BROOMIA, THE OLDEST KNOWN MILLERETTID REPTILE

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ABSTRACT. *Broomia perplexa* is a primitive sauropsid reptile from the Middle Permian of South Africa. Preparation of the type specimen indicates that Watson's original description was in error in describing features of palate, carpus, and tarsus that appeared to distinguish the specimen from other primitive reptiles. *Broomia* is a millerettid, apparently descended directly from the romeriid captorhinomorphs. It is considerably older than other millerettids, and so is of considerable evolutionary and taxonomic importance.

THE most primitive known reptiles, the romeriid captorhinomorphs, appear in the fossil record in the Carboniferous and Lower Permian. Thorough descriptions of members of this ancestral anapsid family (Clark and Carroll 1973; Carroll and Baird 1972) indicate they are antecedent to all advanced members of the Reptilia.

Two broad groups of higher reptiles are recognized: the Theropsida and the Sauropsida. The evolutionary history of the Theropsida is well preserved and it is clear they give rise to mammals before becoming extinct in the Middle Jurassic. The latter group includes all the familiar living orders: Crocodilia, Squamata, Chelonia, and Sphenodontidae, as well as the extinct dinosaurs and the sauropsid ancestors of birds.

A hiatus in the fossil record separates the primitive captorhinomorphs, not known after the Lower Permian, and a number of distinct groups known first from the Middle and later Permian—namely, the Eosuchia, Prolacertilia, and Millerosauria. The specific origins of these groups remain to be established. The millerosaurs appear closest to the romeriids in their general anatomy, and appear relatively early in the Middle Permian. The oldest species attributed to this group is *Broomia perplexa* from the *Tapinocephalus* zone of South Africa known only by the type specimen. This fossil, preserved in a block of quartzitic sandstone, was recovered from Hottentots River, Beaufort, South Africa (Kitching 1977). *Broomia* is considerably older than the well-known millerettids of the *Daptocephalus* and the *Cistecephalus* zones which have been described by Watson (1957) and Gow (1972) and might be expected to cast some light on the origin of the group.

Watson (1957) cites *Mesenosaurus romeri* as the oldest reptile related to the millerettids, but a recent redescription of this genus indicates (Ivakhnenko and Kurzanov 1978) that it is a diapsid, possibly ancestral to the archosaurs. This leaves *Broomia* as the oldest-known link between the romeriids and the millerettids.

Watson's original description (1914), based on the unprepared specimen and carried out at a time when nothing was known of the romeriids, depicts *Broomia* as a unique 'lizard-like' form which could not be placed in any of the known orders of reptiles. This was based on the seemingly peculiar nature of the carpus, tarsus, pectoral girdle, and skull. In a later review (1957) he mentioned that new casts revealed previous errors in skull proportions and he noted similarities between *Broomia* and the millerettids.

Mr. R. Croucher of the British Museum (Natural History) has since prepared the specimen by etching away the bone with hydrochloric acid to leave a high fidelity mould in the acid resistant matrix. Silicone rubber and latex casts from this mould indicate that many of the unique features attributed to *Broomia* are, in fact, artifacts of preservation and that the anatomy is even closer to that of later millerettids than Watson suspected.

Correction of these errors is among several reasons for publishing a rather detailed description

of this fossil. The carpus and tarsus are much more completely ossified than in later millerosaurs and so provide much more information. This is the oldest animal with specific millerosaur affinities and hence may be expected to provide a valuable basis for evaluating the origin of the group.

The skeleton of *Broomia* (text-fig. 1) has been exposed primarily in ventral view. The skull is represented by little more than the buccal surface of the palate. The anterior trunk and more posterior caudal vertebrae are not exposed. The tarsus, in ventral view, and the carpus in dorsal view, are beautifully preserved. All other elements are at least present, and a fairly complete account of the animal's structure is possible. The specimen is extremely well ossified and so presumably represents a fully mature individual of close to maximum size.

The skull and lower jaw

The palate is primitive in most respects and can be readily derived from that in *Paleothyris acadiana* (Carroll 1969), a Pennsylvanian romeriid. It differs from the eosuchians and *Petrolacosaurus kansensis*, the oldest-known diapsid (Reisz 1977), in lacking a suborbital vacuity between the ectopterygoid and palatine elements. All the advanced characters exhibited in the palate are identical to those found in millerosaurs. Both *Broomia* and the millerettids have the quadrate condyle anterior to the basioccipital and there is a lower temporal opening. The exact nature of this opening appears to be variable within the millerettid group (Gow 1972). The palate in *Broomia* differs from Watson's original description (1914) in the location of the internal nares and the proportions of the elements (text-fig. 2A).

The occipital condyle and exoccipitals are present but show little detail. The parasphenoid resembles that of *Protorothyris* and other Pennsylvanian romeriids. The very long and narrow cultriform process projects a considerable distance anteriorly. The parasphenoid does not terminate posteriorly as a diamond-shaped expansion on the lower surface of the basisphenoid as was suggested by Watson but forms a broad concave sheet under the basioccipital. There are no carotid foramina but it is possible that the internal carotids followed grooves running anteriorly just lateral to the base of the cultriform process into the brain-case. Small teeth are present, lateral to the base of the parasphenoid rostrum, but the exact number is not discernible. The narrow rostrum seems to have carried no teeth. All the above features (text-fig. 2B) are to be found in *Milleretta* (Gow 1972) and *Paleothyris* (Carroll 1969), except that *Paleothyris* lacks denticles on the body and cultriform process, while *Milleretta* possesses denticles on both of these elements. Fox and Bowman (1966) discussed the irregularity of occurrence of teeth on the parasphenoid in primitive reptiles.

The basisphenoid is visible from below only at the basipterygoid processes. The forwardly directed processes are beautifully preserved, and as reported by Watson, lie above the general level of the lower surface of the bone and project at nearly right angles to the length of the skull. The convex anterior articular facets suggest that the basal articulation with the palatal complex would have facilitated dorsoventral movement of the brain-case on the palate.

The pterygoids in *Broomia* are large elements which have been preserved throughout much of their length. Their shape and size resemble those of the Pennsylvanian romeriid *Paleothyris*, as well as those of the millerosaurs. The unusually long interpterygoid vacuity is a characteristic shared with the millerettids. The quadrate ramus extends back to the quadrate as a narrow, tapered element. The palatal portion of the pterygoid bears three raised ridges, each covered with small closely set denticles. The transverse flange of the pterygoid is large and bears a single row of teeth. The second, anteriorly directed ridge is continuous with that on the palatine and bears two rows of fairly large denticles. The third ridge forms the inner margin of the pterygoid bone and runs anteriorly as far as the bone is preserved. This ridge is covered with a number of irregular rows of teeth. A few denticles are also found scattered in the depressions between these ridges. All in all, this is a primitive pattern comparable to that seen in *Milleretta*, romeriids, and primitive eosuchians. The lateral orientation of the transverse flange of the pterygoid in *Broomia* is intermediate between the posteriorly directed flange in *Protorothyris* and the more downturned flange of *Millerosaurus*. There is no evidence that the pterygoids do not meet anteriorly. The
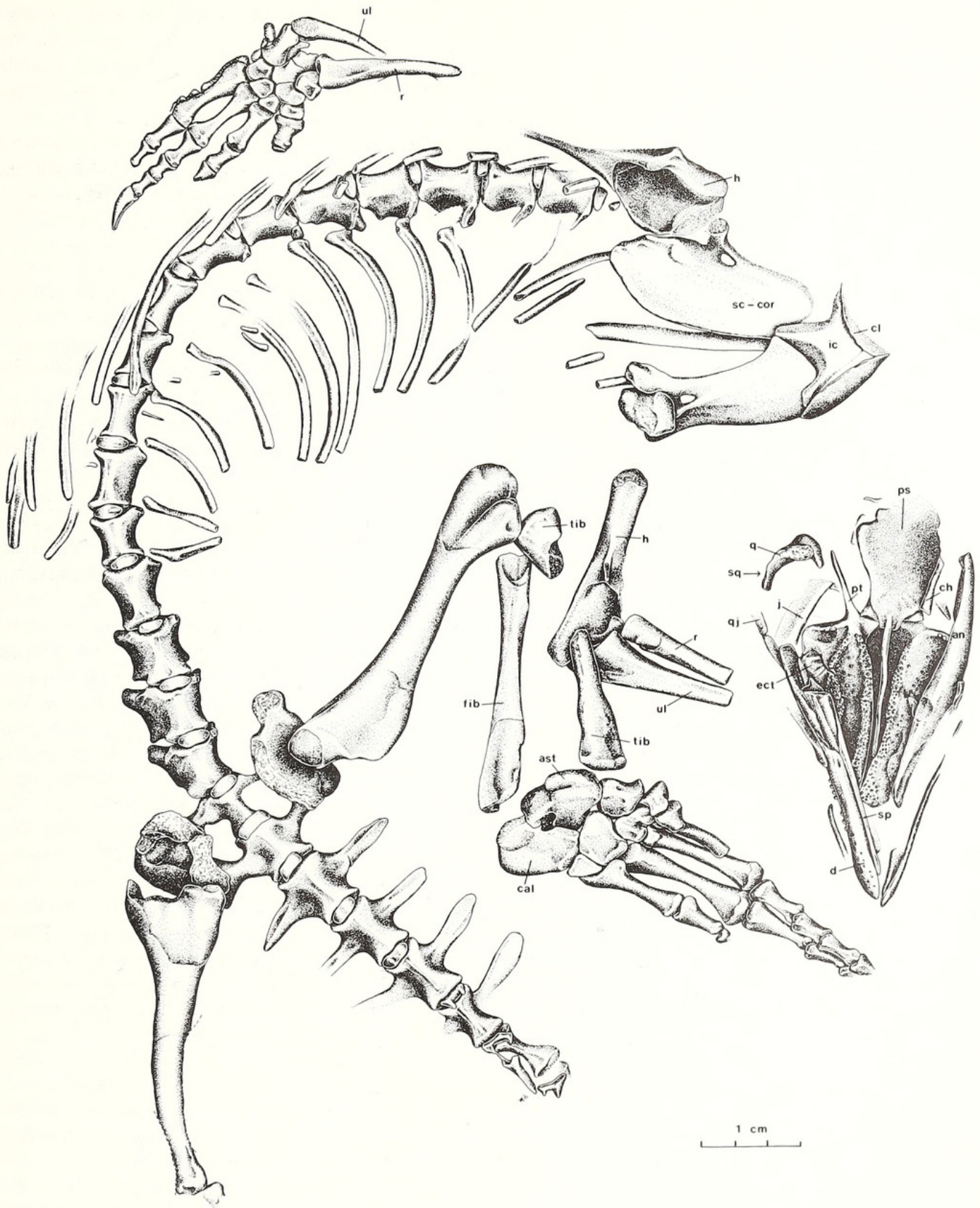
TEXT-FIG. 1. Skeleton of *Broomia perplexa*, drawn from a latex cast. British Museum (Natural History) no. 4065, × 1 ½. Abbreviations used in figures: an, angular; ast, astragalus; bo, basioccipital; cal, calcaneum; cen, centrale; ch, ceratohyal; cl, clavicle; d, dentary; ect, ectopterygoid; fib, fibula; h, humerus; i, intermedium; ic, interclavicle; j, jugal; lc, lateral centrale; m, maxilla; mc, medial centrale; op, opisthotic; p, pisiform; pal, palatine; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; r, radius; rad, radiale; sc-cor, scapulocoracoid; sp, splenial; sq, squamosal; st, stapes; tib, tibia; u, ulnare; ul, ulna; v, vomer; 1–5, distal tarsals and carpals; I–V, metatarsals and metacarpals.
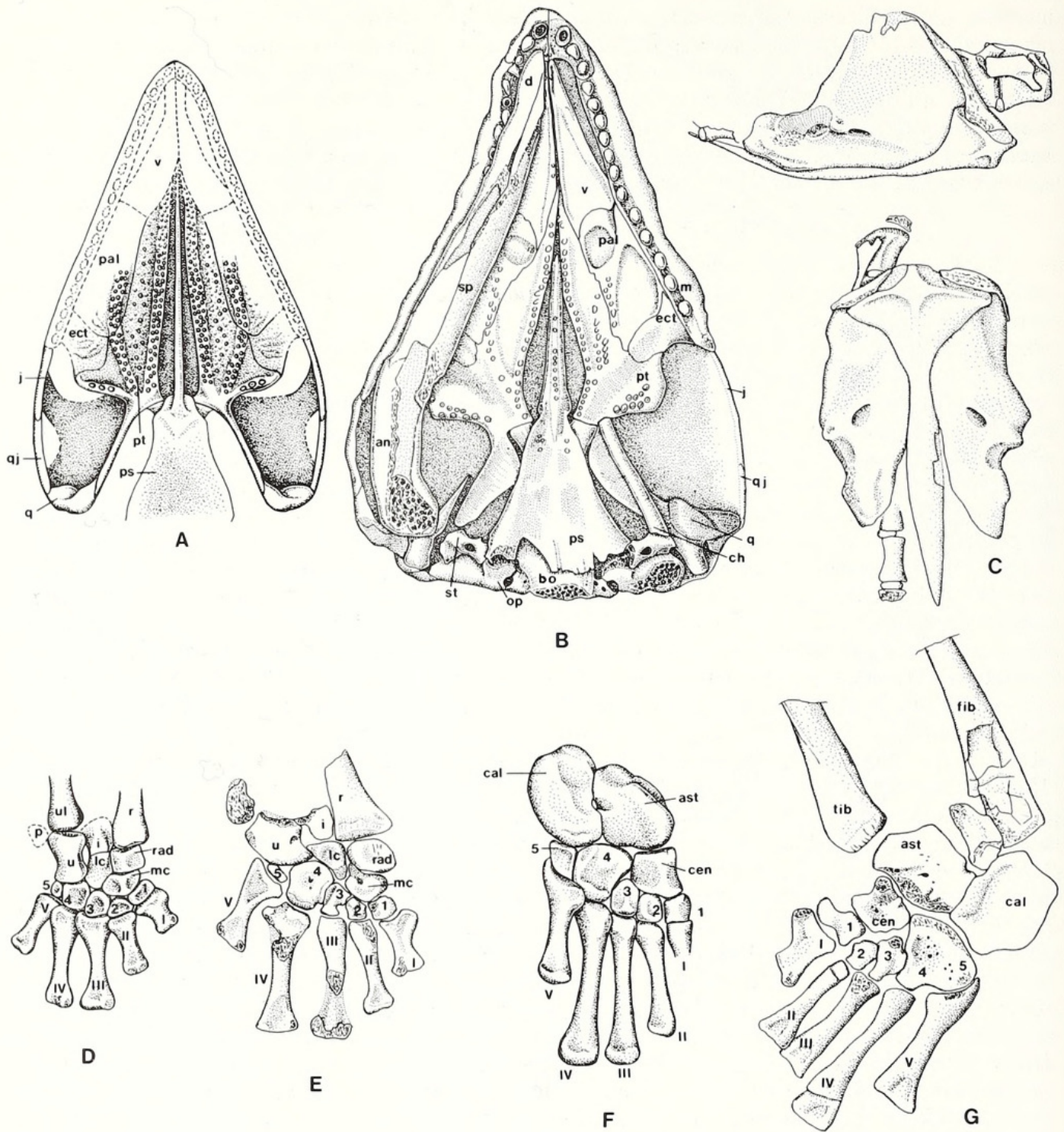
TEXT-FIG. 2. A, Restoration of the palate of *Broomia perplexa*, ×1½. B, *Milleretta rubidgei*, Rubidge collection no. 70, ×2. C, Lateral and ventral views of the pectoral girdle of *Milleretta rubidgei*, Bernard Price Institute for Palaeontological Research no. 2610, ×2. D, Carpus of *Broomia perplexa*, ×1½. E, Carpus of *Milleropsis pricei*, Bernard Price Institute for Palaeontological Research no. 4203, ×3. F, Tarsus of *Broomia perplexa*, ×1½. G, Tarsus of *Milleropsis pricei*, Bernard Price Institute for Palaeontological Research no. 4203, ×3.

anterior sutures of the pterygoids cannot be readily traced. Watson (1914) states that the anterior end of the pterygoid and vomer seem to show a natural border at the back of the internal nares. There is no indication of internal nares in this position in this cast, but rather, the region is filled with matrix which imparts a smooth surface to this area. A sliver of bone, presumably the vomer, is all that can be identified. The relationship between the anterior borders of the pterygoids and the choanae suggested by Watson is improbable. One would expect that *Broomia* possessed a pattern more comparable to that found in *Paleothyris* where only the palatine and vomer border the posterior margin of the internal naris.

The ectopterygoid is a large, structurally important element which lacks denticles. Its posterior borders are readily traced, but the anterior region is covered by the broken fragment of the mandible. Its primitive nature, characteristic of the millerettids as defined by Gow (1972), is in contrast with that of the early diapsids, *Petrolacosaurus* (Reisz 1977) and *Youngina* (Carroll 1977) in which there is a large suborbital fenestra.

Both maxillae are covered by the mandibles. Originally, the dentary was mistaken for this bone (Broom 1941; Watson 1957).

The quadrate of *Broomia* is of a primitive type comparable with that found in *Captorhinus*. There is a narrow articular surface, the exact nature of which is obscured with bits of the articular. The quadrate has an irregular medial surface to which the quadrate ramus of the pterygoid would have been immovably attached. The squamosal appears on its dorso-lateral surface extending toward the articulating surface. The large jugal can be seen in medial view anterior to the quadrate. The posterior margin of the jugal is smooth where it apparently formed the margin of a lower temporal opening. A fairly narrow quadratojugal can be seen to extend posteriorly toward the quadrate. The quadratojugal and jugal form an interdigitating joint. The quadratojugal cannot be seen to extend posteriorly to the quadrate, but the length and nature of the broken edge indicates that it formed a lower temporal arcade. This implies that the temporal region in *Broomia* does not, as Watson suggested (1914), resemble that found in lizards. In *Milleretta* and *Milleropsis* (Gow 1972) the quadratojugal is associated with the quadrate but typically does not reach the jugal.

Running along the left side of the skull is the anterior half of the mandible. Only the posterior half of the right lower jaw remains. At the back of the mandible the prearticular is discernible, although not all of its extent can be traced. The angular is well preserved on the left side and extends anteriorly as a boat-shaped element, two-thirds the length of the jaw. The dentary and splenial elements have become disarticulated and can be seen as thin narrow bones lateral to the remaining elements of the right jaw. The angular is only partially preserved in the left mandible, but the left dentary is well exposed. Eight teeth can be seen, the exact nature of which cannot be determined in this cast. Based on estimates of tooth row length, *Broomia* does not possess more than 20 teeth in the dentary. Gow (1972) indicates *Milleretta rubidgei* has 13 functional maxillary or dentary teeth, while Clark and Carroll (1973) report 35 in *Protorothyris*. A number of foramina are evident on the lateral border of the dentary. Along the inside border of the dentary runs the splenial, extending half the length of the jaw. The length of the jaw confirms that the quadrate is in its natural position, and hence was located anterior to the basioccipital condyle.

Preserved along the lateral edge of the parasphenoid is a portion of the left ceratohyal; a short rod-shaped element.

The skull is equivalent in length to approximately 7 anterior trunk vertebrae. This is similar to skull proportions described in *Milleretta* and the ancestral lizard *Palaeagama*. Somewhat similar skull proportions are also noted in early diapsids (Table 1). Among romeriid reptiles there is, in contrast, a steady increase in proportional skull length with time, from a skull length equivalent to 8 vertebrae in the early romeriid *Hylonomus* to 13·5 in the last genus known from articulated material, *Protorothyris*. Clearly, the Middle and Upper Permian forms, and diapsids in general, represent a distinct departure from the primitive pattern. Presumably the development of temporal openings allowed a reduction in skull size, or changes in diet and feeding behaviour favoured a smaller skull–trunk ratio.

TABLE 1. Skull—trunk proportions in primitive reptiles, the skull length is expressed in terms of vertebral number.

Romeriidae (listed in approximate order of antiquity)

Protorothyris	13·5
Brouffia	12
Coelostegus	11
Paleothyris	10
Cephalerpeton	9
Hylonomus	8

Millerosaurs

Milleretta	7
Broomia	7

Diapsids

Palaeagama	7
Prolacerta	7
Youngina	10
Heleosaurus	7
Petrolacosaurus	6·5

Vertebrae and ribs

Little has been revealed of the vertebral column since Watson's description (1914). It is basically primitive and unspecialized, consisting of deeply amphicoelous notochordal centra and large intercentra which persist throughout its length.

Except for a trace of the atlas, the anterior vertebrae of *Broomia* are not exposed; hence it is impossible to give an accurate vertebral count. However, as Watson indicates, the whole skeleton appears to be in articulation and it is reasonable to extrapolate 9 missing centra between the skull and the most anteriorly preserved trunk vertebrae. The specimen is therefore reconstructed as having a total of 25 presacrals.

Watson (1957) restores *Milleropsis pricei* as having 31 presacrals, while *Milleretta rubidgei* (Gow 1972) has 24 presacrals. On the other hand, *Paleothyris* (Carroll and Baird 1972) is restored as having 32 while *Captorhinus* has 27. *Petrolacosaurus*, the oldest-known diapsid, has a presacral count of 26.

The centra are all similar in size and form. All preserved have a basic hourglass configuration and are approximately 80% as wide as long. The 5 anterior visible centra are each approximately 10% longer than the posterior 11 vertebrae. Foramina subcentralia are present on all centra, as in primitive lizards. The last presacral indicates that zygapophyseal articulating surfaces were nearly horizontal. As Watson (1914) points out, the transverse processes, best seen in the twelfth and thirteenth presacrals, are short and extend from a point on the arch near or on the neurocentral suture, up to the process which supports the prezygapophysis. The articular facet for the rib begins some distance behind the anterior end of the vertebra.

The large size of the intercentra (approximately 35–40% as long as the centra) and the fact that they are found the length of the column, constitute notably primitive features similar to the condition found in the ancestral romeriid captorhinomorphs. Watson states that an intercentrum was not found between the sacrals, but this cast indicates that one was definitely present. In the late Permian millerettids, small crescentic intercentra are also found throughout the column. Of the caudal vertebrae, only the first five are well preserved, while a badly discernible sixth is also present. They are all of the same length and proportions as the posterior presacral vertebrae. To each centrum, large dorsoventrally flattened ribs are indistinguishably fused. They project from the centrum and are approximately the length of one and one-half centra. The fusion of caudal ribs is a common trend in late Permian reptiles and is of taxonomic value only in distinguishing them from

procolophonids. Crescentric intercentra are present anterior to the first three caudals. Traces of haemal arches are evident more posteriorly.

Cervical ribs are not exposed and only traces of the first few dorsal ribs can be seen. Posteriorly, ribs are present in articulation with all the presacrals except for the three immediately in front of the sacrum. The nature of the transverse processes indicates that ribs probably were originally present in this region as well. The length of the ribs differs greatly; the longest and best preserved are found on the thirteenth and fourteenth vertebrae (presuming the presacral count is correct), and are approximately the length of five posterior dorsal trunk centra. Anteriorly, they shorten in an irregular fashion which indicates incomplete preservation. Posteriorly, they progressively shorten until they are lost at the level of the twenty-second centrum. The presacral ribs are holocephalus, slender, long, and curved. The ribs articulate by a single narrow head to an oblique facet on the anterior part of the lateral surface of the pedicel of the neural arch and centrum.

Watson believed the nature of rib articulation is an 'unusual quality' common to both *Broomia* and millerosaurs. The features mentioned in *Broomia* are identical with those in *Milleropsis*, the eosuchians, and other primitive reptiles, and are of little taxonomic value. *Broomia* does, however, lack the distinctly flattened ribs seen in *Milleretta* (Gow 1972).

The sacrum in *Broomia* is made up of two sacral vertebrae, which is the number found in nearly all primitive reptiles. Each one bears fused ribs without trace of sutures. The anterior pair of sacral ribs are shorter and thicker than the posterior pair. The anterior rib arises from the centrum at a 90 degree angle, and articulates with the ilium via a large flat surface, while the posterior rib—directed at a 45 degree angle from the long axis—has a very large articulation with the ilium. This pattern is common to nearly all primitive reptiles. This region has not been well preserved in the members of the Millerettidae from the latest Permian and so cannot be compared in detail.

Appendicular skeleton

The pectoral girdle in *Broomia* is well preserved, although it is somewhat disarticulated. Ventrally, it appears to be in more or less its correct position relative to the rest of the skeleton. The view of the lateral surface is very limited and the presence of a cleithrum cannot be determined.

In general, *Broomia* possesses a primitive type girdle comparable with that found in the Lower Permian captorhinids and romeriids. The interclavicle in ventral view has the typical primitive T-shape. It consists of a diamond-shaped head and a long stem, the distal end of which extends only a short distance past the coracoids. The stem has been broken and displaced lateral to its original position relative to the head. The rhomboidal head bears recesses along its anterolateral and lateral edges. The anterior recesses are obviously to receive clavicles, while Watson (1914, p. 999) interprets the lateral recesses as serving to accommodate coracoids. As he states, 'this implies that the interclavicles largely lay above the coracoids, a feature only paralleled by the plesiosaurs.' Closer examination of the cast indicates that his interpretation is incorrect and that the apparent arrangement of elements is probably an artifact of preservation. The interclavicle lies ventral to the coracoid; as in all other primitive reptilian groups.

The scapulocoracoid is ossified as a unit, as in early captorhinomorphs. The fully ossified endochondral girdle of *Milleretta* (text-fig. 2c) has a very similar configuration. A specimen of a less mature individual illustrated by Gow shows separation of the scapula and coracoid. Unlike the scapulocoracoid of early lizards, that of *Broomia* and other millerosaurs lacks any evidence of anterior fenestration.

The right coracoid is probably in its natural position dorsal to the interclavicle. A large portion of the border of the left coracoid has been lost. With these facts in mind, it is not hard to envisage the reorientation of elements during preservation into the present confusing configuration. The interclavicular stem was displaced laterally to the hind border of the right coracoid, while the left coracoid was rotated slightly upward on to the interclavicular stem. The position of the left glenoid fossa appears to support this interpretation since it obviously does not lie in its correct position. The posterior recesses of the head of the interclavicle can be interpreted as areas of attachment for the pectoralis major muscle as suggested by Holmes (1977) in *Captorhinus*.

The sculpturing on the ventral surface of the clavicle is probably indicative of a tightly adhering dermis; as in *Captorhinus*. The coracoid is a large, flattish element fused with the scapula. A supracoracoid foramen is present, and it appears the supraglenoid foramen is also present, both in positions comparable to those in captorhinomorphs.

The glenoids are not well exposed. The right glenoid is poorly preserved, while the left retains the proximal end of the humerus in its articulating surface. We can, however, conclude that there was definitely a primitive screw-shaped articulating surface with the humerus, similar to that found in *Protorothyris*. A sternum has not been preserved and presumably was cartilaginous.

The upper part of the right humerus is exposed from below, while the left humerus is badly exposed showing only length and general features of the distal end. Neither articulating surface is well exposed. The humerus of *Broomia* is basically primitive and readily derived from that of *Captorhinus*. The shaft is comparatively longer and slimmer and the proximal and distal ends appear to be proportionately smaller. The shaft width is approximately 10% of the length. A badly preserved entepicondylar foramen is discernible. The capitellum is round and directed at right angles to the shaft. The ulnar articulation is contiguous with the capitellum anteriorly as in *Petrolacosaurus*. It appears that the humerus is about 80% the length of the femur; a ratio which is typical in primitive reptiles.

The epipodials in *Broomia* are not well preserved and hence a detailed comparison with other reptilian groups is not possible. The distal halves of the right radius and ulna can be seen articulating with the right carpus, while the proximal halves of the left epipodials are preserved articulating with the left humerus. Both elements are long and slender with expanded ends. The exact length cannot be determined. The proximal end of the radius is only slightly expanded, while that of the ulna is expanded into a well-ossified olecranon. The distal end of the radius is expanded approximately twice the width of the proximal end. The distal end of the ulna is expanded to approximately the width of the distal end of the radius. The distal articulating surface of both the ulna and radius are basically flat as in *Captorhinus*.

The distal forelimb elements in *Broomia* are readily derived from those of *Paleothyris* (Carroll 1969), although they are proportionately longer and slimmer. Both reptiles possessed lightly built epipodial elements and a prominent well-ossified olecranon.

Watson's (1914) description of *Broomia's* carpus is incomplete. The elements present are well preserved and it appears that *Broomia* possessed a primitive carpus comparable to that found in *Captorhinus* (Holmes 1977) or *Paleothyris* (Carroll 1969). All of the eleven basic elements are present, although the pisiform is displaced and not fully exposed (text-fig. 2D).

As Watson observed, the carpus is remarkable for its thorough ossification and accuracy of fit of its elements. There appears to be no doubt as to the identity of the elements, and more importantly, no evidence of a small additional third centrale which he identified between the ulnare and fourth distal carpal. This is important because the presence of this additional centrale was used to differentiate *Broomia* from all other reptilian groups.

Following the primitive pattern, the ulnare in *Broomia* is by far the largest bone in the carpus. The proportions are as in *Galesphyrus capensis* (Carroll 1976), a primitive eosuchian reptile, and the middle Pennsylvanian captorhinomorph *Paleothyris*. The ulnare of *Petrolacosaurus* (Reisz 1975), the earliest diapsid, is much longer while that of *Captorhinus* is proportionately shorter. The ulnare is not well preserved either in *Milleropsis pricei* (text-fig. 2E) or in *Milleretta rubidgei* but it appears to be comparable to that of *Broomia*. The distal end of the ulna articulated closely with the ulnare in *Broomia*. Unfortunately, the orientation of the bone is such that one cannot examine the surface where the pisiform presumably articulated. The medial margin of the bone is notched to form the lateral surface of the perforating foramen. Distally, the bone expands slightly to articulate with the fourth and fifth distal carpals as well as part of the lateral centrale. The proximal edge of the intermedium is not well preserved, but it appears to have articulated with the ulnare in the typical manner.

The distolateral border of the intermedium appears to have been closely associated with the radius. In *Captorhinus*, the intermedium articulates only with the ulnare while in *Paleothyris* the

situation appears comparable to that in *Broomia*. The intermedium in *Broomia* lacks the sharp constriction between the area of the ulnar and radial articulation found in *Paleothyris*. On the distal border of the intermedium in *Broomia* there is a notch for the perforating foramen.

The radiale in *Broomia* is a roundish element which resembles that found in all primitive reptilian groups. The proximal articular surface is flat, and as in *Captorhinus*, the radiale was probably functionally an extension of the radius. The articulating surfaces between the radius and radiale appear to fit tightly together. Distally, the radiale articulates with the medial centrale, while laterally it articulates with the lateral centrale.

As in *Paleothyris*, the lateral centrale of *Broomia* is an important element integrating the carpus. It articulates distally with the third and fourth distal carpals and the medial centrale. It appears to have also contributed to the margin of the perforating foramen; conforming to the pattern of other primitive reptiles.

The pattern of the distal carpals is as seen in all other early reptiles, particularly close comparison being possible with *Captorhinus* and *Paleothyris*. All of these distal carpals, except the fifth, are well preserved. The fourth is the largest, while the fifth is the smallest.

It is highly unlikely that a transverse joint can be found within the tight mosaic of elements of this carpus. The major wrist joint in *Broomia* would appear to be as in *Captorhinus*, the romeriids, eosuchians, millerettids, and *Petrolacosaurus*, between the distal carpals and the metacarpals. The flat articular surfaces found between these bones in all primitive reptiles is cited by Holmes (1977) as evidence of relative inflexibility. In all these forms, some movement was possible between the ulna and ulnare-intermedium, but because the articulation between the radius and radiale is more distally located in the carpus, a major wrist joint here has to be precluded. Also, as Holmes points out in *Captorhinus*, a joint between the radiale, intermedium, and ulnare and the more distal carpals was blocked by the lateral centrale. No single articulating joint served as a sole wrist joint, but rather, the carpal-metacarpal articulation appears to have been the major wrist joint with some flexibility at all other points of articulation. The structure and functions of the carpus in all known groups of primitive reptiles appear similar and provide little basis for taxonomic differentiation.

The first metacarpal is very short. The next three increase progressively in length. The fifth, largely obscured beneath the fourth, is quite short. Only the third digit is complete, with four phalanges, including a long curving ungual. Presumably the phalangeal count was 2, 3, 4, 5, 3 as in other primitive reptiles.

The pelvic girdle in *Broomia* is incompletely exposed. The pubis and ischium are within the matrix beneath the vertebral column and exposure would almost certainly lead to damage of other elements. Both the left and right ilium are present, but they are poorly preserved and yield little information. A large oval depression testifies to the primitive nature of the acetablum.

The femur of *Broomia* is generally primitive and comparable to those of *Captorhinus* or *Paleothyris*, although it is somewhat slimmer. The width of the proximal and distal ends are respectively approximately 25% and 30% of the length. The shaft narrows to approximately 10% of the length. The bone is approximately the length of six trunk vertebrae. Little can be seen of the ventral surface which would be expected to show the major diagnostic features.

The tibia and fibula are very slender bones. Both are poorly preserved. The proximal and distal ends of the tibia are exposed but the proximal portion of the shaft is missing. The two ends appear in place, however, and the length can be determined. Both the fibula and tibia are approximately 80% the length of the femur. The width of the distal end of the tibia is approximately 15% of its length. The proximal end is wider. These proportions are comparable to those of *Petrolacosaurus* and *Galesphyrus*.

The tarsal elements are fully ossified, beautifully preserved, and fit together in a tight mosaic (text-fig. 2F). Their structure resembles the basal pattern from which all advanced reptilian groups arose. It appears that the confusion in Watson's initial description was the result of identifying a small broken piece of the first metatarsal as the first distal tarsal. This led to his assuming a fibulare to be present.

The general arrangement of the elements resembles that of *Paleothyris*. All the primitive elements

are retained with the exception of the medial centrale. The over-all shape and pattern of the tarsal elements is also very similar to that found in *Galesphyrus*—a primitive eosuchian of the *Cistecephalus* zone. There exist, nevertheless, a number of peculiar features.

As seen in ventral view, the astragalus and calcaneum are approximately the same size. The astragalus appears to be in its natural position—though it has been slightly displaced upwards from the plane of the cast. The tibial facet is confined to the dorsomedial border along the proximal border of the astragalus and is in a more dorsal position than in *Captorhinus*. The tibial surface is convex as in the captorhinids and romeriids. There is a strong ridge on the ventral medial border of the bone which is separated from the tibial articulating surface by a shallow groove. This condition is reminiscent of that found in *Petrolacosaurus* (Reisz 1975), although the orientation of the ridges differs in *Broomia*. The further facet is located along the thickened proximal surface of the dorsoventrally compressed vertical 'arm' of the astragalus. The lateral border of the astragalus articulates tightly with the calcaneum and together they appear to function as a single structural unit. The articulation is interrupted by a large distally directed perforating foramen which appears to be located in a more proximal position than in most primitive forms. Following the primitive pattern, the astragalus articulates distally with the lateral centrale and the fourth distal tarsal.

The calcaneum is a relatively simple, oval, platelike structure as found in *Paleothyris* or *Captorhinus*. The lateral extremity, however, is oriented in a more proximal direction than in *Captorhinus*. Its proximal border contributes with the astragalus to the articulating surface for the fibula. The broad, rounded lateral border of the calcaneum flattens distally where it articulates with the fourth and fifth distal elements. As Schaeffer (1941) points out, the enlarged lateral surface of the calcaneum enables the gastrocnemius to exert a more effective pull on the foot by increasing the angles of application, and hence, the foot can more effectively participate in propulsion.

There is only one single centrale in *Broomia*. It supports the astragalus and articulates with the first four distal tarsals in a manner similar to that of *Paleothyris* and all other early reptilian groups.

All the distal tarsals are well preserved and in place, except for the first which has been displaced medially so that it covers a fair proportion of the second distal element. They collectively conform to the primitive pattern. The fourth is by far the largest and most important as it articulates with both the astragalus and calcaneum proximally, the lateral centrale and the third distal element medially, and with the fifth distal tarsal laterally. The very close association of the fourth and fifth elements may indicate a trend toward fusion as seen in *Milleropsis*. Distally, the fourth distal tarsal articulates with the fourth metatarsal and the medial border of the enlarged head of the fifth metatarsal. All other distal tarsals appear to articulate with only their single corresponding metatarsal.

The articulating surfaces for the tibia and fibula resemble those in *Captorhinus*. The tibial facet is more dorsal upon the astragalus and this would appear to facilitate a crurotarsal hinge. The proximal and distal elements articulate closely. There is no evidence of the rather specific association and large articulating surfaces possessed by these elements when they make up a mesotarsal joint. Some intratarsal hinge movement was possible within the reasonably tight mosaic of tarsal elements, but it is doubtful that a major mesotarsal joint as characterizes squamates and *Sphenodon* was found in this tarsus. Instead, it appears the tarsus retained and improved upon the crurotarsal type joint in *Captorhinus*. Unfortunately, it is not clear what the nature of the tarsal joint was in the later millerettids.

The last four metatarsals in *Broomia* are complete and beautifully preserved. The first remains only as a fragment articulating with the first distal tarsal. In general, the proportions are as in *Paleothyris*, the fourth and third being the longest while the first was probably the smallest, judging by the nature of its proximal head. They are all slender, fairly long bones with large articulating proximal heads. The proximal head of the fifth metatarsal is particularly large, curving up and around the lateral side of the fifth tarsal element, while its medial edge extends to articulate with part of the fourth distal tarsal. The fifth metatarsal is only slightly more than half as long as the fourth. It lies parallel with the other metatarsals and is not directed laterally. The fifth metatarsal lacks any 'hooked' nature; a feature commonly associated with the presence of an intertarsal joint

(Robinson 1975). Collectively, the proximal heads of the metatarsals overlap and form a tight structural unit. The presence of a tightly consolidated metatarsal unit would facilitate more effective lever action.

No ventral scales are preserved in *Broomia*.

DISCUSSION

Broomia resembles the Late Permian millerosaurs in the following features: jaw articulation anterior to occipital condyle, presence of a lateral temporal opening, absence of a suborbital fenestra, close integration of the fourth and fifth distal tarsals, the curving of the head of the fifth metatarsal around the fifth distal tarsal.

Broomia is advanced over the romeriids in the presence of a lateral temporal opening, the anterior position of the jaw articulation, and the fusion of the caudal ribs to the centra. The relatively small size of the skull in probably a specialization, although it might be retained from a primitive level of romeriid evolution. The tarsus is highly unified, restricting movement primarily to the crurotarsal joint.

Broomia is more primitive than *Milleretta* in not fusing the fourth and fifth distal tarsals, although the fifth metatarsal articulates with both elements. The sutural union between the jugal and quadratojugal is typically lost in more advanced millerosaurs. No other features known in common to *Broomia* and later millerosaurs can be used to differentiate the two groups.

Broomia reinforces the concept of an early differentiation of millerosaurs and their close affinities with the captorhinomorphs, as opposed to any of the diapsid groups. Millerosaurs parallel some of the adaptations of early lizards, notably toward small size and the development of an impedance matching ear, but do not show evidence of an ossified sternum, fenestration of the scapulocoracoid noted in early lizards, or the initiation of an intratarsal joint. At least in the Karroo beds of South Africa, the lizards succeed the millerosaurs in time (Carroll 1977). Fossils of lizards are so rare that failure to find them in the Middle Permian beds may not be significant. Recognizable ancestors of the Late Permian and Early Triassic paliguanids must have been present in some region at this time, although they may not have become common until after the demise of the millerosaurs.

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