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NELDASAURUS WRIGHTAE,
A NEW RHACHITOMOUS LABYRINTHODONT
FROM THE TEXAS LOWER PERMIAN

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WITH FIVE PLATES

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Labyrinthodont from the Texas Lower Permian*¹

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¹ This paper is part of a thesis submitted to the Department of Biology of Harvard University as partial fulfillment of the requirements for the degree of Doctor of Philosophy, August, 1962.

INTRODUCTION

Since their discovery in 1875, the Lower Permian redbeds of north central Texas have been an important source of fossil vertebrates. Until recent decades, however, the fauna of this region (mainly described by Cope, Case, and Williston) was derived from a very limited series of horizons, which include the upper portions of the Wichita Group and the lowest part of the overlying Clear Fork. Collections made in the uppermost beds of the Clear Fork by Olson (1948, 1951 a-c, 1955) and in the Lower Wichita formations by Romer and associates (Romer, 1935, 1947, 1958) have extended our knowledge and given us some concept of the faunal assemblages that preceded and followed those of the typical Lower Permian faunas. This paper is concerned with certain amphibian remains recovered from the lower levels of the Wichita.

A number of expeditions from the Museum of Comparative Zoology at Harvard College have been made to the Texas redbeds from 1934 onward. In most cases these had the special objective of obtaining remains from the lower horizons of the Wichita Group—the Putnam, Moran and Pueblo formations in descending order. The finds have included numerous identifiable amphibian specimens (mainly from the Putnam and Moran) which, for the most part, pertain to genera already well known from the higher, “classic,” Wichita formations, the Admiral and the Belle Plains. These include such forms as *Trimerorhachis*, *Eryops*, *Broiliellus*, *Tersomius*, *Parioxys* and *Acheloma*. However, the lower formations showed indication of a somewhat different and more primitive faunal assemblage, particularly in the occurrence of the primitive rhachitome, *Edops* (Romer and Witter, 1942).

A further indication of the faunal difference between the upper, typical, Wichita and the lower Wichita formations was the recovery in the earlier trips to these lower beds of remains of an obviously new rhachitome too fragmentary to permit adequate description. Vertebral and limb materials showed some similarity to *Trimerorhachis*, a form not identified with certainty below the Putnam (Olson, 1955), but such skull remains as were recovered indicated a narrow, attenuated snout quite different from that of *Trimerorhachis*.

A collecting trip from the Museum of Comparative Zoology in 1954 under the direction of Dr. Alfred S. Romer resulted in the

recovery of a nearly complete skull of this problematical form, with attached lower jaws and some postcranial material in a common block. The certain association of the skull with postcranial materials made possible for the first time a comprehensive description of this new form and the assignment of the specimens in previous collections to a new genus.

The fossil material described in this paper is assigned to a new genus and species of rhachitomous labyrinthodont for which I propose the name *Neldasaurus wrightae*. Both generic and specific designations are in honor of Miss Nelda E. Wright, Research Assistant and Editor of Publications of the Museum of Comparative Zoology, who discovered the holotype specimen.

ACKNOWLEDGEMENTS

My appreciation is due to several persons whose aid I received during the course of this study. I should like first to express my sincere thanks to Dr. Alfred S. Romer, under whose inspiring direction this work was undertaken and whose continued interest and advice have been of invaluable assistance. I am indebted to Dr. Donald Baird of Princeton for many helpful suggestions and permission to use his information on the Linton fauna; to Dr. Nicholas Hotton III of the United States National Museum for information on *Acropylous vorax*; to Dr. Edwin H. Colbert of the American Museum of Natural History for access to specimens of *Trimerorhachis*; to Dr. Craig C. Black of the Carnegie Museum for the loan of specimens; to Dr. Robert Carroll then at the Museum of Comparative Zoology for information pertaining to early edopsoids; to Dr. Carl Gans of the University of Buffalo and Mr. Frank White of the Biological Laboratories at Harvard for assistance in taking photographs of the specimens. Thanks are also due to Mr. Arnold Lewis of the Museum of Comparative Zoology at Harvard, who gave freely of his time and knowledge in introducing me to the techniques of fossil preparation. Thanks are due also to Dr. Ernest E. Williams and Professor Bryan Patterson of the Museum of Comparative Zoology for critical reading of the manuscript. I am indebted to Miss Nelda Wright for many valuable suggestions during the preparation of this paper.

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SYSTEMATIC DESCRIPTION¹

Class AMPHIBIA
Order TEMNOSPONDYLI
Suborder RHACHITOMI
Superfamily TRIMERORHACHOIDEA
Family TRIMERORHACHIDAE
NELDASAURUS, gen. n.

Type species. *Neldasaurus wrightae* sp.n.

Generic Diagnosis. — A low-skulled labyrinthodont amphibian which closely resembles *Trimerorhachis* in size, many skull proportions, body and limbs, dermal roof pattern, and palate. *Neldasaurus* differs from *Trimerorhachis* in the following respects: orbits midway between snout and occiput; snout narrow; lacrimal elongate but not reaching the external naris; nasals, prefrontals and frontals elongate; external nares close together, their long axes more or less parallel; jugal entering the orbital border; prevomers elongate and the choanae broadly separated from the anterior border of the interpterygoid vacuities; larger number of teeth than in *Trimerorhachis* in the lower jaw and the marginal series of the upper jaw; a tusk pair on the ectopterygoid; a foramen in the lower jaw for the reception of vomerine tusks; opisthotic and prootic unossified; pleurocentra as high as the intercentra; clavicles meeting in front of the interclavicle.

NELDASAURUS WRIGHTAE sp. n.

Holotype. — MCZ 2200, including a nearly complete skull and attached lower jaws, central and neural arch vertebral elements, a partial pectoral girdle, limb bones and remnants of dermal armor.

Type Locality and Horizon. — Terrapin School, Section A-1266, BBB + CRR Survey, Archer County, Texas; Moran Formation, Wichita Group, Permian. Collected by A. S. Romer party, 1954.

Diagnosis. — As for genus.

Referred Specimens. — MCZ Nos. 1371, 1381, 1438, 1463, 2404, 2406, 2407, 2516, 2518, 2519.

¹ The classification used here follows Romer (1947).

DESCRIPTIVE LIST OF MATERIALS

The material consists of the holotype and the following specimens, all from the Wichita Group of the Texas Lower Permian.

MCZ 1371. A partial skull and left lower jaw, dorsal vertebrae — some in articulated series, ribs, a partial clavicle and interclavicle, a nearly complete forelimb, dermal scales and armor. There is also what appears to be a pelycosaur foot bone. Putnam Formation, Table Branch, South Fork of the Little Wichita River, G. W. Stell Survey, Section A-382, 10 miles west of Anarene in Archer County. Collected by R. V. Witter party, 1936.

MCZ 1381. Fragmentary remains of several small individuals. Same data as for MCZ 1371.

MCZ 1438. Poorly preserved remains of skulls and postcranial materials of at least two individuals of little use for purposes of description. Putnam Formation, 1 mile west of Archer City in the Archer City bone bed, Section 151, American Tribune New Colony Subdivision, southwest part Archer County. Collected by R. V. Witter party, 1936.

MCZ 1463. Fragmentary cranial and postcranial materials in a limey nodule. Section 16, Falls County School Land, Archer County, about 7 miles southwest of Anarene. Collected by R. V. Witter party, 1936. The formation is either Putnam or Moran.

MCZ 2404. Fragmentary portions of lower jaw and postcranial materials. Moran formation at Terrapin School, BBB + CRR Survey, A-1266 in southern Archer County. Collected by A. S. Romer party, 1950.

MCZ 2406. A large number of discrete skull and postcranial materials, mostly fragmentary, including the proximal ends of a humerus and a femur. There is also a *Trimerorhachis*-like intercentrum, a complete ring central element and scraps of a larger labyrinthodont. Moran Formation near Padgett in the northeast part of William Tryndale Survey, Young County. Collected by A. S. Romer, 1942.

MCZ 2407. Fragmentary vertebral materials, the distal ends of a radius and a femur and portions of a pterygoid. Collection site as for MCZ 2406. Collected by R. V. Witter, 1942.

MCZ 2516. Separate and disarticulated elements, mostly incomplete; including parts of a lower jaw, a right femur, an ilium, and vertebrae. Moran Formation, $\frac{3}{4}$ mile north and 1 mile west of Padgett Schoolhouse, Young County. Collected by R. V. Witter party, 1936.

MCZ 2518. Fragmentary skull and jaw materials, numerous partial vertebral elements, ribs, pectoral plates and two ilia, probably all pertaining to one individual. Moran Formation in Padgett, the northwest part of the William Tryndale Survey, MCZ Field No. 9, Young County. Collected by A. S. Romer, 1951.

MCZ 2519. A partial intercentrum. Moran Formation west of Cottonwood Creek, about Section 48, County School Land, Archer County. Collected by A. S. Romer, 1954.

ANATOMICAL DESCRIPTION OF GENUS AND SPECIES

GENERAL SKULL MORPHOLOGY

Of the three principal skull specimens, the holotype, MCZ 2200 (Pls. 1 and 2), is the most complete. The figures and description are primarily based on this specimen, but supplementary information was obtained from MCZ 1371 (Pl. 3), MCZ 1438 (Pl. 4), and also the fragments included in MCZ 2518. The holotype skull is described first.

The dermal roof, although fairly complete, is displaced to the left in relation to the palate and has been subjected to post-mortem crushing so that the skull appears to have retained its original depth only in the right suborbital region. Horizontal pressures have caused some overlapping of the medial boundaries of the central dermal bones.

Intrusion of the articular portions of the lower jaws from below partially obscures the relationships of the quadrate region. The anterior extremity of the snout is incomplete in all of the specimens, but the portions that remain permit a reasonable restoration. The right lower jaw of the holotype has retained a fairly normal position throughout much of its length so that most of the lateral skull margin is visible. However, the posterior quarter of the ventrolateral border of the skull roof has been damaged and details of structure are hard to trace.

Post-mortem flattening of the skull and damage to the skull margins introduce some uncertainty in the determination of cranial dimensions. However, the figures obtained from the reconstructed skull roof, the palate and the lower jaw, give the general dimensions, as set forth in Table 1, with a fair degree of accuracy. Determination of the depth of the skull was based primarily on the transverse dimensions of the palate and the resultant restoration of the skull roof to fit these dimensions.

The skull (Figs. 1, 2, 3 and 5) is of moderate size. The snout is narrow but bluntly rounded anteriorly, the skull increasing in breadth toward the back, having its greatest width in the occipital region. Allowing for a slight backward projection of the condyle from the occipital border, the suspensorium is about 1.5 cm behind the level of the condyle. However, the otic notch is not as highly developed as in *Trimerorhachis*, and the contour of the central posterior rim of the skull table is less concave than it is in that animal.

The occiput slopes downward and backward at an angle of approximately 23° from the vertical in the preserved skull. But, though some degree of slope may be normal, the occiput may have been more nearly vertical in life.

The depth of the skull midway between the orbits and the end of the snout is approximately 13 mm, and the height of the cheek below the orbit is 14 mm. The height of the occiput is about 39 mm. Thus, the depth of the skull increases from front to back, the increase being considerably more pronounced in the postorbital region, the snout being generally flattened.

Determination of the original skull roof topography is difficult because of post-mortem distortion. The evidence seems to indicate a more or less flat or slightly concave surface in the central region of the skull table bounded by a low ridge on each side which runs from the tabular to the outer posterior corner of the orbit. The outer face of the ridge slopes gently downward, becoming confluent with the cheek, and the inner face dips down to the central region of the skull table.

The mid-orbit to snout length is approximately 49.3 per cent of the midline skull length. The dorsally directed orbits are oval in shape and somewhat smaller in relation to overall skull size than those of *Trimerorhachis*¹, though, as in *Trimerorhachis*, the interorbital space is narrow. The inner border of the orbit is slightly elevated above the surface of the skull roof, the smooth, medial margin having a depth of 3 mm. The rest of the margin, which shows no appreciable elevation, is not as thick.

A small parietal foramen is present in the midline between the parietals, 2.9 cm behind the posterior orbital border. The distance from the orbit to the parietal foramen is equal to 38 per cent of the skull table length, a shorter distance than that seen in *Trimerorhachis*, where the comparable figure is 50 per cent.

¹ This comparison is based on the ratio of skull width \times skull length/orbit width \times orbit length.

In agreement with the dimensions of the rostrum, the external nares are not as widely separated as they are in other trimororhachoids. The medial margin of the naris is slightly elevated above the surface of the internarial region, and the opening is somewhat constricted in its posterior third. The lateral border of the naris is separated from the skull margin by a dorsal exposure of the premaxilla and the maxilla of approximately 5.5 mm.

Skull MCZ 1371 (Pl. 3) exhibits overall dimensions that are closely comparable to those of the holotype, and the dimensions given in Table 1 can be accepted with a fair degree of certainty. Extreme flattening makes the determination of skull height difficult, but it appears to agree closely with that of MCZ 2200.

The preserved portions of skull MCZ 1438 (Pl. 4) appear to represent a somewhat larger animal than the preceding forms. Overall length cannot be determined, but the dimensions of the preorbital region suggest proportions similar to those of MCZ 2200 and 1371.

The dermal roof bones of MCZ 2518 are disarticulated and incomplete so that comparison of general dimensions of this specimen and the others is impossible.

TABLE I

Measurements (in mm) of Dermal Skull Roof

| | MCZ No. | MCZ No. | MCZ No. |
|-----------------------------|------------|------------|------------|
| <i>Length</i> | 2200 | 1371 | 1438 |
| Snout to end of skull table | 158 | — | — |
| Snout to quadrate | 173 | 174 | — |
| Snout to mid-orbit | 78 | 80 | 86 |
| Orbit | 20 | 20 (est.) | — |
| External naris | 13 | — | 14 |
| <i>Width</i> | | | |
| Snout behind naris | 40 | 42 | 46 |
| Orbital region | 70 | 74 | — |
| Quadrate level | 120 | — | — |
| Orbit | 16 | 15 (est.) | — |
| External naris | 8 | — | 8 |
| Internarial | 10 | — | 12 |
| <i>Height</i> | | | |
| Mid-rostral | 13 | — | 13 (est.) |
| Suborbital | 14 | 14 (est.) | 15 (est.) |
| Occiput | 39 | — | — |

BONES OF THE DERMAL SKULL ROOF

(Figures 1 and 2)

Some sutures on one or another of the skull specimens, MCZ 2200, 1371, 1438, 2418, were readily traced, but the location of others, which were not recognizable per se, was based on the sculpture patterns of individual bones. Centers of ossification were determined by considering their relationship to the sensory canal system, which is typically associated with the center of growth in each bone (Bystrow, 1935; Westoll, 1943; Parrington, 1949). I believe that the general pattern of the skull roof of MCZ 2200, as figured, is reasonably accurate.

The dermal roof pattern closely resembles that of *Trimerorhachis*. Differences in the shape of individual bones in the two animals are obviously due in large measure to the differences in skull proportions mentioned above.

The dermal bones of the skull roof are treated here as comprising four groups: (1) the paired elements of the dorsal midline, (2) the circumorbital bones, (3) the bones of the temporal region that form the lateral margin of the skull table, and (4) the marginal tooth-bearing bones and the cheek bones.

(1) The nasals are long, roughly rectangular bones which extend more than half the distance from the naris to the orbit, their shape sharply contrasted to the squarish nasals in *Trimerorhachis*.

The elongate frontals, with over half their length extending into the preorbital region are also in contrast to conditions in *Trimerorhachis*, in which form the nasals make a much greater contribution to the midfacial area than do the frontals.

The parietals form most of the central portion of the skull table, extending from the posterior border of the frontals to the postparietal suture. A parietal opening of modest size is located centrally between them.

The roughly pentagonal postparietals are relatively small bones. Posteriorly, they turn down over the rim of the skull table in an occipital exposure. A stout occipital flange of the postparietal, which rests on a dorsal extension of the exoccipital, bounds the supraoccipital region laterally and forms the medial rim of the posttemporal fenestra (Fig. 5). The tabular does not appear to take part in the formation of the descending flange.

(2) The circumorbital series, including the prefrontal, postfrontal, postorbital, jugal, and lacrimal, is complete.

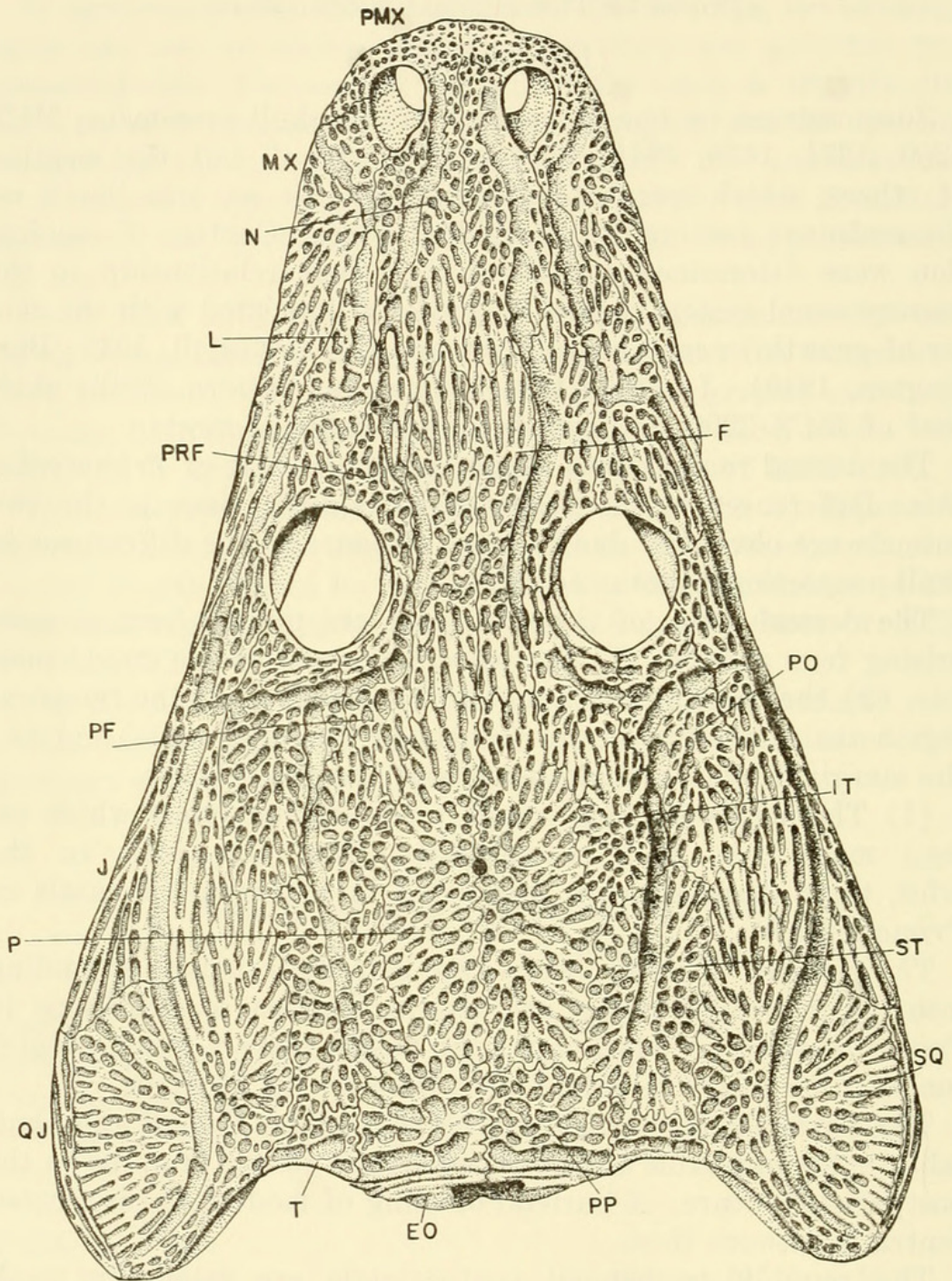


FIG. 1. Dorsal view of skull roof of *Neldasaurus wrightae*, n. gen., n. sp., restored, $\times .75$. Portions of the sensory canal grooves and some sutures on the right have been restored to agree with conditions on the left. Abbreviations: EO, exoccipital; F, frontal; IT, intertemporal; J, jugal; L, lacrimal; MX, maxilla; N, nasal; P, parietal; PF, postfrontal; PMX, premaxilla; PO, postorbital; PP, postparietal; PRF, prefrontal; QJ, quadratejugal; SQ, squamosal; ST, supratemporal; T, tabular.

The prefrontal is a narrow bone which forms the anteromedial margin of the orbit, ending halfway back on the medial rim.

The postfrontal is narrow anteriorly where it joins the prefrontal to complete the medial rim of the orbit. Behind the orbit it becomes somewhat wider.

The jugal is a large bone approximately 7 cm long, and the longest skull roof bone, aside from the maxilla. Unfortunately, the suborbital region in all of the specimens is poorly preserved or damaged, but a break in the surface contour of the right cheek below the orbit in MCZ 2200 and the pattern of the sculpture in this area suggest that there was a lacrimal-jugal suture about halfway back on the lateral rim of the orbit. If this interpretation is correct, the jugal forms at least a small part of the orbital border.

The postorbital forms most of the posterior orbital rim, meeting the jugal laterally on the outer margin of the orbit, though the exact position of the suture is not known.

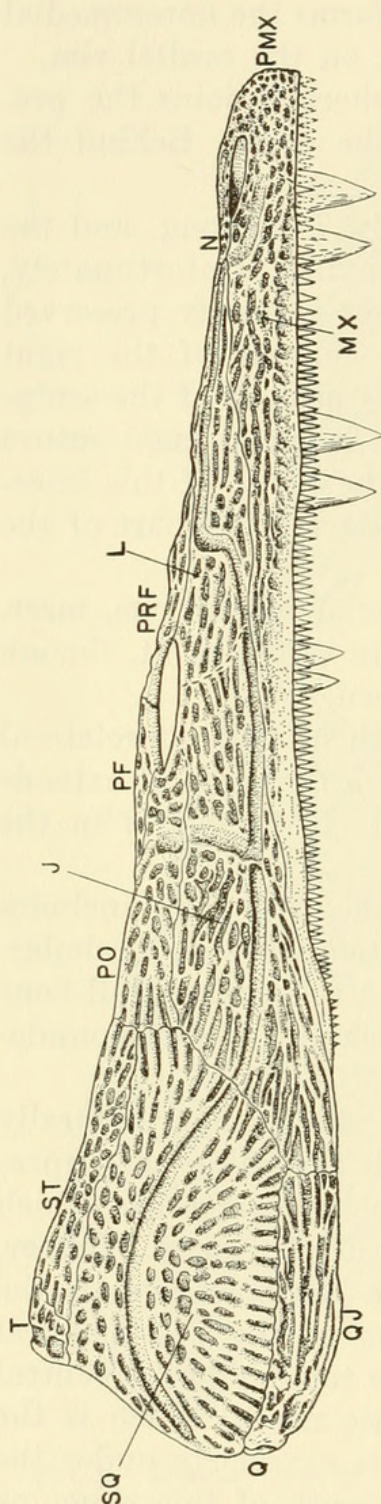
The lacrimal is elongate. It forms much of the anterolateral rim of the orbit and, though it fails to reach the naris, it extends four-fifths of the distance from the orbit to the naris in the holotype skull.

(3) Primitively, the lateral margin of the skull table includes an intertemporal bone as well as supratemporal and tabular. The posterior limits of the intertemporal, a relatively small bone here, were difficult to trace but the anterior and medial boundaries were well defined on MCZ 2200 and MCZ 2518.

The tabular is the smallest bone in the skull table. Laterally it has a short contact with the squamosal, excluding the supratemporal from the margin of the otic notch, a feature which tends to accompany modest development of the latter (Romer, 1947, p. 24). Medially, where it meets the postparietal, the tabular forms most of the dorsal margin of the posttemporal fossa. Midway in its posterior border the tabular has a ventral projection, near the inner edge of the otic notch, which is the posterior end of a low ridge that continues anteriorly under the skull roof for a distance of 7 mm. The depth of this ridge, or flange, is approximately 3 mm.¹

Immediately anterior to its posterior border the ventral surface of the tabular is excavated so that a depression is formed,

¹ Case (1935) mentions a "low rugose line" running forward and inward on the under surface of the tabular from the inner edge of the otic notch in his *Trimero-rhachis* specimen 16002, which may be comparable to the structure described here.



bounded medially by the "flange" described above and posteriorly by the posterior rim of the tabular. Laterally this fossa, which is about 9 mm wide, is bounded by a ventrally-directed process from the posteromedial edge of the squamosal. Little of the underside of the skull roof of this region can be seen and its precise character, partially visible only in the holotype, is difficult to interpret because of its imperfect condition.

(4) The boundaries of the marginal tooth-bearing bones, the premaxilla and maxilla, were hard to find in the rostral region. Their outlines as finally determined are a composite of the patterns that could be seen on parts of four specimens, MCZ 2200, 1371, 1438, and 2518. The premaxilla, seen best in MCZ 1438, apparently had a small dorsal exposure anteriorly, separating the anterior rim of the external naris from the rostral border by a distance of approximately 3 mm. The union of the premaxilla with the nasal posteriorly appears to have been close to the anterior narial rim on the medial side. Medially, the premaxilla joins its fellow of the opposite side, and posteriorly, lateral to the naris, it joins the maxilla near the middle of the lateral rim of the naris.

FIG. 2. Skull of *Neldasaurus wrightae*, in lateral aspect. Restored, $\times .75$. Abbreviation: Q, quadrate. Other abbreviations as in Figure 1.

The maxilla extends along the lateral margin of the skull for about two-thirds of the skull length, its dorsal exposure dwindling rapidly towards the rear. Posteriorly, it comes close to the quadratojugal. Conditions here are uncertain, but the jugal appears to enter the skull margin for a short distance between the maxilla and quadratojugal.

The postorbital cheek region is formed in typical fashion by the squamosal and quadratojugal. Posteriorly the squamosal has a contact with the anterior portion of the quadrate and forms part of the outer margin of the otic notch. On the inner posterior margin of the cheek it has a ventral and anteriorly directed process, about 6 mm deep, which joins the quadrate ramus of the pterygoid on its lateral edge.

The quadratojugal forms the posterolateral margin of the skull below the squamosal. Conditions in the left quadrate region of MCZ 2200, as near as can be determined, are like those in MCZ 1371, where it is better preserved. The posterior edge of the quadratojugal, forming a shallow, concave rim, is separated from the lateral margin by a sharp angle. The inner posterior end of the bone forms a medial projection posterior to the sutural surface for the squamosal. The posterior rim of this medial process probably formed part of the border of the quadrate foramen. The sutural face on the quadratojugal for articulation with the squamosal, therefore, does not reach the anterior edge of the foramen, and the squamosal does not reach its border. The remainder of the border of the quadrate foramen was apparently formed by the quadrate. Conditions here appear to be comparable to those seen in *Trimerorhachis* (Case, 1935, fig. 4; Williston, 1915, fig. 3).

The pattern of the dermal roof bones of MCZ 1371 (Pl. 3) appears to be identical to that of the holotype. This specimen offers further evidence of the relations of the lacrimal, which is here prevented from reaching the posterior narial border by a union of the maxilla and the nasal. Also, although the situation is not entirely clear, the lacrimal appears to have a stout union with the jugal below the orbit so that the jugal forms more than half of the lateral orbital border.

The skull roof of MCZ 1438 (Pl. 4) is incomplete, but it appears to follow the general pattern seen in MCZ 2200 and 1371. In contrast to its form in the other skulls, the lacrimal here reaches to, or nearly to, the external naris. The only other apparent difference is in the slightly larger dimensions of the

individual bones, which agree with the general proportions of the skull.

As stated earlier, the skull roof of MCZ 2518 consists of a number of isolated fragments. In so far as it can be traced, the dermal roof pattern is like that of the holotype.

The sculpture of the dermal roof bones consists of ridges and pits, or grooves, radiating from a center of ossification in each bone. Notable differences between the sculpture pattern in *Neldasaurus* and *Trimerorhachis* are obviously correlated with differences in the shape of individual bones in the two animals. As any figure shows (Bystrow, 1938, fig. 11), there is no linear sculpture in *Trimerorhachis*, whereas in *Neldasaurus* there is a suggestion of linear sculpture on adjacent regions of the frontals and nasals and on the frontals and parietals. The sculpture also tends to become linear in portions of other long bones in *Neldasaurus* such as the lacrimal and jugal.

THE SENSORY CANAL SYSTEM

The channels of a sensory canal system are well defined on the surface of the dermal roof bones in *Neldasaurus* (Figs. 1 and 2). In all the specimens the pattern of these channels is remarkably constant, and, except for the anterior rostral portions of the supraorbital and infraorbital channels, the pattern is clear.

The pattern of the sensory canal system generally resembles that of *Trimerorhachis* (Case, 1935, fig. 5 A) but differs in some particulars. In *Neldasaurus* the supraorbital groove crosses the postfrontal, prefrontal, and nasal but does not enter the lacrimal as in *Trimerorhachis*. The anterior portion of the infraorbital groove in *Neldasaurus* runs from the jugal along the suture between the maxilla and lacrimal, then continues for some distance on the lacrimal. The anterior portion of the infraorbital groove in *Trimerorhachis* is confined to the maxilla except for a short loop onto the lacrimal.

The position of the temporal groove in *Neldasaurus* is essentially as in *Trimerorhachis*, though it is slightly more medial in *Neldasaurus*. A jugal sulcus of the sensory canal system, separated by a short gap from the infraorbital groove on the jugal, crosses the jugal-squamosal suture near its midpoint and has the shape of a medially convex curve on the central region of the squamosal, swinging laterally near the posterior margin

to end at the posterolateral corner of the bone. It does not appear to have passed across the quadratojugal, but over the posterior border of the squamosal, just behind the end of the quadratojugal, to its connection with the lower jaw system. This groove is unknown in *Trimerorhachis*.

The courses traced by the sensory canal grooves of MCZ 1371, 1438 and 2518, where they can be seen, are the same as those on the holotype.

PALATE AND PALATOQUADRATE

(Figure 3 and Plate 2)

In all of the skull specimens the lower jaws lay in more or less normal closed position against the ventral surface of the skull, thus obscuring the lateral palatal surface. Fortunately, it was possible to expose this region by removing the right lower jaw ramus and 2.5 cm of the anterior end of the left jaw ramus from the ventral surface of the holotype skull. The description and reconstruction of the palate and the ventral skull surface, as shown in Figure 3, were mainly based on this specimen. Restored portions are hatched in the figure.

The general form and proportions of the central and posterior portions of the palate in *Neldasaurus*, including the presence of large interpterygoid vacuities, resemble conditions in *Trimororhachis*. However, the region of the palate in front of the interpterygoid vacuities in *Neldasaurus*, reflecting the proportions of the elongate snout, is more extensive.

The anterior end of the palate is incomplete, but the evidence suggests that the premaxilla had a moderate palatal exposure. The ventral exposure of the maxilla, throughout most of its length, represents little more than the width of the tooth row.

The maxilla accounts for nearly two-thirds of the lateral margin; its posterior end briefly enters the anterior portion of the lateral rim of the subtemporal fossa. The jugal apparently enters for a short distance into the ventral margin of the skull posterior to the maxilla, but most of the lateral border of the fossa is formed by the quadratojugal.

Determination of the extent of the palatal exposure of the maxilla adjacent to the internal naris was difficult, and some uncertainty exists. Since the palatine appears to form most if not all of the lateral border of the choana, the maxilla could enter

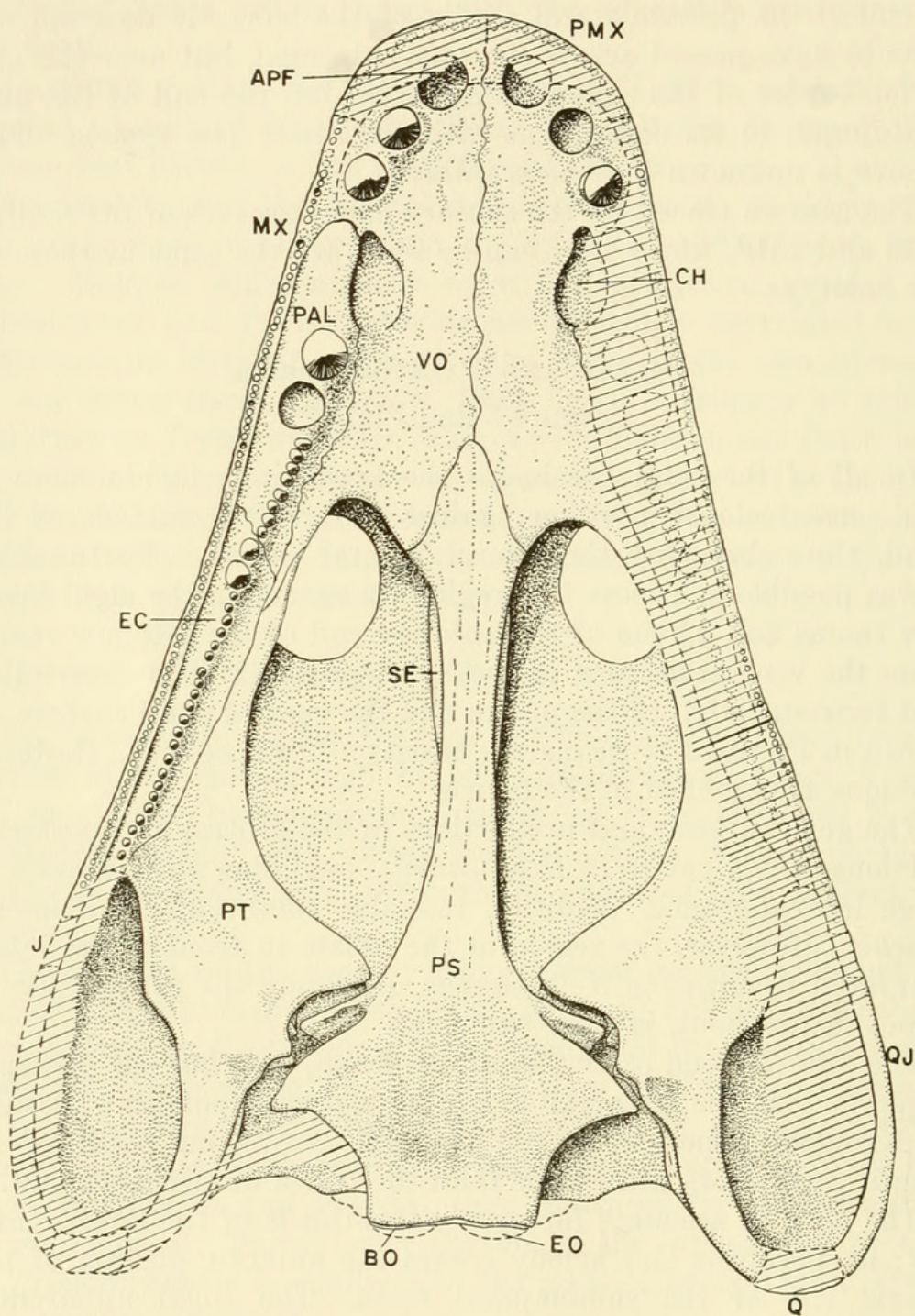


FIG. 3. Reconstruction of skull of *Neldasaurus wrightae* in palatal aspect, $\times .75$. Restored areas are hatched. Abbreviations: APF, anterior palatal fenestra; BO, basioccipital; CH, choana; EC, ectopterygoid; EO, exoccipital; J, jugal; MX, maxilla; PAL, palatine; PMX, premaxilla; PS, parasphenoid; PT, pterygoid; Q, quadrate; QJ, quadratojugal; SE, sphenethmoid; VO, vomer.

its border (if at all) only at the outer anterior corner. Exclusion of the maxilla from the lateral rim of the choana by a union of the vomer and the palatine, which appears to be the case here, is to my knowledge reported in only one other form, *Eobrachyops townendi* (Watson, 1956). The suture between the maxilla and premaxilla can not be seen in ventral aspect. Nevertheless, on the basis of its location on the lateral skull margin, it probably lies close to the level of the anterior member of the vomerine tusk pair.

The marginal teeth are small, crowded and numerous. By counting the teeth in areas where they can be seen, it was possible to estimate a total number of 93 maxillary teeth. The anterior teeth are less than 1 mm in diameter, and in the anterior portion of the maxilla there are slightly less than 10 teeth per cm, while towards the posterior end, where the teeth are still smaller, there are approximately 11 per cm. The length of the tooth-bearing margin of the premaxilla, as reconstructed, is approximately 2.5 cm. The narrow palatal exposure of this bone suggests small tooth size in this region also and, allowing for some decrease in the number of teeth per unit area, the premaxilla should have held at least 15 teeth. In some regions of the maxilla it was noted that teeth alternated with replacement sockets, though no consistent pattern could be seen.

Although the anterior portion of the palate in MCZ 2200 is damaged, there is evidence of the presence of two sets of openings, the anterior palatine fenestrae and the choanae. Immediately anterior, and slightly medial, to the anterior vomerine tusk on each side there is an opening in the palate. In the matrix deposited in this region, on both sides, there are remnants of the upper ends of symphysial tusks belonging to the lower jaw. It appears that anterior palatal fenestrae were present on the suture between the premaxillae and the vomers in *Neldasaurus*. The matrix-filled space containing the upper end of the tusk is confluent with a gap in the anterior part of the floor of the external naris in MCZ 2200. The condition of this region in MCZ 1371 and 1438 is not clear but appears to be similar in the former at least. A comparable situation exists in *Eupelor* (*Buettneria*).

The choanae are located halfway between the anterior end of the interpterygoid vacuities and the end of the snout. They are suboval in outline, with a length of approximately 1.5 cm and a greatest width of .6 cm. Anteriorly, they are constricted by a lateral curvature of the medial border. The lateral margin of

the choana is formed in the main, and perhaps entirely, by the palatine, the anterior and medial margins by the vomer. Although the palate was crushed against the ventral surface of the skull roof in this region of the type specimen, it is apparent that the vomer formed a stout rim on the medial and anterior borders of the opening. The anterior ends of the choanae are 1 cm behind the level of the posterior rims of the external nares. Therefore, to reach the internal naris from the outside, air had to pass backward through a short passageway between the skull roof and the palate—a passageway surely enclosed in a cartilaginous nasal capsule.

The central palatal surface anterior to the interpterygoid vacuities is formed by the vomers. These bones, conforming to the contours of the snout, are approximately four times as long as they are wide. Anteriorly, the vomer is bounded by the premaxilla, and forms the posterior rim of the anterior palatal fenestra; laterally, it joins the maxilla and the palatine, and forms the medial and posterior boundaries of the choana. The vomer meets the palatine midway on the posterior rim of the choana. The suture between the two bones appears to run diagonally backward and outward, medial to the palatine tooth-row. Posteriorly, the vomer forms the anterior margin of the interpterygoid vacuity, but the two vomers are separated in the midline, posteriorly, by the wedge-shaped anterior end of the cultriform process of the parasphenoid. At the point where the vomers meet medially the end of the cultriform process appears to pass dorsal to them.

The posterolateral sutural relations of the vomers are obscured by numerous cracks and the poor preservation of the palatal surface. However, it appears that the vomer formed the anterolateral border of the interpterygoid vacuity, retaining a primitive contact with the pterygoid medially near the anterior end of that opening.

The palatine is bounded laterally by the maxilla and medially by the vomer. Posteriorly, the palatine meets the ectopterygoid. This suture was hard to find but appears to run diagonally forward across the palatal toothrow immediately in front of an enlarged tooth pair and 2.5 cm behind a pair of palatine tusks. If this is the correct position of the suture, the ectopterygoid bears a pair of tusks at its anterior end. It is of interest to note that in *Trimerorhachis*, as described by Case (1915), the ectopterygoid is a short bone, and the palatine supports not only an anterior

fang pair but a second pair of enlarged teeth as well. No enlarged tusks occur on the ectopterygoid in that form. A review of the literature failed to uncover any different description of the palatine-ectopterygoid suture in *Trimerorhachis*. Thus, if the present interpretation is correct, *Neldasaurus* is more primitive than *Trimerorhachis* in this respect.

Assuming that the position of the suture is correct, the ectopterygoid is a long bone, about equal in length to the palatine. Medially, it is bounded by the palatal ramus of the pterygoid and laterally by the maxilla. Posteriorly, where it enters the anterior border of the subtemporal fossa, it is very narrow.

The palatine and ectopterygoid are thickened under the palatal tooth row, and join the maxilla in a firm articulation on the medial surface of that bone. The palatine is stouter than the ectopterygoid. The union of these lateral palatal bones with the maxilla does not reach the ventral edge of the latter with the result that, in ventral aspect, there is a shallow longitudinal groove along the lateral edge of the palate just inside the skull margin.

In primitive fashion, the vomer, the palatine and, apparently, the ectopterygoid each bears a pair of tusks. Those of the palatine are the largest and those of the ectopterygoid are the smallest. It was not possible to determine whether or not any small teeth were present on the vomers between the choanae. However, both the palatine and ectopterygoid tusks are accompanied by a single row of small teeth.

On the left side of the palate in the type specimen the vomerine tusk pair is represented by an empty socket with a tusk behind it. On the right the conditions are reversed. The vomerine tusk is .5 cm in diameter near the base and is somewhat over 1 cm long.

The right palatine bone also supports a tusk pair at its anterior end, the posterior tusk represented by an empty socket. The palatine tusk preserved is larger than that of the vomer, with a diameter at the base of .6 cm and an approximate length of 1.2 cm. Behind the tusk pair on the palatine is a close-set row of 8 small teeth. The more anterior ones are oval in outline, their long axes perpendicular to the tooth row. The posterior ones are round in section. Larger than the maxillary teeth, the palatine teeth average 2 mm in diameter. The third pair of tusks is located at the anterior end of the ectopterygoid. The anterior member of the pair has a basal diameter of 3 mm,

and the posterior a diameter of 4 mm. Behind these, extending nearly to the end of the ectopterygoid, is a row of 21 teeth, decreasing slightly in size towards the posterior end of the row. Their diameter at the base is about 1 mm.

The pterygoid of the type specimen, though damaged, is nearly complete. There are also portions of pterygoid bones in MCZ 2406 and 2407.

The pterygoid consists of a horizontal palatal ramus, a stout central body and a vertical quadrate ramus. The curved, medial margin of the palatal ramus forms the lateral and posterolateral borders of the interpterygoid vacuity. The bone in general is fairly stout but is thin at its medial edge. The palatal ramus has a narrow anterior process, bounded laterally by the ectopterygoid, which articulates with the vomer anteriorly. The posterior portion of the palatal ramus is expanded horizontally. The outer edge of the pterygoid is here thickened and turned ventrally to form a flange about 1 mm deep which forms the anterior portion of the medial border of the subtemporal fossa; the remainder of the border is supplied by the central body and the quadrate ramus of the pterygoid.

The basal articulation was apparently movable (Fig. 4, A). The thickened, horizontal body of the pterygoid opposite the

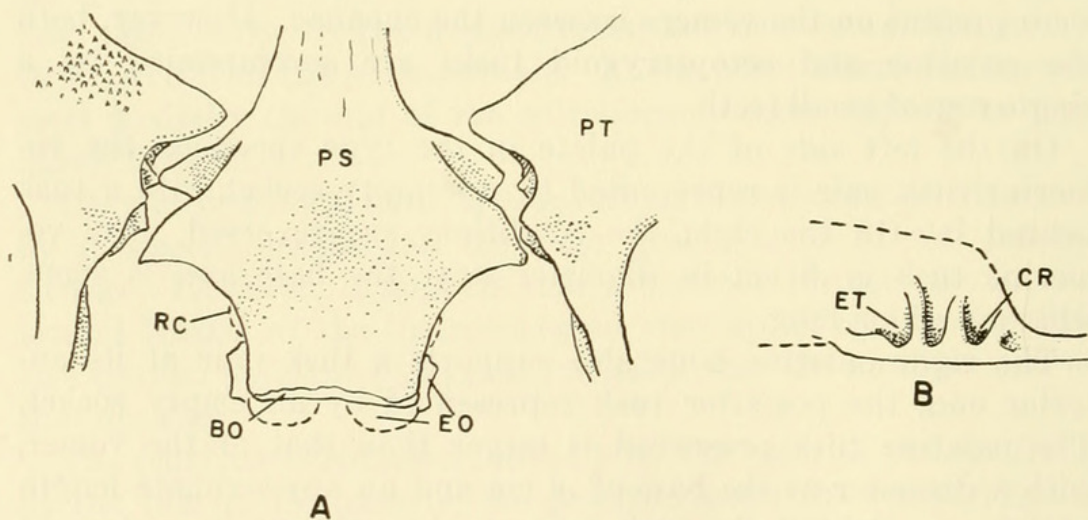


FIG. 4. *Neldasaurus wrightae*. A, reconstruction of the basal articular region of the skull of MCZ 2200 in ventral view, $\times .75$. (Evidence for the presence of the teeth shown on the right pterygoid based on MCZ 2406 and 2407). B, projection of a portion of the medial surface of the left palatoquadrate of MCZ 2200, $\times .75$. Abbreviations: BO, basioccipital; CR, conical recess; EO, exoccipital; ET, "excavatio tympanica"; PS, parasphenoid; PT, pterygoid; RC, pocket for rectus capitus muscle ?

basal articular region of the basisphenoid has an internal process that presumably articulated with the basipterygoid process of the braincase. The internal process, seen best on the right in MCZ 2200, curves dorsally from the level of the central body of the pterygoid so that its tip is nearly .5 cm above the lower surface of the bone. An ascending process rises from the medial edge of the pterygoid just behind the tip of the internal process. Its height above the internal process is about .5 cm, but it rises rapidly posterior to this point to a height of 1.7—1.8 cm opposite the basipterygoid process of the braincase. The concave posterior face of the internal process of the pterygoid forms the anterior and ventral walls of a socket or "conical recess" for the reception of the basipterygoid process of the braincase. The back wall of the "conical recess" is formed by an essentially vertical ridge that rises from the dorsal surface of the pterygoid, just inside the medial edge of the bone, about 1 cm behind the tip of the internal process. This leaves a very limited socket for the reception of the basipterygoid process. Behind the ridge there is a vertical groove, about 5 mm wide, which separates the ridge from the anterior end of the vertical quadrate ramus (Fig. 4, B). The latter, rising above a small medial projection of the pterygoid, forms a second ridge posterior to the groove. The posterior face of the ridge thus produced at the root of the quadrate ramus, and the medial face of the quadrate ramus adjacent to it, share a concavity just above the ventral surface of the pterygoid. It is obvious that this deeply excavated area represents the "excavatio tympanica" of Bystrow and Efremov (1940). It appears that *Neldasaurus* is unusual in that the posterior wall of the "conical recess" is separated by a groove from the ascending ridge at the base of the quadrate ramus which forms the anterior wall of the tympanic excavation.

The quadrate ramus of the pterygoid is approximately 4 cm long and curves outward slightly as it proceeds from its root to an attachment with the quadrate at the outer posterior corner of the skull. Just behind the root, the quadrate ramus, as noted, becomes more or less vertical in the skull, apparently ascending dorsally and somewhat medially. Near the level of, or just anterior to, the otic notch the vertical flange of the quadrate ramus overlaps on the medial side a vertically descending flange of the squamosal. The posteromedial face of the quadrate ramus appears to have had an irregular surface, marked by longitudinally oriented ridges and grooves. There is a prominent, more or

less horizontal, elongate groove in the quadrate ramus, just below its connection with the descending flange of the squamosal. Although post-mortem flattening of this region has introduced some uncertainty in dorsoventral relationships, it seems highly probable that this groove is homologous with the groove in the posteromedial face of the quadrate ramus of *Trimerorhachis*, which apparently serves as a floor for the tympanic cavity (Watson, 1956).

Little can be seen of the quadrate bone. On the medial side of the left cheek in the holotype, however, an anterior extension of the quadrate, which diminishes in size anteriorly, meets the squamosal dorsally and the quadrate ramus of the pterygoid ventromedially.

There is no evidence of an ossified epipterygoid in *Neldasaurus*. A review of the *Trimerorhachis* materials in the collection of the Museum of Comparative Zoology confirmed earlier reports that there is no ossified epipterygoid in that form either.

The obstinate character of the matrix left no indication of palatal teeth in areas other than those described in MCZ 2200, but the fragments of the pterygoid bones in MCZ 2406 and 2407 show that the horizontal flange and part of the palatal ramus are covered by a densely-packed shagreen of small teeth except at the medial edge of the bone.

PARASPHENOID AND BRAINCASE

The braincase is fairly complete in ventral aspect in the holotype specimen. The dorsal surface is crushed against the underside of the skull roof and little can be seen of the lateral surface. The only other braincase material consists of a badly weathered partial parasphenoid with MCZ 1438 and a small portion of the left side of an isolated parasphenoid in MCZ 2518. The description of the parasphenoid and the braincase is based on the holotype.

The proportions of the braincase are remarkably similar to those of *Trimerorhachis* (Case, 1935; Watson, 1956). The sphenethmoid region is narrow, but behind its articulation with the pterygoids the braincase is expanded and more or less flattened. As is usual, the ventral surface of the braincase is sheathed by the parasphenoid.

The parasphenoid narrows gradually in front of the basiptyergoid process of the braincase, giving rise to an anteriorly

directed cultriform process, which forms the medial border of each interpterygoid vacuity. The cultriform process is about 6.6 cm long, fairly broad at each end, but narrow in the central region. The anterior end of the process is wider than in *Trimerorhachis*, but it does not project as far forward into the anterior palatal surface as it does in such forms as *Saurerpeton* or the Triassic metoposaurs.

The anterior and posterior portions of the ventral surface of the cultriform process are nearly flat; the central portion is ventrally convex in cross section, the lateral edge being approximately 2 mm above the level of the ventral surface. The surface of the cultriform process is marked by fine longitudinal ridges and grooves, which also appear to some extent on the main body of the parasphenoid. There is no evidence of teeth on the ventral surface of the parasphenoid, though the rigorous preparation required to remove the matrix could have obscured them.

The main body of the parasphenoid is broad and essentially flat in ventral view (Fig. 4, A). Behind the root of the cultriform process the parasphenoid expands laterally, the central region between the laterally expanded "wings" being moderately concave. Laterally, the parasphenoid sheaths the anterior, ventral and posterolateral faces of the basipterygoid process. The "core" of the process, ossified as part of the basisphenoid in many labyrinthodonts, was here apparently cartilaginous. It would have been exposed at the tip of the process above the parasphenoid, where it could have entered the "conical recess" of the pterygoid to meet the cartilaginous epipterygoid. The anterior margin of the parasphenoid covering the basipterygoid process is directed diagonally outward and backward in direct apposition to the posterior margin of the internal process of the pterygoid. As in *Trimerorhachis*, but in no other Permian temnospondyl, the articular process of the parasphenoid is set off from the main body of the bone by a groove which runs diagonally outward and backward, widening and increasing in depth distally. The anteroventral rim of the articular process of the parasphenoid issues from the side of the braincase on the same level as the ventral surface of the main body of the bone.

Behind the basipterygoid processes, the parasphenoid expands laterally to a width of approximately 5 cm. The margin of the bone then curves sharply inward, matching posteriorly the width of the basioccipital which is 2.2 cm across the base. The posterior border of the braincase has been damaged, but it appears

that the parasphenoid reaches, or nearly reaches, the posterior ventral rim of the basioccipital, although it is extremely thin at this point.

A lateral extension of the parasphenoid turns upward on either side around the basioccipital, gaining a narrow exposure on the lateral face of the braincase at the level of the condyle. Anteriorly this lateral exposure increases, attaining a height of nearly 5 mm ventral to the fenestra ovalis, the ventral rim of which was apparently formed by the parasphenoid. The dorsal and lateral margins are incomplete. In *Trimerorhachis* the lateral concave face of the parasphenoid behind the basipterygoid process contains a deep pocket ventral to the fenestra ovalis, which Watson suggests could have received a rectus capitus muscle. Although this region in *Neldasaurus* is not complete, the details that can be seen suggest that a similar, though less pronounced, fossa for muscle insertion was present.

Careful scrutiny failed to disclose the presence of any openings for the palatine or internal carotid arteries in the ventral or lateral surfaces of the parasphenoid. However, these openings are often small and are not consistently demonstrable even in a well known form like *Trimerorhachis*. Failure to find them in *Neldasaurus* can probably be attributed to their small size or to the rigorous treatment necessarily employed in removing the matrix from the surface of the bone.

Some features of the dorsal surface of the parasphenoid can be determined from exposed portions of the lateral edges, and from the face of a break which runs diagonally across the main body of the braincase. The outer end of a broad groove in the dorsal surface of the parasphenoid can be seen on the lateral surface of the braincase above the laterally expanded "wing." The groove is 6 mm wide at its lateral end and is directed anteromedially. It appears to be comparable to a similar groove on the upper surface of the parasphenoid in *Trimerorhachis* and, as Watson (1956) suggests, probably sheathed the lower medial end of the prootic.

Immediately anterior to the basipterygoid process, the lateral edge of the parasphenoid is thin, but both faces of a break in this region exhibit a thickened mass of bone. Although the form of this thickened mass is partially obscured by matrix, it appears to be part of a strongly developed transverse ridge of bone on the upper surface of the parasphenoid between the roots of the basipterygoid processes. The ridge could occupy the position to

be expected of the posterior rim of a depression for the pituitary.

Reduction of ossification in the braincase is well advanced. The basisphenoid and otic capsule were apparently cartilaginous, since neither is preserved in the holotype. There is, however, evidence of an ossified sphenethmoid. A flat bone about 1 cm high appears to occupy the space between the cultriform process and the skull roof from the anterior end of the interpterygoid vacuity back to a point not far in front of the level of the parietal foramen, a distance of about 4 cm. This bony sheet, bounding laterally the space above the cultriform process, undoubtedly represents an ossified sphenethmoid of the right side. There is no evidence that there was any lateral expansion of the bone like that seen in *Edops* and *Eryops*. Unfortunately, the stapes is not preserved in any specimen.

OCCIPUT

(Figure 5)

The occipital region of the holotype, though damaged, is nearly complete and can be restored. An isolated partial condyle among the materials associated with MCZ 1371 also offers some information, but the description is based mainly on the holotype. The occipital region of MCZ 2200 has been subjected to post-mortem flattening, resulting in some dislocation of its parts. The dorsal portions of the exoccipitals are missing, and only the left side of the condyle is reasonably intact.

The incomplete nature of the exoccipitals hindered an attempt to get an accurate picture of the proportions of the occiput.

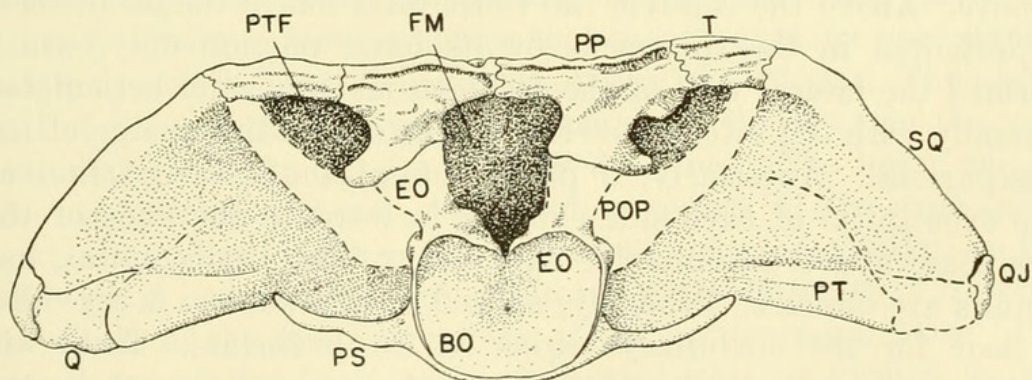


FIG. 5. *Neldasaurus wrightae* (MCZ 2200 and MCZ 1371). Reconstruction of the skull in occipital aspect, $\times .75$ approx. Abbreviations: BO, basioccipital; FM, foramen magnum; POP, paraoccipital process; PS, parasphenoid; PT, pterygoid; PTF, posttemporal fossa. Other abbreviations as in Figure 1. Restored features are in dotted lines.

However, on the basis of the general similarity of the structure and proportions of the occipital region of *Neldasaurus* and *Trimerorhachis*, the height of the dorsal portions of the exoccipitals of *Neldasaurus* was estimated by comparison with Watson's figures for *Trimerorhachis*. Accordingly, the height of the occiput of *Neldasaurus* was approximately 3.9 cm. As noted earlier, the backward slope of the occiput was probably not pronounced in life.

The occipital condyle is a single, subcircular structure with a concave posterior face. Its lower division is formed by the basioccipital, best seen in MCZ 1371. The basioccipital is wedge-shaped in lateral view and extends forward ventrally into the floor of the braincase for a distance of approximately 1.5 cm. The dorsal surface of this anterior extension is unfinished. As said earlier, the parasphenoid covers the ventral surface of the basioccipital to, or nearly to, its posterior border. As in *Trimerorhachis*, the ventral surface of the basioccipital has longitudinal ridges which were in contact with the upper surface of the parasphenoid.

The exoccipitals, resting directly on the basioccipital, form the dorsolateral portions of the condyle and complete its concave posterior face. The position of the suture between the basioccipital and exoccipital can not be determined with certainty but appears to be about half-way between the base and the top of the condyle. Dorsally, the condylar portions of the exoccipitals are well separated, but they approach each other in the midline ventrally. Above the center of the condyle, which contains a notochordal pit, the exoccipitals are only separated by a narrow groove. Above the condyle the exoccipital had a dorsal process, represented in the specimens by its basal portion only, which formed the lateral wall of the foramen magnum and articulated dorsally with the inferior surface of the descending flange of the postparietal. Anteriorly, a projection of the basal portion of the exoccipital of each side extends forward in the floor of the braincase above the anterior extension of the basioccipital, but details are obscure. Probably, as in *Trimerorhachis*, it provided a floor for the medullary region of the braincase. These anterior extensions of the exoccipitals do not quite meet in the midline. The structure of this region, in so far as it can be determined, corresponds generally to that described for *Trimerorhachis* by Watson.

Anterior and somewhat lateral to the base of the dorsal extension of the exoccipital, there is a small process of the exoccipital which forms the anterior wall of the vagal foramen. The posterior wall of the foramen is formed by the base of the ascending process of the bone. Just posterior to the vagal foramen the lateral wall of the exoccipital is pierced by a single foramen for nerve XII. The inner opening of this foramen is in the medial surface of the bone, anterior and slightly ventral to its lateral exit, as seen in MCZ 1371.

The ventral surface of the condyle is broad and more or less flat. The width of the condyle in MCZ 2200 is 2.2 cm and its height is 1.7 cm, while the isolated condyle of MCZ 1371, with a width of 2.3 cm and a height of 1.3 cm, is even lower. These proportions seem to reflect a general trend towards flattening in *Neldasaurus*. The lateral sides of the condyle rise abruptly from the more or less flattened base. In lateral aspect they are considerably narrower than the sides of the condyle in *Trimerorhachis*. Taken together, these characteristics of the condyle resemble the proportions of the intercentra of *Neldasaurus*, in which slender, upright lateral processes arise from the edges of a broad ventral base.

The occipital exposure of the postparietal has a slight backward slope, which is interpreted as being normal. There is no supraoccipital ossification. The ventral articular surface of the postparietal flange slants laterally and ventrally at an angle of 45 degrees to the horizontal, ending laterally in a blunt point. The medial portion of this flange presumably articulated with the upper end of the exoccipital; the laterally projecting outer corner may have rested on the base of a cartilaginous paroccipital bar. There is some evidence that a cartilaginous paroccipital bar extended between the exoccipital and the tabular. The upper end of the bar could have been received in the fossa in the ventral surface of the tabular already described. The lower end of the bar presumably met the anterior surface of the exoccipital ventromedially. There is no indication that the tabular or the exoccipital invaded the paroccipital bar, the latter thus forming the whole of the lower boundary of the posttemporal fossa. The remainder of the fossa, as in *Trimerorhachis*, is formed by the postparietal and the tabular.

LOWER JAW

(Figure 6)

All of the lower jaw specimens have suffered some post-mortem damage and distortion, especially in the articular region. The most complete jaws, MCZ 2200, 1371 and the anterior portions of 1438, are crushed against the ventral surface of the skull so that much of their dorsal and medial surfaces is obscured. Fragments of lower jaws are also present in MCZ 2516, 1381, 1463, 2406, 2404, and 2518.

The right jaw of the holotype specimen is well preserved throughout its prearticular extent, the articular region being hidden. The left jaw is nearly complete from front to back in ventral aspect, the articular region, though twisted, retaining its connection with the prearticular ramus. The infradentary portions of both jaws have been flattened against the palate, losing their original relation to the vertical plane of the dentary.

The left lower jaw of MCZ 1371 (Fig. 6, A) has undergone some distortion and damage, but the preservation of the surface permits a more accurate tracing of the suture pattern than either jaw in MCZ 2200. The anterior tip is missing, but the contours of the preserved portion permit an accurate restoration. Also, though it is incomplete, the articular region is more readily visible in this specimen.

The reconstruction of the lower jaw shown in Figure 6, B is a composite, based primarily on MCZ 2200 and 1371. The relation of the articular region to the ventral rim of the jaw is based on this portion of a small jaw in MCZ 1381, but this relationship is, admittedly, subject to some uncertainty in the larger specimens where the articular region has shared in the general flattening of the ramus.

Aside from a few details, the lower jaw of *Neldasaurus* closely resembles the lower jaw of *Trimerorhachis*. Viewed from below, the anterior end of the jaw is bluntly rounded, the end of each ramus swinging abruptly towards the symphysis from its lateral border, thus paralleling the blunt contours of the snout. The jaw is very shallow anteriorly, its strongly curved outer surface directed as much ventrally as it is laterally. Posteriorly, it becomes progressively deeper, and the convexity of the lateral surface, though continued, is less pronounced. The ventral rim of the jaw was apparently medial to the plane of the dorsal rim

in life. The medial surface, forming a sharp angle with the lateral surface ventrally, is essentially vertical. Posteriorly, the ventral margin of the jaw curves sharply upward to the articular region. There is a modest retroarticular process which extends for a distance of 6 mm behind the posterior rim of the glenoid fossa on the medial side of the jaw. Two cm behind the anterior end of the jaw the dorsal edge of the dentary rises to a point 3 mm above its anterior level; 3 cm behind this point a second, though less abrupt, increase in height occurs. From here, the dorsal margin of the jaw rises gradually to the articular region.

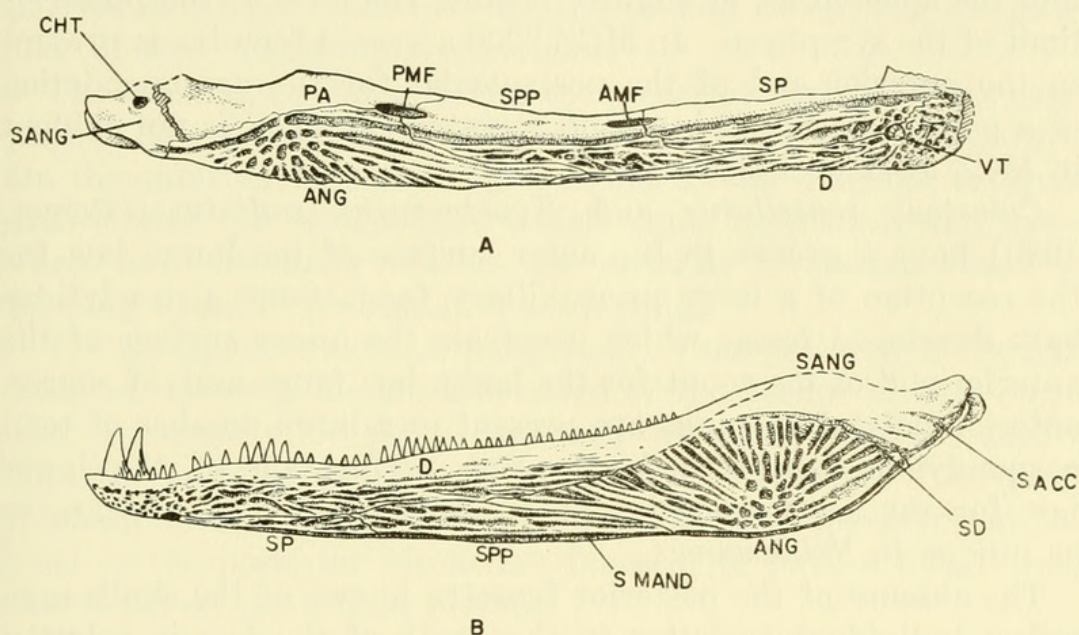


FIG. 6. Lower jaw of *Neldasaurus wrightae* $\times .50$. A, ventral view of left ramus of MCZ 1371. B, external view of left ramus restored (based mostly on MCZ 2200 and MCZ 1371). Abbreviations: AMF, anterior Meckelian fenestra; ANG, angular; CHT, foramen for chorda tympani; D, dentary; PA, prearticular; PMF, posterior Meckelian fenestra; SACC, accessory sulcus; SANG, surangular; SD, dentary sulcus; S MAND, mandibular sulcus; SP, splenial; SPP, posterior splenial; VT, fenestra for reception of vomerine tusk.

The bones of the outer surface of the jaw are sculptured. The medial surface and the ventral rim are smooth.

Two narrow, elongate Meckelian fossae are present just above the ventral margin on the inner surface of the jaw. There is a foramen for the chorda tympani just under the edge of the glenoid fossa at the root of the retroarticular process on the medial surface of the jaw.

In the discussion of the palatal dentition, a fenestra for the reception of a vomerine tusk in the lower jaw was mentioned. In both lower jaws of MCZ 2200 and 1438 and the single jaw of 1371 there is a hole that penetrates the jaw from top to bottom to accommodate the tip of a vomerine tusk. That this is not the result of post-mortem flattening of the skull is shown by the absence of breakage of the surface bones and the finished rim of the opening. The opening of the fenestra in the ventral surface of the jaw is suboval in outline, the long dimension being directed anteromedially. It is approximately 4 mm wide and 5 mm long, and is located on the suture between the dentary and the splenial at, or slightly behind, the level of the posterior limit of the symphysis. In MCZ 2200 a second fenestra is present in the anterior end of the postsplenial for the accommodation of a palatine tusk. This second fenestra, however, is not evident in MCZ 1371 or 1438.

Colosteus scutellatus and *Erpetosaurus radiatus* (Romer, 1930) have a groove in the outer surface of the lower jaw for the reception of a large premaxillary fang. Some Crocodylidae have developed fossae which penetrate the upper surface of the anterior end of the snout for the lower jaw fangs and, of course, anterior palatal openings are present in a large number of temnospondylous labyrinthodonts. But perforation of the lower jaw for the accommodation of an upper jaw tusk appears to be unique in *Neldasaurus*.

The absence of the posterior fenestra in two of the skulls may reflect individual variation in the depth of the jaw in relation to the length of the tusks, or perhaps in older animals large tusks may gradually wear a smooth opening through the lower jaw.

The symphysis is formed by the dentary anteriorly, and the splenial (presplenial) forms the posterior half. Ventrally, it is approximately 1.5 cm long; dorsally it is 2.2 cm long. A medial expansion of the splenial near its anterior end meets a similar expansion from the opposite side, thus lengthening the extent of the symphysis dorsally. The posterior border of the medial process so formed lies 1 cm above the ventral rim of the jaw. A somewhat similar condition appears to obtain in *Trimero-rhachis*, though developed to a lesser degree.

The dentary occupies most of the upper portion of the lateral surface of the jaw ramus and, as already shown, forms most of

the anterior end of the jaw. Except for some uncertainty concerning the posterior extent of the dentary, its relation to the other dermal elements is similar to that of other rhachitomes. It is bounded ventrally by the splenial, postsplenial and angular from front to back, and overlaps each of these elements to a variable extent. The dentary narrows abruptly at the back, its ventral edge ascending diagonally upward and backward. Although its relation to the surangular is not clear, an anterior process of the surangular appears to be interjected between the upturned posterior end of the dentary and the dorsal border of the angular. Much of the dentary is sculptured, but the dorsal portion along the tooth row is quite smooth except for the presence of fine, longitudinal striations.

The splenial, as stated, forms the posterior portion of the symphysis, its anterior end meeting the dentary in a serrate suture. On the outer surface of the jaw it has a long diagonal external suture with the postsplenial, which slants downward and backward, and internally reaches the anterior Meckelian fenestra, forming the anterior rim of that opening.

The postsplenial extends posteriorly to the posterior Meckelian fenestra, forming the anterior third of the border of that opening. Posteriorly, it has a ventrally directed, diagonal suture with the angular on the lateral surface of the jaw. The postsplenial turns over the ventral rim of the jaw, appearing at the level of the posterior Meckelian fenestra to have a height well over 1 cm on the medial surface.

The large angular forms the posteroventral rim and most of the lateral surface of the jaw below and anterior to the articulation. Posteriorly and dorsally the angular is bounded by the surangular, anteriorly and dorsally by the dentary. It has a rather long anterior extension, confined to the lateral face of the ramus, which projects between the postsplenial and the dentary in a gradually narrowed process. Ventrally, a suture between the angular and the prearticular is located on, or just medial to, the ventral rim of the jaw.

The surangular is not complete in any of the specimens. However, on the medial surface of the articular region of the jaw of MCZ 1371 a rather large crack slants upward and backward from the end of the angular to the lip of the glenoid fossa. In the absence of other evidence, and because of its position, this "crack" is tentatively identified as the suture between the surangular and the prearticular. Thus, the surangular would

form the posterior border of the glenoid fossa. Immediately posterior to the "suture," and, as noted previously, just under the edge of the glenoid fossa, is a foramen for the chorda tympani. Its dorsal position and the fact that it is nearly, if not completely, surrounded by the surangular contrasts to the situation in *Trimerorhachis*. In that form, the surangular, angular and prearticular all contribute to the borders of the foramen, according to Case's figures, and its position is more ventral. The foramen for the chorda tympani in MCZ 2200 has a lower position than that observed in MCZ 1371, suggesting that its location is subject to individual variation.

The limits of the articular bone can not be determined and a dorsal view of the glenoid fossa is seen only in MCZ 1371. Unfortunately, it has been damaged. The fossa consists of a concave depression passing diagonally inward from the outer posterior corner of the jaw. A slight ridge separates an outer articular facet from a longer facet on the inner side of the fossa.

The full extent of the prearticular can not be determined, nor can its relation with the coronoids be seen in surface view. In typical fashion it forms the medial wall of the adductor fossa above the angular and postsplenial. Its anterior end extends for some distance in front of the posterior Meckelian fenestra. The medial edge of the adductor fossa is, as typically, lower than the lateral edge. The fossa appears to end anteriorly at the level of the posterior rim of the posterior Meckelian fenestra, having a length of approximately 4 cm.

Unfortunately, the coronoid series is not visible in any of the specimens. The only source of information is that supplied by cross sections of the right lower jaw of MCZ 2200 (Fig. 7). A section through the anterior coronoid, Section J₁, shows three small teeth in a transverse series. Presumably these teeth represent the condition continued throughout the rest of the bone. Traces of similar small teeth were also found in sections showing the other coronoid elements in *Neldasaurus*.

Section J₁ was made approximately 3.5 cm behind the tip of the jaw and 2.3 cm in front of the anterior end of the anterior Meckelian foramen. It should, therefore, pass through the dentary, the splenial and the anterior coronoid. As can be seen in the figure, some distortion is evident, but the three elements can be identified.

A comparison of this section with a section taken through the anterior end of the jaw of *Trimerorhachis* (Broom, 1913, fig.

9D) demonstrates a basic similarity in structure, though the jaw of *Neldasaurus* is relatively more narrow.

Section J₂ was made approximately 1 cm in front of the posterior Meckelian foramen. This section shows very clearly a medial extension of the dentary below the tooth row and above the Meckelian space. The lower portion of the jaw has been folded medially to the vertical plane of the dentary. If this were drawn back to a reasonably normal position, the height of the jaw at this level would be approximately 1.8 cm and the ventral rim would lie a considerable distance medial to the lateral surface of the upper border of the dentary.

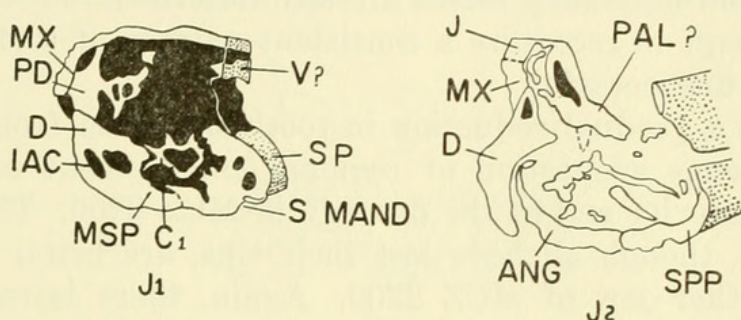


FIG. 7. Transverse sections of the right lower jaw and lateral palatal border of MCZ 2200, $\times 1$. J₁, Section 3.5 cm behind the anterior end of the ramus; J₂, Section 1 cm in front of the posterior Meckelian foramen. Abbreviations: C₁, anterior coronoid; IAC, inferior alveolar canal; MSP, Meckelian space; PD, palatal debris; V?, vomer. Other abbreviations as in previous figures.

The sensory canal system of the lower jaw appears to be represented by three lateral line grooves — a mandibular, a dentary, and an accessory. The mandibular sulcus originates on the posterior margin of the jaw, lateral to the retroarticular process. Its course is readily traced in MCZ 1371 and 2200, where it proceeds along the ventrolateral edge of the jaw, just above the ventral rim, to the posterior border of the symphysis.

The dentary sensory groove arises from the mandibular groove below the articular region, and runs forward along the upper margin of the angular. Anterior to the midpoint of the angular it can not be traced with certainty.

There is some evidence in MCZ 1463 and in the small jaw of 1381 of the presence of an accessory sulcus, dorsal to the dentary sulcus, at the posterior end of the jaw. Due to poor preservation it can not be positively identified in either 1371 or 2200.

By piecing together the information that can be obtained from MCZ 2200 and 1371, it is possible to give a fairly complete account of the lower jaw dentition. *Neldasaurus* possesses a pair of prominent symphyseal tusks on either ramus, each with a diameter at the base of about 5 mm and a height of at least 1 cm.

The teeth of the dentary series in MCZ 2200 and 1371 agree generally in size and number in comparable sections of the jaws of the two specimens, and it appears that the lower jaw of *Neldasaurus* contained 60 or so teeth. The teeth are more crowded than they are in *Trimerorhachis* (where there are about 48 teeth in the lower jaw), a feature which reflects the high tooth count of the maxillary series already described.

An attempt to recognize a consistent pattern of tooth replacement was unsuccessful.

There is a gradual reduction in tooth size from front to back, but with some suggestion of regional enlargement not far behind the anterior end of the dentary in MCZ 2200. The teeth in MCZ 1371, though all have lost their tips, are better preserved than in either jaw of MCZ 2200. Again, there is regional enlargement of the teeth somewhat behind the anterior end of the tooth row. Near the anterior end of the dentary the teeth have a diameter at the base of 1.75 mm. The enlarged teeth that follow have a diameter of 2.5-3.0 mm. In the lower jaw tooth series here described, teeth 18-22 are enlarged, 21 and 22 being the largest. Comparison of the position of this series with the palatal dentition shows that these teeth would be located between the vomerine and palatine tusks, though closer to the latter. Behind this series a second, though less pronounced, enlargement occurs in teeth 33-38.

VERTEBRAL COLUMN

(Figures 8 and 9)

In addition to numerous isolated elements, mostly centra and intercentra, three specimens show associated vertebral material in more or less continuous series.

The vertebral column of MCZ 2200 is distorted and much of the detail is obscure. However, it is possible to trace a reasonably continuous presacral column in which there were approximately 34 vertebrae. MCZ 2518 includes a number of blocks containing presacral vertebrae and several isolated elements, including 33 intercentra. Twenty-five vertebrae can be accounted

for in MCZ 1371. It seems probable, therefore, considering the possibility of loss of some elements, that *Neldasaurus* had approximately 34 presacral vertebrae. The estimated number for *Trimerorhachis* is 31 (Williston, 1915; Case, 1935).

Unfortunately, no atlas vertebra was found and there are only three elements possibly belonging to the caudal series.

On the basis of the relative positions of the vertebral elements in blocks, variations in size of the elements, and variations in the height of the rib facets on centra and intercentra, the presacral vertebral columns of MCZ 2200, 1371 and 2518 were reconstructed.¹ The similarity of the vertebrae of all the *Neldasaurus* specimens makes a detailed description of each specimen unnecessary.

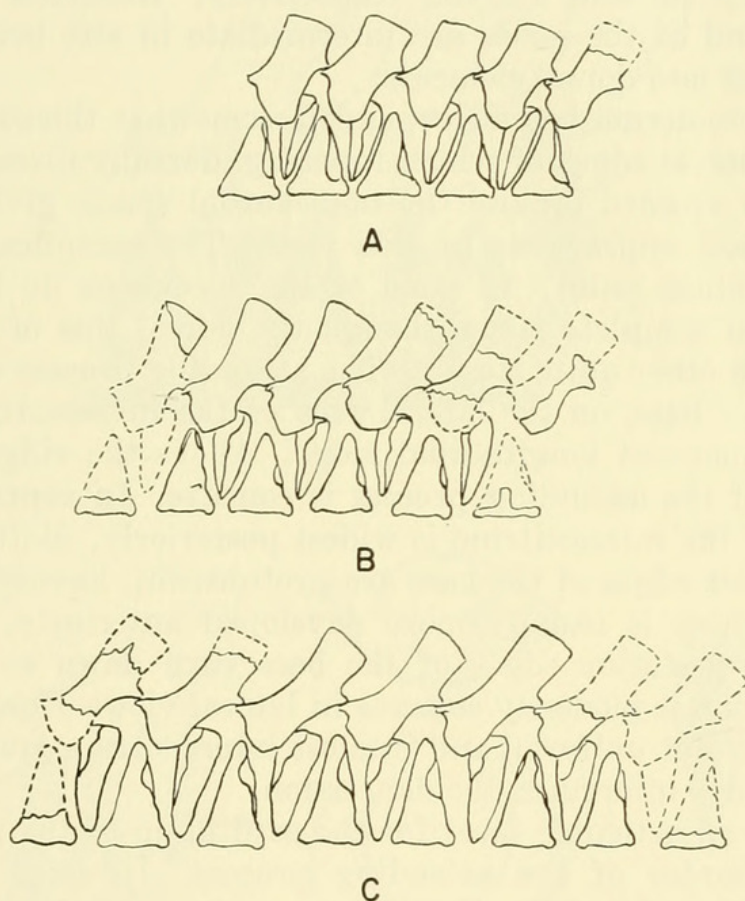


FIG. 8. Partial reconstruction of presacral vertebral column of *Neldasaurus wrightae*, $\times .5$. A, vertebrae 2-5; B, vertebrae 11-16; C, vertebrae 19-26.

¹A detailed description of the reconstruction of the vertebral column for each specimen is given in the thesis on which this paper is based, on file at Harvard University.

The *Neldasaurus* vertebrae conform closely to the typical rhachitinous pattern. Each vertebra consists of a neurocentrum, a single intercentrum open at the top, and paired lateral pleurocentra. The latter are well developed and have a height approximately equal to that of the intercentra. Figure 9, A and B, shows three vertebrae from the mid-dorsal region and two vertebrae from the anterior dorsal region of MCZ 1371.

There is little regional difference in the size of the intercentra and pleurocentra of the presacral vertebral column. Those of the mid-dorsal region are slightly larger than the elements of the anterior and posterior regions. The average height of the first ten intercentra in MCZ 1371 is 1.9 cm, and the average length of the base is 1.2 cm. In the mid-dorsal region these figures are 2.2 cm and 1.5 cm, respectively. Elements near the posterior end of the series are intermediate in size between the anterior and mid-dorsal elements.

The intercentrum has an expanded, somewhat thickened base, from the lateral edges of which tapering, dorsally-directed processes curve upward around the notochordal space, giving a tall wedge-shaped appearance in side view. The ascending process ends in a blunt point. In none of the specimens do the intercentra form complete rings, though the dorsal tips of some approach each other quite closely. The ascending process is marked off from the base, on the lateral face of the intercentrum, by a usually prominent longitudinal ridge. Above the ridge the lateral face of the ascending process is concave. In ventral aspect the base of the intercentrum is widest posteriorly. Both anterior and posterior edges of the base are protuberant, having a medial swelling which is usually more developed anteriorly. The anterior and posterior edges of the base turn down so that the central region is modestly concave in lateral view. However, this concavity is not uniform, and in most intercentra a low, median, rounded ridge interrupts the depression.

There is an articular facet for the capitulum of the rib on the posterior border of the ascending process. In some instances this is a strong laterally directed projection, in others it is less pronounced. The height of the facet above the base of the intercentrum becomes progressively greater from front to back in the vertebral column. In some anterior intercentra the facet is at the very base of the lateral face, while in the posterior ones it is at the tip of the ascending process. The intercentra are stouter and better ossified than those of *Trimerorhachis*, so that the notochordal canal is relatively smaller than in that animal.

However, the base of the intercentrum is not as highly ossified as it is in *Eryops*. The ventral face and the ascending process are sheathed by dense periosteal bone, but on the lateral face of the latter the finished bone does not quite reach the edge or the tip of the process. The ventral and lateral faces of some intercentra are marked to varying degrees by small pits, while others have a smooth surface. The occurrence and development of pits is highly variable in intercentra of comparable size, even from the same individual. Prominent longitudinal ridges are not a common feature of the outer surface of the base and ascending process of the intercentra of *Neldasaurus* as they are in *Trimerorhachis*.

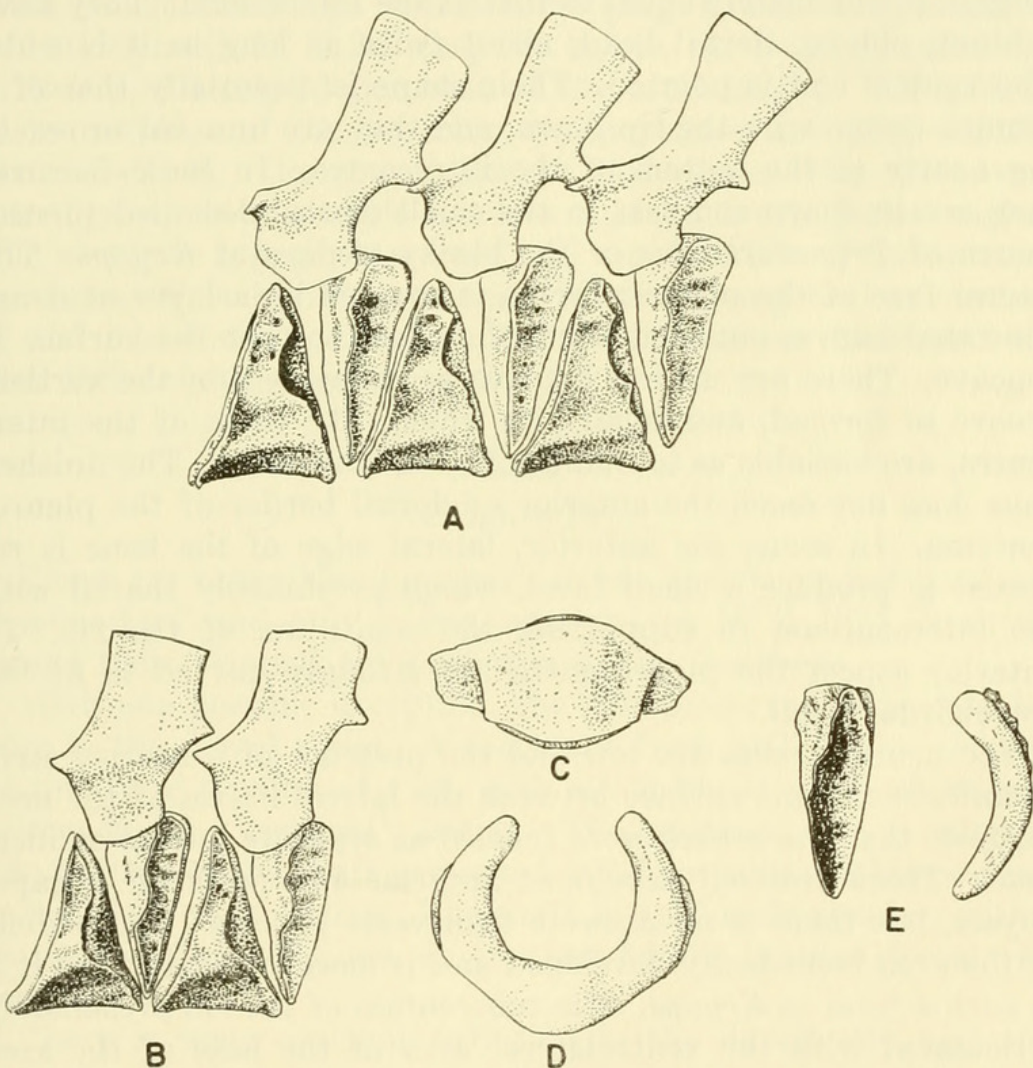


FIG. 9. Vertebral elements of *Neldasaurus wrightae*, MCZ 1371. A, mid-dorsal vertebrae, left lateral aspect. B, anterior dorsal vertebrae, left lateral aspect. C and D, ventral and anterior view of an intercentrum. E, lateral and anterior view of a left pleurocentrum. All $\times 1$.

Three partial intercentra, possibly referable to the caudal series, are present among the specimens. Two are associated with MCZ 2200; the other is an isolated element associated with MCZ 2518. The base is not flattened but strongly curved. Dense perichondral bone is confined to the ventral surface and one edge of the ascending process, the top of which is missing. The intercentrum base is thickened dorsally by endochondral bone which constricts the notochordal space. There is no evidence of haemal arches. In the absence of other information these elements are presumably intercentra of proximal caudals.

The pleurocentra, like the intercentra, are very uniform in structure. They are prominent elements, and, as noted, have a height approximately equal to that of the intercentra. They have a blunt, oblong, dorsal head, about twice as long as it is wide. The ventral end is pointed. Their shape is essentially that of a slender wedge with the tip down, and they are unusual in reaching nearly to the bottom of the intercentra. In these features they are in sharp contrast to the small diamond-shaped pleurocentra of *Trimerorhachis* or the blocky wedges of *Eryops*. The lateral face of the pleurocentrum is covered by a layer of dense bone that curves outward along the edges so that the surface is concave. There are modest transverse ridges within the vertical groove so formed, and small pits which, like those of the intercentra, are variable as to number and arrangement. The finished bone does not reach the anterior or dorsal border of the pleurocentrum. In some, the anterior, lateral edge of the bone is reflected to produce a small facet, which presumably shared with the intercentrum in supporting the capitulum of the rib. In anterior aspect the pleurocentra are strongly curved to fit the notochordal canal.

The neural arches are low and the presence of a narrow strip of unfinished bone surface between the lateral halves of the arch suggests that the arches were formed as separate lateral ossifications. There are well developed anterior and posterior zygapophyses, but there is no discrete transverse process. The pedicle of the arch is modestly developed and is more truncate than it is in such a form as *Eryops*. The tuberculum of the rib presumably articulated with the ventrolateral area of the base of the arch pedicle.

The articular faces of the zygapophyses are roughened, and that of the anterior zygapophysis slopes inward for the reception of the posteriorly and ventrally directed face of the posterior

zygapophysis of the preceding arch. The neural spines are low and only moderately expanded from front to back.

The neural arch elements show greater regional variation than the central elements. Thus, the neural arches of the "cervical" region (Fig. 9, B) have low neural spines, the fourth neural arch from the front as preserved in MCZ 1371 being 2 cm high, the arch pedicle accounting for 50 per cent of the total height. The pedicle descends for a short distance below the zygapophysis, and is curved sharply outward in a strong lateral projection — an incompletely ossified transverse process. The neural spines of this region have a slight backward tilt. The neural elements of the mid-dorsal region are taller, the additional height resulting from elongation of the neural spine (Fig. 9, A). The height of neural element 12 is 2.4 cm; the height of the arch above the pedicle is 1.8 cm, 75 per cent of the total height. The pedicle is truncated and the anterior zygapophyses are only slightly above its base. The neural arch of this region does not have a laterally directed pedicle as does that of the anterior region. The posterior zygapophyses are well separated from the anterior processes on each arch as a result of the strong backward slant of the mid-dorsal spines, which have a sharper backward tilt than those of the anterior region.

RIBS

(Figure 10)

There are many ribs preserved in the specimens but most are fragmentary and only a few, confined to MCZ 1371, have retained their original association with the vertebrae.

With one possible exception, the ribs preserved appear to belong to the dorsal series. A fragment from MCZ 2200 seems to be the distal portion of a rib with a "finished" end, which may belong to the "cervical" region. The proximal end is missing. The portion of the shaft preserved is 2.2 cm long, slightly curved and oval in cross section. The shaft is uniformly slender, with a diameter of only 0.2 cm, in contrast to the heavier dorsal ribs described below.

There is some regional variation in the dorsal ribs and also variation between specimens, but a common pattern can be traced. The shafts of the dorsal ribs are only slightly curved, so that the distal ends of the ribs of opposite sides are well separated ventrally. A rough calculation of the distance spanned by

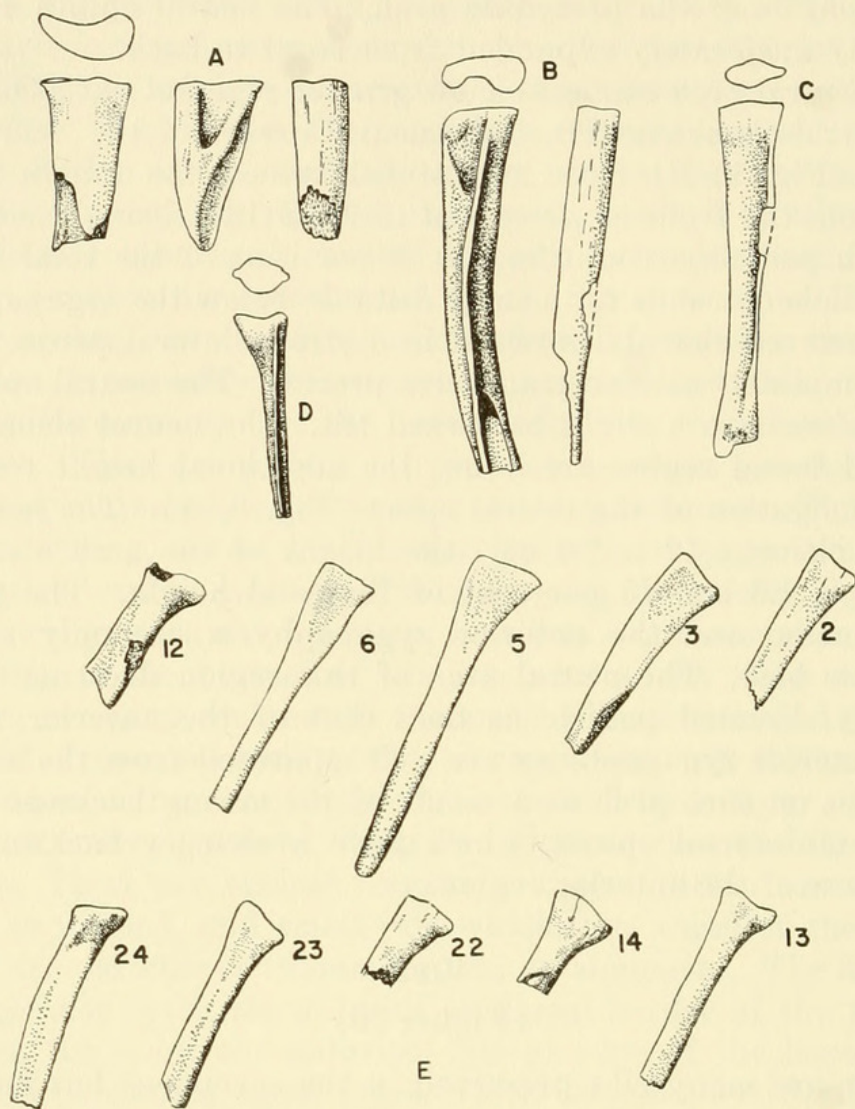


FIG. 10. Ribs of *Neldasaurus wrightae*. A and B, partial anterior ribs. C, partial rib from the mid-dorsal region. D, partial rib from the posterior presacral region. Other ribs as numbered. All from MCZ 1371. All $\times .75$, approx.

opposing ribs articulating with the vertebral column gives a figure of 11.5 cm. If articulated, the ribs would appear to run essentially straight out, suggesting a flat back (and belly) in *Neldasaurus*. As the longest ribs preserved are incomplete distally, and since no provision was made for a possible cartilaginous cap on the rib head, this figure is reasonable when compared to the width of the pectoral girdle, which is 13.6 cm. Though most of the ribs taper distally, a few appear to have had a modest expansion of the distal portion of the shaft. Proximally the shafts are more or less triangular in section; distally they are

elliptical, the long axis of the ellipse oriented dorsoventrally. The rib heads are expanded, though single, and some distinction can be made between confluent capitular and tubercular articular areas.

As noted, there is variation between specimens, so the rib series of MCZ 2200 and MCZ 1371 are described separately. The ten largest ribs preserved in MCZ 2200 probably belong to the anterior region of the dorsal series, and are all of comparable size. Of these ribs, the longest as preserved is 4.5 cm and is representative (Fig. 10, B). The head, which was presumably continued in cartilage, is broad, measuring 1.0 cm in the long axis. Proximally the shaft is stout, having a width of .6 cm on the "capitular" (medial) side and tapering distally to a diameter of .4 cm at the end as preserved. There is no clear division of capitulum and tuberculum on the anterior face of the rib head but the posterior face contains a shallow V-shaped depression in the central proximal region separating a rounded capitular area from a narrow tubercular area. The lateral edge of the shaft bears a low, narrow keel. Behind the keel, along the posterodorsal surface of the rib, a groove runs the length of the shaft.

There are parts of 12 slightly smaller ribs, mostly fragments of the shaft region, presumed to belong to the mid-dorsal series. The longest and most complete of these is shown in Figure 10, C. The rib is incomplete distally but is 4.2 cm long. It is less massive than the anterior ribs; the shaft is more slender and the groove along the posterodorsal border of the shaft is less pronounced. Unlike the anterior ribs, the shaft is straight. There is almost no distinction between capitular and tubercular areas, though the head is flattened.

Posterior dorsal ribs are represented by a single incomplete rib and fragments of two others. The former consists of the head and 2.5 cm of the proximal portion of the shaft (Fig. 10, D). The shaft is slender, the lateral margin forming a thin keel. It does not appear to be grooved. The medial surface is not visible. The head, which is .7 cm long, is thickened and is expanded medially in the central proximal region, so that it forms a nearly oval articular area in end view, and is more sharply marked off from the shaft than the heads of the anterior ribs. There is no separation of capitular and tubercular regions.

The ribs of MCZ 1371 (Fig. 10, E) are similar to those of MCZ 2200, but none are as massive as the anterior dorsal ribs of

the latter. Regional differentiation is less marked in this specimen. The longest rib as preserved, associated with the 5th vertebra of the anterior portion of the vertebral column, is 4.4 cm long. The shaft tapers distally and is slightly curved. The head is flattened, being .8 cm wide, but there is little differentiation between capitular and tubercular areas. The depression noted in the rib heads of MCZ 2200 is lacking. There is a keel along the lateral edge in the proximal half of the rib shaft.

The ribs associated with the mid-dorsal vertebrae in this specimen differ from the anterior ribs in that the heads, though broad, are less flattened. There is some indication of a longitudinal groove like that seen in the ribs of the holotype specimen. The ribs associated with the more posterior series of vertebrae here resemble the mid-dorsal ribs. They are all incomplete distally, the longest being 3.0 cm long.

Thus, the ribs of *Neldasaurus* show some decrease in size from front to back. The heads of the anterior and mid-dorsal ribs are more or less flattened, and the posterior ribs have an expanded head, oval in end view. In some (MCZ 2200), distinction between capitular and tubercular areas is strongly pronounced in the anterior ribs, modest or lacking in the mid-dorsal ribs. A lateral keel appears to be a common feature of the rib shaft. The rib shafts show little curvature.

APPENDICULAR SKELETON

Shoulder Girdle. Parts of the dermal pectoral girdle can be seen in three specimens. MCZ 2200 shows the ventral surface of the clavicles and part of the interclavicle on the underside of the block behind the skull (Plate 2). The anterior end of the right clavicle was broken off but remained in the matrix. The clavicles are pushed together along the mid-line, so that there is little ventral exposure of the interclavicle. Part of the lateral edge of the left clavicle can be seen in dorsal view on the upper side of the block. MCZ 1371 includes the posterior half of a clavicle and a small portion of the interclavicle. MCZ 2518 includes a number of sculptured fragments of the clavicular girdle.

The dermal pectoral girdle of *Neldasaurus* has been restored in ventral aspect in Figure 11. The clavicles are based mainly on MCZ 2200. The posterior portion of the interclavicle is drawn from MCZ 1371. Although the latter animal was somewhat larger than the holotype, the structure and proportions of the girdle are apparently identical.

The ventral dermal girdle of *Neldasaurus* forms a broad thoracic shield whose anterior end appears to have extended forward under the braincase to the level of the posterior end of the basiptyergoid process of the paraspheniod.

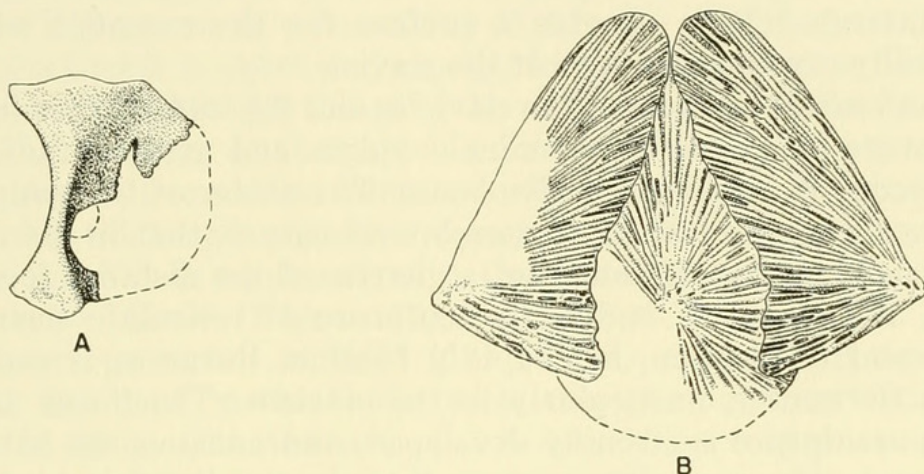


FIG. 11. Pectoral girdle of *Neldasaurus wrightae*, MCZ 2200. A, left scapulocoracoid in medial aspect, $\times .75$. B, restoration of the dermal pectoral girdle, $\times .375$.

The greatest width of the dermal clavicular girdle nearly equals the width of the skull. The clavicle has a roughly triangular outline. Its medial border is irregular but essentially straight; the posterior border is more or less transverse but slants diagonally forward and outward in normal position. The width of the clavicle across the base is 4.4 cm; its length is approximately 8.8 cm. A similar ratio obtains in MCZ 1371. There is a modest medial projection of the posteromedial corner of the bone. The lateral border curves inward anteriorly, but this curvature is not as pronounced as it is in such trimororhachids as *Trimerorhachis* or *Acroplous* (Hotton, 1959). The outline in general closely resembles that of *Buettneria* (Case, 1922).

The lateral edge of the clavicle is curved upward throughout most of its length. About 3 cm anterior to the posterolateral corner of the bone, the upturned lateral edge thickens and rises, forming a stout ridge, the base of the scapular process, which increases in height posteriorly. The dorsal tip of this process is missing.

Although the interclavicle is obscured ventrally in MCZ 2200, its dorsal surface in that specimen and the portion preserved in MCZ 1371 show that it is a sizable element with a length somewhat greater than that of the clavicles. Its posterior end is

bluntly truncated and extends only a short distance beyond the posterior borders of the clavicles. Anteriorly its ventral exposure is reduced by the converging medial edges of the clavicles, whose anterior ends seem to meet in front of it. An unsculptured, but striated flange of bone projects from the anterolateral edge of the interclavicle to provide a surface for the reception of the ventrally overlapping edge of the clavicle.

The ventral surfaces of the clavicles and the interclavicle have a sculpture consisting of prominent ridges and grooves radiating from centers in the respective bones. The center of the sculpture in the clavicle is near the posterolateral corner, that in the interclavicle is in the midline about a quarter of the distance forward from the posterior end. The sculpture is reticulate near the center of ossification, but rapidly becomes linear as it radiates from the center, particularly in the clavicle. The linear aspect of the sculpture is strongly developed, and anastomoses between adjacent ridges are less evident than in the thoracic girdle of *Trimerorhachis*. No cleithrum has been found.

The only trace of the endochondral shoulder girdle is a damaged left scapulocoracoid in MCZ 2200 (Fig. 11, A). The anterior margin is incomplete and a large part of the central region is missing. The general shape of the remaining portion is remarkably similar to the scapulocoracoid of *Trimerorhachis* (Williston, 1915, fig. 5, B, C, D; Case, 1935, figs. 15 and 16), and the missing portions have been restored by reference to that form as well as by continuation of the contours suggested by the broken edges of the bone.

The scapulocoracoid of *Neldasaurus* consists of an expanded blade above the articular surface of the glenoid region. In lateral view the anterior border as restored has a convex outline and the outline of the posterior border is strongly concave dorsally, less so ventrally. The bone as preserved is 3 cm high and its greatest anteroposterior extent was presumably about 2.5 cm. Thus, correlated with the flat body of *Neldasaurus*, it is proportionately shorter than the scapulocoracoid of a form like *Eryops*. The dorsal and ventral edges are unfinished and were presumably continued by cartilage. The thickness of the edges of the bone as preserved suggests that the anterior edge was thinner than the dorsal and posterior margins.

The posterior margin is thickened and rounded, the lower two-thirds being confluent with a modest vertical ridge on the medial side of the bone above the articular surface of the glenoid

region. Anterior to this ridge the posterior portion of the scapular blade is pierced by an oval supraglenoid foramen about one-third of the way above the base.

Although the general form of the scapulocoracoid of *Neldasaurus* is strikingly similar to that of *Trimerorhachis* there are marked differences in proportion. Where the scapulocoracoid of *Trimerorhachis* is short and stocky, in *Neldasaurus* it is lightly constructed, taller and thinner; the articular area of the base is only half as large as that area in *Trimerorhachis*. The vertical ridge above the articular surface in *Trimerorhachis* is separated from the thickened posterior margin of the bone, whereas in *Neldasaurus* it is confluent with the posterior margin.

Anterior Limb (Figure 12). A partial left forelimb and manus are preserved in MCZ 1371 (Pl. 5). The manus as preserved has four metacarpals, with two phalanges articulated with the third and one with the fourth. The carpus was not preserved and was presumably unossified.

There is an incomplete, disarticulated right forelimb in MCZ 2200.

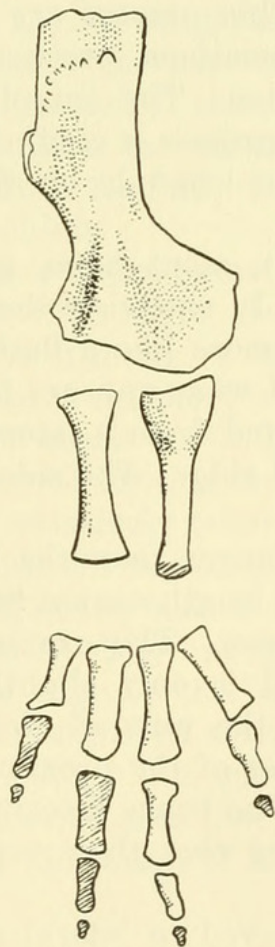


FIG. 12. *Neldasaurus wrightae*. Left anterior limb restored from MCZ 2200 and MCZ 1371, $\times .75$. Restored areas are hatched.

Partial humeri associated with MCZ 2516, 2518, and 2406 show some surfaces not visible in the specimens described above.

The reconstruction of the left forelimb of *Neldasaurus* is based mainly on MCZ 1371 with the proximal end of the ulna added from MCZ 2200. As can be seen from Plate 5, some re-orientation is necessary to put the elements in good articulation.

The forelimb is small for an animal the size of *Neldasaurus*. The humerus, which is relatively long, is of the type seen in *Trimerorhachis*. It is about 4.5 cm long and shows some development of a shaft region. The width of the distal end is 2.3 cm; the proximal end is only 1.2 cm wide. The ends are "twisted" so that the planes of their surfaces form an angle of 27 degrees. There is a well developed deltoid crest on the radial edge of the humerus, just above the middle of the bone, from which an unfinished area along the radial border reaches nearly to the proximal articular surface. There is a small process .5 cm below the top of the humerus on the lateral face as seen in MCZ 2518. In the normally oriented limb its position is near the posterior edge and it probably represents the processus latissimus dorsi. The deltoid crest and this process are connected by a curved band of short, radial striations, presumably supplying part of the deltopectoral insertion. The entepicondyle is strongly developed. The supinator process is continuous with a ridge which projects beyond the ectepicondyle on the distal radial margin of the bone.

The radius is a short, stout bone, about 2.2 cm long, and expanded at both ends. In end view the proximal end is nearly circular, the distal end more like a flattened oval. The bone is not evenly rounded, and what appears to be the medial surface is rather sharply separated from a lateral-anterior surface by a pronounced longitudinal ridge. The side of the shaft opposed to the ulna is concave.

The ulna is slightly longer than the radius, as would be expected, though the exact length cannot be determined. The shaft is curved and very narrow. The proximal end is strongly expanded. The distal end is only slightly expanded. A ridge, similar to that seen in the ulna of *Trimerorhachis*, occurs on the inner posterior border of the proximal end of the bone.

The articular ends of the bones described above are unfinished and excavated, indicating that they were originally capped by cartilage.

The manus was preserved in lateral aspect. The limb bones on the slab are seen from the medial aspect and must be turned

over to agree with the position of the manus. This move correctly places the radius above the first metacarpal.

There are four digits in the manus. The phalangeal count as restored is 2.3.3.2. The metacarpals are relatively long, slender bones and have a flattened-oval outline in cross section. The two central metacarpals are the longest. The first metacarpal, on the radial side of the manus, is the shortest, and is only a little more than half as long as the second and third. The fourth metacarpal is smaller than the middle two but larger than the first. The phalanges as preserved are slender bones, with the articular swelling at the distal end less pronounced than that at the proximal end. In both metacarpals and phalanges, as is fairly common, most distal articular surfaces are convex, whereas the proximal articulations are flattened.

The pectoral limb of *Neldasaurus* is strikingly similar to that of *Trimerorhachis*. It would be difficult, if not impossible, to distinguish between individual bones of the two forms. As can be seen in Case's reconstruction (Case, 1935, fig. 26, p. 267), the restored manus of *Neldasaurus* matches that of *Trimerorhachis*.¹

Pelvic Girdle (Figure 13). MCZ 2518 contains the only pelvic girdle material. There are two ilia with this specimen. The left ilium is seen from the medial side. The lower part of the right ilium is separated from the blade, which is in the same block, and can be seen both medially and laterally. There are no remains of pubis or ischium.

The height of the ilium is approximately 3.3 cm; the expanded base is 2 cm across. The iliac blade, slender but expanded distally, is directed dorsally. The tip of the blade is 1.2 cm long, but its width in the middle of the shaft is only .5 cm. The slender proportions of the ilium recall the slight construction of the scapulocoracoid. The general form is similar to that of *Trimerorhachis*, but the ilium is relatively taller and more slender than in that animal. The lateral surface of the base is somewhat concave. The central portion of the base is strongly produced medially and somewhat ventrally. The upper portion of the acetabulum is located above the edge of the base in the center of the lateral concave face. The unfinished articular surface is bounded by an upraised ridge dorsally. The ventral surface of the ilium shows an unfinished, excavated area that was formerly continued in cartilage. There is no indication of an attachment area for a

¹ Case has reversed the position of the radius and ulna in his figures.

sacral rib on the inner side of the iliac blade. The top of the iliac blade is unfinished and was presumably continued in cartilage.

Posterior Limb (Figure 13). Pelvic limb material is fragmentary and poorly represented. Portions of femora include the damaged proximal and distal ends of a right femur from MCZ 2406, an incomplete shaft from MCZ 2518, a damaged distal end of a femur from MCZ 2407, and the proximal end of a small femur and the distal end of another in scrap associated with MCZ 2404. The last named elements are about half the size of those from MCZ 2406 but the structure is the same. The femur is of the peculiar *Trimerorhachis* type, with a cylindrical shaft and expanded ends. There is a shallow depression on the ventral proximal surface, bounded anteriorly by a projecting trochanter. The outer edge of the latter curves inward toward the shaft distally. The posterior margin of the depression opposite the trochanter is not strongly developed, so that the Y-shaped pattern of ventral ridges common in this area (Romer, 1947) is lacking. The adductor crest is represented by a modest, narrow ridge. Distally, this ridge ends in the center of the ventral surface, a short distance above the end of the bone. Below it,

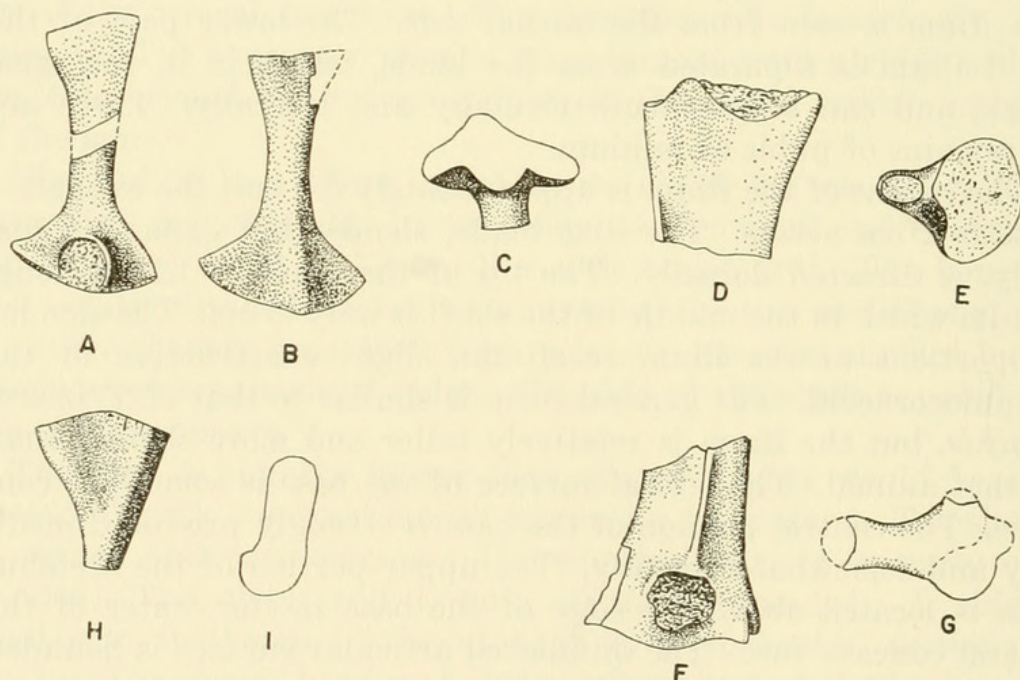


FIG. 13. Pelvic girdle and limb elements of *Neldasaurus*. A, right ilium, outer side. B, left ilium, inner side. C, right ilium, distal surface. A-C, MCZ 2518, $\times .75$ approx. D and E, ventral and proximal views of proximal end of femur. F and G, ventral and distal views of distal end of femur. D-G, MCZ 2406, $\times 1.5$ approx. H and I, inner and proximal view of proximal end of a right tibia of MCZ 2404, $\times .75$ approx.

centrally, is a popliteal space. In MCZ 2407 this is a smooth depression, but in MCZ 2406 it is a rugose, unfinished surface, bounded dorsally by a low upraised ridge. The distal end of the femur has a double condylar area for the head of the tibia and a smaller, lateral condyle for the fibula.

The lower limb bones are represented by the proximal portion of a right tibia and the distal end of a fibula from MCZ 2404, and a similar fragment of fibula from MCZ 2407. The proximal end of the tibia is massive and there is a well developed cnemial crest. The bone tapers rapidly to a slender shaft below the head. The width of the proximal end is 1.7 cm, while the shaft, which is oval in cross section, is only 5 mm across (Fig. 13, H and I).

The fragment assigned to the fibula shows a sub-oval shaft, below which the distal end is considerably expanded, though flattened. Identification of this bone is uncertain.

As far as known, the posterior limb bones of *Neldasaurus* are indistinguishable from those of *Trimerorhachis*, with the possible exception of the distal end of the femur of MCZ 2406. Review of the *Trimerorhachis* material in the collection of the Museum of Comparative Zoology failed to uncover any femora with the peculiar popliteal fossa of that bone.

Assignment of these materials to *Neldasaurus* is not as certain as was the case with the pectoral limb. A single intercentrum of *Trimerorhachis*-type is present in MCZ 2404 and another in MCZ 2406. MCZ 2516 contains two small *Trimerorhachis*-like intercentra and a pleurocentrum. However, all of these specimens are from the Moran formation, from which there has been no definite evidence of the occurrence of *Trimerorhachis* (Olson, 1955). Most of the materials included in the specimens listed here are *Neldasaurus*-like, and the limb materials described compare favorably in size with the other *Neldasaurus* elements in these specimens. For this reason, and because the few *Trimerorhachis*-like vertebral elements do not seem sufficient evidence on which to establish the presence of that animal in the Moran, reference of the posterior limb elements to *Neldasaurus* seems reasonable.

SCALES

Remnants of dermal armor consisting of thin, imbricated bony scales are preserved in a number of places in the specimens. Isolated patches of integumental material are present in MCZ 2200 and MCZ 2518, and in MCZ 1371 considerable areas are

preserved. The pattern of scale distribution is obscure, but the occurrence of scale material in association with much of the skeleton suggests that scales covered most of the dorsal surface of the body.

Scale structure and arrangement is best seen in MCZ 1371 (Fig. 14). In most cases the dermal covering as preserved consists of groups of small, parallel bony rods, the longest about 1 cm long, covering all parts of the skeleton with the exception of the skull and dermal shoulder girdle. Isolated patches of rods were found on the posterior portions of the clavicles and inter-clavicle but their separation from the main mass of integumental material suggests post-mortem displacement. In a number of areas the integument appears to have contained as many as seven layers of bony rods, one above the other. This condition is similar to that of the layers of "bony fibrillae" described by Williston (1916) in *Trimerorhachis*.

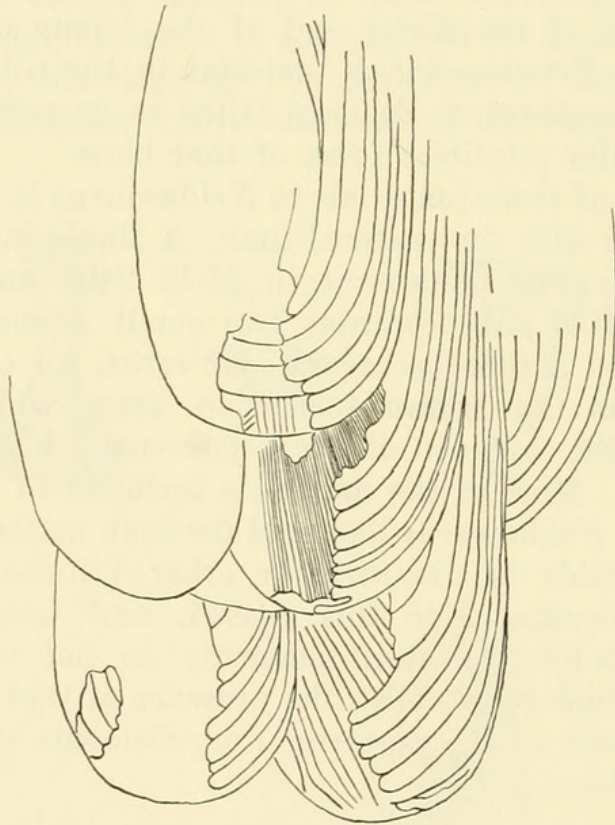


FIG. 14. Dermal scales of *Neldasaurus wrightae*, MCZ 1371, $\times 5$.

More or less complete scales are seen in only a few places. The scales are elongate and rounded at both ends. As near as can be determined, they are 10-12 mm long and 4-5 mm wide,

and, as shown by their layered condition, overlapped to a considerable degree. However, they are very thin, and even in areas where they are in several layers they easily conform to the contours of the underlying skeleton. Colbert (1955) has shown that the "bony fibrillae" described by Williston were in fact remnants of elongate bony scales in *Trimerorhachis*. Comparison of the scales of *Neldasaurus* with the scales of *Trimerorhachis* from the specimens on which Colbert based his paper shows the squamation of the two forms to be alike. As in *Trimerorhachis*, some scales have a superficial layer of fine longitudinal striations, below which is a layer of bony rods of variable width arranged in concentric rings. The presence of the superficial layer, however, is rare in *Neldasaurus* specimens.

OTHER OCCURRENCES OF *NELDASAURUS*

Fragmentary remains of small rhachitinous amphibians have been recovered from several Dunkard localities in West Virginia (Romer, 1952). Early collections of some of these were referred to *Trimerorhachis* (Whipple and Case, 1930; Tilton, 1926). Romer (1952), noting the absence of proof of the existence of *Trimerorhachis* in these beds, described a series of vertebrae from these collections, comparing them with "a rhachitome from the lower Wichita formations (Putnam, Moran) of Texas" in reference to the then undescribed *Neldasaurus*. Comparison of an isolated intercentrum from locality 28 in the Greene Group and an articulated series of three vertebrae from locality 4 of the Washington Group of West Virginia (Moran, 1952; Romer, 1952) (Carnegie Museum nos. 8568 and 8569) has been made with comparable elements for *Neldasaurus*. These elements, (see Romer, 1952, fig. 2, p. 65 and pl. 2, figs. 3 and 4) are remarkably similar to those of *Neldasaurus*, particularly in the height of the pleurocentra and narrow dimensions of the ascending processes of the intercentra.

Hotton (1959) compared vertebral elements of *Acroplous* with those described by Romer, along with some other material from the Dunkard region, finding an isolated parasphenoid and the vertebral elements to bear a close resemblance to those of *Acroplous*.

Correlation of the continental deposits of the Dunkard with Texas beds is somewhat uncertain, but it is generally assumed that the Washington and Greene Groups of the Dunkard are equivalent in age to the Wichita in Texas (Romer, 1958) and

represent the base of the Lower Permian in that region. Further, Romer (1952) has demonstrated a general similarity in the faunal assemblages of the Dunkard and the Lower Permian redbeds of Texas.

On the basis of the resemblance of the circumchordal elements of *Neldasaurus* and the Dunkard specimens, and the approximate correlation of the Texas and West Virginia beds, there is a strong likelihood that *Neldasaurus* (and/or *Acroplous*) or some closely related form was present in the Dunkard.

DISCUSSION

COMPARISON OF *Neldasaurus* WITH OTHER GENERA OF TRIMERORHACHOIDS

The description of this new genus, obviously comparable in many ways to *Trimerorhachis*, suggests the advisability of a general review of the trimerorhachoids — the membership of this group of labyrinthodonts, their structural patterns, classification and relationships. To this end, the first portion of the discussion consists of a morphological comparison of *Neldasaurus* with the other trimerorhachoid genera.

Animals which have been suggested by various authors as belonging to the trimerorhachoid complex include, *Trimerorhachis*, *Saurerpeton*, *Eobrachyops*, *Acroplous*, *Dvinosaurus*, *Chalcosaurus*, *Slaughenhopia*, *Eugyrinus* and other "peliontids," and *Dawsonia*. Although the entire group is reviewed, detailed comparisons are confined to those genera about whose structure we have sufficient knowledge.

Before proceeding with individual comparisons, we may note that the elongate snout of *Neldasaurus* is sharply contrasted to the abbreviated snout of other members of the group. Other features apparently related to snout proportions in which *Neldasaurus* differs from typical trimerorhachoids include elongation of the dermal bones of the face and palate, failure of the lacrimal to reach the naris, and broad separation of the choanae from the interpterygoid vacuities.

NELDASAURUS and TRIMERORHACHIS (Fig. 15). It is obvious from the description given that *Neldasaurus*, apart from facial length, has the combination of primitive and advanced characters seen in the Trimerorhachioidea, as this term is used by Romer. Further, except in this one feature, *Neldasaurus* is obviously closely related to *Trimerorhachis* and will fit into the family

Trimerorhachidae (Romer, 1947, p. 312). *Trimerorhachis* is a well known form from the Texas redbeds whose anatomy has been described by Cope (1878), Broom (1913), Williston (1915, 1916), Case (1911, 1935), and Watson (1956).

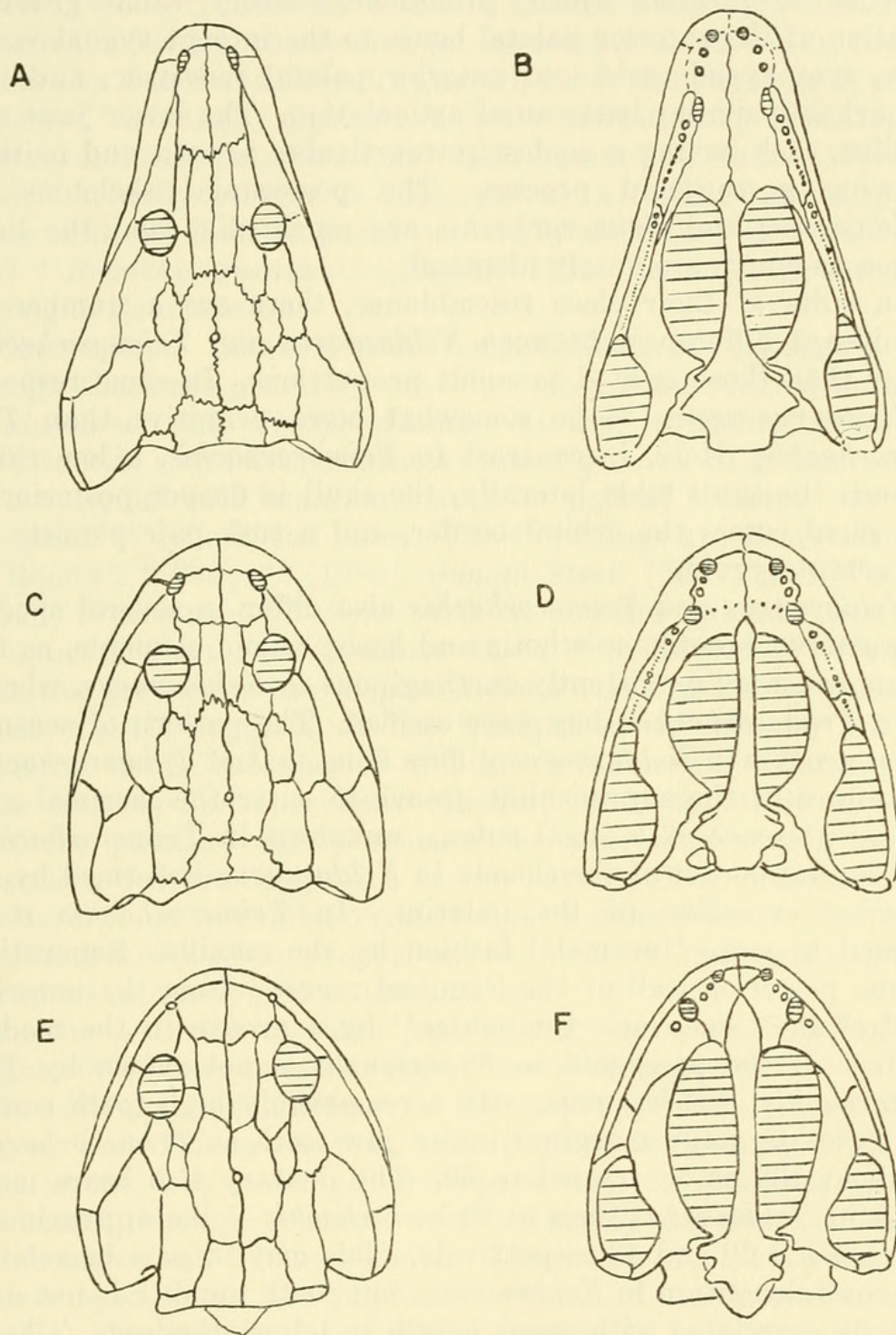


FIG. 15. Trimerorhachid skulls reduced to the same width. Dorsal and palatal views of A-B, *Neldasaurus*; C-D *Trimerorhachis* after Case; E-F, *Saurerpeton* after Romer and Watson.

In addition to the resemblances between *Neldasaurus* and *Trimerorhachis* related to general level of organization, the two show numerous close resemblances of a special nature. The skulls are alike in such features as the general pattern of dermal bones, narrow interorbital width, prominent sensory canal grooves, relation of the anterior palatal bones to the interpterygoid vacuities, symphysial tusks and anterior palatal fenestrae, and the remarkably similar basicranial articulation. The lower jaws are similar, each having a modest retroarticular process and neither showing a coronoid process. The postcranial skeletons of *Neldasaurus* and *Trimerorhachis* are much alike and the limb bones, as noted, are nearly identical.

In spite of their close resemblance, there are a number of significant differences between *Neldasaurus* and *Trimerorhachis* other than those related to snout proportions. In some respects *Neldasaurus* seems to be somewhat more primitive than *Trimerorhachis*. Here, in contrast to *Trimerorhachis*, a low ridge bounds the skull table laterally, the skull is deeper posteriorly, the jugal enters the orbital border, and a tusk pair persists on the ectopterygoid.

Neldasaurus and *Trimerorhachis* also differ in several special characters. Prootic, opisthotic and basisphenoid elements, as far as known, were persistently cartilaginous in *Neldasaurus*, whereas in *Trimerorhachis* they were ossified. The pattern of sensory canal grooves in *Neldasaurus* differs from that of *Trimerorhachis* in failure of the supraorbital groove to enter the lacrimal and in the presence of a jugal sulcus, unknown in *Trimerorhachis*. The lateral border of the choana in *Neldasaurus* is formed by an anterior extension of the palatine. In *Trimerorhachis* it is formed in more "normal" fashion by the maxilla. Separation of the posterior wall of the "conical recess" from the anterior wall of the "excavatio tympanica" by a groove in the medial surface of the pterygoid in *Neldasaurus* is not shown by *Trimerorhachis*. *Neldasaurus*, with a remarkably high tooth count, has twice as many marginal upper jaw teeth as *Trimerorhachis* — about 108 as contrasted to 50. The dentary also bears more teeth in *Neldasaurus* than in *Trimerorhachis* — the approximate count being 60 and 43 respectively. This may in part be related to snout elongation in *Neldasaurus*, but tooth number is not necessarily correlated with snout length in labyrinthodonts (Chase, 1963).

A notable difference in the proportions of pleurocentra and intercentra is seen in the vertebral columns of *Neldasaurus* and *Trimerorhachis*.

SAURERPETON (Fig. 15). This small trimerorhachoid, known mainly from the Upper Pennsylvanian of Linton, Ohio, has been suggested as being closely related to *Trimerorhachis* (Romer, 1947). Romer further believed that "*Pelion lyelli*," also from Linton, was a trimerorhachoid and erected a family Peliontidae within the Trimerorhachioidea for its reception. However, recent studies by Baird and Carroll (Carroll, 1964) show that the type of "*Pelion*" is actually a primitive dissorophid of the genus *Amphibamus*, and that the characters which Romer gave to the "Peliontidae" actually pertain to *Saurerpeton*. All other Linton specimens with an intertemporal previously described as "*Pelion*," and "*Branchiosauravus*" (Romer, 1930) as well, apparently belong to *Saurerpeton*.

Saurerpeton shows definite trimerorhachoid characters although these are generally developed to a lesser degree than in *Neldasaurus* and *Trimerorhachis*. It also resembles them in such special characters as sensory canal grooves on at least some of the dermal roof bones, and anterior palatal fenestrae for the reception of symphysial tusks. These openings are clearly shown in Romer's "*Pelion*" (1930), though Steen (1931) and Watson (1956) reconstruct "*Pelion*" without anterior palatal fenestrae. It appears from Steen's figure 15 of "*Pelion lyelli*" Wyman that the prevomers are displaced from right to left so that, as Romer (1947) suggests, she has interpreted the anterior palatal fenestrae as the choanae. In this she is followed by Watson. In some *Saurerpeton* specimens (Romer, 1930, fig. 6) it appears that the palatine nearly reaches the prevomer lateral to the choana, a feature suggestive of the pattern in *Neldasaurus*.

Saurerpeton resembles *Trimerorhachis* more than *Neldasaurus* in such features as the proportions of the antorbital region and in the small ectopterygoid in the palate.

In the retention of three palatal tusk pairs, *Saurerpeton* resembles *Neldasaurus* rather than *Trimerorhachis*.

In several significant features *Saurerpeton* differs from *Neldasaurus* and *Trimerorhachis*, and in part, in keeping with its greater age, it is seemingly more primitive. In *Saurerpeton* the otic notch, though reduced, is more highly developed than in *Neldasaurus* and *Trimerorhachis*. The orbits in *Saurerpeton* are widely spaced and the jugal forms most of the lateral orbital border. The skull in *Saurerpeton* appears to be deeper than in *Neldasaurus* and *Trimerorhachis*. Watson (1956) estimates a width to height skull ratio in "*Pelion*" of 1:1. The ratio in *Neldasaurus* is 3:1 and in *Trimerorhachis* (Watson, 1956) it is

4.4:1. *Saurerpeton* has fewer marginal upper jaw teeth (about 38) than *Neldasaurus* and *Trimerorhachis* and also lacks the large number of small palatal teeth seen in them.

Saurerpeton differs from *Neldasaurus* and *Trimerorhachis* in several special characters as follows :

- (1) The occiput projects posteriorly beyond the skull table.
- (2) The quadrate condyle appears to have been somewhat anterior to the occipital condyle and well below the level of the floor of the braincase.
- (3) The tabulars are remarkably small.
- (4) The palatine enters the border of the interpterygoid vacuity between the vomer and the pterygoid.
- (5) The maxilla is truncated posteriorly and does not reach the subtemporal fossa.
- (6) The quadrate ramus of the pterygoid is short and has a vertical, ventrally directed flange laterally.
- (7) There is a coronoid process in the lower jaw.

The very long skull table in *Saurerpeton* is a remarkable feature (Romer, 1947), and both supratemporal and squamosal share in the elongation to an extent not seen in *Neldasaurus* and *Trimerorhachis*.

EOBRACHYOPS (Fig. 16). This genus has been described by Watson (1956) on the basis of a specimen from the Lower Permian of Texas. There is no preserved record concerning the collection of the specimen, but the matrix strongly suggests the Clear Fork and, since no materials of that group from higher levels were collected before Olson's recent work, it is highly probable that *Eobrachyops* comes from the Arroyo Formation. Watson's specimen lacked the anterior end of both palate and lower jaw. *Eobrachyops* resembles other trimerorhachoids in its general level of organization and can readily be admitted to the Trimerorhachoidea by accepting Hotton's modification of Romer's definition of the superfamily to include the phrase, "otic notch often poorly developed or lacking" (Hotton, 1959).

Eobrachyops differs from *Neldasaurus*, *Trimerorhachis* and *Saurerpeton* in some special characters. It apparently had an ossified supraoccipital; the lacrimal is confined to the orbital region, its usual area being provided for by an enlarged septo-maxilla; the prefrontal reaches from orbit to naris; sensory canal grooves are essentially confined to circumorbital rings.

In some ways *Eobrachyops* appears to be advanced beyond the level of the other animals so far considered. The exoccipitals

are expanded, enclosing the vagal foramen and meeting the tabulars, thus sheathing posteriorly the cartilaginous paroccipital. Sphenethmoid and quadrate, as well as the prootic elements, are unossified. The interpterygoid vacuities are larger than in

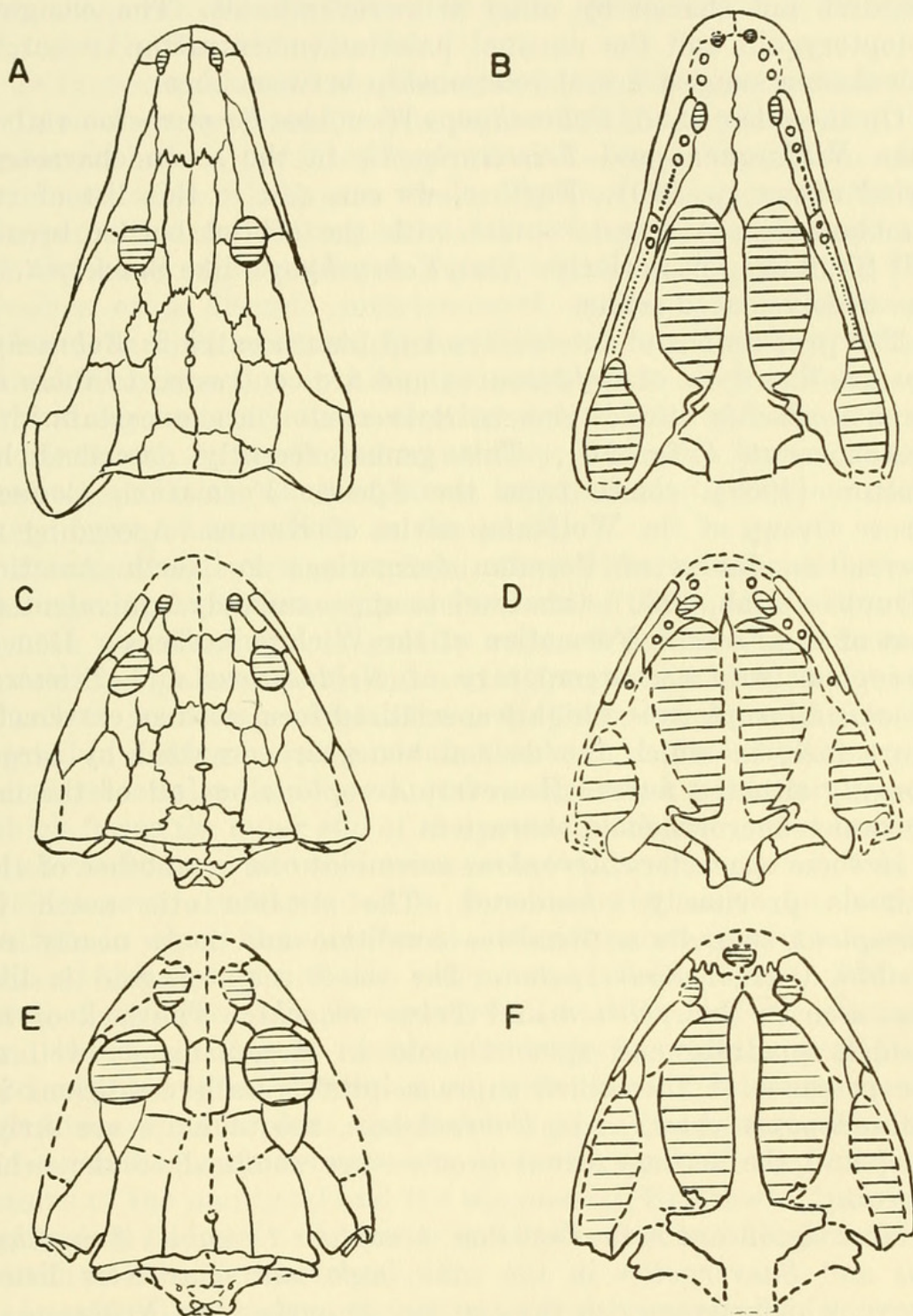


FIG. 16. Trimerorhachid skulls reduced to the same width. Dorsal and palatal views of A-B, *Neldasaurus*; C-D, *Eobrachyops* after Watson; E-F, *Acroploous* after Hotton.

the previously discussed trimerorhachoids, being separated from the choanae only by a narrow strip of bone. The tabulars are reduced to narrow strips. There is no otic notch.

Eobrachyops resembles *Neldasaurus* in two important skull features not shared by other trimerorhachoids. The elongate ectopterygoid and the unusual palatine-vomer union lateral to the choana suggest a real relationship between them.

On the other hand, *Eobrachyops* resembles *Saurerpeton* rather than *Neldasaurus* and *Trimerorhachis* in the seven characters listed above (p. 210). Further, we can add to this list of resemblances: (8) Jugal contact with the orbital border broad. (9) Skull deep posteriorly. Also, *Eobrachyops*, like *Saurerpeton*, has widely-spaced orbits.

The proportions of intercentra and pleurocentra in *Eobrachyops* are like those of *Neldasaurus* and are contrasted to those of *Trimerorhachis*. Conditions in *Saurerpeton* are uncertain.

Acroplous (Fig. 16). This genus, recently described by Hotton (1959), comes from the Speiser Formation, Council Grove Group of the Wolfcamp series of Kansas. According to correlation tables of Permian formations in North America (Dunbar et al., 1960), this level is approximately equivalent to that of the Putnam Formation of the Wichita in Texas. Hence, *Acroplous* was a contemporary of *Neldasaurus* and *Trimerorhachis*. *Acroplous* is a highly specialized form with an extremely short face, in which the dermal bones are crowded by large, dorsally situated nares. However, *Acroplous* has all of the important trimerorhachoid characters.

In some characters *Acroplous* resembles one or another of the animals previously considered. The slit-like otic notch in *Acroplous* suggests a primitive condition and most nearly resembles that of *Saurerpeton*. The small ectopterygoid is like that seen in *Saurerpeton* and *Trimerorhachis*. The lack of an ossified quadrate and sphenethmoid in *Acroplous*, as well as the presence of an ossified supraoccipital, recalls conditions in *Eobrachyops*. Also, as in *Eobrachyops*, the tabulars are strip-like, and the sensory canal grooves are confined to the orbit region.

Most significant is the fact that *Acroplous* resembles *Eobrachyops* and *Saurerpeton* in the nine important characters listed above, which distinguish the last two animals from *Neldasaurus* and *Trimerorhachis*.

The proportions of the intercentra and pleurocentra of *Acroplous* resemble those of *Neldasaurus* and *Eobrachyops*.

DVINOSAURUS. This perennibranchiate labyrinthodont of the Russian Upper Permian has been described by Amalitsky (1924), Sushkin (1936), and Bystrow (1938). *Dvinosaurus* has a short face, anteriorly placed orbits, a very short skull, and lacks an intertemporal element. Some of these characters may be associated with "larval tendencies."

Dvinosaurus shows resemblance to the earlier trimerorhachoids in almost every feature. The only notable exceptions are the apparent lack of the intertemporal and — most important — the shortness of the skull as a whole. Bystrow suggests a probably compound nature of the postorbital — the posteromedial portion of the bone representing a fused intertemporal moiety. The absence of a discrete intertemporal is, therefore, no bar to trimerorhachoid relationship for *Dvinosaurus*. Further, though the skull is short, even here the proportions of pre- and post-orbital segments are those of trimerorhachoids, and the general shortness can be attributed to neoteny, since it is known in several cases that the skull of larval labyrinthodonts is proportionately much shorter than in the adult.

Dvinosaurus is set apart from other trimerorhachoids by certain special characters, such as enclosure of the quadrate foramen by the quadratojugal, a greatly reduced palatine, a somewhat specialized palatal dentition, and a long-stemmed interclavicle. Further, it shows several advanced characters, as might be expected in a late-surviving trimerorhachoid. In two skull features — an essentially double occipital condyle and a tabular process which forms the outer end of the paroccipital bar — *Dvinosaurus* is advanced over all other trimerorhachoids. The exoccipitals in *Dvinosaurus* are expanded to surround the vagal foramen, a feature in which *Dvinosaurus* is more advanced than other members of this group with the exception of *Eobrachyops*. The degree of ossification in *Dvinosaurus*, in which the otic elements and the sphenethmoid remain cartilaginous while a small ossified supraoccipital occurs in at least some specimens, recalls conditions in *Acroplous* and *Eobrachyops*. *Dvinosaurus* also has an unossified gap between the posterior end of the quadrate ramus of the pterygoid and the squamosal (Bystrow's "pterygo-squamosal fissure"). A similar condition obtains in *Eobrachyops* but in no other trimerorhachoid.

In several characters *Dvinosaurus* seems to resemble *Saurerpeton*, *Acroplous* and *Eobrachyops* rather than *Neldasaurus* and *Trimerorhachis*, although in *Dvinosaurus* these characters are

generally developed to a lesser degree. In *Dvinosaurus* the occiput projects behind the skull table, the quadrate condyle is about even with or slightly in advance of the level of the occipital condyle and lies below the level of the ventral surface of the parasphenoid, the pterygoid has a ventral flange laterally, the jugal has a broad contact with the orbital border, the orbits are wide-spaced, and there is a coronoid process in the lower jaw.

Although the skull of *Dvinosaurus* is deepened posteriorly, it is considerably flatter than in *Saurerpeton*, *Acroploous* or *Eobrachyops*. Furthermore, *Dvinosaurus* resembles *Neldasaurus* and *Trimerorhachis* and is in contrast to the other three animals in several important characters. In *Dvinosaurus* the otic notch is reduced and is essentially comparable to the otic notch in *Neldasaurus* and *Trimerorhachis*. The tabular is small, though it is not reduced to a narrow strip. The pattern of the sensory canal grooves on the dermal roof bones of *Dvinosaurus* closely resembles that of *Trimerorhachis* and is nearly identical to that of *Neldasaurus*.

In *Dvinosaurus*, as in *Neldasaurus* and *Trimerorhachis*, there is a union of the vomer and the palatine in the palate, and the maxilla is not truncated posteriorly but reaches the anterior end of the subtemporal fossa.

The vertebral elements of *Dvinosaurus* are most like those of *Trimerorhachis*.

CHALCOSAURUS. This poorly known labyrinthodont was tentatively assigned to the Trimerorhachidae by Romer (1947). The original specimen has been lost, but Efremov redescribed the genus on the basis of the literature and published a figure (1940, pl. II, fig. 2). On the basis of the description, assignment of *Chalcosaurus* to the trimerorhachid group seems reasonable, but knowledge of this animal is too scanty to permit definitive comparisons.

SLAUGENHOPIA. This genus, recently described by Olson (1962), is based on partial skull material from the San Angelo of Texas and a partial lower jaw from the same horizon (Olson and Beerbower, 1953). The incomplete nature of the remains precludes definitive discussion and we here provisionally accept Olson's assignment of *Slaughenhopia* to the Trimerorhachidae.

EUGYRINUS. This small, short-faced genus from the Pennsylvanian Coal Measures in Lancashire has been described by Woodward (1891), and by Watson (1921, 1940), and its phylogenetic position has been considered by Romer (1947). Romer assigned it to the "Peliontidae," a group now known to be

unreal, and considered it a young, though probably post-larval member of the primitive rhachitome group. Further, Watson (1940) has compared *Eugyrinus* with *Dendrerpeton*. More recent unpublished studies by Carroll indicate that *Eugyrinus* is more closely allied to the edopsoids than to the trimerorhachoids, and should probably be removed from the trimerorhachoid complex and placed near the base of the edopsoid group. Hence, *Eugyrinus* is not here considered as a trimerorhachoid.

OTHER "PELIONTIDS." Included tentatively in Romer's family Peliontidae with "*Pelion*" and *Eugyrinus* were *Erpetocephalus* and various Mazon Creek "larvae."

The position of *Erpetocephalus* is problematical. Aside from traces of shoulder girdle, only the dorsal surface of the head is known (Romer, 1947). According to Baird (*in litteris*), "*Erpetocephalus* is a labyrinthodont of uncertain position; Romer (1945) very plausibly classified it as a dendrerpetontid edopsoid." There seems to be no strong argument for assigning it to the trimerorhachoid complex.

Baird's studies have further shown that the Mazon Creek larvae are either indeterminate or that they are not trimororhachoids.

DAWSONIA POLYDENS was based on a number of fragmentary remains of Carboniferous age (Fritsch, 1901). Romer (1945) reviewed the material, finding identification uncertain. Figures (Fritsch, 1901, vol. 1, figs. 42, 43) and copper casts of the original specimens support the assumption that we are here dealing with a primitive temnospondyl of indeterminate affinities.

INTERRELATIONSHIPS OF TRIMERORHACHOID GENERA

The genera here considered trimerorhachoids, in spite of many variations in structure, share a large number of characters related to their general level of organization. The resemblances that in combination suggest the Trimerorhachoidea to have been a natural group are:

- (1) Presence of an intertemporal element — the compound nature of the postorbital in *Dvinosaurus* justifies its inclusion here.
- (2) Single occipital condyle — the condyle tending towards a double condition in *Dvinosaurus*; conditions in *Acropylous* are incompletely known.
- (3) A movable basal articulation.

- (4) Tendency towards flattening of the skull, at least in the antorbital region.
- (5) Otic notch small, poorly developed or lacking.
- (6) Postorbital segment of the skull expanded.
- (7) Usually short-faced — *Neldasaurus* is the only exception.
- (8) Quadrate close to the level of the occipital condyle.
- (9) Presence of sensory canal grooves on the dermal roof bones, often well developed.
- (10) Interpterygoid vacuities enlarged.
- (11) Broad cultriform process of the parasphenoid.
- (12) Anterior palatal fenestrae and symphysial tusks, where known.
- (13) A modest retroarticular process in the lower jaw.
- (14) Ventral dermal shoulder girdle expanded.
- (15) Body flattened.
- (16) Limbs small.

Phylogenetic relationships and classification of the trimororhachoids have been recently treated, principally by Romer (1947), Watson (1956), and Hotton (1959), with varying results. The description of *Neldasaurus* and the discussion of trimororhachoids in the last section provide an opportunity to review relationships within the group.

Neldasaurus resembles *Trimerorhachis* more closely than any other trimororhachoid. However, these animals differ in special characters, some of advanced nature, which indicate that the relationship between them is probably not an ancestor-descendant one. Their typically trimororhachoid features and their appearance near the base of the Permian suggest that they probably arose from a trimororhachoid ancestor in the Pennsylvanian. *Saurerpeton* has been suggested as being closely related to the ancestry of *Trimerorhachis* by Romer (1947) and Hotton (1959). Several primitive features in *Saurerpeton* anticipate conditions in *Neldasaurus* and *Trimerorhachis*. However, some characters, e.g. the anterior position of the quadrate condyle, and failure of the pterygoids to meet the vomers, suggest that *Saurerpeton* has already advanced beyond the evolutionary stage represented by *Neldasaurus* and *Trimerorhachis*. We are thus led to the conclusion that *Saurerpeton*, though close to the ancestry of *Neldasaurus* and *Trimerorhachis*, is not directly ancestral to them.

Eobrachyops, though sharing some special characters with *Neldasaurus* and *Trimerorhachis*, shares a long list of important characters with *Saurerpeton* which are in contrast to conditions

in *Neldasaurus* and *Trimerorhachis*. The combination of primitive and special characters shown by *Saurerpeton* would logically place it close to the ancestry of *Eobrachyops*.

Acroplous has been shown to resemble *Saurerpeton* and *Eobrachyops* in characters that distinguish them from *Neldasaurus* and *Trimerorhachis*. Hotton (1959) recognized the similarity of *Acroplous* to *Eobrachyops*, but placed it closer to *Trimerorhachis* mainly on the basis of three characters. These were:

- (1) The presence of narrow midline elements in *Acroplous* and *Trimerorhachis*.
- (2) Symphysial tusks and anterior palatal fenestrae in *Acroplous* and *Trimerorhachis*.
- (3) The "normal" pattern of palatal bones adjacent to the choana in *Acroplous* and *Trimerorhachis*, as opposed to the "peculiar" situation in *Eobrachyops*, where the palatine provides the lateral boundary of the choana.

A review of these differences suggests that they may not support closer relationship of *Acroplous* to *Trimerorhachis* than to *Eobrachyops*.

- (1) The narrow midline elements in *Trimerorhachis*, as well as in *Neldasaurus*, appear to result from a medial shift in the position of the orbits. In primitive temnospondyls the orbits are widely separated, the postorbital is confined to the posterior border of the orbit and the jugal forms much of the lateral border. With a medial shift in position, the orbit would, in effect, "move away" from the jugal, the postorbital would have a more lateral position relative to the orbit and by an anterior extension could replace (cf. *Trimerorhachis*) or nearly replace (cf. *Neldasaurus*) the jugal on the outer orbital border; the midline elements would at the same time be constricted. In *Acroplous* the strong jugal contact with the lateral border of the orbit and the position of the postorbital immediately behind the orbit suggest that the narrow midline elements here are the result of absolute increase in size of the orbits rather than a shift in position.
- (2) The anterior end of the palate and the lower jaw in *Eobrachyops* are not known, and hence we do not know whether symphysial tusks and anterior palatal fenestrae were present or not in *Eobrachyops*.

- (3) The unusual union of the palatine with the vomer on the lateral border of the choana in *Eobrachyops* is a real difference between *Eobrachyops* and *Acroplous*. However, the occurrence of a similar pattern in *Neldasaurus*, as noted above, a form obviously close to *Trimerorhachis*, suggests that the "normal" pattern may have been modified in parallel fashion in *Eobrachyops* and *Neldasaurus*.

Although in many respects, as Hotton noted, *Acroplous* appears to be a morphological intermediate between *Saurerpeton* and *Eobrachyops*, special characters in *Acroplous* suggest that it probably represents a specialized side branch of the line leading from *Saurerpeton* to *Eobrachyops*.

The aberrant structure of *Dvinosaurus* appears to remove it from close relationship to any trimerorhachoid. Romer (1947) and Hotton (1959) suggested relationship of *Dvinosaurus* to *Trimerorhachis* and *Saurerpeton*; Watson (1956) placed it in the line stemming from *Eobrachyops* to the Triassic brachyopids. In spite of resemblances of *Acroplous* and *Eobrachyops* to *Dvinosaurus*, these animals are too specialized to be reasonably considered ancestral to *Dvinosaurus*. Further, *Dvinosaurus* shares with *Neldasaurus* and *Trimerorhachis* a significant number of those characters which support separation of *Neldasaurus* and *Trimerorhachis* from *Acroplous* and *Eobrachyops*. Hence, we arrive at the conclusion that, as suggested by Romer and Hotton, *Dvinosaurus* is related to *Trimerorhachis* and might reasonably be considered a terminal member of the *Trimerorhachis-Neldasaurus* group.

Review of the Trimerorhachoidea supports the assumption that they form a natural group. The superfamily can be defined by the characters listed on pages 215-216. The phylogenetic conclusions reached above suggest the existence of three subgroups within the Trimerorhachoidea. The families Trimerorhachidae and Dvinosauridae of Romer can be retained, the first including *Trimerorhachis*, *Neldasaurus*, *Chalcosaurus* and *Slaughenhopia*, the second containing *Dvinosaurus*. I propose the erection of a new family Saurerpetontidae, with *Saurerpeton* as the type genus, for the reception of *Saurerpeton*, *Acroplous* and *Eobrachyops*.

The definitions of these families are as follows (Table 2) :

TABLE 2

| <i>Family Saurerpetontidae nov.</i> | <i>Family Trimerorhachidae</i> | <i>Family Drinosauridae</i> |
|--|---|--|
| Tendency towards flattening of skull mostly confined to antorbital region. | Tendency towards flattening of skull in general. | Tendency towards flattening of skull in general but more pronounced in antorbital region. |
| Cheek deep posteriorly; quadrate well below level of ventral surface of parasphenoid. | Cheek not deep posteriorly; quadrate on level of ventral surface of parasphenoid. | Cheek moderately deep posteriorly; quadrate below level of ventral surface of parasphenoid. |
| Quadrate in advance of level of occipital condyle. | Quadrate at or behind level of occipital condyle. | Quadrate at level of occipital condyle. |
| Occiput projecting posterior to skull table. | Occiput not notably projecting posterior to skull table. | Occiput projecting posterior to skull table, but to a lesser degree than in saurerpetontids. |
| Tabulars reduced to narrow strips. | Tabulars small but not reduced to narrow strips. | Tabulars small but not reduced to narrow strips. |
| Jugal contact with orbital border broad. | Jugal contact with orbital border brief or lacking. | Jugal contact with orbital border broad. |
| Palatine entering border of interpterygoid vacuity; pterygoids not meeting vomers anteriorly. | Palatine excluded from border of interpterygoid vacuity by a union of pterygoid and vomer. | Palatine excluded from the border of interpterygoid vacuity by a union of the pterygoid and vomer. |
| Pronounced ventrally directed flange of pterygoid bordering subtemporal fossa. | No ventrally directed flange of pterygoid bordering subtemporal fossa. | Modest ventrally directed flange of pterygoid bordering subtemporal fossa. |
| Maxilla truncated, not reaching level of anterior end of subtemporal fossa posteriorly. | Maxilla not truncated, reaching level of anterior end of subtemporal fossa posteriorly. | Maxilla not truncated, reaching level of anterior end of subtemporal fossa posteriorly. |
| Palatal tusks not usually accompanied by small palatal teeth on vomer, palatine and ectopterygoid. | Palatal tusks usually accompanied by a row of small palatal teeth on vomer, palatine and ectopterygoid. | Palatal tusks on vomer and ectopterygoid accompanied by a row of small palatal teeth. |

TRIMERORHACHOID ORIGINS AND RELATIONSHIPS

The origin of the trimerorhachoids is problematical. Some characters of this group are advanced and of a sort typically met with in Triassic labyrinthodonts. On the other hand, a number of primitive features in the trimerorhachoids, notably single condyle, movable basal articulation, and retention of intertemporal, are not found in labyrinthodonts above the edopsoid level and hence suggest an origin of the trimerorhachoids from an early member of the edopsoid group.

Among the earliest edopsoids are such Pennsylvanian forms as *Gaudrya* from Nýřany, the dendrerpetontids from Joggins, and the English edopsoid-like labyrinthodont, *Eugyrinus*. A trend in dermal roof pattern in edopsoids, characterized by withdrawal of the lacrimal from the anterior orbital border, is already well established in *Gaudrya* and the dendrerpetontids, which would bar them from being directly ancestral to the trimerorhachoids.

Eugyrinus shows a number of characters that might be expected in a trimerorhachoid ancestor, such as: (a) short skull, (b) broad snout, (c) short face, (d) small otic notch, (e) skull table moderately expanded, (f) apparently single condyle, (g) parietal foramen close to orbits, (h) primitive dermal roof pattern, including intertemporal, (i) traces of lateral line grooves on dermal bones of skull roof, (j) open palate, but with pterygoids still extending anteriorly to nearly meet cultriform processes on the anteromedial edges of the interpterygoid vacuities, (k) apparently movable basal articulation, (l) lower jaw with a modest retroarticular process and coronoid process, the last named structure occurring in many, though not all trimororhachoids.

Only in one specific point is *Eugyrinus* too specialized to be a trimerorhachoid ancestor—the fact that, unlike conditions in any trimerorhachoid, the quadratojugal enters into the jaw articulation. However, an edopsoid resembling *Eugyrinus* in all features except this one specialization would be a reasonable trimerorhachoid ancestor.

The possible relationship of trimerorhachoids to the Triassic brachyopids has been treated by Watson, Nilsson and Romer. Watson (1956) proposes *Eobrachyops* and *Dvinosaurus* (1919, 1956) as ancestors of the Triassic brachyopids; *Dvinosaurus*, according to that author, represents a more or less intermediate stage in a line stemming from an ancestral form close to

Eobrachyops in the Lower Permian. Nilsson (1937) agrees in general that *Dvinosaurus*, though not directly ancestral, may be close to the ancestry of brachyopids. Romer (1947) denied relationship of *Dvinosaurus* to the brachyopids, considering it closer to *Saurerpeton* and *Trimerorhachis*, and suggested the metoposaurs as brachyopid ancestors.

In its parabolic skull outline and anteriorly placed orbits, *Dvinosaurus* superficially resembles the brachyopids. However, the pattern of dermal bones in the skull roof of *Dvinosaurus*, including reduction of the postparietal and the topography of the postorbital region, is in contrast to conditions in the brachyopids where the postparietals are not notably reduced and the postfrontal-supratemporal contact, as Romer points out, is more reasonably derived from the more "normal" pattern of typical rhachitomes. Further, the lacrimal contact with the orbit and naris in *Dvinosaurus* differs from the brachyopid condition, in which the lacrimal is typically reduced and withdrawn from the orbit border. The skull table of *Dvinosaurus* is shorter than in the brachyopids. Watson "writes off" such features as a movable basal articulation and the greater anterior extent of the pterygoids in *Dvinosaurus* as merely the retention of primitive characters. However, the retention of such a remarkably primitive feature as a movable basal articulation at such a late date is a condition one would hardly expect if we were, in *Dvinosaurus*, confronted by an immediate brachyopid ancestor.

Other palatal structures of *Dvinosaurus* are also features hardly to be expected in an immediate ancestor of the brachyopids. In *Dvinosaurus*, the vomers are expanded to meet the pterygoids on the lateral border of the interpterygoid vacuities, so that the palatine, which in *Dvinosaurus* is a remarkably small bone, takes no part in the border of the interpterygoid vacuity, whereas in brachyopids the palatine forms the anterior border of that opening. Perhaps significant is the presence of anterior palatal fenestrae in *Dvinosaurus* — none are recorded in the brachyopids.

Some differences between *Dvinosaurus* and the brachyopids may reflect a more primitive level of organization in *Dvinosaurus* and its obvious neoteny. However, the number of morphological differences that exist between *Dvinosaurus* and the brachyopids rule against a close relationship.

Eobrachyops is more like the brachyopids than is *Dvinosaurus* in such features as: less broadly rounded snout; nares, though

widely separated, closer together than in *Dvinosaurus*; orbits of more "normal" proportions; very shallow cheek below orbit; pattern of postorbital region; lacrimal, though still in contact with orbit, greatly reduced; longer skull table than in *Dvinosaurus*; entrance of palatine into the margin of interpterygoid vacuity.

On the other hand, such specialized characters in *Eobrachyops* as tiny tabulars, great reduction of sensory canal grooves, abbreviated maxilla, peculiar pattern of palatal bones adjacent to choanae, and position of quadrate articulation further forward than in some brachyopids, tend to remove it from a directly ancestral position.

In placing *Eobrachyops* close to the ancestry of the brachyopids, Watson listed five characters in which *Eobrachyops* and *Dvinosaurus* resemble the brachyopids and "differ from all other labyrinthodonts" (1956, p. 365). This, which would appear to be a clinching argument, loses strength on closer examination. Two of the five characters, it is true, are found only in *Eobrachyops*, *Dvinosaurus* and brachyopids. These are: (1) a distinct space, formerly occupied by a cartilaginous ridge on the posterior surface of the quadrate, separates the hinder border of the pterygoid from those of the squamosal and quadratojugal; (2) the outer surface of the squamosal and quadratojugal passes round onto the posterior face of the quadrate and there forms a laterally concave, nearly vertical surface.

However, the other three characters cited by Watson are not exclusive to *Eobrachyops*, *Dvinosaurus* and the brachyopids, but are present in other trimerorhachoids (*Saurerpeton*, *Acropylous*), and two of the three — projecting occiput (metoposaurs, plagiosaurs) and ventral position of the quadrate condyle (edopsoids, eryopsoids) — may also be found in other labyrinthodont groups.

If *Eobrachyops* is a Permian representative of the brachyopids, special characters and typically advanced features in *Eobrachyops* would certainly debar *Dvinosaurus* from a position intermediate between *Eobrachyops* and later brachyopids.

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