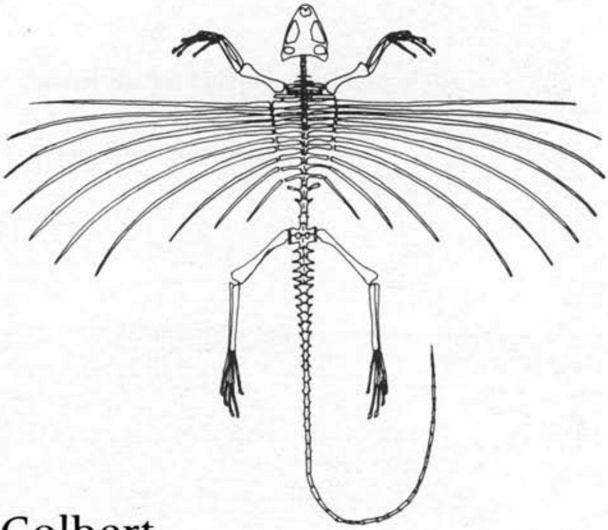
ASPECTS OF VERTEBRATE HISTORY



Essays
In Honor of
Edwin Harris Colbert

Louis L. Jacobs, *editor*

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THE MORPHOLOGY, AFFINITIES, AND AGE OF THE DICYNODONT REPTILE *GEIKIA ELGINENSIS*

by Timothy Rowe

Introduction

In 1886 R. H. Traquair reported the discovery of a dicynodont, tentatively identified as *Dicynodon* sp., from Cuttie's Hillock, near Elgin in northern Scotland (Figure 16.1). This was the first discovery of therapsid reptile remains from western Europe. During the next six years several more specimens were collected from this locality. The first detailed description of this material was by Newton (1893), who described two new dicynodont genera, *Geikia* and *Gordonia*, and a new pareiasaur, *Elginia*. Traquair's specimen was referred to *Gordonia*.

Traquair (1886), Smith Woodward and Sherborn (1890), and Smith Woodward (1898) tentatively considered the Cuttie's Hillock fauna to be of Late Triassic age. Newton (1893) believed that it correlates with Upper Permian or Lower Triassic faunas of India and South Africa. Most later authors (Watson, 1909; Watson and Hickling, 1914; von Huene, 1913, 1940; Westoll, 1951; Romer, 1966) have considered it to be of Late Permian age. Walker (1973), however, believed that the Cuttie's Hillock fauna correlates with a position in the South African Beaufort Series lying between a level high in the *Cistecephalus* Zone (equivalent to the *Daptocephalus* Zone of most recent usage, Kitching, 1970, 1977) to one low in the *Lystrosaurus* Zone, i.e., a position between levels closely bracketing the Permo-Triassic boundary. Walker pointed out that the Permo-Triassic boundary within these almost entirely nonmarine sediments is difficult to correlate with the type marine sections, and consequently the dating of the Cuttie's Hillock fauna is tentative and likely to remain so. An additional problem is that the Cuttie's Hillock fauna consists of only three genera, whose relationships to members of better known faunas is currently unclear, making precise correlation difficult.

At the time of discovery of the Cuttie's Hillock fauna, therapsids of Late Permian to Early Triassic age were known only from South Africa and India. Since then, therapsids of this age have been reported from East Africa, South America, China, Indochina, U.S.S.R., Antarctica; many new forms have also been described from South Africa and India. Despite the many discoveries elsewhere, *Geikia* and *Gordonia* remain the only known therapsids of Late Permian or Early Triassic age from western Europe.

The type-species of *Geikia*, *G. elginensis* Newton (1893), is known from a single specimen. As will be seen, *Dicynodon locusticeps* von Huene (1942), also known from only one specimen, is here referred as a valid species of *Geikia*, *G. locusticeps* (see "Affinities of *Geikia*" for discussion). The purpose of this paper is to redescribe

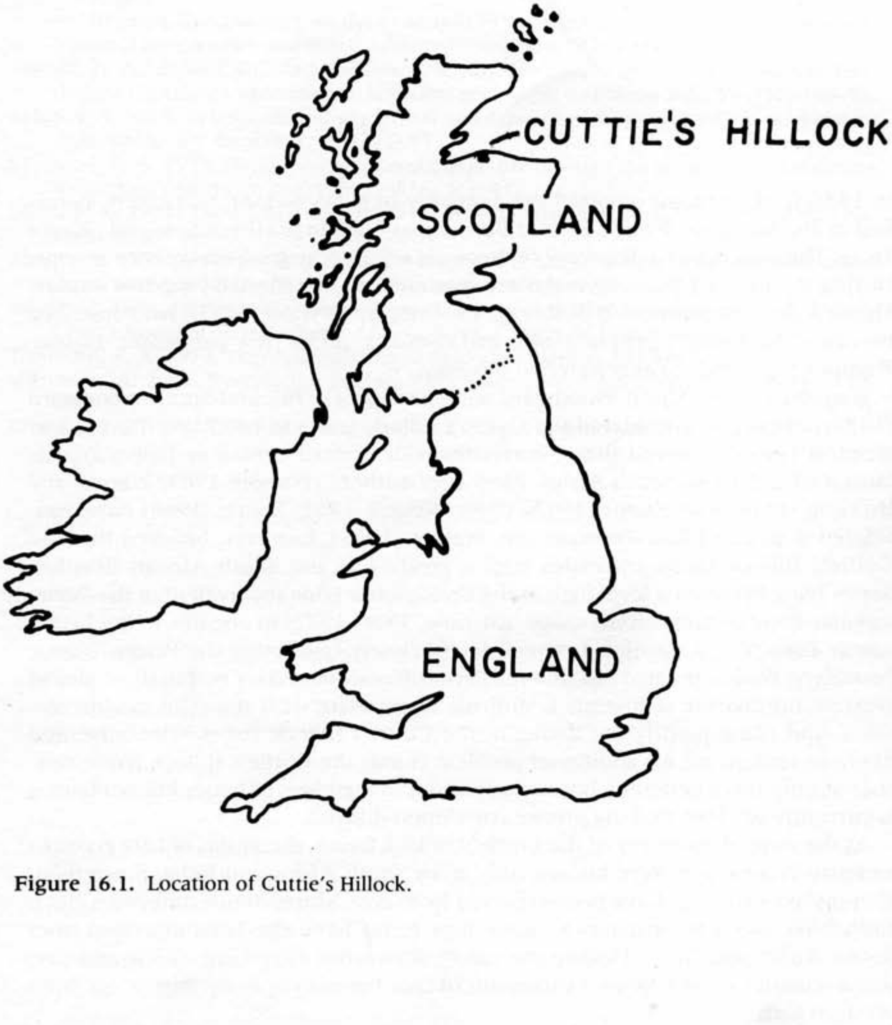

Figure 16.1. Location of Cuttie's Hillock.

Geikia elginensis and to reassess its affinities in light of recent developments in our understanding of dicynodont systematics.

Systematics

Class: Reptilia
 Order: Therapsida
  Suborder: Anomodontia (*sensu* Romer, 1966)
   Infraorder: Dicynodontia (*sensu* Romer, 1966)
    Family: Cryptodontidae (*sensu* Toerien, 1953; Haughton and Brink, 1954)
     Genus: *Geikia* Newton (1893)

Generic Diagnosis: Dicynodonts having no tusk or postcanine teeth; highly vaulted palate; anterior palatal ridges of premaxilla reduced or absent; large palatine having rugose palatal surface; palatine having extensive contact with maxilla and premaxilla; length of interpterygoidal vacuity not less than half the length of the interpterygoidal fossa; interpterygoidal vacuity lying entirely within roof of interpterygoidal fossa; well developed maxillary caniniform process having pronounced lateral ridge; sharp occlusal margin of beak; sharp ridge or "keel" developed on ventral edge of maxilla behind caniniform process; septomaxilla having exposure on lateral surface of snout behind external nares; anterior surface of premaxilla flat, oriented vertically, and meeting lateral surface of premaxilla in abrupt "corner"; single, prominent preorbital protuberance.

Type-Species: *Geikia elginensis* Newton (1893)

Holotype: Natural mold of single nearly complete skull and mandible, associated left humerus, and one isolated metapodial or proximal phalanx. The block containing the natural mold is broken into several pieces housed in the Institute of Geological Sciences, London, G.S.M. 90998–91015.

Locality: Cuttie's Hillock, near Elgin in northern Scotland.

Horizon: Upper Permian, Cuttie's Hillock Sandstone; equivalent to *Daptocephalus* Zone of Beaufort Series, South Africa.

Specific Diagnosis: Interorbital region approximately twice as wide as intertemporal region; width across temporal arches greater than sagittal length of skull; orbit expanded such that its greatest horizontal length is more than one-third of the sagittal length of the skull; very prominent preorbital protuberance expanding anteriorly to lie in front of the vertical anterior surface of the premaxilla.

Referred Species: *Dicynodon locusticeps* von Huene 1942, p. 159; *Geikia locusticeps* new combination.

Holotype: Single skull lacking tip of premaxilla, right quadrate, left temporal arch, and mandible; Institut für Geologie und Paläontologie, Tübingen, K. 87.

Locality: Near the village of Kingori, Songea District, Tanzania (see Nowack, 1937, Figure 5, for detailed description of locality).

Horizon: Upper Permian, Kawinga Formation (Charig, 1963); equivalent to *Daptocephalus* Zone of Beaufort Series, South Africa (Haughton, 1932).

Specific Diagnosis: Intertemporal width and interorbital width approximately equal; width across temporal arches less than sagittal length of skull; greatest horizontal length of orbit approximately one-quarter of the sagittal length of skull; anterior surface of premaxilla extends forward beyond anterior surface of preorbital protuberance.

Material

Geikia elginensis is known from a single specimen that occurs as a natural mold in a pebbly sandstone. The block containing the mold is broken into several pieces, but by reuniting various combinations of pieces most parts of the specimen have been cast. The specimen consists of a nearly complete skull, mandible, left humerus, and an isolated metapodial or proximal phalanx. The skull is of an unusual shape which tends to give one the impression that it may have been severely distorted. However, comparing the right and left sides of the specimen shows evidence of only very minor asymmetrical distortion. Natural openings in the skull such as the foramen magnum and the interpterygoidal vacuity are symmetrical about the sagittal plane and show no evidence of crushing. The right and left orbits, temporal fenestrae, and temporal arches are of nearly identical shapes and show evidence of only minor distortion. It seems quite unlikely that distortion has contributed significantly to the shape of this specimen. The specimen was described from polyvinylchloride casts made by Dr. Alick Walker of the University of Newcastle-upon-Tyne. They generally show well preserved bone in fine detail, but in a number of small localized areas the bone left no impression or only a vague impression on the natural mold and detail is lost.

Geikia locusticeps is known from a single skull lacking the tip of the premaxilla, right quadrate, left temporal arch, and mandible. Preservation of the bone is good, although some of the bone surface appears to have been ground away during preparation.

Description of *Geikia elginensis*

The skull of *Geikia elginensis* is unusual in shape compared to most other dicynodonts. *Geikia* is a medium-sized dicynodont, its skull length being about 110 mm. The greatest width of the skull, between the temporal arches, is slightly greater than its sagittal length. The skull is quite deep, its height from the bottom of the quadrate to the top of the parietals is about 67 mm. The orbits are very large, the interorbital region broad, and pronounced preorbital protuberances extend far anterolaterally from the anterodorsal "corners" of the orbits. The extreme degree of development of the protuberances is greater than in any other dicynodont and is one of the most striking features of the skull. The snout is abruptly terminated and down-turned such that the orbits lie very near the front of the skull. The beak is square, delicately built with a sharp slender maxillary caniniform process, and lies almost directly below the orbits. The overall impression is of a rather delicately built, box-like skull with a large deep temporal region, very large orbits, a flat vertical face, and a relatively small beak and mouth.

Skull Roof (Figure 16.2)

The entire skull roof is preserved but some of its detail has been lost, and a seam in the mold has obscured the pineal region. The interorbital region is quite broad, being slightly more than twice as wide as the intertemporal region. The interorbital region, measured along the midline from the front of the vertical anterior surface of the premaxilla to the back of the postorbital bar, is nearly twice as long as the intertemporal region, measured from the back of the postorbital bar to the occipital plate. The dorsal edges of the orbits are raised some 20 mm above the

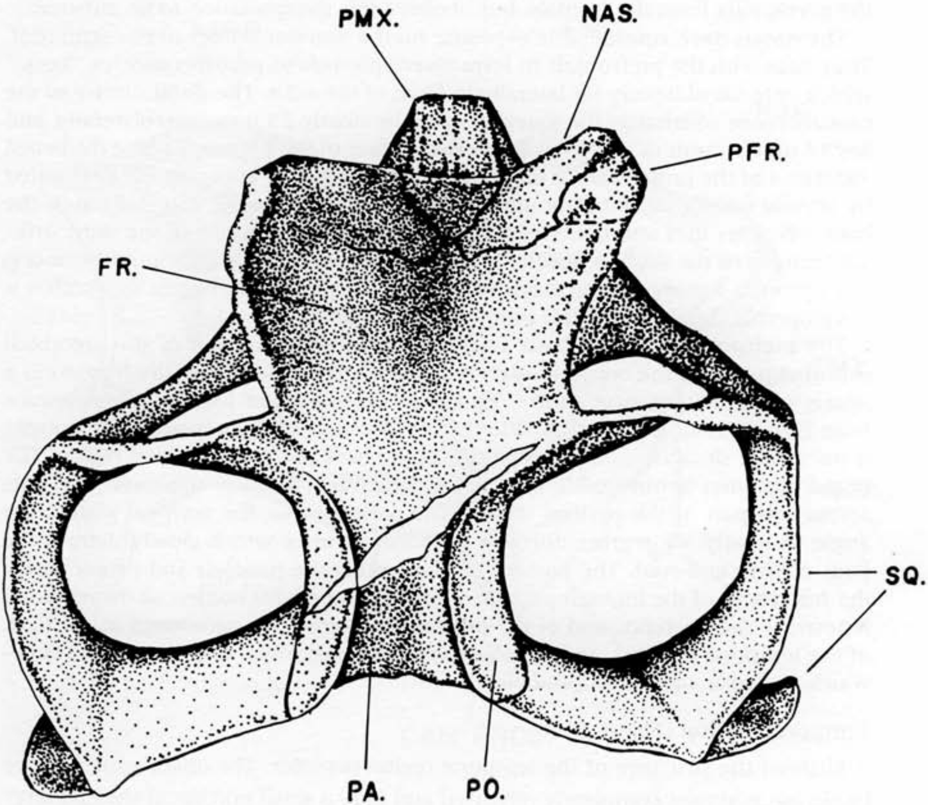

Figure 16.2. *Geikia elginensis*, dorsal view. × 0.85.

midline of the interorbital region, creating a deep trough in the skull roof between the orbits.

The premaxilla extends onto the skull roof as a triangular process. The posterolateral edges of this triangle meet the nasals. Sutures in this region are not clear, but the nasals do not appear to meet along the midline and the tip of the premaxilla has a short contact with the frontals. Walker (1973, figure 3b) figured the skull roof of *Geikia elginensis* with the nasals meeting along the midline, thus separating the premaxilla from the frontals, but I believe this interpretation to be incorrect.

The nasals have considerable exposure on the anterior border of the skull roof. They fuse with the prefrontals to form a very prominent protuberance, or "boss," which extends obliquely far laterally in front of the orbit. The distal surface of the protuberance overhangs the external nares by nearly 25 mm anterolaterally, and lies 12 mm in front of the vertical anterior surface of the premaxilla. The thickened distal end of the protuberance has a rugose surface which appears to be perforated by several small nutrient foramina. More medially, above the external nares, the bone becomes thin and flat. The preorbital protuberance is one of the most striking features of the skull. A smaller protuberance (or several smaller protuberances) is a common feature among dicynodonts, but the prominent degree to which it is developed in *Geikia elginensis* is unique.

The prefrontal is a small bone confined to the posterior part of the preorbital protuberance and the dorsal border of the orbit. The nasals meet the frontals in a nearly straight transverse suture, similar to the condition found in *Pelanomodon* (von Huene, 1942, plate 28-2). Whether postfrontals and a preparietal are present is uncertain, since no sutures are visible at the back of the interorbital region. The pineal foramen is not visible but this is owing to a seam in the mold that cuts across this part of the parietal region. The parietals join the occipital plate at an angle of nearly 90 degrees, forming an abrupt corner which clearly defines the back of the skull roof. The postorbitals lie against the parietals and extend along the full length of the intertemporal bar, forming the medial borders of the temporal fenestrae. The posterior end of the postorbital overlies the squamosal at the back of the temporal fenestra, and the squamosal and postorbital together project backwards to overhang the occipital plate.

Temporal Region (Figure 16.3)

Little of the structure of the temporal region is visible. The lateral aspect of the braincase is almost completely obscured and only a small portion of the epipterygoid and the lateral part of the prootic can be seen. The epipterygoid slants slightly anteriorly as it rises towards the skull roof, but neither end of the bone is visible. The prootic extends laterally to meet the ventral flange of the squamosal and, dorsolaterally, it meets the supraoccipital in a sutural contact. A wide, shallow, indistinct groove lies on the anterior surface of the prootic, in approximately the same position as a groove in *Kingoria,* interpreted by Cox (1959) as marking the course of the *vena capitis dorsalis.*

The temporal fossa is partially roofed by a narrow lateral extension of the parietal and postorbital. The temporal arches expand far laterally so that the transverse width across the arches exceeds the sagittal length of the skull (beak tip to occiput). In dorsal view the temporal fenestrae are almost rectangular in outline, being slightly wider than long.

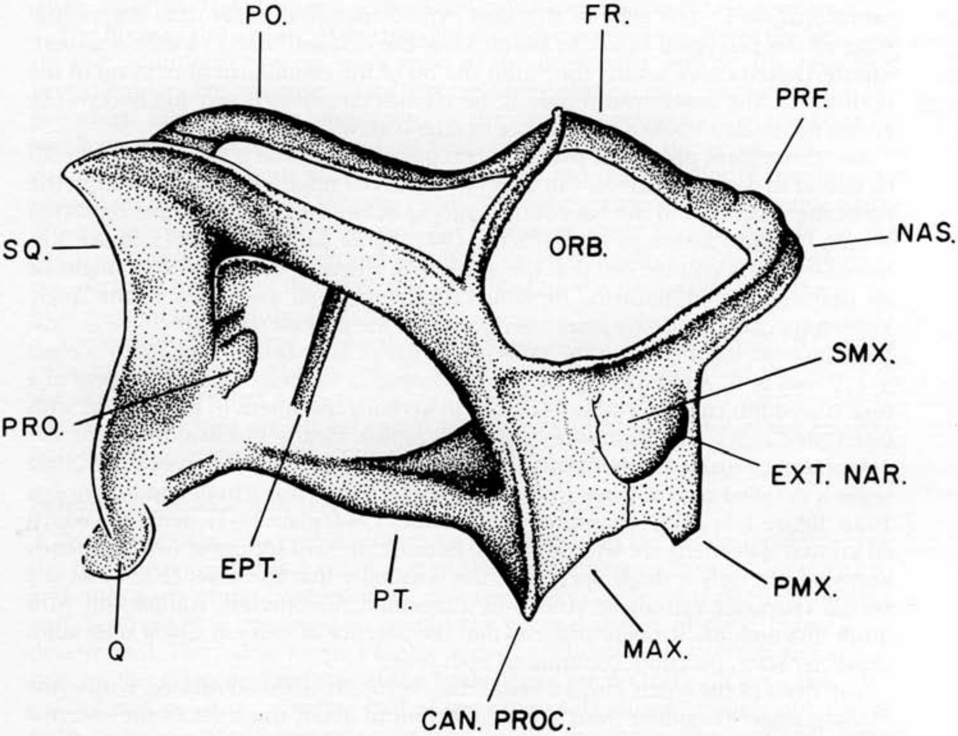

Figure 16.3. *Geikia elginensis,* lateral view, composite illustration from right and left sides. × 0.87.

Snout (Figure 16.3)

The snout is nearly complete and is generally well-preserved, although few of the facial sutures are visible. The occlusal margin of the beak is formed by the maxilla and premaxilla. These bones meet in an indistinct suture that extends vertically from the occlusal margin to the bottom of the external nares. The bone in this region is thin and tapers ventrally to form a sharp cutting edge. The edge remains sharp from the tip of the beak backwards to the caniniform process of the maxilla, and continues behind the caniniform process as a sharp ridge or "post-caninform keel." The edge of this keel extends posterodorsally onto the ventral edge of the pterygoid bone. In lateral view the occlusal margin forms a smooth uninterrupted curve which rises from the tip of the caniniform process up to the premaxilla. The anteriormost part of the premaxilla curves down and backwards, giving the beak a hooked appearance in lateral view.

The caniniform process of the maxilla is quite slender and is without a tusk. On its lateral surface is a narrow but prominent curved ridge which extends from the tip of the process onto the base of the zygoma below the orbit. A similar condition is seen in *Geikia locusticeps* (von Huene, 1942, figure 3a; Walker, 1973, figure 3d). Newton (1893) pointed out that the absence of a tusk in *Geikia elginensis* might be an indication of immaturity. Newton's comment could also apply to the single known specimen of *Geikia locusticeps*. However, the delicate structure of the caniniform process, together with the rather large size of both skulls (beak tip to occiput = 110 mm in *G. elginensis;* 150 mm in *G. locusticeps*), suggests that the absence of a tusk is an adult character state in *Geikia*. In juvenile specimens of *Lystrosaurus* with unerupted tusks, the caniniform process is robust, clearly foreshadowing the development of tusks. Furthermore, the caniniform process in both species of *Geikia* bears a detailed resemblance to those found in *Oudenodon* (Broili and Schroeder, 1936, figure 1-5) and *Pelanomodon* (von Huene, 1942, plate 28-1), genera in which all known specimens are without tusks. Because the two species of *Geikia* are each known from only a single specimen, the possibility that the absence of tusks is a sexual character cannot be ruled out altogether. Nonetheless, comparison with other dicynodonts strongly suggests that the absence of tusks in *Geikia* is an adult character state, probably common to both sexes.

The front of the snout forms a broad, flat, vertically oriented surface, with a low median ridge extending from the beak tip up to about the level of the external nares. The lateral surface of the snout is also flat and joins the anterior surface at a 60 degree angle. The junction between the flat lateral and anterior surfaces forms a prominent corner which extends vertically from the beak margin up to the level of the top of the nares, where the frontoparietal plane of the skull roof meets the premaxillary plane. The snout thus appears to be box-like, abruptly terminated, and downturned very much like, although not as deep as, the snout of *Lystrosaurus*.

The external nares are located on the lateral surface of the snout, approximately midway between the ventral margin of the orbit and the cutting edge of the beak. Sutures between the bones which form this region are not clearly visible, and difficulty in distinguishing between bone and artifacts in the cast make a detailed interpretation of this region difficult. Judging from the condition found in other dicynodonts, the roof of the narial aperture is formed by the nasal, and the anterior wall and anterior part of the floor are formed by the premaxilla (Cluver, 1971). The posterior part of the floor and the rear wall are formed by the septomaxilla.

On the right side of the specimen the maxilla can be seen overlapping the septomaxilla behind the nares, but only a small portion of their contact is visible and the precise geometry of the septomaxilla cannot be determined. No sutures are visible on the left side. Posteriorly, the septomaxilla lies exposed on the lateral surface of the snout in a plane with the maxilla, while anteriorly it gradually slopes medially into the narial aperture without forming a distinct posterior narial border. Newton's (1893) figure is therefore incorrect, as he illustrated a distinct posterior narial border. A similar condition to that of *Geikia* is found in *Pelanomodon* (von Huene, 1942, plate 28-1). Whether a septomaxillary foramen is present is uncertain.

The bone of the surface of the maxilla along the occlusal margin of the beak and on the caniniform process, over most of the premaxilla, and on the preorbital protuberances has a rugose, pitted texture. Some of the pitting, particularly on the preorbital protuberances, appears to be the result of perforation of the bone by small nutrient foramina. It has long been recognized that the occlusal margin of the beak in dicynodonts was covered by horn, and that this horny covering extended onto the face (e.g., Watson 1948). The precise extent of the covering varies among species. The distribution of the rugose punctate surface texture on the snout of *Geikia elginensis* indicates that horn covered much of the caniniform process, occlusal margin of the beak, and extended up the premaxilla onto the preorbital protuberance of the skull roof.

The orbit is quite large. Its greatest length, measured along a horizontal line in a parasagittal plane, is 40 mm, which is slightly more than one-third the length of the skull. The greatest vertical height of the orbit is 34 mm. When compared to *G. locusticeps*, much of the orbital expansion appears to be the result of the extreme anterior development of the preorbital protuberances.

Palate and Basicranium (Figure 16.4)

The entire palate and the basicranium back almost to the basioccipital tuberosities are preserved. Only a small part of the premaxillomaxillary suture is visible, and only parts of the borders of the palatine bones can be seen clearly. However, sufficient detail is preserved to permit the general shapes of these bones to be determined. The palate forms a highly arched vault bounded laterally and anteriorly by the sharp occlusal rim of the beak. There are no teeth on the palate. The palatal surface of the anterior half of the premaxilla curves strongly anteroventrally to form a nearly vertical wall at the front of the palate. The premaxilla bears the two anterior palatal ridges that are present in many dicynodont genera (e.g., *Pelanomodon*, Figure 16.8), but they are much reduced, being very short, narrow, and of low relief. A pronounced median ridge is developed on the rear half of the premaxilla in the usual dicynodont fashion. Its anterior end lies midway between the caniniform process and the tip of the beak. Its posterior end meets the vomer at the back of the palate, but no suture is visible.

The maxillae slant steeply ventrolaterally, forming the steep lateral walls of the palate. The back of the palate is formed by the palatine bones, which meet the maxilla and premaxilla in a broad sutural contact. The palatal surface of the palatine slants posteroventrally, curving down and away from the horizontal surface of the posterior half of the premaxilla. The bone on the surface of the palatine has a rugose texture and is perforated by small nutrient foramina. This texture appears

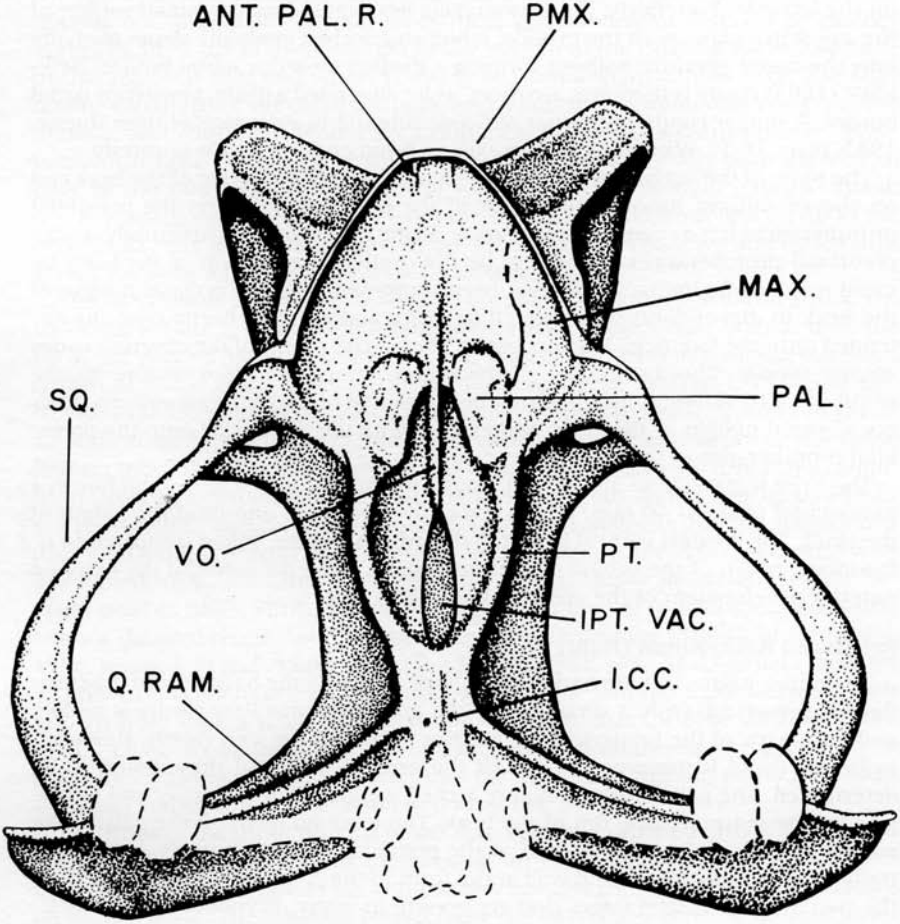

Figure 16.4. *Geikia elginensis,* ventral view, palate and basicranium illustrated from one cast; the remainder of the shaded portion is a composite illustration from several casts; dashed lines surrounding unshaded areas are restorations of unpreserved regions. × 0.96.

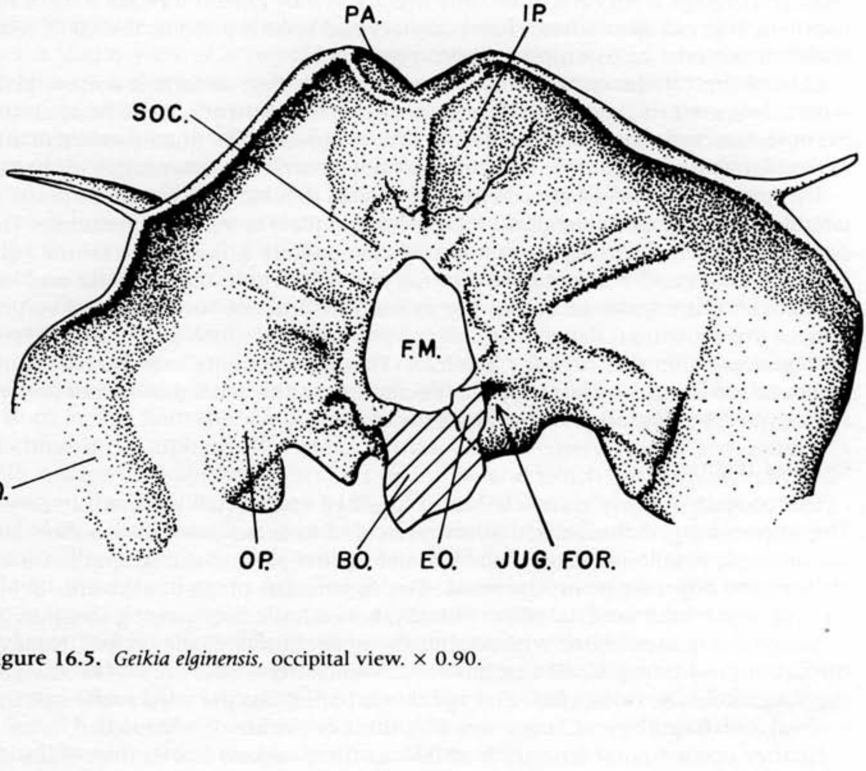

Figure 16.5. *Geikia elginensis,* occipital view. × 0.90.

to extend onto the adjacent parts of the maxilla, but, as no nutrient foramina are visible here, its presence on the maxilla is probably an artifact.

The premaxilla forms the anterior border of the choanae and the palatine forms the anterolateral and lateral borders. The choanae are divided by the vomer, which forms a deep thin septum descending from the roof of the interpterygoidal fossa. The vomer splits posteriorly, forming the anterior and lateral borders of the interpterygoidal vacuity. The interpterygoidal fossa is deep, and the interpterygoidal vacuity lies entirely within its roof. The vacuity is narrow and is two-thirds as long as the fossa. The pterygoids, which form the lateral walls of the fossa, are lightly built and diverge from each other only slightly as they extend forward toward the maxillae. It is not clear whether an ectopterygoid bone is present. The labial fossa is absent, as is the case in most other cryptodontids.

Behind the interpterygoidal fossa, the pterygoids fuse to form a narrow plate with a low median ridge. Posterior to this plate the structure of the basicranium becomes obscure. The basioccipital tuberosities appear to be quite prominent and extend far ventrally, but their distal ends are not preserved. Neither stapes is present.

The quadrate ramus of the pterygoid is a deep, thin bar which extends posterolaterally from the posterior part of the pterygoid plate towards the quadrate. The contact between the quadrate ramus and the quadrate is not visible on the right side, where a quadrate is present. On the left side, where the quadrate was lost postmortem, the quadrate ramus lies against the anterior surface of the ventral part of the squamosal flange, extending a short distance into a smooth, shallow, oblong depression that held the quadrate. The right quadrate is in place but only its lateral surface is visible; it appears to conform to the usual dicynodont pattern as described by Watson (1948) and Cluver (1971).

Occiput (Figure 16.5)

The occiput is nearly complete but in localized areas detail was not preserved. The impressions of the bone that are preserved indicate good preservation and considerable detail, but most of the left and ventral parts of the occiput have left only vague impressions on the mold. The squamosals project backwards about 18 mm beyond the occipital plate. Dorsally, beneath the overhanging squamosals, is a large interparietal bone which forms the upper border of the occiput. None of the sutures bordering the tabular bones are visible. No sutures are visible between the supraoccipital, exoccipital, and opisthotic bones, but the preservation of this general area is quite good, suggesting that these bones are tightly fused.

Neither posttemporal fenestra is visible, as these regions left no impression on the mold. The posttemporal fenestra has been thought to be characteristic of all dicynodonts, and was therefore probably present in *Geikia*. However, an undescribed specimen in the Museum of Paleontology, University of California, Berkeley, (UCMP 42401) from Krugerskraal, South Africa (*Daptocephalus* Zone), has a completely preserved fully prepared occiput in which the posttemporal fenestra is absent. This specimen is referable to the Cryptodontidae with close affinities to *Geikia* and, therefore, a remote possibility does exist that the posttemporal fenestra was absent in *Geikia elginensis*.

The foramen magnum is quite large, its greatest vertical dimension being 20 mm and its greatest horizontal dimension 15 mm. The condylar portions of the basioccipital and exoccipital bones are missing and appear to have been broken off prior to fossilization. On either side, ventrolateral to the foramen magnum, is a rather large jugular canal which pierces the opisthotic and communicates with the floor of the braincase through the exoccipital, just inside the foramen magnum. Immediately behind this opening, the hypoglossal foramen pierces the exoccipital and courses ventrolaterally to communicate with the jugular canal. The paraoccipital process of the opisthotic expands laterally where it abuts against the squamosal, and apparently also contracts the quadrate ramus of the pterygoid, and the quadrate.

Mandible (Figure 16.6)

The mandible is not completely preserved, but by combining the right and left sides a lateral view of a complete ramus can be reconstructed, and most of the symphyseal and articular regions can be seen clearly. The mandible is preserved in a position such that the mouth is gaping open at 90 degrees, with the right articular nearly touching the right quadrate and the left articular lying close to the lower edge of the left squamosal, although the quadrate has dropped off on this side.

Anteriorly, the fused dentaries form an upturned symphysis. The tip of the symphysis is broken, but the preserved portion extends 5 mm above the dorsal edges of the dentary ramus, and its contours indicate that it may have extended another 4 mm dorsally (and possibly further). In dorsal view, a 5 mm wide concave dentary table is developed medially in the symphyseal region. The concavity of its surface extends posteriorly along the dorsal edge of the dentary as a narrow groove which almost reaches the dentary-surangular contact. The bone of the anterior and lateral surface of the symphysis has a rough, pitted texture and was probably covered by horn in life. Both the symphysis and the rami appear to be rather lightly built.

Behind the symphysis, the lateral surface of the dentary bears a low, rounded shelf. A large mandibular fenestra is present, behind which lies the large reflected lamina of the angular. Newton (1893) illustrated the reflected lamina as being divided by a horizontal line, giving the appearance of a bipartite structure with the dorsal half merging anteriorly with the body of the angular, and the separate ventral half attaching along its dorsal edge to the bottom of the ramus. This interpretation is incorrect, however, for, as in other dicynodonts, the reflected lamina is a single continuous sheet of bone. It merges anteriorly with the body of the angular, while posteriorly it forms a broad, continuous sheet with free dorsal, ventral, and posterior edges lying lateral to the ramus. The reflected lamina undulates gently, its dorsal half is convex and its ventral half is concave. The surface of the angular behind the reflected lamina is smooth and flat.

The articular is divided into two condyles, a large lateral condyle, and a relatively shallower medial condyle. The lateral condyle is divided into an anterior concave surface (condylar recess of Crompton and Hotton, 1967) and a convex posterior surface which curves back and down nearly 10 mm below the ventral edge of the ramus onto the prominent retroarticular process.

Postcranium (Figure 16.7)

An impression of a left humerus was found lying about 2 mm from the left temporal arch of the skull (Walker, written communication, 1979). The proximal articular surface is missing and most of the distal articular surface left no impression on the mold. Some damage to the entepicondyle and the ectepicondyle ap-

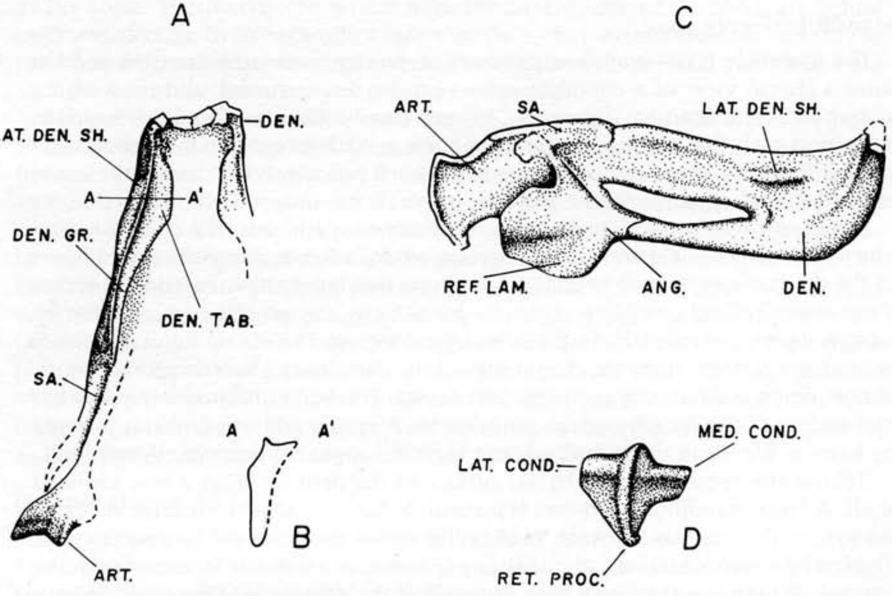

Figure 16.6. *Geikia elginensis*, mandible, A) dorsal view; B) section through A–A' of right ramus; C) composite illustration from right and left sides of lateral view; D) posterior view of left articular. × 0.63.

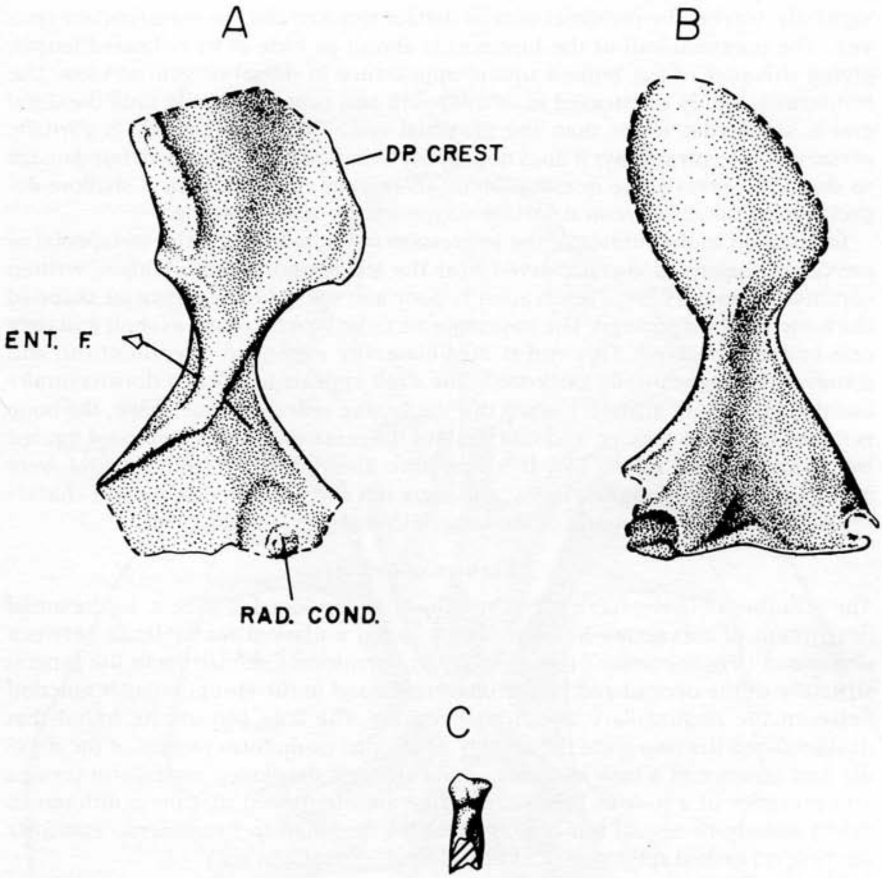

Figure 16.7. *Geikia elginensis,* postcranium, A) left humerus ventral view; B) left humerus dorsal view; C) proximal phalanx or metapodial in (?)ventral view. Dashed lines indicate margins of cast; solid lines are natural borders of bone; cross-hatched area in C is broken surface. × 0.72.

pears to have occurred prior to fossilization. The humerus is twisted such that the deltopectoral crest lies at an angle of about 50 degrees to the widest part of the distal end of the bone. The deltopectoral crest is quite broad and curves anteroventrally, leaving the proximal ventral surface concave and the dorsal surface convex. The proximal half of the humerus is almost as wide as its estimated length, giving this part of the bone a square appearance in dorsal or ventral view. The humerus is tightly constricted at its midpoint, and expands distally until the distal end is somewhat wider than the proximal end. The radial condyle is partially preserved in ventral view; it does not appear to be strongly developed, but damage to this area leaves some question about its original configuration. A shallow depression on the distal ventral surface surrounds the radial condyle.

In addition to the humerus, the impression of an isolated, partial metapodial or proximal phalanx is also preserved near the left temporal arch (Walker, written communication, 1979). Preservation is poor and only the most general shape of the bone can be discerned. The bone appears to be broken across its shaft and only one end is preserved. This end is mediolaterally expanded, asymmetrical, and somewhat dorsoventrally thickened. The shaft appears to thicken dorsoventrally but this may be an artifact. Even if this thickening reflects its true shape, the bone is rather long and slender, and it resembles the metacarpals of *Diaelurodon* figured by Watson (1960, figure 14). It is therefore likely that the feet of *Geikia* were relatively long with slender digits, and were not the shortened, stout feet characteristic of *Placerias* and many of the larger dicynodonts (Camp, 1956).

Affinities of *Geikia*

The affinities of *Geikia* have been the subject of considerable debate. In the initial description of this genus Newton (1893) noted a marked resemblance between *Geikia* and "*Ptychognathus*" (= *Lystrosaurus*), mentioning similarities in the general structure of the occiput and interorbital region and in the abrupt angular junction between the premaxillary and frontal regions. The only features he found that distinguished the two were the weakly developed caniniform process of the maxilla and absence of a tusk in *Geikia*, and a strongly developed caniniform process and presence of a tusk in *Lystrosaurus*. Newton mentioned that these differences might merely be sexual but did not refer his specimen to *Lystrosaurus*, primarily because no tusked specimens had been found in the Elgin area.

Watson (1909) accepted Newton's opinion regarding the close relationship between *Geikia* and *Lystrosaurus*. Watson and Hickling (1914), however, departed from this view and stated that *Geikia* "is not paralleled by any other known form, but is simply derived from *Dicynodon* by the development of horns [*sic*] on the nasals" (p. 399). They also noted a general tendency among dicynodonts towards the development of nasal bosses.

Von Huene (1940) stated that the short wide skull roof of *Geikia* resembled that of *Cistecephalus*. Any resemblance between the two is, however, superficial at best, since the broadening of the cistecephalid skull roof occurs in the parietals whereas in *Geikia* the frontals have widened while the parietal region remains relatively narrow. Later, von Huene (1948, 1956) erected the monotypic family Geikiidae to accommodate *Geikia*. The apparent basis for establishing this familial distinction was his belief that *Geikia* lacked a preparietal (von Huene, 1956). His reasoning is difficult to understand since Newton (1893, p. 466) stated that none of the skull

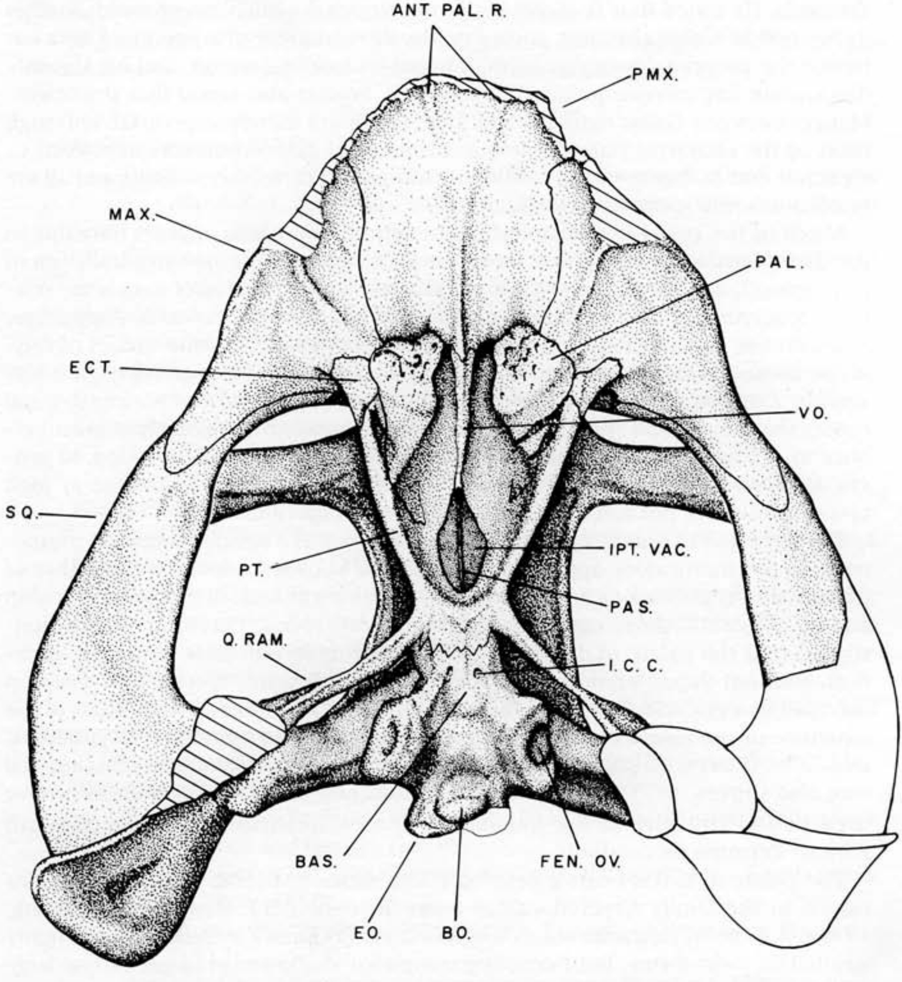

Figure 16.8. *Pelanomodon moschops* (type, AMNH 5325) ventral view. Unshaded regions are restored; cross-hatched regions are broken surfaces. × 0.54.

roof sutures are visible and the condition of the preparietal is therefore indeterminate. Von Huene believed the Geikiidae to be most closely related to the Lystrosauridae and considered the two families to represent a "specialized sidebranch" of the Anomodontia.

Walker (1973) suggested that *Geikia elginensis* was derived from *Dicynodon locusticeps* von Huene (1942), from the Kawinga Formation (Charig, 1963) of Kingori, Tanzania. He stated that *D. locusticeps* demonstrates the initiation of trends further developed in *Geikia elginensis*, including the development of a depressed area between the preorbital protuberances, a broad interorbital region, and an abruptly descending flat anterior premaxillary surface. Walker also stated that the resemblances between *Geikia elginensis* and *Lystrosaurus* are merely superficial, although most of the character states he lists as evidence of close relationship between *G. elginensis* and *D. locusticeps* are found in a number of other dicynodonts and all are present in some species of *Lystrosaurus*.

Much of the confusion surrounding the affinities of *Geikia* appears traceable to the use of only a few characters, most of which seem to be subject to parallelism in phylogenetic analyses. A good example of a problematic character state is the relative broadening of the interorbital region. This has occurred in *Geikia, Platycyclops, Pelanomodon, Aulacocephalodon;* to a lesser extent in *Kingoria*, some species of *Dicynodon* (*sensu* Hotton and Cluver, in preparation) and other Permian forms; it is also seen in *Lystrosaurus* and most large Triassic forms. Similarly, the prefronto-nasal bosses that have fused and expanded to form the pronounced preorbital protuberance in *Geikia* are developed to some degree, although generally unfused, in genera assigned to a number of families. Such characters have little value at high taxonomic levels, but can be useful at a generic or specific level.

The structure of the dicynodont palate, which forms a tightly integrated component of the masticatory apparatus, has become known in detail in a number of genera, and is proving to be quite useful in arriving at hypotheses of relationship and phylogenetic classification at high taxonomic levels. Cluver (1970) demonstrated that the palate of dicynodonts is subject to considerable structural variation, and that the differences may be associated with taxon-specific differences in the masticatory cycle. Toerien (1953) demonstrated the potential usefulness of the structure of the palate in arriving at a phylogenetic classification of dicynodonts, and Cox (1964) used palatal structure to revise the dicynodont genus *Endothiodon* (see also Cluver, 1975). More recently, Hotton and Cluver (in preparation) have used palatal structure as the foundation of a comprehensive revision of South African Permian dicynodonts.

The palate of *Geikia* bears a detailed resemblance to palates of dicynodonts assigned to the family Cryptodontidae (*sensu* Toerien, 1953; Haughton and Brink, 1954). A suite of character states diagnostic of this family includes: palate highly vaulted in most forms, but becoming somewhat shallower in larger forms; large palatines having rugose palatal surface; palatine having wide contact with premaxilla and maxilla; palatal surface of palatine slanting posteroventrally relative to palatal surface of rear part of premaxilla; absence of tusk; absence of postcanine teeth; delicate sharp caniniform process of maxilla, having pronounced lateral ridge; palatal rim strongly developed in front of caniniform process; strongly developed ridge or "keel" on ventral edge of maxilla behind caniniform process; pterygoid separated from maxilla by ectopterygoid and palatine bones; interpterygoidal vacuity lying entirely within roof of interpterygoidal fossa; interpterygoidal vacuity long, approximately equal to or greater than one-half the length of the interpterygoidal fossa.

In *Geikia elginensis* all but one of these character states are known to exist. The single exception involves the separation of the pterygoid from the maxilla by the ectopterygoid. Whether an ectopterygoid is present in *Geikia* is not known, so the presence of this character state can not be confirmed.

Using the above criteria, the following genera can be assigned to the Cryptodontidae (zone definitions and locality data from Kitching, 1977):

Family Cryptodontidae

Geikia Newton (1893)
  Horizon: Upper Permian: Cuttie's Hillock Sandstone, Scotland (*Daptocephalus* Zone); Kawinga Formation, Tanzania (*Cistecephalus* Zone; Haughton, 1932).
  Comments: Here considered to include "*Dicynodon*" *locusticeps* (von Huene, 1942) as valid species, *Geikia* ~~*elginensis*~~. locusticeps
Neomegacyclops Boonstra (1953)
  Synonyms: *Megacyclops* Broom (1931)
  Horizon: Upper Permian: *Cistecephalus* Zone, Beaufort Series, South Africa; Kawinga Formation, Tanzania (*Cistecephalus* Zone; Haughton, 1932).
Pelorocyclops Van Hoepen (1934)
  Horizon: Upper Permian: Beaufort Series, South Africa.
  Comments: Locality data lost, but probably from *Cistecephalus* Zone.
Eocyclops Broom (1913)
  Horizon: Upper Permian: *Cistecephalus* Zone, Beaufort Series, South Africa.
Rhachiocephalus Seeley (1898)
  Horizon: Upper Permian: *Cistecephalus* Zone and *Daptocephalus* Zone, Beaufort Series, South Africa; Upper Madumabisa Mudstone, Zambia (*Daptocephalus* Zone; Kemp, 1975).
Propelanomodon Toerien (1955)
  Horizon: Upper Permian: *Daptocephalus* Zone, Beaufort Series, South Africa.
  Pelanomodon Broom (1938)
  Horizon: Upper Permian: *Daptocephalus* Zone, Beaufort Series, South Africa.
Platycyclops Broom (1932)
  Horizon: Upper Permian: *Cistecephalus* Zone, Beaufort Series, South Africa.
Kitchingia Broom and George (1950)
  Horizon: Upper Permian: *Cistecephalus* Zone, Beaufort Series, South Africa.
Oudenodon Owen (1860)
  Synonyms: *Mastocephalus* Van Hoepen (1934); *Chelyrhynchus* Haughton (1917).
  Horizon: Upper Permian: *Cistecephalus* Zone and *Daptocephalus* Zone, Beaufort Series, South Africa; Upper Madumabisa Mudstone, Zambia (*Daptocephalus* Zone; Kemp, 1975).

Cryptodontidae *incertae sedis*
Haughtoniana Boonstra (1938)
  Horizon: Upper Permian: Upper Madumabisa Mudstone, Zambia (*Daptocephalus* Zone; Kemp, 1975).
  Comments: Palate not preserved.

This list includes, in addition to *Geikia*, only genera recognized by Haughton and Brink (1954). It is not intended to be a revision of the family, which is beyond the scope of this paper. It should be noted, however, that Keyser (1972) suggested that *Rhachiocephalus, Eocyclops, Neomegacyclops, Platycyclops, Pelorocyclops*, and *Kitchingia* may prove to be synonymous. Kitching (1977) believed that *Kitchingia* is a junior synonym of *Rhachiocephalus*, and assigned *Pelanomodon* to the Aulacocephalodontidae. Toerien (1953) assigned only *Oudenodon, Kitchingia, Platycyclops*, and *Pelanomodon* to the Cryptodontidae, but dealt with only a few genera and did not attempt a complete revision of the family. Haughton and Brink (1954) included all of the genera listed above, except *Geikia*, but also included *Eosimops* and *Digalodon*, whose palates differ from the other genera.

In addition to the genera listed above, the type specimens of *''Dicynodon'' sidneyi* Broom (1940) and *''Dicynodon'' tylorhinus* Broom (1913), and an undescribed specimen in the University of California (Berkeley) Museum of Paleontology (UCMP 42401) are referable to the Cryptodontidae. Whether these specimens warrant generic distinction or can be assigned to previously established genera is difficult to assess at present. They are noted here because they may be closely related to *Geikia* and consideration of them in a more detailed analysis of the interrelationships of cryptodontids may require modification of the following discussion.

Below the family level, the palatal structure of cryptodontids becomes less useful in assessing relationships, because differences in character states are largely a result of subtle proportional changes, and few character states are either present or absent. Using such character states is often difficult because nearly all dicynodont specimens have been distorted to a greater or lesser degree, making accurate measurement difficult and often impossible. Furthermore, Hecht (1976) and Hecht and Edwards (1976) pointed out that proportional changes in bony structures are often the result of simple allometric relationships or simple growth patterns, and that this mechanism of morphologic change is highly susceptible to parallelism.

Parallelism has certainly occurred in a number of cranial character states among cryptodontids, but identification of instances of parallel evolution of a given character state at this low taxonomic level is difficult. The polarities of character states can generally be determined by comparison with other taxa believed to be more primitive. In this case the endothiodontinid genera *Brachyprosopus* and *Tropidostoma* were believed to be structurally ancestral to the Cryptodontidae, and the genus *Oudenodon* was considered to be the most primitive cryptodontid (a complete discussion of this will be presented elsewhere; Rowe, in preparation). The major assumption in assessing the affinities of *Geikia*, then, is that the character states found in *Brachyprosopus, Tropidostoma*, and *Oudenodon* are generally primitive for the Cryptodontidae. Even when the polarities of character states are known, however, the identification of parallelism involves a certain element of subjectivity for, in any given group of genera and character states, several phylogenies can be arrived at depending on which shared derived character states are believed to represent true synapomorphies and which have evolved in parallel.

Geikia elginensis was compared to the cryptodontids *Geikia locusticeps, Pelanomodon moschops, Propelanomodon devillersi, Oudenodon marlothi, ''Dicynodon'' tylorhinus*, and the endothiodontinids *Brachyprosopus broomi* and *Tropidostoma microtrema*. Seven characters were compared. Although it would be desirable to use more characters, the incompleteness of several specimens made this difficult. Table 16.1 summarizes the distribution of these character states.

The character states used in this analysis include the relations of the septomaxilla, the degree of development of the anterior palatal ridges, the width of the interorbital region relative to the intertemporal region, size of the preorbital protuberance or boss, composition of the preorbital protuberance, shape of the premaxilla, and relationship of the premaxilla to the frontals.

In *Tropidostoma* and *Brachyprosopus* and most cryptodontids the septomaxilla lies entirely within the external nares, with no exposure on the lateral surface of the snout. The exposure of the septomaxilla on the side of the snout which occurs in *Geikia* and *Pelanomodon* appears to be a good derived character. In most endothiodontinids and cryptodontids the frontals are separated from the premaxilla by the nasals, which meet along the midline. Contact between the frontals and the premaxilla is, therefore, probably also a derived character state within the Cryptodontidae. However, the distribution of this derived character state conflicts with that of the septomaxilla. Contact between the frontals and the premaxilla occurs in *Propelanomodon* and *Geikia elginensis,* but not in *G. locusticeps.* Since both species of *Geikia* and *Pelanomodon* share other derived character states that are not present in *Propelanomodon,* it seems likely that the frontal-premaxilla contact developed independently in *Geikia* and *Propelanomodon.*

The "square" premaxilla found in both species of *Geikia* and the fusion of the prefrontal and nasal to form a single large protuberance are unusual among dicynodonts, and both appear to represent good derived character states within the Cryptodontidae. It is difficult to be certain of the primitive condition of the preorbital protuberance or bosses. Certainly the presence of a small nasal boss is primitive, but whether a separate small prefrontal boss is primitive or if it has developed independently several times is not clear, since *Oudenodon* has both a prefrontal and nasal boss while *Brachyprosopus, Tropidostoma* (usually, but not always), and *Propelanomodon* have only a nasal boss.

The size of the anterior palatal ridges is subject to a wide range of variation among endothiodontinids and cryptodontids. The large robust ridges in *Oudenodon* are probably not primitive since these ridges are not especially pronounced in *Tropidostoma* and are absent in *Brachyprosopus.* The moderate development of the ridges seen in *Tropidostoma* and *Pelanomodon* may represent the primitive condition, while their enlargement in *Oudenodon* and their reduction and loss in *Geikia* may both be derived states.

Geikia elginensis was found to share the most derived character states with *Geikia* (*Dicynodon*) *locusticeps,* including a "square" premaxilla, single large preorbital protuberance composed of fused nasal and prefrontal bones, and the septomaxilla having exposure on the lateral surface of the snout behind the external nares. Because of this close resemblance, "*Dicynodon*" *locusticeps* is here referred to *Geikia* as a valid species, *Geikia locusticeps.* This assignment may not be altogether satisfactory because considerable differences do exist in the proportions of the interorbital/intertemporal region, the size of the preorbital protuberance, and the relationship between the frontals and the premaxilla. However, a similar range of variation is recognized in the dicynodont genus *Lystrosaurus* (e.g., Cluver, 1971) and, until a comprehensive revision of the Cryptodontidae is available, it seems even more unjustifiable to erect a new genus for this specimen. Walker (1973) believed that

TABLE 16.1

Distribution of character states used in assessing affinities of *Geikia elginensis* to other cryptodontids.

	Geikia elginensis	*Geikia locusticeps*	*Pelanomodon moschops*	*Oudenodon marlothi*	*Propelanomodon devillersi*	*"Dicynodon" tylorhinus*	*Tropidostoma microtrema*	*Brachyprosopus broomi*
Anterior Palatal Ridges (large; reduced; absent)	reduced	absent	reduced	large	absent	reduced	reduced	absent
Interorbital Width (greater than intertemporal width; equal to intertemporal width)	greater	greater	greater	equal	equal	greater	equal	equal
Septomaxilla (exposure on lateral surface of snout; no exposure on snout)	exposure	exposure	exposure	no exposure	no exposure	?	no exposure	no exposure
Preorbital Protuberance(s) Size (large; medium; small)	large	large	medium	small	large	large	small	small
Preorbital Protuberance Composition (nasal only; unfused nasal and prefrontal; fused nasal and prefrontal)	fused prefrontal and nasal	fused prefrontal and nasal	unfused prefrontal and nasal	unfused prefrontal and nasal	nasal only	fused prefrontal and nasal	nasal only	nasal only
Premaxilla Shape (beak tip square; beak tip rounded)	square	square	rounded	rounded	rounded	rounded	rounded	rounded
Frontals-Premaxilla Relations (contact; no contact)	contact	no contact	no contact	no contact	contact	?	no contact	no contact

Dicynodon locusticeps is structurally ancestral to *Geikia elginensis,* and his conclusion is supported by this study.

Among the other cryptodontids, *Geikia* closely resembles *Pelanomodon* in that both genera have the septomaxilla exposed on the lateral side of the snout behind the external nares, the preorbital protuberance involves both enlarged prefrontal and nasal bones although they are unfused in *Pelanomodon,* and the interorbital region is substantially wider than the intertemporal region. In the type specimen of *''Dicynodon'' tylorhinus* the prefrontals and nasals fuse to form a large preorbital protuberance and the interorbital region is much wider than the intertemporal region. It therefore may share a more recent common ancestor with *Geikia* than *Pelanomodon* does, but the condition of the septomaxilla is currently unknown, leaving its position uncertain.

Age of Cuttie's Hillock

With the exception of *Geikia elginensis,* all known cryptodontids are from South Africa, Zambia, and Tanzania. They occur in continental sediments of Late Permian age which correlate with the *Cistecephalus* Zone and *Daptocephalus* Zone of the Beaufort Series of South Africa. *Geikia locusticeps* is from a horizon that correlates with the *Daptocephalus* Zone (Haughton, 1932). The stratigraphic range of other cryptodontids favors a Late Permian age rather than an Early Triassic age, and therefore a correlation of the Cuttie's Hillock Sandstone with the *Daptocephalus* Zone. The presence of the pareiasaur *Elginia* in the Cuttie's Hillock fauna tends to support this suggestion inasmuch as pareiasaurs are common members of *Daptocephalus* Zone faunas but are not known to extend into the overlying Early Triassic *Lystrosaurus* Zone. Walker (1973) favored a correlation with the *Lystrosaurus* Zone because the skull of *Elginia* is more spinose than pareiasaurs from the latest known faunas elsewhere. He apparently believed that this extreme specialization required more time to evolve, and consequently *Elginia* is younger than other pareiasaurs. This argument, however, requires tacit assumptions regarding pareiasaur phylogeny and evolutionary rates, for which there seems to be little evidence. The available evidence favors a Late Permian age and *Daptocephalus* Zone correlation for the Cuttie's Hillock fauna.

Summary

The dicynodonts *Geikia* and *Gordonia* are the only known therapsid reptiles from the Late Permian of Europe. Some authors believe that they may be as young as Triassic, but the available evidence favors a Late Permian age, and correlation with the *Daptocephalus* Zone of the Beaufort Series of South Africa. *Geikia elginensis* is assigned to the Cryptodontidae (*sensu* Toerien, 1953; Haughton and Brink, 1954), and is the only member of this family occurring outside of Africa. It is distinctive in the marked enlargement of its preorbital protuberances, its short box-like snout, and the general proportions of its skull. *''Dicynodon'' locusticeps* (von Huene, 1942) is assigned as a valid species of *Geikia, G. locusticeps.* Among cryptodontids, *Geikia* is considered to be most closely related to *Pelanomodon.*

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Abbreviations for Figures

ANG.—angular
ANT. PAL. R.—anterior palatal ridge
ART.—articular
BAS.—basisphenoid
BO.—basioccipital
CAN. PROC.—caniniform process of maxilla
DEN.—dentary
DEN. GR.—dentary groove
DEN. TAB.—dentary table
DP. CREST—deltopectoral crest
ECT.—ectopterygoid
ENT. F.—entepicondylar foramen
EO.—exoccipital
EPT.—epipterygoid
EXT. NAR.—external nares
F. M.—foramen magnum
FEN. OV.—fenestra ovalis
FR.—frontal
I.C.C.—internal carotid canal
IP.—interparietal
IPT. VAC.—interpterygoidal vacuity
JUG. FOR.—jugular foramen
LAT. COND.—lateral condyle of articular
LAT. DEN. SH.—lateral dentary shelf
MAX.—maxilla
MED. COND.—medial condyle of articular
NAS.—nasal
OP.—opisthotic
ORB.—orbit
PA.—parietal
PAL.—palatine
PAS.—parasphenoid
PMX.—premaxilla
PO.—postorbital
PRF.—prefrontal
PRO.—prootic
PT.—pterygoid
Q.—quadrate
Q. RAM.—quadrate ramus of pterygoid
RAD. COND.—radial condyle
REF. LAM.—reflected lamina of angular
RET. PROC.—retroarticular process
SA.—surangular
SMX.—septomaxilla
SOC.—supraoccipital
SQ.—squamosal
VO.—vomer