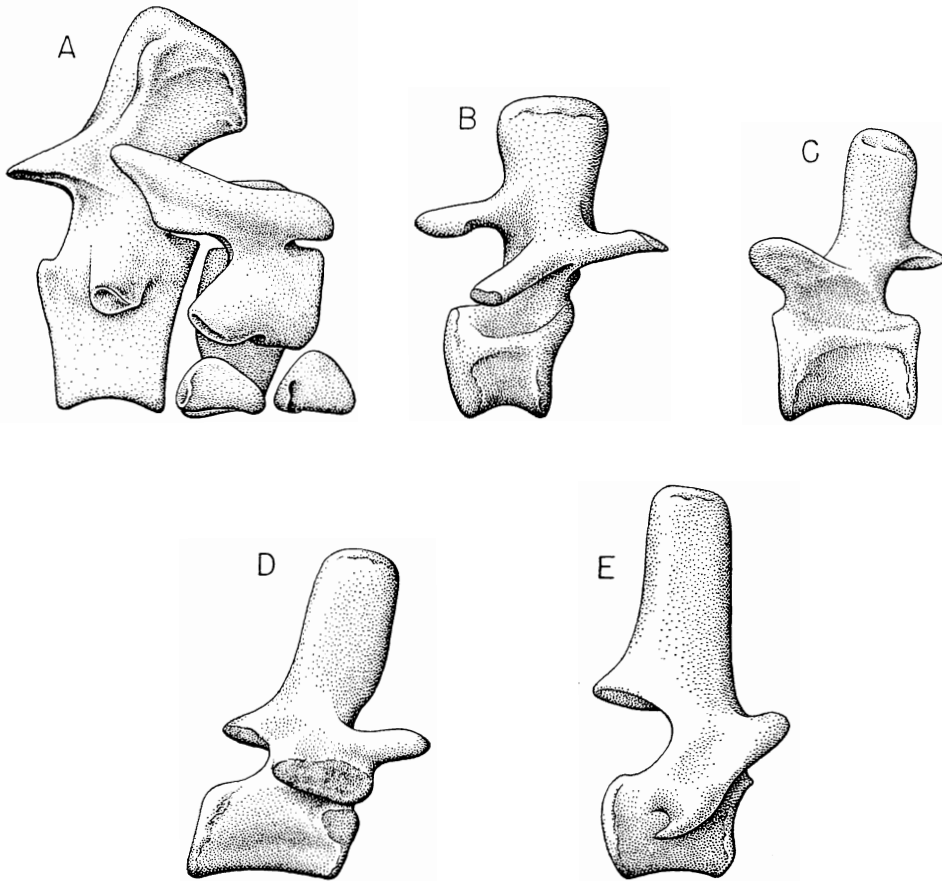
Fig. 1. Lateral views of representative vertebrae, in side view. A, atlas-axis, × ⅔; B, vertebra 6, × ½; C, vertebra 12, × ⅓; D, vertebra 21, × ⅓; E, proximal caudal, × ½.

wise beneath the base of the transverse process.

The ends of the centrum are of a typical pelycosaurian nature—essentially circular in outline, with thickened edges. At either end this circle contains a cone-shaped depression for the notochord, the two cones connected by a small foramen. Both anteriorly and posteriorly the rim of the centrum is somewhat thickened laterally for the articulation of the capitulum, which was thus inter-central in position.

The transverse processes are highly developed in this region, extending outward on either side to a distance from the midline approximately equal to the vertebral length. In edaphosauroid fashion the transverse processes arise from a far anterior position on the neural arch, and their front margins extend almost directly outward from the level of the prezygapophyses. There is in this region no ventral expansion of the process, which is thin dorsoventrally but broad anteroposteriorly; there is thus no continuum in articular areas between capitulum and tuberculum. The transverse process here is directed almost straight laterally, with, however, a slight upward and forward tilt, rather than the downward slant of most pelycosaurs (*Casea* excepted). The base of the process is very broad, extending nearly the whole length of the vertebra.
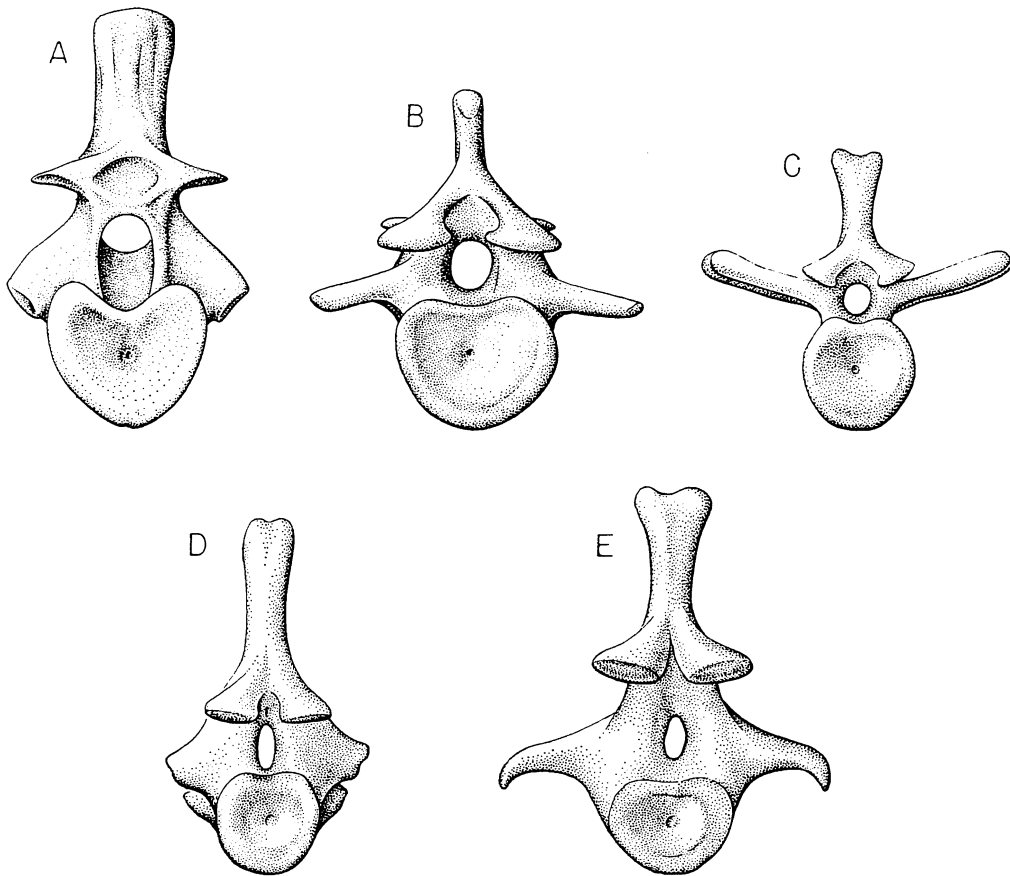
Fig. 2. Posterior views of the same vertebrae as those of Figure 1.

The broad articular surface for the tuberculum faces ventrally and only slightly laterally on the under surface of the process. Since the tuberculum is little raised, the proximal portion of the rib continues outward in the line of the transverse process. The zygapophyses are normally constructed, with a very slight median tilt of the articular surfaces. The neural arches, as in edaphosaurs generally, lack the lateral excavation seen in sphenacodontoids above the transverse processes. The neural spines, as in *Casea*, are slender transversely but long anteroposteriorly, and are low (although not as low, relatively, as in the last-named genus). In such mid-dorsals as are completely preserved the rugose end of the spine is expanded laterally on either side and indented medially, to give a somewhat bifurcate appearance, much as in, for example, some parts of the *Eryops* column.

Cervicals. Progressing forward through the anterior dorsals into the cervical series, the vertebrae are increasingly lightly built, as tends to be true of pelycosaurs generally, but more especially of edaphosauroids, such as *Cotylorhynchus*, in which the head is relatively small. The centra decrease steadily in diameter and length anteriorly, and the width tends to equal the length. In the 6th vertebra of 4-0-4, for example (Figs. 1B, 2B), the length is about 50 mm, the

width about 45 mm. The flattened ventral surface of the centra persists into the cervical region. In the cervicals the transverse processes are shorter and lightly built, in correlation with the decreased size of the ribs. Anteriorly, the cleft in the summit of the neural spines disappears, although some distal expansion may persist; the spines become shorter and somewhat more rounded —ovoid—in section. Proceeding forward, the direction of the transverse processes gradually shifts. In a typical dorsal it points somewhat forward and upward, but in the cervicals the processes become somewhat ventrally and posteriorly directed, in correlation with the direction of the ribs in the relatively slender neck region. Even as far forward as vertebra 3, the capitular facet is high up on the rim of the centrum, showing little of the tendency to descend anteriorly, seen in most pelycosaurs. The cervical zygapophyses are, like the dorsals, widely separated and with essentially horizontal articular surfaces.

Atlas-axis. The atlas-axis complex is present and well preserved in 4-0-6, and is present also in 4-0-4 (Figs. 1A, 2A). A facet on the atlas neural arch indicates the presence in life of a proatlas. The atlas arch is bipartite and typically pelycosaurian, with a long posterior process articulating with the prezygapophysis of the axis and with a spur running farther back along the side of the axis neural arch. There is a short but distinct transverse process for rib attachment, turned strongly downward and backward. The atlantal intercentrum is highly developed for cranial articulation; laterally there is a distinct facet for the rib capitulum. As is well known, the atlas centrum is variable in development in pelycosaurs, reaching the ventral surface in *Dimetrodon*, for example, but excluded from this surface by the second intercentrum in *Ophiacodon*. The situation in *Cotylorhynchus* is not too clear. In both specimens in which the atlas-axis is preserved, there is a distinct ventral gap between intercentra 1 and 2, but the atlas centrum does

not reach the surface here; possibly this gap may have been filled by a ventral cartilaginous continuation of the bone.

Intercentrum 2 is very well developed and bears a distinct rib facet. The axis centrum and arch are built in typically pelycosaurian—and especially edaphosaurian—fashion. The transverse process slants strongly downward and to a slight degree backward. The neural spine is, for an axis, rather short, but is stout, long anteroposteriorly, and expanded in a 3-pronged arrangement posteriorly toward the summit.

Posterior dorsals. Passing backward along the dorsal series, the vertebral centra increase somewhat in length to about vertebrae 17–19, beyond which a progressive reduction takes place so that beyond this point (as is also the case anteriorly) width exceeds length. In 4-0-4, for example, the length of vertebra 21 (Figs. 1D, 2D) is 51 mm, the breadth about 55 mm. An increase in central width, however, persists, width reaching its maximum in the sacral region, and the posterior dorsals are the most massive vertebrae in the column. In the more posterior presacrals the neural spines are increasingly long fore-and-aft and increasingly narrow in transverse diameter, although the arches are broadly expanded at the spine bases. In the posterior dorsal series the two members of each pair of prezygapophyses are joined by a horizontal ridge of bone bridging the space between them and forming a strengthening transverse element which crosses the front end of the vertebra between the ribs of either side. Progressing backward, the transverse processes are increasingly stout but decrease in length. In the last members of the series the processes are fused with the ribs. In the posterior vertebrae the area of attachment of the rib capitulum moves upward and backward to an oval area on the anterodorsal surface of the side of the centrum below the transverse process. Here, as in the transverse process, fusion with the rib takes place in the last few members of the dorsal series.
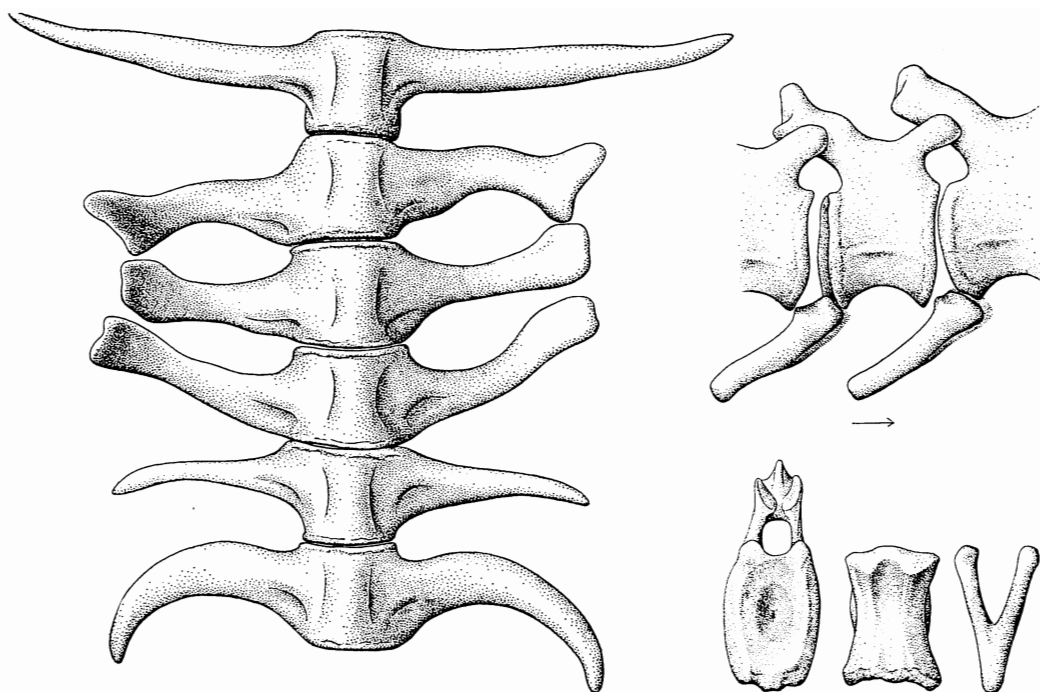
Fig. 3. *Left,* ventral view of last presacral, the three sacrals, and first two caudal vertebrae, $\times$ ¼. *Right, above,* lateral view of mid-caudal vertebrae, $\times$ ½. *Right, below,* posterior and ventral views of a mid-caudal vertebra and a mid-caudal chevron, $\times$ ½.

Sacrals (Fig. 3). Three sacral vertebrae are present, as noted in the description of the ribs. The centra are broad but appear to be shallow dorsoventrally (an effect perhaps due to crushing). In one specimen. at least, the centra of the first and second sacrals appear to be fused; whether the last two were fused is uncertain. On the first sacral the zygapophyses are still well separated, but on the third vertebra the two members of each pair are much closer together, a situation transitional to that in the tail. There appears to be no ossification of apposed zygapophyses. The transverse processes—firmly fused to the ribs—are short, but very stout, and are continuous with a large area on the centrum representing the capitular attachment. A depression which represents the point of junction of tubercular and capitular areas is seen in some specimens; it cannot be determined whether an arterial foramen perforates the structure. The neural spines of the first two sacrals are similar to those of the "lumbars"; that of sacral 3 is shorter fore-and-aft and less compressed from side to side.

Caudals (Figs. 1E, 2E, 3). The most anterior caudals resemble the last sacral closely. The breadth of the centrum is greater than the length or height; the rib attachment areas are short but greatly expanded, with a groove, presumably for an intersegmental artery, marking the line of distinction between tubercular and capitular components. More posteriorly, the transverse processes become greatly reduced in size (with a concomitant reduction in rib size), and process and rib have essentially disappeared by vertebra 12, although a slightly projecting ridge is present as far as vertebra 20. Meanwhile, the centra have begun a change in their proportions. so that by mid-length of the tail the length is considerably greater than the width and the
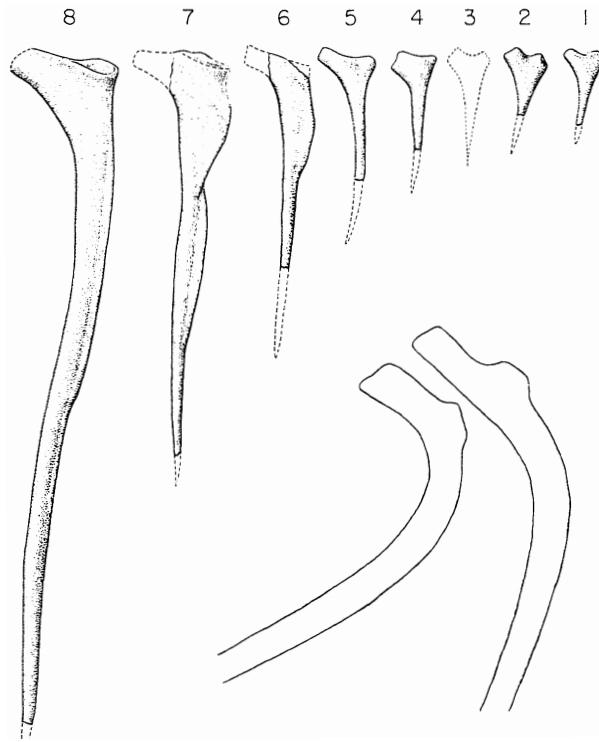
Fig. 4. Above, right ribs 1–8, seen from the posterior aspect, × ¼. Below, the heads of right and left ribs from the same mid-dorsal segment of a single individual, to show contrasts in post-mortem distortion, × ¼.

height also exceeds the width. The zygapophysial pairs have come to lie close to each other near the mid-line, and their articular surfaces have become sharply tilted to a plane close to the vertical. There is, further, a gradual reduction in height and stoutness of the neural spines, so that by the time the mid-caudals are reached, the spine is a low nubbin projecting a short distance above the postzygapophyses. The neural arch as a whole is much reduced, and in the most posterior part of the tail the material shows little evidence of any structure above the centra.

The first of the chevrons appears, in the CNHM specimen (No. 272), between the 3rd and 4th caudals; they continue back as far as vertebra 36, at least in one specimen. The first elements are stoutly built, with a length equal to two centra; as is normal, the length decreases posteriorly, although but slowly. In one specimen, as in pelycosaurs generally (and in *Casea*), there is, in the proximal elements, a basal intercentral component connecting the two arms of the chevron; but in the CNHM specimen not even the most proximal chevrons have a proper intercentrum, there being merely an enlargement of each of the two proximal ends of the chevron structure. Although both of the adjacent centra are bevelled for reception of a chevron, the centrum anterior to the chevron has the most obvious articulations: it bears ventrally a pair of well developed facets, each supported by a longitudinal ridge on the centrum. In the tail the bottom of the centrum shows a longitudinal depression, bounded on either side by these ridges.
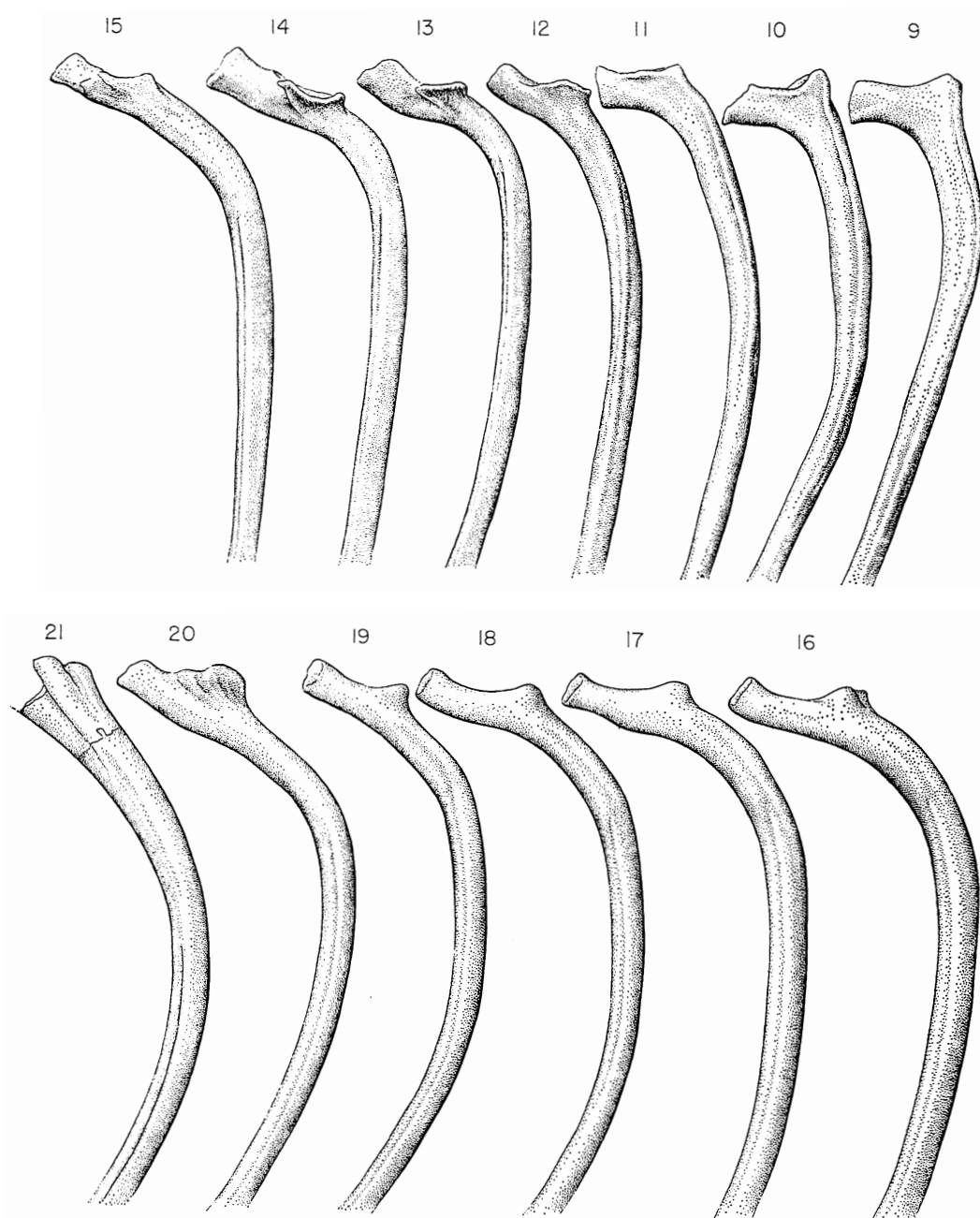
Fig. 5.   The proximal part of right ribs 9–21, seen from the posterior aspect, × ¼.

RIBS

As in all known pelycosaurs, ribs were present on every vertebra from the atlas to and including the proximal caudals. For most parts of the series, specimens 4-0-6 and CNHM 272 furnish the best material.

Dorsal ribs (Fig. 5). In a typical dorsal rib the shaft extends outward (and in life somewhat upward) from the capitulum, the articular surface of which is an oval, narrow anteroposteriorly, occupying the entire head of the rib. The tuberculum in the mid-dorsals does not project to any marked degree from the shaft; it apposes to the transverse process a concave articular surface with an oval shape, broader distally, the length about twice the width.

The proximal end of the rib appears to run distally slightly upward to and past the tubercular region. Shortly beyond this point the rib curves markedly outward and downward to encase the flank. The degree of curvature in life is difficult to determine, due to variable post-mortem crushing and compression; see, for example, the marked contrast between the two members of a rib-pair from the same segment of a single individual shown in Figure 4. In most instances there is a considerable segment of the rib, lying beyond the point of proximal curvature, which is nearly straight; this includes about half the total rib length. This segment appears to have been directed diagonally outward and downward. Distally, beyond this straight section, the rib curves gradually inward toward the mid-line. Although seldom is a complete rib length preserved, it would appear that the greatest length of a rib (measured from the tuberculum) is about the length of 13 dorsal centra; two mid-dorsals of CNHM 272 measure 721 and 718 mm. In such dorsals as are completely preserved the distal end of the rib exhibits a cupped termination with which the cartilaginous section of the rib presumably articulated.

Despite the handicap noted as due to post-mortem distortion, articulation of ribs

and vertebrae gives, on the average, a picture closely comparable to that given by Williston (1911: pl. XVII, fig. 1) for a *Casea* mid-dorsal, and shows the presence of a very broad, barrel-like trunk, with a probable transverse diameter of about 60 cm—i.e., about two feet.

Except for the rather flattened capitular region, typical dorsal ribs are essentially oval in section, and so tilted in life that the long axis of the oval slants downward and forward well over 45°, with the two major surfaces essentially anterior and posterior in position. The anterior margin is in all typical dorsals smoothly rounded. On the posterior surface a ridge develops at a point somewhat distal to the tuberculum and rather toward the ventral margin. This ridge extends outward along the straight lateral segment of the rib, gradually approaching the ventral margin of the rib and, decreasing in prominence, disappears at about the point where the median curvature begins.

There is little expansion of typical dorsal ribs at any region. The diameter of the rib is greatest a short distance distal to the tuberculum; beyond this region there is generally a very gradual decrease to a minimum of about two-thirds of the maximum.

Progressing anteriorly, from such a typical dorsal as that described, to rib 9, a series of gradual changes may be observed. The length decreases, rib 9 in 4-0-6, for example, being but 430 mm in length, i.e. about 60 per cent as long as the longest rib, and the ribs are more lightly built. In anterior dorsals, in contrast with mid-dorsals, the tuberculum projects markedly above the general outline of the dorsal rib margin, and, in contrast, the capitulum is sharply turned downward medially from the line of the shaft. There is here only a slight curvature beyond the tubercular region; when the rib is articulated with the vertebra, it is obvious that its shaft runs more directly downward than in the typical dorsals, indicating a narrowing of the body in the "chest" region, as the level of the shoulder girdle is approached. Distal to the straight

descending portion of the shaft, there is a final segment curving somewhat inward. The total distance from the tuberculum to the beginning of the median curvature is little less than in rib 14, indicating that the "chest" is nearly as deep as the belly, although narrower.

The longitudinal ridge found on the posterior rib surface changes in position as one progresses forward. It has shifted upward, so that its proximal portion lies along the dorsal margin of the rib, and its distal end lies at about the middle of the posterior surface, rather than toward its ventral margin. It has, further, moved proximally, so that its proximal end has attained the distal margin of the tubercular projection, and its distal end extends only part-way down the vertical segment of the rib. Distally the anterior dorsal ribs remain sub-circular in section. Proximally, however, the posterior surface becomes much hollowed out, with the proximal part of the longitudinal ridge forming a very prominent projection dorsally. As far as can be determined in the usually crushed condition of the specimens, the most anterior dorsal ribs are somewhat expanded distally—notably rib 9 in 4-0-6.

Cervical ribs (Fig. 4). In the few previously known pelycosaurs in which the distal ends of the ribs have been well preserved, it appeared that rib 8 was stout distally and presumably had a sternal connection, establishing 7 as the probable number of non-sternal, i.e., cervical, ribs. In 4-0-6, however, rib 8, although elongate (with a length of about 360 mm) and resembling the dorsal rib following it in most regards, tapers to a point distally. It thus failed, obviously, to reach the sternum and must be considered technically to be a cervical.

In 4-0-6, remains of all the cervical ribs are present (but the third is poorly preserved). Although the rib-tips are incomplete, it is clear that all were slender and pointed distally. From rib 8 forward to rib 4 there is a sharp and steady diminution in length, and the preserved portions of the most anterior ribs indicate that these ribs were shorter still. In correlation with the wide separation of the two points of attachment to the vertebrae, tuberculum and capitulum are strongly divergent, giving a V-shape to the proximal part of the rib. The slender distal portions of the ribs appear to be somewhat compressed anteroposteriorly.

In the cervicals, as in the most anterior dorsals, the rib shaft runs straight distally from the tuberculum, indicating a narrow neck region; the tuberculum, as far as preserved in these ribs, retains the somewhat distinct character seen in the most anterior dorsals. On rib 8 the longitudinal ridge retains the character seen in the rib following for much of the proximal half of the shaft, forming a sharp dorsal margin of the rather thin rib, but it fails to reach the tuberculum. On rib 7, the ridge is present on the middle third of the shaft; on the more anterior ribs it has disappeared. It is in a sense replaced by a thin dorsal flange extending distally on rib 7 a short distance outward from the tuberculum, but not continuous distally with the typical dorsal ridge. This flange is present in reduced form on rib 6; more anteriorly, as far as can be seen from the material, no noticeable structures are present on the rib shafts. Ribs 6–8 appear to have lain beneath the scapula; these reduced flanges, presumably functioning for the origin of serratus musculature, contrast with the much greater flange development seen in many early tetrapods.

Posterior dorsal ribs (Fig. 6). Proceeding backward along the dorsal series, the posterior dorsal ribs as far as about rib 20 appear to be essentially similar to more anterior dorsals in character, and show little decrease in length; however, the proximal end of the longitudinal ridge described for the anterior dorsals retreats distally to a small extent in this region. Rib 20 becomes broader proximally; in the posterior ribs there is a gradual approximation of tubercular and capitular heads so that, from about rib 22 back, capitular and tubercular
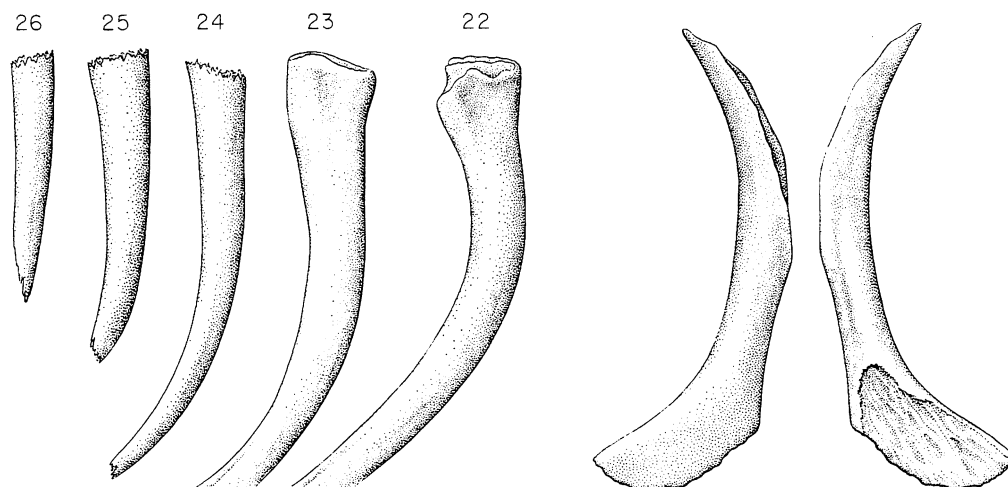
Fig. 6. *Left, posterior presacral ribs of the right side,* × ½. *Right, left clavicle, external and internal views,* × ¼.

areas are essentially fused into a single articular surface. A decrease in length of ribs is not marked until approximately rib 23, which is notably shorter than that preceding it (with a length in CNHM 272, as preserved, of 413 mm) and ribs 24–26 are increasingly short, the last being about 158 mm long in CNHM 272. As in pelycosaurs generally, the freedom of rib articulation with the vertebrae decreases posteriorly; the last 3 short ribs appear to be well fused and immovable and hence are to be considered as lumbars, and the next preceding may also have been immovable in life, although in 4-0-4 a suture between rib and vertebra was seen during preparation for the fourth presacral.

All the more posterior ribs tend to have shafts which are relatively broad and thin for most of their length; the last 5, however, definitely taper to a point distally, and thus lack a sternal connection, and the same may be true of rib 21. As far as segment 23 the ribs continue to be curved, turning downward and backward in life. Ribs 24–26, however, are nearly straight and directed laterally, their length being little more than that of the proximal nearly straight segment of rib 23. The breadth of the proximal part of the ribs increases pos-teriorly to a maximum in rib 24, which is very broad in proportion to its length.

Sacral ribs (Fig. 3). In correlation with the width of the trunk and pelvic region, the sacral ribs are longer than in sphenacodonts and ophiacodonts. Three sacral ribs are present. These are tightly fused to their vertebrae over a broad area; this includes the short transverse processes which arise from much of the lateral surface of the centra. No clear sutures are seen, but dorsally a rugose anteroposterior ridge marks the line of fusion of rib and transverse process. The rib head is deep dorsoventrally, as well as anteroposteriorly. Distinction between capitular and tubercular attachment is indicated by depressions on both anterior and posterior surfaces about half way down; these depressions have not been excavated, but may have been connected by a canal for the intervertebral artery.

The first sacral rib is short but stout. Beyond the head it contracts somewhat in width and extends outward horizontally and slightly posteriorly to terminate in a relatively thin expanded blade extending downward and apposed laterally to the inner face of the ilium. The second rib extends directly laterally; it is similar to the first but slightly less developed. The third rib
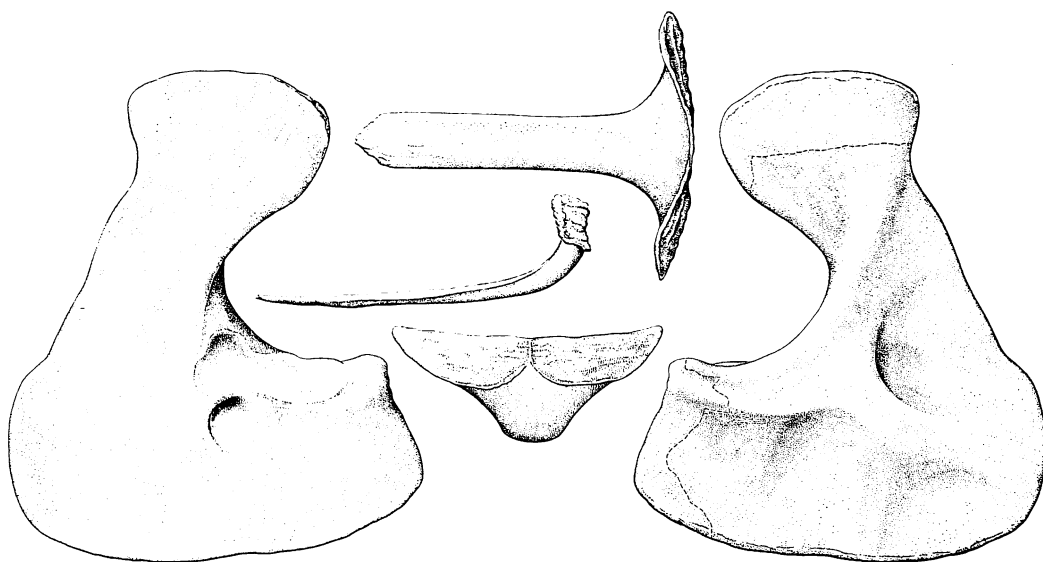
Fig. 7. *Left, external, and right, internal views of the left scapulocoracoid. Broken lines on the internal view outline the portion preserved in No. 4-0-6. Center, dorsal, right lateral, and anterior views of the interclavicle.* × ⅙.

is essentially accessory in nature; it is more slenderly built and curves forward to buttress the second rib as well as apposing the ilium with an only slightly expanded tip.

The first two sacral ribs are fairly comparable to those of *Casea*. In that genus, however, sacral rib 3 is well developed, and *Cotylorhynchus* here exhibits a condition which is less advanced. *Edaphosaurus* shows an intermediate condition in the development of sacral rib 3.

Caudal ribs. As in pelycosaurs generally, ribs are present in the proximal tail region. The first five show a fused attachment to transverse process and centrum with a pattern similar to that of the sacrals, although with a steadily diminishing attachment area; the heads are pierced anteroposteriorly by canals for the intervertebral artery. The first caudal is comparable to the third sacral in most regards, but it extends directly laterally, with a slight distal posterior curvature, to terminate in a pointed tip. Posterior to this, all the caudal ribs, as in pelycosaurs generally, continue to extend outward in a horizontal plane and to taper to distal extremities. In caudals 2–5 a back-

ward curvature of the distal end is pronounced. These ribs show a steady decrease in length and stoutness. Rib 6 is notably shorter, with little development of a distal curved segment, and from this point back the caudal ribs, fused to the transverse processes, are laterally projecting, tapering, and pointed structures which decrease to small nubbins and disappear, except for low rugosities, beyond vertebra 11. In general the caudal ribs are comparable to those of *Casea*.

GIRDLES

Shoulder girdle. A nearly complete scapulocoracoid, as seen from the inner side, is present in 4-0-6, and the figure is based primarily on this specimen. The outer surface is not available in this specimen, but several others show this aspect. The scapular blade, incomplete in 4-0-6, is better preserved in other specimens; its exact height, however, is difficult to determine, due to the lack of distinctive features in this area. The blade in large specimens may have been somewhat more developed. In

all available specimens the dorsal margin of the blade shows an unfinished surface, so that there may have been a considerable cartilaginous suprascapula. No sutures between the presumed three elements could be determined.

The scapulocoracoid (Fig. 7) is edaphosaurian in general character. It is short dorsoventrally, broad anteroposteriorly, with much the proportions of *Lupeosaurus* (*Casea*, presumably in relation to its smaller size, has a girdle of more slender build). The scapular blade is very short and broad, its breadth distally due to a backward flare of the posterior margin greater than is seen in any other pelycosaur. Below the point of clavicular attachment the margin of the scapula curves out widely anteriorly, to give great breadth to the lower part of the blade, as in *Edaphosaurus* and *Lupeosaurus*. In contrast to *Edaphosaurus* and *Lupeosaurus*, but in agreement with *Casea*, *Nitosaurus*, and *Mycterosaurus*, there is no supraglenoid foramen. There is, as in all pelycosaurs, a screw-shaped glenoid cavity; it is here, as in other edaphosaurians, remarkably deep anteriorly. Below its anterior end is the external opening of the supracoracoid foramen. Posteriorly, the coracoid region shows little development of a tubercle for origin of the coracoid head of the triceps. On the inner surface, the upper portion of the subcoracoscapular fossa is shallow, in correlation with the absence of a supraglenoid foramen.

No cleithrum is present in the available material. Much of the clavicles and the interclavicle are present in 4-0-6 and in the type (Figs. 6, 7). In contrast to *Edaphosaurus* and sphenacodonts, there is little ventral expansion of the clavicle (the clavicle of *Casea* is unknown). Its upper portion is well grooved posteriorly to clasp the anterior edge of the scapula. The blade of the interclavicle is unusually broad and short, and there is no development of the longitudinal ridge seen on the ventral surface of the shaft in most pelycosaurs. As preserved, the head turns sharply upward on the shaft,

in contrast to the gentler curvature found in pelycosaurs generally, so that the surfaces apposed to the clavicles are essentially in a vertical plane. The head of the interclavicle is short and T-shaped, in contrast to the diamond-shaped head of many pelycosaurs, and is nearly completely occupied by the pair of crescent-shaped surfaces for the clavicles. These surfaces, which extend far laterally, are covered by rugose striations; the areas on the clavicles which meet them are similarly rugose, and set in distinctly below the general level of the "inner" surfaces of that bone. Obviously the contact between clavicles and interclavicle was an intimate one.

Pelvic girdle. Pelvic girdle material (Fig. 8) is relatively poorly represented. The *Cotylorhynchus* skeletons were nearly all buried with the dorsal surface upward; the ilia in consequence have been generally subject either to damage by crushing during entombment or to erosion prior to discovery, and this element is well preserved in only a few cases. The iliac blade is moderately high, as in sphenacodonts and other edaphosaurians, and in contrast to ophiacodonts, and agrees with other edaphosaurians in that (in contrast with sphenacodonts) there is little posterior elongation. There is a narrow but well-defined longitudinal area for muscle attachment at the top of the inner surface, above the areas for the sacral ribs. The first sacral appears to have been in contact with a depressed area at the anterior margin of the inner surface of the blade, the second presumably apposed to a flat area posterior to this; still farther posteriorly, a well-marked internal depression received the small distal end of the third sacral.

The acetabular region is of a typical pelycosaurian nature, with the usual primitive dorsal buttress. In most specimens sutures between the three pelvic elements are not clearly seen; in one specimen part of the sutures could be made out on the external surface, and in several instances lines of striae on the inner surface indicated the
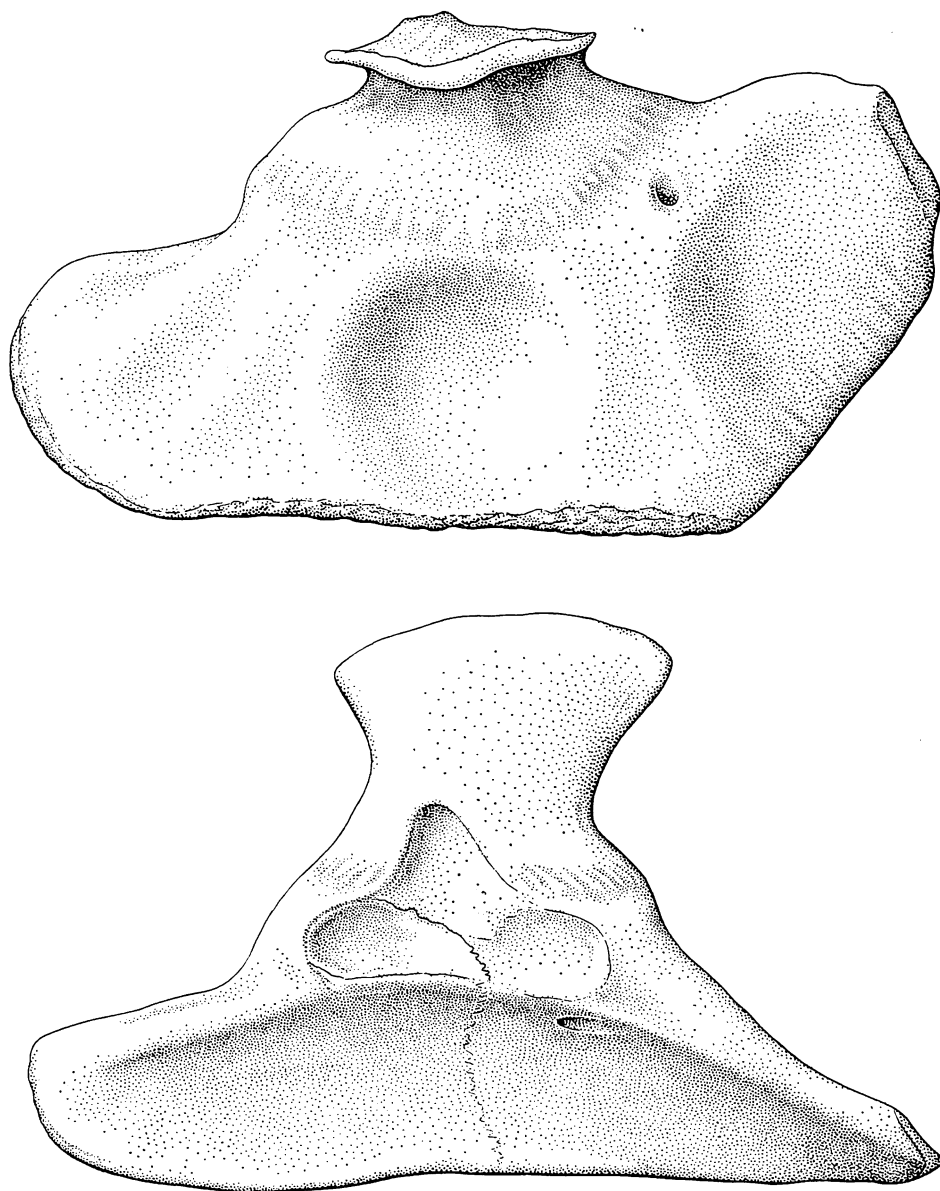
Fig. 8.   Right pelvic girdle in dorsal and lateral views, ✕ ⅓

areas of fusion of ilium with pubis and ischium.

The puboischiadic plate is of very large size, with an anteroposterior length in 4-0-4, for example, of 380 mm, a depth below and internal to the base of the ilium of 112 mm and a breadth of the pubis, measured at right angles from the front end of the pubic symphysis, of 173 mm. There is but a slight indication in the material of the development of a pubic tubercle, such as is found in *Edaphosaurus, Nitosaurus,* and *Casea.* The great development of the puboischiadic plate is comparable to the type of structure

seen in *Edaphosaurus* and *Casea*, and is associated with bodily breadth, present in the pelvic region as well as farther forward. The plate was strongly tilted outward at somewhat more than a 45° angle, so that it is not seen to any great degree in side view.

Internally, the puboischiadic plate exhibits, as in pelycosaurs generally, a gently hollowed out area, in which the bone is relatively thin, along the middle third of its length. Anterior and posterior to this, on pubis and ischium respectively, thickened bony areas—essentially supporting struts—descend from the iliac region to the symphysis. The presence of these thickened areas is reflected in the symphysis, which is thickened in both pubic and ischiadic regions, with a relatively thin intermediate zone. Anterior to the ridge descending the pubis is a very broad area of origin for puboischiofemoralis internus, which is but slightly turned outward from the general plane of the internal surface of the plate. Within this area is the usual internal opening of the obturator foramen which opens externally below the pubic portion of the acetabulum. There is a slight indication in certain specimens of a small area along the dorsal margin of the ischium for an ischiotrochantericus origin.

LIMB ELEMENTS

In almost all instances the limb elements have been crushed and flattened dorsoventrally, so that they are essentially two-dimensional—a situation making correct reconstruction difficult.

The major elements differ markedly from those of little *Casea*, and to a lesser extent from those of *Edaphosaurus* and *Lupeosaurus*, in the fact that they are very stoutly built. This is, of course, a feature associated with the large size and great weight of *Cotylorhynchus*. In most regards, however, they are not only typically pelycosaurian but show a number of distinctive edaphosauroid features. In few instances do we find all, or most, of the major limb elements present

and well preserved in a single specimen. The pose was obviously that common to all pelycosaurs, with humerus and femur projecting nearly straight outward horizontally, and with the lower limb segment essentially vertical in position. Front and hind legs appear to be nearly equal in length, but with the humerus slightly shorter in overall length than the femur. In all pelycosaurs the lower limb is much shorter than the proximal segment, but this relative shortness is very marked in *Cotylorhynchus*. Here radius and tibia are only approximately 60 per cent as long as humerus and femur, respectively. In *Ophiacodon* the radius is about 77 per cent of the humeral length, the tibia about 83 per cent of the length of the femur; in *Dimetrodon* the comparable figures are 82 and 83 per cent. The *Cotylorhynchus* proportions, however, are comparable to those in other edaphosauroids; in *Edaphosaurus boanerges* we find figures of 62 and 57 per cent. Like other edaphosauroids, *Cotylorhynchus* was "low-slung."

Humerus (**Fig. 9**). The humerus is of the primitive tetrahedral type, although the shaft is stouter than in typical (and smaller) pelycosaurs. As figured, the "twist" of the ends on one another is extreme; this, however, appears to be due to crushing of the (none too well preserved) specimens upon which the drawing is based; specimen 4-0-3 shows the "twist" to have been one of approximately 90°. As is sphenacodonts and edaphosauroids generally, the proximal articular surface curves posteriorly well down onto the ventral surface of the head. In its very considerable proximo-distal breadth the entepicondyle is edaphosauroid. The entepicondylar foramen appears to have been unusually large.

The region of the ectepicondyle and the supinator process is imperfect in most specimens. In small specimens, such as University of Oklahoma specimens bearing the numbers 4-0-3 and 23–38, in which the distal end is well preserved, the supinator process is broad and close to the ectepicondyle but
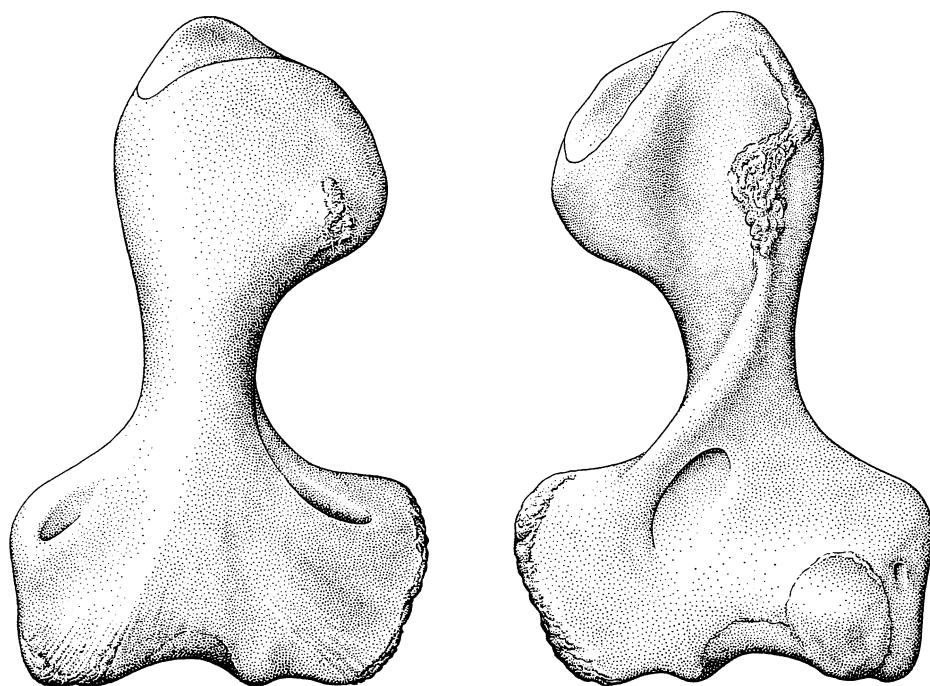
Fig. 9. Right humerus, viewed in dorsal and ventral aspects in the plane of the distal end, × ¼

separated from it by the notch typical of pelycosaurs. This separation, however, is obviously a growth stage only, for in 4-0-16 and a further University of Oklahoma specimen of uncertain number the notch is closed and an ectepicondylar foramen present. The foramen is otherwise found in pelycosaurs only in *Edaphosaurus*, and it is stated to be absent in *Casea*. In *Casea*, however, the gap between the tip of the supinator process and the ectepicondyle is small, and may well have been bridged in cartilage. It is obvious that the ectepicondylar foramen has developed more than once, in parallel fashion, in early reptiles; its presence here may perhaps be correlated with changes in limb mechanics and musculature, due to increased size, rather than attributed to inheritance from a basal edaphosauroid ancestor.

Radius (Fig. 10). The radius is preserved (although not too well preserved) in several instances. As noted above, it is

short, with a length rather less than three-fifths that of the humerus. Although the effect is in all specimens accentuated by crushing, the bone was obviously relatively thin dorsoventrally, as in pelycosaurs generally. As in the case of other limb bones of *Cotylorhynchus*, the radius is broad in proportion to its length.

The proximal articular surface, where preserved, has the appearance of an oval, thin dorsoventrally; presumably it was subcircular in life. The dorsal (extensor) surface of the shaft is convex in section; the ventral surface apparently was flattened. A rugose area for ligament or muscle attachment is visible on the lateral edge of the dorsal surface just below the head of the bone. From the head the bone (when uncrushed) constricts to a somewhat thinner shaft. A short distance below the head, however, a ridge arises on the medial surface of the bone. Proximally it begins somewhat toward the ventral surface; it ex-
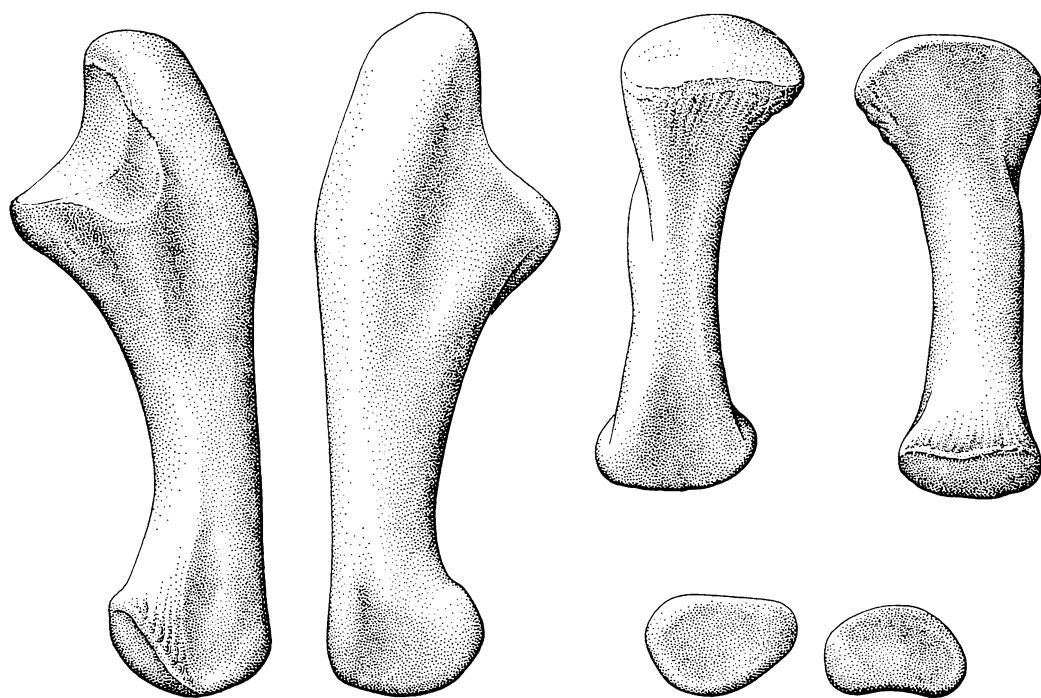
Fig. 10. *Left, left ulna in extensor and flexor aspects. Right, comparable views of the radius. Right, below, proximal and distal surfaces of radius (dorsal aspect above).* × ⅓.

pands, however, to attain the lateral margin and runs downward much of the length of the bone. Distally, the ridge is absorbed in a distal expansion of the bone leading toward the terminal articulation. As in pelycosaurs generally, the distal end of the bone is somewhat curved ventrally, so that the oval distal articular surface (for the radiale) faces somewhat ventrally as well as distally. The lateral margin of the shaft is also rather thin, but there is no development of a projecting ridge. Medioventrally there is an abrupt out-turning of the lateral margin above the articular surface.

Ulna (Fig. 10). The olecranon appears to have become well developed at a relatively early stage of growth, for it is nearly complete (although with a small unfinished terminal surface) in University of Oklahoma specimen N-7-37, a small specimen. As preserved, the head of the ulna is thin where seen, but this is presumably an effect

due to crushing; very probably the head in life was as thick as in *Edaphosaurus*. As in the case of the radius, the bone is very short compared with the humerus. It is, further, exceedingly broad; the breadth of the distal end in one complete specimen measures about 40 per cent of the length of the bone as measured from the lower margin of the sigmoid notch; and the proximal width, across the notch, is about 50 per cent of the length. These figures are far in excess of those of other groups, in which the highest figures available to me are 29 per cent and 39 per cent for a specimen of *Ophiacodon*.

Femur (Fig. 11). The femur is typically edaphosaurian in nature, closely comparable in every major way to a well-preserved *Lupeosaurus* femur in the Harvard collection and likewise comparable, except for its stouter build, to the femora of *Casea* and *Edaphosaurus*. As in other edaphosaurs,
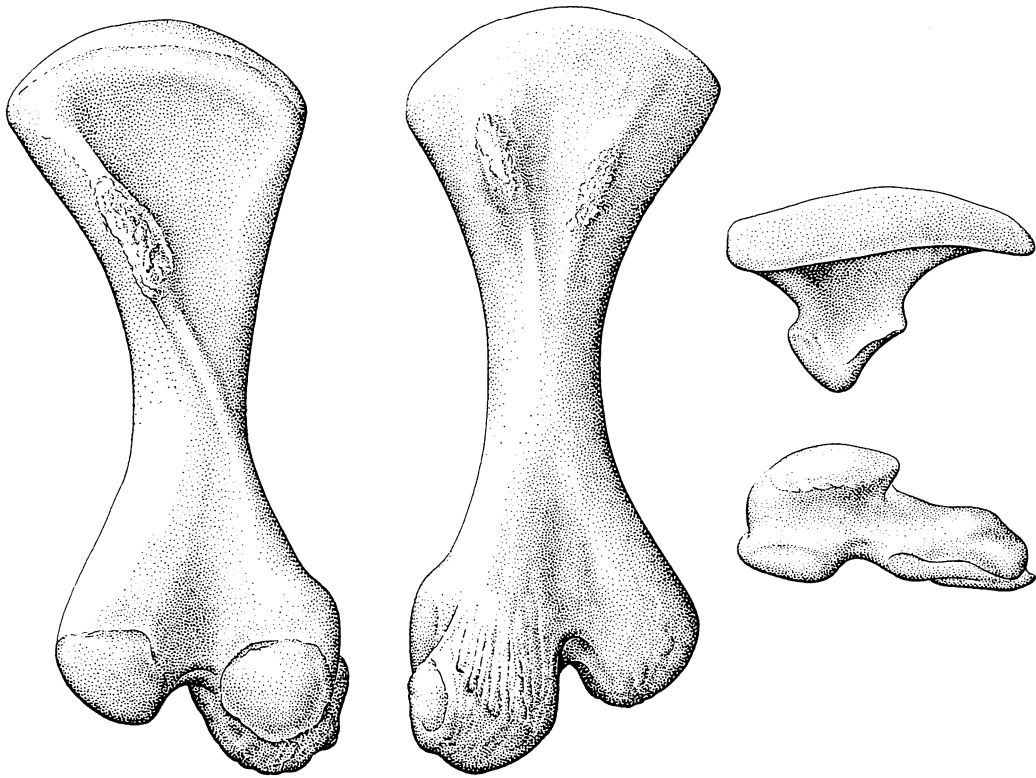
Fig. 11. Right femur, in ventral and dorsal views; at *right*, proximal and distal views (dorsal aspect above). $\times$ ⅓.

the curvature of the shaft characteristic of sphenacodonts is absent. Particularly characteristic is the ventral trochanteric system. There is a well-developed internal trochanter from which, in contrast to sphenacodonts and ophiacodonts, a ridge descends the under side of the shaft diagonally toward the external condyle. There is little indication of a distinct fourth trochanter along this ridge, and likewise little development of the posterior proximal branch of the Y-shaped ridge system, the intertrochanteric fossa thus being shallow posteriorly. In sphenacodonts, and to a lesser degree in some ophiacodonts, the proximal articular surface extends along the proximal portion of the posterior margin of the shaft; here, as in other edaphosaurs, this surface is confined to the proximal end of the bone. Proximally, on the dorsal surface of the

shaft, there is sometimes seen, toward the posterior margin, a rugose area for muscle attachment. Unique is the presence at the anterior margin of a very distinct rugose ridge, about 25 mm long, likewise presumably for muscle attachment; this is clearly seen in two specimens. The external condyle, as in other edaphosauroids, projects very markedly beyond the internal (medial) one, and in a well developed specimen the tip of this condyle markedly overhangs the articular surface for the tibia below it, as it does in other edaphosauroid femora in which ossification is well advanced.

Tibia (Fig. 12). The tibia is, as noted earlier, relatively short, with a length only three-fifths or less that of the femur. As with other limb bones, the tibia is very broad, notably its head. The width of the head in one specimen is about 57 per cent
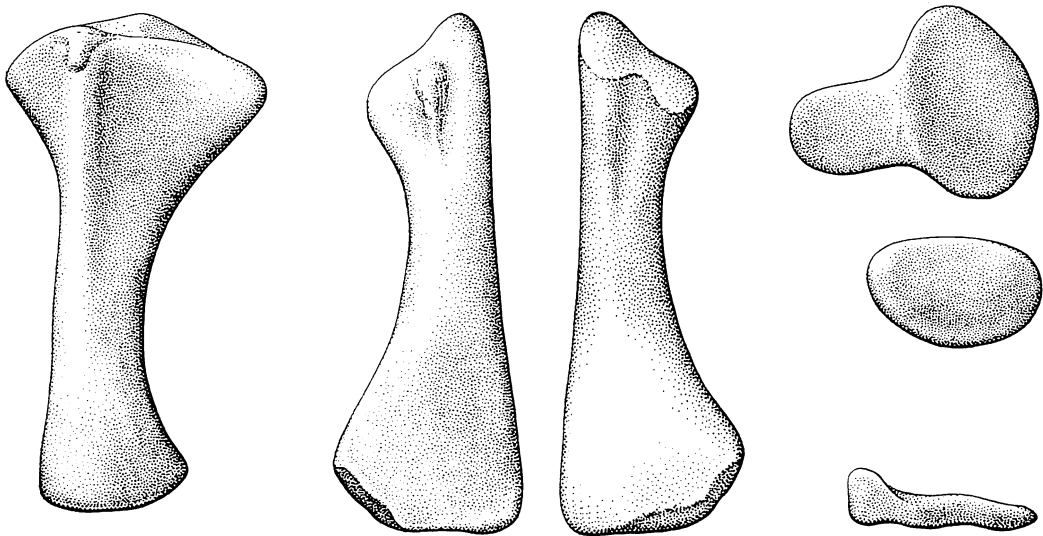
Fig. 12. *Left*, extensor aspect of right tibia; *center*, extensor and flexor aspects of right fibula; *right*, *above*, proximal and distal surfaces of tibia, and *below*, distal surface of fibula, extensor surface above. × ⅓.

the length of the bone, and the distal width nearly 33 per cent of the length. The closest approach to these proportions is in *Edaphosaurus*, in which these two figures approximate 50 per cent and 30 per cent. In all other known pelycosaurs the figures are much lower—*Dimetrodon limbatus*, for example, giving figures of 38 per cent and 22 per cent, *Ophiacodon* 37 per cent and 26 per cent. The two articular surfaces of the head are distinctly separated and set off from one another at a considerable angle. As in other ophiacodonts, the lateral femoral articular area is relatively narrow dorsoventrally. The cnemial crest is little developed. As in *Edaphosaurus*, and in contrast with most other non-edaphosaurian pelycosaurs, the distal articular surface curves strongly toward the lateral side of the bone.

Fibula (Fig. 12). As in the case of the tibia, the fibula is very short as compared with the femur, and is very broad distally. The mean breadth here in three specimens is 38 per cent of the length. This figure is comparable in *Edaphosaurus*, but pelycosaurs generally have a much slimmer

fibula, with distal widths in *Dimetrodon* and *Ophiacodon*, for example, of 20 per cent and 29 per cent of the length.

FEET

Manus (Figs. 13, 14). As noted above, the specimens of *Cotylorhynchus* are not infrequently found in articulated fashion, and the feet are sometimes well preserved. We may note, for example, well preserved front feet in 4-0-1, 4-0-6 and 4-1-S2, hind feet in 4-0-10, 4-0-2 (1249), and both front and hind feet in the Chicago skeleton. Between the various specimens nearly all features of carpus, tarsus and digits are seen. As in the case of the major limb bones, the feet are broad and short, and thus differ considerably at first glance from those of most pelycosaurs. Study, however, shows that, apart from questions of proportions related to the size of the animals the feet are typically pelycosaurian and, despite the contrast in shape, resemble closely those of *Casea*.

The manus has the usual pelycosaur elements, including a pisiforme, two centralia and a series of five distal carpals. The
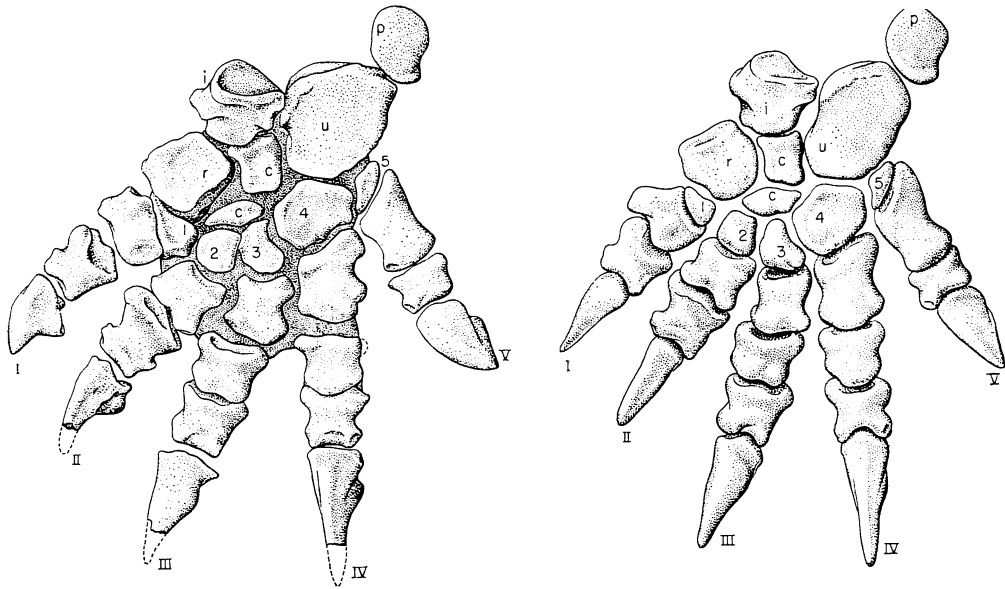
Fig. 13. *Left*, left manus of No. 4-0-6; *right*, restored left manus. X ¼. Abbreviations for Figs. 13–16: a, astragalus; c, centralia; cal, calcaneum; F, fibula; i, intermedium; p, pisiforme; R, radius; r, radiale; T, tibia; U, ulna; u, ulnare; 1–5, distal carpals or tarsals; I–V, digits.

radiale has a very deep, essentially square, proximal articular surface for the foot of the radius. The intermedium is short and broad, with well developed processes on both radial and ulnar sides at mid-height, and a broad proximal articular surface for the ulna. The ulnare is far shorter than in most pelycosaurs, but comparable in proportions to that of *Casea*. The proximal end is much less convex in outline than in most pelycosaurs; it forms a nearly continuous articular surface for the very broad ulna; this surface extends medially from a contact with the intermedium to a lateral facet for the pisiforme. This last element, as usual, is a thin plate. In 4-0-6 the bone is curved sharply toward the ventral surface at its outer margin; this may, however, be an effect of crushing. The medial or proximal centrale is again relatively short. The usual arterial gap is present between proximal centrale, intermedium and ulnare. The lateral centrale is not too well preserved; it is, as in pelycosaurs generally, a small element when viewed from the exterior sur-

face, short proximodistally, broad mediolaterally. The articulated feet suggest that it was placed well in toward the center of the manus, with an unossified gap between radiale and distal carpal 1.

Distal carpal 1 appears to be essentially a simple rectangle in dorsal outline, short proximodistally but broad mediolaterally, covering the entire width of the head of metacarpal I. Element 2 is longer but less broad, its width less than the overall width of its metacarpal; its lateral border is straight, its proximal and medial borders a continuous curve. Element 3 is about as broad as 2, but longer proximodistally. As in pelycosaurs generally, 4 is by far the largest of the distal series, with a width double that of element 3 and a somewhat greater length proximodistally. Its proximal end has, as in pelycosaurs generally, two articular faces at somewhat of an angle to each other, a laterally tilted surface for apposition to the ulnare, a shorter medially tilted face for the proximal centrale. Distally the bone articulates broadly with the ex-
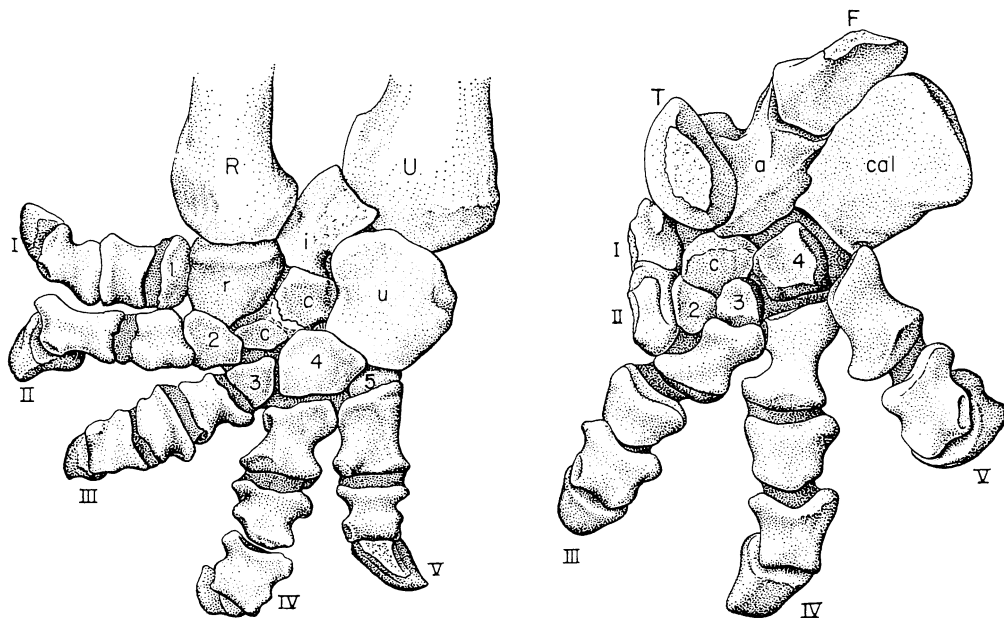
Fig. 14. Left, left manus of No. 4-1-S2; right, left pes of No. 4-0-10. × ⅓   Abbreviations as in Fig. 13.

panded head of metacarpal IV. Element 5 is narrow proximodistally but is expanded mediolaterally to meet the entire breadth of metacarpal V. Proximomedial and proximolateral surfaces meet element 4 and the ulnare, respectively.

In the metapodials (and in the phalanges) the shortness and breadth of the elements and the almost complete absence of a distinct shaft region give the foot a clumsy appearance. There is a steady increase in length from metacarpal I to metacarpal IV, and metacarpal V is, exceptionally, somewhat longer still. Metacarpal I appears to have a broad, flat head; in metacarpals II and III the proximal articular surface is a concave area not occupying the full width of the bone. In metacarpal IV the proximal articulation is a concavity, but a very broad one. In metacarpals II and III there is a pronounced expansion of the head toward the lateral side, and in IV this lateral extension is very pronounced. In metapodial V the proximal articulation does not appear to be cupped; it is tilted so that the outer

margin is much more proximal than the medial.

The phalanges, like the metapodials, are short and massive in appearance. The nature and structure of the articulations of the elements is in general of a typically pelycosaurian type (Romer and Price, 1940: 167–169). From the massive build of the feet and the presumed herbivorous habits of the animal, one would expect the toes to terminate, like those of diadectids or pareiasaurs, in hoof-like structures. Instead, however, there are (as in *Casea*) long and powerful bony claw supports, suggesting that in life the animal did considerable digging for its food supply.

Pelycosaurs, in which good articulated feet are known, typically have a phalangeal formula in the manus of 2-3-4-5-3.[1] *Cotylorhynchus*, as is definitely proven by the material, has the surprisingly low formula of 2-2-3-3-2—even lower than in typical therapsids and rivalled for reduction among

---

[1] *Edaphosaurus*, formerly in doubt, is now known to have this formula also.
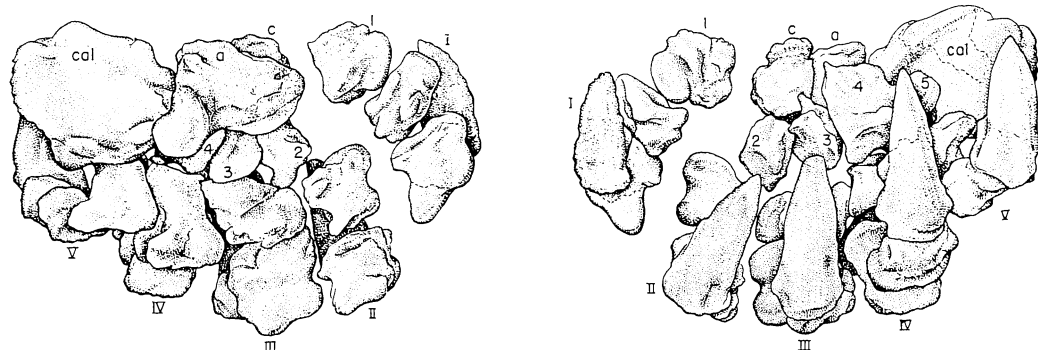
Fig. 15. Dorsal and ventral views of right pes of CNHM 272; the clawed toes are strongly flexed and bent under the tarsus. X ⅓. Abbreviations as in Fig. 13.

Paleozoic reptiles only by the pareiasaurs. In Williston's material of *Casea*, the manus was nearly complete but for the most part disarticulated. Williston, not expecting reduction, utilized the material available to give a manus with the typical reptilian formula (1911: fig. 13). To do this he was forced to assume that a number of elements were missing from the toes. However, new material described by Olson (1954) shows that the formula of the manus was 2-3-3-4-3—a definite reduction, although not as marked as in its giant relative. The series of elements present in Williston's specimen was, thus, actually nearly complete.

Pes (Figs. 14, 15, 16). Although the material of the hind foot is not as good as that of the manus, nearly all the structure can be clearly made out. There is a series of typical tarsal elements—astragalus and calcaneum proximally, and five distal tarsals; there is a lateral centrale, but whether a small medial centrale was present is uncertain. The proximal tarsal elements are relatively short, as compared with those of most other pelycosaurs except for the ophiacodonts; this presumably in relation to ponderous build. The astragalus appears to have had a relatively flat facet for the tibia. There is a typical arterial notch between artragalus and calcaneum.

As in the manus, the reduced phalangeal formula of 2-2-3-3-2 was present. Williston attempted to restore the foot of *Casea* with the primitive formula. But, as his description suggests, little of the material was actually articulated and it seems reasonable to believe that *Casea* had a reduced phalangeal formula in the pes similar to that in the manus; if so, Williston's foot material was nearly complete.

ABDOMINAL RIBS

In agreement, it would seem, with the fact that in the Edaphosauria generally the gastralia are little developed, no trace of abdominal ribs was discovered during preparation of the materials except in one instance. Here there were found numerous slender elements with tapering ends. The maximum length as preserved was 65 mm; the widths 3 to 5 mm. The material was not sufficient to determine their arrangement, although they were presumably arrayed in the usual series of V-shaped segments along the course of the abdomen.

RESTORATION

A lateral view of a restoration is shown in Figure 17, based on the series of larger specimens. The general appearance is comparable to that shown in restorations of its smaller relative, *Casea* (Williston, 1911: frontispiece; Romer and Price, 1940: fig. 71), except for the somewhat more massive build of *Cotylorhynchus* associated with its
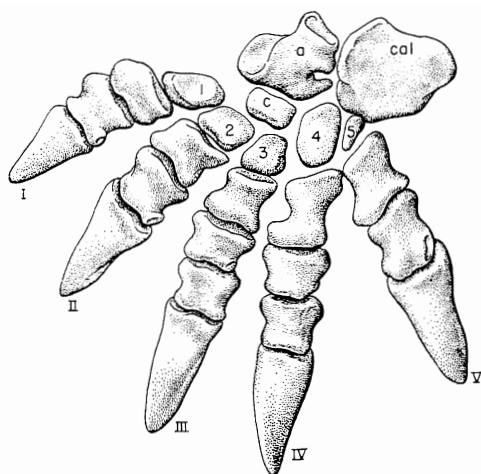
Fig. 16. Restored left pes, × ¼. Abbreviations as in Fig. 13.

larger size, and the absurdly small size of the head. The lateral view does not, of course, give proper emphasis to the great breadth of the barrel-like trunk, commented on previously, and well shown in Williston's photograph of the mounted *Casea*. The build of *Cotylorhynchus* is in agreement with the portrait of a generalized edaphosaurian given by Romer and Price (1940: 377):

"We find a tiny head armed with a powerful battery of blunt teeth, the trunk a large, broadly rounded barrel, the legs spread out broadly, but the lower segments so short that the belly cannot have been far clear of the ground. Such an animal was obviously not a carnivore, and, in the discussion of habits, we have already cited data supporting Williston's belief that these reptiles were herbivores. The enormous storage capacity of the abdomen further suggests that the food was probably of a bulky, watery nature, low in nutritive value, so that it was necessary for the animal to ingest large quantities. The curiously small head of the advanced edaphosaurs is matched among later plant-eating reptiles by the sauropods, whose food may have been of a comparable type."

Cotylorhynchus romeri exceeds in bulk any of the known pelycosaurs from the typical Texas Wichita and Clear Fork redbeds deposits, and is exceeded only by its presumed descendant, *C. hancocki* from the
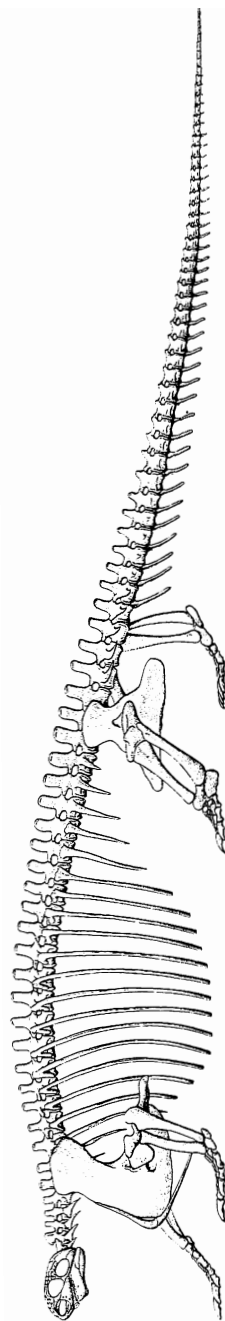

Fig. 17. Restoration of *Cotylorhynchus romeri*, 1/16 the size of a mature specimen.

San Angelo (Olson and Beerbower, 1953; Olson, 1962: 28–45). In the study of pelycosaurs generally, Romer (Romer and Price, 1940; Romer, 1948) used as an index to relative size—and weight—an "orthometric linear unit" based on the dimensions of dorsal vertebrae. At the time of publication of the "Review of the Pelycosauria" such information as was then available concerning *C. romeri* suggested that this unit was approximately 8.32, and this appears still to be a reasonable figure. Closest to *Cotylorhynchus romeri* among Wichita and Clear Fork pelycosaurs were the large terminal member of the *Ophiacodon* phylum, *O. major*, with an orthometric linear unit of 7.37, and the large terminal Clear Fork *Dimetrodon grandis*, at 7.61. Since the *Casea* unit is but 3.30, the average linear measurements of elements of *Cotylorhynchus* should be approximately two and one-half times that of *Casea*, and the weight more than 15 times as great. With an estimated weight of about 331 kg—roughly about one-third of a ton—*Cotylorhynchus* was the giant of its times.

RELATIONSHIPS

When *Casea* was first described it occupied an isolated position among pelycosaurs—so isolated, indeed, that Watson (1917: 173) suggested that it was not a pelycosaur at all. Possibly *Trichasaurus* (cf. Romer and Price, 1940: 422–423) is a relative, but until the discovery of *Cotylorhynchus* no further members of the family Caseidae were recognized. In recent years, however, Olson (1962: 24–47; and earlier papers) has added a number of new forms to the group from the middle and upper Clear Fork formations and the lower part of the Pease River group, including further species of *Casea* and *Cotylorhynchus*, and the new genera *Caseoides*, *Caseopsis*, and *Angelosaurus*; further, the caseids are now known to have ranged widely, for *Ennatosaurus* of the Russian Kazanian is clearly a caseid (as is possibly the poorly known *Phreatophasma*).

The caseids are the last major group of pelycosaurs to appear in the geological record. *Casea broilii*, the earliest acknowledged member of the family, only appears at about the Arroyo-Vale boundary in the Clear Fork group; other forms occur in the later Clear Fork formations and the roughly equivalent Hennessey of Oklahoma, or the still later Pease River group of Texas and the Russian Kazanian. Although some millions of years must be allowed for the development of caseid specializations, it is quite possible for the family to have evolved from some more generalized group during Wichita and early Clear Fork times. Until recently clues as to caseid ancestry were few. *Trichasaurus* of the Arroyo Formation and *Glaucosaurus* of the Clyde Formation of Texas were suggested by Romer and Price (1940: 421–423) as presumed edaphosauroids possibly related to the caseids. In the first-named genus the skull is unknown.[1] The second is represented only by a single small skull which is extremely short-faced and with an isodont dentition; this suggests possibilities of relationship to the caseid pedigree. As to a more remote ancestry, it was suggested by Romer (Romer, 1937; Romer and Price, 1940: 405–412) that *Mycterosaurus* and *Nitosaurus*, small early Permian pelycosaurs which seemed to be primitive in many ways but showed definite edaphosaurian characters in the postcranial skeleton, might represent the ancestral stock of the caseids and perhaps of the edaphosaurians as a whole.

In recent years several new finds have added somewhat to the picture. Vaughn (1958) has described as *Colobomycter* an imperfect skull from the Fort Sill quarry (an Arroyo equivalent in Oklahoma), and considers, reasonably, that its characters indicate that "it provides a good structural if not an actual ancestor for the family Caseidae." Fox (1962) has described as *Delo-*

---

[1] A toothplate provisionally referred to this genus (Romer and Price 1940: 423) is now known to pertain to the cotylosaur *Labidosaurikos*.

rhynchus three isolated maxillae from this same quarry; the bone itself is caseid-like, but the dentition is primitive and hence Fox classes it amongst the presumably ancestral Nitosauridae rather than placing it in the Caseidae. As noted by Langston (1965) there is little to distinguish *Delorhynchus* from its quarry-mate *Colobomycter*. Langston (1965) has recently described as *Oedaleops* a small pelycosaur from the New Mexican Permian represented by two skulls and other fragmentary material. As Langston points out, the *Oedaleops* skull is of a type quite surely expected in a caseid ancestor, but differs from proper members of that family in that, for example, the face is not as abbreviated and, most especially, the dentition is primitive; as proper for a primitive pelycosaur of any sort, the teeth are sharp-pointed and somewhat recurved and with a modest development of a maximum tooth size in the canine region, in one specimen, at least. As possibly attributable to *Oedaleops*, Langston describes a number of small postcranial elements found in the same quarry. Of these, the ilium, as Langston notes, is of a very primitive type, certainly not expected in a pre-caseid. Other elements, most notably the scapulocoracoid (lacking, significantly, the supraglenoid foramen), are comparable to those of *Nitosaurus* and caseids. They may well pertain to *Nitosaurus*.

Moreover, may not *Oedaleops* and *Nitosaurus*, contemporaries from the same region and horizon, be identical? Of *Oedaleops* we have no certain knowledge of postcranial material; of *Nitosaurus* we have no skull material except of maxilla. Langston briefly mentions this possibility but says that *Nitosaurus* "had longer jaws, a more slender dentary, considerably more teeth (subisodont in form) and a higher maxillary bone." But (1) we do not have a complete jaw in *Nitosaurus*; (2) the seeming slenderness of the *Nitosaurus* dentary is probably due to loss of the thin lower margin (cf. Romer and Price: fig. 70, and Langston: fig. 2a); (3) there is no evidence that *Nito-*

saurus had more teeth than *Oedaleops*. In the latter genus the dentary is not known from associated material. In the two maxillae of *Oedaleops* found by Langston, the tooth counts appear to be 18 and 16; in the incomplete *Nitosaurus* maxilla 15 teeth and alveoli are present, and the total count was probably about 18. (4) There appears to be no significant difference in the height of the maxilla between *Oedaleops* and *Nitosaurus*—particularly if the obvious crushing undergone by the *Oedaleops* skull be taken into account.

The one possibly valid generic distinction lies in the greater isodonty of the maxillary dentition in *Oedaleops*. In the type there is a modest development of a "canine" pair at maxillary positions 2 and 3; in a second specimen the third tooth is large; in the *Nitosaurus* maxilla a maximum is not gained until we reach teeth 4 and 5. Considering the constant tooth replacement characteristic of reptiles and the consequent continual changes in the aspect of a dentition, this one feature seems hardly safe ground for generic distinction.[1]

Although the material of the genera discussed above is quite incomplete, in most instances, it appears that in this we have at least the beginnings of a phyletic series leading from such a primitive but edaphosauroid pelycosaur as *Mycterosaurus* upward toward the caseid condition. A complicating and confusing factor in the situation, however, was introduced by Watson (1954: 356) with his suggestion that *Eothyris* might be related to caseid ancestry. Both Vaughn and Langston have adopted this point of view, placing such forms as *Colobomycter* and *Oedaleops* in the Eothyrididae, and Langston goes to the extreme of excluding the Nitosauridae from any relationship to the Caseidae, despite the numerous and surely significant postcranial resemblances between the two.

The basic reason for considering *Eothyris*

---

[1] A subordinal distinction, actually, in Langston's chart, page 43.

as a possible relative of the caseids is, of course, the fact that *Eothyris*, like the caseids, is remarkably short-faced. This in itself is no more a valid reason for associating them than would be the association of the sphenacodont *Secodontosaurus* with the ophiacodont *Varanosaurus* because they are both extremely long-snouted. If the *Eothyris*-caseid relationship is to be substantiated, more positive reasons must be developed.

Langston (1965: 21) cites fourteen points in which *Oedaleops* and *Eothyris* are in partial or complete agreement. As he says, this seems to be, at first sight, an imposing list. Included, of course, is the fact that the face is short, not necessarily meaningful, and the fact, of no systematic value, that both are small. Correlated with small size, and hence likewise without other necessary significance, is the relatively large size of the orbits and of the pineal foramen. A number of other common features are such as are liable to be present in any relatively primitive pelycosaur, including: (1) relatively flat skull; (2) jaw articulation on a level with the toothrow, as in the Ophiacodontia, the primitive sphenacodont *Varanops*, and *Mycterosaurus*; (3) outward slope of cheek plates (contrasting with sphenacodonts); (4) a primitive long lacrimal; (5) normal relationship of roofing bones; (6) an unusually large supratemporal; (7) a long, tapering postorbital (as, for example, in the ophiacodont *Varanosaurus*, and the sphenacodont *Varanops*); (8) some indications in the tabular-supratemporal region of the otic notch of ancestral types; (9) a differentiated dentition, as in most pelycosaurs except *Edaphosaurus* and caseids.

The two genera, thus, are short-faced, small in size, and have both retained various primitive characters. Little remains of the original fourteen points which can be construed as positive indication of relationship. Langston cites "relative position of orbits and pineal opening," but there does not appear to be any unusual condition here in either case. With regard to "enlarged nares and obtuse rostrum," the nares in *Eothyris* do not appear to be any larger, proportionately, than in many other pelycosaurs, and the rostrum does not appear to be any more obtuse than in pelycosaurs generally. The *Eothyris* prefrontals are said to be "inflated" (i.e., somewhat expanded), but this does not seem significant.

There is thus little positive reason to associate *Eothyris* with caseid ancestry, and one very strong objection—the dentition. In all early pelycosaurs—indeed, in nearly all primitive tetrapods generally—there is a trend for the development of somewhat enlarged teeth near the front of the maxilla as an incipient "canine" region. In sphenacodonts and their therapsid descendants this trend is accentuated; in edaphosaurians —both *Edaphosaurus* and the caseids— there is an opposite trend toward isodonty. In such forms as *Oedaleops* there is but a mild, essentially primitive, development of a canine "maximum" such as might be expected in any relatively primitive pelycosaurs. In *Eothyris*, on the other hand, we find the greatest exaggeration of canine tusks to be found in any pelycosaur. In their dentition, *Eothyris* and the caseids have evolved in such diametrically opposite directions that it is difficult to believe that they are at all closely related.

But even if (as is not too probably the case) *Eothyris* should prove to be related to the caseids, it is dangerous to base hypotheses of broader relationships on the "family Eothyrididae," as has been done by Langston and, to a lesser degree, by Vaughn. As I have pointed out (Romer and Price, 1940: 247; Romer, 1956: 676), this family is a purely provisional one, set up to receive forms, presumably highly predaceous, which have marked canine development but are not members of the Sphenacodontia. Any unity the group might have is based on this dental feature—which is, of course, the one point in which all of them notably differ from the trend toward isodonty expected in caseid ancestors. There is no

evidence that any form assigned to this family. other than *Eothyris*, was short-faced. Such postcranial material as can be associated with any of the genera included in this provisional family lacks any features indicative of caseid relationships, and such indications of systematic position as are shown by *Stereorhachis*, *Stereophallodon*, and *Baldwinonus* suggest the Ophiacodontia. With regard to *Eothyris*, the lack of postcranial data is a stumbling block.

On the assumption that the Ophiacodontia represent the basal stock of the Pelycosauria, it is a reasonable assumption that the caseids are of ultimate ophiacodontian derivation; but that any of the "eothyrids" are connecting links is very dubious.

Romer and Price (1940: 366–376) pointed out numerous skeletal features which *Edaphosaurus* and *Casea*, as two extremes, have in common. and advocated their being placed in a common suborder. There is, however, a seeming difficulty in assuming a common ancestry. because of chronological factors. The caseids seem quite surely to have specialized from primitive ancestors at a late date, for no form attributable to this stock is known earlier than fairly early Wichita times; on the other hand, *Edaphosaurus* had already evolved by the late Pennsylvanian. If both *Edaphosaurus* and the caseids evolved from essentially primitive edaphosaurians, such as the nitosaurs, this must have been, as Langston (1965: 58) notes, a very bradytelic group, and nitosaurs should have been in existence in the Pennsylvanian.

This appears to have been the case. It seems highly probable that *Petrolacosaurus*. from the Pennsylvanian Garnett shales of Kansas (Lane. 1945; Peabody. 1949, 1952). is a primitive edaphosauroid.

Lane. and Peabody at first. concluded that this small reptile was a pelycosaur. The latter author. however. impressed by cranial resemblances to *Prolacerta* (with which he was familiar). argued that *Petrolacosaurus* was an eosuchian—a primitive diapsid. There is no morphological proof, one way

or another. of this suggestion. There was a lateral temporal opening, but the cheek is poorly preserved, and whether an additional upper opening was present cannot be determined. Apart from the possible but unproven diapsid nature of the temporal region, there is no reason to assign *Petrolacosaurus* to the Eosuchia. Peabody points out a number of common features of the skulls in *Petrolacosaurus* and *Prolacerta*, but these are essentially primitive characters which could have been inherited by both from captorhinomorph cotylosaurian ancestors. The time of appearance of *Petrolacosaurus* is one at which an eosuchian is hardly to be expected. There are no traces of any diapsid in the Lower Permian, and no sure evidence in the Middle Permian; the first certain diapsid is Upper Permian in age—a full period after *Petrolacosaurus*— and Watson (1957) has argued that diapsids were only then evolving from millerettid cotylosaur derivatives.

If, then, we abandon the possible but improbable suggestion that *Petrolacosaurus* was a precocious diapsid, all the features of this little reptile agree with the assumption that we are dealing with a pelycosaur, and several characters point strongly to the suggestion that it is a primitive edaphosaurian. The skull is primitive and generalized. as it is in such archaic ophiacodonts as *Clepsydrops* and *Varanosaurus*, such a sphenacodontian as *Varanops*, and such a nitosaurian as *Mycterosaurus*. Diagnostic features, however, can be found in the postcranial skeleton. (1) The postcervical vertebral centra are rounded ventrally as in ophiacodonts and edaphosaurs, in contrast to the keeled sphenacodonts. (2) In the carpus the ulnare is short, in contrast to advanced sphenacodonts and as in ophiacodonts and edaphosaurs (however, *Varanops* among the sphenacodonts also has a short ulnare). (3) In the tarsus there is a broad, highly developed. medial centrale forming the sole connection between astragalus and distal tarsals 1 and 2; edaphosaurs and sphenacodonts are similar, but ophia-

codonts have two small centralia of sub-equal size in this position. (4) On the femur, the ventral system of trochanters and ridges is one found among pelycosaurs in edaphosaurs only (cf. Romer and Price, 1940: fig. 37). Distal to the internal trochanter an adductor crest slants diagonally across the bone towards the external trochanter. In sphenacodonts there is a pronounced fourth trochanter but no adductor crest; in ophiacodonts the crest descends the external margin of the bone. (5) Both Lane and Peabody ascribe to *Petrolacosaurus* a pelvis (University of Kansas no. 1425) which is very distinctively edaphosaurian. It is of a type strongly contrasting with that of any other reptilian group—most notably in the shovel-shaped iliac blade, tall but without a marked posterior projection. Were this pelvis definitely associated, *Petrolacosaurus* could be assigned to the Edaphosauria without hesitation. It was, however, found isolated, and since a specimen of *Edaphosaurus* has been found in the quarry, this pelvis may pertain to that genus. Several pelves with low, long ilia of ophiacodont type are also present in the material; but these, too, lack association, and may belong to an ophiacodont, also present in the Garnett material.

There are, thus, in the postcranial skeleton of *Petrolacosaurus* a number of features which strongly indicate that this genus belongs to a group of archaic edaphosaurians from which both *Edaphosaurus* and, at a much later time, the caseids may have arisen.

LITERATURE CITED

Fox, R. C. 1962. Two new pelycosaurs from the Lower Permian of Oklahoma. Univ. Kansas Publ. Mus. Nat. Hist., **12**: 297–307.

Lane, H. H. 1945. New mid-Pennsylvanian reptiles from Kansas. Trans. Kansas Acad. Sci., **47**: 381–396.

Langston, W. 1965. *Oedaleops campi* (Reptilia: Pelycosauria). A new genus and species from the Lower Permian of New Mexico, and the family Eothyrididae. Bull. Texas Mem. Mus., **9**: 1–46.

Olson, E. C. 1954. Fauna of the Vale and Choza. 7. Pelycosauria: family Caseidae. Fieldiana, Geology, **10**: 193–204.

———. 1962. Late Permian terrestrial vertebrates, U.S.A. and U.S.S.R. Trans. Amer. Philos. Soc., (N.S.) **52** (part 2): 1–196.

Olson, E. C. and J. R. Beerbower, Jr. 1953. The San Angelo Formation, Permian of Texas, and its vertebrates. Jour. Geol., **61**: 381–423.

Peabody, F. E. 1949. Mid-Pennsylvanian pelycosaurs from Kansas. Bull. Geol. Soc. Amer., **60**: 1913.

———. 1952. *Petrolacosaurus kansensis* Lane, a Pennsylvanian reptile from Kansas. Univ. Kansas, Paleont. Contrib. Vertebrata, **1**: 1–41.

Romer, A. S. 1937. New genera and species of pelycosaurian reptiles. Proc. New England Zool. Club, **16**: 89–96.

———. 1948. Relative growth in pelycosaurian reptiles. Robert Broom Commemorative Volume. Pp. 45–55.

———. 1956. Osteology of the reptiles. Chicago, Univ. Chicago Press, xxi + 772 pp.

Romer, A. S. and L. I. Price. 1940. Review of the Pelycosauria. Geol. Soc. Amer., Spec. Pap. No. **28**: 1–538.

Shuler, E. W. and R. V. Witter. 1942. The mounted skeleton of *Edaphosaurus boanerges* Romer at Southern Methodist University. Field and Laboratory, **10** (2): 140–144.

Stovall, J. W. 1937. *Cotylorhynchus romeri*, a new genus and species of pelycosaurian reptile from Oklahoma. Amer. Jour. Sci., (5) **34**: 308–313.

Vaughn, P. P. 1958. On a new pelycosaur from the Lower Permian of Oklahoma, and on the origin of the family Caseidae. Jour. Paleont., **32**: 981–991.

Watson, D. M. S. 1913. The Beaufort Beds of the Karroo System of South Africa. Geol. Mag., (5) **10**: 388–393.

———. 1917. A sketch classification of the pre-Jurassic tetrapod vertebrates. Proc. Zool. Soc. London, 1917: 167–186.

———. 1954. On *Bolosaurus* and the origin and classification of reptiles. Bull. Mus. Comp. Zool., **111**: 295–449.

———. 1957. On *Millerosaurus* and the early history of the sauropsid reptiles. Philos. Trans. Roy. Soc. London, (B) **240**: 325–400.

Williston, S. W. 1910. New Permian reptiles: rhachitomous vertebrae. Jour. Geol., **18**: 585–600.

———. 1911. American Permian vertebrates. Chicago, Univ. Chicago Press, 145 pp.