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OWENETTA KITCHINGORUM, SP. NOV., A SMALL PARAREPTILE (PROCOLOPHONIA: OWENETTIDAE) FROM THE LOWER TRIASSIC OF SOUTH AFRICA

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ABSTRACT—The parareptile *Owenetta rubidgei* is known from several skulls, all found in Upper Permian sediments of South Africa. The anatomy of a new species of *Owenetta*, *O. kitchingorum*, from the Early Triassic is described here on the basis of three nearly complete skeletons. This new species is distinguished from *O. rubidgei* on the basis of three dental and three cranial features. Postcranial features cannot be used in the diagnosis because the postcranial anatomy of *O. rubidgei* is unknown. The small parareptile *Barasaurus* from the Late Permian of Madagascar and *Owenetta* are united in the clade Owenettidae, as the sister-taxon of Procolophonidae. Controversies surrounding parareptilian phylogeny are discussed as they relate to *Owenetta*.

INTRODUCTION

The small amniote *Owenetta* was originally named and described briefly by R. Broom (1939) on the basis of a partial skull (R50, Rubidge Collection, Wellwood Museum) from New Bethesda Commonage, Graaf-Reinet, South Africa (*Cistecephalus* Assemblage Zone, Upper Permian). He distinguished it from *Procolophon* and erected the family Owenettidae within Procolophonia for its placement. Although more than a dozen Upper Permian specimens of the type species *O. rubidgei* have been collected subsequently, all are partial or complete skulls, ranging in length from 17 to 35 mm and lack postcrania. Subsequent work on this small parareptile was restricted to a brief study on its general cranial anatomy by Gow (1977).

Two small blocks containing the remains of *Owenetta* were discovered by Dr. James Kitching in 1968 at Donovan's Kop, Tweefontein, Bethulie District, in the *Lystrosaurus* Assemblage Zone (Lower Triassic). This discovery was startling because it not only extended the fossil record of this taxon across the Permo-Triassic boundary (as defined in South Africa), but also included postcranial remains. Preparation of one of the blocks revealed two nearly complete, articulated skeletons in close apposition to each other (Reisz and Laurin, 1991). These skeletons were the first to offer detailed information on the postcranial anatomy of this small parareptile, and they form the basis of the present description. A third skeleton was collected by Dr. Anne Warren in 1992 at the same site, but has been only partially prepared.

The detailed description of *Owenetta* is particularly important because this small reptile can provide valuable new data for analyses of procolophonian evolution. *Owenetta* has also attracted attention because it was used to argue that parareptiles are more closely related to turtles than are captorhinids (Reisz and Laurin, 1991). This hypothesis has led to a renewed interest in parareptiles (Lee, 1993, 1995, 1996, 1997; DeBraga and Reisz, 1996; Rieppel and DeBraga, 1996; DeBraga and Rieppel, 1997; Rieppel and Reisz, 1999). The three articulated skeletons that form the basis of the present study can be distinguished both morphologically and stratigraphically from the genotype, and therefore represent a new species.

SYSTEMATIC PALEONTOLOGY

PARAREPTILIA Olson 1947
PROCOLOPHONIA Seeley 1888
PROCOLOPHONOIDEA Romer 1956

Revised Diagnosis—Small procolophonian parareptiles characterized by the reduced sculpturing on the skull roof, presence of a well developed tongue-like medial process of the prefrontal, distinct doming of the large, smooth supratemporal; absence of postparietal; presence of elongate frontals, the longest paired elements of the skull roof midline; absence of teeth on the transverse flange of pterygoid.

Family OWENETTIDAE Broom 1939

Revised Diagnosis—Small procolophonoid parareptiles characterized by the presence of large postfrontal, eliminating contact between postorbital and parietal; deep temporal emargination between jugal and quadratojugal, reducing the contact between these two bones to less than 1/5 of the height of these bones; large, rectangular supratemporal forms skull table lateral to parietal; humerus lacks entepicondylar foramen.

OWENETTA Broom 1939

Type Species—*OWENETTA RUBIDGEI* Broom 1939

Revised Diagnosis—Small owenettid parareptile characterized by the presence of a shallow depression of the parietal surface surrounding the pineal foramen, presence of a supratemporal that has a lateral notch near the posterior border of the bone. Postcranially, the humerus and femur are long and slender compared to those of *Barasaurus*, femur equivalent in length to 6.5 dorsal vertebrae, tibia/femur ratio is 0.7. Differs from other procolophonoids in having only slightly, rather than strongly, swollen neural arches.

OWENETTA KITCHINGORUM, sp. nov.

Diagnosis—Distinguished from *Owenetta rubidgei* by the presence of a caniniform region in short maxilla which could have accommodated no more than 20 sharply pointed, recurved teeth; medial contact between prefrontals anterior to frontals; and the presence of small postparietals at the back of the skull table.

Holotype—BP/1/4195a (Bernard Price Institute for Paleontology, University of Witwatersrand) an articulated skeleton preserving the skull and anterior part of the skeleton of subadult individual (Fig. 1).

Referred Specimens—BP/1/4195b, the postcranial skeleton of a second subadult individual located in the same block as the holotype (Fig. 1); BP/1/4196, badly crushed skull with anterior part of vertebral column; BP/1/5398, collected by Dr. Anne Warren in 1992, an articulated skeleton with left manus left pes, and most of tail missing, with the skull roof and left

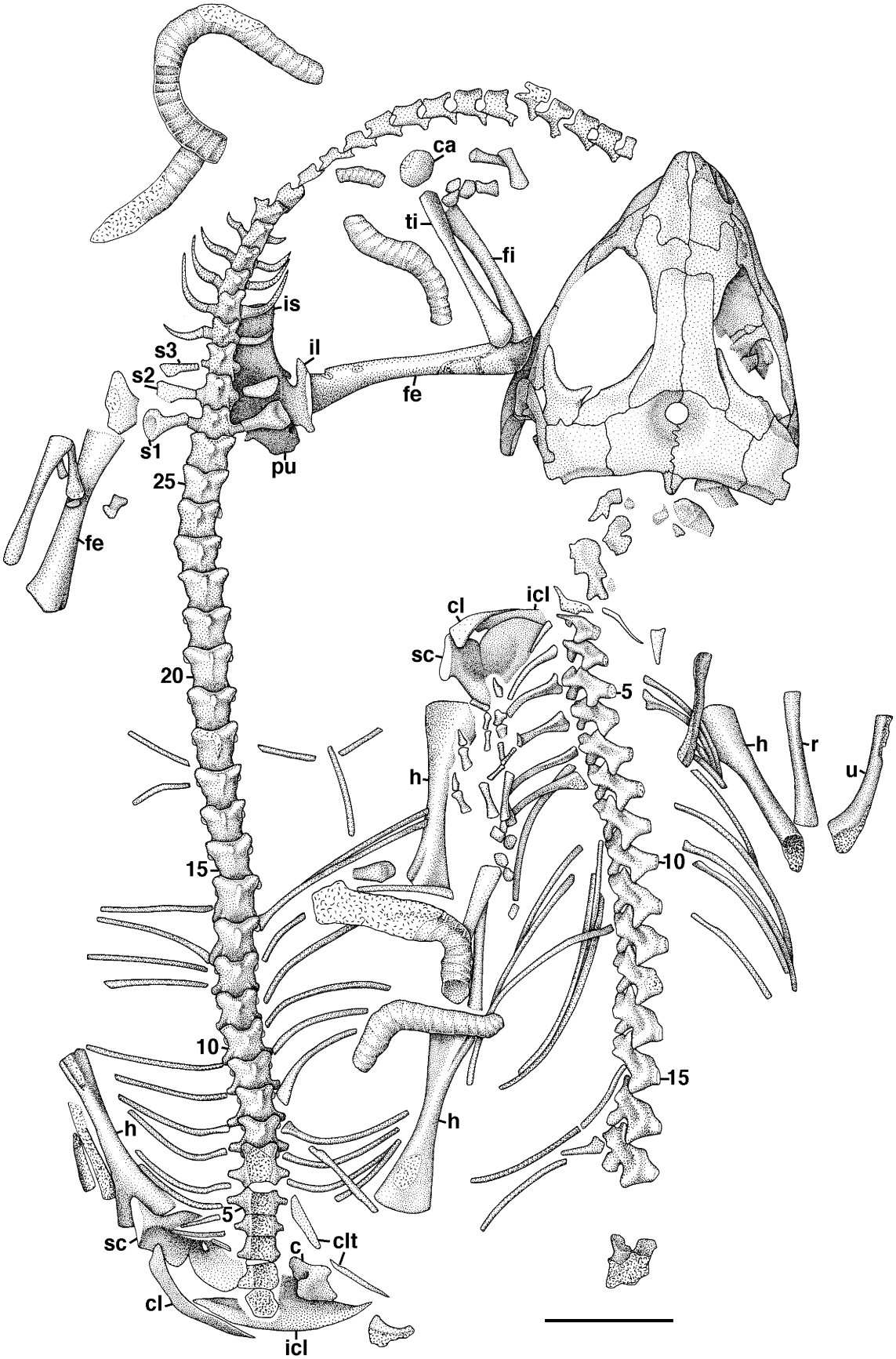

FIGURE 1. *Owenetta kitchingorum* BP/1/4195a and b. Two nearly complete, articulated skeletons in dorsal view. **Abbreviations**: **atc**, atlas centr um; **atn**, atlas neural arch; **axc**, axial centrum; **axn**, axial neural arch; **c**, coracoid; **ca**, calcaneum; **cl**, clavicle; **clt**, cleithrum ; **h**, humerus; **fe**, femur; **fi**, fibula; **icl**, interclavicle; **il**, ilium; **is**, ischium; **pu**, pubis; **r**, radius; **s1, s2, s3**, sacral ribs; **sc**, scapula; **ti**, tibia; **u**, ulna; **5, 10, 15, 20, 25**, vertebra number. Scale equals 1 cm.

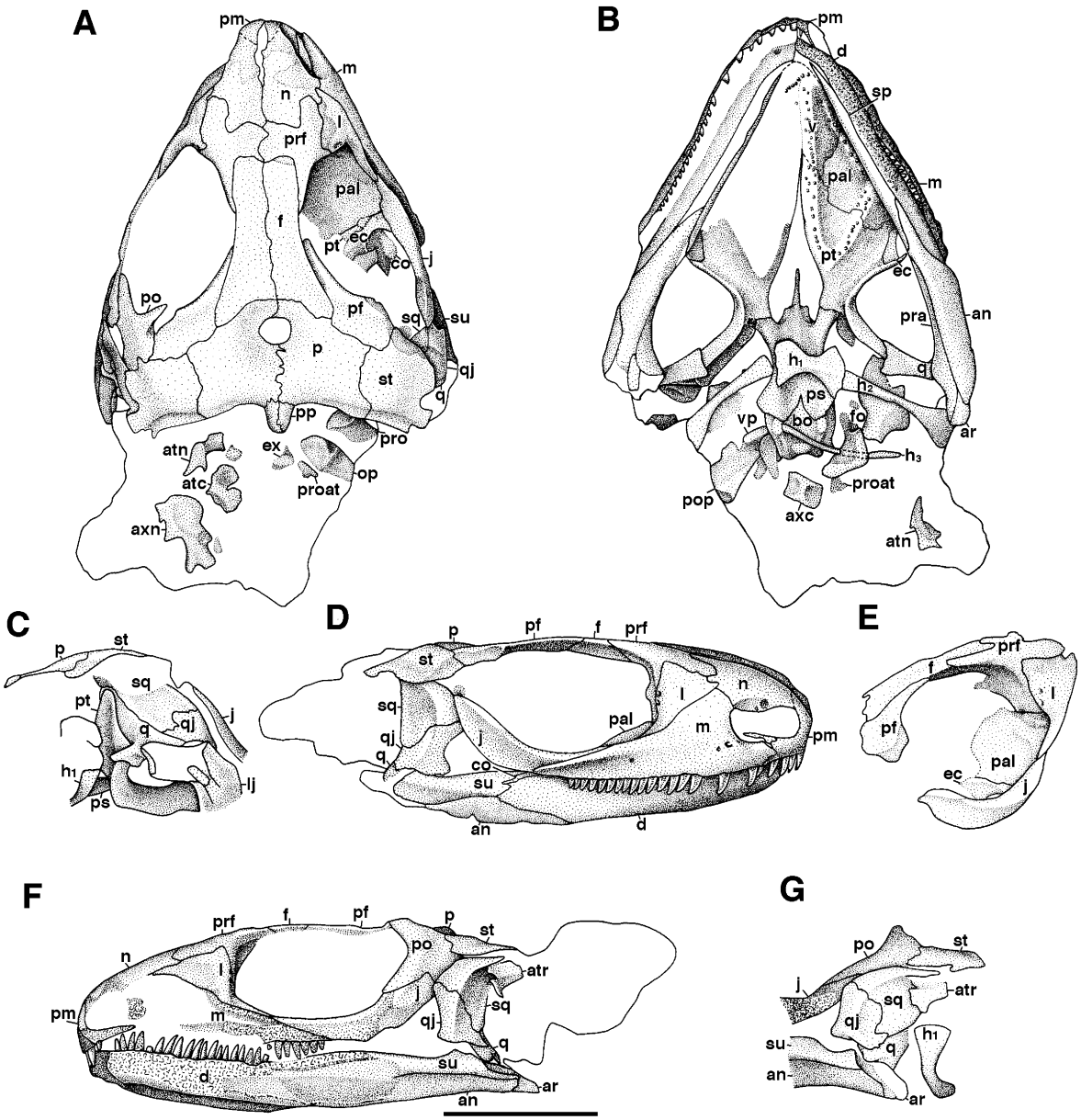

FIGURE 2. *Owenetta kitchingorum* BP/1/4195a. Skull of holotype in (**A**) dorsal, (**B**) palatal, (**D**) right lateral, and (**F**) left lateral views. Details of the (**C**) partial right occiput, (**E**) right anterior orbital, and (**G**) partial occipital view of left temporal region. **Abbreviations**: **an**, angular; **ar**, articular; **atc**, atlas centrum; **atn**, atlas neural arch; **axc**, axial centrum; **axn**, axial neural arch; **bo**, basioccipital; **co**, coronoid; **d**, dentary; **ec**, ectopterygoid; **ex**, exoccipital; **f**, frontal; **fo**, fenestra ovale; **h1**, corpus hyoideum; **h2**, first branchial cornua; **h3**, second branchial cornua; **j**, jugal; **l**, lacrimal; **lj**, lower jaw; **m**, maxilla; **n**, nasal; **op**, opisthotic; **p**, parietal; **pal**, palatine; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pop**, paroccipital process; **pp**, postparietal; **pra**, prearticular; **prf**, prefrontal; **pro**, prootic; **proat**, proatlas; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sp**, splenial; **sq**, squamosal; **st**, supratemporal; **su**, surangular; **v**, vomer; **vp**, ventral process. Scale equals 1 cm.

side of skull and mandible exposed to show critical areas of the cranial anatomy.

Horizon and Locality—Donovan's Kop, Tweefontein, South Africa; *Lystrosaurus* Assemblage Zone, Lower Triassic.

Etymology—Named in honor of the Kitching family, and the greatest collector of Karroo fossils, Dr. James Kitching.

DESCRIPTION AND COMPARISONS

This description of the skull of *Owenetta kitchingorum* is based primarily on BP/1/4195 (Figs. 1, 2), with reference to BP/1/5398. Comparisons with *O. rubidgei*, are based on information provided by the holotype of this species RC 50 (Fig. 3), and the much better preserved referred specimen, SAM (South African Museum, Cape Town) PK K7582 (Figs. 4, 5). The description of the postcranial skeleton is by necessity, restricted to BP/1/ 4195 because no specimens of *Owenetta rubidgei* have postcranial remains, and the skeleton of BP/1/5398 has not been prepared.

Skull

Slight distortion has displaced the skull roof to the right in BP/1/4195 (Fig. 1). In addition, parts of the braincase have disarticulated from the rest of the skull, and moved posteriorly. During initial preparation the skull was removed from the rest

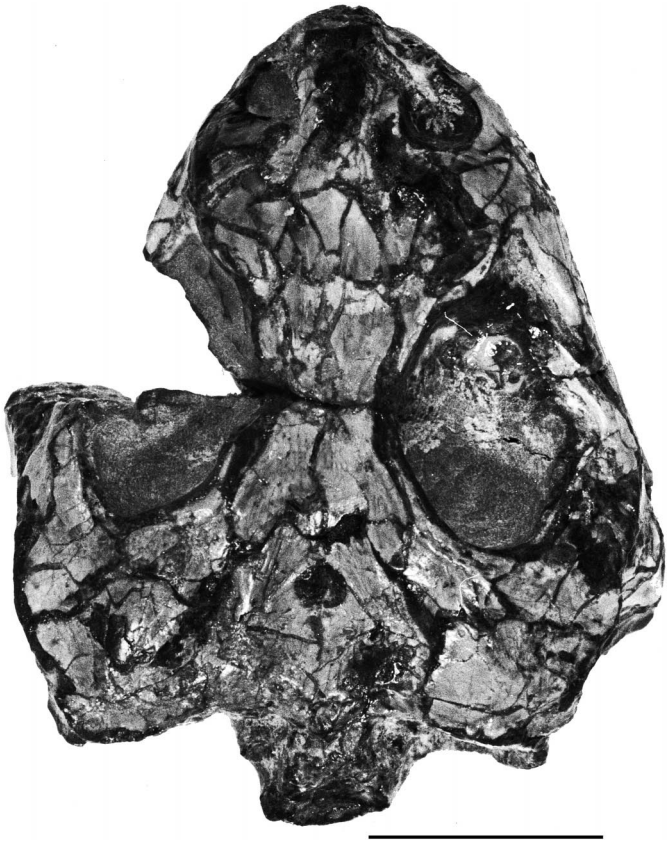

FIGURE 3. *Owenetta rubidgei*. RC 50, Hopotypic skull in dorsal view. Scale equals 1 cm.

of the skeleton, causing some damage to the left side of the snout, with part of this region of the skull remaining on the main block. Otherwise the skull is perfectly preserved, allowing a complete reconstruction. The apparent ease with which the opisthotics, prootics, and supraoccipital have separated from each other suggests that this skeleton represents a subadult individual. This interpretation is supported by evidence from the postcranial skeleton, as the atlas-axis complex has come apart, the fusion of the scapulocoracoid is incomplete, and the carpals and tarsals are only partially ossified. This suggests that a typical adult *Owenetta* may have been significantly larger than this specimen. BP/1/5398 appears also to represent a juvenile individual, and is only about 10 percent larger than BP/1/4195. This is surprising because all known specimens of this genus are either similar in size to the skulls of these apparently immature individuals, or smaller. Nevertheless, several skulls of *Owenetta rubidgei* are much more completely ossified than the holotype of *Owenetta kitchingorum* despite being similar to it in size. This suggests either that the Triassic representative of this genus may have been larger than the Late Permian forms, or that they are less well ossified as adults.

The cranial anatomy of *Owenetta* is poorly known, warranting an extensive description of the skull and mandible. Much of this anatomy can be discerned from the reconstruction, but salient points will be emphasized.

Dermal Skull Roof—The tip of the snout is formed by the premaxilla. As in other parareptiles, this element has a slender dorsal process that does not extend far onto the dorsal surface of the skull. There is place for 5 premaxillary teeth, the socket of the last tooth being covered laterally by the anterior process of the maxilla. Most of the anterior border of the narial opening is entirely made up by the premaxilla. Both the premaxilla and maxilla contribute to the ventral border of the external naris, whereas most of the dorsal border is formed by the nasal. The nasal contributes significantly to the gently domed snout and also forms a narrow dorsal narial shelf.

As indicated in the diagnosis, *Owenetta kitchingorum* has a highly unusual prefrontal. In most Paleozoic amniotes, the prefrontal is a paired circumorbital element that is located lateral to the median nasal and frontal. In *O. kitchingorum*, however, the prefrontal has a large medial process that reaches the midline in front of the orbit, and separates the nasal and frontal bones (Figs. 1A, 6A). The size of this medial process suggests that it probably separated completely these two skull roof elements, even though it is not possible to prepare the ventral surface of this part of the skull roof. The prefrontal also has a large ventral process that is buttressed against the palate and supports medially the relatively delicate lacrimal. This ventral, orbital process of the prefrontal is wide, extending far medially and forming a wide anterior orbital shelf. In addition, there is a well developed medial, tongue-like process of this orbital shelf, as is characteristic of all procolophonoids. As a consequence of the unusual prefrontal anatomy, the frontal does not extend as far anteriorly as in *Owenetta rubidgei*, where it is wedged slightly between the nasal and prefrontal. In *O. kitchingorum*, the frontal is truncated anteriorly and has a subrectagular outline. This configuration of the frontal and prefrontal bones is clearly not pathological, or anomalous as it is also present in the second known skull, BP/1/5398. Above the orbits, the frontal has a wide contribution to the dorsal orbital margin. Posteriorly, the frontal has a posterolateral flange that is interposed between the postfrontal and parietal bones.

The main portion of the skull table is formed by the large parietal, a broad midline element that surrounds anteriorly the well developed pineal foramen. In the region of the pineal foramen, the parietal has a broad, bowl-like depression. The sutural pattern of this bone is unusual, being bordered anteriorly by the frontal and postfrontal, and laterally by the supratemporal. As in *O. rubidgei*, the parietal of *O. kitchingorum* does not contact either the squamosal or the postorbital. Posteriorly, the parietal has a modest occipital flange near its lateral edge, but contacts medially the small postparietal. *O. kitchingorum* differs from *O. rubidgei* and other procolophonoids by having small, paired postparietal at the posterior end of the skull table. This dorsal position of the postparietal is similar to that seen in pareiasaurs, but in the latter, the postparietal is a large, median element. More basal parareptiles have paired, occipital postparietals.

In contrast to procolophonids, the postfrontal is a large element in *Owenetta*. The posfrontal not only has a long anterior process that contributes to the dorsal orbital margin, but also has a broad, slightly concave dorsal surface that forms the anterolateral portion of the skull table. The presence of this large posterior portion of the postfrontal distinguishes owenettids from procolophonids. The condition of a narrow postfrontal may be an autapomorphy of procolophonids because in that family the posterior enlargement of the orbit appears to be mainly at the expense of the postfrontal. The supratemporal occupies the posterolateral corner of the skull table. In both *Owenetta* species, as in *Procolophon*, the supratemporal is a domed element, contacting the postorbital and postfrontal anteriorly, the parietal medially, and overlying the squamosal laterally. The lateral edge of the supratemporal is slightly notched near its posterolateral corner, a distinctive feature of the genus *Owenetta*. In addition, the occipital edge of this bone is beveled, forming an occipital shelf that is contiguous with that of the parietal.

The postorbital is a relatively short, mediolaterally broad element that is located primarily on the lateral surface of the

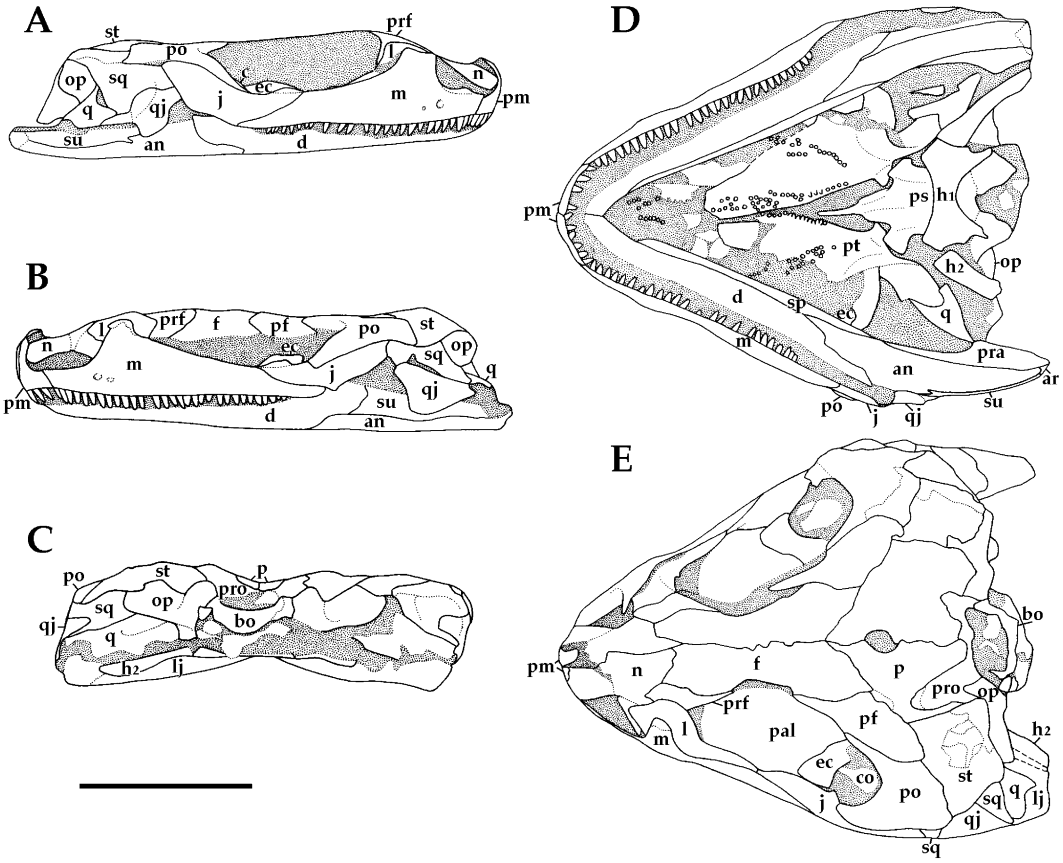

FIGURE 4. *Owenetta rubidgei*. Skull of referred specimen (SAM PK K 7582) in (**A**) right lateral, (**B**) left lateral, (**C**) occipital, (**D**) palatal, and (**E**) dorsal views. **Abbreviations**: see Figure 2. Scale equals 1 cm.

skull, but also has a modest contribution to the skull table immediately in front of the supratemporal. The slight posterior expansion of the orbit of owenettids is probably associated with the emargination of this bone along its orbital margin, forming the strongly curved posterodorsal corner of the orbit.

The maxilla is the largest element of the snout, with well developed premaxillary, anterodorsal and suborbital rami (Fig. 2D). The posterior and most of the ventral borders of the external naris are formed by the maxilla. The presence in *Owenetta* of a distinct anterolateral maxillary foramen, just ventral to the posterior narial border also characterizes most parareptiles, including procolophonids and pareiasaurs (DeBraga and Reisz, 1996). The anterodorsal process of the maxilla is large in *Owenetta kitchingorum*, nearly making contact with the prefrontal (Figs. 2D, 4A, B, 6D). Although this part of the maxilla is usually damaged in *O. rubidgei*, both the holotype (RC 50) and the referred specimen show a similarly tall anterodorsal ramus. However, the holotype of *O. kitchingorum* has a distinctly less elongate suborbital ramus of the maxilla than that of *O. rubidgei*. This structure extends well beyond the mid-level of the orbit in the latter, in strong contrast to the condition in the former where the ramus extends only to the level of the midpoint of the orbit. It is partly for this reason that the maxillary tooth row of the new species is significantly shorter than that of *O. rubidgei*, having space for only 20 teeth rather than the full complement of 30 seen in *O. rubidgei*. In addition, there is a distinct caniniform region in *O. kitchingorum*, with the teeth being larger than those in *O. rubidgei* and having broader bases. The teeth also differ slightly between the two species in that those of *O. rubidgei* are simple and conical whereas those of *O. kitchingorum* are sharply pointed and recurved.

The lacrimal is a relatively large element in *Owenetta*, despite the large size of the maxilla in general, and the great height of the maxillary anterodorsal ramus in particular. The lacrimal has a thin, tall antorbital blade, which is pierced by the lacrimal puncti halfway along its height, and a slender, delicate suborbital ramus that contacts the anterior process of the jugal. In *Owenetta*, the jugal is a relatively simple cranial element, with a vaguely boomerang-shaped outline that wraps around the posteroventral corner of the orbit. Its postorbital ramus has a long slanting sutural contact with the postorbital, but little contact with the quadratojugal and squamosal bones. Anteriorly, the jugal contacts the lacrimal and maxilla (Fig. 2A, E). The jugal has a modest medial buttress where it meets the narrow lateral process of the ectopterygoid and the palatine. A deep temporal emargination separates the jugal from the quadratojugal. The anterior and posterior edges of this deep emargination, formed by the jugal and quadratojugal respectively, contact each other at an acute angle far above the ventral edge of the skull and level with the mid-point of the orbit. Recent evidence indicates that several parareptiles possessed a lower temporal fenestra (DeBraga and Reisz, 1996), raising the possibility that the condition seen in *Owenetta* may represent an example of the loss of the lower temporal bar.

The body of the quadratojugal is short in the anteroposterior dimension, but appears well developed and extends dorsally to the mid-height of the skull. Posteriorly, it is strongly concave where it forms an anteroventral ridge for the probable attach-

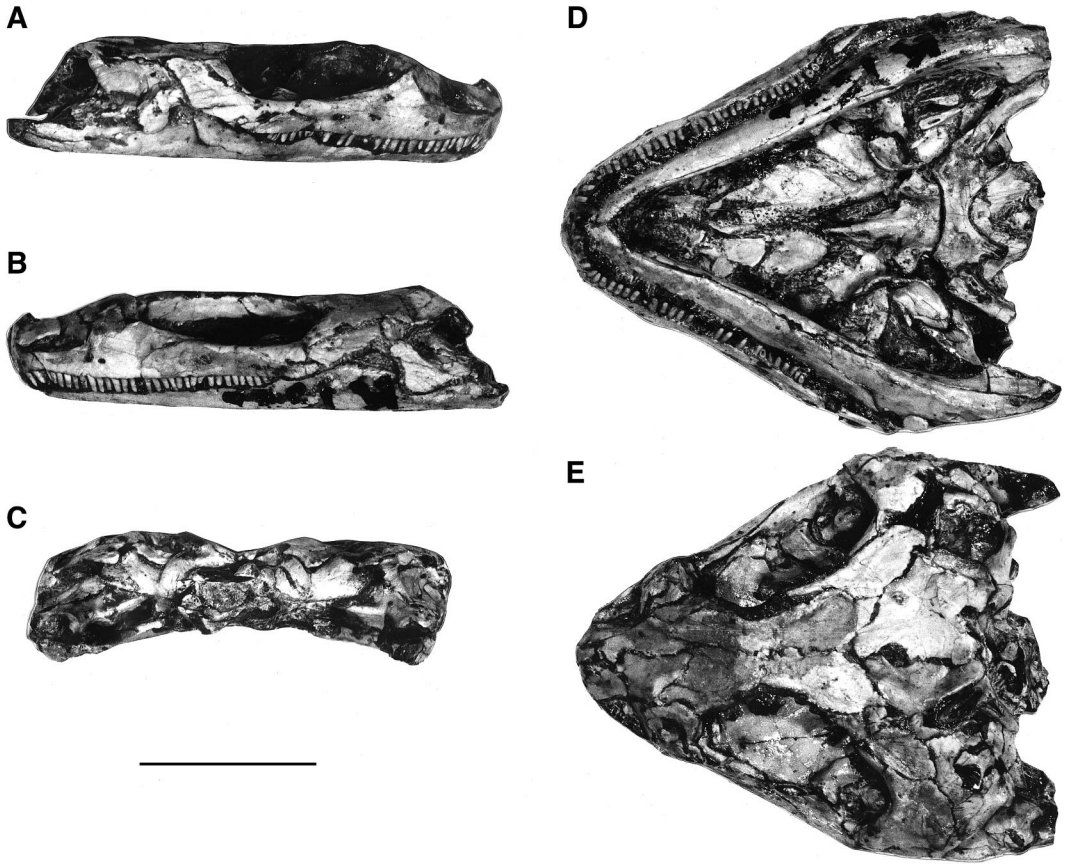

FIGURE 5. *Owenetta rubidgei*. Photographs of referred specimen (SAM PK K 7582) in (**A**) right lateral, (**B**) left lateral, (**C**) occipital, (**D**) palatal, and (**E**) dorsal views. Scale equals 1 cm.

ment of a tympanum. The quadratojugal does not cover the quadrate posteriorly. The gently slanting dorsal edge of the quadratojugal contacts the squamosal (Fig. 2C, D, F, G).

The squamosal is one of the most complex elements of the skull roof, making attachments to the quadratojugal and quadrate ventrally, the postorbital anteriorly, the supratemporal dorsally, and the opisthotic and pterygoids medially (Fig. 2C, D, F, G). Along its lateral surface, the squamosal also has a tympanic ridge that is a dorsal extension of the same type of ridge of the quadratojugal. Posterior to this ridge, the squamosal wraps partly around the posterodorsal process of the quadrate. Mediodorsally, the squamosal has a well developed process that buttresses the supratemporal from beneath. This process of the squamosal is in turn supported by the quadrate and a narrow dorsal process of the quadrate ramus of the pterygoid. There are, therefore, three cranial elements that come together to form a strongly buttressed posterodorsal corner of the skull roof: the supratemporal, squamosal, and quadrate. In addition, the pterygoid provides additional support in this area.

Palate—The palate is formed by the paired vomer, palatine, ectopterygoid, and pterygoid bones. The vomer lies on either side of the midline, in the region of the elongate internal nares (Fig. 2B). In contrast to the condition in both synapsids and eureptiles, the vomers are in contact with each other along nearly their whole length, rather than being wedged apart by a long anterior process of the pterygoid. In both species of *Owenetta*, the ventral surface of the vomer has two major tooth-bearing ridges, one that extends longitudinally near the midline, and another that runs parallel to the maxilla. The ridges meet anteriorly, near the sutural contact with the premaxilla, and extend along the entire length of the vomer. Posteriorly, these tooth-bearing ridges are continued on both the pterygoid and palatine. On the palatine, the ridge at first continues parallel to the edge of the maxilla, but approximately at the middle of the palatine ventral surface turns posteromedially. On either side of this tooth-bearing ridge, the ventral surface of the bone is concave. The proportions of the palatine conform to the general parareptilian pattern, being a mediolaterally broad, relatively short element (Fig. 2A, B, E). The palatine bone has extensive sutural contacts with the vomer anteriorly and the pterygoid posteromedially, but also appears to be thickened laterally to contact the maxilla as well as the jugal and lacrimal laterally (Fig. 2E). The palatine–prefrontal contact is short and buttress-like, enclosing the foramen orbito-nasale.

As in other amniotes, the pterygoid is the largest, most complex element of the palate (Fig. 2B, C). It is composed of two main regions: a large anterior palatal portion which terminates posteriorly in the basi-pterygoid process and the transverse process, and a narrow, tall posterolateral process that extends to the quadrate and the skull roof. An unusual feature of *Owenetta kitchingorum*, which cannot be confirmed in *O. rubidgei* is the presence of a slender lateral process of the pterygoid that is interposed between the palatine and ectopterygoid (Fig. 2A, B). This lateral process of the pterygoid appears to reach the small suborbital foramen. The two palatal tooth-bearing ridges continue on the pterygoid, and converge posteriorly to meet near the edge of the interpterygoid vacuity. In contrast to the condition found in most non-procolophonoid amniotes, these palatal tooth rows do not reach the level of the basicranial articulation. In addition, the anterolaterally tilted transverse flange

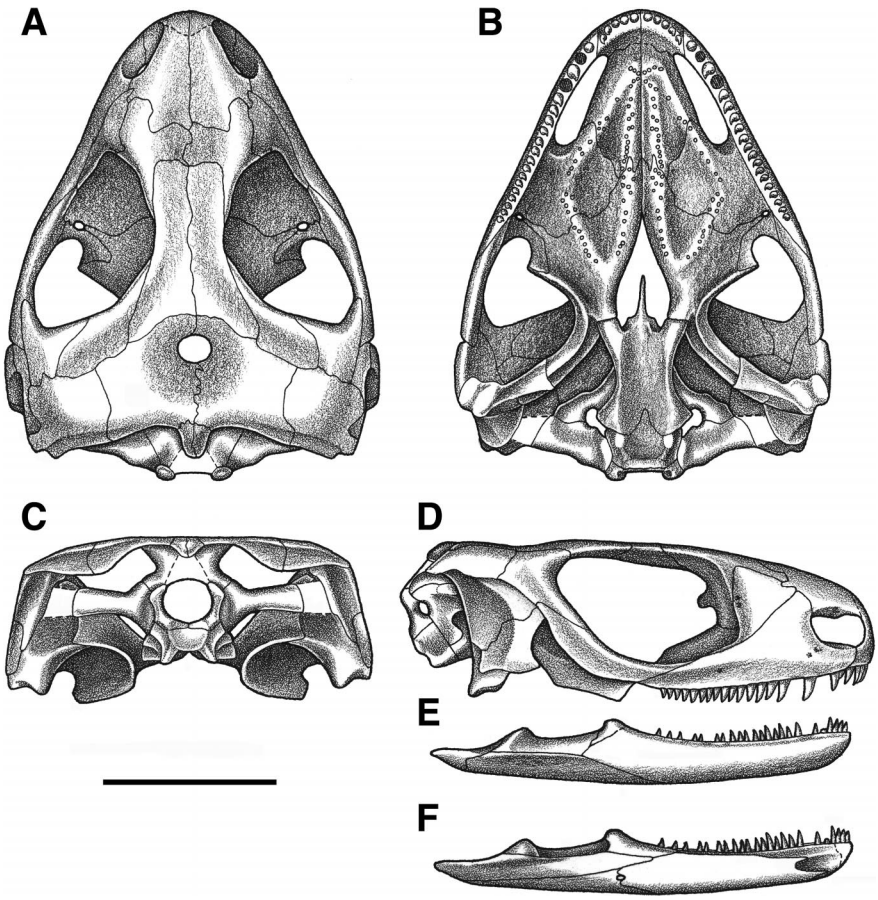

FIGURE 6. *Owenetta kitchingorum*. Skull reconstruction in (**A**) dorsal, (**B**) palatal, (**C**) occipital, and (**D**) right lateral views. Reconstruction of mandible in (**E**) lateral and (**F**) medial views. Scale equals 1 cm.

of the pterygoid is devoid of teeth. Instead, the posterior edge of the flange has a sharp ventral ridge. This ridge extends in a smooth curve posteriorly, onto the quadrate ramus of the pterygoid. Medially, the palatal surface of the pterygoid forms the curved edge of the interpterygoid vacuity and terminates in a butt-like articulation with the parasphenoid. Posterolateral to this basi-cranial articulation, the pterygoid extends only a short distance to reach the anteromedial process of the quadrate The quadrate process of the pterygoid has a flat, slightly expanded ventral surface, whereas the posterodorsal process is a thin, nearly vertical blade that nearly reaches the skull table (Fig. 2C). Between these two parts of the posterior ramus of the pterygoid, a strongly developed concavity extends all the way to the basicranial articulation. This space may contain the middle ear cavity. Although reduced to a small anterolateral extension of the transverse flange, the ectopterygoid remains a distinct element of the palate (Fig. 2 A, B, E). In its position as a brace between the distal end of the transverse flange and the cheek, the ectopterygoid is deep dorsoventrally, and encloses the notch in the anterior border of the adductor fossa.

The quadrate is largely covered by the surrounding bones, but its anatomy can be readily discerned (Fig. 2B, C, G). It is relatively massive, with a well developed dicondylic articulation for the mandible. Above this region, the dorsal process of the quadrate is not constricted, as is normal in most Paleozoic amniotes. Instead, the dorsal process remains broad and gently rounded for part of the region that is not covered by the quadratojugal and squamosal. Immediately above this rounded area, the quadrate has a groove that expands progressively anterodorsally, separating the body of the bone into two major areas, a large anteromedial process and a slender dorsal process. The anteromedial process has an expanded ventral plate that covers part of the quadrate ramus of the pterygoid, and cradles the posteroventral process of that bone. The dorsal process is reinforced towards its distal end by the posterodorsal process of the pterygoid, and by an expanded mediodorsal flange of the squamosal. Between these two edges, the quadrate contributes to the presumed middle ear cavity.

Braincase—The braincase clearly indicates that the skull BP/1/4195 belonged to a subadult individual. Although the ventral elements, the parasphenoid and basioccipital are not displaced, the paired prootic and opisthotic have rotated out of position, and the median supraoccipital has probably collapsed forward (Fig. 2A, B). No stapes have been recovered. In the holotype of *Owenetta kitchingorum* the distal end of the paroccipital process terminates in unfinished bone, indicating that the opisthotic continued laterally in cartilage. This is the expected condition for a subadult individual. In contrast to this condition, the referred specimen of *O. rubidgei* SAM PK K7582 (Figs. 4, 5) has a much larger, completely ossified paroccipital process that reaches the squamosal bone. As in other procolophonians, the paroccipital process is nearly horizontal, with its greatest dimension being in the anteroposterior plane. A well developed ventral process is exposed in ventral view on the right opisthotic. This ventral process would have attached to the rest of the braincase to the lateral wall of the basioccipital, and probably forms the posterior edge of the fenestra ovalis. The latter appears to be small, as in other parareptiles where this can be

discerned (DeBraga and Reisz, 1996). A rounded swelling on the body of the opisthotic extends vertically along the height of the bone, indicating the presence of one of the semicircular canals in this area. This swelling continues on the prootic. The most significant discernable feature of the prootic is the rounded fenestra ovalis that it forms together with the opisthotic. Few additional features of the prootic can be described beyond those shown in the skull reconstruction. Although the supraoccipital could not be found in *Owenetta kitchingorum*, the space available in the reconstruction and the anatomy of this bone in the other species of *Owenetta*, indicate that it was a small element. There appears to be no opisthotic-supraoccipital contact in occipital view (Fig. 6). This can be determined because prootic-opisthotic contacts match completely, leaving no sutural area on the opisthotic for the supraoccipital.

The floor of the braincase is formed by the parasphenoid and basioccipital bones (Figs. 2B, 4B). The parasphenoid is a large element, generally subdivided into two regions, the anterior cultriform process and basicranial tubera, and the posterior plate. The cultriform process is short in *Owenetta*, extending only half-way along the length of the interpterygoid vacuity, and is also slender. However, the base from which the cultriform process arises is wide and well developed, extending to the level of the basicranial articulation. The parasphenoid portion of the basicranial articulation is in the form of two relatively large tubera that extend mainly anteriorly and slightly laterally. However, the surfaces of articulation appear to face forward. The main body of the parasphenoid has the outline of a broadly waisted hourglass, widening anteriorly and posteriorly. Anteriorly, the expanded lateral edges of the hourglass are formed by the bodies of the tubera. The central, narrowed portion of the parasphenoidal plate is gently concave between the ridged lateral edges. The posterior widening is formed by the cristae ventrolaterales that cover part of the basioccipital. These cristae are separated posteromedially by a narrow gap. The whole plate of the parasphenoid, representing the portion of the bone that lies posterior to the cultriform process, is gently concave medially. The basioccipital is unusually long in ventral view, being approximately equal to one-half the length of the parasphenoid plate. Its ventral surface has two prominent tubera that are at the posteriormost tip of the parasphenoidal cristae. These two tubera are connected to a posteriorly directed pair of narrow ridges that extend to the occipital condyle. Attached to the posterodorsal part of the basioccipital is the paired exoccipital. This element, seen with difficulty in *Owenetta kitchingorum* because of the presence of the postcranial elements behind the head, as well as the partial disarticulation of the braincase, nevertheless appears indistinguishable from that of *O. rubidgei*. In normal basal amniote fashion, the exoccipitals meet in the midline, contribute to the occipital condyle, and form the lateral walls of the foramen magnum. Dorsally their contact with the supraoccipital is obscure.

Mandible

The mandible of *Owenetta kitchingorum* appears to be indistinguishable from that of *O. rubidgei*, except for the length of dentary, and the number of teeth carried by this bone. The dentary is shorter in *O. kitchingorum* (Fig. 2B, D, F) occupying less of the jaw length than in *O. rubidgei* (Figs. 4, 5). This is probably related to the maximum number of teeth and tooth positions that can fit on the dentary: In *O. kitchingorum* there is place for only 28 teeth, whereas the dentary of *O. rubidgei* can accommodate 34 or 35 teeth. The dentary is covered medially by the splenial. The anterior end of the splenial does not reach the symphysis, which is formed entirely by the dentary. The anterior edge of the splenial is concave in outline, between the dorsal and ventral areas of contact with the dentary. Posteriorly the splenial contributes to the formation of the meckelian foramen. The coronoid bone is exposed in both lateral and medial views, and forms the anterior border of the adductor fossa. It also has a well developed dorsally oriented process, exposed in the dorsal view of the skull (Figs. 1, 2A). On the medial side of the mandible, the coronoid contacts the prearticular and the posterior end of the splenial. Laterally, the coronoid sits mainly above the dentary.

The angular and surangular form the lateral wall of the mandible in the region of the adductor fossa. The surangular has an unusually low profile in lateral view, and its dorsal edge is concave between the coronoid eminence and the anterior edge of the articular cotyle. The angular is not only longer than the surangular, extending posteriorly from the level of the last tooth position well beyond the articular cotyle, but also extends onto the medial surface of the mandible. It therefore wraps around the ventral surface in the posterior half of the mandible. The prearticular is a slender element, restricted mainly to the medial surface of the mandible, but it also wraps around the articular, extending slightly dorsally. Despite its slender outline, its dorsal edge is only slightly below that of the surangular. As a consequence, the adductor fossa faces mainly dorsally. Posteriorly, the prearticular covers much of the large articular, and contributes extensively to the retroarticular process (Fig. 2B). The cotyles are slightly slanted, so that most of the surface of articulation is tilted gently upwards. The articular has a well developed retroarticular process (Fig. 2A, F), with a gently concave dorsal surface. This concavity extends medially along the length of the retroarticular process. The process is supported laterally and ventrally by the angular.

Hyoid Ossifications

Parareptiles commonly preserve the hyoid apparatus (Lee, 1995; Ivachnenko et al., 1997). Frequently, in *Owenetta* specimens, a central hyoid ossification called the corpus hyoideum is preserved lying across the neck of the parasphenoid. In BP/1/4195 the corpus has moved only slightly to the left of the midline (Figs. 2B, 4B). As in other procolophonians, it has an outline similar to a bow tie. In almost perfect articulation to this corpus is a pair of slender elongate bones, with slightly expanded proximal and distal heads, here interpreted as the first pair of ossified branchial horns or cornua. They are directed posterolaterally and wrap around the partly disarticulated braincase, extending dorsally at the tips. This pattern is clearly seen in ventral view of the skull. However, in *Owenetta kitchingorum*, an additional and more slender long rod, here interpreted as the ossified left second branchial horn, is preserved lying across the basioccipital and left opisthotic. It would probably have attached to the small, narrow posterior process of the corpus.

Axial Skeleton

In both specimens, the vertebral column is preserved in dorsal view, making determination of the centra and intercentra difficult for most of the column. In the headless skeleton the presence of intercentra can be confirmed in the cervical series, the last presacral vertebra, and in the caudals. It is therefore reasonable to assume that they were present throughout the skeleton. In the other skeleton it has been possible to remove some of the matrix and expose the centra in the middorsal region, as well as the intercentra between vertebrae 13, 14, and 15.

Part of the atlas-axis complex is preserved in the skeleton with the skull. The component parts have disarticulated, emphasizing the immaturity of this skeleton. The proatlas, although preserved, is mostly covered by other elements of the skeleton. It is paired, and appears to be an anteroposteriorly

elongate oval element. The bone that is identified as the atlantal centrum has the axial intercentrum fused to it. Both halves of the atlantal neural arch are preserved, and the arch appears similar to that of Paleozoic amniotes. A small neural spine is present on each atlantal neural arch, extending posterodorsally from the body of the arch. The axial centrum is separated from the axial neural arch. The axial neural arch has a well developed hatchet-shaped neural spine, and a ventrolaterally oriented transverse process. The neural spine is thin in transverse section, and the neural arch beneath it is not swollen.

Cervical vertebrae are present in both skeletons, but preserved in slightly different views. In the headless skeleton, the top of the neural arches have been lost prior to discovery, and only their bases are preserved in direct dorsal view. However, these neural arches retain short transverse processes that extend directly laterally. Among the anteriormost vertebrae, these transverse processes appear to increase gradually in size, and extend farthest laterally on the fifth of the series that are exposed. Fortunately, it has been possible to prepare downwards into the vertebrae that have lost most of their neural arches, exposing the centra of these cervicals in dorsal view. This is the only part of the skeleton in which the centra are exposed, but as only the dorsal portions of the centra are visible, the presence of preserved intercentra is uncertain in this specimen. The cervical vertebrae of the other skeleton are preserved in partial lateral view, exposing most of their neural arches, as well as the posterodorsal edge of the centra. This skeleton shows that the cervical and anterior dorsal vertebrae have relatively tall, blade-like neural spines, and that the neural arches are not swollen. Nevertheless, the neural arches are excavated between the zygapophyses, as in procolophonids and pareiasaurs.

The transverse processes vary in size and lateral extent along the vertebral column, allowing us to determine the presacral vertebral count. In the specimen with the skull, vertebrae five and six have the largest transverse processes, extending farthest laterally of all the vertebrae in the whole column. It is therefore possible to determine on the other, headless skeleton, that the first centrum in the series represents either the atlas or the axis. Therefore, the presacral count for *Owenetta* is either 26 or 27. Posteriorly along the column, the transverse processes diminish in size gradually. However, only the first 17 vertebrae have the transverse processes exposed on the partial vertebral column. In the headless skeleton the last presacral is exposed, showing that there is no transverse process on this vertebra. It is not possible to identify a distinct transition from cervical to dorsal vertebrae because the vertebral anatomy changes only gradually along the column, and also because the cervical ribs are not markedly different from those in the dorsal series. Throughout most of the vertebral column the neural arches show clear evidence of swelling, caused by the robust postzygapophyses. A thick ridge extends anteriorly from the postzygapophyses, between the neural spine above and the lateral excavation of the arch below. The neural spines are relatively tall anteriorly and have a slender anterior blade-like extension over the body of the arch, but become small, nubbin-like protrusions farther back along the vertebral column, with a reduced anterior ridge extending over the top of the arch.

Three sacral vertebrae are present. The first sacral has widely spaced prezygapophyses and closely set postzygapophyses that attach to similarly set prezygapophyses on the second sacral. This position of the zygapophyses, closer to the midline than in dorsal vertebrae, characterizes not only the second and third sacrals, but also the caudals. This is possibly because of the different weight bearing needs of these vertebrae from those in the dorsal region. Although only a portion of the caudal series is preserved in the holotype, their configuration indicates that *Owenetta* had an elongate tail, unlike *Procolophon* and pareiasaurs. In all caudals the centra are indistinguishably fused to the neural arches. No haemal arches have been exposed.

Many of the ribs appear to have been displaced by postmortem scavenging by the millepedes that are preserved around and next to both skeletons. A small, double-headed rib that is attached to the left side of the skull in the squamosal notch is probably the atlantal rib. All other cervical ribs appear to be quite slender, in contrast to the short and distally expanded cervical ribs characteristic of most Paleozoic amniotes. For example the rib of the fifth vertebra appears in dorsal view to be approximately 50% of the length of the rib on vertebra 14, but this appearance is partly due to the stronger dorsoventral curvature of the cervical rib. The morphology of the ribs indicates that there were probably 6 cervical vertebrae in *Owenetta*. There is no evidence of ribs beyond vertebra 17, either because an elongated lumbar region was present or because the ribs were displaced by the millepedes. The rib attached to vertebra 17 on the skeleton with the head is complete and significantly shorter than the 15th rib, raising the possibility that there may indeed have been a distinct lumbar region in *Owenetta*. It is quite clear that *Owenetta* had a relatively long, sausage shaped body, as indicated by the shape of the ribs and the length of the vertebral column. The proximal end of each presacral rib has a dorsoventrally expanded tuberculum that matches the shape of the articulating facet of the respective transverse process. A separate capitulum appears to extend to the intercentrum, but is only slightly separated from the tuberculum. The shaft of the presacral ribs are rounded in cross-section for most of their lengths. Despite the small size of this species, there are three sacral ribs that extend laterally from the vertebral column to the expanded ilium. The first sacral rib is the largest of the series and widest distally, the third being the most slender. These ribs appear to have little contact with one another. The caudal ribs have the typical morphology seen in many Paleozoic amniotes, extending laterally from the body of the vertebra and then bending posteriorly. Only the anterior 5 caudal vertebrae bear ribs. At least one additional caudal vertebra bears a small lateral spine-like process, which is probably a modified transverse process.

Appendicular Skeleton

Both skeletons have been preserved in such a way that the shoulder girdles can be viewed only from above. It is therefore difficult to present a detailed description of this part of the skeleton. It is possible to determine that the interclavicle is anchor-shaped, as in all ankyramorph (DeBraga and Reisz, 1996) parareptiles, with a gently curving anterior end that accommodated the slender heads of the clavicles. However, no information is available on either the ventral surface of this bone, or the size and shape of its stem. The clavicles wrap around the head of the interclavicle, and each has a slender, long dorsally oriented shaft that probably extended along the anterior edge of the scapula. A thin, elongate element on the left side of the headless skeleton is tentatively identified as a cleithrum. The anterior part of the scapulocoracoid is exposed in dorsal view in both specimens. It is possible to determine that the anterior coracoid is not fused to the scapula, probably because of the immaturity of both individuals. This immaturity is also indicated by the gentle anterior indentation at the contact between the scapula and anterior coracoid, representing an area of incomplete ossification. The medial opening of the coracoid foramen is exposed on both sides of the headless skeleton. Although preserved in near vertical orientation, it is clear that the scapulae of both individuals are tall and slender, as in other ankyramorphs. There is no evidence of a medial opening of the supraglenoid foramen, indicating that such a foramen was absent in *Owenetta*.

The orientation of the four humeri preserved in these skeletons, and their level of immaturity allow us to determine only that this element is long and quite slender in *Owenetta*. There is clear evidence of a groove that separates the supinator process from the body of the humerus, but it is not possible to determine if there was a fully enclosed ectepicondylar foramen distally. There is, however, no doubt about the absence of an entepicondylar foramen. This condition is also found in *Barasaurus*, generally accepted as the closest known relative of *Owenetta*. Both the radius and ulna are very slender and about 20% shorter than the humerus. Although immature, it is clear that the ulna does not have a well developed olecranon. The rest of the forelimb is poorly ossified and difficult to interpret.

On the headless skeleton, the left side of the pelvic girdle is exposed almost completely in dorsal view with the vertebral column covering only the midline. The pubis is a short, compact element that appears to have a short anteromedial process. The ischium, on the other hand, appears to be quite elongate and broad, extending far posterior to the presumed region of the acetabulum. The ilium is located directly above the acetabulum and has an expanded blade that can accommodate all three sacral ribs. The iliac blade is oriented mainly dorsally above the acetabulum, as there appears to be only a modest anterior expansion and a slightly more substantial posterior expansion of the blade.

The femur is an exceedingly long, slender element, with only slightly expanded proximal and distal ends. It is about 25% longer than the humerus, and has a well developed sigmoid curvature of its shaft. Neither end of the bone is exposed sufficiently for detailed description. The tibia and fibula are both slender and delicately constructed, and only 72% of the length of the femur. The rest of the hindlimb is poorly ossified and difficult to interpret beyond the simple identification of a calcaneum and scattered tarsals.

PHYLOGENETIC RELATIONSHIPS

Recent studies on particular parareptile taxa (Meckert, 1995; DeBraga and Reisz, 1996; Lee et al., 1997) have changed dramatically both our understanding of parareptilian anatomy, and the pattern of relationships within the group. Other studies (Laurin and Reisz, 1995; Lee, 1995, 1997; DeBraga and Rieppel, 1997; Modesto, 1999) have presented large scale phylogenetic analyses with conflicting hypotheses of relationships, but have failed to generate a consensus of parareptile relationships. These controversies can be resolved through a gradual approach, with careful anatomical studies being incorporated into a growing database for evaluating parareptile relationships. Within this context, *Owenetta kitchingorum* is an important taxon because of its excellent, virtually complete preservation. However, one major drawback in the use of these two skeletons for phylogenetic analysis is their obvious immaturity. The recent study of *Barasaurus* (Meckert, 1995) has been very useful in this regard because this taxon is represented by both juvenile and mature individuals. It has therefore become possible to reevaluate the morphology of *Owenetta kitchingorum* and incorporate with confidence many of its postcranial features into a phylogenetic analysis.

The most recent phylogenetic analysis of parareptiles using only direct observations from specimens (DeBraga and Reisz, 1996) used Procolophonia as a terminal taxon. We will not repeat that phylogenetic analysis, but rather use it as a starting point, and consider the interrelationships among members of Procolophonia by investigating the phylogenetic placement of *Barasaurus* and *Owenetta* relative to procolophonids and pareiasaurids. In addition, we exclude turtles from this study because their membership within this clade has once again become controversial (DeBraga and Rieppel, 1997; Rieppel and Reisz, 1999). Although Lee has included the parareptile taxa *Nycteroleter*, *Nyctiphruretus*, and *Sclerosaurus* in his phylogenetic analyses, these forms will not be considered at this time because their anatomy remain inadequately known. Although the data exist, careful, adequately illustrated anatomical studies of these taxa still remain to be done. It is therefore preferable to exclude them from consideration, rather than using incorrect or poorly documented data. In addition, some of the specimens previously identified as *Nycteroleter*, and used in previous analyses, have now been recognized as the new genus *Bashkyroleter* (Ivachnenko et al., 1997).

Pareiasaurian phylogeny has been studied in detail by Lee, and this clade will be used as a single terminal taxon on the basis of his data (Lee, 1995, 1997). The phylogeny of Procolophonidae is a different matter, with detailed studies of members of this group still awaiting completion. The anatomy of the earliest, probably most basal procolophonid *Procolophon* will be used, with most of the data derived from direct studies of specimens that have been included in an unfinished Ph.D. thesis by Michael DeBraga. *Macroleter* is now known from several excellent specimens (Ivachnenko et al., 1997), and is in the process of being redescribed by the authors. The ingroup therefore consists of *Macroleter*, *Acleistorhinus*, Lanthanosuchidae, Pareiasauridae, *Procolophon*, and the owenettids *Barasaurus* and *Owenetta*.

A new phylogenetic analysis of parareptile relationships includes the characters employed by DeBraga and Reisz (1996), but three sets of changes were made:

(1) Characters states for mesosaurs were modified in accordance with new morphological data presented by Modesto (1999).

(2) The following additional twelve (12) new characters were added to the analysis in order to evaluate procolophonian relationships:

61-Supratemporal elongate and slender, less than 1/3rd of parietal width (0), or unusually broad, width > length, and forms skull table lateral to parietal (1).

62-Postorbital–parietal contact: present (0), or absent (1) because of large posterior process of postfrontal.

63-Temporal region: flat expanse of bone (0), or interrupted by deep temporal emargination forming acute angle between jugal and quadratojugal (1).

64-Humerus: entepicondylar foramen present (0), or absent (1).

65-Humerus: ectepicondylar foramen absent (0), or present (1).

66-Prefrontal: tongue-like medial process absent (0), or present (1).

67-Supratemporal doming absent (0), or present (1).

68-Occipital flange of supratemporal absent (0), or present, contiguous with similar structure on parietal (1).

69-Postparietal present (0), or absent (1).

70-Transverse flange of pterygoid has tooth row along posterior edge (0), or is edentulous (1).

71-Frontal length similar to parietal length (0), or longest element of paired median skull roof series (1).

72-Interpterygoid vacuity elongate, extending beyond posterior edge of palatine (0), or short (1).

(3) Two additional skeletal features were added to help resolve the position of mesosaurs:

73-Posterior margin of skull roof roughly straight (0); with a single, median embayment (1), or deeply embayed bilaterally (2).

74-Atlantal neural arch possesses (0) or lacks (1) an epipophysis.

The phylogenetic analysis of parareptile relationships using 11 taxa and 74 characters for investigating the minimum number of evolutionary steps and maximum parsimony (PAUP)

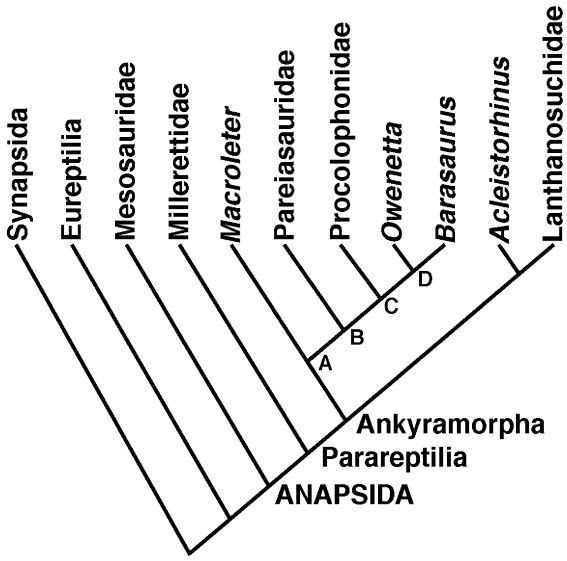

FIGURE 7. Cladogram showing the relationships of *Owenetta* and other parareptiles. Autapomorphies defining Anapsida: 10*, 32*,41*, 57, 58, 65, 68, −73 (1), 74*; Parareptilia: 1*, 3, 16*, 17*, 18, −26*, 35*, 40, 45; Ankyramorpha: 2, 4, 8*, 11*, 14, 23, 25, 27*, 29, 33, 43, 47, 48, 50, 52, 53, 54; Node A: 9*, 13, 15*, 24*, 40*, 55, 72; Node B: −16*, −17*, 28, 30, 31, −39, 42(2), 51, 59, 67; Node C: −25, −65*, 66, 69, 70, 71; and Node D: −11*, 19*, 22*, 61, 62, 63, 64, −74*. Characters indicated by an asterisk have an ambiguous history and could diagnose a more inclusive clade. Reversal are shown by a negative sign. Brackets surround derived state for multistate characters. Characters used in the analysis and their numbering follow that of beBraga and Reisz (1996), with additions listed in the text.

yielded a single tree with a length of 142 steps, with a consistency index of 0.683, and a homoplasy index of 0.415. The data associated with this analysis and its results are presented in Appendix 1.

The family Owenettidae was erected for *Owenetta*, its sole member at that time (Broom, 1939). This taxonomic unit has been largely ignored, but comparisons between *Owenetta*, *Barasaurus*, procolophonids and pareiasaurs, and the phylogenetic analysis indicate that the first two genera are closely related to each other, forming a clade that is the sister taxon of Procolophonidae. *Barasaurus* and *Owenetta* (Fig. 7, Node D, chars. 61–64) show the following four unique morphological features: (1) the supratemporal is an unusually broad element, its width (maximum mediolateral dimension) being greater than its length (maximum anteroposterior dimension); (2) the emargination of the temporal region is narrow and deep, forming in lateral view an acute angle between the jugal and quadratojugal; (3) the postfrontal has a large posterior process that contacts the supratemporal, eliminating contact between the parietal bone and the temporal series; (4) both *Barasaurus* and *Qwenetta* lack an entepicondylar foramen on the distal head of the humerus. These osteological features are autapomorphies that diagnose Owenettidae, and are found in the primitive condition in members of the ingroups and other ankyramorph parareptiles.

Synapomorphies of Owenettidae and Procolophonidae (Fig. 7, Node C, chars. 25, 66–71) include: (1) presence of elongate frontals, the longest paired elements of the skull roof midline; (2) well developed occipital flange of the supratemporal bone which is a lateral continuation of the occipital flange of the parietal; (3) presence of tongue-like medial process of the prefrontal that extend nearly to the midline; (4) absence of teeth on the transverse flange of pterygoid; (5) loss of postparietal (reversed in *Owenetta kitchingorum*), (6) reduced sculpturing of dermal skull elements.

The Procolophonia is diagnosed by numerous autapomorphies discussed elsewhere (DeBraga and Reisz, 1996; DeBraga and Rieppel, 1997), including: (1) Pineal foramen located close to anterior border of parietal; (2) pterygoid fails to extend anteriorly to level of internal nares; (3) anterolaterally directed transverse flange of pterygoid; (4) supraoccipital narrowed to pillar-like structure; (5) retroarticular process broad with concave dorsal surface.

DISCUSSION

The discovery of the articulated skeletons of *Owenetta* has attracted the attention of the senior author for several reasons: firstly, they provide important new osteological information about the poorly known genus *Owenetta*, both in terms of its cranial and postcranial anatomy. Secondly, these new specimens are significantly younger than the genotype, extending significantly the fossil record of this genus, from the late Permian into the early Triassic. This is particularly important because the extended range of this taxon straddles the Permo–Triassic boundary, which has been proposed as the largest known extinction event. In this respect, *Owenetta* is one of the terrestrial vertebrates to survive this extinction event. Thirdly, the anatomy of this parareptile showed numerous skeletal features that were also present in basal turtles. The initial report on the specimens described here (Reisz and Laurin, 1991) ignited a lively debate on turtle origins, and it is mainly for this reason that this topic is discussed below.

Turtle Origins

The origin and relationships of turtles attracted considerable attention during the first half of this century. Gregory (1946) reviewed previous ideas of turtle relationships and compared the osteology and myology of a broad range of extinct and living taxa, and included in his study placodonts, pareiasaurs, diadectomorphs, and captorhinids. He concluded, like some earlier authors, that turtles were derived from Paleozoic ''cotylosaurs.'' He argued, however, that among ''cotylosaurs,'' pareiasaurs approached the Triassic turtles more closely than did the older diadectids. He furthermore concluded that placodonts, especially *Henodus*, had evolved an amazingly turtle-like appearance, but were not related to turtles. Most significantly, he recognized that convergent evolution, especially related to dermal armor, represents a serious problem in recognizing chelonian relationships.

In a large study on diadectids, Olson (1947) reconsidered the origin of turtles as part of a reevaluation of Paleozoic and Mesozoic amniotes. Olson argued for a basic division of amniotes into Parareptilia and Eureptilia, and suggested a derivation of turtles from basal parareptiles, but diadectids rather than pareiasaurs. In Olson's opinion ''appearances of relationships based on the postcranial structures were likely to be deceptive'' (Olson, 1947:47–48), and turtles, ''while not coming from any known diadectid, arose from a stock that was leading to the family at a time prior to the appearance of many of the pareiasaurian specializations'' (Olson, 1947:51). Much later, R. L. Carroll (1969) argued for the first time for the origin of turtles from among basal captorhinids. In particular, he noted the loss of the tabular and ectopterygoid as features shared by captorhinids and turtles.

The advent of cladistics caused a major shift in the methods used in investigating the origin of turtles. The first publication of a large scale computer assisted phylogenetic analysis of amniote relationships (Gauthier et al., 1988) yielded the same conclusion (turtle–captorhinid clade) as had been reached by Carroll (1969). Two important changes proposed by Gauthier et al.

(1988) were the separation of diadectomorphs from the crown group of amniotes, and the recognition of parareptiles (including mesosaurs, millerosaurs, pareiasaurs and procolophonids) as a distinct clade. This clade was poorly supported, however, largely because detailed anatomical information about its members was lacking at the time. The hypothesis of close captorhinid–turtle relationships was also accepted by E. S. Gaffney in his monographic description of *Proganochelys* (Gaffney, 1990).

Largely based on the data provided by the two specimens of *Owenetta*, Reisz and Laurin (1991) proposed an alternative hypothesis of relationships, i.e., that turtles were nested within parareptiles and were probably closely related to Procolophonoidea. Although hampered by lack of detailed anatomical information on other parareptiles, this paper prompted a renewed interest in studies of this important clade of early amniotes. For example, Lee's (1993) study of pareiasaurs led him to conclude that it is this group, rather than procolophonids, that contains the closest known relatives of turtles. In contrast to Gregory's (1946) work, Lee emphasized the dermal armor of pareiasaurs as homologous to that of turtles, and proposed an evolutionary scenario around this hypothesis to explain the unique turtle body plan.

All the new characters cited by Lee (1993) were incorporated into a broad phylogenetic analysis of amniote relationships by Laurin and Reisz (1995) which also showed, on the basis of the data available at that time, that procolophonids were the closest relatives of turtles. *Owenetta* was not included by Laurin and Reisz (1995) because the main purpose of that study was directed towards testing the phylogenetic relationships of early amniotes. Subsequently, Lee (1995) presented new data on pareiasaur anatomy that strengthened his case for their sister-taxon status to turtles, but his phylogenetic analysis could not be duplicated (Rieppel, 1996). After several additional studies and publications (Laurin and Reisz, 1995; Lee, 1995, 1996, 1997), a general consensus of parareptile phylogeny has failed to emerge. The placement of turtles also remains in dispute, with both parareptiles and diapsids (DeBraga and Rieppel, 1997; Lee, 1997; Rieppel and Reisz, 1999) as proposed relatives of turtles. The most recent phylogenetic analysis (Modesto, 1999) of parareptilian phylogeny places mesosaurs as the sister taxon of Parareptilia (Fig. 7).

Considerations of relationships between turtles and other amniotes is beyond the scope of this paper, but we would like to emphasize that new detailed studies of parareptiles such as *Owenetta*, and subsequent phylogenetic analyses are critical to future evaluations of turtle relationships. In this context studies of Permian and Early Triassic parareptiles are critical in any future endeavors to test hypotheses of chelonian relationships (Rieppel and Reisz, 1999).

Owenetta and the Permo–Triassic Extinction Event

The stratigraphic of distribution of *Owenetta* is unusual when compared to other parareptiles and amniotes. Millerosaurs, pareiasaurs, and all the poorly known Russian basal parareptiles, such as *Lanthanosuchus*, *Lanthaniscus*, *Nycteroleter*, *Nyctiphruretus*, and *Macroleter* are restricted to the Paleozoic. Even *Barasaurus* is only known from Upper Permian sediments. Procolophonids, however, are largely a Triassic group of parareptiles, with only fragmentary remains of possible basal taxa being preserved in Permian strata. Among parareptiles, the genus *Owenetta* spans the Late Permian and Early Triassic, extending across the presumed large extinction event that is associated with the Permo-Triassic boundary.

The Known Distribution and Stratigraphic Range of *Owenetta*

Skulls of *Owenetta rubidgei* have been collected (Kitching, 1977) from the following Permian localities: Graaf-Reinet Commonage (*Cistecephalus* Assemblage Zone); Beeldhouersfontein, Murraysburg; Doornplaas (Rust), Graaf-Reinet; Hoeksplaas, Murraysburg; Katbosch, Graaf-Reinet; Melsetter, Middleburg or Richmond; New Bethesda Commonage, Graaf-Reinet; and Oudeberg, Graaf-Reinet (*Dicynodon* Asemblage Zone).

Three skeletons of *Owenetta kitchingorum* have been collected from the Triassic locality of Tweefontein, Bethulie (*Lystrosaurus* Assemblage Zone).

An additional partial skeleton, collected from the Thaba Nchu Commonage, near Bloemfontein and described as a new short limbed lizard *Colubrifer campi* (Carroll, 1982) is probably *Owenetta*. Dr. Susan Evans seems to have come to the same conclusion independently. However, the precise age of this locality is difficult to determine, since at Thaba Nchu the section is very thin, but appears to extend from the *Dicynodon* into the *Lystrosaurus* Assemblage Zones.

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APPENDIX 1

Data matrix used in this study. Polymorphism is indicated by the states present in the second line below the relevant taxa. List of features 1–60 and their character states as in deBraga and Reisz 1996, 61–72 as listed in text, 73–74, as in Modesto 1999.

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                                  111111111122222222223333333333444444444455555555
Taxon                             123456789012345678901234567890123456789012345678
Synapsida                         000000000000000110000000000000100000000000000000000000000
                                                                          1       1
Eureptilia                        000000000001100000000000010000000000001001000100100000010 0
                                            1   1                         1               2
Mesosauridae                      000001000?000000000?100001?0000??20?0?0010000?001?11000111
Millerettidae                     ?010100001000001010001000000000100100011010011001000000111
                                                      1
Macroleter                        111000001?101111110100111010100110100010111011111102111111
Acleistorhinus                    111101112?000102111100102010100111011 1?111111011?10???????
Lanthanosuchidae                  11?011110?100102110000001000101011011111111?1101????21101??
                                     1                    1
Owenetta                          11110?0111001?100110011100111111110?000001210011111112111111
                                                                                  1
Barasaurus                        11110?011??01?1001?00?110011111110?000001210111?1??2110111
Procolophonidae                   11110?011110111001000011001111111 0?000001210111111112111211
Pareiasauridae                    10100?020?1011000?000010101111110 0?000001210111110121 11?11
                                     1                            1
                                                                 5666666666677777
Taxon                                                            9012345678901234
                                                                 0000000000000020
Synapsida                                                        0100000000000020
Eureptilia                                                       0100001011110111
Mesosauridae                                                     ?100001001000010
Millerettidae                                                    0100001001000111
Macroleter                                                       ??010??01000001?
Acleistorhinus                                                   ??000??00200001?
Lanthanosuchidae                                                 ?11111?111011110
Owenetta                                                                   1
Barasaurus                                                       ?11111?11111111?
Procolophonidae                                                  1100000111111111
Pareiasauridae                                                   1100001010000111
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