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AEROSAURUS WELLESI, NEW SPECIES, A VARANOPSEID MAMMAL-LIKE REPTILE (SYNAPSIDA : PELYCOSAURIA) FROM THE LOWER PERMIAN OF NEW MEXICO

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ABSTRACT—*Aerosaurus wellesi* n. sp. is based upon two nearly complete articulated skeletons from the Lower Permian deposits near Arroyo del Agua, New Mexico. Study of these superbly preserved specimens indicates that the genus *Aerosaurus* is distinguishable from most other pelycosaurs, including *Varanops* and *Varanodon*, in having fewer maxillary and dentary teeth, all of which are more laterally compressed and more strongly recurved. The parasphenoid is uniquely expanded laterally and posteriorly, and bears rows of teeth on ridges. *Aerosaurus* also differs from all other pelycosaurs in which the braincase is adequately known in the formation of the *dorsum sellae* mainly from the basisphenoid. *Aerosaurus* was probably an aggressive predator of lizard-like habitus, with an unusually long tail for a pelycosaur . *Aerosaurus, Varanops*, and *Varanodon* are the only pelycosaurs that can be included in the family Varanopseidae with certainty; however, *Basicranodon* may also be a varanopseid. The possibility that the alleged antorbital fenestra in *Varanodon* may be artificial casts further doubt on the suggestion that *Varanodon*, and by extension the Varanopseidae, was involved in the ancestry of archosaurs.

INTRODUCTION

Fossil vertebrates have been known from the Permian redbeds of New Mexico for over a century. Although these widely exposed deposits have been intensively searched by paleontologists, they have yielded disappointingly few good articulated specimens. Prior to recent discoveries by Vaughn (1969) , Berman (1973, 1976, 1977), and Berman and Reisz (in press), most of the important specimens came from bonebeds in the Lower Permian Abo/Cutler Formation, near the settlement of Arroyo del Agua in south-central Rio Arriba County (Langston, 1953).

One of the most interesting of these bonebeds is the University of California's Camp Quarry (UCMP Loc. V-2814) discovered by the late Professor Charles L. Camp in 1928. In 1935, a team headed by Dr. Samuel P. Welles removed six large blocks of red siltstone that represented about thirty square feet of the quarry floor. Besides many dissociated bones of several amphibians (Langston, 1966), the blocks contained two incomplete skulls of a small mammal-like reptile, *Oedaleops campi* Langston, 1965, and two nearly complete skeletons of a medium-sized pelycosaur. Although differing in size, these skeletons clearly belong to a single new species of varanopseid pelycosaur closely related to *Aerosaurus greenleeorum* Romer. They are characterized by, among other things, a uniquely expanded parasphenoidal plate which bears rows of teeth.

Aerosaurus greenleeorum Romer, 1937, is based on a "double handful of bones and bone fregments, not articulated but presumably from a single individual" (Romer and Price, 1940:277). That material was collected by Romer in El Cobre Canyon, about 28 km ENE of Arroyo del Agua, in the Abo/Cutler Formation. The vertebrate-bearing deposits in El Cobre Canyon, once believed to be older than those at Arroyo del Agua, have in recent years been regarded as roughly contemporaneous, of Early Permian (Wolfcampian) age (Langston, 1953; Vaughn, 1963). However, Fracasso (1980) advocates a Pennsylvanian (Missourian) age for these sediments.

Examination of the fragmentary holotype of *Aerosaurus greenleeorum* Romer (FMNH U.C. 464) has revealed an expanded tooth-bearing parasphenoidal plate similar to that of the Camp Quarry varanopseid. Comparisons between this material and the Camp Quarry skeletons leave no doubt that all specimens belong to *Aerosaurus*.

No study of *Aerosaurus* has appeared since the brief description in the "Review of the Pelycosauria" by Romer and Price (1940). The specimens from the Camp Quarry add to our knowledge of the genus, and they confirm the earlier assignment of *Aerosaurus* to the sphenacodont family Varanopseidae. Osteological comparisons of this varanopseid within the family are made mainly with *Varanops*, because the structure of other varanopseids is poorly known. As the best preserved varanopseid, *Aerosaurus*

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sheds new light on the relationships of this pelycosaurian family.

Abbreviations designating museum numbers are: UCMP, Museum of Paleontology, University of California, Berkeley; and FMNH, Field Museum of Natural History, Chicago.

SYSTEMATIC PALEONTOLOGY

Class REPTILIA
Subclass SYNAPSIDA
Order PELYCOSAURIA Cope, 1878
Suborder SPHENACODONTIA Marsh, 1878
Family VARANOPSEIDAE Romer and Price, 1940

A brief comment concerning the formation and spelling of the family name is appropriate here. Williston (1914) coined the generic name *Varanoops* in a footnote ("Osteology of some American Permian Vertebrates," p. 130), but never gave its derivation. Certainly, "varano" must refer to the genus *Varanus* (Vara-NL) as it does in *Varanosaurus* Broili (which name had been applied incorrectly to the species *V. brevirostris* throughout Williston's "American Permian Vertebrates"). The Greek ending ops (face) is not as appropriate in this context as is Greek *opsis* (aspect) because the whole animal, not just the face, probably resembled a varanid lizard. The first "o" in *Varanoops* is optional in transliteration and is customarily omitted. Thus, the correct construction of the family name apparently is Varanopseidae. Although commonly used, Varanopsidae is incorrect even if the termination of the generic name was intended to be Greek ops (face). For a discussion of a similar nomenclatural situation see Welles and Peachy (1953).

AEROSAURUS Romer, 1937

Revised Diagnosis—Varanopseid pelycosaur about one meter long. Differs from all other pelycosaurs in which the braincase is adequately known by formation of the *dorsum sellae* principally from basisphenoid. Distinguished from *Varanops* by proportionately smaller, more delicately constructed skull; fewer maxillary and dentary teeth, which are more laterally compressed and more strongly recurved; laterally and posteriorly expanded parasphenoid bearing rows of teeth; lower neural spines; greater lateral excavation of neural arches on dorsal vertebrae; and larger deltopectoral crest on the humerus. Differs from *Varanodon* in its smaller size; fewer premaxillary and maxillary teeth; shorter premaxilla; shorter cervical centra; shorter neural spines on the dorsal vertebrae; proportionately smaller lateral centrale and fourth metacarpal; and much shorter anterior chevron bones.

AEROSAURUS WELLESI, new species
(Figs. 1–14, 16, 17A)

Holotype—A nearly complete articulated skeleton prepared in shallow relief in a large block of matrix, UCMP 40096.

Referred Specimens—An incomplete but partly articulated skeleton of a large individual, UCMP 40097; an isolated braincase, UCMP 35762; some dissociated elements of a large individual preserved in a block of matrix, UCMP 40098; additional unnumbered specimens representing at least three individuals are scattered throughout two other blocks from the Camp Quarry, UCMP 40094 and 40095, which also contain remains of other vertebrates.

Locality and Horizon—UCMP Loc. V-2813 (Camp Quarry), on the southeast slope of a small butte called Loma Salazar, 440 m south of New Mexico State Highway 96, about 840 m southeast of the Rio Puerco bridge at Arroyo del Agua, section 8, T. 22 N., R. 3 E., Rio Arriba County, New Mexico. Soft, brick-red siltstone containing numerous reduction spheres, Abo/Cutler Formation, Wolfcampian, Lower Permian, about 36 m below the top of the butte. Berman and Reisz reopened this quarry in 1979, but despite extensive digging by a team of five people, only a few scattered bone fragments were recovered. It appears that the site has been completely exhausted.

Diagnosis—Differs from *A. greenleeorum* in its smaller size, less robust ilium and iliac blade, supraglenoid foramen closer to the glenoid fossa on the scapula, shorter cervical centra with less developed keels, longer dorsal centra, absence of a ventral lip on cervical or dorsal centra.

Etymology—Named after Dr. Samuel P. Welles who, as a member (1934) and leader (1935) of the University of California field parties to Arroyo del Agua, was instrumental in assembling the extensive collections of Permian vertebrates in the University of California Museum of Paleontology at Berkeley.

Description

The type specimen (UCMP 40096) is exposed from the dorsal side and lies in an extended position, with the limbs of the left side projecting sharply laterally (Figs. 1, 3). All ventral surfaces are hidden in matrix. The right forelimb and pectoral girdle, distal portions of the right hindlimb, lower part of the pelvis, mid-dorsal vertebrae and ribs, and mid-caudal and posterior caudal vertebrae are missing or not exposed. The flattened skull roof is completely exposed only on the left and dorsal surfaces. The parasphenoid and elements of the occiput are displaced and exposed beyond the posterior edge of the skull table. Only the dorsal half of the left mandible and its dentition are visible. This individual is certainly immature; the ends of the bones, including the neural spines, are incompletely ossified, and the olecranon, which is well developed in the larger specimens, is lacking here.

The referred specimen (UCMP 40097) is a partly articulated skeleton about twice as large as the type, and is probably an adult. The mandibles, some palatal bones, and a part of the braincase are all that remains of the skull, but this specimen also contains a sequence of dorsal ver-

FIGURE 1. *Aerosaurus wellesi* n. sp., holotype UCMP 40096, and associated reptilian and amphibian remains. Scale equals 10 cm.

tebrae and some ribs, several articulated segments of the tail, associated but disarticulated pectoral and pelvic girdles, and the right and incomplete left hind limbs with partly articulated feet. A few gastralia are also preserved. For measurements see Table 1.

Skull

The skull (Figs. 2, 4, 5), as reconstructed, comprises about one-fourth of the precaudal length of the skeleton, and is equal in length to nine mid-dorsal vertebrae. It is depressed to a degree intermediate between the reconstructions of *Varanops* given by Romer and Price (1940, Pl. 5) and Williston (1911, Fig. 25). The jaw articulation is situated as far back as in *Varanops* and at about the level of the tooth row. Although the distance from orbit to jaw articulation is about the same as in *Varanops*, the skull table in *A. wellesi* seems relatively abbreviated because of the emargination of its transverse occipital margin. In lateral aspect, the rostrum appears moderately long and low.

FIGURE 2. *Aerosaurus wellesi* n. sp., anterior part of holotype UCMP 40096. Scale equals 5 cm.

As in *Varanops* and *Varanodon*, the posterior edge of the skull slopes gently from the posterolateral corner of the skull table to the jaw articulation. This edge of the skull is as long as in *Varanops* but shorter than in *Varanodon* (Olson, 1965). The occiput, poorly known in other varanopseids, was much less steeply inclined than in non-varanopseid sphenacodonts.

A few of the dermal bones are lightly sculptured with shallow, irregular pits and grooves. Below the orbit, the lateral edge of the jugal forms a low lateral crest that bears a series of blunt, saw-like serrations unreported in other pelycosaurs.

As in all varanopseids, the skull roof is emarginated above the large, round orbits, so that the frontal bones enter the orbital margins without the usual pelycosaurian lateral process. It is uncertain whether the prefrontal was expanded laterally in front of the orbit as in *Varanops*, because crushing has distorted this region of the skull. Although the postorbital is incomplete, the shape of this bone suggests that a lateral postorbital prominence, found in sphenacodonts, was present in *A. wellesi*. As in *Varanops*, the postorbital and suborbital bars are very slender. The lacrimal and jugal unite beneath the orbits and exclude the maxilla from its rim, exactly as in *Varanops* and *Varanodon*. The pineal foramen is relatively as well as absolutely larger than in non-varanopseid sphenacodonts, and is similar in size to that in *Varanops* and *Varanodon*. As in all advanced pelycosaurs, the foramen is situated far back on the abbreviated skull table, near the posterior edge. As in *Varanops* and *Varanodon*, the lateral temporal fenestra of *Aerosaurus* is relatively large for a pelycosaur. Its maximum horizontal dimension is greater than its maximum vertical dimension. The surrounding bones are thin and narrow, especially below the fenestra. As in other varanopseids, the posterior border of the lateral temporal fenestra forms an acute angle with the horizontal ventral border. There is no antorbital fenestra as reported in *Varanodon* (Olson, 1965), however, the bones in this area are thin.

DERMAL SKULL ELEMENTS—The premaxilla appears delicate because of the relatively large size of the naris. The dorsal ramus of the premaxilla appears to slope slightly anteriorly in the type specimen. This is probably the result of postmortem distortion of the skull, which has tended to displace the skull table anteriorly relative to the maxilla. No septomaxilla is evident.

The maxilla is expanded dorsally above its largest teeth,

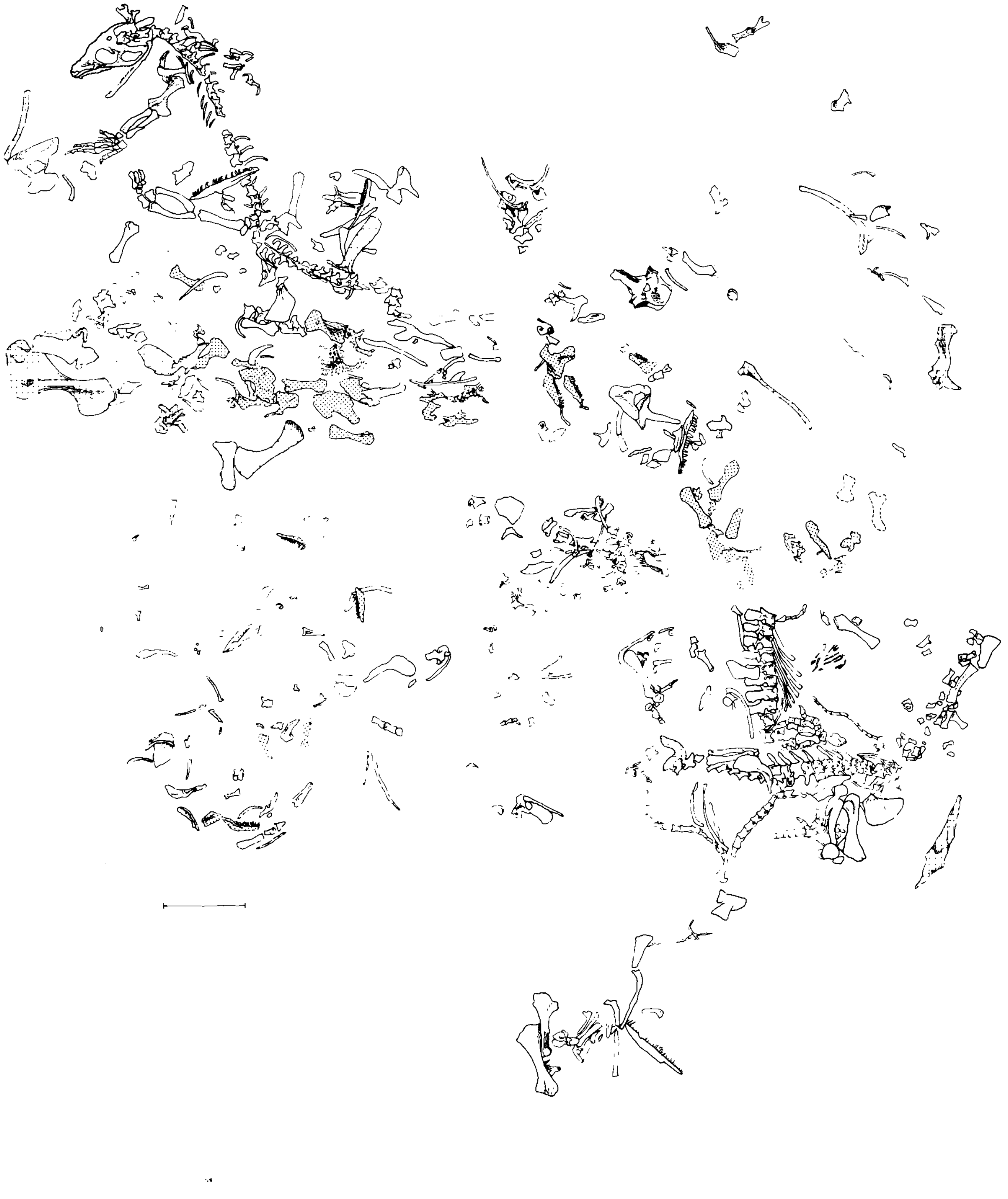

FIGURE 3. Diagram of Camp Quarry fossils showing relationships between the holotype of *Aerosaurus wellesi* n. sp., (UCMP 40096, upper left), and the principal referred specimen (UCMP 40097, lower right). Bones of *Aerosaurus* are left unshaded; diagonal squares, *Eryops*; horizontal lines, *Limnosceloides*; vertical lines, unidentified pelycosaurs; dots, *Oedaleops*; squares, *Sphenacodon*. Scale equals 10 cm.

and there is a suggestion of a lateral ridge similar to, but less accentuated than, the supracaniniform swelling in *Varanops* and *Varanodon*. Dissociated maxillae (Fig. 6) show no enlargement on the medial side such as occurs above the caniniform teeth in advanced sphenacodonts, nor is there a vertical brace here, as in *Ophiacodon*. The posterior end of the maxilla is narrow dorsoventrally; it is partly covered laterally by the jugal. The maxilla extends posteriorly as far as the center of the lateral temporal fenestra, where it contacts the quadratojugal. As in *Varanops* and *Varanodon*, the maxilla of *Aerosaurus* is relatively longer than in most pelycosaurs.

The lacrimal is a broad sheet of bone that forms much of the anterior orbital margin. It is slightly constricted in front of the orbit by the dorsal expansion of the maxilla. From here it extends almost undiminished to the external naris, where it forms the entire posterior narial margin. A well developed posteroventral process meets the jugal beneath the orbit.

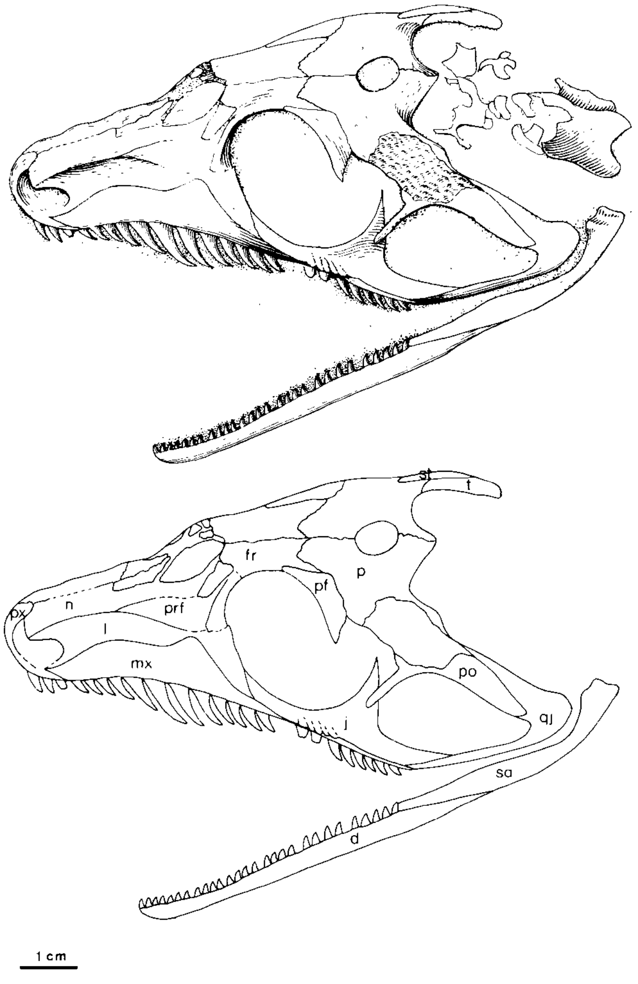

FIGURE 4. *Aerosaurus wellesi* n. sp., skull of holotype UCMP 40096 as exposed in shallow relief. The posterolateral corner of the skull table is damaged and only its general outline is definable. Abbreviations: ***fr***, frontal; ***d***, dentary; ***j***, jugal; ***l***, lacrimal; ***mx***, maxilla; ***n***, nasal; ***p***, parietal; ***pf***, postfrontal; ***po***, postorbital; ***prf***, prefrontal; ***px***, premaxilla; ***qj***, quadratojugal; ***sa***, surangular; ***sq***, squamosal; ***st***, supratemporal; ***t***, tabular.

The jugal resembles that of *Varanops*, except for its unique lateral serrations and a relatively narrow postorbital ramus. As in *Varanops* and *Varanodon*, the jugal is excluded from the ventral margin of the skull by the junction of the maxilla and quadratojugal.

The quadratojugal, best seen in UCMP 40096, has a long, slender ventral ramus that extends anteriorly to meet the jugal and the posterior tip of the maxilla. A long, slender dorsal process apparently lay beneath the edge of the squamosal, but this was largely obscured by the squamosal in lateral aspect. The quadratojugal forms the acute posteroventral corner of the lateral temporal opening and also bounds it to a considerable extent below and behind.

The exact length of the nasal is difficult to determine because of extensive fragmentation of the skull table in the region of the nasal-frontal suture. The bone was apparently long, slender, and similar in shape and size to that in *Varanops*, but it contributed less to the narial opening.

The frontal is long and slender. There is no lateral expansion above the orbits. As in *Varanops*, and in contrast to the condition in non-varanopseid sphenacodonts, the posterior end of the frontal in *Aerosaurus* does not extend as far back as the posterior margin of the orbit.

The postfrontal, because of the extensive contribution of the frontal to the orbital margin, is relatively small and restricted to the skull table.

The preserved portion of the postorbital includes a long, slender ventral ramus that projected down along the posterior orbital margin. As in *Varanops*, a second ramus that extended posteriorly is broader and longer than the ventral process.

The squamosal is seen only in the type specimen and is only partly preserved. What remains indicates that the bone had a long and narrow descending ramus, whose remnants can be seen outlining the posterolateral edge of the skull. This ramus is unusually narrow, even narrower than in *Varanops*.

The parietal is a large, broad element with a well developed posterolateral process. The slender supratemporal element is situated in a shallow groove in this process.

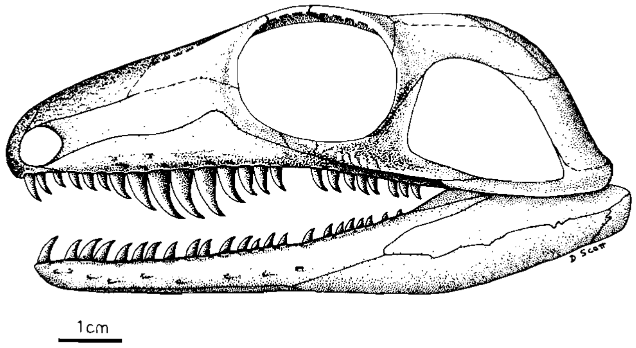

FIGURE 5. *Aerosaurus wellesi* n. sp., reconstruction of skull in lateral view, based upon UCMP 40096 and 40097.

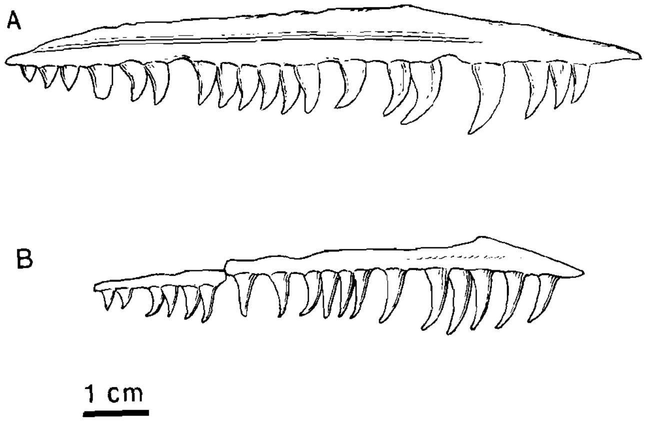

FIGURE 6. *Aerosaurus wellesi* n. sp., referred maxillae showing variation in dentitions. ***A***, left maxilla in medial view, UCMP 40097; ***B***, right maxilla in lateral view, UCMP 40094. Both specimens have lost some of the dorsal edges.

The posterior edge of the parietal is deeply emarginated between the posterolateral process and the midline. From the skull table, the parietals curve ventrally onto the occipital surface along a poorly defined transverse occipital crest. The interparietal, although not preserved, apparently was a broadly triangular bone that did not reach the table.

A right pterygoid, exposed in palatal aspect, is associated with the larger skeleton (UCMP 40097). The three processes of the pterygoid, the transverse flange, the quadrate ramus, and the palatal ramus are partly preserved. The transverse flange resembles that of *Haptodus* (Currie, 1979), and is intermediate in size between pterygoids of *Sphenacodon* and *Ophiacodon*. This flange bore a single row of large teeth, four of which are represented by broken bases. There is also room on the flange for four or five additional teeth of the same size, evidenced by sockets. The long palatal ramus of the pterygoid is well developed. Although its anterior end, marked by a sutural surface for the vomer, is preserved, it is not clear whether the lateral edge is intact. The palatal ramus bears on its medial margin a thickened, tooth-bearing, longitudinal ridge which arises immediately anterior to the junction of the three pterygoid rami. As in *Haptodus* (Currie, 1979), a second, less robust and shorter denticulate ridge occurs parallel and lateral to the first, separated from it by a shallow longitudinal groove. The quadrate ramus, distorted and incomplete in this specimen, appears to be a dorsoventrally wide, thin sheet of bone. Its ventral margin forms a longitudinal ridge that, in normal position, probably corresponded to the more completely formed shelf of bone present in *Haptodus*. The position of the basicranial articulation is not determinable, but a deep medial excavation just posterior to the junction of the three pterygoid rami may have been associated with the basipterygoid articulation. Thus, the articulation with the braincase occurred farther forward than in *Sphenacodon* or *Dimetrodon*, and probably at a more ventral position on the pterygoid. This condition is similar to that of *Haptodus* (Currie, 1979). A second, smaller pterygoid in block UCMP 40096, exposed from above, confirms this interpretation.

What may be a part of the palatine was removed from one of the blocks. It is covered with a shagreen of fine denticles, but the shape of the bone cannot be determined. It is not even certain that this fragment belongs to *Aerosaurus*, because some *Sphenacodon* skeletal elements have been recognized in the Camp Quarry material.

BRAINCASE—The braincase is remarkably well preserved in UCMP 35762 and 40097 (Figs. 7–12). UCMP 35762 displays all external surfaces and lacks only the cultriform process. Although this specimen is well ossified, many of the sutures are still discernible. This is in contrast to the condition in most pelycosaurs, where a strong tendency toward fusion of the braincase elements exists. The braincase forms a structural unit that is buttressed against the skull roof and cheeks through the thin dorsal edge of the supraoccipital, the massive lateral process of the supraoccipital, and the wide paroccipital process of the opisthotic, respectively. The structure is box-like, with posterodorsal (supraoccipital) and anteroventral (parasphenoid) surfaces almost parallel to one another. The occipital surface of the braincase, preserved in UCMP 35762, is plate-like as in all pelycosaurs, and tilts anterodorsally. This large plate is formed by the medial portion and the lateral process of the supraoccipital and opisthotic. The massive lateral processes of the supraoccipital are separated by deep, narrow posttemporal fossae from the broad but anteroposteriorly thin paroccipital processes of the opisthotic (Fig. 10). The paroccipital processes are inclined posterolaterally in characteristic sphenacodont fashion. The combined paraspenoid and basisphenoid bones have an unusual shape for a pelycosaur—that of a large shovel—with a large cultriform process (parasphenoid rostrum) and a thick, widely expanded posterior plate. This complex has separated from the rest of the braincase in UCMP 40097; because it has been exposed by the superior surface, it provides much information about the floor of the braincase (Fig. 12).

The parasphenoid is the largest element of the braincase. It is solidly attached to the ventral surface of the basisphenoid so that only a trace of the suture between them is discernible. Posteriorly, the parasphenoid slightly overlaps the basioccipital and forms the ventral margin of the *fenestra ovalis*. As in other pelycosaurs, the cultriform process is large, comprising about two-thirds of the length of the parasphenoid. The parasphenoid expands laterally from the narrow cultriform process to its maximum width in the region of the basipterygoid tubercles of the basisphenoid. The lateral edges of the posterior third of the parasphenoid are approximately parallel to the long axis of the skull, and are in line with the tips of the basipterygoid processes. The lateral edge of the parasphenoid is contiguous with the basisphenoid to form the venrolaterally expanded *cristae ventrolaterales*. Both the parasphenoid

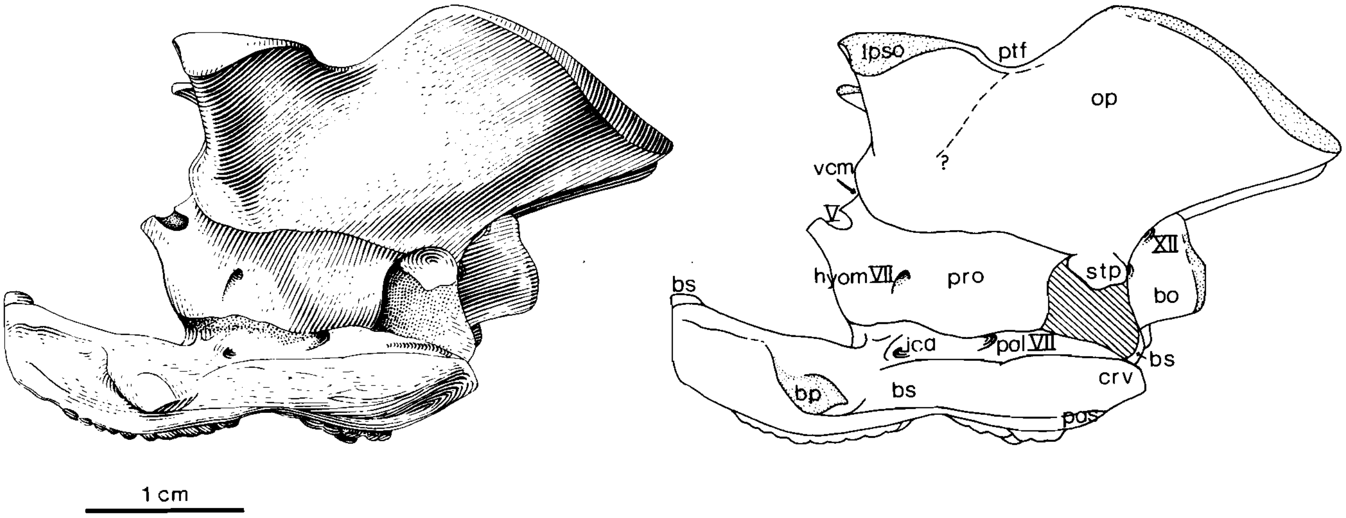

FIGURE 7. *Aerosaurus wellesi* n. sp., referred braincase UCMP 35762 in left lateral view. Broken line represents the inferred position of junction between supraoccipital and prootic drawn from right side of specimen. Abbreviations: ***bo***, basioccipital; ***bp***, basipterygoid process of basisphenoid; ***bs***, basisphenoid; ***crv***, *crista ventrolateralis*; ***hyom VII***, supposed channel for hyomandibular branch of the facial nerve; ***ica***, foramen for internal carotid artery; ***lpso***, lateral process of supraoccipital; ***op***, opisthotic; ***pal VII***, foramen for palatine branch of facial nerve; ***pas***, parasphenoid; ***pro***, prootic; ***ptf***, posttemporal fossa; ***stp***, process for footplate of stapes; ***vcm***, notch for *vena cerebralis medius*; ***V***, notch for the trigeminal nerve; ***XII***, foramen for the hypoglossal nerve.

and basisphenoid have longitudinal striations on the cristae, which arise from the dorsal surface and cross diagonally over the lateral edge. This imparts a fibrous appearance to the sides of the *cristae ventrolaterales* that has not been reported in any other pelycosaur, but is somewhat reminiscent of the *torus transiliens* on the lateral edges of the pterygoid flanges in crocodilians. The *cristae ventrolaterales* appear crescentic in posterior aspect, but are flatter and much wider than is usual for sphenacodont pelycosaurs. The relatively short and broad shape of the cristae accentuates the box-like appearance of the braincase. The cristae are separated from each other by the broad and relatively deep median trough of the parasphenoid. This trough ends posteriorly in a delicately serrated edge below the basioccipital.

The most striking feature of the basal side of the braincase is the presence on the parasphenoid of numerous strong, pointed, and recurved teeth (Fig. 8). These teeth are arranged in three groups in a definite pattern. A posterior group occupies a broadly U-shaped band on a transverse bridge of bone at about the mid-length of the expanded parasphenoid plate. Anteriorly, near the basipterygoid processes, two narrower series of up to three teeth in width are borne on ventral ridges of bone that follow the downturned lateral edges of the parasphenoid plate. These merge anteriorly and continue a short distance onto the cultriform process. Farther anteriorly, the cultriform process has a median ventral ridge with teeth that are more widely spaced and less regularly disposed than those of the lateral series. How far these continue anteriorly on the process cannot be determined. In addition, occasional teeth appear randomly on the ventral surface of the parasphenoid.

Much of the parasphenoid is covered dorsally by the basisphenoid. The exposed areas in UCMP 40097 include the anterior portion of the cultriform process and the posterior portion of the expanded plate (Fig. 12). Dorsally, the cultriform process forms a broadly U-shaped longitudinal trough whose relatively low sides subside anteriorly until they disappear at the tip of the process. The sides and bottom of the trough are finely striated longitudinally. The parasphenoid displays a broad, coarse surface in the area of its posterior emergence from beneath the basisphenoid (Fig. 12). Medially, the dorsal surface of the parasphenoid has fine longitudinal striations in the area of its attachment to the overlying basioccipital. On the superior surface of the *crista ventrolateralis*, anterior to the *fenestra ovalis*, the pattern of coarse ridges and grooves is irregular.

The basisphenoid is a large and complex element that is difficult to consider apart from the parasphenoid. These two bones are so extensively co-ossified that a vague division between them can be discerned only posterolaterally (UCMP 35762). Here a suture extends a short distance anteriorly from the *fenestra ovalis*, along a narrow lateral groove beneath, but close to, the base of the basipterygoid process; it disappears into the lateral corner of a deep oval pit (possibly a foramen) near the anteroventral corner of the basipterygoid process (Fig. 7).

The most distinctive structures of the basisphenoid are the large basipterygoid processes or tubera. They extend laterally far from the base of the cultriform process. The distance between the lateral tips of the basipterygoid processes is unusually wide in *Aerosaurus*, nearly equal to that between the posterolateral corners of the parasphenoid-basisphenoid complex, and equal to one-half of the distance between the lateral edges of the paroccipital process.

The dorsal and anterior surfaces of the massive triangular processes are scarred for the attachment of the cartilaginous sheet that lined the synovial joint between the basisphenoid and the epipterygoid. An anterodorsal scarred ridge that extends from the base of the basipterygoid process to its acuminate lateral end separates the dorsal and anterior surfaces.

The posterior one-fifth of the trough in the cultriform process of UCMP 40097 is occupied by the ossified part of the basisphenoidal rostrum, which ends anteriorly in a poorly ossified, unfinished surface. The trough continues posteriorly on the basisphenoid, but there its surface is not striated. The trough becomes shallow posteriorly and disappears at an indistinct transverse elevation at the rim of the retractor pit (= *sella turcica*, see below). Dorsally, the basisphenoid rostrum has a mid-longitudinal ridge in the area where the cultriform process is broken. The ridge disappears posteriorly into a short and deep median fossa. The fossa ends posteriorly at a small transverse elevation, but its lateral edges are thick and transversely rounded. These edges, the *cristae trabeculares*, continue posteriorly as parts of the transverse elevation, joining across the midline in a narrow ridge. Posteriorly, the depression contains an opening which probably transmitted the internal carotid. Posterior to this anterior foramen of the internal carotid is a depression commonly called *sella turcica*. This feature, however, is better termed the retractor pit (Heaton, 1979). This pit is located slightly posterior to a plane through the basipterygoid processes, and is relatively small in comparison to the size of the paraphenoid-basisphenoid complex. Rising posteriorly and above the pit is the *dorsum sellae* (UCMP 35762).

The *dorsum sellae* appears lower than in *Dimetrodon* and is less thoroughly ossified. In *Aerosaurus*, the basi-

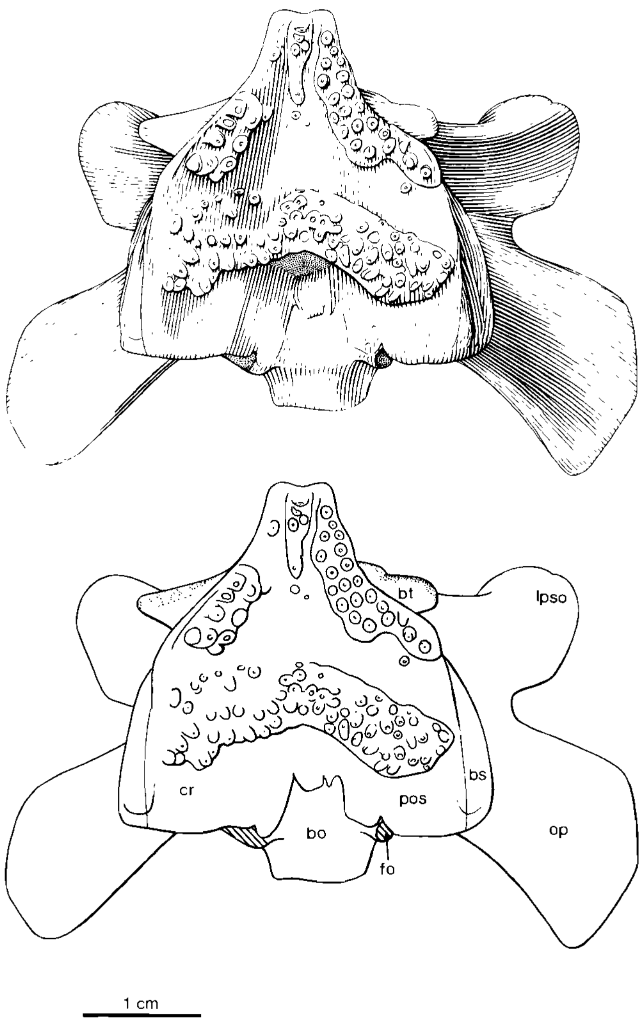

FIGURE 8. *Aerosaurus wellesi* n. sp., referred braincase UCMP 35762 in ventral view. Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **bt**, basipterygoid process of basisphenoid; **cr**, *crista ventrolateralis*; **fo**, *fenestra ovalis*; **lpso**, lateral process of supraoccipital; **op**, opisthotic; **pas**, parasphenoid.

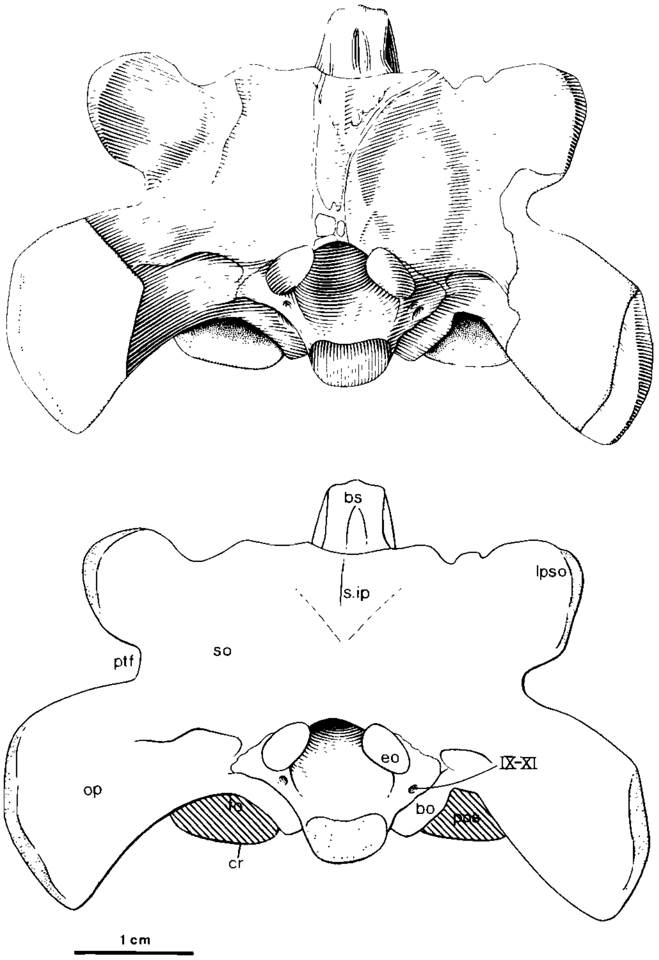

FIGURE 9. *Aerosaurus wellesi* n. sp., referred braincase UCMP 35762 in dorsal view. Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **cr**, *crista ventrolateralis*; **eo**, exoccipital; **fo**, *fenestra ovalis*; **lpso**, lateral process of supraoccipital; **op**, opisthotic; **pas**, parasphenoid; **ptf**, posttemporal fenestra; **s.ip**, sutural surface on supraoccipital for interparietal; **so**, supraoccipital; **IX-XI**, jugular foramen.

sphenoid is the principal contributor to the *dorsum sellae*. This is in contrast to the condition in other pelycosaurs, in which there is little (if any) basisphenoid participation in the dorsum. In living reptiles and in captorhinids, however, the basisphenoid is the main contributor (Heaton, 1979). In UCMP 35762 the *dorsum sellae* comprises a massive pillar, termed *processus sellaris* by Heaton (1979) and prootic process by Romer and Price (1940), that arises from the *processus clinoideus* on either side of the retractor pit. The suture between the prootic and basisphenoid extends upward and around the anterior edge of the *processus sellaris*, traverses the process diagonally above the anterior abducens foramen, and crosses the *crista sellaris* of the *dorsum sellae* just below its dorsal edge.

This construction of the *dorsum sellae* is unique among the pelycosaurs, and what can be seen of the braincase in UCMP 40097 confirms the condition in UCMP 35762. A pair of massive pillars arise from the basisphenoid, form the abducens foramen (where they are broken off), and attain a greater height medially than laterally. It is probable that the dorsum did not contain a median opening; a vertically oval fenestration in UCMP 35762 is probably an artifact of preparation. The transverse wall of the *crista sellaris* is incomplete in UCMP 40097, but the preserved portion suggests that there was no fenestration in this area.

Posterior to the *dorsum sellae*, the basisphenoid forms a dorsal cover to the parasphenoid that is partly marked by sharp ridges and grooves. The ridges extend onto the lateral surface of the parasphenoid-basisphenoid complex. The medial edge of the dorsal surface of the basisphenoid extends from the *dorsum sellae* to the posterolateral corner of the *crista ventrolateralis*.

In lateral view, the basisphenoid displays a long, poorly defined suture with the prootic. This suture extends posteriorly from the *processus clinoideus* to the *fenestra ovalis*. Ventral to this suture, the basisphenoid forms a low, nearly vertical wall that is separated from the horizontal dorsal surface of this bone by a deep trough. In this trough are two foramina, an anteromedial excavation for the palatine (vidian) ramus of the facial nerve, and a posterior, narrow channel that extends over the dorsal surface of the basisphenoid to the posterolateral corner of the *crista ventrolateralis*.

The two foramina just noted are probably for the palatine (vidian) ramus of the facial nerve and the internal carotid, respectively. The elongate posterior foramen

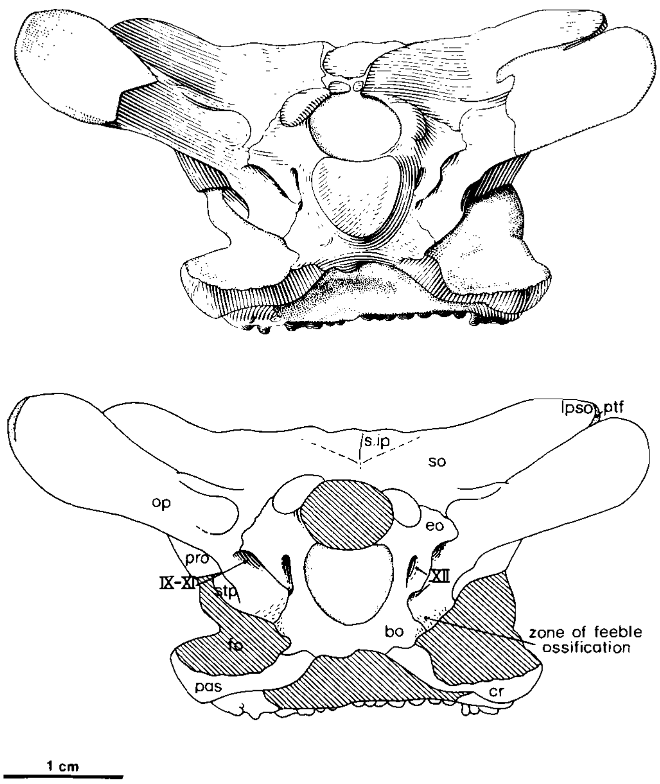

FIGURE 10. *Aerosaurus wellesi* n. sp., referred braincase UCMP 35762 in occipital view. Abbreviations: ***bo***, basioccipital; ***cr***, *crista ventrolateralis*; ***eo***, exoccipital; ***fo***, *fenestra ovalis*; ***lpso***, lateral process of supraoccipital; ***op***, opisthotic; ***pas***, parasphenoid; ***pro***, prootic; ***ptf***, posttemporal fenestra; ***s.ip***, sutural surface on supraoccipital for interparietal; ***so***, supraoccipital; ***stp***, process for footplate of stapes; ***IX-XI***, jugular foramen; ***XII***, foramen for hypoglossal nerve.

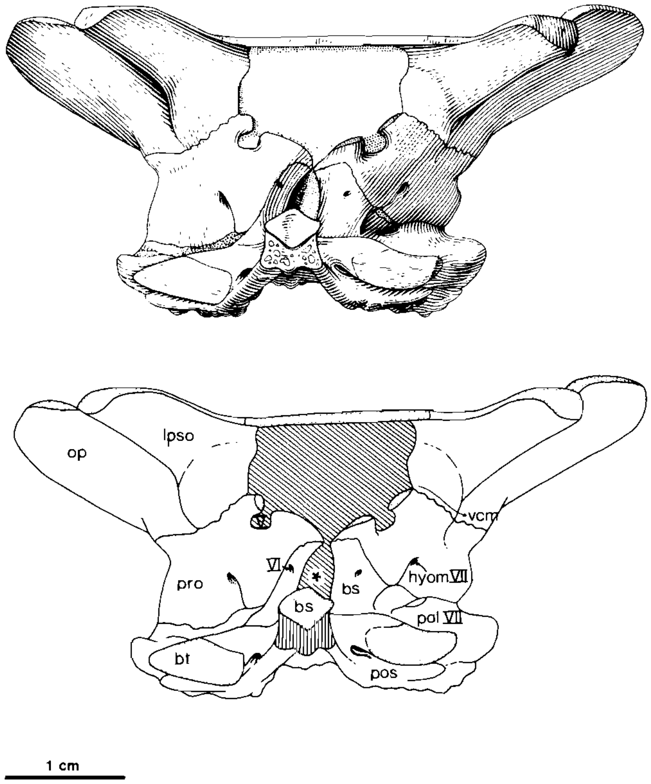

FIGURE 11. *Aerosaurus wellesi* n. sp., referred braincase UCMP 35762 in anterior view. Asterisk indicates posterior area in *dorsum sellae* damaged during preparation and appearing as a fenestra in the specimen. Abbreviations: ***bs***, basisphenoid; ***bt***, basipterygoid process of basisphenoid; ***hyom VII***, foramen for palatine branch of facial nerve; ***pas***, parasphenoid; ***pro***, prootic; ***vcm***, notch for *vena cerebralis medius*; ***V***, notch for trigeminal nerve; ***VI***, foramen for abducens nerve.

probably transmitted the palatine ramus of the facial nerve. This large foramen opens anterolaterally between the prootic and basisphenoid. It is clearly defined only when these two bones are suturally attached, as in UCMP 35762. Otherwise, the basisphenoid portion of the foramen has a notch on the dorsal edge of the bone (UCMP 40097). The anterior foramen, probably for the internal carotid, is located just posterior to the *processus clinoideus* and opens posterolaterally. The long channel probably carried the internal carotid anteromedially, across the superior surface of the basisphenoid and to this foramen. This is the most direct route for the internal carotid, but the position of both the canal and the foramen is unusual. If the carotid looped around the basipterygoid process and entered the basicranium through the foramen located at the base of the process, the close apposition of the basipterygoid processes to the parasphenoid plate would have restricted the vidian sulcus and would have necessitated the rerouting or loss of the artery. It is also possible that the apparent foramen at the anteroventral corner of the basipterygoid process is only a deep pocket formed when the laterally spreading parasphenoid plate became closely appressed to the ventral surfaces of the process.

The prootic is a relatively large element that comprises most of the ventrolateral wall of the braincase. It surrounds a part of the internal ear cavity externally, contributes to the dorsal part of the *dorsum sellae*, and forms the anterior margin of the *fenestra ovalis* (Figs. 7, 11). Ventrally, the prootic is sutured to the basisphenoid, anteriorly, it contributes to the anterior edge of the braincase as the *processus sellaris*. Between the *processi sellates* the prootic forms a narrow bridging sheet of bone, the *criata sellaris* of the *dorsum sellae*. The anterodorsal portion of the prootic bounds the trigeminal notch. The notch represents the largest of the lateral cranial foramina. Its dorsal edge was not ossified, but it is surrounded by more bone than is usual in pelycosaurs. Dorsally, the prootic has an unusually long sutural contact with the supraoccipital and opisthotic. Posteriorly, the prootic enters the anterior border of the *fenestra ovalis*. An exit for the hyoid ramus of the facial nerve occuts slightly anterior to the center of the prootic. A foramen for the palatine branch of the facial nerve is represented by a matrix-filled gap between the prootic and basisphenoid. The palatine foramen is oval, faces anterolaterally, and is larger than the hyoid foramen. It opens into a wide basin near the dorsal edge of the basisphenoid (Figs. 7 and 12), which may have lodged the geniculate ganglion.

The supraoccipital is a wide median element with a low sagittal crest and shallow excavations posterodorsally on either side of the crest, for insertion of the *M. rectus capitis* (Fig. 10). A wide triangular sutural area situated anterodorsally is probably for the interparietal. The roof of the supraoccipital is thin. Its anterior edge is wide and has an unfinished border that does not project as far anteriorly as in *Sphenacodon* or *Dimetrodon* (Romer and Price, 1940). The large lateral process of the supraoccipital is braced anteroventrally by a massive ridge that abuts upon the prootic ventrally (Fig. 11). The distal surface of the lateral

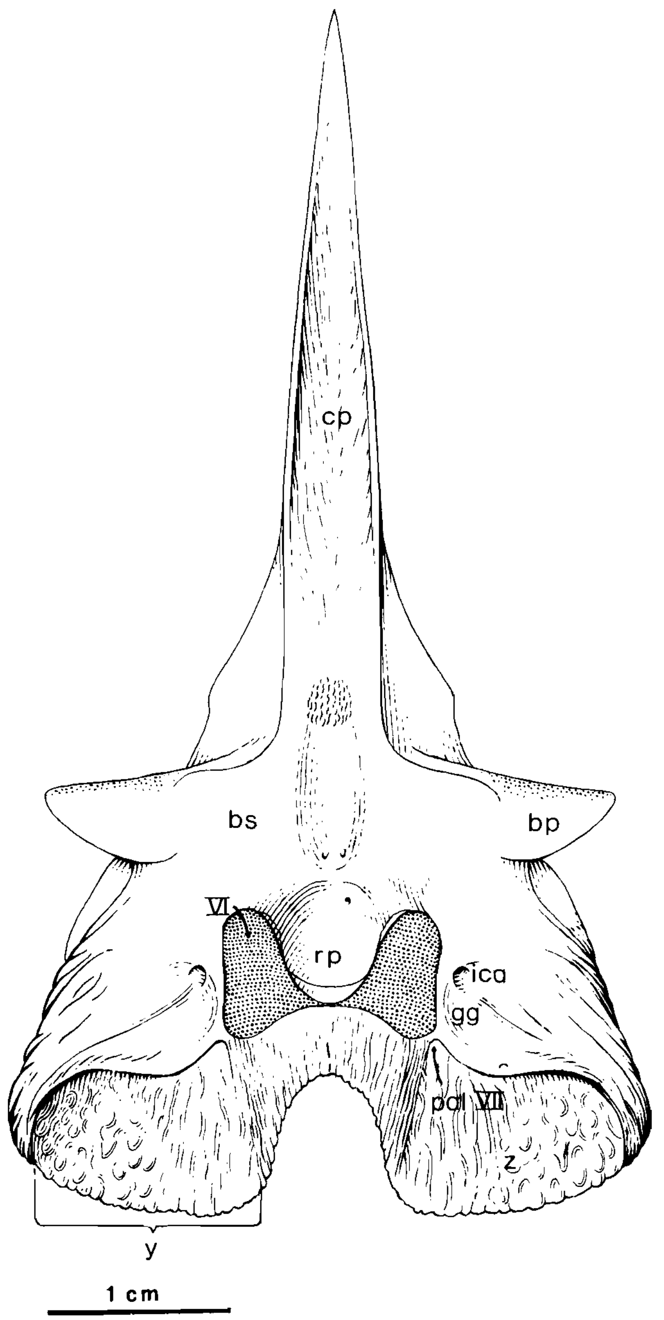

FIGURE 12. *Aerosaurus wellesi* n. sp., basicranium of referred specimen UCMP 40097 in dorsal view. Stippling indicates spongy basisphenoid bone approximately at the contact surface underlying the otic segment of the braincase (details of this surface have been largely destroyed). Abbreviations: ***bp***, basipterygoid process of basisphenoid; ***bs***, basisphenoid; ***cp***, cultriform process; ***gg***, excavation probably occupied in part by the geniculate ganglion; ***ica***, foramen for internal carotid artery; ***pal VII***, foramen for palatine branch of facial nerve; ***rp***, retractor pit; ***y***, parasphenoidal edge of the *fenestra ovalis*; ***z***, basin in upper surface of parasphenoid-basisphenoid complex occupied in life by cartilaginous extension of the otic elements beneath the vestibule; ***VI***, foramen for the abducens nerve.

process of the supraoccipital is unfinished. A so-called venous notch (Romer and Price, 1940, Fig. 10) is located just above the trigeminal notch, at the anterior junction of the supraoccipital and the prootic. The notch is bordered above by a bulge in the anteroventral corner of the supraoccipital buttress (Figs. 7 and 11). It is shallower than in *Dimetrodon*. The suture between the prootic and supraoccipital extends from the venous notch posteriorly and approximately parallel to the basicranial axis, and reaches the anterodorsal edge of the *fenestra ovalis*. How much of the braincase above the *fenestra ovalis* is formed by the supraoccipital is uncertain because of the absence of a distinct division between this bone and the opisthotic. A fine line stained red by matrix is discernible on the right side of the specimen between the lateral process and the paroccipital process. If this marks the suture between the supraoccipital and the opisthotic, then the opisthotic forms not only most of the dorsolateral wall of the braincase, but also all (or most) of the paroccipital processes.

The opisthotic appears to be a relatively large element and the paroccipital processes are unusually well developed for a pelycosaur. The opisthotic is poorly ossified in the region of the *fenestra ovalis*. The left paroccipital process has been broken in UCMP 35762, revealing the cross section at about mid-length. The walls of the process are thin and the interior of the bone is cancellous. A low ridge originates from the posterodorsal surface of the paroccipital process in a short distance medial to the fracture. This ridge becomes larger as it passes ventromedially toward the *foramen magnum*, and for a short distance forms the sharp superior edge of a shallow groove. This groove widens medially and ends near the exoccipital in a shallow, ovate depression presumably for the insertion of the *M. obliquus capitis inferior*. Possibly, the contact between the supraoccipital and opisthotic on the occipital plate is associated with this ridge and groove, but no suture is visible. The anteroventral surface of the paroccipital process is gently convex , but, in contrast to the condition in other sphenacodonts, the proximal part of this surface is smooth. In sphenacodonts this area has a long massive ridge for the dorsal process of the stapes.

The paroccipital process has a slightly concave, keeled ventral edge that extends from the region of the *fenestra ovalis* to the expanded lateral head of the process. Proximally, it ends at a pit that lies above the posterodorsal edge of the *fenestra ovalis* (Fig. 10). This pit corresponds to a similar excavation in sphenacodonts, where it is associated with a well developed ventral flange that forms the border of the *fenestra ovalis*. The pit and flange of the opisthotic provide support for the large stapedial footplate in *Dimetrodon* (Romer and Price, 1940). In *Aerosaurus* the posteroventral excavation probably served the same function, but the ventral flange is very small. The posterior surface of the opisthotic is unfinished below the flange, and it is probable that the *fenestra ovalis* was completed in cartilage in this region. The *fenestra ovalis* appears to extend dorsally between the stapedial pit of the opisthotic and the posterior margin of the prootic to the base of the paroccipital process. This suggests that the area posterodorsal to the *fenestra ovalis* was also persistently cartilaginous.

As in *Captorhinus* (Heaton, 1979), in pelycosaurs a notch usually occurs on the ventral edge of the paroccipital process, opposite a corresponding notch between the dorsal process of the stapes and the footplate. When the stapes is in position, these opposing notches form a foramen for the passage of the *vena capitis lateralis* and the hyoid ramus of the facial nerve (Heaton, 1979). The notch on the paroccipital process, common to other pelycosaurs, is not present in *A. wellesi*. Neither is there a distinct area on the opisthotic for attachment of the dorsal process of the stapes.

A large ovate jugular foramen issues from the braincase in the exoccipital-opisthotic suture, at about the level of the braincase floor and below the lateral apex of the exoccipital, and dorsolateral of the paired hypoglossal foramina (Fig. 10). As in *Varanops* and most other pelycosaurs, a well developed and fully ossified ventral ramus of the opisthotic abuts against the lateral flange of the basioccipital.

The exposed surfaces of the basioccipital and exoccipitals join without any trace of a suture (Fig. 10). The union between the supraoccipital and these otic elements, often obliterated in adult sphenacodonts, can be seen in places in UCMP 35762 and may be inferred in others. The occipital condyle is apparently formed mainly by the basioccipital. As in *Varanops*, but in contrast to most other pelycosaurs, the occipital condyle is borne on a strong neck (Romer and Price, 1940). The surface of the articulation is flat to slightly concave at its center, but the edges of the condyle are rounded. On either side of the *cavum cranii* a lateral flange of the basioccipital truncates the posteroventral edge of the opisthotic and thus forms the osseous ventrolateral rim of the *fenestra ovalis*. The flange has an anteroventral extension below the fenestra that disappears into a matrix-filled opening in UCMP 35762. The basioccipital, together with the parasphenoid below, forms a floor of indeterminable extent beneath the vestibular region. The bone is sheathed ventrally by a thin sheet of parasphenoid. In ventral aspect, the basioccipital disappears anteriorly toward the apex of the *cavum cranii*, between the *cristae ventrolaterales*; however, it contributes to the exposed surface of the floor of the *cavum cranii*.

The exoccipitals form the usual incomplete ring around the *foramen magnum* (Fig. 10), but it is not clear how much of the braincase is floored by them. They are separated above the *foramen magnum* by the supraoccipital. A prominent pseudozygapophyseal facet for the proatlas occurs on the dorsal process of the exoccipital on either side of the *foramen magnum* (Fig. 10). Paired hypoglossal foramina emerge from the exoccipital. The larger of the two openings is oval and lies dorsal to the smaller, round foramen, at about the level of the braincase floor.

Mandible

The mandible (Fig. 13) is long and slender, resembling *Varanops* in many features. Some of the external surfaces are lightly sculptured with grooves and pits like those on the skull roof. As in *Varanops*, a "sphenacodont notch" and reflected lamina characteristic of more advanced sphenacodonts are lacking. The mandibular symphysis is small, in accordance with the generally slender construction of the jaw. Opposing surfaces are striated, indicating restricted inter-ramal flexibility in life.

The long dentary has a well developed posterodorsal process that overlaps the surangular and extends into the posterior quarter of the lower jaw. The angular and prearticular bones are also long. The splenial is nearly as long as the tooth-bearing part of the dentary. Anteriorly, it extends as a thin, almost slender sheet of bone to the mandibular symphysis but does not enter into it. As in *Varanops*, and in contrast to other pelycosaurs, the splenial is completely covered in lateral view by the dentary. Coronoids have not been identified in the specimens, but a groove on the medial surface of the right dentary in UCMP 40097 indicates that the anterior coronoid may have extended forward to the base of the tenth tooth. As in *Varanops* and *Ophiacodon*, there appears to be a long, slender *foramen intermandibularis caudalis* on the medial surface of the mandible. The articular bone is not well exposed, but it appears to have been more primitively constructed than in *Sphenacodon*. The medial tilt of the articular surface is slight, whereas in sphenacodontids the articular surface is turned down medially and ventrally. The small retroarticular process of the articular, best preserved in UCMP 40096, is slightly curved medially.

Dentition

There are spaces for about 26 marginal teeth in the jaws of *A. wellesi*, significantly fewer than reported for *Varanops* (44) or *Varanodon* (38–40). The upper teeth are longer than in either of those genera and appear flattened laterally, especially near the base. Most of the teeth are more strongly recurved than the teeth of any other well known pelycosaur. Some of the teeth have a triangular depression on the medial surface near the base, as in *Ophiacodon*, but the rectangular section seen in large teeth of advanced sphenacodonts is not apparent. Implantation appears to be subthecodont. Enamel surfaces are smooth and there are no carinae on the upper teeth. Three teeth are preserved in the exposed premaxilla (UCMP 40096), but one more tooth may have been present. The arrangement of the teeth is shown in Figure 5. Several maxillae show that the number of teeth varies from about 18 to 20, with gaps for one to three more teeth, respectively. Size distribution is also variable (Fig. 6A, B). In one maxilla (UCMP 40097) the seven largest teeth are located anteriorly, whereas in another maxilla (UCMP 40096) an equivalent group of large teeth is preceded by three very small teeth. Although present in all specimens, caniniform teeth are not sharply differentiated from other maxillary teeth. The teeth decrease gradually in length posterior to the caniniforms. Two teeth below the orbit, near the serrated edge of the jugal, appear peg-like in UCMP 40096,

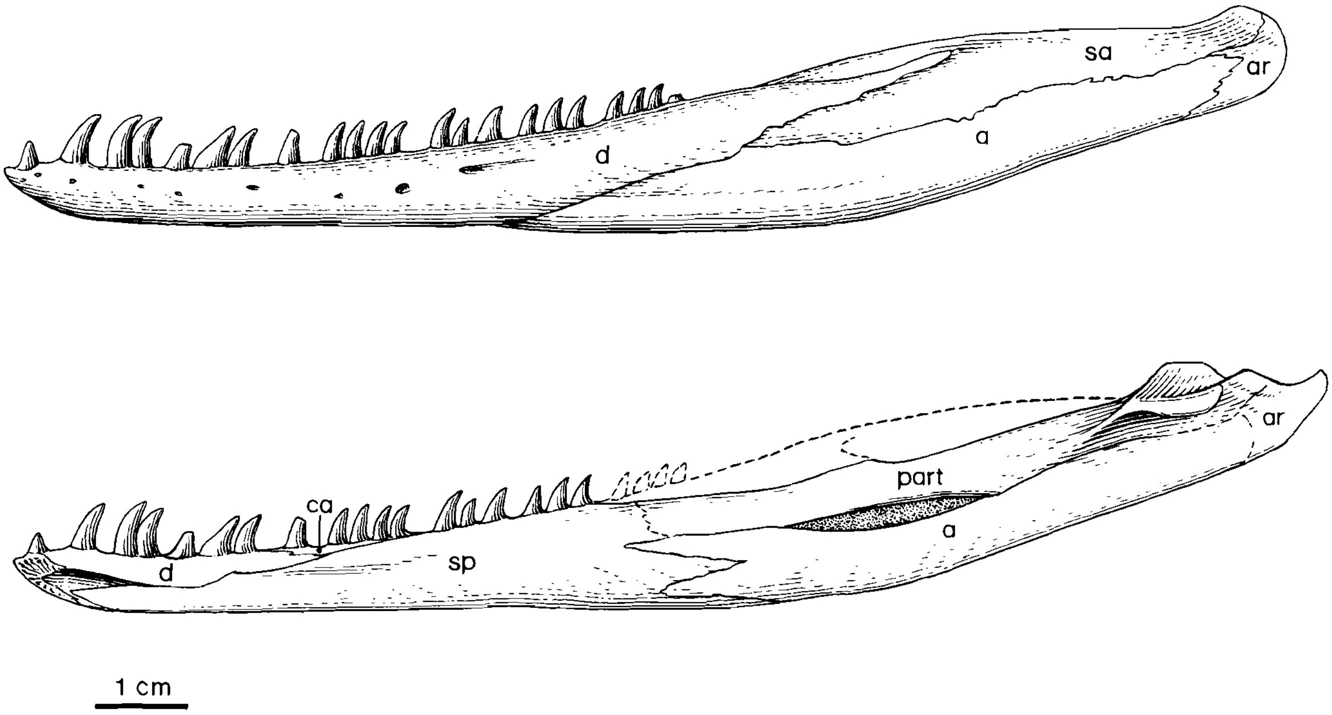

FIGURE 13. *Aerosaurus wellesi* n. sp., mandible of referred specimen UCMP 40097. ***A***, left ramus in lateral view; ***B***, right ramus in medial veiw. The posterior ends of the rami appear different, possibly as the result of damage to the specimen. Abbreviations: ***a***, angular; ***ar***, articular; ***ca***, anterior coronoid; ***d***, dentary; ***part***, prearticular; ***sa***, surangular; ***sp***, splenial.

because their medial sides have been crushed. An additional six long, slender, and recurved teeth occur posterior to these teeth, and ventral to the postorbital bar and the lateral temporal opening in this specimen. It is not clear how these long, curved posterior teeth were used unless the jaws could be very widely opened.

The strongly recurved mandibular teeth are smaller, more closely spaced, and more uniform in size than those of the maxilla. A few of the lower teeth have a sharp carina on the anterior edge of the crown, and it is probable that this was present in all the teeth. The teeth on the dentary gradually decrease in size posteriorly, but this is subject to some variation. The dentary of UCMP 40096 contains 28 teeth, with replacement gaps for at least four more teeth. In the UCMP 40097 there are 22 teeth and 8 gaps in the right dentary.

Vertebrae

Twenty-six presacral vertebrae, including a proatlas, are preserved in the type skeleton. One or two mid-dorsal vertebrae are missing due to erosion that has cut a channel through the thoracic region. Five or six of the anterior vertebrae may be regarded as cervicals. Three sacral vertebrae are present. No preserved series of caudal vertebrae is complete. Three disjointed segments from the large skeleton (UCMP 40097) contain at least 70 caudal vertebrae; although this is the minimum number of caudal vertebrae for this species, it is greater than the numbers usually reported in other pelycosaurs.

The vertebrae (Fig. 14F) resemble those of *Varanops*, but despite the greater maturity of the individual specimens of *A. wellesi* they have significantly shorter neural spines than those of immature *Varanops*. This is unexpected because the anteroposterior dimensions of the neural spines and of the centra are nearly identical in the two species. The excavation of the neural arches of the dorsal vertebrae appears deeper in *A. wellesi* than in *Varanops* and is more reminiscent of the condition seen in advanced sphenacodonts.

The bipartite proatlas arch is represented by fragments in UCMP 40096. The short neural arch of the atlas is characteristically double and bears a small posterior spine, which passes lateral to the zygapophyses and overlaps the base of the axial spine for about one-half of its length. The axis is approximately equal to the other cervicals in length. The pedicel of the axial neural arch is relatively shorter anteroposteriorly than pedicels of the other cervical vertebrae. Its spine is longer anteroposteriorly, but is of similar height to the other cervicals. Its dorsal edge is thickened and nearly horizontal, as in *Varanops*, and more like in ophiacodonts than sphenacodonts. Cervical centra are either hidden in matrix or are badly distorted in all specimens. The dorsal centra are deeply amphicoelous and probably perforate. Their form is also difficult to define owing to postmortem distortion of most of the exposed bones. In the type specimen, where they have been crushed dorsoventrally, the mid-dorsal centra are spool-shaped and appear much longer than high. Ventrally, these centra have a well developed longitudinal ridge that is less pronounced than that of *Varanops* or other sphenacodonts. Bevelling for intercentra is not pronounced. All the vertebrae are well ossified; there is no suture visible between the neural arch and centrum on the vertebrae of any specimen. Pedicels of the dorsal vertebrae are slightly shorter anteroposteriorly than their respective centra; they are deeply notched behind and extend far anteriorly, thus giving the impression of relative shortness. The neural spines of the dorsal vertebrae are low; maximum height of about 18 mm is reached at vertebra 18. Spines, particularly toward the front of the series, appear flared at the top when seen from the side. The dorsal edge of all presacral spines is flat, suggesting close approximation to the skin, or possibly the presence of a cartilaginous cap. The transverse processes of the presacral vertebrae are well developed, moderately wide anteroposteriorly, and project laterally at right angles to the neural arches. The transverse processes of anterior dorsal vertebrae are longer than those of cervical or more posterior dorsal vertebrae, but none approaches the elongate, slender construction found in *Dimetrodon* or *Sphenacodon*.

In contrast to the condition in *Varanops*, where the spines of the posterior dorsal vertebrae are much shorter anteroposteriorly than in other presacral vertebrae, the corresponding spines in *A. wellesi*, although lower, retain the same anteroposterior dimensions as in the other dorsal vertebrae. In addition, the neural spines of successive sacral vertebrae decrease gradually in anteroposterior diameter. Neural spines of anterior caudal vertebrae are much narrower in lateral view than are those of presacral vertebrae. The neural spines diminish gradually in size posteriorly and are never longer than the height of their respective centra. Neural spines disappear as discrete processes at approximately the 25th caudal. Prezygapophyses project anteriorly beyond the centra through much of the caudal series. The first seven caudal vertebrae bear ribs in UCMP 40096.

Intercentra are present in the dorsal series; chevrons begin with about the fifth caudal vertebra. Only the most anterior chevrons are as long as the height of their respective vertebrae, and are not greatly expanded distally. Some anterior chevrons appear to have been "closed" proximally by a thin transverse bar of bone, the intercentrum. The distal caudal vertebrae, although poorly preserved, seem to be slender and cylindrical.

Ribs

All presacral vertebrae bear slender double-headed ribs. Although many of the ribs are articulated in the specimens, it is not possible to tell which of them are the longest. Some dorsal ribs (UCMP 40097) are slightly expanded distally. There are three sacral ribs in UCMP 40096. The two anterior sacral ribs are fused to the vertebrae. The first is the most massive of the three; it appears Y-shaped in dorsal view, with a thick iliac process and a long, slender posterior branch that partly overlaps the second sacral rib. The second rib is similar, though smaller and with shorter processes. A third sacral rib, seen on the left side of UCMP 40096, is detached from its vertebra, but lies nearby in the matrix. This rib lacks the strong processes of the two preceding ribs, but is short and thickened distally. The first caudal vertebra bears a characteristic pelycosaurian caudal rib that curves posteriorly, overlapping succeeding ribs as far back as the fourth or fifth vertebra. Other anterior caudal ribs have the same form, but are successively shorter. Beyond the fifth vertebra, "ribs" are simply short lateral processes which disappear in the vicinity of the ninth caudal.

Gastralia are represented by a small cluster of tiny rods lying near the distal ends of several articulated ribs in UCMP 40097. Their manner of preservation does not permit either determination of orientations or configuration at the midline. In other pelycosaurs, gastralia are long, narrow plates rather than rods (Reisz, 1975). In one specimen of *Archeothyris* from Linton, Ohio, gastral scales are preserved in both ventral and dorsal views. The dorsal view shows that the edges of some scales are curled inwards, giving them the appearance of rods rather than narrow plates. Probably the same preservational artifact has occurred in UCMP 40097.

Appendicular Skeleton

PECTORAL GIRDLE—The entire pectoral girdle is probably preserved in the type specimen, but only the medial surface of the left scapula is partially exposed. The right endochondral shoulder girdle of UCMP 40097, complete except for its anterodorsal edge, has been freed from the matrix. A clavicle of this specimen is also preserved. An interclavicle probably belonging to the same species (if not to this individual) is present in a block of matrix labelled

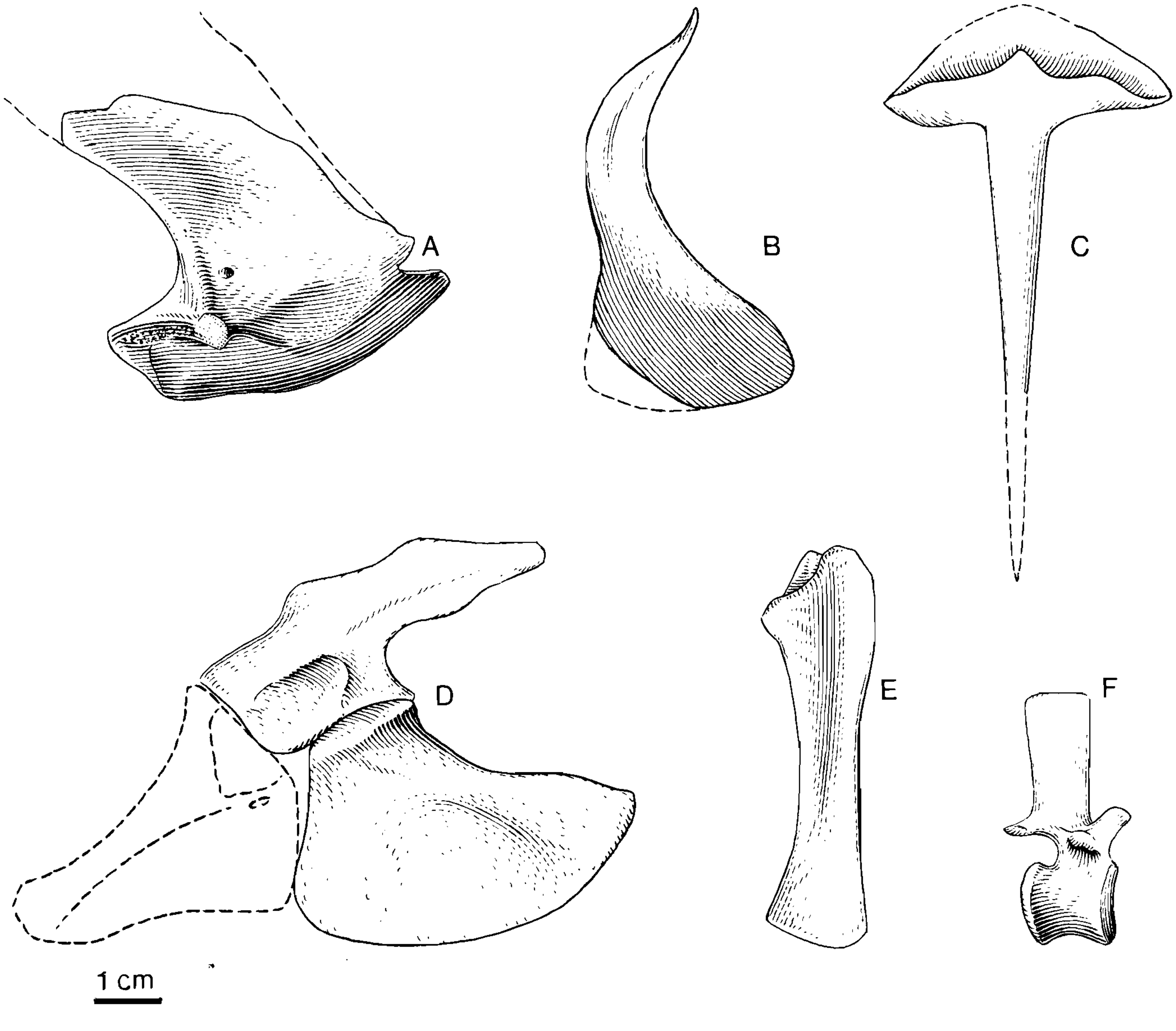

FIGURE 14. *Aerosaurus wellesi* n. sp., postcranial elements of referred specimen UCMP 40097. ***A***, right scapulocoracoid in lateral view; ***B***, right clavicle in lateral view; ***C***, interclavicle in ventral view; ***D***, left pelvis with pubis in lateral view, restored after *Varanops*; ***E***, ulna in ventral view; ***F***, twelfth presacral vertebra in lateral view.

UCMP 40094. No cleithrum has been identified in the collection.

The shoulder girdle differs little from that of *Varanops* (see Williston, 1911, Pl. 5). The scapulocoracoid (Fig. 14A) is broad, but owing to damage the outline of the anterior edge and the height of the blade cannot be determined. The blade appears to have curved more strongly posteriorly than in *Varanops*, but this may result from crushing. The anterior edge of the scapulocoracoid is sharply emarginated opposite the glenoid. It is not clear whether this notch occurs only on the coracoid, as in *Varanops*, or is shared by the scapula, because no sutures are discernible between the bones. The supraglenoid buttress is wide at its base, but narrows rapidly upward and the scapular blade thins transversely. A small supraglenoid foramen occurs on the scapular blade; it is closer to the posterior edge or to the buttress than in *Varanops*; and more ventrally on the blade and nearer the glenoid fossa than in the type of *A. greenleeorum*. The anterior buttress of the glenoid is massive, and is presumably composed of scapula and coracoid.

The clavicle (Fig. 14B) seems slightly more robust than in *Varanops*. It is not clear to what extent the proximal head of the bone flared anteriorly, but it is considerably expanded anteroposteriorly. The T-shaped interclavicle (Fig. 14C) is better preserved than in other varanopseids, and is more like that of *Ophiacodon* than *Varanops* (cf. Romer and Price, 1941, Fig. 21).

PELVIC GIRDLE—The pelvic girdle is only partly exposed in UCMP 40096. The elements are not co-ossified (Fig. 14D). Relative to the size of the girdle, the posteriorly

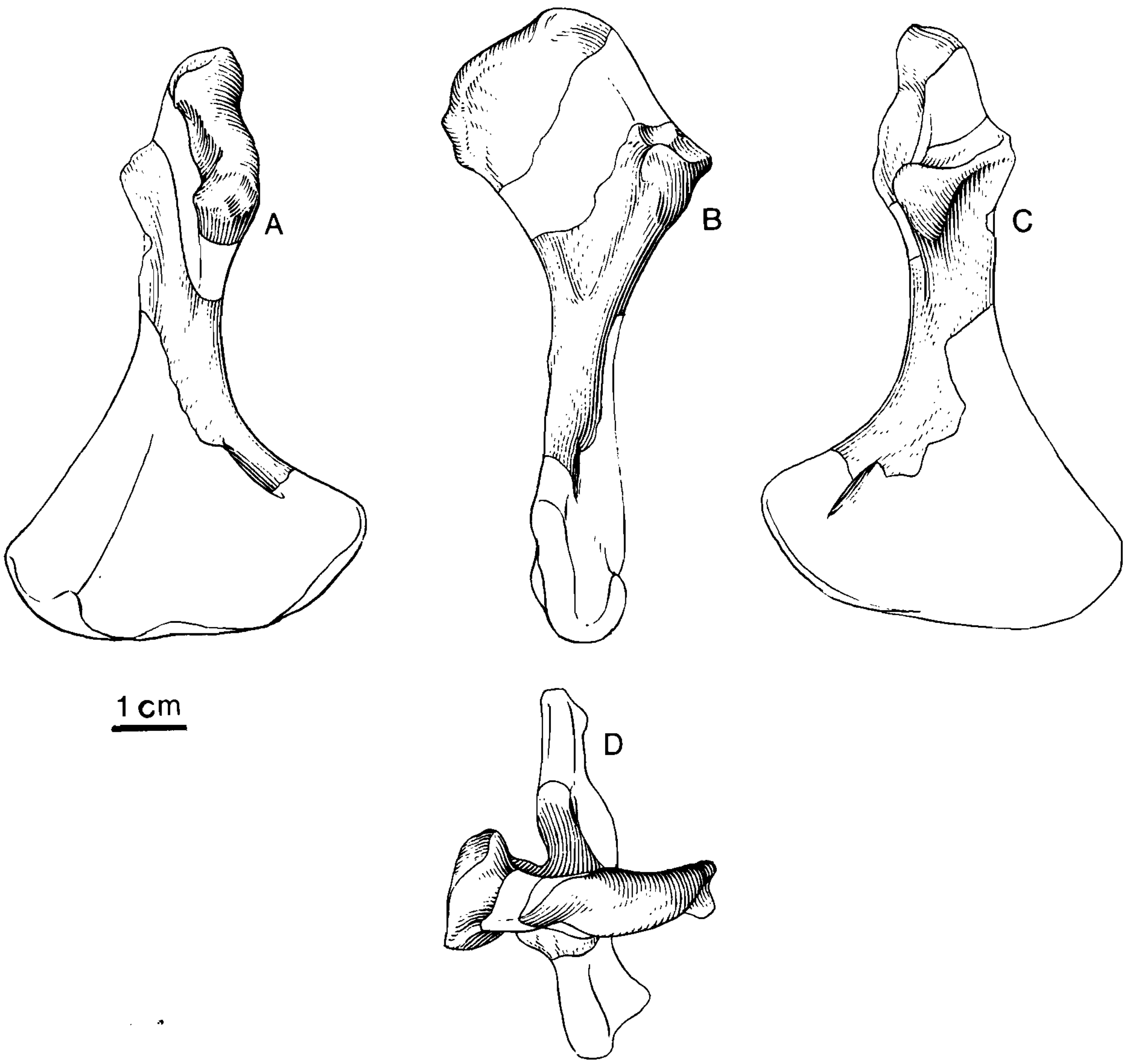

FIGURE 15. *Aerosaurus greenleeorum* Romer, left humerus of type specimen FMNH U.C. 464. ***A***, distal dorsal surface; ***B***, proximal ventral surface; ***C***, distal ventral surface; ***D***, proximal end. The distal end is restored after the humerus of UCMP 40096, which is from an immature individual.

directed iliac blade is somewhat longer and more slender than in *Varanops*. The longitudinal dorsal trough of the iliac blade, present in ophiacodonts but lost in advanced sphenacodonts, is clearly seen here. The presence of this trough is believed to represent a primitive condition for the Pelycosauria. In *A. wellesi* the trough is smaller and shallower than in ophiacodonts. The acetabulum, although better defined than in *Varanops*, has edges that are less well ossified than in the type of *A. greenleeorum*. The neck of the iliac blade seems narrower than in either *Varanops* or *A. greenleeorum*. The ischium is longer and better ossified than in *Varanops*. Its median edge, which no doubt continued as cartilage in life, is convex. The dorsal edge is not so strongly ridged and thickened as in *Varanops*, and does not extend so steeply ventrally as in that genus. In contrast to *Ophiacodon* and *Varanops*, the dorsal edge of the ischium has a slight dorsal flare distally. This condition is also seen is sphenacodontids (Romer and Price, 1940, Figs. 26, 27), but there the dorsal flare is much greater than in *A. wellesi*. The pubis is inadequately exposed and cannot be described.

LIMBS—The limbs of the left side are well preserved and nearly complete in UCMP 40096. The forelimb is about twenty percent shorter than the hindlimb. As in other, more advanced sphenacodonts, the humerus and femur are only slightly longer than the respective lower legs. This allowed for a higher posture and longer stride, and it is probably related to a predaceous mode of life. The incompletely ossified humerus of UCMP 40096 (Fig. 2) is more expanded distally and thicker in the shaft than the humerus of *Varanops*, which was even less ossified. In dorsal aspect, the entepicondylar foramen appears longer than that in *Varanops*. The supinator process is less sharply differentiated, although it is relatively longer than in *Varanops*. There is only a slight indication of an ectepicondylar notch below the supinator process. The character of the deltopectoral crest is not known, but Romer (1937) notes

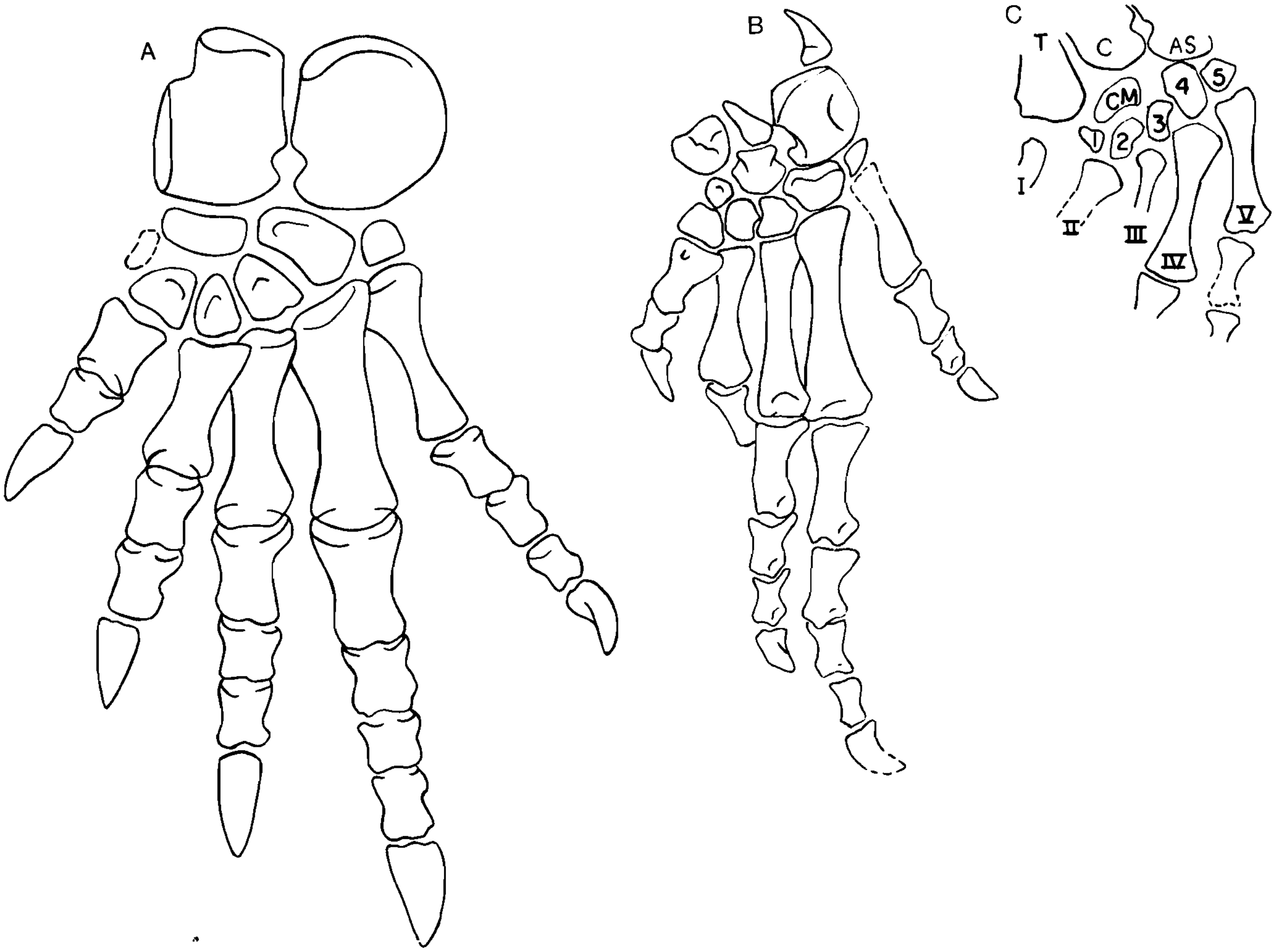

FIGURE 16. *Aerosaurus wellesi* n. sp. ***A***, composite reconstruction of left pes based on all available material and drawn to scale of UCMP 40097; ***B***, left manus in dorsal view, UCMP 40096 (type); ***C***, left pes of referred specimen UCMP 70083, as preserved. Abbreviations: ***as***, astragalus; ***c***, calcaneum; ***cm***, medial centrale; ***t***, tibia; ***1–5***, distal tarsals; ***I–V***, matatarsals.

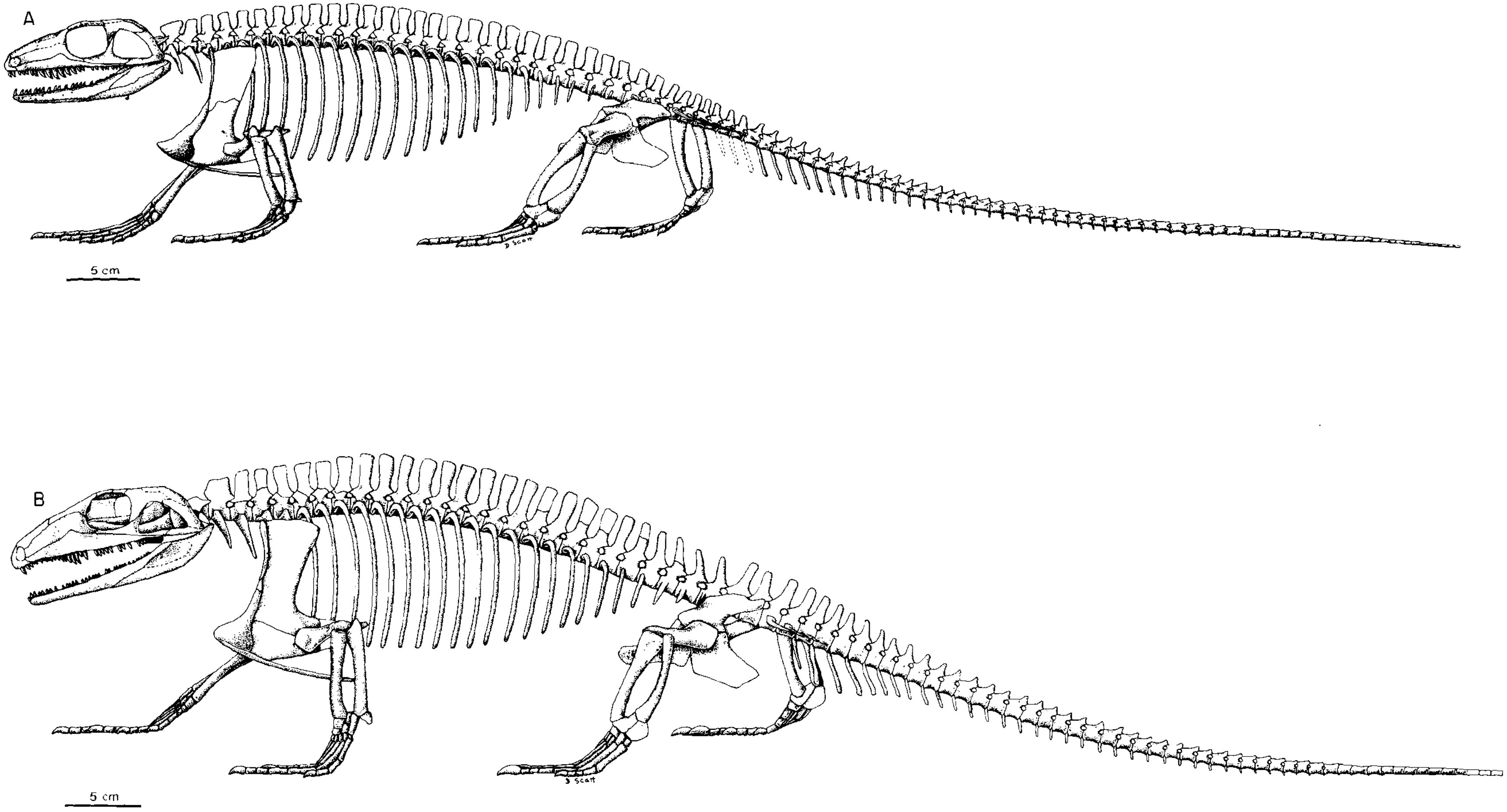

FIGURE 17. Reconstructions of the skeletons of (**A**) *Aerosaurus wellesi* n. sp. (composite), and (**B**) *Varanops brevirostris* (after Romer and Price, 1940).

TABLE 1. Measurements (in millimeters) of *Varanops brevirostris* and *Aerosaurus wellesi* n. sp. *uncorrected for distortion, **measurements considered unreliable; ***after Romer and Price (1940, Tables 1–4).

	Varanops ***	*Aerosaurus**	
		No. 40096	No. 40097
Length of skull from snout to quadrate	140.0	99.0	—
Length of face from snout to orbit	55.0	38.0	—
Anteroposterior diameter of orbit	34.0	28.0	—
Length of skull from orbit to quadrate	50.0	33.0	—
Height of skull at orbit	33.0	26.0	—
Length of mandible	140.0	94.0	151.0
Length of upper tooth row	99.0	65.6	—
Length of lower tooth row	—	50.0	77.6
Length of centra			
Axis	15.0	9.0	—
Fourth cervical	16.0	10.5	—
Middorsal	14.0	11.4	12.8
Posterior dorsal	15.0	—	12.5
Anterior caudal	13.0	—	12.9
Midcaudal	10.5	9.0	11.5
Width of centra (posterior)			
Middorsal	12.5	8.9	—
Posterior dorsal	13.0	—	13.0
Height of centra (posterior)			
Middorsal	14.0	8.1	12.0
Posterior dorsal	14.0	—	12.0
Anterior caudal	10.0	—	11.6
Midcaudal	6.0	6.0	8.0
Overall height of vertebrae			
Axis	18.0	15.7	—
Fourth cervical	—	16.4	—
Middorsal	44.0	26.9	37.0
Posterior dorsal	42.0	—	38.5
Anterior caudal	36.0	—	38.5
Midcaudal	18.0	13.6	16.0
Length of clavicle	70.0	—	62.0
Width of clavicle	32.0	—	26.0+
Distance from top of anterior end of glenoid to top of scapula	70.0	—	43.0+
Length of glenoid	—	—	21.6
Length of humerus	72.0	53.0	—
Width of humerus at proximal end	35.0	22.3**	—
Width of humerus at distal end	41.0	32.2	—
Length of radius	59.0	41.8	55.0
Width of radius at proximal end	13.0	9.0+	12.5
Width of radius at distal end	12.0	9.0	13.0
Length of ulna from lower end of sigmoid notch	57.0	45.0	54.4
Width of ulna at proximal end	18.0	10.2	18.0
Width of ulna at distal end	15.0	10.9	15.0
Length of ilium	52.0	34.7	56.0
Width of iliac neck	24.0	13.0	18.4
Width of iliac base	38.0	23.6	33.4
Length of ischium	58.0	—	52.0
Height of ischium	35.0	—	42.7
Length of femur	87.0	62.5	85.3
Width of femur at proximal end	30.0	17.0	29.0**
Width of femur at distal end	30.0	—	23.0**
Length of tibia	72.0	52.4	60.5
Width of tibia at proximal end	26.0	13.0	—
Width of tibia at distal end	18.0	—	12.0
Length of fibula	75.0	64.0	55.0
Width of fibula at proximal end	18.0	12.8	8.6
Width of fibula at distal end	19.0	—	12.3

TABLE 1. Measurements (in millimeters) of *Varanops brevirostris* and *Aerosaurus wellesi* n. sp. *uncorrected for distortion, **measurements considered unreliable; ***after Romer and Price (1940, Tables 1–4).

	Varanops ***	*Aerosaurus**	
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Posterior dorsal	15.0	—	12.5
Anterior caudal	13.0	—	12.9
Midcaudal	10.5	9.0	11.5
Width of centra (posterior)			
Middorsal	12.5	8.9	—
Posterior dorsal	13.0	—	13.0
Height of centra (posterior)			
Middorsal	14.0	8.1	12.0
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Middorsal	44.0	26.9	37.0
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Midcaudal	18.0	13.6	16.0
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Width of clavicle	32.0	—	26.0+
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Length of glenoid	—	—	21.6
Length of humerus	72.0	53.0	—
Width of humerus at proximal end	35.0	22.3**	—
Width of humerus at distal end	41.0	32.2	—
Length of radius	59.0	41.8	55.0
Width of radius at proximal end	13.0	9.0+	12.5
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Width of iliac base	38.0	23.6	33.4
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Height of ischium	35.0	—	42.7
Length of femur	87.0	62.5	85.3
Width of femur at proximal end	30.0	17.0	29.0**
Width of femur at distal end	30.0	—	23.0**
Length of tibia	72.0	52.4	60.5
Width of tibia at proximal end	26.0	13.0	—
Width of tibia at distal end	18.0	—	12.0
Length of fibula	75.0	64.0	55.0
Width of fibula at proximal end	18.0	12.8	8.6
Width of fibula at distal end	19.0	—	12.3

that the crest in the type of *A. greenleeorum* is unusually massive for the size of the animal and is turned sharply downward and posteriorly. Figure 15 shows the humerus of *A. greenleeorum* (FMNH U.C. 464) with the missing parts restored after the smaller humerus of *A. wellesi* (UCMP 40096).

The ulna (Fig. 14E) has a straight, thick shaft with the ends less expanded than in *Varanops*. The olecranon is moderately well developed in the large skeleton (UCMP 40097), but the sigmoid notch is not developed to the high degree seen in advanced sphenacodonts. The radius is neither greatly expanded at the ends nor much constricted in the shaft; the entire forearm appears more robust than in *Varanops*.

The left manus of UCMP 40096 (Fig. 16B) is visible in dorsal aspect. It is probably complete, but the second digit is bent underneath the third, obscuring some of the phalanges. The bones are well articulated except for the proximal carpals that were moved slightly apart. The carpus comprises about one-fifth of the total length of the extended manus. The medial centrale and the fifth distal carpal are completely ossified. The pisiform is not completely exposed in the specimen, but it was probably smaller than that in *Varanops*. Metacarpals have the same proportions as in *Varanops*, except that the first metacarpal is relatively somewhat longer in *Aerosautus*. The proximal phalanges are approximately two-thirds the length of their respective metacarpals. Terminal phalanges are simple, short, and somewhat recurved claws. The phalangeal formula is 2:3:4:5:3.

Both femora are preserved in the type specimen as well as in the larger, partially articulated skeleton. The shaft is straight and moderately thick, and the ends are not greatly enlarged. The internal trochanter (exposed only in UCMP 40097) appears to be broader than in *Varanops*. There is no notch proximally between this trochanter and the head of the femur. A small isolated femur in block UCMP 40096 shows the area for attachment for the internal and external *M. puboischiofemoralis* (cf. Romer and Price, 1941, Fig. 35). This area is large for a sphenacodont and is much better developed than in *Varanops*. The ventral surface of the femur is not exposed in any specimen.

The tibia is massive and more strongly bowed than in *Varanops*. The fibula is slightly longer than the tibia. It is more strongly bent in the opposite direction and its distal end is expanded. Large facets are present for articulation with the pes.

The incomplete left pes of UCMP 40096 retains only the proximal tarsals, some distal tarsals, and three incomplete metatarsals. Partially articulated parts of both pedes are preserved in the larger specimen. A third specimen (UCMP 70083), which has the proximal part of the left pes appressed to parts of another foot, was collected from the surface at the Camp Quarry. This specimen (Fig. 16C), which is about the size of the pes in the holotype, supplements the other material and permits a reconstruction of the pes (Fig. 16A). The pes is larger than the manus. As in *Varanops*, the calcaneum has a broadly arcuate lateral outline. Its length barely exceeds the width. The astragalus is also short and square-cut, as in *Varanops*, without the long proximal neck seen in most sphenacodonts. The articular surface for the fibula is about two-thirds as wide as that for the tibia. As in *Varanops*, a perforating foramen occurs near the distal end of the articulation, between the astragalus and calcaneum, and is bounded equally by these bones. A large medial centrale is present in UCMP 70083. All metatarsals, but especially the second, are relatively shorter and thicker than in *Varanops*. Proximal ends of metatarsals II through V slightly overlap each other. All phalanges are short and thick. As in some more advanced sphenacodonts, the antepenultimate phalanges tend to be shorter than the others, at least on digits III and IV. The claws appear to have been flattened dorsoventrally toward the tips, but they are more strongly curved than those of the manus. These claws are only slightly longer than the penultimate phalanges. The phalangeal formula is 2:3:4:5:4.

Discussion

Except for a few elements of the foot, the type of *Aerosaurus greenleeorum* consists only of fragments of bone, thus making comparison with the Camp Quarry specimen difficult. The key to the identity of the Camp Quarry varanopseid is in the parasphenoid dentition. Preparation of the fragmentary parasphenoid of the holotype of *A. greenleeorum* revealed the broken bases of two teeth belonging to a lateral group similar to that seen in the Camp Quarry specimens. In addition, on the posterior part of the parasphenoid there is a heavy transverse "pad" of bone with scars where other teeth have been broken off. Thus, there are no observable differences between the parasphenoid dentitions in the type of *A. greenleeorum* and in the Camp Quarry specimens.

Obvious structural differences in the postcranial skeleton include poorer development of ventral keels, lesser lateral constriction of the cervical centra, absence of a typical sphenacodont ventral lip on the centra, and a more anteroventral position of the supraglenoid foramen in *A. wellesi*. The facet on the astragalus that opposed the fourth distal tarsal is not as distinctly formed as in *A. greenleeorum*.

None of the Camp Quarry specimens had attained the size of the type of *A. greenleeorum*, but UCMP 40097 is almost as large. Romer and Price (1940:7–10) devised a "linear unit" for comparing proportions of pelycosaur skeletons. Unfortunately, the incomplete condition of *A. greenleeorum* and the difficulty of obtaining critical measurements from the *A. wellesi* specimens render the linear unit comparisons useless. In addition, Currie (1978) has shown that the orthometric linear unit should not be used to compare individuals of differing levels of maturity. From a purely qualitative viewpoint it is obvious that the ilium is less robust, the centra of the cervical vertebrae are shorter, and the dorsal centra are longer than in *A. greenleeorum*. The glenoid fossa and the proximal end of the humerus are preserved in *A. greenleeorum* but are so distorted in *A. wellesi* that detailed comparisons cannot be made.

The Permian sediments at Arroyo del Agua and El Cobre Canyon, from which all the known *Aerosaurus* material has been taken, have also yielded a number of fragmentary remains of other tetrapods, whose systematic positions are poorly understood. Their possible relationships to *Aerosaurus* have to be examined.

The only other small reptile associated with *A. wellesi* in the Camp Quarry is *Oedaleops campi*, a very primitive caseosaur allied to *Eothyris* (Langston, 1965; Reisz, 1980). This small pelycosaur bears no resemblance to *Aerosaurus*. *Nitosaurus jacksonorum* Romer is based on poorly preserved fragmentary remains from El Cobre Canyon (Romer, 1937; Romer and Price, 1940). The completely dissociated skeletal elements include limb bones, partial pelvic girdles, and some scraps of vertebrae, all of which are difficult to identify. There is also a poorly preserved skull fragment (premaxilla, maxilla, and an impression of the dentary). The postcranial elements are too large to be associated with the skull fragment, even if the small-headed caseids are used for comparison. The skull fragments resemble closely the small pelycosaur *Oedaleops*, whereas the postcranial skeleton, which is comparable in size to *Aerosaurus*, was thought by Romer and Price (1940) to point to edaphosaurian affinities. It seems likely that the holotype of *Nitosaurus jacksonorum* is composite. It is clear, however, that no relationship to *Aerosaurus* exists. *Baldwinonus trux* Romer and Price, from El Cobre Canyon, is so poorly known that it was lumped in the Eothyrididae for want of a better receptacle (Romer and Price, 1940). The fragmentary type specimen seems to include the remains of two different pelycosaurs. One of us (RR) has studied the specimen, and is convinced that the maxilla belongs to a large sphenacodont, whereas the vertebrae are typically ophiacodont (Reisz, 1980). *Puercosaurus obtusidens* Williston is a tiny captorhinomorph which bears no resemblance to *Aerosaurus*. *Chamasaurus dolichognathus* Williston, from El Cobre Canyon, is known only from a slender dentary with small, closely spaced teeth. Unlike *Aerosaurus*, the bone is heavily sculptured. It almost certainly does not belong to a pelycosaur and may be of amphibian derivation.

Other scrappy New Mexico pelycosaurian remains include *Arribasaurus* Williston, *Poliosaurus* Case, and *Dimetrodon navajovicus* Case that have all been assigned to *Ophiacodon* by Romer and Price (1940). *Scoliomus* Williston and Case, from the Arroyo del Agua area, is known from two limb elements probably belonging to a large sphenacodont, possibly *Sphenacodon*.

The similarities between *Aerosaurus* and *Varanops* indicate that these genera are closely related (Fig. 17). Observed differences are:

1. *Aerosaurus* is slightly smaller than *Varanops*, but its skeleton is better ossified.

2. The length of the skull relative to presacral length is smaller in *Aerosaurus* than in *Varanops*.

3. Caniniform teeth are less differentiated in *Aerosaurus*. Most of the larger teeth lie farther anteriorly than in *Varanops*. While occupying about the same relative length of the jaw, the upper dentition of *Aerosaurus* contains only about 26 teeth, as compared to about 43 in *Varanops*. There are fewer "pre-canines" in the maxilla of *Aerosaurus*, (about 5 compared to 11 in *Varanops*), but all the teeth are as closely spaced as in *Varanops*. These differences are primarily the result of the greater anteroposterior width of the tooth bases in *Aerosaurus*, and only partly reflect its relatively shorter face.

4. Excavations of the neural arches in the posterior dorsal vertebrae appear deeper in *Aerosaurus* than in *Varanops*. Neural spines are lower and relatively wider in *Aerosaurus*.

5. The tail of *Aerosaurus* is longer than in any other known pelycosaur, but it is closest to *Varanops* in the number of caudal vertebrae (more than 69 compared to about 60 inferred in *Varanops*).

6. All limb and foot elements are relatively shorter and heavier in *Aerosaurus*. Even in a juvenile, the carpus is better ossified than in the supposedly immature specimens of *Varanops*.

The inferred immaturity of all known individuals of *Varanops* makes the significance of some of these differences difficult to assess. Some evaluation of their importance can be made, however, because the type specimen of *A. wellesi* also appears to be immature. The available evidence suggests that *Varanops* is the less specialized of the two genera.

THE FAMILY VARANOPSEIDAE

Olson (1965) reviewed the genera that had been assigned to the Varanopseidae. He concluded that besides *Varanops* and *Varanodon* only the South African *Elliotsmithia* should be included in this family. The Varanopseidae were relatively long-lived geologically, ranging from the Early into the Late Permian. Included forms are strikingly similar, indicating that the varanopseids represent a relatively conservative lineage.

Varanodon agilis Olson (1965), from the Upper Permian of Oklahoma, is the youngest North American varanopseid. It is known from an almost complete skeleton, which closely resembles both *Aerosaurus* and *Varanops*. A completely unexpected skeletal feature reported by Olson for *V. agilis* is the presence of an antorbital fenestra. Careful examination of the specimen has revealed that the preserved portions of the lacrimal are very thin, and that the anterior part of this bone is completely separated from its posterior part by the supposed fenestra. Furthermore, the edges of the opening are irregular. These facts suggest that the "fenestra" is the result of either postmortem damage or overpreparation. As in *Varanops*, the bones of the face of *Aerosaurus* are obviously very thin and delicate except in the vicinity of the antorbital ridge. This ridge, which is strongly expressed in *Varanops, Varanodon,* and *Aerosaurus*, probably added strength to the upper jaw that was otherwise being weakened by thinning of the facial bones. The suspensorium, though farther back in *Aerosaurus* than in most pelycosaurs, is relatively anterior for a varanopseid and resembles *Varanops* more than *Varanodon*. In the latter form, "...at least one-half of the temporal fenestra lies back of the occipital condyle" (Olson, 1965: 50). The shape of the posterior cheek region of *Varanodon* shows the greatest specialization. The temporal fenestra is lower and longer than in any other pelycosaur, and the squamosal and postorbital bones are correspondingly expanded. *Aerosaurus* resembles *Varanops* more closely than *Varanodon* in this feature.

Particularly significant is the unusual way in which the quadratojugal and maxilla meet below the jugal in the temporal arcade in all the three genera: the maxilla is unusually long and its posterior process extends under the lateral temporal opening. Elsewhere in pelycosaurs, the quadratojugal meets the maxilla in *Eothyris* and *Oedaleops*, but there it is the quadratojugal that has a long anterior process that meets a maxilla of normal length. The upper tooth row is relatively longer in *Varanodon* than in *Aerosaurus*, but this is probably related to the greater specialization of the skull in *Varanodon*. The dentition of *Aerosaurus* is intermediate between *Varanodon* and *Varanops* in heterodonty. As described by Olson (1965), the teeth of *Varanodon*, although strongly recurved, are essentially homodont.

Neither *Varanodon* nor *Aerosaurus* have a lateral mandibular fenestra. This strengthens the possibility that the opening is also lacking in *Varanops*, where the condition of preservation leaves some uncertainty, however (Williston, 1911; Romer and Price, 1940). The mandible of *Varanodon* is extremely slender. It apparently shows the most advanced condition of madibular elongation, with *Aerosaurus* occupying an intermediate position between *Varanodon* and *Varanops*. The humerus is not adequately known in *Varanodon*, but Olson's illustration (1965, Fig. 4d) suggests that the proximal end bore a massive deltopectoral crest similar in proportions to that of *Aerosaurus greenleeorum*. The ulna appears to resemble that of the large *Aerosaurus wellesi* specimen. A remarkable feature of the manus in *Varanodon* is the great size of the fourth digit and particularly of the fourth metacarpal. This bone appears to have had a volume equal to all the other matacarpals combined, and it is unique among pelycosaurs. The fourth digit and its metacarpals are the longest of the series also in *Varanops* and *Aerosaurus*, but neither of these genera displays the tendency toward hypertrophy seen in *Varanodon*. The carpus of *Varanodon* is also highly specialized in having an unusually large, well ossified lateral centrale and the fourth carpal. In *Aerosaurus* the lateral centrale of the carpus is well ossified but small, whereas in *Varanops* it is apparently unossified (Romer and Price, 1940). The fourth carpal in *Aerosaurus* and *Varanops* is comparable in size to that in other sphenacodont pelycosaurs.

The long haemal arches of *Varanodon* are unlike anything seen elsewhere in pelycosaurs, for the chevrons of the "...sixth and seventh caudals are long, measuring about 10 cm" (Olson, 1965:53). This exceeds the length of the humerus by almost twenty per cent. In contrast, the corresponding chevrons in *Varanops* and *Aerosaurus* are little more than one-third as long as the humerus. Olson believed that the deep and narrow tail of *Varanodon* was well adapted for swimming.

The elongated centra of the cervical vertebrae in *Varanodon* and *Varanops* decrease gradually in length towards the thoracic region. The difference in lengths of the cervical centra is the greatest in *Varanodon*, where the axial centrum is nearly twice as long as that of the seventh vertebra. Elongation of the cervical vertebrae, especially the axis, is probably correlated with the increased distance between the occipital condyle and the jaw joint. Although the condition in *Aerosaurus* is not clear, it is probable that the cervical centra were also elongated.

In his discussion of varanopseids, Olson (1965:57) noted that "With the few forms known at present, statements about trends within the varanopsid group are hardly justifiable." However, he did not take *Aerosaurus* into acount. *Aerosaurus*, *Varanops*, and *Varanodon* occur at widely separated localities in New Mexico, Texas, and Oklahoma, respectively, and at successively higher horizons. Although *Aerosaurus* is the oldest known varanopseid, it appears intermediate in many structural features between *Varanops* and *Varanodon*. It is probably more primitive than *Varanops* only in the height of the presacral neural spines. The better ossified feet and exceedingly long tail suggest that *Aerosaurus* was a more agile terrestrial carnivore than *Varanops*. Resemblances in head proportions and the nature of the teeth suggest a closer relationship between *Aerosaurus* and *Varanodon* than between *Varanops* and *Varanodon*.

Three other Permian reptiles, *Basicranodon fortsillensis*, *Milosaurus mecordi*, and *Elliotsmithia longiceps* have been regarded as varanopseid pelycosaurs.

Basicranodon fortsillensis Vaughn, 1958, from the Early Permian fissure deposits near Fort Sill, Oklahoma, is represented only by a cranium, but similarities to *Aerosaurus* in this part of the skull are obvious. *Basicranodon* has a number of teeth on the parasphenoid, which are arranged in a fashion similar to those on the anterior part of the plate in *Aerosaurus*. The teeth, however, are relatively larger and less numerous in *Basicranodon*, and there is no posterior transverse series as in *Aerosaurus*. Teeth on the parasphenoid are significant at higher taxonomic levels. They have been noted in some caseid pelycosaurs (Olson, 1968; Sigogneau-Russell and Russell, 1974), some millerosaurs (Gow, 1972), a few captorhinids (Heaton, 1979), and in *Petrolacosaurus* (Reisz, 1977). More significantly, the parasphenoid-basisphenoid complex of *Basicranodon* is laterally expanded as in *Aerosaurus*. Vaughn (1958:46) describes "a deep ventral trough between each basipterygoid process and the ipsilateral wall of the dentigerous concavity" in *Basicranodon*. As in *Aerosaurus*, the basipterygoid processes are directed more horizontally than is usual for non-varanopseid pelycosaurs. The trough in *Basicranodon* corresponds to the groove between the parasphenoid and basipterygoid process of *Aerosaurus*. In *Basicranodon*, however, the internal carotid entered the braincase "midway in the length of the trough, at its vertex," having followed the trough from behind in concert with the palatine branch of the facial nerve (Vaughn, 1958). Such a course was probably still possible in *Basicranodon* because the basal plate is less expanded than in *Aerosaurus*, but the carotid has apparently shifted from its more usual position between the basipterygoid processes. The altered routes of the artery and nerve inferred for *Aerosaurus* are probably a necessary consequence of lateral expansion of the parasphenoid-basisphenoid complex. The condition in *Basicranodon* appears structurally intermediate between that in *Aerosaurus* and the arrangement seen in such sphenacodonts as *Dimetrodon*. *Aerosaurus* and *Basicranodon* also agree in having paired carotid foramina in front of the retractor pit, whereas Romer and Price (1940:76) have noted that "...two unpaired openings are seen in several genera [of pelycosaurs], one in the floor of the sella, another more anteriorly placed." This arrangement is thought to have resulted from a "squeezing together" of the carotids in the development of a highly tropibasic braincase. The basicranium of both *Basicranodon* and *Aerosaurus* is not so narrow as that of *Dimetrodon*, and the carotids may have remained separate. The presence of a median ridge in the floor of the retractor pit and the reduced contribution of the basisphenoid in the *dorsum sellae* of *Basicranodon* are different from *Aerosaurus*, but in light of the otherwise broad agreement between the two, they do not appear to be significant. *Basicranodon* was probably a varanopseid, but its place within the family remains obscure.

Milosaurus mecordi DeMar, 1970, is represented by an incomplete articulated postcranial skeleton including the pelvis, hind limb and pes, and a series of caudal vertebrae. Referred material includes a small fragment of the maxilla with teeth and fragments of vertebrae. *Milosaurus* is an advanced pelycosaur, possibly a sphenacodont according to DeMar, because the pes has a large medial centrale, elongate astragalus and calcaneum, a first metatarsal with an expanded proximal articular surface, a relatively elongate fifth digit, and hooked terminal phalanges. In addition, the referred lumbar vertebra has a ventral keel. De Mar included *Milosaurus* among the varanopseids because this species displays primitive features that bar it from inclusion among advanced sphenacodonts.

Inclusion of *Milosaurus mecordi* in the family Varanopseidae seems questionable because no diagnostic features of this family have been identified in *Milosaurus*. On the contrary, the structure of the astragalus-calcaneum complex appears more elongate and hence more advanced than in *Varanops* or *Aerosaurus*; the elongation of the fifth digit seen in *Milosaurus* is also an advanced condition not present in *Varanodon* or *Aerosaurus*. More specimens of *Milosaurus* are needed before its taxonomic position among pelycosaurs can be established with certainty.

Elliotsmithia longiceps Broom, 1937, from the Middle Permian of South Africa, is known only from a small incomplete skull and jaws that have proportions similar to those of *Varanops*. The resemblances to *Varanops* noted by Romer and Price (1940) apply to *Aerosaurus* as well. The lateral outline of the skull with its remarkably drawn-out suspensorium resembles that of varanopseids. The posterior teeth (the only ones preserved) are flattened and recurved. They are relatively larger than in *Varanops*, suggesting that there were relatively few teeth in the maxilla, as in *Aerosaurus*. The maxillary dentition and the maxilla do not extend as far posteriorly as in the North American varanopseids. According to Romer and Price (1940) and Broom (1937), a distinctive feature of *Elliotsmithia* is the elongation of the postfrontal. This does not occur in any North American varanopseid, where parietal lappets (absent in *Elliotsmithia*) show the usual pelycosaurian development. Thus, despite some similarities to varanopseids, the peculiar skull morphology of *Elliotsmithia* precludes positive assignment to the Varanopseidae.

Note may be taken here of the suggestion by Reig (1967, 1970) that varanopseids were ancestral to the archosaurs. Romer (1971) dealt with Reig's argument point by point and concluded that it was highly improbable. Among the supposed resemblances between varanopseids and archosaurs, and, indeed, possibly at the root of Reig's idea, was the alleged presence of an antorbital fenestra in *Varanodon*. Our interpretation of the *Varanodon* condition as owing to postmortem effects removes what Romer termed "...one possible escape from the conclusion that *Varanodon* has nothing to do with archosaurs," namely that *Varanodon* may have evolved directly from captorhinomorphs "...and is on the way toward the archosaurs" (Romer, 1971:107).

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