

# ANALYSIS OF MILLERETTID PARAREPTILE RELATIONSHIPS IN THE LIGHT OF NEW MATERIAL OF *BROOMIA PERPLEXA* WATSON, 1914, FROM THE PERMIAN OF SOUTH AFRICA

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**SYNOPSIS** A second specimen of the poorly known millerettid *Broomia perplexa* is reported. It consists of a cranium and partially articulated postcranium. As indicated by its small size (*ca.* 35% shorter skull than the holotype) and unfused pelvis and limbs, the new specimen is a sub-adult individual. Comparison with the holotype reveals only minor differences that are ascribed to ontogenetic or individual variation. Accordingly we consider the new specimen to represent the second record of *Broomia*, discovered 90 years after the description of the holotype. A preliminary phylogenetic analysis of millerettid inter-relationships identifies *Broomia* as a millerettid related to the genus *Millerosaurus*. The enigmatic parareptile *Eunotosaurus africanus* is nested within Millerettidae as the sister taxon of *Milleretta rubidgei*. Whereas millerettids are well known from the latest Permian *Dicynodon* Assemblage Zone of the Beaufort Group of South Africa, *Broomia* and *Eunotosaurus* are found in the Middle Permian *Tapinocephalus* Assemblage Zone. The new *Broomia* specimen not only complements our knowledge of this early millerettid but also shows, in addition to recent findings in the same area, that the lowermost Beaufort Group is at least 1200 m thick in this area compared with *ca.* 2500 m in the western part of the Karoo Basin.

**KEY WORDS** Parareptilia, phylogeny, Gondwana, Middle Permian, *Tapinocephalus* Assemblage Zone

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## INTRODUCTION

Millerettids are small lizard-like reptiles considered to be the basalmost members of the Parareptilia (Laurin & Reisz 1995; deBraga & Reisz 1996; Modesto 1999; Berman *et al.* 2000; Reisz & Scott 2002). Some features of the group include a cranial ornamentation formed by shallow tubercles and the presence of a temporal fenestra (Gow 1972). Five species are known: *Milleretta rubidgei* Broom, 1938, *Millerosaurus ornatus* Broom, 1948, *Millerosaurus nuffieldi* Watson, 1957, *Milleropsis pricei* (Watson, 1957) and *Broomia perplexa* Watson, 1914. All are from the Permian of the Karoo Basin in South Africa. Whereas the millerettids from the latest Permian *Dicynodon* Assemblage Zone (AZ) are known from several specimens, the Middle Permian *Broomia perplexa* is the only millerettid from the *Tapinocephalus* AZ, and it is represented only by the holotype (Kitching 1977).

In the past, *Broomia* has been considered by several authors to be a taxon that is closely related, or ancestral, to the Millerettidae (Broom 1921, 1941; Romer 1956; Watson 1957; Kuhn 1969), but was not mentioned in the review of the Millerettidae by Gow (1972). The taxon has also been regarded as a probable araeoscelid diapsid (Nopcsa 1923; Piveteau 1955) or procolophonoid parareptile (Romer 1966). In a detailed and well-illustrated re-description of the genus, Thommasen & Carroll (1981) justified the classification of this taxon as a millerettid mainly on the basis of palatal features, but they could not evaluate the presence of distinctive millerettid features in other areas of the skull because the roof of the cranium is not preserved in the holotype. *Broomia* was also excluded from the phylogenetic definition of the group proposed by Laurin & Reisz (1995) and was not included in any other reptilian group by these authors. Scepticism in regarding *Broomia* as a millerettid may be due to the incompleteness of the holotype, which lacks the roof of the cranium, where some features that diagnose the Millerettidae are located (Gow 1972; Laurin & Reisz 1995). In addition, a considerable stratigraphical gap exists between *Broomia*, known from the *Tapinocephalus* AZ, and the millerettids from the *Dicynodon* AZ. This paper reports a new parareptile specimen from the *Tapinocephalus* AZ in Eastern Cape Province that can be clearly identified as a millerettid and exhibits features that are comparable with only *Broomia perplexa*. The new specimen also provides important cranial information not present in the holotype. The stratigraphical implications of the presence of *Broomia* in Eastern Cape Province are discussed.

## Institutional abbreviations

BMNH = Natural History Museum, London.

BP = Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg.

RC = Rubidge Collection, Wellwood, Camdeboo (formerly Graaff-Reinet) Municipality, Eastern Cape, South Africa.

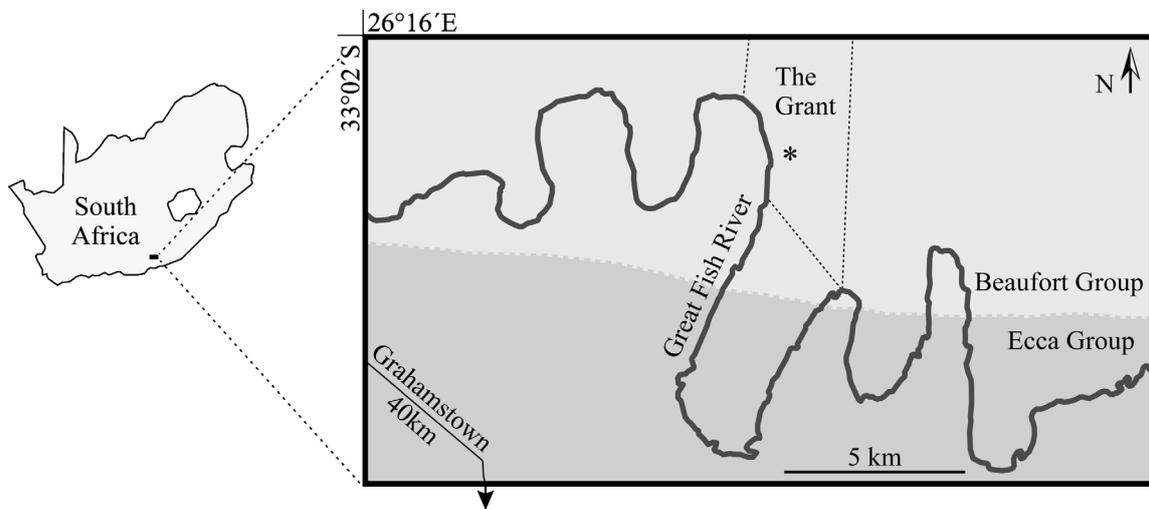
## MATERIAL AND METHODS

The new specimen, BP/1/6222, comprises a skull and postcranial elements. Most of the specimen had been exposed by erosion and was badly weathered, with only the impression of bone preserved in places. An air hammer was used as the main instrument to prepare the palate, but manual cleaning with fine needles was employed for delicate areas. The pelvic girdle and the right hindlimb were preserved largely as impressions in the mudstone, and negative preparation (i.e. the remaining bone was removed) was undertaken on these areas. This procedure was not applied to the right knee because in this area the bone is in good condition. The pelvis and right hindlimb areas that had been negatively prepared were filled with silicone in order to produce a positive cast for study. Numerous morphological details of the palate and the manus became visible only through the application of immersion oil.

The holotype of *Broomia perplexa*, BMNH R4065, consists of a natural impression and a silicone cast was employed for its study. Other comparative material included: *Milleretta rubidgei*, BP/1/2040, BP/1/2610, BP/1/2614, BP/1/2876, BP/1/3818, BP/1/3821, BP/1/3822, RC 14 (holotype) and RC 70; *Millerosaurus ornatus*, RC 78 (holotype); *Milleropsis pricei*, BP/1/720 (a block with at least eight specimens, including the holotype) and BP/1/4203.

## GEOLOGICAL SETTING

BP/1/6222 was discovered by Charlton Dube on the farm, The Grant, in Eastern Cape Province (Fig. 1). It was recovered from an argillaceous interval comprising dark olive-green mudstone with minor sandstones, 1705 m above the Ecca/Beaufort boundary. Stratigraphically the locality falls



**Figure 1** Locality map showing part of the Grahamstown area of South Africa and the farm The Grant. The site where the specimen was recovered is indicated by an asterisk.

within the middle part of the Koonap Formation (lower Beaufort Group), which is considered to have been deposited in a subaerial delta plain setting (Johnson & le Roux 1994).

At present the biostratigraphy of this part of the Karoo Basin is poorly known (Rubidge 1995). However, as a result of recent collecting activities in the area, dinocephalians (Modesto *et al.* 2001), scylacosaurid therocephalians and the parareptile *Eunotosaurus* have been found on The Grant, thus indicating that the lowermost Beaufort *Tapinocephalus* AZ (Boonstra 1969; Smith & Keyser 1995) is present in the area. This is in addition to an earlier discovery of *Eunotosaurus* 15 km to the east (Gow & de Klerk 1997).

## SYSTEMATIC PALAEOLOGY

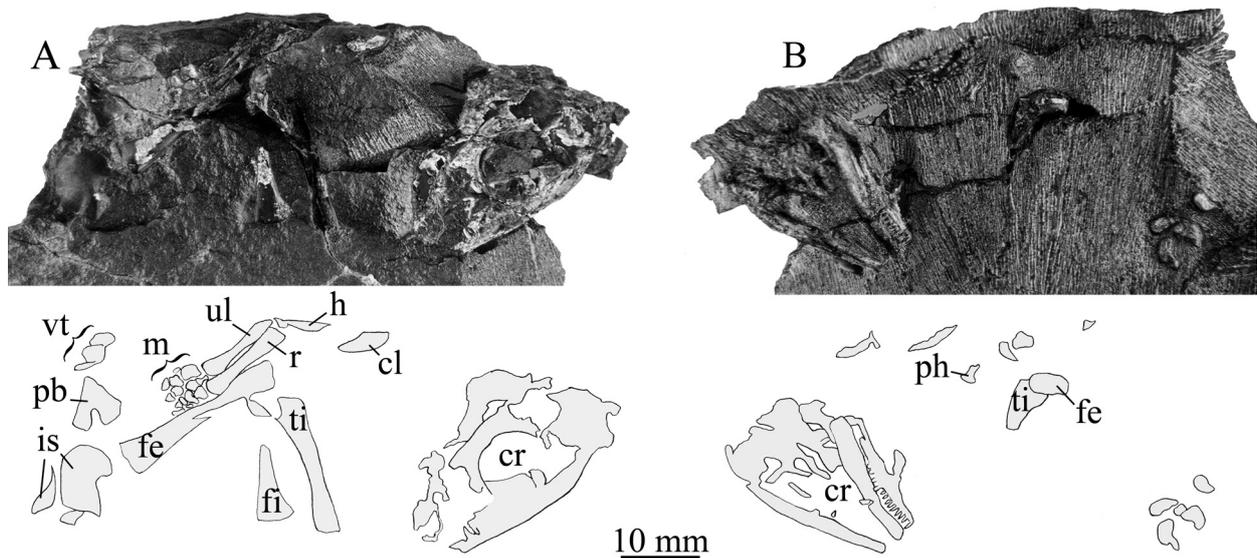
**PARAREPTILIA** Olson, 1947 *sensu* deBraga & Reisz, 1996

**MILLERETTIDAE** Romer, 1956

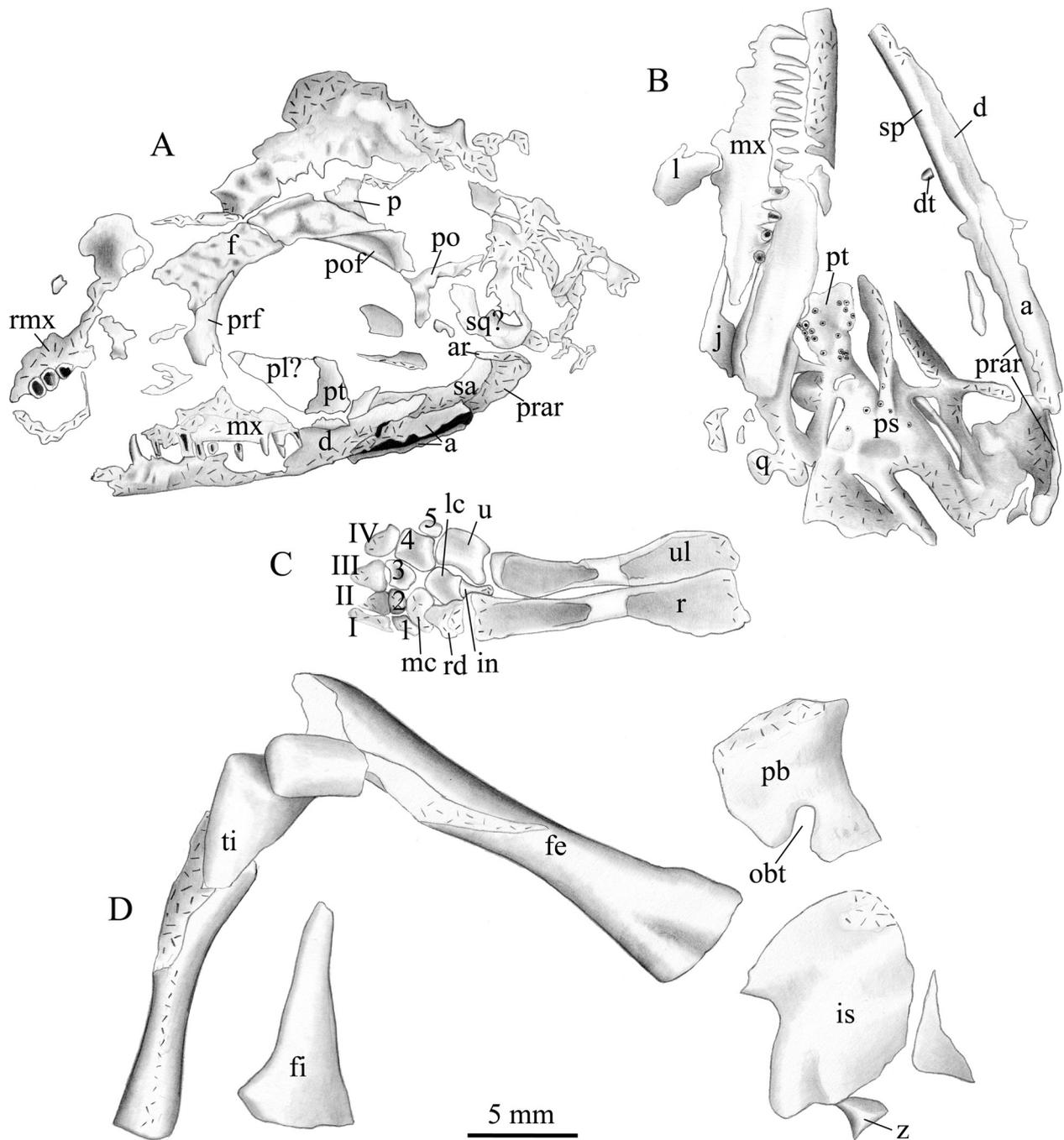
**NEW DEFINITION.** A clade that comprises all taxa more related to *Milleretta rubidgei* Broom, 1938, than to *Macroleter poezicus* Tverdokhlebova & Ivakhnenko, 1984.

***Broomia perplexa*** Watson, 1914 (Figs 2–3)

**HOLOTYPE.** BMNH R4065, an impression of a skull and fairly complete and articulated postcranium in ventral view.



**Figure 2** *Broomia perplexa* BP/1/6222. **A**, block containing the fossil, most elements are exposed in dorsal view. Pelvis and right hindlimb are shown prior to negative preparation. **B**, reverse side of the block, showing palate, the tibia–femur articulation and some unidentified postcranial elements. Abbreviations: cr, cranium; cl, clavicle; fe, femur; fi, fibula; h, humerus; is, ischia; ph, phalanx; m, manus; pb, pubis; r, radius; ti, tibia; ul, ulna; vt, vertebrae.



**Figure 3** *Broomia perplexa* BP/1/6222. **A**, cranium, left lateral and dorsal surfaces. **B**, cranium in palatal view and attached mandible. **C**, antebrachium and carpus in dorsal view. **D**, pelvis and hind limb in ventral view, draw from silicon casts, except for the tibia–femur articulation, drawn from the actual bone and superimposed onto the illustration. Abbreviations: a, angular; ar, articular; d, dentary; dt, dentary tooth; f, frontal; fe, femur; fi, fibula; in, intermedium; is, ischium; j, jugal; l, lacrimal; lc, lateral centrale; mc, medial centrale; mx, maxilla; obt, obturator foramen; p, parietal; pb, pubis; pl?, palatine?; po, postorbital; pof, postfrontal; prar, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; r, radius; rd, radiale; rmx, right maxilla; sa, surangular; sp, splenial; sq?, squamosal?; ti, tibia; u, ulnare; ul, ulna; z, zygopophysis. Metacarpals and distal carpals are indicated by Arabic and Roman numerals, respectively.

REFERRED SPECIMEN. BP/1/6222, a partial, articulated small skull and postcranium with some areas preserved as impressions.

REVISED DIAGNOSIS. Among millerettids, the following features are known only in *Broomia perplexa*: palate bearing longitudinal ridges with multiple rows of denticles, shagreen of denticles present in the depression between these ridges,

ulnare proximodistally elongated, and wholly or partially fused lateral centrale and intermedium (suture still visible). Autapomorphies in the manus are preliminary because the postcrania of *Millerosaurus ornatus* and *M. nuffieldi* are not known.

PROVENANCE. BMNH R4065 was collected at the farm Hotentots Rivier 296 (32° 23' S; 21° 58' E), Beaufort West

district, Western Cape Province, Republic of South Africa. BP/1/6222 was collected from the farm The Grant (33° 03' S; 26° 23' E), Grahamstown district, Eastern Cape Province, Republic of South Africa. *Tapinocephalus* AZ (Kitching 1977), Koonap Formation, Middle Permian (Guadalupian).

## DESCRIPTION

The specimen appears to have been buried in a curled-up position. A curled-up posture in our specimen is inferred from the proximity of the right hindlimb to the head, which in turn, faces posteriorly (Fig. 2A). A curled-up position is also displayed by the holotype of *Broomia perplexa*.

### Cranial skeleton

The skull has been dorsolaterally compressed (Fig. 3A) with the result that the right side of the skull has collapsed, whereas the left side and the skull roof are preserved in the same plane, opposite the palate. The tip of the snout and most of the basiocranium are missing. Sculpturing, consisting of a melange of tubercles and minor rugosities, covers the external surfaces of the cranium including all skull-roof bones and the dentary. No pits, ridges, or large bosses are present. There is no evidence of osteoderms.

Most of the right maxilla is preserved (Fig. 3B). This bone is elongated anteroposteriorly and, although it is weathered, its irregular surface suggests the presence of ornamentation. Dorsally, part of the contact of the maxilla with the nasal is present, whereas posterior to the nasal, the maxilla contributes to the rim of the orbit. This area is not well preserved. Posteroventrally the maxilla thins progressively as it contacts the jugal. The right maxilla bears at least 13 teeth, which are all thin, conical and slightly recurved posteriorly. The anteriormost tooth is the largest in the maxilla and the following teeth progressively decrease in size toward the posterior end. Part of the right maxilla is exposed in medial view (Fig. 3A) and shows sections of three maxillary teeth. Only a small portion of the left maxilla is preserved. Eight teeth are present, among which the largest tooth is exposed in longitudinal section, showing a shallow root that is ankylosed to the bone. No foramina could be distinguished on either maxilla.

The posterior portion of the right lacrimal is present (Fig. 3B). It contacts the maxilla ventrally and contributes to the orbital rim. The left prefrontal is partially preserved and forms the anterior part of the orbital margin, whereas dorsally it contacts the frontal. A long and thin process of the prefrontal extends posteriorly along the rim of the orbit. The right frontal is well preserved and its dorsal surface is extensively sculptured. This roughly rectangular bone contacts the nasal anteriorly, the prefrontal and the postfrontal laterally, the parietal posteriorly and it contributes to the orbital rim. The postfrontal is a triangular bone with an acute process that extends anteriorly and contributes to the dorsal margin of the orbit. Only a small portion of the left parietal is present and it is in sutural contact with the frontal. A larger portion of the right parietal is preserved and it exhibits a highly ornamented surface. The margins of this bone, except for the medial margin, are not clear. A small crescentic notch along the medial margin of the right parietal probably constitutes the right border of the pineal foramen.

A small portion of the left postorbital is present and forms the posterior border of the orbit. Part of the right jugal, which is slightly dislocated from its natural position, is exposed in ventral view (Fig. 3B). The posterior margin of this bone is a vertical edge that could be either a sutural contact with the quadratojugal, or the margin of a temporal fenestra. As the temporal region is damaged on both sides of the cranium, it is not possible to determine whether the new specimen possesses a temporal fenestra. A bone fragment in the left temporal region is tentatively identified as the squamosal. Additional small bones that are visible beneath the orbit in dorsal view include small portions of the palatine and possibly the pterygoid.

The posterior portion of the palate has been prepared (Fig. 3B), but matrix has been left in the anterior portion to avoid weakening the fragile skull. No sutures are visible in the palate and only general features are described here. The palate was covered by several minute denticles but these delicate elements were lost during mechanical preparation. Some of their pulp cavities are visible through the use of immersion oil. The general morphology of this region does not differ from that of other millerettids. A long interpterygoid vacuity is partially visible, and its borders are formed by ridges of relatively thick bone. Clusters of pulp cavities visible on the ridge along the right border of the interpterygoid vacuity indicate that multiple rows of denticles were present along the medial margin of the pterygoid. A second ridge in the pterygoid projects obliquely towards the palatine from the medial ridge. This pterygo-palatine ridge has at least two rows of denticles. A few sparse pulp cavities are present in the depression between the pterygo-palatine ridge and the medial ridge, indicating that this area was covered with a shagreen of denticles. The posterior edges of the pterygoid transverse flanges are damaged, so it is not possible to determine if denticles are present. As in other millerettids, the quadrate process of the pterygoid projects posterolaterally. A small lamina of bone attached to the right quadrate process may be a distorted portion of the pterygoid or a dislocated bone from the cranial roof. The parasphenoid body is basically triangular. A small oval depression is present on its anterior ventral surface and some denticles are visible adjacent to the base of the parasphenoid rostrum. The posterior ventral surface of the parasphenoid body is badly preserved. The cultriform process is long and narrow and it bears some denticles on its base; possibly more teeth were present along the cultriform process but most of its ventral surface is damaged. The quadrate condyle is situated anterior to the occiput, at the mid-length of the parasphenoid corpus. No other elements are visible or preserved in the palate or the braincase.

The mandible, most of which is preserved apart from the symphysis, is tightly occluded to the skull and, as a result, is only partially visible. It is slender, slightly shorter than the skull and in general morphology does not differ from that of other millerettids. The right dentary is exposed better than the left one and has sculpturing on the anterior end. Most of the lateral surface of the lower jaw comprises the dentary, which thins posteriorly, where it contacts the angular and overlaps the anterior portion of the surangular. Only one tooth is visible on the left dentary. This is long, conical and slightly recurved posteriorly. The splenial is only partially visible in ventral view and forms the antero-medial portion of the mandible. The right coronoid is not exposed and the left coronoid is missing. The ventrolateral margin of the posterior portion of the mandible comprises

an elongated angular. Dorsally the angular is bordered by the prearticular and the surangular. A fracture on the right angular has exposed an endocast of the Meckelian canal (represented in black on Fig. 3A). The thin surangular, which is shorter than the angular, is slightly recurved dorsally at its posterior end where it contacts the articular. Only portions of the right prearticular are visible, but a fortuitous fracture on the right lower jaw has exposed part of the prearticular in lateral view. The articular is a small splinter of bone positioned obliquely on the posterodorsal extremity of the jaw that contacts the surangular, the prearticular and, presumably, the angular.

### Postcranial skeleton

The vertebral column is missing, except for the badly preserved partial moulds of three posterior presacral vertebrae. Most of the pectoral girdle is lost, but a small crescentic plate between the humerus and the cranium represents the distal portion of the right clavicle. The left limbs are missing. The unfused state of the pelvic girdle elements suggests that the specimen is a juvenile (Fig. 3D). The pelvis is represented by elements of the right ischium and pubis. The pubis is missing its anterior and medial margins, but despite this it is apparent that the medial portion of the bone is slightly recurved dorsally and the obturator foramen is not closed. The right ischium and a tiny portion of the left, are present. This bone forms an oval plate and has a concave lateral margin. A shallow depression protrudes medially from the edge of the lateral concavity and a second, curved depression is visible on the posterior portion of this bone. The morphology of the pelvic elements of BP/1/6222 is entirely compatible with those of BP/1/3821, a much smaller juvenile *Milleretta* individual described by Gow (1972: figs 14, 17b). A small fragment of bone preserved posterior to the right ischium is probably a zygopophysis.

Only a portion of the right humerus is preserved, but this is badly weathered and is uninformative. The radius, the ulna and many elements of the manus are exposed in ventral view (Fig. 3C). A long fracture, present on both the radius and the ulna, has resulted in the separation of longitudinal sections of both bones that reveal wide medullary cavities in each. The ulna is shorter than the radius and articulates distally with the ulnare and the intermedium. The radius articulates distally with the radiale and more laterally with the intermedium. Ten carpal elements are present and are well ossified, despite the immaturity of the specimen. The ulnare is the largest element in the carpus of BP/1/6222 and is a proximodistally elongated, subrectangular bone. Its anterior and lateral margins are slightly convex whereas the medial and posterior margins are concave. The ulnare articulates medially with the lateral centrale and the intermedium. The lateral centrale is a pentagonal bone, equivalent in length and width, and its lateral, medial and posterior margins are concave. The anterior and posterior ends of this bone are slightly thicker, creating a shallow depression that extends from the medial to the lateral margin. The intermedium is firmly attached to the posterior border of the lateral centrale, indicating that these bones are wholly or partially fused. Medial to the lateral centrale is the incompletely preserved radiale. Anterior to the radiale is the medial centrale, which is a thin, semilunar bone, with a posterior notch for the radiale articulation. Five distal carpals are present. The largest of

these is the fourth distal carpal, which is *ca.* 50% wider than the neighbouring third distal carpal, which exhibits a shallow oval ventral depression. Only the most proximal portions of metacarpals I–IV are preserved.

The right hind limb is preserved in ventral view but lacks the pes (Fig. 3D). The unossified femoral ends are another indication that the specimen is immature. The preserved portion is long and gracile and it resembles the femur of the juvenile specimen of *Milleretta*, BP/1/3821 (Gow 1972: figs 17d–g). The tibia, which is preserved in articulation with the femur, is fractured across the shaft. The proximal end is not very prominent, but this may be a result of the juvenile status of the specimen. Only the distal portion of the fibula is preserved.

### Comparisons with other millerettids

BP/1/6222 displays a cranial ornamentation formed by gently domed tuberosities, a long inter-ptyergoid vacuity and denticles on the cultriform process and the ventral plate of the parasphenoid. These three features are considered diagnostic characters of the Millerettidae (Gow 1972; Thommasen & Carroll 1981; Laurin & Reisz 1995). The carpus of BP/1/6222 is long and slender, a character previously considered diagnostic of millerettids (Laurin & Reisz 1995), but which is now known to be also present in bolosaurids (Berman *et al.* 2000) and in basal procolophonoids (J.C.C., pers. obs.). On the basis of cranial features we identify the new specimen as a millerettid parareptile. As the palate and carpus of the new specimen are the best-preserved elements, comparisons with other millerettids will be restricted to these elements.

*Milleropsis pricei* is characterised by, among other characters, a narrow cranium and a long snout. Although the snout is not complete in BP/1/6222, its palate is clearly wider than that of *Milleropsis* and the proximity of the anterior ends of the two lower jaws indicates that only small portions of the mandible and the snout are missing, which in turn indicates that the cranium of BP/1/6222 was not elongated. The maxillary dentition of *Milleropsis pricei* is isodont, in contrast to that of BP/1/6222, which shows a caniniform region and an enlarged anterior caniniform in the maxilla. The carpus of *Milleropsis* differs from that described for the new specimen (Thommasen & Carroll 1981: fig. 2e) in that the ulnare of *Milleropsis* is considerably wider than long, the lateral centrale is a triangular element with only a short contact with the intermedium, the posterior margin of the fourth distal carpal of *Milleropsis* is convex and has a large contact with the lateral centrale and the third distal tarsal possesses a ventral ridge.

Comparisons with the genus *Millerosaurus* are more difficult. The two species within this genus are represented only by holotypic material and their postcrania are unknown. We were unable to examine the holotype of *Millerosaurus nuffieldi* (held in the Museum of Zoology, Cambridge). *Millerosaurus ornatus* is represented by a partial skull, RC 78, which consists of several elements not preserved on BP/1/6222, including the diagnostic supratemporal. However, the presence of single rows of pterygoid denticles in this genus (Watson 1957) indicates that the new specimen cannot be referred to *Millerosaurus*.

The palate of BP/1/6222 exhibits some similarities with that of *Milleretta rubidgei*. That species typically has single

denticle rows in the palate (Thommasen & Carroll 1981: fig. 2b), but the presence of double denticle rows in the palate of the holotype (RC 14) (Gow 1972: pl. 2) suggests that the condition is variable within the species. However, none of the specimens referred to *Milleretta* exhibits a shagreen of denticles between the pterygo–palatine row and the pterygoid medial row, a character which is present in the new specimen and represents a major difference between *Milleretta* and BP/1/6222. A partial carpus of *Milleretta* is known in the juvenile individual BP/1/3821 and it exhibits a rounded medial centrale and a proximodistally compressed, semilunar lateral centrale (Gow 1972: fig. 16i), which both differ from the morphology seen in BP/1/6222. Based on the differences in the palate and the carpus we do not consider BP/1/6222 to be referable to *Milleretta*.

The palate of the holotype of *Broomia perplexa* (BMNH R4065) has a multiple row of denticles along the medial edge of the pterygoid and another shorter multiple row on the pterygo–palatine ridge. These rows of denticles are more abundant than those in *Milleretta* (RC 14) or any other millerettid specimen. As in BP/1/6222, the holotype of *Broomia perplexa* shows a palatal shagreen in the depression between the two main palatal denticle rows. A character in BMNH R4065 that may differ from our specimen is the probable absence of denticles along the cultriform process. Watson (1957) reported and figured denticles along the cultriform process of the holotype of *Broomia perplexa*, but Thommasen & Carroll (1981) did not report the presence of this character and we cannot confirm this feature in our silicone cast of the holotype. The general morphology of the carpus of the new specimen is more compatible with that of BMNH R4065 (Thommasen & Carroll 1981: figs 1, 2d) than with those of *Milleretta* or *Milleropsis*. The carpi of BMNH R4065 and BP/1/6222 share a proximodistally elongated ulnare, a fused lateral centrale and intermedium, an anteroposteriorly compressed and crescentic medial centrale and a third distal carpal bearing a ventral depression. The only difference between the carpus of the holotype of *Broomia perplexa* and that of our specimen is the concave lateral border of the ulnare of the former, contrary to the convex lateral margin in our specimen. This minor difference may be attributed to ontogenetic or individual variation. Based on the comparisons presented above, we consider that our specimen is morphologically more similar to *Broomia* than other millerettids and, as such, is only the second record of this genus.

## INTERRELATIONSHIPS OF THE MILLERETTIDAE

### Methods

Early workers (e.g. Broom 1921, 1941; Watson 1957) proposed that *Broomia* occupies a basal position in relation to the end-Permian millerettids, a hypothesis that is, in part, suggested by the early age of *Broomia*. In order to investigate the phylogenetic position of *Broomia* we performed a cladistic analysis of millerettids. Previous analyses have merely evaluated the relationships of Millerettidae within Parareptilia; hence, the present analysis is intended as a preliminary study of millerettid interrelationships. This phylo-

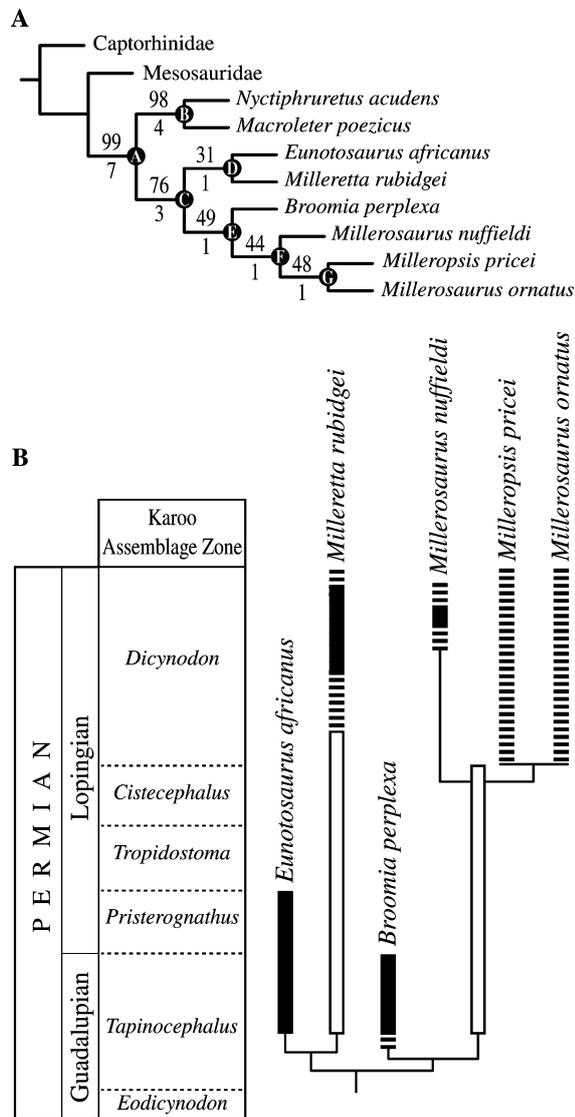
genetic analysis includes the five known millerettid species and the parareptile *Eunotosaurus africanus* as operational taxonomic units (OTUs). Previous workers (Gow 1997; Gow & de Klerk 1997) proposed that *Eunotosaurus* is closely related to the millerettids, a hypothesis that has gained support from recent cladistic studies (Tsuji 2006; Reisz *et al.* 2007). The clade Ankyramorpha (*sensu* deBraga & Reisz 1996) is represented in our analysis by *Nyctiphruetus acudens* and *Macroleter poezicus* (Efremov 1940; Ivakhnenko 1987; Tsuji 2006; Müller & Tsuji 2007; Reisz *et al.* 2007). Mesosauridae, a group considered to be the sister taxon of Parareptilia (Modesto 1999), has also been included. The outgroup is Captorhinidae (Romer 1956; Heaton 1979; Modesto *et al.* 2007). A character list was compiled largely based on Laurin & Reisz (1995) following modifications by Modesto (2000), Tsuji (2006) and this study. Other characters were taken or adapted from deBraga & Reisz (1996), deBraga & Rieppel (1997) and Gow & de Klerk (1997). Characters 3, 4, 8, 9, 14 and 19 are new to this study. All characters are informative of parsimony and were given equal weighting. Only character 10 was ordered. The analysis was run using TNT 1.1 (Goloboff *et al.* 2003) using the Implicit Enumeration algorithm, which provides exact solutions, and collapsing branches with ambiguous support.

### Results

One most parsimonious tree (MPT) with 59 steps was found (Fig. 4A). The analysis recognises a well-supported, monophyletic Millerettidae (clade C). The group is diagnosed by six non-ambiguous synapomorphies, including a cranial sculpturing consisting of low tubercles and a long interpterygoid vacuity. The analysis recognises *Eunotosaurus* as the sister taxon of *Milleretta*, a relationship supported by the presence of thickened and overlapping trunk ribs (state 1 of characters 28 and 29). Accordingly, *Eunotosaurus* is identified in this study as a millerettid. *Broomia perplexa* is identified by TNT as a member of a group of millerettids (clade E, Fig. 4A) that are characterised by having temporal openings in an adult stage (character 11, state 1). Although the presence of this character state could not be confirmed in the new specimen, the morphology of the jugal in the holotype is consistent with the presence of a temporal opening. Our results indicate that the genus *Millerosaurus* is paraphyletic. However, clade F is poorly supported and, given the preliminary nature of the analysis, it seems premature to make *Milleropsis* a junior synonym of *Millerosaurus* or to allocate *Millerosaurus nuffieldi* to a new genus.

### Discussion

Overall, relationships within Millerettidae are poorly supported in this analysis. This phenomenon is probably related to the incompleteness of our current knowledge of some taxa. The genus *Eunotosaurus* is better known from postcranial material but both species of the genus *Millerosaurus* are known exclusively from incomplete holotypic cranial material, making many character state comparisons impracticable. The taxonomy of millerettids as currently established (Gow 1972) relies heavily on the structure of the temporal region, but this area is poorly preserved in both *Broomia* specimens and the morphology of the temporal fenestrae in this taxon is not well understood.



**Figure 4** **A**, Single most parsimonious tree (MPT) produced by TNT. Tree length = 59; consistency index = 0.746; retention index = 0.766. Symmetric resampling and decay index values (above and below, respectively) are given next to each node. Decay index values were calculated from 212 trees. Symmetric resampling was performed using 5000 replicates and 10 repetitions ( $P = 0.33$ ) using the Traditional Search option (random addition sequences plus tree bisection–reconnection). Non-ambiguous synapomorphies (with character states in parentheses): clade A (Parareptilia): 10(1), 12(1), 15(1), 18(1), 21(1), 22(1), 23(1), 30(1), 34(1); clade B (Ankyramorpha) 7(1), 25(1), 31(1), 32(1), 33(1); clade C (Millerettidae): 2(1), 4(2), 17(1), 19(1), 20(1), 26(1); clade D: 28(1), 29(1); clade E: 11(1); clade F: 8(1); clade G: 13(1). **B**, Phylogenetic relationships of Millerettidae within a biostratigraphical context. Ghost lineages and/or taxa are represented by open bars.

*Broomia* and *Eunotosaurus* are separated by a considerable geological gap from *Milleretta*, *Millerosaurus* and *Milleropsis* (Fig. 4). Our results indicate that *Milleretta*, despite its latest Permian age, is as basal as *Broomia*. Accordingly, at least two ghost lineages link the millerettids from the *Dicynodon* AZ to those from the *Tapinocephalus* AZ.

The new specimen represents only the second record of *Broomia perplexa*, 90 years after the description of the holotype. The new material, which possesses a skull more complete than that of the holotype and displays, among other features, the characteristic cranial sculpturing of the Millerettidae, provides important additional evidence that *Broomia* is indeed a millerettid, despite the long stratigraphical gap that separates this taxon from the genera recorded in the *Dicynodon* AZ. In addition, a phylogenetic analysis supports recent hypotheses that the problematic taxon *Eunotosaurus*, which is contemporaneous with *Broomia* in the *Tapinocephalus* AZ, has millerettid affinities.

Stratigraphical logging on The Grant and neighbouring farms in the Grahamstown area (Mason 2007), in concert with the prospecting that yielded the new specimen of *Broomia*, dinocephalians (Modesto *et al.* 2001), scylacosaurid therocephalians and the parareptile *Eunotosaurus*, indicates that the *Tapinocephalus* AZ is up to 1700 m thick in the southeastern part of the Karoo Basin, compared with about 2500 m in the western part (Kitching 1977; Smith & Keyser 1995). The *Tapinocephalus* AZ thus thins toward the east and is not as completely preserved as in the west. This thinning of the *Tapinocephalus* AZ, together with the absence of deposits of the *Eodicynodon* AZ in this part of the basin (Mason 2007), supports earlier conclusions (Rubidge *et al.* 2000; Rubidge 2005) that the earliest terrestrial deposition in the Karoo Basin took place later in the southeastern part of the basin than on the southwestern side.

## CONCLUSIONS

The new *Broomia perplexa* material clarifies the relationships of this species, showing that this taxon is indeed a millerettid reptile. A phylogenetic analysis shows that Millerettidae is a well supported, monophyletic clade within Parareptilia. This analysis indicates that *Broomia* is closely related to *Milleropsis* and *Millerosaurus*. The enigmatic genus *Eunotosaurus* is recognised as a true millerettid, being the sister taxon of *Milleretta*. Despite their Middle Permian age, *Broomia* and *Eunotosaurus* are more related to the end-Permian millerettids than to each other, resulting in two long ghost lineages within the group. The presence of *Broomia* in the Grahamstown area reinforces previous suggestions that the *Tapinocephalus* AZ is thinner in the east than in the west of the Karoo Basin.

## ACKNOWLEDGEMENTS

We are grateful to Colin and Richard Were for hospitality and access to their properties in the Eastern Cape for fieldwork over many years, Billy de Klerk of the Albany Museum for logistical support and Sandra Chapman from the Natural History Museum, London, for the loan of a cast of the holotype of *Broomia perplexa*. Suggestions from Sean Modesto, Johannes Müller and two anonymous referees greatly improved this work. Our research was financially supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil), Department of Science and Technology (DST, South Africa), National Research Foundation (NRF, South Africa) and the Palaeontological Scientific Trust (PAST, South Africa).

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## APPENDIX A: CHARACTER LIST

Sources for each character are given within square brackets [authors and former character numbers]; asterisks indicate characters that have been modified.

A, Laurin & Reisz (1995); B, deBraga & Reisz (1996); C, deBraga & Rieppel (1997); D, Gow & de Klerk (1997); E, Tsuji (2006).

0. Pits on dermal sculpturing: present (0), absent (1). [A:38\*]
1. Tuberosities on dermal sculpturing: absent (0), gently domed (1), prominent (2). [A:38\*]
2. Maxilla and quadratojugal: in contact (0), separated (1). [A:22]

