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The Triassic Reptile *Prolacerta* in Antarctica

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ABSTRACT

The prolacertid reptile, *Prolacerta broomi*, hitherto known from the *Lystrosaurus* Zone of the Middle Beaufort beds of South Africa, is described from specimens including two skulls with jaws, other fragments with skulls and jaws, and various postcranial elements, found in the Fremouw Formation of the Transantarctic Mountains. The Antarctic fossils represent individuals generally somewhat smaller than those known from South Africa, with slightly fewer teeth in the upper and lower jaws, and with other minor differences. These variations are, however, probably attributable to age differences and perhaps geographic separation rather than to any specific distinctions. A partial

skeleton, including hind limbs and some caudal vertebrae of prolacertilian relationships, likewise would seem to represent an individual somewhat smaller than the South African species. The presence of *Prolacerta broomi*—in addition to a lydekkerinid amphibian *Cryobatrachus kitchingi*, the dicynodont reptiles *Lystrosaurus murrayi*, *Lystrosaurus curvatus*, *Lystrosaurus mccaigi*, and *Myosaurus gracilis*, the procolophonid *Procolophon trigoniceps*, and the theriodonts *Thrinaxodon liorhinus* and *Eriolacerta parva*—corroborates the close relationships between Antarctica and South Africa and their probable connection during Early Triassic time.

INTRODUCTION

The collection of fossil tetrapods secured from the Lower Triassic Fremouw Formation of Antarctica during the austral summers of 1969–1970 and 1970–1971 contains various remains representative of the diapsid reptiles, these being specifically prolacertilians and thecodonts. All of these specimens

were found during the second field season, and were collected in the vicinity of the junction between McGregor and Shackleton glaciers, at about latitude 85°13'S and longitude 174°30'E. The fossils were collected by Dr. James W. Kitching of the Bernard Price Institute for Palaeontological Research, Uni-

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versity of the Witwatersrand, Johannesburg, and his associates, namely John Ruben, then of the University of California, Berkeley, and Thomas Rich, then of the American Museum of Natural History, New York.

At this point I wish to acknowledge advice and comments from Dr. Robert Carroll of the Redpath Museum, McGill University, Montreal; from Dr. Peter Galton, of the Peabody Museum, Yale University, New Haven, Connecticut, and the University of Bridgeport, Bridgeport, Connecticut; and from the late Professor Georg Haas, The Hebrew University, Jerusalem, Israel. Consultations with these authorities were most helpful; it must be emphasized, however, that all conclusions reached in this paper are solely the responsibility of the author.

The drawings were made by Miss Pamela Lungé; the photographs by Mr. Mark Middleton, both of the Museum of Northern Arizona.

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STRATIGRAPHIC RELATIONSHIPS

For the benefit of those unfamiliar with previous papers in this series describing Triassic tetrapods from Antarctica, a few remarks will be included here concerning the stratigraphic relationships of the Fremouw Formation. This, the lowest unit in the Antarctic Triassic sequence, overlies the Permian Buckley Formation, from which it is separated by a disconformity, and in turn it is overlain by the Falla Formation and above that the Prebble Formation, both of Triassic age. The Prebble Formation is separated by a disconformity from overlying Jurassic volcanic rocks, the Ferrar Dolerite, which may also be intruded into the Triassic sediments. The Fremouw Formation in the Transantarctic Mountains may reach thicknesses of 650 m.

The sediments of the Fremouw Formation are cyclic in nature, ranging from coarse, conglomeratic channel deposits at the base of the cycle to fine floodplain deposits at the top. The specimens described in this paper were collected from the fine-grained sediments that

are prevalent in the vicinity of McGregor and Shackleton glaciers.

In the previous papers of this series it has been shown that the fossil tetrapods from the Fremouw Formation are closely related to those occurring in the Lower Triassic *Lystrosaurus* Zone, Middle Beaufort beds of the Karroo Series in southern Africa.

DESCRIPTIONS OF FOSSILS

SYSTEMATICS

CLASS REPTILIA

SUBCLASS DIAPSIDA

ORDER EOSUCHIA

FAMILY PROLACERTIDAE

Comments: The family Prolacertidae was established by Parrington in 1935, in his original description of *Prolacerta broomi*, new genus and species. He said about the higher taxonomic relationships of the genus and species:

Though most closely allied to the Eosuchia *Prolacerta* cannot, I think, be included among them, since they are the most primitive diapsids and the basal group from which all later, specialized, forms may have evolved. It is excluded from the Squamata by the presence of part of the quadratojugal and the fact that the quadrate is fixed. [But the quadrate is not fixed, as was shown by Camp in 1945 and by Gow in 1975.] The proper place seems to be in a new family of the Thecodontia, for which the name Prolacertidae is proposed. (Parrington, 1935: 205)

In his paper describing in detail the skull of *Prolacerta*, Camp (1945: 95) stated that for *Prolacerta* the "concert of characters seems to place it in the Protorosauria (=Eosuchia), and within the family Protorosauridae."

The family Prolacertidae was placed within the order Eosuchia by Romer in 1956 and 1966, and by Piveteau in 1955. It was included within the Lacertilia by Tatarinov (*in* Rozhdestvenskii and Tatarinov) in 1964. In 1956 von Huene included *Prolacerta* in his underorder Prolacertilia, but did not designate a family to contain the genus.

Kuhn-Schnyder (1962: 132) described a skull of *Macrocnemus* and showed its close similarities to the skull of *Prolacerta*. He felt, however, that the relationships of the higher taxa of lepidosaurians were too uncertain to warrant a definitive position for *Prolacerta* and its relatives. "The relationships between Eosuchians, Archosaurians and Prolacertilians are by no means clear. Therefore we at pres-

ent classify only the Prolacertilians with the Lepidosaurians."

Pamela Robinson, in her paper of 1967 on "The Evolution of the Lacertilia," placed the origin of this order among eosuchian diapsids such as *Prolacerta*. However she did not attempt formal designations of the higher taxa of these reptiles.

In his definitive study of *Prolacerta*, Gow (1975: 118) established a new order, Parathecodontia, for the family Prolacertidae—probably to be included within the Lepidosauria. His justification for setting up this new order of reptiles was as follows: "It is thus clear that *Prolacerta* is representative of an as yet poorly known group of early Triassic prearchosaurian thecodonts which in all probability gave rise to the later *Macrocnemus* and *Tanystropheus*. These can then be regarded as a sterile group which paralleled the Squamata in the loss of the lower temporal arcade."

Although the Prolacertidae probably do represent a group separate from both the eosuchians and the lacertilians in the strict sense of the two terms, it seems premature to set up a new reptilian order for the three genera involved. Since *Prolacerta* seemingly is not directly ancestral to the true lizards, perhaps the best course at the present time is to retain the family Prolacertidae in the Eosuchia, realizing that a satisfactory definition of the Eosuchia is not now possible.

This is substantially the procedure followed by Evans (1980). She recognized the subclass Diapsida to contain three infraclasses, namely Eosuchia, Archosauria and Squamata, and she placed the Prolacertidae along with 14 other families within the Eosuchia. Moreover, she indicated the Eosuchia as equally ancestral to the other two infraclasses. She admitted (1980: 257) that: "This is an artificial arrangement since the Eosuchia becomes a receptacle for a wide range of genera, but it has the advantage of leaving the two probably monophyletic groups—the Archosauria and the Squamata—as independent infraclasses. The term Lepidosauria becomes (? temporarily) redundant.

Prolacerta Parrington, 1935

Prolacerta Parrington, 1935: 197–206.

TYPE SPECIES: *Prolacerta broomi* Parrington.

HORIZON AND LOCALITY OF TYPE SPECIES: Lower Triassic, Middle Beaufort beds, *Lystrosaurus* Zone, Katberg Formation, South Africa.

GENERIC DIAGNOSIS: Small lepidosaurs, with a narrow skull, a somewhat elongated preorbital region, and a large orbit. Lower

temporal arch incomplete, the jugal terminating posteriorly in a point that does not reach the quadrate. Quadratojugal persisting, but very slender. Supratemporal fenestra rather large. Nasals extensive, overlapped by maxillae. Numerous palatal teeth on pterygoid and palatine. Lower jaw slender, probably with a ligamentous symphysis. Teeth pleurothecodont. Five premaxillary teeth, more than 20 maxillary teeth extending to a position beneath front of orbit; more than 20 dentary teeth. Vertebrae amphicoelous. Postcranial skeleton slender; bones frequently hollow or internally cancellous. Pectoral girdle with expanded, very thin scapulocoracoid, heavy clavicle and long interclavicle; pelvic girdle with broad puboischiatic plate. Limbs slender; hind limb much longer than forelimb. Ankle with large astragalus-calcaneum. "Hooked" fifth metatarsal, with fifth digit offset from the other digits. Typical reptilian phalangeal formula.

Prolacerta broomi Parrington

Prolacerta broomi Parrington, 1935: 197–205, figs. 1–3, pl. 9.

TYPE: A skull in the Museum of Zoology, Cambridge University, from Harrismith, Orange Free State, South Africa.

HORIZONS AND LOCALITIES: Lower Triassic; Middle Beaufort beds, *Lystrosaurus* Zone, Katberg Formation, South Africa; Fremouw Formation, from localities in the Transantarctic Mountains, Antarctica.

DIAGNOSIS: See generic diagnosis above.

ANTARCTIC SPECIMENS UNDER CONSIDERATION

The Antarctic specimens of *Prolacerta broomi* were found at several localities, namely: Halfmoon Bluff, Shackleton Glacier, near its junction with McGregor Glacier, Central Transantarctic Mountains; Mt. Kenyon, about 10 km due east of Halfmoon Bluff; *Thrinaxodon* Col., about 12 km east and slightly north of Halfmoon Bluff; Kitching Ridge, on the western side of Shackleton Glacier, about 14 km directly west of Halfmoon Bluff; also Graphite Peak, approximately 108 km west by north of Halfmoon Bluff.

TABLE 1
Prolacerta broomi
(measurements of skull in millimeters)

	AMNH 9520	AMNH 9521	Type (Parrington, 1935)	UCMP ^a 37151	BPI ^b 2675 2676
Skull pmx.-quad.	29	35 ^c	57	54	68
pmx.-ant. bord. orbit (A)	13.5	—	29	28	35
ant. bord. orbit-quad. (B)	15.5	—	28	26	33
Ratio A/B	0.87		1.03	1.07	1.06

^a University of California Museum of Paleontology, from Camp, 1945.

^b Bernard Price Institute, from Gow, 1975.

^c Estimated measurement.

All of the Antarctic specimens of *Prolacerta broomi* are preserved as rather fragile fossils in blocks of fine sandstone or siltstone matrix. In many of these blocks the fossils are remarkably abundant, but extremely fragmentary. Consequently, the descriptions that follow are based on a few selected specimens.

From Halfmoon Bluff

AMNH 9520. A somewhat distorted skull with lower jaw, in the rock, with the left side and top of the skull visible.

AMNH 9521. A skull with lower jaw, in the rock. The specimen is crushed dorsoventrally and many of the bones are incomplete or out of place.

AMNH 9522. Numerous bone fragments of the skull and postcranial skeleton, including an interorbital region (the frontals) seen in ventral view, and a fragmentary maxilla with five teeth.

AMNH 9526. Fragment of a mandibular ramus with teeth; also a palatine with several alveoli, as well as various skull fragments. In addition, some postcranial bones, including metatarsals and phalanges.

AMNH 9551. Humerus, and various bone fragments (from Sentinel Hill, near Halfmoon Bluff).

AMNH 9561. Ten articulated presacral vertebrae, with ribs; also caudal vertebra. Various other bones, including paired ischia (seen ventrally), part of a femoral shaft, a fragment of a scapulacoracoid with the proximal end of crushed humerus, and a jaw fragment with four alveoli.

AMNH 9574. Three articulated vertebrae and limb bones.

From Mt. Kenyon

AMNH 9558. A partially preserved skull and isolated disarticulated skull elements with lower jaws; anterior fragments of right and left dentaries with teeth; various articulated vertebrae and limb bones; preserved in a heavy block of matrix.

From Thrinaxodon Col.

AMNH 9552. Postcranial bones in matrix.

AMNH 9557. This species? Humerus, bone fragments.

From Kitching Ridge

AMNH 9513. Fragment of small maxilla with five teeth.

AMNH 9535. A few small vertebral fragments, in series.

AMNH 9564. Fragmentary cervical vertebrae.

AMNH 9568. A block containing a right pterygoid seen in dorsal view, two cervical vertebrae, and six posterior caudal vertebrae.

AMNH 9573. Part of a scapulacoracoid, two humeri, and other bones.

AMNH 9502. A slab containing a left premaxilla with two teeth, some skull fragments, including what appears to be a part of the anterior region of the skull, a left pterygoid, an elongated bone that may be a palatine, a large isolated tooth, an incomplete pelvic girdle with both ilia, and fragments of other elements, both hind limbs, the right one with a complete articulated pes, part of a sacrum, five incomplete posterior presacral vertebrae, some with articulated holocephalous ribs, and 15 caudal vertebrae with chevrons.

From Graphite Peak

AMNH 9560. A possible skull fragment, with fragments of the cranial roof. Jaw fragment with six teeth. Several vertebrae, including a series of about eight very fragmentary caudal vertebrae. A hind limb, and other fragments of limb bones.

DISCUSSION

In the execution of this study, close comparisons have been made between *Prolacerta* from Antarctica and similar fossils from the Karroo sequence of Africa, notably *Prolacerta broomi*, *Pricea*, *Palaeagama*, *Pali-guana*, *Saurosternon*, *Helosaurus*, *Galesphyrus*, and *Youngina*. These several forms have been described in papers by Broom and Robinson (1948), Camp (1945), Carroll (1975a, 1975b, 1976a, 1976b, 1977), Gow (1975), and Parrington (1935). Other papers bearing on this study have been the classic classification of lizards by Camp (1923), the anatomy of the head of *Ctenosaura* by Oelrich (1956), and Cruickshank's 1972 paper on proterosuchian thecodonts.

THE SKULL AND DENTITION

The description of the skull, jaws, and dentition that follows is based largely on AMNH 9520, with additional information from AMNH 9521, when such is available and pertinent. Remarks concerning other specimens listed above as belonging to the species will also be included, particularly in considering the postcranial skeleton.

In this connection it should be pointed out that *Prolacerta broomi* occurs in considerable abundance within the Fremouw Formation of Antarctica, a marked contrast to its relative scarcity within the *Lystrosaurus* Zone of South Africa. The difference may represent the accidents of collecting, but in view of the extensive exploration that has been carried on in the *Lystrosaurus* Zone over a period of a century or more, as compared with the necessarily brief time that has been spent in the Fremouw Formation, the difference probably indicates environmental conditions in Antarctica that favored the relative abundant burial and fossilization of *Prolacerta*, which seemingly was not the case in South Africa.

It would appear that *Prolacerta* from Ant-



Fig. 1. *Prolacerta broomi* Parrington. AMNH 9520, skull and mandible. Left lateral view, $\times 2$.

arctica is significantly smaller than *Prolacerta* from Africa. The two Antarctic skulls, AMNH 9520 and 9521, which are closely comparable in size, are only slightly more than half as large in linear dimensions as is the type skull, based on Parrington's 1935 restoration of the type, and the same size relationships pertain in a comparison of the Antarctic specimens with the skull described by Camp in 1945. They are even relatively smaller when compared with the skull described and figured by Gow (1975), being less than half as large as this specimen.

A certain size range is evident in *Prolacerta broomi*. It would appear however, that the largest elements in the Antarctic fossils do not significantly overlap, either by direct measurement or by extrapolation, the smallest comparable elements among the African fossils. Although this contrast in size might possibly be a manifestation of a specific separation between the African and Antarctic fossils, it is here proposed that (in light of the close morphological similarities involved) the size differences may be attributed to variability within a single species, and probably for the most part to growth factors. There is reason to think that some of the Antarctic material, because of its small size, especially as exemplified by AMNH 9520 and 9521, may represent juvenile specimens.

There also are some differences in skull



Fig. 2. *Prolacerta broomi* Parrington. AMNH 9520, skull and mandible. Left lateral view, $\times 4$.

proportions. That part of the Antarctic skull (AMNH 9520) anterior to the front of the orbit is relatively shorter than the region posterior to the antorbital margin, as compared with specimens from Africa, as described by Parrington (1935), Camp (1945), and Gow (1975). The comparatively shorter preorbital skull region in the Antarctic specimen is perhaps a function of the relatively large orbit in this specimen, which in turn indicates the

possibility that this fossil represents a young individual.

A key diagnostic feature of *Prolacerta* is the incomplete jugal bar. In African specimens the jugal is a crescentic-shaped bone in lateral view, bounding the lower border of the orbit and terminating in two posterior points, one directed dorsally to embrace the ventral prong of the postorbital bone and the other directed posteriorly toward the quad-



Fig. 3. *Prolacerta broomi* Parrington. AMNH 9521, skull and associated bones. Dorsal view, $\times 2$.

rate-quadratojugal. The bone in the Antarctic *Prolacerta*, AMNH 9521 drawn in figure 4, is similar in its shape and relationships to the same element in *Prolacerta broomi* from Africa, especially as figured by Gow in 1975. In this respect the prolacertilian nature of the Antarctic form is well established.

Naturally there is a gap between the posterior point of the jugal and the quadrate, so that the quadrate, thus released from any contact with a jugal bar, may have been a movable bone with its distal end enabled to rock back and forth by virtue of an active articulation between the proximal end of this bone and the squamosal. Whether the skull in *Prolacerta broomi* was truly streptostylic is a debatable point, as will be noted below.

In African specimens the quadratojugal is a small splintlike bone attached to the anterior border of the quadrate; the preservation of the Antarctic materials is not sufficient in this area of the skull to determine whether the same is true.

The nasal opening in the Antarctic skull (AMNH 9520) would appear to be rather elongated, with a narrow median bridge between the two apertures, formed by the confluent premaxillae. In front of the nasal opening is a small foramen in the premaxilla as in some modern lizards, evidently for the passage of the medial ethmoidal nerves. It is probable that the maxilla is excluded from the nasal opening by the premaxilla, but this cannot be conclusively established on the basis of AMNH 9520. The maxilla and nasal are large, and the nasal is overlapped by the deep vertical wall of the maxilla.

The prefrontal has a narrow posterior point extending back over the anterosuperior border of the orbit. The exact dimensions of this bone cannot be ascertained because of poor preservation of its more anterior region. It possibly was expanded anteriorly to border the posterolateral edge of the nasal, thus intervening between this latter bone and the lacrimal. The lacrimal in turn is not well defined, but it would seem to be a small bone between the prefrontal above and the posterior part of the maxilla below. It may form a small segment of the anterior border of the orbit. There is apparently a small foramen immediately in front of the lower anteroventral border of the orbit, this being identified

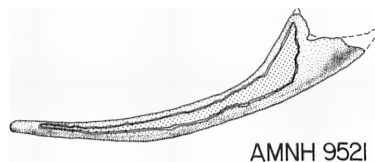


Fig. 4. *Prolacerta broomi* Parrington. AMNH 9521, left jugal. Lateral view, $\times 4$.

as a lacrimal foramen. It is quite possible that there is another foramen in a slightly more anterior position; if so, the Antarctic specimen would resemble *Prolacerta broomi* as described by Gow in having two such foramina.

The frontals form a narrow cranial roof between the large orbits. These are elongated bones, reaching from about opposite the anterior borders of the orbits to their probably sinuous posterior terminations, more or less opposite the posterior borders of the orbits. Of course the frontals join the parietals in this latter region, where the cranial roof is somewhat expanded by the increased width of the parietals as compared with the frontals. A long posterior process or wing extends back from each parietal to articulate with the squamosal, the limits and shape of this latter bone not being discernable. The ventral surface of the frontals may be seen in AMNH 9522, a block containing a miscellany of broken bones. In AMNH 9520 there is an elongated bone behind and parallel to the posterior process of the left parietal; this bone may be identified as a displaced paroccipital process of the opisthotic. It seems evident that there is a pineal foramen in AMNH 9520. In the descriptions of *Prolacerta broomi* by Parrington and by Camp no such foramen was perceived, but Gow's description (1975: 102) clearly indicated a pineal foramen in one specimen. As this author remarked, "B.P.I. 2675 is the only *Prolacerta* skull with a substantial pineal opening midway along the parietal suture; in the other described specimens there is no sign of this opening; this must be taken to be a variable character."

In the typical *Prolacerta broomi* a very small, splintlike supratemporal participates in the articulation between the parietal wing and the squamosal. The Antarctic materials are not preserved sufficiently to determine whether the same is true.

A large postorbital forms much of the posterior border of the orbit in AMNH 9520. This bone does not show the triradiate structure that is typical of the postorbital in many reptiles; it is evident that the posterior prong of the bone has been broken away. Dorsally this bone comes to a point and the anterior edge of the bone beneath this point articulates for some distance with the posterior edge of the postfrontal. The ventral termination of the postorbital appears to be blunt, but this probably is a result of damage to the end of the bone. The remnants of a postfrontal may be seen along the posterodorsal border of the orbit in this specimen.

AMNH 9560 is a block containing various skeletal elements, among them a part of the orbital region of a skull with a postorbital, some bone fragments that may be of the frontal area, and a piece of maxilla with four teeth. The postorbital of this specimen preserves slightly more of its middle portion than is present in AMNH 9520, to indicate that the bone is somewhat more robust than the postorbital of the African fossils as illustrated by Camp (1945) and by Gow (1975).

The jugal is not clearly discernable in AMNH 9520. Fortunately a reasonably well-preserved right jugal is present in AMNH 9521 and, as has been described in a preceding paragraph, the bone does not make contact with the quadrate.

A broad and robust bone is situated within the supratemporal fenestra of AMNH 9520, contiguous to the posterior process of the parietal. This element is here interpreted as the displaced right quadrate, its posterior concave surface lying uppermost, exposed to view. What is here taken to be its proximal end takes the form of a rounded articular surface, which might have afforded an active, movable articulation with the squamosal. Gow was convinced that the skull of *Prolacerta* was streptostylic, stating that (1975: 112), "the quadrate is free to move anteroposteriorly as a result of the loss of the lower temporal bar."

In the original description of *Prolacerta broomi*, Parrington did not express an opinion as to possible streptostyly in this reptile, but in his paper of 1945, Camp listed a "streptostylic quadrate" as one of the diagnostic characters of *Prolacerta*. Other authors

have questioned this; for example, Carroll (1977: 387) has stated that: "The squamosal retains an extensive ventral process, however, greatly limiting the motility of the quadrate."

So the matter stands. In this connection it can only be said that the upper end of the quadrate in the Antarctic specimen would seem to indicate a bone capable of movement.

The distal end of this bone is not well preserved; it would appear that there probably was a transversely broad articular surface. A rather poorly defined bone occupies the place of the left quadrate. Its distal end appears to lie within the articulating surface of the articular. The bone is anteriorly convex, and the anterior surface shows a series of denticulate points, possibly for contact with a quadratojugal.

Several fragmentary bones from the ventral part of the skull are present in certain blocks of Antarctic matrix containing the fossil remains of *Prolacerta*. AMNH 9522 contains a partially preserved parabasisphenoid element. This element is characterized by its broad posterior region, with strong basipterygoid processes, for articulation with the pterygoids. The parasphenoid rostrum extends anteriorly to a broken termination which exposes the hollow cancellous interior of the bone. It seems probable that the complete rostrum extended forward as a very thin, bladelikey process.

In the block numbered AMNH 9568 there is a right pterygoid of an individual considerably larger than the two skulls, AMNH 9520 and 9521. The bone is exposed in dorsal view so that pterygoid teeth are not evident except at its posterior end, where breakage reveals four small, pointed teeth. In shape the bone resembles the pterygoid in *Prolacerta* as figured by Gow; it points anteriorly and broadens posteriorly into a robust pterygoid flange, the lateral edge of which would have limited movement of the lower jaw during closure. The quadrate process is widely expanded.

A small fragment in block number AMNH 9526 may be a part of a palatine containing a row of very small alveoli along one edge.

The lower jaw as seen in AMNH 9520 is slender, and there is little dorsal expansion

in the coronoid region. Anteriorly the dentary shows a short symphyseal region; its surface is marked by a number of small foramina in line beneath the anterior dentary teeth. Perhaps there was a ligamentous symphysis. It would appear that the border between the dentary and the surangular and angular bones is located approximately beneath the middle region of the orbit. Posteriorly there is a large retroarticular process, forming much of the articular bone.

The dentition is pleurothecodont and the teeth are held in the alveoli by bone of attachment, nicely seen in AMNH 9520. The maxillary teeth extend back to a point beneath the anterior part of the orbit, a resemblance to South African specimens.

In block number AMNH 9558 there are two associated dentary fragments from the symphyseal region and the rami immediately posterior to the symphysis, the left dentary containing eight teeth, the right containing seven teeth, all somewhat laterally compressed and most of them separated by intervening sockets, or perhaps very large resorption pits. The mesial ventral borders of these sockets or pits extend down on the medial surface of the dentary. The first five teeth in the right dentary are regularly arranged, with an empty socket or pit between each of them. There is some confusion as to the next two teeth, in part because of the manner of preservation, but the last four teeth, like the anterior five, are regularly arranged with intervening pits or sockets. These pits may be equated with the medial resorption pits described by Gow in *Prolacerta broomi*.

In AMNH 9520 the premaxillae are broken and distorted to such a degree that the number of teeth cannot be satisfactorily determined. Both Camp (1945) and Gow (1975) indicated five premaxillary teeth in *Prolacerta broomi*. The premaxilla of AMNH 9502 reveals only four teeth, as noted below. The number of maxillary teeth cannot be determined in this specimen, but in AMNH 9521 there are at least 21 maxillary teeth. In this same specimen there are seemingly 23 dentary teeth. In *Prolacerta broomi* Gow, as mentioned, has determined 5 premaxillary teeth and 25 maxillary teeth, making a total of 30 teeth in the upper dentition. He indicates 27 dentary teeth. Thus *Prolacerta*

broomi as exemplified by AMNH 9520 and 9521 seems to have four fewer teeth, above and below, than does the African variant. This seems reasonable in view of the somewhat shorter preorbital region of the Antarctic form as compared with its African counterpart.

In the original description (1935: 198) of *Prolacerta broomi*, Parrington characterized the teeth as being "small, slightly compressed, and hooked." Likewise, Camp (1945: 11) described the teeth as "small, slightly compressed and recurved at their tips." Gow (1975: 100) characterized the teeth as "laterally compressed, with sharp unserrated edges and are recurved." The same applies to the teeth of *Prolacerta* from Antarctica, except that in some specimens, notably AMNH 9520 and AMNH 9521, they are not compressed but rather are rounded or elliptical in cross section. The teeth in the Antarctic fossils are entirely coated by enamel, as is true of the African specimens.

A left premaxilla, nicely preserved in AMNH 9502, shows the lower border of a rather large nasal opening, and posteriorly an ascending sutural border for articulation with the maxilla. The first and third premaxillary teeth are present, the space between them being occupied by the socket for the second tooth, and the space behind the third tooth showing a socket for a fourth member of the premaxillary series. Nutrient foramina are present on the surface of the bone above the alveolar edges, the one above the alveolus for the fourth tooth being rather large. The teeth are laterally compressed, posteriorly recurved to some degree, and without serrations. Behind the premaxilla is a rather large isolated tooth, evidently from the maxilla. It too lacks serration.

The apparent difference between the premaxilla, AMNH 9502, as well as the dentaries, AMNH 9558, and some other Antarctic specimens, such as AMNH 9520 and 9521, so far as lateral compression or rounded cross sections of the teeth are concerned, perhaps is not so great as it first appears. AMNH 9502 represents an individual considerably larger than either AMNH 9520 or AMNH 9521 and comparable in size to the adult *Prolacerta* described and figured by Camp and by Gow. Might there be an ontogenetic or a positional

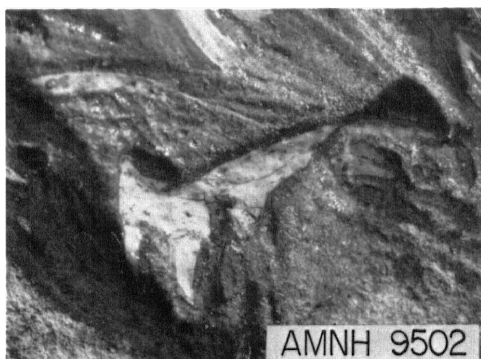


Fig. 5. *Prolacerta broomi* Parrington. AMNH 9502, left premaxilla. Lateral view, $\times 4$.

difference involved? As for the latter possibility, AMNH 9521 does show positional differences, the more anterior maxillary teeth being rounded in cross section, the more posterior teeth showing some lateral compression.

Other preserved parts of the skull in AMNH 9502 are of an equivocal nature, and difficult to interpret. As noted, there appears to be the anterior part of a snout, which, if the identification is correct, is narrow and elongated. In this respect it shows some resemblance to the snout of *Proterosuchus*, but it is so poorly preserved that no definite comparison is here implied.

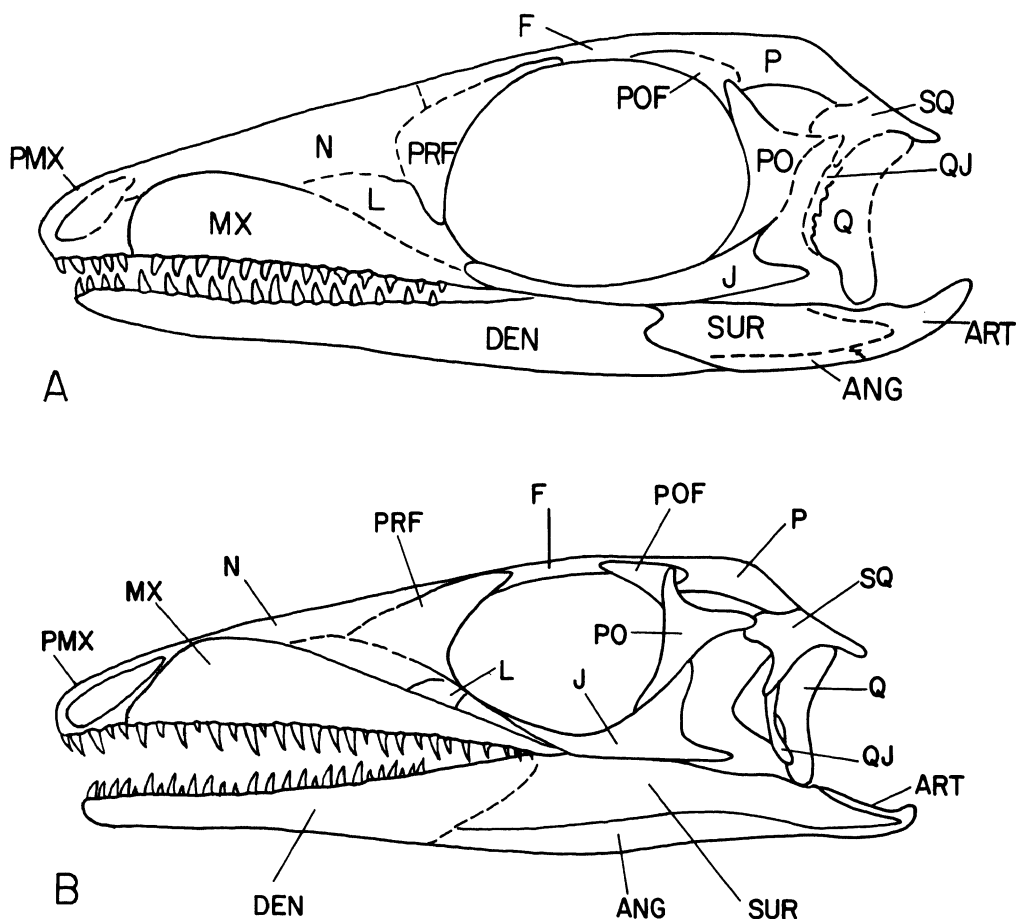


Fig. 6. A. *Prolacerta broomi* Parrington. Restoration of skull from Antarctica in left lateral view, $\times 4$. B. *Prolacerta broomi* Parrington. Restoration of skull from South Africa, in left lateral view, after Gow, $\times 1.5$. Abbreviations: ANG, angular; ART, articular; DEN, dentary; F, frontal; J, jugal; L, lacrimal; MX, maxilla; N, nasal; P, parietal; PMX, premaxilla; PO, postorbital; POF, postfrontal; PRF, prefrontal; Q, quadrate; QJ, quadratojugal; SUR, surangular; SQ, squamosal.

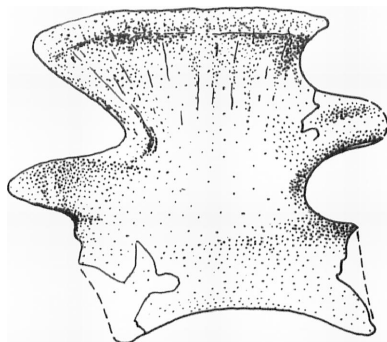
On the basis of the information available as described above, a restoration of the skull of *Prolacerta* from Antarctica, and a similar restoration of *Prolacerta* from Africa, are shown in figure 6.

THE AXIAL SKELETON

Several blocks of matrix from the Fremouw Formation contain various elements of the postcranial skeleton of *Prolacerta*. Cervical vertebrae are seen in AMNH 9558 with 9 vertebrae, and AMNH 9564 with 2 vertebrae; 10 dorsals and a caudal are exposed in AMNH 9561, 2 cervicals are exposed in AMNH 9568, 3 dorsals in AMNH 9574, while in AMNH 9502 there are 5 incomplete posterior dorsals and 15 caudal vertebrae.

The cervical vertebrae from Antarctica, here identified as of *Prolacerta*, are elongated, perhaps to about the same degree as would seem to be characteristic of *Prolacerta broomi*, but with taller spines. The skull length of *Prolacerta* as illustrated by Gow (1975), is about equal to the articular length of four cervicals; as illustrated by Camp (1945) to the articular length of about five cervicals. Unfortunately there is no specimen in the Antarctic materials with an associated skull and cervical vertebrae, but it would appear that the ratio of skull length to cervical length, as based on a comparison of AMNH 9520 and AMNH 9521 with AMNH 9558 (probably representing a larger individual than represented by the skulls) is on the order of about four cervicals. The cervicals in the Antarctic materials have, as mentioned, somewhat taller spines than those from Africa, and these spines are relatively long, there being but little distance between the anterior and posterior ends of spines of adjacent vertebrae. One of the two cervicals in the block numbered AMNH 9568 has a very long spine, the anterior end of which projects toward the anterior zygapophyses, an indication that this is the third vertebra in the cervical series. The cervicals seen in AMNH 9558 do not show the low, lateral horizontal ridge that characterizes comparable vertebrae from Africa, but the two vertebrae of AMNH 9568, which are exceptionally well preserved, do have this feature.

The dorsal vertebrae are shorter than the



AMNH 9568

Fig. 7. *Prolacerta broomi* Parrington. AMNH 9568, cervical vertebra. Left lateral view, $\times 4$.

cervicals, as is the case in the African fossils, but differ in that the spines are slanted posteriorly to a slight degree. Gow showed the dorsal vertebrae as having vertical spines. When seen in ventral view, as shown by AMNH 9561, the dorsal centra are "pinched" laterally so that each vertebra has a pronounced ventral ridge. The rib facets are not prominent and it appears that in the more posterior ribs the facets had merged so that these ribs were essentially holocephalous. There are well-developed intercentra in the dorsal series.

The posterior presacral vertebrae, which are seen in AMNH 9502, have strong zygapophyses, and on each vertebra a rather tall, strong spine rising from the posterior part of the neural arch, its posterior edge being above the posterior zygapophyses. Each of these vertebrae is characterized by a single anterior facet on each side of the neural arch, directly beneath the anterior zygapophyses, for articulation with a holocephalous rib.

The imperfectly preserved sacrum of this specimen shows at least one broad sacral rib, distally expanded, evidently for a junction with a second sacral rib. It indicates that the sacrum was rather broad in this reptile.

The considerable series of caudal vertebrae, so nicely preserved in AMNH 9502, are seen in ventral aspect, so it is not possible to determine the height or strength of the neural spines. The centra are expanded at their articulating ends, the medial part of each vertebra being contracted, thus giving to each

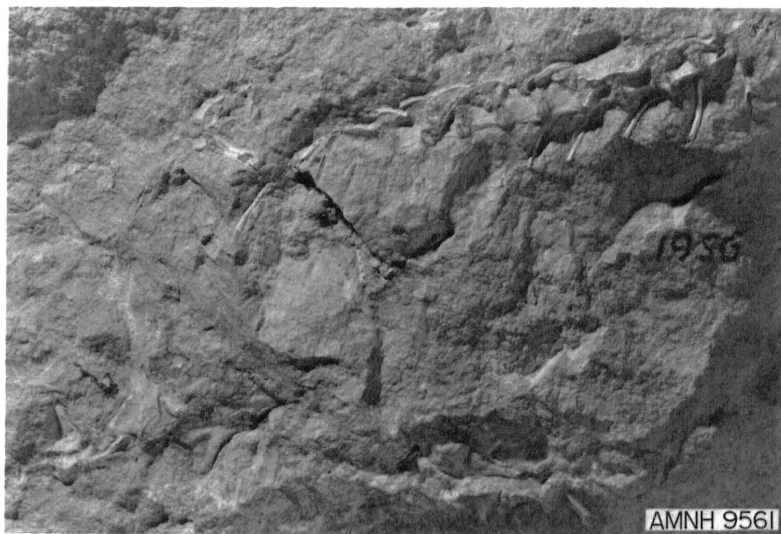


Fig. 8. *Prolacerta broomi* Parrington. AMNH 9561, a block containing a series of articulated presacral vertebrae with ribs and associated bones. Oblique ventral view, $\times 1$.

centrum something of a hourglass shape. The transverse processes are long. Elongated chevrons, distally expanded, are articulated between most of the exposed caudal vertebrae. The broken base of a chevron occupies

the space between the anterior face of the first vertebra carrying a complete chevron and the posterior face of the immediately preceding vertebra.

THE APPENDICULAR SKELETON—FORELIMB

Elements of the pectoral girdle and the forelimb are visible in several blocks, namely, AMNH 9526, 9551, 9557, 9558, 9561, and 9573.

The upper part of what may be a right scapulacoracoid is present in block AMNH 9573. The vertebral edge appears to be broken in a straight line across the blade of the bone, while the posterior edge of the bone descends in a gentle, sweeping curve. Anteriorly the bone is greatly expanded, very much as illustrated by Gow in his figure of the scapulacoracoid of *Prolacerta broomi*. Ventrally the bone is poorly preserved.

Humeri are preserved in each of the blocks numbered AMNH 9551, 9561, 9557, and 9573. In 9551 and 9557 only the distal half of the bone is preserved. In 9561 the bone is crushed and only partially preserved. In 9573 there are two humeri, one fairly well preserved, the other consisting of a partial shaft.

In describing the humerus of *Prolacerta broomi*, Gow observed (1975: 109) that the

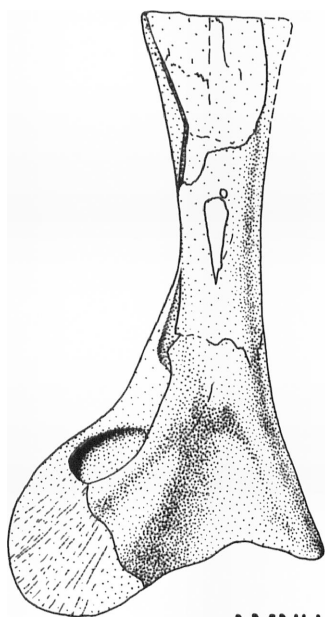


Fig. 9. *Prolacerta broomi* Parrington. AMNH 9551, partial left humerus. Dorsal view, $\times 4$.



Fig. 10. *Prolacerta broomi* Parrington. AMNH 9502, caudal vertebrae with chevrons, part of a tibia and a left pes, $\times 1.4$.

bone is "primitive and simple, though the entepicondylar foramen has been lost; there is a deep ectepicondyla groove." So far as they are preserved, this description applies to the bones from Antarctica. In blocks

AMNH 9551 and 9573 the humeri are distally expanded to an even greater degree than shown by Gow. Numbers AMNH 9552 and 9573 are considerably wider distally than is 9557, so the possibility exists that the latter

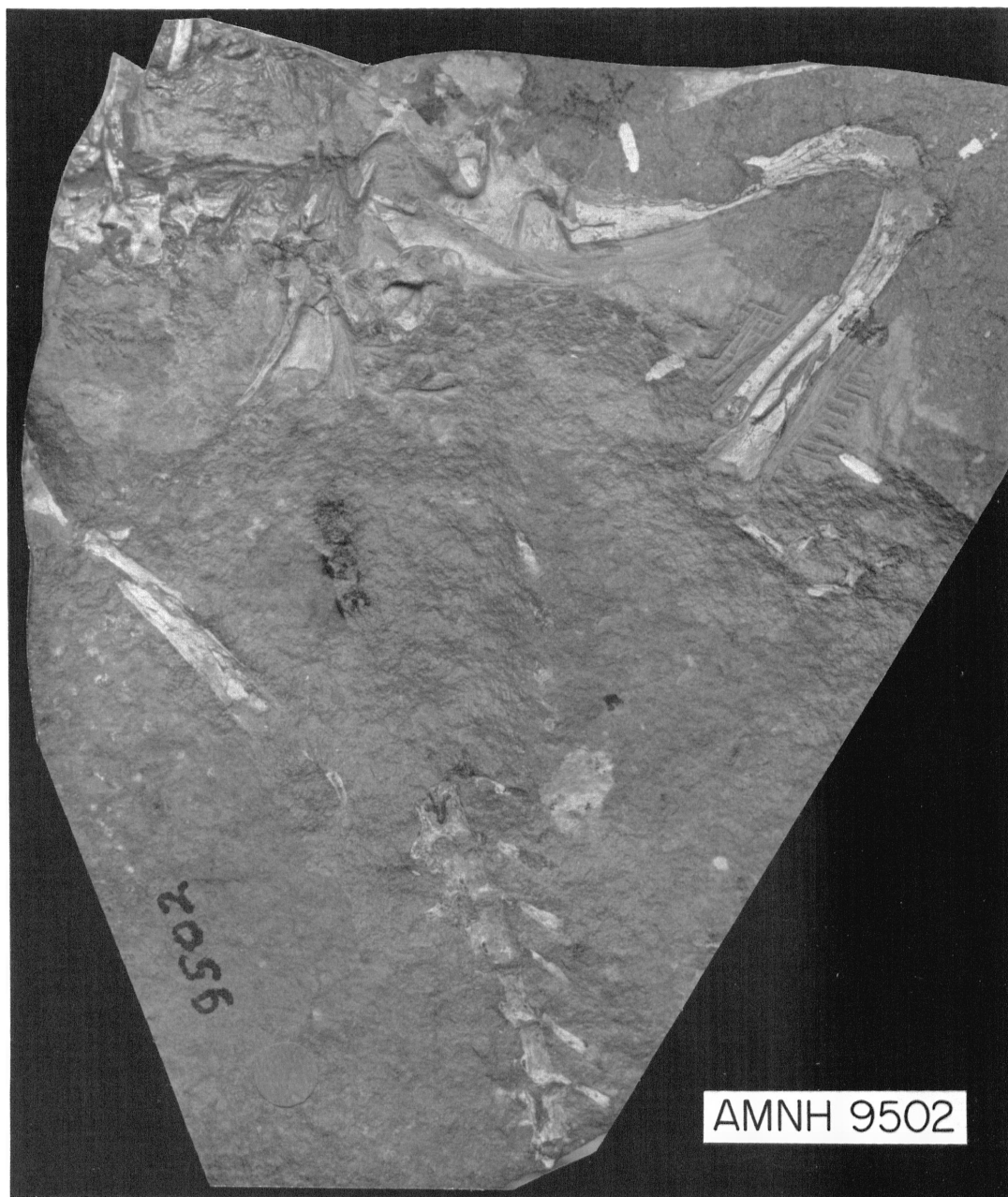


Fig. 11. *Prolacerta broomi* Parrington. AMNH 9502, a partial counterpart of the slab shown in figure 10. Caudal vertebrae and tibia below, hind limb parts of pelvis and presacral vertebrae above, $\times 1.4$.

is not to be identified as *Prolacerta*. The two humeri to be seen in the block numbered AMNH 9573 are robust bones, but in each the ends are too crushed to yield useful information about the humerus.

An elongated, slender bone in block number AMNH 9558 is here considered as probably a radius. One end of the bone is crushed to such a degree that it is not possible to determine satisfactorily its length or shape.

It is essentially a straight, slender bone, the ends of which are slightly expanded. The length of the bone would appear to be somewhat less than the estimated lengths of the humeri described above, which would be in accordance with the relationship between humerus and radius-ulna in *Prolacerta*.

THE APPENDICULAR SKELETON—HIND LIMB

Block number AMNH 9561 contains a part of the mid-shaft of a femur. This is a large bone, somewhat curved, its diameter being closely comparable to the diameter of the femur of *Prolacerta broomi* as figured by Gow. It is also a large hollow bone, the walls of the shaft being comparatively thin.

Our knowledge of the hind limb in *Prolacerta broomi* from Antarctica is best obtained from the partial skeleton, AMNH 9502. The ilium is rather tall, its anterior border being quite straight; this is in contrast with the ilium of *Prolacerta* as figured by Gow. It would appear that the superior border of the bone forms a sweeping curve, extending back and down, so that there is considerable posterior extension. The ventral part of the ilium where it articulates with the pubis and ischium is only partially preserved, a rather large acetabular depression is evident.

Both the pubis and the ischium are large and platelike. The pubis terminates ventrally in a rather straight, thickened, and somewhat everted border. The pubis is not sufficiently well preserved to indicate the presence or absence of an obturator foramen.

The two ischia preserved in the block numbered AMNH 9561 are platelike, each resembling in shape the ischium of *Prolacerta broomi* as figured by Gow. There is a ventrally directed, low ridge on the medial surface of the bone, and posteriorly it terminates acutely.

The femur of AMNH 9502 is a strong bone, curved posteriorly at its distal end. Although somewhat crushed proximally, it would appear that there is a large internal trochanter, separated from the head of the bone by an intertrochanteric fossa. The proximal articular end of the femur appears to have been rounded. The shaft of the bone is smooth, without muscle scars.

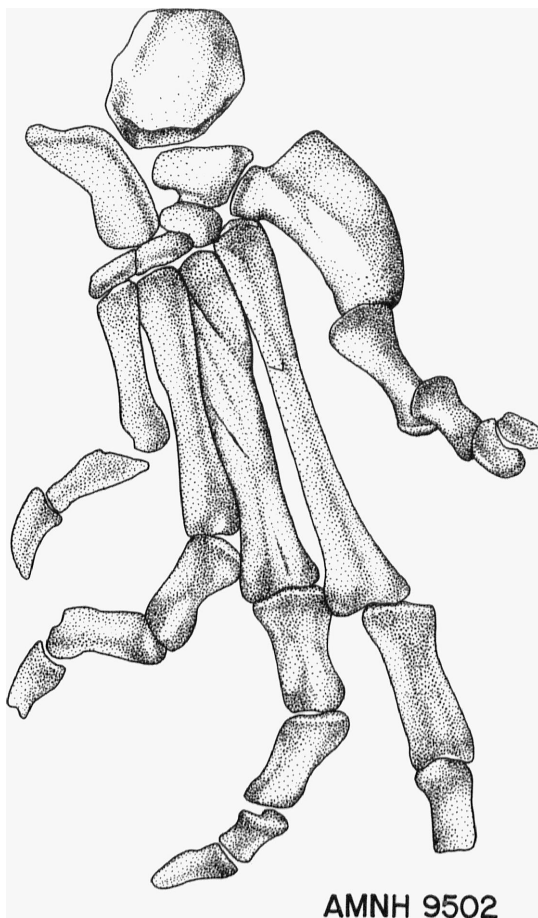


Fig. 12. *Prolacerta broomi* Parrington. AMNH 9502, left pes. Dorsal view, $\times 3.4$.

The tibia is a stout, straight bone, equal to the femur in length. This contrasts with the hind limb of *Prolacerta* as described by Gow, in which the lower bones are somewhat longer than the femur. The fibula is of course much smaller in diameter than the tibia, yet the shaft of this bone is strong and rounded in cross section.

A nicely articulated pes completes the specimen here described. There are two large proximal bones in the tarsus. One of these, a large, rounded element obviously is the calcaneum. A transversely elongated bone situated immediately medial to the calcaneum is here interpreted as a large astragalus (or perhaps a fused astragalus and centrale), articulating with both the tibia and fibula, much

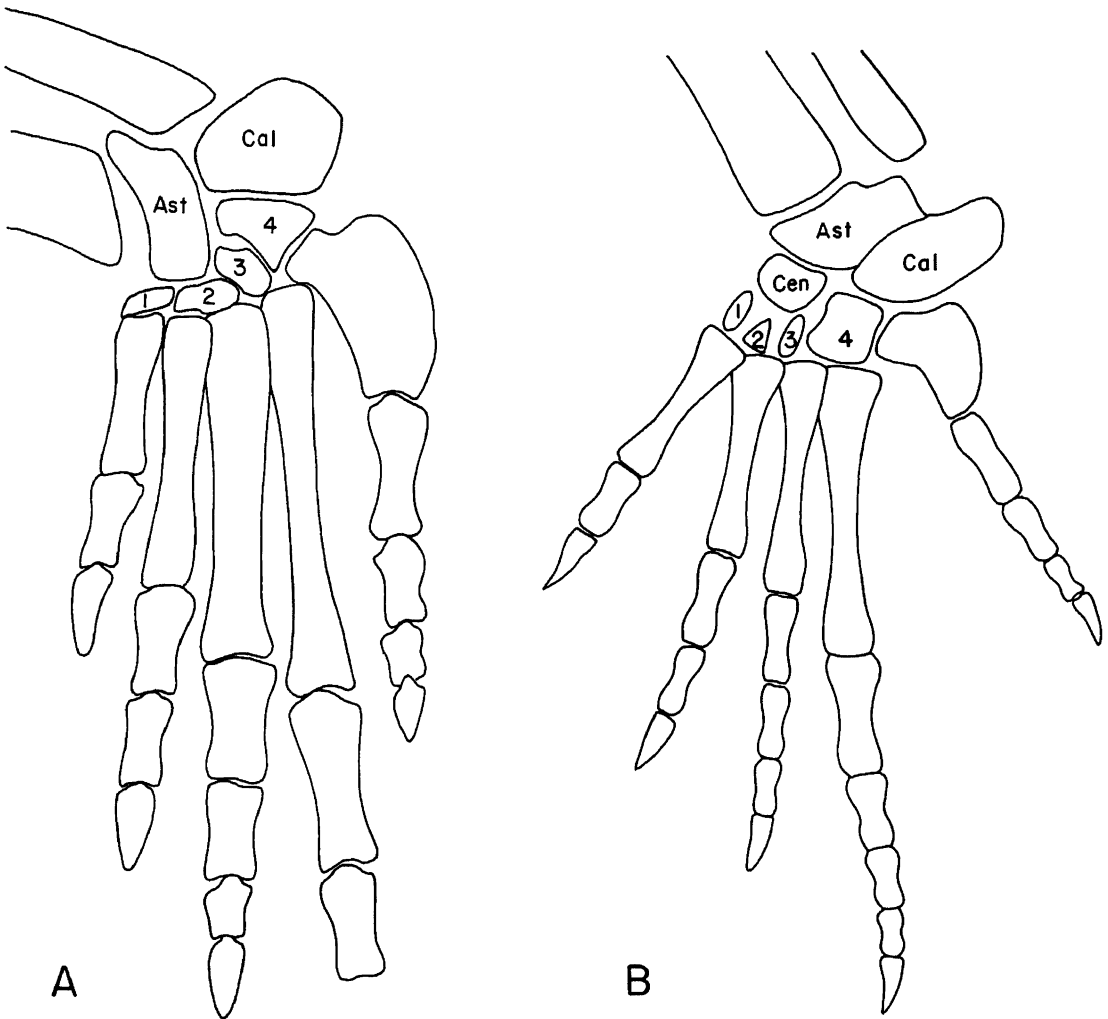


Fig. 13. **A.** *Prolacerta broomi* Parrington. AMNH 9502, left pes. Dorsal view, $\times 3.4$. **B.** *Prolacerta broomi* Parrington. Pes, after Gow. Dorsal view, $\times 3.4$. Abbreviations: Ast, astragalus; Cal, calcaneum; Cen, centrale; 1, 2, 3, 4, tarsals.

as Gow has shown for *Prolacerta*. Gow showed a small centrale in contact with the astragalus in *Prolacerta*, but such an element is not discernable in the specimen at hand. Yet, generally speaking, the disposition of the proximal tarsals in the present specimen accords closely with the arrangement seen in *Prolacerta*.

There are four distal tarsal bones, the first three articulating with the proximal ends of the first three metatarsals. The fourth distal tarsal is larger than its fellows, and is related in small part with the proximal end of the

fourth metatarsal, and to a larger degree with the proximal end of the fifth metatarsal. Proximally it articulates with both the astragalus and the calcaneum.

There are five well-developed metatarsals, progressively increasing in length from the first to the fourth member of the series. The fifth metatarsal is approximately equal to the first in length. There are two phalanges in the first digit, three in the second, four in the third, and four in the fifth. Only the two large proximal phalanges are preserved in the fourth digit, but it seems quite probable that



Fig. 14. *Prolacerta broomi* Parrington. AMNH 9560, right hind limb with fragments of the pelvis and parts of the pes, $\times 1$.

there were five present. Therefore there is every reason to think that the phalangeal formula of this foot was characteristically reptilian, namely 2-3-4-5-4.

The fifth metatarsal merits special attention. As noted, it is about equal to the first metatarsal in length, but it is very broad, and divergent from the rest of the foot. It does not, however, have the hooked shape so characteristic of thecodont reptiles; rather its medial edge is curved. The same is true of the lateral edge, which forms a strong curve leading to a broad flange lateral to the proximal articulation of the bone. In a general way this bone resembles the fifth metatarsal of *Prolacerta*, as figured by Gow. It is distinguished, however, by its very strong proximal articulation.

An articulated right hind limb, with an incomplete foot and a very fragmentary pelvis, is present in block AMNH 9560. The pelvis is seen in ventral view, with both ischia poorly preserved though, visible. A small part of

the right pubis is also visible. The femur, its head in articulation with the pelvis, is a long, slender bone, slightly expanded proximally and distally. It evidently represents an individual considerably smaller than those represented by AMNH 9502 and by the humeri, described above. The tibia and fibula are in articulation with the femur. The distal ends of these bones are missing as are any elements of the tarsus. As in AMNH 9502, the tibia and fibula are approximately equal to the femur in length. The metatarsals are present although incompletely preserved. They do show, however, an increase in length from the first through the fourth metatarsal, as would be expected. The fifth metatarsal can be seen as a short, broad bone, being particularly wide at its proximal end, but it is so incompletely visible that no exact determination can be made as to its shape. Poorly preserved articulated phalanges are to be seen distal to the second and third metatarsals. These show the expected numbers of three and four, respectively.

CONCLUSION

The discovery of *Prolacerta broomi* in the Lower Triassic Fremouw Formation of the Transantarctic Mountains forms one more link in the paleontological evidence showing the very close paleozoological relationships between Antarctica and southern Africa at the beginning of Triassic time. These relationships are exemplified by the presence in Antarctica of the labyrinthodont amphibians *Austrobrachyops* and *Cryobatrachus*, the former comparable to the South African *Cynognathus* Zone brachyopid *Batrachosuchus*, the latter to the South African *Lystrosaurus* Zone lydekkerinids *Lydekkerina* and *Limnoiketes* (Colbert and Cosgriff, 1974). The two continental regions are further linked among the reptiles by the specific identities between dicynodonts, procolophonids, cynodonts, and scaloposaurians. Thus *Lystrosaurus murrayi* and *Lystrosaurus curvatus* (Colbert, 1974), *Lystrosaurus mccaigi* (Cosgriff et al., 1982), *Myosaurus gracilis* (Hammer and Cosgriff, 1981), *Procolophon trigoniceps* (Colbert and Kitching, 1975), *Thrinaxodon liorhinus* (Colbert and Kitching, 1977), and *Ericiolacerta parva* (Colbert and Kitching, 1981), found in

the Fremouw Formation, extend the ranges of these species into East Antarctica from their original distributions in the *Lystrosaurus* Zone of the Karroo beds. In addition, other scaposaurian reptiles enlarge the relationship, although not down to the generic or specific levels. *Prolacerta broomi* does, however, add to the record still another genus and species common to the two regions. One can only conclude that this reptile, like the other tetrapods from the Fremouw Formation, indicates most clearly that there was a close ligation between East Antarctica and southern Africa, with the range of the *Lystrosaurus* fauna extending across what was once a unified geographic region.

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