Palaeont. afr., **34**, 33-42 (1997)

A REASSESSMENT OF *EUNOTOSAURUS AFRICANUS* SEELEY (AMNIOTA: PARAREPTILIA).

by

Chris E. Gow

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg,
Private Bag 3, Wits 2050, South Africa

ABSTRACT

This paper provides an almost complete description of the Permian fossil reptile *Eunotosaurus* for the first time. Taphonomy indicates that these were terrestrial animals; dentition suggests that they preyed on small invertebrates; while the broad, imbricating ribs point to a slow moving animal with a protective, turtle-like carapace. Temporal emargination and the fan-like iliac blade serve to align these animals with Parareptilia, sensu Laurin and Reisz (1995). *Eunotosaurus* and millerettids are sister taxa on the basis of stapes and rib morphology, and together they constitute the sister taxon to Ankyramopha (Debraga and Reisz 1996), having eight characters in which they are less derived than the latter.

KEYWORDS: *Eunotosaurus, parareptiles*

INTRODUCTION

The late Permian reptile *Eunotosaurus africanus* Seeley 1892, was revised by Cox (1969), and the first and only good skull was described by Keyser and Gow (1981). The available material has generally been too poor to yield detailed, definitive information about the osteology, biology, and relationships of the animal. The limbs in particular have remained poorly known until recently (Gow and De Klerk 1997).

Great advances have been made in the study of amniote phylogeny in recent years, yet much remains to be done.

According to recent work of Laurin and Reisz (1995), and Debraga and Reisz (1996), Amniota is comprised of three major monophyletic groups, plus the poorly understood Mesosauridae.

These groups are, i) Synapsida including mammals, ii) Eureptilia, including living reptiles except testudines and birds, and iii) Parareptilia including testudines. These groups diverged approximately 300 million years ago in the Upper Carboniferous: mesosaurs and parareptiles have no fossil history prior to the Middle Permian.

Early amniotes share numerous plesiomorphies, and it has not been easy to find synapomorphies defining the major groups, for example, Laurin and Reisz (1995) listed 14 apomorphies for Parareptilia, while Debraga and Reisz (1996) halved this number.

Eunotosaurus has been so poorly known that it has had to be omitted from most recent phylogenetic studies; Lee (1993) however, has expressed the opinion that it is a synapsid. The present study clearly demonstrates that it is a good parareptile, sharing several derived characters with the slightly younger millerettids.

MATERIAL AND METHODS

Renewed interest in *Eunotosaurus* arose with the discovery of a large specimen which has a skull and pectoral girdle and anterior part of the trunk, all in articulation – M777 in the collections of the Council for Geosciences (formerly the Geological Survey), Keyser & Gow 1981). This specimen has well preserved bone in a very hard, fine grained, green mudstone matrix: it was mechanically prepared at the Council for Geosciences, and unfortunately separation between hard matrix and softer bone is poor, with the result that much surface detail, such as ornamentation of the dermal bones of the skull, was lost during preparation.

Subsequently J. Welman recovered a small articulated specimen form the Free State (NMQR 3299 in the collections of the National Museum, Bloemfontein) which is extremely poorly preserved, the mudstone matrix being deeply weathered, and the weathered and eroded bone in very poor condition; it includes a partial skull lacking braincase and palate, and with maxillary teeth represented by impressions only; much of the trunk including parts of both limb girdles, and parts of the forelimbs. The main value of this specimen is that it confirms some of the sutural details of the skull roof as determined from M777.

In 1995 the Albany Museum, Grahamstown, acquired an excellent specimen (AM5999) from the Eastern Cape (Gow & de Klerk 1997). This small specimen exists mostly as high fidelity impression in a block of fine grained sandstone; it is headless, but has most of the limbs, including a partial manus and compete pes, and a tail which is almost complete.

Several other specimens are represented in various museum collections, but generally consist of only the carapace-like trunk portion comprised of articulated vertebrae and ribs: in some cases it appears that parts of these specimens may have been overlooked in the field (this is mentioned as a caution for the future rather than a criticism of past collecting). The matrix of some specimens is so heavily indurated as to defy preparation.

Specimens which add useful information are: GM71 in the collections of the Council for Geosciences, being a block of articulated mid-dorsal vertebrae and ribs, which also has six dissociated caudal vertebrae; and a small unnumbered specimen from the same collection which includes parts of a macerated skull. The BPI material (BP/1/3516) which had been acid prepared by Cox (1969) has also been examined.

Eunotosaurus occurs in the upper half of the *Tapinocephalus* assemblage zone and throughout the *Pristerognathus* assemblage zone of the Beaufort (Smith & Keyser 1995). According to Roger Smith (pers. com.) *Eunotosaurus* specimens are always preserved in crevasse splay situations, either in mudrocks, or less commonly fine-grained sandstone. Being broad bodied they are invariably preserved lying on their ventral surface.

Specimens have been variously prepared as appropriate: Cox (1969) had some success with acetic acid, extensive use has been made of mechanical preparation, and the Albany specimen was studied by means of latex peels and X-rays. However, some material simply cannot be adequately prepared with currently available techniques.

DESCRIPTION

The Skull. Figures 1, 2, 3 & 4.

This description refers to the specimen M777, except where otherwise stated. It is important to appreciate that most of the dorsal surface ornamentation of the skull of M777 was removed with the matrix, and that much of the surface of the occiput adheres to the matrix attached to the main block. Also important to note is that at some stage the skull roof of M777 was broken off and reattached with a thick layer of epoxy cement. The skull of M777 is slightly dorso-ventrally crushed. Some ornamentation is preserved on the National Museum skull (NAMQR3299); Figure 3 attempts to illustrate this.

The skull is triangular in dorsal view, quite deep, and blunt-snouted, with a backwardly sloping occiput. It is superficially similar to that of modern tortoises. The pattern of tuberosities is closely comparable to that seen in millerettids, a character regarded by Laurin and Reisz (1995) as an autapomorphy of millerettids.

Nothing useful can be said about the lower jaws as they are damaged and show hardly any sutural detail.

Premaxilla.

The premaxillae meet the nasal above, and have oblique sutural contacts with the maxillae laterally below the nares. It is difficult to estimate the original size of the nares as their margins are damaged. Each premaxilla bore three sharply pointed teeth, circular in cross section.

Maxilla.

The facial region is damaged, so the outlines of the maxillae as illustrated are not true surface suture lines. Posteriorly both maxillae are slightly incomplete, and, because of this and the effects of distortion, it is not possible to determine their true relationship to the jugals: I would not like to have to decide whether or not the maxillae enter the orbits. In this specimen there are approximately 20 tooth positions in the maxilla: maxillary teeth are smaller than those of the premaxilla; they are also rounded in section and taper to a point, they decrease in size posteriad; gaps between teeth indicate ongoing replacement.

Nasal, lacrimal and prefrontal.

These elements are so badly damaged that nothing useful can be said about the superficial relationships: the lacrimal region (but not the prefrontal) was prepared in the left orbit, where the lacrimal canal can be seen.

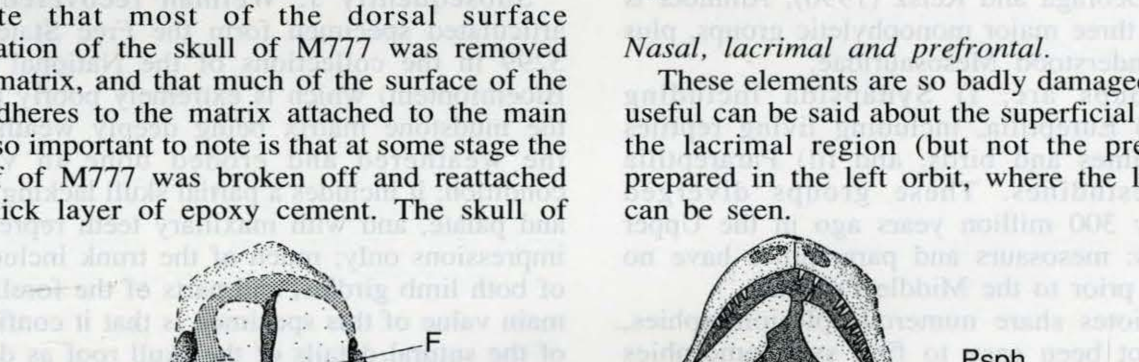

Figure 1. *Eunotosaurus* M777
Dorsal and ventral views of the skull. Dense texturing is matrix, more open dots indicate epoxy cement.

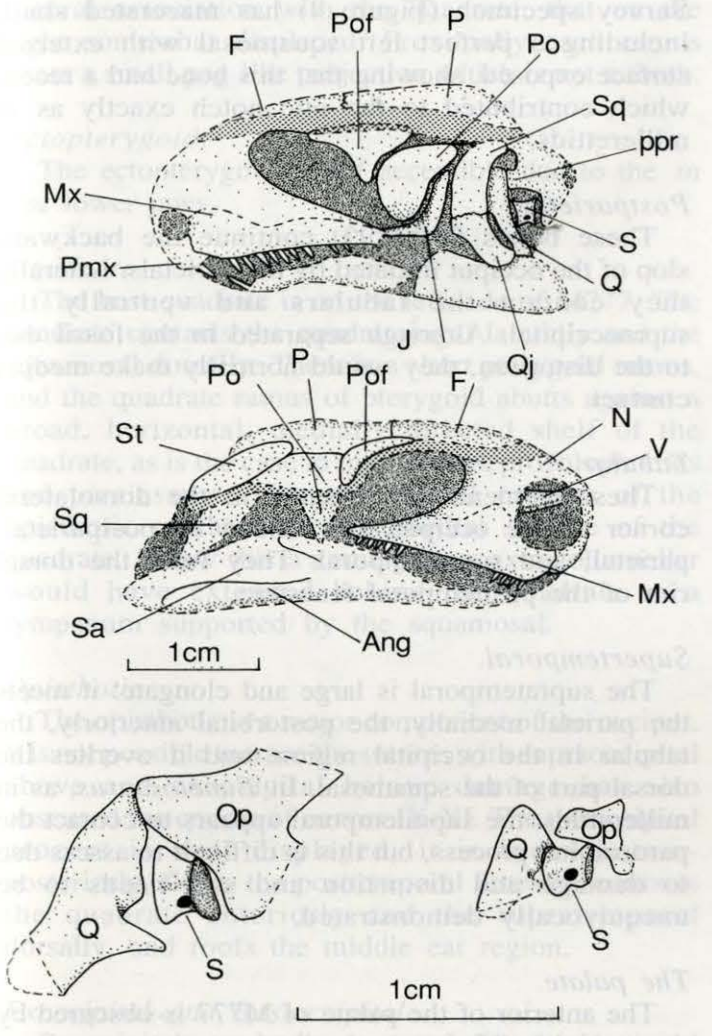

Figure 2. Above. Lateral views of *Eunotosaurus* skull M777. Dense texturising is matrix, more open dots indicate epoxy cement. Below. The stapes of *Eunotosaurus* M777 left, compared with *Milleretta* BP/1/3821 on the right.

Frontal.

The frontals are large, bordered anteriorly by the nasals, laterally by pre- and postfrontals, and posteriorly by the parietals. Their dorsal surfaces are sculpted. It is not possible to determine if they were excluded from the dorsal rim of the orbit by pre- and postfrontals.

Parietal.

The parietals form the broadest part of the skull table: they surround a fairly large pineal foramen. The parietal makes sutural contact with the frontal anteriorly, postfrontal, postorbital and supratemporal laterally, and curves onto the occiput to meet the postparietal and tabular. The parietals overlap the dorsal part of the supraoccipital: this is seen in QR3299 where the parietals are damaged in this region.

Postfrontal.

Large postfrontals straddle the fronto-parietal suture dorsolaterally and make sutural contact with the postorbitals laterally (bones of the cheek region are displaced in M777 due to distortion and virtually absent in QR3299).

Postorbital.

This is a robust element with a distinct lateral tuberosity. It is in sutural contact with the postfrontal anteriorly, the parietal and supratemporal dorsally and the jugal posteriorly.

Jugal.

Relationships of the jugal cannot be satisfactorily determined as only the left jugal of M777 is preserved,

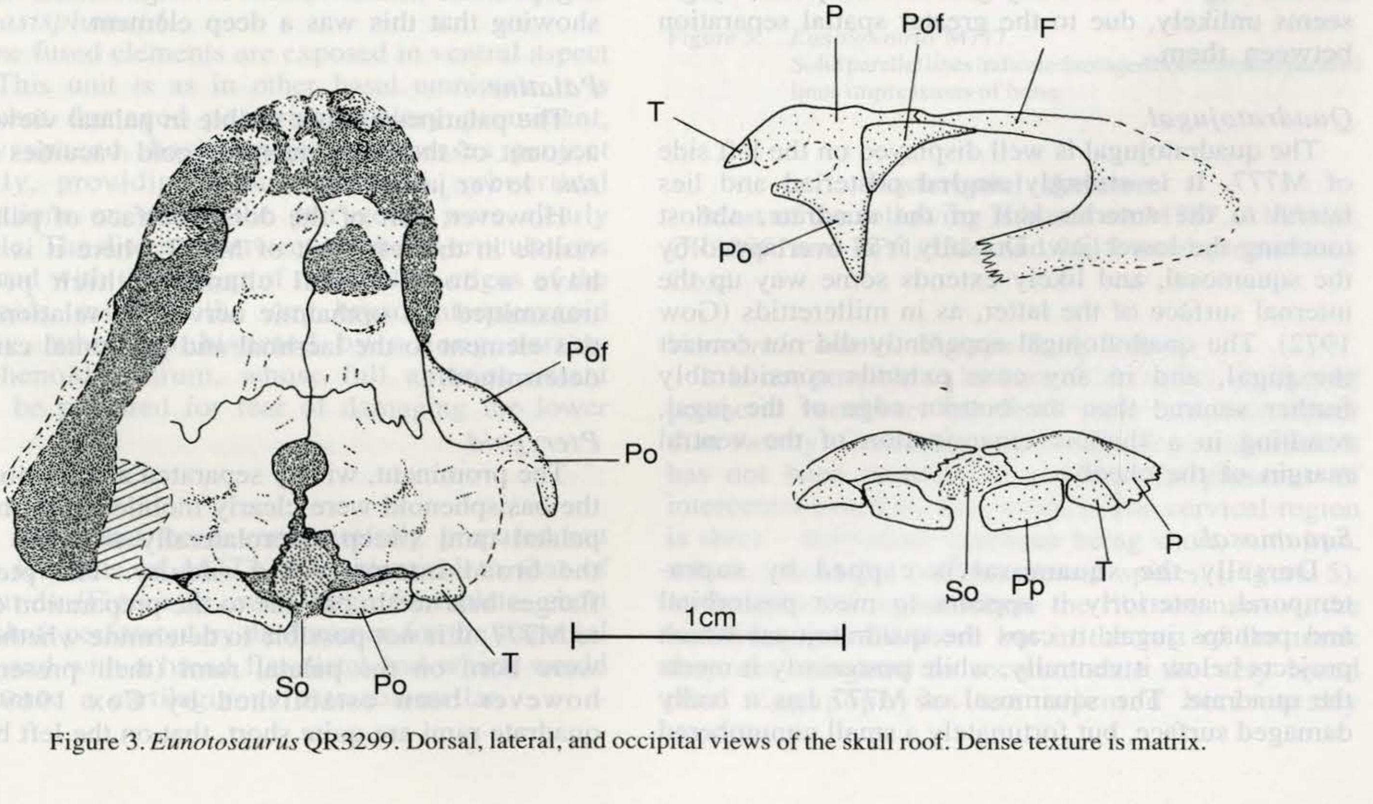

Figure 3. *Eunotosaurus* QR3299. Dorsal, lateral, and occipital views of the skull roof. Dense texture is matrix.

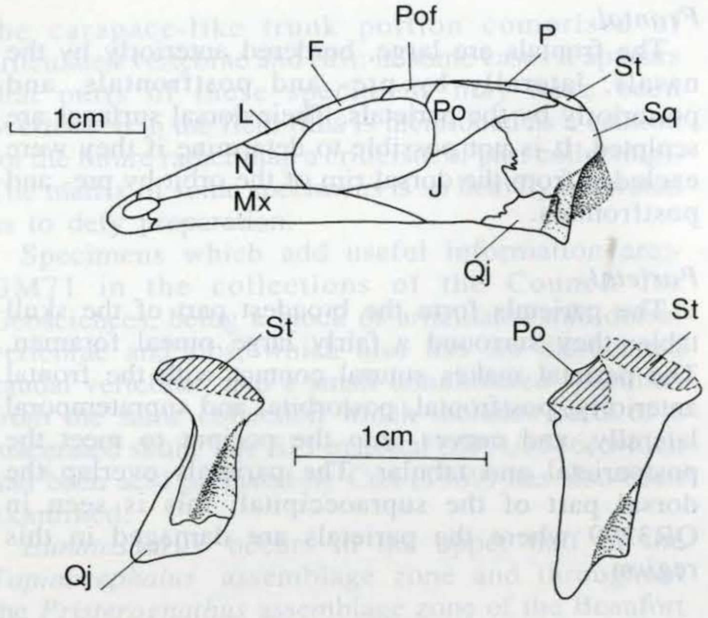

Figure 4. Lateral view of the skull of *Milleretta* RC70 (from Gow 1972) to show the relationships of the squamosal, and below on the left squamosal and quadratojugal of *Milleropsis* BP/1/720 (Gow 1972), and right, the squamosal of *Eunotosaurus*.

and it is displaced and probably damaged; also the orbit is distorted and the maxilla damaged. It is impossible therefore to determine whether the jugal entered the orbital rim ventrally. The full extent of the sutural contact with the postorbital can also not be determined, but it was certainly extensive. The posterior edge is sharply angled, conferring a boomerang shape to the bone. It is not possible to determine whether the posterior edge of the jugal made sutural contact with the squamosal; whether or not this was so, contact of jugal with the quadratojugal seems unlikely, due to the greater spatial separation between them.

Quadratojugal.

The quadratojugal is well displayed on the left side of M777. It is strongly angled posteriad and lies lateral to the anterior half of the quadrate, almost touching the lower jaw. Dorsally it is overlapped by the squamosal, and likely extends some way up the internal surface of the latter, as in millerettids (Gow 1972). The quadratojugal apparently did not contact the jugal, and in any case extends considerably further ventrad than the bottom edge of the jugal, resulting in a shallow emargination of the ventral margin of the cheek.

Squamosal.

Dorsally the squamosal is capped by supratemporal, anteriorly it appears to meet postorbital and perhaps jugal; it caps the quadratojugal which projects below it ventrally, while posteriorly it meets the quadrate. The squamosal of M777 has a badly damaged surface, but fortunately a small unnumbered Survey specimen (Figure 4) has macerated skull, including a perfect left squamosal with external surface exposed, showing that this bone had a recess which contributed to the otic notch exactly as in millerettids.

Postparietal.

These bones (QR3299) continue the backward slop of the occiput initiated by the parietals. Laterally they contact the tabulars and ventrally the supraoccipital. Although separated in the fossil due to the distortion, they would normally make median contact.

Tabular.

These elements are situated in the dorsolateral corner of the occiput, surrounded by postparietal, parietal, and supratemporal. They form the dorsal rim of the posttemporal fenestrae.

Supertemporal.

The supratemporal is large and elongate: it meets the parietal medially, the postorbital anteriorly, the tabular in the occipital region, and it overlies the dorsal part of the squamosal. In *Eunotosaurus*, as in millerettids, the supratemporal appears to contact the paroccipital process, but this is difficult to assess due to damage and distortion and still needs to be unequivocally demonstrated.

The palate.

The anterior of the palate of M777 is obscured by the articulated lower jaws.

Vomer.

Part of a dorsally displaced vomer is visible through a gap in the cheek behind the right narial opening, showing that this was a deep element.

Palatine.

The palatines are not visible in palatal view on the account of the large interpterygoid vacuities and *in situ* lower jaws.

However, part of the dorsal surface of palatine is visible in the left orbit of M777 where it is seen to have a dorso-lateral channel which probably transmitted the opthalmic nerve: the relationship of this element to the lacrimal and prefrontal cannot be determined.

Pterygoid.

The prominent, widely separated articulations with the basisphenoid were clearly mobile: from these the palatal rami sweep anterolaterally to curve around the broad interpterygoid vacuity. The pterygoid flanges bear teeth, but due to the preparation damage to M777, it is not possible to determine whether teeth were born on the palatal rami (their presence has however been established by Cox 1969). The quadrate rami are quite short, that on the left being in natural association with the quadrate, that on the right somewhat displaced. Proximally each ramus bears a small peg-like projection which is not a tooth.

Ectopterygoid.

The ectopterygoid is not accessible due to the *in situ* lower jaws.

Quadrate.

The best quadrate is on the left side of M777. The quadrate contacts the quadratojugal laterally and the squamosal dorsally. There is a short pterygoid ramus, and the quadrate ramus of pterygoid abutts against a broad, horizontal, medially directed shelf of the quadrate, as is the case in millerettids, procolophonids and pareiasaurs. The paroccipital process of the opisthotic reaches the dorsomedial surface of the quadrate. Below this a cartilaginous extracollumellar would have extended behind the quadrate to a tympanum supported by the squamosal.

Opisthotic.

The opisthotic is a major component of the occiput. It is not possible to trace the sutures with supraoccipital above and exoccipital below: damage has also obscured the course of nerves IX-XI. The paroccipital process is well displayed; it is broad anteroposteriorly, floors the posttemporal fenestra, contacts the quadrate anteriorly and the supratemporal dorsally, and roofs the middle ear region.

Exoccipital and Basioccipital.

Exoccipitals are badly damaged. The basioccipital floors the braincase and contributes the single occipital condyle: much of it is covered ventrally by parabasisphenoid.

Parabasisphenoid.

These fused elements are exposed in ventral aspect only. This unit is as in other basal amniotes; it is somewhat damaged posteriorly. Very prominent, widely spaced, basipterygoid processes project laterally, providing hemicylindrical, subvertical articulations on which the pterygoids were clearly movable. The distance between the basal articulations combined with the sweep of the median edges of the pterygoids, result in the very broad interpterygoid vacuity, which is bisected by a long narrow parasphenoid rostrum, whose full anterior extent cannot be prepared for fear of damaging the lower jaws.

Stapes.

The stapes has been very carefully prepared out on the left side of M777; it is identical to that of millerettids (Figure 2), with large foot plate, short broad shaft perforated by the foramen for the stapedial artery, and with a broad flat distal end which would have borne a cartilaginous extracolumellar.

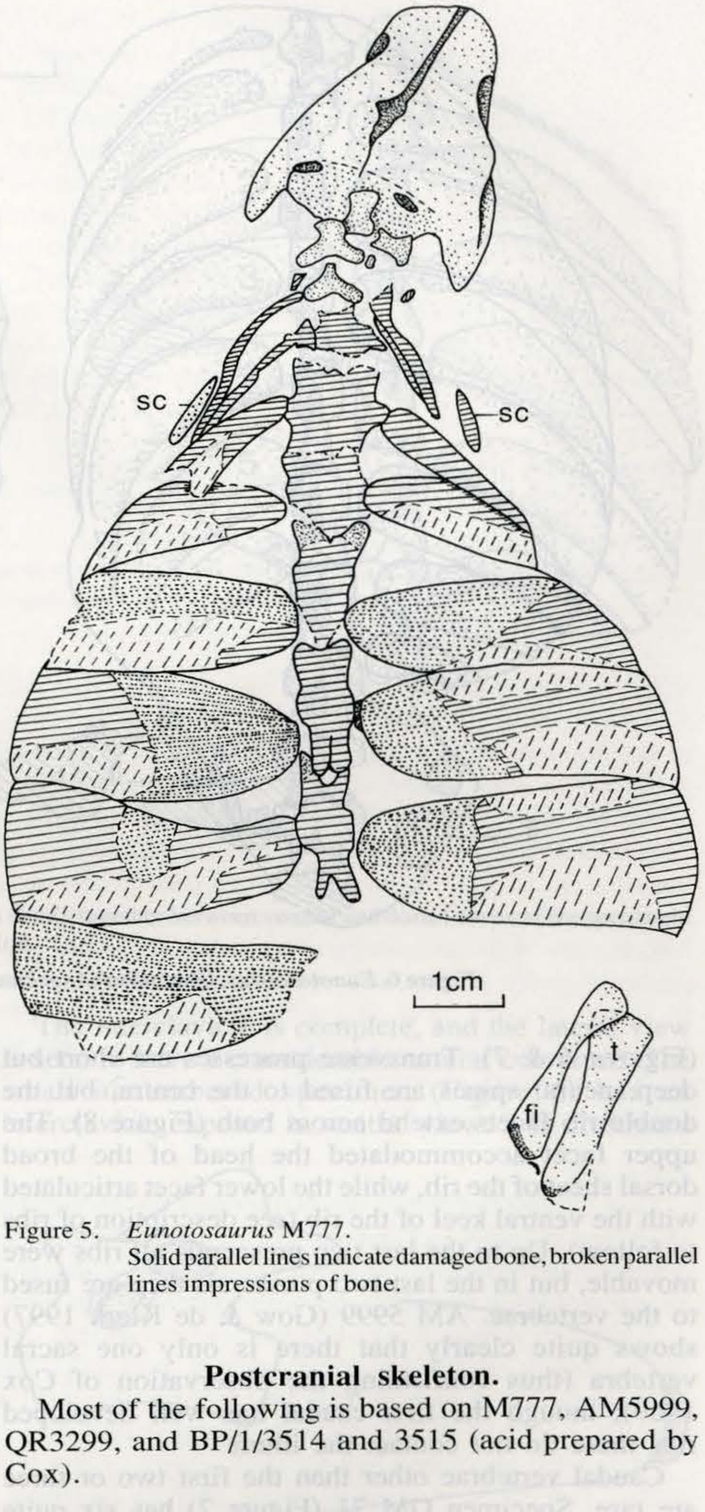

Figure 5. *Eunotosaurus* M777.
Solid parallel lines indicate damaged bone, broken parallel lines impressions of bone.

Postcranial skeleton.

Most of the following is based on M777, AM5999, QR3299, and BP/1/3514 and 3515 (acid prepared by Cox).

Vertebral column. Figures 5, 6, 7 & 8.

It is not possible to be sure of the exact number of presacral vertebrae, but there were certainly fewer than twenty. Centra are apparently all notochordal. It has not been possible to confirm the presence of intercentra noted by Cox (1969). The cervical region is short – individual vertebrae being short, with low, robust, markedly bulbous neural spines (Figure 5). In the pectoral region where the ribs are narrow, the vertebrae are still short, but in the rest of the trunk they are elongated to accommodate the very broad ribs. Zygapophyses are oriented horizontally

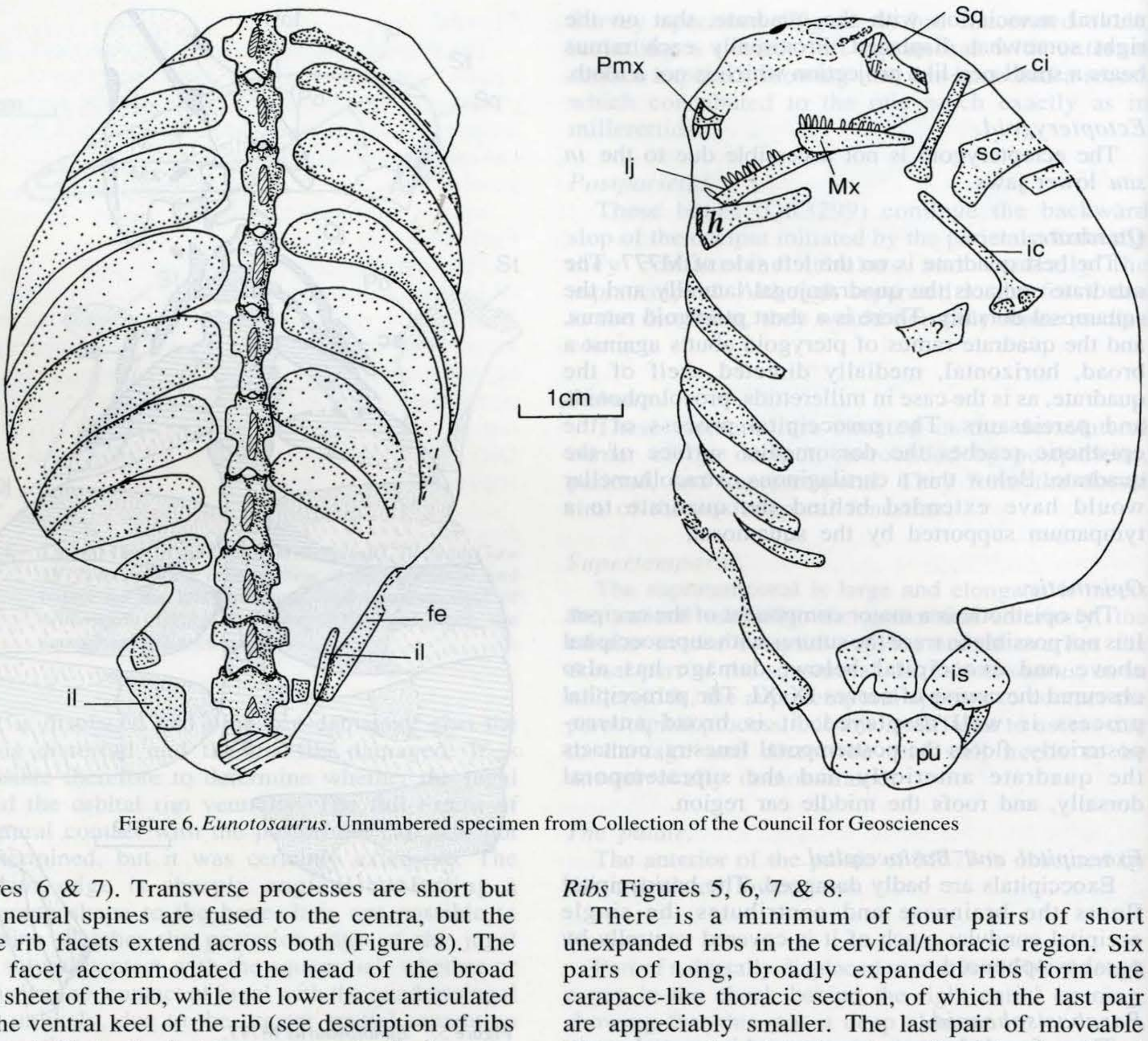

Figure 6. *Eunotosaurus*. Unnumbered specimen from Collection of the Council for Geosciences

(Figures 6 & 7). Transverse processes are short but deep: neural spines are fused to the centra, but the double rib facets extend across both (Figure 8). The upper facet accommodated the head of the broad dorsal sheet of the rib, while the lower facet articulated with the ventral keel of the rib (see description of ribs to follow). Up to the last two presacrals all ribs were movable, but in the last two presacrals they are fused to the vertebrae. AM 5999 (Gow & de Klerk 1997) shows quite clearly that there is only one sacral vertebra (thus confirming the observation of Cox 1969); though the first caudal has well developed ribs these do not contact the ilium.

Caudal vertebrae other than the first two or three are rare. Specimen GM 71 (Figure 7) has six quite large, scattered posterior caudals (no transverse processes), which clearly indicate the presence of a long tail. As revealed by X-ray, the block containing AM 5999 also contains a long fully articulated tail, this lies *below* the rest of the skeleton, and separated from it, but almost certainly belongs to the skeleton. There are 3 proximal caudals in articulation with the sacrum, and the disarticulated portion of the tail comprises at least 27 vertebrae (with significant neural spines and no haemal arches), thus a minimum count of 30 caudals supported a long slender tail.

Ribs Figures 5, 6, 7 & 8.

There is a minimum of four pairs of short unexpanded ribs in the cervical/thoracic region. Six pairs of long, broadly expanded ribs form the carapace-like thoracic section, of which the last pair are appreciably smaller. The last pair of moveable ribs are much reduced and confined to the dorsal region of the body. The two lumbar vertebrae have fused ribs which project laterally.

All *Eunotosaurus* specimens seen by the author have straight vertebral columns in the trunk region, and some degree of imbrication of the ribs. The ribs have a longitudinal fibrous surface texture, first noted by Cox (1969). Cox shows the dorsal ribs tapering ventrad from a postero-lateral projection: this in an artifact resulting from abrasion during weathering and the cross-sectional shape of the ribs. The ribs actually curve quite sharply onto the ventral surface of the animal, where they taper gradually. Several specimens have suffered dorso-ventral diagenetic compression which has caused the distal portions of trunk ribs to snap off and fold flat. Cox presents accurate cross-sections showing how the ribs consist of a broad blade dorsally and a ventral keel. Morphology varies along the shaft of each rib, but generally most of the expansion is behind the

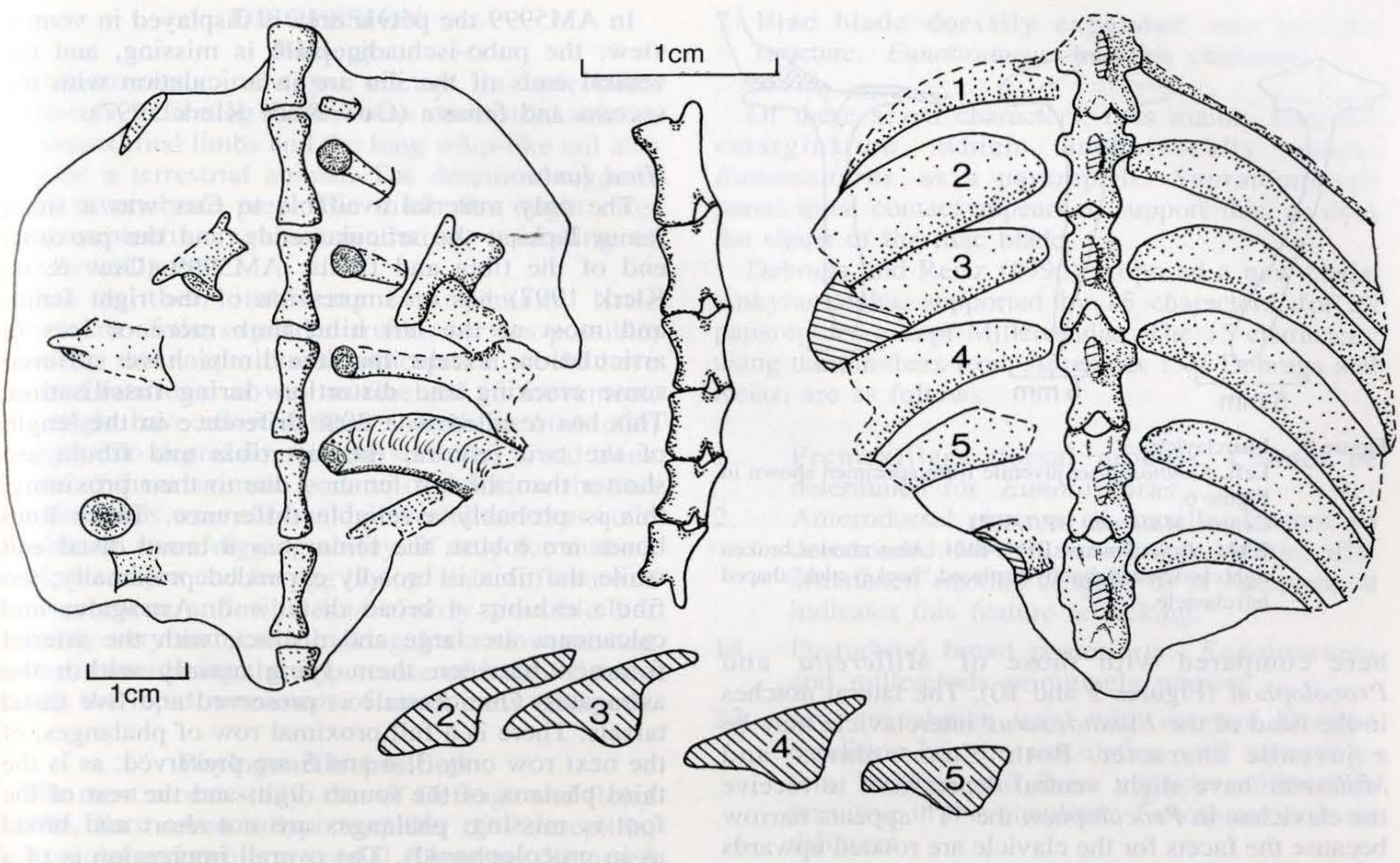

Figure 7. *Eunotosaurus*. GM71. Scattered caudal vertebrae are shown strung together between ventral and dorsal views of the specimen. Cross sections of correspondingly numbered ribs shown below.

keel, allowing each rib to overlap onto its posterior neighbour. The articulation of the ribs with the transverse processes is remarkable (Figure 8), being a simple modification of the primitive holocephalous condition. Each rib effectively has two heads, a dorsal head formed at the proximal end of the broadly expanded blade, which is drawn down to a rounded articular surface. A second head is formed on the ventral keel and projects a little further mesiad. Articulations on the transverse processes are described above. This arrangement would allow restricted but quite complex movements (see discussion).

Pectoral girdle. Figures 5, 6, 9, & 10.

M777 allows some addition to Cox's generally adequate description. A block containing the left scapula and most of the left humerus has been broken off and its counterpart on the main block prepared, resulting unfortunately in considerable loss of bone. The scapulocoracoids are fused in this large specimen, indicating that it was a mature animal.

The outline of the left scapula, including the dorsal margin, is complete. The scapula is a tall, thick rectangular element, fused with a single coracoid ventrally: the median surface rises to a central convexity which is slightly damaged as indicated in Figure 10.

The interclavicle is complete, and the lateral view is seen to have a considerable natural curvature. The small unnumbered specimen (Figure 6) has an interclavicle exposed in ventral view: it is illustrated

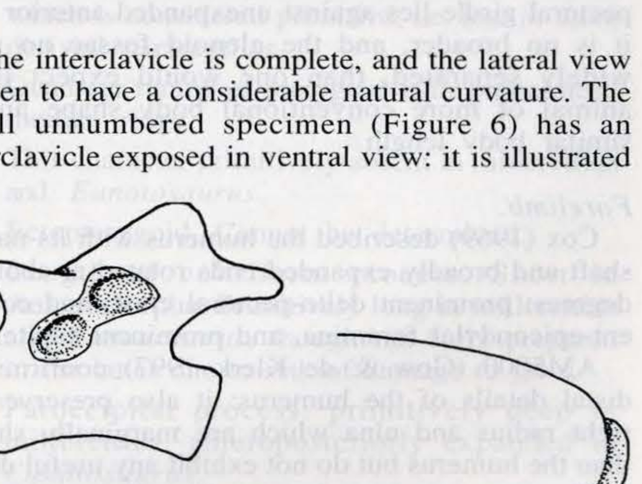

Figure 8. *Eunotosaurus*. Diagramatic sketches to show articulation for rib on trunk vertebra, and the dual head – broad sheet above narrow shaft.

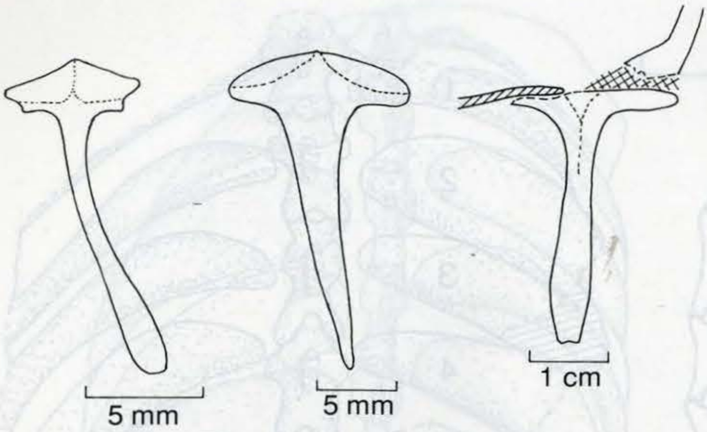

Figure 9. Interclavicles
Left. *Eunotosaurus* juvenile from specimen shown in Figure 6.
Centre. *Milleretta* BP/1/3821
Right. *Procolophon* BP/1/4014. Also shown broken right clavicle and slightly displaced, "hockey stick" shaped left clavicle.

here compared with those of *Milleretta* and *Procolophon* (Figures 9 and 10). The lateral notches in the head of the *Eunotosaurus* interclavicle may be a juvenile character. Both *Eunotosaurus* and *Milleretta* have slight ventral depressions to receive the clavicles: in *Procolophon* the "T" appears narrow because the facets for the clavicle are rotated upwards at 90 degrees. Substantial clavicles are incomplete, but of conventional design. As noted by Cox the pectoral girdle lies against unexpanded anterior ribs; it is no broader, and the glenoid fossae no more widely separated, than one would expect in an animal of more conventional body shape and of similar body length.

Forelimb.

Cox (1969) described the humerus with its narrow shaft and broadly expanded ends rotated at about 50 degrees; prominent delto-pectoral crest, and ect-and ent-epicondylar foramina, and prominent capitellum.

AM5000 (Gow & de Klerk 1997) confirms the distal details of the humerus: it also preserves the right radius and ulna which are marginally shorter than the humerus but do not exhibit any useful detail.

The same specimen has the first digits of the left manus preserved, two with distal carpals attached.

Pelvic Girdle. Figure 6.

Cox (1969) provides an adequate description of the pelvic girdle of a mature individual, including the fact that there is only one sacral rib facet on the tall narrow ilium, and that the acetabulum is only buttressed anteriorly. The ilium is moderately expanded before tapering to a blunt point dorsally. Pubes and ischia fuse to form a broad flat plate. In the unnumbered juvenile (Figure 6) pubes and ischia are not fused and the obturator foramen is an open notch. In that specimen the sacral rib is also not fused to the vertebra.

In AM5999 the pelvic area is displayed in ventral view: the pubo-ischiadic plate is missing, and the ventral ends of the ilia are in articulation with the sacrum and femora (Gow & de Klerk 1997).

Hind limb.

The only material available to Cox was a small femur lacking the articular ends, and the proximal end of the tibia and fibula. AM5999 (Gow & de Klerk 1997) has an impression of the right femur and most of the left hind limb more or less in articulation, except that the limbs have suffered some cracking and distortion during fossilisation. This has resulted in a 20% difference in the length of the two femora; the left tibia and fibula are shorter than the left femur – due to their proximity, this is probably a reliable difference. These limb bones are robust; the femur has a broad distal end while the tibia is broadly expanded proximally; the fibula exhibits a broad distal end. Astragalus and calcaneum are large and distinct, with the arterial foramen between them lying mainly within the astragalus. One centrale is preserved and five distal tarsals. There is a full proximal row of phalanges, of the next row only 3, 4 and 5 are preserved, as is the third phalanx of the fourth digit; and the rest of the foot is missing: phalanges are not short and broad as in procolophonids. The overall impression is of a powerful hind limb, with moderately short, broad foot.

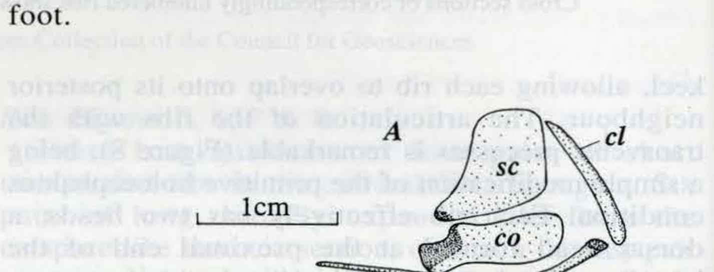

Figure 10. A. *Milleretta* BP/1/3821 juvenile pectoral girdle; note natural curvature of interclavicle. B., C., and D. *Eunotosaurus* M777. B. Median view of left scapula, clavicle and humerus. C. Right lateral view of pectoral girdle; note natural curvature of interclavicle. D. Ventral view of pectoral girdle.

DISCUSSION

Biology

Eunotosaurus always occurs in overbank sediments, indicating that this was a terrestrial animal: the unmodified limbs and the long whip-like tail also indicate a terrestrial animal. The dentition suggests small invertebrate prey. The thick ribs might offer some protection against predation, trampling or burrow collapse.

Due to their imbricate arrangement, little movement of the expanded trunk ribs was possible; however, the unique double articulation would have allowed rotational as well as fore and aft movement; this might have allowed these animals to *inter alia*, wriggle into depressions in the soil. The broad trunk region of these animals tends to overshadow the fact that the limbs were short and powerful and thus quite capable of some digging ability, if only for making shallow scrapes and for egg laying. Lateral flexure of the vertebrae and ribs was clearly possible but certainly very restricted, making for a slow moving animal, considering the importance of lateral flexure during the rapid movement of small early tetrapods.

Phylogenetic position

The most recent study, that of Debraga and Reisz (1996), lists seven autapomorphies of Parareptilia, five cranial and two post cranial. These are discussed below particularly as they relate to *Eunotosaurus*.

1. Anterolateral maxillary foramen present and significantly larger than all other foramina in maxilla. This is normally an easily observable character, but it cannot be determined for *Eunotosaurus* on the available material.
2. Foramen orbitonasale entirely surrounded by bone. This is a difficult character to evaluate in many fossils, and requires that the relevant bones be undisturbed. *Eunotosaurus* had a dorsal channel in the palatine for the optic nerve, but it is not possible to say whether this was roofed by prefrontal and lacrimal. Detailed comparative studies of this region are needed.
3. Temporal emargination formed by quadratojugal and squamosal. This character is present in *Eunotosaurus*.
4. Ectopterygoid teeth absent. Impossible to determine in unique material in an intractable matrix and with lower jaws in place.
5. Paroccipital process – supratemporal contact present. Determination of this character requires undistorted, perfectly prepared material. The supratemporal on the right side of M777 appears to make contact with the paroccipital process: the left supratemporal is missing. This character also appears to be present in millerettids, but for both animals confirmation is needed.
6. Sacral ribs only slightly in contact with one another distally or not at all. Not applicable to *Eunotosaurus* which has only one pair of sacral ribs.
7. Iliac blade dorsally expanded into fan-like structure. *Eunotosaurus* has this character.

Of these seven characters, it is mainly temporal emargination which unequivocally marks *Eunotosaurus* as a parareptile. Supratemporal/paroccipital contact appears to support this, as does the shape of the iliac blade.

Debraga and Reisz (1996) proposed a new clade, Ankyramorpha, supported by 15 characters, for all papareptiles except Millerettidae. The 15 characters, using the numbers from Appendix of Debraga and Reisz, are as follows:

1. Premaxillary dorsal process. Cannot be determined for *Eunotosaurus*.
2. Anterodorsal process of maxilla. Cannot be determined for *Eunotosaurus*. If the disarticulated maxilla (Figure 6) is complete, it indicates this feature is lacking.

14. Postorbital broad posteriorly. *Eunotosaurus* and millerettids primitively narrow.

23. Jaw articulation level with occiput. Derived condition has the articulation well anterior to this. Debraga and Reisz consider millerettids primitive in this character: *Eunotosaurus* is no different.

25. Dermal sculpturing. Millerettids and *Eunotosaurus* very similar in this character, which is considered primitive, i.e. lost in more derived parareptiles.

29. Quadrate ramus of pterygoid with pronounced median ridge.

    This character primitively absent in millerettids and *Eunotosaurus*.

33. Ectopterygoid. Cannot be determined.

41. Length of cultriform process. Short in Ankyramorpha. Primitively long in millerettids and *Eunotosaurus*, though not fully prepared in the latter due to risk of damage to jaws.

43. Paroccipital process: primitively deep in millerettids, anteroposteriorly expanded in *Eunotosaurus*.

47. Quadrate condyle: cannot be determined for *Eunotosaurus*.

48. + 50. Characters of lower jaw which cannot be determined for *Eunotosaurus*.

52. Trunk neural arches. Primitive in millerettids and *Eunotosaurus*.

53. Interclavicular head T-shaped rather than diamond-shaped.

    Cladistic analyses are often published ahead of osteological descriptions, so it is sometimes not clear what is meant by character descriptions: this is a case in point, where a character needs to be more precisely defined: *Eunotosaurus* and millerettids certainly have a more "diamond shaped" interclavicular head, compared with, for example, *Procolophon*, in which the facets for the clavicles appear to be oriented virtically, thus making the head more narrowly T-shaped in ventral view.

54. Interclavicle recessed for reception of clavicles. In *Eunotosaurus* and millerettids and facets for clavicles are barely perceptible depressions.

Thus of the 15 characters, nine can be determined for millerettids and *Eunotosaurus*. In eight of these they are both primitive with respect to Ankyramorpha. To these can be added the remarkable similarity in stapes morphology, which is a synapomorphy of Millerettidae plus *Eunotosaurus* (the stapedial foramen appears late in synapsid evolution: it is not known in pelycosaurs), and broad ribs, also a synapomorphy of these two taxa (as distinct from the pachyostotic ribs of mesosaurs and caseids).

Millerettidae and *Eunotosaurus* are thus sister taxa and together they constitute a sister clade to Ankyramorpha.

Eunotosaurus shares one derived character with Ankyramorpha, namely the anteroposteriorly expanded paroccipital process. The fine marginal dentition is convergent with that of *Owenetta*, while the low presacral count is convergent with pareiasaurs and turtles. Uniquely among parareptiles *Eunotosaurus* has a single sacral vertebra, bulbous cervical neural spines, and specialised (double) rib articulations.

ACKNOWLEDGEMENTS

The palaeontological staff of the Council for Geosciences, the National Museum, and the Albany Museum, are thanked for the extended loan of material. Michael Lee and Michael de Braga are cordially thanked for refereeing this paper, and constructive suggestions.

LIST OF ABBREVIATIONS

Cranial

Ang	angular
Bo	basioccipital
F	frontal
J	jugal
L	lacrimal
Mx	maxilla
N	nasal
Op	opisthotic
P	parietal
Pmx	premaxilla
Po	postorbital
Pof	postfrontal
Pp	postparietal
ppr	paroccipital process
Psph	parasphenoid
Ptgd	pterygoid
Q	quadrate
Qj	quadratojugal
S	stapes
Sa	surangular
So	supraoccipital
Sq	squamosal
St	supratemporal
T	tabular
V	vomer

Postcranial

cl	clavicle
co	coracoid
cof	coracoid foramen
fe	femur
fi	fibula
h	humerus
ic	interclavicle
il	ilium
is	ischium
lj	lower jaw
pu	pubis
sc	scapula
t	tibia

REFERENCES

COX, C.B. 1969. The problematic Permian reptile *Eunotosaurus*. Bulletin of the British Museum (Geology), **18**(5), 165-196.

DEBRAGA, M. & REISZ, R.R. 1996. The Early Permian reptile *Acleistorhinus pteroticus* and its phylogenetic position. *J. Vert. Palaeont*, **16**(3). 384-395.

GOW, C.E. 1972. The osteology and relationships of the Millerettidae (Reptilia; Cotylosauria) *J. Zool. Lond*., **167**, 219-264.

KEYSER, A.W. & GOW, C.E. 1981. First complete skull of the Permian reptile *Eunotosaurus africanus* Seeley. *S. Afr. J. Sci*., **77**, 417-420.

LAURIN, M. & REISZ, R.R. 1995. A re-evaluation of early amniote phylogeny. *Zool. J. Lin. Soc*., **113**, 165-223.

LEE, M.S.Y. 1993. The origin of the turtle body plan: bridging a famous morphological gap. Science, **261**, 1716-1720.

SMITH, R.M.H. & KEYSER, A.W. 1995. Biostratigraphy of the *Taphinocephalus* Assemblage Zone. p.8-12. In B.S. Rubidge Ed. Biostratigraphy of the Beaufort Group (Karoo Supergroup). South African Committee for Stratigraphy (SACS), Biostratigraphic Series No. 1, Council for Geosciences, Dept. of Mineral and Energy Affairs. 46p.

-------- Biostratigraphy of the *Pristerognathus* Assemblage Zone. p.13-17. In B.S. Rubidge Ed. Biostratigraphy of the Beaufort Group (Karoo Supergroup). South African Committee for Stratigraphy (SACS), Biostratigraphic Series No. 1, Council for Geosciences, Dept. of Mineral and Energy Affairs. 46p.