THE UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

VERTEBRATA

ARTICLE 8
Pages 1-24, Figures 1-21

A NEW ARMORED DINOSAUR FROM THE CRETACEOUS OF KANSAS

By THEODORE H. EATON, JR.
(Contribution from the Museum of Natural History)

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A NEW ARMORED DINOSAUR FROM THE CRETACEOUS OF KANSAS

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ILLUSTRATIONS

ABSTRACT

The skull and partial skeleton of an ankylosaur, family Nodosauridae, new genus and species, are described from the Terra Cotta clay member of the Dakota Formation (Cretaceous), Ottawa County, Kansas. The premaxillaries bear blunt, conical teeth; the pterygoids, although expanded posteriorly, do not fuse with the quadrates; the sacrum contains six fused vertebrae with sacral ribs, plus a presacral rod of five additional fused vertebrae. The new genus is probably ancestral to *Edmontonia,* and perhaps to other Late Cretaceous American genera. The environment was that of a warm-temperate deciduous forest.

INTRODUCTION

Although the sedimentary rocks of Kansas are rich in fossil animals, these are mostly marine invertebrates and fishes, with a scattering of large aquatic reptiles, a few primitive sea birds, and land mammals of relatively late geological age. Dinosaurs are rare. Only five specimens have been reported hitherto from Kansas, and four of these consist only of fragments. The armored dinosaurs, suborder Ankylosauria, are represented by two species from the Upper Cretaceous Niobrara Chalk, a marine deposit in which the remains were buried, probably as a result of drifting from nearby shores. One of these species, described by Wieland (1909) as *Hierosaurus sternbergii,* is known only from a few bony plates and some parts of the internal skeleton. The other, from a much more complete specimen, was described as *H. coleii* by Mehl (1936), who considered it to be aquatic; this interpretation is doubtful.

The ankylosaur reported in the present paper was found by Mr. Warren H. Condray on his farm in Ottawa County, ten miles south of Miltonvale, Kansas. He wrote to Senator Frank C. Carlson, who communicated with Chancellor Franklin D. Murphy of the University of Kansas. Mr. Russell R. Camp, preparator in vertebrate paleontology at the Museum of Natural History, investigated the find, and in July, 1955, with Mr. Condray's help, removed the specimen. Its preparation in the laboratory was a tedious and difficult task on account of the hard, "ironstone" matrix and the fragility of many of the bones. Mr. Camp was assisted, in the course of this work, by a student, Mr. Glenn E. Marihugh.

The skeleton lay partly exposed in the bed of an intermittent stream, and was damaged by cattle trampling, stream erosion, and weathering. Many elements were missing, but a few isolated fragments were recovered as far as 50 yards downstream. In addition, the bones had been partly dissociated at their original burial, probably by action of currents. Limb bones (except a femur and one phalanx), pectoral girdle, and much of the tail are lacking. The specimen is, however, one of the better preserved ankylosaurs, especially as to the skull, vertebral column, and sacrum.

Stratigraphically the site stands midway in the Terra Cotta clay member of the Dakota Formation, hence about one third of the way up in the Dakota (now classified as uppermost Lower Cretaceous in the Kansas region). The rock is a hard, fine-grained, cross-bedded sandstone, reddish, gray and brown, and has many concretions containing limonite. Fossil leaves of oak, beech, sycamore and sassafras indicate that the animal lived in a warm-temperate forest like that of the southeastern Piedmont today. Central Kansas in Dakota time was probably a coastal plain of low relief, in which aggrading streams deposited sediments from higher land to the west. The site is approximately 12 miles west of the present eastern margin of Cretaceous exposures.

To Prof. Robert W. Wilson and Mr. Camp I am grateful for consultation and aid in interpreting the material, and to Prof. E. Raymond Hall for making the specimen available. I thank Mr. Merton C. Bowman and Mrs. Lorna Cordonnier for assistance with drawings, and Miss Sarah Gayle Seevers both for drawings and for help in preparing the description.

The dinosaur belongs to the order Ornithischia, suborder Ankylosauria and family Nodosauridae, but represents a heretofore unnamed genus and species that is named and described below.

DESCRIPTION

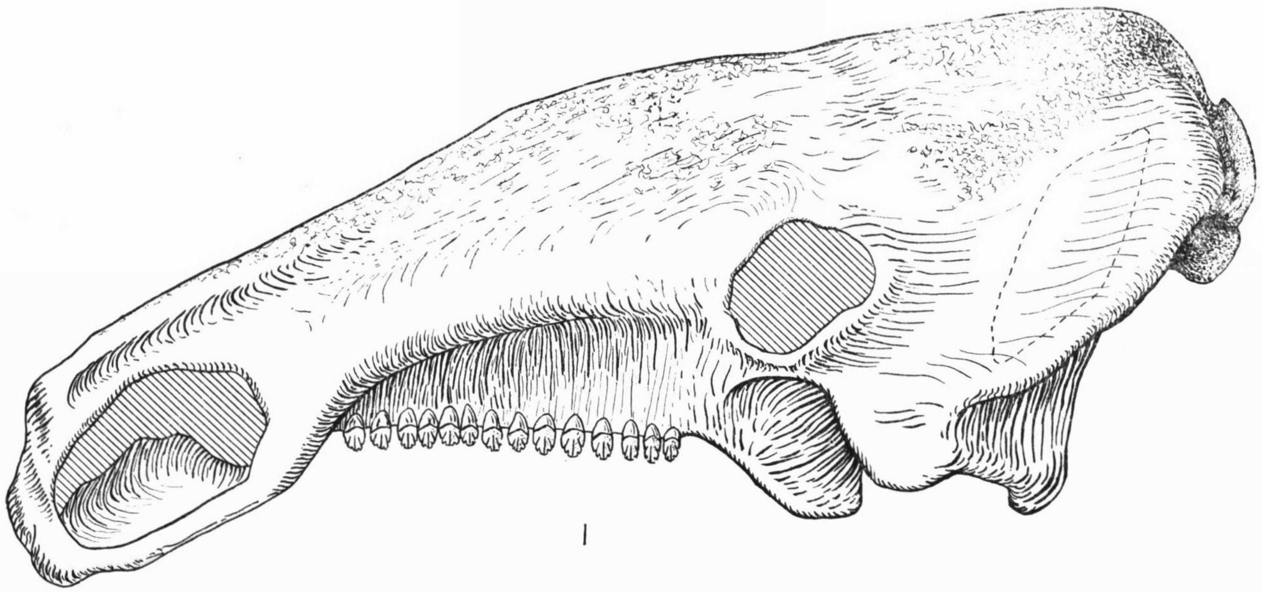
SILVISAURUS CONDRAYI, n.gen., n.sp.

The type specimen consists of a partial skeleton, including the skull, No. 10296 Univ. Kansas Mus. Nat. Hist., obtained in July, 1955, by Russell R. Camp, in SW¼ sec. 8, T. 10 S., R. 1 W., Ottawa County, Kansas, midway in the Terra Cotta clay member of the Dakota Formation, Lower Cretaceous.

DIAGNOSIS

Armored dinosaur approximately ten feet long; skull pear-shaped, about three fourths as wide as long, widest at posterior margins of orbits; dermal armor concealing antorbital and temporal fenestrae, but lacking prominent processes; condyle only slightly decurved; palate with two deep, elongated clefts, at posterior ends of which pterygoids form thin-walled pouches; pterygoids meeting but not fusing with quadrates; premaxillary teeth eight or nine, bluntly conical, slightly serrate, lacking cingulum; maxillary teeth 17 or 18, crowns spatulate, margins having 7 to 9 serrations from which grooves extend about halfway down flat sides; cingulum strong but not rugose; mandibular teeth about 27, similar to those of maxillary.

Sacrum includes 6 fused vertebrae with sacral ribs, and presacral rod of 5 additional fused vertebrae; ribs in trunk have T-shaped or L-shaped cross sec-



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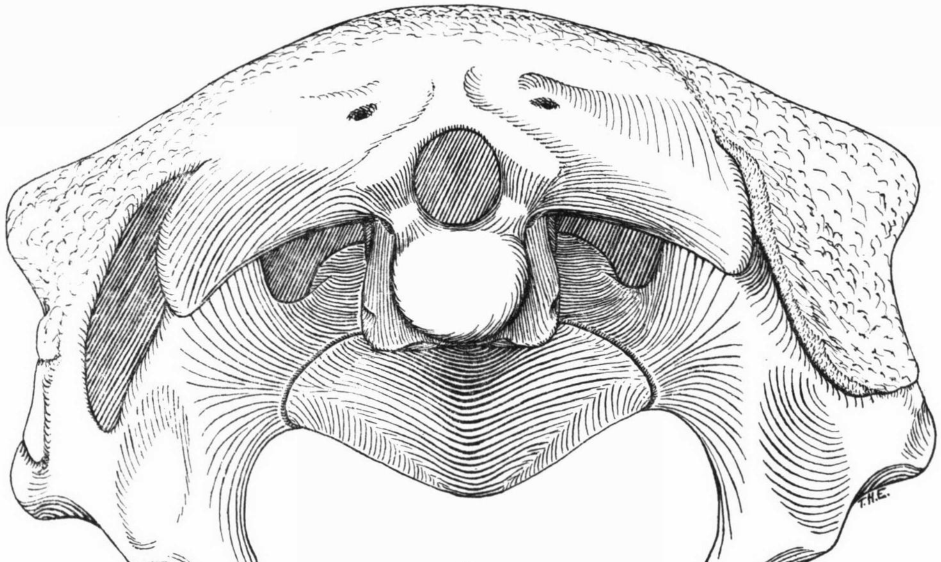

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FIGURES 1, 2. Skull of *Silvisaurus condrayi*, ×0.5.———1, Lateral view.———2, Occipital view.

tions; dermal armor immobile in sacral region; dorsum covered with flattened polygonal or rounded plates; tail and part of trunk bearing lateral dermal spikes.

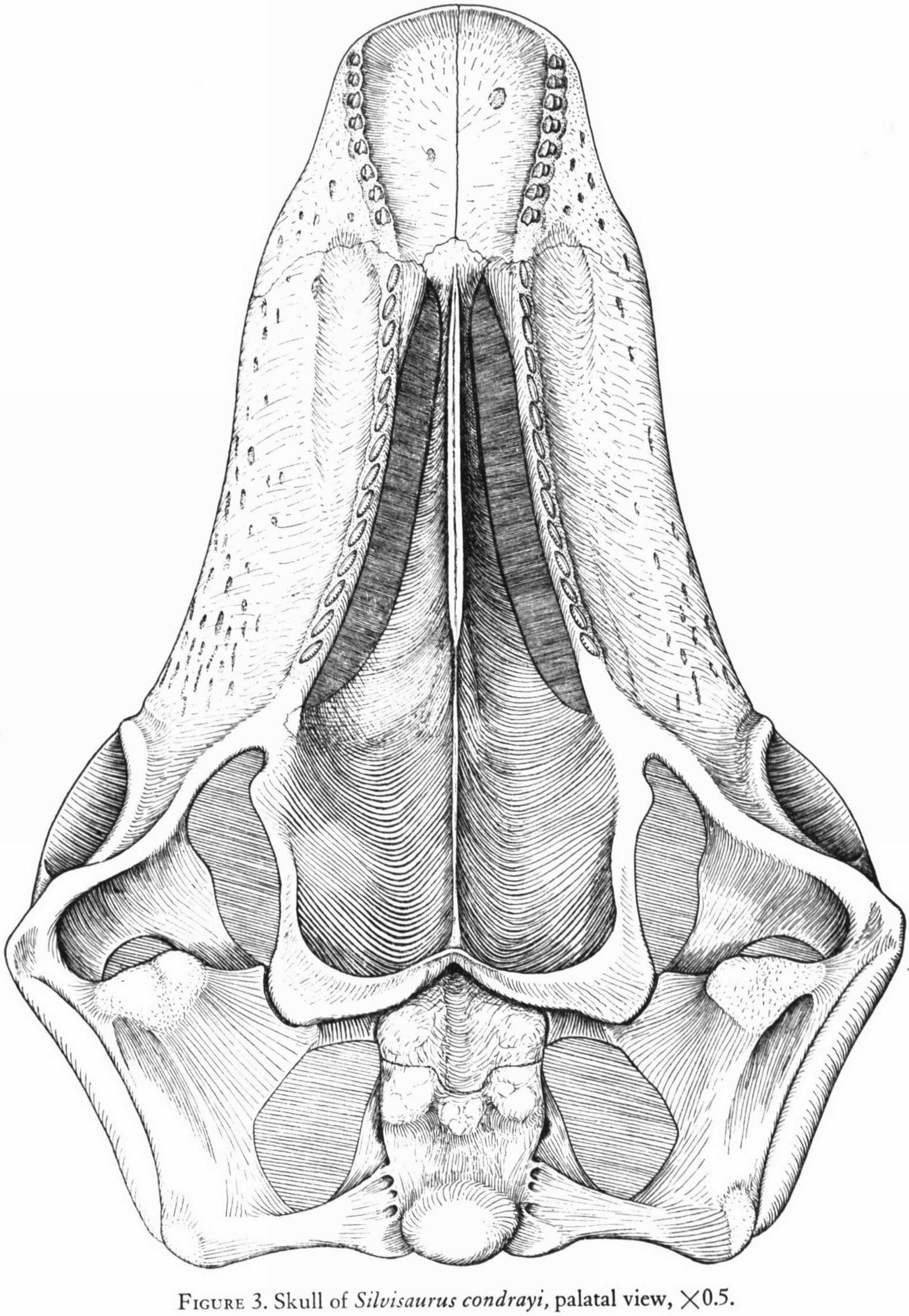


FIGURE 3. Skull of *Silvisaurus condrayi*, palatal view, ×0.5.

SKULL

DORSAL SURFACE AND FENESTRAE

Figures 1-6

The skull of *Silvisaurus* was originally overlain dorsally and laterally by a dermal armor of bony plates which, however, are poorly preserved in the type. Above the right orbit, three of these plates can be distinguished clearly enough to show that they resembled those of *Edmontonia longiceps* (STERNBERG, 1928) in the same area. Middorsally and anteriorly much of the armor is missing, and the surface of the skull proper is exposed. A shallow median groove runs forward on the snout, becoming more distinct anteriorly where it is formed by the nasal and premaxillary bones. The premaxillaries meet the nasals directly above and medial to the anterior margins of the nares, and bear slightly depressed lateral surfaces that may have supported the proximal edges of a horny beak.

The narial opening, as shown on the left side of the specimen, is large, about 40 mm. high and 50 mm. wide. But the nostril may have been further restricted by the dermal plates and the margin of the beak, to an extent not apparent in the specimen.

The orbits, slightly overhung dorsally by the dermal armor, are so placed as to suggest that the visual axis of each eye was at an angle of about 60 degrees from the axis of the head, in the horizontal plane. The orbital cast formed by matrix is sufficiently exposed on the right side to show that its maximum diameter, at right angles to the axis of the eye, is slightly more than 60 mm., but the external diameter of the orbit, shown on the left, is about 35 mm.

In dinosaurs as a rule the skull appears to be lightly built because the deep temporal fossa opens laterally by two fenestrae, ventrally by a wide subtemporal fenestra, and also to the orbit through the incomplete floor of the latter; usually an antorbital fenestra opens into the nasal passage or a passage confluent with this. In *Silvisaurus* all these openings are present in the skull, but the antorbital and the two temporal fenestrae are concealed outwardly by the dermal armor. The antorbital fenestra is clearly visible from within the palatal vacuities. Looking dorsad in the temporal fossa, one can see the superior temporal fenestra, completely covered; the lateral fenestra, a long oval opening with its axis tilted anteroventrally, is nearly covered. The dermal armor extends to the lower edge of this fenestra but is not firmly attached there; the opening is not visible from above.

The spacious temporal fossa, occupied in life by the jaw muscles, opens ventrally beneath the orbit by way of a subtemporal fenestra, through which these muscles reached the mandible. The cavity of the orbit is confluent medioventrally with that of the temporal fossa, since the orbital floor is incomplete. On the floor of the temporal fossa behind the quadrate and pterygoid, but anterior to the exoccipital and opisthotic, is another fenestra that probably accommodated a sheet of connective tissue.

OCCIPITAL SURFACE

Figure 2

Scarcely any clear sutures can be seen in this part of the skull. A suture probably separates each exoccipital from the basioccipital immediately above the condyle. At the point where the lower end of the quadratojugal reaches the external surface of the quadrate there is also a probable suture. The pterygoids expand laterally and their dorsolateral surfaces, as seen from behind, occupy broad depressions on the medial faces of the quadrates, but this contact is not a suture, since the bones separate readily, leaving smooth surfaces. Presumably the joint was, in life, a syndesmosis, with slight if any mobility.

The opisthotics, extending laterally at the level of the foramen magnum, terminate in broad, rugose paroccipital processes, the function of which probably was to provide for the insertion of strong rectus capitis and levator scapulae muscles. Most of the remaining occipital surface, above and medial to these processes, must have received the spinalis capitis and longissimus muscles of the neck. Even so, with a head of this size, the area for muscle attachment seems inadequate for long-sustained support.

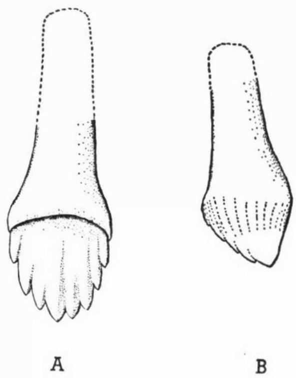


FIGURE 4. *Silvisaurus condrayi;* lateral views of (A) maxillary tooth (no. 14, right) and (B) premaxillary tooth (no. 7, left). ×2.

PALATE AND UPPER DENTITION

Figures 2-4

In ventral aspect the most conspicuous features of the skull are a narrowing of the palate (between the maxillary tooth-rows) to less than half the width of the skull, and an extraordinary deepening of the palate dorsad into a pair of narrow clefts that extend about 60 per cent of the total length of the skull. In their anterior and narrowest half these clefts are bounded laterally by the maxillaries, each of which bears, on a strong alveolar ridge, approximately 17 teeth.

Individual teeth of the maxillary series are compressed (see Fig. 4) in their distal portions (the parts exposed in life). Each tooth bears from seven to nine serrations on its cutting edge. At the base of the flattened part is a prominent collar-like cingulum; grooves between successive serrations do not extend all the way to the cingulum. Proximal to the latter the root of the tooth consists of a columnar peg fitting into the alveolus. The maxillary teeth stand diagonally, so that the anterior margin of each lies mediad to the posterior margin of the tooth next in front of it. The crown height of each tooth, from cingulum to tip, is 5 to 7 mm.; the greatest antero-posterior length is about 7 mm. The size of these teeth diminishes gradually in an anterior direction.

The premaxillary bones together form a shallow inverted scoop with thin edges that probably supported a horny turtle-like beak. The premaxillary teeth numbered eight or possibly nine, as shown on the left side where six are in place. Anteriorly each tooth-row flares laterally, toward the outer margin of the jaw, but posteriorly is in line with the maxillary teeth.

The premaxillary teeth are about half as large as those of the maxillary series, and of a different shape. The distal portion is barely flattened on the side, but makes a bulging cone. The peg-like base of the tooth is much narrower than the conical tip. This cone turns slightly posteriorly, forming a blunt hook, on the edge of which are four to six small serrations corresponding to those of the maxillary teeth. Evidently the premaxillary series was used to supplement the beak in tearing away leaves or stems from plants, whereas the maxillary series was more suitable for chopping or slicing.

The deep palatal clefts mentioned above are bordered posteriorly by ectopterygoids and pterygoids, the latter forming a thin transverse crest in line with the ventral ends of the quadrates. Apparently the clefts represent greatly elongated choanae, but it is not likely that they were open for their entire length in life. In the related genus *Edmontonia* a strong inward process from each ectopterygoid obviously marked the anterior limits of the functional choanae, opposite the posterior end of the maxillary tooth-row. In the present specimen there is a break in the ectopterygoids, and the processes, if they existed, are lost, but a smooth, shallow concavity on the lateral wall of each cleft behind this break shows where the air passage was situated.

A thin, vertical septum stands between the palatal clefts; in its anterior half it comes as far ventrally as the alveolar ridges of the maxillaries, and is composed here of the united vomers. Probably this septum supported either a soft or a horny secondary palate that reached as far back as the anterior ends of the ectopterygoids. The distance from the ventral, posterior edge of the median septum to the roof of either nasal cavity is about 65 mm. vertically. These cavities expand laterally as far as the antorbital fenestrae, which are covered externally by the dermal armor. The nasal cavities (palatal clefts) also extend back as far as the thin transverse pterygoid walls. The posterior part of each cavity seems to have constituted a sinus or diverticulum, situated behind the descending air passage, and covered ventrally by a connective tissue sheet attached to the rim of the pterygoid. These sinuses are not simply excavations of otherwise massive bones, but are almost balloon-like inflations of the thin pterygoids. Such an extraordinary modification must have had some important function. As the walls are too delicate to provide any resistance to pressure or to the pull of muscles, and as they obviously comprise the surfaces of air chambers close to the stream of respired air, the only function which comes to mind is that of resonance. It seems likely that these chambers amplified the sound-vibrations produced by air passing them, perhaps in the manner of a voice-box. Assuming that the pitch is determined by the size of the resonating chamber (diameter approximately 50 mm.), this sound may have been about E or F, four octaves above middle C.

The more dorsal and medial part of each pterygoid articulates with the basisphenoid and, in part, the presphenoid. There may have been a slight mobility of the basipterygoid joint. Lateral to this joint each pterygoid extends to the quadrate, which it meets in a suture. But the ventral part of the posterior edge of the pterygoid, in association with the developing air cavities already mentioned, flares ventrally and laterally so far as to meet the quadrate again in what appears to be a secondary joint, where the lateral surface of the pterygoid lies in a smooth, shallow recess in the quadrate. There may not have been a direct contact of the bones here, but a gap occupied by connective tissue or cartilage. In later ankylosaurs, such as *Edmontonia,* there is no indication of any such gap, and the basipterygoid articulation seems to have closed solidly, eliminating any possible kineticism.

In *Alligator* and *Crocodylus* the only median bone anterior to the braincase is the presphenoid, of trapezoid shape, standing vertically between the orbits and ventral to the olfactory and optic foramina. It touches the dorsal surface of both pterygoids. Anterior to it, between the orbits, is a large median window bounded above by the frontals and below by the pterygoids. Immediately anterior to the window the prefrontal on each side sends a process down to meet a short upward process of the palatine. The basioccipital comes forward as far as a median foramen (Eustachian tube), and the bone at the sides and in front of this foramen is the basisphenoid, which has a sutural articulation with the pterygoids. Evidently in Crocodilia the loss of kineticism is accompanied by union of the pterygoids with (1) basisphenoid, and (2) quadrates; the latter connection may amount to complete fusion.

Therefore the loss of kineticism in ankylosaurs, at least, must have been independent of that in Crocodilia, because the connection between pterygoids and basisphenoid in *Silvisaurus* is not yet firm, although it becomes so in the later ankylosaurs.

In *Silvisaurus* a median vertical plate of bone lies dorsal to the posterior portion of the fused pterygoids, over the location of the posterior nares. The plate is in the correct position for a presphenoid, and is separate from the small median keel of the basisphenoid (which stands immediately in front of the internal carotid foramina). This supposed presphenoid has a vertical extent, along its broken edge, of 58 mm., and maximum thickness of 13 mm. Just ventral to this bone there is apparently another, immediately anterior to the basisphenoid, and wedged between the posterior inflated walls of the pterygoids. If separate from the presphenoid, it must be the parasphenoid; its size and shape cannot be seen clearly.

In most Ornithischia the orbit is bounded anteriorly by the prefrontal and lacrimal, and ventrally by the jugal. Primitively the jugal also forms the ventral edge of the lower temporal fenestra, but the quadratojugal and quadrate sometimes take part in this. In *Silvisaurus* the quadrate forms the posterior margin of the fenestra, the quadratojugal forms part of the ventral margin, and the jugal meets the quadratojugal, probably at the point of greatest breadth of the skull. But sutures bounding the prefrontal, lacrimal, jugal and quadratojugal cannot be distinguished. Under the edge of the right orbit, anteriorly, a broken surface of bone extends down and meets the pterygoid (and palatine?) wall; presumably this bone is the prefrontal. It makes a hook posteriorly, by means of which its contact with and support of the pterygoid is extended.

BRAINCASE

Figure 5

Owing to the manner in which the skull was broken, many details of the deeper cranium can be observed which in an intact skull would be concealed. The broken surfaces are on the left and right sides, about an inch out from the walls of the braincase, and also across the front of it in the olfactory region of the cranial cavity, anterior to the optic foramina. Thus the entire series of cranial nerve foramina is visible on one side or the other, and the endocranial cavity, although not entirely clear of matrix, can be viewed from both ends; it is closely similar in shape, position and relative size to that of *Stegosaurus,* as figured by GILMORE (1914). In its anterior aspect the ventral half of the braincase, below the level of the optic foramina, has been bent to the right, so that its midpoint, between the internal carotid foramina, lies 8 to 10 mm. from its normal position. This has resulted in displacement of the lower foramina of right and left sides. The right internal carotid foramen, for example, is concealed by the edge of the basisphenoid, but the left one is not.

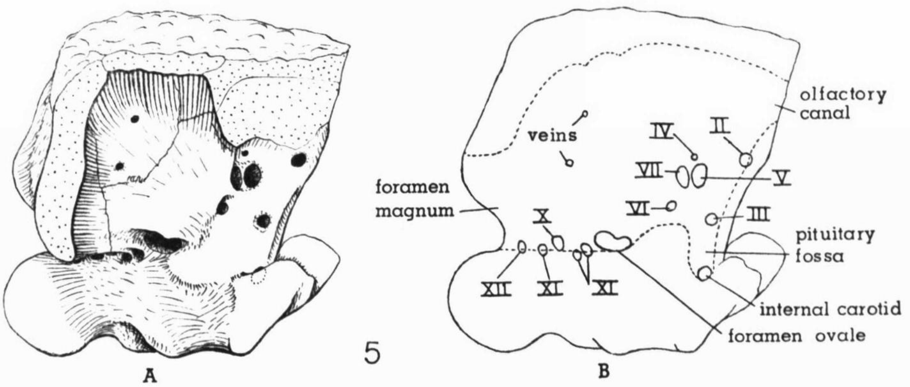
Endocranial cavity. The foramen magnum (diameter dorso-ventrally 25 mm., transversely 23 mm.) opens some 30 mm. below the dorsal edge of the occipital surface, and the floor of the endocranial cavity is approximately horizontal for the greater part of its length; anteriorly it rises slightly (Fig. 5B). The roof (internally) ascends steeply from behind forward, so that its thickness from the inner to outer surface is not more than 10 to 12 mm.; in the middorsal portion the roof is about 8 mm. thick. In the otic region the endocranial cavity remains the same width as the foramen magnum, but anterior to the inner ear, and dorsally, it broadens to a maximum of 35 mm., and the depth there, not including the pituitary fossa, is approximately 50 mm. The volume of space cleared in the endocranial cavity is 53 cc. as measured by sand in a graduated cylinder. Of this about 3 cc. is in the inner ear cavities. Approximately 30 per cent of the cavity has not been cleared because of danger to preservation of the walls, so that the total endocranial volume would be close to 70 cc. The brain probably did not fill the endocranial cavity in life, but in several places the form of the brain influenced that of the inner surface of the cavity.

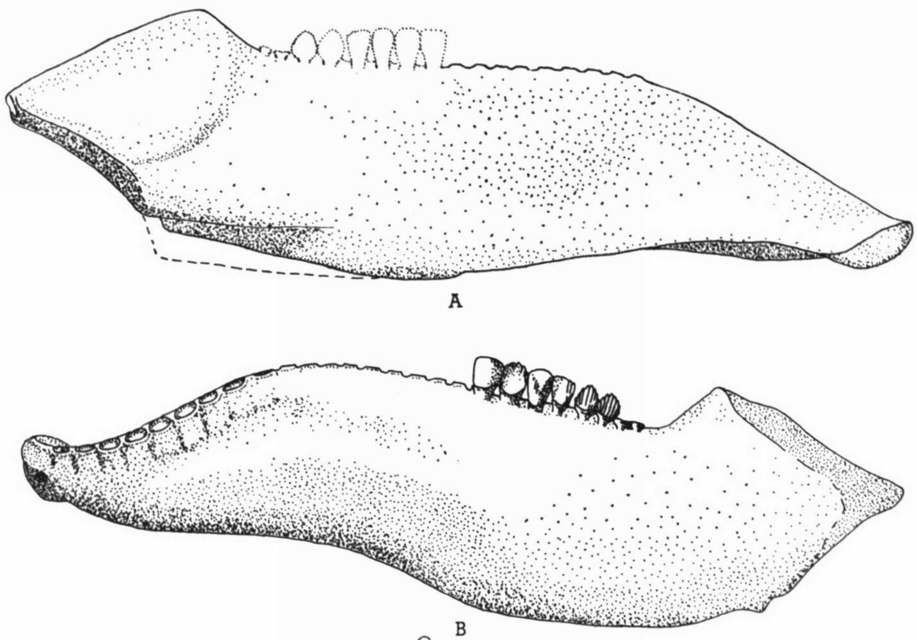
The level at which the braincase broke off from the more anterior part of the skull is that at which the endocranial cavity narrows to a diameter of 17 mm. transversely, and where, therefore, the olfactory tracts probably became distinguishable from the remainder of the cerebrum. The inner surface of the cavity behind this point is smooth and rounded dorsally and laterally, but there is no indication dorsally of a median separation of the hemispheres from each other. Ventrally the matrix has not been removed, and the exact shape of the cavity in this important region cannot be determined. At about 42 mm. posterior to the break there is a low arching ridge on the inner surface of the endocranial cavity where the cerebrum was separated from the optic lobes. Impressions of the latter show clearly immediately behind the ridge, and the right and left are distinguishable from each other in the middle line; their anteroposterior extent is about 8 to 9 mm., and they slant anteroventrally on the sides of the cavity, disappearing as clear impressions some 20 mm. from the middorsal line. Another low ridge, sharper and narrower than the preceding, separates the impression of the optic lobes from that of the cerebellum, which shows as a single median concavity in the roof.

Directly ventral to the position of the optic lobes and cerebellum, on either side, a large lateral concavity in the wall is interpreted as marking the anterolateral portion of the medulla, in the region of the origin of the fifth and seventh nerves. This part of the brain must have been relatively larger than in the alligator (ROMER, 1956, Fig. 14), and the foramina for nerves V and VII are both large in *Silvisaurus.*

Foramina and related features of braincase. Sutures between supraoccipital, exoccipitals and basioccipital are not certainly visible, and that between basioccipital and basisphenoid is open to some doubt (Fig. 5). The latter bone bears on its anterolateral face the basipterygoid articulating surface, but there is no prominent process. Anterodorsally, immediately in front of the cranial cavity, the basisphenoid narrows and forms an upright crest; this rests against the upright presphenoid, which extends forward between the pterygoids.

The internal carotid foramen is immediately behind the upright crest of the basisphenoid and is some 20 mm. ventral to the optic foramen. Presumably the pituitary fossa reached at least as far ventrally as the internal carotid foramen, which opened into it on either side, but the fossa is filled with matrix and its size cannot be determined; its depth was probably 15 mm. or more. On the anterolateral face of the braincase, midway between its dorsal and ventral limits, are three large foramina in a horizontal series, for the optic, trigeminal and facial nerves. The latter two are largest and separated from each other by only a thin partition. Possibly the foramen taken to be that of the facial nerve also carried one or two rami of the trigeminal, as suggested in the figure of the *Protoceratops* braincase by BROWN & SCHLAIKJER (1940, fig. 15), but there is not, as there was in *Protoceratops,* another foramen that could be considered facial. The fact that the axes of these two large foramina





FIGURES 5, 6. *Silvisaurus condrayi.*——5, Braincase, (A) right lateral view and (B) outline, showing foramina and endocranial cavity, ×0.5.————6, Left ramus of mandible, (A) medial view (teeth concealed by matrix) and (B) lateral view, ×0.5.

converge toward each other outwardly, rather than inwardly, suggests that they bore two separate nerves instead of the rami of one. The oculomotor foramen opens 8 mm. below that of the trigeminal, and the abducent foramen is 5 mm. posteroventral to the facial. The trochlear foramen is about 6 mm. above the trigeminal and is the smallest of the series, less than 2 mm. in diameter.

A lateral bulge of the cranium separates these anterior foramina from the posterior group. The first of the latter is the foramen ovale; it lies in a narrow recess, and has a diameter antero-ventrally of 8 mm., postero-ventrally 5 mm. From the foramen ovale to the edge of the foramen magnum is 25 mm. in a horizontal line, and 5 more foramina occur in this distance. The first two of these, nearest the foramen ovale, evidently bore two divisions of the glossopharyngeal nerve; the two foramina are confluent with each other inwardly. The last three are presumably for the vagus, spinal accessory and hypoglossal nerves.

Two other distinct foramina occur on the wall of the braincase, well above the level of the inner ear. They are interpreted as probably for cerebral veins. A conspicuous foramen, probably with the same function, occurs on the occipital face of the skull on each side of the foramen magnum and a little distance above it.

As seen from inside the foramen magnum, the medial wall of each inner ear cavity has been broken open. Although none of its details are visible, the diameter of the inner ear was probably about 12 mm.

MANDIBLE

Figure 6

The left mandible is in fairly good condition as far back as the end of the tooth-row, but the articular portion is lacking. Alveoli and teeth still present show that there were about 27 teeth in the series, with a form and arrangement like those of the maxillary series. The distance in a straight line from the most posterior alveolus to the anterior end of the mandible, at the symphysis, is 170 mm. The more anterior third of the tooth-bearing edge curves strongly downward, and the dentary then swings medially toward the symphysis, becoming toothless for about 25 mm. There is no indication of a predentary, but probably a horny beak encased this part of the jaw, much smaller, however, than the upper beak. Along the external surface, parallel with the tooth-row and below it, is a shallow trench, at the lower edge of which the fleshy cheek must have attached. As a result, the horizontal portion of the tooth-row is set inward 20 to 25 mm. from the most lateral surface of the mandible. On the medial surface, although much of the upper edge is still concealed by matrix, there appears a row of nutrient foramina serving the roots of the teeth; each foramen is about 3 mm. in diameter, and they lie within 4 or 5 mm. of the alveolar edge of the bone.

The more important measurements of the skull of *Silvisaurus condrayi* are given in Table 1.

TABLE I. *Measurements of Skull of* Silvisaurus condrayi, *in Millimeters*

Total length	332
Maximum width, behind orbits	253
Width between tips of paroccipital processes	160
Anteroposterior length of premaxillary in midline	79
From posterior end of premaxillary to posterior face of pterygoid crest in midline	173
From posterior face of pterygoid crest to posterior edge of condyle, horizontally	80
Depth of skull from boss to base of quadrate	153
Depth to posterior end of maxillary ridge	93

VERTEBRAE AND RIBS

CERVICAL REGION

Figures 7-9

The material consists of five cervical vertebrae and the impressions of at least three more, which were anterior to the figured series, judging by the positions of their transverse processes. The impressions are partial and scattered, but the five vertebrae are apparently in sequence and are complete except for the lower half of the first centrum. Unfortunately the atlas and axis, usually fused in this family, have not been found. When the series is set together, there is a gap of about 12 mm. between the centra, which may have been occupied by cartilage on the articular surfaces.

Although they are not evenly progressive, the following changes occur in the series, going posteriorly: (1) the transverse processes become longer, more massive, and tilted upward; (2) the neural spine becomes slightly higher and curves posteriorly; (3) the centrum becomes more deeply hollowed on the side below the diapophysis, and slightly larger; (4) the position of the parapophysis becomes progressively higher and more posterior on the centrum; (5) anteriorly the transverse processes stand in the same plane as the pre- and post-zygapophyses, but, more posteriorly, above this plane, margins of the zygapophyses become increasingly confluent with those of the transverse processes; (6) the base of the transverse process rises higher on the neural arch and the peduncles below it become longer, but this is not accompanied by any clear increase in the diameter of the neural canal or of the centrum; (7) the pre- and post-zygapophyses become more tilted upward and the latter more confluent with the neural spine, the prezygapophyses becoming shorter.

Four separate Y-shaped cervical ribs have been found. The tuberculum is a little shorter and slightly bigger at the tip than the capitulum. The shaft is a little longer than the capitulum and curves posteroventrally. On the basis of curvature, two of the ribs appear to be from the right side and two from the left. Obviously, the cervical ribs took no part in the support of dermal armor, and this accounts for their retention of the primitive movable articulations with the vertebrae.

THORACIC REGION

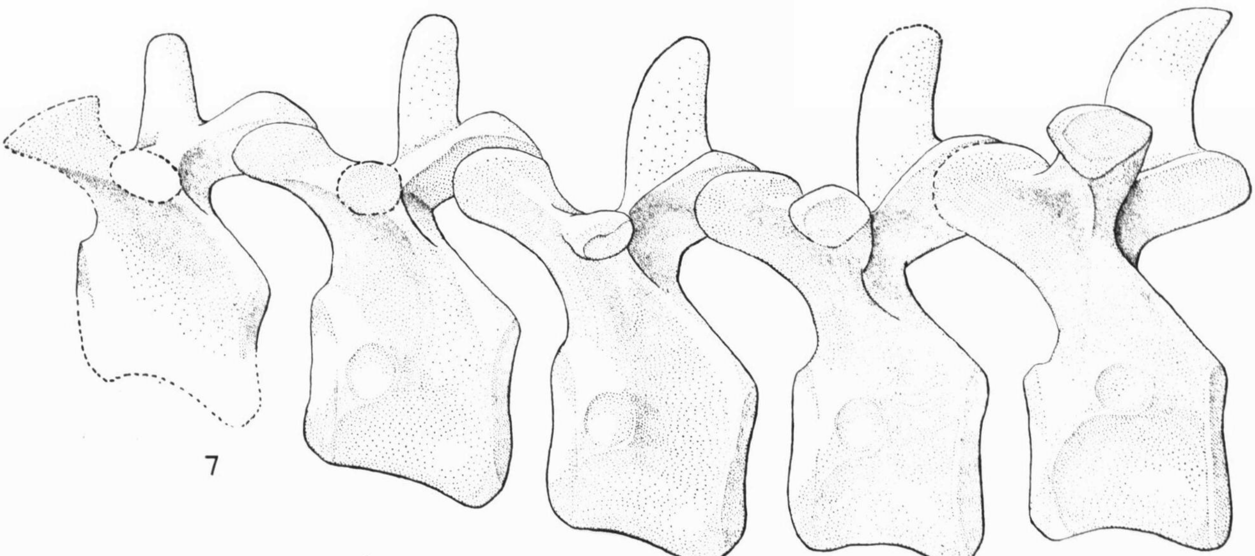
Figures 10, 11

One or two vertebrae may be missing between the last cervical and the first thoracic, but the fit is close. Differences between these regions are correlated with support of armor in the trunk and corresponding rib enlargement.

Of the five recognizable thoracic vertebrae, the first two are still in original contact. The remainder are judged to be posterior to the first two because they continue the trend toward enlargement of the neural spine, and because the space and angle between the prezygapophyses of the first two thoracic vertebrae are intermediate between those of the widely spaced cervicals and the narrowly spaced thoracics.

The five thoracics all have long, strong, broad transverse processes, standing at an angle of about 45 degrees above the horizontal plane, and lacking a distinct articular facet for the capitulum. The facet for the tuberculum shows as an enlarged rough depression laterally, on the end of the transverse process.

The thoracic ribs become large, high-arched, T-shaped or L-shaped in cross section, flat on top for carrying dermal armor, and have their proximal ends snugly fitted against



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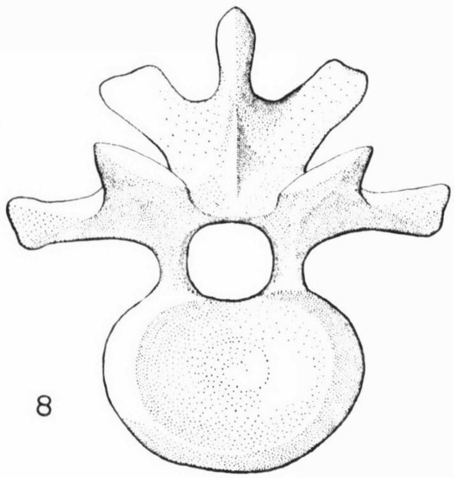

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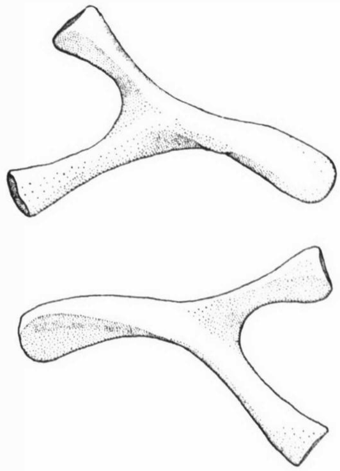

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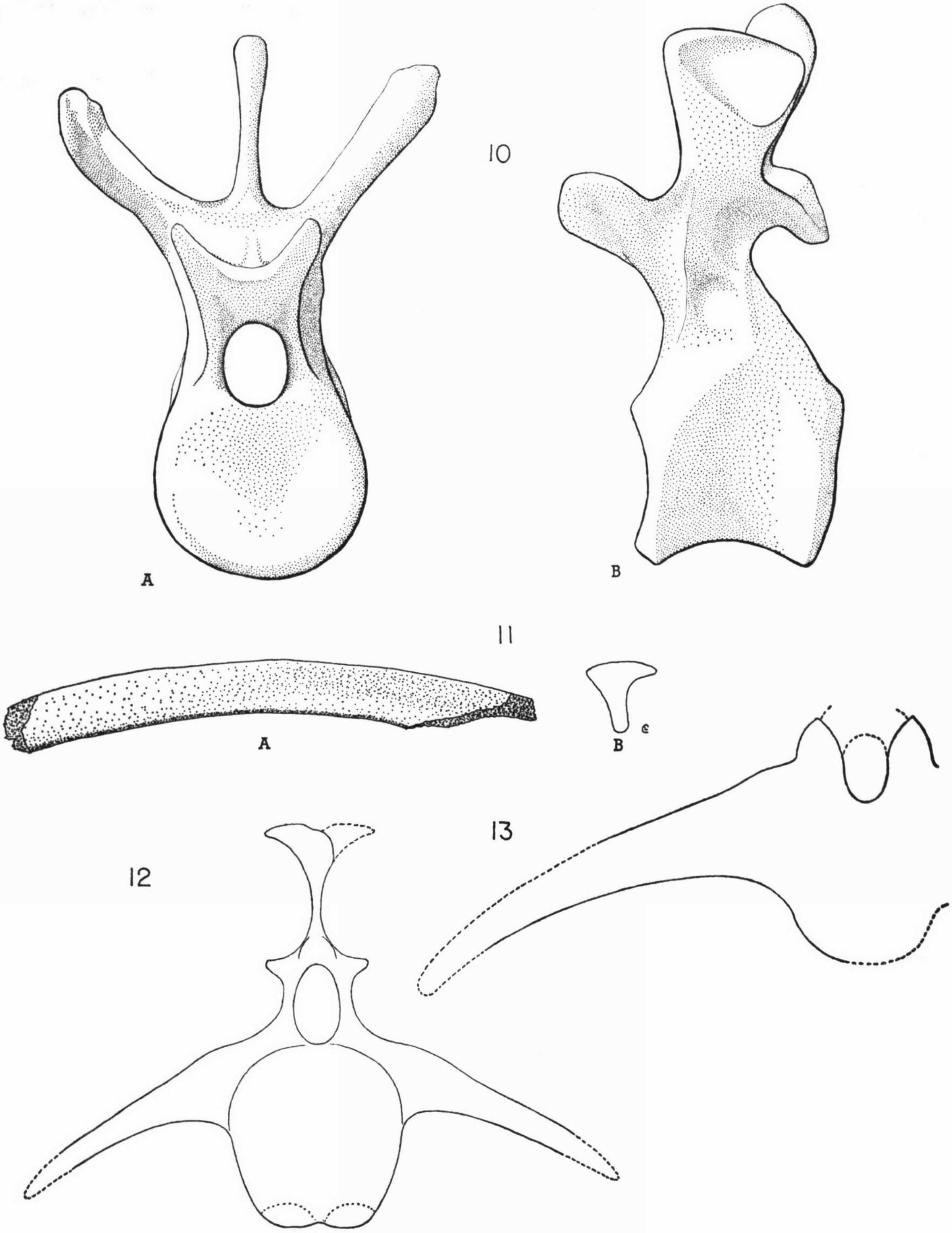
FIGURES 7-9. *Silvisaurus condrayi.*———7, Cervical vertebrae (probably nos. 4 to 8), left lateral view, ×0.5. ———8, Cervical vertebra (probably no. 5), anterior view, ×0.5.———9, Left cervical rib, anterior view (above) and posterior view (below), ×0.5.



FIGURES 10-13. *Silvisaurus condrayi.*———10, Thoracic vertebra, (A) anterior view and (B) left lateral view, ×0.5. ———11, Portion of thoracic rib, (A) anterior view and (B) cross section, ×0.5.———12, Caudal vertebra, anterior view, ×0.5.———13, Another caudal vertebra, posterior view, ×0.5.

TABLE 2. *Measurements of* Vertebrae, *in Millimeters*

	Cervical					Thoracic				
	1	2	3	4	5	1	2	3	4	5
Centrum, post. vert. diam.	?	54	56	54	55	56	?	51?	?	?
Centrum, max. horiz. diam.	70	75	76	77	75	79	80	66	?	60
Centrum, max. horiz. ant.-post. length	53	58	59	52	58	70	68?	62	65	67
Neural canal, post. horiz. diam.	22	23	22	25	26	23	21	17	15	15
Neural canal, post. vert. diam.	24	25	25	26	26	25	27	31	31	24
Neural spine, height above neural canal	44	55	59	63	71	82	83	91	90	98
Neural spine, ant.-post. width at middle	14	19	24	23	24	27	31	22	42	42
Neural spine, transv. width at middle	11	10	11	10	9	9	7	6	6	5
Total width across transv. process	145	125	130	156	158	146	124	116	116	102
Total height, mid-line	?	133	139	145	152	160	164	170	182	167?
Total width, ant.-post. length at zygapophyses	93	92	88	90	97	115	?	?	?	99
Width across prezygapophyses	99	73	77	91	86	73	65	50	?	30?
Width across postzygapophyses	68	74	76	74	64	67	?	?	31	30

Caudal Vertebra		Sacrum		Neural Canal	
Centrum, horizontal anterior-posterior length	42	Length, median(a)	375	Anterior horizontal diameter	64
Centrum, vertical diameter	52	Length, lateral	361	Anterior vertical diameter	64?
Centrum, horizontal diameter	61	Width, anterior	445	Posterior horizontal diameter	17
Neural canal, horizontal diameter	13	Width, posterior	294	Posterior vertical diameter	20

the lateroventral surfaces of the transverse processes. But there is no evidence that they became fused to the vertebrae, as in several other genera of Ankylosauria. There are also some flat, spatulate ribs, that probably were attached to the presacral rod, as in *Polacanthus.*

SACRUM

Figure 14

Six fused vertebrae with their heavy, elongate transverse processes and fused sacral ribs constitute the sacrum proper, but a presacral rod of five additional fused vertebrae extends forward. The total length of this structure medially is 645 mm., of which 370 mm. is in the sacrum itself, 205 mm. in the preserved part of the presacral rod, and 70 mm. missing between the two. The length of this gap can be measured from the impressions on the adjacent matrix, and indeed much of the evidence regarding details of this region is available from such impressions. The width of the sacrum anteriorly is 310 mm.

The diameter of the neural canal at the anterior end of the sacrum proper is about 64 mm., both vertically and horizontally, as compared with diameters ranging from 20 mm. to 31 mm. in cervical and thoracic vertebrae (Table 2). This great expansion, indicating a spindle-shaped enlargement of the spinal cord, evidently extends forward through at least three or four vertebrae of the "presacral rod," as well as posteriorly for about the same distance in the sacrum, where the cavity can be seen clearly as it tapers down to a diameter of 21 mm. posteriorly.

Anteriorly the presacral rod shows a broken surface, but this surface must be close to the actual anterior end, where the last free thoracic vertebra articulated with it, because the dorsal portions of this vertebra, separated from the presacral rod, are present above it. The neural spine and transverse processes are of the same shape as those in the other thoracic vertebrae, but larger, the height of the neural spine measuring 112 mm. above the neural canal, and the width across the transverse processes 106 mm. The neural spines and zygapophyses of some of the vertebrae incorporated in the presacral rod can be seen indistinctly and appear to fuse above the intervertebral (spinal nerve) foramina. The height of the neural spines diminishes rapidly to less than 25 mm. in the sacrum proper, although the upper surfaces there are damaged by weathering, and measurements cannot be made.

The dorsal, median part of the sacrum proper is made up of the fused, broadened pre- and post-zygapophyses and neural arches; below these are the foramina for sacral nerves. Six vertebrae apparently made contact with the ilium, by means of elongated transverse processes fused with sacral ribs. The more anterior four of these show the distinction between the process (dorsal), which is flattened for support of dermal plates, and the rib (ventral), which emerges from the level of the centrum; in cross-section the two show an hourglass form, not entirely separate from each other at any point. But it is clear that the process and rib are both present in each lateral bar of the sacrum, by comparison with MEHL's (1936, pl. 3) figure of the sacrum of *Hierosaurus coleii,* an ankylosaur in which both are present and separate from each other. The last two sacral vertebrae in *Silvisaurus* bear lateral bars in which the transverse processes and ribs are completely joined, so that it is impossible to see any distinction, except that the lower part of each bar emerges from the centrum, and the upper from the neural arch.

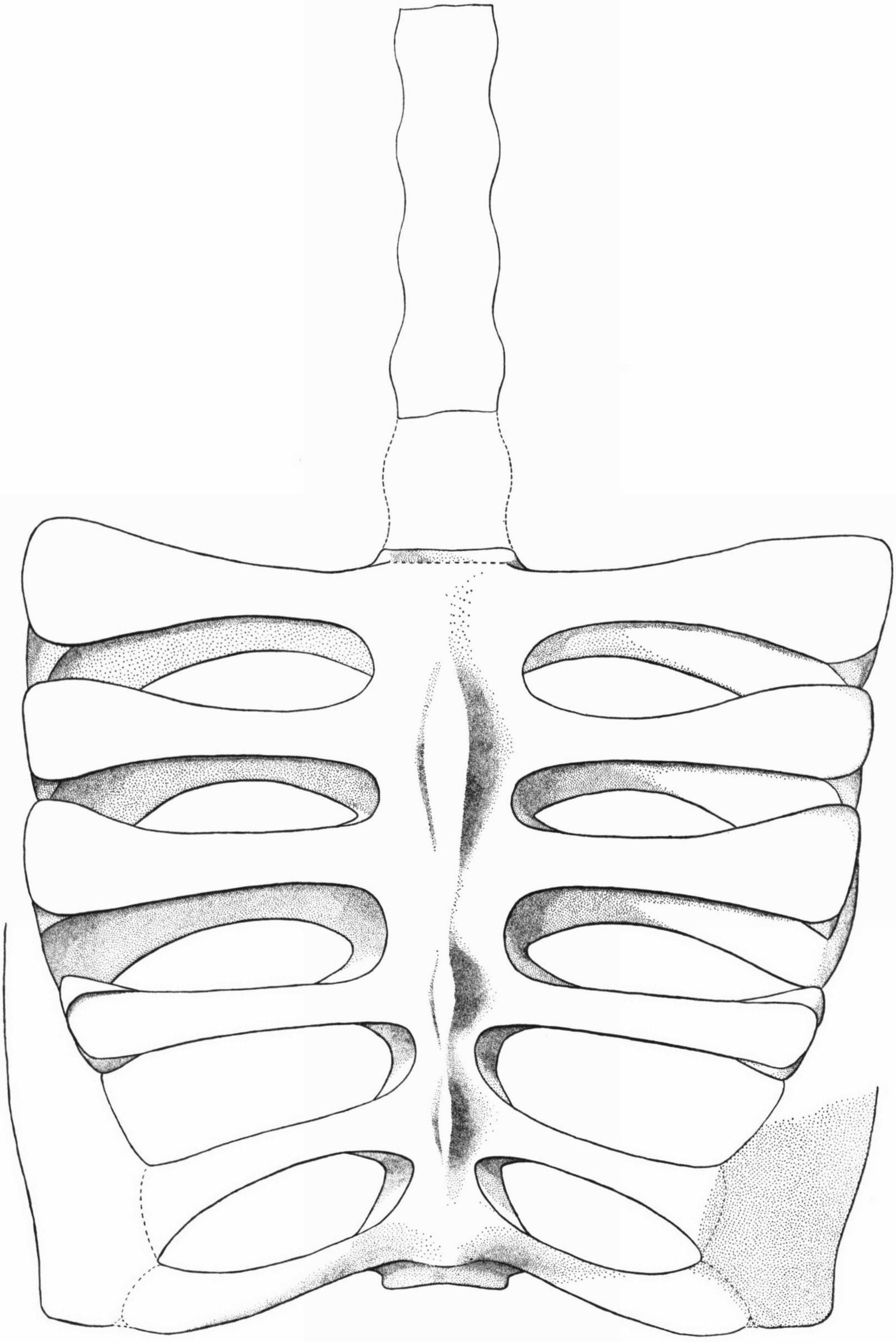
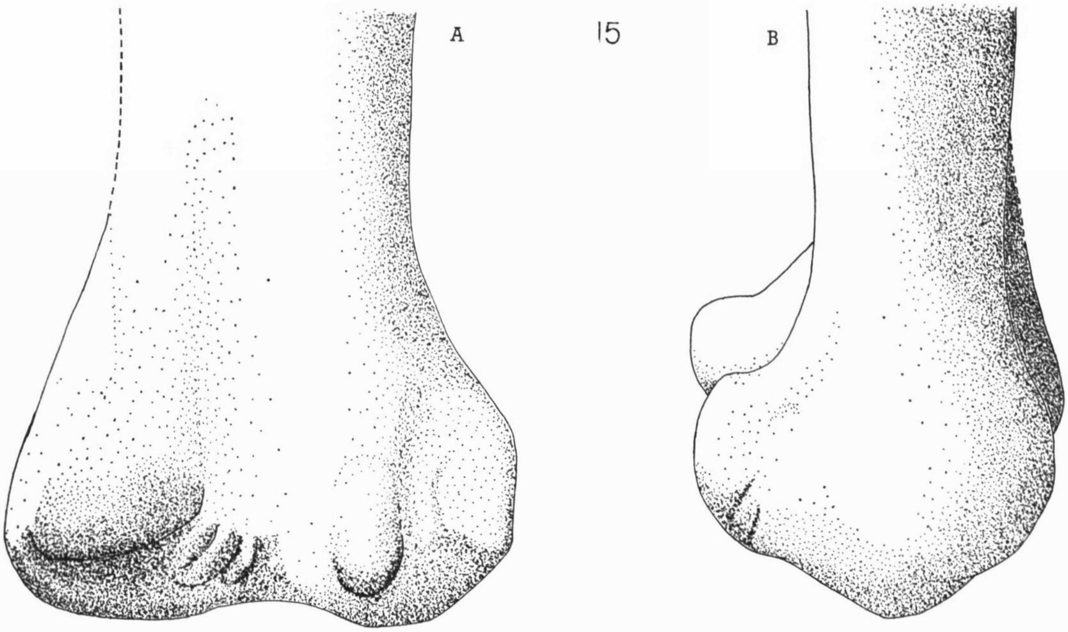


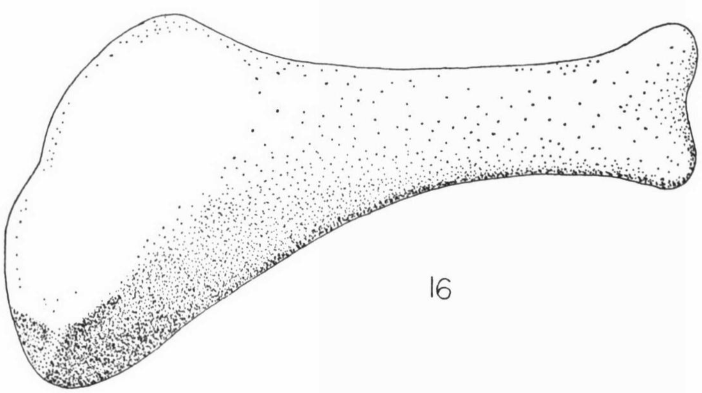
Figure 14. *Silvisaurus condrayi,* sacrum and presacral rod, dorsal view, ×0.3.

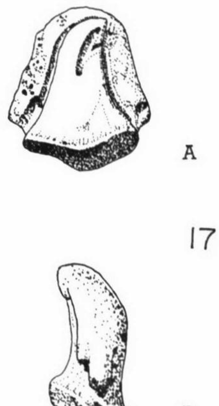
CAUDAL REGION

Figures 12, 13

The specimen contains three partial molds and two fairly complete examples of caudal vertebrae. There is no direct contact with the sacrum, and probably none of the vertebrae fits immediately behind it, but one may be the second or third of the caudal series, judging by measurements. Figure 12 shows a well-preserved caudal vertebra, perhaps midway in the tail, with fused ribs curved down and posteriorly. Other features of this vertebra are the high neural spine, expanded distally for support of a dermal plate, and two blunt prominences on the anteroventral edge of the centrum, for articulation of a chevron bone. The fusion of caudal ribs with their vertebrae is reported almost universally in reptiles (ROMER, 1956), but they are unusually massive in *Silvisaurus,* probably to serve for the insertions of muscles that swung the tail, and also for the support of dermal spikes comparable to those pictured by MATTHEW (1922) in his restoration of *Palaeoscincus*. The specimen has some dermal plates almost in place on the ends of the ribs, and a pair tilted upward on either side of the base of the neural spine, but none of these is clear enough for satisfactory illustration. In Figure 13 the ribs are even longer and heavier, but the centrum is narrower, suggesting that this vertebra was farther back but carried more prominent spikes.







FIGURES 15-17. *Silvisaurus condrayi.*———15, Right femur, distal portion, (A) lateral and (B) posterior views, ×0.5.———16, Left pubis, external view, ×0.5.———17, Terminal phalanx, (A) ventral and (B) lateral views, ×0.5.

PELVIS AND LIMBS

Figures 14-17

Most of the appendicular skeleton is missing from this specimen. The only part of the pelvis clearly connected with the rest of the skeleton is the posterior end of the ilium, shown in Figure 14. Numerous dissociated fragments and impressions in matrix can probably be referred to the ilium and ischium, but prolonged study of these has failed to show that they fit together. The only other bone of the pelvis is a presumed left pubis (Fig. 16), but the identification of this bone as a pubis entails some doubt as to determinations in published descriptions of related genera; this will be discussed below.

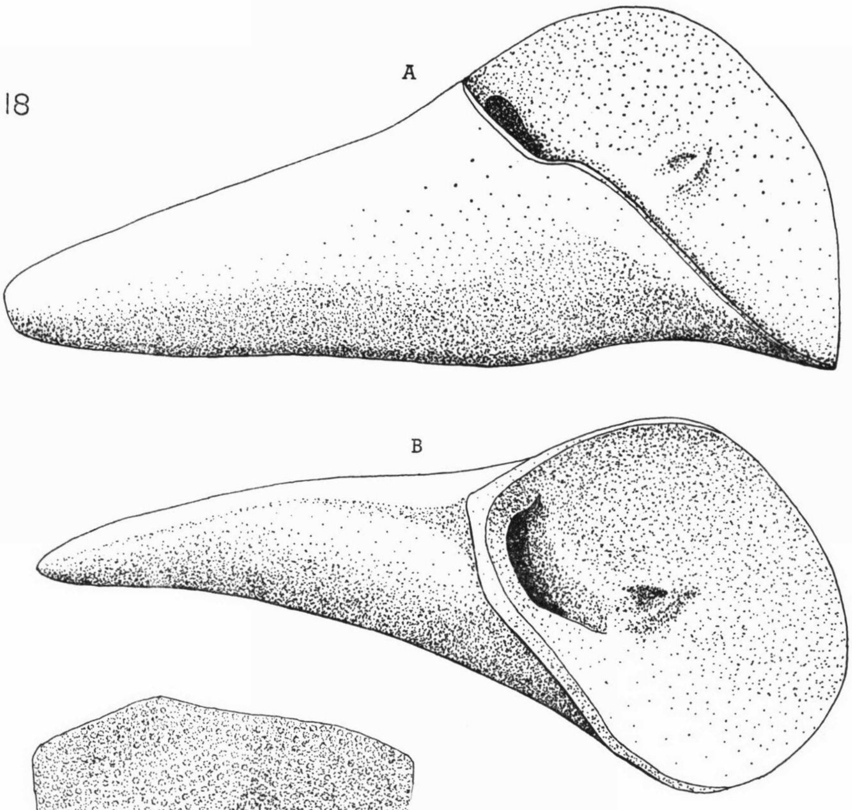
The distal end of the right femur is shown in Figure 15; its proportions suggest a total length of about 400 mm. Figure 17 shows a terminal phalanx, but it is uncertain whether this belongs to the fore foot or hind foot. There are no other limb bones.

DERMAL ARMOR

Figures 18-20

Numerous dermal plates are scattered among the other elements of the skeleton, but they show almost no meaningful association. The largest units are illustrated (Figs. 18-20). Indirect evidence concerning this armor comes from the shape of the ribs, sacrum and caudal vertebrae; the part covering the skull has been described already. The armor of *Palaeoscincus, Nodosaurus,* and *Polacanthus* has been described by others, and gives some basis for inferring the arrangement in *Silvisaurus*.

18



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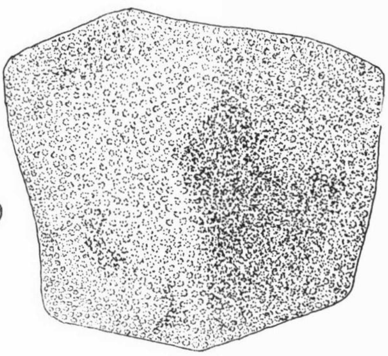

FIGURES 18, 19. *Silvisaurus condrayi.*———18, Dermal spine (probably of shoulder), (A) ventral and (B) posterior views, ×0.5.———19, Dermal plate (probably from trunk), external surface, ×0.5.

It seems that polygonal or rounded scutes lay across the trunk in transverse rows, each row supported by one pair of dorsally flattened ribs, and that between successive rows the skin either was unarmored or contained small ossicles. Undoubtedly the neural spines of most vertebrae supported median scutes, but the armor known in the specimen does not include pieces showing clear bilateral symmetry.

Over the sacrum and the presacral rod there probably lay an inflexible shield, the units of which corresponded to those more anteriorly supported by ribs. The large, irregularly crested plates (Fig. 20) may have lain in a series (not necessarily in the order in which they are drawn) along one shoulder; the strong, curved spine in Fig. 18, suggestive of those in *Palaeoscincus* and *Hoplitosaurus,* is probably a local extension of a sharp crest in the same series. On either side of the tail, the extended caudal ribs, fused with the vertebrae, probably supported successive dermal spikes or cones, but of these no direct evidence remains.

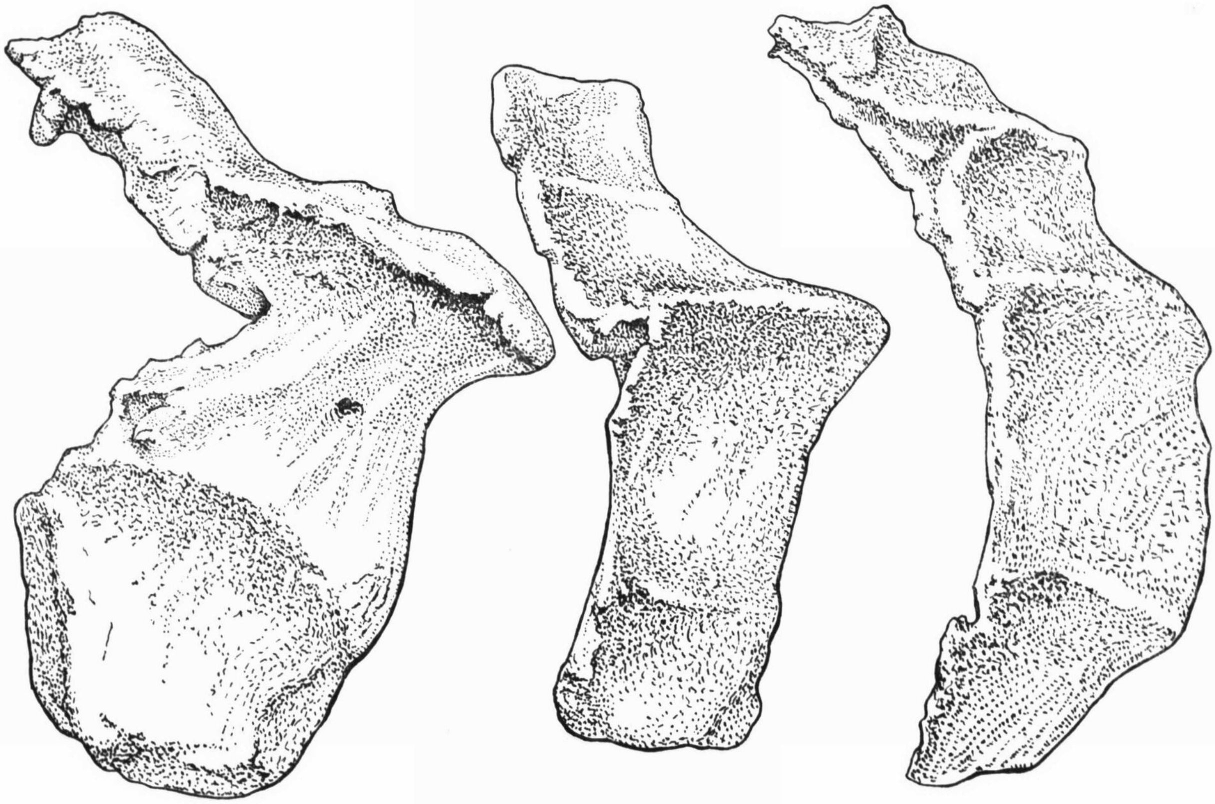

Figure 20. *Silvisaurus condrayi,* dermal plates (probably from shoulder), ×0.5.

COMPARISONS AND DISCUSSION

Nearly all papers on Ankylosauria have described new material and attempted some comparison with that already known. But the group is not yet well understood, for few of the descriptions are thorough, and many good specimens are neither described nor figured. Several genera and species are known only from small fragments. When a comprehensive study of ankylosaurs is made, their taxonomy probably will be changed greatly, but in the meantime some comments are desirable on the information obtained from the specimen of *Silvisaurus.*

Among North American Ankylosauria it is probably the oldest geologically, and the presence of premaxillary teeth, the failure of the pterygoids to fuse with the quadrates, the lack of fusion of trunk ribs with vertebrae, and the moderately long neck are probably primitive characters in the family Nodosauridae. The head shows none of the extraordinary triangular form seen in *Ankylosaurus,* in which the temporal region on either side extends as a broad horn, nor is there evidence of a ponderous club-shaped tail. Thus *Silvisaurus* may be little changed anatomically from the Old World acanthopholids (in the sense of ROMER, 1956), and such nodosaurs as *Polacanthus.*

Nevertheless many details show a similarity between *Silvisaurus* and *Edmontonia,* from the Upper Cretaceous of Montana and Alberta. The skull of *E. rugosidens* is broader and heavier than that of *Silvisaurus,* the pterygo-quadrate joint has disappeared, and the premaxillary is toothless, but otherwise the two genera are evidently closely allied. We may infer that *Silvisaurus* was, at least approximately, ancestral to *Edmontonia.*

RUSSELL (1940) figured the scapulocoracoid of *Edmontonia rugosidens* as a single, robust bone with shallow glenoid fossa and a blunt acromion. There is no reason to doubt this determination, but it is in sharp contrast with the condition in *Palaeoscincus costatus,* the mounted skeleton of which (AMNH-5665) shows the coracoid and scapula quite separate from each other, as in most dinosaurs. RUSSELL also figured a pair of wedge-shaped bones as clavicles, but so far as the present writer can discover, no clavicles have been reported in other ankylosaurs (and almost none in other dinosaurs); RUSSELL was not able to say how they articulated with the scapulocoracoid of *Edmontonia.* In the specimen of *Silvisaurus* there is one such bone, unmistakably like the supposed "clavicle" of *Edmontonia,* but it seems much more probably a pubis. The narrow end in our specimen has two separate roughened swellings with a smooth gap between; these would hardly be understandable in a clavicle, but at the posterior (proximal) end of the pubis it is suggested that either (1) the smaller rough process was for articulation with the ilium and the larger, below, for the ischium, or (2) the smaller was for the ischium only, while the more ventral prominence bore a vestige of the postpubic process, supposedly missing in ankylosaurs. The latter is thought to be the more likely alternative. The bone is similar to the pubis of some other Ornithischia if the postpubic process of the latter were removed. ROMER (1927) suggested that the pubis in *Ankylosaurus* is fused with the ischium, but a good ischium, presumably of this genus, in the American Museum (AMNH5403) shows two prominent articular processes anteriorly, the upper of which must have met a preacetabular part of the ilium, while the lower evidently received the posterior end of the loosely articulated pubis. GILMORE's (1930) figure of a pubis of *Edmontonia* shows a small bone with a large, lateral, arched process labelled by him "postpubic process"; if the argument above is correct, GILMORE's bone can hardly be a pubis.

A pair of deep palatal clefts separated by a narrow median partition can be seen in the skulls of *Edmontonia, Silvisaurus, Ankylosaurus* and *Palaeoscincus costatus* (mounted in the American Museum of Natural History) and is probably a characteristic of Ankylosauria in general. Teeth with serrate crowns, in both maxillary and premaxillary, may be a primitive feature of the group, and so may the expanded sacral canal, and the rows of dermal ossicles, supported in part by the axial skeleton. All these, however, are also features of the suborder Stegosauria, in its more generalized members, such as *Scelidosaurus* and *Kentrosaurus.* The skull of *Stegosaurus* shows similar deep, palatal clefts, although this animal is certainly a specialized member of the suborder. The braincase and endocranial cavity of *Silvisaurus* appear to be closely similar to those of *Stegosaurus.* For these reasons the writer regards the Ankylosauria and Stegosauria as probably directly and rather closely

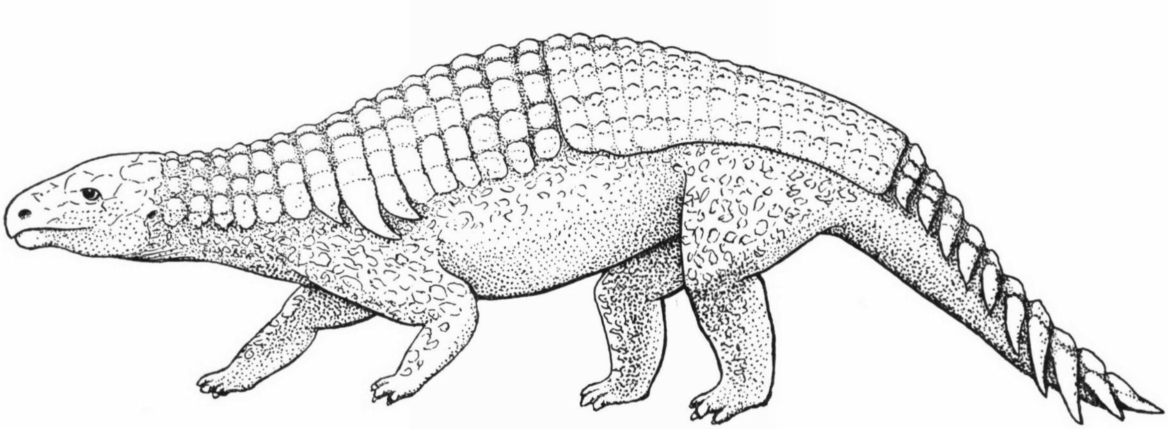

FIGURE 21. *Silvisaurus condrayi,* probable appearance in life, ×0.04.

related to each other, both derived from a common early Jurassic ancestor that was already armored and quadrupedal. Specialization within the Ankylosauria then consisted of a broadening of the body, increased dermal armor laterally on the trunk and tail, subsequent development of a sacral "carapace," and fusion of trunk ribs with vertebrae. Stegosauria, however, became dorsally arched, the head remaining small and low, while armor became specialized dorsally rather than laterally. Premaxillary teeth persisted in some Ankylosauria, but were lost (1) in Stegosauria and (2) in advanced ankylosaurs, independently. The postpubic process, on the other hand, persisted in Stegosauria but not in Ankylosauria, perhaps because the latter came to resemble armored tanks, not much elevated from the ground.

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