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Erratum

INSECT FAUNAS OF SOUTH AFRICA FROM THE UPPER PERMIAN AND THE PERMIAN/ TRIASSIC BOUNDARY

by

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ABSTRACT

Those sites in South Africa where more than one insect fossil specimen has been found have been interpreted as younger than Middle Triassic or as Late Permian. One site which has yielded a number of specimens and is apparently near the Permian/Triassic boundary is a quarry in the town of Bulwer KwaZulu-Natal. There are six sites with more than one insect specimen which are stratigraphically lower than Bulwer, namely Escourt (a new site), Far End, Mooi River (National Road), Mount West, Balgowan and Lidgetton. According to the 1984 1:1 000 000 Geological Map of Southern Africa Bulwer is situated in the Tarkastad Subgroup of the Beaufort Group near its lower boundary; the Tarkastad has been considered as Triassic. The remaining sites, except Balgowan and Lidgetton, fall in the Estcourt Formation of the Beaufort Group, as do all the sites with single Late Permian specimens except for one similarly aged specimen from the more easterly Emakwezeni Formation. The stratigraphically lowest sites are Lidgetton and slightly younger Balgowan; both are mapped as Volksrust Formation of the Ecca Group. An analysis is made of vertical distribution of taxa, with those of Lidgetton and Balgowan grouped together as a lower unit, of Bulwer as upper unit, and of the Estcourt Formation sites and Emakwezini site as a middle unit. No obvious break between the three units has been noted.

KEYWORDS: Insects, Upper Permian; Permian/Triassic Boundary; Estcourt Formation; Volksrust Formation; Tarkastad Subgroup.

INTRODUCTION

Thirty years ago there were only two described African (Zaïre and Zimbabwe) fossil insect specimens and another two South African specimens awaiting study. Since then the number of specimens of insects of Palaeozoic and possibly Lower Triassic age in Africa has grown to hundreds, most of which have come from an area about 90km from north to south and 50km from west to east in Kwazulu-Natal (Figure 1). This area includes the sites of all but one of the Upper Permian and possibly Lower Triassic specimens (the exception being from Emakwezini, further east) and all the Palaeozoic sites which have so far yielded more than one specimen. Most of the specimens from this area are in the Natal Museum, with a few, including some types, in the collections of the Bernard Price Institute for Palaeontological Research (BPI), University of the Witwatersrand, Johannesburg. These two collections include all the described material. A photographic record of types, and other important specimens, including undescribed taxa, is being compiled. Sufficient information is available to permit an analysis of the stratigraphic distribution of taxa.

MATERIALS AND METHODS

All the material in the Natal Museum has been studied and many types and other important specimens were photographed either previously, or recently. The types from the Bernard Price Institute were photographed in September 1996. Two insect fossils from a new site in Estcourt are represented by photographs supplied by Mr. D. Green. A small number of specimens has been discovered recently during a further splitting of material collected several years ago. Of these, one significant specimen which has not yet been accessioned has been included in the analysis of distributions. Photographs which included a millimetre scale and were enlarged similarly, greatly aided comparisons of specimens within a site and between sites. Specimens in which the radial vein appeared negative, i.e. as a trough instead of a ridge, were often also photographed with posterior lighting, which reversed the relief. By scanning photographs into a computer manipulations such as adjustments in size and reversals of wings to a standard apex-right view were made simple.

The specimens were grouped as members of three units, corresponding to divisions on the 1984 1:1000 000 Geological Map of Southern Africa: an upper unit for Bulwer specimens (Tarkastad Subgroup of the Beaufort Group), a lower unit for specimens from Lidgetton and Balgowan (Volkrust Formation of the Ecca Group), and middle unit for all the other Palaeozoic Kwazulu-Natal sites (Estcourt or Emakwezini Formations). It should be noted that Triassic fossils occur quite low in the Tarkastad Subgroup.

For the stratigraphic distribution of the insect groups, reference was made to Riek (1970) and Kukalová-Peck (1991). The sequence of insect groups in the latter was followed. The stratigraphic range of the Trichoptera is shown in the Triassic in Kukalová-Peck (1991), but in the Permian in Riek (1970), who unlike Kukalová, includes the stem-

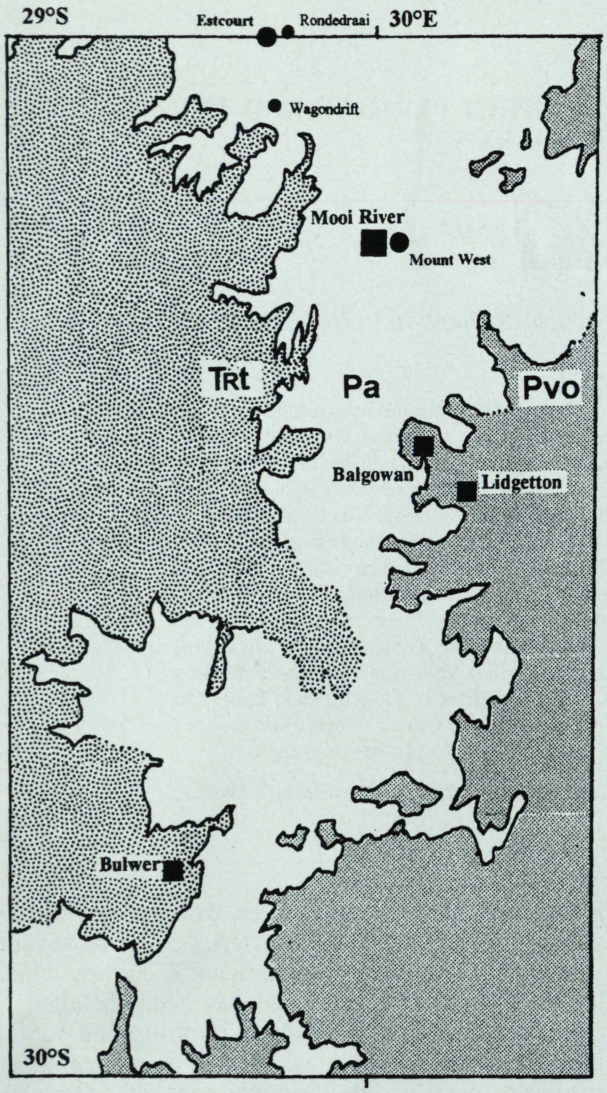


Figure 1. Map showing the study area, and the three units, the lowest being in the East, the highest in the West. TRt = Tarkastad Subgroup of the Beaufort Group; Pa = Estcourt Formation of the Beaufort Group; Pvo = Volksrust Formation of the Ecca Group. Boundaries are represented by dotted lines when they are obscured by dolerite intrusions.

group Amphiesmenoptera (Permian to Triassic) in the Trichoptera. The stratigraphic units form the upper two-thirds of the Carboniferous to the lower two-thirds of the Cretaceous were rescaled to a million years per millimetre, to represent the geological periods in proportion (Figure 2). The lengths of the three units under study have been arbitrarily made the same length, and together shown as considerably more of the Permian than they really represent. Species are represented as narrow lines, monospecific genera as broad lines.

RESULTS

The orders Paraplecoptera; Plecoptera; Orthoptera; Protelytroptera; Hemiptera; Mecoptera; and Neuroptera are apparently represented by the same taxon (genera and sometimes species) in more than one of the units (Table 1). In the case of Orthoptera, the taxon *Eolocustopsis* Riek 1976, is represented by a wing in one unit (middle one – Mooi River) and by specimens which include a thorax with wingbase only, at the other (lower – Lidgetton) unit. Protelytroptera, represented by *Phyllelytron acuminatum* Riek 1976, and Neuroptera, represented by *Archeosmylus*, have been found only in the upper two units.

The stratigraphic occurrence of the Protelytroptera shown in Riek (1970) ends in the Permian, but they are shown as extending into the early Cretaceous in Kukalová-Peck (1991). The remaining four orders each have one genus which possibly extends from the lower to the upper unit. They are: Paraplecoptera, *Mioloptera* Riek 1973 (Figure 3); Plecoptera, *Euxenoperla* Riek 1973; Hemiptera, *Beauforticus* Riek 1976 – in lower and upper units only (Figure 4, note caption); and Mecoptera, *Prochoristella* Riek 1953 (Figure 5), the first record of the genus in South Africa being the species *P. hartmani* Riek 1976.

The taxa reported as shared between the lower and middle units, are the following. Paraplecoptera: *Mioloptoides* Riek 1976; Hemiptera: an undescribed stenovicid (see Van Dijk 1978: p.57, figures 70, 71); *Orthoscytina* Tillyard 1926, with some doubt about the specimen from the lower unit; *Aleuronympha* Riek 1974; and two species of a new permaleurid nymph (Riek 1974 figure 74). The new taxa reported as shared between the middle and upper units are the following. Paraplecoptera: *Miolopterina* Riek 1976

TABLE 1.

Stratigraphic distribution of Taxa known from more than one level, the three levels being represented by the sites listed.

Lidgetton Balgowan	Mooi River Far End Wagondrift Mt. West Rondedraai Estcourt Emakwezini	Bulwer
Paraplecoptera: *Mioloptera*		
Plecoptera: *Euxenoperla*		
Hemiptera: *Beaufortiscus*		
Mecoptera: *Prochoristella*		
Paraplecoptera: *Mioloptoides*		
Hemiptera: Stenovicid		
Hemiptera: *Orthoscytina*		
Hemiptera: *Aleuronympha*		
Hemiptera: Permaleurid		
	Paraplecoptera: *Miolopterina*	
	Paraplecoptera: *Liomopteroides*	
	Protelytroptera: *Phyllelytron*	
	Hemiptera: *Austroprosboloides*	
	Hemiptera: *Dysmorphoscartella*	
	Neuroptera: *Archeosmylus*	

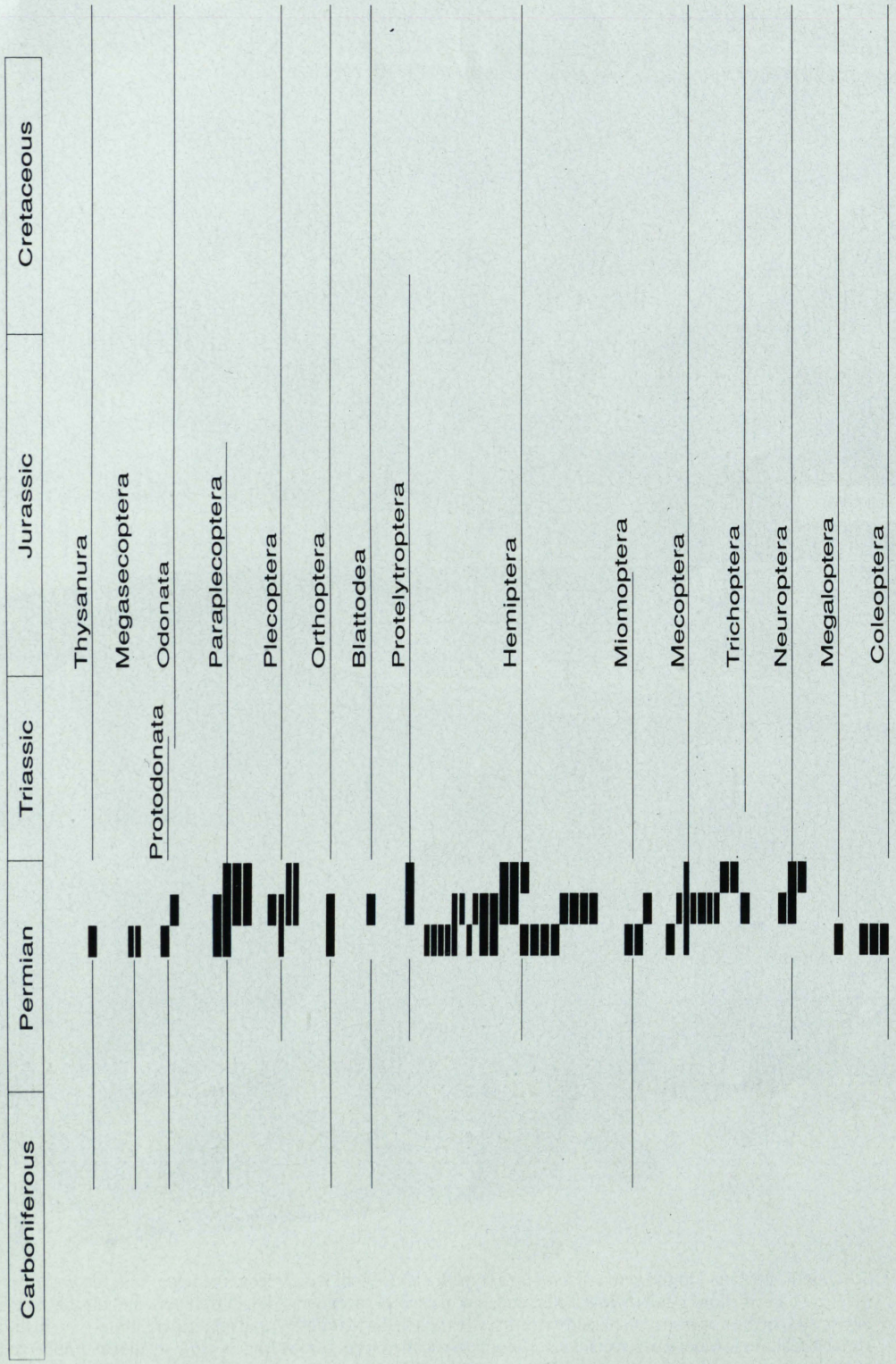


Figure 2. Fossil insect taxa reported from Kwazulu-Natal, South Africa, and the stratigraphic ranges of the groups after Kukalová-Peck (1991). (0.81 mm = 1 million years)

and *Liomopteroides* Riek 1973 (synonym *Liompterina*, according to Riek 1976); Protelytroptera: *Phyllelytron* Kukalová 1966; Hemiptera: *Austroprosboloides* Riek 1973 and *Dysmorphoscartella* Riek 1973; Neuroptera: *Archeosmylus*.

Overall 30 recognisable genera are found in only one of the three units, 13 are found in two units, and three in all three units.

DISCUSSION AND CONCLUSIONS

There is no obvious discontinuity either between the lowest and middle unit or between the middle and

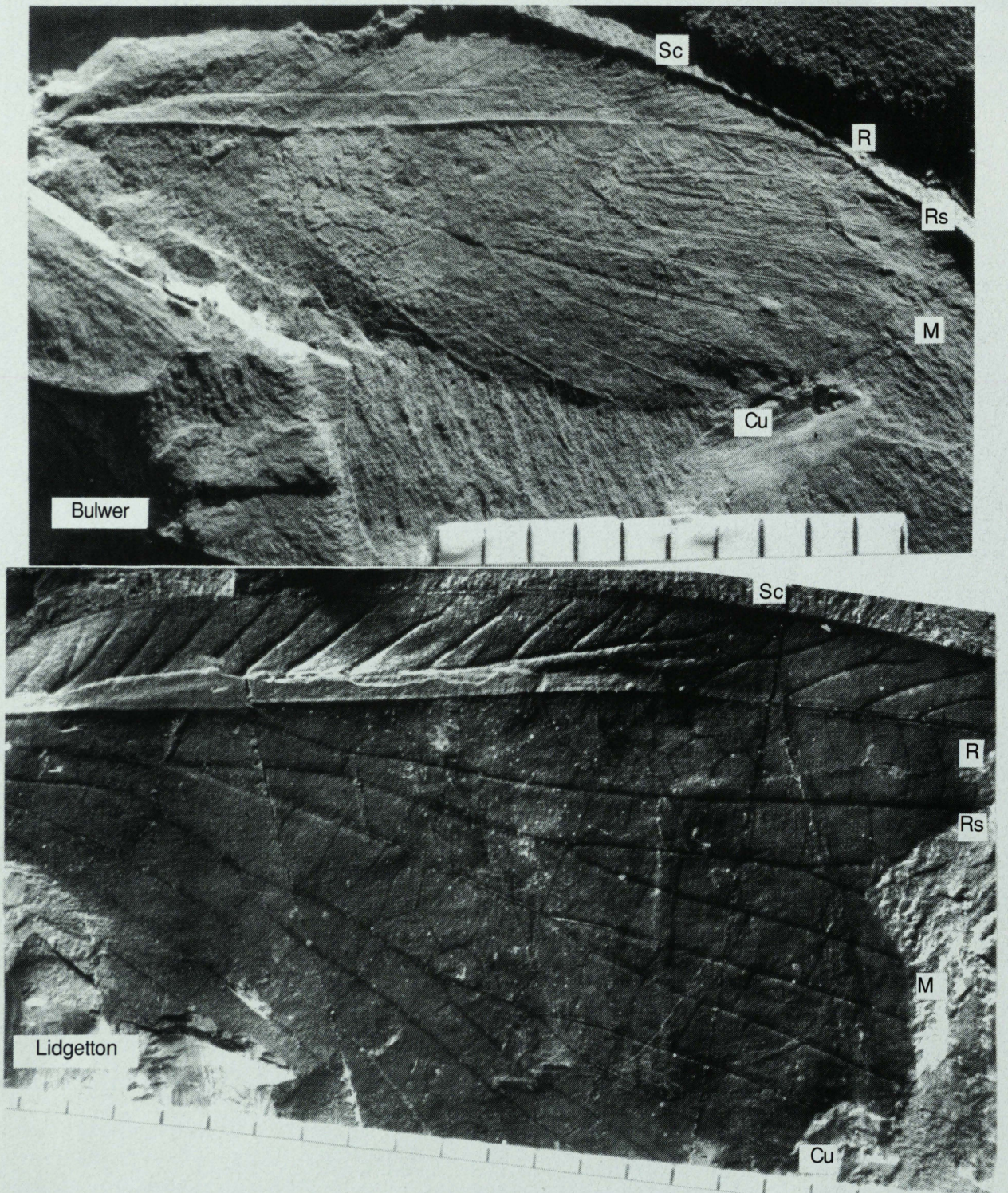


Figure 3. Specimens attributed to the genus *Mioloptera* (type locality Mooi River) from the upper unit (above, Bulwer; only specimen; reversed), and the lower unit (below, Lidgetton, one of several specimens); x8. Differences include the extra branch of the Radial Sector (Rs) in the upper specimen, and extra distal branch in the Medial (M) and (anterior) Cubital (Cu) in the lower specimen, all variable features in Mooi River specimens. The upper specimen appears to be considerably smaller (c. 20mm) and the lower specimen considerably larger than the estimated 26mm of the Mooi River type.

highest unit. The flora, rather poorly represented in the lower unit (Lidgetton and Balgowan), is similar in the three units. Anderson & Anderson (1985) treat all the sites as Permian. Bulwer is shown as in the Estcourt Formation in their Map 2.8 (Anderson & Anderson 1985 p.34). The map is based on Map 1 of Anderson (1977), derived from a palynological study. Among the assemblages selected for the study by Anderson & Anderson there were none in the *Lystrosaurus* Assemblage Zone and two in the *Dicynodon* Assemblage Zone (which corresponds to the Estcourt Formation). Carbonaceous material does occur at Bulwer, and has been sampled by A.J. Tankard, but no palynological results of a study of this material are known which might provide information indicating a Permian or Triassic age of

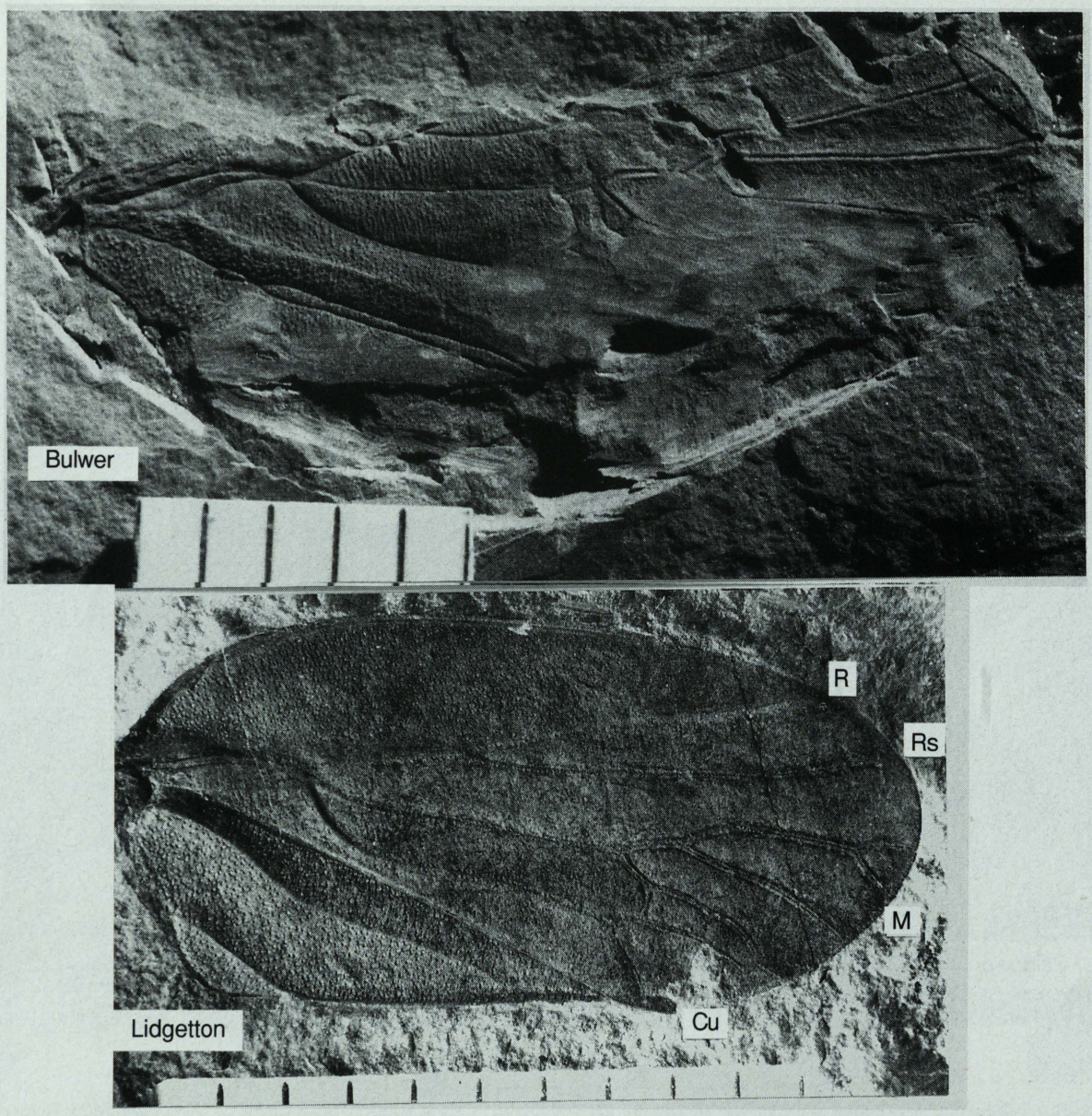


Figure 4. Specimen attributed to the genus *Beaufortiscus* (above, Bulwer, only specimen; reversed) and the type specimen of the genus from Lidgetton (below); x 8,8. The upper specimen shows a number of differences from the type. These include the lesser curvature of the Medial and Cubital veins at their common origin with the Radial, the more proximal branching of the Medial, and straighter marginal branches. These are at least specific differences, and may be generic ones.

the site. The inclusion of the Bulwer area in the Tarkastad Subgroup during mapping was presumably based on local lithology independent of biostratigraphic relationship to the Estcourt Formation. There are three chrono-stratigraphic alternatives for the Bulwer site, namely Permian, at the Permian/Triassic boundary, or Triassic. The transition from *Glossopteris*-dominated to *Dicroidium*-dominated floras seems to have occurred during the Early or Middle Triassic, a period for which the fossil record of the floras and the associated insect faunas in South Africa is poor. As with the flora, the insect fauna of the Bulwer site shows affinities with the older sites.

Further work at the Mooi River site is not feasible, as the site is covered by a broad highway, the N3 National Road. A test excavation made during the road-making into the road cutting yielded plants of inferior quality and no insects. A quarry just above the road cutting, on the farm Far End, yielded a small number of insects. The productive layers are probably exhausted. Some material from Far End was collected and stored, and has yet to be studied. The Balgowan site is a small road cutting which probably could be further studied. Some Lidgetton material is being studied at present. Further study of the Bulwer site has been planned. In the town of Bulwer, this site is a disused quarry with great potential for further continued study provided steps are taken to stop the invasion of the site by wattle trees. As this is the productive site closest to the Permian/Triassic boundary, intensive study may be well rewarded.

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The information in the catalogue of the Natal Museum used is largely dependent on the researches of Dr Edgar Riek, who is accordingly warmly acknowledged. Any errors in the present work must be attributed to me. Mrs Bianca Lawrence is acknowledged for

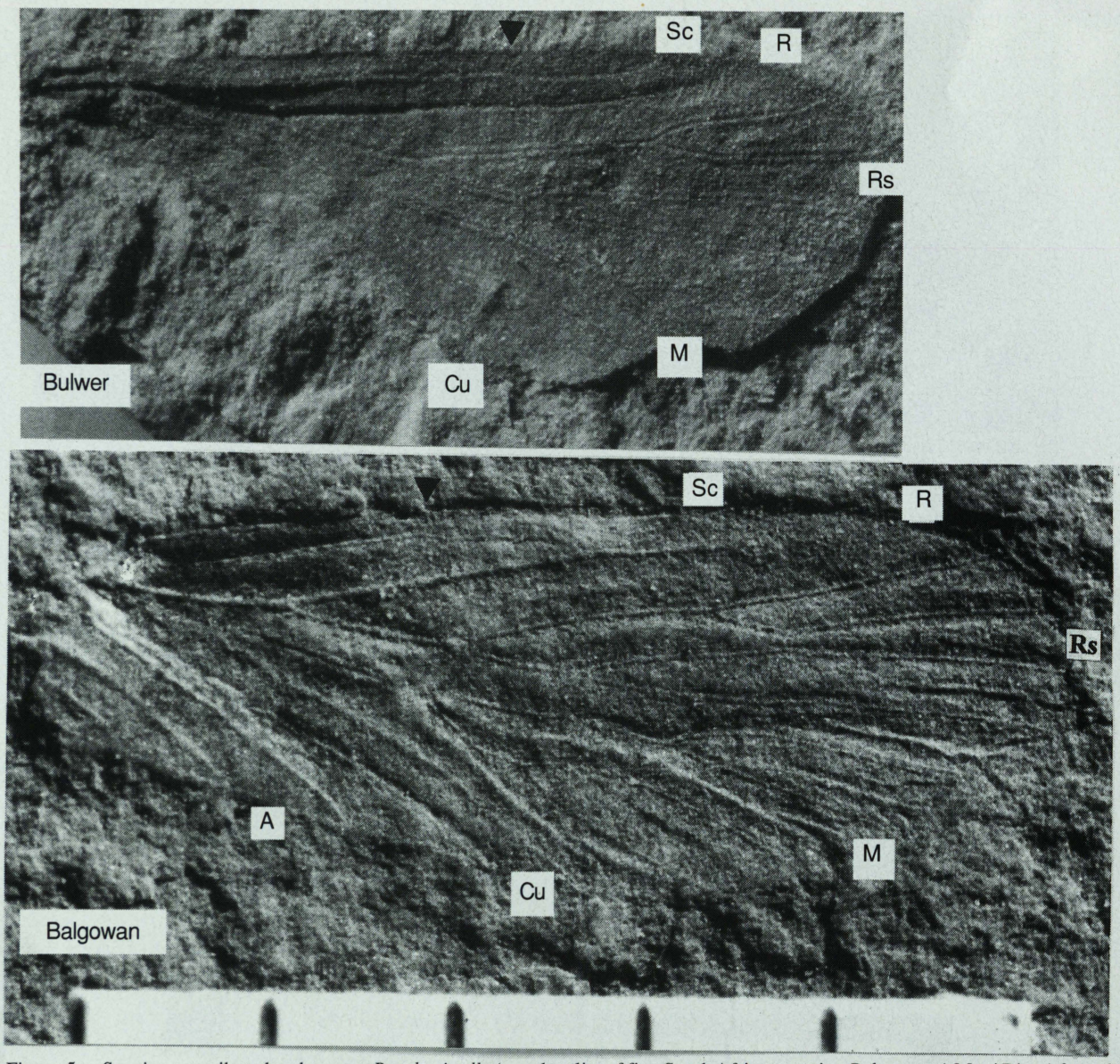


Figure 5. Specimens atributed to the genus *Prochoristella* (type locality of first South African species, *P. hartmani*, Mooi River) from the upper unit (above, Bulwer, only specimen) and the lower unit (below, Balgowan, only specimen; reversed); x27. Note that the upper specimen has the opposite (uncorrected) relief to the lower specimen. Note also that the lower specimen has folds (mainly raised) between some of the veins. In the upper specimen the Radial is parallel to the front edge of the wing for some distance, unlike the Radial of the lower specimen. The Subcosta (Sc) of the upper specimen has a branch and a kink well beyond the level of the first forking of the Radial Sector, whereas the branching and kink in the Subcosta of the lower specimen is proximal to this fork. These differences at about the specific level. The upper specimen is smaller than the lower one.

making it possible for me to work on the Natal Museum material at a distance, not only by loan of specimens, but also by painstakingly matching photographs with specimens. Dr Mike Raath is acknowledged for making it possible for me to photograph the BPI types during the September 1996 Palaeontological Society Symposium. Dr Henk Geertsema is acknowledged for making valuable comments on the original manuscript and on a final version with minor changes, which version also benefited from scrutiny by Dr Juri van den Heever.

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THE OLDEST PROCOLOPHONOID (AMNIOTA: PARAREPTILIA) – NEW DISCOVERY FROM THE LOWER BEAUFORT OF SOUTH AFRICA.

by

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ABSTRACT

Until now the earliest recognised procolophonoid (*sensu* Laurin & Reisz 1995) reptile has been *Owenetta*, which ranges from the *Cistecephalus* assemblage zone (Upper Permian) to the *Lystrosaurus* assemblage zone (Lower Triassic) of the Beaufort Group of South Africa. This paper records the presence of a new even older form from low in the underlying *Tapinocephalus* assemblage zone.

KEYWORDS: Anapsida, Procolophonoidea, Procolophonidae, parareptiles.

INTRODUCTION

The Procolophonoidea are a group of anapsid reptiles which have attracted attention recently as the group most closely similar to turtles. Reisz and Laurin (1991) proposed the procolophonoid *Owenetta* as the sister taxon of turtles, while Lee (1993) has made the same claim for pareiasaurs. The oldest fossils of turtles, of which three genera have been described, occur in Upper Triassic rocks from Germany and Argentina (Rougier *et al* 1995).

The family Procolophonidae Lydekker 1880 (*sensu* Laurin & Reisz 1995) includes the genera *Anomoiodon*, *Burtensia*, *Candelaria*, *Contritosaurus*, *Eumetabolodon*, *Hypsognathus*, *Kapes*, *Koiloskiosaurus*, *Leptopleuron*, *Macrophon*, *Microthelodon*, *Myocephalus*, *Neoprocolophon*, *Orenburgia*, *Paoteodon*, *Procolophon*, and *Thelegnathus* (Laurin & Reisz 1995). As Lee (1995) has pointed out, Reisz and Laurin (1991) previously extended the definition of the family to include *Owenetta*. The family has a cosmopolitan distribution – including Europe, Asia, and Africa. With the exception of *Owenetta*, all of the procolophonoid genera are Triassic in age. In South Africa *Owenetta* occurs in the Triassic *Lystrosaurus* Assemblage Zone, but also occurs in the Upper Permian *Cistecephalus* and *Dicynodon* assemblage zones of the Beaufort Group (Kitching 1995, Kitching & Groenewald 1995, Smith & Keyser 1995). The oldest species is *Owenetta rubidgei* from the *Cistecephalus* assemblage zone of middle Tatarian age.

In this paper the first procolophonoid from the underlying *Tapinocephalus* Assemblage Zone of the Beaufort Group is described, which is thus the earliest known specimen of the group. The specimen was found by Mr. Patrick Bender on the farm Blaaukranz in the Price Albert District which is considered to be low in the *Tapinocephalus* Assemblage Zone (Kitching 1977). In close proximity fossils of the pareiasaur *Bradysaurus*, the dicynodont *Diictodon*, the dinocephalian *Anteosaurus* and fragments of tapinocephalid dinocephalians were recovered.

MATERIAL

The specimen NMQR 3061 in the collections of the National Museum, Bloemfontein, was found in two blocks, one containing an articulated series of nine precaudal vertebrae, and the other thirteen proximal caudals, a partial right pubis, and articulated distal femur plus tibia and fibula. In spite of a thorough search the anterior half of the specimen could not be found. There is no clear fit of the two blocks, but very little appears to be missing as the anteriormost preserved caudal vertebrae are considered to be the first and second caudals. The bones are encased in a fine grained green mudstone containing scattered millimetre cubes of haematite, pseudomorphs after pyrite. The specimen is difficult to prepare as the matrix does not part easily from the bone. Bone surfaces (black) are only well defined where they have been exposed by natural erosion. In preparation it was found that organic acids do attack the matrix, but also adversely affect the bone which is extremely thin-walled, and hence acid preparation was not pursued further. Because of the difficulties experienced in preparation only conservative mechanical preparation has been undertaken.

DESCRIPTION (Figures 1, 2 &3)

A total of 22 vertebrae are preserved, and it is possible to differentiate 9 dorsals and 13 caudals. The anteriormost 5 dorsal vertebrae are reasonably complete and well preserved. In the posterior dorsal vertebrae the pleurocentra have been weathered, thus exposing a horizontal cross-section of some. From this it is evident that the pleurocentra are

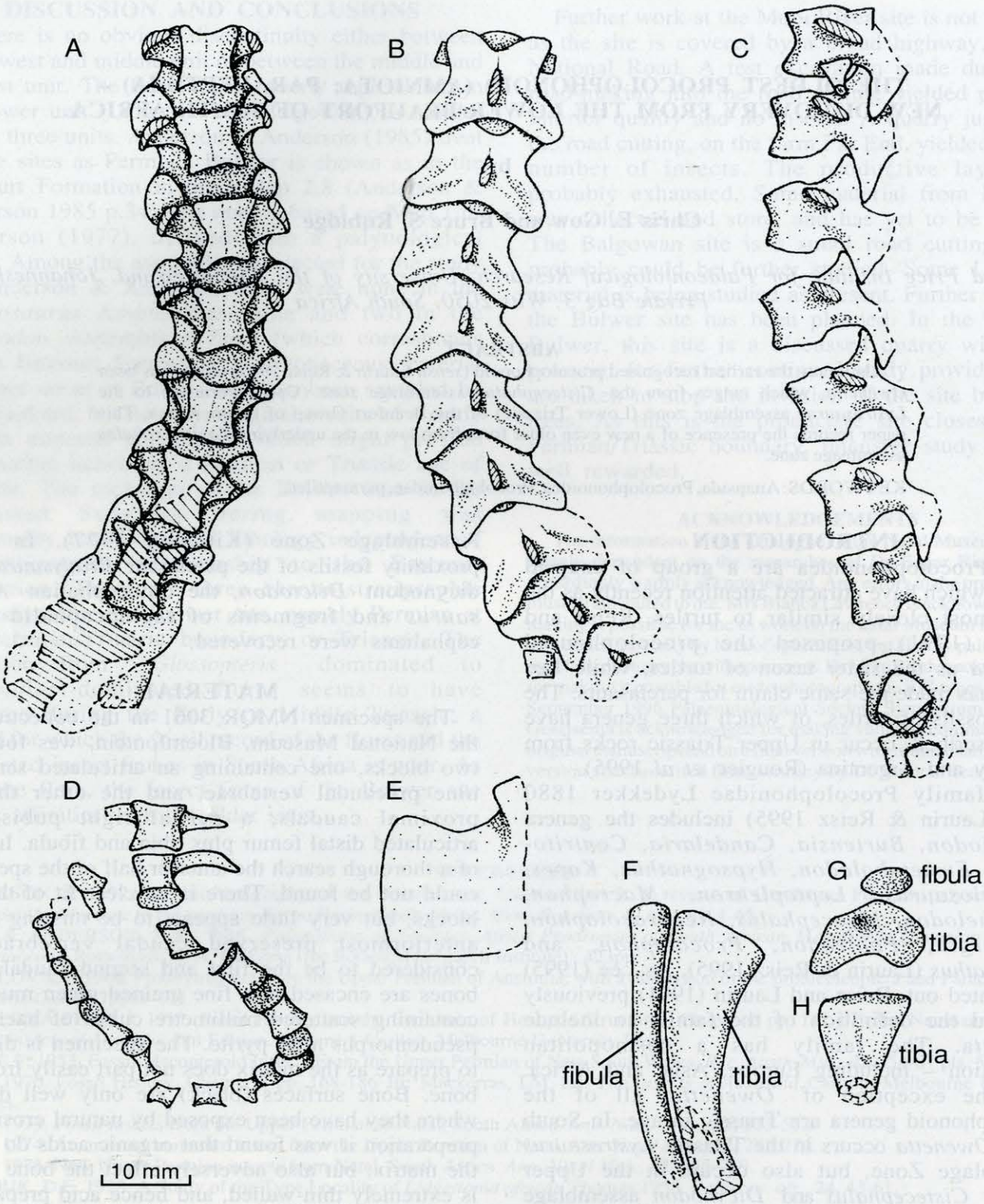


Figure 1: Procolophonoid specimen NMQR 3061: A) trunk vertebrae, ventral view; B) trunk vertebrae, dorsal view; C) trunk vertebra lateral view; D) caudal vetebrae, vental view; E) pubic (?) fragment, ventral view; F) proximal ends of tibia, dorsal aspect, G) articular ends of tibia and fibula; H) tibia ventral view.

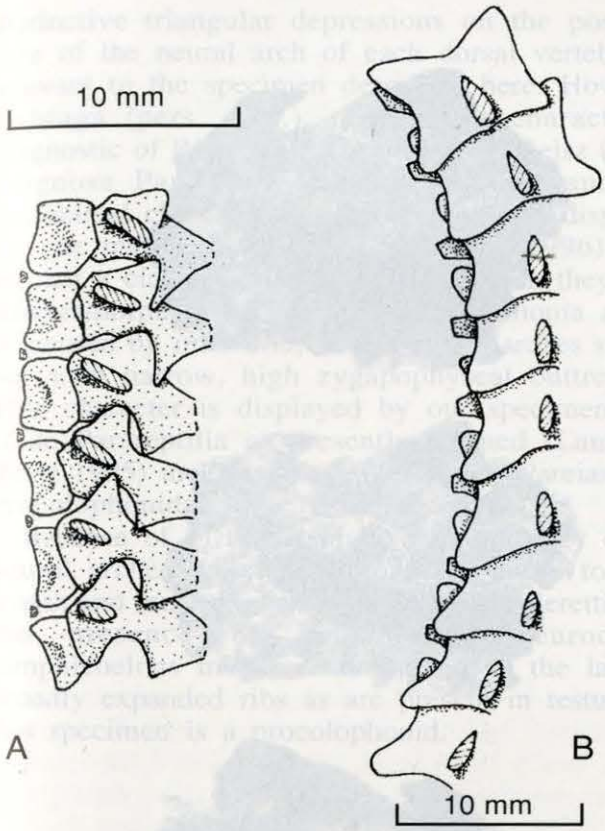


Figure 2: *Procolophon trigoniceps*.
A) Left BP/1/2854. B) Right BP/1/2278.
Both drawn from casts of impressions taken from natural molds.

notochordal. When viewed from the ventral side the pleurocentra are spindle-shaped and both ends of the centra are slightly bevelled; the ventral surfaces are not ridged. From the bevelled nature of the ventral side of the ends of the pleurocentra, as well as the wide spacing between the ventral surfaces of successive articulated vertebrae, it is evident that large intercentra were probably present between all the well preserved vertebrae, but are not preserved now (large intercentral spaces are also present in *Procolophon* – pers. com. Michael Debraga). Where broken it can be seen that the vertebrae are remarkably spongey and thin walled.

The neural arches of the preserved dorsal vertebrae have large, extensively overlapping and horizontally oriented zygapophyses. The dorsal surfaces of the postero-laterally projecting postzygapophyses are swollen, and the postzygapophyses have indentations on their anterior surfaces. In contrast the anterior zygapophyses have an anterolateral orientation, but the dorsal surface is more flattened and slightly concave to accomodate the articular surface of the postzygapophyses of the preceding vertebra with which they make a horizontally oriented articulation. The neural spines are very low and are ovoid in cross-section with the broader end posterior. The postero-dorsal surfaces of the neural arches bear a pair of triangular depressions. The neural arches are fused to the pleurocentra indicating that the animal was mature.

As the posterior dorsal vertebrae have been weathered it is difficult to differentiate between lumbar and sacral vertebrae. However, as the posterior 2 precaudal vertebrae are abruptly smaller and have less prominent zygapophyses than those preceding them, they are considered to be sacral. There is no evidence for a third sacral, though it is possible that the critical area may be missing.

The vertebrae in the second block are smaller than the rest and become progressively smaller posteriad. The zygapophyses are less pronounced and from the distinctive morphology of the transverse processes – large, laterally projecting on the first, large and strongly curved posteriad on the second -, they are considered to be the first and second caudals. These vertebrae are visible only in ventral view and like the dorsal vertebrae also have spindle shaped pleurocentra. The ventral surface of the anteriormost two caudal vertebrae is rounded, but those more posteriorly situated have a flattened ventral surface with a narrow midline keel. The lack of spacing between successive pleurocentra, which are preserved in close articulation, suggests that haemal arches if present would have been small.

Only a few fragmentary ribs and very few rib heads are preserved. From these and the single facetted attachments on the transverse processes, it is evident that the ribs were single headed and relatively slender structures.

The bone here identified as a partial pubis is large, plate-like and unfenestrated as is typical of basal parareptiles. Only the distal portion of the right femur is present; it is almost square in cross section at its distal end. In dorsal view it displays a slight depression, the intercondylar fossa, at the distal end.

The distal ends of both the tibia and fibula and most of the foot, except for part of an astragalus or calcaneum, are missing. The proximal articular surface of the tibia displays a central pit which is probably a natural feature which would have afforded purchase to a tendon or ligament. When viewed from the lateral side the tibia is a curved bone which is broad proximally and thins towards the distal end which is weathered. In dorsal view the tibia is crescent shaped, rounded anteriorly with a concavity on the posterior side. The fibula is less robust than the tibia but is not well exposed from the matrix. This bone is also slightly curved and has a prominent articular facet at the distal end.

DISCUSSION

Laurin & Reisz (1995) list 14 synapomorphies of the Parareptilia, ten of which are cranial characters and only four postcranial. However these postcranial characters are all in elements which are not preserved in specimen NMQR 3061. Lee (1995) on the other hand lists 18 characters of which only four pertain to the postcranium and only one (pair of

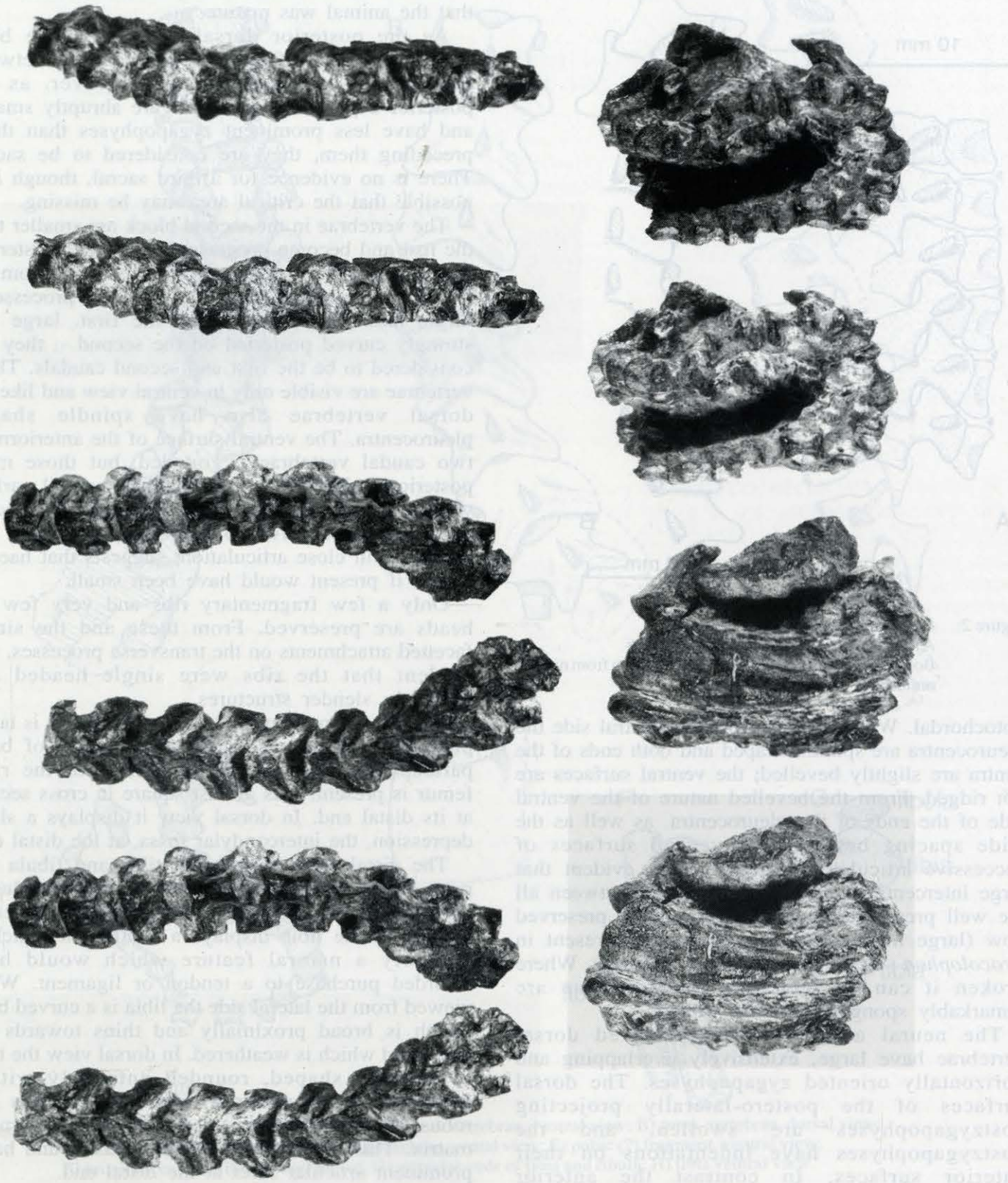


Figure 3: NMQR 3061. Stereophotographs. Left, dorsal vertebrae in dorsal, ventral, and left lateral views. Right, limb bones and caudal vertebrae. Scale bar = 10 mm.

distinctive triangular depressions on the posterior face of the neural arch of each dorsal vertebra) is relevant to the specimen described here. However, Debraga (pers. com.), rejects this character as diagnostic of Parareptilia. Debraga and Reisz (1996) diagnose Parareptilia on five cranial and two postcranial characters, none of which are displayed by our material. Debraga and Reisz(1996) have erected a clade within Parareptilia which they term Ankyramorpha; this includes Procolophonia and is diagnosed by *inter alia*," trunk neural arches swolen but with narrow, high zygapophyseal buttresses;" This character is displayed by our specimen. The clade Parareptilia as presently defined (Laurin & Reisz 1995) includes the Millerettidae, Pareiasauria, Procolophonidae and Testudines.

Because of 1) the distinctive morphology of the neural arches which are broader relative to their length and much bigger than those of millerettids, 2) the presence of notochordal pleurocentra (amphicoelous in pareiasaurs), and 3) the lack of broadly expanded ribs as are present in testudines, this specimen is a procolophonid.

The specimen is much larger than *Owenetta*, but falls within the size range of *Procolophon*. The pleurocentra are notochordal but they are not "pinched" laterally as is the case in *P. trigoniceps*.

Because of the fragmentary nature of the specimen it is difficult to assign it to a particular genus. It probably represents a new taxon but we feel that it would be undesirable to name such an undiagnostic specimen. So far the only parareptiles from the *Tapinocephalus* assemblage Zone are the pareiasaurids *Bradysaurus* and *Embrithosaurus*, the millerettid *Broomia* ((Watson 1914, Thommason & Carroll 1981), and *Eunotosaurus* (which is clearly a parareptile, Gow in prep.). Specimen NMQR 3061 is the first procolophonoid from this zone and shows that the group is not as young as previously supposed (Laurin & Reisz 1991).

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A NOTE ON THE POSTCRANIAL SKELETON OF *MILLERETTA* (AMNIOTA: PARAREPTILIA).

by

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ABSTRACT

This description of a partial postcranial skeleton of a mature individual of *Milleretta rubidgei* shows that it has very broad (laterally expanded) ribs, and growth of limb bones had ceased. Previously the only described postcranial skeleton was that of a young individual in which the ribs are not as broad and the ends of the limb bones were still formed of cartilage.

KEYWORDS: *Milleretta*, parareptiles

INTRODUCTION

The monospecific genus *Milleretta* is the least derived member of the Millerettidae, which also includes *Millerosaurus* and *Milleropsis* (Gow 1972). The family is remarkable for the development of a lateral temporal opening, and it is only adult *Milleretta* which have a completely closed temporal region. Until now the post cranial skeleton of *Milleretta* has been known from a single, nearly complete (including the skull), articulated juvenile individual, BP/1/3821. In the juvenile the ribs are moderately laterally expanded, but they do not overlap, thus, though the specimen described below was familiar to the writer, because of its greatly expanded ribs, it did not occur to him until recently that it might be a millerettid.

MATERIAL

The specimen, number BP/1/2040, was collected by J.W. Kitching in 1950 on the farm Wilgebosch, district New Bethesda, from the *Dicynodon* Assemblage zone (formerly *Daptocephalus* zone). It is thus the same age and from the same geographic region, as previously described millerettid material. Minimal mechanical preparation was required.

DESCRIPTION

The specimen is articulated, but somewhat laterally crushed. There are 15 presacral vertebrae, two sacrals, and three caudals, all with their ribs in fair condition on at least one side. Most of the pelvic girdle is preserved, also the left femur and proximal ends of tibia and fibula (Figure 1).

Vertebrae have the broad neural arches typical of fossil parareptiles; the spines have been eroded off. Transverse processes are prominent; widely spaced zygapophyses are oriented horizontally. Centra are amphicoelous and narrow ventrally. Intercentra are present. These vertebrae are indistinguishable from those of the juvenile, except that arch and centrum are fused in the adult.

Ribs (Figure 2) are very robust dorsally, and postero-laterally they have extensive caudad expansions which overlap the next rib posteriorly. Expansion has resulted from a drawing out of the posterior margin of each rib into a thin sheet; the posterior edge of each expanded rib bears fine crennelations. Ribs are holocephalus.

Gastralia are preserved along the full length of the trunk as previously recorded for *M. rubidgei* (Gow 1972).

Pubes and ischia are fused together, but the two plates have shifted relative to one another and appear to have been loosely connected.

Only the left ilium is complete; the dorsal blade is broadly expanded relative to the neck of the bone, with most of the expansion directed posteriad. The acetabular region is damaged on the right side and obscured by the femur on the left.

Whereas the limb bones of the juvenile skeleton have unfinished extremities, the femur of this specimen (Figure 2) is fully ossified, a clear indication that the animal was full grown.

The femur is drawn foreward displaying the large internal trochanter and intercondylar fossa. Only the proximal ends of tibia and fibula are preserved, in articulation with the femur.

DISCUSSION

The skeleton described above is the same geological age as the only other *Milleretta* skeleton known (Gow 1972), which is that of a juvenile. The new skeleton is clearly that of an adult as demonstrated by fusion of the elements of the vertebrae and the fully formed articular ends of the limb bones. In view of correspondence in provinence and morphology, there can be no doubt that this is a *Milleretta* skeleton. Expansion of the ribs increases considerably with age, resulting in considerable overlap of adjacent prelumbar ribs. Why the animal should have such robust, imbricating ribs is not obvious, particularly as the

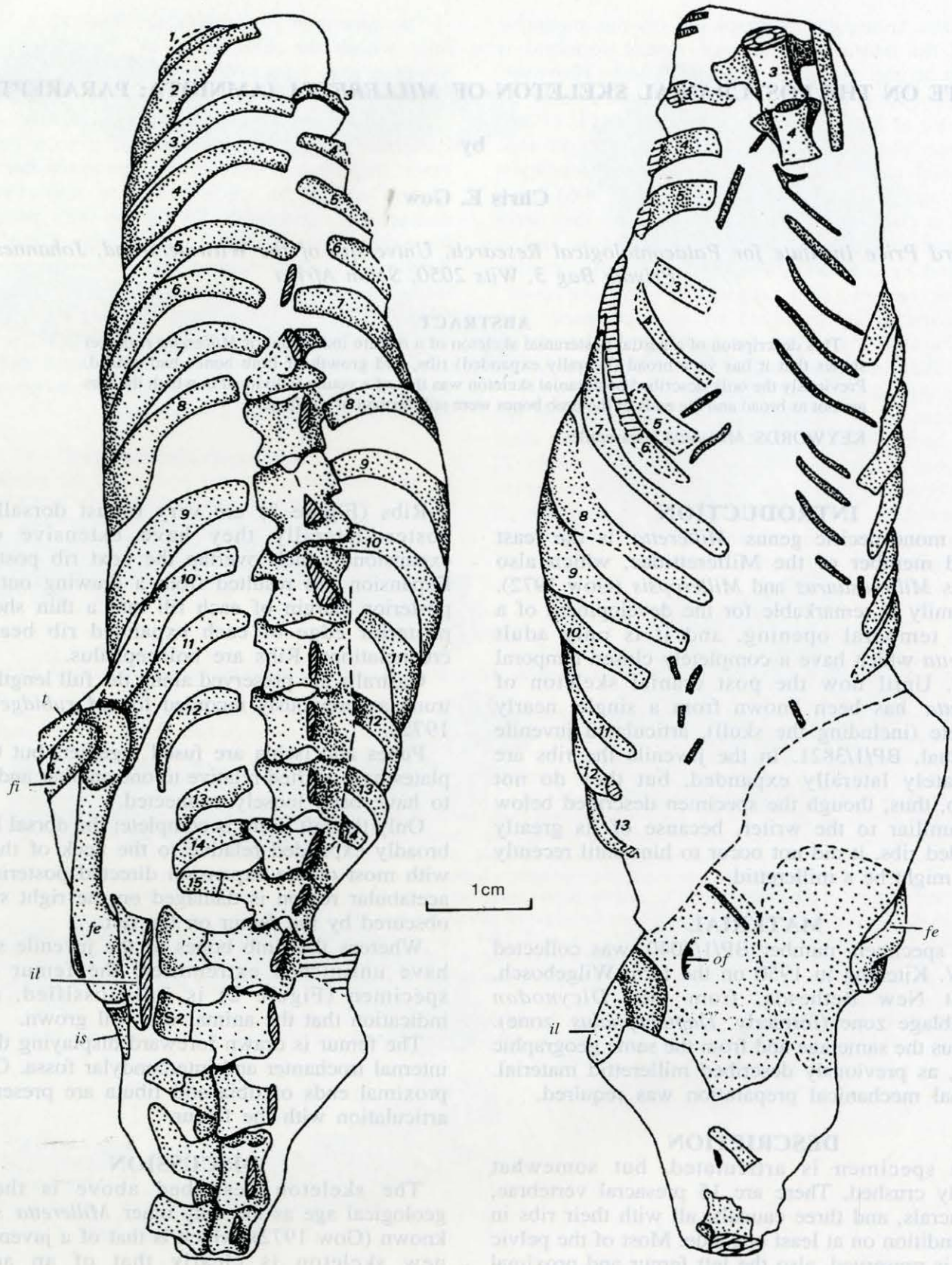


Figure 1. *Milleretta* BP/1/2040 postcranial skeleton in dorsal and ventral views.

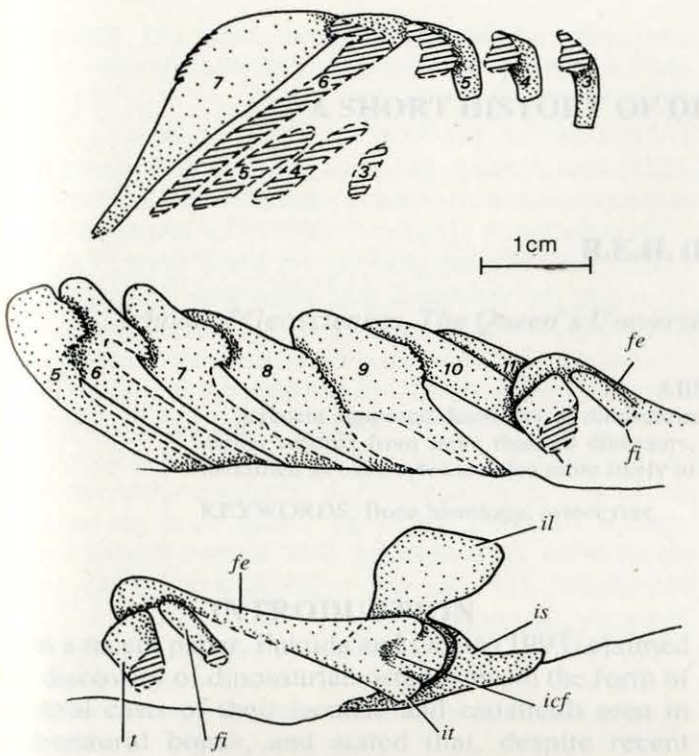


Figure 2. *Milleretta* BP/1/2040. Top to bottom: anterior ribs of right side; posterior ribs of left side and part of hind limb; left pelvic girdle and hind limb.

related *Millerosaurus* and *Millerops*is have slender ribs. Certainly thick ribs offer considerable physical protection; they could also limit the degree of lateral flexure of the body, which might reduce speed, but on the other hand facilitate sustained slow locomotion (a well known capability of modern day Karoo tortoises, for example). It could be that a more rigid trunk in adults is an adaptation to burrowing; foot morphology could have a bearing on this suggestion, but the feet are not known at this time.

It is argued elsewhere (Gow in prep.), that millerettids and *Eunotosaurus* are sister taxa lying outside Ankyramorpha (Debraga and Reisz 1996) in Parareptilia. However, rib morphology should not be regarded uncritically as an additional synapomorphy, as it has been attained rather differently in the two genera. In *Milleretta* the vertebrae are plesiomorphic, while the ribs are broadened by simply drawing out the shaft to an airfoil like section; in contrast, the *Eunotosaurus* trunk vertebrae are elongated and the ribs have double articulations and a drawn out "T" shaped section. If there is a synapomorphy it cannot be stated more precisely that "ribs thickened".

ABBREVIATIONS

fe	femur
fi	fibula
h	humerus
icf	intercondylar fossa
il	ilium
is	ischium
it	internal trochanter
of	obturator foramen
t	tibia

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A SHORT HISTORY OF DINOSAURIAN OSTEOCYTES.

by

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ABSRACT

A recent supposed discovery of dinosaurian osteocytes by Fukuda and Obata (1993) ignored earlier records from more than 20 dinosaurs, dating back 150 years. Some of the bodies they identified as osteocytes are also more likely to represent chondrocytes.

KEYWORDS: Bone histology, osteocytes.

INTRODUCTION

In a recent paper, Fukuda and Obata (1993) claimed the discovery of dinosaurian osteocytes, in the form of mineral casts of their lacunae and canaliculi seen in hadrosaurid bones, and stated that, despite recent histological studies, ". . . there is no information on osteocytes in dinosaur bone tissues" (p. 99, para. 1). At that date, however, earlier studies outlined here contained records from more than 20 dinosaurs, dating back 150 years (Quelett 1849), and even electron microscope photographs had been in print since 1966 (Pawlicki, Korbel & Kubiak 1966). This note reviews a range of relevant references, for readers not familiar with them, and also shows that some bodies identified as osteocytes by Fukuda and Obata in the articular surface of a dinosaur limb bone, are more likely to represent chondrocytes.

Historical outline

First, under the old name "bone cells", the presence of osteocyte lacunae was recorded from bones of the ornithopod *Iguanodon* by Quekett (1849) and of the sauropod *Pelorosaurus* by Mantell (1850). These are the oldest ornithischian and saurischian records respectively. Strictly, Quekett (p. 57) only stated that bones of *Iguanodon* do not differ from those of modern lizards in minute structure; but his numerous figures of lacunae and canaliculi from modern forms (plates 5-8) and from a pterosaur (plate 8, Figure 2) leave no doubt of what he meant. Subsequently Hasse (1878) recorded osteocyte lacunae in a vertebra ascribed to the prosauropod *Thecodontosaurus*, contrasting spindle-shaped examples from periosteal bone with stellate forms seen in a nothosaur (p. 499), and giving a figure which shows their presence in endochondral bone (Figure 24b). Their presence is seen readily in some of Seitz's (1907) photographic figures e.g. Figure 57, *Megalosaurus*; Figures 59-61, *Iguanodon*; Figure 76, "*Trachodon*" (*Anatosaurus*); and his text, in which he called them "bone corpuscles" (Knochenkörperchen), contains records of their presence and arrangement in bones of *Plateosaurus* (p. 265), *Megalosaurus* (p. 288) *Brontosaurus* (pp. 302, 303), *Diplodocus* (pp. 304, 306), *Camarasaurus* (p. 311, as "*Morosaurus*" pp. 322, 324), *Haplocanthosaurus* (pp.313, 314), *Allosaurus* (pp. 315, 316), *Stegosaurus* (p. 321) *Iguanodon* (pp. 326-328), *Dryptosaurus* (p. 344), *Triceratops* (p. 346), and *Anatosaurus* (pp. 348-350), as "*Trachodon*". Osteocyte *Stegosaurus* lacunae recorded as from *Zanclodon* (p. 262), which is now considered indeterminate, are probably from a prosauropod (c.f. Benton 1986, pp. 295-297). A preserved canalicular network was noted in *Brontosaurus* (p. 302), though not illustrated, and lacunae affected by fungal enlargement, mineral infilling, loss of canaliculae or complete obliteration were reported from various genera. Records from prosauropods, sauropods, theropods, ornithopods, a stegosaur and a ceratopsian have thus been in print for most of this century; and Seitz's (1970) study contains more such records than any other single paper.

In later work, Moodie (1928) reported the presence of lacunae and canaliculae in Haversian bone from "ossified tendons" of *Anatosaurus* (as "*Trachodon*") and *Ankylosaurus* (p.2), and that of lucunae is obvious in some of his "*Trachodon*" figures (Figures 2b, 6a & 6b). Bacterial enlargement of lacunae was also reported (p.2 and Figure 6a). Nopcsa and Heidsieck (1933) found lacunae and canaliculae in periosteal and Haversian bone from a half-grown *Hypacrosaurus*, and in fibro-lamellar tissue from a juvenile *Procheneosaurus* (as "*Tetragonosaurus*"), reporting round and polygonal lacunae as having diameters between 3-7μ, and spindle-shaped examples short diameters between 2-4μ (pp. 222, 224, 225). In the juvenile, the presence of lacunae is obvious in their figure (Figure 2); and they reported canaliculae connecting them as forming a network with meshes "about 4μ" wide (p. 225). Gross (1934, pp. 755-759) reported the presence and arrangement of lacunae in bone from *Plateosaurus*, *Brachiosaurus* and *Iguanodon*, calling them "bone cells" (Knochenzellen) or simply "cells" (Zellen), and gave figures showing obvious examples in *Brachiosaurus* tissues

(Figures 19 and 20), also noting contrasting arrangements in different parts of secondary osteons (Figure 20). De Lapparent (1947), Figure 6 and Plate 6, figures 1-4, 6) figured bone showing lacunae and canaliculae in *Rhabdodon*, with a drawn figure showing the canalicular network (figure 6c); and Pawlicki, Korbel & Kubiak (1966, Figures 1 and 3) used transmission EM photographs to illustrate these features as seen in an unnamed Gobi dinosaur. Later, Pawlicki (1977) reported concentration of mucopolysaccharide traces around lucunae and canaliculae in *Tarbosaurus*; used optical, transmission EM and SEM photographs (1978, Figures 1-6) to illustrate their form in this genus, also noting two types of fusiform lacunae with differently arranged canaliculae; and discussed (1984) the metabolic significance of dinosaurian lacunae and canaliculae. Reid (1984a, Figure 1) figured mineral filled lacunae and canaliculae from *Iguanodon*, mentioned Mantell's *Pelorosaurus* record (p. 629), and pointed out lacunae shown in Seitz's *Anatosaurus* figure (Reid 1985, p. 141), besides figuring bone with obvious lacunae from *Cetiosaurus*, *Valdosaurus*, *Aristosuchus* (1984a, Figures 2, 3 and 15; 1985, Figures 3, 4 and 8) and *Hypsilophodon* (1984b, Figure 1j). Besides lacunae, canaliculi can be seen in the 1985 *Aristosuchus* Figure; and Chinsamy (1990, p. 78) reported strongly branched examples from *Syntarsus*.

DISCUSSION

As noted at the start of this study, Fukuda and Oblata's (1993) paper involves two distinct problems. First, it is clear that they were wrong to suppose that nothing was known of dinosaurian osteocytes; and why they should have thought so is puzzling, when so much had been known for so long. Genera cited above, from which preserved lacunae were then known, total two (three?) prosauropods, seven sauropods, six theropods, five ornithopods, including three hadrosaurs, a stegosaur, an ankylosaur and a ceratopsian. The persistence of lacunae in dinosaurian bones had been known for 144 years (Quekett 1848); many details of their form, arrangement and preservation in over a dozen dinosaurs for 86 years (Seitz 1907); and their dimentions in two hadrosaurs, including a juvenile, for 60 years (Nopcsa & Heidsieck 1933). A transmission EM photograph had been in print for 27 years (Pawlicki, Korbel & Kubiak 1966), and scanning EM photographs for 15 years (Pawlicki 1978). Some of the relevant publications are probably not widely known (e.g. Hasse 1878); but *Nature*, in which the first EM photograph appeared, is not an obscure journal, and Seitz's classic "Vergleichende Studien" (1907) is required basic reading for anyone working on fossil bone. Perhaps, however, the answer is that osteocytes have not been involved in the controversy over dinosaurian physiology, except indirectly as secondary markers of different types of bone at fibrillar level (e.g. de Ricqlès 1975, p. 59 and Figure 1), and have hence received little or no attention in papers concerned with that topic (e.g. de Ricqles 1980; Reid 1987). Persons not familiar with studies of bone histology could thus get a false impression that nothing was known about them. Hopefully, this note will make how much we know more widely known.

Second, Fukuda and Obata's sample from a juvenile *Maiasaura* was stated to be compact bone from the upper articular surface of a limb bone (pp. 99-101), and was found to contain casts of lacunae which did not emit canaliculi (p. 101 and Figure 6). This they ascribed to "retardation of bone calcification in the juvenile" and taphonomic damage (pp. 101 and 102). But the articular faces of dinosaurian limb bones are not formed from compact bone, whose presence there would block growth in length, but from calcified cartilage, representing the deep parts of the growth plates under which new endochondral bone was formed (e.g. Reid 1984a, pp. 645 and 646 and Figures 24-27, *Iguanodon*; Reid 1996, Figures 38 and 39, *Allosaurus*; Figures 41 and 81, *Camptosaurus*); and a characteristic of cartilage is that the lacunae occupied by its chondrocytes do not emit canaliculi. Hence it seems likely that the tissue called compact bone was really calcified cartilage; and this would fit the style of calcification which their Figure 6 shows. The preservation of calcified cartilage in dinosaurian bones is again no new discovery, having first been figured by Hasse (1878, Figure 24a) from *Thecodontosaurus*.

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