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Scaloposaurian Reptiles from the Triassic of Antarctica

EDWIN H. COLBERT[1] AND JAMES W. KITCHING[2]

ABSTRACT

Among the theriodont reptiles discovered in the Lower Triassic Fremouw Formation of Antarctica during the austral summer of 1970–1971, are several scaloposaurian skulls, jaws, and parts of postcranial skeletons. Of particular significance are an associated mandibular ramus and pterygoids, as well as the hind limbs of a second specimen, all identified as *Ericiolacerta parva,* the type of which comes from the *Lystrosaurus* zone of the Karroo sequence of South Africa. In addition, two new genera and species are described: *Pedaeosaurus parvus* and *Rhigosaurus glacialis,* the former a very small scaloposaurid rather similar to *Ericiolacerta,* but with a flat skull roof pierced by a pineal foramen and with numerous simple teeth; the latter a comparatively robust form (although small in size) lacking a pineal foramen, with a strong jugal arch, a rather heavy dentary, and enlarged canines followed by a limited number of simple, pointed postcanine teeth. A small maxilla with an associated dentary is included in this paper, although its identity as a scaloposaurian theriodont cannot be verified. It is therefore designated as Theriodontia, *incertae sedis.* As in the case of previously described tetrapods from the Fremouw Formation, the scaloposaurians show some close resemblances with, and some differences from, fossils in the *Lystrosaurus* zone fauna of Africa. This is to be expected among two assemblages that had terrestrial connections, yet at the time were separated by a distance of perhaps 1500 km.

INTRODUCTION

Among the fossil reptiles collected from the Lower Triassic Fremouw Formation in the Transantarctic Mountains of East Antarctica, during the austral summer of 1970–1971, are several specimens of scaloposaurid theriodonts. The fossils, five in number, were obtained by one of us (J.W.K.) in the vicinity of Shackleton Glacier, two having been found on Kitching Ridge immediately to the east of the glacier and two at *Thrinaxodon* Col, some 15 km. west of the glacier and about 5 km. south of McGregor Glacier, not far from the confluence of these two great ice streams. Kitching Ridge is at lati-

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tude 85° 12′ S and longitude 177° 06′ W, whereas *Thrinaxodon* Col is at latitude 85° 12′ S; its longitude is about 174° 19′ W.

The scaloposaurids found at *Thrinaxodon* Col are from a locality at which several specimens of the cynodont genus, *Thrinaxodon,* occurred—hence the name given to this topographic feature. The Antarctic *Thrinaxodon,* belonging to the same species found in South Africa, namely *T. liorhinus,* has recently been described by us. The presence of scaloposaurids associated with *Thrinaxodon* in Antarctica repeats the occurrences of reptiles that so characterize the *Lystrosaurus* zone of the Middle Beaufort beds of South Africa. (Colbert and Kitching, 1977.)

The drawings illustrating this paper were made by Miss Pamela Lungé and the photographs were taken by Mr. Mark Middleton, both of the Museum of Northern Arizona, Flagstaff.

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STRATIGRAPHIC RELATIONSHIPS

The stratigraphic relationships of the Fremouw Formation have been described in several publications, most notably in a paper by Elliot, Collinson, and Powell (1972), dealing with the stratigraphy of the Triassic tetrapod-bearing beds of Antarctica, as well as in the preceding papers of this series describing some of the tetrapods from the Fremouw Formation, particularly *Lystrosaurus* (Colbert, 1974; Colbert and Cosgriff, 1974; Colbert and Kitching, 1975). In the light of previous descriptions, no detailed consideration of the Fremouw Formation is presented in this paper. For the benefit of readers who may not have access to the publications cited, a few remarks are, however, offered here.

The Lower Triassic Fremouw Formation, which rests disconformably on the Permian Buckley Formation in the Transantarctic Mountains, and may reach thicknesses of some 650 m., is succeeded by the Triassic Falla Formation. The Fremouw sediments are characterized by fining-upward cycles, consisting of coarse channel deposits of continental sandstones at the base, with the higher siltstones and mudstones forming fine-grained floodplain deposits. Several such cycles are contained within the Fremouw Formation. In the area of the McGregor and Shackleton glaciers there are bedding plane exposures consisting of fine-grained mudstones and sandstones, and it is from these exposures that the bones and skeletons of fossil vertebrates have been obtained.

The upper horizons of the Fremouw Formation also contain fossil logs and coal, and near the top of the sequence are leaves of the widely distributed Gondwana plant, *Dicroidium.*

As has been pointed out, the fauna from the Fremouw Formation is closely related to the Lower Triassic *Lystrosaurus* zone fauna from the Middle Beaufort beds of South Africa, listed by Kitching in 1968 and 1977.

DESCRIPTION OF FOSSILS

SYSTEMATICS

CLASS REPTILIA

ORDER THERAPSIDA

SUBORDER THERIODONTIA

INFRAORDER SCALOPOSAURIA

FAMILY SCALOPOSAURIDAE

The Scaloposauria constitute a group of small, Middle Permian to Lower Triassic theriodonts, probably derived independently from an early Permian sphenacodont pelycosaur stock, but separated from their sphenacodont precursors by a substantial time gap.

In the South African Beaufort Group, they make their first appearance in the lower horizons of the *Tapinocephalus* zone at the same time as the more primitive pristerognathid theriodonts and persist into the middle horizons of the Lower Triassic, *Lystrosaurus* zone, whereas the pristerognathid-like forms become extinct at the end of the Middle Permian *Tapinocephalus* zone.

Since the description of *Scaloposaurus* *constrictus*, Owen, 1876, these small theriodonts with exceptionally low and slender snouts (of which a large number of described and new specimens are housed in South African institutions) have been variously classifed and defined by authors such as Boonstra, 1934, 1953, and 1972; Brink, 1965; Broom, 1910 and 1932; Crompton, 1955; Haughton and Brink, 1954; Piveteau, 1961; Romer, 1969; Watson, 1931; Watson and Romer, 1956; Mendrez, 1975; and others.

Watson, 1931, in his description of the skeleton of the "bauriamorph" (*Ericiolacerta parva*), excludes the scaloposaurids from the infraorder Therocephalia and in his summary suggests that the great suborder Therocephalia can probably be subdivided into smaller groups.

Boonstra, 1953 (p. 605) suggested that it may be taxonomically convenient to subdivide the suborder Therocephalia into two superfamilies, Pristerosauria and Scaloposauria, the former to contain the more primitive pristerognathids and the latter the more advanced scaloposaurids. However, in 1972 he discarded his superfamilies Pristerosauria and Scaloposauria, using the orders Therocephalia and Scaloposauria and gave useful definitions for both orders.

In their classification of the therapsid reptiles, Watson and Romer, 1956, include the scaloposaurids in the infraorder Bauriamorpha and restrict the use of the infraorder Therocephalia to the more primitive pristerognathids and whaitsiids. Romer, 1969, once again expands the infraorder Bauriamorpha to include the *Scaloposaurus*-like forms, while Brink, 1965, favors the inclusion of all the ictidosuchid-bauriamorph (scaloposauriid-bauriamorph) forms under the infraorder Scaloposauria. This, he suggests, could then be divided into two superfamilies, the earlier Ictidosuchoidea (with the families Ictidosuchidae and Scaloposauridae) and the later Bauriamorpha (containing only the family Bauriidae). He gives very useful definitions for his familial division (Brink, 1965; p. 137).

Kitching, 1977, modified the taxonomy of the scaloposaurids by combining Brink's 1965 classification with those of earlier authors, resulting in the adoption of the infraorders Scaloposauria and Bauriamorpha. This was based on his close association with Brink's work and on his own observations and studies during detailed preparation of new material and additional preparation of many existing, incompletely prepared specimens of both therocephalians and scaloposaurids.

Based on the various classifications and definitions of the above-mentioned authors and by Kitching (in preparation) the Scaloposauria can be redefined as follows.

Small theriodonts with lightly built skulls. Snout region long and shallow with slight maxillary flare. Parietal forms part of the relatively small temporal fossa. Postorbital arches slender, complete or incomplete (in many instances incomplete due to prefossilization damage). No postorbital. No preparietal. Pineal foramen absent or very small if present. Postfrontals always absent. Intertemporal region narrow with sagittal crest or broad and flat. Occipital crest low or incipient. Zygomatic arches slender. Secondary palate elementary or closing, in some forms incipiently mammal-like. Epipterygoid generally slender, but sometimes broad and partially incorporated into the sidewall of the brain case. Pterygoid vacuities oval or elongate. Suborbital fenestra small and round to oval. Occipital condyle single (incipiently double in the Bauriidae). Dentition less heterodont than in the infraorder Therocephalia with canines frequently reduced in prominence. Cheek teeth small, conical, and numerous (7–12), but in some forms posteriorly incipiently tricuspid. Six incisors—not enlarged; two to three pre-canine maxillary teeth not uncommon in the Ictidosuchidae. Dentary long and exceptionally slender with an almost continuously curved lower border and long ascending coronoid process rising slightly above the surangular (excessive protrusion of the coronoid process beyond the surangular can in many instances be attributed to postmortem distortion). Postdentary bones either well developed or weak; no postventral angle to the dentary.

In general many of the above characters are applicable to the known specimens of the family Scaloposauridae and particularly to *Scaloposaurus* and *Ericiolacerta* (if the latter is indeed a separate genus and not merely a juvenile of the former), from the Lower Triassic *Lystrosaurus* zone of South Africa.

Recent advances in the study of therocephalians and scaloposaurids (Brink, 1965; Mendrez, 1972, 1973, and 1975; Kitching, 1977, and in preparation) indicate that some "scaloposaurids" described as new genera and species are merely juveniles or junior synonyms of existing taxa, some of them therocephalian. Two examples will illustrate the misinterpretations that have occurred. *Homodontosaurus kitchingi* Broom, 1949, has proved on further preparation to be a junior synonym of the scaloposaurid *Tetracynodon tenuis* Broom and Robinson 1948 (Kitching, 1977); more recently, additional preparation of the type of the "scaloposaurid" *Olivieria parringtoni* revealed that it is a juvenile of the therocephalian *Moschorhinus*. This conclusion is based on morphological features of the skull and on the fact that the type of *Olivieria* was recovered from the same locality and horizon as two adult *Moschorhinus* specimens.

The authors are thus aware of some difficulties in the concept of the scaloposaurs and have relied on their redefinition of the Scaloposauria and on the definitions of the families Ictidosuchidae and Scaloposauridae advanced by the authors mentioned above in identifying the scaloposaurids from the Lower Triassic Fremouw Formation of Antarctica.

[After the manuscript of the paper was submitted for publication, a posthumous paper by Mendrez-Carroll was received devoted to a new study of the skull of *Scaloposaurus constrictus*. She limits the family Scaloposauridae to *Scaloposaurus* and *Nanictocephalus,* which genera she regards as being restricted to the "*Cistecephalus*-zone" of late Permian age. Scaloposaurians in the *Lystrosaurus* zone of early Triassic age are considered by her to be contained within the genera *Ericiolacerta* and *Scalopolacerta* (this latter a new genus based on *Scaloposaurus hoffmani*), belonging to the family Ericiolacertidae. We are, however, retaining the more inclusive concept for the Scaloposauridae.]

Ericiolacerta Watson, 1931

Ericiolacerta Watson, 1931, p. 1163–1180, figs. 1–14, 16.

TYPE SPECIES: *Ericiolacerta parva* Watson.

HORIZON AND LOCALITY OF TYPE SPECIES: From the *Lystrosaurus* zone, Middle Beaufort beds, Karroo Series, near Harrismith, Orange Free State, South Africa.

GENERIC DIAGNOSIS: A small theriodont. Skull low, snout long and slender, postorbital bar incomplete, temporal region short. Parietal region fairly large and flat, with no parietal foramen. Pterygoids tetraradiate with large interpterygoid vacuity. Secondary palate, formed largely by the premaxilla and maxilla; secondary palate closing. Lower jaw slender, with little development of the coronoid. Teeth rather numerous and irregular, with no distinctive canine. Some mandibular postcanines are bicuspid or tricuspid. Skeleton slender with elongated scapula, flat pelvic girdle, slender limbs and feet and a tuber on the calcaneum.

(We are inclined to regard *Eriociolacerta parva* Watson, 1931, based upon a single badly distorted specimen that came from a horizon on the Harrismith Commange that yielded a number of specimens of *Scaloposaurus,* as synonymous with *Scaloposaurus constrictus* Owen, 1876. For now, however, we are accepting *Ericiolacerta* as a valid genus, with *Ericiolacerta parva* the type species. Our decision follows the judgment of the late Dr. Christiane Mendrez-Carroll, who had done extensive research on the Scaloposauridae.)

Ericiolacerta parva Watson, 1931

Ericiolacerta parva Watson, 1931, pp. 1163–1180, figs. 1–14, 16.

TYPE: Distorted skull and almost complete skeleton; Museum of Zoology, Cambridge University, Cat. No. R377/T.369.

HORIZONS AND LOCALITIES: From the Lower Triassic, Middle Beaufort beds, *Lystrosaurus* zone; Harrismith, Orange Free State, South Africa. The Antarctic specimen is from the Lower Triassic Fremouw Formation, and was found near the confluence of McGregor and Shackleton glaciers, Transantarctic Mountains, Antarctica.

DIAGNOSIS: See generic diagnosis, above.

ANTARCTIC SPECIMENS UNDER CONSIDERATION

AMNH 9542, the pterygoids of the palate and a left mandibular ramus with teeth. From Kitching Ridge,[3] 25 km. due east of *Thrinaxodon* Col, at approximately 85° 12′ S and 177° 06′ W.

AMNH 9550, hind limbs and part of a pelvis with some vertebrae. From Kitching Ridge.

DISCUSSION

Number 9542 can be identified as *Ericiolacerta parva* with a considerable degree of confidence. As noted above, it consists of the pterygoids and a left mandibular ramus (fig. 1) and scanty as is this evidence, the elements preserved compare so closely with those of the type specimen of *Ericiolacerta parva,* as described and figured by Watson (1931), that the identity of the Antarctic fossil would seem to be well established.

The paired pterygoids are tetraradiate, bounding an elongated interpterygoid vacuity with inner vertical faces. These elements are slightly smaller than the pterygoids of *Scaloposaurus constrictus,* and slightly larger than those of *Ericiolacerta parva* as figured by Watson (1931) and by Mendrez (1975). Even though, as noted above, *Ericiolacerta parva* is considered by us as possibly synonymous with *Scaloposaurus constrictus,* Watson's name is used in the following discussion. The interpterygoid vacuity, broad and somewhat rounded anteriorly, is constricted to a narrow channel posteriorly within the boundaries of the two pterygoids. In this respect the Antarctic specimen differs slightly from the type of *Scaloposaurus constrictus,* in which the posterior portion of the interpterygoid vacuity is more widely open, perhaps owing to distortion, but it resembles closely the type of *Ericiolacerta parva.* Another difference is the lateral reach of the quadrate rami of the pterygoids. In the Antarctic specimen the tips of the rami are lateral (and of course posterior) to the pterygoid flanges; in *Scaloposaurus* they are close to an anteroposterior line with the pterygoid flanges; in *Ericiolacerta* they are medial to anteroposterior lines projected back from the pterygoid flanges.

In all essential features, the pterygoids of the Antarctic specimen coincide closely with those of *Ericiolacerta parva* and *Scaloposaurus,* as known from *S. constrictus.* The outer margins of the quadrate rami are strongly ridged, whereas medially, between these ridged outer margins and the interpterygoid vacuity, there are thin bony plates. The fossa between each ramus and the basisphenoid and paroccipital is wide. The transverse ramus or flange of each pterygoid is robust, and somewhat flared laterally, and ends in a rather broad knob on its posterior half with an anterior thin plate. Its ventral surface is slightly concave. The palatal surfaces of the two pterygoids unite in a firm suture and this junction seems to be along a low median ridge, with grooves on each side of this ridge, as is typical of *Ericiolacerta* and *Scaloposaurus.* It seems likely that these grooves would have passed anteriorly into the choanae although not enough of the specimen is preserved to make a definite determination on this point.

A comparison of the pterygoids of AMNH 9542 with those of *Ericiolacerta parva* and *Scaloposaurus constrictus* is shown in figure 3.

So far as the lower jaw is concerned, the resemblance between the Antarctic specimen and the mandible of *Ericiolacerta* is striking. The Antarctic specimen is somewhat bigger than the jaw figured by Watson, but is essentially the same size as that of *Scaloposaurus constrictus.* All three jaws are long and low, and lack a free upright coronoid. They show an expansion in the symphyseal region, which is shorter in the Antarctic specimen, and in *Scaloposaurus,* than in *Ericiolacerta.* The Antarctic jaw lacks the postdentary elements, but in view of the

[3] For the latitudes and longitudes of Kitching Ridge and *Thrinaxodon* Col, see Alberts, 1977.

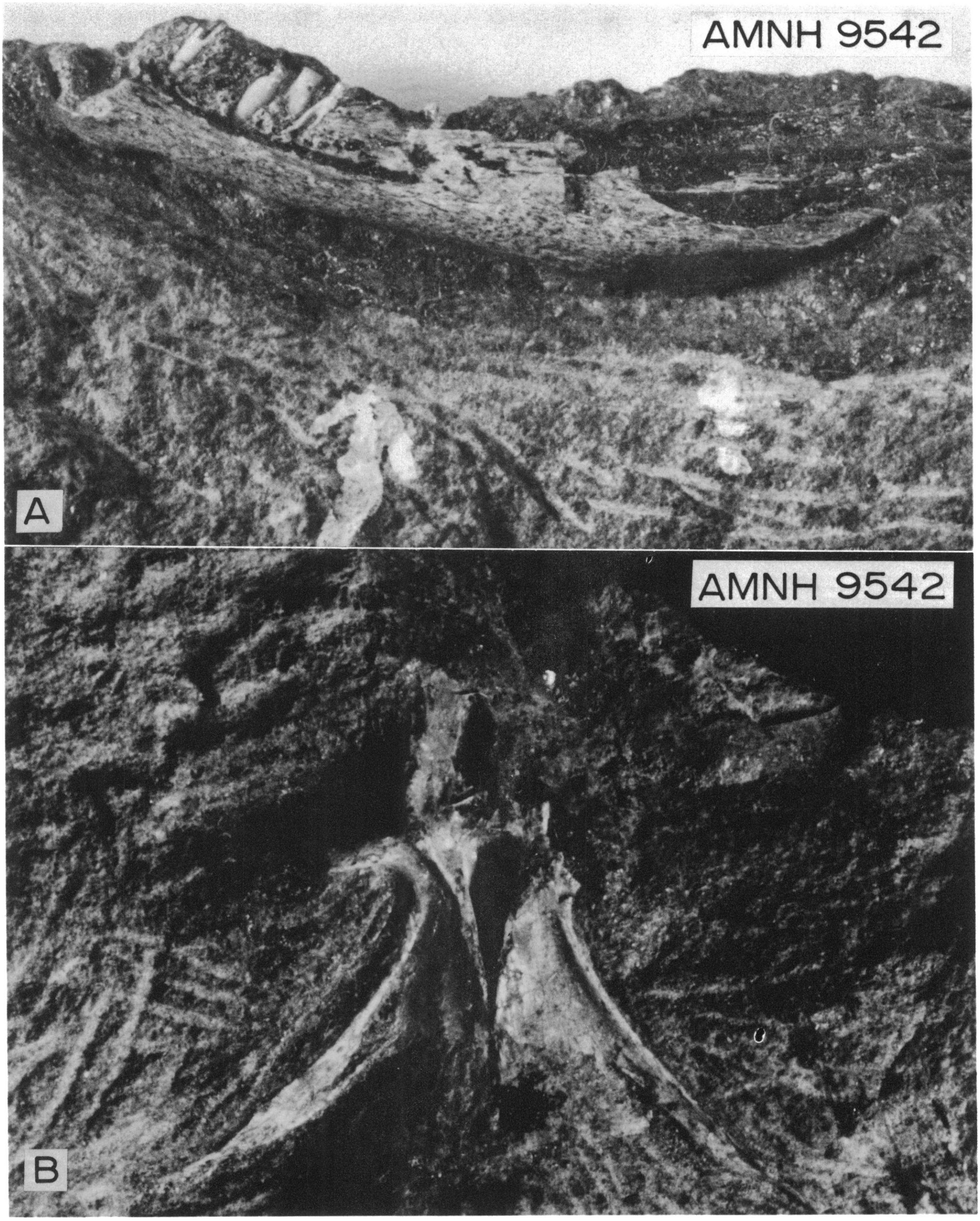

FIG. 1. *Ericiolacerta parva* Watson. AMNH 9542. A. Part of a left manidbular ramus, lateral view. B. Pterygoids, palatal view. Both ×3.

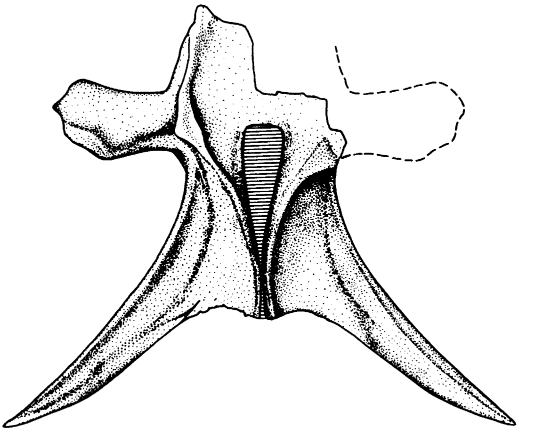

FIG. 2. *Ericiolacerta parva* Watson. AMNH 9542. Pterygoids, palatal view. ×2.

close correspondence in shape between it and *Ericiolacerta* as well as *Scaloposaurus* in the posterior dentary region, which slopes back as a long process, it seems probable that these bones in the Antarctic fossil were similar to those in the African specimens.

The lower teeth of *Ericiolacerta* are noteworthy because of their generally small size and irregularity, a character that certainly holds in the Antarctic specimen. From the remnants of the basal part of an alveolus it appears that the first dentary tooth in this fossil was a large cylindrical incisor, not quite so procumbent as in *Ericiolacerta,* and separated by a small gap from the next tooth behind it. This second tooth is quite small in *Ericiolacerta* from Africa; it would appear to be relatively larger in the Antarctic fossil.

One of the striking features of *Ericiolacerta* is the lack of enlarged canines, above and below, and certainly the Antarctic jaw shows no sign of a canine.

In this specimen there is an irregular arrangement of very small teeth behind the first two dentary teeth—six in number. In *Ericiolacerta* as figured by Watson nine such unevenly spaced teeth are shown. In the Antarctic specimen there are large gaps between the second and third dentary teeth (as preserved) and between the fifth and sixth teeth, thus allowing space for several more teeth to have been present in the sequence. Consequently, one may assume that the number of dentary teeth in the Antarctic specimen was closely comparable to that characteristic of *Ericiolacerta*. The posterior teeth in the African specimen have bulbous crowns and are tricuspid, with the cusps arranged in an anteroposterior plane and the central cusp the largest. The teeth in the Antarctic fossil have suffered from erosion, but the features of the last tooth in the series seem to indicate that the characters enumerated above could have applied to this

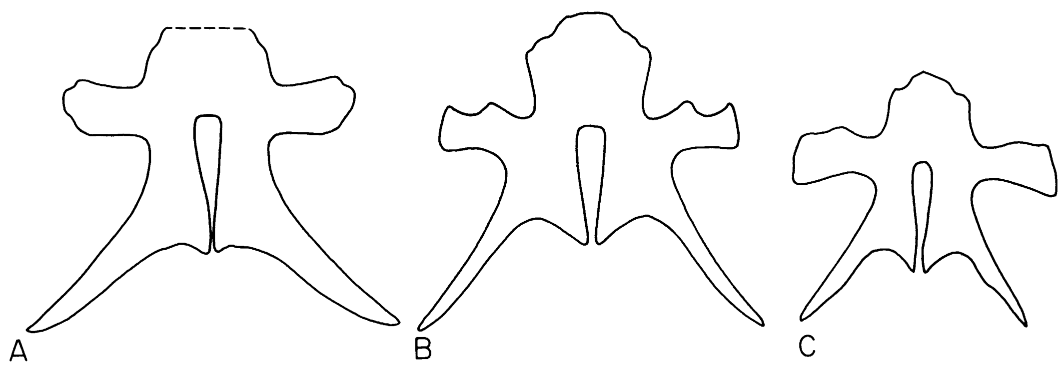

FIG. 3. A comparison of the pterygoids in scaloposaurians. A. *Ericiolacerta parva* Watson. AMNH 9542. B. *Scaloposaurus constrictus* Owen. Adapted from Mendrez, 1975. C. *Ericiolacerta parva* Watson. Adapted from Mendrez, 1975. A ×1.5, B and C ×2.

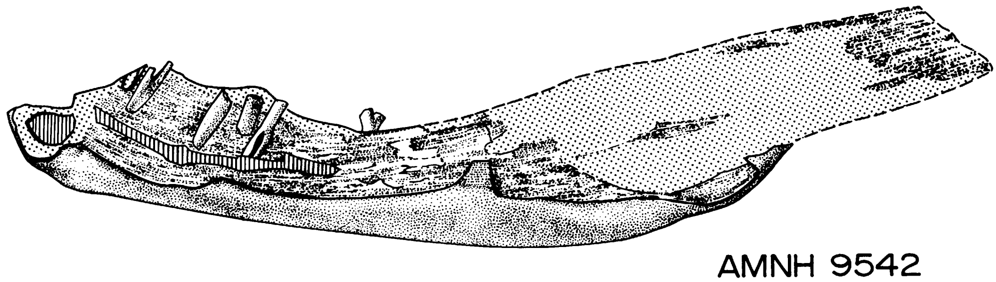

FIG. 4. *Ericiolacerta parva* Watson. AMNH 9542. Left manidibular ramus, lateral view. ×3.

tooth, and probably to the teeth in front of it.

Such are the comparisons of AMNH 9542 to *Ericiolacerta parva* and to *Scaloposaurus constrictus* from the *Lystrosaurus* zone of South Africa. The teeth of *Ericiolacerta parva* were also described in detail by Crompton (1962). It is here maintained that the comparisons justify the conclusion that this species was common to what is now southern Africa and what is now Antarctica during early Triassic time, thus constituting one more link in the evidence pointing to the close ligation of these two regions at that period of earth history.

AMNH 9550, a part of a pelvis with vertebrae and the hind limbs in articulation, is also identified as *Ericiolacerta parva*. It was found on Kitching Ridge, not far from AMNH 9542, and both specimens are within exactly the same type of matrix, namely a red silty sandstone containing flecks of feldspar with clay inclusions in the shape of little pellets. The possibility of numbers AMNH 9542 and 9550 representing the same individual is a debatable question. In Watson's description of *Ericiolacerta parva*, he shows a reconstruction of the skeleton with the femur having about the same length as the dentary. The lengths of the two elements according to his restoration would be 29.6 mm. for the dentary and 26.7 mm. for the femur. The fe-

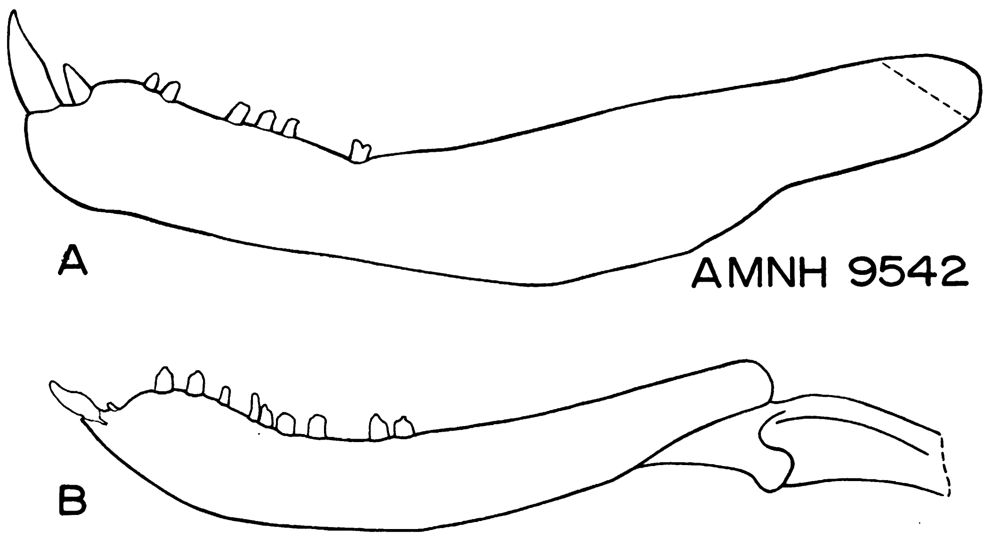

FIG. 5. *Ericiolacerta parva* Watson. Mandibular rami as restored in left lateral views. A. AMNH 9542. B. The type, after the figure by Watson. Both ×3.

mur of the type of *Ericiolacerta parva* is, however, incomplete at its distal end, and it is possible that Watson may have made it too long in his restoration. Watson states that although the femur is incomplete, "its length can be calculated from the angle it makes with the tibia and fibula" (Watson, 1931, p. 1177). The dentary of the Antarctic specimen is 42.2 mm. long, whereas the femur is 23.8 mm. long, slightly more than half the length of the dentary. If these same proportions were applied to *Ericiolacerta* the femur would be about 17 mm. in length, which seems short. Thus, it seems likely that AMNH 9550, with a much shorter femur than the dentary, 9542, may represent a somewhat smaller individual.

The pelvis of AMNH 9550, seen in ventral aspect, is incompletely preserved. Considerable parts of the two ischia are visible, and these are broad along their symphyseal borders and flat, narrowing to the acetabular articulation, very much as Watson has indicated in his drawing of the ischia of *Ericiolacerta*. The same may be true for the pubes, although these are not so well preserved in the Antarctic specimen as are the ischia. However, the ischia would seem to be relatively narrower in the Antarctic specimen than in the type of *Ericiolacerta parva*.

In the pelvic region there are several dislocated sacral ribs, behind which are four centra, and the four anterior caudals, above the posterior part of the ischia. Anterior to the mass of sacral ribs are three presacral centra in articulation with associated ribs. From this specimen it is not possible to determine precisely the number of sacral vertebrae, but it is assumed that there probably were three. This number is indicated by Watson for *Ericiolacerta parva* and it is a characteristic number for therapsid reptiles, although many genera show an incorporation of additional vertebrae into the sacrum.

The femur and tibia of AMNH 9550 are approximately equal in length. The femur is a strong bone, with the head set at a slight angle to the shaft, and with the proximal end of the bone expanded relative to its distal end, this expansion being the result of a well-developed ridge running down the shaft from the great trochanter.

The tibia, a heavy bone, is proximally and distally expanded. The well-developed fibula, which crosses the tibia from an internal position proximally to an external position distally, is expanded at each end. It is a sturdy bone relative to the tibia.

The pedes are preserved, but the bones have been somewhat displaced in each foot. It is possible, however, to get a fair impression as to the nature of the pes in this specimen. The feet are large, and strongly developed, probably about four-fifths the length of the tibia when extended. There is an astragalus, rather round in outline, except for a notch on what is presumed to be the side articulating with the calcaneum. Perhaps this is an arterial notch. A very large bone in the left foot is here tentatively considered to be the calcaneum. On one side it is thickened, whereas on the other it is considerably thinner, there being a sharp transition between these two areas of the bone. No calcis tuber can be seen, and this throws some doubt on the true nature of this bone. A tuber is prominent in *Ericiolacerta parva,* and it is characteristic for closely related therocephalians. Another rounded element in the left foot is tentatively identified as a centrale. It seems probable that there was a full complement of tarsals in this specimen, that is, astragalus and calcaneum, centrale and four distal tarsals.

The two feet indicate that there are five digits with strong metatarsals, of which the first is shorter than the remaining four. It appears that the fourth metatarsal is the longest of the group, and the fifth metatarsal, only slightly shorter than the fourth, is a relatively heavy bone. The phalanges are robust, the unguals being sharply pointed. It appears evident from the fossil that the phalangeal formula is 2-3-3-3-3.

The measurements show clearly the disparity in the length of the femur as compared with the dentary in the Antarctic materials, in contrast to the rather similar lengths of femur and dentary in the type of *Ericiolacerta parva*. Thus, the probability of the Ant-

FIG. 6. *Ericiolacerta parva* Watson. AMNH 9550. Hind limbs, with a fragment of the pelvis. ×3.

arctic materials representing two individuals, as already mentioned in a previous paragraph, is evident.

Watson shows the femur of *Ericiolacerta parva* as being slightly shorter than the tibia, but in AMNH 9550 the femur is slightly long-

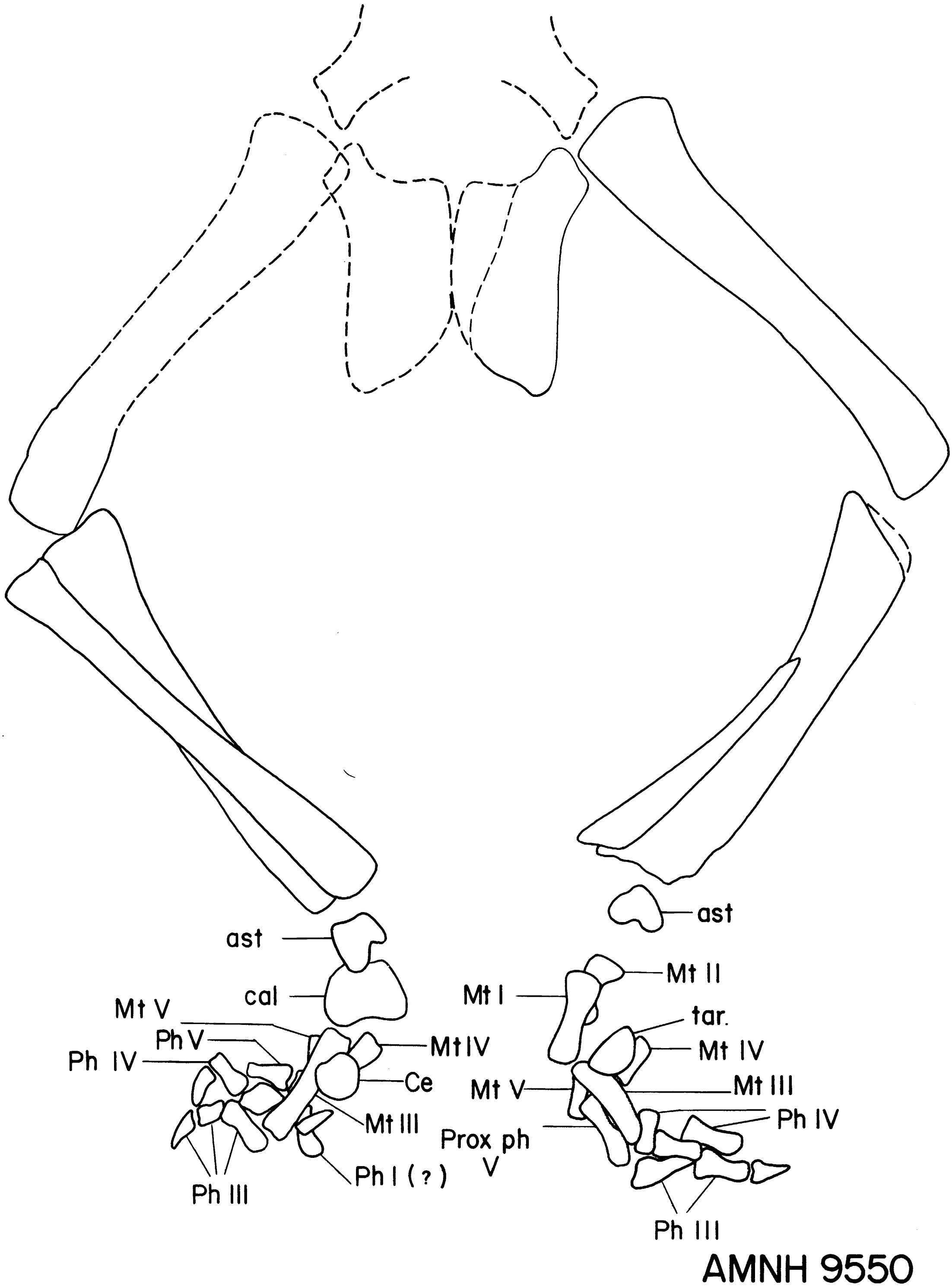

FIG. 7. *Ericiolacerta parva* Watson. AMNH 9550. Key to bones of the pedes, shown in figure 6. ast—astragalus; cal—calcaneum; ce—centrale; Mt—metatarsal; Ph—phalanx; Prox ph—proximal phalanx; tar—tarsal.

er than the tibia. This difference cannot, however, be accorded much significance, especially in view of the fact that the femur and tibia in Watson's specimen are incomplete, so that there is the possibility of some error in Watson's restorations of the lengths of these bones.

TABLE 1
Measurements (in Millimeters) of *Ericiolacerta parva*

	AMNH 9542	Watson, 1931	*Scaloposaurus constrictus*[a]
Dentary, length	42.2	29.6	40.0
Dentary, depth	4.8	4.0	—
Pterygoid, width across flanges	17.4	17.0	21.4
Pterygoid, width across quadrate rami	32.0	13.5	23.4
	AMNH 9550		
Ischium, breadth	4.6	10.2	—
Femur, length	23.8	26.7	—
Tibia, length	22.3	28.4	—
Fibula, length	22.3	28.4	—
Mt III, length	6.2	28.4	—

[a]As measured from figures; Watson, 1931.

PEDAEOSAURUS, NEW GENUS

TYPE SPECIES: *Pedaeosaurus parvus*, new species.

GENERIC DIAGNOSIS: A very small scaloposaurid, approximately 20 to 30 percent smaller in linear dimensions than *Ericiolacerta*. The characters of the skull and dentition are in general those seen in *Ericiolacerta*, but this form differs because of the presence of a well-defined pineal foramen.

ETYMOLOGY: *Pedae*, from Greek *pedai*, meaning a shackle, in reference to the Shackleton Glacier, near which the specimen was found: *saurus*, from Greek *sauros*, meaning a lizard, or reptile.

Pedaeosaurus parvus, new species

TYPE: AMNH 9548, a partial skull with mandible, associated with right and left femora and tibiae.

HORIZON AND LOCALITY: From the Lower Triassic Fremouw Formation at Kitching Ridge, about 5 m. above the confluence of this glacier with McGregor Glacier, at about latitude 85° 3′ S and longitude 177° 06′ W.

DIAGNOSIS: See generic diagnosis, above.

ETYMOLOGY: *parvus*, from Latin *parvus*, meaning small.

The specimen AMNH 9548 is noteworthy because of its very small size. If we are correct in placing it within the Scaloposauridae it may be the smallest known example of these theriodonts, being even smaller than the South African form, *Homodontosaurus* (which is here considered to be a juvenile *Tetracynodon*; see Mendrez, 1973) from the *Daptocephalus* zone. The manner of preservation is such that some of the characters typical of the Scaloposauridae cannot be determined, yet sufficient details can be seen so that the fossil may be assigned to the above family with some justification.

In addition to its small size, the skull is low, as is the posterior part of the dentary. In other words, the coronoid region is not elevated. Moreover, the dentary is slender, as is characteristic of the Scaloposauridae. The frontals are long, and the preorbital portion of the skull also would appear to be somewhat elongated. The temporal region is short, a character typical of this family. The parietals are broad and flat, a scaloposaurid feature, but are distinctive in being pierced by a well-formed parietal foramen, which could be a juvenile feature. This is in contrast with *Ericiolacerta*, in which no parietal foramen is present. In this respect we point out that Watson's figure of *Ericiolacerta* (1931) shows an opening in the midline of the parietals, but this is an artifact. Watson clearly states that "there is no pineal foramen" in *Scaloposaurus*. The lack of such a foramen is also characteristic of his *Ericiolacerta*.

In this connection note that Crompton, in his 1955 revision of the Scaloposauridae, recognized four "groups" of these reptiles, designated A–D, which show increasing stages

FIG. 8. *Pedaeosaurus parvus,* new genus and species. AMNH 9548. Skull and mandible in ventral view with parts of hind limbs. ×3.

of advancement. In this type of arrangement the more primitive scaloposaurids, included in his groups A and B, are characterized by a pineal foramen. In the more advanced forms, including *Scaloposaurus* and *Ericiolacerta,* it seems that the foramen has been lost. Therefore, it may be assumed that the Antarctic specimen retains a primitive feature in this respect.

In other ways, however, the Antarctic fossil shows various advanced features that typify *Scaloposaurus* itself as well as *Ericiolacerta*. The skull is not sufficiently complete to be certain as to the nature of the postor-

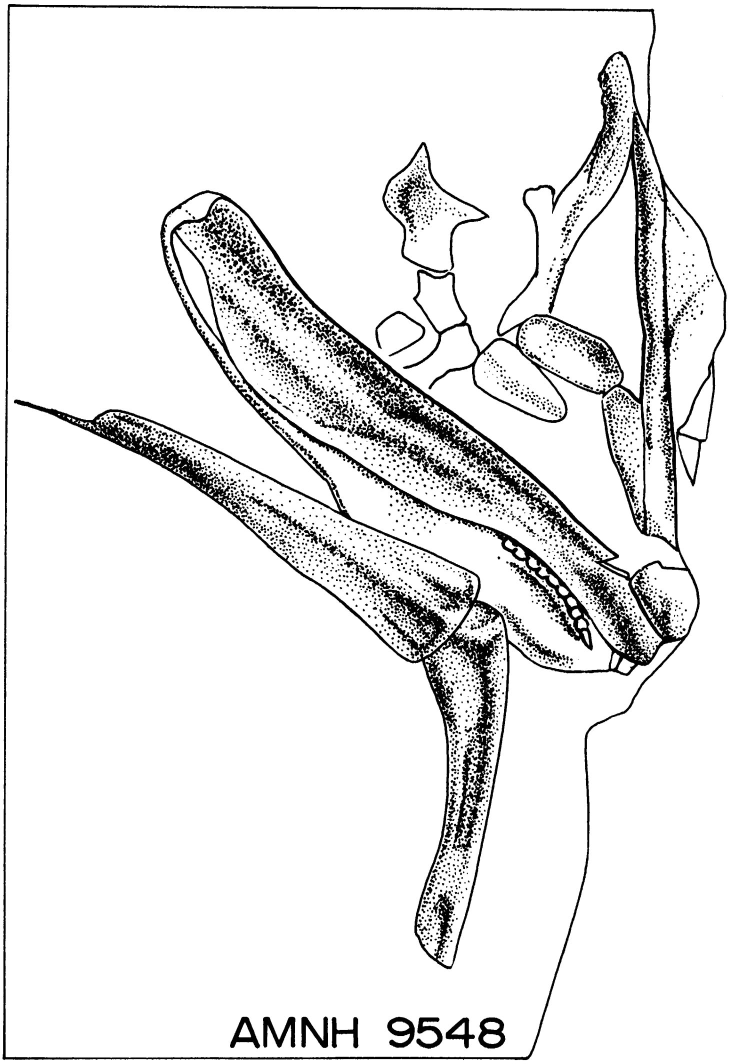

FIG. 9. *Pedaeosaurus parvus,* new genus and species. AMNH 9548. Mandible and left maxilla with alveoli for teeth in ventral view, certain palatal bones, and associated partial femur and tibia. ×3.

bital bar, but from the rather flat, delicate nature of the skull roof, it seems probable that the bar was incomplete, as it is in all but the most primitive scaloposaurids.

The palatal-basicranial regions of the skull are rather difficult to interpret because of fragmentation of the bones that occurred before or during fossilization. In addition the skull and jaws are contained within three separate pieces; (1) a block of matrix in which are preserved parts of the lower jaws and skull fragments; (2) a smaller block of matrix which separated from the parent block, containing the major part of the skull and the jaws, as well as the bones of the hind limbs, and (3) a still smaller fragment that separated itself during preparation—a fortuitous circumstance because the separation was clean, and as a result the skull roof, hitherto hidden by a hard, thick layer of matrix, was exposed.

Little can be said as to the ventral aspect of the skull and jaws. Anteriorly, between the anterior parts of the mandibular rami, near their junction, are two flat fragments of bone, here interpreted as parts of the palatal plates of the maxillae, or perhaps the premaxillae. Immediately behind them are two paired bones of indefinite shape which may be the displaced vomers. Abutting against the right member of the pair is the broken end of the right dentary, this bone being shifted so that it extends diagonally into the palatal region. The back end of this mandibular ramus is in place, and in contact with the quadrate, as is the case with the opposite ramus as well. Opposite the posterior ends of the two rami, and more or less on the midline, is a rather broad bone with a shallowly concave or dishlike surface, having a well-defined lateral edge flaring posteriorly, and a posterior transverse sutural edge, obviously for articulation with a more posterior element. This is taken to be the righthand part of the basisphenoid-basioccipital complex, which in the scaloposaurids is characterized by abrupt widening posteriorly.

In several other respects the Antarctic specimen shows resemblances to the more advanced scaloposaurids, as typified by *Scaloposaurus*. Thus, there are numerous teeth in both the skull and the dentary, and they are very small. There seems to be no indication of an enlarged upper canine, again an advanced character in the scaloposaurids, exemplified especially well in *Scaloposaurus* and *Ericiolacerta*. It is not possible to be confident as to the nature of the crowns in the postcanine teeth—whether they were simple or cusped. It appears, however, that the teeth were simple, as seems to be indicated by four fragmentary teeth—two in the maxilla and two in the dentary. An anterior maxillary tooth, with part of its distal region broken away, has all the appearance of being a simple peg. It is somewhat procumbent in the socket—pointing forward. In a more posterior part of the maxilla the point of an erupting tooth can be seen. There is an anterior dentary tooth of some size and quite simple in form. It is not, however, at the tip of the jaw, as is the large procumbent incisor in *Scaloposaurus* and *Ericiolacerta*. In what may be the second alveolus behind it is a simple, pointed tooth. There are at least nine alveoli in the skull, probably all in the maxilla. It appears that there is a fairly long premaxillary region that probably contained several incisors.

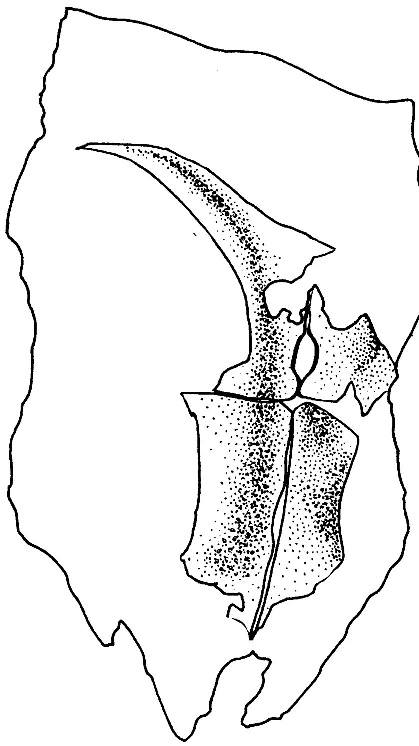

FIG. 10. *Pedaeosaurus parvus*, new genus and species. AMNH 9548. Parts of frontals and right parietal in dorsal view. ×3.

Articulated femora and tibiae are associated with the skull, being in contact with the left maxilla. Interestingly enough, these bones, which resemble the same bones of *Ericiolacerta parva* from Antarctica described above, are in the same pose as the

TABLE 2
Measurements (in Millimeters) of *Pedaeosaurus parvus*

Skull length (approximate)	28.0
Preorbital length (approximate)	14.0
Skull width, posterior	21.2
Interorbital width	5.1
Dentary length (approximate)	28.0
Femur length	17.7
Tibia length	23.2

Ericiolacerta limbs with the articulations between the two bones extended laterally. The femur is somewhat shorter than the skull, as in the case of the *Ericiolacerta* skeleton described by Watson, and the tibia apparently is slightly shorter than the femur—a resemblance to the Antarctic specimen of *Ericiolacerta*.

RHIGOSAURUS, NEW GENUS

TYPE SPECIES: *Rhigosaurus glacialis*, new species.

HORIZON AND LOCALITY OF TYPE SPECIES: From the Lower Triassic Fremouw Formation, at McGregor Glacier, *Thrinaxodon* Col, Mount Kenyon, Central Transantarctic Mountains, Antarctica.

GENERIC DIAGNOSIS: A small theriodont reptile, with relatively large orbits and a broad temporal region; frontals between the orbits are broad, parietals broad and flat; no pineal foramen; temporal fenestra broad and postorbital bar probably incomplete; jugal-squamosal bar deep beneath the temporal opening. There are at least four upper incisors followed by an enlarged canine. The 7 + simple, pointed postcanine teeth are approximately equal to each other in size and regularly spaced. The dentary is straight and seemingly rather heavy—not slender; several lower incisors; postcanine teeth similar to those in the maxilla.

ETYMOLOGY: *Rhigo*, from Greek *rhigos*, meaning frost or cold; *saurus*, from Greek *sauros*, meaning lizard or reptile.

Rhigosaurus glacialis, new species

TYPE: AMNH 9525, a partial skull with an anterior part of the lower jaw.

HORIZON AND LOCALITY: From the Lower Triassic Fremouw Formation at *Thrinaxodon* Col, Mount Kenyon, about 7 km. south of McGregor Glacier and some 14 km. west of Shackleton Glacier, in the area between the junction of these two glaciers, at about latitude 85° 12′ S and longitude 174° 19′ W, Central Transantarctic Mountains, Antarctica.

DIAGNOSIS: See generic diagnosis, above.

ETYMOLOGY: *glacialis*, from Latin *glacialis*, meaning icy or frozen.

The specimen AMNH 9525 is with some hesitation placed within the Scaloposauridae. In some respects, notably the small size, the wide, flat parietals lacking a pineal opening, and what appears to be an incomplete postorbital bar, AMNH 9525 seems to agree favorably with some Scaloposauridae. In other respects, especially the regular dentition and the large canine, the fossil is perhaps not typically scaloposaurid, but could belong to the family Ictidosuchidae, within the Scaloposauria.[4] It should be noted, however, that Crompton in his revision of the Scaloposauridae (1955) placed *Ictidosuchops intermedius*, originally described as *Ictidosuchoides intermedius*, within the Scaloposauridae, and this form is characterized by a regular dentition and well-defined canine. With this precedent in mind, it seems reasonable, therefore, to regard *Rhigosaurus* as coming within the limits of the scaloposaurids as defined in this paper.

The specimen consists of a skull and a part of the lower jaw in the rock. The anterior part of the skull in front of the orbit is rotated about the longitudinal axis at approximately 90 degrees with relation to the back of the skull. Consequently, as it is exposed, the front of the skull is seen in internal lateral view so that the left side of the facial region is preserved, whereas the back of the skull

[4] The infraorder Scaloposauria as here defined contains the families Scaloposauridae and Ictidosuchidae. In 1972 Boonstra recognized the Scaloposauria as an order, containing the suborders Ictidosuchia and Bauriamorpha. In Africa ictidosuchids range from the *Tapinocephalus* zone (Boonstra, 1954; Kitching, 1977) to the first 50 ft. (±18) of the *Lystrosaurus* zone.

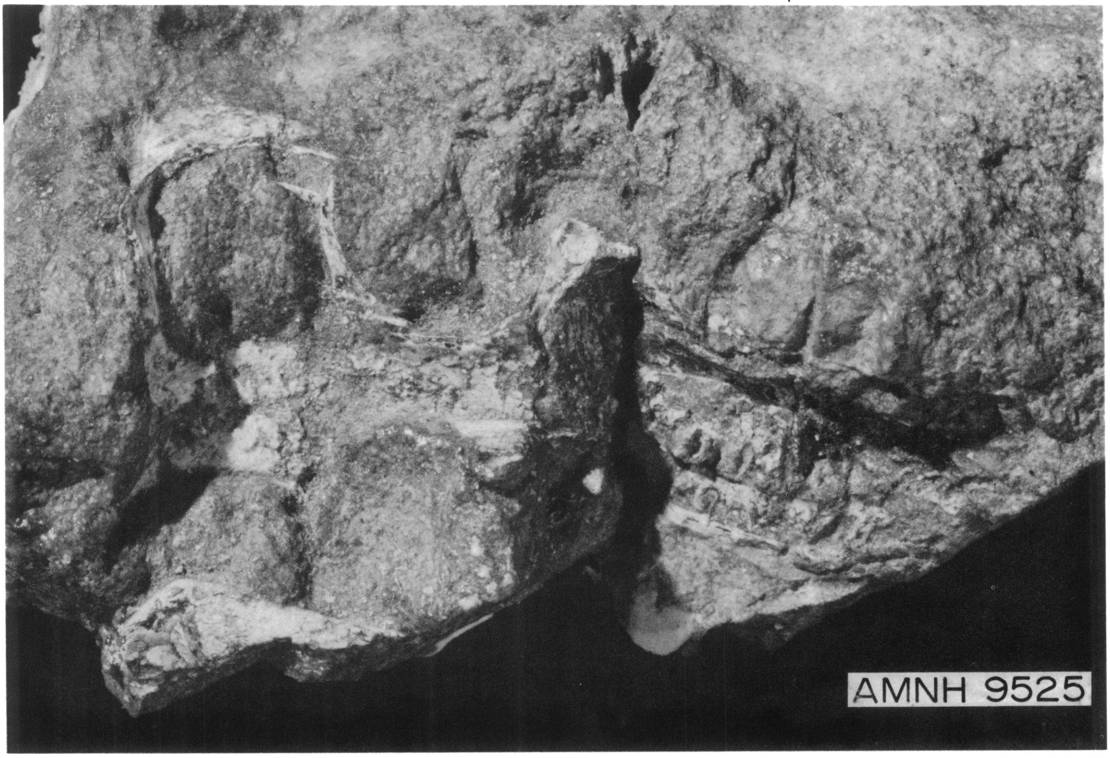

FIG. 11. *Rhigosaurus glacialis,* new genus and species. AMNH 9525. Skull, the posterior part in dorsal view, the anterior part in partial lateral view. ×3.

is seen in dorsal view. It would seem that the skull was fractured transversely, perhaps at some time prior to fossilization, with the resultant rotation of one segment in relation to the other. Yet the fracturing did not separate the two pieces which are still in contact.

The skull is small, being about 40 millimeters in length. The parietals are broad and very flat, and as mentioned there is no pineal foramen present. It would appear that the postorbital bar is incomplete, which is typical of the scaloposaurids, and forms the anterior margin of a short and wide temporal fenestra. Beneath the fenestra is a rather deep jugal-squamosal bar. The orbit is relatively large.

In the features of the dentition this specimen is unlike scaloposaurids such as *Scaloposaurus,* but is similar to *Ictidosuchoides longiceps* Brink, 1960, the inclusion of which within the Ictidosuchidae broadens the diagnostic characters of that family, especially so far as the dentition is concerned. It may be compared as well with *Regisaurus jacobi* Mendrez, 1972. The canine is large as in *Ictidosuchops* and *Ictidosuchoides,* whereas behind the canine there are visible seven regularly spaced, rather robust cheek teeth. In *Ictidosuchops* there are nine such teeth, but it is possible that one or two teeth may be lost in the Antarctic specimen because of the fracture just behind the last of the cheek teeth along which the front part of the skull was rotated in relation to its back section. There is a rather long maxillary-premaxillary complex in front of the canine, containing several teeth. Four are visible but there may have been more, since this part of the skull is not well preserved. In *Ictidosuchops* there are three small maxillary teeth in front of the canine, and five premaxillary teeth.

The front part of the dentary is present,

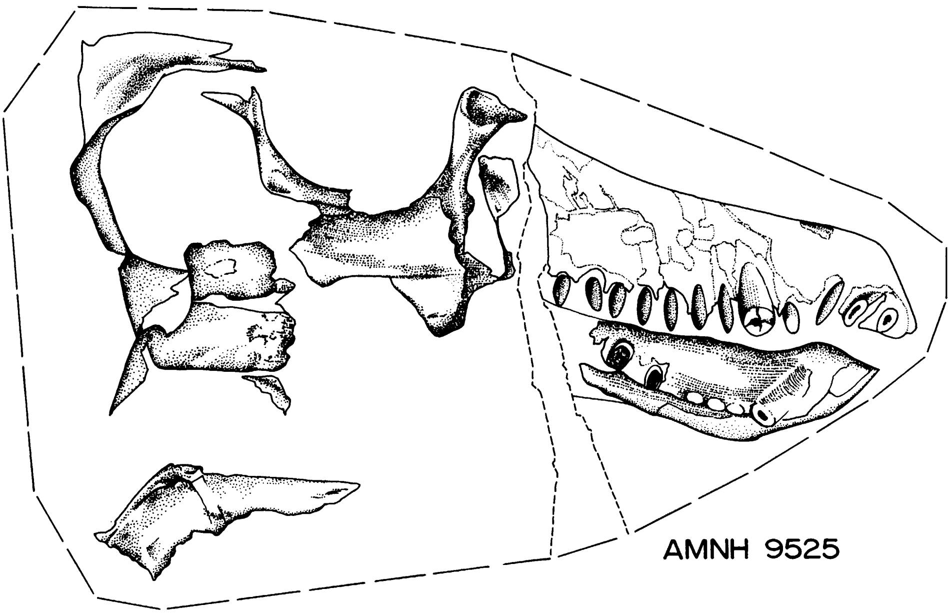

FIG. 12. *Rhigosaurus glacialis,* new genus and species. AMNH 9525. Skull as shown in figure 11. ×3.

with the alveolus for a large canine, and sockets for several postcanine teeth. It appears that the front of the dentary is rather deep, to accommodate the canine, and that the bone diminishes in depth somewhat behind the canine. A similar configuration in the dentary is seen in *Ictidosuchops*.

It is probable that *Rhigosaurus glacialis* is more closely comparable to *Ictidosuchops intermedius* (Crompton, 1955) than to any other of the other known scaloposaurid genera and species. Thus, it is small—a common scaloposaurid character—but not as large as the African form.[5] But like *Ictidosuchops,* it has a large canine and postcanine teeth regularly spaced and similar to each other in size. Moreover, it seems probable that there are several maxillary and premaxillary teeth occupying an elongated muzzle in front of the canine.

The skull characters are typically scaloposaurian. The parietals are broad and flat, but lack the pineal opening that characterizes *Ictidosuchops* and *Ictidosuchoides*. However, other scaloposaurids, such as *Scaloposaurus* and *Tetracynodon* (Sigogneau, 1963), lack a pineal opening. The postorbital bar, although incomplete, seemingly is longer than the same element in *Ictidosuchops,* resembling in this respect the postorbital bar in *Scaloposaurus* and *Tetracynodon*. It would appear that the jugal-squamosal bar along the lower border of the temporal fenestra is relatively heavier than it is in *Ictidosuchops,* resembling in this feature the bar in *Ericiolacerta* as figured by Watson, and by extension the bar in *Scaloposaurus*. Finally, the dentary as preserved would seem to be rather deep—heavier than in *Ictidosuchops* and *Scaloposaurus,* and perhaps more like the dentary of *Olivieria* (Brink, 1965) with regard to proportions.

[5] The length of the skull of *Rhigosaurus glacialis* is 36 mm. (See accompanying table of measurements.) Skulls of *Ictidosuchops intermedius* in the collections of the Bernard Price Institute for Palaeontological Research in Johannesburg range in length from 55 mm. to 175 mm.

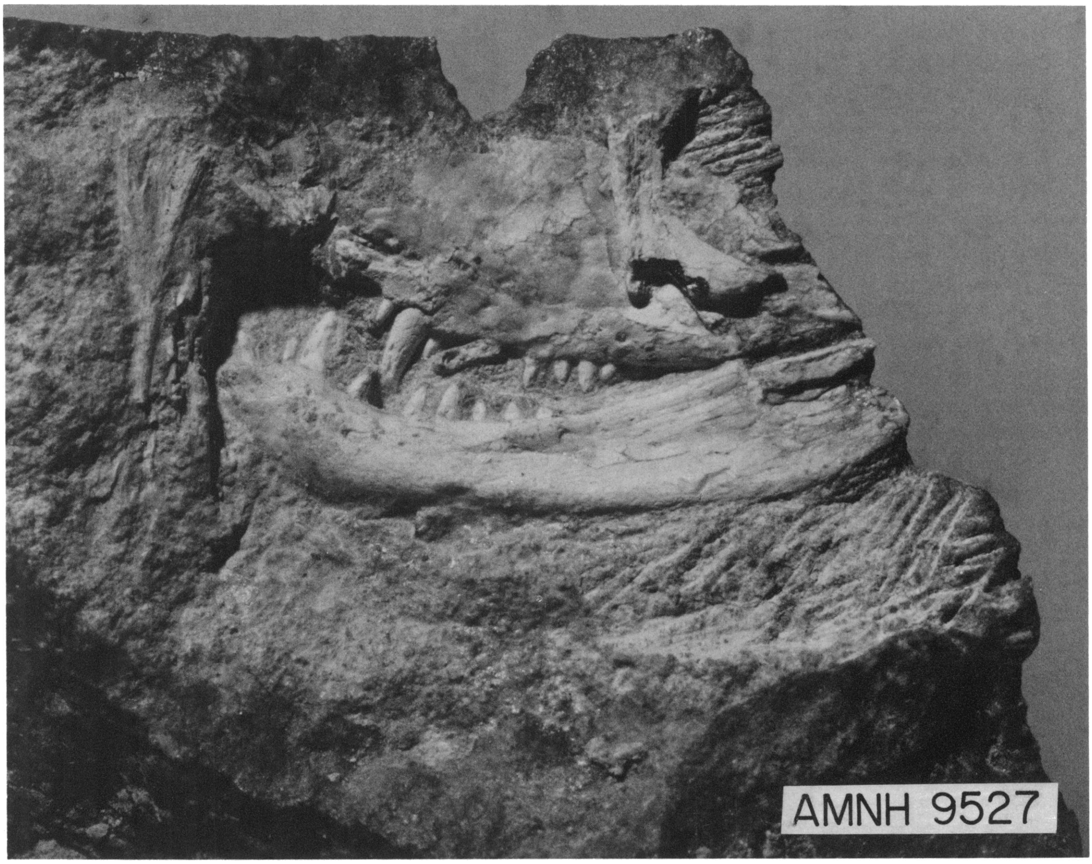

FIG. 13. Theriodontia, *incertae sedis*. AMNH 9527. Part of left maxilla with broken jugal, and mandible. ×4.

THERIODONTIA, *INCERTAE SEDIS*

Specimen under consideration; AMNH 9527, the greater part of a left maxilla with a broken fragment of the left jugal and an associated left dentary, from the Lower Triassic Fremouw Formation as Shackleton Glacier, Halfmoon Bluff, Sentinel Hill, Central Transantarctic Mountains.

The specimen, which unexpectedly came to light during the preparation of eosuchian postcranial bones from the Fremouw Formation, is that of a rather small theriodont reptile with a deep maxilla (which in all probability can be attributed to postmortem distortion or flattening of the bone), a fairly well-developed jugal arch and a rather slender scaloposaurid-like dentary. The dentary is characterized by a sharp angle between the anterior symphyseal and ventral borders of the dentary which could be compared with that of the small therocephalian *Hofmeyria*, and by a low coronoid process. The canines in both the maxilla and dentary are large. There is a small tooth immediately in front

TABLE 3
Measurements (in Millimeters) of *Rhigosaurus glacialis*

Skull length	36.0
Preorbital length	20.0
Skull width, posterior	26.0

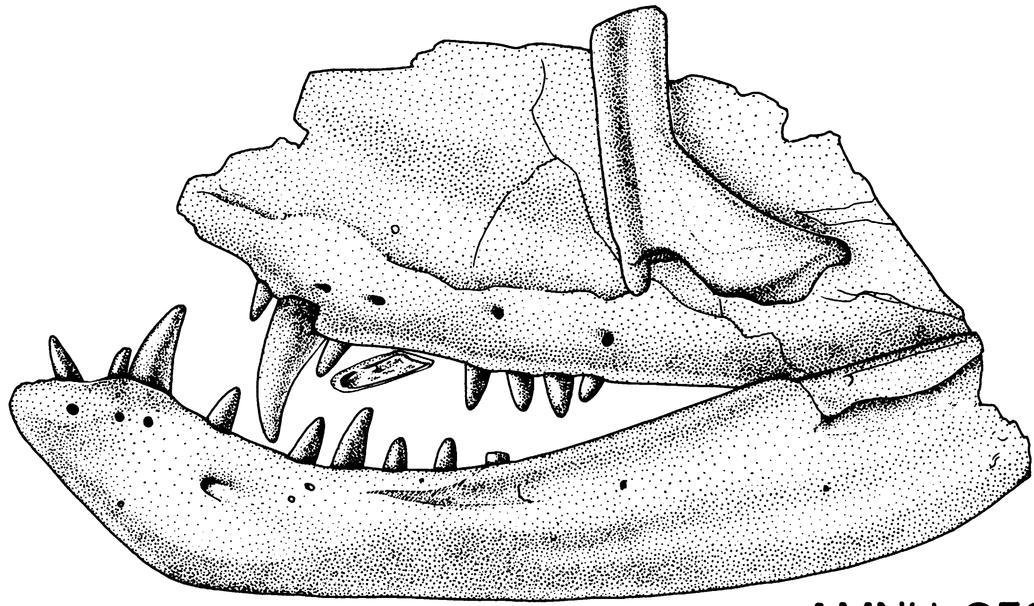

FIG. 14. Theriodontia, *incertae sedis*. AMNH 9527. Part of left maxilla with broken jugal, and mandible. ×5.

of the upper canine, and at the back of the canine there are six postcanine teeth preserved in the form of simple cones. The lower jaw is displaced, with the result that the lower canine bites into a socket in front of the small tooth immediately anterior to the upper canine. Two well-defined teeth are preserved immediately in front of the lower canine and it appears that four such teeth were originally present. There are six lower postcanine teeth preserved in the form of simple cones, the first of which is quite close to the canine as in most scaloposaurids. All the postcanine teeth in the maxilla and dentary are widely spaced. A wide gap between the first and third upper postcanine teeth is occupied by a displaced tooth. There is also an exceptionally large space between the first and second lower postcanine teeth. The wide spaces are most probably due to postmortem loss of teeth which were either in the process of replacement or were newly erupted and as yet not firmly embedded in the alveoli. Loss of teeth during the lifetime of an animal and the alveoli closing up completely is also not an uncommon feature in the theriodonts. With these gaps between the preserved upper and lower teeth it thus appears that the specimen probably had a minimum dental formula of eight upper and seven lower postcanine teeth.

As preserved, it is difficult to establish a close concordance between AMNH 9527 and the various other theriodonts from the Lower Triassic *Lystrosaurus* zone or for that matter with those from the Middle and Upper Permian forms from the Beaufort Group in South Africa. In certain features the specimen compares favorably with *Scaloposaurus constrictus* but the enlarged canines eliminate it from a close relationship with this form. The large canines are normally features seen in the genera *Ictidosuchoides* and *Ictidosuchops*, the latter ranging from the Upper Permian *Cistecephalus* zone into the Lower Triassic *Lystrosaurus* zone of South Africa. AMNH 9527 is much smaller than *Ictidosuchops* but it might be a juvenile of this form, which in the adult stage has a dental formula of between nine and 12 closely spaced postcanine teeth.

In some respects the specimen may be compared with the cynodonts, *Thrinaxodon* and *Galesaurus*, both from the South African *Lystrosaurus* zone, but it differs markedly from these forms in that the postcanine teeth are simple conelike pegs showing none of the cuspidation that is typical of the galesaurids.

Because of the lack of more definitive characters, easily comparable with some of the known genera mentioned above, we believe that the assignment of a new generic and specific name to AMNH 9527 is not justified. It is merely included in this paper as a record. Perhaps at a future date more complete and definitive specimens may be recovered from the Antarctic sediments that will establish the exact relationships of this particular specimen. There are, indeed, many lacunae to be filled in the tetrapod fauna of the Fremouw Formation.

CONCLUSIONS

It is evident that the various Antarctic scaloposaurians described in the present paper show characters relating them to several genera within the infraorder, notably *Scaloposaurus, Ericiolacerta, Ictidosuchops,* and *Ictidosuchoides*. It is not surprising, however, that in spite of these resemblances to known scaloposaurians the Antarctic fossils also show differences from the African forms. As is seen from the studies of Antarctic amphibians (Colbert and Cosgriff, 1974) and other reptiles from the Fremouw Formation (Colbert, 1974; Colbert and Kitching, 1975, 1977) some of the tetrapods are generically different from their nearest African counterparts, whereas other genera and even species are identical in the two continents. This illustrates the fact that the Fremouw fauna is a *Lystrosaurus* zone fauna with some differences, as might be expected in two assemblages that occupied a single continental area yet were separated each from the other during early Triassic time by a distance of perhaps 1500 km.

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