The cranial anatomy and relationships of *Secodontosaurus*, an unusual mammal-like reptile (Synapsida: Sphenacodontidae) from the early Permian of Texas

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The cranial anatomy of the Early Permian sphenacodontid synapsid *Secodontosaurus* is redescribed. There is no evidence for recognition of more than one species of *Secodontosaurus*, and *S. willistoni* is declared a junior subjective synonym of *S. obtusidens*. Numerous derived characters (autapomorphies), mainly related to the unusually slender and slightly elongated skull, distinguish *Secodontosaurus*. The cranial specializations are interpreted as an adaptation toward a feeding strategy which involved preying upon small tetrapods that attempted to avoid capture by hiding in crevices and burrows. A cladistic analysis supports the following hypotheses of relationships: (a) the Sphenacodontidae is the nearest sister taxon of Therapsida; (b) *Secodontosaurus*, *Sphenacodon*, *Ctenospondylus* and *Dimetrodon* share a more recent common ancestor with one another than any of them do with *Haptodus*, and (c) *Secodontosaurus* shares a more recent common ancestor with *Dimetrodon* than with either *Sphenacodon* or *Ctenospondylus*. The latter hypothesis suggests that the sphenacodont subfamily 'Sphenacodontinae' is paraphyletic and, therefore, invalid.

KEY WORDS:—*Secodontosaurus* – Synapsida – Sphenacodontidae – mammal-like reptile – Palaeozoic – osteology – phylogeny.

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INTRODUCTION

Sphenacodontids are Late Pennsylvanian to Early Permian synapsid amniotes (often termed 'mammal-like reptiles') that became the dominant Laurasian terrestrial predators during the Early Permian. They are representatives of the primitive grade of synapsids traditionally called pelycosaurs. We recognize that 'Pelycosauria' is not a clade, and only use the term pelycosaur in an informal sense.

Romer & Price (1940) placed eight genera in the Sphenacodontidae and subdivided this group into three subfamilies, the Haptodontinae, Sphenacodontinae and Secodontosaurinae. Their classification reflected the dominant view of the time, that taxa should be ordered into groups on the basis of overall phenetic similarity. They also tended to construct evolutionary scenarios by creating phyletic lines from generalized, primitive forms to specialized, advanced taxa. Consequently, they included the small, insectivorous *Haptodus* in the Sphenacodontidae because it was viewed as being sufficiently 'generalized and primitive' to be ancestral to the larger, more specialized members of that family. Among the Sphenacodontidae only the unusual and rare *Secodontosaurus* has been studied since its brief description by Romer & Price (1940).

The taxonomic history of *Secodontosaurus* is confusing because this synapsid eluded recognition as a distinct taxon for over six decades. In 1880, Cope described *Theropleura obtusidens* on the basis of skeletal remains of various reptiles and amphibians (AMNH 4007) from the Admiral Formation, Wichita Group, near Mount Barry, Wichita County, Texas. These remains include part of an occiput and atlas exposed on one side of a 10 cm long slab and parts of a slender mandible and maxilla of *Secodontosaurus* on the other side. In a review of pelycosaurs, Case (1907), assuming that all the synapsid material of AMNH 4007 pertained to a single individual, assigned *Theropleura obtusidens* to *Dimetrodon* because of the presence of typical sphenacodontid vertebrae. In addition, Case (1907: 57) erected a new species, *Dimetrodon longiramus*, on the basis of a sphenacodontid scapula and a slender mandible (AMNH 4091) from the Belle Plains Formation, Wichita Group, at Tit Mountain near Dundee, Archer County, Texas. This material was also assigned subsequently to *Secodontosaurus* (Romer & Price, 1940). Further reference to skeletal remains of this peculiar early synapsid was made by Williston (1916), who described and figured (pp. 188–189, fig. 36) a long, slender maxilla and dentary (FMNH 754) from the Arroyo Formation, Clear Fork Group, at the Craddock Ranch, Baylor County, Texas. Williston indicated that these elements probably represented a new taxon, but mistakenly considered them to be an ophiacodontid. In his *Osteology of the Reptiles*, Williston (1925: 233) included the name '*Secodontosaurus*' under the ophiacodontids, but did not assign a holotype or offer any description of this previously unmentioned new taxon.

Romer (1936) re-examined all of the above skeletal materials and agreed with Williston that they represented a new taxon. He felt that Williston intended the name *Secodontosaurus* to apply to the present form and, therefore, used this name for the slender jawed sphenacodontid. However, he took as the type species the established Wichita species *D. longiramus* (Romer, 1936: 91). Romer & Price (1940) recognized that remains of *Secodontosaurus* had been recovered from both

Wichita and Clear Fork Group beds and established a separate species for each level. For the Wichita specimens the species name *Secodontosaurus obtusidens* (Cope) had priority, whereas the name *S. willistoni* was proposed for the Clear Fork specimen (Romer, 1936: 91). However, in the present study, we find no basis for the recognition of more than one species of *Secodontosaurus*, and *S. willistoni* is considered a junior subjective synonym of *S. obtusidens*.

In addition to the specimens mentioned above, four others from the Lower Permian strata of Texas are used in this study of the cranial anatomy of *Secodontosaurus*. Most important among these is MCZ 1124, consisting of a complete skull with closely attached left mandible, parts of the right mandible, cervical and anterior dorsal vertebrae, and scapulocoracoids from the Admiral Formation, Wichita Group, at Rattlesnake Canyon, Archer County. The skull of MCZ 1124 was used in the partial reconstruction in lateral view by Romer & Price (1940: pl. 16) and is the principal specimen of this study (Figs 6–11). The remaining cranial specimens include a partial braincase, AMNH 4062, from the Belle Plains Formation, Wichita Group, at Beaver Creek, Wichita County, and a nearly complete articular, part of AMNH 4826, from the Admiral Formation, Wichita Group, at Godwin Creek, Baylor County.

Romer & Price (1940) also considered the phylogenetic relationships of *Secodontosaurus*. They offered two alternative hypotheses, either *Secodontosaurus* could be a specialized offshoot of an advanced sphenacodontid in which the skull has become secondarily low and slender and the marginal dentition reverted to a relatively primitive condition, or *Secodontosaurus* could have developed from a primitive sphenacodontid stage, as represented by *Haptodus*. It is this second hypothesis that was preferred by Romer & Price (1940) and supported by Currie (1979). Recent cladistic analyses that considered early synapsid phylogeny, have placed *Haptodus* outside of Sphenacodontidae + Therapsida (Gauthier *et al.*, 1989; Laurin, 1990). The present study permits a re-evaluation of the phylogenetic relationships of *Secodontosaurus*, as well as the testing of the hypotheses presented above.

AMNH, FMNH (WM), KUVP and MCZ refer, respectively, to collections at: American Museum of Natural History, New York; Field Museum of Natural History, Chicago; University of Kansas Museum of Natural History, Lawrence; and the Museum of Comparative Zoology, Cambridge. CAT is an acronym for Computerized Axial Tomography.

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903 (Pelycosauria)
Sphenacodontia Romer & Price, 1940
Sphenacodontidae Williston, 1912
Secodontosaurus *Romer, 1936*

Synonymy. Theropleura obtusidens Cope, 1880: 41–42.
          Dimetrodon longiramus Case, 1907: 54–55, 134–137.
Type species. Secodontosaurus obtusidens (Cope, 1880).
Revised diagnosis. Sphenacodontid synapsid distinguished from other members of the family by the following autapomorphic features: skull roof elements unusually thin; the parietal forms part of the dorsal border of the temporal

fenestra and postorbital does not contact the supratemporal; skull and mandible unusually low and narrow and snout slightly elongated, resulting in a narrow dorsal process of the premaxilla and anterior process of nasal, reduced nasal width, poorly developed supracanine buttress, reduced ventral palatal process of lacrimal, and reduced orbital process of frontal; the posterolateral wing of parietal greatly reduced in width and directed mainly posteriorly; relatively large postparietal covers large area of supraoccipital; elongate paroccipital process of opisthotic curved strongly posteriorly; stapes slender and shortened; dorsal and lateral processes of supraoccipital reduced; lateral exposure of prefrontal reduced; height of suborbital and subtemporal rami of jugal reduced; elongate palatal surface; transverse flange of pterygoid reduced in width and palatal exposures of palatine, vomer, and ectopterygoid greatly reduced and lacking teeth; dorsal process of quadrate tilted slightly anterodorsally; lateral condyle of quadrate extends beyond lateral edge of skull roof; first mandibular tooth directed forward; no dramatic increase in height of anterior premaxillary and dentary teeth; retroarticular process is widely separated anteroposteriorly from reflected lamina of angular; and mandibular symphysis reduced and restricted to the dentary.

Secodontosaurus obtusidens (Cope, 1880)

Synonymy. Secodontosaurus willistoni Romer, 1936, p. 91.

Diagnosis. As for genus.

Holotype. AMNH 4007 (in part), partial lower jaws, right squamosal, partial right parietal, braincase, atlantal neural arch, and axial intercentrum.

Referred specimens. MCZ 1124, a nearly complete skull with left mandible (Figs 6–11), cervical and anterior dorsal vertebrae, and scapulocoracoids. Additional isolated fragments attributed to this specimen include parts of the right mandible. Though the isolated fragments and skull match each other in preservational characteristics and associated matrix, their association must remain tentative. There is no doubt, however, that the isolated fragments pertain to *Secodontosaurus.* MCZ 2749, large, badly encrusted skull roof, complete left mandible, and articulated vertebral column with sail; MCZ 2944, partial skull with braincase, lower jaw, and extensive postcranial material, including articulated vertebral column with well-preserved neural spines; MCZ 5134, 6382–6384, and 6998, disarticulated skull elements, including maxillae, transverse flange of pterygoid, articulars, dentaries and lower jaw fragments representing at least five individuals. FMNH (WM) 745 (holotype of *Secodontosaurus willistoni* Romer, 1936), maxilla (Fig. 12) and dentary; AMNH 4062, nearly complete braincase (Fig. 13) and partial vertebral column; AMNH 4091 (holotype of *Dimetrodon longiramus* Case, 1907), large, nearly complete left mandible (Figs 14, 15) and scapulocoracoid; AMNH 4826, nearly complete articular (Fig. 16), fragment of left transverse flange of pterygoid, and fragments of four vertebrae, including numerous spine fragments.

Horizon and locality. All specimens from the Lower Permian of Texas. MCZ 1124, Admiral Formation, Wichita Group, of Rattlesnake Canyon, Archer County; MCZ 2749, Admiral Formation, Wichita Group, of the south side of Godwin Creek and near its mouth (J.J. Long Surv. A-833), Archer County; MCZ 2944, Belle Plains Formation, Wichita Group, of south side of Little

Wichita River; MCZ 5134, 6382–6384, and 6998, Admiral Formation, Wichita Group, of the Briar Creek bonebed, School Land Section 32, Archer County; AMNH 4007, holotype, Admiral Formation, Wichita Group, of Mount Barry, a small elevation 16 km (10 mi) west of Wichita Falls, Wichita County; AMNH 4091, Belle Plains Formation, Wichita Group, of Tit Mountain, Archer County; AMNH 4826, Admiral Formation, Wichita Group, of Godwin Creek, Baylor County; FMNH (WM) 754, Arroyo Formation, Clear Fork Group, of Craddock bonebed, Craddock Ranch, Baylor County.

DESCRIPTION AND COMPARISONS

Reconstruction of skull

The outline of the skull in lateral view (Fig. 1A) was derived mainly from the left side of MCZ 1124 (Figs 6, 7), whereas the sutures of the cheek and temporal region were produced by careful cross-checking of the patterns on both sides of the specimen. The sutural patterns are slightly different on the two sides of MCZ 1124, because the left side was originally exposed by grinding, which removed a thin layer of the left lateral surface. For example, the suture between the lacrimal and prefrontal was based on the right side (Figs 8, 9), because the contact between these elements on the left side represents part of the internal overlapping suture. The outline of the maxilla, however, is best represented on the left side because the dorsal lamina of the right maxilla has been displaced slightly over the body of the element. The shape and length of the posterior
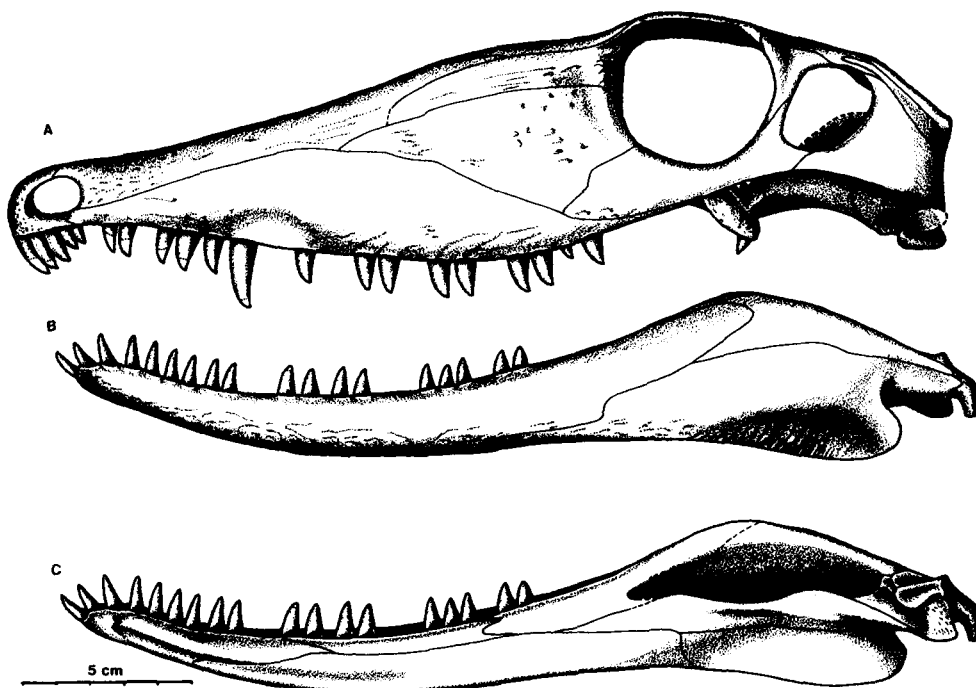

Figure 1. Reconstruction of *Secodontosaurus obtusidens*. A, Skull in lateral view; lower jaw in B, lateral, and C, medial views. Scale bar = 5 cm.

process of the maxilla was determined by combining the evidence provided by the partial posterior process of the right maxilla and the groove for its reception preserved on the left jugal. The configuration of the upper tooth row is based also on the left side of MCZ 1124, as was the curvature of the ventral edge of the skull. Reconstruction of the squamosal was particularly difficult and is based on both the holotype (AMNH 4007, Figs 4, 5) and MCZ 1124. Nevertheless, it was not possible to determine its lateral extent until the width of the skull at the level of the quadrate and the adductor fossa was established.

Reconstruction of the skull in palatal view was based on direct information from exposed areas and transverse sections provided by natural breaks (Fig. 10), and 32 CAT scans (Fig. 11) of the skull in MCZ 1124. For example, the width of the snout was determined by direct observation of the palatal surface of the premaxilla and aided by measurements taken from the CAT scans. The central portion of the palate between the transverse flange and internal nares was reconstructed also by direct observations of the exposed areas in conjunction with the transverse sections of the skull at natural breaks. The resulting tentative reconstruction was then carefully checked and corrected with the use of the CAT scans. The palate is not exposed in the region of the internal nares, and its configuration was determined entirely by transverse breaks of the skull (Fig. 10i, ii) and the CAT scans (Fig. 11B–D), whereas the width of the internal nares could only be estimated as the space that remained between the vomers and the reconstructed alveolar shelf of the maxilla. The transverse flange of the left pterygoid is exposed in MCZ 1124 (Figs 6–9), but its size and configuration was checked against the unexposed right transverse flange using the CAT scans (Fig. 11G–J). Together, these two sources of information on MCZ 1124 confirmed the unusually small transverse dimension of the flanges in *Secodontosaurus*. The size of the teeth on the transverse flange was based on one partially preserved tooth on the exposed left pterygoid and the diameters of the remaining two sockets.

The outline of the braincase in palatal view (Fig. 2B) was derived mainly from the isolated braincase AMNH 4062 (Fig. 13). Unfortunately, the anterior two-thirds of the parasphenoid and the stapes are not preserved in this specimen. A sequence of CAT scans were therefore used to determine the shape and dimensions of the parasphenoid concealed within the skull of MCZ 1124 (Fig. 11H–L), whereas details of the posteroventral surface were taken from AMNH 4062 (Fig. 13C). The partially exposed stapes in MCZ 1124 (Figs 8, 9) was used in the reconstruction. The orientation of the quadrate ramus of the pterygoid was drafted to extend lateral to the braincase. The ventral view of the quadrate was reconstructed using both elements of MCZ 1124, but mainly the right quadrate, which has been partially separated from adjoining elements.

The reconstruction of the skull in dorsal view (Fig. 2A) was based directly on MCZ 1124. The skull table and supraorbital region were relatively easy to reproduce, even though the component skull elements have either separated or telescoped to some extent along the sutures (Figs 8, 9). The width of the frontals in the antorbital region was determined using CAT scans (Fig. 11E–G) and a transverse section (Fig. 10iii), as the frontals in this region are covered by the prefrontals. The width of the antorbital region of the skull was determined indirectly, using the reconstructed width of the palatal elements together with the width of the marginal elements of the skull roof (premaxilla, maxilla, jugal).
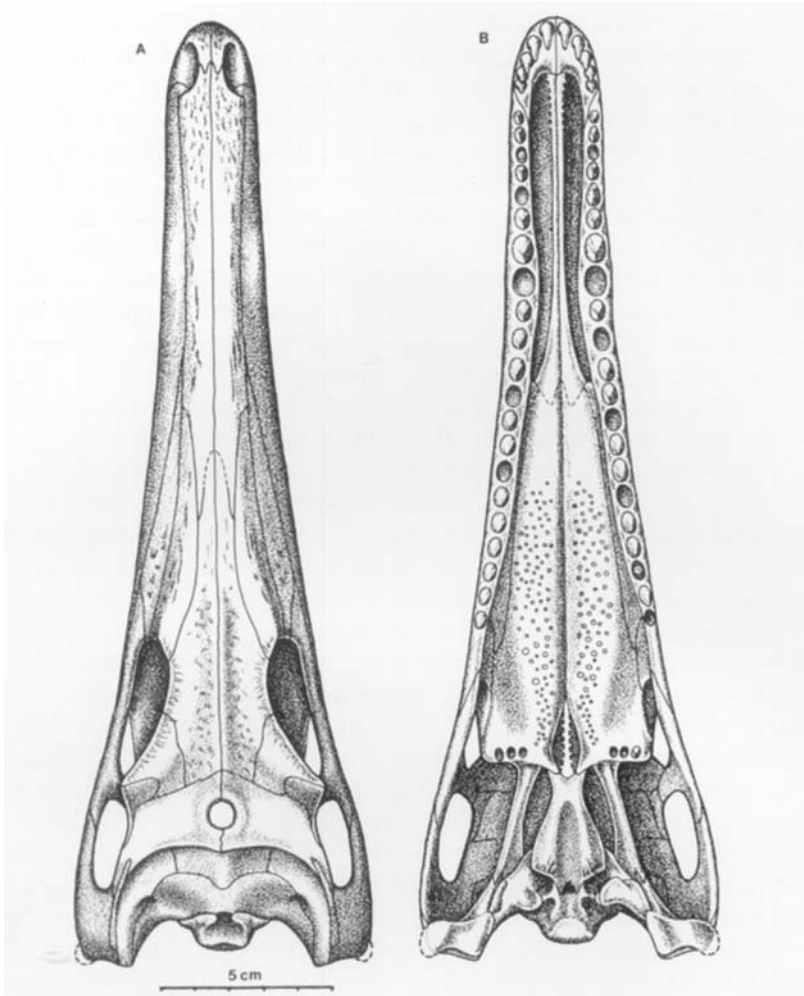
Figure 2. Reconstruction of skull of *Secodontosaurus obtusidens*. A, Dorsal; B, ventral (palatal) views. Scale bar = 5 cm.
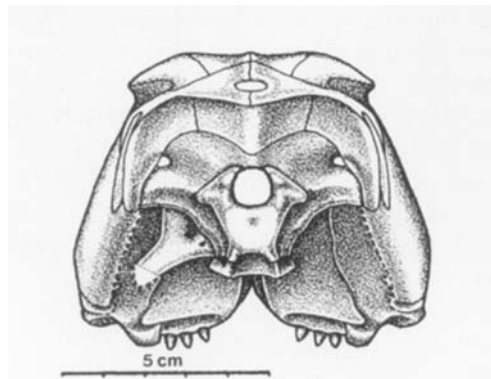

Figure 3. Reconstruction of skull of *Secodontosaurus obtusidens* in posterior (occipital) view. Scale bar = 5 cm.

The undistorted curvature of the right prefrontal and nasal was then used to determine the outline of the sutures for the dorsal view of the antorbital region.

Three specimens (AMNH 4007 and 4062, MCZ 1124) were used to reconstruct the occiput (Fig. 3), although compensation for size differences had to be made. The orientation and spatial relationships of the various processes were taken from the undistorted partial braincase AMNH 4062 (Fig. 13A). The length of the paroccipital process and the shape and size of the postparietal were taken from MCZ 1124 (Figs 8, 9). The length of the tabular, especially its posteroventral process, was determined using measurements of the holotype AMNH 4007 (Figs 4, 5). The basioccipital–exoccipital complex was reconstructed from MCZ 1124, but its spatial relationships with the rest of the braincase was based on AMNH 4062.

The occipital view of the skull (Fig. 3) was drafted mainly by combining the reconstructions of the occiput and the ventral and dorsal views of the skull roof. The occipital view of the quadrate, including the unusual condyles, was taken from the right side of MCZ 1124. The occipital extent of the squamosal and quadratojugal could be determined only from the sutural scars on the dorsal ramus of the right quadrate in MCZ 1124. A shallow indentation at the base of the medial condyle of the same quadrate was also used to determine the posterior extent of the quadrate ramus of the pterygoid.

In order to reconstruct the mandible (Fig. 1B, C) information from the complete but partially covered left mandible of MCZ 1124 was supplemented with that from four additional partial or fragmentary mandibles. The outline of the mandible in lateral view is based on the left of MCZ 1124, with some additional information from that of AMNH 4091 (Fig. 14). The sutural pattern of the lateral surface was determined using the left mandible of MCZ 1124, but with extensive cross-correlations with AMNH 4091. This strategy for determining the suture pattern of the lower jaw was necessary because the lateral surface of the left lower jaw of MCZ 1124 is damaged, probably the result of initial preparation using relatively coarse grinding tools. The posterior extents of the angular and surangular were determined by the sutural scars preserved on the isolated articular of AMNH 4826. The pattern of sculpturing was based entirely on information from AMNH 4091 (Fig. 14A), inasmuch as the sculpturing on the mandibles of MCZ 1124 (Figs 6, 7) was obliterated by previous preparators. The dental pattern was based on MCZ 1124, but the unusual orientation of the first tooth is confirmed in AMNH 4091.

The nearly complete left mandible of AMNH 4091 was the primary source of information for the medial view of the jaw. The fragmentary right mandible (not figured) attributed to MCZ 1124 provided information on the posterior portion of the medial surface, including details of the base of the reflected lamina and articular. The isolated articular AMNH 4826 (Fig. 16A, B) confirmed the structure of this region of the mandible based on MCZ 1124. The mandibular symphysis is damaged in all specimens, but AMNH 4091 (Fig. 14B) was sufficiently well preserved to allow its reconstruction.

General osteology

The skull of *Secodontosaurus* is unusually low and narrow, with a very long antorbital region (Figs 1–3). The bones of the snout are extremely thin except

for the tooth-bearing aveolar ridges. In lateral view the ventral edge of the skull is gently concave in the anterior region of the snout, gently convex for the remainder of the snout, and moderately concave in the postorbital region. The circumorbital bones are thickened along the orbital rim, especially dorsally, where they form a well-developed supraorbital ridge. This ridge extends anteriorly as a moderately developed antorbital ridge. The single temporal fenestra is directly behind the orbit. The skull is very narrow in dorsal view, with a long, slender snout, a narrow interorbital region with slightly concave edges, and a short, narrow skull table. The widest portion of the skull roof is in the postorbital region.

The occipital surface of the skull (Fig. 3) is strongly concave on either side of the midline and is inclined slightly forward. Therefore, the central portion of the occiput lies far anterior to the level of the posterolateral corners of the skull roof, and the occipital condyle lies a short distance anterior to the level of the suspensorium. A well-developed median, occipital crest extends between the skull table and the foramen magnum.

The internal nares are unusually long and narrow (Fig. 2). The palatal surface of the pterygoid is covered with a shagreen of small, peg-like teeth, extending from a short distance behind the choanae to the transverse flange. An unusually narrow, but well-developed, toothed transverse flange of the pterygoid extends far below the level of the ventral edge of the skull. Posterior to the transverse flange a tall, vertical quadrate process of the pterygoid is sutured to the quadrate, bracing the skull roof and occiput to the palate. The ventral edge of the process is moderately concave in lateral view and extends well below the ventral edge of the cheek.

The mandible (Fig. 1B, C) is unusually slender throughout its length. The tooth-bearing margin of the mandible is slightly concave in lateral view. Posterior to the tooth row the dorsal edge of the mandible curves upward, forming a slightly domed coronoid region. The reflected lamina of the angular is long, extending ventrolaterally from the central body of the mandible. The paired fossae of the jaw articulation are well below the level of the coronoid expansion and face dorsomedially.

Skull roof

Premaxilla. The premaxilla, preserved only in MCZ 1124, is a small, lightly built element that forms the tip of the snout and bears five teeth. The surface sculpturing of the premaxilla is limited to a few shallow pits that probably served for the passage of blood vessels and nerves to the skin of the snout. Of the three processes that are typically present in all primitive reptiles, the maxillary process is the largest in *Secodontosaurus*. It has a long lateral exposure that borders most of the ventral margin of the external naris, then continues posteriorly for a considerable distance in contact with the medial surface of the premaxillary process of the maxilla. As in *Sphenacodon*, that portion of the maxillary process in contact with the maxilla is edentulous and contributes to the lateral border of the internal naris. As in most primitive reptiles, the first tooth of the premaxillary series is the largest, with the following teeth decreasing gradually posteriorly. The size difference between the first and last premaxillary teeth is not as marked as in *Sphenacodon* or *Dimetrodon*. Although all the premaxillary

teeth are somewhat damaged, it is possible to discern that there are no anterior or posterior cutting edges. The first and second teeth have a relatively shallow implantation in *Secodontosaurus* in contrast to the condition seen in *Sphenacodon*, *Dimetrodon*, or even large specimens of *Haptodus*, where the teeth are deeply implanted in the body of the premaxilla.

The joined, paired dorsal processes of the premaxillae curve posterodorsally and run between the nasals for a very short distance. Although the dorsal processes of the premaxillae in MCZ 1124 are incomplete, it is clear that in *Secodontosaurus* they are narrower in cross-section and curve more abruptly posterodorsally than in either *Haptodus*, *Sphenacodon* or *Dimetrodon*. This may be related to the relatively smaller size of the anterior premaxillary teeth and their shallower implantation. Careful preparation of the palatal surface of the right premaxilla has exposed the anterior border of the internal naris. There is no evidence of a medial palatal process of the premaxilla in *Secodontosaurus*, and the vomer contacts the premaxilla in a short butt joint on the anteromedial narial border. The palatal process is very small in *Sphenacodon* (Eberth, 1985), whereas a well-developed, slender process is present in *Haptodus garnettensis* (personal observation). Despite the slender appearance of the premaxilla, especially when compared with that of *Sphenacodon* or *Dimetrodon*, the median sutural surface of the premaxillae is large.

In lateral view the ventral margin of the premaxilla slopes slightly anteroventrally, giving the snout a distinct hooked appearance, as in other sphenacodontids.

Septomaxilla. Both septomaxillae are preserved in the posterior portion of the external nares of MCZ 1124, but have been displaced slightly posteriorly. In addition, the right and left septomaxillae have been rotated clockwise and counterclockwise, respectively. Consequently, much of the body of the septomaxilla, as well as its dorsal process, is covered by the nasal. The exposed parts, the anterior part of the footplate and the transverse shelf (medial shelf of Eberth, 1985), are similar to the respective parts of the septomaxillae of *Sphenacodon* and *Dimetrodon* (Eberth, 1985; Romer & Price, 1940). The reconstruction of the septomaxilla offered by Romer & Price (1940: pl. 16) is not justified on the basis of the information available in MCZ 1124, the only specimen of *Secodontosaurus* in which the element is preserved.

Nasal. In MCZ 1124 the right nasal has been displaced under the left and is also covered posteriorly by the right prefrontal. The left nasal, on the other hand, is completely exposed, but its external surface has been slightly ground away during earlier preparation. Consequently, its external sutures with the lacrimal and prefrontal are distorted to the point that now they actually represent in part the internal contacts between these highly overlapping elements.

The nasal is unusually elongate in *Secodontosaurus*, occupying nearly 50% of the skull length. In contrast to the condition seen in *Haptodus*, *Sphenacodon* or *Dimetrodon*, where the nasal is a relatively broad sheet of bone with an expanded anterior end, the nasal in *Secodontosaurus* is a slender, long element that forms the roof of the narrow, long snout. Transverse sections of the snout of MCZ 1124 indicate that the nasal is very thin, even along its medial edge. The midline sutural surface of the left nasal, as exposed at the level of the twelfth maxillary tooth position, is unusually thin (2 mm) for such a large skull, less than one-third the thickness of the same sutural surface in the skulls of *Sphenacodon* or *Dimetrodon*

of similar length. The narrow premaxillary process underlies the dorsal process of the premaxilla and contributes to the posterodorsal border of the external naris. The width of the premaxillary process of the nasal and the dorsal process of the premaxilla are equal in *Secodontosaurus*, resulting in a narrow supranarial shelf. In contrast, the premaxillary process of the nasal is wider than the dorsal process of the premaxilla in *Dimetrodon* (Romer & Price, 1940), and the premaxilla is excluded from the dorsal border of the external naris. The posterior border of the external naris is formed entirely by the nasal, and it is likely, therefore, that the nasal-septomaxillary contact is extensive as in *Sphenacodon* and *Dimetrodon*. The nearly straight, long lateral border of the nasal continues from contact with the maxilla to contact with the lacrimal. Posterior to this level there is a marked narrowing of the external exposure of the nasals, as they wedge between the anterior ends of the prefrontals. The same condition is also found in *Dimetrodon* and *Sphenacodon*. There is, however, a greater degree of overlap between the nasal and frontal and between the nasal and prefrontal in *Secodontosaurus* (Fig. 10iii) than in either *Sphenacodon* (Eberth, 1985) or *Haptodus* (personal observation).

Frontal. The frontals are long and very slender, but exhibit the basically triradiate pattern of sphenacodontids, with anterior, orbital and posterior processes. Despite being markedly more slender, the frontals of *Secodontosaurus* are strikingly similar in shape and general proportions to those of *Dimetrodon*.

The straight midline suture of the frontals is elevated slightly on a narrow ridge above the general surface of the skull roof, as are their thickened orbital margins. As a result, shallow longitudinal troughs are formed between the raised areas. Although the anterior processes of the frontals are partially covered in MCZ 1124 by the prefrontals, their size and sutural relationships can be easily determined. As in *Sphenacodon* and *Dimetrodon*, the anterior process of the frontal is the longest, diminishing gradually in width as it extends forward from the orbital margin to its narrow contact with the nasal; the anterior end of the joined frontals extends far forward underneath the nasals, as indicated by the transverse sections of the skull (Figs 10, 11). The frontal–prefrontal contact changes from a thick abutment joint posteriorly to an increasingly overlapping joint anteriorly, with the prefrontal overlapping the frontal. Consequently, one-half of the width of the frontal is covered by the prefrontal just posterior to the frontal-nasal suture (Fig. 8). The orbital process of the frontal is poorly developed in *Secodontosaurus*, extending only a very short distance laterally, as would be expected with the overall slenderness of the skull. It is supported ventrally by a short posteromedial projection of the prefrontal. In contrast, the orbital process in *Sphenacodon* and *Dimetrodon* is well-developed, extending far laterally between the prefrontal and postfrontal. A slight separation of the postfrontal and parietal from the posterior process of the frontal on the right side of MCZ 1124 reveals these contacts to be thick and essentially non-overlapping sutures.

The ventral surface of the left frontal has been exposed in the region of the orbit, revealing a massive ridge whose medial edge is step-like. The ridge extends anteriorly from the suture with the parietal for most of its length, then curves laterally at the level of the antorbital buttress of the prefrontal. The medial edge of the ridge apparently marks the edge of the contact of the frontal with the planum supraseptale (Eberth, 1985).

Parietal. The only skull table element present in the holotype (AMNH 4007,
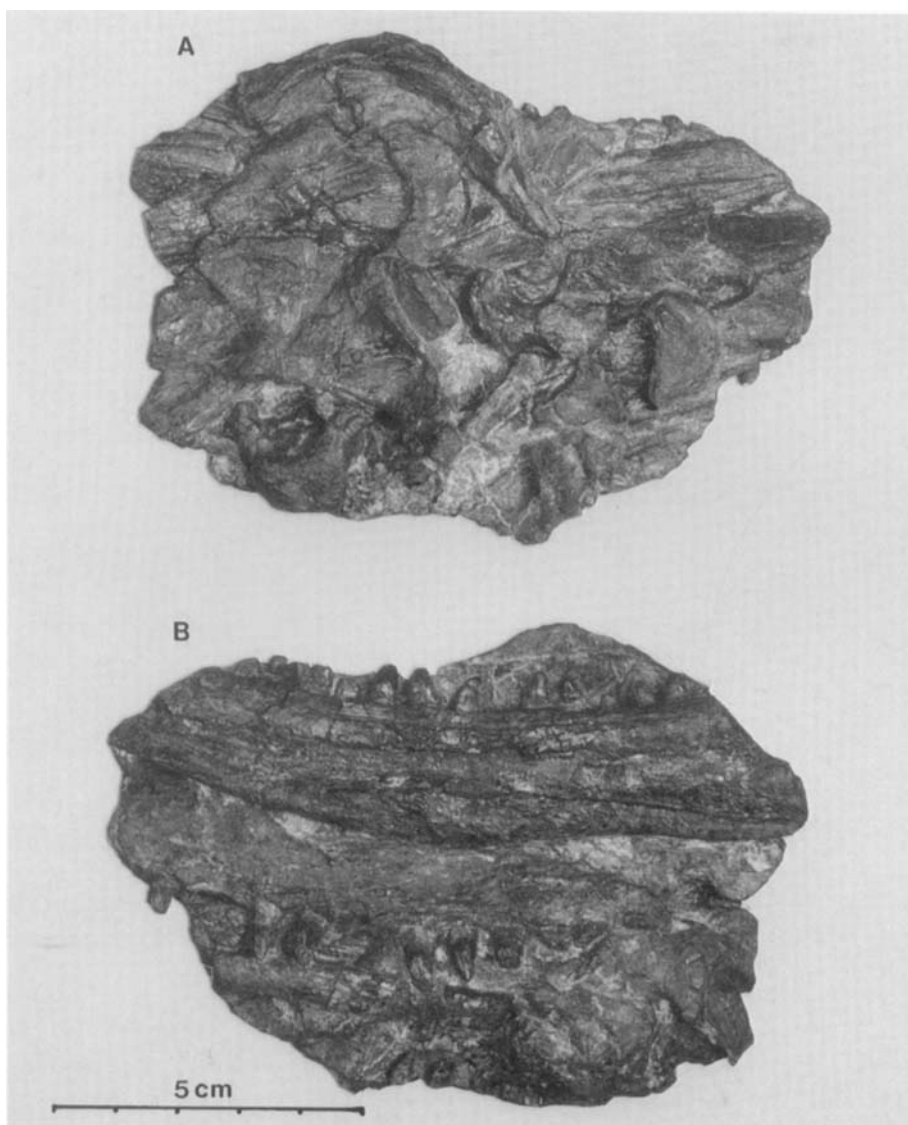
Figure 4. *Secodontosaurus obtusidens*, holotype, AMNH 4007. Photograph of block containing specimen shown in opposing views. Scale bar = 5 cm.

Fig. 4) is the right parietal, of which only its posterior edge remains. The paired parietals are well preserved in MCZ 1124, although the right parietal has been separated from the general surface of the skull table and displaced slightly anteroventrally.

The parietal is short, extends nearly the full width of the skull table, and is slightly domed at its centre of ossification. A well-developed posterolaterally projecting wing separates the occipital and temporal regions of the skull. In *Secodontosaurus*, as in *Dimetrodon* and *Haptodus*, the pineal foramen is located posterior of the midlength of the parietal and close to the posterior edge of the skull table. The immediate area surrounding the pineal foramen is raised slightly
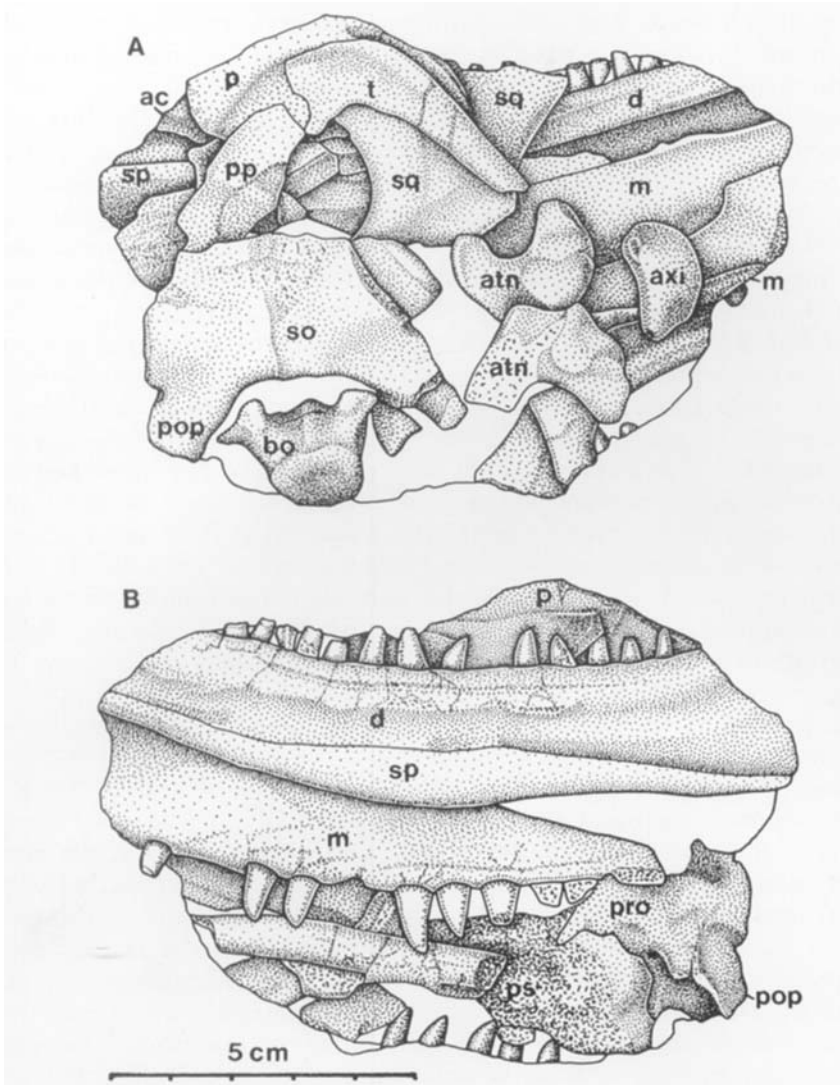
Figure 5. *Secodontosaurus obtusidens*, holotype, AMNH 4007. Block containing specimen illustrated as in Fig. 4 showing in A, occiput, medial surface of left upper and lower jaws, and elements of the atlas–axis complex; and in B, lateral surface of left upper and lower jaws, anteroventral surface of braincase, and five partial, isolated maxillary teeth. Scale bar = 5 cm.

above the general surface of the parietal. The anterior sutural contacts with the frontal and postfrontal are thick and strongly interdigitating, whereas laterally, the parietal contacts the postorbital and squamosal in simple overlapping sutures. The occipital margin is strongly concave on either side of the midline, and the angular contact between the skull table and the occiput is abrupt. Both the holotype (AMNH 4007) and MCZ 1124 show the presence of a large occipital flange of the parietal that underlies the postparietal and tabular. The posterolateral wing of the parietal is long and slender in *Secodontosaurus* and projects mainly posteriorly and only slightly laterally, in strong contrast to the condition in *Sphenacodon* and *Dimetrodon*, where the parietal wing is broad and

projects mainly laterally and only slightly posteriorly. On the dorsal surface of the posterolateral wing is a deep, narrow, longitudinally striated groove that carried the slender, anterior portion of the supratemporal.

Exposure of the ventral surface of the parietal has revealed a highly unusual feature in the temporal region of *Secodontosaurus*, the lateral edge of the parietal contributes to the dorsal border of the temporal fenestra. The slight separation of the left parietal from the postorbital and squamosal in MCZ 1124 has exposed the sutural surfaces. The extent of the contacts between the parietal and the posterior process of the postorbital and the anterodorsal process of the squamosal are defined precisely by the slightly grooved sutural scars on the ventral surface of the parietal. The available evidence indicates that the squamosal does extend anteriorly to reach the postorbital, but that this contact occurs only beneath the parietal and medial to the lateral edge of the posterolateral parietal wing. The lateral edge of the parietal contributes, therefore, to the dorsal edge of the temporal fenestra. This feature has not been described in any other pelycosaur.

Postparietal. A single, median postparietal, restricted entirely to the occiput, is preserved in both the holotype (AMNH 4007) and MCZ 1124. It is essentially a transversely elongate, rectangular plate-like bone except for a short, rounded mid-ventral process. A low, median ridge extends the full midline length of its posteriorly exposed surface, becoming more pronounced ventrally. Both the sutural striations on the supraoccipital for the postparietal and the size of the midvental process of the postparietal indicate that the latter element covered a significant portion of the supraoccipital, extending close to the dorsal edge of the foramen magnum.

Prefrontal. The prefrontal, both of which are well-preserved in MCZ 1124 (Figs 5, 6), contacts the nasal and frontal dorsomedially and lacrimal ventrally, forms part of the orbital margin posteriorly, and wedges between the lacrimal and nasal anteriorly. Its orbital margin is massive, whereas anteriorly it forms a long, thin, sheet-like extension. The prefrontal has a posterodorsal process that contributes to the supraorbital shelf, then continues a short distance posteromedially beneath the frontal. The contact between the prefrontal and frontal above the orbit is very deep and interdigitating, similar to that in *Sphenacodon* and *Dimetrodon*. A narrow process of the prefrontal extends far ventrally on the anterior wall of the orbit medial to the lacrimal. The orbital margin of the prefrontal is sculptured with shallow horizontal grooves and small nutrient foramina. Although the prefrontal contributes to a supraorbital shelf, it is less well developed than in *Sphenacodon* or *Dimetrodon*, and there is only a shallow preorbital fossa on the lateral surface of the skull. A particularly well-preserved skull of the primitive sphenacodont *Haptodus garnettensis* (uncatalogued specimen of the Royal Ontario Museum, Toronto) not only has a poorly developed supraorbital shelf of similar size to that in *Secodontosaurus*, but also has a shallow preorbital fossa.

The anterior sheet-like process of the prefrontal is slightly convex laterally and not only contributes to the vertical lateral surface of the snout, but also extends slightly onto the dorsal surface of the skull. The anterior process is long and unusually narrow dorsoventrally, a condition that is probably attributable to the elongation and low profile of the snout.

Postfrontal. The postfrontal is roughly triangular in outline and is restricted to the skull table. It has deep interdigitating sutures with the frontal, parietal and
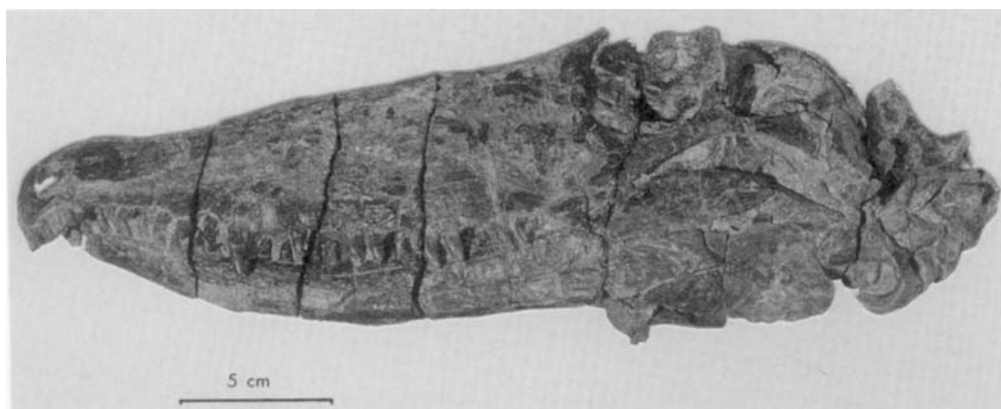
Figure 6. *Secodontosaurus obtusidens*, MCZ 1124. Photograph of skull, lower jaw and atlas–axis complex, in left lateral view. Scale bar = 5 cm.

postorbital and forms the posterior one-third of the dorsal orbital margin. The postfrontal is relatively thin in cross-section along the orbital margin, but gradually thickens toward its contacts with the skull table elements. Because the lateral process of the frontal is poorly developed in *Secodontosaurus*, its contact with the postfrontal is significantly shorter than in *Sphenacodon* or *Dimetrodon*. Nevertheless, the postfrontal contributes to a narrow, but distinct supraorbital shelf. As revealed by minor disarticulation on both sides of the skull of MCZ 1124, the posterolateral margin of the postfrontal has a deep, slightly underlapping contact with the postorbital. The supraorbital shelf ends posteriorly on the postfrontal in a slight buttress.

Postorbital. The postorbital is preserved on both sides of the skull MCZ 1124, though displaced slightly as a result of the distortion of the skull table. The postorbital is a triradiate element, with a short anteromedial process that overlaps the postfrontal, a long, slender, ventral process that forms the dorsal half of the postorbital bar, and a relatively short, robust posterior process that contributes to the dorsal border of the temporal fenestra. The posterior process is long and narrow in *Sphenacodon* and *Dimetrodon*, wedging between the parietal and squamosal and extending beyond the temporal fenestra to contact the supratemporal, whereas in *Secodontosaurus* it is relatively short and robust, and fails to reach the supratemporal. The posterior process is not wedged between the parietal and squamosal, as in other pelycosaurs, but rather underlies the parietal and contacts the blade-like anterodorsal process of the squamosal medial to the lateral border of the parietal. The posterior process remains surprisingly robust and dorsoventrally thick to provide support for the thin posterolateral wing of the parietal. The dorsal surface of the process is therefore grooved to match the ventral sutural surface of the parietal. The groove does not extend forward to the anteromedial process of the postorbital as in *Sphenacodon* (Eberth, 1985) and *Dimetrodon*, because the sutural relationships between the postfrontal and postorbital appear to be reversed in the massive sphenacodontine skulls. As described and illustrated by Eberth (1985: fig. 11c), the postfrontal overlaps broadly the postorbital in *Sphenacodon*, creating a buttress at the posterodorsal margin of the orbit and an associated recess behind it. In *Secodontosaurus*, it is the

postorbital that overlaps anteromedially the postfrontal, and the buttress is less well developed. The vental process of the postorbital is essentially triangular in horizontal cross section. In lateral view the process is very slender, but the anteriorly facing surface is considerably broader. Although the ventral process is broken off on both sides of the skull, the distal end of the left postorbital is preserved sutured to the medial surface of the jugal.

Maxilla. The maxilla consists of a long, thickened, tooth-bearing alveolar ridge and a thin vertical lamina or sheet that forms much of the antorbital cheek region. In lateral view the maxilla has the general outline of a long, low, isosceles triangle, though the ventral edge and associated tooth row are slightly convex. In MCZ 1124, there are 15 teeth on the right maxilla and 16 teeth on the left, with spaces for eight additional teeth on the right and seven on the left for a total of 23 maxillary tooth positions. As in *Dimetrodon* and *Sphenacodon*, the canine is at last twice as large as the other maxillary teeth. In large specimens of *Haptodus* the relative serial position of the canine is the same as for *Secodontosaurus* (MCZ 1124), with six or seven precanines and 16 postcanines. In contrast to this count, *Sphenacodon* maxillae from the Anderson Quarry, New Mexico, vary from zero to four precanine and 12 to 15 postcanine tooth positions at different ontogenetic stages (Eberth, 1985). In all of the above sphenacodontids there are two canine tooth positions, but typically only one canine is fully developed.

Some details of the sutural pattern of the maxilla with the surrounding elements of the cheek can be discerned in MCZ 1124. The maxilla appears to overlap the nasal slightly, but is in turn overlapped by the lacrimal. Along the maxillary-jugal contact the maxilla appears to contact the lacrimal medial to the jugal. Anteriorly, the maxilla has a long overlapping suture with the maxillary process of the premaxilla, but makes only a very small contribution to the external narial opening. The long, narrow posterior process of the maxilla is edentulous, forming an unusually slender ventral boundary to the jugal that extends slightly beyond midlength of the orbit. The lateral surface of the right maxilla of MCZ 1124 is well preserved and exhibits numerous shallow grooves and vessel scars that extend posterodorsally from the ventral edge of the maxilla, then curve posteriorly.

The medial surface of the maxilla is exposed only in the holotype of *Secodontosaurus willistoni*, FMNH (WM) 754 (Fig. 12). Medial view of this specimen indicates that the suture for the premaxilla is unusually long in *Secodontosaurus*, extending from the anterior tip of the alveolar shelf halfway to the canine tooth position. Above this area the wide overlapping suture with the nasal demonstrates that the maxilla overlaps the nasal in front of the canines. Dorsal and immediately posterior to the canines the nasal is still overlapped by the maxilla, but the ventral edge of the nasal inserts into a slight trough in the maxilla. A short anterior portion of the sutural surface for the lacrimal, also preserved in this specimen, indicates that the maxilla overlaps the lacrimal in this region. Farther posteriorly, the dorsal edge of the maxilla is not preserved.

The medial surface of the alveolar shelf in FMNH (WM) 754 is smooth from the level of the third precanine to that of the third postcanine, indicating that the internal narial opening is unusually long in *Secodontosaurus*. The supracanine buttress is well-developed in *Secodontosaurus* to accommodate the deep tooth implantation of the paired canines, and there is no dorsal precanine step of the ventral jaw margin as in other advanced, large sphenacodontids. The
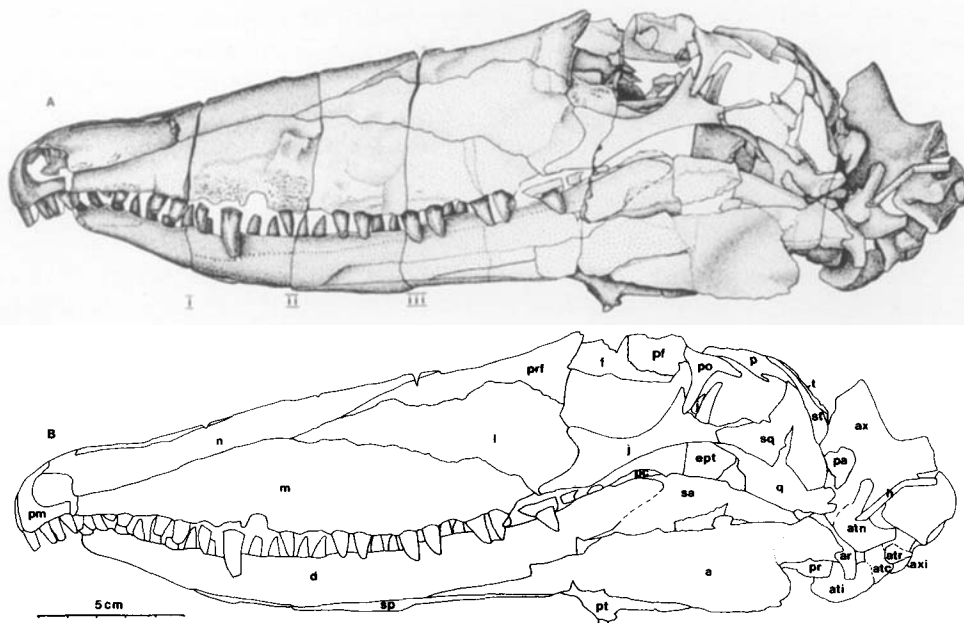
Figure 7. A, Stipple drawing, and B, outline sketch to indicate individual elements and other structures of *Secodontosaurus obtusidens*, MCZ 1124, as shown in Fig. 6. i, ii and iii represent natural breaks in the specimen that permit the transverse illustrations of skull shown in Fig. 10. Scale bar = 5 cm.

supracanine buttress appears to be reinforced dorsally by two distinct ridges that extend onto the vertical maxillary sheet. Posterior to the region of the canines the alveolar shelf exhibits sutural scars for the palatine and ectopterygoid.

The maxilla of FMNH (WM) 754 has places for seven precanines, two canines, and 17 postcanines, for a maximum count of 26. Although incomplete, comparisons of the height and width of the alveolar shelf of FMNH (WM) 754 with that of MCZ 1124 indicate that it is unlikely that the former had places for any additional teeth.

Lacrimal. From its small contribution to the orbital margin, the large plate-like lacrimal extends anteriorly on the lateral surface of the skull, reaching only halfway to the tip of the snout, then terminates by wedging between the nasal and the maxilla. Two small foramina on the posterior surface of the orbital margin of the lacrimal mark, the openings of the lacrimal duct. The anterior extent of the lacrimal duct cannot be determined precisely. A fortuitous break in the skull halfway along the length of the lacrimal, however, reveals a small (less than 1 mm in diameter) anteroposteriorly directed canal that may represent the passage for the lacrimal duct. This small canal does not appear to extend the entire length of the lacrimal, as indicated by Figs 10 and 11. The dorsal margin of the lacrimal overlaps the nasal and prefrontal. Although there is no direct evidence for the presence of a medial bracing lacrimal footplate, it is probably rudimentarily developed in *Secodontosaurus*. In advanced pelycosaurs such as *Haptodus*, *Sphenacodon* and *Ianthasaurus*, this supporting structure, which contacts the alveolar shelf of the maxilla, is well developed.

Jugal. The left jugal of MCZ 1124 is preserved in its entirety, but its external surface has been damaged from earlier mechanical preparation, whereas only the anterior portion of the right is preserved. The jugal extends as a narrow bar along the ventral skull edge as it forms the ventral borders of the orbit and temporal fenestra. As in other sphenacodontids, the anterior portion of the jugal expands into a large sheet-like antorbital process. The antorbital sheet is unusually large in *Secodontosaurus* and is entirely underlain by the lacrimal. The antorbital process of the jugal is excluded from the ventral edge of the skull by a very narrow, splint-shaped process of the maxilla that extends posteriorly to a level slightly beyond the midlength of the orbit. The suborbital bar of the jugal is much narrower dorsoventrally than in *Dimetrodon* or *Sphenacodon*, but is relatively wider mediolaterally than in other sphenacodontids. The dorsal process of the jugal which forms the ventral half of the postorbital bar is also robust in *Secodontosaurus*, more massively developed relative to the rest of the jugal than in other sphenacodontids. This process is preserved only on the left side of MCZ 1124, although the dorsal tip has been broken off and displaced a short distance posterolaterally to rest against the postorbital. The two elements of the postorbital bar are separated except for a small, splint-like piece of the postorbital (not visible in the figures) that remains attached to the dorsal process of the jugal, indicating that the latter was incised anteriorly to receive the ventral process of the postorbital. In lateral view, the exposed portion of the posterior process of the jugal is similar in size to the dorsal process, but is more slender mediolaterally. Much of the posterior process, however, is covered by an anterior process of the squamosal. The overlapped portion of the jugal is broadly expanded posteriorly, and its dorsal and ventral margins coincide exactly with the edges of the overlapping squamosal. The free ventral edge of the jugal is only slightly concave, intermediate between the nearly straight and strongly concave conditions of *Haptodus* and *Sphenacodon*, respectively.

Quadratojugal. The quadratojugal is rarely preserved in advanced pelycosaurs. Fragments of this element are preserved on the left side of MCZ 1124 (not visible in the figures), lying between the squamosal and the quadrate. Available evidence indicates that the quadratojugal is a slender, probably tall element, with a reduced anterior process. In lateral view the quadratojugal is covered almost completely by the squamosal. The quadratojugal extends anteriorly a short distance underneath the squamosal along the ventral edge of the skull, ending far short of the jugal. At the posteroventral corner of the skull the quadratojugal is thickened slightly where it abuts the lateral condyle of the quadrate. A small, somewhat damaged part of this process of the quadratojugal is exposed at the posteroventral corner of the skull, where the medial flange of the squamosal has been lost.

The presence of a tall, narrow quadratojugal with a short anteroventral process has also been observed in sphenacodontids (Eberth, 1985), as well as in *Haptodus* (personal observations).

Squamosal. The right squamosal is partially covered by the tabular and the opisthotic in the holotype (AMNH 4007), and those of MCZ 1124 are damaged as a result of crushing. The squamosal of *Secodontosaurus*, although relatively smaller, is like that of *Haptodus* or *Sphenacodon* in having a broad, subtriangular exposure on the lateral surface of the skull but wrapping around the posterior margin of the cheek, where it has a narrow exposure. In lateral view, the
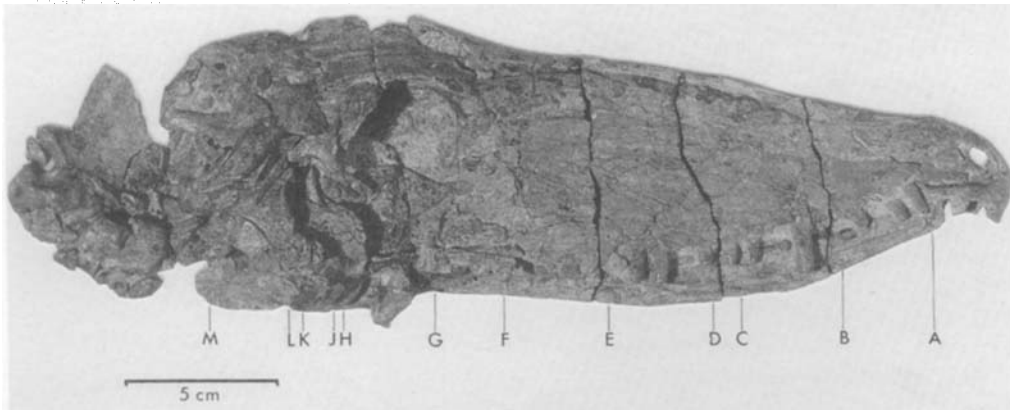
Figure 8. *Secodontosaurus obtusidens*, MCZ 1124. Photograph of skull and atlas–axis complex in right lateral view and left lower jaw in partial medial view. Letters A–M indicate levels of CAT scans shown in Fig. 11. Scale bar = 5 cm.

squamosal has two well-developed anterior processes, the postorbital and jugal processes, which extend along the posterodorsal and posteroventral margins of the lateral temporal fenestra, respectively. In lateral view, the long, slender postorbital process extends only a short distance along the posterodorsal margin of the temporal fenestra, but has an unusually large, medial expansion that not only underlaps the parietal, but also extends anteriorly to reach the postorbital. In sphenacodontids such as *Sphenacodon*, the postorbital process of the squamosal is also very slender in lateral view, but extends farther forward along the dorsal edge of the temporal fenestra and has an extensive overlapping contact with not only the parietal, but also the postorbital. The more robust jugal process overlaps the posterior process of the jugal. The distal end of the jugal process is missing in both specimens, but its shape can be deduced from the sutural scar on the jugal.

All the preserved squamosals exhibit a large trough-like concavity that extends across the suturally overlapping dorsal surface from the anterior end of the postorbital process to the posterodorsal corner of the element. The dorsolaterally facing concavity underlies the posterolateral wing of the parietal, the elongate supratemporal, and the laterally exposed wing of the tabular. In MCZ 1124, the dorsal sutural surface of the squamosal is complete and is correctly and fully articulated with the adjoining elements. It is, therefore, surprising that this concave surface extends posteroventrally beyond the supratemporal and probably close to the level of the suspensorium. The squamosal, however, is incomplete below the posteroventral end of the tabular in both specimens, and the medial flange of the squamosal that normally covers the dorsal process of the quadrate, as in other sphenacodontids, is not preserved.

Supratemporal. The small supratemporal, rarely preserved in advanced pelycosaurs because of its superficial position on the skull roof, has remained in place on the left side of MCZ 1124. In addition, two small fragments of bone on the right side are probably pieces of the supratemporal that have been displaced as a result of the separation of the parietal and squamosal. The supratemporal is a long, slender, wedge-shaped element, widening from only 1.5 mm at its
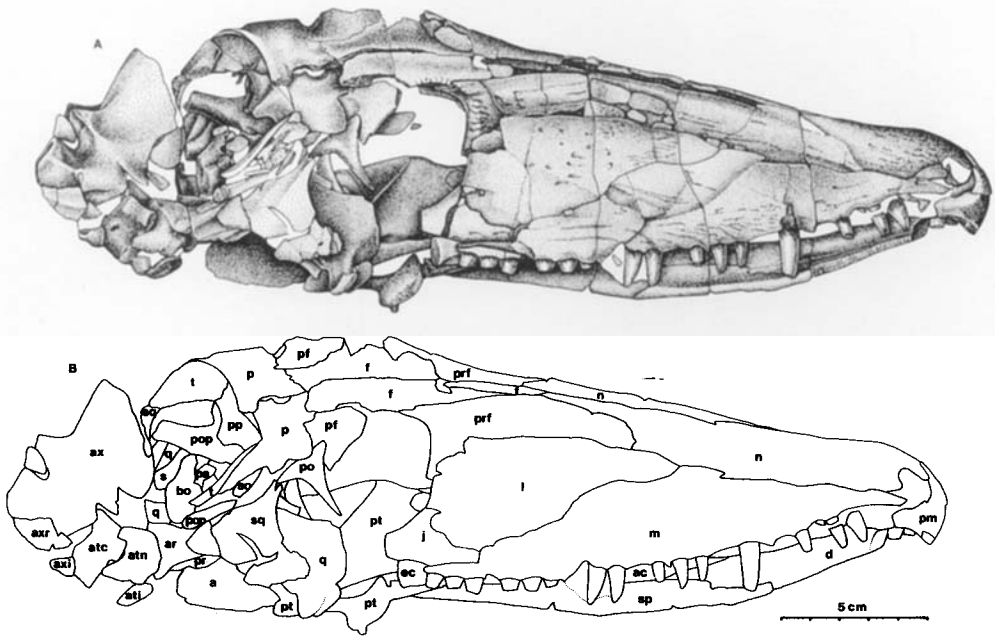
Figure 9. A, Stipple drawing, and B, outline sketch to indicate individual elements and other structures of *Secodontosaurus obtusidens*, MCZ 1124, as shown in Fig. 8. Scale bar = 5 cm.

anterior end to 5.5 mm at its posterior end. Its anterior half overlaps the posterolateral wing of the parietal, whereas posteriorly it extends along the squamosal–tabular contact. In the holotype (AMNH 4007) a well-preserved deep, narrow, striated groove on the parietal that receives the supratemporal varies in width from 1.5 to 2.0 mm, and is *c.* 2 mm deep and *c.* 20 mm long. As in *Dimetrodon* and *Sphenacodon*, the supratemporal is exposed in lateral view. According to Romer & Price (1940: pl. 10) and Eberth (1985: fig. 3) the supratemporal straddles the dorsolateral curvature of the skull in these sphenacodontids, but is of sufficient size to be visible in lateral view of the skull. In *Secodontosaurus*, however, the supratemporal extends from a dorsal position along its suture with the parietal to a largely lateral orientation along its suture with the squamosal. Thus, the expanded posterior half of the supratemporal faces mainly laterally.

Tabular. The holotype (AMNH 4007) has a complete right tabular preserved in articulation with the parietal, and in MCZ 1124 both tabulars are preserved in place on the occiput, but appear to lack the ventral end.

The tabular is a relatively large, sheet-like element that forms the posterodorsal edge of the skull roof and extends onto the occipital surface of the skull, connecting the occiput to the skull table dorsally and the cheek laterally. The tabular contacts the postparietal medially, forms the lateral margin, the posttemporal fenestra, and covers the lateral process of the supraoccipital and the distal end of the paroccipital process of the opisthotic. The narrow, ventral end of the tabular probably extends to the ventrolaterial tip of the paroccipital process. Much of the body of the tabular appears to be supported by the parietal

and squamosal, and it is likely that it also contacts the dorsal process of the quadrate.

Palate

Vomer. The vomer is exposed only in cross-section at several levels in MCZ 1124 (Fig. 10). At the level of the internal nares the vomer appears as a much more slender element than that in either *Haptodus, Dimetrodon* or *Sphenacodon.* A cross-sectional view of the vomer at the level of the last precanine reveals it as trough-shaped and only *c.* 2 mm wide. The CAT scans (Fig. 11) indicate that the vomer remains very slender throughout most of its length, becoming broader posteriorly at the level of the third or fourth postcanine tooth. A second cross-sectional view of the skull at the level of the third postcanine shows the vomers as more robust than in the anterior portion of the snout. Numerous small canals seem to extend anteroposteriorly through the vomer. The slivers of bone located above the robust, trough-like portion of the vomers represent broken fragments of the delicate, medial ascending process. Two slightly thicker, curved slivers, one above each vomer (Fig. 10), are undoubtedly the tips of the anterior processes of the pterygoids that overlap the vomers, as in *Dimetrodon.* The precise suture between these two elements cannot be discerned.
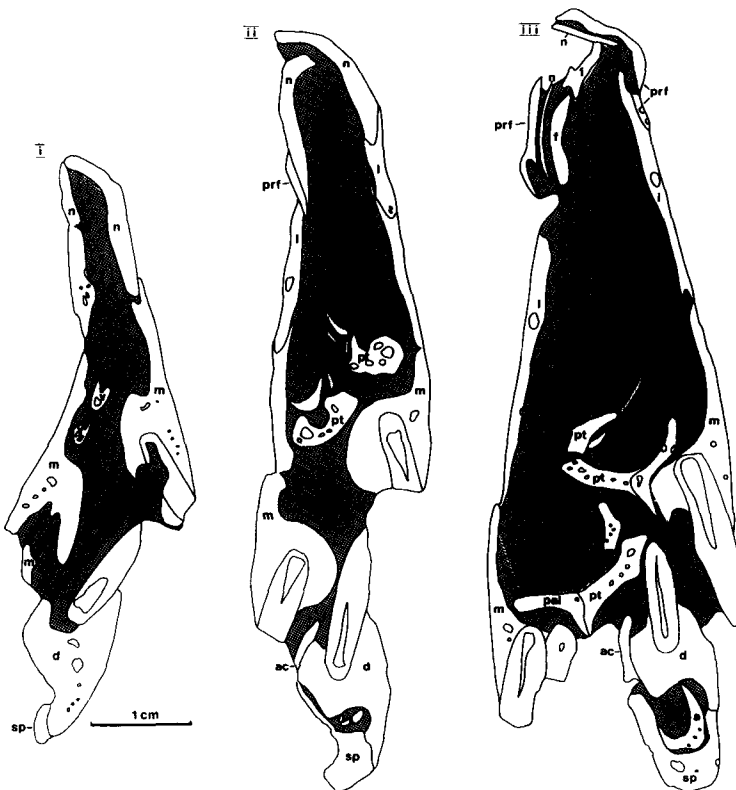
Figure 10. Transverse sections of skull and left lower jaw, MCZ 1124, drawn at natural breaks, i, ii and iii, as indicated in Fig. 7A. Scale bar = 1 cm.
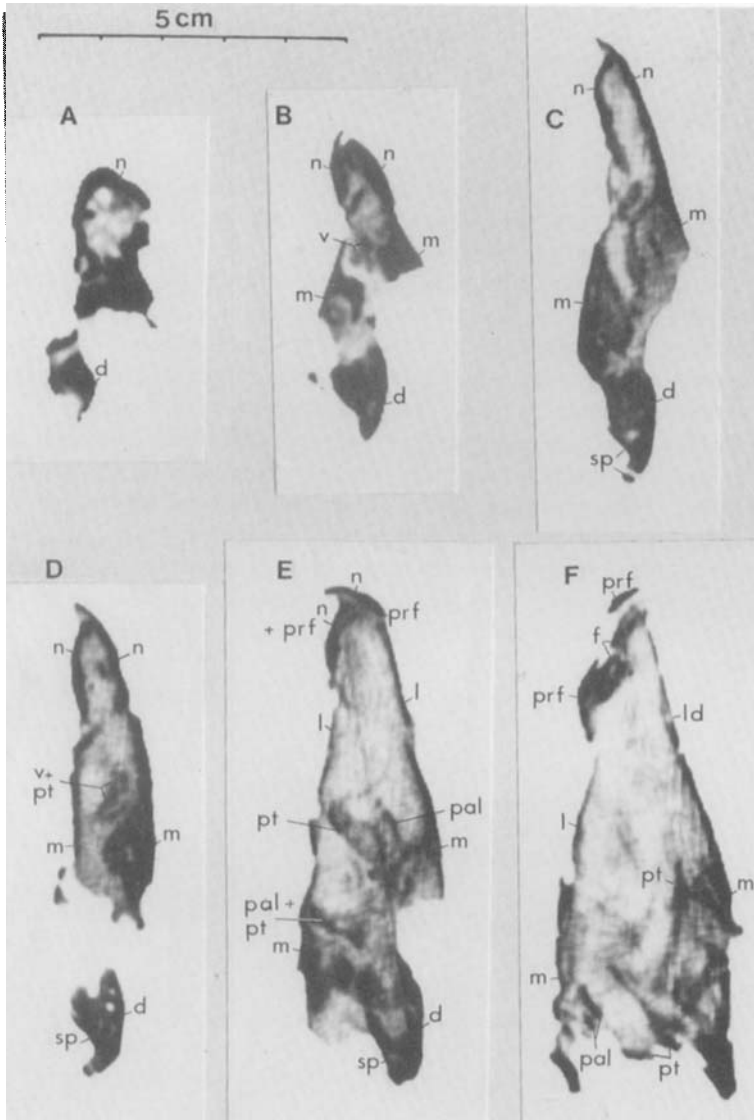
Figure 11. Photographic reproductions of transverse CAT scans of the skull and left lower jaw of *Secodontosaurus obtusidens*, MCZ 1124. Levels of CAT scans A–M are indicated in Fig. 8.

The CAT scans indicate that the vomers extend posteriorly only to the level of the third or fourth postcanine. Nevertheless, this element is unusually long in *Secodontosaurus*, longer than in *Dimetrodon* or *Sphenacodon*, and is undoubtedly due to the elongation of the precanine portion of the snout.

Palatine. The left palatine is exposed in MCZ 1124 in both partial ventral view and cross-sectional view through a transverse break at the level of the eighth postcanine tooth position. This, together with CAT scans, reveals that the palatine is relatively long and exceedingly slender, being at least 80 mm long and never more than 7 mm wide. Its extent is similar to that of *Dimetrodon*, extending from the posterior border of the internal naris to the end of the tooth
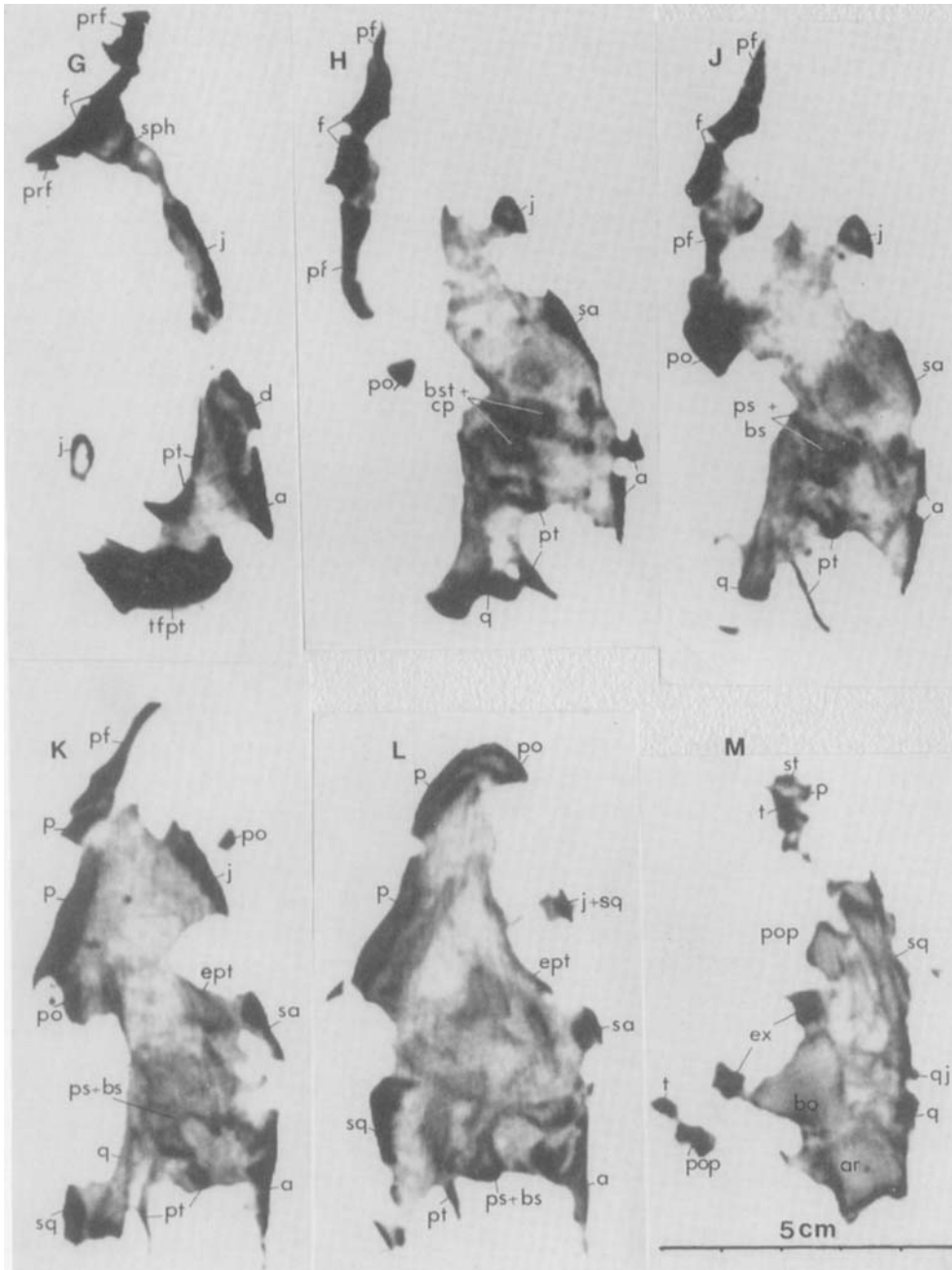
row. However, the width of the palatine is greatly reduced in *Secodontosaurus* when compared with that of *Dimetrodon* or *Haptodus*. The reduced width of the palatine is probably related to the reduced skull width.

Anteriorly, the palatine probably formed the posterior border of the internal naris, but unfortunately this portion of the palate is not exposed. Details of the

palatine–ectopterygoid suture can be seen in ventral view (not seen in figures), where the ectopterygoid has separated slightly from the medial palatal elements. The palatine extends posteriorly as a narrow wedge between the ectopterygoid and the pterygoid and may have supported the ectopterygoid from above. The suture between the palatine and pterygoid extends the full length of the former and appears in ventral view as a slightly sigmoid curve. The transverse section of the skull at the level of the eighth postcanine (Fig. 10iii) shows an unusually thick palatine-pterygoid suture in *Secodontosaurus*.

The most striking feature of the palatine is its contact with the maxilla. Typically in pelycosaurs, the palatine attaches to the maxilla along the medial, highly rugose surface of the alveolar shelf. In *Secodontosaurus*, the palatine-maxilla contact is more extensive, with the palatine extending laterally onto the dorsal surface of the alveolar shelf to reach the dorsal lamina of the maxilla. Although it is impossible to determine whether this supra-alveolar extension of the palatine is suturally attached to the maxilla, it certainly reinforced the marginal tooth row from above. The ventral surface of the palatine does not carry any teeth, in strong contrast to the condition in *Haptodus, Dimetrodon* and *Sphenacodon*.

Ectopterygoid. A small, flat piece of bone in MCZ 1124 is identified as the right ectopterygoid because of the position it occupies relative to the palatine and pterygoid. It appears to be only slightly out of position, having rotated ventrolaterally and shifted a short distance medially beneath the pterygoid. Medially, the ectopterygoid is a thin sheet of bone, but is thickened posteriorly, where it forms the anterior border of a narrow, longitudinal depression that extends posteriorly along the lateral edge of the pterygoid to the subtemporal fossa. The ectopterygoid is also thickened laterally, where it appears to be suturally attached to the alveolar shelf of the maxilla, but the configuration of this contact cannot be determined. The ectopterygoid also has no teeth on its ventral surface.

Pterygoid. Both pterygoids are exposed in cross-sectional breaks at two levels along the snout in MCZ 1124, and the right pterygoid is also partially exposed ventrally. In many respects the pterygoid of *Secodontosaurus* is similar to that of *Sphenacodon* and *Dimetrodon*, but there are a number of noteworthy differences. The three major structural components of the pterygoid are the anterior process (palatal surface), the transverse flange and the posterior quadrate process. Although similar in structure to those of *Haptodus* or *Dimetrodon*, they have different proportions in *Secodontosaurus* as a consequence of the elongation and narrowing of the skull. The anterior process occupies most of the palatal surface of the skull and is slightly longer than in *Dimetrodon*. In contrast to the condition seen in both *Haptodus* and *Dimetrodon*, where the anterior process is L-shaped in ventral view because its posterior one-third is greatly expanded laterally, the process remains relatively narrow in *Secodontosaurus*. The transverse flange and the quadrate process are also significantly reduced in width, and both are less than half the width of the respective processes of sphenacodontine skulls of similar length. As a result of the reduced width, the transverse flange of the pterygoid is only wide enough to hold three teeth, rather than the six or more teeth present on those of *Sphenacodon* or *Dimetrodon*. The transverse section of the skull (Fig. 10iii) and the CAT scans indicates that the dorsally expanded flange of the anterior process is also relatively low in *Secodontosaurus*. The dorsal flange of the quadrate process of the pterygoid, visible through the right orbit, as well as

in the CAT scans, is also reduced in height in proportion to the reduction in height of the skull roof. In addition, however, it appears that the process is shorter than in other sphenacodontids, occupying only 12% of the skull length, whereas in *Dimetrodon* and *Haptodus* it is 21% of the skull length.

The medial edge of the pterygoid is gently concave in ventral view at the level of the transverse flange. This curvature, togeher with the parasphenoid, defines a relatively narrow, small interpterygoid vacuity. The presence of a small, posteromedially inflected process extending from the transverse flange of the pterygoid indicates that the epipterygoid extended far anteroventrally, reaching the dorsal surface of the process and close to the ventral surface of the palate.

Palatoquadrate

Quadrate. The quadrate is preserved only in MCZ 1124, where both are partially exposed. Only the condyles, the anteroventral portion of the dorsal process and the dorsal tip of the left quadrate are exposed as a result of slight anteroventral rotation. The rest of the left quadrate is covered by the squamosal, jugal and quadratojugal. As a result of extensive anterior displacement, all but the posterodorsal part of the dorsal process of the right quadrate has been exposed in lateral view.

The quadrate is a relatively large bone, with two large ventral condyles and a flattened, blade-like dorsal process. The condyles extend medially and laterally from the dorsal process, with the medial condyle positioned slightly anterior and ventral to the lateral condyle. In ventral view, the articulating surface of the medial condyle is elongate anteroposteriorly, narrow mediolaterally, and has a strongly developed ventral ridge close to the medial edge of the condyle. The lateral condyle is broad and has an anteroposteriorly oriented ventral ridge positioned near the groove separating the condyles and parallel to that of the medial condyle. The lateral condyle ridge is not sharply set off from the rest of the lateral condyle, but rather is continuous laterally with its gently curving articulating surface. In most sphenacodontids the two condyles are essentially ventral expansions of the massive dorsal blade-like process and are separated from each other by a deep, narrow groove, whereas in *Secodontosaurus* the condyles are set off at a sharp angle from the dorsal blade and are separated from each other by a relatively broad groove. Consequently, in the skull reconstructions the lateral condyle extends laterally beyond the edge of the skull roof and could probably be seen even in dorsal view (Fig. 2A), whereas the medial condyle extends medially beyond the level of the paroccipital processes and probably obscured them in ventral view (Fig. 2B).

As in sphenacodontids, the dorsal process of the quadrate probably had massive sutural contacts with the squamosal posteriorly, the paroccipital process of the opisthotic medially, the pterygoid anteriorly and possibly the epipterygoid dorsally. Of these sutural surfaces only the ventral part of the contact with the squamosal is exposed. The overall shape of the dorsal process indicates that the pattern of these sutures is similar to that in both *Sphenacodon* and *Haptodus*. The only discernible difference between the quadrate dorsal processes of *Sphenacodon* and *Secodontosaurus* is probably related to differences in skull proportions. That is, the dorsal process in *Sphenacodon* is relatively taller when compared with the anteroposterior dimensions of the process and the size of the condyles.

Epipterygoid. The left epipterygoid is partially exposed in MCZ 1124 (Figs 6, 7). As in other primitive reptiles, the epipterygoid has a broad, triangular base with a tall, posterodorsally oriented pillar-like process. Only the posterior two-thirds of the base is exposed, and a desciption and interpretation of the basicranial recess is, therefore, not possible. The precise relationship between the ptyergoid and epipterygoid cannot be determined, preventing reconstruction of their association. It is nevertheless possible to determine from comparisons between the height of the skull and the size of the epipterygoid that the pillar-like process extended nearly to the pineal foramen, and the anteroventral corner of the triangular base extended far ventrally. The pillar-like process appears shorter and somewhat more robust than that in *Dimetrodon*, features that are probably related to the reduced skull height in *Secodontosaurus*. The structure of the pterygoid in the region medial to the transverse flange at the base of the quadrate process indicates that the basicranial articulation was located far ventrally, close to the ventral surface of the palate. This is in strong contrast to the condition seen in both *Haptodus* (Currie, 1979) and *Dimetrodon* (Romer & Price, 1940), where the basicranial recess of the epipterygoid is attached to the pterygoid near the dorsal edge of the quadrate process, well above the level of the palate.

Braincase

As in other advanced pelycosaurs, the braincase of *Secodontosaurus* (Fig. 3) forms a massive structural unit that is buttressed dorsally against the skull roof by the sphenethmoid anteriorly and the dorsal edge of the supraoccipital posteriorly. Laterally, the braincase is attached solidly to the cheeks via the massive, lateral process of the supraoccipital and the paroccipital process of the opisthotic. Ventrally, the braincase is supported against the palate through the basipterygoid tubera and the epipterygoid anteriorly, and against the quadrate through the paroccipital processes laterally and stapes posteriorly. Most of the braincase forms a massive box-like structure, with extensive fusion of the component elements. Thus, the paired exoccipitals and the basioccipital are fused indistinguishably, as are the supraoccipital, opisthotic and prootic elements. The most striking feature of the braincase of *Secodontosaurus* is its overall similarity to that of *Sphenacodon* or *Dimetrodon*. A few detectable differences in proportion are probably related to the unusual dimensions of the skull of *Secodontosaurus*.

Basioccipital–exoccipital complex. The elements of this complex, preserved in the holotype (AMNH 4007), MCZ 1124 and AMNH 4062, form the occipital condyle, as well as the lateral walls of the foramen magnum. The exposed parts of the complex indicate that in most features it is similar to that in *Sphenacodon* or *Dimetrodon*. The size of the complex relative to the overall size of the occiput, however, is greater in *Secodontosaurus* than in the above sphenacodontids. The ratio of the width of the braincase (measured across the paroccipital processes) to the maximum width of the occipital condyle is 6:1 in *Dimetrodon limbatus* and 3.5:1 in *Secodontosaurus*. As in other pelycosaurs, the floor of the foramen magnum is formed entirely by the exoccipitals, a slight midline rugosity marking their fusion on the dorsal surface of the complex. It is, therefore, likely that part of the occipital condyle is formed by the exoccipitals, but fusion has obliterated any

trace of a basioccipital–exoccipital suture. The vertical pillar-like extension of the exoccipitals form the lateral walls of the foramen magnum, but the dorsomedial extent of the pillar is not as great as in *Dimetrodon*. Dorsally, the exoccipital bears the elongate articular facets for the proatlantal arches. The area of contact between the exoccipitals and the supraoccipital is demarcated by exposed articulating facets on the supraoccipitals of AMNH 4062 and MCZ 1124. The locations of the exits for cranial nerves IX–XI between the dorsal extension of the exoccipital and the opisthotic and for the two small foramina for cranial nerve XII on the lateral surface of the basioccipital– exoccipital are the same as in other sphenacodontids. It has been possible to prepare much of the medial surface of the exoccipital, exposing a large foramen at the base of the pillar that undoubtedly represents the passage of cranial nerve X.

The basioccipital portion of the complex undoubtedly forms the major portion of the occipital condyle. The articular surface of the condyle faces mainly posteriorly, where a slight dimple-like recess represents a remnant of the notochord. Beneath this recess the gently rounded condyle extends ventrally and anteroventrally, as the articulating surface with the atlas-axis complex extends onto the ventral surface of the basioccipital. The ventral portion of the articulating surface has the outline of an isosceles triangle when viewed ventrally, and its unfinished surface is raised from the rest of the basioccipital along the two sides of the triangle. Anteriorly, the basioccipital is covered by a thin posterior projection of the parasphenoid that is attached to narrow longitudinal striations of the basioccipital in a strongly interdigitating suture. Immediately lateral to the posterior projection of the parasphenoid, the lateral edges of the basioccipital appear to contribute to the medial wall of the inner ear cavity and to the medial edge of the fenestra ovalis but, as in *Dimetrodon* and *Aerosaurus*, there is no perichondral bone cover in this area. The extent to which this surface is depressed from the margin of the neighbouring opisthotic and parasphenoid suggests that it was covered by a relatively thick layer of cartilage. The unusually well-developed anterior ossification of the basioccipital can be seen through the large fenestra ovalis (Fig. 13B). In AMNH 4062, the massive anterior ossification of the basioccipital is in contact with the basisphenoid, but also abuts against a massive posterior ossification of the prootic. A similar arrangement has been shown in *Dimetrodon* by Romer & Price (1940: fig. 10, but is less massively ossified.

Supraoccipital–opisthotic–prootic complex. The supraoccipital and opisthotics form the massive occipital plate, whereas the prootics form the lateral walls of the braincase and the dorsum sellae. This complex is generally smaller and less massive in *Secodontosaurus* than in skulls of *Dimetrodon* or *Sphenacodon* of similar size. This is partly due to the smaller dimensions of the occiput of *Secodontosaurus* compared to those of other sphenacodontids of similar skull lengths.

The supraoccipital portion of the complex is exposed in posterior view in the holotype (AMNH 4007) and is partially preserved in AMNH 4062. In MCZ 1124, the supraoccipital is broken along the midline and is almost completely covered by the postparietal and tabulars. The massive mid-dorsal process of the supraoccipital is broad in *Secodontosaurus* and ends in a thick, unfinished surface, and its posterior surface is scarred in AMNH 4007, marking the extent of its overlap by the postparietal. The lateral areas of the mid-dorsal
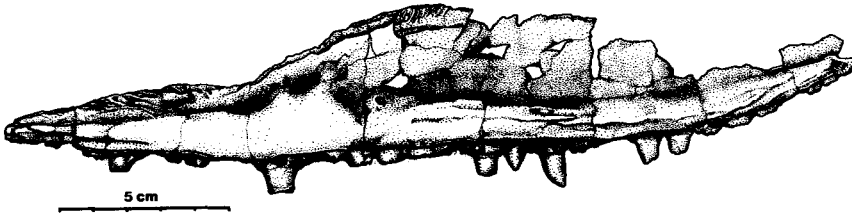
Figure 12. *Secodontosaurus 'willistoni'* Romer (1936), holotype, FMNH (WM) 754. Medial view of right maxilla. Scale bar = 5 cm.

process that would have been covered by the tabular are poorly preserved in AMNH 4007, broken off in AMNH 4062, and covered by dermal bones in MCZ 1124. The massive, paired lateral processes extend dorsolaterally between the mid-dorsal process and the paroccipital processes. The end of the lateral process, preserved on the right side of the supraoccipital of AMNH 4007 and in 4062, is thick and roughened where it would have been covered by the tabular. A shallow notch between the lateral process and the paroccipital process represents the small posttemporal fenestra and probably lies on the union of the supraoccipital and opisthotic. If the lateral extent of the lateral processes are defined by the distance they extend beyond the medial border of the post-temporal fenestra, then they are noticeably shorter than those in *Dimetrodon* or *Sphenacodon*. A vertical median ridge on the occipital surface of the complex in the holotype (AMNH 4007) marks an area of insertion of nuchal ligaments. The ridge is developed to a lesser degree in *Secodontosaurus* than in other sphenacodontids of similar skull length. The supraoccipital contributes to the dorsal border of the foramen magnum between the dorsal pillars of the exoccipitals.

The opisthotic portion of the complex is well-preserved in the isolated braincase AMNH 4062, although the distal portion of both paroccipital processes has been lost. The process is exposed in occipital view in MCZ 1124 and partial anterior view in the holotype AMNH 4007. Significant differences between the opisthotic of *Secodontosaurus* and those of haptodontine and sphenacodontine sphenacodontids are related to the size and shape of the paroccipital process. In all sphenacodontids the paroccipital process is a relatively well-developed structure that extends ventrolaterally from the occipital plate. In *Haptodus*, the paroccipital process is a relatively broad, sheet-like structure throughout most of its length and becomes rod-like only distally. In *Sphenacodon* and *Dimetrodon*, the paroccipital process is broad proximally, but its rod-like distal portion extends much farther ventrolaterally than in *Haptodus*. In *Secodontosaurus*, the process is massive and broad at its base, as in other sphenacodontids, but is slender and rod-like for most of its length. The long rod-like portion of the process is curved strongly posteriorly and slightly ventrally. The exposed portion of the anterolateral surface of the paroccipital indicates that the articulation for the dorsal process of the stapes is identical to that in *Sphenacodon* (Eberth, 1985) and *Dimetrodon* (Romer & Price, 1940), consisting of a wide, shallow socket surrounded by a narrow articular ridge of unfinished bone. Directly above the articulating facet for the dorsal process of the stapes the distal end of the paroccipital process is strongly striated for articulation with the dorsal process of the quadrate.
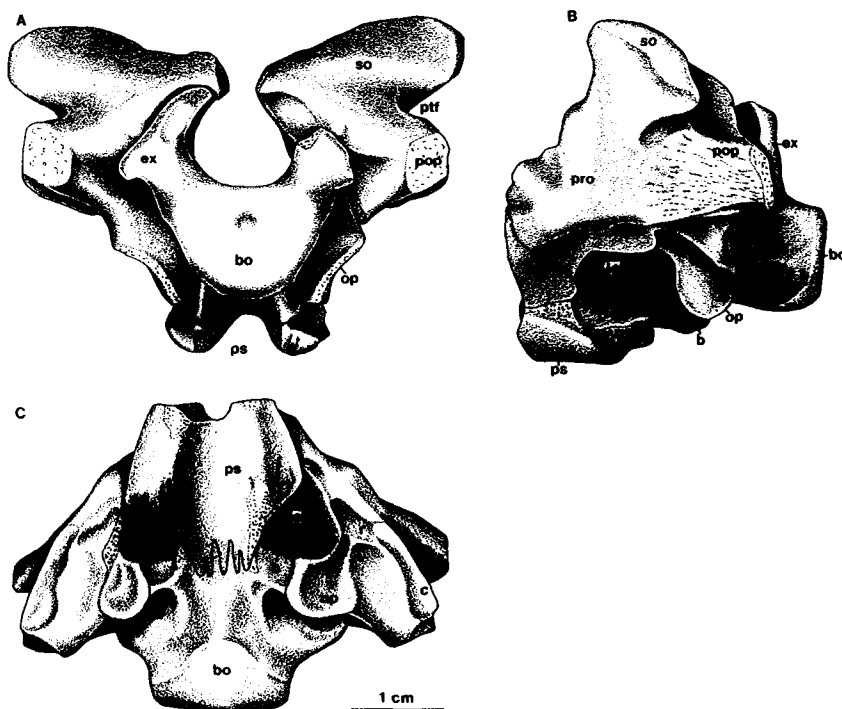
Figure 13. *Secodontosaurus obtusidens*, AMNH 4062. Partial braincase in A, posterior (occipital), B, left lateral, and C, ventral (palatal) views. Scale bar = 1 cm.

The prootic region of the braincase is partially preserved in AMNH 4062 (Fig. 13B). As in other sphenacodontids, it is indistinguishably fused to the rest of the braincase in *Secodontosaurus*. The preserved parts of the element are virtually identical to those of *Dimetrodon* (Romer & Price, 1940: fig. 10) both in shape and relationships to the surrounding elements.

Basiparasphenoid. AMNH 4062 has the posterior portion of this fused complex preserved in articulation with the rest of the braincase. Although the basiparasphenoid is not exposed in any of the other specimens used in this study, information was gained from CAT scans of MCZ 1124 (Fig. 11). In addition, the outline of the cristae ventrolaterales is discernible on the holotype, despite being covered by badly worn and damaged bone of an unidentified element. The available evidence indicates that in *Secodontosaurus*, as in *Sphenacodon* and *Dimetrodon*, the posterior portion of the parasphenoid is narrower than in *Haptodus*, and the narrow cristae ventrolaterales are separated by a narrow, deep median groove. Posteriorly, the ventral surface of the cristae are heavily marked by striae, in a manner similar to that seen in other sphenacodontids. Some significant features of the basiparasphenoid not exposed in AMNH 4062 can be deduced from the CAT scans of MCZ 1124. The transverse sections of the skull indicate that the basiparasphenoid has been rotated ventrolaterally toward the right by about 40°. These images are sufficiently detailed to show the passage of the canal for the carotids through the basiparasphenoid (Fig. 11). It is also evident from the CAT scans that the complex forms a narrow, solid neck-like region just posterior to the basipterygoid processes. The shape of the

basipterygoid processes can also be seen in Fig. 11. They appear vertically oval in outline and lie close to the midline. The processes lie just slightly ventral to the base of the transversely narrow, anterodorsally directed cultriform process, most of which has been lost in MCZ 1124.

Stapes. A nearly complete left stapes has been exposed in MCZ 1124. It has been little disturbed from its attachment to the braincase, and consequently the articulating facets of the dorsal process and of the footplate have not been exposed. Both of these processes are significantly smaller than in sphenacodontids of similar skull length. As in other advanced pelycosaurs, the dorsal process is at least twice as large in the transverse plane as the footplate. The stapedial foramen is also unusually small in *Secodontosaurus*, probably a consequence of the reduced size of the footplate. As in *Dimetrodon* the articulating surface of the footplate probably covered part of the opisthotic, and was much too small to cover the large opening of the inner ear, commonly called the fenestra ovalis. It is possible that this large opening represents an artifact of preparation, because the stapes does cover completely the fenestra ovalis in *Dimetrodon*. The evidence that both the footplate and dorsal process abut against opisthotic supports the hypothesis that the pelycosaurian stapes served mainly to brace the braincase against the quadrate, rather than as an acoustic transducer of vibrations. Although the distal portion of the shaft is incompletely preserved, reconstruction of this region of the skull indicates that the shaft must have been unusually short for a sphenacodontid, probably a consequence of the reduced skull width and height.

Mandible

The lower jaw of *Secodontosaurus* conforms to the pattern expected in a sphenacodontid pelycosaur (Fig. 1), but is unusually elongate and slender. As in other pelycosaurs the ossified mandibular elements include a single endochondral bone, the articular, and seven dermal elements, the dentary, angular, surangular, splenial, prearticular and two coronoids (Figs 4, 6, 7, 10, 14–16). The dentary, angular and surangular form almost all of the lateral surface of the mandible, whereas the other dermal elements are associated primarily with the medial surface.

Dentary. As in all pelycosaurs, the dentary is the longest element of the lower jaw, and that of *Secodontosaurus* occupies 76% of the length of the lower jaw. The dorsal edge of the dentary in MCZ 1124 is not exposed sufficiently to permit a tooth count, but the larger, isolated left lower jaw of AMNH 4091 (Fig. 14) shows 23 teeth, including incomplete teeth, and 12 resorption pits for a total count of 35. In none of the specimens available for study is there a marked difference in the size of the teeth along the series except for a small, gradual decrease toward the posterior end. This is in strong contrast to the heterodonty present in *Haptodus*, *Dimetrodon* and *Sphenacodon*. In adult specimens of *Haptodus garnettensis*, the second and third teeth of the dentary are usually larger than the rest of the series, whereas in *Dimetrodon* and *Sphenacodon*, they are greatly enlarged and can be described as caniniform. In order to accommodate these larger teeth in *Haptodus*, *Dimetrodon* and *Sphenacodon*, the dentary is swollen mediolaterally. On the other hand, in AMNH 4091 the second and third teeth of the mandibular series are only slightly larger than the rest, and in MCZ 1124 there is no
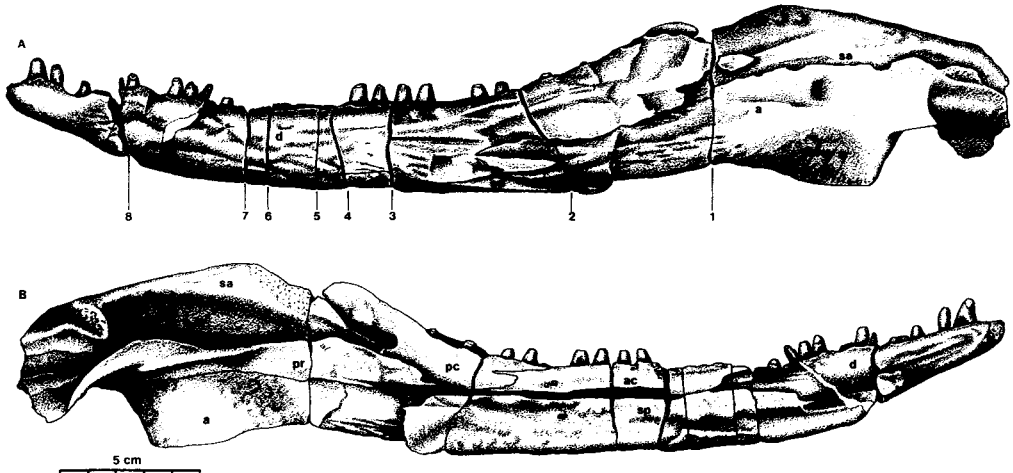
Figure 14. *Secodontosaurus obtusidens*, AMNH 4091. Partial left lower jaw in A, lateral, and B, medial views. The numbers 1–8 indicate seven natural breaks and a mechanical cut (5) that permit the transverse illustrations shown in Fig. 15. Scale bar = 5 cm.

noticeable difference in the sizes of the anterior teeth. In contrast to the condition seen in all other known pelycosaurs, the first three teeth of the dentary in *Secodontosaurus* point markedly anteriorly, with the first tooth directed nearly straight forward and in line with the shallow ventral margin of the lower jaw. The dorsal edge of the dentary is concave in lateral view, giving the anterior two-thirds of the lower jaw a slightly upward curvature. The anteriormost portion of the lower jaw, anterior to tooth position 6, consists entirely of the unusually slender dentary. In this region the dentary becomes increasingly more slender in strong contrast to the opposite condition in other sphenacodontids. The narrow meckelian canal of the dentary is exposed medially as it emerges from beneath the anterior margin of the splenial, becoming progressively shallower as it extends toward the symphysis. The mandibular symphysis of *Secodontosaurus* is very small relative to the length of the lower jaw, and is far less developed than in other pelycosaurs of comparable skull length. The symphyseal surface is restricted to the dentary and is not strongly rugose as in other sphenacodontids but rather gently pitted, suggesting that more movement may have been possible between the rami of *Secodontosaurus* than in other sphenacodontids. In most pelycosaurs, including *Haptodus* and *Dimetrodon*, the symphysis extends posteroventrally and incorporates the splenial. Posterior to tooth position 12 the alveolar shelf of the dentary is covered medially by the two coronoids. Despite the slender appearance of the mandible, the dentary remains relatively robust. This is partly because the meckelian canal is unusually narrow in *Secodontosaurus* (Fig. 15, sections 3–7), and the anterior portion of the angular does not extend as far anteriorly as in *Dimetrodon* (Romer & Price, 1940: fig. 14, section 2). As documented by the transverse sections of AMNH 4091 (Fig. 15, sections 2–8), the alveolar shelf is well developed both dorsoventrally and mediolaterally. Posteriorly, the dentary overlaps on the lateral surface the angular and surangular, and supports the posterior coronoid medially.
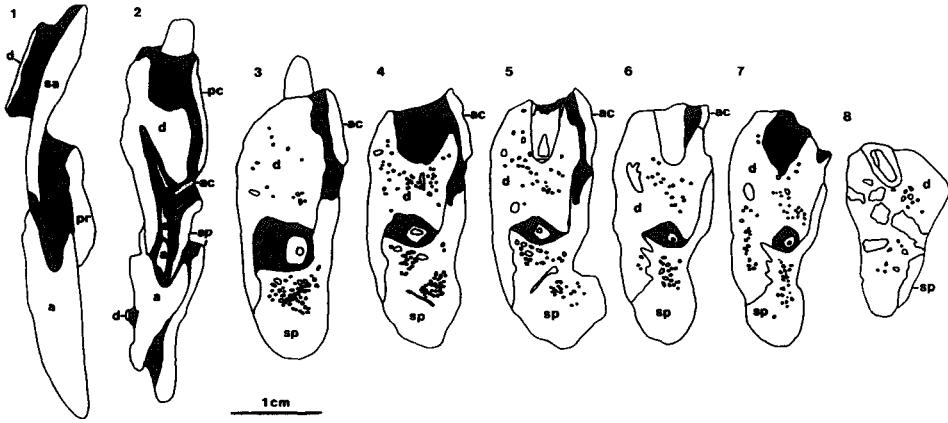
Figure 15. Transverse sections through the left lower jaw of AMNH 4091 drawn at seven natural breaks and a mechanical cut (5) at levels 1–8 as indicated in Fig. 14. Scale bar = 1 cm.

Splenial. Medial view of the mandible of AMNH 4091 exhibits the splenial as a long, narrow, subrectangular element (Fig. 14B). In contrast to other sphenacodontids, the splenial does not contribute to the symphysis in *Secodontosaurus*, but terminates at about the level of the sixth tooth position. There is a small notch in the anterior margin of the splenial where it covers medially the meckelian canal. The splenial is attached to the lateral margin of the alveolar shelf along most of its length (Fig. 15, sections 3–8) and also probably contacted the ventral margins of the anterior and posterior coronoids. Beneath the meckelian canal the splenial has an extensive sutural contact with the medial surface of the dentary. A distinct scar on the medial surface of the angular between transverse sections 1 and 2 of AMNH 4091 (Fig. 14B) at the anterior end of the medial exposure of the angular indicates that the splenial is incomplete posteriorly. The splenial undoubtedly overlapped the angular in this region of the mandible, extending posteriorly beyond the anterior edge of the adductor fossa. In this feature, *Secodontosaurus* differs from the other sphenacodontids, where the splenial terminates posteriorly at a level well anterior of the adductor fossa. Posteroventrally, the splenial contacts the anterior end of the angular along the ventral edge of the mandible, whereas more anteriorly it wraps around the ventral edge of the mandible to contact the dentary on the lateral surface of the mandible (Figs 14A, 15, sections 3–7). The splenial forms, therefore, a significant portion of the mandibular ventral edge.

Coronoids. As in all other pelycosaurs, there are two coronoids in *Secodontosaurus*, and both are well preserved in AMNH 4091. The anterior coronoid extends along the central portion of the alveolar shelf of the dentary from the 16th to the 28th tooth position and has an interdigitating suture with the posterior coronoid. The posterior coronoid continues along the remaining medial surface of the alveolar shelf to the anterior edge of the adductor fossa. Here, as in *Sphenacodon* and *Dimetrodon*, the posterior coronoid is subdivided into two processes. A large posterodorsal process overlaps medially the surangular along the lower half of the low coronoid eminence, and a second, short posteromedial process first makes a short contribution to the anteromedial border of the adductor fossa

before being overlapped medially by the prearticular. In contrast to the anterior coronoid, which is entirely restricted to the medial surface of the alveolar shelf, the posterior coronoid has a narrow lateral exposure along the anterodorsal edge of the coronoid eminence of the mandible.

Surangular. The surangular, visible in lateral and medial views of the mandible, is exposed in both MCZ 1124 and AMNH 4091. The massive dorsal edge of the surangular forms most of the low, broadly convex coronoid eminence. In lateral view, much of this large element is covered by the dentary and angular. A slender, thin lateral exposure of the surangular, present in both MCZ 1124 and AMNH 4091, extends far posteriorly to overlap the lateral surface of the prearticular–articular complex as it extends to the base of the retroarticular process. In medial view, the surangular forms the lateral wall of the adductor fossa. In MCZ 1124, a large knob-like process extends medially from the posterior portion of the surangular and ends in an unfinished sutural surface for attachment to the articular.

Angular. The angular is a large, elongate, flattened element that is exposed in both the medial and lateral views of AMNH 4091 and lateral view of MCZ 1124. It is attached anteriorly to the splenial and dentary, dorsolaterally to the surangular, and dorsomedially to the prearticular and forms the posteroventral portion of the lower jaw. Throughout most of its anterior length the angular is V-shaped in cross-section, and forms, as in other sphenacodontids, a ventrally projecting blade beneath the adductor fossa, referred to as the reflected lamina. The lamina is similar in size to that in *Dimetrodon* and much larger than that in *Haptodus*. As in *Dimetrodon*, the lateral surface of the lamina is strongly pitted and grooved. Although generally similar to that of other sphenacodontids, the reflected lamina of *Secodontosaurus* is distinct in being elongate rather than deep, and having a thin rather than thick ventral edge. Posterior to the reflected lamina, the angular has a well-developed horizontal process that supports the articular directly beneath the condylar recesses. A posterior process of the angular extends to the base of the retroarticular process.

Prearticular. As in other sphenacodontids, the prearticular is a narrow, twisted element that extends along the ventromedial border of the adductor fossa. Anteriorly, the prearticular is wedged between the posterior coronoid and the splenial, whereas posteriorly, it extends to the pterygoideus process of the articular, where it wraps around the ventral edge of that element. Available evidence indicates that the complex contact between the prearticular and articular is similar in *Secodontosaurus* and *Sphenacodon*. The only notable difference between the two taxa relates to the degree of downward curvature of the complex at the posterior end of the lower jaw. In *Secodontosaurus*, the prearticular–articular complex and the area of its attachment on the angular are not curved ventrally as in *Sphenacodon*, but rather extend posteriorly, with the ventral edge of the complex being parallel to the long axis of the jaw.

Articular. The articular, best preserved in AMNH 4826 (Fig. 16), is a small, robust, complex bone with two distinct recesses for articulation with the quadrate, a posteriorly projecting retroarticular process, and a ventromedial pterygoideus process. The articular of *Secodontosaurus* is not as compact and massive as in *Dimetrodon* or *Sphenacodon* and appears to be more elongate anteroposteriorly. In the isolated articular AMNH 4826, most of the sutural surfaces for adjoining elements are completely preserved. Laterally, the central
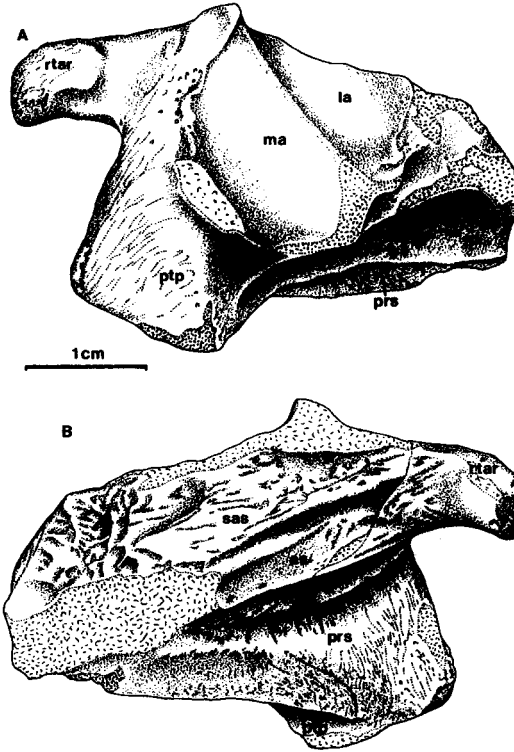
Figure 16. *Secodontosaurus obtusidens*. AMNH 4826. Articular in approximately A, medial, and B, lateral views. Scale bar = 1 cm.

portion of the articular has deep, strongly rugose sutural surfaces for the surangular and angular that are separated by a well-developed longitudinal ridge. The sutural surface for the angular appears to extend over a sharp, ventrally facing ridge that is an anterior extension of the ventral edge of the retroarticular process and terminates ventrally along the base of the pterygoideus process. Thus, the main body of the articular and the base of the pterygoideus process were supported by a trough-shaped posterior process of the angular. However, most of the area ventral to this sharp ridge forms a slightly rugose sutural surface for the prearticular, and only the tip of the pterygoideus process is not covered laterally by the prearticular. In medial view, the sutural surface for the prearticular is long and narrow (Fig. 16A), and the reconstructed medial sutural edge is unusually long and angled anterodorsally (Fig. 1C). The pterygoideus process is well developed and appears more robust than in sphenacodontids of similar skull length. In *Secodontosaurus*, the retroarticular process extends posteriorly beyond the ends of the angular and surangular, then turns sharply ventrally. The articular of other sphenacodontids is stouter than that of *Secodontosaurus*, and the entire retroarticular process extends ventrally.

The two recesses for articulation with the quadrate face mediodorsally and only slightly anteriorly. The lateral recess is larger, and a well-developed buttress on the posteriomedial margin of its surface probably served to prevent forward dislocation of the jaw. A well-developed ridge extends anteromedially from this

buttress. Except for the posteromedial buttress, the lateral recess is gently concave, and its central longitudinal trough is open anteromedially. The medial recess is bound laterally by the ridge and medially by a well-developed buttress, and the central longitudinal trough is open at both ends. The two longitudinal troughs are approximately parallel to one another, and their long axes are oriented anteromedially.

Dentition

The marginal dentition of *Secodontosaurus* is partially preserved in the holotype AMNH 4007 and in MCZ 1124. Although most of the teeth are somewhat broken either at the base or at the tip, some have remained undamaged, allowing description of the dental series. The premaxillary teeth are relatively slender, sharply pointed and lack any anterior or posterior cutting edges. All the preserved maxillary teeth have anterior and posterior cutting edges, but they lack serrations. The anterior cutting edge is present only along the apical half of the tooth and extends from the medial surface basally onto the anterior edge apically. The posterior cutting edge extends vertically almost the entire height of the tooth. The anterior maxillary teeth are more robust than the premaxillary teeth, but are not as robust as the posterior maxillary teeth. The posterior maxillary teeth are broad anteroposteriorly at the base and remain broad throughout most of their lengths.

The anterior dentary teeth are slender and sharply pointed, more slender than any tooth of the upper marginal series. The posterior dentary teeth are robust, even near the tips. Nevertheless, they are not as broad anteroposteriorly as the posterior maxillary teeth. All the preserved dentary teeth have cutting edges of similar design to those on the maxillary series and also lack serrations. All the teeth on the pterygoid have the shape of simple cones, without any cutting edges.

PHYLOGENETIC RELATIONSHIPS

Secodontosaurus was included by Romer & Price (1940) in the synapsid family Sphenacodontidae as the sole representative of the 'subfamily Secodontosaurinae'. Their subdivision of this family into the 'Haptodontinae', 'Sphenacodontinae' and 'Secodontosaurinae' reflects the view that sphenacodontids include the ancestral, primitive form, *Haptodus*, from which three advanced groups evolved: the Early Permian sphenacodontines and secodontosaurines, and the Late Permian therapsids. Although the hypothesis of close relationships between advanced pelycosaurs and therapsids is widely accepted, a detailed analysis of phylogenetic relationships of the above taxa has not been undertaken. In order to resolve the evolutionary relationships of *Secodontosaurus*, it is necessary to analyse the phylogenetic relationships of sphenacodontids (*sensu* Romer & Price, 1940). Such an analysis is also expected to clarify what taxon among sphenacodontids is the nearest relative of therapsids.

Most recent classifications of synapsids divide them into the sister taxa Caseasauria and Eupelycosauria (Kemp, 1982; Reisz, 1986). Caseasuria, which includes the families Eothyrididae and Caseidae, is not directly relevant to the

problem at hand. Eupelycosauria includes the non-therapsid families Varanopseidae, Ophiacodontidae, Edaphosauridae, Sphenacodontidae, as well as all the advanced synapsids, the Therapsida (Reisz, 1986). Given our current knowledge of these groups, the following inclusive terminal taxa have been selected for standard cladistic analysis:

Family Varanopseidae. The following genera have been used to infer the ancestral condition for this family: the small varanopseid *Mycterosaurus* (significantly more primitive than other members of this family), the lightly built, but much larger carnivores *Varanops*, *Aerosaurus* and *Varanodon*. *Mycterosaurus* and *Aerosaurus* have been redescribed recently (Berman & Reisz, 1983; Langston & Reisz, 1981). *Varanops* and *Varanodon* have been carefully examined by the senior author for the purposes of this study.

Family Ophiacodontidae. The following genera have been used to infer the ancestral condition for this family: *Archaeothyris*, a small ophiacodontid from the Middle Pennsylvanian of Nova Scotia (Reisz, 1972), a small, primitive, undescribed new species of *Ophiacodon* from the Late Pennsylvanian near Garnett, Kansas (Wilson, 1989). *Varanosaurus*, a highly specialized representative of this group has also been examined for the purposes of this study by the authors.

Family Edaphosauridae. The two genera that have been included in this family are *Ianthasaurus*, a small insectivorous form from the Late Pennsylvanian of Kansas (Reisz & Berman, 1986; Modesto & Reisz, 1990) and *Edaphosaurus*, the large Permo-Carboniferous herbivores from North America (Modesto, 1991). These genera have been used to infer the ancestral condition for this family.

The following genera have been included in the analysis as synapsids that have been placed previously in the Sphenacodontidae: *Haptodus* has been included in the family by several authors (Romer & Price, 1940; Reisz, 1986), but recent cladistic analyses have suggested that this genus falls outside the clade formed by the other members of this family (Gauthier *et al.*, 1989). The cranial anatomy of *H. baylei* has been described in detail by Currie (1979), whereas recently discovered skulls of *Haptodus garnettensis* add significant new information about the cranial anatomy of the genus, especially in the region of the occiput, braincase and mandible (Laurin, 1990). *Dimetrodon* and *Sphenacodon* have been described and illustrated in detail (Romer & Price, 1940; Eberth, 1985), but *Ctenospondylus* is less well known than the other sphenacodontids, especially postcranially. *Secodontosaurus* is also included in this analysis on the basis of new osteological information presented above. Although two species of *Secodontosaurus* have been named (Romer, 1936), we propose in the Systematic Palaeontology section that *Secodontosaurus willistoni* is a junior subjective synonym of *Secodontosaurus obtusidens*.

Therapsida. The following genera have been used to infer the ancestral state for this taxon: The large, carnivorous *Titanophoneus* from the Permian of U.S.S.R. is known by excellent cranial and postcranial materials; other therapsids from the U.S.S.R. include *Biarmosuchus*, *Syodon* and *Venjukovia*. These therapsids were re-examined by the first author.

In all, 97 osteological features or characters (Appendix 1) were used in the phylogenetic analysis of the above taxa. Some of these characters are utilized for the first time, but the majority come from previous studies (Brinkman & Eberth,
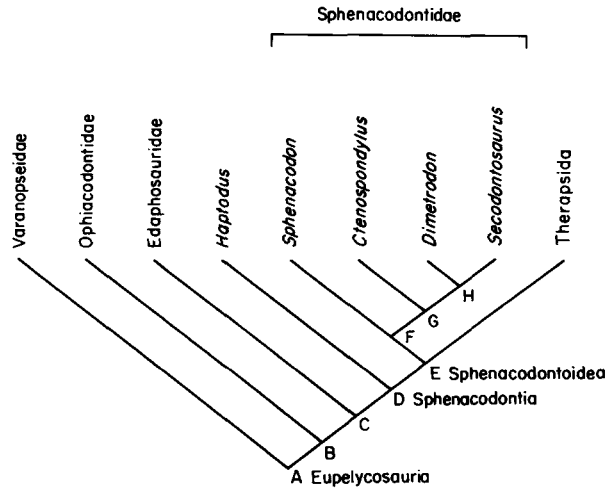
Figure 17. Cladograms illustrating hypothesis of phylogenetic relationships of sphenacodontid synapsids (see text for explanations).

1983; Reisz, 1986; Gauthier, Kluge & Rowe, 1988). The resultant data matrix (Appendix 2) was subjected to the branch and bound algorithm of PAUP 3.0, which guarantees to find all of the most parsimonious trees. The analysis was performed with the assistance of Mr Michel Laurin on a MacIntosh Plus computer, using the MacIntosh version of PAUP 3.0 (Swofford, 1989). In this program the trees were rooted using the outgroup method, and the character state optimization was minimum F-value, which tends to remove tree length from interior branches toward peripheral branches wherever possible. The character states were left unordered. Only one most parsimonious tree was found (Fig. 17). It requires 150 steps and has an overall consistency index of 0.801. As expected, the results of this analysis indicate that *Haptodus*, the sphenacodontids and *Secodontosaurus*, and the Therapsida form a clade, and the Edaphosauridae, Ophiacodontidae and Varanopseidae are progressively more distant sister taxa to this clade. However, the new hypotheses of phylogenetic relationships between *Haptodus*, *Sphenacodon Ctenospondylus*, *Secodontosaurus*, *Dimetrodon* and Therapsida are dramatically different from previous proposals, requiring a new taxonomic scheme and new diagnoses. The cladogram of Fig. 17 suggests the following indented taxonomic scheme (Ax, 1987):

Sphenacodontia (Romer & Price, 1940)
    Haptodus (Gaudry, 1886)
    Sphenacodontoidea (new combination)
        Therapsida (Broom, 1905)
        Sphenacodontidae (Case, 1915)
            Sphenacodon (Marsh, 1878)
            Node G
                Ctenospondylus (Romer, 1936)
                Node H
                    Dimetrodon (Cope, 1878)
                    Secodontosaurus (Romer, 1936)

Whereas Sphenacodontia and Sphenacodontidae have been previously used in slightly different contexts, the Sphenacodontoidea represents a new taxonomic unit. The procedure of defining taxa in terms of common ancestry and providing provisional diagnoses in the form of lists of synapomorphies will be followed here (Gauthier *et al.*, 1988). Thus, the shared derived characters, or synapomorphies, listed below are grouped according to which of the nodes (D–H of the cladogram of Fig. 17), or the taxonomic units listed above that they diagnose. Nodes D–F have been assigned the formal taxonomic names Sphenacodontia, Sphenacodontoidea (new combination) and Sphenacodontidae, respectively. Synapomorphies of nodes A–C are given in Appendix 1, but are not discussed in the text. Preceding each synapomorphy is a capitalized letter that denotes the node diagnosed by the synapomorphy, and by an arabic number that identifies the synapomorphy at that node. In the discussion of each synapomorphy, the character states are indicated by bracketed arabic numbers (0–3), denoting unordered states. Some patterns of synapomorphy, when analysed, were determined to be ambiguous, in that more than one transformational series were equally parsimonious. Those ambiguous characters that could apply at more than one node are identified with a question mark (?).

Sphenacodontia: *Haptodus,* Sphenacodontidae, Therapsida and all synapsids that share a more recent common ancestry with them than with edaphosaurids.

D1, Ventral edge of the premaxilla slopes anteroventrally, giving the snout a slightly hooked appearance. The premaxilla is directed slightly anteroventrally (1), similar to, but not as strongly angled, as that in captorhinid reptiles. This orientation of the premaxilla is most noticeable if the ventral edge of the premaxilla is compared with that of the anterior portion of the maxilla. The slightly hooked appearance of the sphenacodont premaxilla may be related to deeper implantation of the larger first and second premaxillary teeth relative to those in other primitive eupelycosaurs. The primitive condition of the premaxilla, seen in all other primitive eupelycosaurs, is a snout in which the ventral edge of the premaxilla is in line with that of the anterior portion of the maxilla (0). Therapsids appear to show the secondarily derived condition of an anterodorsal slope (2).

?D2, The latent surface of the prefrontal is recessed in front of the orbit. The presence of a slight depression on the lateral surface of the prefrontal (1) near the anterodorsal corner of the orbit may be related to the development of the supraorbital shelf. The depression is shallow in *Haptodus* and *Secodontosaurus*, but is deep in other sphenacodontids and therapsids. Ophiacodontids also appear to have a shallow lateral depression of the prefrontal, making this synapomorphy ambiguous.

?D3, The posterolateral wing of the parietal is transversely broad, and

?D4, The lateral edge of the parietal posterolateral wing is convex. The posterolateral wing of the parietal normally supports the supratemporal in primitive synapsids and its lateral edge is either slightly concave or straight (0) and does not project laterally beyond the supratemporal. In *Haptodus* and sphenacodontids, the wing extends laterally beyond the lateral edge of the supratemporal in a slightly convex margin, giving the parietal a transversely broad appearance (1) in this region. In therapsids, this region of the skull has been modified dramatically, making these synapomorphies ambiguous.

D5, Supracanine buttress is present on the medial surface of maxilla, but lacks a dorsal ascending process. The presence of a well-developed canine buttress (1) is related to the increased size of the canines and their deep implantation into the alveolar shelf. The alveolar shelf is thickened both medially and dorsally where the canines are inserted deeply. Small, immature individuals of *Haptodus* show only a moderate degree of enlargement of the alveolar shelf in the region of the canines. The primitive condition for synapsids is the presence of caniniform teeth without a buttress (0), as in *Oedaleops* (Langston, 1965). The supracanine buttress in ophiacodontids has probably been derived independently from that of sphenacodontids, judging from the differences in the morphology of this area in the two groups. In ophiacodontids there is a moderate thickening of the alveolar shelf which is supported by an ascending process that extends dorsally from the alveolar shelf along the medial surface of the maxilla (2).

D6, Ventral lamina of angular is strongly convex posteriorly. The ventral lamina of the angular has a gently convex posteroventral edge (0) in both ophiacodontids and edaphosaurids, where this element extends toward the posterior end of the mandible. In *Haptodus*, sphenacodontids and primitive therapsids the ventral edge is strongly convex (1), and the ventral lamina does not extend to the posterior end of the jaw. This condition is not directly related to the reflection of the lamina seen in sphenacodontids and therapsids, because *Haptodus* shows this condition even though its lamina extends ventrally directly beneath the body of the mandible, as in *Ianthasaurus* and *Ophiacodon*.

D7, First premaxillary tooth is greatly enlarged and similar in length to the enlarged canine. In *Haptodus*, *Dimetrodon* and *Sphenacodon* there is a well-developed canine and an enlarged first premaxillary tooth, both significantly larger than the other teeth on the premaxilla and maxilla (1). Although *Secodontosaurus* has a well-developed canine, the first premaxillary tooth, though enlarged, is not as large as in the above sphenacodontids. We interpret the dental pattern seen in *Secodontosaurus* as secondarily derived within the Sphenacodontidae and related to the adaptational complex associated with the evolution of a narrow, low skull with a slightly elongated snout. The primitive condition, seen in part in other Permian synapsids, is the possession of a moderately developed caniniform tooth, and a slightly enlarged first premaxillary tooth (0). This condition is exemplified by *Oedaleops* (Langston, 1965). Therapsids show a second derived condition of all premaxillary teeth being enlarged and equal in length (2).

D8, Second dentary tooth is greatly enlarged. In the lower jaw of *Haptodus*, *Dimetrodon*, *Sphenacodon* and *Ctenospondylus*, the second tooth is significantly larger than all the other teeth of the series (1). We interpret the condition seen in *Secodontosaurus*, where this tooth is not enlarged, as a reversal associated with the evolution of a slender lower jaw. The primitive condition, seen in ophiacodontids, is the presence of slightly enlarged anterior dentary teeth (0). Therapsids such as *Titanophoneus* and *Biarmosuchus* show a second derived condition of all four anterior dentary teeth being greatly enlarged (2).

D9, Premaxillary tooth count is less than five. *Haptodus*, *Dimetrodon*, *Sphenacodon*, *Ctenospondylus* and therapsids have four or three premaxillary teeth (1), whereas *Varanops*, *Ophiacodon* and other primitive eupelycosaurs have five or six premaxillary teeth (0). We interpret the presence of six premaxillary teeth in *Secodontosaurus* as a reversal associated with slight elongation of its snout.

D10, The triceps process on the posterior coracoid is large. The triceps process is

unusually large and broad anteroposteriorly (1) in *Haptodus*, sphenacodontids and therapsids. In *Ianthasaurus* and *Ophiacodon* the process is moderately developed relative to the size of the posterior coracoid (0). The posterior coracoid tends to be poorly ossified in *Varanops*, but is moderately developed in the varanopseid *Aerosaurus*. The triceps process appears to be large in therapsids primitively.

D11, Ventral adductor ridges of femur are poorly developed. The ventral adductor ridge that extends distally from the fourth trochanter is poorly developed (1) in *Haptodus*, sphenacodontids and therapsids. In addition, the rugose areas representing the fourth trochanter and the internal trochanter do not extend far ventrally from the body of the femur. The primitive condition, seen in edaphosaurs and ophiacodontids and varanopseids, is the presence of prominent ridges and trochanters on the ventral surface of the femur (0).

Comments. The Sphenacodontia was first erected by Romer & Price (1940), and included the families Varanopseidae and Sphenacodontidae. The distribution of the synapomorphies D1–D11 indicates that *Haptodus*, the sphenacodontids, therapsids and all other advanced synapsids (including mammals) form a clade, and to this monophyletic group we propose to assign the formal taxonomic designation of Sphenacodontia. Edaphosauridae, Ophiacodontidae and Varanopseidae represent progressively more distant sister taxa to the Sphenacodontia.

Sphenacodontoidea: Sphenacodontidae, therapsids and all synapsids that share a more recent common ancestry with them than with *Haptodus*.

E1, The body of the premaxilla is robustly constructed. The relative size and shape of the premaxilla is variable in synapsids, but the massive configuration of the body of this element (3) is restricted to sphenacodontids and primitive therapsids. *Ophiacodon* and *Varanops* exhibit two other derived states, elongate, slender (1) and wide (2) premaxillary body, respectively, whereas *Ianthasaurus* and *Eothyris* have the primitive character state of lightly built, short premaxillary body (0).

E2, Maximum length of nasal is greater than that of the frontal. This derived condition (1), seen in all sphenacodontids and in therapsids, may be related to the increase in the length of the muzzle region relative to that of the orbital region. The increase in muzzle length is not evident (0) in *Haptodus* or *Ianthasaurus* and is judged as the primitive state. We interpret the elongated condition of the nasal in *Ophiacodon* to have been derived independently from that of sphenacodontoids. All other early synapsids, including caseids and varanopseids, also exhibit the primitive state for the length of the nasal.

E3, Nasal has a posteroventral narial process. Primitively, the posterior border of the external naris is formed by the lacrimal (0), as seen in *Varanops*, *Ophiacodon*, *Ianthasaurus* and *Haptodus*. With the exclusion of the lacrimal from the external naris in sphenacodontids and therapsids, a ventral extension of the nasal forms the posterior border of the naris (1). In the varanopseid *Mycterosaurus* the lacrimal is also excluded from the naris, but it is a dorsal process of the maxilla that replaces the lacrimal rather than the nasal.

E4, Frontal orbital lappet extends far laterally. Primitively, synapsids lack an orbital process of the frontal (0), as seen in varanopseids and ophiacodontids. Both *Ianthasaurus* and *Haptodus* possess a small orbital lappet (1), whereas sphenacodontids and therapsids have broad lappets that extend far laterally (2).

The advanced edaphosaur *Edaphosaurus* has a well-developed orbital lappet, but we interpret this condition as independently derived from the intermediate condition (1). The progressive modification of the lappet within this genus (Modesto, personal communication) provides support for this hypothesis.

E5, Postfrontal is deeply incised posteriorly by the postorbital. In most early synapsids the posterior border of the postfrontal contacts the parietal and postorbital in a slightly interdigitating suture that extends laterally or posterolaterally. The contact of the postfrontal with the parietal and postorbital is nearly straight in *Haptodus*, conforming to the primitive condition (Currie, 1979). As in most other early synapsids, in *Haptodus* the postorbital–postfrontal contact is an abutment joint (0). In sphenacodontids and in therapsids (Reisz, personal observations) there is a deep, concave encroachment into the posterior border of the postfrontal by the postorbital. In addition, an anterodorsal process of the postorbital overlaps the dorsal surface of the postfrontal to sheath a concave depression behind the supraorbital shelf (1).

E6, Pineal ridge surrounds pineal foramen. In all sphenacodontids the pineal foramen is located on a slightly raised area of the parietal and is bordered by a distinct, rounded ridge (1). The primitive condition, seen in all other Lower Permian synapsids, is that the pineal foramen simply opens on the flat surface of the skull table (0). The derived condition is also found in primitive therapsids.

E7, Lateral surface of postorbital is strongly recessed. In both *Ianthasaurus* and *Haptodus*, the supraorbital region of the skull roof is expanded laterally to form a supraorbital shelf or hood above the orbit. This shelf is supported posteriorly by a buttress formed by the postfrontal and postorbital. Behind this buttress the lateral margin of the postorbital appears gently concave in dorsal view (1). In sphenacodontids and therapsids, the postorbital buttress is particularly well developed, and consequently the lateral surface of the postorbital is strongly recessed (2) as it extends from the buttress to the posterolateral corner of the skull table. Thus, the posterior process of the postorbital appears strongly concave in dorsal view. Ophiacodontids, caseasaurs and varanopseids exhibit the primitive condition for synapsids, with the lateral surface of the postorbital being nearly flat (0).

E8, Ventral margin of maxilla is strongly convex. The ventral edge of the maxilla is slightly convex in *Eothyris*, ophiacodontids, *Ianthasaurus* and *Haptodus* (1), whereas *Sphenacodon*, *Dimetrodon*, *Ctenospondylus* and therapsids exhibit the derived condition of the ventral margin being strongly convex (2). We interpret the condition seen in *Secodontosaurus*, where the ventral edge is only gently convex, as a character reversal associated with the evolution of a slender, low skull.

E9, Lacrimal is exluded from the naris. In sphenacodontoids the lacrimal is reduced in length anteriorly and fails to reach the external naris, allowing the contact between the nasal and maxilla (1). *Haptodus* exhibits the primitive condition of a long, slender lacrimal that extends from the orbit to the external naris, completely separating the maxilla and nasal (0). In the varanopseid *Mycterosaurus*, the lacrimal is also excluded from the external naris, but this condition has been interpreted as independently derived (Berman & Reisz, 1983). In another varanopseid, *Varanodon*, the lacrimal is reduced in length, but is not excluded from the external naris because the latter is greatly expanded posteriorly. The derived state of the reduced length of the lacrimal, excluding it from the external naris, is found in sphenacodontids and therapsids, but the

shape of the lacrimal is different in two groups, being wedge-shaped in the former and subrectangular in the latter. This suggests that these states may have been derived independently.

E10, Suborbital process of jugal is expanded anterodorsally at the anteroventral corner of the orbit. In all early synapsids, the jugal is a triradiate element with discrete suborbital, postorbital and subtemporal processes. Primitively, as in *Varanops, Ophiacodon, Ianthasaurus* and *Haptodus*, the suborbital process extends anteriorly beneath the orbit and meets a distinct posteroventral orbital process of the lacrimal (0). In sphenacodontids and therapsids, the suborbital process extends far anteriorly and even dorsally to form a portion of the anteroventral orbital border that is otherwise occupied by the lacrimal (1).

E11, Basicranial articulation is located posterior to the level of the transverse flange of the pterygoid. *Sphenacodon, Ctenospondylus, Dimetrodon* and therapsids show the derived condition of the basicranial articulation being at a level posterior to the pterygoid flange (1), whereas in *Secodontosaurus*, the primitive condition of both structures being at approximately the same level (0) occurs. We interpret the condition in *Secodontosaurus* as a possible reversal associated with the reduction in the height and width of the skull.

E12, Paroccipital process of opisthotic extends ventrolaterally. In sphenocodontids and therapsids the paroccipital process extends ventrolaterally (1), as indicated by the curvature of its ventral edge. The primitive condition, with the process extending laterally, its ventral edge being nearly horizontal (0), is seen in *Haptodus*.

E13, Paroccipital process of opisthotic extends posteriorly. This character state is difficult to interpret because the known specimens of *Haptodus* are strongly flattened postmortally and the curvature of its opisthotic is uncertain. The available evidence, however, suggests that the moderate posterior curvature of the sphenacodontid and therapsid paroccipital process (1) is greater than the straight, or nearly straight process (0) of *Haptodus*. *Secodontosaurus*, on the other hand, shows the second derived condition of a sharply recurved paroccipital process (2).

E14, Paroccipital process is narrow, blade-like. *Sphenacodon, Ctenospondylus, Dimetrodon* and therapsids show the derived condition of a narrow, blade-like paroccipital process (1), whereas *Secodontosaurus* has the second derived condition of a narrow, rod-like process (2). The primitive condition of a broad, blade-like structure (0) is seen not only in *Haptodus*, but also in *Varanops*.

E15, Reflected lamina is present on angular. A reflected lamina of the angular is a distinct morphological feature of all sphenacodontids and therapsids, in which it curves posterolaterally from the main body of the mandible (1), whereas in *Haptodus* and other non-sphenacodontid pelycosaurs, the ventral flange or lamina of the angular is directly beneath the main body of the mandible (0). The reflected lamina of sphenacodontids occupies *c.* half the height of the lower jaw just anterior to the level of the jaw articulation. In this taxa the posterior portion of the lamina is separated laterally from the prearticular and the slender posterior process of the angular, and its posterior edge forms a distinct notch anteroventral to the jaw articulation. The notch is best seen in lateral view of the mandible. The reflected lamina also creates a wide groove between itself and the angular surface of the main body of the mandible that extends anteriorly from the level of the jaw articulation. The groove is formed entirely by the angular

and lies between a medial flange that is attached to the prearticular and the reflected lamina that lies lateral to the main body of the mandible. The reflected lamina is further modified in therapsids.

E16, Retroarticular process is well developed and is formed by the articular. Primitively, the articular either lacks a clearly defined retroarticular process, as in *Ophiacodon*, *Ianthasaurus* and *Haptodus*, or it is a multipartite process (0), as in *Varanops*. In sphenacodontids and therapsids, a distinct retroarticular process is formed entirely by the articular (1).

E17, Retroarticular process is curved ventrally. Primitively, as exemplified by *Varanops*, the retroarticular process extends posteriorly from the level of the suspensorium (0). The derived condition of a ventrally curved process (1) occurs in all sphenacodontids and is apparently also present in primitive therapsids (Hopson & Barghusen, 1986).

E18, Marginal teeth possess anterior and posterior cutting edges. Sphenacodontids and most primitive therapsids have anterior and posterior cutting edges along the apical two-thirds of the maxillary, premaxillary and dentary teeth (1). Primitively, synapsids such as *Ophiacodon*, *Ianthasaurus* and *Haptodus* lack this feature (0). The derived condition, seen in *Varanops* and other varanopseids, was probably acquired independently of that seen in sphenacodontoids.

E19, Canines are more than twice as large as all other maxillary teeth. Primitively, synapsids possess caniniform teeth, but these are only slightly larger (0) than the other teeth on the maxilla. In sphenacodontids and primitive therapsids, the canines are at least twice as large as any other maxillary teeth (1). Although the canines appear relatively smaller in *Secodontosaurus* than those in other sphenacodontids, this is partly an illusion created by the elongation of the marginal tooth row.

E20, Number of precanine maxillary teeth reduced to less than four. The apparent primitive condition of six precanine maxillary teeth (0) in *Secodontosaurus* is interpreted here as a character reversal, associated with the autapomorphy of snout elongation. All other sphenacodontids and therapsids show the derived condition of less than four precanine maxillary teeth (1).

E21, Vomerine teeth absent. In *Haptodus* and *Ophiacodon* the relatively slender vomer carries small teeth on its ventral surface (0). This primitive condition is seen in all other early synapsids except sphenacodontids, where this region of the palate is exposed. Sphenacodontids and therapsids lack vomerine teeth (1).

E22, Lateral surfaces of presacral neural arches are deeply excavated. The primitive neural arch morphology for synapsids is the lack of excavation on the lateral surfaces of the presacral vertebrae (0), as seen in caseasaurs. The derived condition of slightly excavated neural arches occurs in the primitive eupelycosaurs, *Varanops* and *Ianthasaurus*, as well as *Haptodus* (1). Sphenacodontids and therapsids have the second derived condition of deeply excavated neural arches (2). The absence of excavation in *Ophiacodon* is interpreted here as a character reversal and autapomorphic for the Ophiacodontidae.

E23, Scapular blade is narrow distally, and

E24, Scapular blade is narrow at the base. Primitively, synapsids possess a large scapular blade which is broad both proximally and distally (0). Sphenacodontids and therapsids have the derived conditions of the reduced scapular blade both distally and at the base (1), giving the shoulder girdle its distinctly tall and slender appearance.

E25, Iliac blade has an anterodorsal process. Primitively, the synapsid iliac blade only has a long, slender posterodorsal process and lacks an anterodorsal extension (0). This condition is seen in primitive eupelycosaurs, including *Haptodus*. The derived condition of an iliac anterodorsal process (1) occurs in all sphenacodontids, as well as in primitive therapsids.

E26, Intertrochanteric fossa of femur is shallow. A deep intertrochanteric fossa (0) makes the ventral surface of the femoral proximal head deeply concave, as seen in synapsids primitively. The proximal head of the femur of most primitive synapsids appears, therefore, relatively thin in transverse section, and its articular surface is elongate anteroposteriorly, but narrow dorsoventrally. In sphenacodontids the proximal head of the femur is more robust than in other early synapsids, and the intertrochanteric fossa is therefore shallow (1). Consequently, the proximal articular surface for the acetabulum is also robust and wide in its dorsoventral dimension.

E27, Lateral centrale pedis is absent. Although complete pedes are rarely preserved, we have been able to determine that two centralia pedes (0) are present in *Varanops*, *Ophiacodon* and *Haptodus*, representing the primitive condition. The lateral centrale is absent in sphenacodontids where this part of the skeleton is well preserved, and is also absent in therapsids.

Comments. The hypothesis of close relationships between sphenacodontids and therapsids is strongly supported by 27 synapomorphies. This, in turn, permits the following conclusions:

(1) The sphenacodontids and therapsids (including mammals) form a clade, designated here as Sphenacodontoidea. In evolutionary terms the presumed common ancestor of therapsids and sphenacodontids was a carnivorous synapsid of moderate to large size that resembled more closely the sphenacodontids that dominated the terrestrial scene during the Early Permian than the small *Haptodus*. Osteological features that diagnose this clade probably represent an adaptational complex that allowed sphenacodontids and therapsids to maintain their dominant role among terrestrial vertebrates during the Permian.

(2) *Haptodus* is the nearest sister taxon to Sphenacodontoidea. Thus, *Haptodus* falls outside the clade that includes the sphenacodontids and therapsids. Taxonomically, this requires the removal of *Haptodus* from Sphenacodontidae. In the most recent review of this genus a large number of formerly distinct taxa were placed into two species, *Haptodus baylei* and *H. garnettensis* (Currie, 1979). *Haptodus saxonicus*, *H. longicaudatus*, *H. gaudryi*, *H. macrourus* and *Cutleria wilmarthi* were all made junior synonyms of *H. baylei*, but without a thorough, direct study of the majority of the type specimens. Ongoing studies of these specimens (Michel Laurin) has revealed the likelihood that the synonomy was invalid, but this does not alter significantly the above conclusion, because none of these taxa belong in Sphenacodontoidea.

Sphenacodontidae: *Sphenacodon, Ctenospondylus, Dimetrodon, Secodontosaurus* and all other sphenacodontoids that share a more recent common ancestry with them than with therapsids.

F1, Premaxilla lacks a distinct palatal process. The premaxilla of reptiles is composed primitively of three major processes that extend from its main body: a dorsal process extends to the nasal, a posterolateral process contacts the maxilla in a long, oblique suture and the posterior palatal process contacts the vomer in

a long oblique suture. The primitive pattern of all three processes being retained (0) is seen in most early synapsids, including *Haptodus* and primitive therapsids. In sphenacodontids, including *Secodontosaurus*, the palatal process of the premaxilla has been essentially lost, so that the vomer forms the entire medial border of the internal naris, and the premaxilla–vomer contact is very narrow (1). Although the palatal process of the premaxilla is retained in therapsids, it is relatively shorter than in either *Haptodus* or *Ophiacodon* (Reisz, personal observations).

F2, Anterior process of frontal is narrower than posterior process. In sphenacodontids the width of the anterior process of the frontal is *c.* one-half that of the posterior process (1). Other eupelycosaurs, including *Haptodus* and therapsids, retain the presumed primitive state of subequal widths of the anterior and posterior processes (0). The reduced width of the anterior process of the frontal in *Secodontosaurus* appears to be related to the extensive overlap of the frontal by the prefrontal, as shown by cross-sectional views of the skull of MCZ 1124 (Fig. 10). Isolated frontals of *Sphenacodon* (Eberth, 1985) and reconstructions of *Dimetrodon* (Romer & Price, 1940) show a similar pattern of overlap.

F3, Frontal has long anterior process. In all primitive synapsids the frontal is a supraorbital element with distinct anterior and posterior processes. In *Ianthasaurus* and *Haptodus* the anterior process is slightly longer than the posterior process due to moderate anterior elongation of the former. In sphenacodontids the anterior elongation of the frontal is significantly greater (1) than in either *Haptodus* or therapsids, with the antorbital process being at least three times as long as the postorbital process. *Ophiacodon* also shows this derived state, but is interpreted as derived independently from the condition seen in sphenacodontids as a result of the elongation of the snout.

?F4, Parasphenoid plate is transversely narrow and has a deep median groove. Primitively, the posterior portion of the parasphenoid has the form of a wide plate with a broad shallow groove separating well-developed cristae ventrolaterales (0). This character state is seen in *Haptodus*. *Ophiacodon* and therapsids exhibit the derived condition of a narrow parasphenoid plate that lacks a deep median groove (1). Sphenacodontids exhibit a second derived condition in which the plate is narrow and possesses a deep median groove (2). This pattern of distribution makes the derivation of this synapomorphy of sphenacodontids ambiguous only because it is equally parsimonious to derive it from either state (0) or (1).

F5, Axis neural spine is narrow dorsally. The neural spine of the axis is moderately expanded anteroposteriorly (0) in *Haptodus, Ianthasaurus* and therapsids (0). Sphenacodontids show the derived condition of a relatively tall axial neural spine that is anteroposteriorly broad proximally, but becomes narrow distally (1).

F6, Cervical centra are keeled ventrally. In *Haptodus garnettensis*, the cervical vertebrae have a longitudinal ventral ridge that extends the length of the centrum. This ridge lacks a keel ventrally (0). Sphenacodontids exhibit the derived condition of a sharp ventral keel on the cervical centra (1).

F7, Dorsal centra are keeled ventrally. As in the cervical region, the dorsal vertebrae of *Haptodus garnettensis* have a longitudinal ridge ventrally, and lack a distinct keel (0). In sphenacodontids, the anterior and mid-dorsal vertebrae show the derived condition of a sharp ventral keel (1).

F8, Neural spines are elongate. Neural spine elongation is a derived feature of presacral vertebrae that is frequently encountered in early synapsids. There is strong evidence to indicate that this condition has been developed independently in several eupelycosaur families (Sphenacodontidae, Edaphosauridae and Ophiacodontidae). Among the sphenacodonts, *Haptodus* exhibits the primitive condition in having blade-like neural spines of moderate height (neural spine height 25% to 50% greater than centrum height) (0). Among synapsids the primitive state (0) is also seen in members of Caseidae, Varanopseidae and Ophiacodontidae. In *Sphenacodon* the neural spines of the presacral vertebrae show elongation, with the height of the spines always being at least three times the height of the centra (1).

F9, Ischium (distal portion) is expanded posterodorsally. The primitive state, the ischium being slender distally (0), occurs in *Varanops, Haptodus, Ophiacodon* and therapsids. Although large species of *Edaphosaurus* also exhibit the derived state of a distal posterodorsal expansion of the ischium (1), it is interpreted as derived independently from the primitive condition because the small edaphosaur *Ianthasaurus* exhibits the primitive state (0).

Comments. The Sphenacodontidae, first erected by Case (1915), was modified by Romer & Price (1940) to include some fragmentary sphenacodont materials, *Haptodus, Secodontosaurus, Sphenacodon, Dimetrodon* and the fragmentary *Ctenospondylus.* Romer & Price (1940) proposed two alternative hypotheses of relationships for *Haptodus,* the 'sphenacodontines', and *Secodontosaurus.* One hyothesis was that *Secodontosaurus* could be a specialized off-shoot of an advanced sphenacodont, such as *Sphenacodon,* in which the skull became secondarily low and slender. The alternative hypothesis proposed that *Secodontosaurus* could have developed from a primitive sphenacodont, such as *Haptodus,* with the skull becoming secondarily elongated. Placed in a cladistic framework these two hypotheses of relationships can be stated as follows: (A) *Sphenacodon, Ctenospondylus, Dimetrodon* and *Secodontosaurus* are more closely related to each other than either is to *Haptodus* and share a more recent common ancestor than either does with *Haptodus,* or (B) *Secodontosaurus* and *Haptodus* are more closely related to each other than either is to *Sphenacodon, Ctenospondylus* and *Dimetrodon* and share a more recent common ancestor than either does with these sphenacodontines.

All the known osteological features shared by *Haptodus* and *Secodontosaurus* are ancestral for sphenocodontoids and, therefore, of no value in evaluating phylogenetic relationships within this group. No derived features have been discovered that are shared by *Haptodus* and *Secodontosaurus* which appear in the primitive state in *Dimetrodon, Sphenacodon* or *Ctenospondylus.* The available evidence, therefore, supports hypothesis A, that *Secodontosaurus* and the other sphenacodontids are more closely related to each other and share a more recent common ancestor than any of them does with *Haptodus.* Therefore, the Sphenacodontidae, as defined here, forms a monophyletic taxon, or clade, rather than a paraphyletic grade, and is the nearest sister group of therapsids (including mammals).

Node G: The common ancestor of *Ctenospondylus, Dimetrodon, Secodontosaurus* and all of its descendants that share a more recent common ancestry with them than with *Sphenacodon.*

G1, Neural spines are greatly elongated. The presence of greatly elongated neural spines (taller than five times the height of the centrum) in *Secodontosaurus* dorsal vertebrae was suspected by Romer & Price (1940), but has been confirmed only in the present study. The primitive condition of neural spine height of dorsal vertebrae being less than five times the height of the centra is seen in *Sphenacodon.*

G2, Neural spines have anterior and posterior shoulder-like constrictions. The primitive condition, seen in *Sphenacodon* and *Haptodus,* is the presence of a laterally flattened, blade-like neural spine in which the anterior and posterior edges are essentially straight throughout their lengths (0). In *Ctenospondylus, Dimetrodon* and *Secodontosaurus* the neural spine is subdivided into distinct proximal and distal portions marked by a rather abrupt, shoulder-like convergence of the fore and aft edges of the spine (0). This can result in an anteroposteriorly narrower distal portion of the spine, as seen in *Dimetrodon,* or even an anteroposterior expansion of the distal portion of the spine, as exhibited by the presacral vertebrae of *Ctenospondylus.* The shoulder-like constriction probably marks the dorsal limit of the epaxial musculature. A similar pattern of neural spine morphology is present in edaphosaurs, and is considered to have been probably acquired independently in that group.

Node H: The common ancestor of *Dimetrodon* and *Secodontosaurus* and all its descendants that share a more recent common ancestry with them than with *Ctenospondylus.*

H1, Nasal-maxillary suture is longer than nasal-lacrimal suture. The primitive condition appears to be the presence of a relatively short nasal-maxillary suture, as seen in *Ctenospondylus* and *Sphenacodon,* that is shorter than the nasal-lacrimal suture (1). In *Dimetrodon* and *Secodontosaurus* the derived condition of this character is a suture between these elements that is longer than the suture between the nasal and lacrimal (2). The condition of very long nasal-maxillary suture and absence of nasal-lacrimal suture seen in therapsids is considered to have been independently derived.

H2, Neural spines are rounded in cross-section. In both *Dimetrodon* and *Secodontosaurus* the greatly elongated neural spines are rounded in transverse section above the shoulder-like proximal constriction (1). This derived condition is also present in edaphosaurs (and the enigmatic *Lupeosaurus*), but is interpreted here as independently acquired from that seen in the above sphenacodontids. The primitive condition, seen in all other synapsids, is the presence of laterally flattened, blade-like neural spines (0).

H3, Anterior and posterior grooves are present on neural spines. In both *Dimetrodon* and *Secodontosaurus* the anterior and posterior surfaces of the greatly elongated neural spines exhibit well-developed longitudinal grooves (1). Such grooves are not present (0) in any other synapsid.

Comments. In order to evaluate the phylogenetic relationships between *Secodontosaurus* and other sphenacodontids, two alternative hypotheses must be compared and tested. The first hypothesis reflects the subdivision of sphenacodontids into the two subfamilies erected by Romer & Price (1940), Sphenacodontinae and Secodontosaurinae. In this scheme, *Sphenacodon, Ctenospondylus* and *Dimetrodon* form a clade, and are more closely related to each other than any is to *Secodontosaurus.* Superficially, this hypothesis appears reasonable, especially when the great phenetic similarity between the skulls of

Sphenacodon, *Ctenospondylus* and *Dimetrodon* is taken into account. There are only two possible synapomorphies that may test the above hypothesis of relationships: presence of a maxillary step anterior to the canines, and the number of precanine maxillary teeth reduced to less than three. However, both of these character states appear to be size related, because small species of *Dimetrodon* (Romer & Price, 1940) and juvenile, small specimens of *Sphenacodon* show the intermediate or primitive condition. For example, Eberth (1985) has shown that precanine tooth counts decrease during ontogeny, and the degree of development of the maxillary step is also ontogenetically variable in the specimens of *Sphenacodon* from the Anderson quarry of New Mexico. In addition, this hypothesis necessitates the independent acquisition of five derived characters: G1–G2, H1–H3.

The second hypothesis of relationship views *Dimetrodon* and *Secodontosaurus* as sister taxa and, therefore, more closely related to each other than either is to *Sphenacodon* or *Ctenospondylus*. Although there is little to differentiate the skulls of the sphenacodontines *Dimetrodon*, *Sphenacodon* and *Ctenospondylus*, and the skull of *Secodontosaurus* is highly autapomorphic, this hypothesis is supported by one cranial (H1) and two postcranial (H2 and H3) synapomorphies. In this context the skull pattern of *Secodontosaurus* can be viewed as having been derived from that of a sphenacodontid through slight elongation of the snout and great reduction in height and width. Under this hypothesis the similarities between the skulls of *Sphenacodon*, *Dimetrodon* and *Ctenospondylus* represent symplesiomorphies for sphenacodontids, and the shared derived characters listed above test and falsify the first and widely accepted concept of relationships.

Less well supported by the distribution of synapomorphies is the hypothesis that *Ctenospondylus* is the nearest sister taxon to the clade formed by *Dimetrodon* and *Secodontosaurus*. Synapomorphies G1, great elongation of the neural spines, and G2, presence of anterior and posterior shoulder-like constrictions of the neural spines, are not very convincing characters, given the distinct morphology of the *Ctenospondylus* neural spines, and the frequent derivation of spine elongation within primitive synapsids. Nevertheless, the taxonomic consequence of these hypotheses is that the traditional subfamily Sphenacodontinae is paraphyletic and no longer valid.

Secodontosaurus: This taxon is diagnosed by a large number of autapomorphies:

(I) *Skull and mandible are unusually low and narrow.* A large number of autapomorphic features of *Secodontosaurus* can be attributed to its unusual, low, narrow skull: (a) Dorsal process of the premaxilla is narrow. *Haptodus*, *Dimetrodon* and *Sphenacodon* share the condition of a broad well-developed dorsal process associated with a robust premaxilla (E1). The narrow dorsal process of the premaxilla of *Secodontosaurus* is obviously related to its slender, narrow snout, and should be considered a derived feature. (b) Premaxillary process of nasal is narrow and reduced in length. In most early synapsids, including sphenacodontids and *Haptodus*, the long premaxillary process of the nasal extends far anteriorly and lateral to the dorsal process of the premaxilla to form most of the dorsal edge of the external naris. In *Secodontosaurus*, however, the premaxillary process of the nasal is narrow and short and has an underlapping contact with the dorsal process of the premaxilla. Consequently, the dorsal

margin of the external naris is formed nearly equally by both elements. (c) Supracanine buttress is poorly developed. The canines are well developed in *Secodontosaurus*. Typically, canines of the size of those in MCZ 1124 and FMNH (WM) 753 would be set in deep sockets and associated with a large buttress. Two features of the maxilla, however, suggest that implantation of the canines in *Secodontosaurus* is not as well developed as in other sphenacodontids of comparable size. The lateral swelling of the maxilla directly above the canines is barely noticeable in *Secodontosaurus*, in contrast to the marked swelling in *Dimetrodon*, *Sphenacodon* and *Ctenospondylus*. The height of the maxilla at the level of the canines is only slightly greater than the length of the canine in *Secodontosaurus*, whereas in other sphenacodontids the height of the maxilla is *c.* twice the length of the canines. (d) Nasal is reduced in width throughout its length. (e) Ventral palatal process of lacrimal is reduced. In most Early Permian synapsids in which the snout is known in medial view, there is a well-developed ventromedial process of the lacrimal at the level of the anterior orbital margin that extends to the palate. This process is particularly well developed in *Sphenacodon*, *Dimetrodon* and *Haptodus* (Eberth, 1985; Romer & Price, 1940, personal observations), and is also found in *Ianthasaurus*. In *Secodontosaurus* this process appears to be either reduced or completely absent, judging from cross-sectional breaks of the skull and the CAT scans of MCZ 1124. (f) Orbital lappet of frontal is reduced. *Ianthasaurus*, *Haptodus*, sphenacodontids and therapsids are characterized by the presence of a supraorbital shelf that is formed in part by an orbital lappet or lateral process on the frontal (E4–1). *Sphenacodon*, *Dimetrodon* and therapsids have large orbital lappets of the frontals (E4–2). The orbital lappet in *Secodontosaurus*, although present, is modest, and as a consequence the interorbital width of the skull is also greatly reduced. Even though specimens of *Haptodus garnettensis* show the ancestral condition of a modest orbital lappet, it is still slightly better developed than that in *Secodontosaurus*. (g) Parietal forms part of the dorsal border of the temporal fenestra. In all other early synapsids the dorsal border of the temporal opening is formed by the postorbital and the squamosal. As a possible consequence of a greatly narrowed skull, the posterior process of the postorbital may have been reduced, and the anterior process of the squamosal became restricted mainly to the ventral surface of the parietal. Even though the lateral edge of the parietal contributes to the superficial surface of the dorsal rim of the temporal fenestra, the postorbital–squamosal contact is retained medial to the edge of the fenestra on the ventral surface of the parietal. (h) Postorbital does not contact the supratemporal. In most primitive synapsids the long posterior process of the postorbital contacts the supratemporal. This condition, considered to be primitive for amniotes, is found not only in *Eothyris* and *Oedaleops*, where both the postorbital and supratemporal are large, sheet-like elements, but also in *Ophiacodon*, *Sphenacodon* and *Dimetrodon*, where the postorbital and supratemporal are slender. The loss of contact between these two elements in *Secodontosaurus* is probably the result of the reduction in the length of the posterior process of the postorbital, rather than the supratemporal. An analogous condition is apparently present in the varanopseids *Varanodon* and *Varanops*, where the posterior process of the postorbital is completely replaced by the squamosal, resulting in a loss of contact between the supratemporal and postorbital (Reisz, personal observations). The dermal skull roof is so highly modified in the temporal region of *Varanodon* that we conclude that the loss of the

supratemporal–postorbital contact has been achieved independently in these taxa. The polarity of this character is ambiguous within the Eupelycosauria because both *Ianthasaurs* and *Haptodus* appear to have lost the postorbital–supratemporal contact. (i) Posterolateral wing of parietal is greatly reduced in width and directed mainly posteriorly. In *Haptodus, Sphenacodon* and *Dimetrodon,* the posterolateral wing of the parietal is broad and extends mainly laterally and slightly posteriorly. The same condition is present in *Eothyris* and a wide variety of other early synapsids and is therefore presumed to be primitive. In *Secodontosaurus,* on the other hand, the process projects almost directly posteriorly. (j) Relatively large postparietal covers large area of supraoccipital. Primitively, the occipital exposure of the supraoccipital is large in sphenacodontids, and the postparietal covers only a small portion of this large plate-like element. In *Secodontosaurus,* as a consequence of the reduced skull height, the supraoccipital is reduced in height, but the postparietal remains relatively large and covers a significant portion of its posterior surface. (k) Elongate paroccipital process of opisthotic is narrow and rod-like. In *Haptodus,* sphenacodontids and therapsids, the paroccipital process of the opisthotic is narrow and blade-like. In *Secodontosaurus,* the paroccipital process has been reduced to a rod-like shaft of bone. (l) Stapes is slender and the shaft is reduced in length. In *Dimetrodon* and *Sphenacodon,* the stapes is a large, stout, robust element, with a broad dorsal process, a slightly smaller, rounded footplate, well-developed stapedial foramen, and a large anteroposteriorly flattened shaft. The stapes of *Haptodus garnettensis* (personal observations) is similar, but slightly less stoutly constructed than those of the above sphenacodontids. The stapes in *Secodontosaurus* is morphologically distinguishable from those of other sphenacodontids, because the shaft is more slender and the footplate, dorsal process and stapedial foramen are all smaller relative to the skull. Possibly because the relative width and height of the skull in the occipital region is reduced, the length of the stapedial shaft has also become reduced. (m) Dorsal and lateral processes of supraoccipital are reduced. In sphenacodontids, the primitive condition is represented by large, well-developed dorsal and lateral processes on the supraoccipital. In *Secodontosaurus,* these processes are reduced, the dorsal process being reduced both in width and height and the lateral processes in height. (n) Lateral surface of prefrontal is reduced in height. Primitively, in sphenacodontids the prefrontal is a relatively large element that contributes significantly to the lateral surface of the cheek. In *Secodontosaurus,* the prefrontal is unusually long and slender and its contribution to the height of the snout is modest, possibly as a consequence of the reduction in the height of the skull. (o) Suborbital and subtemporal rami of jugal are reduced in height. In *Dimetrodon* and *Secodontosaurus,* the jugal is a relatively tall element, with large, plate-like suborbital and subtemporal rami. Both the suborbital and subtemporal rami of the jugal are greatly reduced in height in *Secodontosaurus.* (p) Jaw articulation is at the level of the tooth row. In *Ianthasaurus, Haptodus* and *Dimetrodon,* the jaw articulation is below the level of the tooth row. This is one of the derived character states shared by edaphosaurid and sphenacodont synapsids (Reisz, 1986) and, thus, can be considered to be the primitive state for sphenacodontids. The location of the jaw articulation at the level of the tooth row in *Secodontosaurus,* therefore, represents a character reversal and an autapomorphic feature of this taxon. (q) Transverse flange of pterygoid is reduced in width. The transverse flange of the pterygoid is a large structure in

early synapsids that extends far ventrally from the general palatal surface and supports either a battery of small or a single row of large teeth. *Haptodus*, *Dimetrodon* and *Sphenacodon* have large, well-developed transverse flanges that accommodate a row of seven to 12 large teeth. In *Secodontosaurus*, the transverse flange of the pterygoid is robust and still extends ventrally far below the general palatal surface, but has been greatly reduced in width. Consequently, there is room for only three teeth on its reduced flange. The teeth, however, are still comparable in size to those on the transverse flanges of *Sphenacodon* and *Dimetrodon* specimens of similar skull length. (r) Palatal exposure of palatine is greatly reduced. The extreme reduction in the palatal exposure of the palatine is a highly unusual autapomorphic feature of *Secodontosaurus*. All other Early Permian synapsids, including *Haptodus* and *Dimetrodon*, exhibit the primitive condition of a large palatine with a large palatal exposure that forms nearly half of the palatal surface between the internal naris and the transverse flange of the pterygoid. In *Secodontosaurus*, the palatine forms less than 10% of the palatal surface. (s) Vomer is greatly reduced in width. The autapomorphic feature of a greatly reduced width of the vomer in *Secodontosaurus* does not appear as dramatic as the reduction of the palatine, because the vomers in early synapsids are generally slender midline elements which form the medial border of the internal nares. The vomers have become, nevertheless, even more slender in *Secodontosaurus* than in other early synapsids, being *c.* one-third the width of the vomers of *Dimetrodon* or *Sphenacodon* skulls of comparable size. (t) Ectopterygoid is greatly reduced in width. As a palatal element located immediately posterior to the palatine, it is not entirely unexpected that the ectopterygoid is also reduced in width in *Secodontosaurus*. The reduction in width also appears less dramatic than that of the palatine, because the ectopterygoid of the eupelycosaurian palate is a relatively small element. (u) Palatine and ectopterygoid lack dentition. The absence of teeth on the palatine and ectopterygoid in *Secodontosaurus* is probably related to the restriction of these elements to very narrow bands along the lateral margins of the palate, where the presence of teeth would have no functional value. *Haptodus* and *Dimetrodon* and other early synapsids have numerous teeth on the palatine and ectopterygoid (Romer & Price, 1940). (v) Dorsal process of quadrate is inclined slightly anteriorly. In all sphenacodontids the quadrate is a well-developed element, with a large, robust dorsal process. This condition is retained in *Secodontosaurus*, but in contrast to other sphenacodontids, the dorsal process is tilted anteriorly in response to the reduced height of the skull. (w) There is no marked increase in the height of anterior premaxillary or dentary teeth. Primitively, sphenacodontids have greatly enlarged anterior premaxillary and dentary teeth and well-developed canines, at least twice as large as the other marginal teeth. The anterior premaxillary and dentary teeth are also enlarged in *Secodontosaurus*, but not to the extent seen in either *Haptodus* or *Dimetrodon*. The condition in *Secodontosaurus* appears to represent a character reversal. (x) Mandibular symphysis is reduced and restricted to the dentary. *Haptodus*, *Dimetrodon* and *Sphenacodon* share the primitive synapsid character state of a massive, large mandibular symphysis that is formed by the dentary and splenial. As a result of the reduced height of the mandible, the symphysis is reduced in *Secodontosaurus*, with the splenial being excluded from the symphyseal area. (y) Skull roof elements and reflected lamina of angular are reduced in thickness. In the sphenacodontids *Haptodus*, *Sphenacodon*

and *Dimetrodon*, the skull roof and lower jaw elements are robust relative to the size of the skull. Despite the large size of the skull of *Secodontosaurus*, the roofing elements are unusually thin. They are similar in thickness to the dermal elements of *Haptodus*, even though the latter is less than one-half the length of the skull of *Secodontosaurus*. The reflected lamina of the angular is also unusually thin in cross-section in *Secodontosaurus*, significantly thinner than that in either *Sphenacodon* or *Dimetrodon*.

(II) *Snout is slightly elongated.* The antorbital region of the skull varies greatly in length among synapsids. It is, therefore, difficult to establish the primitive condition for this character. The evidence provided by *Eothyris* and *Oedaleops* suggests that a short antorbital region, less than one-half of the total skull length, may represent the primitive condition. Among edaphosaurids and sphenacondontids, it is likely that the primitive condition is represented by *Haptodus* and *Ianthasaurus*, where the antorbital region is *c.* one-half the total skull length. Large sphenacodontids, including the various species of *Dimetrodon* and *Sphenacodon*, exhibit some elongation of the snout, ranging from 54.2 to 62.9% of the skull length. The skull of *Secodontosaurus* has a slightly greater elongation of the snout than that of all other sphenacodontids, with the antorbital region forming 65.6% of the skull length. Two other derived characters can be attributed to the relative lengthening of the snout: (a) Palatal surface is elongated. The general palatal surface, extending from the posterior border of the internal naris to the transverse flange of the pterygoid, occupies 31 to 35% of the total skull length in *Haptodus* and in *Dimetrodon*. *Secodontosaurus* also has an elongated palatal surface, occuping 40% of the total skull length, that is undoubtedly the result of snout elongation. (b) Maxillary-nasal contact is unusually long. The presence of a nasal-maxillary suture is a derived character shared by *Dimetrodon*, *Sphenacodon* and *Secodontosaurus*. The length of this suture varies among these taxa from 19 to 37% of the length of the antorbital region. In *Secodontosaurus*, the maxillary-nasal suture is unusually long, occupying 43% of the antorbital region.

(III) *Reflected lamina of angular and retroarticular process are widely separated anteroposteriorly.* The presence of a reflected lamina on the angular and a well-developed retroarticular process are derived characters shared by sphenacodontids. These two structures are located close to each other in the massively constructed articular region of the lower jaw. In *Secodontosaurus*, these structures are widely separated by a long posterior process of the angular that extends between the bases of the reflected lamina and the retroarticular process.

(IV) *Splenial is elongated but does not extend to the mandibular symphysis.* In most early synapsids, including *Haptodus*, *Dimetrodon* and *Sphenacodon*, the splenial extends far anteriorly on the medial surface of the lower jaw and contributes to the mandibular symphysis. In the above sphenacodonts, the splenial occupies 42–48% of the lower jaw length, whereas in *Secodontosaurus* the long, slender splenial occupies 56% of the lower jaw. Despite this elongation, the splenial extends anteriorly only to the level of the seventh tooth position and does not reach the mandibular symphysis.

(V) *Lateral condyle of quadrate extends far beyond the lateral margin of the skull roof.* In all early synapsids the articular surface of the quadrate is formed by two condyles separated by a groove. Among other sphenacodontids and in early carnivorous therapsids, the two condyles are close to each other and directly

below the dorsal process. *Secodontosaurus* exhibits the highly unusual feature of the condyles being widely separated and extending far medially and laterally from beneath the dorsal process. Although the lateral condyle is incomplete, and we have reconstructed its lateral extent conservatively, it obviously extended laterally beyond the edge of the skull roof.

(VI) *First mandibular tooth is directed anteriorly.* In most primitive synapsids the first mandibular tooth points directly dorsally or slightly anteriorly. The first mandibular tooth points dorsally in *Haptodus* and anterodorsally in *Dimetrodon* and *Sphenacodon*. The forward projecting first mandibular tooth of *Secodontosaurus* can, therefore, be considered to represent an autapomorphic feature of this taxon.

Comments. Most, if not all of the autapomorphic features listed above could be readily interpreted as consequences of developing a slender, slightly elongated, low skull from the sphenacodontid skull pattern. Even character states IV–VI represent modifications that are indirectly related to the development of a slightly elongated, low, slender skull. Because it is quite easy to differentiate *Dimetrodon* and *Secodontosaurus* specimens on the basis of even small cranial fragments, it has been possible to re-examine the Lower Permian collections and recognize several partial skeletons of *Secodontosaurus* that were misidentified as *Dimetrodon*. These specimens confirm unequivocably that *Secodontosaurus* possessed a *Dimetrodon*-like vertebral sail. It is important to note, however, that because *Secodontosaurus* and *Dimetrodon* appear to be virtually identical postcranially, numerous specimens lacking cranial materials are therefore now unidentifiable at the generic level. These specimens, although assigned to *Dimetrodon*, could just as well be *Secodontosaurus*. It is therefore necessary to re-examine in detail all the relevant specimens with the purpose of identifying possible postcranial autapomorphies of *Dimetrodon* or *Secodontosaurus*. If such features can be found, we might be able to separate the postcranial remains of *Dimetrodon*, the dominant Early Permian carnivore, from those of the slender snouted *Secodontosaurus*.

The great similarity between *Secodontosaurus* and other sphenacodontids in the postcranial skeleton, and the numerous cranial autapomorphies of *Secodontosaurus* toward a more slender, lower, elongated skull than that of the other sphenacodontids, leads us to conclude the following: (i) *Secodontosaurus* evolved from an advanced sphenacodontid similar in cranial and postcranial features to those of *Dimetrodon*; (ii) *Secodontosaurus* evolved toward a very specialized feeding strategy, perhaps preying upon small tetrapods that attempted to avoid capture by hiding in crevices and burrows. This is suggested by its long, low, narrow skull, forward projecting anteriormost dentary teeth, and less heterodont dentition than other sphenacodontids. The suggestion that *Secodontosaurus* may have been a fish eater is not supported by the postcranial features, especially the tall sail.

scans of MCZ 1124 used in Figure 11. We are also grateful to Mr Michel Laurin who provided a great deal of assistance in the use of the MacIntosh version of PAUP 3.0. Support for this research was provided by a grant from the Natural Sciences and Engineering Research Council of Canada (to RRR).

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INDEX OF ABBREVIATIONS

a	angular	atr	atlantal rib
ac	anterior coracoid	ax	axial neural arch
ar	articular	axi	axial intercentrum
as	suture for angular	axr	axial rib
atc	atlantal centrum	b	unfinished surface of bo
ati	atlantal intercentrum	bst	basipterygoid tubera
atn	atlantal neural arch	bo	basioccipital

c	contact for stapes	pop	paroccipital process
ct	cultriform process	pr	prearticular
d	dentary	prf	prefrontal
ec	ectopterygoid	pro	prootic
ept	epipterygoid	prs	suture for pa
ex	exoccipital	ps	parasphenoid
f	frontal	pt	pterygoid
h	hyoid element	ptf	postemporal fenestra
ie	internal ear	ptp	pterygoideus process
j	jugal	q	quadrate
l	lacrimal	r	stapedial recess
la	lateral condylar recess	rtar	retroarticular process
ld	lacrimal duct	s	stapes
m	maxilla	sa	surangular
ma	medial condylar recess	sas	suture for sa
n	nasal	so	supraoccipital
op	opisthotic	sp	splenial
p	parietal	sph	sphenethmoid
pa	proatlas	sq	squamosal
pal	palatine	st	supratemporal
pc	posterior coracoid	t	tabular
pf	postfrontal	tfpt	transverse flange of pterygoid
pm	premaxilla	v	vomer
po	postorbital	x	septomaxilla

APPENDIX 1

Description of character states used in the cladograms. The character states are listed according to their location on the skull or the postcranial skeleton (numbers 1–97 in the first column). In the second column the capitalized letters followed by a number denote the node of the cladogram they define in Fig. 17 and the synapomorphy at that node, respectively (A1–H3). The bracketed number (0, 1, 2 or 3) in the second column refers to the character state listed in the third column. The underlined capitalized letter $\underline{S}$ refers to autapomorphies of *Secodontosaurus*. Other capitalized letters refer to the following synapsid taxa: I, Edaphosauridae; O, Ophiacodontidae; T, Therapsida; V, Varanopseidae. The asterisk (*) denotes a character reversal.

Character	Nodes and autapomorphies	Description of characters
		Skull
1.	$\underline{S}$	Skull and mandible: High (0); low, narrow (1)
2.	O, $\underline{S}$	Snout: Short (0); elongate (1)
3.	D1, T(2)	Premaxilla: Ventral edge straight (0), sloping anteroventrally (1), sloping anterodorsally (2)
4.	F1	Premaxilla: With (0); without palatal process (1)
5.	E1(3), O(1), V(2)	Premaxilla: Short (0); long, slender (1); wide (2); robust (3)
6.	T, V	Septomaxilla: Small, inside naris (0); large, superficial (1)
7.	E2, O7	Nasal: Shorter or equal to frontal (0); longer than frontal (1)
8.	E3	Nasal: Without (0), with posteroventral narial process (1)
9.	D2, O	Prefrontal: Without (0), with antorbital recess (1)
10.	H1(2)	Nasal-maxillary suture: No contact (0); shorter than (1), longer than nasal-lacrimal suture (2)
11.	C1(1), E4(2)	Frontal: No orbital lappet (0); orbital lappet small (1); extends far laterally (2)
12.	F2	Frontal: Anterior and posterior processes subequal in width (0); anterior process narrower than posterior process (1)
13.	F3, O	Frontal: Short anterior process (0); long anterior process (1)
14.	A1	Parietal: Equal to 1/4 skull roof length (0); reduced length (1)
15.	D3, T*	Parietal: Narrow (0); broad posterolateral wing (1)
16.	D4, T*	Parietal: Lateral edge concave or straight (0); lateral edge convex (1)

APPENDIX 1—*continued*

Character	Nodes and autapomorphies	Description of characters
17.	A2	Pineal foramen: 1/5 or more of parietal width (0); less than 1/5th of par. width (1)
18.	E5	Postfrontal: Straight postorbital suture (0); incised posteriorly by postorbital (1)
19.	E6	Pineal ridge: Absent (0); present (1)
20.	S(1)	Postorbital–supratemporal contact: Present (0); narrow separation (1); wide separation (2)
21.	C2(1), E7(2)	Postorbital: Lateral surface flat (0); gently recessed (1); strongly recessed (2)
22.	C3	Postorbital: Posterior process broad (0); narrow in dorsal view (1)
23.	A4	Postorbital region relative to preorbital length. Subequal (0); preorbital longer (1)
24.	B1	Postparietal: Paired (0); fused (1)
25.	B2(1), E8(2), S*	Maxilla ventral margin: Straight (0); gently convex (1); strongly convex (2)
26.	V	Posterior tip of maxilla: Anterior to postorbital bar (0); beyond postorbital bar (1)
27.	D5(1), O(2)	Maxilla supracanine buttress: Absent (0); present (1); present with ascending process (2)
28.	T, V	Maxilla preorbital dorsal process: Absent (0); present (1)
29.	V	Narial opening: Small (0); enlarged antero-posteriorly (1)
30.	E9	Lacrimal: Contacts naris (0); excluded from naris (1)
31.	C4(2), O(1)	Jugal: Excluded from ventral edge of skull (0); narrow contribution to ventral edge (1); wide contribution (2)
32.	E10	Jugal suborbital process: Narrow anteriorly (0); expanded anterodorsally (1)
33.	C5(1)	Quadratojugal anterior process: Long (0); absent (1)
34.	B3	Squamosal: Excluded from (0); or contributes to zygomatic arch (1)
35.	B4	Ventral margin of postorbital region: Straight (0); concave (1)
36.	B5	Pterygoid anterior process: Low dorsal flange (0); tall dorsal flange (1)
37.	C6	Pterygoid quadrate process: Has medial shelf (0); lacks medial shelf (1)
38.	B6	Pterygoid quadrate process: Short (0); long (1)
39.	B7(1), T(2)	Stapes dorsal process: Free (0); attaches to pop (1); no dorsal process (2)
40.	C7, T(2)	Stapes dorsal process: Slender (0); broad (1); no dorsal process (2)
41.	C8, T*	Stapes: Rod-like shaft (0); blade-like shaft (1)
42.	E11, S*	Basicranial articulation: Level with pterygoid transverse flange (0); posterior to tr. fl. (1)
43.	C9(1), O(2)	Basisphenoid tubera: Large, laterally oriented (0); small anterolaterally (1); small anteriorly (2)
44.	F4(2), T*, O(1)	Parasphenoid plate: Broad (0); narrow (1); narrow with deep median groove (2)
45.	C10(2), O(1)	Parasphenoid plate: Posterior accessory shelf dentigerous (0); small, edentulous shelf (1); no shelf (2)
46.	E12	Opisthotic: Paroccipital process extends horizontally (0); ventrolaterally (1)
47.	E13	Opisthotic: Paroccipital process extends laterally (0); or posteriorly (1)
48.	E14(1), S(2)	Opisthotic: Paroccipital process broad, blade-like (0); narrow, blade-like (1), narrow, rod-like (2)
49.	O	Lateral mandibular fenestra: absent (0); present (1)
50.	B8	Ventral edge of angular: Ridged (0); keeled (1)
51.	C11	Coronoid region of mandible: Gently convex (0); strongly convex (1)
52.	C12	Prearticular: Nearly straight (0); twisted posteriorly (1)
53.	C13	Pterygoideus process: Formed by articular and prearticular (0); mainly by articular, sheathed by prearticular (1)
54.	E15	Angular reflected lamina: Absent (0); present (1)

APPENDIX 1—*continued*

Character	Nodes and autapomorphies	Description of characters
55.	D6	Angular ven. lamina: Gently convex (0); strongly convex posteriorly (1)
56.	E16	Retroarticular process: Composite (0); formed by articular (1)
57.	E17	Retroarticular process: Horizontal (0); curved ventrally (1)
58.	E18, V	Marginal dentition: No anterior and posterior cutting edges (0); cutting edges present (1)
59.	E19	Canine length: <2× other maxillary teeth (0); >2× other maxillary teeth (1)
60.	D7(1), S̱*, T(2)	Premaxillary teeth: Small (0); 1st stage (1); all large (2)
61.	D8(1), S̱*, T(2)	Anterior dentary teeth: Small (0); 2nd large (1); all large (2)
62.	E20, S̱*	Precanine maxillary teeth: Four or more (0); less than four (1)
63.	D9, S̱*	Premaxillary teeth: Five or more (0); less than five (1)
64.	E21	Vomerine teeth: Present (0); absent (1)
65.	S̱, T	Ectopterygoid teeth: Present (0); absent (1)
66.	C14	Pterygoid teeth: Arranged in three groups (0); two groups (1)

Postcranial skeleton

Character	Nodes and autapomorphies	Description of characters
67.	C15	Intercentrum 1 and 2: In contact ventrally (0); separated by atlas pleurocentrum (1)
68.	F5	Axis: Neural spine expanded anteroposteriorly (0); narrow dorsally (1)
69.	F6	Cervical centra: Ridged (0); keeled ventrally (1)
70.	C13, T*	Length of cervical centra: Equal (0); longer than dorsal centra (1)
71.	F7	Dorsal centra: Ridged (0); keeled ventrally (1)
72.	C16	Sacral vertebrae: Two or less (0); at least three (1)
73.	F8(1)	Neural spines: Short (0); elongate (1)
74.	G1, I	Neural spines: Less than (0); or more than (1) five times the height of the centrum
75.	H2, I	Neural spines: Blade-like (0); rounded in cross-section (1)
76.	G2, I	Neural spine shoulders: Absent (0); present (1)
77.	I	Neural spines: Lateral tubercles absent (0); present (1)
78.	H3	Neural spines: Anterior and posterior grooves absent (0); present (1)
79.	C17(1), E22(2)	Neural arches: Not excavated laterally (0); shallow excavation (1); deep excavation (2)

Appendicular skeleton

Character	Nodes and autapomorphies	Description of characters
80.	E23, V	Scapula: Broad (0); narrow distally (1)
81.	E24	Scapula: Broad (0); narrow at base (1)
82.	O*, V*, T	Supraglenoid foramen: On posterior surface (0); on lateral surface of scapula (1); no foramen (2)
83.	D10	Posterior coracoid: Triceps process small (0); large (1)
84.	O*, V*	Limbs: Short and stout (0); long and slender (1)
85.	B9	Humerus: Deltopectoral ridge double (0); single (1)
86.	C18, T(2)	Ulna: Broad olecranon (0); narrow, elongate olecranon (1); small (2)
87.	C19	Ilium dorsal groove: Present (0); absent (1)
88.	C20	Ilium posterior process: Long, extends to posterior limit of ischium (0); short (1)
89.	E25	Ilium: Anterodorsal process absent (0); present (1)
90.	C21	Pubis: Lateral public tubercle present (0); absent (1)
91.	F9	Ischium: Slender distally (0); expanded posterodorsally (1)
92.	E26	Femur: Intertrochanteric fossa prominent (0); reduced (1)
93.	D11	Femoral ventral ridge system: Prominent (0); feeble (1)
94.	I*, O*	Fibula: Distal head/shaft diameter less than 3/1 (0); equal or greater than 3/1
95.	I*, O*	Astragalus: Proximal neck region short (0); long (1)
96.	C22	Calcaneum: Width and length subequal (0); length greater than width (1)
97.	E27	Lateral centrale: Present (0); absent (1)

APPENDIX 2

Distribution of the character states among the taxa included in the cladogram. The numbers at the top (1–97) refer to the description of the character states in Appendix 1. The question marks indicate that the character could not be coded, either because of missing data, or because the character does not apply

Character
number   1 2 3 4 5 6 7 8 9 0 ... 9 7

Taxon:

Varanopseidae
Ophiacodontidae

Edaphosauridae
Haplodus
Sphenacodon
Ctenospondylus
Dimetrodon

Secontosaurus
Therapsida